

# **Growth and Longevity in Surfclams East of Nantucket**

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## **Introduction**

Analysis of the distribution of Atlantic surfclams showed that submarket and small market-size 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 that historically showed highest landings. Few small surfclams were found inshore where most reported landings originated. The catch of submarket and small market-size surfclams (surfclams <150 mm) generally overlapped wherever they occurred. The catches of the two size classes were significantly correlated (Pearson correlation:  $r = 0.93$ ;  $P < 0.0001$ ). In contrast, medium and large market-size surfclams (surfclams  $\geq 150$  mm) were found on the most extreme southwestern edge of the HMA and inshore to the EEZ boundary. The two larger size classes were very similarly distributed and their catches were significantly correlated (Pearson correlation:  $r = 0.80$ ,  $P < 0.0001$ ). 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 catches of the two size groups, animals <150 mm and  $\geq 150$  mm, were not correlated (Pearson correlation:  $r = 0.10$ ,  $P > 0.05$ ), demonstrating their differential distributions.

The hypothesis was raised that the differential distribution of surfclams reflected recent colonization in deeper water consistent with the known offshore expansion of the surfclam's range documented throughout the Mid-Atlantic Bight and on Georges Bank. Support for this

view came from the relationship between surfclam shell and the abundance of large ( $\geq 150$  mm) and small ( $< 150$  mm) surfclams. The probability that the abundance of large surfclams in the catch exceeding the median abundance 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 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 additional expectation was that stations in which the abundance of small surfclams exceeded the median would not coincide with stations in which catches of surfclam shell rose above the median catch. This 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 ( $\geq 150$  mm) surfclams, indicative of long-term occupation of this habitat by surfclams. Lower catches of shell in regions where smaller surfclams were abundant supported recent colonization

The presence of smaller surfclams in the HMA, however, could be the result of recent colonization or slow growth in suboptimal habitat. Accordingly, Atlantic surfclams from selected stations were aged and their growth rates measured.

#### **Methods:** *Ageing of Atlantic surfclams*

At four stations (A3, C3, I1, I4 at depths , respectively, 26, 39, 84, 74 m), surfclams representing the range of sizes caught were selected, shucked, and the articulated valves returned to the laboratory for ageing. Atlantic surfclams lay down annual growth increments as a consequent of the seasonal cycle of their growth (Jones, 1981; Ivany, Wilkinson & Jones, 2003), that can be used to estimate their age (Ropes & Jearld, 1987; Jacobson et al., 2006; Chute, McBride, Emery & Robillard, 2016). In the laboratory, paired valves were dipped in a diluted bleach solution, 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  $\mu\text{m}$  and 1  $\mu\text{m}$  polycrystalline diamond suspension. 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. 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, Virginia Institute of Marine Science, and the NMFS Northeast Fisheries Science Center (see also Jacobson et al., 2006).

A 3-parameter von Bertalanffy growth model was used to evaluate both individual and population growth rates (see also Chintala & Grassle, 2001; Munroe et al., 2016; Chute, McBride, Emery & Robillard, 2016). All growth increment datasets passed normality and heteroscedasticity tests. 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. 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, Powell & Mann (2018), Picariello (2006), and Chute, McBride, Emery & Robillard. (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). *A posteriori* tests used least squares means.

## **Results**

### *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 two shallow-water sites contained surfclams from a broad range of ages from young to surfclams older than 20 yr (Fig. 1). This age distribution is typical of mature population dynamics characterized by recruitment, growth, and mortality over a relatively long time (Weinberg, 1999). The two deeper-water sites were characterized by young surfclams; the oldest surfclam aged was 13 years old, having recruited to the area in 2004.

### *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 date significant as a covariate or as a component

of an interaction term (Tables 1, 2).

Growth increments from age 3 to age 4 were strongly influenced by birth date (Tables 1, 2). 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. 2). 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. 3). Surfclam growth rates from age 3 to age 4 at the shallow stations were modestly significantly different from growth rates at the deeper stations (Table 2); 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. 2). 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 2). 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. 3) also explained the modestly significant interaction term between birth date and group (shallow vs. deep stations) (Table 2).

Surfclam growth increments from age 7 to age 8 did not differ significantly between shallow and deep stations, nor was birth date significant as a covariate or as a component of an interaction term (Tables 1, 2). An *a posteriori* test showed that surfclams at deeper station I1 grew significantly faster than surfclams at either shallow station (Table 2); 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 & Grassle, 2001; Chute, McBride, Emery & Robillard, 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 significant 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 3. The  $L_{\infty}$  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  $L_{\infty}$  and has the potential to also affect  $k$ .

## Discussion

### *Perspective*

Over much of the geographic range, warming seawater temperatures are forcing surfclams to move north and offshore (Narváez et al., 2015; Powell, Kuykendall & Moreno, 2017; Hofmann et al., in press). This process is well documented in the Mid-Atlantic where surfclams have moved offshore off New Jersey (Weinberg, Powell, Pickett, Nordahl & Jacobson, 2005) and mass mortality events have occurred inshore off Delmarva (Kim & Powell, 2004). Powell, Kuykendall & Moreno (2017) 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, Powell, Klinck, Mann & Hofmann, 2013; Narváez et al., 2015). Consequences of this physiology include lower condition offshore (Marzec, Kim & Powell 2010), declining maximum size ( $L_{\infty}$ : Munroe et al., 2016), and a differential distribution of surfclam shell and living surfclams (Powell, Kuykendall & Moreno, 2017). In the latter case, a characteristic of recent colonization is living surfclams with little co-occurring shell.

Off Nantucket, the primary demographic difference observed is the dichotomous distribution of large (>150 mm) and smaller surfclams. The largest surfclams are nearly completely restricted to the shallower depths <35 m. Smaller surfclams are distributed over a broader area, but highest densities are found at deeper depths. Surfclams have been fished in the region for decades, with landings coming historically from shallower depths. The size differential is obverse to an anticipated effect of fishing, wherein truncation of the size frequency in the areas historically fished might be expected (e.g., Rice, Hickox & Zehra, 1989; Kraeuter, Ford & Cummings, 2007; Munroe et al., 2016). In this case the region less fished has the truncated size-frequency distribution. 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. In addition, the distribution of abundance has shifted towards the range boundary rather than being situated in the center of the range, an outcome commonly encountered in the terrestrial world (Dallas, Decker & Hastings, 2017)

#### *Evidence for a surfclam range shift off Nantucket*

The two deeper-water stations yielded surfclams no older than 13 yr, whereas the shallow-water stations 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 & 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, McBride, Emery & Robillard (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 only recently inhabited by surfclams. The 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, 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.

#### *Physiological implications of deep-water colonization*

The biological exigencies associated with occupation of new habitat along the leading edge of a species' range has received considerable attention relative to the genetic implications of early colonization (Holt, 2003; Hughes, Dytham & Hill, 2007; Hellman, Pelini, Prior & Dzurisin, 2008; Excoffier, Fall & Petit, 2009), but the immediate physiological challenges that may effect success and the subsequent degree to which the colonizing populations takes 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, Jones & Thompson, 1980; Munroe, Powell, Klinck, Mann & Hofmann, 2013; Narváez et al., 2015; Broell, McCain, & Taggart, 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, Hilbish, Helmuth, Jones & Wetthey (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). Deficit stress is the primary reason for range recession at the warm-temperature boundary of the surfclam's range. On the other hand, temperatures below optimal reduce both respiratory rate and filtration rate and consequently also should reduce the rate of growth, an expectation at the cold-temperature boundary of the surfclam's range.

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 & Ropes, 1977; Chintala & Grassle, 1995; Chute, McBride, Emery & Robillard, 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  $L_{\infty}$  values observed elsewhere by Munroe et al. (2016) in the 2000s and as large as observed by them off New Jersey in the 1980s (see also NEFSC, 2017). These stations 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 for growth 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 surfclams in shallower water. 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 surfclams in shallower water. Thus, the physiological penalty imposed by colonization pushing the range boundary into deeper water lasted no more than 4-5 years.

The rapidity of this occupation, taking place approximately on a 5-year time scale, might

be 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, however (Timbs et al., submitted). 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, Powell, Mann & Long., 2017) 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.

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Table 1. Growth increments in mm yr<sup>-1</sup> rendered as mean (median) ± standard deviation for each of the four stations and for the depth-dependent station groups.

Station	Year 1 to Year 2	Year 3 to Year 4	Year 7 to Year 8
A3	25.8 (27.8) ± 9.5	38.1 (29.9) ± 7.4	6.1 (5.7) ± 2.6
C3	25.8 (26.3) ± 9.1	28.0 (29.5) ± 6.1	7.0 (6.1) ± 3.7
I1	26.3 (26.9) ± 7.3	26.0 (28.5) ± 10.1	11.0 (12.1) ± 2.4
I4	28.2 (25.5) ± 10.5	25.9 (24.8) ± 7.9	8.4 (7.0) ± 3.6
Group			
Shallow	25.8 (27.8) ± 9.1	30.7 (39.8) ± 7.1	6.5 (6.1) ± 3.1
Deep	27.1 (26.6) ± 8.7	26.0 (23.0) ± 9.1	9.6 (10.2) ± 3.3

Table 2. 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 date was calculated from the date of death (August, 2017). Least squares means tests for cases where at least one comparison between stations was significant at  $\alpha = 0.05$ .

	Group	Station(Group)	Birth Date	Group*Birth Date
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	C3	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	C3	I1	I4
A3	P > 0.05	P = 0.0026	P = 0.05
C3		P=0.0067	P > 0.05
I1			P > 0.05

Table 3. Von Bertalanffy growth curve parameters for surfclams from each locale and for the combination of shallow sites (A3+C3) and deep sites (I1+I4).

	Von Bertalanffy Parameters		
Locale	$L_{\infty}$ (cm)	$k$ (yr <sup>-1</sup> )	$t_0$ (yr)
A3	169.8	0.255	1.047
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

Figure 1. 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 age frequency of the surfclams that were aged from each site.

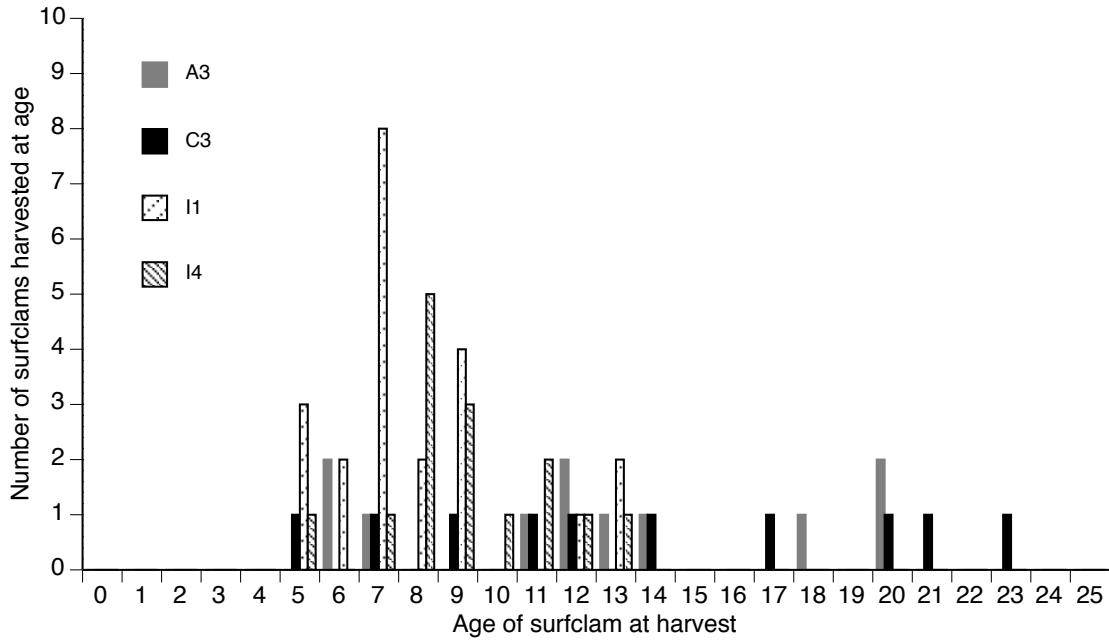


Figure 2. Growth increment from age 3 to age 4 for surfclams from the deeper-water stations I1 and I4 (Table 1) versus birth year. The diagonal line is an ordinary least squares regression line.

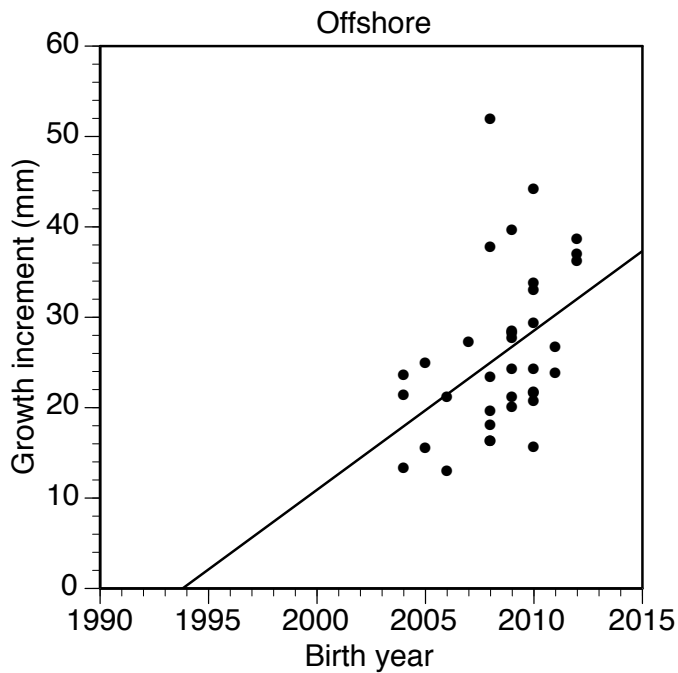


Figure 3. Growth increment from age3 to age 4 for surfclams from the shoaler-water stations A3 and C3 (Table 1) versus birth year.

