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## DEFINING PATTERNS IN OCEAN QUAHOG (*ARCTICA ISLANDICA*) SEXUAL DIMORPHISM ALONG THE MID-ATLANTIC BIGHT

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**ABSTRACT** The ocean quahog, *Arctica islandica* (Linnaeus 1767), is a commercially important species along the western Atlantic continental shelf. It is a long-lived species, frequently reaching ages over 200 y. Uniquely, it is one of the few bivalves to display sexual dimorphism, in that females grow to sizes larger than those of males. This phenomenon is believed to occur because males reach sexual maturity before females and, thus, have slower growth rates earlier. The growth rates of *A. islandica* from four sites across the Mid-Atlantic Bight, Georges Bank, Long Island (LI), and north and south of the Hudson Canyon, were measured to determine patterns in growth between males and females. Females begin to outgrow males between the ages of 5 and 15 y 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 y 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 LI 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, these rare outcomes have limited influence on the population so that female-to-male ratio consistently 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. 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. Egg sizes in *A. islandica* are larger than those of most other bivalves with planktotrophic larvae. Accordingly, another 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.

**KEY WORDS:** ocean quahog, *Arctica islandica*, sexual dimorphism, Mid-Atlantic Bight, growth rate

### INTRODUCTION

The ocean quahog (*Arctica islandica*) is an infaunal, non-colonial 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. unpublished) 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, García-Rodríguez et al. 2000, Colloca 2002). 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 (Chávez-Villalba et al. 2011); and 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 *A. islandica* (Ropes et al. 1984a, Fritz 1991, Steingrímsson & Thórarinsdóttir 1995, Thórarinsdóttir & Steingrímsson 2000, Hemeon et al. 2021).

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

As *Arctica 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. unpublished). Based on

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these same studies, some have hypothesized that the difference in overall size between males and females is that males mature at a younger age (Thórarinsdóttir & Steingrímsson 2000). To explore this hypothesis further, the growth increments of four populations of *A. islandica* from the Mid-Atlantic Bight (MAB) and Georges Bank (GB) were examined to define statistically when during ontogeny sex-based differences begin to occur. Environmental factors were also analyzed to determine potential causes for these observed differences in growth by site.

## MATERIALS AND METHODS

### Sample Collection

In 2017 and 2019, *Arctica 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 GB, off LI, and north (NJ1) and south (NJ2) of Hudson Canyon off New Jersey (see Table 1, Fig. 1). Each clam was shucked, sex was determined, processed for aging (for methods, see Pace et al. 2017a, Hemeon et al. 2021), and analyzed to determine age frequencies and growth rates.

### Aging and Growth Measurements

This species deposits growth lines in their umbo each year (Jones 1980, Thompson et al. 1980a), termed annuli. Murawski et al. (1982) and Ropes et al. (1984b) confirmed these lines as yearly increments, permitting *Arctica islandica* age determination. Images of the umbo region of each animal were taken using a combination microscope and camera (example image in Fig. 2). These images were then uploaded into the opensource software ImageJ with the ObjectJ plugin (see Pace et al. 2017a, 2017b for more information). Each annulus was marked using this software to determine age, and the distance between markers was calculated in pixels. Pixel distance was first converted to a proportion of growth per year, then translated to total length in mm to get total growth per year using the overall length of each clam.

### Dataset Organization and Environmental Mitigation

Maturity and sexual differentiation in *Arctica islandica* can occur at 5 y 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

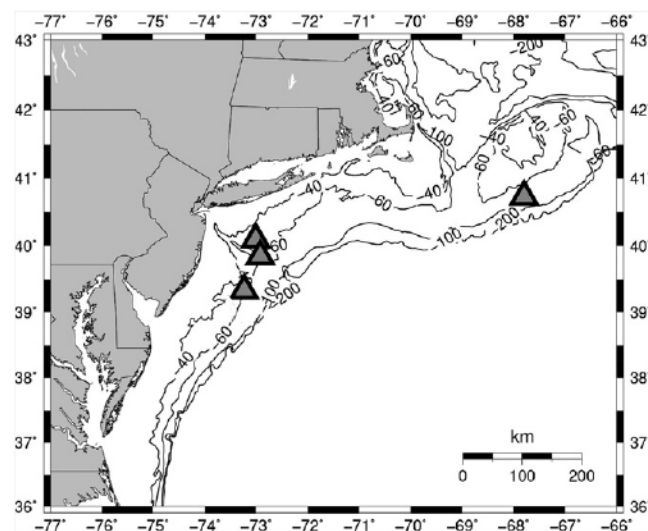


Figure 1. Sample locations. From north to south, sites are Georges Bank (GB), Long Island (LI), New Jersey north (NJ1), and New Jersey south (NJ2).

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 with 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 *Arctica islandica* in these datasets spans 13–310 y, and each dataset contains over 600 aged animals (Hemeon et al. 2021, Hemeon et al. unpublished, Sower et al. unpublished). 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 multidecadal 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 by 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 three of the four sites, 1910–1950. Only GB was lacking sufficient animals in the 1950s.

### Sample Analysis

Growth rates of males and females born each decade were averaged across 5-y increments in mm (i.e., age classes) between the ages of 5 and 50 y. 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

TABLE 1.

Locations of each of the four study sites in decimal degrees.

| 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      |

GB, Georges Bank; LI, Long Island; NJ1, Northern New Jersey; NJ2, Southern New Jersey.

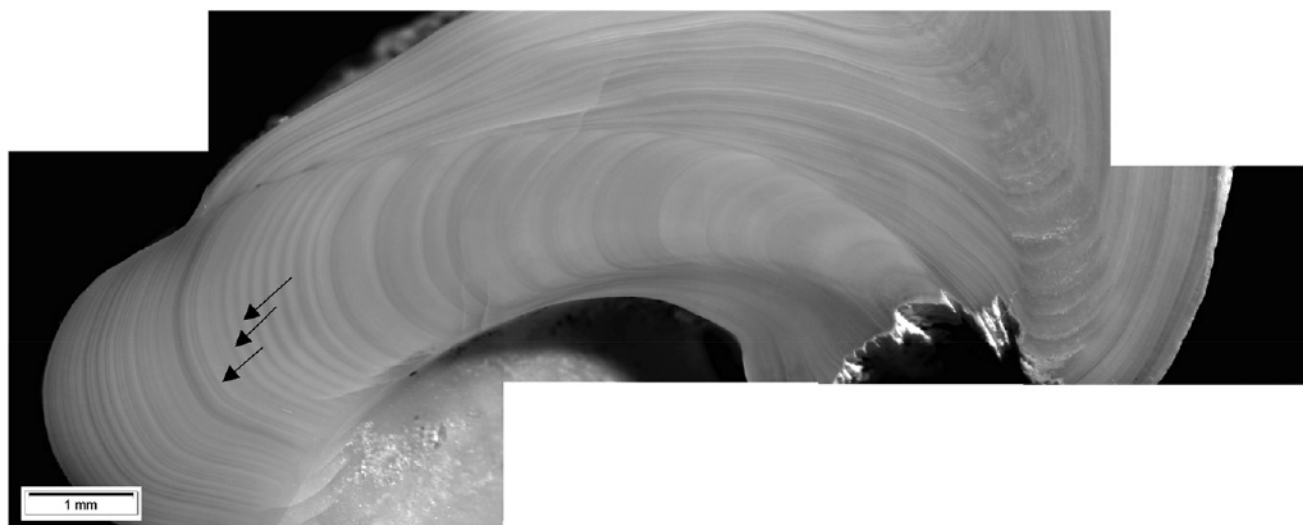


Figure 2. *Arctica islandica* hinge plate with prominent annuli, indicated by arrows.

sample sizes differ (Welch 1938, 1947, Derrick et al. 2016). Welch's test also performs as well as the nonparametric Mann–Whitney *U* 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 whether any patterns unique to said site became apparent.

#### Cold Pool Dynamics

The southern extension of the range of *Arctica islandica* 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.

## RESULTS

#### Statistical Tests

Welch's *t*-test was used in lieu of Student's test and performance compared with the alternative nonparametric

Mann–Whitney *U* test using a subset of the sites and decades. Though results were not exactly the same, patterns were consistent (Table 2).

#### Site-Specific Trends

##### Georges Bank

A total of 233 animals born in the decades 1910–1940 were analyzed from GB. 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 for the 1910s, by age 15 for decades 1920–1930, and at age 30 for the 1940s (Fig. 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 (Fig. 4). By age 50, these differences were magnified. For example, females were at least 4 mm larger at 83 mm compared with 79 mm in males for animals born in the 1940s (Table 3), and females were 9 mm larger, at 84 mm compared with 75 mm in males, for animals born in the 1910s.

TABLE 2.

Welch's *t*-test results compared with Mann–Whitney *U* (MWU) test results per birth decade at two sites with the highest number of animals born.

| Decade | Site | Age | Welch's <i>t</i> -test<br>( <i>P</i> value) | MWU test<br>( <i>P</i> 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                      |

NJ1, Northern New Jersey; NJ2, Southern New Jersey.

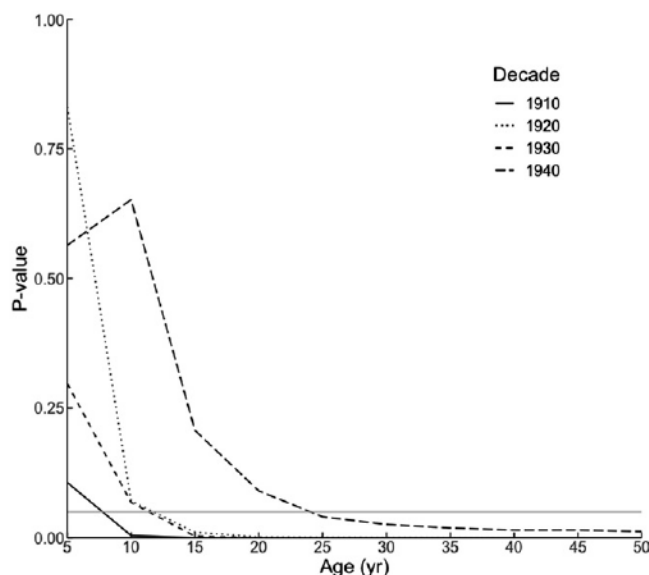


Figure 3. Trends in  $P$  value per decade obtained using Welch's  $t$ -test for animals from Georges Bank. The horizontal gray line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

#### Long Island

A total of 377 animals across five decades were analyzed from LI. Early in ontogeny, the growth rates of males and females did not differ significantly for three of five decades and four of five discounting the first few years of life for the 1910s (Fig. 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.

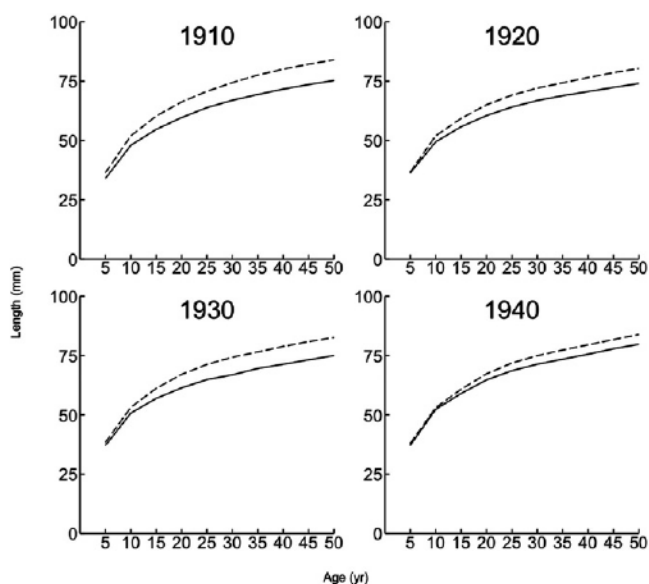


Figure 4. Growth differentials for female and male *Arctica islandica* at Georges Bank for animals born during the decades 1910–1940. Dashed line = females, solid line = males.

In contrast, male and female sizes were significantly different in the 1950s at all ages (Fig. 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 y, respectively, Table 4, Fig. 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 (Fig. 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.

#### Northern New Jersey (NJ1)

A total of 438 animals were analyzed from NJ1. Early in ontogeny, the growth rates of males and females did not differ significantly for three of the five decades, 1920–1940, though 1920 was nearly significant at age 5. For 1930 and 1940, females diverged significantly by ages 12 and 14, respectively (Fig. 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 (Fig. 8, Table 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 (Fig. 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 (Fig. 8).

#### Southern New Jersey (NJ2)

A total of 172 animals were analyzed from the NJ2. This site has the broadest age distribution in the population age frequency (our unpubl. data), 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 with the other three sites. Males and females diverged significantly in size in three decades, two at age 35 and one at age 40 (Fig. 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 age 35 (Fig. 10, Table 6). As was observed at the other three sites, females continued to grow larger relative to males 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-y timeline. Interestingly, in the 1930s,

TABLE 3.  
Average lengths (mm) of males (M) and females (F) at Georges Bank at each age and decade.

| Decade | Sex | Age (year) |        |        |        |       |       |       |       |       |       |
|--------|-----|------------|--------|--------|--------|-------|-------|-------|-------|-------|-------|
|        |     | 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 |

\* Denotes at which age and corresponding length statistical significance ( $P < 0.05$ ) was reached.

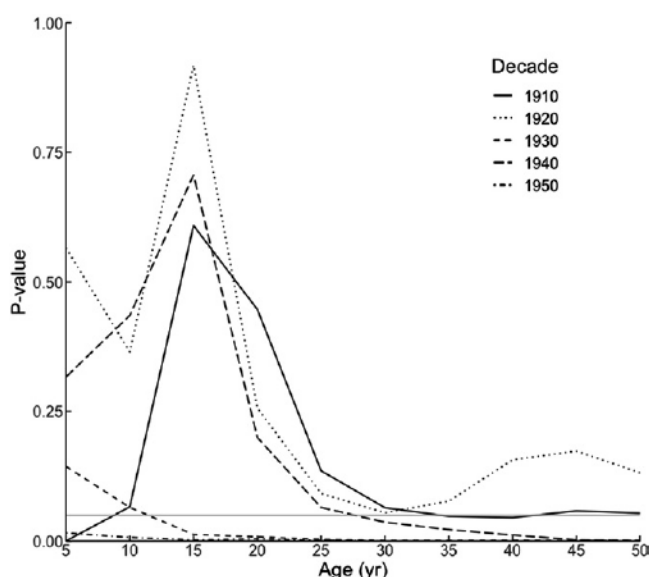


Figure 5. Trends in  $P$  values obtained using Welch's  $t$ -test for animals from Long Island. The horizontal gray line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

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.

#### 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 (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 age 15, even if differences were not statistically significant. At this age, across decadal groups, the lengths of both males and females ranged from 47 to 61 mm, with an average of 56.3 mm and a SD 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 GB, 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, SD 2.75 mm, and the average size of females is 56.70 mm, SD 2.42 mm.

TABLE 4.  
Average lengths (mm) of males (M) and females (F) from Long Island at all ages and decades.

| Decade | Sex | Age (year) |       |        |       |       |        |        |       |       |       |
|--------|-----|------------|-------|--------|-------|-------|--------|--------|-------|-------|-------|
|        |     | 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 |

\* Denotes at which age and corresponding length statistical significance ( $P < 0.05$ ) was reached.

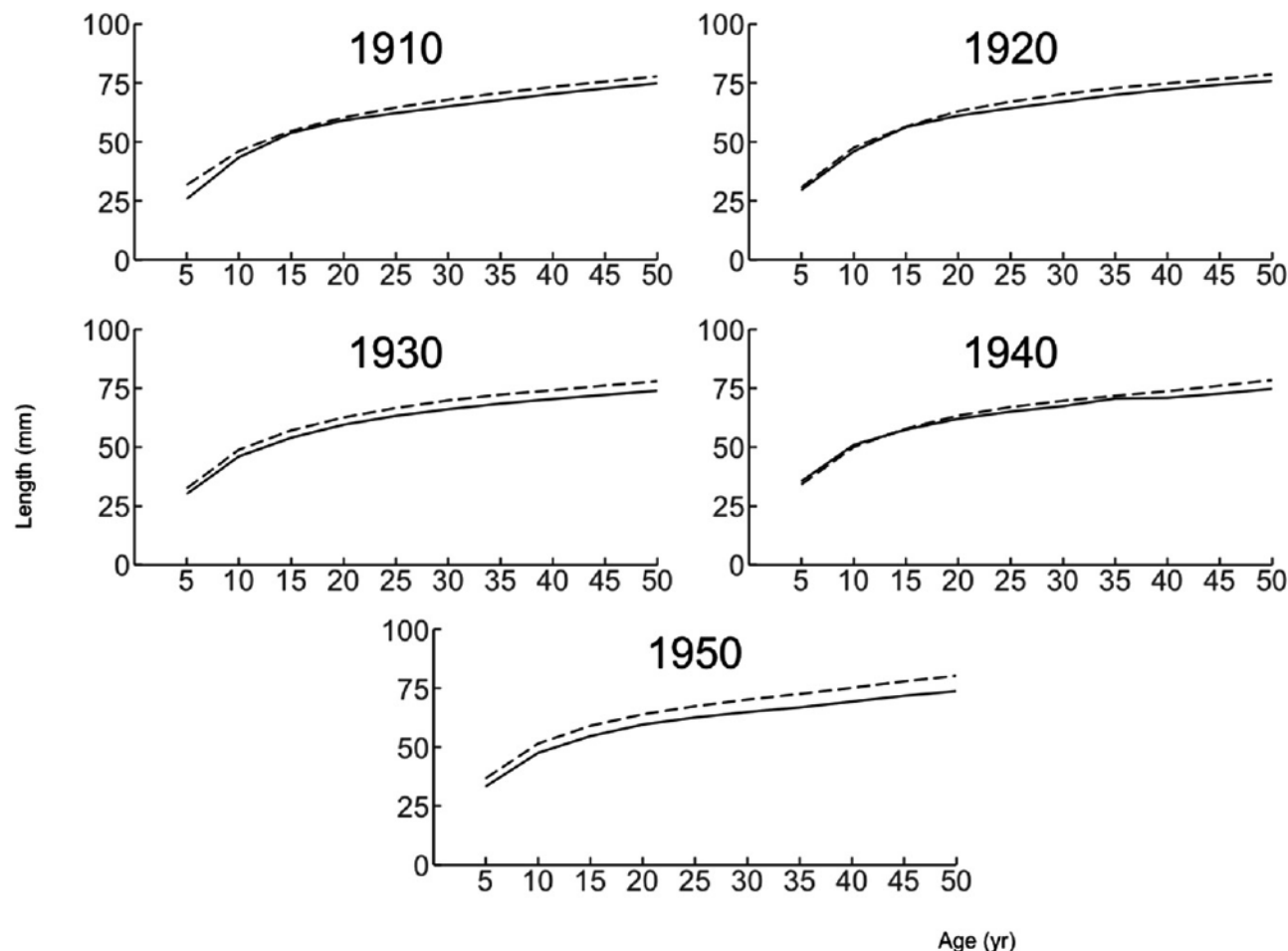


Figure 6. Growth differentials for male and female *Arctica islandica* for Long Island for animals born during the decades 1910–1950. Dashed line = females, solid line = males.

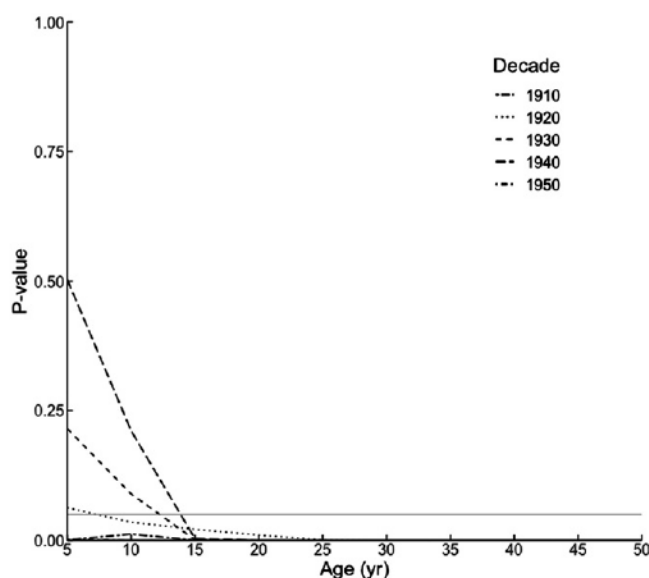


Figure 7. Trends in *P* values obtained using Welch's *t*-test for animals from Northern New Jersey (NJ1). The horizontal gray line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

## DISCUSSION

### Sexual Dimorphism

Hemeon et al. (2021, unpublished) detailed the differential in sizes between male and female *Arctica islandica* over their life span, confirming and extending earlier reports by Ropes et al. (1984a), Fritz (1991), 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 LI were 6 y old, with an average of 9.8 y in males and 13.2 y in females. The 6-y-old mature animals were 36–60 mm long, whereas 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.

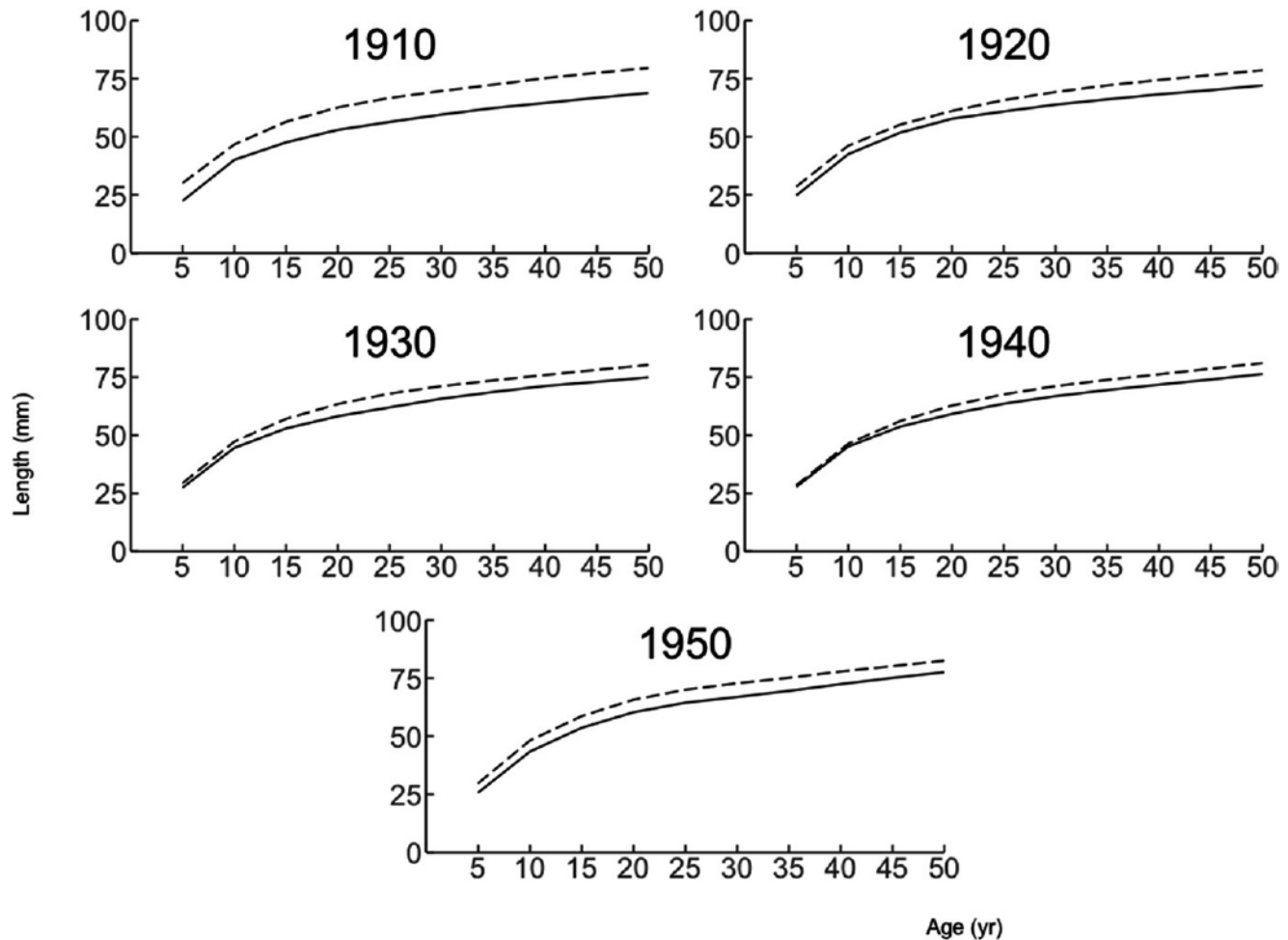


Figure 8. Growth differentials for male and female *Arctica islandica* for Northern New Jersey (NJ1) for animals born during the decades 1910–1950. Dashed line = females, solid line = males.

#### *Spatial Heterogeneity and Cold Pool Influences on Growth*

The metabolic energetics of *Arctica islandica* are notably sensitive to temperature with a  $Q_{10}$  as high as four recorded for respiration (Begum et al. 2009) and demonstrate 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, Cargnelli et al. 1999a). An increase of 1°C can cause a mass mortality event (Merrill et al. 1969). Correspondingly, in the MAB, significant numbers of *A. islandica* are rarely found where mean summer bottom water temperatures exceed 13.5°C (Sower et al. unpublished). 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 GB presumably due to the warmer bottom water temperatures experienced there, for example.

Growth rates 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 among 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) were accessed for the time period 2016–2019.

#### *Georges Bank*

Georges Bank is the northernmost and deepest site in this dataset (Table 1). Georges Bank 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).

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

TABLE 5.  
Average lengths (mm) of males (M) and females (F) from northern New Jersey (NJ1) at each age and decade.

| Decade | Sex | Age (year) |        |        |       |       |       |       |       |       |       |
|--------|-----|------------|--------|--------|-------|-------|-------|-------|-------|-------|-------|
|        |     | 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 |

\* Denotes at which age and corresponding length when statistical significance ( $P < 0.05$ ) was reached.

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 *Arctica islandica* in the MAB. Pace et al. (2018) and Hemeon et al. (2021) 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*.

#### Long Island

The LI site is located at a depth of 47.5 m and is the most inshore site of the four (Fig. 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 7). Data from recent years also suggest that LI occasionally experiences near-lethal temperatures (Table 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.

#### Northern New Jersey (NJ1)

Even though NJ1 is slightly south of LI, it is farther offshore at 60 m depth. One might expect that *Arctica islandica* from this site experience cooler temperatures during the summer. In fact, the temperature regime is similar to that of the LI site with the exception that the extreme temperatures are 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.

#### 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

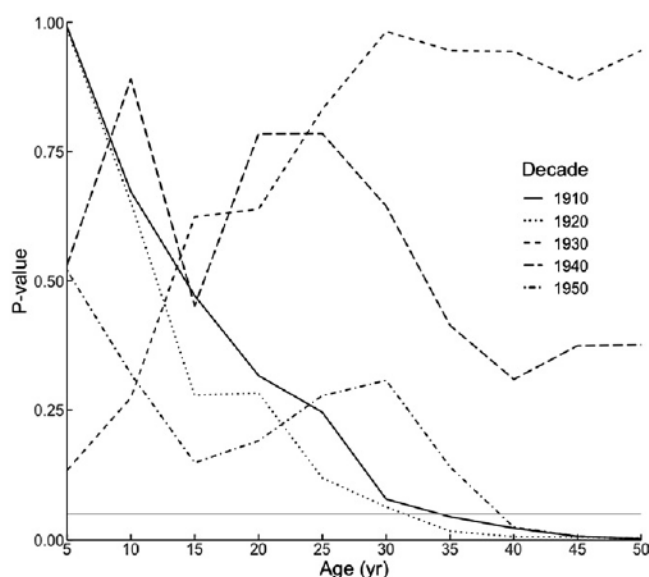


Figure 9. Trends in  $P$  values obtained using Welch's  $t$ -test for animals from Southern New Jersey (NJ2). The horizontal gray line indicates an alpha value of 0.05. Values falling below this line were considered statistically significant.

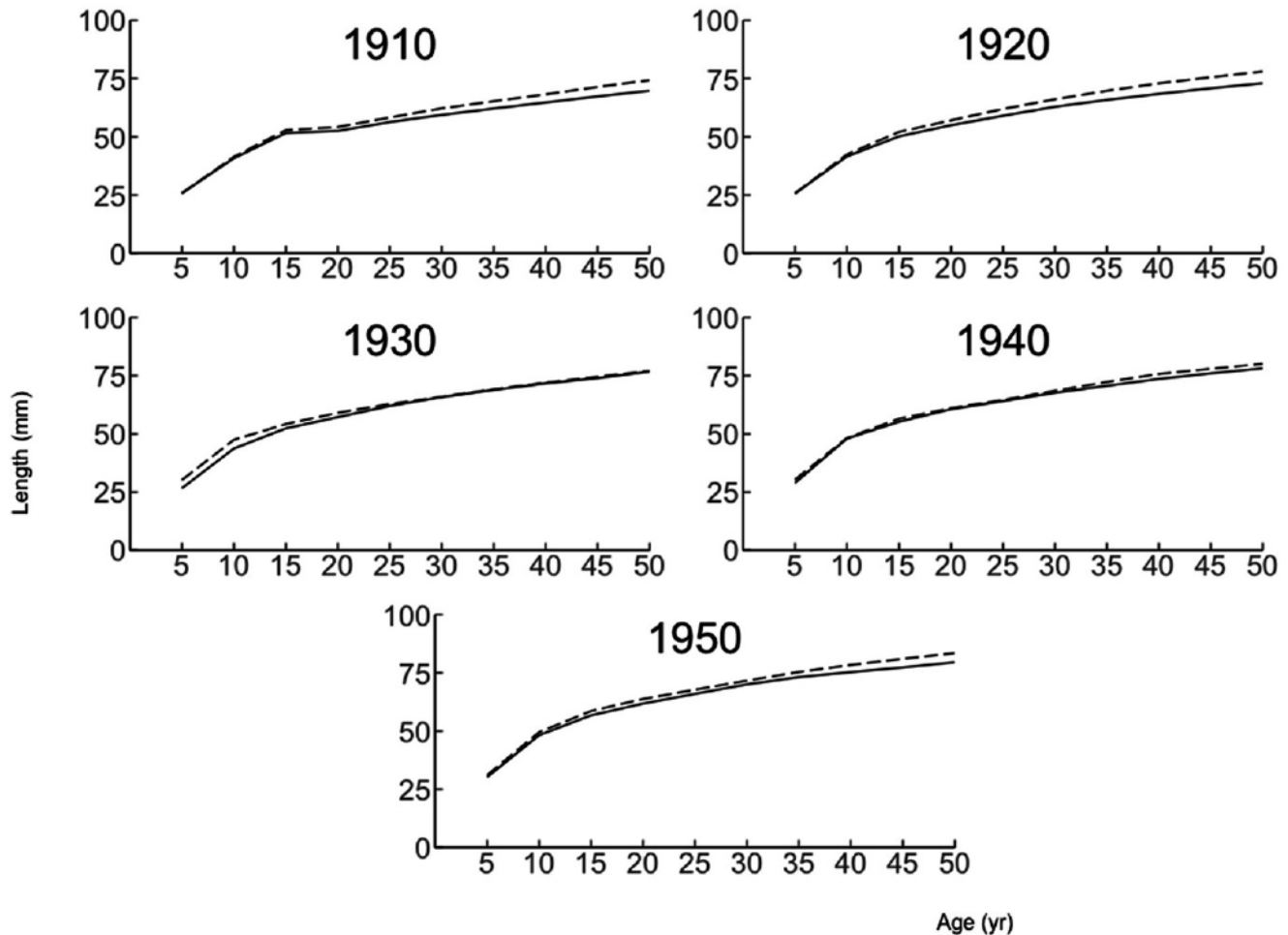


Figure 10. Growth differentials for male and female *Arctica islandica* for Southern New Jersey (NJ2) for animals born during the decades 1910–1950. Dashed line = females, solid line = males.

over the studied decades. Unlike the other sites, in two of five cases, male and female growth rates do not diverge significantly. The NJ2 site 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 y of life. When decades did reach statistical significance, it was not until the animals were 35 y 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.

#### 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 y 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 LI 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 among sites, limiting interpretation of variable growth outcomes as a function of temperatures, but the sensitivity of *Arctica 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, unpublished) found strong evidence for

TABLE 6.  
Average lengths (mm) of males (M) and females (F) of southern New Jersey (NJ2) at each age and decade.

| Decade | Sex | Age (year) |       |       |       |       |       |        |        |       |       |
|--------|-----|------------|-------|-------|-------|-------|-------|--------|--------|-------|-------|
|        |     | 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 |

\* Denotes at which age and corresponding length if statistical significance ( $P < 0.05$ ) was reached.

this expectation, suggesting a 52-mm size at maturity at GB and LI for populations with approximately 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 3–5). Southern New Jersey (NJ2) animals do not display differences in growth between sexes, until year 35 and at sizes 65 mm and greater, and never in some decades, but overall, *Arctica islandica* are observed 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.

*Why might the sex-specific size difference in Arctica islandica exist?*

#### Protandry

One hypothesis for smaller males and larger females is that *Arctica 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 sampled during the sex change (Harding et al. 2013, Powell et al. 2013). Protandry results in an age-dependent

TABLE 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  | Lower    | Upper    | Minimum | Maximum | Median |
|--------------|-------|-----------|----------|----------|---------|---------|--------|
|              |       | Deviation | Quartile | Quartile |         |         |        |
| 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  |

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 & Thórarinsdóttir 1995, Thórarinsdóttir & Steingrímsson 2000). Given these findings, protandry is not a probable cause for the size difference between sexes in *A. islandica*.

#### Difference in lifespan/mortality

A second hypothesis posed is that male *Arctica islandica* may have higher rates of mortality and, thus, live shorter lives compared with 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. (unpublished) 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 y, whereas the oldest female was 224 y. At LI, males again were older, with the oldest male aged at 310 y, whereas the oldest female was only 272 y (Hemeon et al. unpublished). In NJ1, the oldest female was aged at 286 y, whereas the oldest male was aged at 279 y. In NJ2, the oldest female was 270, whereas the oldest male was 278. Thus, in *A. islandica*, males and females do not display strong differences in estimated longevity.

#### 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, Luttikhuisen 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” toward a member of the opposite sex. This behavior has not been documented in *Arctica 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 toward females with less energy expenditure, and, thus, have increased chances for successful reproduction.

#### 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 *Arctica islandica*, it might

be energetically beneficial for a female to focus on growth for a longer period of time, and then switch to producing gametes once an adequate size is 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 with similar species would provide clearer reasoning on smaller male sizes.

Consequently, the uniqueness of sexual dimorphism in *Arctica islandica* within the Venerida coupled with their long life span would suggest that differential growth rates between sexes provide increased fitness for both sexes 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 with the northern quahog (hard clams, *Mercenaria mercenaria*), surf clams (*Spisula solidissima*), Manila clams (*Lajonkairia lajonkairii*), and other clams (Gallager & Mann 1986, Toba & Miyama 1994, Cargnelli et al. 1999b, Jagadis 2011). Mann (unpublished) 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 with 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 surf clams, however, which arguably live in a more energetic environment. Conversely, larval life spans are relatively long in *Arctica 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 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 *Arctica islandica*, is not more commonly encountered in bivalves. This

species is the only known extant member of the family Arcticiidae (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 size. These traits may have developed due to *A. islandica* residing in boreal waters, so close inspection of sex-based lengths and gamete sizes of other boreal species is recommended to provide clarity.

### CONCLUSION

The ocean quahog, *Arctica islandica*, is greatly influenced by the temperature in its environment. Temperature clearly impacts growth rates, causing variations from location to location and birth year to birth year. It is still unclear whether maturity is a function of growth or age in *A. islandica*; many studies (Ropes et al. 1984a, Rowell et al. 1990, Steingrímsson & Thórarindóttir 1995, Hemeon et al. 2021), 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 and 15 y and 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 neither 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.

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### LITERATURE CITED

- Ballesta-Artero, I., R. Witbaard, M. L. Carroll & J. van der Meer. 2017. Environmental factors regulating gaping activity of the bivalve *Arctica islandica* in northern Norway. *Mar. Biol.* 146:15.
- Begum, S., L. Basova, J. Strahl, A. Sukhotin, O. Heilmayer, E. Philipp, T. Brey & D. Abele. 2009. A metabolic model for the ocean quahog *Arctica islandica*—effects of animal mass and age, temperature, salinity, and geography on respiration rate. *J. Shellfish Res.* 28:533–539.
- Begum, S., L. Basova, O. Heilmayer, E. E. R. Philipp, D. Abele & T. Brey. 2010. Growth and energy budget models of the bivalve *Arctica islandica* at six different sites in the northeast Atlantic realm. *J. Shellfish Res.* 29:107–115.
- Brusher, H. A., W. C. Renfro & R. A. Neal. 1972. Notes on distribution, size, and ovarian development of some penaeid shrimps in the northwestern Gulf of Mexico 1961–62. *Contrib. Mar. Sci.* 16:75–87.
- Butler, P. G., A. D. Wanamaker, J. D. Scourse, C. A. Richardson & D. J. Reynolds. 2013. Variability of marine climate on the North Icelandic Shelf in a 1357-year proxy archive based on growth increments in the bivalve *A. islandica*. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 373:141–151.
- Cargnelli, L., S. Griesbach, D. Packer & E. Weissberger. 1999a. Essential fish habitat source document: ocean quahog, *Arctica islandica*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-148. 12 pp.
- Cargnelli, L., S. Griesbach, D. Packer & E. Weissberger. 1999b. Essential fish habitat source document: Atlantic surfclam, *Spisula solidissima*, life history and habitat characteristics. NOAA Tech. Memo. NMFS-NE-142. Woods Hole, MA: U.S. Department of Commerce. 13 pp.
- Charnov, E. L., R. Warne & M. Moses. 2007. Lifetime reproductive effort. *Am. Nat.* 170:129–142.
- Chávez-Villalba, J., C. Soye, A. Huvet, Y. Gueguen, C. Lo & G. Le Moullac. 2011. Determination of gender in the pearl oyster *Pinctada margaritifera*. *J. Shellfish Res.* 30:231–240.
- Chen, Z. & E. Curchitser. 2020. Interannual variability of the Mid-Atlantic Bight Cold Pool. *J. Geophys. Res. Oceans* 125:e2020JC016445.
- Chen, Z., E. Curchitser, R. Chant & D. Kang. 2018. Seasonal variability of the Cold Pool over the Mid-Atlantic Bight continental shelf. *J. Geophys. Res. Oceans* 123:8203–8226.
- Coe, W. R. 1934. Alteration of sexuality in oysters. *Am. Nat.* 68:236–251.
- Collin, R. 2006. Sex ratio, life-history invariants, and patterns of sex change in a family of protandrous gastropods. *Evolution* 60:735–745.
- Colloca, F. 2002. Life cycle of the deep-water pandalid shrimp *Plesionika edwardsii* (Decapoda, Caridea) in the central Mediterranean Sea. *J. Crustac. Biol.* 22:775–783.
- Dahlgren, T. G., J. R. Weinberg & K. M. Halanych. 2000. Phylogeography of the ocean quahog (*Arctica islandica*): influences of paleoclimate on genetic diversity and species range. *Mar. Biol.* 137:487–495.
- Derrick, B., D. Toher & P. White. 2016. Why Welch's test is Type I error robust. *Quant. Methods Psychol.* 12:30–38.
- Dinamani, P. 1974. Reproductive cycle and gonadal changes in the New Zealand rock oyster *Crassostrea glomerata*. *N. Z. J. Mar. Freshw. Res.* 8:39–65.
- Fotheringham, N. 1971. Life history patterns of the littoral gastropods *Shaskyus festivus* (Hinds) and *Ocenebra poulsoni* Carpenter (Prosobranchia: Muricidae). *Ecology* 52:742–757.
- Friedland, K. D., R. E. Morse, J. P. Manning, D. C. Melrose, T. Miles, A. G. Goode, D. C. Brady, J. T. Kohut & E. N. Powell. 2020. Trends and change points in surface and bottom thermal environments of the US northeast continental shelf ecosystem. *Fish. Oceanogr.* 29:396–414.
- Friedland, K. D., T. Miles, A. G. Goode, E. N. Powell & D. C. Brady. 2022. The Middle Atlantic Bight Cold Pool is warming and shrinking: indices from *in situ* autumn seafloor temperatures. *Fish. Oceanogr.* 31:217–223.
- Fritz, L. W. 1991. Seasonal condition change, morphometrics, growth and sex ratio of the ocean quahog, *Arctica islandica* (Linnaeus, 1767) off New Jersey, USA. *J. Shellfish Res.* 10:79–88.

- Gallager, S. M. & R. Mann. 1986. Growth and survival of larvae of *Mercenaria mercenaria* (L.) and *Crassostrea virginica* (Gmelin) relative to broodstock conditioning and lipid content of eggs. *Aquaculture* 56:105–121.
- García-Rodríguez, M., A. Esteban & J. L. Perez Gil. 2000. Considerations on the biology of *Plesionika edwardsi* (Brandt, 1851) (Decapoda, Caridea, Pandalidae) from experimental trap catches in the Spanish western Mediterranean Sea. *Sci. Mar.* 64:369–379.
- González-Vallejo, N. E. 2008. Parasitism of *Monogamus minibulla* (Olsson and McGinty, 1958) (Gastropoda: Eulimidae) on the red sea-urchin *Echinometra lucunter* (Linnaeus, 1758) (Echinodermata: Echinometridae) on the Caribbean coast of Mexico. *Nautilus* 122:178–181.
- Harding, J. M., E. N. Powell, R. Mann & M. J. Southworth. 2013. Variations in eastern oyster (*Crassostrea virginica*) sex-ratios from three Virginia estuaries: protandry, growth and demographics. *J. Mar. Biol. Ass. U.K.* 93:519–531.
- Hayward, A. & J. F. Gillooly. 2011. The cost of sex: quantifying energetic investment in gamete production by males and females. *PLOS ONE* 6:e16557.
- Hemeon, K. M., E. N. Powell, S. M. Pace, T. E. Redmond & R. Mann. 2021. Population dynamics of *Arctica islandica* at Georges Bank (USA): an analysis of sex-based demographics. *J. Mar. Biol. Ass. U.K.* 101:1003–1018.
- Henderson, A. C., K. Flannery & J. Dunne. 2002. Growth and reproduction in spiny dogfish *Squalus acanthias* L. (Elasmobranchii: Squalidae), from the West Coast of Ireland. *Sarsia* 87:350–361.
- Houghton, R. W., R. Schlitz, R. C. Beardsley, B. Butman & J. L. Chamberlin. 1982. The Middle Atlantic Bight Cold Pool: evolution of the temperature structure during summer 1979. *J. Phys. Oceanogr.* 12:1019–1029.
- Jagadis, I. 2011. Spawning, larval development and spat settlement in the venus clam *Gafarium tumidum* (Roding, 1798) from south-east coast of India. *Indian J. Fish.* 58:1–5.
- Jones, D. S. 1980. Annual cycle of shell growth increment formation in two continental shelf bivalves and its paleoecologic significance. *Paleobiology* 6:331–340.
- Lentz, S. J. 2017. Seasonal warming of the Middle Atlantic Bight Cold Pool. *J. Geophys. Res. Oceans* 122:941–954.
- Levitan, D. R. 2000. Optimal egg size in marine invertebrates: theory and phylogenetic analysis of the critical relationship between egg size and development time in echinoids. *Am. Nat.* 156:175–192.
- Levitan, D. R. 2006. The relationship between egg size and fertilization success in broadcast-spawning marine invertebrates. *Integr. Comp. Biol.* 46:298–311.
- López, A. G., J. L. Wilkin & J. C. Levin. 2020. Doppio—a ROMS (v3.6)-based circulation model for the Mid-Atlantic Bight and Gulf of Maine: configuration and comparison to integrated coastal observing network observations. *Geosci. Model Dev.* 13:3709–3729.
- Luttikhuisen, P. C., P. J. C. Honkoop & J. Drent. 2011. Intraspecific egg size variation and sperm limitation in the broadcast spawning bivalve *Macoma balthica*. *J. Exp. Mar. Biol. Ecol.* 396:156–161.
- Lutz, R. A., R. Mann, J. G. Goodsell & M. Castagna. 1982. Larval and early post-larval development of *Arctica islandica*. *J. Mar. Biol. Ass. U.K.* 62:745–769.
- MAFMC. 2021. Ocean quahog fishery information document. Dover, DE: Mid-Atlantic Fishery Management Council. 15 pp.
- Mann, R. 1982. The seasonal cycle of gonadal development in *Arctica islandica* from the Southern New England shelf. *Fish Bull.* 80:315–326.
- Mann, R. 1986. *Arctica islandica* (Linné) larvae: active depth regulators or passive particles? *Am. Malacol. Bull.* 3:51–57.
- Mann, R. & C. C. Wolf. 1983. Swimming behaviour of larvae of the ocean quahog *Arctica islandica* in response to pressure and temperature. *Mar. Ecol. Prog. Ser.* 13:211–218.
- McEdward, L. R. & B. G. Miner. 2003. Fecundity-time models of reproductive strategies in marine benthic invertebrates: fitness differences under fluctuating environmental conditions. *Mar. Ecol. Prog. Ser.* 256:111–121.
- Merrill, A. S., J. L. Chamberlin & J. W. Ropes. 1969. Ocean quahog fishery. In: Firth, F. E., editor. Encyclopedia of marine resources. New York, NY: Van Nostrand Reinhold Publishing Co. pp. 125–129.
- Morse, W. W. 1981. Reproduction of the summer flounder, *Paralichthys dentatus* (L.). *J. Fish Biol.* 19:189–203.
- Morton, B. 2011. The biology and functional morphology of *Arctica islandica* (Bivalvia: Arctiidae): a gerontophilic living fossil. *Mar. Biol. Res.* 7:540–553.
- Murawski, S. A., J. W. Ropes & F. M. Serchuk. 1982. Growth of the ocean quahog, *Arctica islandica*, in the Mid-Atlantic Bight. *Fish Bull.* 80:21–34.
- Neuheimer, A. B., M. Hartvig, J. Heuschele, S. Hylander, T. Kiørboe, K. H. Olsson, J. Sainmont & K. H. Andersen. 2015. Adult and off-spring size in the ocean over 17 orders of magnitude follows two life history strategies. *Ecology* 96:3303–3311.
- Nichol, D. G. 1998. Annual and between-sex variability of yellowfin sole, *Pleuronectes asper*, spring-summer distributions in the eastern Bering Sea. *Fish Bull.* 96:547–561.
- Nixon, S. W., S. Granger, B. A. Buckley, M. Lamont & B. Rowell. 2004. A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. *Estuaries* 27:397–404.
- Orton, J. H. 1927. Observation and experiments on sex-change in the European oyster (*O. edulis*). Part I. The change from female to male. *J. Mar. Biol. Ass. U.K.* 14:967–1045.
- Ou, H. W. & R. Houghton. 1982. A model of the summer progression of the Cold-Pool temperature in the Middle Atlantic Bight. *J. Phys. Oceanogr.* 12:1030–1036.
- Pace, S. M., E. N. Powell, R. Mann & M. C. Long. 2017a. Comparison of age-frequency distributions for ocean quahogs *Arctica islandica* on the western Atlantic US continental shelf. *Mar. Ecol. Prog. Ser.* 585:81–98.
- Pace, S. M., E. N. Powell, R. Mann, M. C. Long & J. M. Klinck. 2017b. Development of an age-frequency distribution for ocean quahogs (*Arctica islandica*) on Georges Bank. *J. Shellfish Res.* 36:41–53.
- Pace, S. M., E. N. Powell & R. Mann. 2018. Two-hundred year record of increasing growth rates for ocean quahogs (*Arctica islandica*) from the northwestern Atlantic Ocean. *J. Exp. Mar. Biol. Ecol.* 503:8–22.
- Peharda, M., I. Mladineo, J. Bolotin, L. Kekez & B. Skaramuca. 2006. The reproductive cycle and potential protandric development of the Noah's Ark shell, *Arca noae* L.: implications for aquaculture. *Aquaculture* 252:317–327.
- Powell, E. N., E. A. Bochenek, J. M. Klinck & E. E. Hofmann. 2002. Influence of food quality and quantity on the growth and development of *Crassostrea gigas* larvae: a modeling approach. *Aquaculture* 210:89–117.
- Powell, E. N., J. M. Klinck & E. E. Hofmann. 2011a. Generation time and the stability of sex-determining alleles in oyster populations as deduced using a gene-based population dynamics model. *J. Theor. Biol.* 271:27–43.
- Powell, E. N., J. Morson & J. M. Klinck. 2011b. Application of a gene-based population dynamics model to the optimal egg size problem: why do bivalve planktotrophic eggs vary in size? *J. Shellfish Res.* 30:403–423.
- Powell, E. N., J. M. Morson, K. A. Ashton-Alcox & Y. Kim. 2013. Accommodation of the sex-ratio in eastern oysters *Crassostrea virginica* to variation in growth and mortality across the estuarine salinity gradient. *J. Mar. Biol. Ass. U.K.* 93:533–555.
- Powell, E. N. & R. J. Stanton. 1985. Estimating biomass and energy flow of molluscs in palaeo-communities. *Palaeontology* 28:1–34.
- Robertson, R. 1981. Protandry with only one sex change in an *Epitonium* (Ptenoglossa). *Nautilus* 95:184–186.

- Ropes, J. W., S. A. Murawski & F. M. Serchuk. 1984a. Size, age, sexual maturity, and sex ratio in ocean quahogs, *Arctica islandica* Linné, off Long Island, New York. *Fish Bull.* 82:253–267.
- Ropes, J. W., D. S. Jones, S. A. Murawski, F. M. Serchuk & A. Jearld. 1984b. Documentation of annual growth lines in ocean quahogs, *Arctica islandica* Linné. *Fish Bull.* 82:1–19.
- Rowell, T. W., D. R. Chaisson & J. T. McLane. 1990. Size and age of sexual maturity and annual gametogenic cycle in the ocean quahog, *Arctica islandica* (Linnaeus, 1767), from coastal waters in Nova Scotia, Canada. *J. Shellfish Res.* 9:195–203.
- Ruxton, G. D. 2006. The unequal variance t-test is an underused alternative to Student's *t*-test and the Mann–Whitney *U* test. *Behav. Ecol.* 17:688–690.
- Sastry, A. N. 1979. Pelecypoda (excluding Ostreidae). In: Giese, A. C. & J. S. Pearse, editors. Reproduction of marine invertebrates, vol. 5. New York, NY: Academic Press. pp. 113–292.
- Sha, J., Y. H. Jo, X. H. Yan & W. T. Liu. 2015. The modulation of the seasonal cross-shelf sea level variation by the Cold Pool in the Middle Atlantic Bight. *J. Geophys. Res. Oceans* 120:7182–7194.
- Shuozeng, D. 1995. Life history cycles of flatfish species in the Bohai Sea, China. *Neth. J. Sea Res.* 34:195–210.
- Soong, K. & M. H. Chen. 2003. Sex expression of an immobile coral-inhabiting snail, *Quoyula monodonta*. *Mar. Biol.* 143:351–358.
- Steingrímsson, S. A. & G. Thórarinsdóttir. 1995. Age structure, growth and size at sexual maturity in ocean quahog, *Arctica islandica* (Mollusca: Bivalvia), off NW-Iceland, vol. 54. ICES Document C.M. 1995 K. 17 pp.
- Strahl, J., T. Brey, E. E. R. Philipp, G. Thórarinsdóttir, N. Fischer, W. Wessels & D. Abele. 2011. Physiological responses to self-induced burrowing and metabolic rate depression in the ocean quahog *Arctica islandica*. *J. Exp. Biol.* 214:4221–4231.
- Taylor, A. C. 1976. Burrowing behaviour and anaerobiosis in the bivalve *Arctica islandica* (L.). *J. Mar. Biol. Ass. U.K.* 56:95–109.
- Tettelbach, S. T., J. R. Europe, C. R. H. Tettelbach, J. Havelin, B. S. Rodgers, B. T. Furman & M. Velasquez. 2017. Hard clam walking: active horizontal locomotion of adult *Mercenaria mercenaria* at the sediment surface and behavioral suppression after extensive sampling. *PLOS ONE* 12:e0173626.
- Thompson, I., D. S. Jones & D. Dreibelbis. 1980a. Annual internal growth banding and life history of the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). *Mar. Biol.* 57:25–34.
- Thompson, I., D. S. Jones & J. W. Ropes. 1980b. Advanced age for sexual maturity in the ocean quahog *Arctica islandica* (Mollusca: Bivalvia). *Mar. Biol.* 57:35–39.
- Thórarinsdóttir, G. G. & S. A. Steingrímsson. 2000. Size and age at sexual maturity and sex ratio in ocean quahog, *Arctica islandica* (Linnaeus, 1767), off northwest Iceland. *J. Shellfish Res.* 19:943–947.
- Toba, M. & Y. Miyama. 1994. Relationship of size to gonadal maturation and spawning in artificially conditioned Manila clams (*Ruditapes philippinarum*). *Nippon Suisan Gakkaishi* 60:173–178.
- Turner, R. D. & Y. Yakovlev. 1983. Dwarf males in the Teredinidae (Bivalvia, Pholadacea). *Science* 219:1077–1078.
- Welch, B. L. 1938. The significance of the difference between two means when the population variances are unequal. *Biometrika* 29:350–362.
- Welch, B. L. 1947. The generalization of 'Student's' problem when several different population variances are involved. *Biometrika* 34:28–35.