

Comparison of age–frequency distributions for ocean quahogs *Arctica islandica* on the western Atlantic US continental shelf

Sara M. Pace^{1,*}, Eric N. Powell¹, Roger Mann², M. Chase Long²

¹Gulf Coast Research Laboratory, University of Southern Mississippi, Ocean Springs, MS 39564, USA

²Virginia Institute of Marine Science, The College of William and Mary, Gloucester Point, VA 23062-1346, USA

ABSTRACT: Geographic differences in the age structure of 4 populations of ocean quahogs *Arctica islandica* throughout the range of the stock within the US exclusive economic zone were examined. The ages of animals fully recruited to the commercial fishery (≥ 80 mm shell length) were estimated using annual growth lines in the hinge plate. The observed age frequency from each site was used to develop an age–length key enabling reconstruction of the population age frequency for the site. Within-site variability was high for both age-at-length and length-at-age; a single age–length key could not be applied and would not result in accurate age estimates for populations throughout the northwestern Atlantic. For most sites, the oldest living animals recruited 200–250 years BP, coincident with the ending of the Little Ice Age. The southern populations had the oldest animals, consistent with a presumed warming from the south. All sites experienced an increase in recruitment beginning in the late 1800s to early 1900s depending upon site, whereupon the populations reached carrying capacity and remained so characterized subsequently through more or less continuous low-level recruitment. The lag in population expansion following recruitment of the oldest living animals is consistent with the extended time to maturity in the species and suggests that the oldest animals record initial colonization near the end of the Little Ice Age. All 4 populations show evidence of high recruitment capacity when below carrying capacity and relatively continuous recruitment when at carrying capacity.

KEY WORDS: Ocean quahog · *Arctica islandica* · Age–frequency distribution · Age–length key · Recruitment

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

The ocean quahog *Arctica islandica* (Linnaeus, 1769) is a large, commercially important bivalve mollusc, widely distributed along the continental shelf on both coasts of the North Atlantic basin (Merrill & Ropes 1969, Dahlgren et al. 2000). The species ranges from Cape Hatteras, NC, USA, to Newfoundland, Canada, and from the Bay of Cadiz in Spain north to Iceland (Merrill & Ropes 1969, Dahlgren et al. 2000, for further documentation of the North Atlantic range, see Brey et al. 1990, Rowell et al. 1990, Witbaard et al. 1999, Ragnarsson & Thórarins-

dóttir 2002, Butler et al. 2009). The species has a life span exceeding 500 yr (Butler et al. 2013), growing to a maximum size of approximately 130 mm, with animals > 200 yr old commonly encountered.

A major ocean quahog fishery has existed on the Mid-Atlantic continental shelf of the USA since 1967 (NEFSC 2009). Annual ocean quahog landings peaked at 22 000 mt in 1992; US landings in recent years (2010–2014) have ranged from about 14 000 to 16 000 mt (NEFSC 2009). A small commercial fishery for ocean quahogs began in Iceland in 1995 but was limited to 1 fishing vessel (Thórarinsdóttir & Jacobson 2005, Thórarinsdóttir et al. 2010); the Icelandic

*Corresponding author: sara.pace@usm.edu

fishery is currently artisanal and catches have been negligible since 2005.

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

In addition, recruitment rates for long-lived species are generally thought to be inherently low. Broodstock-recruitment relationships for long-lived finfish often show low steepness, a characteristic of a species with limited recruitment capacity and an extended time frame for population recovery following a population decline (Goodwin et al. 2006, Mangel et al. 2010). The same may be true for many long-lived invertebrates, although documentation is more limited (e.g. Peterson & Summerson 1992, Peterson 2002). Indeed, broodstock-recruitment relationships are rarely reported (e.g. Hancock 1973, Honkoop et al. 1998, Kraeuter et al. 2005, Powell et al. 2009). Often, recruitment rates are low despite high fecundity due to larval and post-settlement mortality (e.g. Thorson 1950, Ólafsson et al. 1994, van der Meer 2003), but Allee effects and broodstock limitation can also be present (Peterson & Summerson 1992, Kraeuter et al. 2005). For ocean quahogs, the time necessary to build a population to carrying capacity after initial colonization or to rebuild a population after overfishing and the ability of the population to

remain at carrying capacity through years of variable recruitment and mortality is poorly known. Ocean quahogs, being extremely long-lived and certainly the most successful of the extremely long-lived non-colonial marine invertebrates, offer a particularly interesting opportunity to study the population dynamics of recruitment during population expansion and when at carrying capacity. Indeed, Pace et al. (2017) suggest that recruitment capacity is high, but scarcely evident at carrying capacity, where only limited recruitment is necessary to balance the low natural mortality rate characteristic of the species.

The objective of this study was to evaluate long-term recruitment patterns of ocean quahogs from 3 sites in the Mid-Atlantic and to compare these patterns to that of the Georges Bank population previously described by Pace et al. (2017) using the age frequencies of the existing populations. Sites were chosen to cover much of the range of the stock in US waters to establish the feasibility of applying a single age-length key to length-frequency data routinely obtained by the stock survey (NEFSC 2017) and to identify geographic variations in recruitment timing and periodicity, such variations being well known for other commercially important shellfish in the region (e.g. *Spisula solidissima*, Weinberg 1999, Chintala and Grassle 2001; *Placopecten magellanicus*, McGarvey et al. 1993, NEFSC 2014). For *A. islandica*, significant recruitment events may occur on decadal to vicennial time scales (Steingrímsson & Thórarinsdóttir 1995, Powell & Mann 2005, Thórarinsdóttir & Jacobson 2005, Harding et al. 2008). However these studies, being based primarily on juvenile surveys, offer information on only a small fraction of the extended life span of this species and cover a restricted geographic range; thus their application to the extended life history of the population is unclear. In addition, in most cases, these studies addressed a species at or near carrying capacity, with the limitation on recruitment anticipated to co-occur (Hughes 1990, Brooks & Powers 2007).

Hennen (2015) assumed a low steepness value in specifying a theoretical broodstock-recruitment relationship for *A. islandica*. Low steepness invokes one of 2 reproductive strategies for long-lived organisms. In one case, recruitment capacity is low and the species relies on limited but routine recruitment over its lifetime, hence low steepness. Alternatively, recruitment capacity is high, but its potential infrequently realized. This may be expressed by the absence of a broodstock-recruitment relationship. The latter, often termed bet-hedging (Stearns 1976) may better apply to bivalves, whereas the former

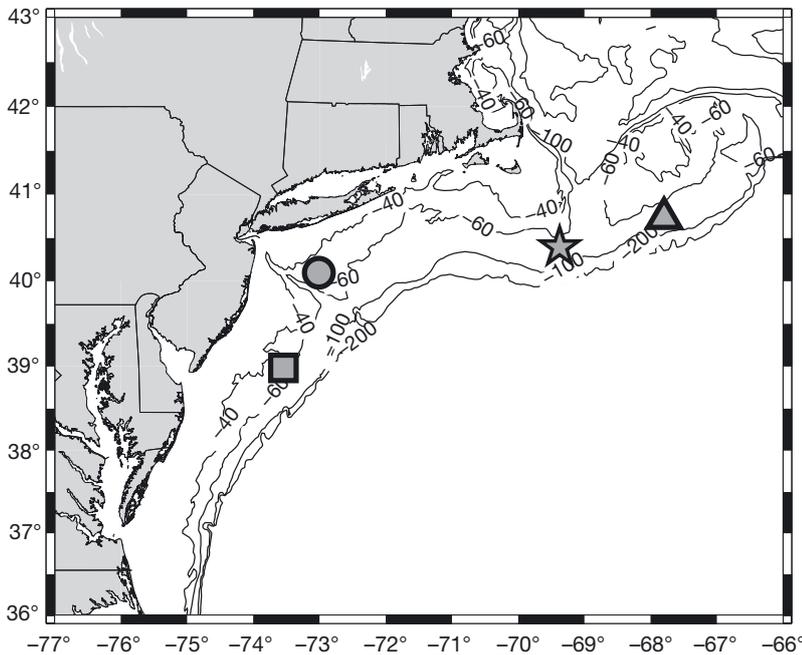


Fig. 1. Location of sample collection sites: New Jersey (square), Long Island (circle), Southern New England (star), and Georges Bank (triangle). Depth in m

may better apply to long-lived fish (Hancock 1973, Goodwin et al. 2006). Regardless, the 2 alternatives lead to substantively different management options. Hennen's (2015) analysis stressed the importance of understanding recruitment over centennial time scales and this is one focus of the present study. The approach used here includes estimation of the age of individuals by counting annual growth lines using photographs of a cross-section of the hinge plate, followed by development of age–length keys for each site from the observed ages-at-length. These then were used to reconstruct the population age frequency from which an evaluation of long-term recruitment patterns could be deduced. This database is then used to address the feasibility of geographic scale assumptions of uniformity in age–length keys and the dynamics of recruitment at centennial scales, knowledge on both being essential to the sustainable management of the ocean quahog fishery.

MATERIALS AND METHODS

Sample collection

Ocean quahog samples were collected from New Jersey and Long Island from the F/V 'Christy' in March 2015; samples from Southern New England

and Georges Bank (Pace et al. 2017) were collected in May 2015 from the F/V 'Pursuit' (Fig. 1). All samples were collected using hydraulic dredges towed for 5 min. Ocean quahogs with shell lengths (anterior–posterior dimension) ≥ 80 mm were targeted by this project, as the sampling gear is nearly 100% selective for this size range (NEFSC 2017). All sites except the Southern New England site required multiple tows in order to obtain sufficient sample sizes; however, all additional tows were taken from as close to the same location as possible so that each sample comprised animals from the same local population. To ensure that each sample contained an adequate number of the largest and presumably oldest animals present in the populations, all live ocean quahogs retained by the dredge were measured to capture the size frequency of each population.

From this group, about 800 animals ≥ 80 mm, relatively evenly distributed across the size range captured, were retained for further study.

Sample preparation

Shucked clams were dipped in diluted bleach, rinsed in water, and air-dried. Intact valves were labeled and archived. At each site, at least 20 clams from each 5 mm size class were haphazardly chosen from the collection, starting with the 80 to <85 mm size class through the maximum available size for each site. Hereafter, the size classes will be referred to using the lower size class boundary, e.g. 80 mm for animals 80 to <85 mm.

Each clam chosen to be aged was sectioned, ground, and polished (see details in Pace et al. 2017). The hinge plate of each clam was photographed using either a high-definition Olympus DP73 digital microscope camera using the Olympus cellSens microscope imaging software or a high definition Olympus America microscope camera using Olympus MicroSuite software. Neither camera could capture a single image of the hinge plate at a magnification high enough to discriminate annual growth lines; multiple images of the hinge were required to produce a complete hinge image. The Olympus cellSens microscope imaging software automatically

stitched images of the hinge together; the hinge photographs taken using the alternative software were stitched together using the open source software ImageJ (FIJI) to create a complete image of the hinge section. Both cameras provided images at a resolution sufficient to distinguish annual growth lines without the use of acetate peels or staining methods. To estimate the age for each clam, its hinge image was examined and each annual growth line annotated using the ObjectJ plugin in the software ImageJ (Fig. 2).

Creating age–length keys

As shown in Pace et al. (2017), the range of observed ages for a sample size of less than 200 individuals at a sample site greatly underrepresents the entire age range present in a population. Consequently, estimating the probability of age-at-length based only on observed ages likely biases the probability of any age occurring at a given length; in particular, some ages present in the population are not observed (Pace et al. 2017). Thus, an age–length key must be constructed from a sparse dataset. This is not an unusual challenge (e.g. MacDonald & Pitcher 1979, Mohn 1994, Stari et al. 2010). In the case of *A. islandica*, the age distributions were typically right-skewed within each 5 mm size class at each site. That is, animals of younger age had a higher probability of occurrence than animals of older age within a size class, and a long tail comprising the rarer and much older animals was present. To address the problem posed by unobserved ages within the observed age range without having knowledge of the underlying age distribution within each size class, 4 metrics were defined for each set of ages within each 5 mm size class; namely, the mean age, the variance in age,

the mean differential in years between consecutive ages ordered from youngest to oldest, and the variance in the mean differential between consecutive ages. Sets of ages were simulated within each 5 mm size class using a Monte Carlo routine, and at least 10 individual sets that fell within a 10th percentile of the position of the observed age group for all 4 metrics were selected and considered valid estimates of the age probability in addition to the observed group. These age groups were used to construct the probability of age-at-length within each size class (for further details on the methodology used, see Pace et al. 2017).

To investigate the representativeness of the set of 20 animals aged per 5 mm size class, a size class with a particularly skewed distribution was chosen from each site. This was a size class that was significantly different from a random draw of ages within the observed age range; that is, a size class with the age distribution least likely to occur by chance based on the 4 defined metrics previously described. An additional 20 animals were haphazardly chosen from the original set of animals obtained that fell within that size class. These animals were aged. This second set of ages was compared to the first set using a permutation test in which 1000 sets of ages were drawn without replacement from the combined dataset and the second set of ages was then compared to the distribution obtained from the probabilities of the 4 metrics to determine the representativeness of the second set of ages and, by inference, the additional 10 sets of simulated ages (Noreen 1989).

Most cases represented a random draw from the combined dataset; this supported the assumption that a sample size of 20 individuals within each size class was sufficient to represent the age distribution. For cases where the second set did not represent a random draw from the combined dataset, the com-

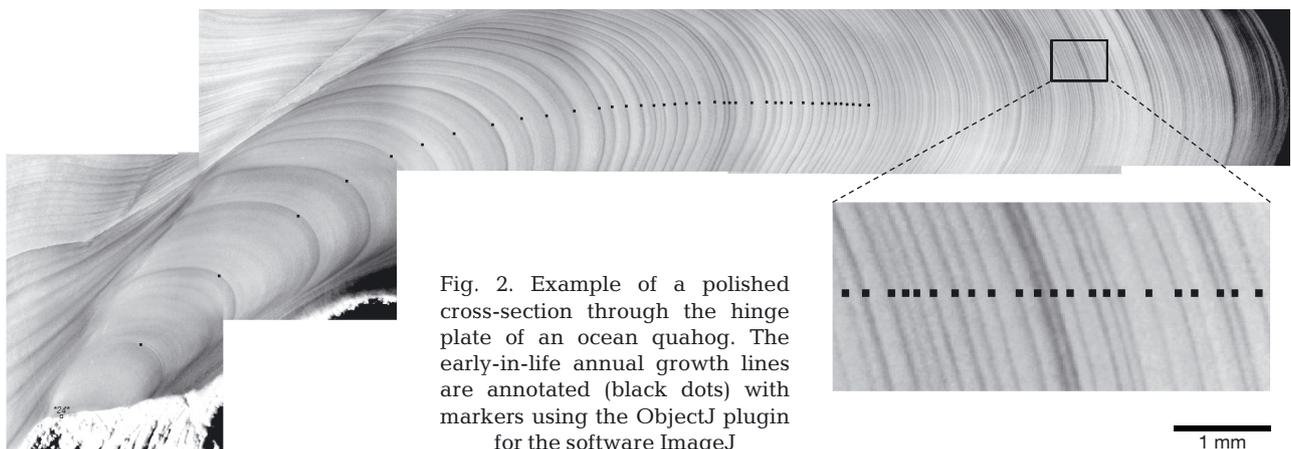


Fig. 2. Example of a polished cross-section through the hinge plate of an ocean quahog. The early-in-life annual growth lines are annotated (black dots) with markers using the ObjectJ plugin for the software ImageJ

bined dataset was resampled again 1000 times, each selection of 20 individuals again evaluated using the permutation test, and the probability of each metric recorded. In this way, the likelihood of the original second set being fairly drawn from the combined dataset could be evaluated. For example, if the original second set of 20 was significantly different from the first for a given metric and that outcome occurred only a few times out of the 1000 independently drawn sets of 20, this analysis would suggest that the age distribution of the second set drawn was highly unlikely to occur again by chance if 40 different clams had been aged. To further investigate the effect of significant differences in age distribution between 2 sets of 20 individuals from the same size class, 2 population age frequencies were generated, the first using the age estimates from the original sample only; the second using the ages from the resample. A Kolmogorov-Smirnov 2-sample test (Daniel 1978) was run to determine if the 2 population age–frequency distributions differed significantly.

The age–length keys were then applied to the complete size distribution for each site to generate a population age frequency, which specifies the proportion of individuals at each age within each population. Recruitment patterns can be interpreted from the number of individuals present at each age under the assumption that mortality rates have not varied much over time, as variations in numbers at age inherently confound variability in recruitment and variability in mortality. The expected conservatism of adult mortality rate is supported by the presence of animals exceeding an age of 200 yr in the population. For this reason, large changes in proportional contribution between age classes is interpreted as evidence of variations in recruitment.

RESULTS

Age and length dynamics

The size–frequency distributions obtained from the measurement of all individuals retained by the dredge at each site are shown in Fig. 3. The total number of clams measured was 2448 (New Jersey), 2443 (Long Island), and 2453 (Southern New England). Of these clams, 189 individuals ≥ 80 mm were aged from New Jersey, 154 from Long Island, and 118 from Southern New England.

The distribution of observed ages-at-length for ocean quahogs from each site is shown in Fig. 4.

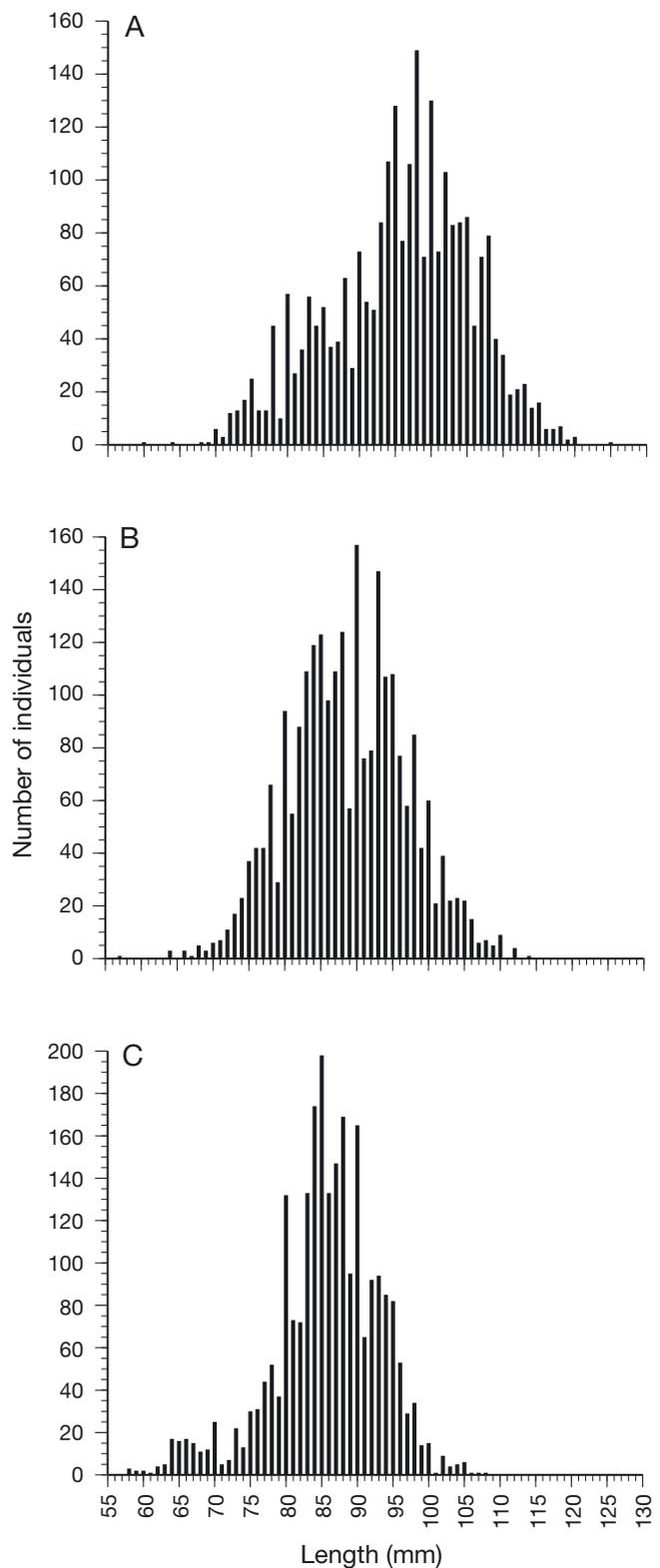


Fig. 3. Size–frequency distribution of all measured clams from (A) New Jersey, (B) Long Island, (C) Southern New England. See Pace et al. (2017), their Fig. 3, for Georges Bank

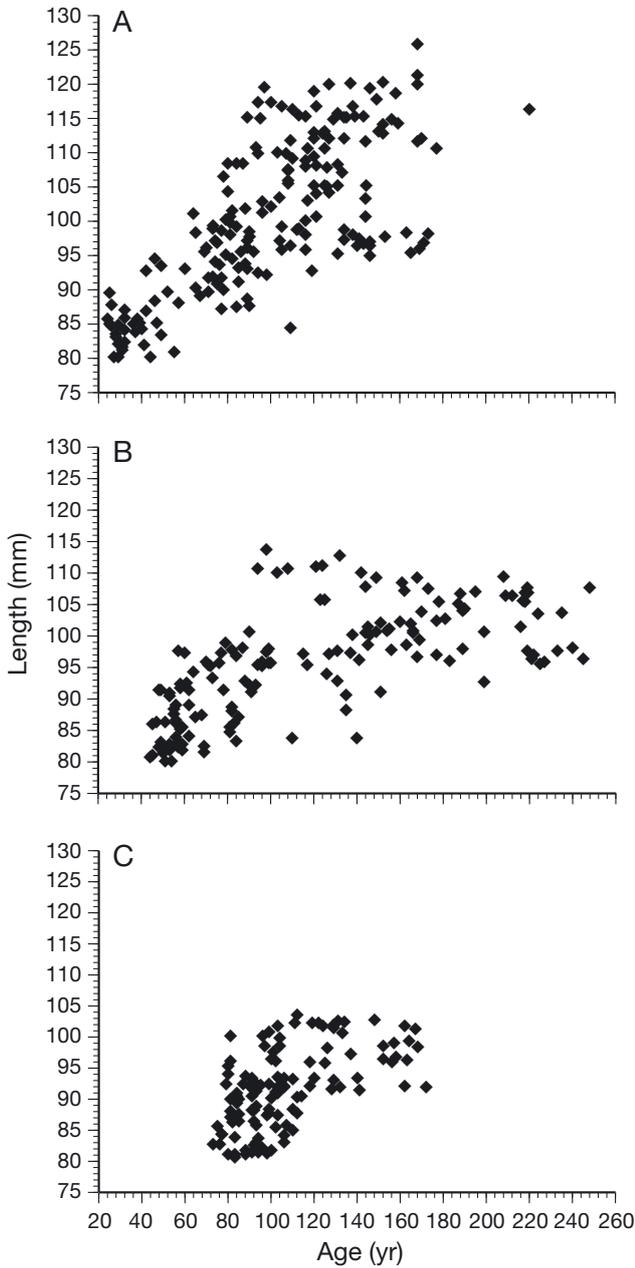


Fig. 4. Age estimates for animals based on direct counts of hinge growth lines. (A) New Jersey, (B) Long Island, (C) Southern New England. See Pace et al. (2017), their Fig. 4, for Georges Bank

Within each size class, ocean quahog populations exhibited a large age range (Fig. 5). The age and size distributions at each site are shown in Table 1. Clams aged from New Jersey ranged from 24 to 220 yr, covering an age range of nearly 200 yr. The age range was nearly the same for Long Island clams: 44 to 248 yr. Clams from Southern New England covered a narrower age range from 73 to 172 yr old. Pace et al.

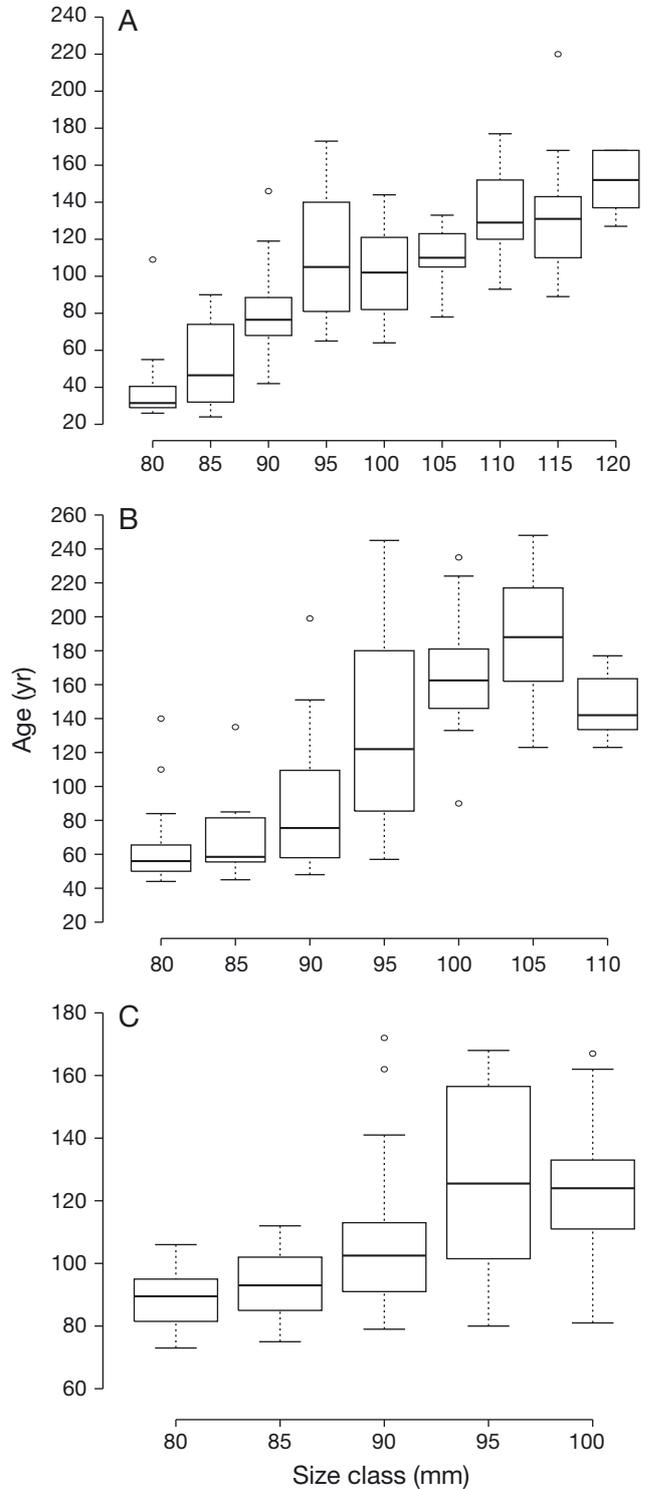


Fig. 5. Observed age range for each size class for (A) New Jersey, (B) Long Island, and (C) Southern New England. Size values represent the lower boundary of each size class. Dark horizontal lines are the median ages of animals plotted in Fig. 4, boxes show the interquartile range (IQR) of these ages, whiskers represent the full age range excluding outliers (circles) ± 1.5 IQR outside of the box

Table 1. Observed age range and largest animal aged at each site. Georges Bank data from Pace et al. (2017)

Region	Age range (yr)	Birth date range	Largest animal (mm)
New Jersey	24–220	1795–1991	125
Long Island	44–248	1767–1971	115
Southern New England	73–172	1843–1942	105
Georges Bank	54–198	1817–1961	116

(2017) reported that clams from a Georges Bank site ranged from 54 to 198 yr. A large size range at age also exists throughout most of the observed age range at all sites (Fig. 4). That is, the age and length relationship for market-size ocean quahogs at each of these sites is highly variable whether described in terms of age-at-length or length-at-age. Moreover, at all sites, the intermediate size classes displayed the largest age ranges. Ages in the 95 mm size class from New Jersey spanned 108 yr. Long Island had the largest age range of 188 yr in the 95 mm size class. In the Southern New England population, ages spanned 93 yr in the 90 mm size class.

The test statistics for each metric used to identify whether the sampled ages within each size class were randomly distributed are shown for each site in Table 2. Shaded boxes indicate cases where the distribution of observed ages was unlikely to be obtained from a random draw of ages within the observed age range. Size classes with the most non-random distributions varied throughout the size-class range. In New Jersey, the 90 mm and the 115 mm size classes had the most non-random age distributions, which might have been anticipated considering the old-age outliers present in both size classes (Fig. 5). The Long Island population provided the most non-random distributions, with 3 of 4 metrics significantly non-random in the 3 smallest size classes, whereas the 2 largest size classes did not diverge from a random distribution in any metric. The Southern New England population had 1 size class (90 mm) with 3 of 4 metrics significantly diverging from random, with the most non-random distribution coinciding with the size class with the largest age range. Pace et al. (2017) found a similar pattern in a Georges Bank population in the 100 mm size class, which exhibited the largest age range of 125 yr, with 3 of 4 significantly non-random metrics.

Based on the statistics shown in Table 2, 10 age groups having a similar age distribution pattern were obtained as simulated datasets. These distributions

Table 2. Test statistics comparing the observed distribution of ages to that expected from a random draw of ages from the age range recorded in the size class for the observed mean (\bar{x}), the observed variance (var), the observed mean of the differences of consecutive pairs of animals ordered by their age ($d\bar{x}$), and the observed variance of these differences ($d\text{var}$) within each size class for each site. Sizes are the lower size boundary of the size class. Cases where the observed distribution of ages were unlikely to be obtained by a random draw of ages in the observed age range are shaded. NJ: New Jersey; LI: Long Island; SNE: Southern New England

	80 mm	85 mm	90 mm	95 mm	100 mm	105 mm	110 mm	115 mm	120 mm
NJ \bar{x}	p < 0.005	0.005 < p < 0.05	p < 0.005	0.05 < p < 0.1	0.5 < p < 0.6	0.9 < p < 0.95	0.5 < p < 0.6	p < 0.005	0.6 < p < 0.7
NJ var	0.1 < p < 0.2	0.3 < p < 0.4	0.005 < p < 0.05	p = 0.6	0.2 < p < 0.3	0.1 < p < 0.2	0.1 < p < 0.2	0.005 < p < 0.05	0.5 < p < 0.6
NJ $d\bar{x}$	p = 0.4	p = 0.4	p = 0.4	0.4 < p < 0.5	0.4 < p < 0.5	p = 0.4	p = 0.4	0.4 < p < 0.5	0.4 < p < 0.5
NJ $d\text{var}$	0.8 < p < 0.9	0.6 < p < 0.7	0.9 < p < 0.95	0.8 < p < 0.9	0.8 < p < 0.9	0.3 < p < 0.4	0.3 < p < 0.4	p > 0.99	0.4 < p < 0.5
LI \bar{x}	p < 0.005	p < 0.005	p < 0.005	0.005 < p < 0.05	0.6 < p < 0.7	0.5 < p < 0.6	0.3 < p < 0.4		
LI var	0.005 < p < 0.05	0.005 < p < 0.05	0.05 < p < 0.1	0.6 < p < 0.7	0.005 < p < 0.05	0.1 < p < 0.2	0.4 < p < 0.5		
LI $d\bar{x}$	p = 0.4	0.4 < p < 0.5	0.4 < p < 0.5	0.4 < p < 0.5	0.95 < p < 0.99	p = 0.4	0.4 < p < 0.5		
LI $d\text{var}$	p > 0.99	p > 0.99	p > 0.99	0.8 < p < 0.9	0.8 < p < 0.9	0.8 < p < 0.9	0.4 < p < 0.5		
SNE \bar{x}	p < 0.005	0.5 < p < 0.6	p < 0.005	0.6 < p < 0.7	0.4 < p < 0.5				
SNE var	p = 0.3	0.2 < p < 0.3	p < 0.005	0.7 < p < 0.8	0.05 < p < 0.1				
SNE $d\bar{x}$	p = 0.6	p = 0.6	p = 0.4	0.4 < p < 0.5	p = 0.4				
SNE $d\text{var}$	0.6 < p < 0.7	0.7 < p < 0.8	p > 0.99	0.8 < p < 0.9	0.3 < p < 0.4				

retained the statistical characteristics for the 4 metrics in that they fell within the shown percentiles and were used in addition to the observed age dataset to establish the probabilities for age-at-length within each size class.

Representativeness of aged subsets

Based on the statistics shown in Table 2 and Fig. 5, one size class with a highly skewed age range was chosen from each site and an additional 20 ocean quahogs were aged to evaluate the representativeness of the original 20 aged animals. Size classes with additional animals sampled were as follows: 95 mm (New Jersey) and 90 mm (Long Island and Southern New England). Table 3 shows the ages for the original and resampled set of animals from each site. Analyses from a Georges Bank population reported by Pace et al. (2017) are also included. Shaded boxes indicate cases where an age present among the resampled 20 individuals was also present in the original set of ages. At all sites, not more than 25% of a second set of 20 animals were of an age identified in

Table 3. Age data from the (1) original 20 clams chosen to be aged and (2) the resample of 20 additional individuals for the New Jersey (NJ) 95 mm size class, the Long Island (LI) 90 mm size class, the Southern New England (SNE) 90 mm size class, and the Georges Bank (GB) 100 mm size class (Pace et al. 2017). Shaded boxes highlight ages present in the first set of 20 that were also observed in the second set of 20. Note the selected size classes correspond to those classes with outliers and extended age ranges (see Fig. 5)

NJ1	NJ2	LI1	LI2	SNE1	SNE2	GB1	GB2
65	73	57	76	79	80	73	81
69	81	60	82	81	87	75	82
70	84	70	84	84	88	79	86
73	89	71	87	84	91	99	90
74	90	72	96	85	92	101	104
75	104	77	99	90	93	103	107
77	116	79	99	91	93	106	109
79	131	94	100	91	93	106	113
81	134	96	115	95	99	107	117
86	134	98	127	103	100	110	122
89	138	117	141	104	102	112	122
90	140	131	156	106	103	114	123
92	141	137	163	114	103	114	125
105	143	145	168	118	103	115	128
105	146	169	183	120	106	118	131
109	146	177	189	128	106	121	135
112	165	221	219	129	110	134	139
113	169	227	222	132	112	165	152
116	171	233	225	162	140	182	166
153	173	240	243	172	141	198	198

the earlier set of 20. Taking the 40 animals as a whole, duplicate ages occurred in no more than 5 cases in any of the 4 size classes sampled twice and as few as 1 in the Long Island and 2 in the Georges Bank cases. Triplicates occurred only twice, both in the Southern New England dataset. Pace et al. (2017) reported that only 2 ages were found in both datasets for a Georges Bank site. Thus, at all sites, the addition of a second set of 20 animals added a large number of ages that were not represented in the first set of ages, confirming that many more animals would need to be aged in order to establish an age-length relationship based solely upon observed ages and lengths.

For each site, a permutation test was run to determine whether the distribution of age estimates from the resampled set deviated significantly from that of the combined set of ages. At 2 of the 3 sites, in addition to the Georges Bank site (Pace et al. 2017), none of the 4 metrics were significantly different; that is, the resample dataset could be obtained as a random draw from the combined set of ages (Table 4). The absence of test metrics diverging from random at the Georges Bank, Long Island, and Southern New England sites suggests that the age distribution derived from the first 20 animals aged adequately represented the distribution function for the age range within that size class. As the analyzed size classes were chosen because the age distributions were ones showing significant deviations from a random distribution of ages, by inference, the age distributions for the remaining size classes are likely also to be representative.

In contrast to the other 3 sites, 3 of 4 test metrics for the resample differed significantly from the combined dataset for the New Jersey population (Table 4), suggesting that the first sample of 20 did not sufficiently describe the age distribution within this size class. Perusal of Table 3 shows that the primary difference between the 2 datasets is that the resample contains many ages falling within a large age gap (116 to 153 yr) in the first set. These 2

Table 4. Permutation test statistics (p) for the observed mean (\bar{x}), observed variance (var), observed mean of the difference in ages of animals ordered by their age ($d\bar{x}$), and the observed variance of these differences ($d\text{ var}$)

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

Table 5. New Jersey age–length key: for convenience, the probability of each decadal age group occurring within each size class is provided. Population age frequencies derived in this study used the probability at each age rather than the decadal age group

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

datasets came from the same group of clams, each chosen haphazardly from the group. To further examine this issue, the combined set of 40 was randomly split in half 1000 times and the permutation test run each time to evaluate the probability of obtaining a split providing 2 datasets as deviant as were the observed 2. In all 3 cases, the observed probability of each test metric occurred less than 7 times out of 1000, twice for the observed mean, thrice for the observed variance, and 7 times for the observed variance in the differences obtained from the set of ordered ages. These results suggest that obtaining the observed split from the set of 40 aged animals is statistically highly improbable. By inference, one would assume that a second set of 20 drawn from any of the remaining size classes would demonstrate a selection of ages diverging in detail from the original set as shown in Table 3, but not diverging in the distribution function for that size class. As it was infeasible to age several scores of animals within each size class from each population due to the time required, even using the advanced camera technology employed in this project, and because at the other 3 sites 20 animals sufficiently described the age distribution of the most extreme size class, 20 animals within each size class were taken as an acceptable sample size to describe the dispersion of ages within a size class.

Age–length keys

Age–length keys for New Jersey (Table 5), Long Island (Table 6), and Southern New England (Table 7) were generated by establishing the probability for each age within each size class, based on the observed age group plus the 10 simulated age groups for each size class. For simplicity of presentation, each key displays decadal age groups and size classes; zero probabilities in the tables indicate the absence of animals at that size and age given the sampling constraints. Population age frequencies shown subsequently, however, were obtained using the probabilities of each observed age in each size class rather than the decadal age groups shown in Tables 5–7.

The population age frequencies are shown in the Supplement at www.int-res.com/articles/suppl/m585p081_supp.pdf for New Jersey (Table S1), Long Island (Table S2) and Southern New England (Table S3). Pace et al. (2017) provide an additional example from a Georges Bank population. The age frequencies display the estimated number of individuals at age in the population sample obtained at each site. The population age frequencies were generated from age–length keys that included observed ages and the 10 simulation groups. The population age frequencies, had the 10 simulated groups not been

Table 6. Long Island age–length key: for convenience, the probability of each decadal age group occurring within each 5 mm size class is provided. Population age frequencies derived in this study used the probability at each age rather than the decadal age group

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

included, are shown in Tables S4–S6 for comparison. The observed age frequencies clearly miss many ages that one may expect are present in the population (see Table 3) given the results of the resampled size classes (Table 3), but are absent from the observed dataset due to the small sample size (compare Tables S1–S3 with Tables S4–S6).

Two additional age frequencies were generated for the New Jersey site to address the issue of significantly different results obtained from the permutation test

Table 7. Southern New England age–length key: for convenience, the probability of each decadal age group occurring within each size class is provided. Population age frequencies derived in this study used the probability at each age rather than the decadal age group

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

when the resample was included, the first using only the original set of ages to represent the 95 mm size class and the second using only the resampled ages. Significant differences between the population age–frequency distributions were not detected (Kolmogorov-Smirnov 2-sample test, $D_{201} = 0.108$, $p > 0.05$), despite the significant difference between the age distributions of the 2 sets of 20 age estimates for this size class. Thus, the differences in the age distributions of the 2 samples in the 95 mm size class did not significantly affect the population age-frequency distribution derived for this population.

Population age frequency

The population age-frequencies for all 4 sites, including the Georges Bank population reported by Pace et al. (2017), are shown in Fig. 6. The age structure differs substantially throughout the New Jersey to Georges Bank region, which encompasses the majority of the US ocean quahog stock. The ocean quahog populations at the New Jersey and Long Island sites have age ranges spanning at least 200 yr. New Jersey had the youngest animals that were fully recruited to the fishery, with animals ≥ 80 mm as young as the low 20s, indicating that ocean quahog populations in New Jersey have the most rapid growth rate of the 4 sites. Compare this to the Southern New England site, where the youngest animals ≥ 80 mm had ages in the low 70s.

Table 8 displays a summary of the age structures including data from Pace et al. (2017). In all 4 cases, the age structure is characterized by a long tail of relatively rare old animals and an extended age range of abundant younger animals, separated by a rapid increase in numbers at age over a relatively short time. In each case, the number of ocean quahogs in the youngest age classes decreases. This is due to the artificial truncation of the dataset at shell length 80 mm, not to a reduction in recruitment or an increase in mortality. All sizes including young of the year would have to be aged in order to completely fill out the population age–frequency distribution.

Unlike the 3 other sample sites, examination of the population age–frequency distributions (Fig. 6) reveals that the New Jersey population does not display a particularly long tail of low numbers of older animals on the right side of the distribution. Few ani-

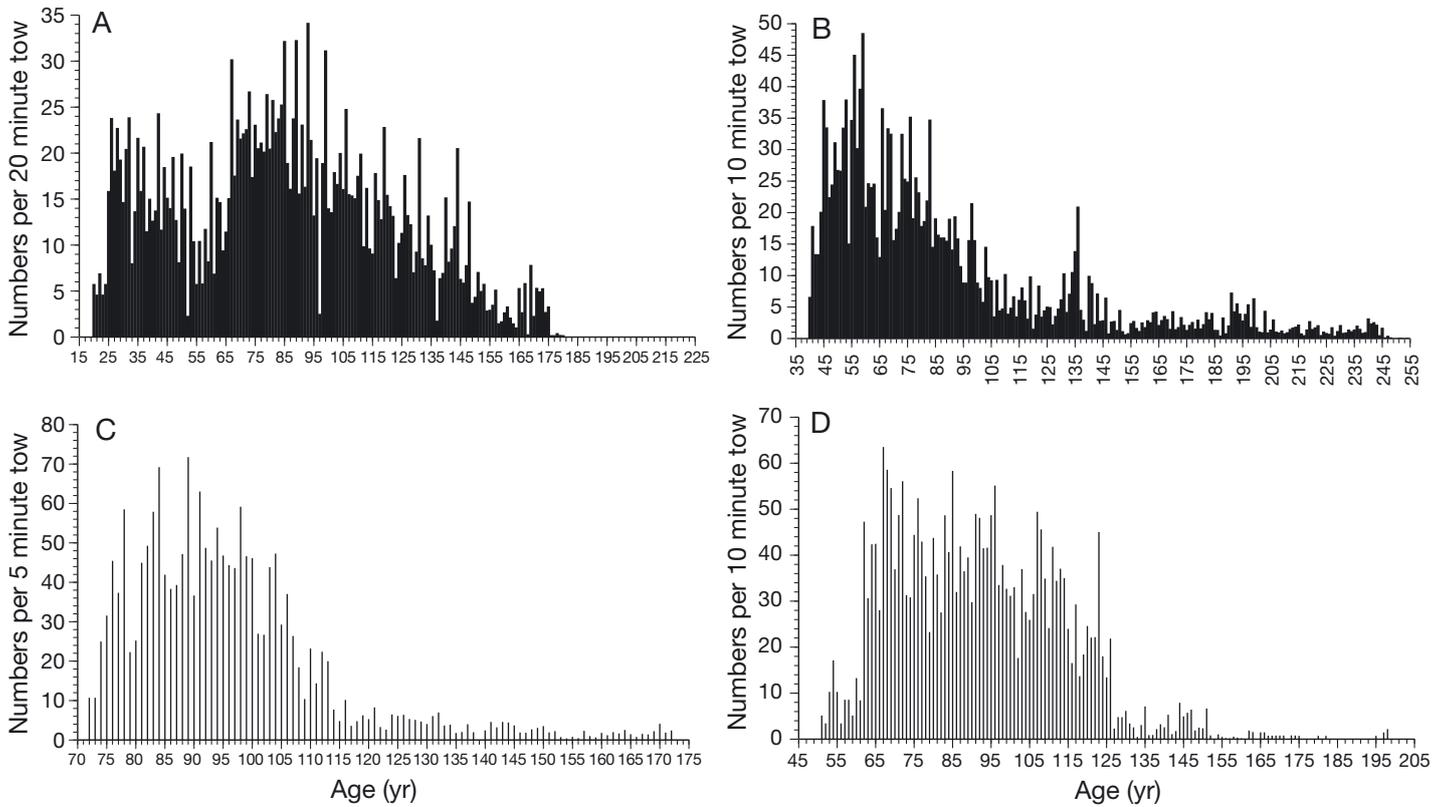


Fig. 6. Age–frequency distributions for (A) New Jersey, (B) Long Island, (C) Southern New England, and (D) Georges Bank (Pace et al. 2017). Truncation at young ages is due to sample truncation at 80 mm; smaller and by inference mostly younger clams were not aged. Note that the x-axis and y-axis scales differ among plots

mals over 200 yr old were present, but the oldest relatively common animals recruited circa 1835, with the population expanding in size relatively continuously from 1855 until approaching an asymptote around 1900 when the population apparently stabilized. The population consists of a small number of animals over 140 yr, a larger number of animals between 100–140 yr, and the largest number of animals <100 yr. An extended period of relatively low recruitment occurred from 1950–1965, as indicated

Table 8. Summary of the age structure and period over which rapid recruitment occurred at each site, including Georges Bank (Pace et al. 2017). Expansion years are visually approximated from Fig. 6. Population age frequencies were used to determine age percentiles. NJ: New Jersey; LI: Long Island; SNE: Southern New England; GB: Georges Bank

Region	Recruitment expansion start	Recruitment expansion end	5th, 25th, 50th, 75th percentile age
NJ	1855	1900	30, 70, 121, 171
LI	1895	1935	50, 93, 147, 200
SNE	1900	1915	77, 97, 122, 147
GB	1890	1920	58, 88, 125, 162

by the reduction in the number of individuals present between the ages of 50–65 yr.

The Long Island population has the longest tail, suggesting that, with the exception of a particularly large year class around 1880, the population remained at low abundance from circa 1765 until approximately 1895. After 1895, the population expanded rapidly over about 40 yr and stabilized in ca. 1935. The population age structure in Long Island consists of a small number of animals between 120–255 yr, with the majority of the population between the ages of 40–120 yr; no obvious hiatuses in recruitment exist, however.

The Southern New England site has been occupied by ocean quahogs since at least the 1840s, the shortest record of occupation of the 4 sites. The population apparently remained small in size until approximately 1900; 15 yr later, by 1915, the population had apparently approached carrying capacity. The population consists of a large number of animals between about 70–100 yr old, fewer animals between 100–115 yr old, and a consistently low number of animals 115–175 yr old (Fig. 6). Recruitment hiatuses are not apparent.

As a comparison, the oldest animals aged from the Georges Bank population, as previously described by Pace et al. (2017), recruited about 200 yr ago, ca. 1815, after which the population remained small in size for about 70 yr, as indicated by the small number of animals older than 125 yr. Around 1890, the population began to increase in size very rapidly, reaching about half of its final asymptotic state in only 5–10 yr; a second population expansion occurred around 1915 and approached a higher asymptote within approximately 5 yr. The population consists of a large number of individuals between the ages of 65–100 yr, with a smaller number of animals in the 100–125 yr range. Following population expansion, recruitment hiatuses are not apparent.

DISCUSSION

Age–length keys

The population dynamics of ocean quahogs are highly variable over the species' range. For the populations on the US East Coast, regional variation is substantial, as is apparent from the age–length keys presented in Tables 5–7. A single age–length key cannot be used to estimate the age structure of populations from these different regions, considering the large variation in age-at-length and the size range of animals present. Fig. 4 demonstrates this large variability in both age-at-length and length-at-age, and the differences in these distributions at each of the 3 sites illustrate why a single age–length key would not result in accurate age estimates throughout the Mid-Atlantic. The youngest animal aged in New Jersey was 24 yr old at 80 mm, whereas the youngest animal of comparable size from Southern New England was 73 yr old. Additionally, the variability in maximum shell length at each site would prohibit accurate age estimates throughout the species range; for example, the maximum shell length of animals aged at Southern New England was 105 mm, whereas the largest animal aged from New Jersey was 125 mm.

The development of an age–length key for ocean quahogs is challenged by the time required to age individual animals, the age range present in most populations, and the presence of individuals of many ages within a narrow size range. Moreover, the population is not composed of a few dominant year classes; indeed, dominant year classes appear to be remarkably rare; even dominant decadal recruitment events appear to be rare. This is true for the 4 populations reviewed here and would appear to be true

for other North Atlantic populations reported in the literature (Steingrímsson & Thórarinsdóttir 1995, Ridgway et al. 2012). Moreover and more unfortunately, the range of ages in a narrow size class (e.g. 5 mm) is large and the dispersion of ages within a narrow size class is rarely random, often being highly right-skewed and typically differing substantively from even the abutting lower and higher size class. As a consequence, a large number of animals must be aged from each size class to support a standard age–length key for a specific population and a large number of populations must be aged to characterize the regional metapopulation. These types of challenges are well known (e.g. MacDonald & Pitcher 1979, Mohn 1994, Stari et al. 2010), but ocean quahogs represent an extreme example of the common challenge of ageing sufficient numbers of animals to characterize the population demographic.

Consequently, any age-dependent analysis of population dynamics requires a way to estimate age-at-length from a sparse dataset. Harding et al. (2008) approached this problem for small and mostly juvenile ocean quahogs by applying a Taylor's power law correction. Essentially, they assumed a normal distribution of ages-at-length with an expanding variance as the age increased. For animals early in their life history, this assumption is generally appropriate (e.g. Craig & Oertel 1966, Hofmann et al. 2006) as it proved to be in the case of Harding et al. (2008). Hofmann et al. (2006) provided a mathematical basis for the description of population age structure based on a bivariate normal distribution function with an increasing right skew with increasing age. Ocean quahogs represent an extreme case in which many age distributions at size are represented by an extended right skew. Consequently, in this study, we utilized an approach that assumed that the age distribution function as observed in a length class from a restricted set of aged animals, 20 in this case, was sufficient to define the age distribution function for the length class. We also assumed that the set of ages observed was a small subset of the sets of ages that might be obtained that remained true to that age distribution function. We tested this in several ways by focusing on a few length classes that contained the most non-random distribution of ages across the observed age range. Despite the significant difference between the age distributions of the original and resampled animals from the 95 mm size class for the New Jersey population, these analyses suggest that a sample size of 20 animals sufficiently represents the age distribution within each size class to develop an age–length key supporting the evalua-

tion of general aspects of the age–frequency distribution, such as periods of curtailed recruitment, the presence of strong year classes, periods of population expansion, and the timing of initial colonization that gave rise to the current populations. Each of these can be estimated from this dataset at all 4 sites.

Details, however, are likely not clearly revealed. Whereas 20 ocean quahogs per 5 mm size class may accurately describe the age distribution, the number of new ages present in the second sample of 20 individuals (Table 3) affirms the postulate that many ages are present in any 1 size class and that a large number of individuals would need to be aged to accurately identify the full number of ages present and to permit small-scale differences in the degree to which certain ages are better represented than others to be distinguished.

A further note is that the additional ages obtained in the second resampling but not observed in the first sampling filled in a gap in the original dataset in almost every case. Thus, for example, the second resampling from New Jersey added additional animals in the younger fraction of the age range, as would be anticipated as the relatively younger ages are disproportionately abundant in nearly all size classes. However, the first 20 animals exhibited a large gap in ages between 116 and 153 yr old. Fully 9 of the 20 ages of the resampled individuals fell into this age gap. Similarly, for Southern New England, the second sampling showed a large age gap between 112 and 140 yr old. Six of 20 animals in the first sampling fell into this age gap. For the Georges Bank dataset reported by Pace et al. (2017), the first sample of 20 showed an age gap between 121 and 134 years old. Six of 20 individuals in the resampling fell into this gap. By inference, age gaps in the datasets in most cases evidence under-sampling rather than recruitment lulls and, in fact, clear intimations of decadal or multidecadal hiatuses in recruitment or below average recruitment are rare in these datasets.

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

Age frequencies and population dynamics

The rarity of old animals in the population suggests that animals older than the oldest animal aged may have been missed. However, the known long life span of ocean quahogs, our oldest animal being less than half the oldest age known (Schöne et al. 2005c, Ridgway & Richardson 2011) and the low mortality rate suggest that animals older than the ones observed are indeed rare. Ocean quahogs shells are widely distributed on the continental shelf along the northeastern coast of the USA (Marchitto et al. 2000, Powell et al. 2017) and the species has an extended fossil record (e.g. Goodfriend & Weidman 2001, Williams et al. 2009, Wanamaker et al. 2011, Crippa et al. 2016). One presumes that their range has shifted repeatedly over prehistoric and historic time with long-term changes in climate. One interpretation of the extended tail of old ages in the populations' age–frequency distributions observed in this study is that the ocean quahog populations of the northeast US continental shelf most recently colonized the presently inhabited area 200–250 years BP. Very little is known about the distribution of ocean quahogs along the northeast US coast over historic time, but recent evidence from Georges Bank shows that an offshore shift in range had occurred prior to the initiation of the National Marine Fisheries Service survey program in 1980 (Powell et al. 2017). We suggest that the long tail in the age distributions record the timing of such an event throughout the northeast continental shelf of the USA.

Basing interpretation on this premise, and recalling that sampling was likely insufficient to fully describe the age frequencies of the oldest living animals at any of the 4 sites, the 2 southern sites displayed the earliest inhabitation by ocean quahogs, beginning approximately 250 yr ago in Long Island, with evidence of recruitment 220 yr ago in New Jersey. Colonization of the Southern New England site seems to have begun approximately 170 yr ago, and the earliest inhabitants of sampled population on Georges Bank recruited about 200 yr ago. All of the populations experienced a period of rapid expansion to what is presumed to be carrying capacity, consistent with the most recent population dynamics assessment that concluded that *A. islandica* was at carrying capacity prior to 1980 and continues to be near this abundance level (NEFSC 2017). Interestingly, the populations at the northern sites began to expand fairly rapidly in the late 1800s and approached carrying capacity within about 15 yr in Southern New England and approximately 30 yr on Georges Bank. At the southern

sites, although ocean quahogs apparently had been present longer than in the northeastern areas, the New Jersey population took nearly 80 yr to approach carrying capacity even though population expansion began much earlier, at around 1835, whereas initiation of the population at the Long Island site began approximately contemporaneously with the Southern New England and Georges Bank populations.

The extended population expansion recorded by the New Jersey population would be consistent with a population at the southern end of the range. For a species with a circumboreal distribution, New Jersey, being situated farther south than is typical of the species' range, is in an area presumably nudging the maximum high temperature tolerance of the species. Increased periods of high bottom-water temperatures might inhibit survival of newly settled individuals when compared to areas with a more consistently suitable temperature range. Additionally, the larval supply and subsequent recruitment may have been more limited if this population was farther from a source population. Furthermore, although consistently small numbers of older individuals were present in the Long Island population for about 130 yr, that population did not exhibit rapid growth until the early 1900s, a distinctly longer period at low abundance than observed for the 2 populations to the northeast, after which the population approached carrying capacity within about 25 yr.

Pace et al. (2017) suggested that the most recent phase of recruitment on the northeast US continental shelf by ocean quahogs co-occurred with the ending of the Little Ice Age, an epoch that concluded in the first half of the 19th century (Schöne et al. 2005b, Mann et al. 2009, Cronin et al. 2010). Moore et al. (2017) recorded significant warming trends in the northwest Atlantic Ocean beginning in the middle of the 19th century consistent with this climate change. Warming bottom-water temperatures would have initiated a range shift to areas that were previously unoccupied. This could explain why the oldest animals are found at the southern sites, as these regions would have warmed up before the more northern sites. Regardless, once the initial recruits began to inhabit the northeastern US continental shelf where they are found today, the populations remained at low levels for an extended period. This is evident from the long tail in the population age frequency (Fig. 6); a time span of nearly 150 yr in Long Island, about 70 yr on Georges Bank, about 55 yr in Southern New England, and presumably so many years off of New Jersey, as indicated by the rarity of animals over the first 60 years of colonization.

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

Oddly enough, the Long Island site apparently experienced colonization prior to the northern sites, yet the rapid population expansion occurred at the Georges Bank and Southern New England sites prior to the expansion in Long Island. Considering the extended period of time of up to 60 d that ocean quahog larvae can remain in the water column (Lutz et al. 1982, Mann 1985), long-distance transport of larvae would be possible. Larval connectivity at mid-shelf where ocean quahogs are found is not well understood. At shallower depths, net transport is west and south alongshore from New England to New Jersey, with a larval retention gyre operating on Georges Bank (Zhang et al. 2015, 2016) and with offshore transport occurring on the continental shelf south of Hudson Canyon, particularly in the fall. Although larvae spawned in the south possibly could reach the Southern New England and Georges Bank sites, a more likely original larval source for colonization is from the northeast, where populations have existed for extended periods of time (Dahlgren et al. 2000, Wanamaker et al. 2009). In fact, the fossil record for ocean quahogs dates at least back to 5000–8000 BP off the western coast of Greenland (Funder & Weidick 1991). Wanamaker et al. (2008) reported that ocean quahogs have been present in the Gulf of Maine at least since 1030 ± 78 AD.

While speculative, one possible source population for the Mid-Atlantic colonization is documented by the presence of ocean quahogs in the northwest Atlantic Ocean for several hundred years prior to the establishment of the New Jersey and Long Island

populations. The incongruity in this ready alternative is that the oldest animals in the present dataset came from the 2 southern sites. The fossil record of ocean quahogs in the Gulf of Maine suggests that the initial populations in the western Atlantic Ocean may have inhabited warmer and shallower waters, as the fossils were collected at a water depth of 38 m (Wanamaker et al. 2009), and Powell et al. (2017) recently reported ocean quahog shells at shallower depths on Georges Bank than presently occupied by the living population, interpreted by them as clear evidence of a historically recent range shift. Thus, an alternative source population for the southwestern sites might be animals living further inshore than they do today. Regardless, explanation for the delayed response at the Long Island site between initial colonization and subsequent population expansion remains uncertain; nevertheless, the possibility that net larval transport south out of the Long Island region may have restricted population expansion off Long Island cannot be discounted and would be consistent with a recent evaluation of surfclam connectivity in the Mid-Atlantic Bight (Zhang et al. 2016).

Unexpectedly little evidence exists of strong year classes in this dataset. Two potential year classes are visible at the Long Island site both early in the population record, the first smaller year class occurring circa 1820, and the second larger year class occurring in approximately 1880. A vague indication exists of a possible year class in New Jersey that probably occurred circa 1845. In both cases, evidence for strong year classes, if any, only exists early on, prior to the population expansion, arguably during a time when the local population was not self-recruiting. As New Jersey and Long Island are the 2 most southern sites, it is conceivable that these populations were farther from the recruitment source of the early populations, which could explain the less consistent recruitment into these populations early in their history as compared to the 2 northern sites. Once population expansion occurred, substantial periods of low recruitment are almost nonexistent, with the only obvious case being the decadal trough in recruitment, perhaps not surprisingly, at the most southern site, New Jersey, from 1950–1965, interestingly coincident with the most recent period of declining temperatures in the Mid-Atlantic Bight (Nixon et al. 2004).

Fishery implications

Ocean quahogs support an East Coast commercial fishery that began ca. 1967 and expanded in the early

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

Several lines of evidence suggest that the fishery has not materially influenced the age frequencies reported herein. (1) The fishing mortality rate over the history of the fishery has never exceeded the natural mortality rate and, for most of the time, has been well below it (NEFSC 2009, 2017), i.e. the fishery has had little impact on the stock. (2) The selfsame trends in the age frequencies observed at the 3 fished sites are also present in the Georges Bank populations, although this population has rarely been fished and, in fact, was closed to fishing over much of the historical fishery (NEFSC 2009). Indeed, the US ocean quahog stock was considered to be at carrying capacity in the late 1960s at the historic start of the ocean quahog fishery (NEFSC 2009) and remains near that today (NEFSC 2017). An asymptote in the age frequency after population expansion at each of the 4 sites is consistent with this interpretation. (3) The vast majority of animals of age 80 yr or higher were fully recruited to the fishery prior to its inception; thus, any fishing would have decremented this group of animals equivalently. These animals are the primary contributors to the age frequencies reported herein, as ageing was restricted to animals ≥ 80 mm. Thus, we have not attempted to correct the age frequencies for bias in a possible over-representation of the youngest clams that grew into market size since the fishery became operational. It is unlikely that the fishery has substantively impacted the age frequencies, nor is it likely that the length frequencies have been truncated.

CONCLUSIONS

As described in Pace et al. (2017), the Georges Bank age–frequency distribution shares many similarities with the published age–frequency distributions for Iceland (Steingrímsson & Thórarinsdóttir 1995) and the Belfast Lough in Northern Ireland (Ridgway et al. 2012). The age–frequency distributions for New Jersey, Long Island, and Southern New England also bear many similarities to that of Georges Bank in that population levels remained low for a period of about 100 yr beginning about 200–250 years ago, after which the population size grew rapidly over a few decades at all sites except New Jersey, whereafter the population increased in size more slowly (Steingrímsson & Thórarinsdóttir 1995, Ridgway et al. 2012, Pace et al. 2017). Similarities between locations as distant as the New Jersey continental shelf and Ireland suggest that this mode of colonization and population expansion may be characteristic of ocean quahogs throughout the North Atlantic basin.

The age–frequency distributions suggest that the living populations of ocean quahogs record the entire history of colonization over a substantial portion of their present North Atlantic range. Setting aside recent non-native invasions (e.g. *Crassostrea gigas*, Troost 2010; *Potamocorbula amurensis*, Carlton et al. 1990), this species may be the only marine species for which such a record exists and very likely the only native species. The characteristics of this colonization and possible biological explanations are as follows. (1) Initial colonization that gave rise to the current populations began towards the end or shortly after the end of the Little Ice Age. Abundances were low as might be anticipated by dependency on an external source for recruitment. Low mortality rates and long life span permits representatives of these initial colonizers to remain present in the living population. Year classes, albeit small, were possibly more common than later, suggesting more sporadic recruitment events from an external source. Small sample sizes, however, limit confidence in this inference. (2) At some point, local reproduction began to contribute to the larval pool; likely this occurred many years following initial colonization due to the extended time to maturity. Alternatively, environmental conditions changed, permitting enhanced recruitment and/or post-settlement survival. (3) Due to local reproduction or to environmental change, the population entered into a rapid expansion that, over a relatively brief period given the life history of the species, raised abundance to near carrying capacity. The population expansion is remarkably rapid given the extended life span of the

species; however, the rapid expansion is consistent with the high recruitment potential of most bivalves due to their high annual fecundity. (4) Population expansion ceased when the population reached carrying capacity. Afterwards, recruitment remained sufficient to balance natural mortality and the population remained at carrying capacity for an extended period of time, rarely interrupted by extended periods of low recruitment. This suggests that ocean quahogs have recruited regularly, certainly more frequently than once per decade, to these populations.

Resiliency of the US East Coast ocean quahog population to fishing has been questioned due to the limited evidence for large recent recruitment events. The population dynamics inferred from the age frequencies described here are consistent with recent inference from stock surveys (NEFSC 2017) that *A. islandica* is near carrying capacity throughout its US range. Low recruitment is the anticipated result for a population near carrying capacity, whereas a much higher recruitment capacity typical of most bivalve species is well demonstrated by the rapid population expansion that occurred during earlier times as the population abundances rose to that level. Expansion of the range northward and offshore, however, which might be anticipated with continued warming of the North Atlantic, may require an extended period of time, as time-to-maturity will likely limit the response time of a newly established population in developing local recruitment potential.

Acknowledgements. We appreciate the assistance of the captain and crew of the F/V 'Pursuit' and the F/V 'Christy', who carried out these sampling tasks over several days at sea. We also thank Melissa Southworth (Virginia Institute of Marine Science) who assisted in sample sorting. This research was supported by the National Science Foundation (NSF) Industry/University Cooperative Research Center SCSMFis (Science Center for Marine Fisheries) through membership fees under the direction of the Industry Advisory Board (IAB). SCSMFis administrative support is provided by NSF award #1266057. Conclusions and opinions expressed herein are solely those of the authors.

LITERATURE CITED

- ✦ Brey T, Arntz WE, Pauly D, Rumohr H (1990) *Arctica (Cyprina) islandica* in Kiel Bay (Western Baltic): growth, production and ecological significance. *J Exp Mar Biol Ecol* 136:217–235
- ✦ Brooks EN, Powers JE (2007) Generalized compensation in stock-recruit functions: properties and implications for management. *ICES J Mar Sci* 64:413–424
- ✦ Butler PG, Richardson CA, Scourse JD, Witbaard R and others (2009) Accurate increment identification and the spatial extent of the common signal in five *Arctica islandica* chronologies from the Fladen Ground, northern North Sea. *Paleoceanography* 24:PA2210

- Butler PG, Wanamaker AD Jr, Scourse JD, Richardson CA, Reynolds DJ (2013) Variability of marine climate on the North Icelandic Shelf in a 1357-year proxy archive based on growth increments in the bivalve *Arctica islandica*. *Palaeogeogr Palaeoclimatol Palaeoecol* 373:141–151
- Carlton JT, Thompson JK, Schemel LE, Nichols FH (1990) Remarkable invasion of San Francisco Bay (California, USA) by the Asian clam, *Potamocorbula amurensis* I. Introduction and dispersal. *Mar Ecol Prog Ser* 66:81–94
- Chintala MM, Grassle JP (2001) Comparison of recruitment frequency and growth of surfclams, *Spisula solidissima* (Dillwyn, 1817), in different inner-shelf habitats of New Jersey. *J Shellfish Res* 20:1177–1186
- Craig G, Oertel G (1966) Deterministic models of living and fossil populations of animals. *Q J Geol Soc Lond* 122: 315–355
- Crippa G, Angiolini L, Bottini C, Erba E and others (2016) Seasonality fluctuations recorded in fossil bivalves during the early Pleistocene: implications for climate change. *Palaeogeogr Palaeoclimatol Palaeoecol* 446: 234–251
- Cronin TM, Hayo K, Thunell RC, Dwyer GS, Saenger C, Willard DA (2010) The Medieval Climate Anomaly and Little Ice Age in Chesapeake Bay and the North Atlantic Ocean. *Palaeogeogr Palaeoclimatol Palaeoecol* 297: 299–310
- Dahlgren TG, Weinberg JR, Halanych KM (2000) Phylogeography of the ocean quahog (*Arctica islandica*): influences of paleoclimate on genetic diversity and species range. *Mar Biol* 137:487–495
- Daniel WW (1978) Applied nonparametric statistics. Houghton Mifflin Company, Boston, MA
- Funder S, Weidick A (1991) Holocene boreal molluscs in Greenland—paleoceanographic implications. *Palaeogeogr Palaeoclimatol Palaeoecol* 85:123–135
- Goodfriend GA, Weidman CR (2001) Ontogenetic trends in aspartic acid racemization and amino acid composition within modern and fossil shells of the bivalve *Arctica*. *Geochim Cosmochim Acta* 65:1921–1933
- Goodwin NB, Grant A, Perry AL, Dulvy NX, Reynolds JD (2006) Life history correlates of density-dependent recruitment in marine fishes. *Can J Fish Aquat Sci* 63: 494–509
- Hancock DA (1973) The relationship between stock and recruitment in exploited invertebrates. *Rapp P-V Réun Cons Int Explor* 164:113–131
- Harding JM, King SE, Powell EN, Mann R (2008) Decadal trends in age structure and recruitment patterns of ocean quahogs *Arctica islandica* from the Mid-Atlantic Bight in relation to water temperatures. *J Shellfish Res* 27: 667–690
- Hennen DR (2015) How should we harvest an animal that can live for centuries? *N Am J Fish Manage* 35:512–527
- Hofmann EE, Klinck JM, Kraeuter JN, Powell EN, Grizzle RE, Buckner SC, Bricelj VM (2006) A population dynamics model of the hard clam, *Mercenaria mercenaria*: development of the age- and length-frequency structure of the population. *J Shellfish Res* 25:417–444
- Honkoop PJC, van der Meer J, Beukema JJ, Kwast D (1998) Does temperature-influenced egg production predict the recruitment in the bivalve *Macoma balthica*? *Mar Ecol Prog Ser* 164:229–235
- Hughes TP (1990) Recruitment limitation, mortality, and population regulation in open systems: a case study. *Ecology* 71:12–20
- Kraeuter JN, Buckner S, Powell EN (2005) A note on a spawner-recruit relationship for a heavily exploited bivalve: the case of northern quahog (hard clams), *Mercenaria mercenaria* in Great South Bay New York. *J Shellfish Res* 24:1043–1052
- Lutz RA, Mann R, Goodsell JG, Castagna M (1982) Larval and early post-larval development of *Arctica islandica*. *J Mar Biol Assoc UK* 62:745–769
- MacDonald PDM, Pitcher TJ (1979) Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. *J Fish Res Board Can* 36: 987–1001
- Mangel M, Brodziak J, DiNardo G (2010) Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish Fish* 11:89–104
- Mann R (1985) Seasonal changes in the depth distribution of bivalve larvae on the southern New England shelf. *J Shellfish Res* 5:57–64
- Mann ME, Zhang Z, Rutherford S, Bradley RS and others (2009) Global signatures and dynamical origins of the Little Ice Age and Medieval Climate Anomaly. *Science* 326:1256–1260
- Marchitto TM Jr, Jones GA, Goodfriend GA, Weidman CR (2000) Precise temporal correlation of Holocene mollusk shells using sclerochronology. *Quat Res* 53:236–246
- McGarvey R, Serchuk FM, McLaren IA (1993) Spatial and parent-age analysis of stock-recruitment in the Georges Bank sea scallop (*Placopecten magellanicus*) population. *Can J Fish Aquat Sci* 50:564–574
- Merrill AS, Ropes JW (1969) The general distribution of the surf clam and ocean quahog. *Proc Nat Shellf Assoc* 59: 40–45
- Mohn R (1994) A comparison of three methods to convert catch at length data into catch at age. *Col Vol Sci Pap ICCAT* 42:110–119
- Moore GWK, Halfar J, Majeed H, Adey W, Kronz A (2017) Amplification of the Atlantic Multidecadal Oscillation associated with the onset of the industrial-era warming. *Sci Rep* 7:40861
- NEFSC (Northeast Fisheries Science Center) (2009) 48th Northeast Regional Stock Assessment Workshop (48th SAW) assessment report. NEFSC Ref Doc 09-15, NOAA Fisheries, Woods Hole, MA
- NEFSC (2014) 59th Northeast Regional Stock Assessment Workshop (59th SAW) assessment summary report. NEFSC Ref Doc 14-07, NOAA Fisheries, Woods Hole, MA
- NEFSC (2017) 63rd Northeast Regional Stock Assessment Workshop (63rd SAW) assessment report. NEFSC Ref Doc 17-10, NOAA Fisheries, Woods Hole, MA
- Nixon SW, Granger S, Buckley BA, Lamont M, Rowell B (2004) A one hundred and seventeen year coastal water temperature record from Woods Hole, Massachusetts. *Estuaries* 27:397–404
- Noreen EW (1989) Computer-intensive methods for testing hypotheses: an introduction. John Wiley & Sons, New York, NY
- Ólafsson EB, Peterson CH, Ambrose WG Jr (1994) Does recruitment limitation structure populations and communities of macro-invertebrates in marine soft sediments: the relative significance of pre- and post- settlement processes. *Oceanogr Mar Biol Annu Rev* 32:65–109
- Pace SM, Powell EN, Mann R, Long MC, Klinck JM (2017) Development of an age–frequency distribution for ocean quahogs (*Arctica islandica*) on Georges Bank. *J Shellfish Res* 36:41–53
- Peterson CH (2002) Recruitment overfishing in a bivalve mollusc fishery: hard clams (*Mercenaria mercenaria*) in North Carolina. *Can J Fish Aquat Sci* 59:96–104

- Peterson CH, Summerson HC (1992) Basin-scale coherences of population dynamics of an exploited marine invertebrate, the bay scallop: implications of recruitment limitation. *Mar Ecol Prog Ser* 90:257–272
- Powell EN, Mann R (2005) Evidence of recent recruitment in the ocean quahog *Arctica islandica* in the Mid-Atlantic Bight. *J Shellfish Res* 24:517–530
- Powell EN, Stanton RJ Jr (1985) Estimating biomass and energy flow of molluscs in paleo-communities. *Paleontology* 28:1–34
- Powell EN, Klinck JM, Ashton-Alcox KA, Kraeuter JN (2009) Multiple stable reference points in oyster populations: biological relationships for the eastern oyster (*Crassostrea virginica*) in Delaware Bay. *Fish Bull* 107:109–132
- Powell EN, Kuykendall KM, Moreno P (2017) The death assemblage as a marker for habitat and an indicator of climate change: Georges Bank, surfclams and ocean quahogs. *Cont Shelf Res* 142:14–31
- Ragnarsson SAG, Þórarinsdóttir G (2002) Abundance of ocean quahog, *Arctica islandica*, assessed by underwater photography and a hydraulic dredge. *J Shellfish Res* 21:673–676
- Ridgway ID, Richardson CA (2011) *Arctica islandica*: the longest lived non colonial animal known to science. *Rev Fish Biol Fish* 21:297–310
- Ridgway ID, Richardson CA, Scourse JD, Butler PG, Reynolds DJ (2012) The population structure and biology of the ocean quahog, *Arctica islandica*, in Belfast Lough, Northern Ireland. *J Mar Biol Assoc UK* 92:539–546
- Ropes JW, Murawski SA, Serchuk FM (1984) Size, age, sexual maturity, and sex ratio in ocean quahog, *Arctica islandica* Linné, off Long Island, New York. *Fish Bull* 82:253–266
- Rowell TW, Chaisson DR, McLane JT (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
- Schöne BR, Houk SD, Freyre Castro AD, Fiebig J, Oschmann W (2005a) Daily growth rates in shells of *Arctica islandica*: assessing sub-seasonal environmental controls on a long-lived bivalve mollusk. *Palaios* 20:78–92
- Schöne BR, Pfeiffer M, Pohlmann T, Seigismund F (2005b) A seasonally resolved bottom-water temperature record for the period AD 1866–2002 based on shells of *Arctica islandica* (Mollusca; North Sea). *Int J Climatol* 25:947–962
- Schöne BR, Fiebig J, Pfeiffer M, Gleß R and others (2005c) Climate records from bivalved Methuselah (*Arctica islandica*, Mollusca; Iceland). *Palaeogeogr Palaeoclimatol Palaeoecol* 228:130–148
- Stari T, Preedy KF, McKenzie E, Gurney WSC, Heuth MR, Kunzlik PA, Speirs DC (2010) Smooth age length keys: observations and implications for data collection on North Sea haddock. *Fish Res* 105:2–12
- Stearns SC (1976) Life-history tactics: a review of the ideas. *Q Rev Biol* 51:3–47
- Steingrímsson SA, Þórarinsdóttir G (1995) Age structure, growth and size at sexual maturity in ocean quahog, *Arctica islandica* (Mollusca: Bivalvia), off NW-Iceland. *ICES CM* 1995/K:54
- Þórarinsdóttir GG, Jacobson LD (2005) Fishery biology and biological reference points for management of ocean quahogs (*Arctica islandica*) off Iceland. *Fish Res* 75:97–106
- Þórarinsdóttir GG, Steingrímsson SA (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
- Þórarinsdóttir GG, Jacobson L, Ragnarsson SA, Garcia EG, Gunnarsson K (2010) Capture efficiency and size selectivity of hydraulic clam dredges used in fishing for ocean quahogs (*Arctica islandica*): simultaneous estimation in the SELECT model. *ICES J Mar Sci* 67:345–354
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. *Biol Rev Camb Philos Soc* 25:1–45
- Troost K (2010) Causes and effects of a highly successful marine invasion: case - study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *J Sea Res* 64:145–165
- van der Meer J, Beukema JJ, Dekker R (2003) Large spatial variability in lifetime egg production in an intertidal Baltic tellin (*Macoma balthica*) population. *Helgol Mar Res* 56:274–278
- Wanamaker AD Jr, Heinemeier J, Scourse JD, Richardson CA, Butler PG, Eiriksson J, Knudsen K (2008) Very long-lived mollusks confirm 17th century AD tephra-based radiocarbon reservoir ages for North Icelandic shelf waters. *Radiocarbon* 50:399–412
- Wanamaker AD Jr, Kreutz KJ, Schöne BR, Maasch KA and others (2009) A late Holocene paleo-productivity record in the western Gulf of Maine, USA, inferred from growth histories of the long-lived ocean quahog (*Arctica islandica*). *Int J Earth Sci* 98:19–29
- Wanamaker AD Jr, Kreutz KJ, Schöne BR, Introne DS (2011) Gulf of Maine shells reveal changes in seawater temperature seasonality during the Medieval Climate Anomaly and the Little Ice Age. *Palaeogeogr Palaeoclimatol Palaeoecol* 302:43–51
- Weinberg JR (1999) Age-structure, recruitment, and adult mortality in populations of the Atlantic surfclam, *Spisula solidissima*, from 1978–1997. *Mar Biol* 134:113–125
- Williams M, Haywood AM, Harper EM, Johnson ALA and others (2009) Pliocene climate and seasonality in North Atlantic shelf seas. *Philos Trans R Soc A* 367:85–108
- Witbaard R, Duineveld GCA, de Wilde PAWJ (1999) Geographical differences in growth rates of *Arctica islandica* (Mollusca: Bivalvia) from the North Sea and adjacent waters. *J Mar Biol Assoc UK* 79:907–915
- Zhang X, Haidvogel D, Munroe D, Powell EN, Klinck J, Mann R, Castruccio FS (2015) Modeling larval connectivity of the Atlantic surfclams within the Middle Atlantic Bight: model development, larval dispersal and metapopulation connectivity. *Estuar Coast Shelf Sci* 153:38–53
- Zhang X, Munroe D, Haidvogel D, Powell EN (2016) Atlantic surfclam connectivity within the Middle Atlantic Bight: mechanisms underlying variation in larval transport and settlement. *Estuar Coast Shelf Sci* 173:65–78