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**THE INFLUENCE OF SPATIALHETEROGENEITY ON OCEAN
QUAHOG (ARCTICA ISLANDICA) POPULATION DYNAMICS
ALONG THE MID-ATLANTIC BIGHT**

Jillian Sower

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THE INFLUENCE OF SPATIAL HETEROGENEITY ON OCEAN QUAHOG
(ARCTICA ISLANDICA) POPULATION DYNAMICS ALONG THE MID-
ATLANTIC BIGHT

by

Jillian R. Sower

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

Approved by:

Dr. Eric N. Powell, Committee Chair
Dr. Roger Mann
Dr. Chet Rakocinski

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ABSTRACT

The ocean quahog (*Arctica islandica*) support an economically important fishery in the US, though little is known about their life history traits. To determine how these traits vary geographically, the age frequencies and growth rates from two New Jersey sites (NJ1 & NJ2) as well as Georges Bank (GB) and Long Island (LI) were analyzed. Though sexual dimorphism in bivalves is rare, recent research has shown that *A. islandica* display distinct differences in sizes between males and females, with females reaching larger sizes than those of males. To determine when this difference in size occurs, the growth rates of males and females were analyzed using Welch's t-test. Results indicate that females begin outgrowing males between the ages of 10-15, at an average size of 50-55 mm. Rarely do males keep pace in growth with females beyond this point. Larger sizes in females may influence their presence in age frequencies based on size selectivity (> 80 mm) by commercial dredge. This is observed in the New Jersey sex ratios, as females are more frequent at a ratio 1:~0.80 at both sites. Age frequencies of NJ1 are very similar to those of LI and GB, yet NJ2 displays recruitment events not observed in any of the other sites. When comparing growth rates, *A. islandica* from southern sites are reaching milestone sizes 2-3x faster than those of Georges Bank, an effect of warmer bottom water temperatures in these southern areas.

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DEDICATION

This thesis is dedicated to my parents, Jennifer and Steve, who supported me the whole way; my dogs, Coco and Tiberius, who always knew how to make me smile; and to Alyssa, Laura, and Kathleen, some of the best friends I've made, who helped me get through it all.

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LIST OF ABBREVIATIONS

ALK	Age-length key
GB	Georges Bank
LI	Long Island
MAB	Mid-Atlantic Bight
NAO	North Atlantic Oscillation
NJ1	Northern New Jersey
NJ2	Southern New Jersey
US	United States of America

CHAPTER I - INTRODUCTION

1.1 Introduction

The ocean quahog, *Arctica islandica*, is a species unlike many other bivalves. This species is long-lived, with many animals reaching 200 years in age, with the oldest documented *A. islandica* aged at 507 years old (Butler et al. 2013). *Arctica islandica* has a strict upper thermal tolerance limit of 15°C, and thus inhabits boreal waters. Its range spans from Newfoundland, Canada, to Virginia, US in the western Atlantic and from Iceland through the Norwegian Sea and to the British Isles in the eastern Atlantic (Dahlgren et al. 2000).

The ocean quahog supports an economically important fishery in the US that began in the late 1960s. The *A. islandica* fishery has shifted its geographic focus as biomass has decreased in abundance in the southern portion of this species' range. Between 1980-1991, the majority of the fishery's landings came from waters off New Jersey, US (NEFSC 2017); however, the fishery is now focused south of Long Island.

Arctica islandica deposit annual growth lines, termed annuli, throughout their shells and hinge plates each year (Jones 1980, Thompson et al. 1980, Ropes et al. 1984a). These annuli can be counted to determine age. Annuli are believed to be deposited during fall and winter, between September and December in conjunction with spawning (Jones 1980). Annual growth is influenced by numerous environmental factors, such as temperature, food availability, and salinity (Schöne et al. 2005, Harding et al. 2008), which can influence an animal's overall length and cause high variability in length at age amongst animals born at a similar time. Variations in length at age present problems for fisheries management, as ages at a given size can span decades if not hundreds of years

of difference. These variations inhibit the use of age-based models for species such as *A. islandica*, and fisheries must rely on length-based models.

1.2 Project Objectives

The first objective of this project is to analyze the degree of sexual dimorphism in *A. islandica*. Sexual dimorphism is rare in bivalves but has been documented for *A. islandica* by numerous studies as females dominate size classes larger than those of males (Ropes et al. 1984b, Rowell 1990, Steingrímsson and Thórarinsdóttir 1995, Hemeon et al. 2021, in prep.). The study presented herein will determine when females begin to outgrow males and what the biological cause might be.

The second and third objectives of this project are to build upon the work of Pace et al. (2017a, 2018) by using larger sample sizes than what were originally used. In the Pace et al. studies, only approximately 200 individuals from one site in New Jersey were used to generate age frequencies and generate age-length keys, as well as analyze growth rates. The studies presented herein utilize age and length data from two sites from off New Jersey, one north and one south of the Hudson Canyon. Each site yielded over 700 *A. islandica* individuals for age frequency and growth rate analysis, as well as sex-based differences and recruitment trends, to provide important information on the status of these populations.

Objectives for this project include comparisons between the two New Jersey sites and two northern sites, Long Island and Georges Bank, as previously analyzed by Hemeon et al. (2021, in prep.). These comparisons will provide key details on how *A. islandica* is affected by environmental heterogeneity, or how environmental variables change geographically, as well as how growth may have fluctuated over time.

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CHAPTER II – DEFINING PATTERNS IN OCEAN QUAHOG (*ARCTICA* *ISLANDICA*) SEXUAL DIMORPHISM ALONG THE MID-ATLANTIC BIGHT & GEORGES BANK

2.1 Introduction

The ocean quahog (*Arctica islandica*) is an infaunal, noncolonial species that ranges from Newfoundland, Canada to Cape Hatteras, NC, USA, and from the Bay of Cadiz in Spain to Iceland and Norway (Cargnelli et al. 1999a, Dahlgren et al. 2000, Ballesta-Artero et al. 2017). This species supports a commercially important fishery along the western Atlantic continental shelf, valued at \$9.1 million and producing more than 11.3 million pounds of meat in 2019 (MAFMC 2021). Despite the economic importance of this species, many of its life history traits remain poorly known, such as the degree of sexual dimorphism in this species (Hemeon et al. 2021, Hemeon et al. in prep.) and the biological origin. Sexual dimorphism can present itself as differences in size, coloration, or some other morphological characteristic and is frequently encountered in many marine species such as flatfish (Morse 1981, Shuozeng 1995, Nichol 1998), sharks (Henderson et al. 2002), shrimps, and other decapods (Brusher et al. 1972, Colloca 2002, Garcia-Rodriguez et al. 2000). Sexual dimorphism is reported in some gastropods (Fotheringham 1971, Soong & Chen 2003, González-Vallejo 2008), but among gastropods, protandry is more common (Robertson 1981, Collin 2006). In comparison to gastropods, sexual dimorphism in bivalves is rare (Sastry 1979) with cases of protandry and sequential hermaphroditism being most common (e.g., some oysters, Orton 1927, Coe 1934, Dinamani 1974; pearl oysters, Chàvez-Villalba et al. 2011; arc shells, Peharda et al. 2006). Cases of dwarf males are rarer still (teredinids, Turner & Yakovlev 1983);

however, evidence of size-based sexual dimorphism has been found in *Arctica islandica* (Ropes et al. 1984a, Fritz 1991, Steingrímsson & Thórarinsdóttir 1995, Thórarinsdóttir & Steingrímsson 2000, Hemeon et al. 2021).

Generally, *A. islandica* grow very rapidly in their youngest years of life, sometimes by as much as 10 mm shell length or more in a single year. After they reach 20 to 30 years of age, growth rate drastically decreases – this is theorized to coincide with the onset of sexual maturity (Begum et al. 2010, Morton 2011). Steingrímsson and Thórarinsdóttir (1995) found that in an Icelandic population most clams reach maturity at 55 mm but at different ages. Age and size at maturity is not consistent across this species, however. Ropes et al. (1984a) found in a population off Long Island that gonadal development (and thus sexual maturity) can begin when animals are as young as 3-5 years old, between sizes 33-38 mm, with complete differentiation occurring between 5-18 years, at sizes 47-55 mm. At each stage in differentiation, males were both younger and smaller than females (Ropes et al. 1984). These observations have been supported by Thompson et al. (1980b) and Rowell et al. (1990).

As *A. islandica* age, males and females consistently display distinct differences in overall size: females tend to dominate size classes larger than those of males (Ropes et al. 1984a, Hemeon et al. 2021, Hemeon et al. in prep.). These studies collectively suggest that the difference in overall size between males and females is that males mature at a younger age. To further explore this hypothesis, the growth increments of four populations of *A. islandica* from the Mid-Atlantic Bight (MAB) and Georges Bank were examined to statistically define when during ontogeny sex-based differences begin to

occur. Environmental factors were also considered to determine potential causes for these observed differences in growth by site.

2.2 Methods

2.2.1 Sample Collection

In 2017 and 2019, *A. islandica* were collected from four different sites along the MAB for age frequency analysis and the creation of age-length keys. These sites are located on Georges Bank (GB), off Long Island (LI), and north (NJ1) and south (NJ2) of Hudson Canyon off New Jersey (see Table 2.1, Figure 2.1). Individuals were shucked, sexes were determined using smear slide, processed for aging (for methods, see Pace et al. 2017a, Hemeon et al. 2021) and analyzed to determine age frequencies and growth rates.

2.2.2 Ageing and Growth Measurements

Arctica islandica deposits growth lines in their umbo each year (Thompson et al. 1980a, Jones 1980), termed annuli. Murawski et al. (1982) and Ropes et al. (1984b) confirmed these lines as yearly increments, permitting *A. islandica* age determination. Images of the umbo region of each animal were taken using a combination microscope and camera (example image in Figure 2.2). These images were then uploaded into the opensource software ImageJ with the ObjectJ plugin. Each annulus was marked using this software to determine age, and the distance between markers (the annual growth increment) was calculated in pixels. Pixel distance was first converted to a proportion of growth per year, then translated to total length in mm to estimate total growth per year using the overall length of each clam.

2.2.3 Dataset Organization and Environmental Mitigation

Maturity and sexual differentiation in *A. islandica* can occur at 5 years old or younger (Thompson et al. 1980b, Ropes et al. 1984a, Rowell et al. 1990, Thórarinsdóttir & Steingrímsson 2000, Morton 2011). Analysis of the present dataset is premised on the hypothesis that growth rates should be similar between sexes prior to sexual differentiation, with possible divergence following the onset of maturity. Hemeon et al. (2021) demonstrated that growth dynamics in *A. islandica* are a function of integrated conditions but highly dependent on birth year within the same population so that size at age varies by birth year. For example, animals born in the 1920s were potentially subject to different bottom water temperatures compared to those born during the 1990s, substantively impacting growth rates at an early age when growth rates were high. Consequently, analysis was further refined to evaluate variations of growth at age between sexes by decade of birth.

The age range of *A. islandica* in these datasets spans from 13-310, and each dataset contains over 600 aged animals (Hemeon et al. 2021, Hemeon et al. in prep., Sower et al. in prep.). To facilitate analysis, each animal was assigned to its respective birth decade. Although year-to-year differences may be important, assigning animals into their respective birth decades and analyzing them within these groups increased statistical strength and permitted multi-decadal comparisons to mitigate growth differences imposed by birth year and subsequent lifetime-integrated environmental conditions. Decades assigned with fewer than 10 males and 10 females born were discarded to prevent error in statistical analysis due to low sample size, as were cases where the same decade was not represented thusly in animals from all four collection sites. As a result,

four decades were identified with sufficient males and females born across all four sites, 1910-1940, and five decades were identified in 3 of the 4 sites, 1910-1950. Only Georges Bank was lacking sufficient animals in the 1950s.

2.2.4 Sample Analysis

Growth rates of males and females born each decade were averaged across five-year increments in mm (i.e., age classes) between the ages of 5-50 years. The average growth rates were then compared using Welch's t-test. Welch's test is preferred over Student's test for smaller sample sizes and is more Type I error robust when sample sizes differ (Welch 1938, Welch 1947, Derrick et al. 2016). Welch's test also performs as well as the nonparametric Mann-Whitney U (MWU) test when variances are equal and better when variances are unequal (Ruxton 2006). To check this, the outcomes from the two tests for a subset of the data were compared.

The p-value obtained from Welch's test was used as a metric to track when the difference in growth became apparent between males and females, with $p < 0.05$ set as the primary threshold indicator. The growth increments at each age class were also summed per animal and then averaged for each sex to determine an average length at age. Each site was then analyzed over time to determine if any patterns unique to said site became apparent.

2.2.5 Cold Pool Dynamics

The southern extension of *A. islandica*'s range into the MAB is facilitated by the Cold Pool, an annual band of cooler bottom water generated by thermal stratification that forms in the spring and breaks down in the fall (Lentz 2017, Friedland et al. 2020). The southern and inshore portion of the Cold Pool varies yearly in the MAB (Sha et al. 2015,

Chen et al. 2018, Friedland et al. 2022). The Cold Pool generates strong onshore-offshore gradients in summer bottom water temperature and also varies downcoast year to year (Houghton et al. 1982, Ou & Houghton 1982, Lentz 2017, Chen et al. 2018, Chen & Curchitser 2020), potentially causing important differences in local bottom water temperatures at each site and over time. Consequently, to determine what aspects of the Cold Pool may have impacted growth in these four populations, monthly-averaged bottom water temperature data estimated from the Doppio hydrodynamic model (López et al. 2020) were accessed for 2016-2019.

2.3 Results

2.3.1 Statistical Tests

Welch's t-test was used in lieu of Student's test and performance compared to the alternative nonparametric Mann-Whitney U (MWU) test using a subset of the sites and decades. Though results were not exactly the same, patterns were consistent (Table 2.2).

2.3.2 Site-Specific Trends

2.3.2.1 Georges Bank

A total of 233 animals born in the decades 1910-1940 were analyzed from Georges Bank. Early in ontogeny, the growth rates of males and females did not differ significantly for any decade. A significant difference in growth between males and females was reached by age 10 in the 1910s, by age 15 for decades 1920-1930, and at age 30 for the 1940s (Figure 2.3). Mean lengths at the significant age reached for males and females for these decades, respectively, were: 1910, 48 mm, 52 mm; 1920, 55 mm, 59 mm; 1930, 56 mm, 61 mm; and 1940, 68 mm, 72 mm. Differences in lengths at these thresholds were 3-5 mm, with the difference continuing to increase as the clams grew

older (Figure 2.4). By age 50 these differences were magnified. For example, females were at least 4 mm larger at 83 mm compared to 79 mm in males for animals born in the 1940s (Table 2.3), and females were 9 mm larger, at 84 mm compared to 75 mm in males, for animals born in the 1910s.

2.3.2.2 Long Island

A total of 377 animals across five decades were analyzed from Long Island. Early in ontogeny, the growth rates of males and females did not differ significantly for 3 of 5 decades and 4 of 5 discounting the first few years of life for the 1910s (Figure 2.5). The 1950s diverged from this pattern in that male and female sizes were significantly different throughout ontogeny. For the remainder, male and female sizes in three of the decades diverged significantly or nearly so at ages 25-35: 1910, 1920, and 1940. For the 1930s, significance was reached at age 15. In contrast, male and female sizes were significantly different in the 1950s at all ages (Figure 2.5). Sizes reached at the age when males and females diverged significantly, however, were often consistent. In 1910 and 1940 females were 70 mm and males 65-67 mm (ages 35 and 30, respectively, Table 2.4, Figure 2.6). In 1920, the p-value was nearly significant at age 30 when again females were 70 mm and males 67 mm. In 1930, significance was reached at age 15 when females were 57 mm and males 53 mm (Figure 2.6). Overall, females consistently began to outgrow males by at least age 25 and were larger than males by 3-7 mm by age 50.

2.3.2.3 Northern New Jersey (NJ1)

A total of 438 animals were analyzed from the northern New Jersey site, NJ1. Early in ontogeny, the growth rates of males and females did not differ significantly for 3 of the 5 decades, 1920-1940, though 1920 was nearly significant at age 5. For 1930 and

1940, females diverged significantly by ages 12 and 14, respectively (Figure 2.7). In the remaining two decades, 1910 and 1950, females outgrew males significantly in the first few years of life. In all five decades females and males displayed significantly different growth by age 15. In 1910, females initially were much larger at 30 mm than males at 22 mm (Figure 2.8, Table 2.5). This difference became as large as 11 mm by age 40. In the 1950s, females were only 4 mm larger than males at age 5 at 29 mm, and only reached a maximum difference of 6 mm at age 30. In the 1920s, females were 4 mm larger at 46 mm than males at age 10, with a maximum difference of 6 mm reached at age 30 (Figure 2.8). In the 1930s, females were 5 mm larger than males at 57 mm at age 15, and differences between the two reached 6 mm by age 50, when females were 80 mm. In the 1940s, females were only 3 mm larger than males at age 15, with an average size of 56 mm. By age 50, this difference grew to 5 mm, with females reaching an average size of 81 mm (Figure 2.8).

2.3.2.4 Southern New Jersey (NJ2)

A total of 172 were analyzed from the southern New Jersey site, NJ2. This site has the broadest age distribution in the population age frequency (see Chapter 3), with high numbers of animals born in decades that did not contain 10 each of males and females at other sites. The differential in growth dynamics between males and females is vastly different at this site in comparison to the other three sites. Males and females diverged significantly in size in three decades, two at age 35 and one at age 40 (Figure 2.9). For the other two decades, males and female sizes remained similar throughout ontogeny and did not display significant differences in size at any age. These are the only two such cases in the entire analyzed dataset across all four sites.

For cases where males and females did diverge in size, this site had the smallest size differences between males and females when significance was reached. Consistently, females only reached sizes 3 mm larger than those of males by year 35 (Figure 2.10, Table 2.6). As was observed at the other three sites, females continued to grow larger relative as time passed, reaching up to 5 mm maximum difference in the 1920s decadal group by age 50. In the 1930s and 1940s, however, males and females remained similar in size throughout the 50-year timeline. Interestingly, in the 1930s females were noticeably larger than males at age 5, but these differences diminished over time. In 1940, though significance was never reached, females were consistently 2 mm larger than males at 72 mm average length by age 35.

2.3.3 Common Trends

At all sites and for nearly all decadal groups, females were larger than males at each year class after early ontogeny. Only in a few instances in the earliest age classes (ages 5-10) were males sometimes the same size as females, or 1-2 mm larger. In these decadal groups, however, females almost always grew to larger sizes than males, even if by only 1-2 mm, by age 50. Females typically began to outgrow males by year 15, even if differences were not statistically significant. At this age, across decadal groups, the lengths of both males and females ranged from 47-61 mm, with an average of 56.3 mm and a standard deviation of 2.92 mm. Only one group displayed an average length below 50 mm, the males aged 15 in 1910 at NJ1. The only three groups to reach or exceed 60 mm average growth were all females at Georges Bank, in the decadal groups 1910, 1930, and 1940. The average size of males at age 15 across sites and decadal groups is 53.87

mm, standard deviation 2.75 mm, and the average size of females is 56.70 mm, standard deviation 2.42 mm.

2.4 Discussion

2.4.1 *Arctica islandica* Sexual Dimorphism

Hemeon et al. (2021, in prep.) detailed the differential in sizes between male and female *A. islandica* over their life span, confirming and extending earlier reports by Fritz (1991), Ropes et al. (1984a), Steingrímsson and Thórarinsdóttir (1995), and Thórarinsdóttir and Steingrímsson (2000). For the majority of sites and decadal groups analyzed in the current study, males and females displayed significant growth differences by year 15, and in some cases even earlier. Ropes et al. (1984a) found that the youngest animals to reach maturity at Long Island were 6 years old, with an average of 9.8 years in males and 13.2 years in females. The 6-year-old mature animals were 36-61 mm long, while males were 47 mm on average, and females 55 mm on average. Similar results were seen by Rowell et al. (1990) off Nova Scotia. These data fit well with the results presented in this study – females begin to grow larger than males very early in life, and this is likely due to males maturing at an earlier age, with the length differential reaching significance most frequently at sizes 50-60 mm.

2.4.2 Spatial Heterogeneity and Cold Pool Influences on Growth

The metabolic energetics of *A. islandica* are notably sensitive to temperature with a Q_{10} as high as 4 recorded for respiration (Begum et al. 2009) and noteworthy responses to variations in food supply and temperature (Ballesta-Artero et al. 2017). This species has a strict upper thermal tolerance limit of 15°C (Merrill et al. 1969, Cagnelli et al. 1999a). An increase in 1°C can cause a mass mortality event (Merrell et al. 1969).

Correspondingly, in the MAB, significant numbers are rarely found where mean summer bottom water temperatures exceed 13.5°C (Sower unpubl. data). The decades considered herein cover a range of temperature regimes. The 1920s were relatively cold, the 1930s and 1940s relatively warm, and temperatures began to decline again in the 1950s leading into the 1960s cold period (Nixon et al. 2004). To what extent these estuarine trends provide inferences on bottom water temperature trends on the middle to outer continental shelf is unknown. Neither is it known to what extent relative differences in bottom water temperatures in recent years might be representative of differentials in past decades. Nonetheless, results by Pace et al. (2017a, 2017b, 2018) and Hemeon et al. (2021) show that growth rates vary substantively between sites within the MAB – animals from New Jersey can grow faster than animals from Georges Bank presumably due to the warmer bottom water temperatures experienced there, for example.

Growth rates also vary with birth dates as warmer temperatures generate faster growth and presumably a shorter time to maturity early in ontogeny. Thus, temperature likely also plays an important role in the growth differentials observed in males and females. Although bottom water temperatures are not available for 1910-1950, comparison of the temperature dynamics between the four sites in more recent years may provide some inferences by analogy. For this purpose, results of the recently-developed Doppio model (López et al. 2020) are accessed for the time period 2016-2019.

2.4.2.1 Georges Bank

Georges Bank is the northernmost and deepest site in this dataset (Table 2.1). GB is also along the northern edge of the Cold Pool and generally experiences the coldest temperatures during the onset of the Cold Pool's annual cycle in spring (Lentz 2017).

Due to stronger tidal currents and thus more rapid vertical mixing, however, warming rates at GB can be higher compared to much of the MAB (Lentz 2017).

Georges Bank had the second-lowest range of variability in growth patterns over time. Three out of the four decadal groups displayed statistically significant differences between males and females by age 15. The fourth decadal group reached significance at age 25. Temperatures at this site are more moderate than at the other three sites, with a distinctly lower chance of an extreme warm event in the fall when stratification breaks down. Based on Doppio model reconstructions of bottom water temperatures for the collection site for 2016-2019 (López et al. 2020), mean temperatures varied from 6.86°C in the spring to 10.78°C in the fall with summer and fall temperatures nearly identical, as were winter and spring (Table 7). A distinct seasonal cycle is present with winter-spring temperatures rising by about 3°C into summer/fall. Maximum summer and fall temperatures did not exceed the 13.5°C mean summer temperature standard for the distribution of *A. islandica* in the MAB. Hemeon et al. (2021) and Pace et al. (2018) documented increasing growth rates at this site over century-long time periods, so that 2016-2019 temperatures probably exceed the century-long conditions experienced by *A. islandica*.

2.4.2.2 Long Island

The Long Island site is located at 47.5 m depth and is the most inshore site of the four (Figure 2.1). This site had the second highest amount of variability in growth patterns over the five decades. This is likely due to the fact that warming rates are higher in this inshore area in the fall as the stratification maintaining the Cold Pool breaks down (Lentz 2017, Chen et al. 2018). The location of this site is also inshore of the center of the

Cold Pool, which lies between the 50 and 80 m isobaths (Houghton et al. 1982), which may account for the higher fall temperatures (Table 2.7). Data from recent years also suggest that LI occasionally experiences near-lethal temperatures (Table 2.7). Maximum temperatures for the 2016-2019 period reached 16.30°C in the fall. Warmer temperatures might allow for males to grow to a larger size before reaching maturity, which might explain why growth rates between males and females do not diverge significantly until year 30 for all decades.

2.4.2.3 Northern New Jersey (NJ1)

Even though the northern New Jersey site, NJ1, is slightly south of LI, it is farther offshore at 60 m depth. One might expect that *A. islandica* from this site experience cooler temperatures during the summer. In fact, the temperature regime is similar to that of the Long Island site with the exception that the extreme temperatures are somewhat lower. Doppio data for 2016-2019 show consistent low temperatures during winter through summer with a distinct warm-up in the fall as stratification breaks down. At this time, like LI, temperatures reach near lethal maximums. At this site, two decades showed statistically significant growth differences by age 5, and all five do so by age 15. Similar to the LI site, females consistently grew faster than males throughout ontogeny, though females begin to diverge earlier than in LI.

2.4.2.4 Southern New Jersey (NJ2)

The southern New Jersey site, NJ2, diverges strongly from the other sites in the relative growth rates of males and females over the studied decades. Unlike the other sites, in two of five cases, male and female growth rates do not diverge significantly. The southern New Jersey is located at 62.5 m depth, south of the Hudson Canyon, but

relatively far north of the southern limit of the Cold Pool (Friedland et al. 2022) and near the cross-shelf center of the Cold Pool. Doppio renderings suggest very limited temperature change during the winter-spring-summer seasonal progression, the lowest temperature change of all 4 sites. Doppio estimates suggest high variability during the stratification breakdown, relative to the other sites, with some temperatures approaching 16°C. At NJ2, two decades did not contain animals that displayed statistically significant differences in growth between sexes, indicating that males and females were growing at the same rate over the first 50 years of life. When decades did reach statistical significance, it was not until the animals were 35 years of age consistently. Potentially, the limited seasonal signal outside of fall warm up could allow for males to obtain similar growth rates to females, in contrast to the other three sites.

2.4.2.5 Site similarities and differences

Each of the sites is unique in some way, but three general sex-dependent growth dynamics can be observed. Most commonly, the two sexes diverge in size with females outpacing males in growth rates after the first 5-15 years of life. This outcome occurs at all sites for some decades and is generally the most common outcome across decades. In a few cases, female growth rates diverge very early in ontogeny. Such cases occur at two sites north of the Hudson Canyon, both on the Long Island continental shelf (LI, NJ1). Most rarely, the two sexes maintain similar growth rates. This is observed for a few decades only at NJ2. Coincidentally, NJ2 is the most southern site.

Temperature data for the decades of interest are not available. For some guidance, reliance is based on Doppio reconstructions of bottom water temperatures for 2016-2019, a time frame of limited applicability. Overall, the temperatures are not greatly dissimilar

between sites, limiting interpretation of variable growth outcomes as a function of temperatures, but the sensitivity of *A. islandica* to temperature may well magnify small changes in temperature into large changes in growth rate. The fact that the one site where males and females do not diverge in growth rate for some decades is also the site with the most variable fall temperatures based on the Doppio model is potentially noteworthy.

In bivalves, maturity is often reached when shell length is approximately 44-51% of maximum length, although considerable variability exists among species (Powell & Stanton 1985). Hemeon et al. (2021, in prep.) found strong evidence for this expectation, suggesting a 52-mm size at maturity at GB and LI for populations with a ~120-mm maximum shell length. In this study, maturity is determined based on the presumption that a divergence in size at age between males and females is an indicator of such, that divergence routinely occurred at sizes in the range 45-60 mm (Tables 2.3-2.5). Southern New Jersey (NJ2) animals do not display differences in growth between sexes, until year 35 at sizes 65 mm+, and never in some decades, but overall, *A. islandica* seems to reach maturity at a size consistent with most bivalves at about 50% of maximum size, while unusually maintaining a different size between sexes for animals born in most decades at all sites.

2.4.3 Why could the sex-specific size difference in *A. islandica* exist?

2.4.3.1 Protandry

One hypothesis for smaller males and larger females is that *A. islandica* exhibits protandry, a form of hermaphroditism in which males change sex to become females. Protandry, though common in some bivalve orders, is not reported in Venerida. Two instances of hermaphroditism in *A. islandica* were found by Mann (1982). Such

occurrences are often found in protandric species when animals are caught during the sex change (Powell et al. 2013, Harding et al. 2013). Protandry results in an age-dependent divergence in sex ratio, however, which was clearly shown not to be present by Hemeon et al. (2021) and strongly suggested not to be present by others (e.g., Ropes et al. 1984a, Steingrímsson and Thórarinsdóttir 1995, Thórarinsdóttir and Steingrímsson 2000). Given these findings, protandry is not a probable cause for the size difference between sexes in *A. islandica*.

2.4.3.2 Difference in lifespan/mortality

A second hypothesis posed is that male *A. islandica* may have higher rates of mortality, and thus live shorter lives compared to their female counterparts (Ropes et al. 1984a, Steingrímsson & Thórarinsdóttir 1995). If this were the case, males might mature earlier to increase their overall fitness, as they would have less time than females to reproduce. In contrast to this hypothesis, Hemeon et al. (2021) and Sower et al. (in prep.) observed that males can live as long as, or longer than, females. At GB, the oldest animals observed were male, as the oldest male was 261 years while the oldest female was 224 years. At LI, males again were older, with the oldest male aged at 310 years, while the oldest female was only 272 years (Hemeon et al. in prep.). In NJ1, the oldest female was aged at 286 years, while the oldest male was aged at 279 years. In NJ2, the oldest female was 270, while the oldest male was 278. Thus, in *A. islandica*, males and females do not display strong differences in longevity.

2.4.3.3 More Reproductive Chances for Males

A third option is movement to facilitate fertilization efficiency. Fertilization efficiency is a serious constraint for free-spawning species (Levitan 2006, Luttikhuizen et

al. 2011). Recently, Tettelbach et al. (2017) found evidence for horizontal movement, dubbed “hard clam walking”, in *Mercenaria mercenaria*, in which both hard clam sexes were equally as likely to ‘walk’ towards a member of the opposite sex. This behavior has not been documented in *A. islandica*, but it has in other clams such as *Spisula solidissima* (Tettelbach et al. 2017). Observations of *A. islandica* movement have been limited to burrowing behavior (Taylor 1976, Strahl et al. 2011), and the degree to which horizontal movement is common within the order Venerida is unknown. If this behavior is displayed in *A. islandica*, smaller sizes in males would allow them to move towards females with less energy expenditure, and thus have increased chances for successful reproduction.

2.4.3.4 Better Reproductive Condition for Females

Larger females may be able to produce more and/or larger eggs and thus be more reproductively fit. In many species, the female gamete (the ovum) is more energetically expensive to generate than the male gamete (sperm) as it is larger (Hayward & Gillooly 2011). Egg quality, often estimated as lipid content, clearly is an important effector of larval success (Gallager & Mann 1986, Powell et al. 2002). Egg size is an important energetic tradeoff relative to larval survival (Gallager & Mann 1986, Levitan 2000, Powell et al. 2011b). Cost of reproduction as measured by mortality rate is also higher in females; thus, increased size might be advantageous in improving overall fitness for females. For a species such as *A. islandica*, it might be energetically beneficial for a female to focus on growth for a longer amount of time, and then switch to producing gametes once an adequate size had been reached. Males, on the other hand, can generate many more gametes for the same energy expenditure overall (Charnov et al. 2007; see also Powell et al. 2011a). Larger females may produce more and/or higher quality eggs.

Larger males could produce larger and/or more sperm, but this would come with a tradeoff of being unable to start producing sperm at a younger age or smaller size at maturity. More research on *A. islandica* sperm size compared to similar species would provide clearer reasoning on smaller male sizes.

Consequently, the uniqueness of sexual dimorphism in *A. islandica* within the Venerida coupled with their long lifespan would suggest that differential growth rates between sexes provide increased fitness for females in terms of lifetime reproductive output. How this advantage manifests itself remains unknown, but the eggs of *A. islandica* are relatively large for Venerida, at about 85-90 μm in diameter (Lutz et al. 1982, Cargnelli et al. 1999a) compared to hard clams (*Mercenaria mercenaria*), surfclams (*Spisula solidissima*), Manila clams (*Lajonkairia lajonkairii*) and other clams (Gallager & Mann 1986; Cargnelli et al. 1999b, Toba & Miyama 1994, Jagadis 2011). R. Mann (pers. comm.) records a smaller, but still large, size of 66 μm for *A. islandica*, which may have arisen due to the difference in egg data collection across studies; however, this size is still considered large compared to these other species. For a given gamete fraction, the number of eggs produced per female would be one-quarter to one-half of that produced by these other species. Thus, the necessity of producing larger eggs would place a premium on faster growth in females permitting an increase in lifetime reproductive output (an important measure of fitness; Charnov et al. 2007) to counterweigh the loss of per-spawn egg production.

Why produce larger eggs? If sperm limitation is an issue, then larger eggs could increase the chance of fertilization success (Neuheimer et al. 2015). Fertilization success would appear to be equally constrained for other continental shelf bivalves such as

surfclams, however, which arguably live in a more energetic environment. On the other hand, larval lifespans are relatively long in *A. islandica*, due likely to the colder temperatures restricting developmental rates (Lutz et al. 1982, Mann 1986) and this might require a larger egg carrying a greater energy store. The veliger stage of *A. islandica* is reached in 3-4 days, during which provisions from the egg would be necessary (Mann & Wolf 1983). Major spawning in the MAB coincides with fall turnover, so food should be plentiful. This does not apply to *A. islandica* outside of the MAB, however, such as those residing in shallower, northern waters, or in much deeper offshore water, where greater energy stores would be beneficial. For example, the oldest-known *A. islandica* was collected off Iceland from depths of 81-83 m (Butler et al. 2013). Larger eggs also might be a response to more restricted food availability in these areas (McEdward & Miner 2003). Regardless of purpose, the large eggs in *A. islandica* are noteworthy and would seem to be a predictable stimulus for more rapid female growth to enhance egg production by providing for the presence of larger females with more reproductive years in the population.

It is unclear why this life history trait, if true for *A. islandica*, is not more commonly encountered in bivalves. This species is the only known extant member of the family Arctiidae (Lutz et al. 1982); perhaps these traits were unique to this family of bivalves. Unfortunately, the lack of living conspecific species prevents direct comparisons of shell length and gamete sizes. These traits may have developed due to *A. islandica* residing in boreal waters, so close inspection of sex-based lengths and gamete size of other boreal species is recommended to provide clarity.

2.5 Summary

Female *A. islandica* begin to outgrow males between the ages of 5-15 years at sizes 50-55 mm, though this varies amongst the sites and between decades. Each of the sites is unique in some way, but three sex-dependent growth dynamics are observed. Most commonly, the two sexes diverge in size with females outpacing males in growth rates after the first 5-15 years of life. This outcome occurs at all sites and is generally the most common outcome across decades. In a few cases, female growth rates outpace the males very early in ontogeny. Such cases occur at two sites north of Hudson Canyon, both on the Long Island continental shelf. Most rarely, the two sexes maintain similar growth rates. This is observed for a few decades at the most southern site. In the population as a whole, rare outcomes have limited influence on the population so that female-to-male ratio increases with increasing size. This sexually dimorphic growth is not caused by protandry, nor is it compensation for a differential mortality rate between the sexes. One viable hypothesis is that differential growth is an adaptation to support the large egg sizes in females where larger female size is essential to counterweigh the consequent reduced fecundity due to larger egg volume.

2.6 Tables

Table 2.1 Locations of each of the four study sites in decimal degrees. GB = Georges Bank; LI = Long Island; NJ1 = northern New Jersey; NJ2 = southern New Jersey.

Site	Date Collected	Latitude	Longitude	Depth (m)
GB	2017	40.72767 N	-67.79850 W	72.5
LI	2017	40.09658 N	-73.01057 W	47.5
NJ1	2019	39.840556 N	-72.821667 W	60.0
NJ2	2019	39.33 N	-73.122778 W	62.5

Table 2.2 Welch's t-test results compared to Mann-Whitney U (MWU) test results per birth decades at two sites with the highest number of animals born. NJ1: Northern New Jersey; NJ2: Southern New Jersey.

Decade	Site	Age	Welch's T-test (p-value)	MWU Test (p-value)
1940	NJ1	5	0.5028	0.5704
		10	0.2111	0.1523
		15	0.003235	0.003372
1990	NJ2	5	0.0747	0.0951
		10	0.003029	0.002392

*Table 2.3 Average lengths (mm) of males (M) and females (F) at Georges Bank at each age and decade; * denotes at which age and corresponding length statistical significance ($p < 0.05$) was reached. M = males, F = females.*

Decade	Sex	Age (yr)									
		5	10	15	20	25	30	35	40	45	50
1910	M	33.98	47.98*	54.69	59.66	63.87	66.95	69.39	71.68	73.60	75.29
	F	36.38	51.94*	60.33	66.23	70.75	74.41	77.62	80.08	82.17	84.02
1920	M	36.24	51.97	55.79*	60.50	64.09	66.85	68.87	70.63	72.38	74.05
	F	36.65	49.42	59.29*	65.05	69.11	72.09	74.33	76.54	78.60	80.37
1930	M	37.07	50.73	56.90*	61.35	64.84	66.82	69.54	71.30	73.16	74.96
	F	38.33	53.14	61.15*	67.02	71.26	74.26	76.48	78.82	80.84	82.61
1940	M	37.13	52.31	58.99	64.69*	68.58	71.32	73.42	75.54	77.83	79.75
	F	37.90	52.98	60.74	67.25*	71.82	74.93	77.29	79.52	81.71	83.86

*Table 2.4 Average lengths (mm) of males (M) and females (F) from Long Island at all ages and decades; * denotes at which age and corresponding length statistical significance ($p < 0.05$) was reached. M = males, F = females.*

Decade	Sex	Age (yr)									
		5	10	15	20	25	30	35	40	45	50
1910	M	25.78	46.06	53.83	59.13	62.20	65.02	67.74*	70.36	72.71	74.86
	F	31.77	43.39	54.61	60.33	64.59	67.90	70.76*	73.32	75.59	77.82
1920	M	29.59	45.95	56.26	61.11	64.27	67.09*	69.93	72.29	74.29	75.88
	F	30.67	47.57	56.43	62.98	67.07	70.26*	72.86	74.79	76.72	78.62
1930	M	30.18	46.08	53.99*	59.53	63.28	66.08	68.46	70.40	72.18	73.96
	F	32.55	48.90	57.09*	62.59	66.63	69.81	72.26	74.16	76.13	77.94
1940	M	35.53	50.96	57.42	62.03	65.08	67.39*	70.63	70.91	72.69	74.74
	F	34.22	50.05	57.84	63.36	67.01	69.63*	71.75	73.72	76.06	78.43
1950	M	33.30*	47.52	54.65	59.54	62.54	64.85	66.79	69.28	71.74	73.69
	F	36.74*	51.47	59.01	63.90	67.28	70.13	72.52	75.10	77.87	80.22

*Table 2.5 Average lengths (mm) of males (M) and females (F) from northern New Jersey (NJ1) at each age and decade; * denotes which age and corresponding lengths when statistical significance ($p < 0.05$) was reached.*

Decade	Sex	Age (yr)									
		5	10	15	20	25	30	35	40	45	50
1910	M	22.40*	40.08	47.61	52.96	56.36	59.51	62.34	64.50	66.78	68.83
	F	30.01*	46.71	56.46	62.59	66.69	69.68	72.39	75.21	77.50	79.59
1920	M	24.78	42.49*	51.79	57.74	60.87	63.79	66.08	68.23	70.06	72.08
	F	28.58	46.15*	55.22	61.08	65.74	69.25	72.09	74.40	76.54	78.62
1930	M	27.54	44.60	52.97*	58.22	62.02	65.77	68.66	71.24	73.03	74.96
	F	29.43	47.29	57.09*	63.48	67.95	71.15	73.63	75.97	78.21	80.32
1940	M	27.90	45.17	53.74*	59.19	63.60	66.87	69.50	71.79	74.04	76.40
	F	28.56	46.36	56.14*	62.80	67.66	71.17	73.86	76.26	78.69	81.13
1950	M	25.74*	43.40	53.64	60.32	64.39	66.87	69.48	72.39	75.09	77.56
	F	29.77*	48.17	58.67	65.69	69.98	72.75	75.13	77.84	80.16	82.50

*Table 2.6 Average lengths (mm) of males (M) and females (F) of southern New Jersey (NJ2) at each age and decade; * denotes at which age and corresponding length if statistical significance ($p < 0.05$) was reached.*

Decade	Sex	Age (yr)									
		5	10	15	20	25	30	35	40	45	50
1910	M	25.78	40.79	51.62	52.54	56.31	59.35	62.11*	64.70	67.31	69.77
	F	25.76	41.42	52.83	54.20	58.22	62.16	65.24*	68.21	71.38	74.27
1920	M	25.66	41.57	50.19	54.99	58.99	62.86	65.80*	68.39	70.80	72.97
	F	25.70	42.41	52.09	57.04	61.91	66.06	69.72*	72.92	75.53	78.01
1930	M	26.71	43.69	52.38	57.18	61.98	65.83	68.89	71.69	73.96	76.76
	F	30.22	47.44	54.20	59.01	62.80	65.91	69.16	71.97	74.55	77.06
1940	M	28.97	47.98	55.26	60.61	64.10	67.68	70.65	73.60	76.03	78.16
	F	30.38	48.21	56.51	61.06	64.57	68.51	72.26	75.74	77.95	80.07
1950	M	30.24	48.23	56.76	61.77	65.94	70.01	73.13	75.28*	77.32	79.52
	F	31.07	49.51	58.58	63.73	67.70	71.60	75.34	78.36*	80.98	83.46

Table 2.7 Metrics of bottom water temperature for the four sampled sites for winter (Jan-Mar), spring (Apr-Jun), summer (Jul-Sep), and fall (Oct-Dec) averaged over 2016-2019 from a simulation produced by the Doppio model (López et al. 2020).

Variable	Mean	Standard Deviation	Lower Quartile	Upper Quartile	Minimum	Maximum	Median
Long Island							
summer	10.21	1.51	9.10	10.77	7.94	13.08	10.27
winter	7.65	1.37	6.75	8.76	5.90	10.22	7.19
spring	6.98	1.13	6.14	7.89	4.47	8.01	7.36
fall	13.62	1.58	12.44	14.82	10.89	16.39	13.53
Georges Bank							
summer	10.55	1.78	9.28	12.03	7.72	13.20	10.42
winter	7.22	1.08	6.70	8.11	5.43	9.07	6.93
spring	6.86	1.13	6.04	7.78	5.03	8.60	6.69
fall	10.78	1.18	9.88	11.81	8.77	12.55	10.74
New Jersey 1							
summer	9.58	1.55	8.40	10.29	7.26	12.48	9.66
winter	8.37	1.18	7.86	9.51	6.36	10.33	8.01
spring	7.23	1.17	6.26	8.18	5.40	8.98	7.42
fall	13.42	1.34	12.61	14.62	11.09	15.59	13.24
New Jersey 2							
summer	9.57	1.00	8.55	10.09	8.18	11.32	9.83
winter	9.42	1.05	8.73	10.10	7.23	11.18	9.57
spring	7.90	1.14	7.30	8.69	5.49	9.54	8.06
fall	12.31	2.23	10.64	13.26	8.67	16.10	12.43

2.7 Figures

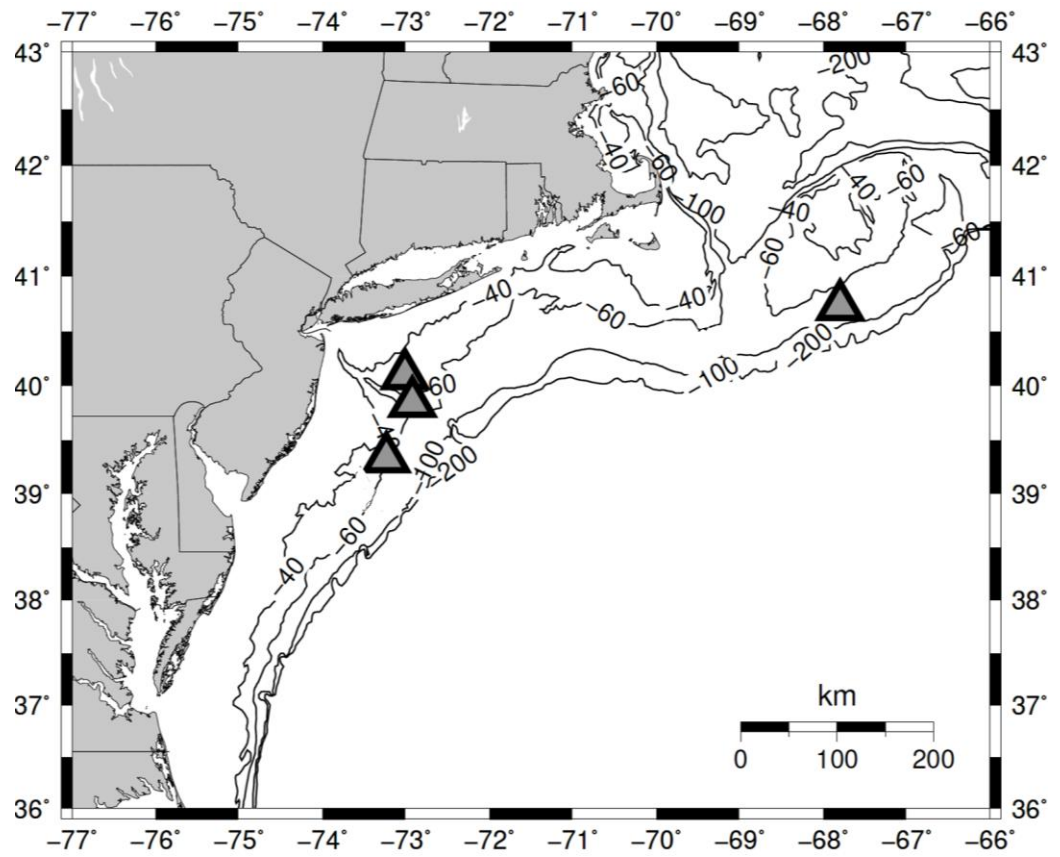


Figure 2.1 Sample locations. From north to south, sites are Georges Bank (GB), Long Island (LI), New Jersey north (NJ1), and New Jersey south (NJ2).

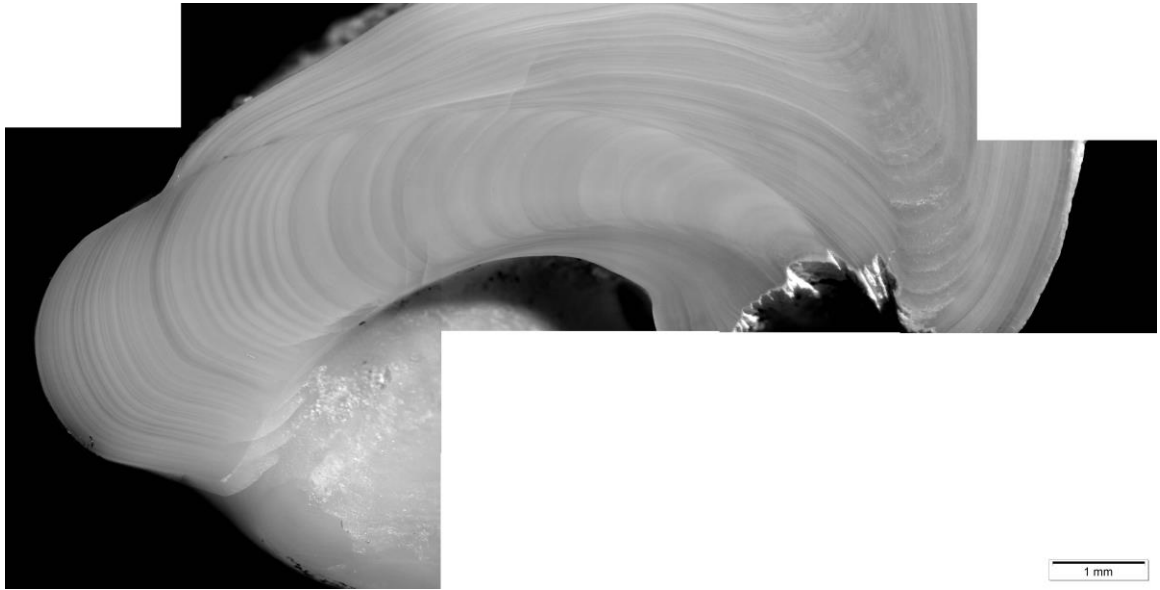


Figure 2.2 Arctica islandica hinge plate with prominent annuli.

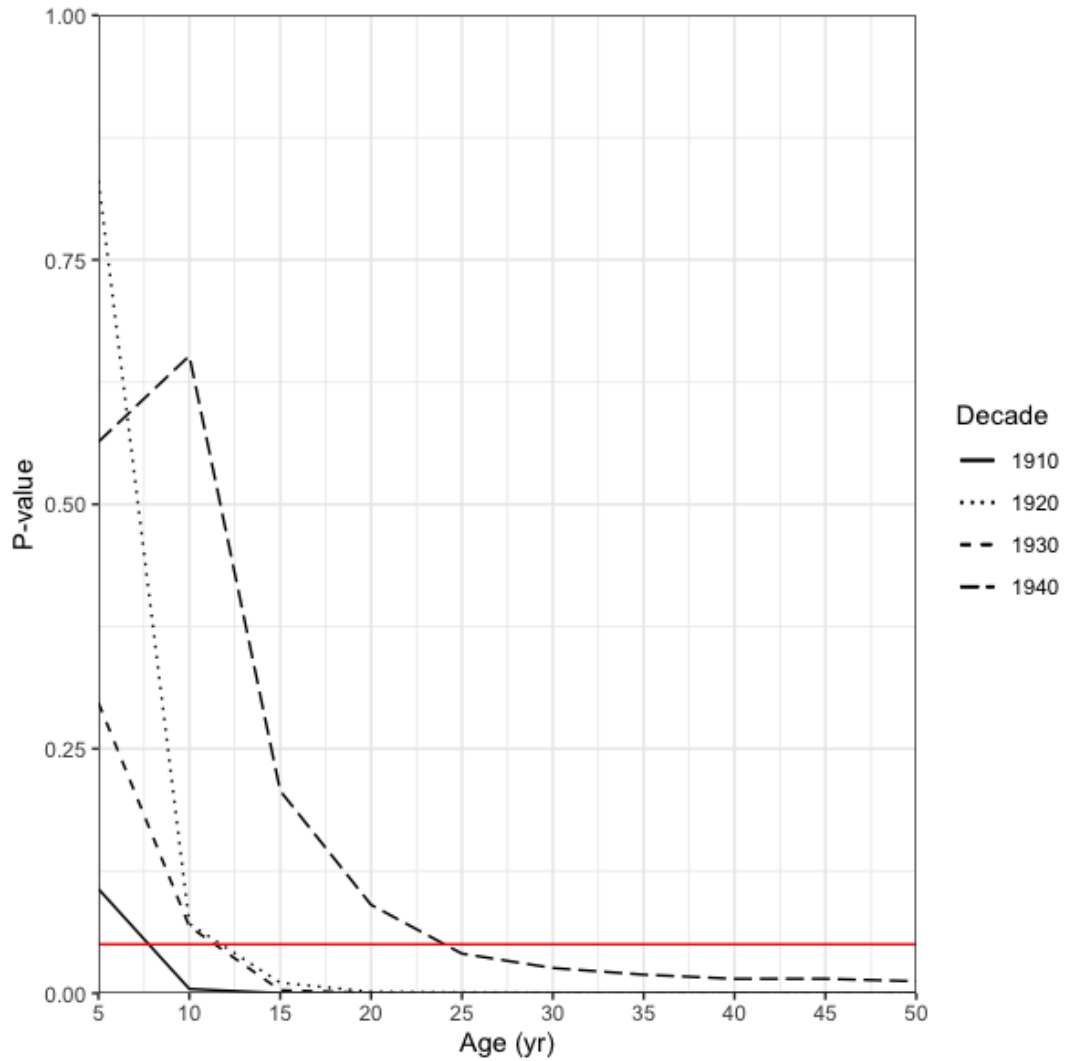


Figure 2.3 Trends in P-value per decade at Georges Bank obtained using Welch's t-test. The horizontal red line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

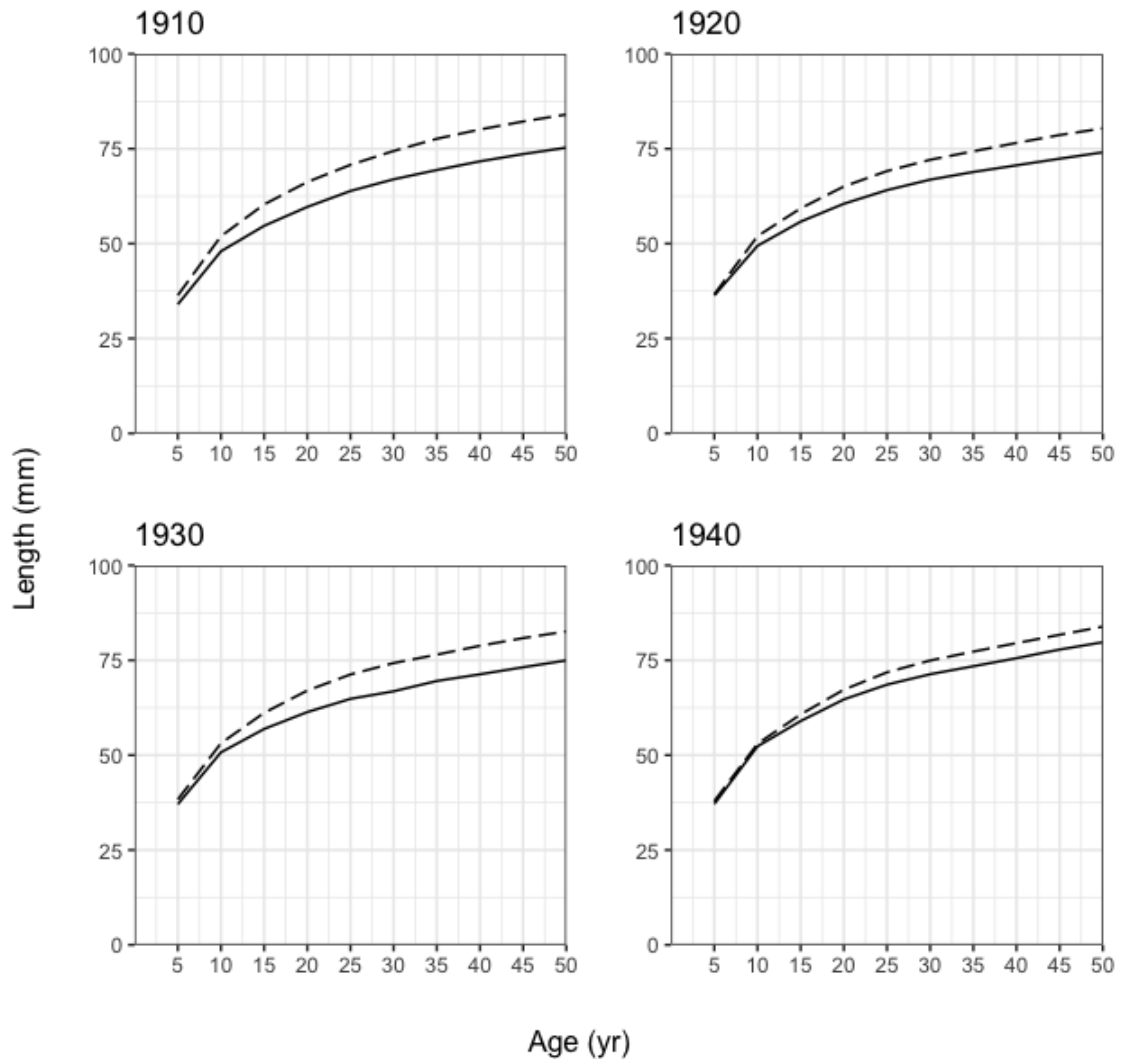


Figure 2.4 Growth differentials for female and male *Arctica islandica* at Georges Bank for animals born during the decades 1910-1940. Dashed line = females, solid line = males.

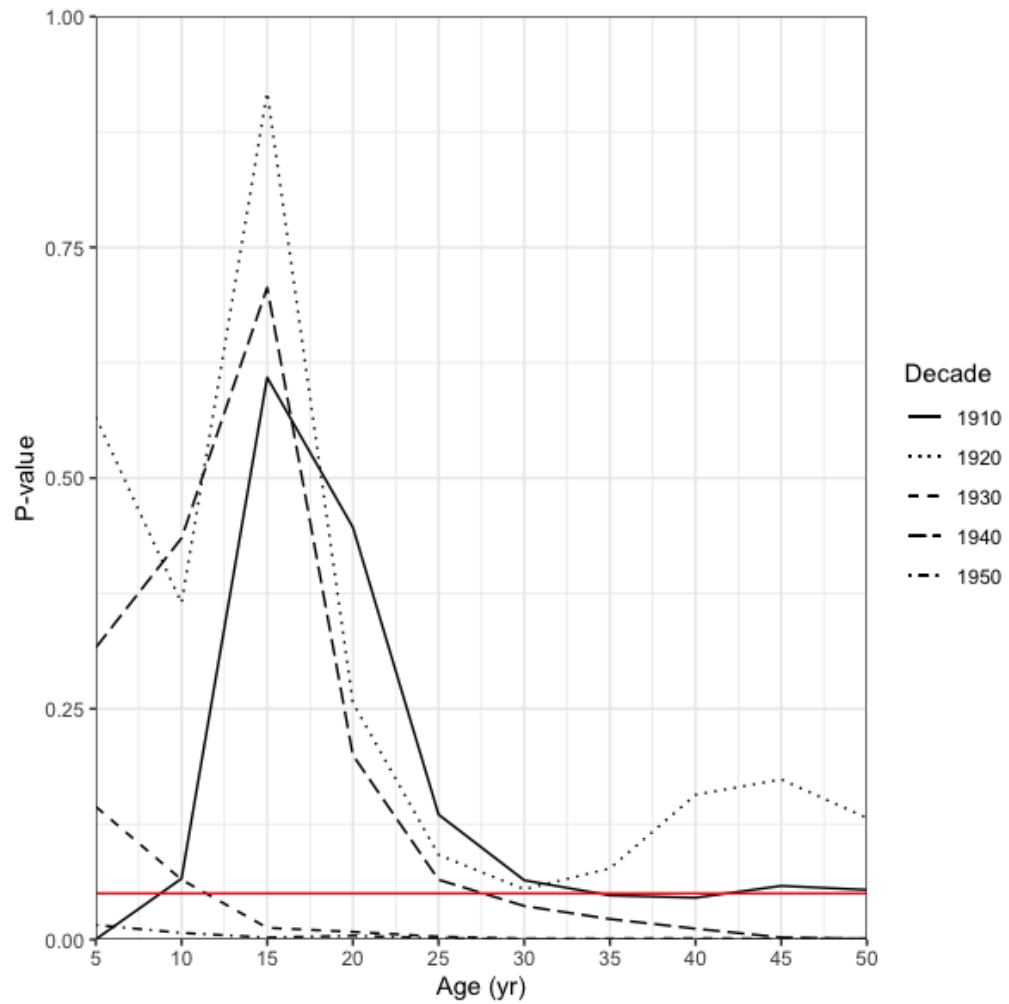


Figure 2.5 Trends in P-values obtained using Welch's t-test for animals from Long Island. The horizontal red line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

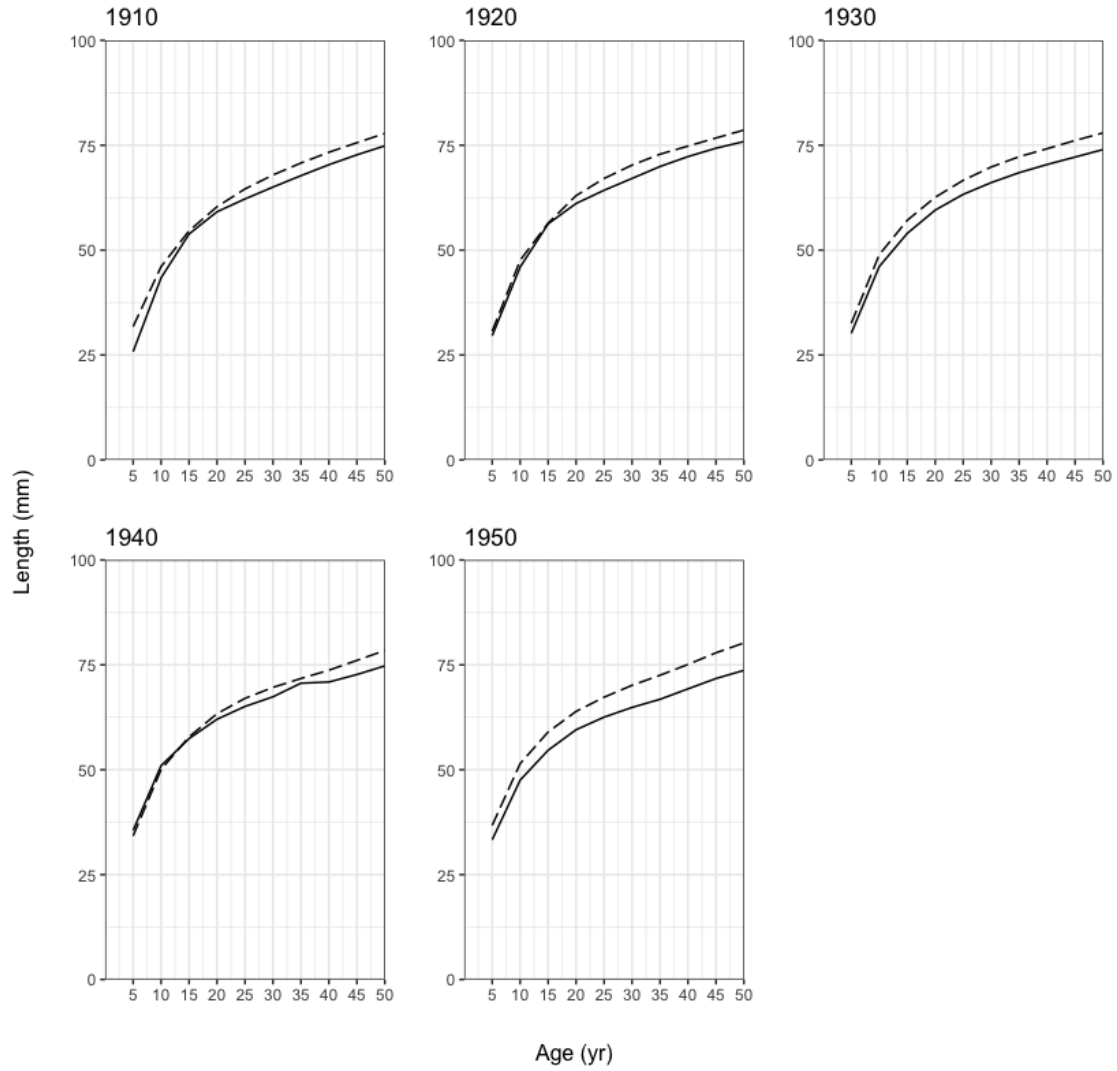


Figure 2.6 Growth differentials for male and female Arctica islandica for Long Island for animals born during the decades 1910-1950. Dashed line = females, solid line = males.

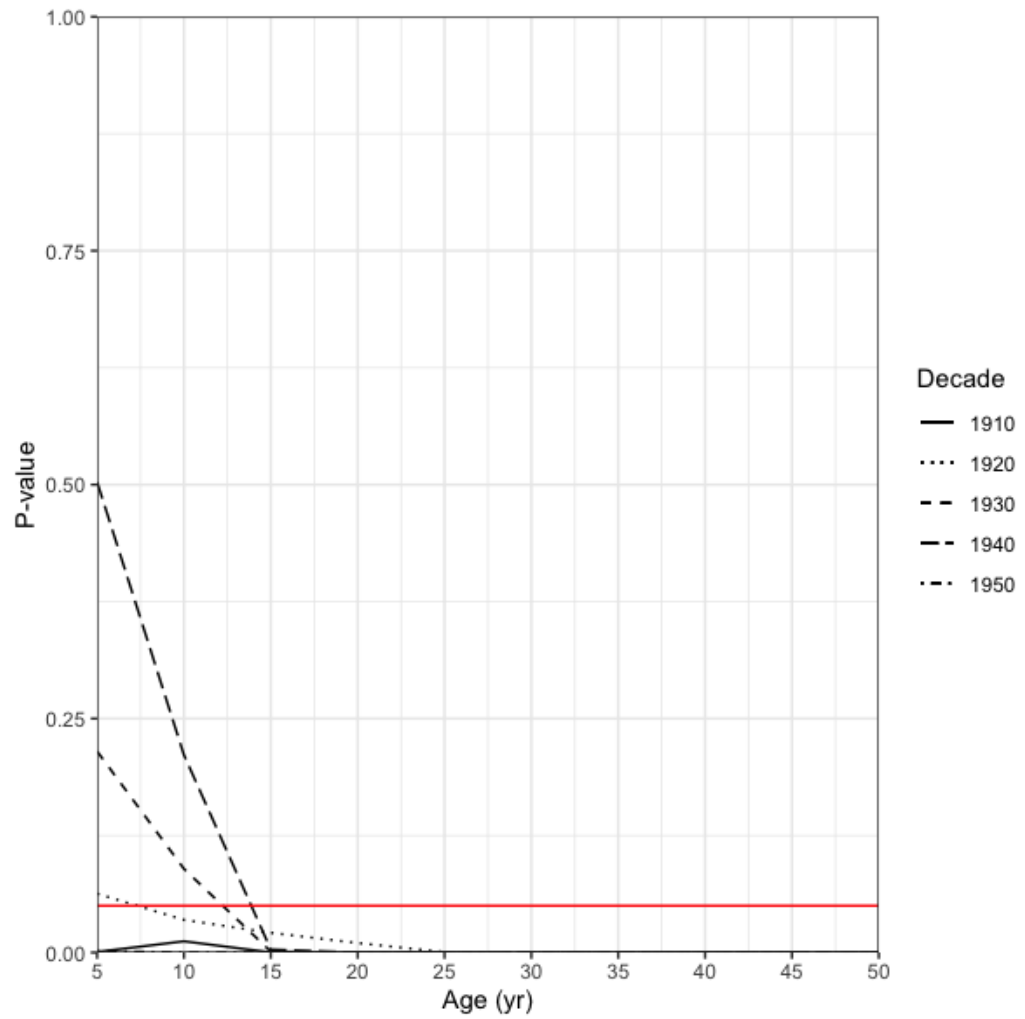


Figure 2.7 Trends in P-values obtained using Welch's t-test for animals from Northern New Jersey (NJ1). The horizontal red line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

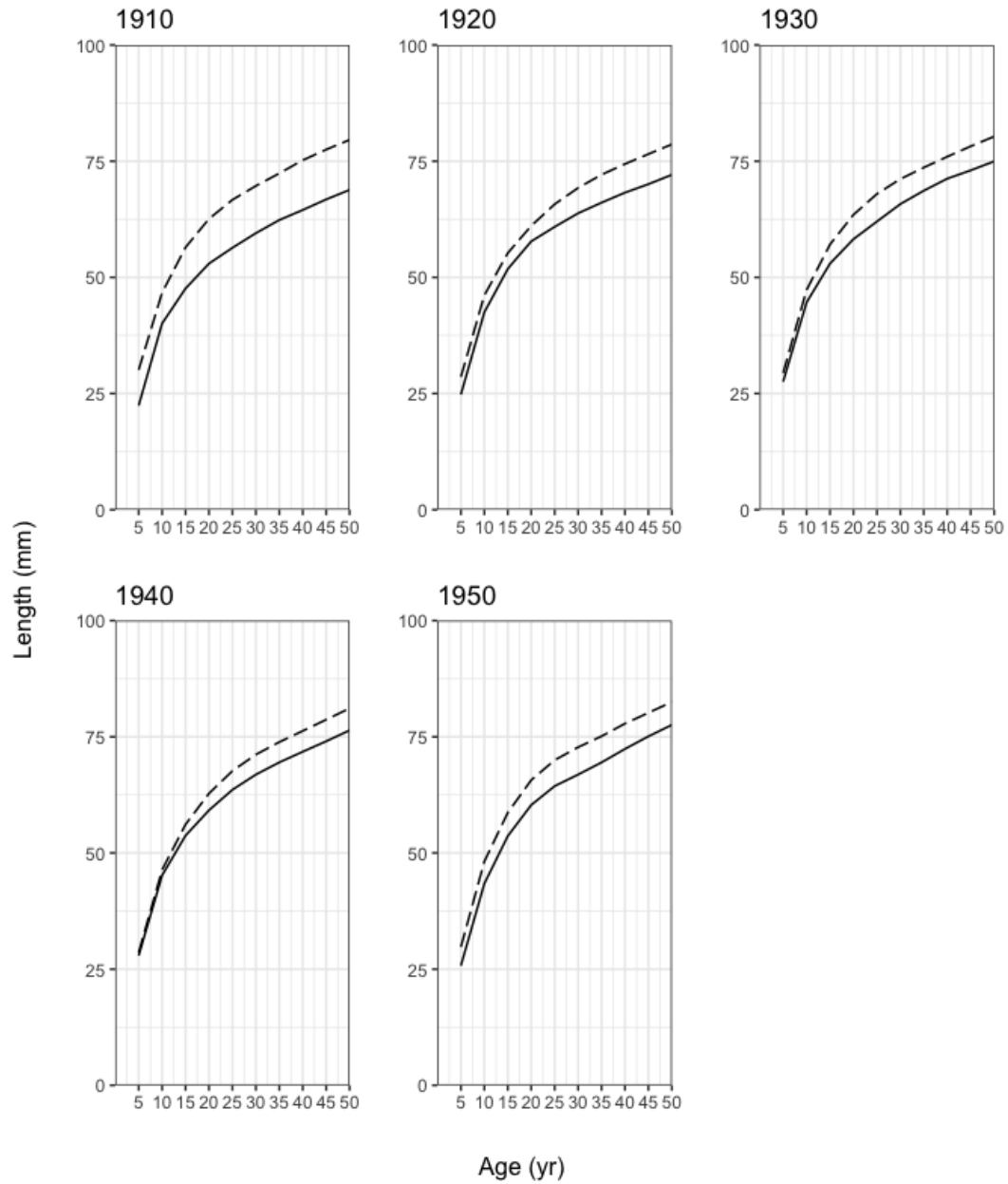


Figure 2.8 Growth differentials for male and female Arctica islandica for Northern New Jersey (NJ1) for animals born during the decades 1910-1950. Dashed line = females, solid line = males.

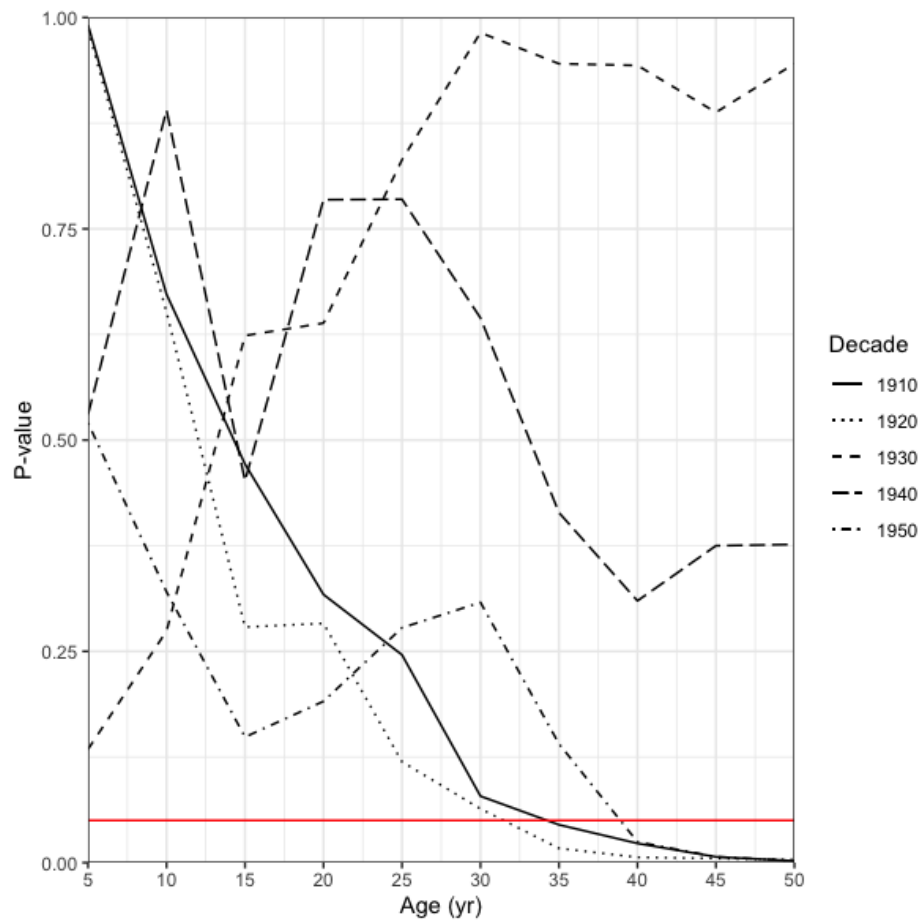


Figure 2.9 Trends in P-values obtained using Welch's t-test for animals from Southern New Jersey (NJ2). The horizontal red line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

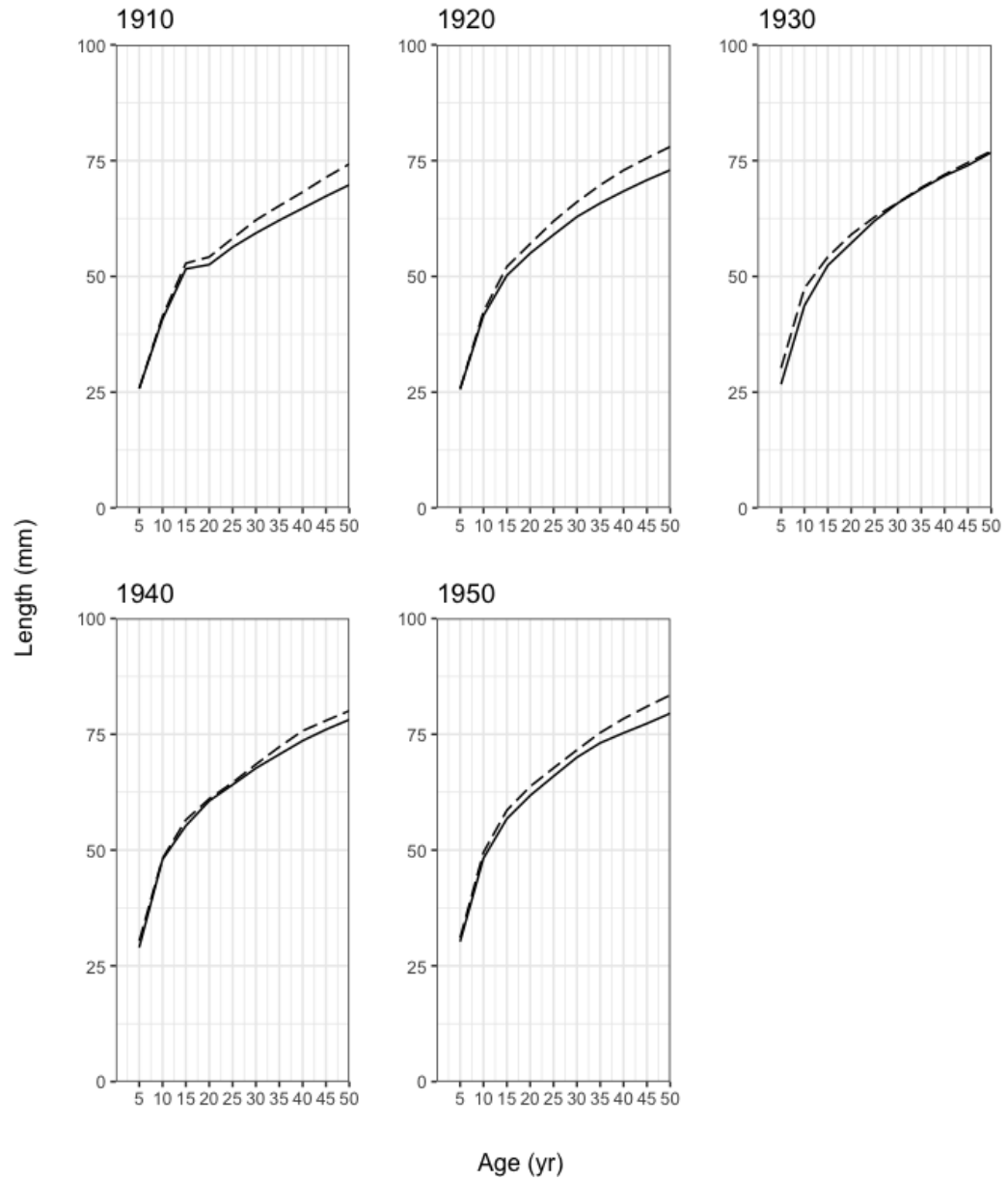


Figure 2.10 Growth differentials for male and female Arctica islandica for Southern New Jersey (NJ2) for animals born during the decades 1910-1950. Dashed line = females, solid line = males.

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CHAPTER III – SPATIAL HETEROGENEITY IN POPULATION AGE FREQUENCY AND RECRUITMENT IN THE OCEAN QUAHOG (*ARCTICA ISLANDICA*)

3.1 Introduction

The ocean quahog, *Arctica islandica*, is the longest-lived, noncolonial species inhabiting the northwestern Atlantic continental shelf. Fisheries for this species began in the United States in 1967, with a \$9.1 million ex-vessel value in 2019 (Pace et al. 2017b; MAFMC 2021). *Arctica islandica* is a boreal species with a range spanning from Newfoundland, Canada, to Cape Hatteras, North Carolina, in the Western Atlantic, and from Iceland and Norway to the Bay of Cadiz, Spain, in Europe (Merrill et al. 1969; Dahlgren et al. 2000; Ballesta-Artero et al. 2017; Pace et al. 2017a, b).

Arctica islandica deposit annual growth lines in their valves, termed annuli, which can be counted to determine age (Jones et al. 1980; Thompson et al. 1980; Murawski et al. 1982; Ropes et al. 1984b). Their lifespan often exceeds 200 years of age, with the oldest-documented *A. islandica* aged at 507 years old (Butler et al. 2013). They can reach sizes of 120 mm shell length, but age can vary greatly at a given size (Pace et al. 2017a, b; Hemeon et al. 2021), which, with its long lifespan, inhibits the use of age-based models to manage this species (NEFSC 2017).

Arctica islandica are sensitive to changes in bottom water temperatures. They have a strict upper thermal tolerance of 15°C – increases of 1°C in this temperature range can cause mass mortality (Merrill et al. 1969; Harding et al. 2008). Temperature can also impact growth rates in *A. islandica*, as observed by Schöne et al. (2005), Ballesta-Artero et al. (2017), Pace et al. (2018), and Hemeon et al. (2021). Thus, it is important to

determine how differing temperatures throughout the range of *A. islandica* have impacted their age structure and growth to inform fisheries of best management practices.

To determine the effects of environmental variance on *A. islandica* growth and recruitment, over 1,500 animals from two New Jersey populations north and south of the Hudson Canyon were analyzed and compared to two northern populations (Hemeon et al. 2021; Hemeon et al. in prep.). New Jersey was chosen due to its southern location and to the decrease in fishery landings in the 1990s. Previously, between 1980-1991, the bulk of landings for the U.S. fishery were caught off New Jersey, but the fishery shifted to the Long Island continental shelf in 1991 due to declining biomass farther south (NEFSC 2017). Previous age and growth studies have been performed on New Jersey *A. islandica* (Pace et al. 2017a; Pace et al. 2018); however, larger sample sizes and sex-based samples were deemed necessary (Hemeon et al. 2021a; 2021b) to establish a more accurate age-length relationship. Results presented for these two sites will be compared to the equivalent analyses for populations from Georges Bank and Long Island to determine how this species' demographics vary across its range (Hemeon et al. 2021a; Hemeon et al. in prep.).

Besides basic demographics, comparison of these four populations can provide additional information on the dynamics of recruitment across the Mid-Atlantic region. The predictability of recruitment of *A. islandica* has been a primary concern in the management of the fishery (NEFSC 2017). Little information is available from surveys, as the age span supporting the fishery is vastly longer than the direct observation of recruitment dynamics (Powell and Mann 2005; Harding et al. 2008; Hemeon et al. 2021a). Age frequencies created using large sample sizes may help identify recruitment

patterns for *A. islandica*, whether major gaps in recruitment efficacy exist or if recruitment events can be correlated with environmental cycles such as the North Atlantic Oscillation. Such data could provide information leading to improved fishery quotas and on the efficiency of *A. islandica* stock recovery in case overfishing ever occurs (Hemeon et al. 2021a).

Arctica islandica males and females have observed growth differentials, with females reaching larger sizes than those of males (Ropes et al. 1984a; Fritz 1991; Thórarinsdóttir and Steingrímsson 2000; Hemeon et al. 2021a; Hemeon et al. in prep.). Sexual dimorphism is rare in bivalves, yet is remarkably apparent in *A. islandica*. Due to the influence that these size differentials may have on length- or age-based models, separate age-length keys by sex may also be necessary to accurately describe and manage each population (Hemeon et al. 2021a). Accordingly, any comparison of between-population demographics and recruitment dynamics must dependently evaluate the potential influence of sexual dimorphism.

The objective of this study is to determine the degree to which a single age-length key can be used for the *A. islandica* of the Mid-Atlantic Bight (MAB) and Georges Bank, and if not, whether each population requires its own unique key or whether geographically close populations, such as Long Island and northern New Jersey, can be described by a single key. Age frequencies will also be examined to determine patterns in recruitment, and whether they differ across the MAB and Georges Bank. Males and females from each population will also be analyzed to determine if sexual dimorphism, leading to variations in age or length frequencies, may warrant separate, sex-based keys for each population.

3.2 Materials & Methods

3.2.1 Sample Collection

In August of 2019, *Arctica islandica* samples were collected by commercial hydraulic dredge from two sites off New Jersey: 39.840556 N, 72.821667 W by the *F/V Big Bob*, and from 39.33 N, 73.545 W by the *F/V John N*. These sites are located respectively north and south of the Hudson Canyon on the Mid-Atlantic continental shelf at 60.0 m and 62.5 m depth. A total of 777 animals were collected from the northern site, herein referred to as NJ1, and 908 were collected from the southern site, NJ2.

Commercial dredges are selective for sizes >80 mm shell length, so this study predominantly focused on animals that have obtained market size and are relevant to the fishery. Animals <80 mm are underrepresented. Samples from Georges Bank (GB) and Long Island (LI) were collected in 2017 from 40.72767 N, 67.79850 W and 40.09658 N, 73.01057 W respectively by the *F/V ESS Pursuit* (Figure 1). At Georges Bank, 615 animals were collected for ageing, while 904 animals were collected for the age sample for Long Island (Hemeon et al. 2021a; Hemeon et al. in prep.).

3.2.2 Sample Preparation

All animals were measured for shell length (mm), shucked, cleaned in a bleach solution, and sexed by gonadal smear slide. Shells were cleaned in a bleach solution, cut to expose the hinge plate using a tile saw, sanded, and polished to clearly display annuli, and imaged using a combination Olympus camera and microscope with cellSens software. For greater detail on processing techniques for *A. islandica*, see Pace et al. (2017a,b) and Hemeon et al. (2021b). Ageing was completed using the opensource software ImageJ with the ObjectJ plugin. In total, 738 animals were aged from NJ1, and

790 were aged from NJ2. A minimum of 100 animals per 5 mm size class were aged, with all animals aged for underrepresented size classes (<80 mm and >105 mm). Some animals were omitted from analyses due to poor image quality and therefore highly uncertain ages, leading to 756 NJ2 and 714 NJ1 available ages to create age-length keys.

3.2.3 Ageing Error Assessment.

To increase confidence in *A. islandica* ages, two readers aged subsamples and compared ages for each population. Hemeon et al. (2021b) utilized 20% subsamples, but southern shells, including Long Island and New Jersey, were anticipated to be more difficult to age compared to Georges Bank due to the increased presence of subannual signatures in animals from these populations (Hemeon et al. in prep.); thus, 30% subsamples were used instead. Readers' ages were measured for bias, precision, and error utilizing the protocol outlined in Hemeon et al. (2021b). Once bias between readers was undetected and ages were precise to an acceptable degree (i.e., non-significant bias levels and error < 10%), one reader continued to age the remainder of each population.

3.2.4 Length Sample

The *A. islandica* collected for ageing at NJ1 and NJ2 sample were also used to create a length frequency for each site. At Georges Bank, 3,159 animals were collected to create the length frequency (Hemeon et al. 2021a), while 2,905 animals provided the length frequency for Long Island (Hemeon et al. in prep.).

3.2.5 Age-Length Keys

Age-length keys (ALKs) describe the probability of an animal's age at a given length. ALKs were created for the NJ1 and NJ2 populations, as well as male and female subsets of each, using their corresponding age samples. ALKs for Georges Bank and

Long Island, including male and female subsets, were previously reported by Hemeon et al. (2021a) and Hemeon et al. (in prep.).

3.2.6 Age-Frequency Distributions

To analyze differences between age frequency distributions, three statistical tests were used: Kolmogorov-Smirnov, Anderson-Darling, and Wald-Wolfowitz Runs. The Kolmogorov-Smirnov (KS) test is sensitive to and is thus used to evaluate deviations between the central portions of two age frequencies, whereas the Anderson-Darling (AD) test is more sensitive to differences at the tail ends of the distributions (Conover 1980; Engmann and Cousineau 2011; Hemeon et al. 2021a). The Wald-Wolfowitz Runs test evaluates the degree to which two distributions cross each other, focusing here on differences in growth rates between males and females (Conover 1980; Hemeon et al. 2021a). Results of all three tests are provided with respect to the $\alpha = 0.05$ and $\alpha = 0.01$ significance levels. The KS and AD tests were two-tailed, while the Runs test is one-tailed to evaluate the ‘low’ condition, which determines whether the distributions failed to cross one another at a minimal frequency expected by chance. Interpretation of the latter test is substantially different if the two frequency distributions cross more or less often than expected by chance.

As the data are heavily right-skewed due to the lack of small and young animals, potentially due to variation in recent recruitment, but more likely due to dredge selectivity, mitigation of the influence of low to zero numbers in the left tail on the statistical evaluation of the distribution is important. Thus, the statistical comparisons also used modified frequency distributions by using the median value of the original distribution to combine adjacent small cells (see Hemeon et al. 2021a for more

information). This type of analysis is herein referred to as median bin modification (Hemeon et al. 2021a). Hereafter, the data will be referred to as either unmodified or the median modified.

To determine the potential of one ALK (e.g., male ALK) to describe another age frequency (e.g., female), 50 Monte-Carlo simulations were performed by randomly sampling with replacement from the true age-length data. New age-length keys were created for each simulation and applied to the comparison length data. The resulting new age frequencies were tested for significant differences from the original ('True') age frequencies by the KS, AD, and Runs statistical tests. For more information, see Hemeon et al. (2021a).

3.2.7 Longevity & Mortality

Longevity and mortality are calculated using the regression of the natural log of the descending right tails of the age frequency for each site (Ridgway et al. 2012; R Core Team 2018; Hemeon et al. 2021a; Hemeon et al. in prep.). The descending left tails were not used due to low frequencies of young animals potentially skewing results. Individuals were consolidated by birth year into 10-year age classes for this purpose. For NJ1, analysis used animals greater than 80 years of age; for NJ2, animals greater than 130 years of age were used.

3.2.8 Sex Ratios & Dimorphism

Males and females may occur in equal proportions across size classes for Venerida (e.g., Guo and Allen 1994; Herrmann et al. 2009; Kavitha et al. 2021; Lopez et al. 2022). To evaluate this in *A. islandica*, animals for each population were divided by sex within their respective 5-mm size class. Binomial tests were used to determine the

extent to which the proportion of males and females diverged from the expected ratio of 1:1 (R Core Team 2018).

3.3 Results

3.3.1 Age-Length Data

For NJ1 and NJ2, the oldest animals were females aged at 286 and 295 years, respectively. The largest animals were also females at both sites, with the largest animal at NJ1 measured at 111.02 mm in NJ1 and 114.74 mm in NJ2. The youngest and smallest animals caught by commercial dredge at both sites were all males. At NJ1, the youngest male was aged at 13 years, while the youngest male was 14 years in NJ2. The smallest animal was measured at 62.73 mm in NJ1, and 74.64 mm in NJ2 (Figures 2 & 3).

In NJ1 females, the ages ranged from 23-286 (median = 88), while males ranged from 17-279 years (median = 73). Mean values for both sexes were larger than median values, with females averaging at 104 years and males averaging at 84 years. In NJ2 females, ages ranged from 15-295 years (median = 113), and male ages ranged 14-278 (median = 100). Opposite of NJ1, the average values were smaller than median values, with the average female age being 105 years and the average male aged 96 years. Lower mean values indicate that the NJ2 ages are more left-skewed than NJ1 (Figures 4 & 5).

In NJ1, the largest range of ages occurred in the 90-mm size class, with ages ranging 162 years for males and 235 years for females. In NJ2, the 95-mm size class contained the largest age ranges, 169 years for males and 175 years for females. These were not the most numerous size classes, however. For both sites, the most numerous size class is the 85-mm size class, with 162 animals total from NJ1 and 124 animals total from NJ2. Broken down into sex, the most numerous size class for females at NJ1 was the 95-

mm size class with 91 animals, and for males 80 mm with 107 animals (Figure 6). For NJ2, the most numerous size class for females was again the 95-mm size class with 74 animals, and for males the 85-mm size class is largest with 78 animals (Figures 7).

3.3.2 Age-Frequency Distributions

At NJ1, females were somewhat older than males (Figure 4). Correspondingly, KS tests for both the unmodified and the median bin modified datasets demonstrated that the two age frequencies are extremely significantly different (Table 1). This result was also true for the AD and Runs tests.

NJ2 age frequencies are somewhat offset, but not to the same degree as in NJ1 (Figure 5). KS test results were significant for the unmodified data file but not for the median bin modification (Table 1). Contrarily, AD test results were significant for the median bin modification but not for the unmodified data file. Runs test results were not significant for the unmodified data file but were significant for the median bin modification.

A comparison of population age frequencies for NJ1 and NJ2 show that they were significantly different. Table 2 displays the number of times simulated age frequencies derived using age-at-length data from one dataset when applied to a length frequency from another dataset produced age frequencies that were different from the ‘True’ age frequency for the second datasets (for more information, see Hemeon et al. 2021a). Runs test results were significantly different in a minimum of 70% of simulations for both the unmodified data comparisons and the median bin modifications (Table 2). AD results were strongly significantly different comparing for the majority of the simulations, but indicate that males were similar when NJ1 is the ‘True’ dataset. However, when NJ2 is

the 'True' dataset, AD tests identify significant differences 82-100% of the time. KS results reveal that the simulated age frequencies between populations, males, and females are different 100% of the time in the unmodified data, but are much less frequently significantly different once the datasets are modified to limit the influence of poorly represented age classes. These results indicate that both the centers and the tails of each populations' distributions are significantly different too frequently for a single age-length key derived from the population at one site to be applied to the other. This result accrues regardless of whether the populations are compared as a whole or by sex.

NJ1 and NJ2 age frequencies were compared directly to those from Georges Bank and Long Island to determine age differences among the MAB populations. Age frequencies from Georges Bank populations when compared to either NJ1 or NJ2 were found to be significantly different in most cases (Table 3). Only the comparison of males between NJ1 and Georges Bank yielded non-significant results for the AD test, suggesting some similarity of the tails between the two age distributions in the unmodified dataset.

Comparisons of age frequencies between the New Jersey sites and the Long Island population showed different trends (Table 4). In the unmodified data, NJ1 males were significantly different in KS and AD tests at both alpha levels. However, once this dataset was modified to the median bins, the KS results were non-significant, and AD results were only significant at the 0.05 level. For females, the KS results were non-significant for both the unmodified and the median bin datasets, but significant for the AD test. Runs test results were only significant at the 0.05 level for males and non-significant at both levels for females. Thus, the NJ1 population differs from the Long

Island population, but the differential is not as strong as that between NJ1 and Georges Bank. This suggests that the frequencies of very old or very young animals may differ more strongly in the Georges Bank than that of Long Island. In contrast, the comparison between NJ2 and Long Island shows consistent significant differences, similar to the comparison between the NJ2 and Georges Bank populations.

3.3.3 Length Frequency

For both New Jersey sites, female sizes were offset to sizes larger than those of males (Figures 8 & 9). For NJ1, the Runs test results between males and females were significantly different in both the unmodified file comparison and the modified bin comparison (Table 1). AD test results were significant at the 0.05 level for the median bin modification and unmodified data files. KS test results were not significant for the median bin modification but very significant for the unmodified data.

For NJ2, KS test results were not significant for the median bin modification but were for the unmodified data. AD tests were statistically significant at the 0.05 level for the median bin modification but were not significant for the unmodified datasets. As with NJ1, Runs test results were very significantly different for both modified and unmodified datasets. Thus, a clear discrepancy in the growth rate exists between male and female *A. islandica* at NJ2.

3.3.4 Longevity & Mortality

For the NJ1 population, the mortality rate is estimated at 0.019 yr^{-1} . For females, the rate is slightly lower at 0.018 yr^{-1} , and for males it is lower still at 0.015 yr^{-1} . The population longevity for this site is 310 years, while for females it is 300 years and males 273 years. For NJ2, the mortality rate is higher than NJ1 at 0.024 yr^{-1} . For females the

rate is 0.026 yr^{-1} , and for males, 0.023 yr^{-1} . Longevity for the NJ2 population is 304 years, while for females it is 277 years and 265 years for males.

3.3.5 Recruitment

In NJ1, a major recruitment event occurred in the 1930s and 1940s, but recruitment decreased substantively thereafter into the 1970s before peaking again in the 1990s. For NJ2, a major recruitment event happened in the mid-late 1800s, and recruitment then decreased until the 1980s-90s when another event occurred (Figures 10 & 11). In both cases, most birth years are represented for the 1800s and 1900s, suggesting yearly recruitment at both sites, with observable year-to-year and decade-to-decade variations in scale.

3.3.6 Sex Ratios & Dimorphism

Males and females dominated different size classes. Males were much more common at sizes 70-89 mm, whereas females were more numerous in size classes 90-105 mm in NJ1 and NJ2. At both sites, females began to outnumber males by the 90-mm size class. The ratios of males and females became close to 1:1 at size class 85 mm at NJ1 and at size class 90 mm at NJ2 (Tables 5 & 6). On a population scale, females are more numerous than males overall in New Jersey. The NJ1 population female:male ratio is 1:0.80, whereas the NJ2 population ratio is 1:0.83. Females reached overall larger sizes than males at both New Jersey sites, as indicated by the statistically significant Runs test results and cumulative length frequencies (Figure 8 & 9).

3.4 Discussion

3.4.1 Cold Pool Dynamics

The Cold Pool is a 20-60 m thick body of uniformly cooler bottom water that forms along the outer continental shelf in the spring (April) annually along the MAB from as thermal stratification traps winter water remnants (Lentz 2017). Consequently, boreal species occupy the continental shelf at latitudes lower than would be anticipated by inshore provincial boundaries (Engle and Summers 1999; Hale 2010). Thus, it permits the extension *A. islandica*'s range as far south as Cape Hatteras, N.C. The Cold Pool dissipates in the fall (October-November) when the thermocline breaks down. Recent interannual variability in the duration and mass of the Cold Pool is well-documented (Chen et al. 2018; Chen and Curchitser 2020, Friedland et al. 2022), but likely occurred throughout much of the Holocene (LeClaire et al. 2022) and likely influences *A. islandica* growth from year to year and from location to location. The Doppio model (López et al. 2020) allows the tracking of annual patterns in temperature data over recent years (2016-2019) which, used here, are assumed to provide guidance as to geographic trends of the past, given the lack of temperature data for the majority of the lifespan of *A. islandica*.

3.4.1.1 Age-Length Key Analysis

Northern (NJ1) and southern (NJ2) New Jersey sites are significantly different for the majority of tests and dataset modifications, at $\alpha = 0.01$. Though they are both east of the New Jersey, they have a major geographical barrier between them - the Hudson Canyon. The Hudson Canyon is the largest US east coast underwater canyon, cutting up to 800 m into the continental slope and extending 370 km into deep water at 7-9 km wide (Keller et al. 1973) and has a substantial influence on current direction and velocity on

the northeast and southwest sides (Castelao et al. 2008), and thus on the dispersion of larvae north-south and across the continental shelf in the region (Zhang et al. 2015, 2016). Thus, the NJ1 and NJ2 populations exist in distinct geographic regions, under conditions of distinct sources for larval supply, which would explain the differences in age frequencies and recruitment events between the two sites.

NJ1 displays low but consistent recruitment throughout the 1800s and early 1900s with a distinct peak in the 1930s-50s. Recruitment picks up at NJ2 and increases to a high proportion of animals born in the mid-late 1800s and suggests a lower recruitment rate in the 1900s until the 1980s, assuming similar mortality rates over this time period. Both sites experience a noticeable decrease in recruitment in the 1960s-1970s (Figures 10a & 11a). This decrease is consistent with the decline in water temperatures during these decades (Nixon et al. 2004). The higher recruitment in the 1930s-1950s is consistent with higher temperatures during that time (Nixon et al. 2004).

The absence of a consistent recruitment index from survey data due to limitations of dredge size selectivity and the short timeframe since survey initiation in the early 1980s (NEFSC 2017) limits the comparison of direct recruitment observations to the age frequency data reported here. Nonetheless, the recruitment peaks are consistent with reports by Harding et al (2008) and Powell and Mann (2005) based on collection of smaller size classes using a lined dredge, suggesting that dredge size selectivity did not substantively bias comparisons reported here for the time period prior to about 2000. The interpretation of the influence of temperature on the probability of recruitment is consistent with Harding et al. (2008) who argued that increases in bottom water temperature result in increased recruitment potential. In addition, LeClaire et al. (2022)

suggested that recruitment has declined over the last 100+ years inshore and south of NJ2 and this is supported by a comparison of the more southerly NJ site reported by Pace et al. (2017b) and the data reported here for NJ2, as well as the lower recruitment rate suggested by the NJ2 age frequency for much of the 20th century. The increase in recruitment at NJ2 late in the 20th century also is mirrored in the age frequency farther south reported by Pace et al. (2017b) and in the reports of recent recruitment in that region by Powell and Mann (2005). These trends suggest some consistency within large geographic regions in recruitment potential that are likely manifested by trends in bottom water temperature as yet poorly understood.

3.4.1.2 Sex Ratios & Dimorphism

Population sex ratios at NJ1 and NJ2 are similar, 1:0.80 and 1:0.83, respectively. Fritz (1991) found a similar sex ratio off New Jersey, 1:0.77 (F:M), indicating that this site is historically female dominated. Examining the individual size classes, NJ1 displays a distinct difference in males and females at most size classes. NJ2 only has 3 classes in which binomial results indicate that there are significantly different numbers of females and males: 85 mm, 100 mm, and 105 mm, suggesting that there is a more even spread of males and females across size classes at NJ2 compared to NJ1. The differential is also consistent with Sower et al. (in press) who interpreted size differentials between males and females as a result of higher growth rates for males at NJ2, and thus fewer size classes where males and females diverge in representation. Not surprisingly, the two sites also differ at which size class has the closest to a 1:1 ratio with NJ2 having the higher value: for NJ1, 85 mm, and for NJ2, 90 mm.

Pace et al. (2017b, 2018) found that southern populations of *A. islandica* tended to have higher growth rates compared to their northern counterparts. Even though NJ2 is relatively geographically close to NJ1, the Hudson Canyon causes different ecological impacts as it acts as a barrier on the Cold Pool and at least a partial barrier on larval transport (Zhang et al. 2016; Chen et al. 2018; Chen and Curchitser 2020). NJ2 experiences increased variation in bottom water temperatures than NJ1 during the fall thermocline breakdown (López et al. 2020), potentially influencing growth and population structure, leading to overall larger animals at age.

At NJ1, females are observed to be older than males (Figure 4) and distinctly larger than males. Commonly, bivalve species with larger, older females and younger, smaller males display protandry, but no evidence for protandry exists for *A. islandica* (Ropes et al. 1984a; Hemeon et al. 2021a). The likely reason behind the differences in ages at NJ1 is that there is an increase in female frequency in the 1920s-1930s that was not observed in males (Figure 10, B & C). Similar periods of differential survival of males were observed by Hemeon et al. (2021a) on Georges Bank. What might facilitate recruitment or survival of one sex over the other is unclear. One hypothesis is that as females grow faster to an overall larger size than males, males may have been subjected to increased predation due to their smaller size. However, information on predators for *A. islandica* beyond *Astropecten americanus* (Franz and Worley 1982) is poorly reported. Another hypothesis relating to size is that larger animals have increased burrowing success compared to smaller animals, so females may have escaped negative environmental influences occurring at this time (Taylor 1976). The burrowing hypothesis is, however, poorly supported because the same influence should exist on all cohorts, not

just males, whereas the occurrence of disproportional survival is cohort-restricted in time. Thus, some influence early in life would appear necessary. Regardless, what is clear is that periods of time when male and female proportions in a cohort differ widely from 1:1 are common and often of multi-year duration and require explanation.

3.4.1.3 Longevity & Mortality

NJ2 had a higher calculated mortality rate and lower overall longevity compared to NJ1, for the population and for males and females. These rates are also somewhat higher than the natural mortality rate of 0.02 yr^{-1} accepted by the NEFSC (2017). This is potentially due to the higher variability in temperatures experienced at NJ2 in the fall stratification breakdown of the Cold Pool compared to NJ1 per the Doppio model results (López et al. 2020). This site experienced the highest variability in temperature (2.23°C) during the thermocline breakdown in recent (2016-2019) years (López et al. 2020). Alternatively, the differential might be explained by a higher fishery catch at NJ2. The differential is well below the estimate of the fishing mortality rate for the stock (Hennen 2015; NEFSC 2017). However, the differential in historical catch between the two sites is not available as catch reports are for a relatively large regional scale and the fishery targets local patches of high density (Solinger et al. in prep.). Regardless of the potential of the fishery, the mortality rates of both populations are very similar to the natural mortality rate of 0.02 yr^{-1} . The fishery has been prosecuted over a very short time in comparison to the age range of the market-size population suggesting limited negative impacts on the age frequencies reported herein from the fishery.

3.4.2 Comparison of All Four Sites

3.4.2.1 Age-Length Key Analysis

Hemeon et al. (in prep.) found that population ALKs created for Georges Bank and Long Island were sufficiently different to produce site-specific age frequencies. When comparing the ALKs of these two sites to New Jersey, however, similarities were observed between Long Island and NJ1. The statistical difference observed between the two is generated by differentials at the tail ends of the distributions, with NJ1 having slightly higher proportions of animals in the 1980-90s compared to Long Island. This is potentially due to the timing of sample collection related to dredge size selectivity; Long Island samples were collected in 2017, whereas NJ1 samples were collected in 2019. Two years could be a sufficient amount of time for young animals to reach a size large enough to be collected by commercial dredge, and thus could be the cause for this singular discrepancy between the two sites.

Given the comparisons between NJ1, NJ2 and Georges Bank and Long Island yielding highly significant results, a single ALK will not provide accurate data for the entirety of the MAB. New Jersey south of the Hudson Canyon should have its own key. North of the Hudson Canyon, NJ1 and Long Island could potentially have combined keys, though more analyses would need to be performed on animals born since the 1990s from Long Island. Georges Bank should also have its own unique key, as it was significantly different from the other three sites (Hemeon et al. in prep.). The results of these analyses identify substantial regionality in the population dynamics consistent with known variations in the oceanography of the regions and suggest that a closer look might be valuable to determine the degree to which age frequencies vary across the Cold Pool.

3.4.2.2 Sex Ratios & Dimorphism

Hemeon et al. (2021a) and Hemeon et al. (in prep.) reported population sex ratios for Georges Bank (1:1.1, F:M) and Long Island (1:1.4, F:M). The most notable difference between the four sites is that Georges Bank and Long Island display mildly-skewed sex ratios favoring males, while both New Jersey sites are skewed in favor of females. One possible reason for the difference in sex bias may be the major recruitment event in the 1980s-1990s in New Jersey not seen in Long Island or Georges Bank. Many of the slower-growing males born during this time period may not have reached a fishable size when New Jersey samples were collected in 2019. A second cause may be the enhanced survivorship of females during certain time periods. Regardless, sex ratios varying modestly from the expected 1:1 ratio are not unusual for *A. islandica*. Variations have been observed at many sites across the northwestern Atlantic continental shelf: F:M, 1:1.35 (Jones 1981), 1:1.09 (Mann 1982), 1:0.93 (Ropes et al. 1984a), 1:2 (Rowell et al. 1990), and 1:0.77 (Fritz 1991). Such inconsistencies may arise due to environmental variation that would promote one sex over the other, or may be caused by differences in sampling techniques, as males and females are concentrated in different size classes so that very small and very large animals are often underrepresented by one of these two sexes. In either case, *A. islandica* populations are typically reported to be biased towards one sex over the other.

Similar age frequencies yet different length frequencies between males and females are representative of a sexually dimorphic species (Hemeon et al. 2021a; Hemeon et al. in prep.). Sexual dimorphism is rare in bivalves (Sastry 1979; Hemeon et al. 2021a), but is demonstrably present in *A. islandica* as shown for populations from the

MAB, Georges Bank, and Iceland (Fritz 1991; Steingrímsson and Thórarinsdóttir 1995; Hemeon et al. 2021a; Hemeon et al. in prep.; Sower et al. in press). Because females grow at faster rates than males, they are likely to reach commercial size (80 mm) at a younger age. Thus, females potentially experience increased fishing pressure relative to males, potentially leading to the need for sex-based models in fisheries assessment, an option typically reserved for protandrous and protogynous species (Alonzo et al. 2008; Drouineau et al. 2012).

3.4.2.3 Longevity & Mortality

Hemeon et al. (2021a) reports mortality values for Georges Bank at 0.04 for the population, 0.05 for females, and 0.04 for males. Longevity values for this population are 257 for the population, 219 for females and 244 for males. For Long Island, mortality estimates are 0.022 for the population, 0.021 for females, and 0.023 for males. Longevity estimates are 347 years for the population, 324 for females, and 316 for males (Hemeon et al. in prep.).

Mortality rates for both NJ1 and NJ2 are lower than those of Long Island and Georges Bank, with NJ1 having the lowest overall calculated mortality rate. Longevity for both sites was lower than Long Island but higher than Georges Bank. At each site, the calculated population longevity is the highest, with females having the second highest at 3 out of the 4 sites, and males usually having the lowest. Trends for mortality rates are more inconsistent. Females have the highest mortality rates in NJ2 and at Georges Bank, yet the lowest at Long Island and NJ1. In New Jersey, males have the lowest mortality rates, yet they have very similar rates to the population mortality rates in Georges Bank and Long Island.

In the Long Island-New Jersey region, fall temperatures of 14-15°C have been reported in recent years (López et al. 2020). Though this temperature is not lethal for *A. islandica*, it is warm enough to potentially negatively impact growth and reproduction. *Arctica islandica* have been reported to burrow in the sediment to escape unfavorable environmental situations, as the sediment provides a temperature buffer (Taylor 1976; Strahl et al. 2011). This behavior likely allows *A. islandica* in this region to escape rising temperatures during the fall breakdown of the Cold Pool, thereby keeping their mortality rates low. The observed mortality rates at Long Island, NJ1, and NJ2 vary little from 0.02 yr⁻¹. The small differentials may be due to the variation in recruitment leading to small differences in the age frequencies used to estimate the mortality rate or may be due to habitat-specific environmental variations. In comparison, Georges Bank's higher mortality rate is noteworthy, though the cause is unclear as Georges Bank is not influenced by the fishery (Hemeon et al. 2021a). One possibility is the rapid rise in temperatures on Georges Bank in comparison to the MAB over the last quarter century (Kavanaugh et al. 2017), although this site has had the least differential yearly temperatures in recent years (López et al. 2020).

3.4.2.4 Recruitment

At Georges Bank and Long Island, recruitment occurred consistently every 8 years (Hemeon et al. 2021a; Hemeon et al. in prep.). Both of these sites display high levels of recruitment in the mid-1900s, similar to that of NJ1. However, Long Island has higher recruitment in the late 1900s, whereas in Georges Bank, recruitment appears to decrease after the 1960s.

Both NJ1 and NJ2 *A. islandica* experienced high recruitment in the 1980s-1990s, but a similar increase was not observed in either the Long Island or Georges Bank populations (see Figure 11 in Hemeon et al. 2021a and Figure 6 in Hemeon et al. in prep). Harding et al. (2008) reported temperature data for 1990-2002 that would have facilitated good recruitment, though animals in the selfsame study for this time period were undersampled. Given the high levels of recruitment in the 1990s reported in this study at NJ1 and NJ2, it is evident that the temperatures reported by Harding et al. (2008) did yield high recruitment. One potential reason this peak in recruitment was not observed in Long Island or Georges Bank is the two-year difference between sample collections. Resampling these sites may yield animals that were born during the 1980s-90s that have since reached a fishable size. Another explanation may arise from the origin of larvae at these sites. Georges Bank is a larval trap, thus being a source and sink (Zhang et al. 2015). Currents in western areas generate a net southwestern larval drift, so that sources tend to be north and east (Zhang et al. 2015, 2016). Thus, larval supply may be different. Finally, early survival post-set is almost certainly influenced by the timing of Cold Pool decay in the fall and the degree to which temperatures rise transiently about 15°C.

Georges Bank, Long Island, and NJ1 all display peaks in recruitment in the 1930s-1950s, indicating similar recruitment trends for these sites with some lags in years. The time period covers a well-described warm period during the mid-20th century, with higher recruitment inferentially explained by temperature relationships reported by Harding et al. (2008). The only population that does not display a recruitment peak during this time period is NJ2. LeClaire et al. (in prep.) discuss an evident decrease in recruitment in populations off Delmarva which began approximately 120 years ago,

potentially due to an increase in bottom water temperature limiting survival of younger animals. The effects of this temperature increase are also likely observed in NJ2, as this site experiences a high peak in recruitment between 1860-1900, and then a continual decrease until ~1980, which is not seen in any of the sites located north of the Hudson Canyon, but is similar to the more southerly population studied by Pace et al. (2017b). Pace et al. (2017b) also observed a population expansion beginning in 1835 in a New Jersey population farther south of NJ2, and that this was potentially due to increased warming trends in the mid-1800s after the Little Ice Age ended ~1850 (Moore et al. 2017).

At both Long Island and Georges Bank, pulses in recruitment occur, on average, every 8 years consistent with the North Atlantic Oscillation (NAO) cycle (Hemeon et al. 2021a; Hemeon et al. in prep.; see Soniat et al. 2009, 2012 for similar periodicity in an estuarine case). The NAO is a climate cycle with an approximately 8-year periodicity, with a direct influence on sea-surface temperature (Hurrell and van Loon 1997; Hurrell et al. 2001). NJ1 and NJ2 had similar recruitment pulses, matching some years of high recruitment at Long Island as noted in Hemeon et al. (in prep.), though coincidence in peak years is not always present (Table 7). Hemeon et al. (in prep.) suggest that lags in recruitment between sites may be due to the movement of Labrador Sea water southward over time, which would explain the slight differences amongst these three sites. Despite this, the age frequencies suggest that the NAO has a similar effect on *A. islandica* recruitment in populations throughout the MAB.

3.5 Summary

The ocean quahog, *Arctica islandica*, is a commercially important species on the northwestern Atlantic continental shelf. The age and length frequencies from two populations collected in 2019 from New Jersey, north and south of Hudson Canyon were analyzed and compared to two northern populations from Long Island and Georges Bank. Sex-specific differences were also analyzed to determine how said differences influenced a range of demographic metrics. Though some similarities in recruitment trends exist, likely caused by large-geographic-scale environmental conditions, each site contains a distinct population with distinct demographics. Recruitment is consistent over hundreds of years, but year-to-year and decadal-length variations are apparent. One age-length key may potentially be used to represent Long Island and northern New Jersey, but the remaining sites are significantly dissimilar. Sex ratios also vary, with differential survival of one sex during certain times in the past partially responsible. Mortality rates for Georges Bank are distinctly higher compared to the other populations. Based on these results, the use of separate age-length keys would seem necessary for each population and each sex.

3.6 Tables

Table 3.1 Results of statistical analyses for various comparisons between age distributions and length distributions. KS: two-tailed Kolmogorov-Smirnov two-sample test; AD: two-tailed Anderson-Darling two-sample test; Runs: one-sided Wald-Wolfowitz Runs test; ns = nonsignificant; F = female, M = Male

Site	Dataset	Comparison	Test	Alpha	Null	Median Bin
NJ1	Length	F-M	KS	0.01	*	ns
				0.05	*	ns
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	ns	ns
				0.05	*	*
	Age	F-M	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	*	*
				0.05	*	*
NJ2	Length	F-M	KS	0.01	*	ns
				0.05	*	ns
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	ns	ns
				0.05	ns	*
	Age	F-M	KS	0.01	*	ns
				0.05	*	ns
			Runs	0.01	ns	*
				0.05	ns	*
			AD	0.01	ns	*
				0.05	ns	*

Table 3.2 Results of Monte Carlo simulations. ALK marks the dataset from which the simulated dataset was taken and the age-length key derived applied to the 'True' length frequency. 'True' is the age frequency to which the simulated age frequencies were compared. Results are the present of simulated datasets yielding a significant difference for the raw datasets (unmodified) and for datasets in which low amplitude age or size classes were combined to increase the number of observations in each size or age class above the original median value for all age or size classes (median). KS: two-tailed Kolmogorov-Smirnov two-sample test; AD: two-tailed Anderson-Darling two-sample test; Runs: one-sided Wald-Wolfowitz Runs test; ns = nonsignificant

Population	True	ALK	Level	Unmodified			Median		
				KS	Runs	AD	KS	Runs	AD
NJ1	Female	Male	0.05	1.00	0.08	1.00	0.18	0.12	1.00
			0.01	1.00	0.04	1.00	0.84	0.06	1.00
	Male	Female	0.05	0.02	0.00	1.00	0.02	0.08	1.00
			0.01	0.38	0.00	1.00	0.00	0.00	1.00
NJ2	Female	Male	0.05	0.84	0.04	1.00	0.02	0.08	1.00
			0.01	0.96	0.00	1.00	0.08	0.00	1.00
	Male	Female	0.05	1.00	0.04	1.00	0.02	0.32	1.00
			0.01	1.00	0.00	1.00	0.36	0.10	1.00
Region	NJ1	NJ2	0.05	1.00	1.00	0.98	0.76	1.00	1.00
	Pop	Pop	0.01	1.00	1.00	0.54	1.00	1.00	0.94
	NJ1 F	NJ2 F	0.05	1.00	1.00	0.98	0.18	1.00	1.00
			0.01	1.00	0.96	0.14	0.60	0.98	1.00
	NJ1 M	NJ2 M	0.05	1.00	0.90	0.02	0.06	0.98	1.00
			0.01	1.00	0.70	0.00	0.78	0.80	1.00
	NJ2	NJ1	0.05	1.00	1.00	1.00	0.02	1.00	1.00
			0.01	1.00	1.00	1.00	0.26	1.00	1.00
	NJ2 F	NJ1 F	0.05	1.00	1.00	1.00	0.02	0.98	1.00
			0.01	1.00	0.92	1.00	0.22	0.88	1.00
	NJ2 M	NJ1 M	0.05	1.00	0.96	1.00	0.08	0.96	1.00
			0.01	1.00	0.82	1.00	0.58	0.84	1.00

Table 3.3 Results of statistical analyses for various comparisons between age distributions of northern (NJ1) and southern (NJ2) New Jersey to Georges Bank. KS: two-tailed Kolmogorov-Smirnov two-sample test; AD: two-tailed Anderson-Darling two-sample test; Runs: one-sided Wald-Wolfowitz Runs test; ns = nonsignificant; F = female, M = male

Site	Dataset	Comparison	Test	Alpha	Null	Median Bin
NJ1	Female	F-F	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	*	*
				0.05	*	*
	Male	M-M	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	ns	*
				0.05	ns	*
NJ2	Female	F-F	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	*	*
				0.05	*	*
	Male	M-M	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	*	*
				0.05	*	*

Table 3.4 Results of statistical analyses for various comparisons between age distributions of northern (NJ1) and southern (NJ2) New Jersey to Long Island. KS: two-tailed Kolmogorov-Smirnov two-sample test; AD: two-tailed Anderson-Darling two-sample test; Runs: one-sided Wald-Wolfowitz Runs test; ns = nonsignificant; F = female, M = male

Site	Dataset	Comparison	Test	Alpha	Null	Median Bin
NJ1	Female	F-F	KS	0.01	ns	ns
				0.05	ns	ns
			Runs	0.01	ns	ns
				0.05	ns	ns
			AD	0.01	*	ns
				0.05	*	*
	Male	M-M	KS	0.01	*	ns
				0.05	*	ns
			Runs	0.01	ns	ns
				0.05	*	*
			AD	0.01	*	ns
				0.05	*	*
NJ2	Female	F-F	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	*	*
				0.05	*	*
	Male	M-M	KS	0.01	*	*
				0.05	*	*
			Runs	0.01	*	*
				0.05	*	*
			AD	0.01	*	*
				0.05	*	*

Table 3.5 Northern New Jersey (NJ1) sex ratios. Significant results represent cases with female:male ratios significantly different from 1:1; ns = nonsignificant

Size Class (mm)	Females	Males	F : M	P-value
60	0	1	-	ns
65	1	0	-	ns
70	2	10	1:5.00	0.036
75	19	32	1:1.68	ns
80	32	107	1:3.34	3.46E-10
85	73	89	1:1.22	ns
90	89	49	1:0.55	9.01E-4
95	91	19	1:0.21	1.29E-11
100	68	9	1:0.13	3.85E-11
105	21	1	1:0.05	1.10E-5
110	1	0	-	ns
Total:	397	317	1:0.80	0.0031

Table 3.6 South New Jersey (NJ2) sex ratios. Significant results represent cases with female:male ratios significantly different from 1:1; ns = nonsignificant

Size Class (mm)	Females	Males	F : M	P-value
60	0	1	-	ns
65	2	0	-	ns
70	13	18	1:1.39	ns
75	33	49	1:1.49	ns
80	39	54	1:1.39	ns
85	46	78	1:1.70	0.0054
90	63	57	1:0.91	ns
95	74	54	1:0.73	ns
100	73	16	1:0.22	2.92E-9
105	49	1	1:0.02	2.99E-11
110	5	0	-	ns
Total:	397	328	1:0.83	0.0116

*Table 3.7 Years of high *Arctica islandica* recruitment in Long Island (LI) as reported by Hemeon et al. (in prep.), northern New Jersey (NJ1), and southern New Jersey (NJ2). High recruitment is identified as peaks in the age frequencies (Figures 10A and 11A)*

LI	NJ1	NJ2
1953	1951	1956
1945	1945	1948
1942	1942	1942
1932	1934	1933
1927	1928	1927
1922	1922	1921
1915	1917	1917
1905	1904	1906
1889	1887	1890

3.7 Figures

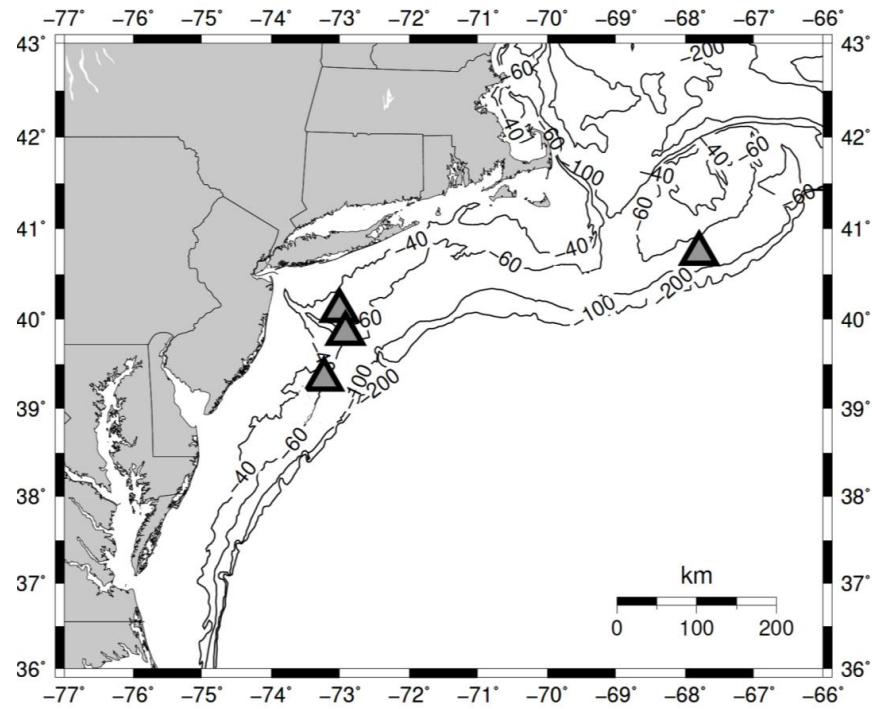


Figure 3.1 Locations of each of the four sampling sites. From north to south, they are Georges Bank (GB), Long Island (LI), New Jersey north (NJ1), and New Jersey south (NJ2)

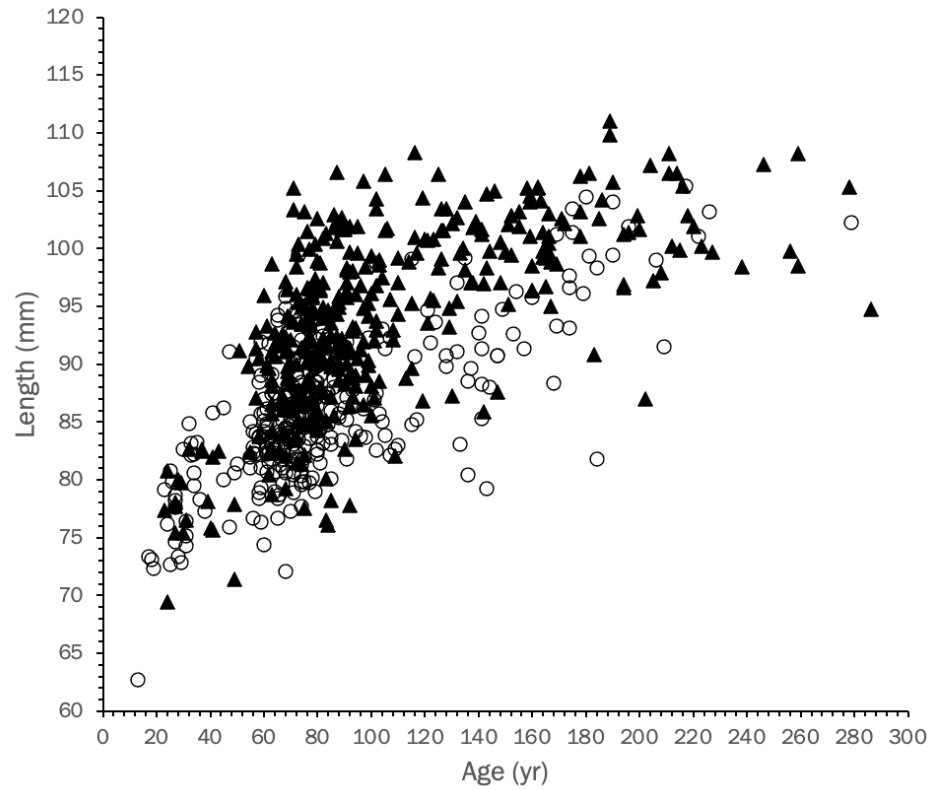


Figure 3.2 Age-length distribution for the northern New Jersey site, NJ1. Solid triangles represent females; hollow circles represent males

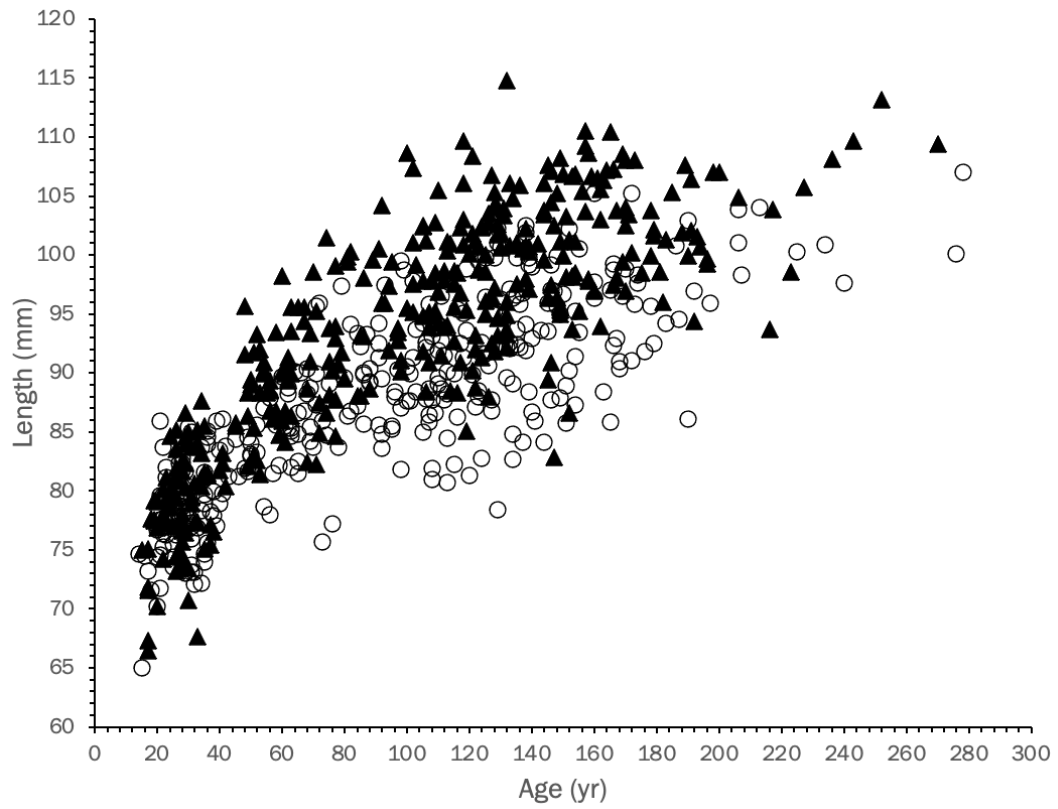


Figure 3.3 Age-length distribution for the southern New Jersey site, NJ2. Solid triangles represent females; hollow circles represent males

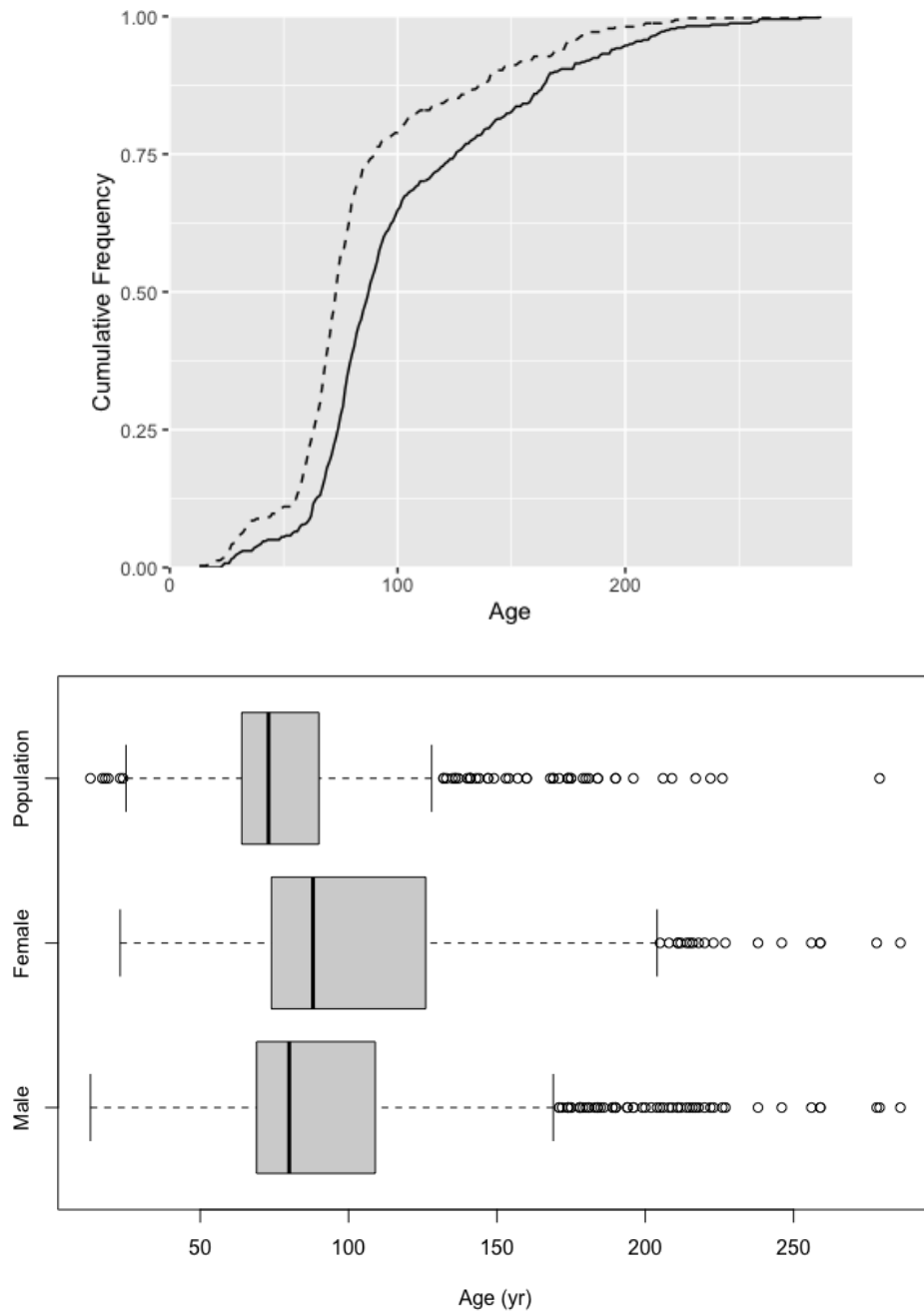


Figure 3.4 Northern New Jersey (NJ1) cumulative age distributions for male (dashed line) and female (solid line) *Arctica islandica* and box and whisker plots of population, females, and males age frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers.

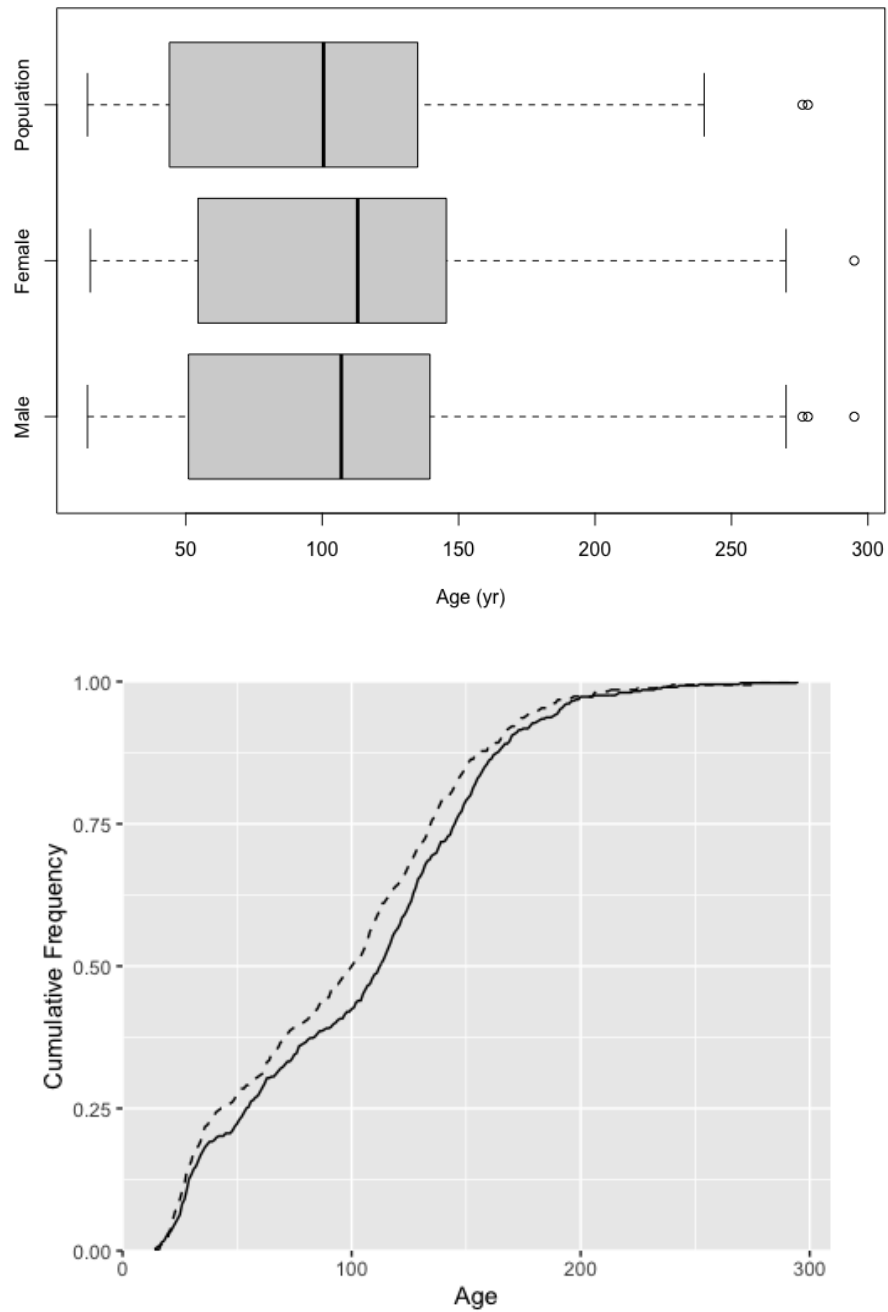


Figure 3.5 Southern New Jersey (NJ2) cumulative age distributions for male (dashed line) and female (solid line) *Arctica islandica* and box and whisker plots of population, females, and males age frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers.

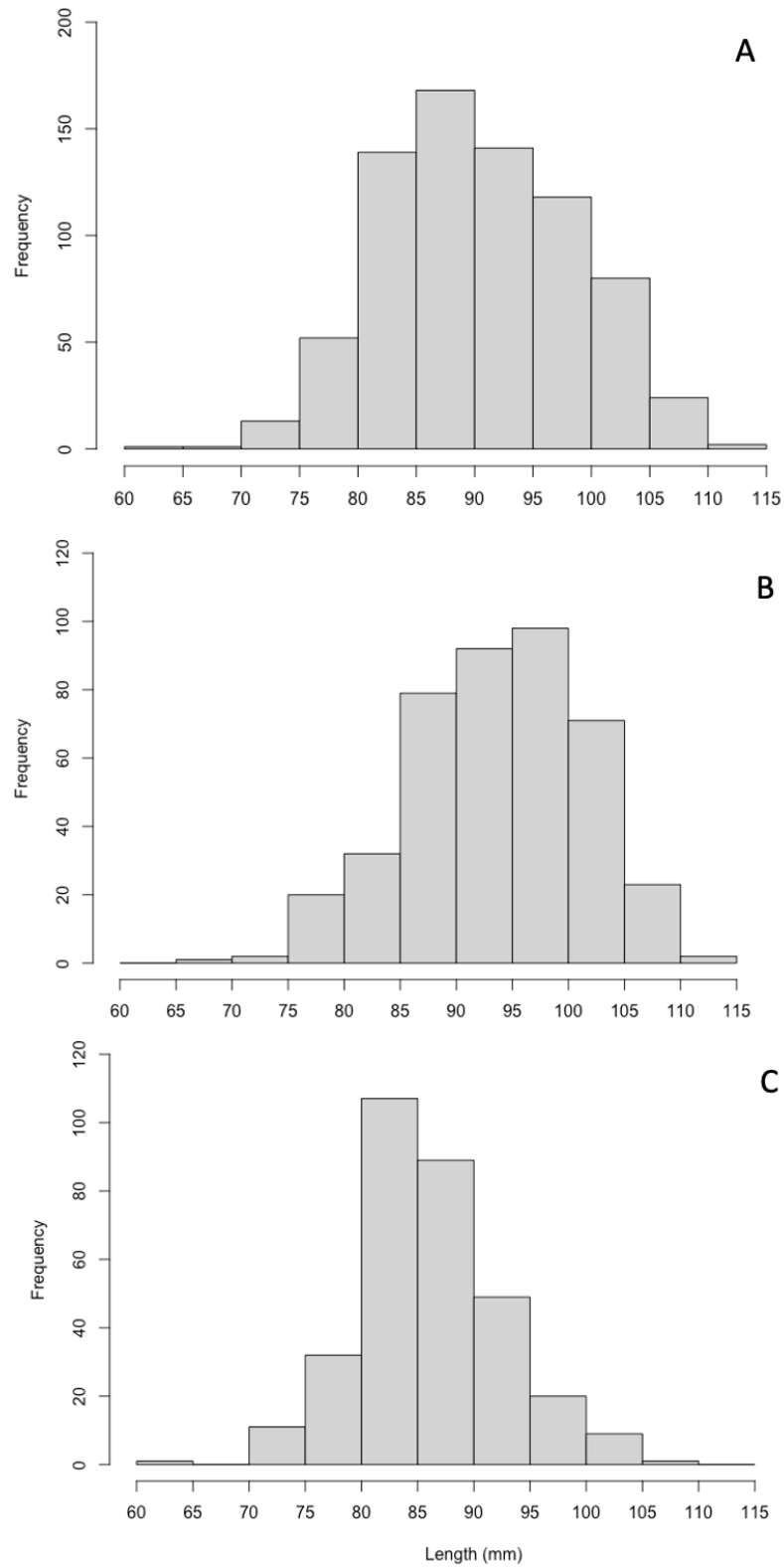


Figure 3.6 NJ1 Population (a), female (b), and male (c) length frequencies. Note the y axis varies between plots

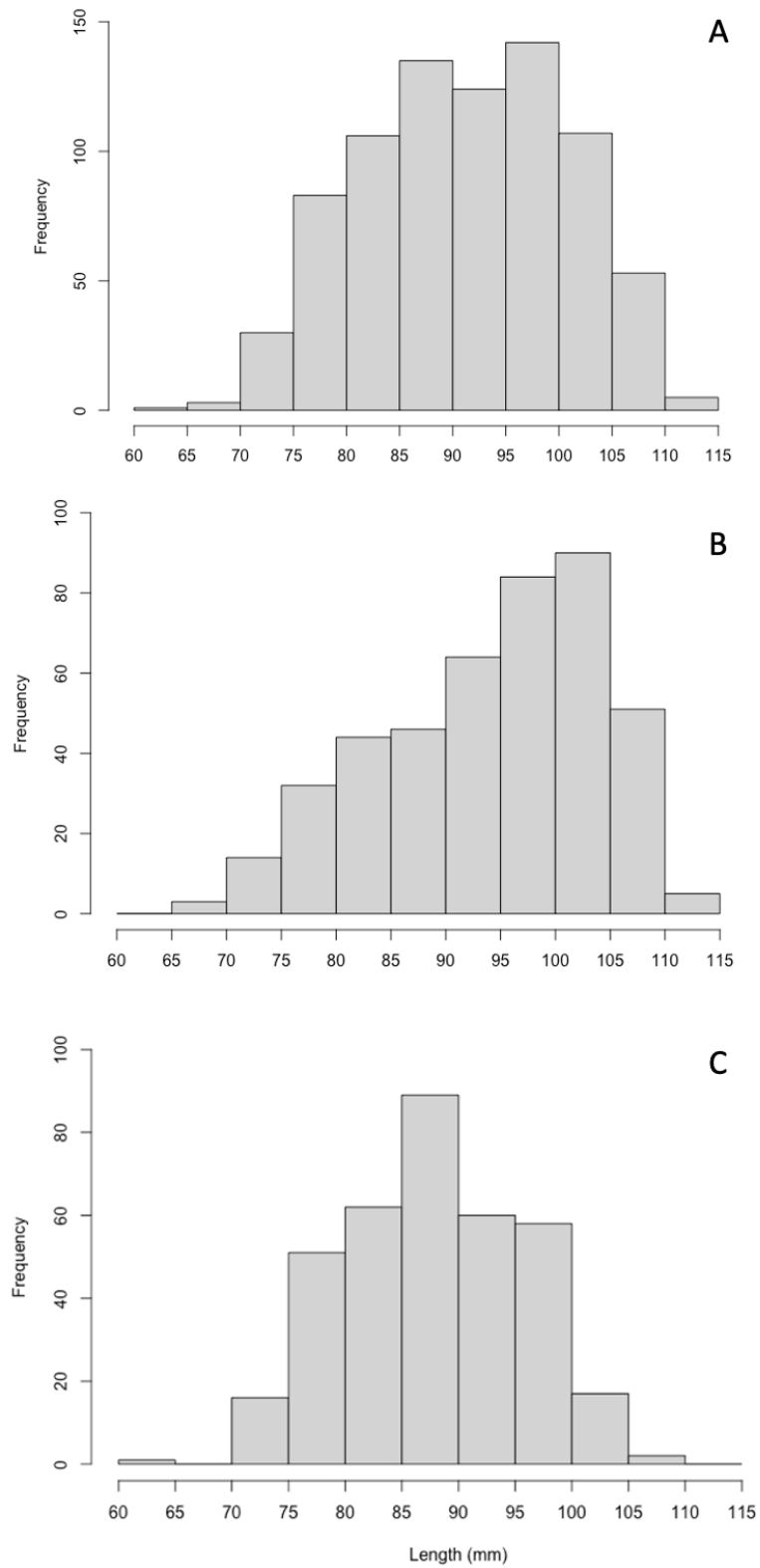


Figure 3.7 NJ2 population (a), female (b), and male (c) length frequencies. Note the y axis scale varies between plots

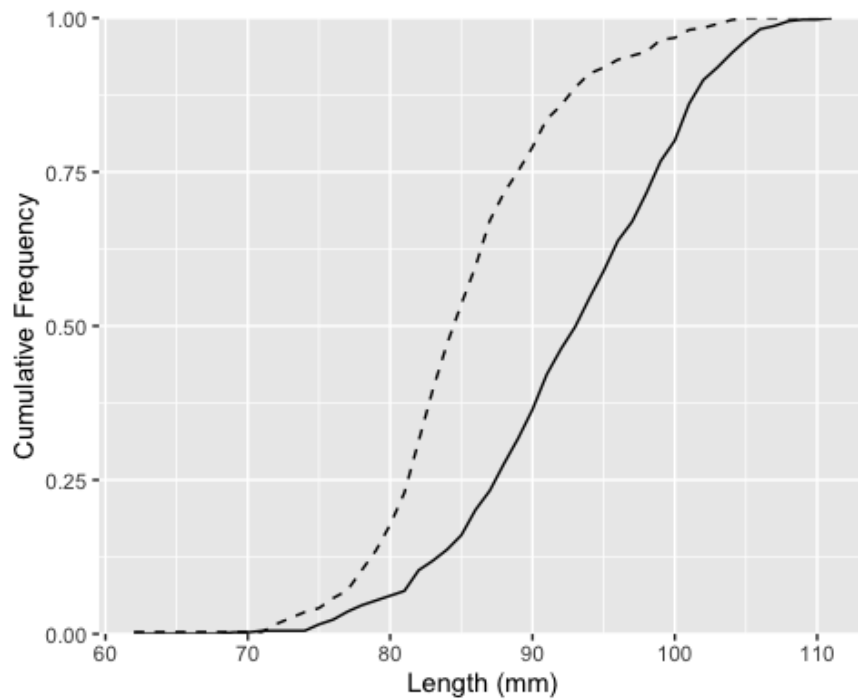
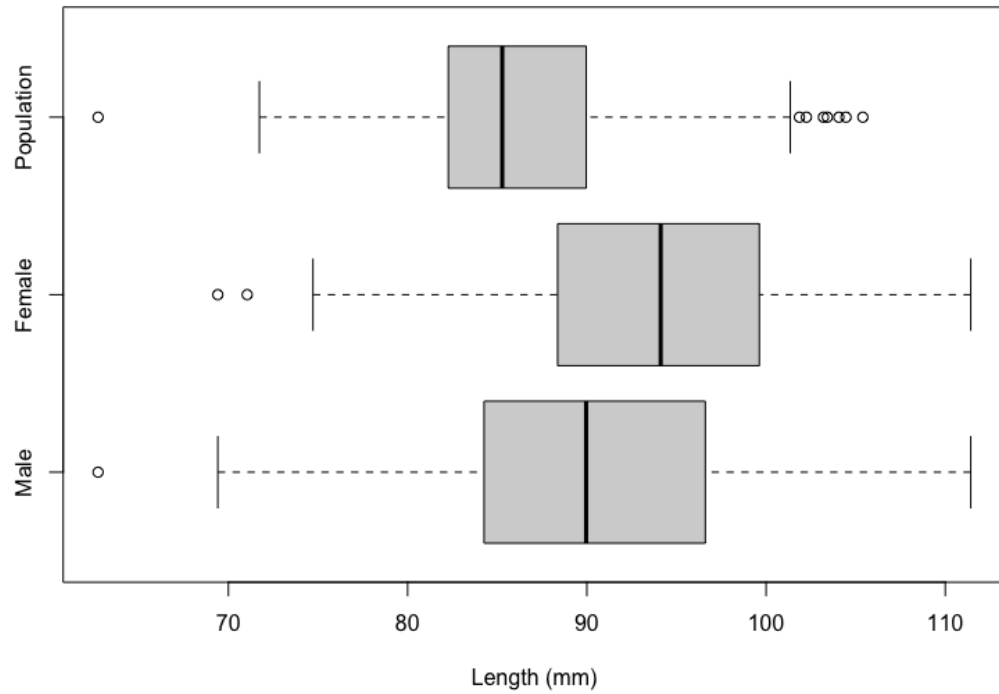


Figure 3.8 Northern New Jersey (NJ1) cumulative length distributions for male (dashed line) and female (solid line) *Arctica islandica* and box and whisker plots of population, females, and males length frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers.

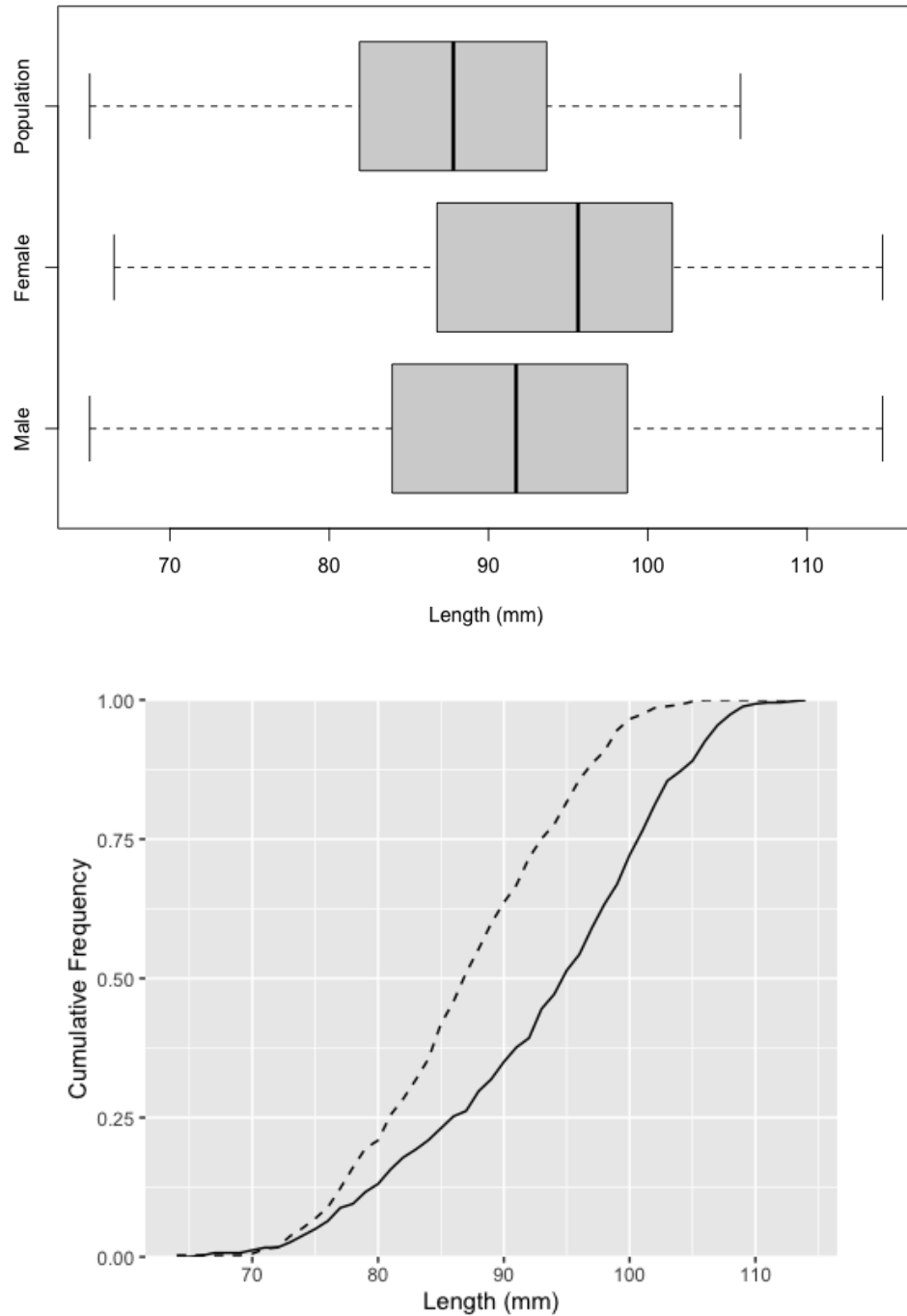


Figure 3.9 Southern New Jersey (NJ2) cumulative length distributions for male (dashed line) and female (solid line) *Arctica islandica* and box and whisker plots of population, females, and males length frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers.

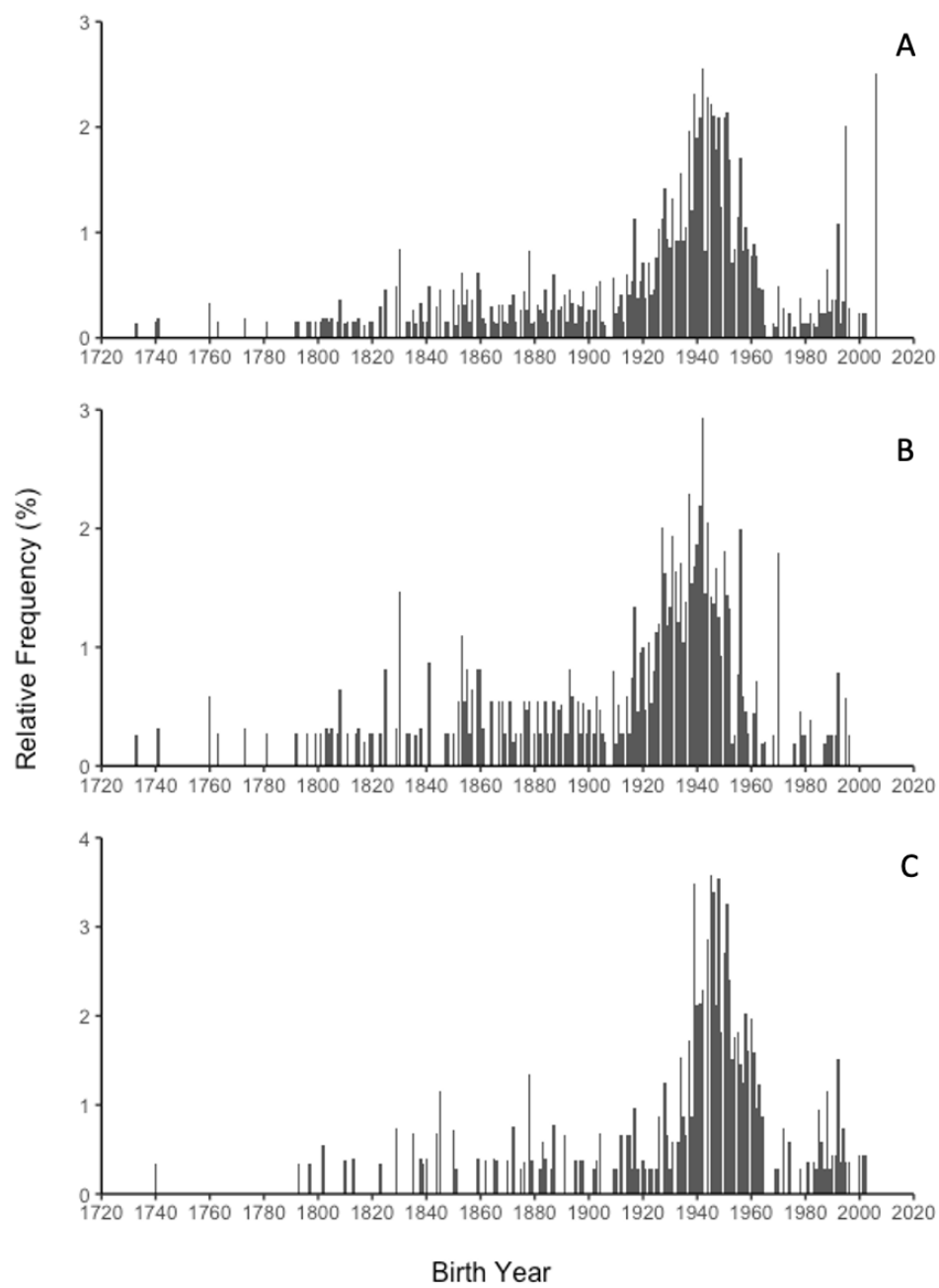


Figure 3.10 Northern New Jersey (NJ1) age frequency; population (A), female (B), male (C)

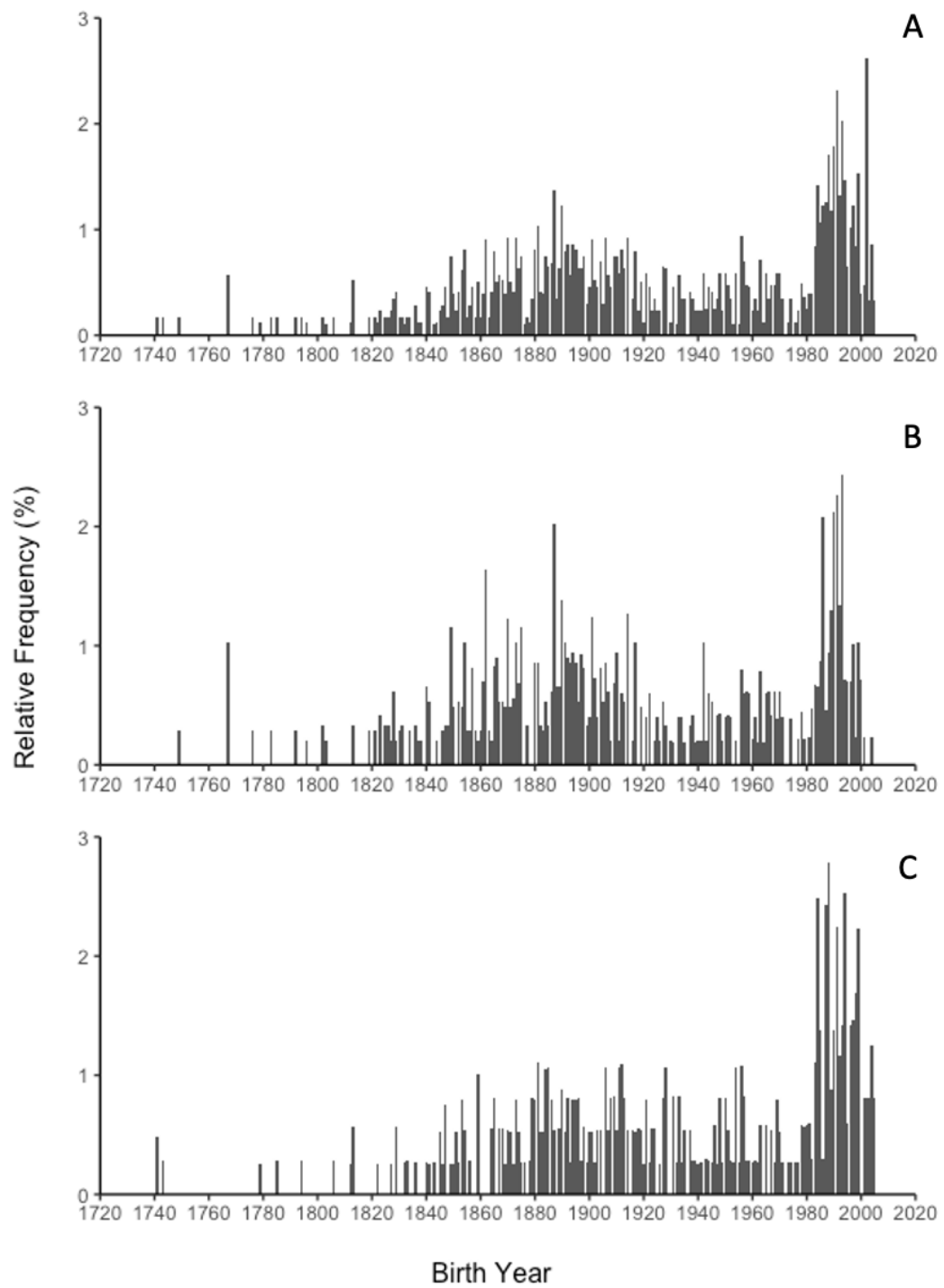


Figure 3.11 Southern New Jersey (NJ2) age frequency; population (A), female (B), male (C)

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CHAPTER IV – OCEAN QUAHOG (*ARCTICA ISLANDICA*) GROWTH RATE
ANALYSES OF FOUR POPULATIONS FROM THE MID-ATLANTIC BIGHT AND
GEORGES BANK

4.1 Introduction

The ocean quahog (*Arctica islandica*) is an extremely long-lived species, often reaching at least 200 years in age, with the oldest-recorded *A. islandica* aged at 507 years (Butler et al 2013) that also supports one of the largest shellfish fisheries in the world (Hennen 2015, NEFSC 2017). Growth rates of extremely long-lived animals such as *A. islandica* can provide proxies of environmental patterns of the past, as they can fluctuate over time with changes in temperature or food availability and quality (Schöne et al. 2005, Wanamaker et al. 2009, Mette et al. 2016, Ballesta-Artero et al. 2017). This species deposits distinct annual growth lines, termed annuli (Thompson et al. 1980, Jones 1980, Ropes et al. 1984b), which can be counted to determine age and their thickness used to determine past environmental fluctuations due to patterns in annuli and growth increments (Murawski et al. 1982, Wanamaker et al. 2008, Marali and Schöne 2015). Bivalves tend to grow faster at higher temperatures (Schöne et al. 2005, Pace et al. 2018); thus, increasing temperatures in recent decades due to climate change may have influenced *A. islandica* growth.

The metabolism of *Arctica islandica* is particularly sensitive to temperature in comparison to most bivalves (Begum et al. 2009), themselves distinctly sensitive (van der Veer et al. 2006, Munroe et al. 2013). New Jersey represents the southern portion of the range of *A. islandica* in the western Atlantic. A study by Pace et al. (2018) on New Jersey *A. islandica* found that animals from southern areas may have faster growth rates than

those of their northern counterparts from Georges Bank and Southern New England, with animals being significantly younger at 60 mm shell length compared to these more northern sites, due to the higher bottom water temperatures experienced there. To build upon the study by Pace et al. (2018), the growth rates from larger sample sizes of *A. islandica* from two New Jersey sites north and south of the Hudson Canyon were measured and compared to those from Long Island and Georges Bank (Hemeon et al. in prep.) to determine how growth rates may change by location. Three models were tested to determine which fits *A. islandica* growth best: von Bertalanffy, which is a commonly used growth model applicable to many marine species (Brey and Gage 1997, Devillers et al. 1998, Helidoniotis and Haddon 2013); Tanaka (1982, 1988), which was developed for animals with indeterminate growth; and a modified Tanaka, with an extra parameter to model growth at older ages (Hemeon et al. in prep.). Pace et al. (2018) considered the influence of warming temperatures since the end of the Little Ice Age as an important effector generating long-term trends in increasing rate of growth and suggested that one reason for the wide range of ages with small size classes (e.g., 5 mm increments) might be the rate of growth in the first several decades of life leading to larger sizes at age for more recent birth years. To examine the potential of warming temperatures interacting with birth years in determining *A. islandica* demographics, time to milestone sizes important to the fishery were also analyzed over time to determine whether growth rates have remained similar over recent centuries, or whether they have fluctuated as a result of changing environmental factors.

4.2 Materials and Methods

4.2.1 Sample Collection

In August of 2019, *Arctica islandica* were sampled from north and south of the Hudson Canyon off New Jersey (Figure 1). The northern New Jersey sample (herein referred to as NJ1) was collected at 39.84056 N, 72.82167 W, while the southern New Jersey sample (NJ2) was collected at 39.33 N, 73.12278 W. The sex of each animal was determined using gonadal smear slide, and shells were processed to expose the hinge plate and annuli for ageing. For more information on shell processing techniques, see Pace et al. (2017a; 2017b) and Hemeon et al. (2021a). Once processed, each shell was photographed using a combination microscope and camera, and said photographs were uploaded into the opensource software ImageJ with the ObjectJ plugin. This software is used to annotate each individual annual line to determine age. Distances between signatures are originally produced as pixels which are then converted to millimeters using a proportion of the animal's overall length to determine annual growth. Samples used for comparison in this study from Long Island and Georges Bank were collected in 2017 and analyzed in Hemeon et al. (in prep.).

4.2.2 Growth Models: Population, Males, Females

Growth increments were cumulatively summed for each individual animal per site. The von Bertalanffy (Eq 1), Tanaka (Eq 2), and modified Tanaka (Eq 3) models were applied to the cumulative growth increments for the population, male, and female groups for both NJ1 and NJ2. The von Bertalanffy model is widely used in fisheries management and is currently used in *A. islandica* management (von Bertalanffy 1938, NEFSC 2017). The Tanaka model was chosen as it fits species with indeterminate growth

(Tanaka 1982, Pace et al. 2017b), as is observed in *A. islandica*. The modified Tanaka is an updated version of the Tanaka that contains an additional parameter, “g”, that better fits *A. islandica* growth at older age classes (Powell & Klinck pers comm).

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

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

$$\text{Eq (3)} \quad L_t = d + \frac{1}{\sqrt{f}} \log(2f(t - c) + 2\sqrt{f^2(t - c)^2 + fa}) + gt^{2.5} .$$

Where t is age in years and L is length in mm

These models were first applied to the overall populations to determine whether distinct differences in growth exist by location. These models were then applied to the male and female components of each population to ascertain if growth rates differ between sexes, as has been hypothesized by Steingrímsson and Thórarinsdóttir (1995) and Hemeon et al. (2021b).

4.2.3 Growth Models: Age-Specific Cohorts

Growth rates are expected to vary over time as environmental conditions change, such as temperature and food availability being the primary determinants of scope for growth in bivalves including *A. islandica* (Schöne et al. 2005, Harding et al. 2008, Canu et al. 2010, Munroe et al. 2013). As *A. islandica* commonly live to 200+ years, variations in growth are expected across generations based on the environmental conditions in their birth years. The populations, males, and females were divided into twenty-year cohorts based on birth year. The same three models were then applied to determine the degree to which growth rates have changed over time in New Jersey *A. islandica*.

4.2.4 Growth Rates

Two sizes, and the time it takes to reach said sizes, are important in *A. islandica* population dynamics, and, as the species is commercially harvested, fisheries management. Most bivalves reach maturity at approximately 50% of their maximum body size, although considerable variability exists (Powell & Stanton 1985). Hemeon et al. (in prep.) concluded in a review of the literature that age at maturity approximated 52 mm in *A. islandica* and Sower et al. (in press) provided supporting information for the sites studied in this contribution. A second milestone for this species is time to 80 mm, which is the minimum size efficiently selected for harvest by commercial dredge (NEFSC 2017). The number of years from birth to these two sizes were analyzed using linear regression for each animal to determine whether the years taken to reach these milestones has fluctuated over the past three centuries. Time between these size milestones is referred to the years of reproduction prior to harvest and is analyzed using the same method.

4.3 Results

4.3.1 Growth Models: Population, Males, Females

The variables used in the Tanaka model can be understood as follows. Parameter c (years) denotes the age at maximum growth rate. At the age of maximum growth, c , the growth rate is $1/\sqrt{a}$. So, parameter a ($\text{yr}^2 \text{ mm}^{-2}$) describes the maximum growth rate which will occur at age c . Parameter f (yr^{-2}) controls the rate at which growth declines with increasing age. For older animals, growth rate reduces to $1/(t\sqrt{f})$. Parameters d (mm) and g ($\text{mm yr}^{-2.5}$) are scalars of size, with g influencing the rate of growth rate decline with increasing age determined by parameter f . All model parameters except d ,

were forced to be ≥ 0 during model convergence to prevent the estimation of negative square roots and logarithms.

Either Tanaka or modified Tanaka fit *A. islandica* growth best, while von Bertalanffy fits routinely yielded an underestimate of length at old age when a strong deviation existed from the other two (Figures 4.2 & 4.3). For NJ1, the a and c parameters are always larger than in NJ2, indicating lower growth rates and higher ages at maximum growth rates (Table 4.1). The d parameter is larger in the population levels and for females in NJ2, but is smaller than NJ1 for males, indicating larger body sizes in the two former groups. The f parameter is larger at all levels in NJ1, indicating lower growth rates at old age at NJ1.

The modified Tanaka parameters yielded somewhat different results than the original Tanaka. The a , c and d parameters were all larger in NJ1 than in NJ2, indicating the same smaller growth rates and higher ages at maximum growth. However, the g parameter, unique to the modified Tanaka model, is larger at all levels in NJ2 than in NJ1, which illustrates larger sizes at older ages for this population.

Females tend to have lower a and c values compared to males at both sites, as well as higher d and g values (Table 4.1), especially in the modified Tanaka model. These consistencies express the fact that the growth of females is higher than that of males, which would allow them to reach the larger body sizes and dominate larger size classes as found in Hemeon et al. (2021b, in prep.) and Sower et al. (in press).

4.3.2 Growth Models: Age-Specific Cohorts

Both the original and modified Tanaka models fit the cohort groups well, yet the von Bertalanffy model continued to perform poorly (Tables A.1 & A.2). Hemeon et al.

(in prep.) advises that L_{inf} parameters derived from von Bertalanffy fits not be used due to their inherent inaccuracy. Sometimes, however, the modified Tanaka yielded overestimates for growth at age on the cohort scale, especially in NJ2 and in cohorts with very few animals ($n < 10$) (Figures 4.4-4.9). Nevertheless, both models indicate increasing growth trends over time. For example, a parameter values steadily decrease as birth year increases for both sites, with some fluctuation (Tables A.3-A.6). This indicates that maximum growth rates have increased over time.

When comparing populations within cohorts, NJ2 a parameter values are almost always smaller than those of NJ1 indicating a more rapid growth rate early in ontogeny, except in the cases of 1760, 1880, 1900, and 1980 (Figure 10). Values for c (Figure 4.11) and d parameters (Figure 4.12) followed similar trends, indicating that *A. islandica* from NJ2 have displayed consistently higher growth rates over the past three centuries. Values for f parameter appeared to steadily increase over time (Figure 4.13), indicating that growth rates at older ages have decreased over time. When comparing sex-based growth, females have also displayed higher growth rates and lower ages at maximum size within cohorts compared to males (Figures 4.10-4.14) over time.

4.3.3 Growth Rates

The metrics integrating growth dynamics were identified to facilitate determination of the degree of change in growth rate with birth year: age at maturity estimated to occur at 52 mm, age at recruitment to the fishery estimated to occur at 80 mm, and the number of years elapsing between these two sizes. Linear regression analysis indicates that these three elapsed times to have decreased as growth rates increased with increasing birth year. For comparison, the age at 52 mm and 80 mm and

the number of years elapsed between them was calculated for three birth years: 1800, 1900, and 2000.

Sower et al. (in press) found that the size of maturity, ~52 mm, is often reached in the first 10-15 years of life. For individuals born in 1800, this value was somewhat higher, at age 26 for NJ1 and age 28 at NJ2 (Table 4.2). For individuals born in 1900, however, these ages decreased to 17 and 18 for NJ1 and NJ2, respectively. These ages decreased further for animals born in 2000, at 9 for NJ1 and 8 for NJ2 (Figures 4.15 & 4.18). These trends are significant, with significance levels for the regressions for both sites less than $2.2\text{E-}16$. R^2 values for both NJ1 and NJ2 are 0.3918 and 0.3697, respectively. Taking into account that the variance is increased by the combination of the two sexes typified by varying growth rates within this age range, these regression coefficients are surprisingly high. The rate of change for NJ1 is -0.085 yr^{-1} and is -0.097 yr^{-1} for NJ2.

Time to commercial size, 80 mm, has also decreased as birth year increased. Years taken to reach commercial size were calculated at 114 and 118 years for NJ1 and NJ2, respectively, for individuals born in 1800. This decreased to 71 and 73 years, respectively, for individuals born in 1900, and decreased further to 28 and 26 years for animals born in 2000. The rate of change for NJ1 was -0.43 yr^{-1} in NJ1 and -0.46 yr^{-1} in NJ2 (Figures 4.16 & 4.19). R^2 values indicate a strong, statistically significant ($p < 2.2\text{E-}16$) relationship to birth year, with values at 0.7059 for NJ1, and 0.6288 for NJ2.

Years of reproduction prior to fishing are defined as the elapsed time between individuals reaching 52 mm and reaching 80 mm. This window of time has also decreased with increasing birth year. The number of years available to reproduce for

animals born in 1800 was 72 at NJ1 and 93 at NJ2. The number of years decreased to 51 and 55 for NJ1 and NJ2 respectively for individuals born in 1900, and decreased further to 30 years in NJ1 and 16 years in NJ2 for individuals born in 2000. The increase in growth rate observed in NJ2 over NJ1 is corroborated by their respective rates of change, with -0.21 yr^{-1} in NJ1 and -0.38 yr^{-1} in NJ2 (Figures 4.17 & 4.20). Linear regressions were also statistically significant, with p-values less than $2.2\text{E-}16$. R^2 revealed a much stronger trend at NJ2 than NJ1, as R^2 values for NJ2 were 0.7697, but 0.2351 for NJ1.

For both NJ1 and NJ2, the last two decades of birth years seem to be characterized by a more rapid reduction in years to market size and a more rapid reduction in the number of years of reproduction before recruitment to the fishery. Insufficient data are available for birth years after 2000 to confirm the presence of these apparently accelerating trends.

4.4 Discussion

4.4.1 Growth Model Implications

The Tanaka and modified Tanaka models fit *A. islandica* growth the best for both populations, with the modified Tanaka often outperforming the Tanaka, as confirmed by AIC results presented in Hemeon et al. (in prep.). The von Bertalanffy model provided the worst fit for both populations, estimating high values at young ages and estimating low values at old ages. This outcome was first considered by Pace et al. (2017a) and subsequently confirmed by Hemeon et al. (in prep.) for the Georges Bank and Long Island sites. Poor fit can lead to a substantial underestimation of length at old age, as one of the salient characteristics of *A. islandica* is the absence of asymptotic growth at old age. For this reason, the von Bertalanffy model cannot be relied upon to describe growth

in this species. Thus, parameters from only the Tanaka and modified Tanaka models will be used to compare *A. islandica* across sites.

As discussed in Results, the g parameter (Figure 4.14) which describes length at older ages, was higher in NJ2 than in NJ1. Modified Tanaka results are very similar to the original Tanaka in NJ1, leading to similar growth predictions. These two populations are separated by the Hudson Canyon, which influences the movement of water between these two sites. Both bottom water temperature and primary productivity could be different between these two sites due to this geographical barrier. Both factors have been observed to greatly impact *A. islandica* growth (Schöne et al. 2005). As NJ2 is south of NJ1, these higher growth rates at older ages at NJ2 are potentially caused by warmer bottom water temperatures at that site. The differential in growth rate at old age, however, is not mirrored early in ontogeny. Time to maturity and time to recruitment into the fishery is very similar between the two sites.

Comparing growth model performance across the 20-year cohort bins shows that the original Tanaka model often underestimates length at old ages. The modified Tanaka, conversely, fits the observed data well, yet often overestimates growth to unobserved length values. Due to this overestimation, the ability to extrapolate growth trends using the modified Tanaka model is very limited, as also observed by Hemeon et al. (in prep.). However, both the original and modified Tanaka models confirm increased growth rates in both populations in recent decades, with estimates for animals born in the 1960s-2000s much higher than those born in the 1700s and 1800s (Figures 4.4-4.9). Thus, growth rates have likely increased consistently with birth year since the late 1700s.

Females and males display distinct differences in growth, with females reaching larger sizes (Ropes et al. 1984a, Hemeon et al. 2021b, in prep.; Sower et al. in press). The higher growth rates experienced by females compared to males discussed here and in Hemeon et al. (in prep.) provide further evidence that this species is sexually dimorphic, even though sexual dimorphism is rarely observed in bivalves. The differential rates of growth by males and females is partly responsible for the wide range of ages at length noted for most 5-mm size classes by Pace et al. (2017b), Hemeon et al. (2021b) and herein.

4.4.2 Growth Rates

Birth year is an important contributor to variation in length at age for ocean quahogs at both NJ1 and NJ1. The impressive influence of birth year is well instantiated by regressions of age-at-specified-length relative to birth year (Figures 4.15-4.20). Three elapsed time periods were used for comparison, the time between birth and maturity, the time between birth and recruitment into the fishery, and the elapsed time between the two representing the number of years of reproduction before exploitation. This latter is an important characteristic influencing the sensitivity of fishing on stock sustainability (Sissenwine and Shepard, 1987; Peterson, 2002). To determine consistent patterns in these three metrics at all four sites, three birth years were examined: 1800, 1900, and 2000. Year 1800 occurred in the last phase of the Little Ice Age (Cronin et al. 2010, Moore et al. 2017), whereas year 1900 occurred within a time period of consistent warming (Nixon et al. 2004). Year 2000 coincides with the initiation of a regime shift that produced rising temperatures throughout much of the Mid-Atlantic Bight (Pershing et al. 2015, Perretti et al. 2017, Powell et al. 2020).

Each site showed decreasing times to the three metric sizes as birthdate increased, though variation among the four sites was observed. *Arctica islandica* from Georges Bank reached 52 mm at the youngest age out of all four sites, at age 18 for animals born in 1800, which decreased by a factor of 2 to age 9 for animals born in 2000. NJ1, NJ2, and Long Island, conversely, reached 52 mm by age 28 for animals born in 1800, which also decreased to age 9 for animals born in 2000, which is a decrease by a factor exceeding 3 (Table 2.2). In all four sites, animals born in 1900 fell almost exactly halfway in elapsed time between the 1800 and 2000 values. Time to commercial size (80 mm) followed the same trends at all four sites, with Georges Bank having the youngest age, 63 years, for animals born in 1800, whereas NJ1, NJ2, and Long Island have ages ranging from 114-119 years born in 1800. By 2000, ages to 80 mm had decreased to 26-28 years in NJ2 and NJ1, respectively, and 34-39 years in Long Island and Georges Bank, respectively. For years of reproduction, NJ2 had the most drastic decrease as birth year increased, with 93 years available for animals born in 1800 decreasing by a factor of 5 to 16 years available for animals born in 2000. Georges Bank displayed the least amount of difference, from 48 years for animals from 1800 to 41 in 2000. Long Island and NJ1 displayed very similar trends, at 79 and 72 years available for animals born in 1800, respectively, to 32 and 30 years available for animals born in 2000.

The influence of birth year on time to milestone size is much more subdued in Georges Bank (Hemeon et al. in prep.) compared to the southern sites. This is consistent with observations by Hemeon et al. (in prep.) that animals at the end of the Little Ice Age were growing fastest in this region, but that growth rates at the other three sites caught up in large measure over the following 200 years (see also Ropes and Pyoas, 1982; Lewis et

al., 2001). These findings are also in agreement with Pace et al. (2018) who examined additional populations off southern New England and further south of Delmarva and, noteworthily, are in agreement with growth rates from subfossil shells measured by LeClaire et al. (in prep.) recovered from the death assemblage off Delmarva. The latitudinal response revealed, in particular, by comparisons of elapsed time from birth to market size define a clear north-to-south gradient in increased growth rates since the end of the Little Ice Age throughout the Mid-Atlantic and Georges Bank region.

The trends in growth rate as a function of birthdate may be due to increasing bottom water temperatures over the last 200 years, though due to the lack of bottom water temperature data throughout the time period represented in the birthdates and ages reported here, one cannot be certain that temperature is the cause. Of particular note is the absence of information on the long-term dynamics of the Cold Pool. Nonetheless, many of the *A. islandica* in this study have lived throughout the entirety of global warming since the end of the Little Ice Age, very likely leaving a record of rising temperatures in the variations in growth rate over that time. Growth rates in most bivalves are strongly influenced by temperature, with growth rates rising over a wide temperature range, but then falling again as optimal temperatures are exceeded. The general pattern in Venerida, of which *A. islandica* is a member, is well described (Hofmann et al. 2006, Flye-Saint-Marie et al. 2007, Munroe et al. 2013), with growth primarily influenced by ever rising respiration rates with rising temperatures, but a parabolic response of filtration rates leading to temperature-dependent changes in scope for growth (Munroe et al. 2013, Beukema et al. 2017). *Arctica islandica* are sensitive to variations in temperature even to a greater degree than most Venerida (Begum et al., 2009, 2010). Thus, the presumption

that the primary growth-influencing agent is rising bottom water temperatures has merit. One cannot exclude the influence of food supply, however, as food supply is an important modulator of rates of growth (Schöne et al. 2005, Wanamaker et al. 2009, Mette et al. 2016, see also LeClaire et al. in prep.), but a centuries-long increase in food supply is unlikely to be an explanatory alternative (Boyce et al. 2010). What is unique for *A. islandica*, due to their long lifespan, is that the differential in growth rate with rising temperatures can be observed within members of the living community born across the centuries and that this record leaves a strong signal of the influence of climate change in the northwestern Atlantic. *Arctica islandica* growth rates have increased by factors of 2 to 3 or more since the end of the 1700s, an extraordinary physiological response to global warming.

4.4.3 Trends in Growth

Hemeon et al. (in prep.) reported model parameters for *A. islandica* from Georges Bank and Long Island in Table 3 in the same study. Those reported parameters will be compared directly to those for NJ1 and NJ2 to determine trends over time. At all four sites, and for both males and females (Figure 4.10), *a* parameter values have been decreasing with slight variation since 1720. These trends indicate that maximum growth rates have increased over time. *C* parameter values have increased steadily over time as well (Figure 4.11). However, this parameter presents anomalous 0 values for many cohort years in the 1700s and 1800s at all four sites. The reasons behind these 0 values are unclear. Interestingly, *d* parameter values have remained consistent since 1720 (Figure 4.12), with slight increases in the most recent cohorts. *D* is a scaler of body size, and may indicate that body sizes have stayed consistent over time, despite increasing growth rates.

The f parameter values have slightly increased over time (Figure 4.13), which indicates decreasing growth at older age. However, this parameter is corrected by the g parameter, which influences the rate of growth rate decline with increasing age. The g parameter has increased since 1720 (Figure 4.14) to a larger degree than the f parameter, potentially indicating that growth at older ages has actually increased rather than decreased.

All four sites have displayed the same trends in parameter variation since 1720. These trends indicate that *A. islandica* growth has increased with some variation. One possible reason for increasing growth is increasing bottom water temperature. However, it is difficult to validate this claim, as bottom water temperature is not available for much of the time represented by *A. islandica* lifespan presented in this study. What could be affecting *A. islandica* growth is likely widescale geographically, given the same trends among all four sites, so increasing temperature is a plausible cause.

4.5 Summary

Growth rates from approximately 1,500 *Arctica islandica* from New Jersey, collected from north and south of the Hudson Canyon, were analyzed and compared to Long Island and Georges Bank. New Jersey represents the southern boundary of *A. islandica* from the Mid-Atlantic Bight, and animals here may experience warmer temperatures compared to their northern counterparts. Results indicate that *A. islandica* from New Jersey have slower maximum growth rates compared to northern *A. islandica*, particularly from off Georges Bank. However, results indicate that *A. islandica* from south of the Hudson Canyon have higher growth rates at older ages compared to the other three sites. Growth rates have been increasing over the past three centuries, potentially due to increasing bottom water temperatures, with time to maturity and time to

commercial size drastically decreasing, leading to fewer years of reproductive ability.

Out of the three models tested, the von Bertalanffy, commonly used in fisheries management, had the worst fit for all populations and at all levels, and should not be used in the management of this species. The Tanaka and modified Tanaka models are recommended in its place, as these models best fit *A. islandica* growth at young (Tanaka) and older (>160 years, modified Tanaka) ages.

4.6 Tables

Table 4.1 Parameter values for von Bertalanffy, Tanaka, and modified Tanaka models of best fit. NJ1 = northern New Jersey; NJ2 = southern New Jersey; SE = standard error.

Model	Group	Parameter	NJ1		NJ2	
			Estimate	SE	Estimate	SE
von Bertalanffy	Population	L_{inf}	1.06E+02	2.18E-01	8.97E+01	7.99E-02
		K	1.33E-02	8.35E-05	3.09E-02	1.48E-04
		t_0	-3.58E+01	2.31E-01	-9.48E+00	9.84E-02
	Male	L_{inf}	8.26E+01	9.45E-02	8.50E+01	1.02E-01
		K	4.91E-02	3.02E-04	3.66E-02	2.57E-04
		t_0	-3.32E+00	7.68E-02	-7.61E+00	1.27E-01
	Female	L_{inf}	1.09E+02	3.17E-01	9.32E+01	1.14E-01
		K	1.18E-02	1.04E-04	2.82E-02	1.77E-04
		t_0	-4.31E+01	3.62E-01	-1.04E+01	1.37E-01
Tanaka	Population	a	2.71E-02	5.88E-04	1.31E-02	6.82E-04
		c	3.98E+00	5.78E-02	1.58E+00	6.42E-02
		d	7.85E+01	1.04E-01	7.95E+01	1.13E-01
		f	4.49E-03	3.27E-05	3.65E-03	2.55E-05
	Male	a	2.62E-02	7.65E-04	1.64E-02	8.01E-04
		c	4.11E+00	7.65E-02	2.46E+00	7.97E-02
		d	7.43E+01	1.49E-01	7.40E+01	1.38E-01
		f	5.11E-03	5.64E-05	4.66E-03	4.77E-05
	Female	a	2.81E-02	7.85E-04	9.12E-03	1.06E-03
		c	4.23E+00	7.70E-02	8.60E-01	9.57E-02
		d	8.00E+01	1.32E-01	8.39E+01	1.69E-01
		f	4.46E-03	4.18E-05	3.07E-03	2.82E-05
Modified Tanaka	Population	a	2.69E-02	6.42E-04	1.69E-02	6.07E-04
		c	3.60E+00	6.84E-02	2.40E+00	6.55E-02
		d	7.99E+01	1.72E-01	7.61E+01	1.62E-01
		f	4.11E-03	4.11E-05	4.34E-03	4.30E-05
		g	0.00E+00	3.55E-07	9.34E-06	3.86E-07
	Male	a	2.63E-02	7.59E-04	1.80E-02	7.20E-04
		c	4.16E+00	8.31E-02	3.07E+00	8.04E-02
		d	7.41E+01	2.19E-01	7.15E+01	1.93E-01
		f	5.18E-03	7.66E-05	5.44E-03	7.63E-05
		g	8.31E-07	5.97E-07	8.20E-06	5.20E-07
	Female	a	2.63E-02	8.95E-04	1.51E-02	9.36E-04
		c	3.14E+00	9.53E-02	1.87E+00	9.77E-02
		d	8.28E+01	2.35E-01	7.99E+01	2.48E-01
		f	3.78E-03	4.91E-05	3.69E-03	4.94E-05
		g	0.00E+00	4.33E-07	9.99E-06	5.41E-07

Table 4.2 Time to milestone sizes at three birth years at northern New Jersey (NJ1), southern New Jersey (NJ2), and Georges Bank (GB) and Long Island (LI), the latter two taken from Hemeon et al. (in prep.). Ages are reported in years.

	Birth Year	NJ1	NJ2	GB	LI
Time to 50% Maturity (52 mm)	1800	26	28	18	28
	1900	17	18	12	16
	2000	9	8	9	9
Time to Commercial Size (80 mm)	1800	114	119	63	114
	1900	71	72	51	74
	2000	28	26	39	34
Years of Reproduction (52 mm-80 mm)	1800	72	93	38	170
	1900	51	55	34	114
	2000	30	16	30	76

4.7 Figures

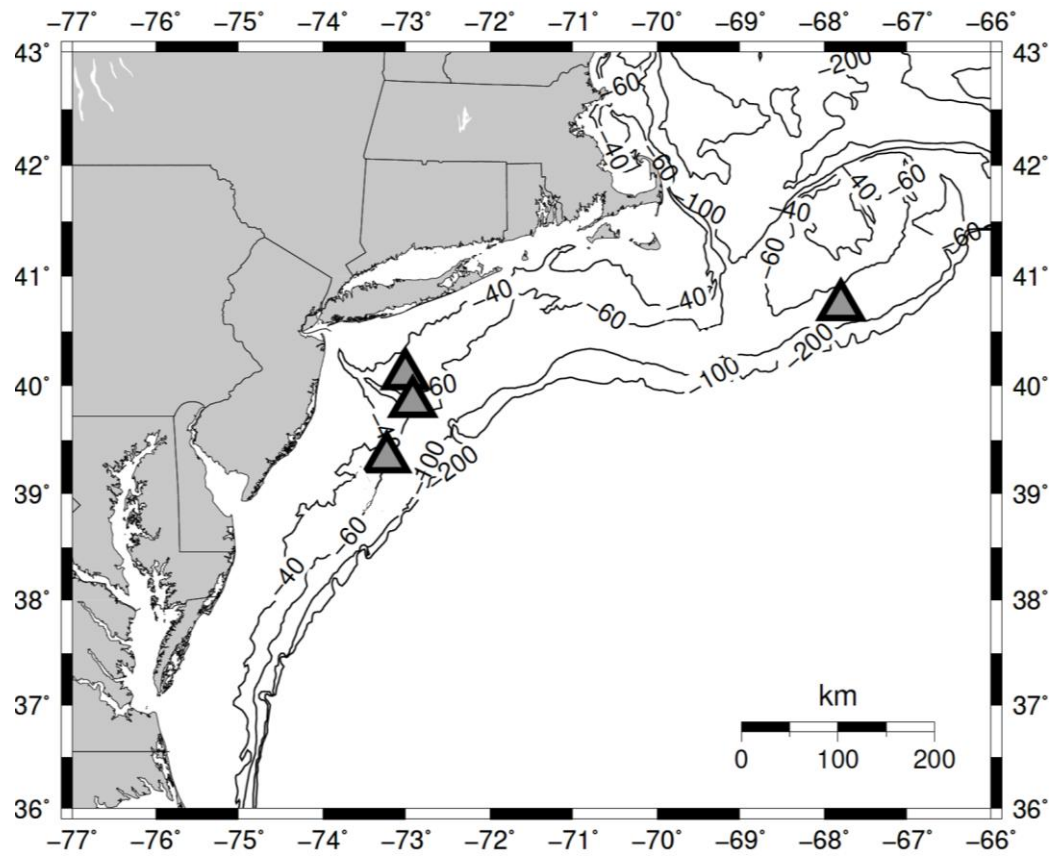


Figure 4.1 Map of sample locations. From north to south, sites are Georges Bank (GB), Long Island (LI), New Jersey north (NJ1), and New Jersey south (NJ2).

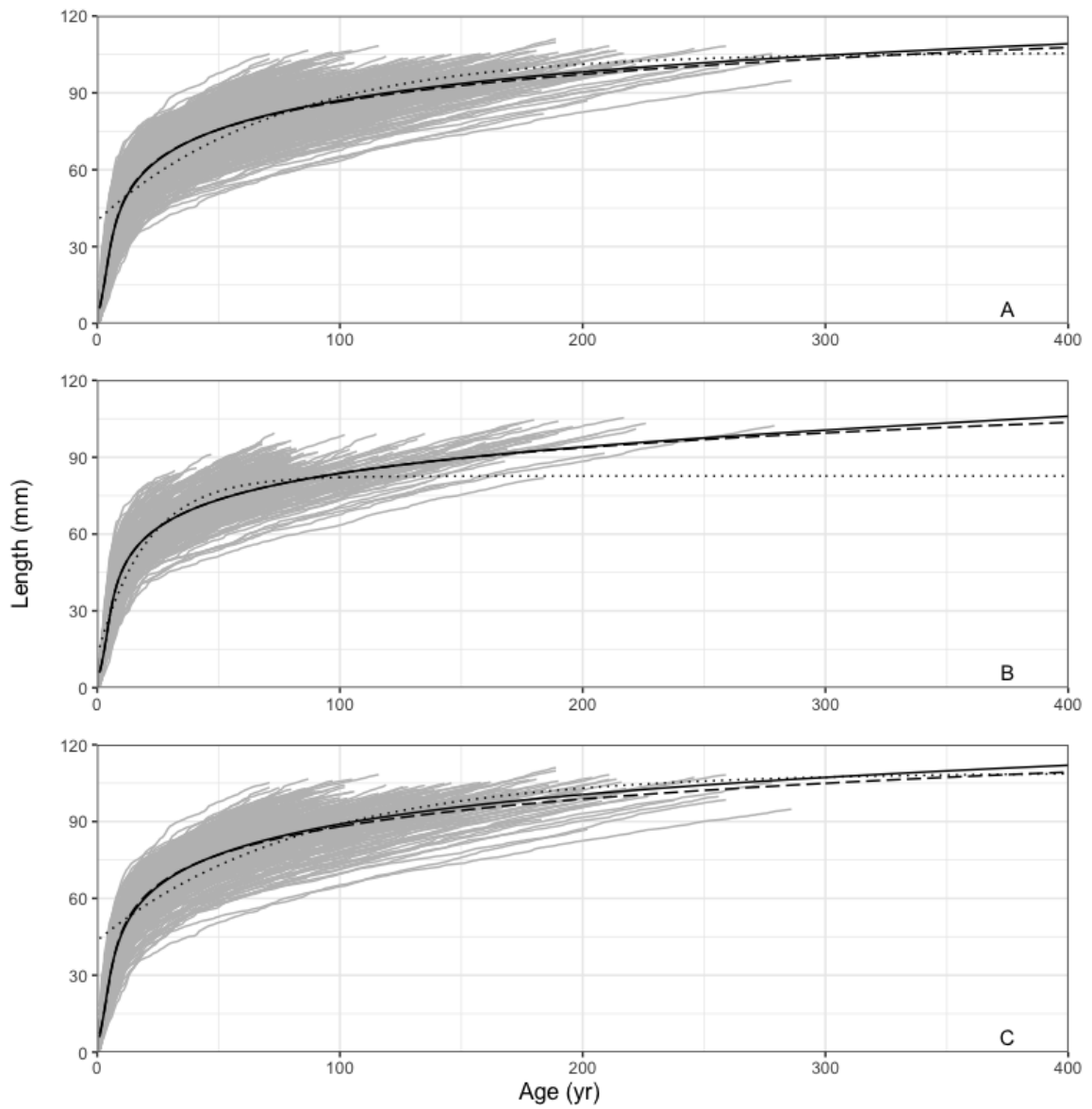


Figure 4.2 Best fit models for NJI population (A), male (B), and female (C). Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

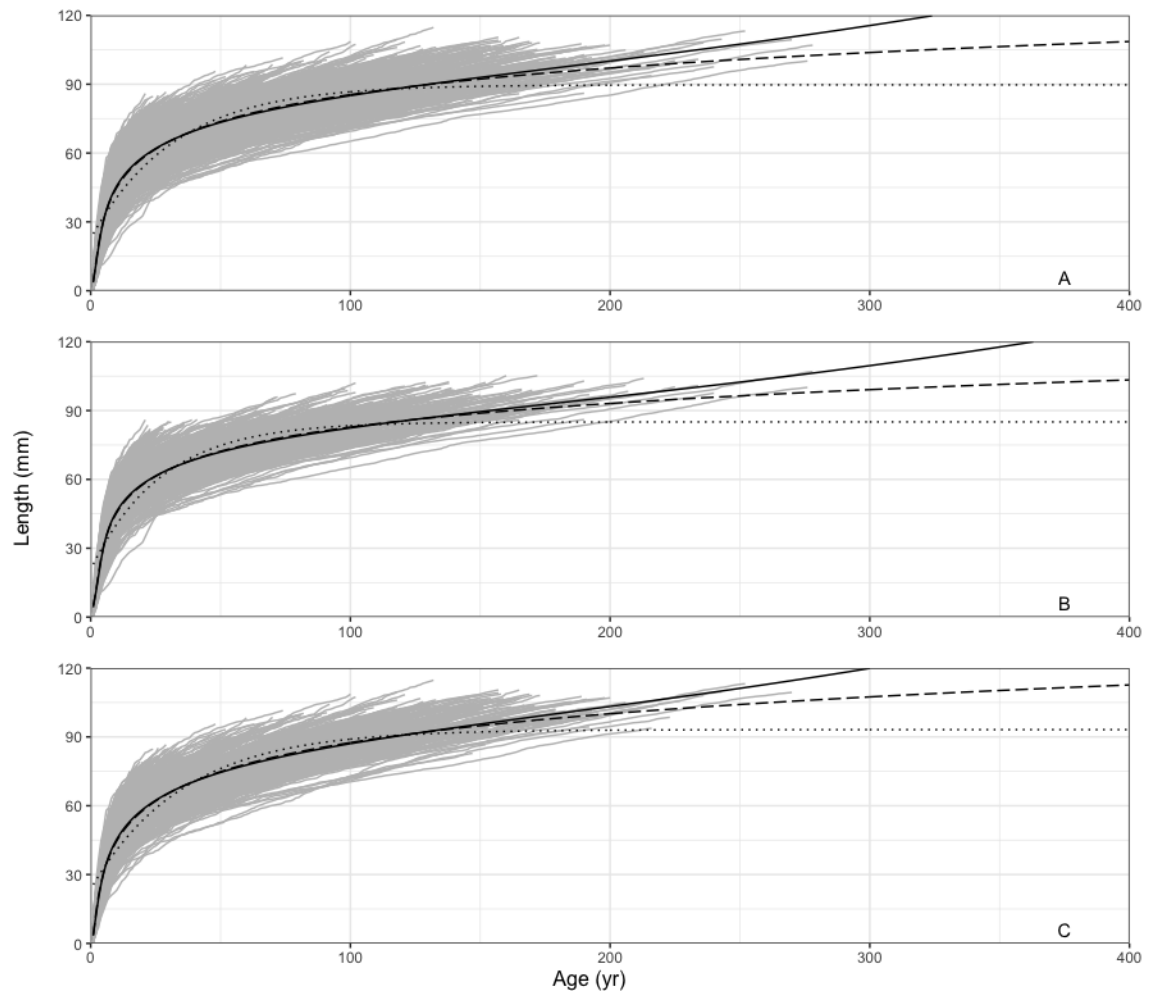


Figure 4.3 Best fit models for NJ2 population (A), male (B), and female (C). Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

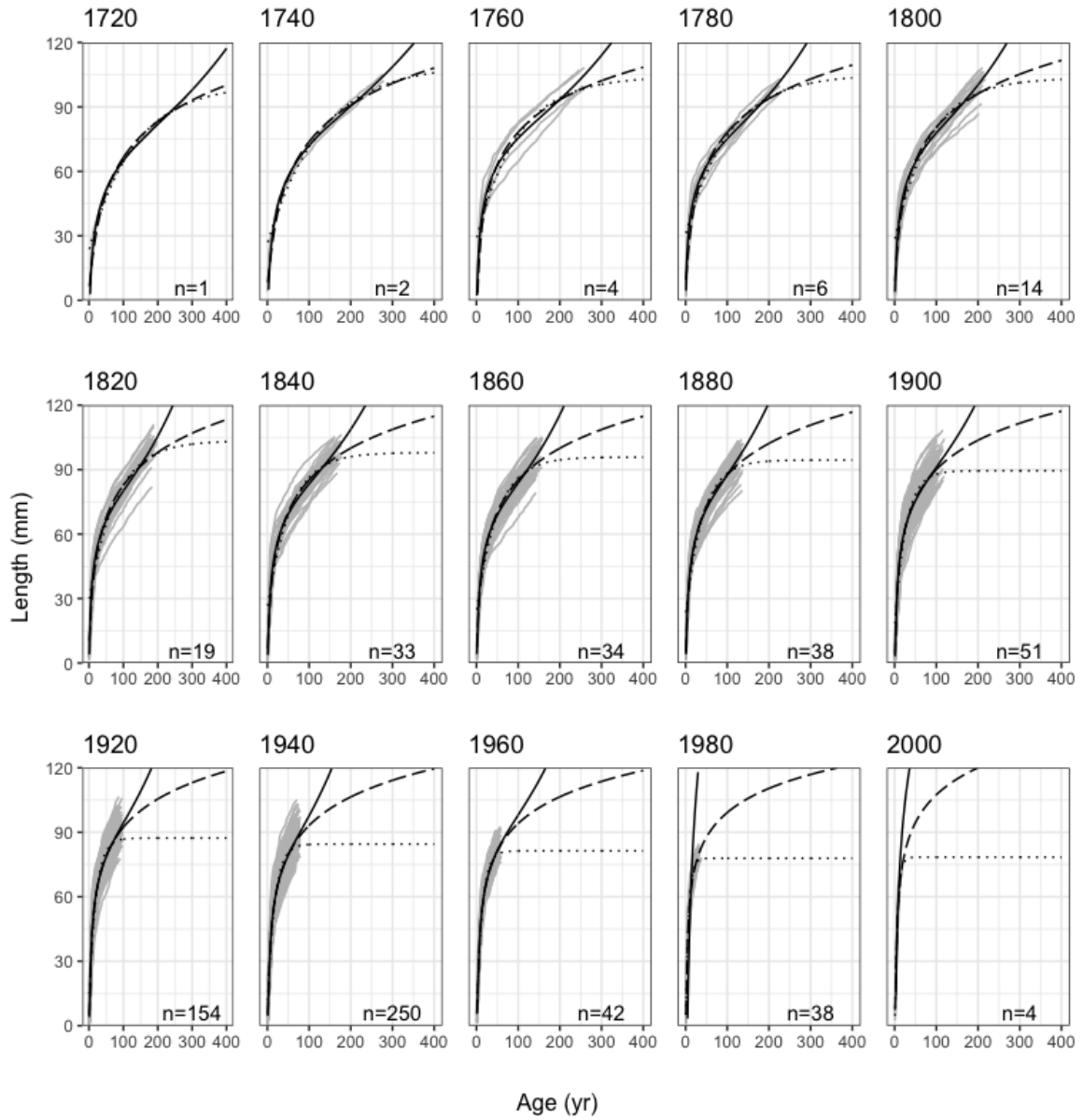


Figure 4.4 Best fit models for NJI population 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

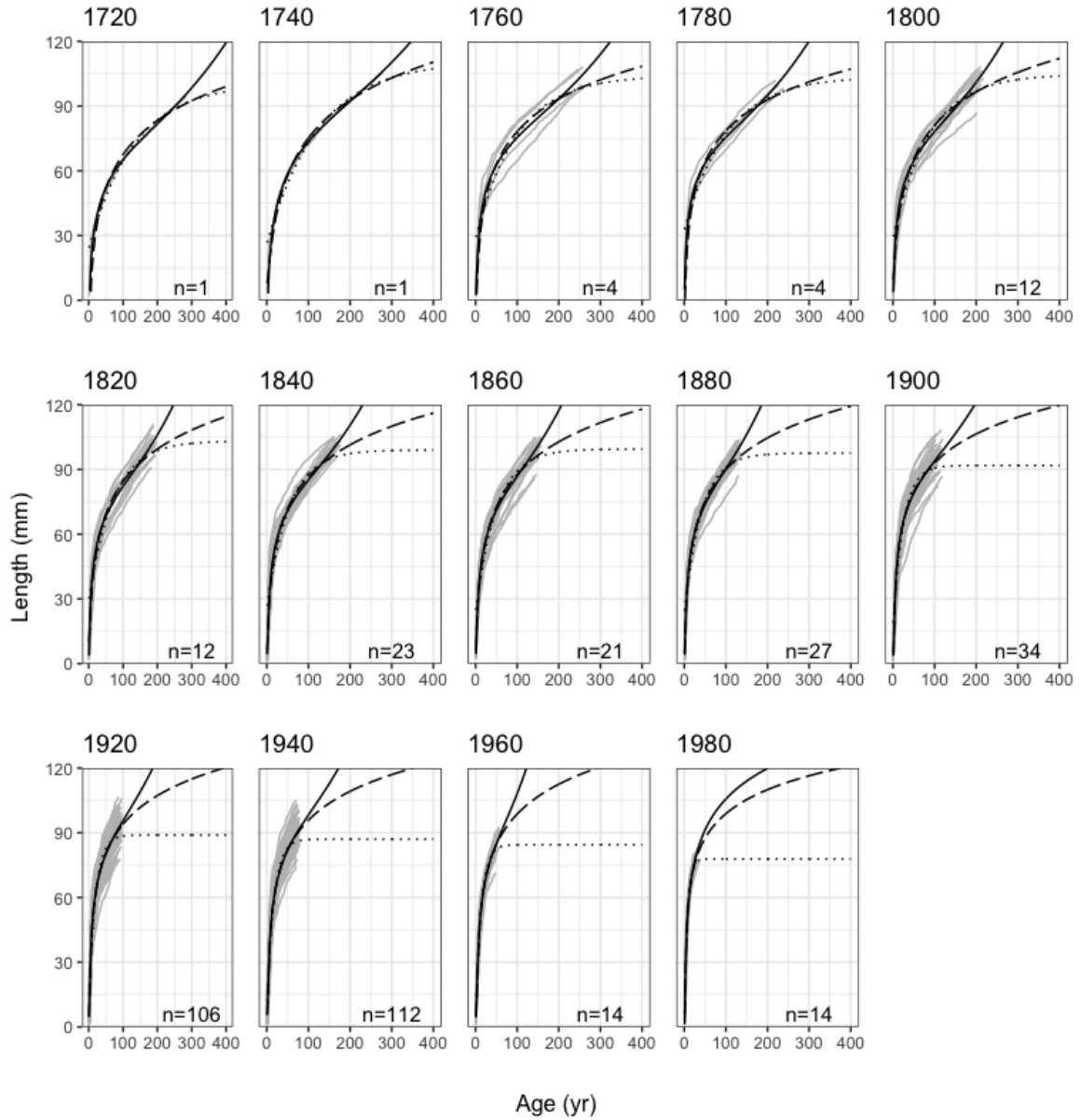


Figure 4.5 Best fit models for NJ female 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

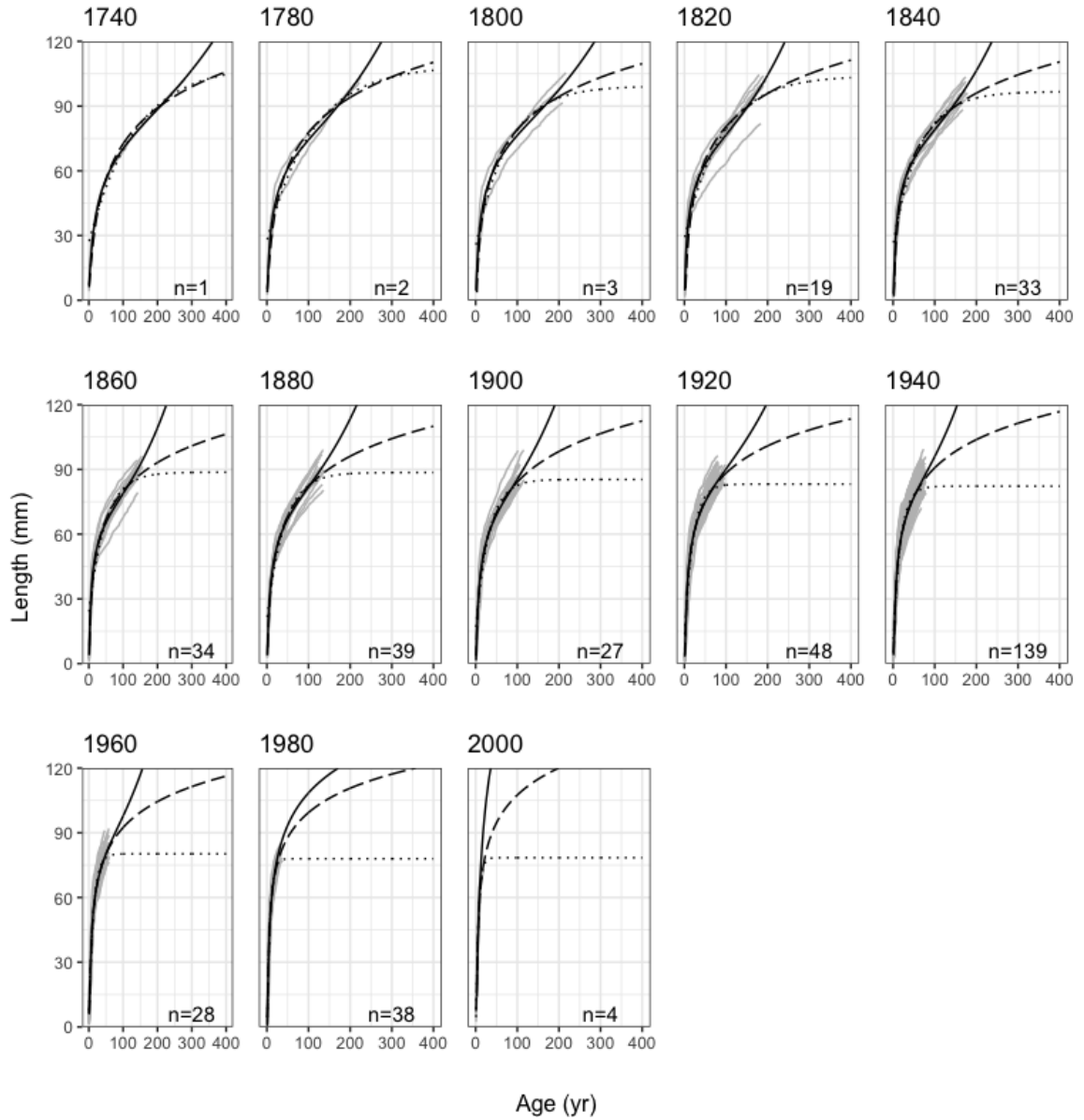


Figure 4.6 Best fit models for NJI male 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

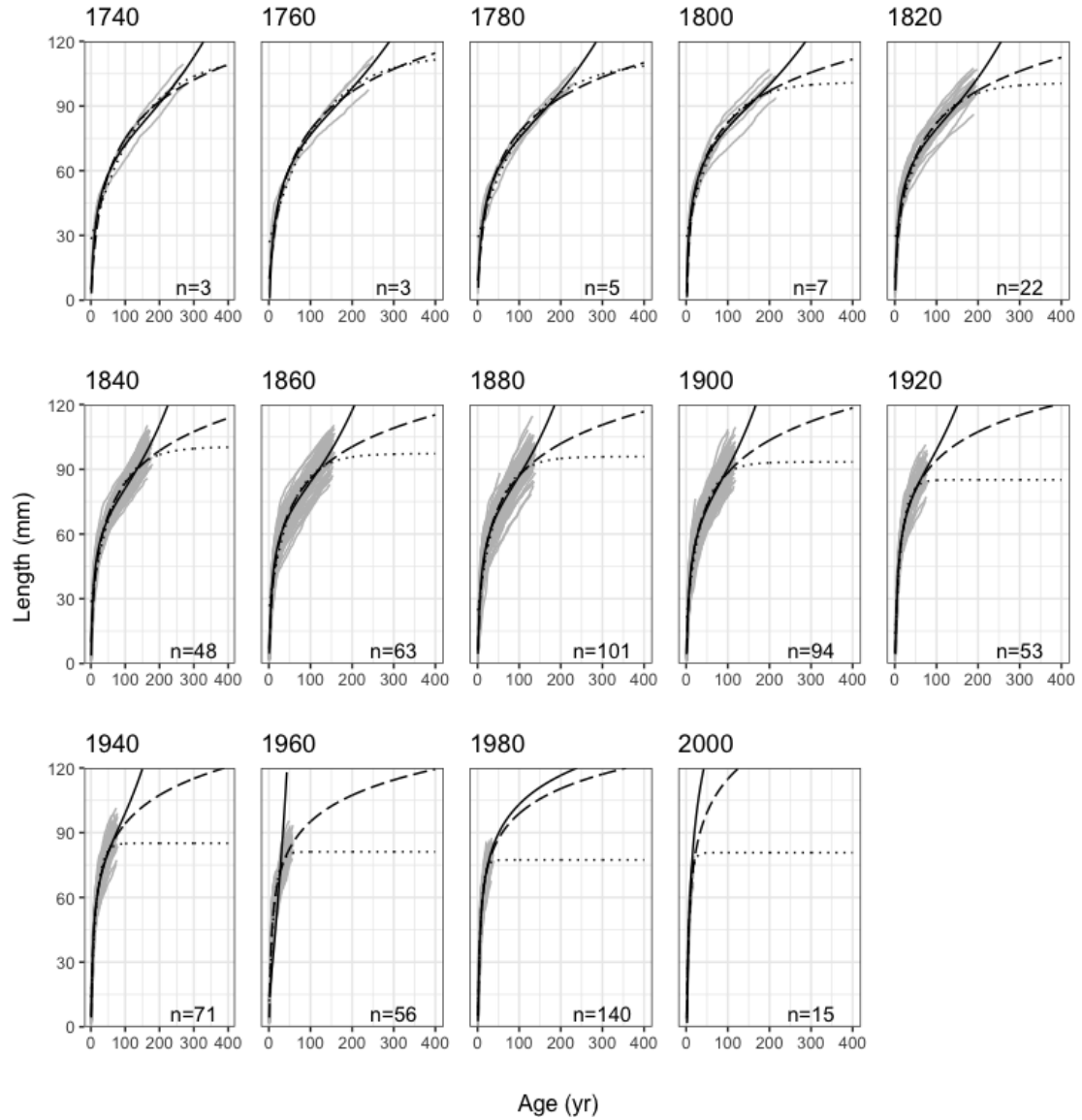


Figure 4.7 Best fit models for NJ2 population 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

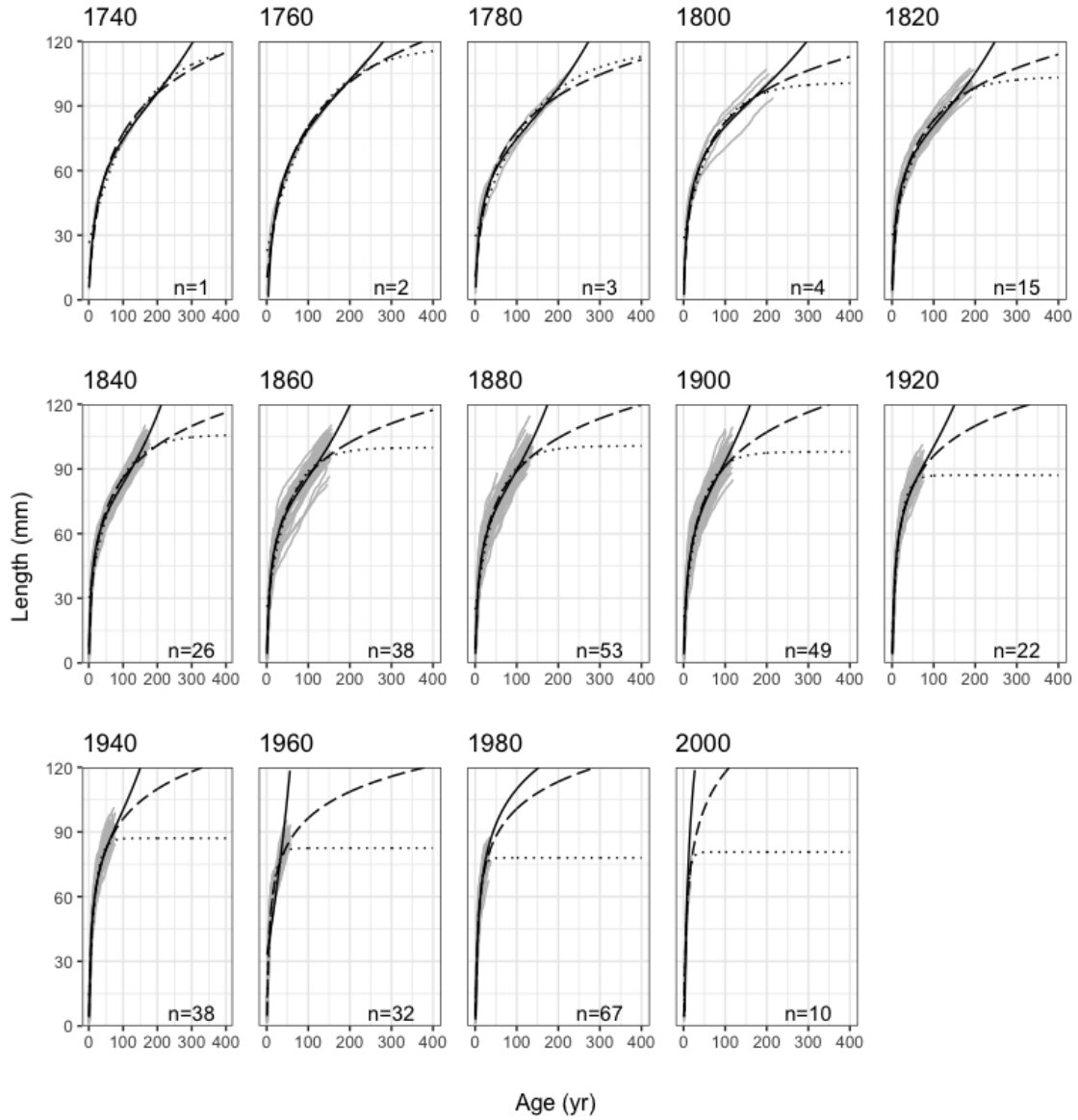


Figure 4.8 Best fit models for NJ2 female 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

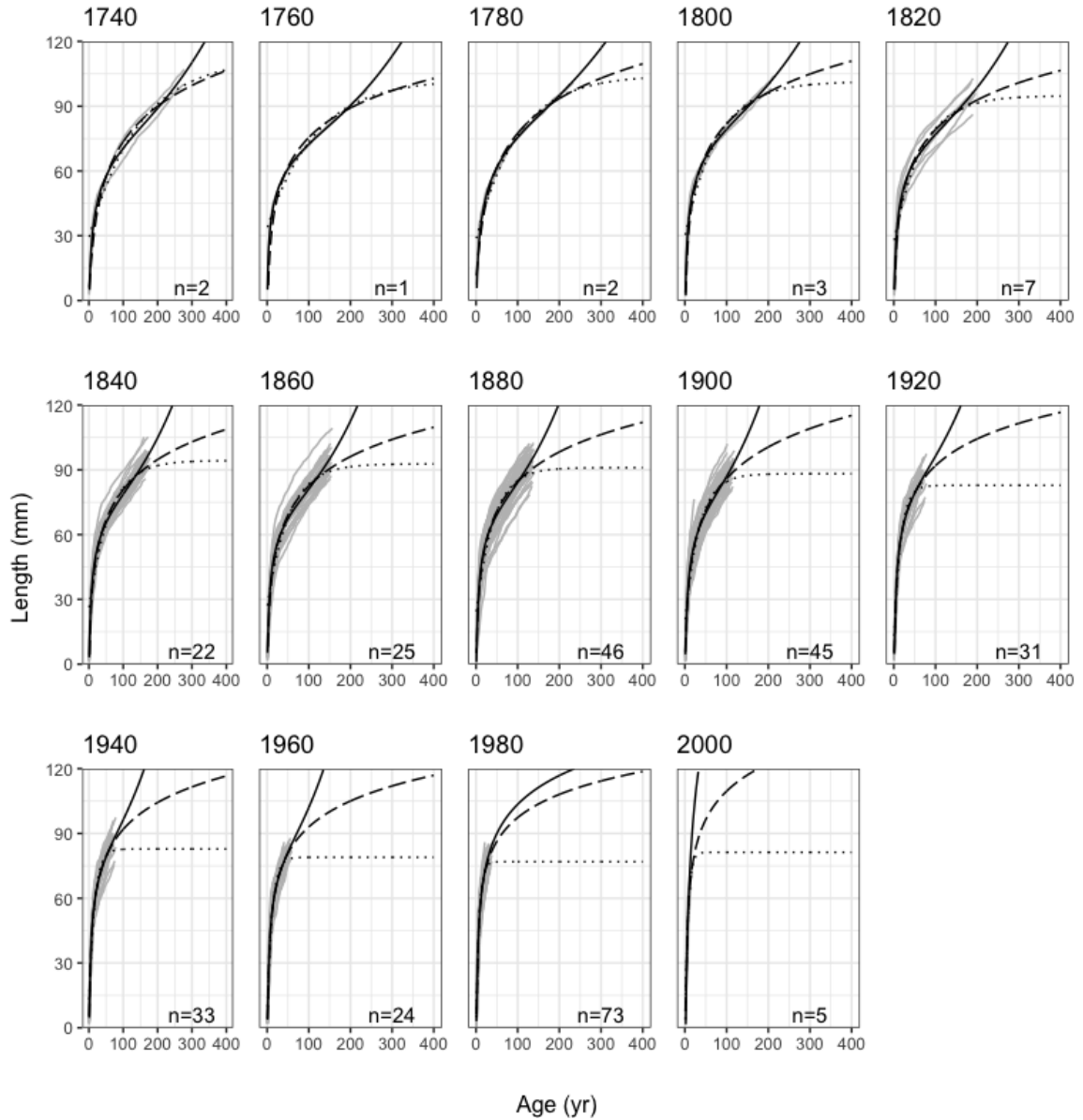


Figure 4.9 Best fit models for NJ2 male 20-year cohorts. Solid line: modified Tanaka; dashed line: Tanaka; dotted line: von Bertalanffy.

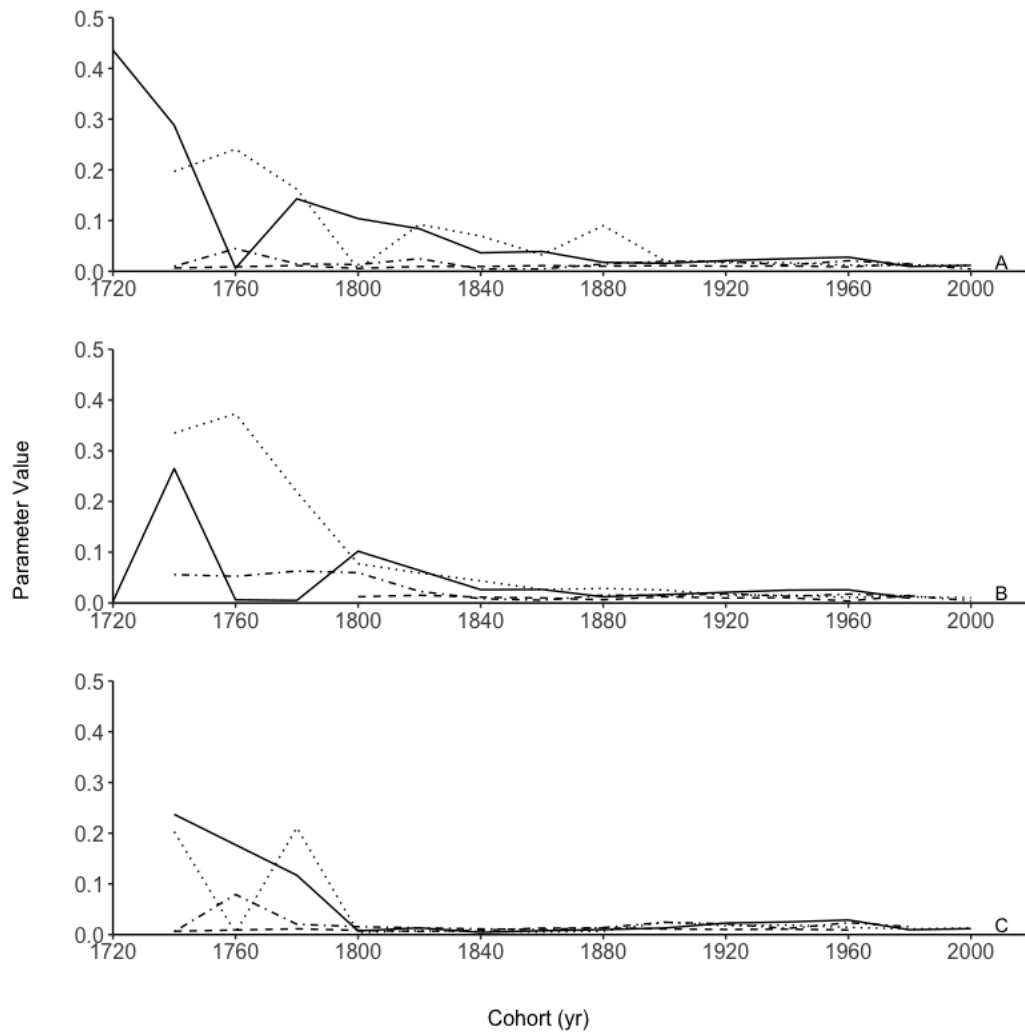


Figure 4.10 Tanaka a parameter values for northern New Jersey New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line) for population (A), female (B), and male (C) cohorts

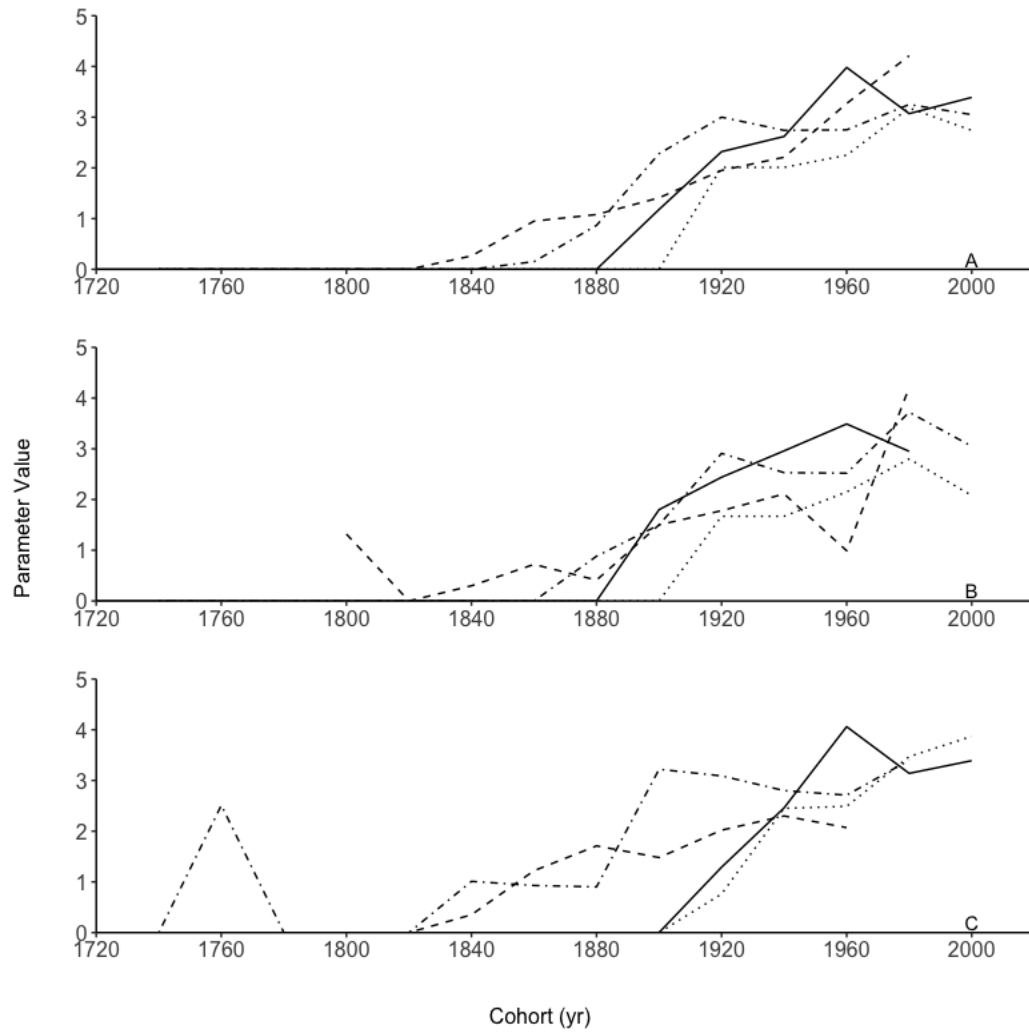


Figure 4.11 Tanaka c parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line) for population (A), female (B), and male (C) cohorts

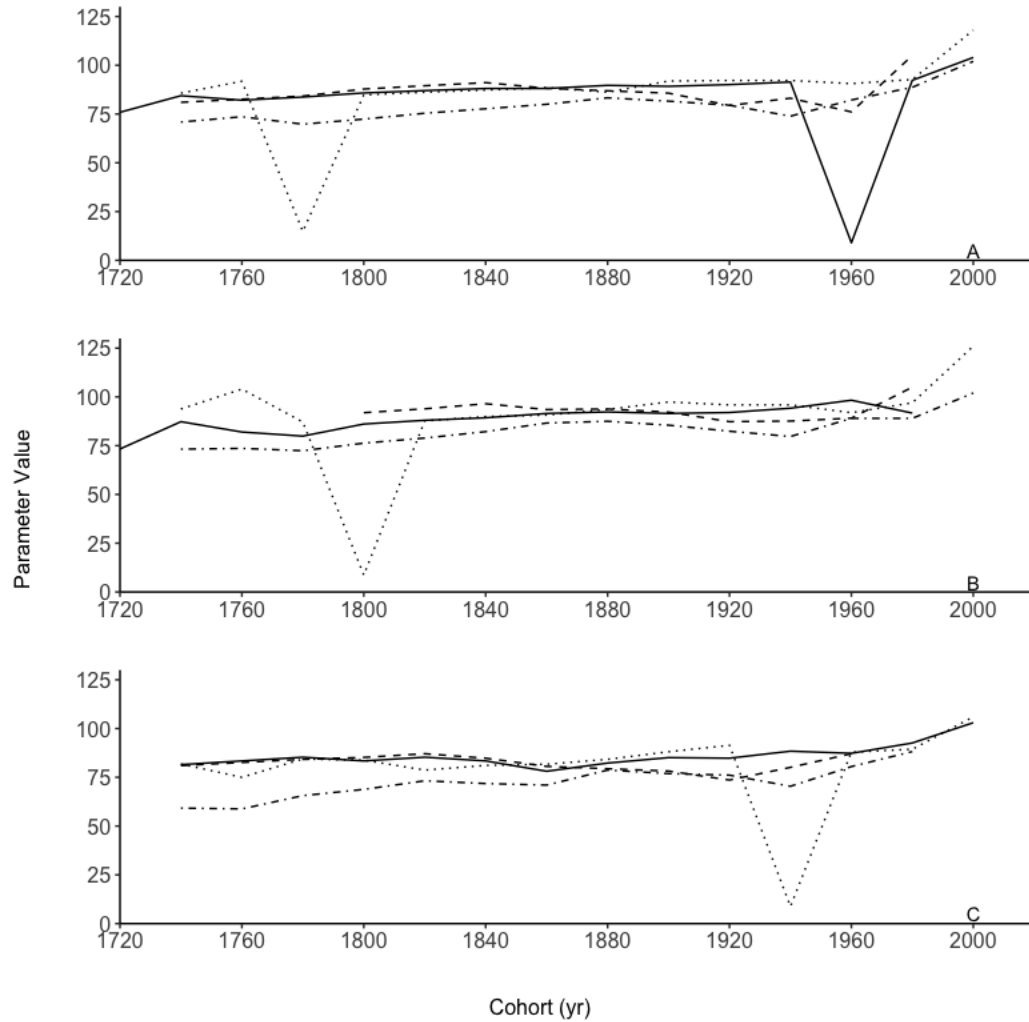


Figure 4.12 Tanaka d parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line) for population (A), female (B), and male (C) cohorts

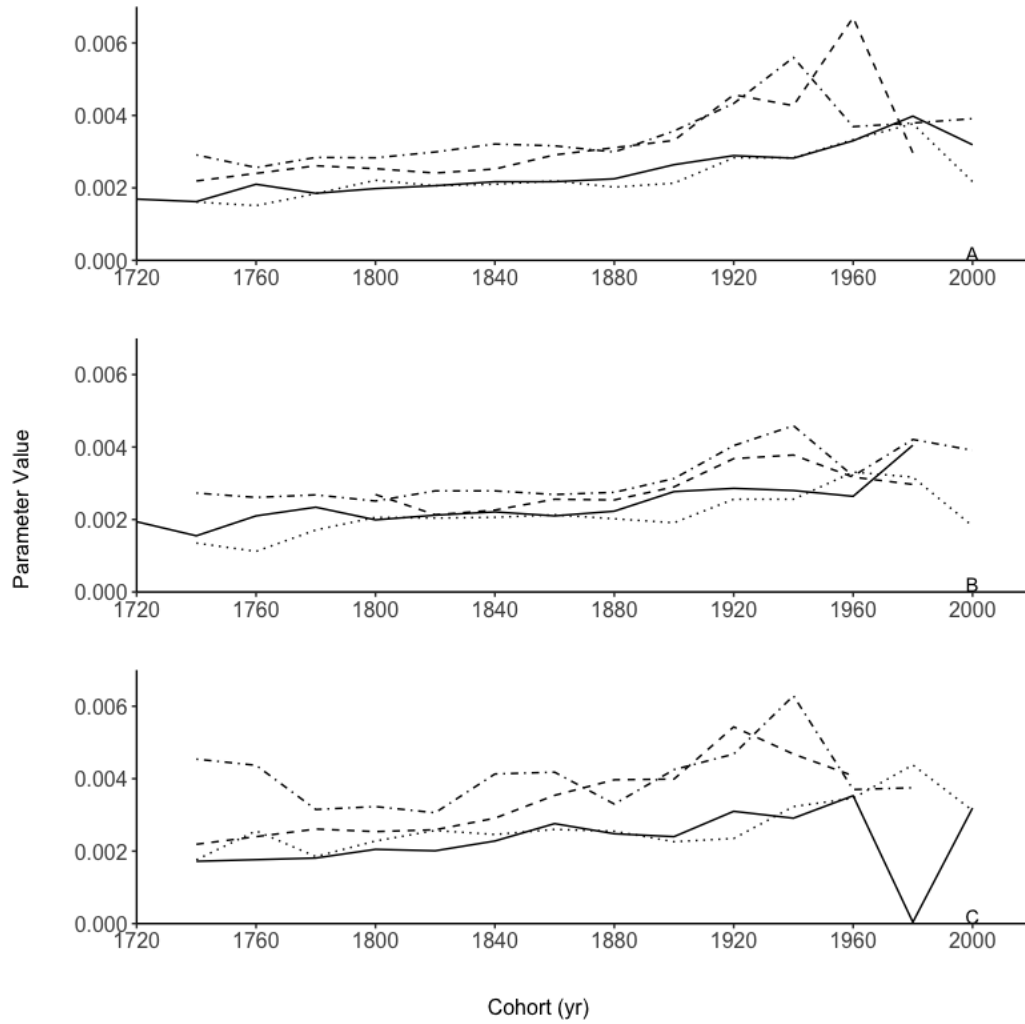


Figure 4.13 Tanaka f parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line) for population (A), female (B), and male (C) cohorts

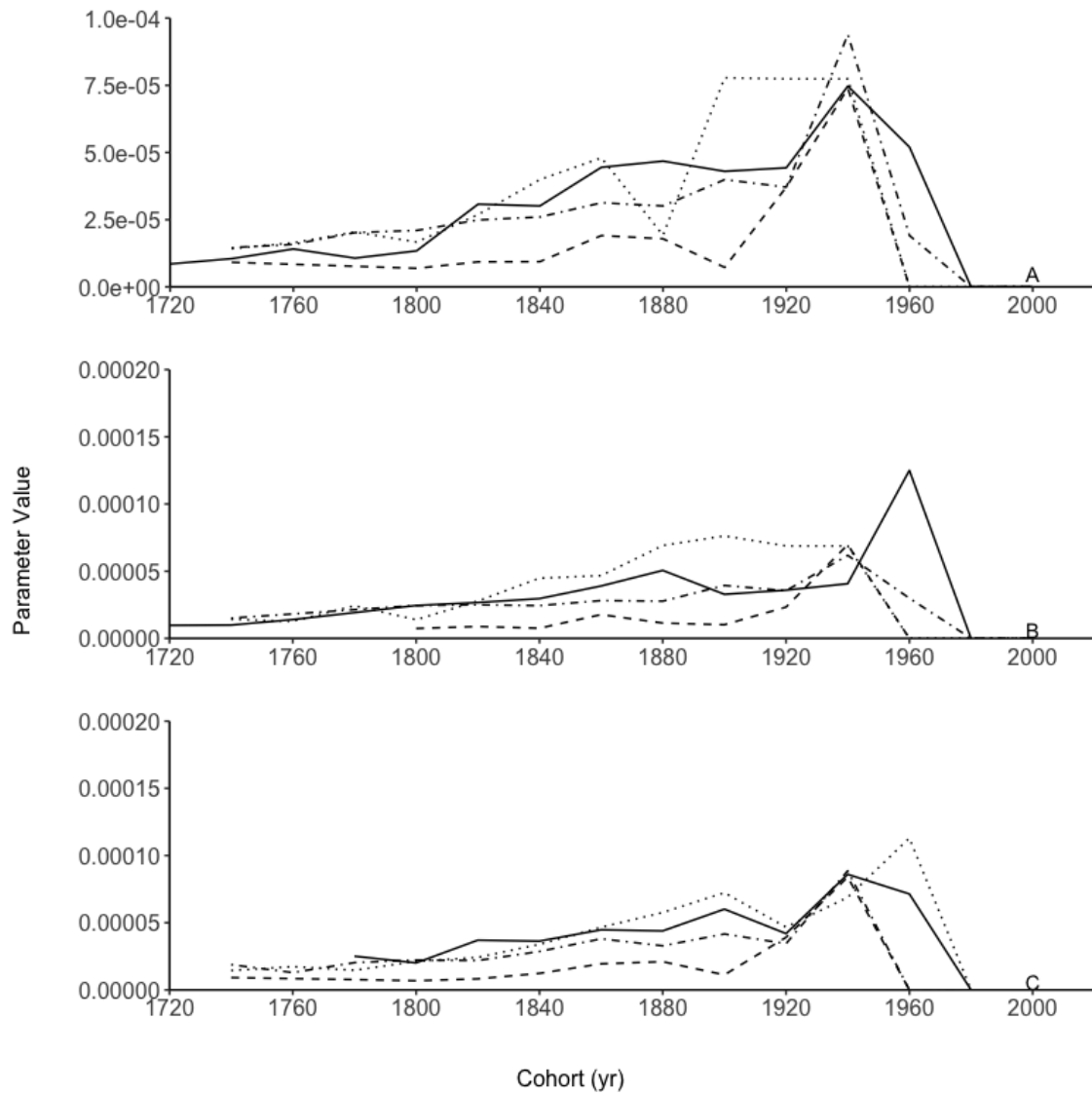


Figure 4.14 Modified Tanaka g parameter values for northern New Jersey (NJ1; solid line), southern New Jersey (NJ2; dotted line), Long Island (dotdash line), and Georges Bank (dashed line) for population (A), female (B), and male (C) cohorts

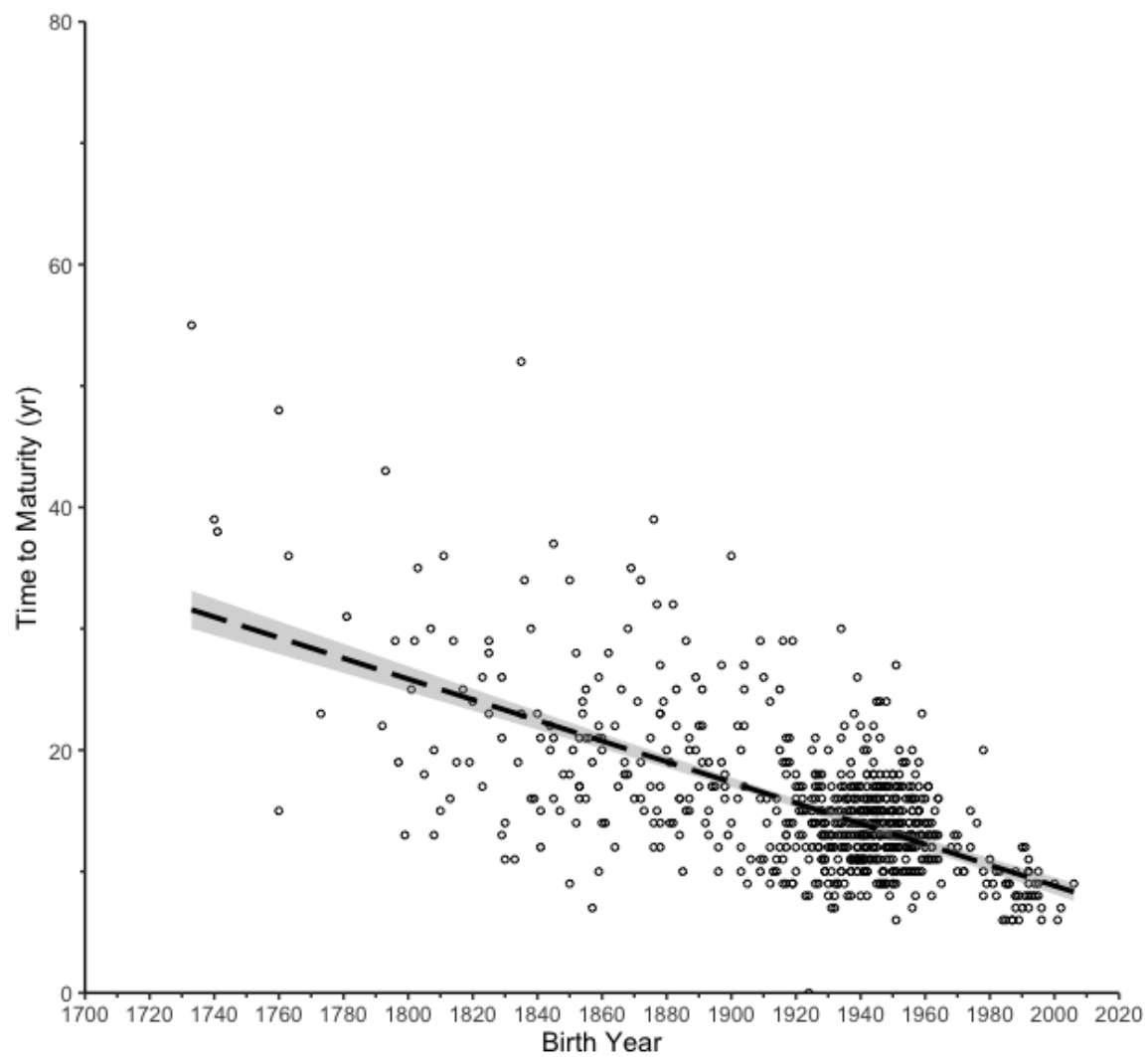


Figure 4.15 Northern New Jersey (NJ1) time to 50% maturity (52 mm). Dashed line = line of regression; equation: $179.12 - 0.085x$

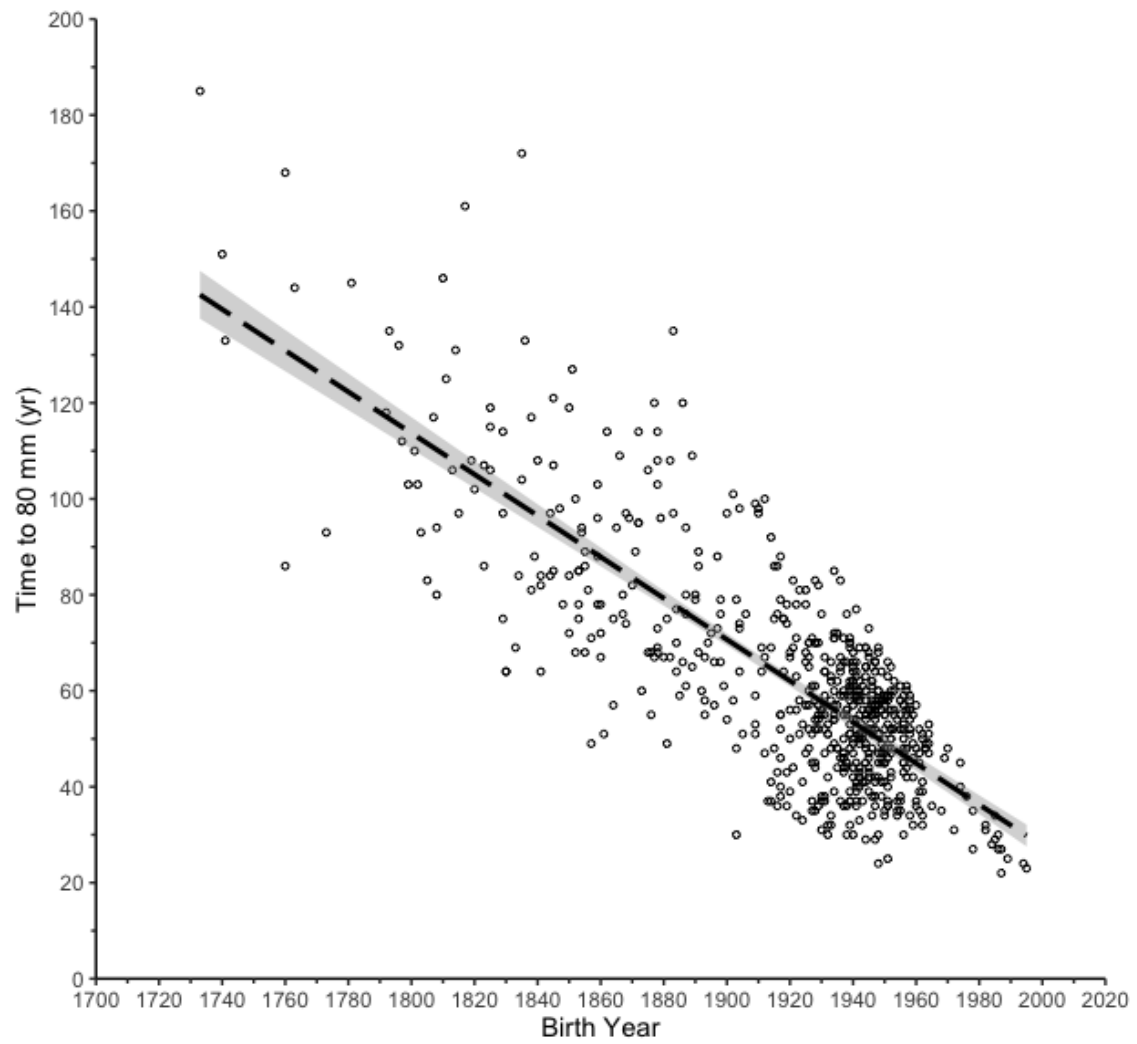


Figure 4.16 Northern New Jersey (NJ1) time to commercial size (80 mm). Dashed line = line of regression; equation: $888.00 - 0.43x$

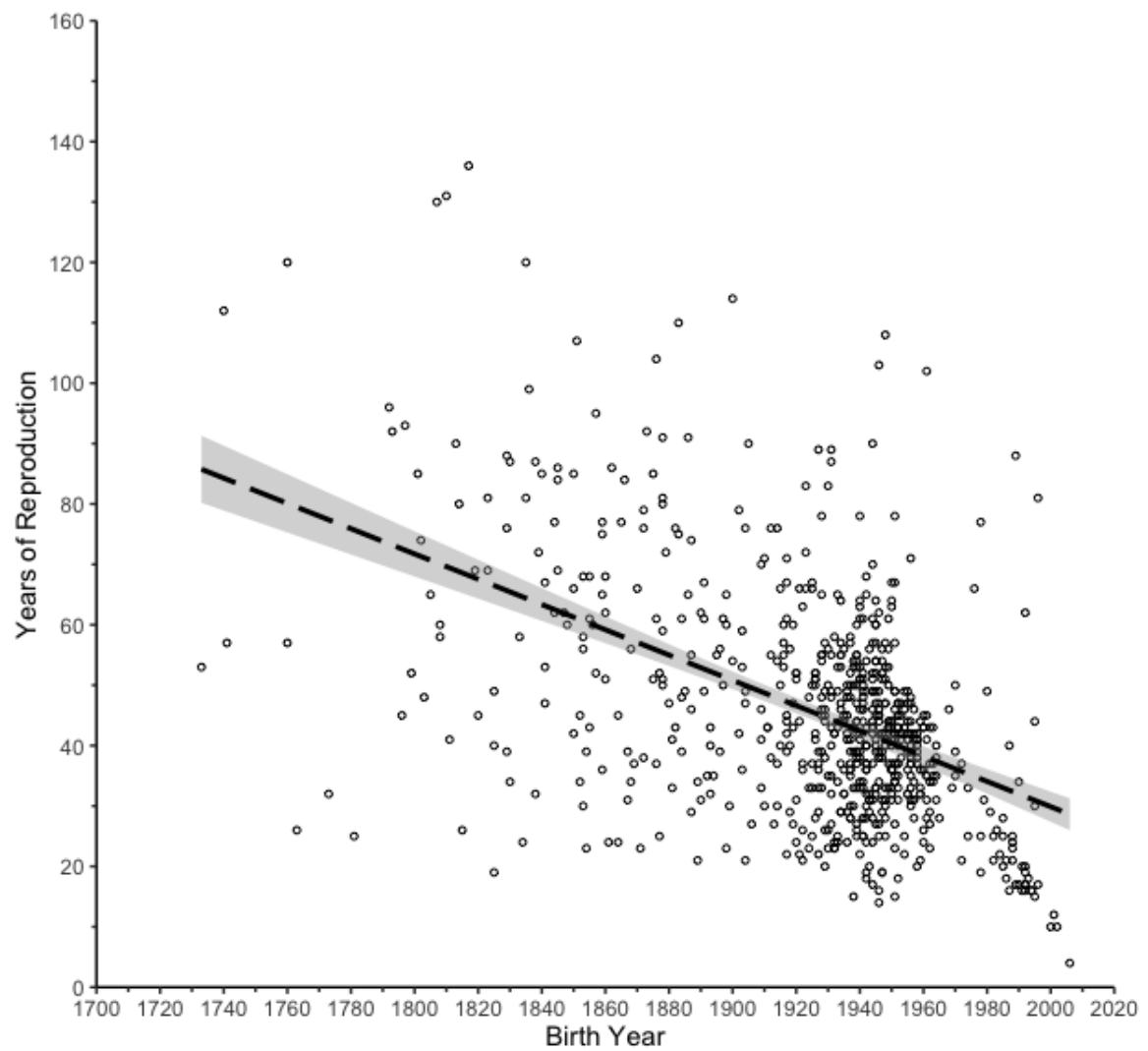


Figure 4.17 Northern New Jersey (NJ1) years of reproduction (time between 52 mm and 80 mm). Dashed line = line of regression; equation: $448.36 - 0.21x$

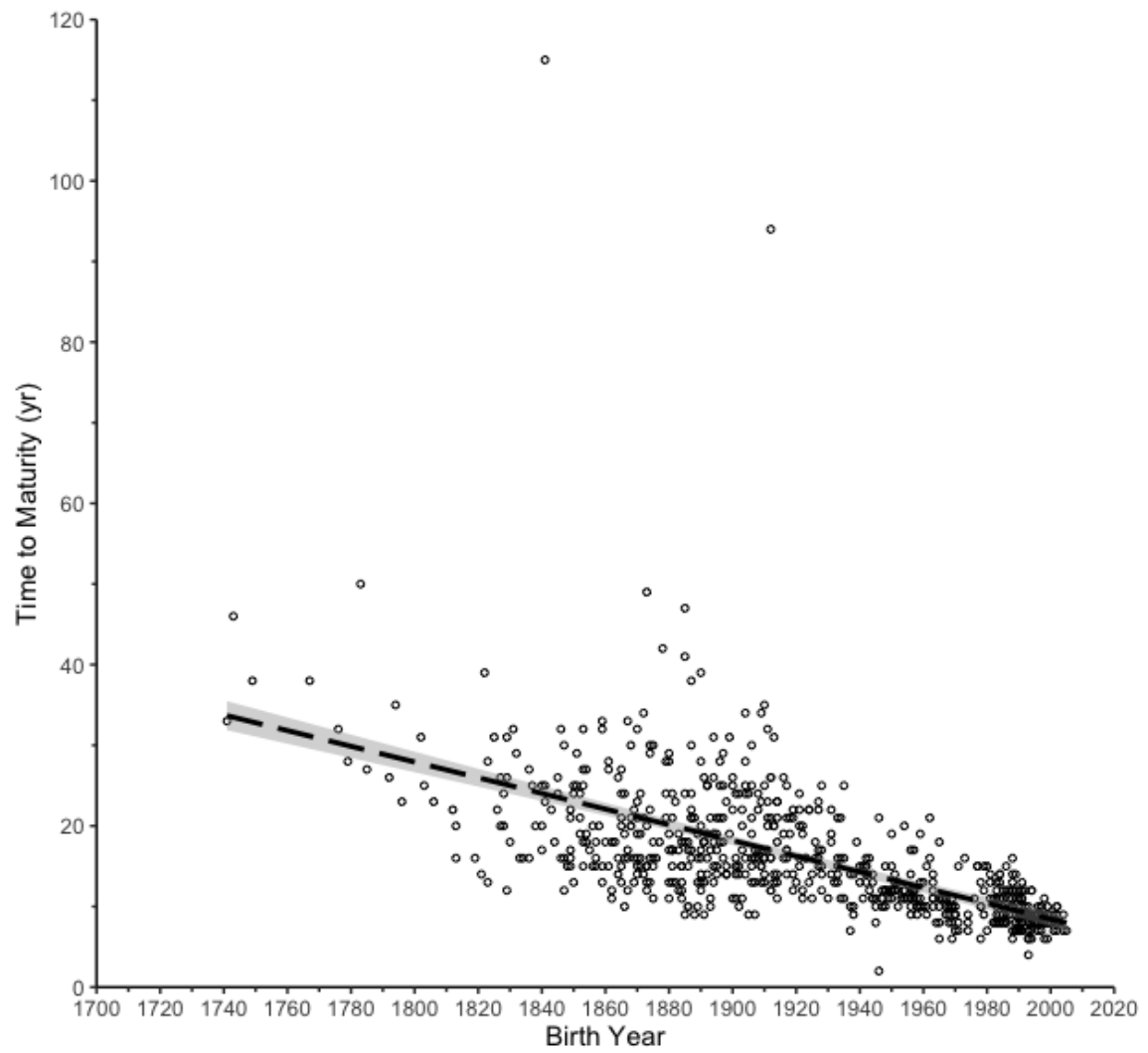


Figure 4.18 Southern New Jersey (NJ2) time to 50% maturity (52 mm). Dashed line = line of regression; equation: $203.18 - 0.097x$

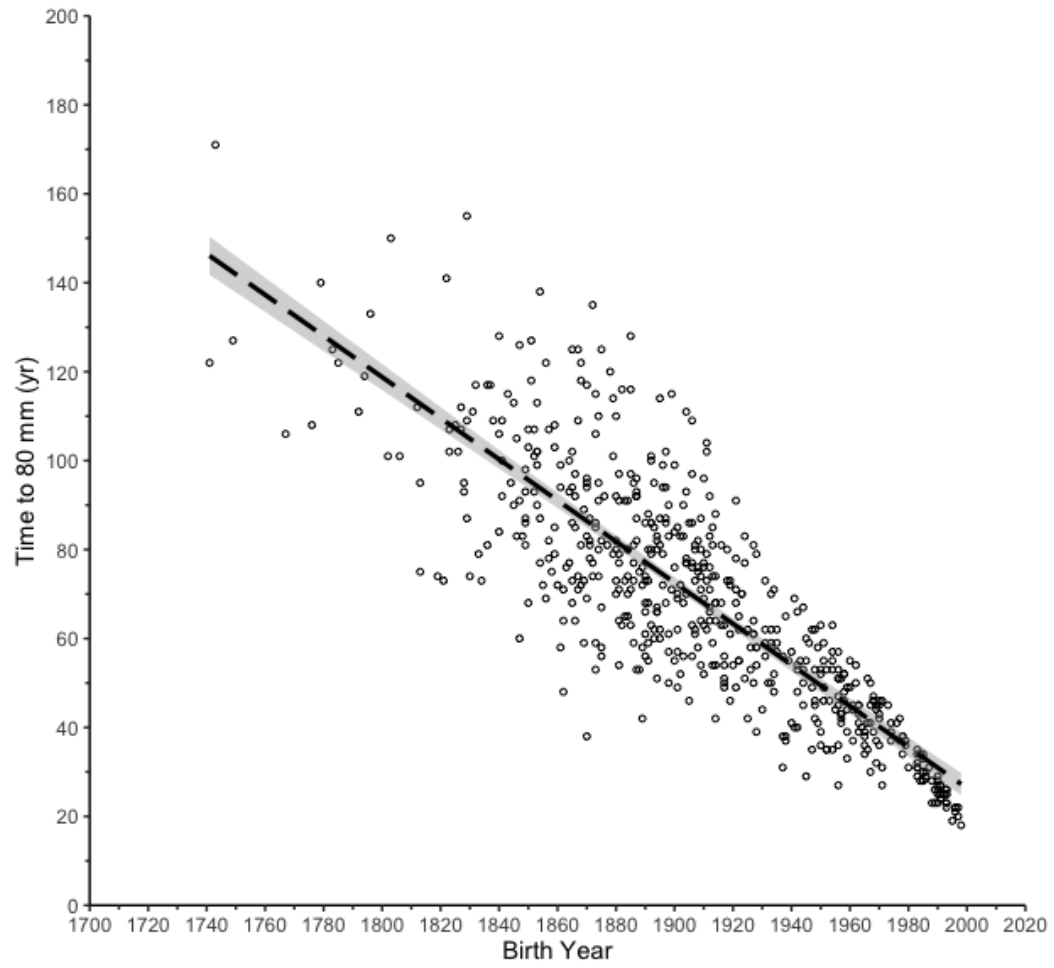


Figure 4.19 Southern New Jersey (NJ2) time to commercial size (80 mm). Dashed line = line of regression; equation: $950.94 - 0.46x$

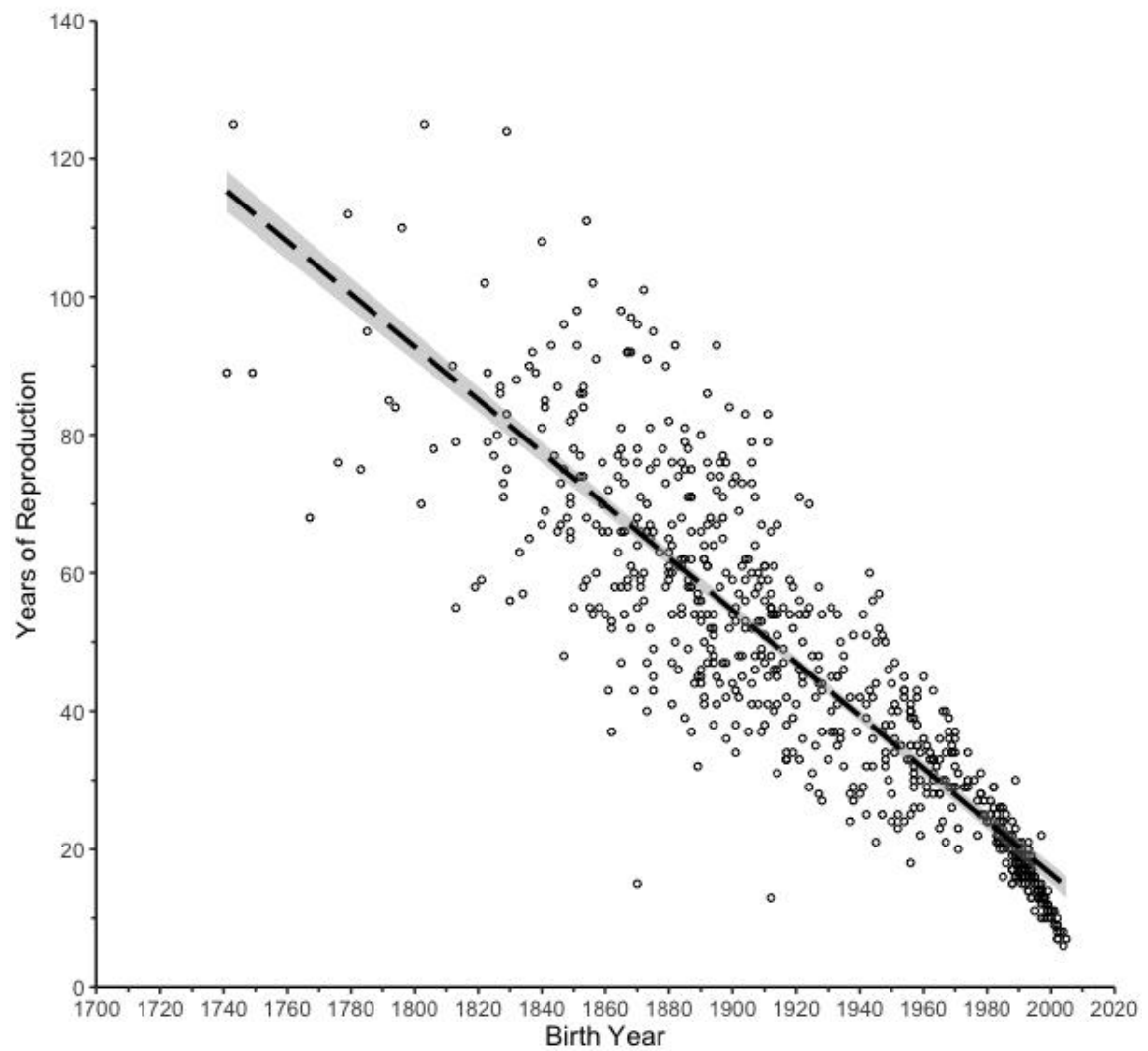


Figure 4.20 Southern New Jersey (NJ2) years of reproduction (time between 52 mm and 80 mm). Dashed line = line of regression; equation: $779.75 - 0.38x$

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CHAPTER V – CONCLUSIONS

5.1 *Arctica islandica* Sexual Dimorphism

The ocean quahog, *Arctica islandica*, is greatly influenced by the temperature in its environment. Temperature clearly impacts growth rates, causing them to vary from location to location and birth year to birth year. It is still unclear if maturity is a function of growth or age in *A. islandica*; many studies (Ropes et al. 1984, Rowell et al. 1990, Steingrímsson & Thórarinsdóttir 1995, Hemeon et al. 2022), including the results seen here, suggest that maturity is size dependent: *A. islandica* reach maturity at about 40-50% of maximum size, around 55 mm in length. As growth rates vary by location, ascertaining a given age at these sizes, and thus age at maturity, is uncertain without local information on age at length.

Females typically begin growing faster than males between the ages of 10-15 at size 56 mm, which is an average of 3 mm larger than males. In some sites and decadal groups, females outgrow males by age 5, though this is rare. Rarer still are the cases in which males grow at the same rate as females, which only occurred in the most southern site, NJ2, and in only two of the five decadal groups. The differences are most likely related to temperature conditions as they differ over time, but in the population as a whole, these rarer outcomes have limited import. In these studied populations, considering all cohorts present, female growth rates always exceed that of males so that the female-to-male ratio increases with increasing size. The reason behind this growth divergence is not protandry, nor is it differential mortality, but perhaps an adaptation to support the large egg sizes in females where larger size is essential to support fecundity. Cases where males grow as fast as females may be just as easily indicative of a constraint

on female growth as a facilitation on male growth. Perhaps these cases mark particularly limited food supplies or temperatures restricting female growth rates.

5.2 New Jersey Population Dynamics

Four sites are compared within the MAB and Georges Bank region with respect to the demographics of *A. islandica*. Age frequencies were dissimilar in important details between these sites. Recruitment is consistent over hundreds of years in that few cohorts are not represented, but year-to-year and decadal-length variations are readily apparent. One ALK may potentially be used to represent Long Island and NJ1, though the absence of recent (1980s-1990s) recruitment at the Long Island site is distinctive if not a result of differential sampling of rapidly growing recent recruits. NJ2 and Georges Bank are significantly dissimilar in age and length frequencies from each other and the other sites. Though some similarities in recruitment trends exist amongst these sites, likely caused by large-geographic-scale environmental conditions, each site clearly contains a distinct population with distinct demographics. Age-at-length relationships are significantly different. Females consistently outgrow males, but the differential between the sexes varies between sites. Sex ratios also vary, with differential survival of one sex during certain times in the past at least partially responsible. Mortality rates are more consistent west of Georges Bank, but the mortality rate for the Georges Bank population is distinctly higher. Based on these results, the use of separate age-length keys would seem necessary for each population and for each sex if detailed reconstruction of age frequency and other demographic traits is critical. *Arctica islandica* is an extremely long-lived species and the differentials observed amongst populations potentially accrue from the accumulation of 200+ years of recruitment, growth, and mortality that likely magnify

between-location differences in environmental history. *Arctica islandica* has received considerable attention for its potential to serve as a proxy source for long-term trends in bottom water temperatures (Butler et al. 2009; Reynolds et al. 2017). Demographic variability suggests that the species may also provide a long-term record of environmental conditions affecting a wide range of demographic processes within the boreal habitat of the northwestern Atlantic.

5.3 Growth Rates

Birth year is an important contributor to variation in length at age for ocean quahogs at both NJ1 and NJ1. The impressive influence of birth year is well instantiated by regressions of age-at-specified-length relative to birth year (Figures 4.14-4.19). Three elapsed time periods were used for comparison, the time between birth and maturity, the time between birth and recruitment into the fishery, and the elapsed time between the two representing the number of years of reproduction before exploitation. This latter is an important characteristic influencing the sensitivity of fishing on stock sustainability (Sissenwine and Shepard, 1987; Peterson, 2002). To determine consistent patterns in these three metrics at all four sites, three birth years were examined: 1800, 1900, and 2000. Year 1800 occurred in the last phase of the Little Ice Age (Cronin et al. 2010, Moore et al. 2017), whereas year 1900 occurred within a time period of consistent warming (Nixon et al. 2004). Year 2000 coincides with the initiation of a regime shift that produced rising temperatures throughout much of the Mid-Atlantic Bight (Pershing et al. 2015, Perretti et al. 2017, Powell et al. 2020).

Each site showed decreasing times to the three metric sizes as birthdate increased, though variation among the four sites was observed. *Arctica islandica* from Georges

Bank reached 52 mm at the youngest age out of all four sites, at age 18 for animals born in 1800, which decreased by a factor of 2 to age 9 for animals born in 2000. NJ1, NJ2, and Long Island, conversely, reached 52 mm by age 28 for animals born in 1800, which also decreased to age 9 for animals born in 2000, which is a decrease by a factor exceeding 3 (Table 2). In all four sites, animals born in 1900 fell almost exactly halfway in elapsed time between the 1800 and 2000 values. Time to commercial size (80 mm) followed the same trends at all four sites, with Georges Bank having the youngest age, 63 years, for animals born in 1800, whereas NJ1, NJ2, and Long Island have ages ranging from 114-119 years born in 1800. By 2000, ages to 80 mm had decreased to 26-28 years in NJ2 and NJ1, respectively, and 34-39 years in Long Island and Georges Bank, respectively. For years of reproduction, NJ2 had the most drastic decrease as birth year increased, with 93 years available for animals born in 1800 decreasing by a factor of 5 to 16 years available for animals born in 2000. Georges Bank displayed the least amount of difference, from 48 years for animals from 1800 to 41 in 2000. Long Island and NJ1 displayed very similar trends, at 79 and 72 years available for animals born in 1800, respectively, to 32 and 30 years available for animals born in 2000.

The influence of birth year on time to milestone size is much more subdued in Georges Bank (Hemeon et al. in prep.) compared to the southern sites. This is consistent with observations by Hemeon et al. (in prep.) that animals at the end of the Little Ice Age were growing fastest in this region, but that growth rates at the other three sites caught up in large measure over the following 200 years (see also Ropes and Pyoas, 1982; Lewis et al., 2001). These findings are also in agreement with Pace et al. (2018) who examined additional populations off southern New England and further south of Delmarva and,

noteworthy, are in agreement with growth rates from subfossil shells measured by LeClaire et al. (in prep.) recovered from the death assemblage off Delmarva. The latitudinal response revealed, in particular, by comparisons of elapsed time from birth to market size define a clear north-to-south gradient in increased growth rates since the end of the Little Ice Age throughout the Mid-Atlantic and Georges Bank region.

The trends in growth rate as a function of birthdate may be due to increasing bottom water temperatures over the last 200 years, though due to the lack of bottom water temperature data throughout the time period represented in the birthdates and ages reported here, one cannot be certain that temperature is the cause. Of particular note is the absence of information on the long-term dynamics of the Cold Pool. Nonetheless, many of the *A. islandica* in this study have lived throughout the entirety of global warming since the end of the Little Ice Age, very likely leaving a record of rising temperatures in the variations in growth rate over that time. Growth rates in most bivalves are strongly influenced by temperature, with growth rates rising over a wide temperature range, but then falling again as optimal temperatures are exceeded. The general pattern in Venerida, of which *A. islandica* is a member, is well described (Hofmann et al. 2006, Flye-Saint-Marie et al. 2007, Munroe et al. 2013), with growth primarily influenced by ever rising respirations rates with rising temperatures, but a parabolic response of filtration rates leading to temperature-dependent changes in scope for growth (Munroe et al. 2013, Beukema et al. 2017). *Arctica islandica* are sensitive to variations in temperature even to a greater degree than most Venerida (Begum et al., 2009, 2010). Thus, the presumption that the primary growth-influencing agent is rising bottom water temperatures has merit. One cannot exclude the influence of food supply, however, as food supply is an important

modulator of rates of growth (Schöne et al. 2005, Wanamaker et al. 2009, Mette et al. 2016, see also LeClaire et al. in prep.), but a centuries-long increase in food supply is unlikely to be an explanatory alternative (Boyce et al. 2010). What is unique for *A. islandica*, due to their long lifespan, is that the differential in growth rate with rising temperatures can be observed within members of the living community born across the centuries and that this record leaves a strong signal of the influence of climate change in the northwestern Atlantic. *Arctica islandica* growth rates have increased by factors of 2 to 3 or more since the end of the 1700s, an extraordinary physiological response to global warming.

APPENDIX A Growth Model Parameter Values for NJ1 and NJ2 Cohorts

Table A. 1 Northern New Jersey (NJ1) von Bertalanffy model parameter values for 20-year cohorts. SE = standard error.

Cohort	Parameter	Population		Female		Male	
		Estimate	SE	Estimate	SE	Estimate	SE
1720	L _{inf}	1.00E+02	1.02E+00	1.00E+02	1.02E+00	-	-
	K	7.64E-03	2.56E-04	7.61E-03	2.55E-04	-	-
	t ₀	-3.45E+01	1.74E+00	-3.56E+01	1.75E+00	-	-
1740	L _{inf}	1.10E+02	8.74E-01	1.11E+02	1.01E+00	1.09E+02	1.18E+00
	K	7.76E-03	2.04E-04	8.08E-03	2.49E-04	7.39E-03	2.56E-04
	t ₀	-3.55E+01	1.35E+00	-3.32E+01	1.55E+00	-3.81E+01	1.81E+00
1760	L _{inf}	1.04E+02	1.09E+00	1.04E+02	1.09E+00	-	-
	K	1.02E-02	4.24E-04	1.02E-02	4.24E-04	-	-
	t ₀	-3.15E+01	2.03E+00	-3.15E+01	2.03E+00	-	-
1780	L _{inf}	1.05E+02	8.98E-01	1.03E+02	1.01E+00	1.09E+02	1.75E+00
	K	9.67E-03	2.95E-04	9.90E-03	3.63E-04	9.15E-03	4.77E-04
	t ₀	-3.55E+01	1.42E+00	-3.75E+01	1.77E+00	-3.17E+01	2.22E+00
1800	L _{inf}	1.03E+02	5.89E-01	1.05E+02	6.96E-01	9.93E+01	1.04E+00
	K	1.19E-02	2.59E-04	1.15E-02	2.88E-04	1.30E-02	5.49E-04
	t ₀	-2.64E+01	8.73E-01	-2.77E+01	1.01E+00	-2.21E+01	1.60E+00
1820	L _{inf}	1.03E+02	6.23E-01	1.03E+00	6.36E-01	1.04E+02	1.28E+00
	K	1.29E-02	2.98E-04	1.41E-02	3.59E-04	1.12E-02	4.65E-04
	t ₀	-2.54E+01	8.56E-01	-2.35E+01	9.34E-01	-2.85E+01	1.55E+01
1840	L _{inf}	9.79E+01	2.89E-01	9.90E+01	3.03E-01	9.67E+01	5.77E-01
	K	1.83E-02	2.43E-04	1.90E-02	2.69E-04	1.58E-02	3.87E-04
	t ₀	-1.64E+01	3.98E-01	-1.56E+01	4.14E-01	-1.94E+01	7.81E-01
1860	L _{inf}	9.58E+01	3.71E-01	9.95E+01	4.29E-01	8.87E+01	4.59E-01
	K	2.01E-02	3.35E-04	1.99E-02	3.68E-04	2.14E-02	5.04E-04
	t ₀	-1.39E+01	4.33E-01	-1.34E+01	4.74E-01	-1.38E+01	6.06E-01
1880	L _{inf}	9.45E+01	3.15E-01	9.76E+01	3.31E-01	8.85E+01	4.80E-01
	K	2.45E-02	3.65E-04	2.43E-02	3.63E-04	2.44E-02	5.88E-04
	t ₀	-1.07E+01	3.24E-01	-1.09E+01	3.27E+01	-1.04E+01	5.23E-01
1900	L _{inf}	8.95E+01	2.67E-01	9.18E+01	2.73E-01	8.53E+01	3.91E-01
	K	3.82E-02	5.88E-04	4.10E-02	6.68E-04	3.24E-02	6.70E-04
	t ₀	-5.04E+00	2.34E-01	-4.65E+00	2.39E-01	-5.84E+00	3.31E-01
1920	L _{inf}	8.73E+01	1.25E-01	8.89E+01	1.46E-01	8.32E+01	1.84E-01
	K	5.01E-02	3.75E-04	5.06E-02	4.40E-04	5.02E-02	5.70E-04
	t ₀	-2.72E+00	8.48E-02	-2.71E+00	9.89E-02	-2.56E+00	1.26E-01
1940	L _{inf}	8.45E+01	1.06E-01	8.71E+01	1.52E-01	8.22E+01	1.27E-01
	K	5.87E-02	3.53E-04	5.98E-02	5.12E-04	5.85E-02	4.29E-04
	t ₀	-1.54E+00	5.34E-02	-1.47E+00	7.60E-02	-1.54E-01	6.48E-02
1960	L _{inf}	8.13E+01	2.80E-01	8.45E+01	5.32E-01	8.02E+01	3.22E-01
	K	7.64E-02	1.17E-03	7.39E-02	1.92E-03	7.66E-02	1.40E-03
	t ₀	-2.30E-01	9.53E-02	-1.67E-01	1.58E-01	-3.11E-01	1.16E-01
1980	L _{inf}	7.79E+01	3.12E-01	7.78E+01	4.84E-01	7.79E+01	4.04E-01
	K	1.42E-01	2.46E-03	1.41E-01	3.87E-03	1.42E-01	3.16E-03
	t ₀	5.18E-01	5.58E-02	3.96E-01	8.99E-02	5.89E-01	7.07E-02
2000	L _{inf}	7.85E+01	2.56E+00	-	-	7.85E+01	2.56E+00
	K	1.57E-01	1.50E-02	-	-	1.57E-01	1.50E-02
	t ₀	6.18E-01	1.80E-01	-	-	6.18E-01	1.80E-01

Table A.2 Southern New Jersey (NJ2) von Bertalanffy parameter values for 20-year cohorts. SE = standard error.

Cohort	Parameter	Population		Female		Male	
		Estimate	SE	Estimate	SE	Estimate	SE
1740	L _{inf}	1.14E+02	1.35E+00	1.19E+02	1.50E+00	1.12E+02	1.70E+00
	K	7.13E-03	2.61E-04	7.24E-03	2.69E-04	6.85E-03	3.19E-04
	t ₀	-3.90E+01	1.88E+00	-3.34E+01	1.76E+00	-4.34E+01	2.51E+00
1760	L _{inf}	1.14E+02	1.28E+00	1.17E+02	8.45E-01	1.02E+02	1.49E+00
	K	8.67E-03	3.12E-04	9.08E-03	2.06E-04	8.67E-03	4.58E-04
	t ₀	-2.98E+01	1.58E+00	-2.25E+01	9.13E-01	-4.54E+01	2.84E+00
1780	L _{inf}	1.11E+02	9.15E-01	1.17E+02	1.63E+00	1.04E+02	7.72E-01
	K	8.51E-03	2.19E-04	7.54E-03	2.99E-04	1.01E-02	2.69E-04
	t ₀	-3.48E+01	1.14E+00	-3.74E+01	1.73E+00	-3.11E+01	1.19E+00
1800	L _{inf}	1.01E+02	6.15E-01	1.01E+02	8.90E-01	1.01E+02	7.57E-01
	K	1.36E-02	3.60E-04	1.40E-02	5.47E-04	1.30E-02	4.13E-04
	t ₀	-2.42E+01	1.05E+00	-2.27E+01	1.51E+00	-2.63E+01	1.29E+00
1820	L _{inf}	1.01E+02	4.38E-01	1.03E+02	5.10E-01	9.48E+01	7.01E-01
	K	1.36E-02	2.37E-04	1.30E-02	2.49E-04	1.50E-02	4.85E-04
	t ₀	-2.43E+01	6.44E-01	-2.52E+01	7.10E-01	-2.22E+01	1.16E+00
1840	L _{inf}	1.00E+02	3.31E-01	1.06E+02	4.68E-01	9.43E+01	3.87E-01
	K	1.51E-02	1.95E-04	1.37E-02	2.21E-04	1.70E-02	2.98E-04
	t ₀	-2.11E+01	4.18E-01	-2.34E+01	5.35E-01	-1.83E+01	5.47E-01
1860	L _{inf}	9.73E+01	3.01E-01	9.99E+01	3.79E-01	9.28E+01	4.24E-01
	K	1.91E-02	2.52E-04	1.91E-02	3.04E-04	1.96E-02	3.98E-04
	t ₀	-1.56E+01	3.59E-01	-1.47E+01	4.25E-01	-1.66E+01	5.65E-01
1880	L _{inf}	1.02E+02	6.50E-01	1.00E+02	3.59E-01	9.10E+01	3.05E-01
	K	1.28E-02	3.33E-04	2.02E-02	2.73E-04	2.44E-02	3.75E-04
	t ₀	-2.50E+01	1.03E+00	-1.29E+01	3.08E-01	-1.18E+01	3.49E-01
1900	L _{inf}	9.34E+01	2.47E-01	9.79E+01	3.60E-01	8.82E+01	2.87E-01
	K	2.69E-02	2.91E-04	2.52E-02	3.58E-04	2.95E-02	4.26E-04
	t ₀	-8.56E+00	1.95E-01	-8.74E+00	2.58E-01	-8.08E+00	2.56E-01
1920	L _{inf}	8.51E+01	1.90E-01	8.71E+01	2.68E-01	8.66E+01	2.70E-01
	K	6.02E-02	6.58E-04	5.76E-02	8.42E-04	4.21E-02	6.10E-04
	t ₀	-1.93E+00	9.77E-02	-2.10E+00	1.34E-01	-3.58E+00	1.80E-01
1940	L _{inf}	8.51E+01	1.90E-01	8.71E+01	2.68E-01	8.28E+01	2.56E-01
	K	6.02E-02	6.58E-04	5.76E-02	8.42E-04	6.39E-02	1.00E-03
	t ₀	-1.93E+00	9.77E-02	-2.10E+00	1.34E-01	-1.69E+00	1.35E-01
1960	L _{inf}	8.11E+01	2.52E-01	8.26E+01	3.16E-01	7.89E+01	3.77E-01
	K	8.45E-02	1.28E-03	8.40E-02	1.61E-03	8.62E-02	1.96E-03
	t ₀	-8.64E-01	9.50E-02	-1.07E+00	1.23E-01	-5.50E-01	1.35E-01
1980	L _{inf}	7.73E+01	2.06E-01	7.80E+01	3.12E-01	7.69E+01	2.72E-01
	K	1.34E-01	1.43E-03	1.25E-01	1.94E-03	1.41E-01	2.06E-03
	t ₀	4.84E-01	3.43E-02	4.16E-01	5.11E-02	5.39E-01	4.56E-02
2000	L _{inf}	8.07E+01	1.36E+00	8.07E+01	1.33E+00	8.13E+01	3.47E+00
	K	1.45E-01	6.69E-03	1.43E-01	6.62E-03	1.46E-01	1.63E-02
	t ₀	6.39E-01	8.51E-02	6.22E-01	8.75E-02	6.62E-01	1.92E-01

Table A.3 Northern New Jersey (NJ1) Tanaka model parameters for 20-year cohorts. SE = standard error; - indicates cohorts with no animals.

Cohort	Parameter	Population		Female		Male	
		Estimate	SE	Estimate	SE	Estimate	SE
1720	a	4.36E-01	1.81E-01	3.12E-03	9.71E-03	-	-
	c	0.00E+00	1.67E+00	0.00E+00	9.46E-01	-	-
	d	7.59E+01	1.18E+00	7.33E+01	1.09E+00	-	-
	f	1.69E-03	1.23E-04	1.94E-03	1.03E-04	-	-
1740	a	2.88E-01	8.99E-02	2.65E-01	9.74E-02	2.37E-01	1.07E-01
	c	0.00E+00	1.29E+01	0.00E+00	2.63E+00	0.00E+00	2.81E+00
	d	8.44E+01	9.42E-01	8.73E+01	1.15E+00	8.15E+01	1.18E+00
	f	1.62E-03	8.39E-05	1.55E-03	9.28E-05	1.72E-03	1.15E-04
1760	a	6.11E-03	1.03E-02	6.11E-03	1.03E-02	-	-
	c	0.00E+00	8.18E-01	0.00E+00	8.18E-01	-	-
	d	8.21E+01	8.73E-01	8.20E+01	8.73E-01	-	-
	f	2.10E-03	9.45E-05	2.10E-03	9.45E-05	-	-
1780	a	1.43E-01	5.30E-02	4.92E-03	7.67E-03	1.17E-01	7.43E-02
	c	0.00E+00	1.61E+00	0.00E+00	6.00E-01	0.00E+00	2.53E+00
	d	8.37E+01	8.68E-01	7.99E+01	6.70E-01	8.53E+01	1.57E+00
	f	1.85E-03	9.45E-05	2.34E-03	8.58E-05	1.81E-03	1.46E-04
1800	a	1.04E-01	3.20E-02	1.02E-01	3.58E-02	7.28E-03	1.09E-02
	c	0.00E+00	1.09E+00	0.00E+00	1.22E+00	0.00E+00	8.62E-01
	d	8.58E+01	6.97E-01	8.61E+01	7.81E-01	8.34E+01	1.07E+00
	f	1.98E-03	1.47E-05	1.99E-03	8.45E-05	2.05E-03	1.04E-04
1820	a	8.39E-02	2.84E-02	6.41E-02	2.69E-02	1.33E-02	1.23E-02
	c	0.00E+00	1.04E+00	0.00E+00	1.06E+00	0.00E+00	8.48E-01
	d	8.70E+01	7.55E-01	8.80E+01	8.10E-01	8.53E+01	1.05E+00
	f	2.06E-03	8.27E-05	2.12E-03	9.18E-05	2.01E-03	9.58E-05
1840	a	3.65E-02	9.06E-03	2.62E-02	7.42E-03	4.42E-03	4.49E-03
	c	0.00E+00	4.37E-01	0.00E+00	3.95E-01	0.00E+00	3.83E-01
	d	8.81E+01	4.29E-01	8.93E+01	4.22E-01	8.34E+01	5.67E-01
	f	2.17E-03	4.67E-05	2.21E-03	4.63E-05	2.28E-03	6.20E-05
1860	a	3.91E-02	1.21E-02	2.66E-02	1.01E-02	7.60E-03	6.29E-03
	c	0.00E+00	5.89E-01	0.00E+00	5.70E-01	0.00E+00	4.20E-01
	d	8.81E+01	6.34E-01	9.15E+01	6.91E-01	7.81E+01	5.59E-01
	f	2.17E-03	6.61E-05	2.10E-03	6.61E-05	2.76E-03	8.51E-05
1880	a	1.78E-02	6.27E-03	1.21E-02	4.55E-03	9.82E-03	7.08E-03
	c	0.00E+00	3.92E-01	0.00E+00	3.21E-01	0.00E+00	4.89E-01
	d	8.97E+01	5.65E-01	9.23E+01	5.11E-01	8.23E+01	7.43E-01
	f	2.25E-03	5.78E-05	2.23E-03	5.03E-05	2.48E-03	8.92E-05
1900	a	1.58E-02	3.48E-03	1.65E-02	2.75E-03	1.29E-02	7.11E-03
	c	1.18E+00	3.13E-01	1.80E+00	2.87E-01	0.00E+00	4.87E-01
	d	8.92E+01	6.45E-01	9.15E+01	6.43E-01	8.51E+01	8.44E-01
	f	2.64E-03	7.83E-05	2.77E-03	8.33E-05	2.40E-03	8.96E-05
1920	a	2.12E-02	1.21E-03	2.10E-02	1.34E-03	2.28E-02	1.86E-03
	c	2.32E+00	1.31E-01	2.44E+00	1.50E-01	1.29E+00	1.86E-01
	d	9.01E+01	3.37E-01	9.20E+01	3.96E-01	8.48E+01	4.53E-01
	f	2.89E-03	4.45E-05	2.86E-03	5.10E-05	3.10E-03	6.82E-05

Table A.3 (continued)

1940	a	2.48E-02	9.43E-04	2.52E-02	1.24E-03	2.49E-02	1.16E-03
	c	2.62E+00	1.07E-01	2.96E+00	1.51E-01	2.46E+00	1.26E-01
	d	9.14E+01	3.29E-01	9.42E+01	4.82E-01	8.84E+01	3.75E-01
	f	2.82E-03	3.92E-05	2.80E-03	5.62E-05	2.91E-03	4.73E-05
1960	a	2.79E-02	1.59E-03	2.59E-02	2.75E-03	2.87E-02	1.94E-03
	c	3.98E+00	2.25E-01	3.49E+00	4.18E-01	4.06E+00	2.63E-01
	d	8.99E+00	9.46E-01	9.83E+01	1.94E+00	8.73+01	1.05E+00
	f	3.30E-03	1.34E-04	2.64E-03	1.83E-04	3.53E-03	1.69E-04
1980	a	9.50E-03	5.50E-04	9.40E-03	8.76E-04	9.53E-03	7.01E-04
	c	3.07E+00	1.32E-01	2.95E+00	2.07E-01	3.14E+00	1.69E-01
	d	9.23E+01	1.20E+00	9.17E+01	1.83E+00	9.26E+01	1.56E+00
	f	3.98E-03	1.90E-04	4.05E-03	3.02E-04	3.95E-05	2.44E-04
2000	a	1.17E-02	2.25E-03	-	-	1.17E-02	2.25E-03
	c	3.39E+00	5.99E-01	-	-	3.39E+00	5.99E-01
	d	1.04E+02	1.02E+01	-	-	1.03E+02	1.02E+01
	f	3.19E-03	9.71E-04	-	-	3.19E-03	9.71E-04

Table A.4 Southern New Jersey (NJ2) Tanaka model parameters for 20-year cohorts. SE = standard error.

Cohort	Parameter	Population		Female		Male	
		Estimate	SE	Estimate	SE	Estimate	SE
1740	a	1.97E-01	8.80E-02	3.35E-01	1.34E-01	2.03E-01	1.14E-01
	c	0.00E+00	2.58E+00	0.00E+00	3.69E+00	0.00E+00	3.10E+00
	d	8.57E+01	1.23E+00	9.38E+01	1.73E+00	8.18E+01	1.35E+00
	f	1.61E-03	1.02E-04	1.35E-03	1.06E-04	1.76E-03	1.36E-04
1760	a	2.41E-01	1.01E-01	3.73E-01	7.76E-02	3.68E-03	1.13E-02
	c	0.00E+00	2.97E+00	0.00E+00	2.41E+00	0.00E+00	8.72E-01
	d	9.18E+01	1.55E+00	1.04E+02	1.36E+00	7.50E+01	8.94E-01
	f	1.51E-03	1.11E-04	1.12E-03	5.61E-05	2.56E-03	1.39E-04
1780	a	1.62E-01	5.30E-02	2.19E-01	9.58E-02	2.11E-01	6.66E-02
	c	0.00E+00	1.58E+00	0.00E+00	2.73E+00	0.00E+00	1.82E+00
	d	1.48E+01	8.57E-01	8.71E+01	1.42E+00	8.44E+01	9.00E-01
	f	1.84E-03	8.60E-05	1.71E-03	1.26E-04	1.85E-03	9.34E-05
1800	a	4.56E-03	5.65E-03	7.73E-02	5.22E-02	4.53E-03	5.77E-03
	c	0.00E+00	4.76E-01	0.00E+00	1.92E+00	0.00E+00	4.76E-01
	d	8.48E+01	6.08E-01	8.65E+00	1.30E+00	8.38E+01	5.94E-01
	f	2.21E-03	6.72E-05	2.06E-03	1.47E-04	2.28E-03	6.97E-05
1820	a	9.24E-02	2.30E-02	5.91E-02	1.71E-02	7.56E-03	9.12E-03
	c	0.00E+00	8.17E-01	0.00E+00	7.15E-01	0.00E+00	6.16E-01
	d	8.62E+01	5.72E-01	8.77E+01	5.76E-01	7.87E+01	6.94E-01
	f	2.06E-03	6.31E-05	2.04E-03	6.00E-05	2.57E-03	1.01E-04
1840	a	6.96E-02	1.31E-02	4.35E-02	1.06E-02	6.16E-03	4.06E-03
	c	0.00E+00	5.20E-01	0.00E+00	5.01E-01	0.00E+00	3.04E-01
	d	8.73E+01	4.33E-01	8.99E+01	4.84E-01	8.11E+01	4.09E-01
	f	2.10E-03	4.66E-05	2.06E-03	4.84E-05	2.46E-03	5.17E-05
1860	a	3.26E-02	8.26E-03	2.65E-02	8.75E-03	5.32E-03	4.53E-03
	c	0.00E+00	4.22E-01	0.00E+00	4.85E-01	0.00E+00	3.43E-01
	d	8.85E+01	4.69E-01	9.07E+01	5.77E-01	8.17E+01	5.03E-01
	f	2.19E-03	4.95E-05	2.13E-03	5.74E-05	2.60E-03	6.77E-05
1880	a	9.01E-02	3.62E-02	2.86E-02	6.96E-03	6.89E-03	3.93E-03
	c	0.00E+00	1.27E+00	0.00E+00	4.05E-01	0.00E+00	2.92E-01
	d	8.62E+01	8.26E-01	9.36E+01	5.61E-01	8.42E+01	4.63E-01
	f	2.02E-03	9.12E-05	2.02E-03	4.79E-05	2.55E-03	5.78E-05
1900	a	2.07E-02	4.65E-03	2.55E-02	6.68E-03	2.44E-02	6.96E-03
	c	0.00E+00	2.99E-01	0.00E+00	4.35E-01	0.00E+00	4.11E-01
	d	9.19E+01	4.94E-01	9.74E+01	7.31E-01	8.81E+01	6.30E-01
	f	2.13E-03	4.37E-05	1.91E-03	5.32E-05	2.26E-03	6.24E-05
1920	a	1.70E-02	1.36E-03	1.54E-02	1.93E-03	1.75E-02	3.85E-03
	c	2.01E+00	1.65E-01	1.67E+00	2.33E-01	7.62E-01	3.22E-01
	d	9.22E+01	5.48E-01	9.59E+01	7.83E-01	9.14E+01	7.23E-01
	f	2.83E-03	6.44E-05	2.56E-03	7.71E-05	2.35E-03	6.89E-05
1940	a	1.70E-02	1.36E-03	1.54E-02	1.93E-03	1.89E-02	1.79E-03
	c	2.01E+00	1.65E-01	1.67E+00	2.33E-01	2.45E+00	2.20E-01
	d	9.22E+01	5.48E-01	9.59E+01	7.83E-01	8.78E+00	7.17E-01
	f	2.83E-03	6.44E-05	2.56E-03	7.71E-05	3.23E-03	1.06E-04
1960	a	1.21E-02	9.79E-04	1.09E-02	1.10E-03	1.42E-02	1.61E-03
	c	2.25E+00	1.60E-01	2.15E+00	1.86E-01	2.49E+00	2.55E-01
	d	9.06E+01	7.69E-01	9.19E+01	9.07E-01	8.79E+01	1.20E+00
	f	3.33E-03	1.07E-04	3.31E-03	1.25E-04	3.46E-03	1.79E-04

Table A.4 (continued)

1980	a	1.17E-02	3.91E-04	1.21E-02	6.31E-04	1.10E-02	5.06E-04
	c	3.18E+00	8.85E-02	2.80E+00	1.46E-01	3.47E+00	1.09E-01
	d	9.27E+01	7.94E-01	9.70E+01	1.28E+00	8.94E+01	9.91E-01
	f	3.77E-03	1.15E-04	3.17E-03	1.40E-04	4.38E-03	1.83E-04
2000	a	1.20E-02	1.13E-03	1.05E-02	1.43E-03	1.29E-02	2.58E-03
	c	2.74E+00	4.02E-01	2.08E+00	4.99E-01	3.87E+00	5.97E-01
	d	1.18E+02	6.74E+00	1.26E+02	7.70E+00	1.06E+02	1.20E+01
	f	2.17E-03	3.41E-04	1.82E-03	2.97E-04	3.12E-03	1.06E-03

Table A.5 Northern New Jersey (NJ1) modified Tanaka model parameter values for 20-year cohorts. SE = standard error.

Cohort	Parameter	Population		Female		Male	
		Estimate	SE	Estimate	SE	Estimate	SE
1720	a	2.74E-02	3.03E-02	9.99E-03	1.21E-02	-	-
	c	0.00E+00	1.05E+00	0.00E+00	6.56E-01	-	-
	d	6.14E+01	8.36E-01	5.94E+01	7.23E-01	-	-
	f	2.92E-03	1.58E-04	3.30E-03	1.57E-04	-	-
	g	8.54E-06	5.19E-07	9.71E-06	5.21E-07	-	-
1740	a	1.17E-02	1.07E-02	7.37E-03	9.71E-03	1.28E-01	4.09E-02
	c	0.00E+00	6.59E-01	0.00E+00	7.19E-01	0.00E+00	1.17E+00
	d	6.98E+01	8.60E-01	7.31E+01	1.10E+00	6.79E+01	7.98E-01
	f	2.66E-03	1.21E-04	2.43E-03	1.29E-04	2.68E-03	1.35E-04
	g	1.05E-05	5.74E-07	9.93E-06	7.19E-07	1.04E-05	4.62E-07
1760	a	3.31E-02	2.03E-02	3.31E-02	2.04E-02	-	-
	c	1.60E+00	1.14E+00	1.60E+00	1.14E+00	-	-
	d	6.77E+01	1.32E+01	6.77E+01	1.32E+00	-	-
	f	3.74E-03	3.47E-04	3.74E-03	3.47E-04	-	-
	g	1.41E-05	1.27E-06	1.40E-05	1.23E-06	-	-
1780	a	1.25E-02	1.09E-02	7.19E-03	1.04E-02	3.89E-02	2.42E-02
	c	3.47E-01	5.88E-01	2.89E-01	6.10E-01	1.28E+00	1.18E+00
	d	6.55E+01	7.19E-01	6.52E+01	7.72E-01	6.52E+01	1.35E+00
	f	4.06E-03	2.12E-04	4.35E-03	2.56E-04	3.82E-03	3.61E-04
	g	1.07E-05	9.06E-07	1.92E-05	1.02E-06	2.51E-05	1.63E-06
1800	a	2.48E-02	9.31E-03	2.14E-02	9.33E-03	4.55E-02	2.65E-02
	c	1.03E+01	5.37E-01	9.96E-01	5.61E-01	1.56E+00	1.35E+00
	d	6.92E+01	7.44E-01	6.92E+0	8.02E-01	6.88E+01	1.69E+00
	f	3.70E-03	1.77E-04	3.77E-03	1.97E-04	3.55E-03	3.84E-04
	g	1.34E-05	1.02E-06	2.45E-05	1.12E-06	2.01E-05	2.17E-06
1820	a	1.72E-02	6.73E-03	1.57E-02	6.93E-03	1.90E-02	1.32E-02
	c	1.09E+00	4.64E-01	1.09E+00	5.15E-01	9.91E-01	7.91E-01
	d	6.98E+01	7.77E-01	7.32E+01	9.26E-01	6.45E+01	1.17E+00
	f	3.97E-03	1.98E-04	3.70E-03	2.06E-04	4.42E-03	3.71E-04
	g	3.08E-05	1.38E-06	2.67E-05	1.57E-06	3.70E-05	2.24E-06
1840	a	2.41E-02	3.22E-03	2.50E-02	3.19E-03	2.47E-02	4.85E-03
	c	1.94E+00	2.59E-01	2.05E+00	2.64E-01	2.11E+00	3.72E-01
	d	7.38E+01	5.23E-01	7.62E+01	5.53E-01	6.70E+01	6.90E-01
	f	3.81E-03	1.16E-04	3.66E-03	1.14E-04	4.53E-03	2.13E-04
	g	3.01E-05	1.14E-06	2.96E-05	1.19E-06	3.63E-05	1.60E-06
1860	a	2.72E-02	4.25E-03	2.27E-02	5.90E-03	2.88E-02	4.05E-03
	c	2.17E+00	3.44E-01	1.34E+00	4.59E-01	2.92E+00	3.38E-01
	d	7.22E+01	7.50E-01	7.89E+01	1.02E+00	6.42E+01	7.07E-01
	f	4.00E-03	1.76E-04	3.17E-03	1.60E-04	5.44E-03	2.86E-04
	g	4.45E-05	2.11E-06	3.90E-05	2.46E-06	4.47E-05	2.48E-06
1880	a	1.97E-02	3.52E-03	1.74E-02	2.84E-03	2.70E-02	6.55E-03
	c	1.57E+00	3.13E-01	1.50E+00	2.71E-01	1.86E+00	5.06E-01
	d	7.75E+01	8.34E-01	8.05E+01	7.67E-01	7.04E+01	1.17E+00
	f	3.48E-03	1.45E-04	3.32E-03	1.21E-04	3.99E-03	2.65E-04
	g	4.68E-05	2.83E-06	5.06E-05	2.58E-06	4.39E-05	4.14E-06

Table A.5 (continued)

1900	a	2.43E-02	2.65E-03	2.08E-02	2.29E-03	3.31E-02	4.90E-03
	c	2.89E+00	3.11E-01	2.91E+00	3.02E-01	2.62E+00	4.42E-01
	d	8.07E+01	1.10E+00	8.53E+01	1.18E+00	7.27E+01	1.29E+00
	f	3.70E-03	1.96E-04	3.53E-03	1.89E-04	3.89E-03	2.60E-04
	g	4.30E-05	5.69E-06	3.28E-05	6.02E-06	6.01E-05	6.51E-06
1920	a	2.39E-02	1.02E-03	2.31E-02	1.17E-03	2.56E-02	1.56E-03
	c	3.21E+00	1.39E-01	3.16E+00	1.65E-01	3.13E+00	1.99E-01
	d	8.44E+01	6.31E-01	8.73E+01	7.68E-01	7.96E+01	8.55E-01
	f	3.59E-03	9.91E-05	3.40E-03	1.10E-04	3.82E-03	1.50E-04
	g	4.43E-05	4.77E-06	3.59E-05	5.59E-06	4.19E-05	6.80E-06
1940	a	2.69E-02	7.70E-04	2.62E-02	1.12E-03	2.75E-02	9.14E-04
	c	3.49E+00	1.12E-01	3.43E+00	1.72E-01	3.47E+00	1.27E-01
	d	8.48E+01	6.10E-01	9.05E+01	9.78E-01	8.11E+01	6.72E-01
	f	3.58E-03	8.98E-05	3.18E-03	1.17E-04	3.83E-03	1.12E-04
	g	7.47E-05	6.79E-06	4.07E-05	1.01E-05	8.60E-05	7.87E-06
1960	a	2.76E-02	1.55E-03	2.59E-02	2.42E-03	2.82E-02	1.89E-03
	c	4.21E+00	2.54E-01	4.03E+00	4.38E-01	4.38E+00	2.86E-01
	d	8.74E+01	1.97E+00	9.20E+01	3.65E+00	8.39E+01	2.14E+00
	f	3.61E-03	2.69E-04	3.21E-03	4.03E-04	4.02E-03	3.51E-04
	g	5.20E-05	3.78E-05	1.25E-04	7.01E-05	7.14E-05	4.24E-05
1980	a	3.05E-05	8.36E-04	4.22E-03	1.37E-03	7.47E-03	1.04E-03
	c	0.00E+00	1.32E+00	1.17E+00	4.09E-01	1.84E+00	3.48E-01
	d	3.44E+02	6.35E+01	1.06E+02	5.74E+00	1.11E+02	5.47E+00
	f	2.43E-04	8.21E-05	2.42E-03	3.56E-04	2.26E-03	2.96E-04
	g	0.00E+00	1.53E-03	0.00E+00	2.65E-04	0.00E+00	2.62E-04
2000	a	3.70E-04	6.82E-03	-	-	3.70E-04	6.82E-03
	c	0.00E+00	5.33E+01	-	-	0.00E+00	5.33E+00
	d	2.29E+02	2.04E+02	-	-	2.29E+02	2.05E+02
	f	5.41E-04	9.50E-04	-	-	5.41E-04	9.50E-04
	g	0.00E+00	1.66E-02	-	-	0.00E+00	1.66E-02

Table A.6 Southern New Jersey (NJ2) modified Tanaka model parameter values for 20-year cohorts. *SE* = standard error.

Cohort	Parameter	Population		Female		Male	
		Estimate	SE	Estimate	SE	Estimate	SE
1740	a	1.38E-02	1.77E-02	1.18E-01	3.92E-02	9.16E-03	1.81E-01
	c	0.00E+00	9.51E-01	0.00E+00	1.32E+00	0.00E+00	9.78E-01
	d	6.71E+01	1.09E+00	7.59E+01	1.11E+00	6.36E+01	1.08E+00
	f	3.02E-03	1.99E-04	2.20E-03	1.24E-04	3.46E-03	2.54E-04
	g	1.42E-05	7.97E-07	1.42E-05	6.02E-07	1.44E-05	8.52E-07
1760	a	1.28E-02	1.57E-02	8.66E-03	8.04E-03	7.38E-05	4.38E-03
	c	0.00E+00	1.02E+00	0.00E+00	7.63E-01	0.00E+00	2.51E-01
	d	7.54E+01	1.54E+00	8.76E+01	1.63E+00	6.10E+01	2.85E-01
	f	2.46E-03	1.80E-04	1.69E-03	9.20E-05	4.92E-03	1.23E-04
	g	1.64E-05	1.25E-06	1.27E-05	1.10E-06	1.73E-05	3.70E-07
1780	a	8.56E-03	8.41E-03	8.12E-03	1.22E-02	9.58E-03	8.13E-03
	c	0.00E+00	5.13E-01	0.00E+00	7.41E-01	0.00E+00	4.97E-01
	d	6.89E+01	7.35E-01	6.78E+01	1.05E+00	7.06E+01	7.20E-01
	f	3.14E-03	1.32E-04	3.22E-03	1.98E-04	3.02E-03	1.21E-04
	g	2.04E-05	7.79E-07	2.43E-05	1.13E-06	1.46E-05	7.42E-07
1800	a	7.33E-03	1.01E-02	8.28E-03	1.74E-02	1.98E-02	5.28E-03
	c	7.12E-02	6.45E-01	0.00E+00	1.12E+00	1.47E+00	3.76E-01
	d	7.34E+01	1.01E+00	7.57E+01	1.79E+00	6.97E+01	5.94E-01
	f	3.31E-03	1.93E-04	3.02E-03	2.90E-04	4.08E-03	1.63E-04
	g	1.67E-05	1.31E-06	1.39E-05	2.18E-06	2.12E-05	8.98E-07
1820	a	1.40E-02	5.60E-03	6.86E-03	5.78E-03	2.85E-02	1.08E-02
	c	6.82E-01	3.63E-01	1.46E-01	3.77E-01	1.79E+00	6.83E-01
	d	6.99E+00	5.87E-01	7.19E+01	6.28E-01	6.60E+01	1.02E+00
	f	3.84E-03	1.42E-04	3.56E-03	1.32E-04	4.52E-03	3.36E-04
	g	2.69E-05	1.01E-06	2.78E-05	1.03E-06	2.42E-05	1.94E-06
1840	a	2.06E-02	2.71E-03	1.60E-02	2.88E-03	2.56E-02	3.82E-03
	c	1.73E+00	2.11E-01	1.31E+00	2.28E-01	2.20E+00	2.92E-01
	d	6.92E+01	4.06E-01	7.15E+01	4.55E-01	6.66E+01	5.43E-01
	f	4.30E-03	1.13E-04	4.03E-03	1.13E-04	4.64E-03	1.74E-04
	g	3.99E-05	9.44E-07	4.48E-05	1.02E-06	3.39E-05	1.31E-06
1860	a	2.41E-02	2.89E-03	2.41E-02	3.89E-03	2.31E-02	3.73E-03
	c	2.17E+00	2.43E-01	1.98E+00	3.28E-01	2.31E+00	3.11E-01
	d	7.15E+01	5.37E-01	7.54E+01	7.48E-01	6.66E+01	6.55E-01
	f	4.27E-03	1.41E-04	3.72E-03	1.53E-04	5.16E-03	2.42E-04
	g	4.80E-05	1.56E-06	4.67E-05	1.98E-06	4.66E-05	2.17E-06
1880	a	1.22E-02	1.06E-02	1.60E-02	3.54E-03	2.53E-02	2.66E-03
	c	3.23E-01	6.45E-01	9.56E-01	2.90E-01	2.71E+00	2.46E-01
	d	7.23+01	9.73E-01	7.79E+01	7.47E-01	6.91E+01	6.14E-01
	f	3.35E-03	1.91E-04	3.26E-03	1.17E-04	4.94E-03	1.98E-04
	g	1.92E-05	1.27E-06	6.91E-05	2.43E-06	5.76E-05	2.53E-06
1900	a	2.15E-02	2.75E-03	1.49E-02	4.68E-03	2.47E-02	2.83E-03
	c	1.50E+00	2.43E-01	5.16E-01	3.93E-01	2.20E+00	2.61E-01
	d	7.78E+01	7.19E-01	8.46E+01	1.16E+00	7.21E+01	7.64E-01
	f	3.37E-03	1.13E-04	2.68E-03	1.24E-04	4.19E-03	1.75E-04
	g	7.78E-05	3.21E-06	7.63E-05	4.44E-06	7.23E-05	3.96E-06

Table A.6 (continued)

1920	a	1.92E-02	1.11E-03	1.81E-02	1.63E-03	2.67E-02	3.16E-03
	c	2.80E+00	1.74E-01	2.45E+00	2.53E-01	2.21E+00	3.44E-01
	d	8.59E+01	1.00E+00	8.98E+01	1.46E+00	8.40E+01	1.34E+00
	f	3.55E-03	1.44E-04	3.13E-03	1.70E-04	3.06E-03	1.65E-04
	g	7.74E-05	1.20E-05	6.88E-05	1.59E-05	4.67E-05	8.39E-06
1940	a	1.92E-02	1.11E-03	1.81E-02	1.63E-03	2.01E-02	1.51E-03
	c	2.80E+00	1.74E-02	2.45E+00	2.53E-01	3.08E+00	2.34E-01
	d	8.59E+00	1.00E+00	8.98E+01	1.46E+00	8.27E+01	1.35E+00
	f	3.55E-03	1.44E-04	3.13E-03	1.70E-04	3.94E-03	2.30E-04
	g	7.74E-05	1.20E-05	6.88E-05	1.59E-05	6.89E-05	1.75E-05
1960	a	4.59E-10	4.00E-12	1.67E-09	1.03E-12	1.44E-02	1.41E-03
	c	1.00E+02	4.98E-02	1.37E+02	8.14E-02	2.86E+00	2.74E-01
	d	4.92E+03	1.40E+00	4.19E+03	1.53E+00	8.35E_01	2.24E+00
	f	2.82E-05	1.51E-08	3.66E-05	1.95E-08	4.06E-03	3.68E-04
	g	0.00E+00	9.27E-05	0.00E+00	6.05E-05	1.13E-04	5.43E-05
1980	a	9.09E-03	4.51E-04	1.09E-02	1.30E-03	9.07E-03	6.24E-04
	c	2.15E+00	1.39E-01	1.58E+00	3.52E-01	2.19E+00	1.93E-01
	d	1.02E+02	2.08E+00	1.17E+02	4.84E+00	1.02E+02	2.90E+00
	f	2.75E-03	1.57E-04	1.88E-03	1.98E-04	2.79E-03	2.23E-04
	g	0.00E+00	1.11E-04	0.00E+00	1.95E-05	0.00E+00	1.54E-04
2000	a	4.86E-04	3.44E-03	1.32E-04	3.19E-03	2.81E-03	1.07E-02
	c	0.00E+00	2.23E+00	0.00E+00	3.65E+00	0.00E+00	7.83E+00
	d	2.06E+02	7.60E+01	2.82E+02	1.82E+02	2.50E+02	2.87E+02
	f	6.48E-04	4.78E-04	3.81E-04	4.66E-04	4.62E-04	1.04E-03
	g	0.00E+00	6.53E-03	0.00E+00	1.42E-02	0.00E+00	2.02E-02