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ORIGINAL PAPER

Examination of spatial heterogeneity in population age frequency and recruitment in the ocean quahog (*Arctica islandica Linnaeus 1767*)

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Abstract

The ocean quahog, *Arctica islandica*, is a commercially important species on the northwestern Atlantic continental shelf. This species can live over 200 years with ages varying widely per 5-mm size class (shell length), making study of age-related demographics difficult. To determine how the demography of this species differs across its range, including age frequencies, age-at-length relationships, and sex ratios, ocean quahogs from multiple sites distributed from the Mid-Atlantic Bight to Georges Bank were studied. The age and length frequencies from two populations collected in 2019 from New Jersey, north and south of Hudson Canyon (39.840556 N, 72.821667 W and 39.33 N, 73.545 W, respectively), were analyzed and compared to two other populations from Long Island (40.09658 N, 73.01057 W) and Georges Bank (40.72767 N, 67.79850 W), previously collected in 2015 and 2017. 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, potentially caused by differential survival of one sex during certain times in the past. 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.

Keywords Ocean quahog · *Arctica islandica* · Mid-Atlantic Bight · Age frequency · Recruitment

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).

The ocean quahog lay down annual growth lines, termed annuli, in both the shell and hinge plate which can be counted to determine age (Jones et al. 1980; Thompson et al. 1980; Murawski et al. 1982; Ropes et al. 1984b). The lifespan of *Arctica islandica* often exceeds 200 years of age, with the oldest documented *A. islandica* aged at 507 years old (Butler et al. 2013). Shell length can exceed sizes of 120 mm, but age can vary greatly at a given size (Pace et al. 2017a, b; Hemeon et al. 2021a), which, with such a long lifespan, limits 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

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of 15–16 °C—increases of 1 °C beyond 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. (2021a). 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. 2021a, 2023). New Jersey was chosen due to its southern location in the *A. islandica* current range and decreased fishery landings in the 1990s. Previously, between 1980 and 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 in response to declining biomass farther south (NEFSC 2017). Previous studies on New Jersey *A. islandica* (Pace et al. 2017a, 2018) indicated larger, gender-specific sample sizes were needed to establish a more accurate age–length relationship (Hemeon et al. 2021a; 2021b). Results presented for these two sites were compared to the equivalent analyses for populations from Georges Bank and Long Island to determine how *A. islandica* population demographics vary across its U.S. range (Hemeon et al. 2021a, 2023).

Comparisons of these four populations can provide additional information on recruitment dynamics 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 better estimates of the *A. islandica* stock recovery time frame if overfishing ever occurs (Hemeon et al. 2021a).

Arctica islandica males and females have observed growth differentials, with females reaching larger sizes than males (Ropes et al. 1984a; Fritz 1991; Thórarinsdóttir and Steingrímsson 2000; Hemeon et al. 2021a, 2023). Sexual dimorphism is rare in bivalves yet is remarkably apparent in *A. islandica*. Due to the influence that size differentials may have on length- or age-based models, separate age–length keys 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 evaluate the potential influence of sexual dimorphism.

The objectives of this study are 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 are examined to determine recruitment patterns and whether they differ across the MAB and Georges Bank. Males and females from each population are also analyzed to determine whether size-based sexual dimorphism leads to variations in age or length frequencies that may warrant separate, sex-based keys for each population.

Materials and methods

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 39.33 N, 73.545 W by the *F/V John N*. These sites are located north and south of the Hudson Canyon on the Mid-Atlantic continental shelf at 60.0 m and 62.5 m depths, respectively. 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 highly selective for sizes > 80 mm shell length (SL), so this study predominantly focused on animals that have obtained market size and are relevant to the fishery. Animals < 80 SL 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* (Fig. 1). Depths for these locations are 72.5 m at Georges Bank and 47.5 m at Long Island.

Sample preparation

All animals were measured for shell length, shucked, and sexed by gonadal smear slide. Shells were cleaned in a bleach solution, cross-sectioned to expose the hinge plate in the umbo region of the valve using a tile saw, sanded, 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

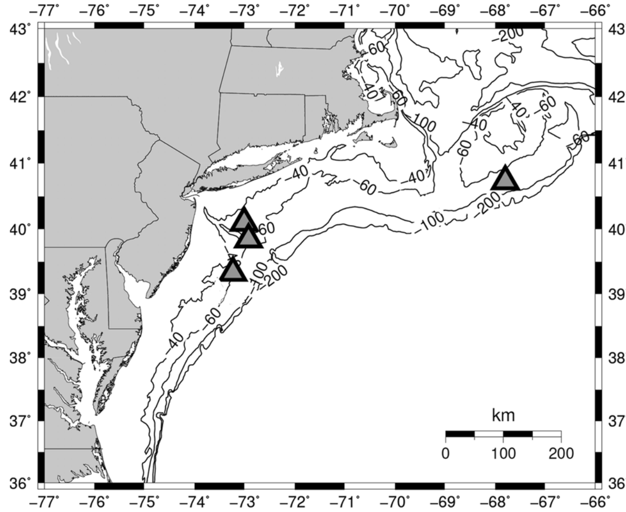


Fig. 1 Locations of each of the four sampling sites. From north to south, they are Georges Bank (GB), Long Island (LI), New Jersey north (NJ1), and New Jersey south (NJ2)

all animals aged for underrepresented size classes (< 80 mm SL and > 105 mm SL). Some animals were omitted from analyses due to poor image quality and, therefore, highly uncertain ages, which reduced the number of shells aged to 756 from NJ2 and 714 from NJ1: these were subsequently used for age–length key construction. 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, 2023).

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 valves from southern locations, 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 markers in animals from these populations (Hemeon et al. 2023); thus, 30% subsamples were used instead. Subannual markers may occur during periods of environmental disturbance or change, such as hurricanes or warmer temperatures leading to rapid growth in a calendar year, as a consequence of spawning, and as a product of the diel cycle. These subannual markers have received considerable attention in *A. islandica* and other bivalves (Weidman et al. 1994; Goodwin et al. 2001; Schöne et al. 2002, 2005) and can normally be recognized by their lighter appearance and failure to extend to both lateral edges of the hinge plate like annual markers do. Age-reader ages were compared and evaluated 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, one reader aged the remainder of each population.

Length sample

The *A. islandica* collected for ageing at NJ1 and NJ2 were used to create a length frequency for each site. At Georges Bank, 3,159 animals were measured to create the length frequency (Hemeon et al. 2021a), while the length of 2,905 animals were used to generate the length frequency for Long Island (Hemeon et al. 2023).

Age–length keys

Age–length keys (ALKs) describe the probability of a potential 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, 2023).

Age–frequency distributions

To analyze potential 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 frequency at 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 are 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.

The age frequency data are heavily left-skewed in part due to the lack of small and young animals, potentially due to variation in recent recruitment, but more likely due to dredge selectivity. More important, however, is the long tail of very old cohorts represented by none to a few old animals in each cohort, as would be anticipated by cohorts exposed to many years of mortality. This long tail can have undue influence on the statistical analysis, when the numbers present are too few to stabilize detailed comparisons between older cohorts. To mitigate the influence of low to zero numbers in the left tail of the age frequency distribution, adjacent ages were combined into larger age bins whenever the sequential sum fell below the median value of the original distribution (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 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. Details of this procedure are provided by Hemeon et al. (2021a).

Longevity and mortality

Longevity is defined as the expected lifespan of the oldest animal from a cohort, while the mortality rate is the probability of death in a given calendar year. Longevity and mortality were calculated using the regression of the natural log of the descending left tails of the age frequency for each site (Ricker 1975; Ridgway et al. 2012; R Core Team 2018; Hemeon et al. 2021a, 2023). Note that throughout the age frequency is described with the oldest age to the left on the x axis consistent with the earliest birth date. Data 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, as these age classes represented the descending left tails of the age distributions.

Sex ratios and 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 sex ratios in *A. islandica*, animals for each population were divided by sex within their respective 5-mm SL size class; for example, animals between 60–64 mm were compiled into the 60 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).

Results

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 111.0 mm in NJ1 and 114.7 mm shell length (SL) 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 62.7 mm in NJ1, and 74.6 mm SL in NJ2 (Figs. 2 and 3).

At NJ1, females ages ranged from 23–286 (median = 88), while male ages ranged from 17 to 279 years (median = 73). Mean values for both sexes were larger than median ages, with female ages averaging at 104 years and male ages averaging at 84 years. At NJ2, female ages ranged from 15 to 295 years (median = 113), and male ages ranged 14–278 (median = 100). Opposite of NJ1, the mean ages were lower than median ages, with a mean female age of 105 years and a mean male age of 96 years. Lower mean ages indicate that the distribution of NJ2 ages included proportionately more younger animals than NJ1 (Figs. 4 and 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 size class with the most animals is the 85-mm size class, with 162 animals total from NJ1 and 124 animals total from NJ2. When examined by 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 (Fig. 6). For NJ2, the largest 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 (Fig. 7).

Age–frequency distributions

NJ1 female age frequencies were offset to older ages than male age frequencies (Fig. 4). Correspondingly, KS tests for both the unmodified and the median bin modified data sets demonstrated that the two age frequencies are significant (Table 1). This result was also true for the AD and Runs tests.

NJ2 male and female age frequencies are offset, but not to the same degree as in NJ1 (Fig. 5). KS test results

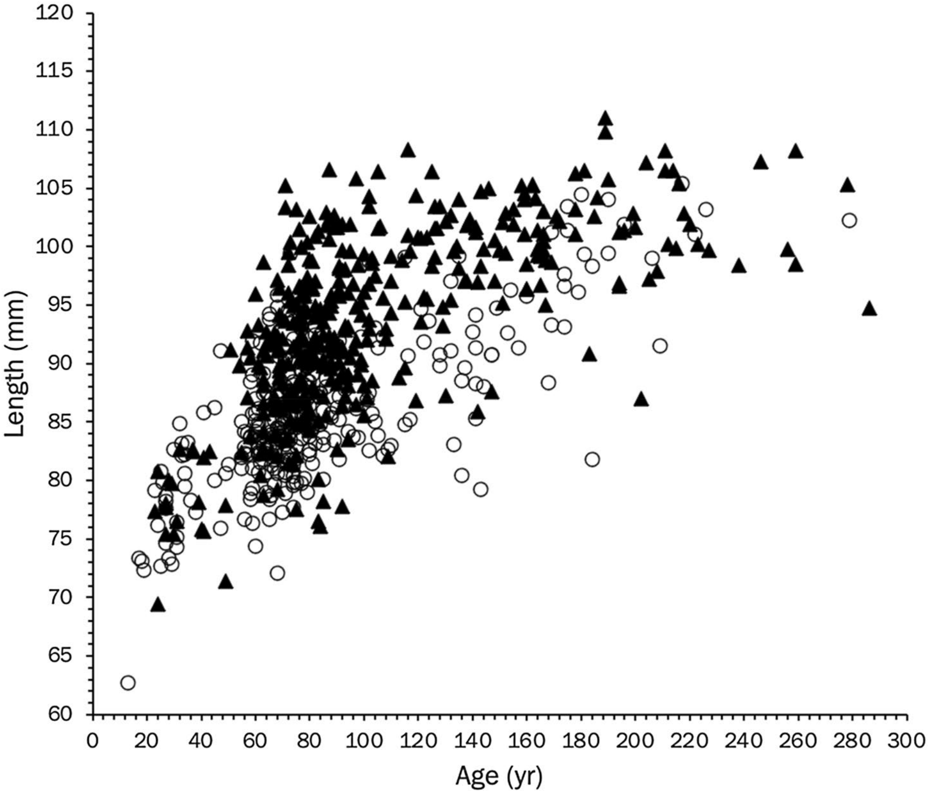


Fig. 2 Age–length distribution for the northern New Jersey site, NJ1. Solid triangles represent females; hollow circles represent males. N = 714

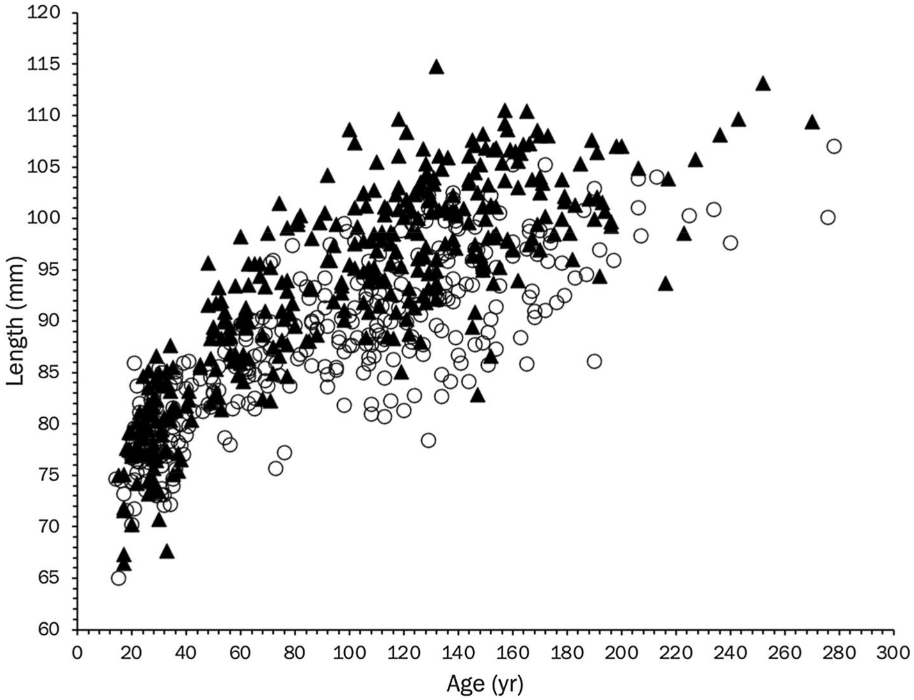


Fig. 3 Age–length distribution for the southern New Jersey site, NJ2. Solid triangles represent females; hollow circles represent males. N = 756

were significant for the unmodified data file but not for the median bin modification, suggesting an increased influence of the extended old-age tail of the distribution (Table 1). Contrarily, but from an equivalent cause, AD test results were significant for the median bin modification but not for the unmodified data file. Not surprisingly, runs test results were not significant for the unmodified data file but were significant for the median bin modification.

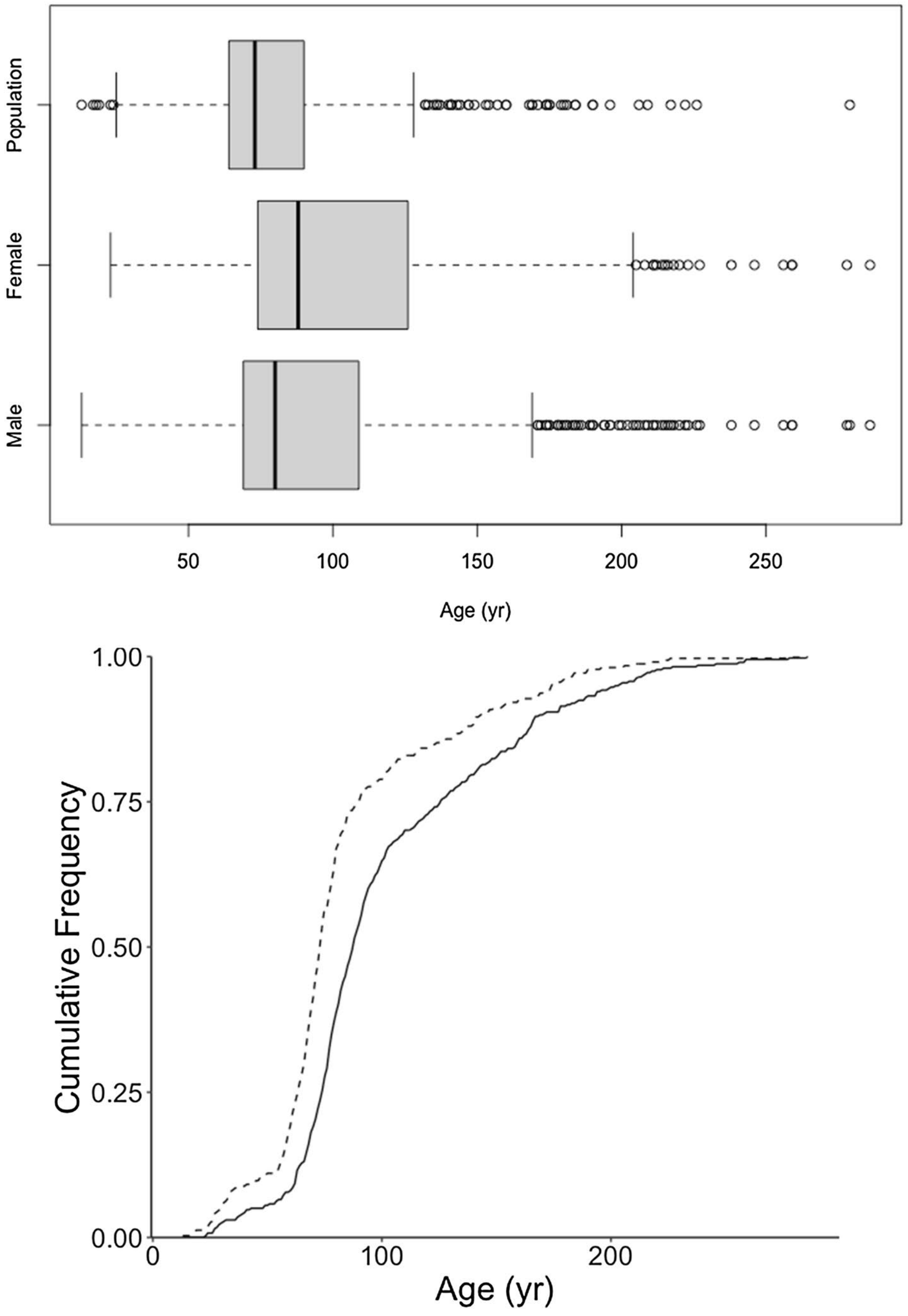


Fig. 4 Cumulative age distributions for male (dashed line) and female (solid line) *Arctica islandica* for northern New Jersey (NJ1) and box and whisker plots of population, females, and males age frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers

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–length-key data from one site when applied to a length frequency from another site produced age frequencies that were different from the 'True' age frequency for the second sites (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 significantly different for the majority of the simulations but indicated that males were similar when NJ1 was the 'True' data set, and the simulated age–length key was from NJ2. However, when NJ2 was the 'True' data set and NJ1 was the simulated age–length key, AD tests identified significant differences 82–100% of the time depending on alpha level. KS results reveal that the simulated age frequencies between populations, males, and females were different 100% of the time in the unmodified data but were much less frequently significantly different once the data sets were modified to limit the influence of poorly represented age classes. These results indicated that both the centers and

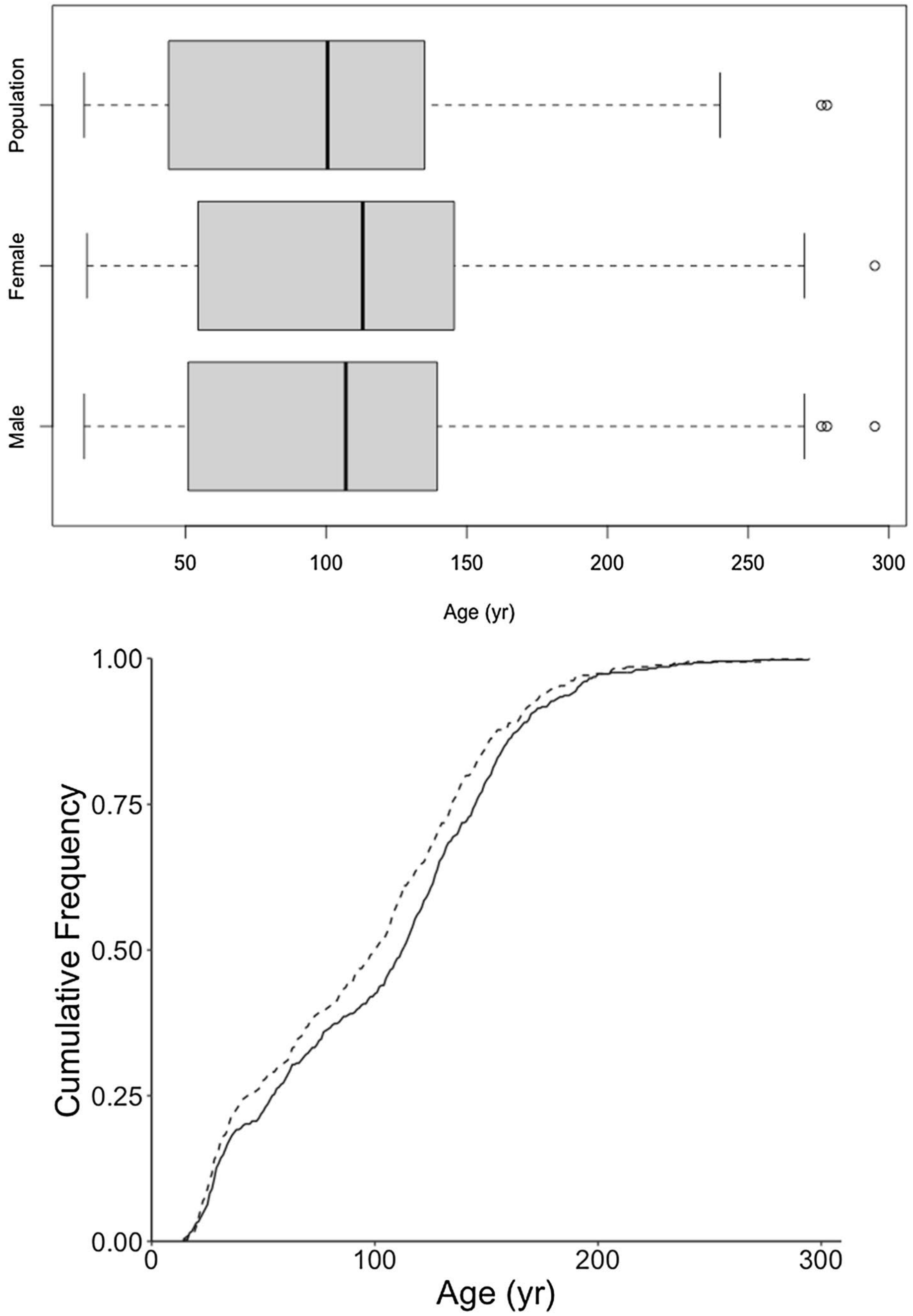


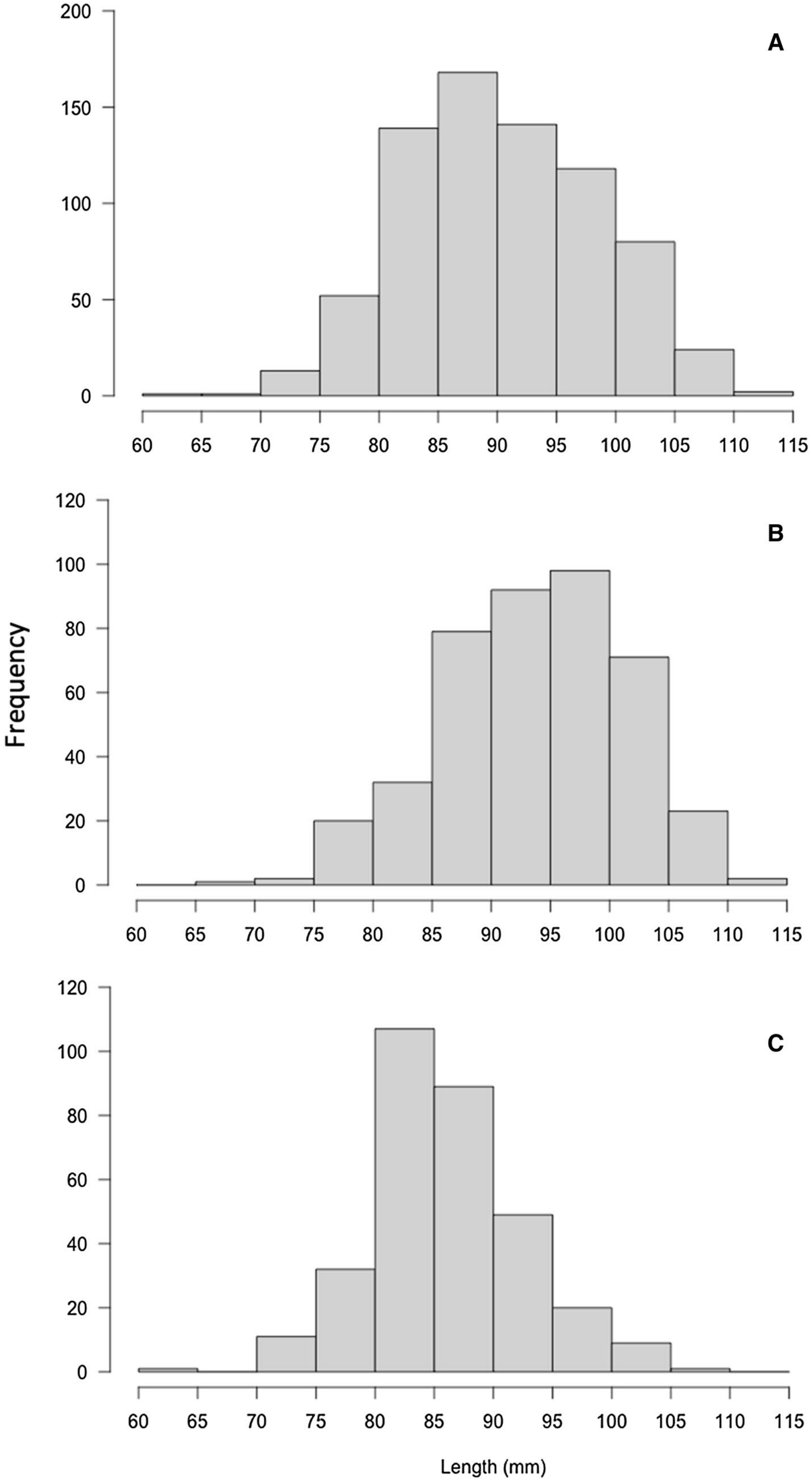
Fig. 5 Cumulative age distributions for male (dashed line) and female (solid line) *Arctica islandica* for southern New Jersey (NJ2) and box and whisker plots of population, females, and males age frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers

the tails of each populations' distributions were 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 were 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 differences among the MAB populations. Age frequencies from Georges Bank populations when compared to those from 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 data set.

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 data set 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

Fig. 6 NJ1 Population (**a**), female (**b**), and male (**c**) length frequencies. Note the y axis varies between plots



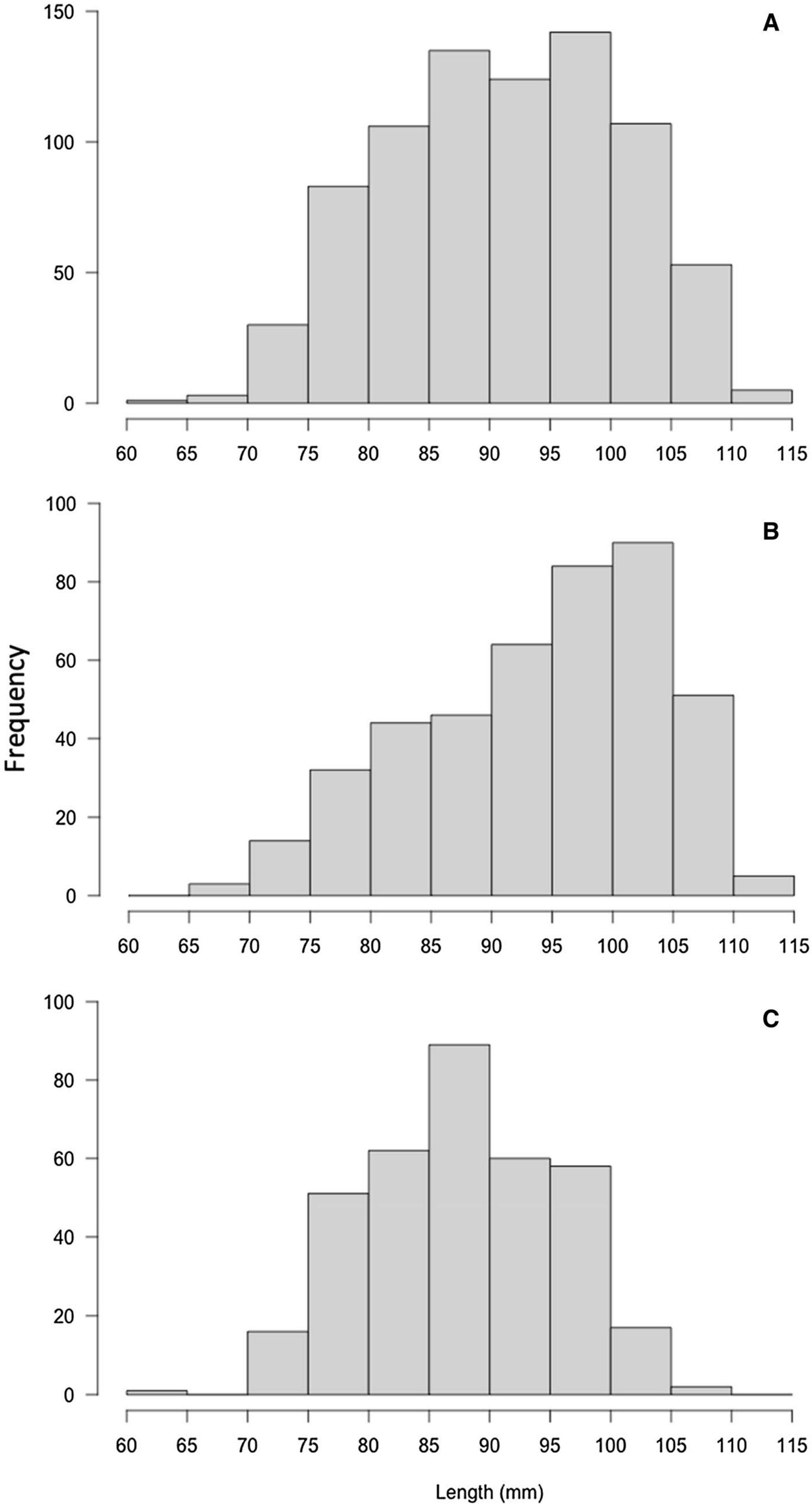


Fig. 7 NJ2 population (**a**), female (**b**), and male (**c**) length frequencies. Note the y axis scale varies between plots

Table 1 Results of statistical analyses for various comparisons between age and length distributions from New Jersey north (NJ1) and New Jersey south (NJ2)

Site	Data set	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	*

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

median bin data sets, 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 to a larger extent in Georges Bank than that of Long Island, indicating larger amounts of young or old animals. In contrast, the comparison between NJ2 and Long Island showed consistent significant differences, similar to the comparison between the NJ2 and Georges Bank populations.

Length frequency

For both New Jersey sites, female sizes were offset to sizes larger than those of males (Figs. 8 and 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). Anderson–Darling 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 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 data sets. As with NJ1, runs test results were significantly different for both modified and unmodified data sets. Thus, a clear discrepancy in the growth rate exists between male and female *A. islandica*.

Longevity and mortality

For the NJ1 population, the total 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; for females longevity is 300 years and males 273 years. For NJ2, the total 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; for females it is 277 years and 265 years for males.

Table 2 Results of Monte Carlo simulations

Population	True	ALK	α 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 Pop	NJ2 Pop	0.05	1.00	1.00	0.98	0.76	1.00	1.00
			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 Pop	NJ1 Pop	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

ALK marks the data set from which the simulated age–length key was derived and then applied to the 'True' length frequency. 'True' is the age frequency to which the simulated age frequencies were compared. Results are the proportion of simulated data sets yielding a significant difference for the raw data sets (unmodified) and for data sets 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

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 (Fig. 10). At NJ2, a substantial recruitment event occurred in the mid-late 1800s, after which recruitment decreased until the 1980s–1990 s when another large recruitment event occurred (Fig. 11). In both cases, most cohorts were represented in the 1800s and 1900s, with at least one animal recruited per year during these centuries, suggesting routine recruitment at both sites, with observable year-to-year and decade-to-decade variations in scale. In addition, NJ1 displayed low but consistent recruitment throughout the 1800s and early 1900s with a distinct peak in the 1930s–1950s. Recruitment picked up at NJ2 and increased to a high proportion of animals born in the mid-late 1800s, but the age frequency suggests a lower recruitment rate in the 1900s until the 1980s, assuming similar mortality rates over this time period. Both sites experienced a noticeable decrease in recruitment in the 1960s–1970s (Figs. 10a and 11a). This decrease in recruitment was consistent with the decline in temperatures during these decades (Nixon et al. 2004). The higher recruitment in the 1930s–1950s was consistent with higher temperatures during that time (Nixon et al. 2004).

Sex ratios and 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 and 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 (Figs. 8 and 9).

Table 3 Results of statistical analyses for various comparisons between age distributions of northern (NJ1) and southern (NJ2) New Jersey to Georges Bank (Hemeon et al. 2021a)

Site	Data set	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	*	*

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

Discussion

Cold pool dynamics

The Cold Pool is a 20–60 m deep body of uniformly cooler bottom water that forms along the outer continental shelf in the spring (April) annually along the MAB 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 (Franz and Merrill 1980; Engle and Summers 1999; Hale 2010). Thus, the Cold Pool permits the range extension of *A. islandica* as far south as Cape Hatteras, NC. The Cold Pool dissipates in the fall (October–November) when the thermocline breaks down. Recent interannual variability in the duration and size 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*.

Direct comparison of both New Jersey sites

Age–length key analysis

Northern (NJ1) and southern (NJ2) New Jersey sites are significantly different for the majority of tests and data set modifications, at $\alpha = 0.01$. Though the sites are relatively close geographically, they have a major geographical barrier between them—the Hudson Canyon. The Hudson Canyon is the largest U.S. 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 with relatively little connectivity for larval

Table 4 Results of statistical analyses for various comparisons between age distributions of northern (NJ1) and southern (NJ2) New Jersey to Long Island (Hemeon et al. 2023)

Site	Data set	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	*	*

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

dispersion, which would explain the differences in age frequencies and recruitment events between the two sites.

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 the year 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 twentieth century. The increase in recruitment at NJ2 late in the twentieth 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.

Sex ratios and 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 significantly different numbers of females and males: 85 mm, 100 mm, and 105 mm, suggesting that males and females are more evenly spread across size classes at NJ2 compared to NJ1. This even spread in NJ2 is consistent with Sower et al. (2022) who observed fewer size differences between males and females as a result of higher growth rates for males at NJ2, and thus fewer size

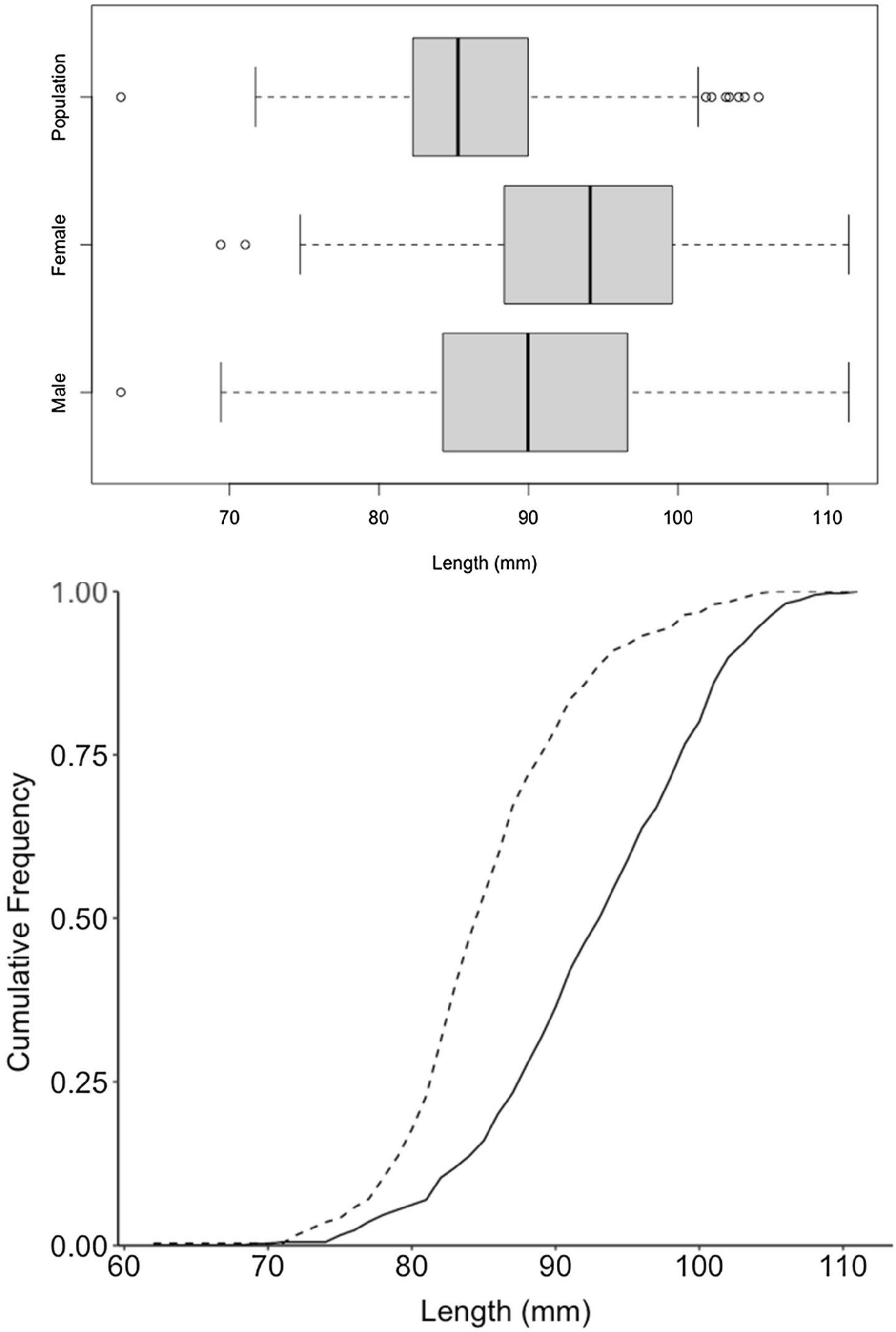


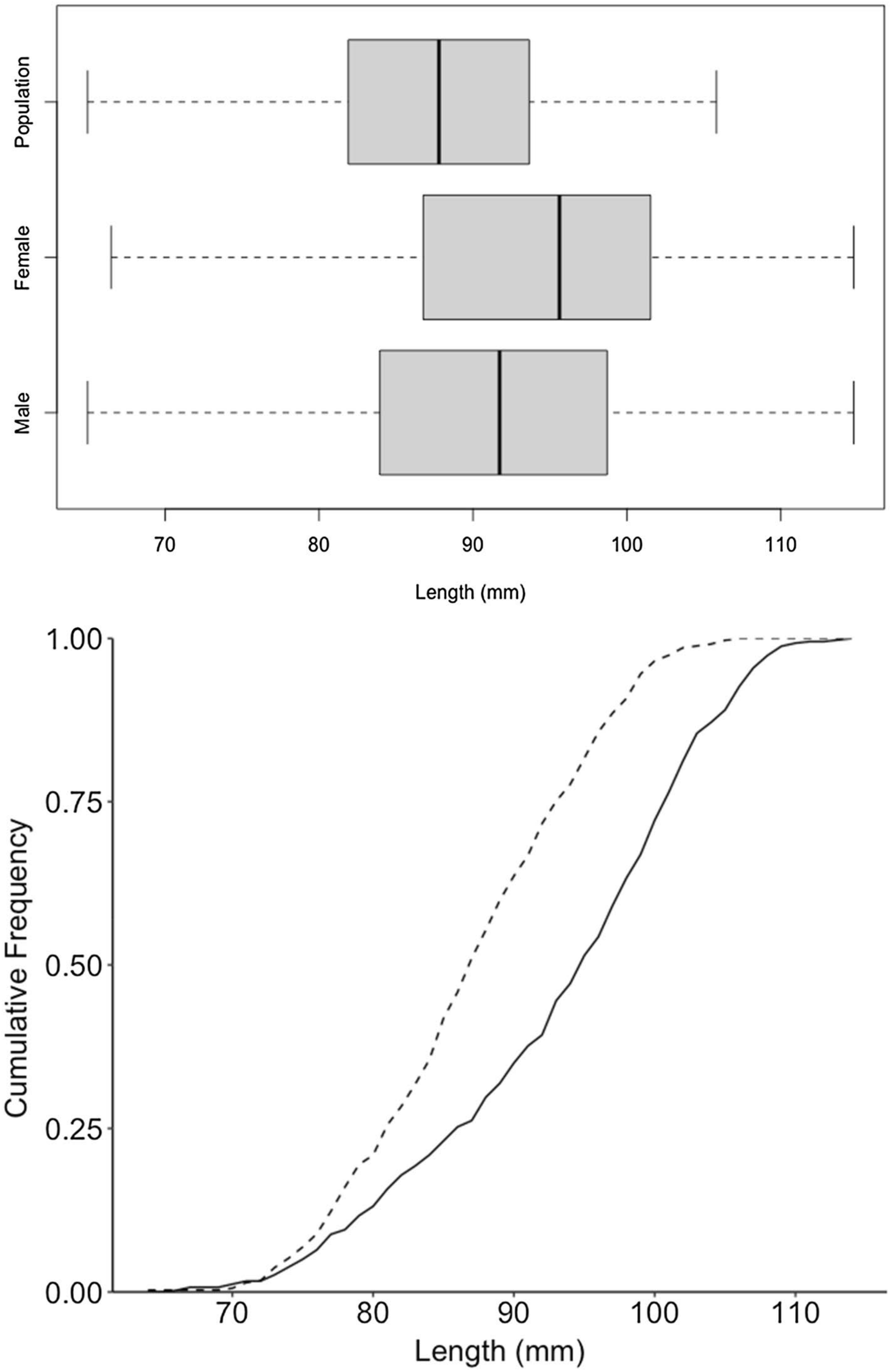
Fig. 8 Cumulative length distributions for male (dashed line) and female (solid line) *Arctica islandica* for northern New Jersey (NJ1) and box and whisker plots of population, female, and male length frequencies. Central line indicates median (50th percentile), 25th and 75th percentiles are represented by the boxes (interquartile range), whiskers represent the minimum and maximum, and hollow circles represent outliers

classes, where males and females diverge in representation. Not surprisingly, the two sites also differ as to 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 acts as a barrier to larval transport (Zhang et al. 2016; Chen et al. 2018; Chen and Curchitser 2020). NJ2 experiences increased variation in bottom water temperatures compared to NJ1 (i.e., warmer temperatures for either longer periods of time or during traditionally cooler times of the year) and particularly during the fall thermocline breakdown (López et al. 2020). Ocean quahog growth rates are very sensitive to temperature (Pace et al. 2018) and this tendency towards warmer temperatures at NJ2 potentially can influence growth, leading overall to larger animals at the same age.

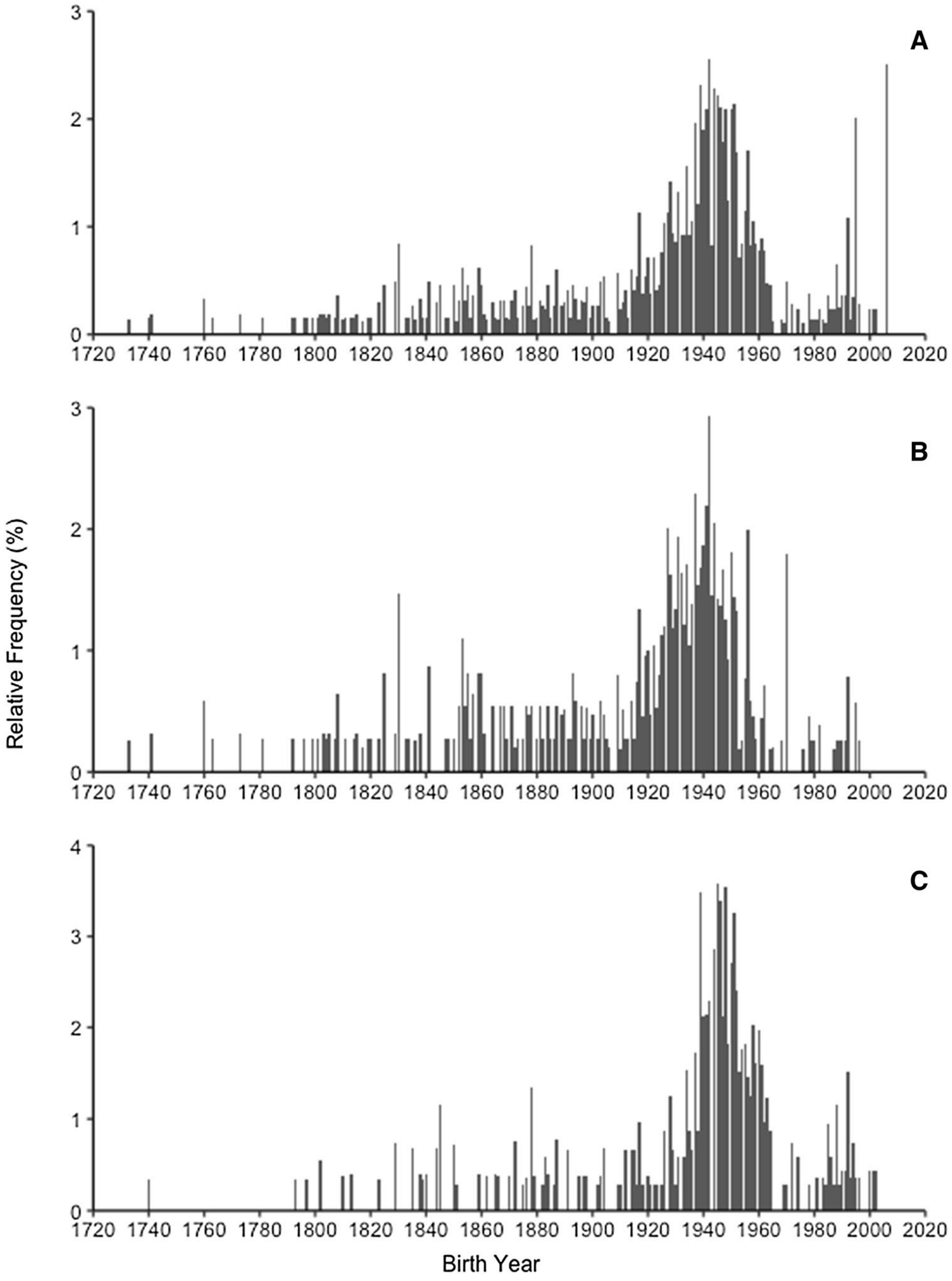
At NJ1, females are observed to be older than males (Fig. 4) and distinctly larger than males. Commonly,

Fig. 9 Cumulative length distributions for male (dashed line) and female (solid line) *Arctica islandica* for southern New Jersey (NJ2) and box and whisker plots of population, female, and male 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



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, 2023). The likely reason behind the differences in ages of males and females at NJ1 is the presence of an increase in female frequency in the 1920s–1930s that was not observed in males (Fig. 10b, 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

Fig. 10 Northern New Jersey (NJ1) age frequency: population (**A**), female (**B**), male (**C**)



smaller animals, so females may have escaped negative environmental conditions during the 1920s–1930 s (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.

Longevity and 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 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). While warmer temperatures may yield higher growth rates, if these same higher temperatures continue to

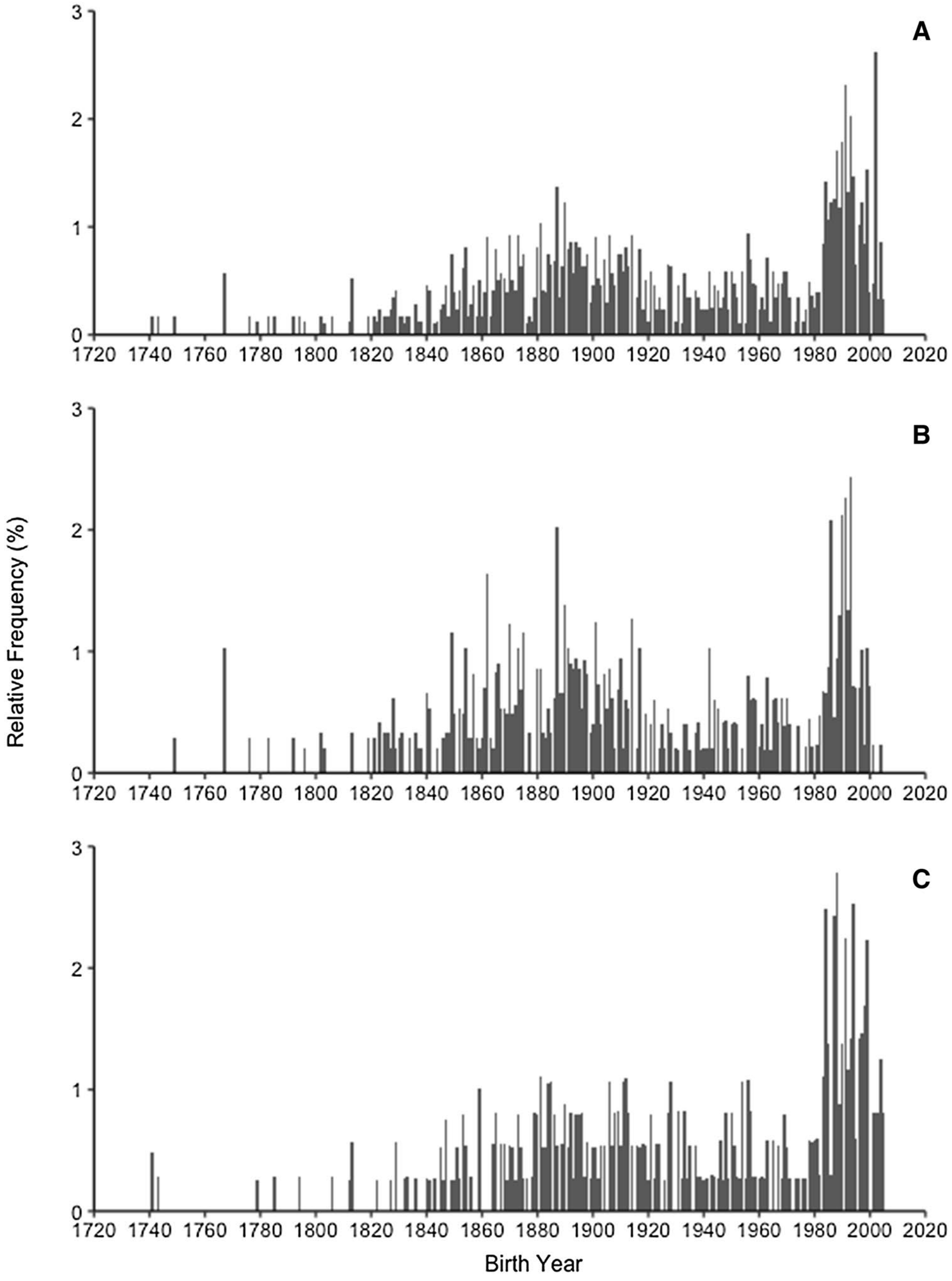


Fig. 11 Southern New Jersey (NJ2) age frequency: population (**A**), female (**B**), male (**C**)

rise and exceed the critical thermal maximum (15–16 °C) of *A. islandica*, then mortality rates could increase. 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 in mortality rate is well below the estimate of the fishing mortality rate for the stock (Hennen 2015; NEFSC 2017). Unfortunately, the differential in historical catch between the two sites is not available as catch reports are for a relatively large regional scale and the offshore clam fishery targets local patches of high density (Solinger et al. 2022). 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} used currently in *A. islandica* population management models (NEFSC 2017). The fishery has been prosecuted over a very short time in comparison with the age range of the market-size population suggesting limited negative impacts on the age frequencies reported herein from the fishery.

Table 5 Northern New Jersey (NJ1) sex ratios

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

Significant results represent cases with female:male ratios significantly different from 1:1; ns = nonsignificant

Table 6 South New Jersey (NJ2) sex ratios

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

Significant results represent cases with female:male ratios significantly different from 1:1; ns = nonsignificant

Comparison of all four sites

Age–length key analysis

Hemeon et al. (2023) 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 differences at the tail ends of the distributions, with NJ1 having slightly higher proportions of animals in the 1980–1990s 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 this could be the cause for this singular discrepancy between the two sites. Dredge selectivity rises rapidly from sizes 50–70 mm SL (NEFSC 2020). Most of the animals born in the 1980s–1990s were between 70–90 mm SL at both New Jersey sites. Thus, most likely, the discrepancies between New Jersey and Long Island are due to lower recruitment in Long Island, rather than a change in dredge selectivity.

Given that comparisons between NJ1, NJ2, Georges Bank, and Long Island yielded 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. 2023). 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 examination might be valuable to determine the degree to which age frequencies vary across the Cold Pool.

Sex ratios and dimorphism

Hemeon et al. (2021a, 2023) 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 recruited 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 at the New Jersey sites 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 in many studies 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 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. Factors that could inhibit one sex while also favoring the other beyond burrowing capabilities as discussed below are not reported, though unknown factors such as differential growth rates varying susceptibility to predation certainly could exist. 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, 2023). Sexual dimorphism is rare in bivalves (Sastry 1979; Hemeon et al. 2021a) but is demonstrably present in *A. islandica* in terms of larger body sizes for females as shown for populations from the MAB, Georges Bank, and Iceland (Fritz 1991; Steingrímsson and Thórarinsdóttir 1995; Hemeon et al. 2021a, 2023; Sower et al. 2022). Because females grow at faster rates than males, they likely 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).

Longevity and mortality

Hemeon et al. (2021a) reported mortality values for Georges Bank at 0.04 yr^{-1} for the population, 0.05 yr^{-1} for females, and 0.04 yr^{-1} 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 yr^{-1} for the population, 0.021 yr^{-1} for females, and 0.023 yr^{-1} for males. Longevity estimates are 347 years for the population, 324 for females, and 316 for males (Hemeon et al. 2023).

Mortality rates for both NJ1 and NJ2 are lower than those for 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, and maximum ages for NJ were comparable to maximum ages at LI. 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 have a potentially negative impact growth and reproduction. This species has 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, higher mortality at Georges Bank 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 with the MAB over the last quarter century (Kavanaugh et al. 2017), although this site has had the least amount of temperature differences in recent years (López et al. 2020).

Recruitment

At Georges Bank and Long Island, recruitment occurred consistently throughout the twentieth century and high recruitment pulses occurred in approximately 8-year intervals (Hemeon et al. 2021a, 2023). 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 at Georges Bank, the absence of cohorts later than the 1960s could either be attributed to reduced recruitment in recent decades, or substantially lower growth rates of these cohorts in comparison with the southern sites prevented young GB *A. islandica* from being sampled by the size-selective dredge.

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 Fig. 11 in Hemeon et al. 2021a and Fig. 6 in Hemeon et al. (2023). Harding et al. (2008) reported temperature data for 1990–2002 that would have facilitated good recruitment, though animals in the present study for this time period were undersampled, likely due to their size and size-limitations of sampling gear. 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 2-year difference between sample collections. Resampling these sites may yield animals that were born during the 1980s–1990s 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 both a source and sink (Davies et al. 2015; Zhang et al. 2015). Currents to the west of this area 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 amount of time the temperature is greater than 15ºC.

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-twentieth 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, south of New Jersey, which began approximately 120 years ago, potentially due to an increase in bottom water temperature beyond the critical thermal maximum 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 and 1900, when temperatures may have been warmer than earlier during the Little Ice Age, yet cooler than in the 1900s, and then a continual decrease until ~ 1980 consistent with overall trends in increasing temperature, 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, 2023; 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. (2023), though coincidence in peak years is not always present (Table 7). Hemeon et al. (2023) suggest that lags in recruitment between sites may be due to the movement of Labrador Sea water southward over time (e.g., Kavanaugh et al. 2017), 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.

Conclusion

Four sites were 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 was 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 varies in age structure and sex ratio. Age-at-length relationships are significantly different. Females consistently outgrow males, but the size difference 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 at the NJ and LI sites, 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 over the range of the species in the northwestern Atlantic.

Table 7 Years of high *Arctica islandica* recruitment in Long Island (LI) as reported by Hemeon et al. (2023), northern New Jersey (NJ1), and southern New Jersey (NJ2)

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

High recruitment is identified as peaks in the age frequencies (Figs. 10A and 11A)

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Data availability The data sets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Conflict of interest The authors have no conflicts of interest.

Ethics approval Ethics approval was not required.

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