

Research papers

Growth and longevity in surfclams east of Nantucket: Range expansion in response to the post-2000 warming of the North Atlantic

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ABSTRACT

The Atlantic surfclam, *Spisula solidissima*, is distinguished by a well-documented shift in range that accelerated in the 2000s as the northwest Atlantic warmed. Here the extension of the Atlantic surfclam into heretofore Acadian Province waters off the island of Nantucket is documented and compared to the distribution of surfclam shell as an indicator of recent colonization, to the timing of range expansion, and to the physiological implications of a range extension into deeper water. The primary demographic difference observed is the dichotomous distribution of sizes. Smaller surfclams averaged higher in abundance at the deeper offshore sites, whereas the number of large animals was distinctly fewer; thus, the size-frequency distributions at deeper sites were shifted towards the smaller sizes, a finding consistent with the expectation of recruitment into deeper water during a period of range expansion. In confirmation, deeper-water stations where surfclams were aged yielded surfclams no older than 13 yr, whereas shallow-water stations had a mature age frequency with some surfclams exceeding 20 yr. Further support for the more recent occupation of deeper-water sites comes from the distribution of surfclam shell, that was found in limited quantities at stations where recent colonization is inferred and in greater quantities in shallower water where longer-term occupation is surmised. For the shallower-water sites with a mature demographic, growth rates were comparable or higher than observed elsewhere in the stock and surfclam maximum sizes were larger than elsewhere in the geographic range. In contrast, surfclams colonizing deeper water post-2000 grew at a slower rate likely due to a lower average temperature near the deep-water range boundary. The penalty for colonization pushing the range boundary into deeper, cooler water lasted no more than 4–5 years, however, after which growth rates increased to rates typical of surfclams in shallower water. Thus, surfclams responded quickly to a period of rapid climate change in contrast to expectation from their known longevity.

1. Introduction

One of the manifestations of the warming of the world's oceans is the latitudinal translation of provincial boundaries chronicled by the shift in range of quintessential species. The western North Atlantic is a bellwether (Briggs and Bowen, 2012), as the rate of warming exceeds most other oceanic regions (Pershing et al., 2015; Saba et al., 2016; Lentz, 2017) and the biomass dominant bivalves found there are particularly sensitive to changes in bottom water temperature (Begum et al., 2009; Hornstein et al., 2018). Consideration of the dynamics of range shifts has spawned a range of modelling approaches for terrestrial and marine

applications focused on the source-sink dichotomy, the dispersal characteristics of geographic spread from the core to range boundaries, the capacity for rapid response to ongoing climate change, the obstacles posed by geographic and, for marine systems, hydrodynamic barriers to dispersal, and the genetic consequences of a shift in range (Gaylord and Gaines, 2000; Holt et al., 2005; Dunstan and Bax, 2007; Butler et al., 2012; Berestyck et al., 2009; Excoffier et al., 2009; Sexton et al., 2009; Woodin et al., 2013). In comparison, documentation of range shift dynamics, beyond the observation of a shift in distributional pattern, is limited (Gilman, 2006; Hellmann et al., 2008; Castaños et al., 2009; Troost, 2010; Woodin et al., 2013) with the dynamic spread of

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introduced species offering a disproportionate number of case histories in the marine realm (Sagarin et al., 1999; Troost, 2010; Dutertre et al., 2010; Wetthey et al., 2016) and with little documentation of range shifts for continental shelf species.

On the continental shelf off the northeast coast of the U.S., two provincial boundaries are in play which delineate respectively the Virginian province historically delineated by Cape Hatteras and Cape Cod (Hale, 2010), inhabited by cold temperate species, and the intrusion of the Acadian Province (Hale, 2010), inhabited by boreal species, into the Mid-Atlantic by the cold pool (Lentz, 2017). The cold pool is an extension of cold water onto the middle and outer continental shelf from southern New England to Delmarva that is maintained as a discrete cold water feature on the bottom for much of the spring and summer by the thermocline (Houghton et al., 1982; Mountain, 2003).

Among the species affected by Mid-Atlantic Bight warming are two key groups, the mobile species headlined by a variety of finfish which have the luxury of following isotherms in real time (Lucy and Nye, 2010; Hare et al., 2016) and the sessile and sedentary species that can only change their range through mortality and recruitment. One of these, the Atlantic surfclam, is of particular interest due to its well-documented shift in range that accelerated in the 2000s. This species has a quasi knife-edge upper thermal optimum near 21°C; scope for growth drops quickly above this thermal optimum (Munroe et al., 2013; Hornstein et al., 2018), rapidly resulting in a reduced rate of filtration, physiological compromise, and ultimately mortality (Kim and Powell, 2004; Weinberg et al., 2005). As a consequence, surfclams are sensitive to warming bottom waters along their southern and inshore range boundaries. Net down-coast water transport in the Mid-Atlantic impedes the movement of surfclams north, but cross-shelf transport facilitates a cross-shelf shift in range into deeper water (Zhang et al., 2015, 2016; Timbs et al., 2019). The dimensions of the resulting range shift in the southern half of the Mid-Atlantic Bight are well documented (Weinberg, 2005; Hofmann et al., 2018; Powell et al., 2020), but few details exist chronicling the temporal progression and physiological implications beyond the circa-2000 mass mortality event off Delmarva that dramatically shifted the southern boundary north from its historical latitudinal extent typical of a species characteristic of the Virginian Province (Hofmann et al., 2018).

Further north, the influence of bottom water warming is less well documented, though a decline in surfclam biomass inshore off Long Island (Hornstein et al., 2018) and evidence from recent offshore surveys off Long Island (NEFSC, 2017) and on Georges Bank (Powell et al., 2017a) of increasing biomass suggest the initiation of a cross-shelf expansion in range. Powell et al. (2017a) suggested that the distribution of surfclam shell might be used to distinguish sites of recent colonization from locations of long-term habitation. The death assemblage is a well-studied archive of the history of community composition and the tendency for the death assemblage to faithfully record species composition (Staff et al., 1986; Olszewski and Kidwell, 2007; Kidwell, 2008) and to an important extent record the rank-order of species dominance (Kidwell, 2002; Lockwood and Chastant, 2006; Tomašových and Kidwell, 2010) supports the likelihood that the history of colonization may be unearthed by its study. Here we document the extension of the Atlantic surfclam into heretofore Acadian Province waters off the island of Nantucket, compare the distribution of surfclam shell to living surfclams as an indicator of recent colonization, and document the timing of range expansion and the physiological implications of an extension of range into deeper water.

2. Methods

2.1. Survey location and design

In August 2017, a survey was conducted to evaluate the distribution of surfclams between Nantucket and the Great South Channel, an area that historically had received limited sampling due to the high current

velocities and rapid shifts in depth that limited safe operations by large research vessels. The survey domain is shown in Fig. 1. The western boundary approximates the inshore EEZ (Exclusive Economic Zone) boundary and the southern boundary abuts, on the lower left, the Nantucket Lightship Closed Area.

A fixed grid design was chosen to ensure that the region was evenly and densely surveyed. Fixed grids are routinely used to evaluate regions initially for later inclusion into a stratified random survey design (e.g., van der Meer, 1997; Morehead et al., 2008; HSRL, 2012; Powell et al., 2017b). A hub-and-spoke fixed grid design was implemented with spokes of 3-NM (5.56 km) length (Fig. 1). This sampling density was chosen to approximate the densest sampling grid theoretically achievable under the NEFSC¹ (1988) survey protocol. A few stations were repositioned under a standard NEFSC protocol permitting repositioning within 1 NM of the designated position. Stations were moved for three reasons: (1) some fell just inshore of the EEZ inshore boundary and were moved offshore across the boundary line; (2) some stations fell just inside of the Nantucket Lightship Closed Area and were moved just north of that closure line; and (3) some stations fell on untowable bottom, always locations too shallow for the vessel to safely tow, and were moved laterally into deeper water. Only 6 of the 63 stations (9.5%) were repositioned.

2.2. Survey towing and on-deck processing protocol

The towing protocol followed that used by NEFSC for the 1982–2011 R/V *Delaware II* surveys in most respects. This protocol was chosen to permit comparison of “bycatch” data routinely collected during the R/V *Delaware II* surveys (see Powell et al., 2017a; Powell et al., 2019). The survey vessel was the F/V *Mariette*, homeport New Bedford, Massachusetts. The dredge was a 99’ hydraulic dredge of standard surfclam design (Lambert and Goudreau, 1996). Bar spacing was 1.875’ on the top, bottom, and knife shelf and 1.75’ on the sides. Selectivity is unknown, but experience with dredges of this type suggests that the dredge will be ~100% selective for surfclams targeted for market (≥ 120 mm) with selectivity declining at smaller sizes. The F/V *Mariette* uses a shaker to remove unwanted material from the catch. The shaker grate was closed to 0.75’ for the survey.

Tows were of 5-min duration in the direction of the next station except where large sand waves restricted towing direction. Tow speed was 3 knots. Most tows lasted 5 min, but excessive catch or rapid shoaling decreased tow time in a few cases. Swept area per tow averaged about 1,250 m² (Table 1). The survey in its entirety sampled about 78,500 m².

The entire catch was sorted using the NEFSC R/V *Delaware II* protocol (Powell et al., 2017a, 2019) that included sorting all surfclams, cobbles, rocks, boulders, associated invertebrates, and shell. Surfclam shell was measured in bushels. All measurable living surfclams were measured to the nearest mm; clams too broken to be measured were assigned proportionally to the distribution of measured sizes.

For presentation and for some subsequent statistical analyses, surfclams were allocated to 4 somewhat arbitrary size categories termed herein: submarket (clams ≤ 120 mm), small market (clams >120 –150 mm), medium market (clams >150 –170 mm), and large market (clams > 170 mm). A minimum size is not enforced in the Atlantic surfclam fishery, but dredge selectivity generally reduces the catch of surfclams <120 mm, hence the use of the term submarket in this study. Abundance maps that follow generally compare two components of the catch. Circle diameters are linearly proportional to catch (in m⁻²), but are not

¹ The National Marine Fisheries Service Northeast Fisheries Science Center (NEFSC) carries out the federal stock survey for Atlantic surfclams. The R/V *Delaware II* was the survey vessel used through 2011, after which it was retired and the survey protocol adapted for use on a fishing vessel, the F/V *Pursuit*, that included the limiting of on-deck processing to the catch of target species.

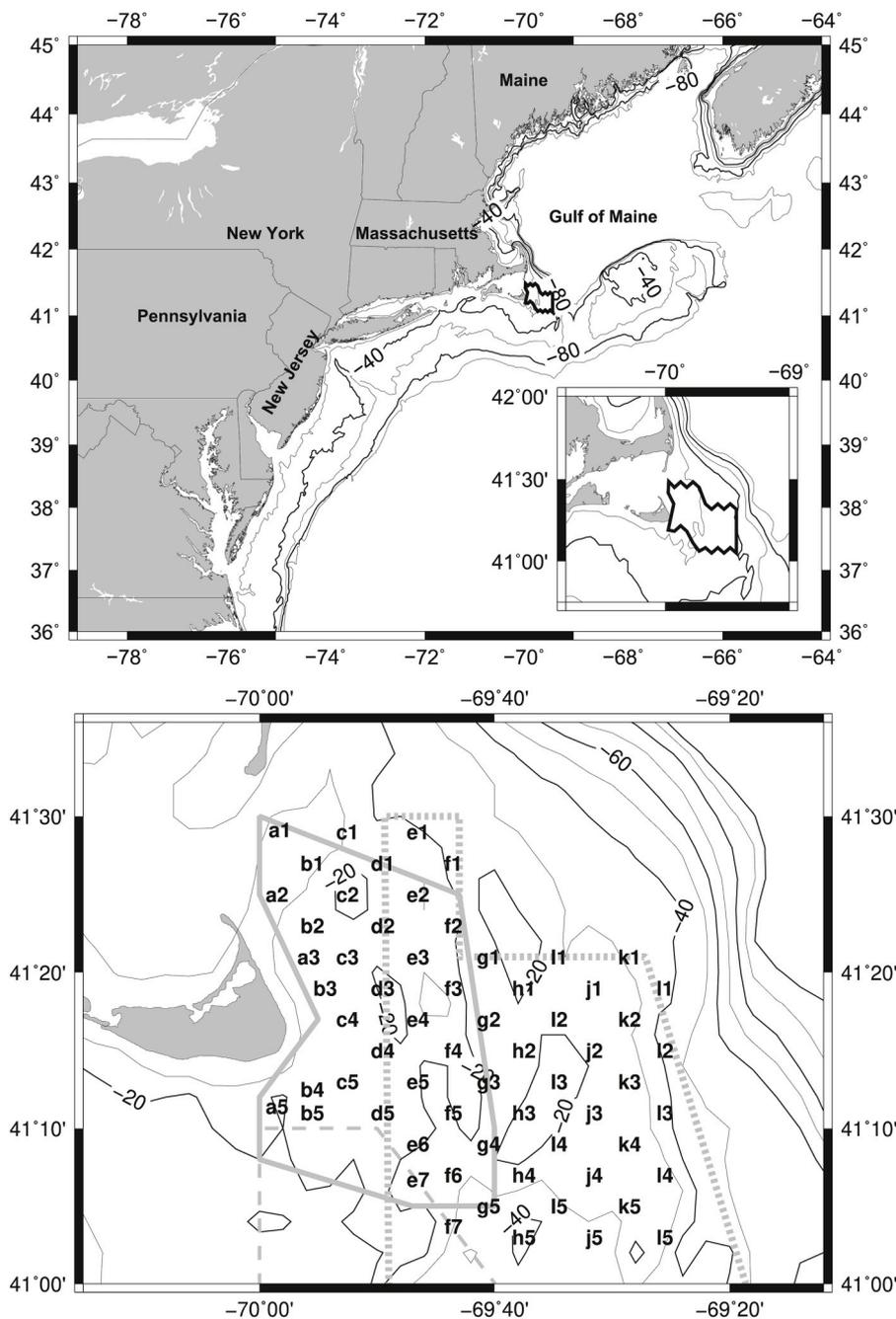


Fig. 1. Top, location of survey outlined by a solid black line just off Massachusetts just east of Nantucket. Bottom, close up of the survey design. Gray solid line outlines the sector historically contributing most of the Atlantic surfclam landings in the surveyed region. Gray dashed line outlines the northern portion of the Nantucket Lightship Habitat Closure Area. Gray dotted line outlines the upper half of the Great South Channel Habitat Management Area. Letters and numbers are station designations for the 63 stations in the survey. Depths are in meters.

Table 1
Tow track statistics. The upper 4 metrics are given in units of tow⁻¹. The sum is the total for all 63 stations occupied.

	Distance (m)	Swept Area (m ²)
Mean	495.9	1,247.0
Standard deviation	52.9	133.0
Median	498.3	1,253.1
Interquartile range	70.8	178.0
Sum	31,242.0	78,561.2

comparable between components. Thus, for example, in a comparison plot of the distribution of submarket and medium-market surfclams (Fig. 2), differential circle sizes for each size class of surfclams record the differences in catch of that size class between stations. However, no valid quantitative comparison can be made between the circle sizes for

surfclam catch of one size class with the circle size of the other. Demarcated regions on each map are: lower left, the upper portion of the Nantucket Lightship Closed Area; upper left, a region demarcated from fishery landing reports representing the portion of the surveyed region contributing most of the reported landings; and center-right, a habitat management area (HMA) designated by the New England Fisheries Management Council (Powell et al., 2019). For ease of description, the location trends in catch will be described relative to these three areas hereafter. Station abundance data are provided as supplementary material by Powell et al. (2019).

2.3. Ageing of atlantic surfclams

At four stations (A3, C3, I1, I4 at depths, respectively, 8, 12, 26, 23 m; see Fig. 1 for locations, see Table 2 for number aged), surfclams representing the range of sizes caught were selected, shucked, and the

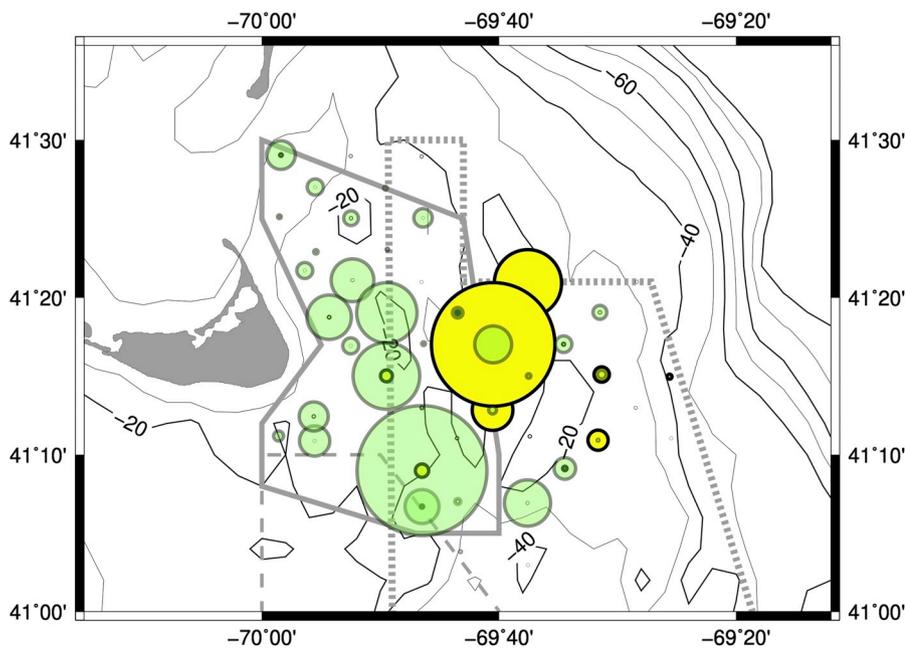


Fig. 2. Catch of submarket (≤ 120 mm) (solid yellow) and medium-market ($>150\text{--}170$ mm) (semi-transparent green) Atlantic surfclams. Variations in green and yellow shading accrue from circle overlap. Circle diameters are linearly proportional to numbers m^{-2} within category only. Abundance comparisons cannot be made across categories. Supporting data are provided as supplementary material in Powell et al. (2019). Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m.

articulated valves returned to the laboratory for ageing. Atlantic surfclams lay down annual growth increments consequent of the seasonal cycle of their growth (Jones, 1981; Ivany et al., 2003), that can be used to estimate their age (Ropes and Jearld, 1987; Jacobson et al., 2006; Chute et al., 2016). In the laboratory, paired valves were dipped in diluted bleach, rinsed with water, and air-dried. The height of each valve was measured (mm), as well as the length and width of each chondrophore. Valves were sectioned using a modified tile saw along the height axis of the shell. The exposed valve was ground with progressively finer grit sandpaper and then polished on a wet polishing wheel with 6 μm and 1 μm polycrystalline diamond suspensions. Each chondrophore was photographed using an Olympus DP73 digital microscope camera using Olympus cellSens microscope imaging software. Using the ObjectJ plugin in the software ImageJ, annual growth lines on the chondrophores were annotated to determine the age of each individual. See Pace et al. (2017a) for additional methodological details. Growth increments, the distance between two consecutive growth lines, were also measured for each individual to evaluate differences in growth rates. Ages of clams were confirmed after inter-calibration between multiple readers at the Gulf Coast Research Laboratory (University of Southern Mississippi), Virginia Institute of Marine Science (College of William & Mary), and the NMFS Northeast Fisheries Science Center (see also Jacobson et al., 2006). Growth increments for each animal were

Table 2
Growth increments in mm yr^{-1} rendered as mean (median) \pm standard deviation for each of the four stations and for the depth-dependent station groups.

Station	Number Aged	Year 1 to Year 2	Year 3 to Year 4	Year 7 to Year 8
A3	11	25.8 (27.8) \pm 9.5	38.1 (29.9) \pm 7.4	6.1 (5.7) \pm 2.6
C3	10	25.8 (26.3) \pm 9.1	28.0 (29.5) \pm 6.1	7.0 (6.1) \pm 3.7
I1	21	26.3 (26.9) \pm 7.3	26.0 (28.5) \pm 10.0	11.0 (12.1) \pm 2.4
I4	15	28.2 (25.5) \pm 10.5	25.9 (24.8) \pm 7.9	8.4 (7.0) \pm 3.6
Group				
Shallow (A3+C3)	21	25.8 (27.8) \pm 9.1	30.7 (39.8) \pm 7.1	6.5 (6.1) \pm 3.1
Deep (I1+I4)	36	27.1 (26.6) \pm 8.7	26.0 (23.0) \pm 9.1	9.6 (10.2) \pm 3.3

inferred based on equivalently proportional growth of chondrophore length and shell length (Jacobson et al., 2006).

A 3-parameter von Bertalanffy growth model was used to evaluate growth rates (see also Chintala and Grassle, 2001; Munroe et al., 2016; Chute et al., 2016). Comparison of growth at age was accomplished by nested ANOVA in which shallow (A3, C3) and deep (I1, I4) stations were grouped as a main effect and in which the main effect of station was nested within depth group. All growth increment datasets passed normality and heteroscedasticity tests. Birth year was included as a covariate with the added assumption that an interaction should exist between birth year and depth group, based on the observations of Pace et al. (2018), Picariello (2006), and Chute et al. (2016) that long-lived bivalves on the U.S. East-coast continental shelf show significant regional variations in growth rate that are often depth related and that growth rate at age may vary in one location depending on changing environmental conditions (Jones, 1980, 1981; Munroe et al., 2016; Pace et al., 2018). *A posteriori* tests used least squares means.

3. Results

3.1. Distribution and abundance of Atlantic surfclams

Atlantic surfclams were found throughout the surveyed region except for the farthest offshore and southern portions of the HMA (Fig. 2). Limited numbers in the south are consistent with minimal NEFSC survey catches in the NEFSC survey strata immediately south of the surveyed area (NEFSC, 2017; Powell et al., 2017a). Highest catches were taken in the central portion of the surveyed region coincident with the north-central portion of the HMA and just outside of the area supporting the majority of reported surfclam landings (Fig. 2).

The surfclam sizes were not equivalently distributed in the survey domain. Submarket and small-market surfclams were found in highest abundance in the central northern portion of the surveyed area coincident with the western half of the HMA and the eastern edge of the region of historically high landings (Fig. 3). Few small surfclams were found inshore where most reported landings originated. Submarket and small-market surfclams generally overlapped wherever they occurred (Fig. 3). Numbers caught per tow for the two smaller size classes were significantly correlated (Pearson product-moment correlation: $r = 0.93$; $P < 0.0001$). In contrast, medium-market and large-market surfclams were

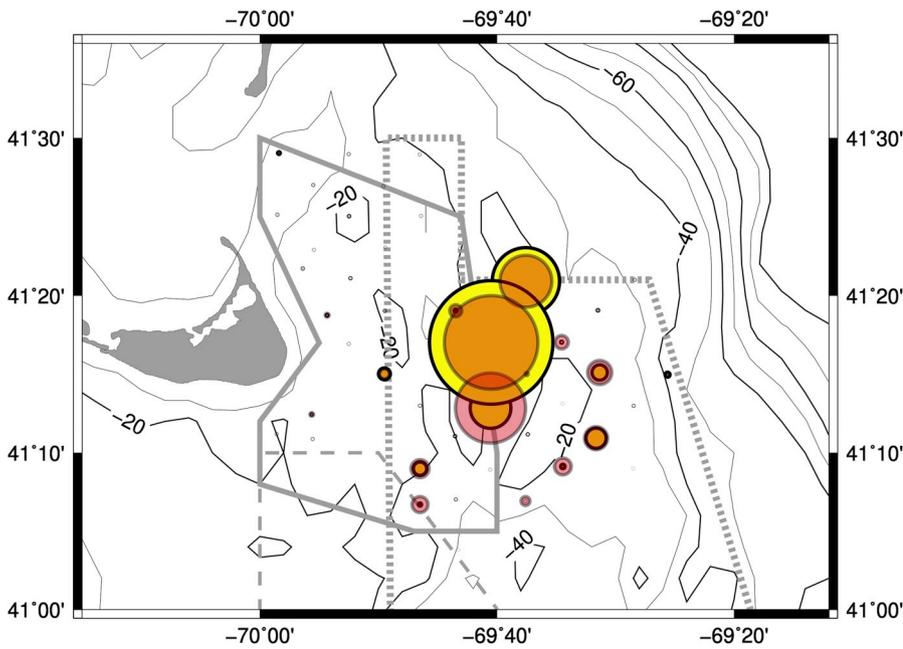


Fig. 3. Catch of submarket (≤ 120 mm) (solid yellow) and small-market (>120 – 150 mm) (semi-transparent red) Atlantic surfclams. Variations in red and yellow shading accrue from circle overlap. Circle diameters are linearly proportional to numbers m^{-2} within category only. Abundance comparisons cannot be made across categories. Supporting data are provided as supplementary material in Powell et al. (2019). Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m.

found on the most extreme southwestern edge of the HMA and inshore to the EEZ boundary (Fig. 4). The two larger size classes were very similarly distributed and the numbers caught per tow also significantly correlated (Pearson product-moment correlation: $r = 0.80$, $P < 0.0001$), but the largest of the surfclams (>170 mm) tended to be disproportionately relatively more common in the most inshore central portions of the survey domain. Animals 150 mm and larger were rarely encountered offshore of this region and extremely large animals (>170 mm) were very rare offshore of this region. The differential in distribution is well depicted by a comparison of submarket and medium-market surfclams (Fig. 2), that shows limited overlap in these two size classes. The submarket animals dominate in water >20 m deep in comparison to the larger surfclams that are generally found at shallower depths. The numbers caught per tow for these two size classes, animals <150 mm and ≥ 150 mm, were not correlated (Pearson product-moment

correlation: $r = 0.10$, $P > 0.05$).

Population size-frequency distributions ordered by depth show that, although some large surfclams are found in deeper water and some small surfclams are found in shallower water, the size frequencies of surfclam populations shifted towards the smaller sizes in deeper water (Fig. 5). Proportionately fewer large animals are found at the deeper-water stations. In contrast, and also clearly evident, is the proportionately fewer numbers of smaller surfclams at the shallow-water stations.

3.2. Atlantic surfclam shell

In the surveyed region, surfclam shell was generally encountered where large-market surfclams were found (Fig. 6), an indication that surfclams have been a dominant benthic inhabitant at these inshore depths for an extended period of time. How long is unclear, but the

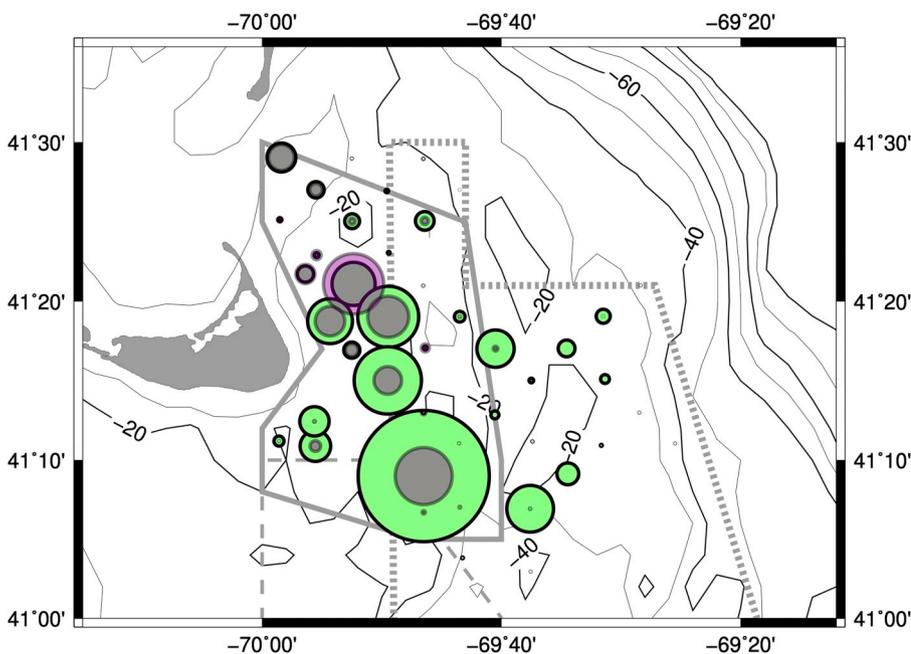


Fig. 4. Catch of medium-market (>150 – 170 mm) (solid green) and large-market (>170 mm) (semi-transparent purple) Atlantic surfclams. Variations in purple and green shading accrue from circle overlap. Circle diameters are linearly proportional to numbers m^{-2} within category only. Abundance comparisons cannot be made across categories. Supporting data are provided as supplementary material in Powell et al. (2019). Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m.

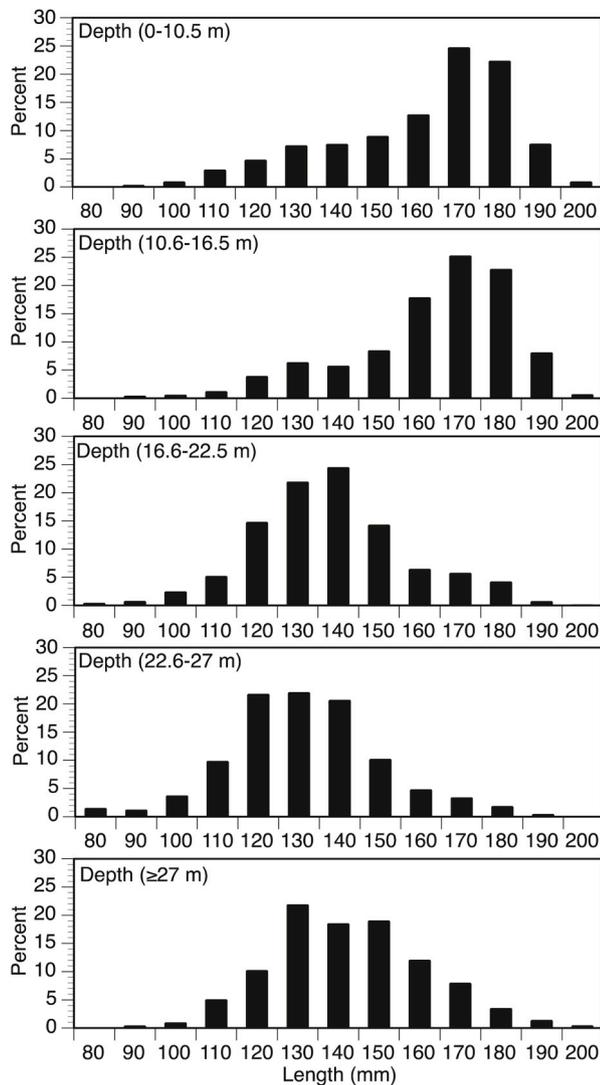


Fig. 5. Population size-frequency distributions for Atlantic surfclams for each of 5 depth zones east of Nantucket. Size frequencies derived from the combined catch from all stations within the denoted depth zone.

maximum life span of ~30 years would suggest that inhabitation has extended over half-century time scales or longer. In contrast, smaller surfclams, found offshore of this region, rarely were found in locales where surfclam shell was abundant (Fig. 7). The inference is that this deeper-water region has been inhabited only recently by surfclams. However, unequivocal discrimination of recent colonization from slower growth, that might also be expected offshore in deeper water (Munroe et al., 2013), requires data on the ages of the living clams.

To further evaluate the relationship between surfclam shell and the abundance of large (≥ 150 mm) and small (< 150 mm) surfclams, the probability that the fraction of large surfclams in the catch exceeding the median fraction and the catch of surfclam shell exceeding the median shell catch was evaluated using a binomial test. The expectation was that stations in which large surfclams were proportionately more abundant and stations where catches of shell rose above the median catch would coincide more frequently than expected by chance. This was the case: $P < 0.01$. The expectation was that stations in which the fraction of small surfclams exceeded the median would not coincide with stations in which catches of surfclam shell rose above the median catch. This too was the case: $P > 0.05$. Thus, catches of surfclam shell above the median catch were much more likely to be present in stations yielding proportionately larger catches of large (≥ 150 mm) surfclams.

3.3. Atlantic surfclam age distributions

The finding of smaller surfclams in deeper water may originate from populations of younger and hence smaller surfclams or surfclams growing slower. The number of animals aged (Table 2) was insufficient to develop a formal population age frequency at any of the 4 sites; however, the two shallow-water sites contained surfclams from a broad range of ages from young to older than 20 yr which was not the case at the two deeper sites (Fig. 8). The wide distribution of ages at the two shallow water sites is typical of mature population dynamics characterized by recruitment, growth, and mortality over a relatively long time (Weinberg, 1999). The two deeper-water sites, in contrast, were characterized by young surfclams; the oldest surfclam aged was 13 years old, having recruited to the area in 2004, and coincidentally with the most recent increase in the rate of oceanic warming in the study region, also in 2004 (Pershing et al., 2015).

3.4. Surfclam growth rates

Growth increments from age 1 to age 2 did not differ between shallow and deep sites or between locales; nor was the influence of birth year significant as a covariate or as a component of an interaction term (Tables 2, 3).

On the other hand, growth increments from age 3 to age 4 were strongly influenced by birth year (Tables 2, 3). Growth was slow for the earliest colonizers (oldest surfclams) at the deeper stations, but rose to a level approximating the growth rate of surfclams in shoaler water for surfclams born later in the 2000s (Fig. 9). In comparison, surfclam growth rates at the shallower stations did not substantively change over the two decades prior to collection, including over the time frame encompassing the initial colonization period at the deeper stations (Fig. 10). Surfclam growth rates from age 3 to age 4 at the shallower stations were modestly significantly different from growth rates at the deeper stations (Table 3); average growth increments were higher for surfclams at the shallower stations due to the slower growth rates for surfclams at the deeper stations in the mid 2000s, the few years following initial colonization (Fig. 9). An *a posteriori* test showed that surfclams at both shallow stations differed significantly in growth rate from the growth rates for surfclams at deeper station I1 and surfclams at one shallow station differed significantly in growth rate from surfclams at deeper station I4 (Table 3). The change in growth rate over time observed for surfclams at the deeper stations compared to consistent growth rates over the same time period for surfclams at the shallower stations (Fig. 10) also explained the modestly significant interaction term between birth date and group (shallow vs. deep stations) (Table 3).

Surfclam growth increments from age 7 to age 8 did not differ significantly between shallow and deep stations, nor was birth year significant as a covariate or as a component of an interaction term (Tables 2, 3). An *a posteriori* test showed that surfclams at deeper station I1 grew significantly faster than surfclams at either shallow station (Table 3); however, the few surfclams exceeding 8 years of age at the deeper stations limit the reliability of this comparison.

Size-at-age data were fit to a 3-parameter von-Bertalanffy function (Chintala and Grasse, 2001; Chute et al., 2016) for each of the four sites and, because the surfclam growth rates at the two shallow-water sites were never significantly different, nor were differences found between the two deep-water sites, a 3-parameter von-Bertalanffy function was fit to the combination of surfclams from the two shallow-water sites and the combination of the two deep-water sites. The parameter values are shown in Table 4. The L_{∞} values for the shallow sites are consistent with values found during the 1980s for the federal surfclam stock, and distinctly above values seen in the 2000s (Munroe et al., 2016). The parameter values for the deeper sites are reported, but are suspect because a mature population age frequency is not present and this will likely bias the estimate of L_{∞} and has the potential to also affect k .

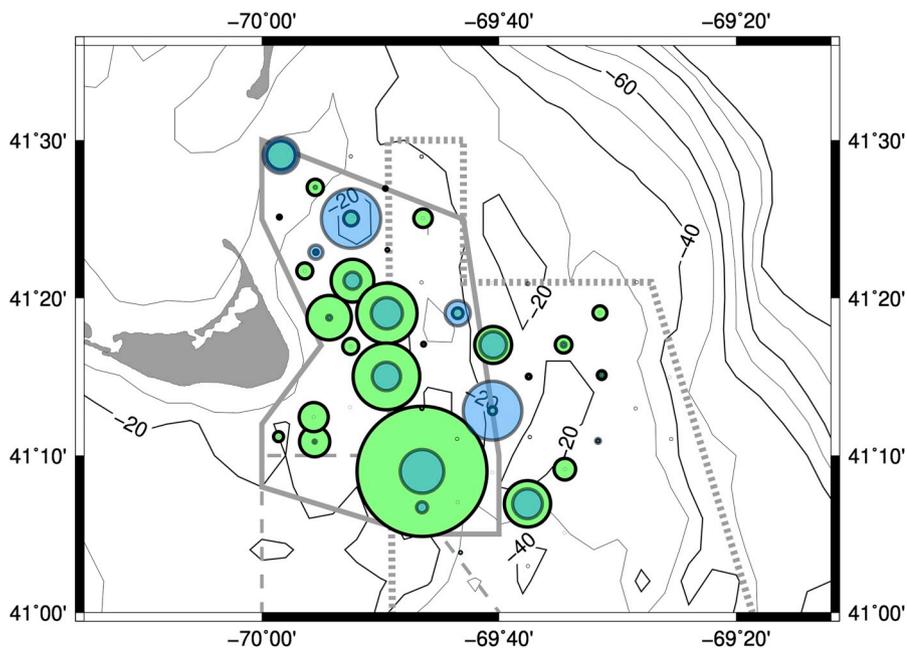


Fig. 6. Catch of surfclam shell (semi-transparent blue) and medium-market (>150–170) Atlantic surfclams (solid green). Variations in blue and green shading accrue from circle overlap. Circle diameters are linearly proportional to numbers m^{-2} for surfclams and $bu\ m^{-2}$ for surfclam shell within category only. Abundance comparisons cannot be made across categories. Supporting data are provided as supplementary material in Powell et al. (2019). Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m.

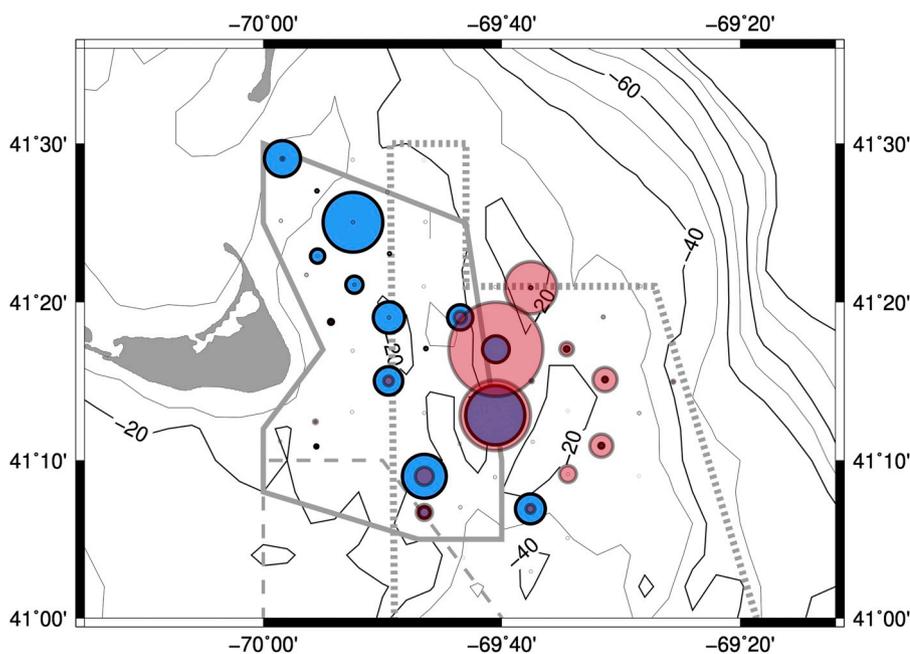


Fig. 7. Catch of surfclam shell (solid blue) and small-market (120–150 mm) Atlantic surfclams (semi-transparent red). Variations in blue and red shading accrue from circle overlap. Circle diameters are linearly proportional to numbers m^{-2} for surfclams and $bu\ m^{-2}$ for surfclam shell within category only. Abundance comparisons cannot be made across categories. Supporting data are provided as supplementary material in Powell et al. (2019). Zero catch stations are not shown (see Fig. 1 for full station complement). Depths in m.

4. Discussion

4.1. Perspective

Over much of the geographic range, warming seawater temperatures are forcing surfclams to move north and offshore (Narváez et al., 2015; Powell et al., 2017a; Hofmann et al., 2018). This process is well documented in the Mid-Atlantic where surfclams have moved offshore off New Jersey (Weinberg et al., 2005) and mass mortality events have occurred inshore off Delmarva (Kim and Powell, 2004). Powell et al. (2017a) and NEFSC (2017) documented the same offshore trends as far north as Georges Bank. NEFSC (2017) found surfclams progressing offshore off eastern Long Island. This nearly stock-wide shift in range is due to the narrow temperature window between temperatures optimal

for surfclams and their upper lethal limit (Munroe et al., 2013; Narváez et al., 2015; Hornstein et al., 2018). Consequences of this physiology include lower condition offshore (Marzec et al., 2010), declining maximum size (L_{∞} : Munroe et al., 2016), and a differential distribution of surfclam shell and living surfclams (Powell et al., 2017a, Powell et al., 2020). In the latter case, a characteristic of recent colonization is living surfclams with little co-occurring shell whereas the opposite is indicative of a range recession, the time frame of which is dependent upon the degree of time averaging (Powell and Davies, 1990; Flessa and Kowalewski, 1994; Kidwell, 2002). Though well described in general, the details of demography and physiology for benthic species colonizing an advancing range boundary during a period of climate change are not well understood. The case of the surfclam provides a particularly good opportunity to examine these aspects of species performance during a

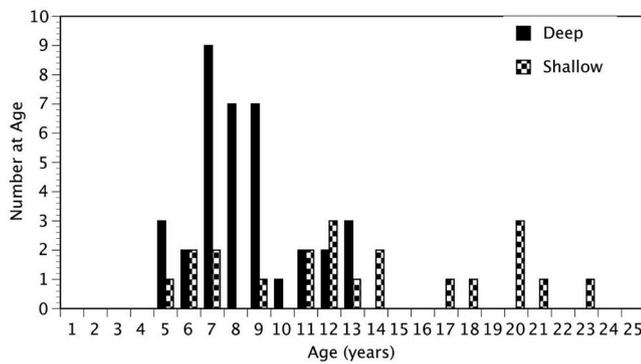


Fig. 8. Number of surfclams aged as a function of their age. Note that the plot does not represent a population age frequency; rather, the plot shows the frequency of ages for the surfclams that were aged from each site group: deep (I1+I4), shallow (A3+C3).

Table 3

Results of a nested ANOVA analysis of growth increments for 3 yearly transitions. Group: shallow (stations A3+C3) vs. deep (stations I1+I4). Station: A3, C3, I1, I4. Birth year was calculated from the year of death (August 2017). Least squares means tests follow for cases where at least one comparison between stations was significant at $\alpha = 0.05$.

	Group	Station (Group)	Birth Year	Group*Birth Year
Growth Increment Year 7 to Year 8	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
Growth Increment Year 3 to Year 4	$P = 0.031$	$P > 0.05$	$P = 0.0026$	$P = 0.031$
Growth Increment Year 1 to Year 2	$P > 0.05$	$P > 0.05$	$P > 0.05$	$P > 0.05$
Growth Increment Year 3 to Year 4				
Station		I1	I4	
A3	$P > 0.05$	$P = 0.0007$	$P = 0.0033$	
C3		$P = 0.043$	$P > 0.05$	
I1			$P > 0.05$	
Growth Increment Year 7 to Year 8				
Station		I1	I4	
A3	$P > 0.05$	$P = 0.0026$	$P = 0.05$	
C3		$P = 0.0067$	$P > 0.05$	
I1			$P > 0.05$	

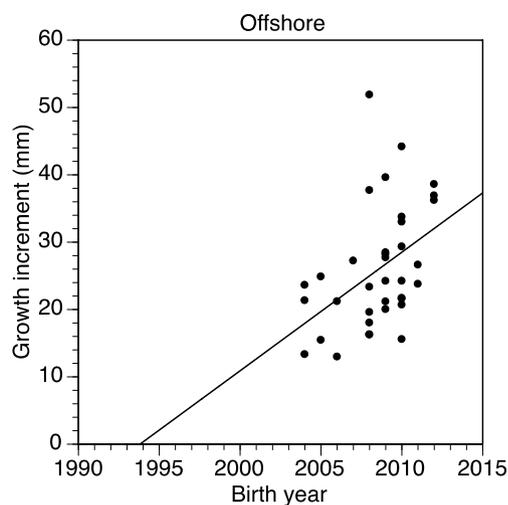


Fig. 9. Growth increment from age 3 to age 4 for surfclams from the deeper-water stations I1 and I4 (Table 2) versus birth year. The diagonal line is an ordinary least squares regression line.

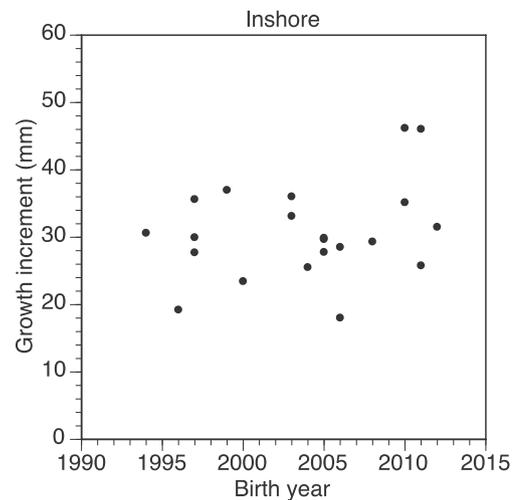


Fig. 10. Growth increment from age 3 to age 4 for surfclams from the shoaler-water stations A3 and C3 (Table 2) versus birth year.

Table 4

Von Bertalanffy growth curve parameters for surfclams from each locale and for the combination of shallow sites (A3+C3) and deep sites (I1+I4).

Locale	Von Bertalanffy Parameters		
	L_{∞} (cm)	k (yr^{-1})	t_0 (yr)
A3	169.8	0.255	1.05
C3	178.2	0.224	0.33
I1	142.4	0.266	1.03
I4	176.0	0.201	0.98
Group			
Shallow	174.2	0.239	0.73
Deep	158.6	0.230	1.01

shift in range.

Off Nantucket, the primary demographic difference observed is the dichotomous distribution of large (>150 mm) and smaller surfclams. The largest surfclams were caught nearly exclusively at the shallower depths <20 m. Smaller surfclams were distributed over a broader area, but highest densities were found at deeper depths. Surfclams have been fished in the region for decades, with landings coming historically from shallower depths (<20 m), although recent catches have come from a broader range of depths. The size differential is contrary to an anticipated effect of fishing, wherein truncation of the size frequency in the areas historically fished might be expected (e.g., Rice et al., 1989; Krauter et al., 2007; Munroe et al., 2016). In the case of surfclams off Nantucket, the region less fished has a size-frequency distribution shifted towards the smaller sizes as often observed in fished populations. Not only are the numbers of smaller clams higher on the average at these deeper sites, but the numbers of large animals are distinctly fewer at these deeper sites; thus, the size-frequency distributions are distinctly shifted towards the smaller size classes. The differential in size frequencies, then, cannot be explained by fishing. In addition, the distribution of abundance has shifted towards the range boundary rather than being situated in the center of the range, a not-unusual outcome during a period of climate change in the terrestrial world (Dallas et al. 2017) and one increasingly observed throughout the range of the Atlantic surfclam (Weinberg et al., 2005; Timbs et al., 2019).

4.2. Evidence for a surfclam range shift off Nantucket

Mid-Atlantic water temperatures have been warming for at least the last 200 years, with a distinct increase in rate since 1970 (Nixon et al., 2004; Fulweiler et al., 2015; Pershing et al., 2015; Steinman et al., 2015;

Kavanaugh et al., 2017; Pace et al., 2018). The disproportionately higher rate of warming in the Gulf of Maine and Mid-Atlantic region relative to the remainder of the world's oceans is now well described (Pershing et al., 2015; Kavanaugh et al., 2017) and is expected to continue (Saba et al., 2016). That warming bottom water temperatures are forcing surfclams to move offshore is well described (see review in Hofmann et al., 2018; Timbs et al., 2019). Throughout much of the species' range, the offshore movement has initiated recruitment within the area occupied by ocean quahogs. This co-habited ecotone is now well documented (Powell et al., 2020), including on the neighboring Georges Bank (Powell et al. 2017a).

The finding of smaller surfclams offshore in the survey east of Nantucket is consistent with the expectation of recent recruitment into deeper water throughout much of the surfclam's range. Indeed, the two deeper-water stations at 23 and 26 m yielded surfclams no older than 13 yr, whereas the two shallower-water stations at 8 and 12 m had a mature age frequency with some surfclams exceeding 20 yr. NEFSC (2017) presents population age frequencies for the federal stock from Delmarva to Georges Bank. Loesch and Ropes (1977) found animals at least 19 years old off Delmarva. Weinberg (1999) evaluated population age frequencies for the stock in the southern portion of the range as it was found in the 1990s, and routinely found animals of 26+ years. Chute et al. (2016) also observed older clams throughout most of the geographic range of the surfclam stock. Thus, the age range of surfclams from the two shallow sites off Nantucket is not unusual, whereas the limited age range in deeper water would be unexpected for a mature population age frequency. The inference is that this deeper-water region has been inhabited only recently by surfclams. This would be consistent with the tricennial shift in surfclams offshore and notably coincident with the most recent acceleration in the rate of warming in the study region (Pershing et al., 2015).

Further support for the newness of occupation of deeper-water sites can be found in the distribution of surfclam shell, which is found in limited quantities in regions where recent colonization is inferred and in greater quantities in water shallower than this. Bivalve shell enters into the taphonomic process after death. Stated simply, various degradational processes such as dissolution, abrasion, and bioerosion operate to destroy the shell (Staff et al., 1986; Powell et al., 1989; Davies et al., 1990) while it is at the surface or in the surficial sediments within the taphonomically-active zone (TAZ; Davies et al., 1989). Burial, on the other hand, removes shell from the TAZ, thereby preserving it for an extended period of time, if not indefinitely (Powell, 1992; Walker and Goldstein, 1999; Olszewski, 2004). The robustness to taphonomic degradation of surfclam shell is unknown, but shells of similar clam species tend to be robust (Callender et al., 1994; Walker and Goldstein, 1999; Powell et al., 2011, Powell et al., 2011). Thus, surfclam shell should remain intact for many decades after death (Powell et al., 2017a).

The signal provided by surfclam shell is clear in the case of the region east of Nantucket where surfclam shell is found predominately in regions where larger surfclams are present. The observation of species present living, but not in the death assemblage, is unusual and normally explained by rarity of occurrence or poor preservability (e.g., Callender and Powell, 2000; Albano, 2014; Martinelli et al., 2016), neither of which is true for Atlantic surfclams in the surveyed region. Long post-mortem shell half-lives impose taphonomic inertia into the system which permits the death assemblage to track the history of occupation (Kidwell, 2008; Poirier et al., 2010; Feser and Miller, 2014), but which also imposes a time delay between initial colonization and representation in the death assemblage (Olszewski, 2012; Feser and Miller, 2014) and a variable signal of range relinquishment depending on the degree of time averaging (e.g., Perry, 1996; García-Ramos et al., 2016; Powell et al., 2020). Thus, range expansion, as inferred from this survey, provides a stronger and less ambiguous signal than range relinquishment. Evidence of range relinquishment is evident along the southern range boundary off Delmarva today (Powell et al., 2020), but no evidence of abandonment of the shallowest waters off Nantucket is provided by the

present survey; rather range expansion is the primary population shift off Nantucket.

4.3. Physiological implications of deep-water colonization

The biological exigencies associated with occupation of new habitat along the leading edge of a species' range have received considerable attention relative to the genetic implications of early colonization (Holt, 2003; Hughes et al., 2007; Hellman et al., 2008; Excoffier et al., 2009), but the immediate physiological challenges that may affect success and the subsequent degree to which the colonizing populations take on the role of source as well as sink are not well understood. Growth rate and maximum size in Atlantic surfclams, like most large bivalves, is strongly temperature dependent (Ambrose et al., 1980; Munroe et al., 2013; Narváez et al., 2015; Broell et al., 2017). This temperature dependency is biphasic; filtration rates follow a strongly left skewed relationship with temperature. As a consequence, scope for growth drops rapidly above an optimal temperature as the clam enters what Woodin et al. (2013) termed the transient event margin, a temperature range that permits survival, but compromises energetics by reducing ingestion relative to respiration. Narváez et al. (2015) referred to the physiological constraint as deficit stress (Getz, 2011). On the other hand, temperatures below optimal reduce both respiratory rate and filtration rate and consequently also should reduce the rate of growth.

Growth rates for clams from the shallower stations off Nantucket are comparable or higher than observed elsewhere in the stock, in contrast with the oft-observed lower rates of growth in the southern portion of the range, particularly inshore where temperatures are warmer (Loesch and Ropes, 1977; Chintala and Grassle, 1995; Chute et al., 2016) consequent of the temperature constraint on scope for growth. Surfclam maximum sizes in the surveyed region are larger than elsewhere in the geographic range with largest sizes clearly larger than L_{∞} values observed elsewhere by Munroe et al. (2016) in the 2000s and as large as those observed off New Jersey in the 1980s (see also NEFSC, 2017). The shallow-water stations surveyed east of Nantucket presently contribute the highest abundance of large surfclams in the stock (NEFSC, 2017). Large size in this region is likely a mixture of optimal temperatures and higher current velocities providing increased food resources.

The surfclams colonizing deeper water post-2000 might be expected to grow slower due to an anticipated lower average temperature near the deep-water range boundary. This is exactly the observation in the first few years after colonization, when growth rates were indeed significantly lower than for clams in shallower water. Such animals can be expected to have lower fecundities for a period of time and, thus, their contribution to population spawning stock biomass will be proportionately lowered. The time frame under which this constraint remains would depend on the rate of climate change introducing more optimal temperatures. Interestingly, off Nantucket, the limitation on growth rate existed for only a few years until warming permitted growth rates to increase to rates typical of clams in shallower water. Thus, the physiological penalty imposed by colonization pushing the range boundary into deeper water lasted no more than 4–5 years. This remarkably rapid achievement of normal growth rates is consistent with the rapid ocean temperature rise well-documented in the Nantucket region (Pershing et al., 2015).

4.4. Regime shift implications

Roy et al. (2001) observed that the range boundaries of large bivalves are particularly sensitive to climate change. Circa-2000 saw a rapid change in population dynamics for many species in the North Atlantic, as far south as the Gulf of Mexico. In the Gulf of Mexico, the dominance of the ENSO (El Niño-Southern Oscillation) signal in oyster (*Crassostrea virginica*) population dynamics ceased, with subsequent changes in maximum size, sex ratio, and mortality throughout the following decade (Powell, 2017). In Delaware Bay, the population

dynamics of *C. virginica* also changed dramatically (Powell et al., 2008). Off the east coast, a surfclam mass mortality event occurred off Delaware (Kim and Powell, 2004), followed shortly thereafter by the disappearance of surfclams from New Jersey state waters (Hofmann et al., 2018). Coincident with these events, all likely a response to rising temperatures, surfclams colonized deeper waters east of Nantucket, pushing into waters heretofore the habitat of boreal species. The timing is consistent with known changes in water temperature in the region (Pershing et al., 2015) and is consistent with the range-wide offshore movement of this species (Powell et al., 2017a; Hofmann et al., 2018; Powell et al., 2020).

The rapidity of this colonization event off Nantucket, taking place approximately on a 5-year time scale, is unexpected given the longevity and sedentariness of the species. The tendency of larval settlement in surfclams to cover a broader area than the range occupied by the adults provides the basis for rapid range shifts to occur (Timbs et al., 2018, 2019). Thus, rapid occupation of the deep water off Nantucket was likely facilitated by the routine tendency for recruits to settle in suboptimal habitat beyond the range boundary of the adults of the species. Once established, the surfclam population rapidly increased in abundance. The timing is about 15% of the known life span of the species and reminiscent of the rapid colonization of the Mid-Atlantic by the much longer lived ocean quahog circa 1900 (Pace et al., 2017b) that took place in 20–30 years, about 10–15% of that species' known life span on the U.S. east-coast continental shelf. The ability to advance a range boundary rapidly is an important adaptation for a long-lived species, as decadal to tricennial shifts in temperature are known accompaniments of climate cycles such as the North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO). The ongoing shift in the range of the Atlantic surfclam is the geographically most extensive documented range shift for a sedentary benthic species. The evidence from Nantucket demonstrates the rapidity of response possible given a rate of climate change rapid enough to minimize the physiological impediments limiting post-colonization population development through suboptimal temperatures restricting post-settlement growth. In this case, continued warming permitted growth rates to reach regional norms in about 5 years and, if the present temperature regime remains, the deeper-water habitat can be expected to develop mature population demographics within the next decade.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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