



## **Genetics, age demographics, and shell size of Atlantic surfclams from the southern edge of their range.**

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Report Issued: November 9, 2022

### **Summary**

Until recently, the federal surfclam fishery had not fished for surfclams on the southern edge of the surfclam range due to low population numbers resulting from mortalities in the 1990s. Catches of surfclams off Virginia in the past two years have raised the question of whether the surfclam population has recovered in the region or if a single large cohort survived to support those catches. The subspecies *Spisula solidissima similis* is a shallow, warm water cryptic subspecies of the Atlantic surfclam. The two subspecies are morphologically indistinguishable; however, *S. s. similis* grows to a smaller overall size and is genetically distinct. Questions have also been raised about the possibility of *S. s. similis* being part of the population fished off the coast of Virginia, and whether the clams being fished there are from a population that derives from regular recruitment. To address these questions, samples of surfclams were taken off the coast of Virginia. Genetic samples were taken and compared to both Atlantic surfclam and the cryptic subspecies in DNA sequences. Surfclams were aged, and length and weight were recorded for each clam. Size and weight were then compared to a New Jersey population of the same ages. Genetic results suggest there is a cyptic subspecies surfclam or a hybrid within the sampled population, surfclams aged 3 to 9 years of age were found within the sample, and the southernmost surclams were smaller than New Jersey clams of the same age.

## Introduction

Atlantic surfclams (*Spisula solidissima*) are a large, long-lived cold-water clam species living on the continental shelf from South Virginia to Canada (Hofmann et al., 2018, Jones et al., 1978, & Narváez et al., 2015). The species supports a large commercial fishery in the United States and generates around 30 million USD each year in revenue from landings alone (Scheld et al. 2022).

The optimal temperature range for Atlantic surfclams is between 16 to 22° Celsius (Narváez et al. 2015), with the southern part of the species' range generally experiencing higher bottom temperatures than more northern regions (Weinberg & Helser, 1996). Higher than normal bottom temperatures can result in elevated stress levels, starvation, and death (Loosenoff and Davis, 1963., Narváez et al., 2015). In the early 1990s higher than normal water temperatures resulted in a major mortality event of Atlantic surfclams on the southern end of the range (Weinberg., 2005). The low population numbers remaining after the mortality event limited Atlantic surfclam fishing efforts in the region.

The cryptic subspecies (*Spisula solidissima similis*) are genetically distinct from Atlantic surfclams, and with the possible exception of one small hinge process they are morphologically indistinguishable (Hare et al., 2010). The cryptic subspecies tends to live in warmer shallower waters and are not a commercially targeted species. The presence of the cryptic subspecies among the Atlantic surfclam population could indicate a possible range shift for the cryptic subspecies into deeper waters. Such a range shift could have repercussions for the federal fishery and management practices due to possible misidentification of the cryptic subspecies as an Atlantic surfclam (Reiss et al. 2009). Hybridization potential between Atlantic surfclams and the cryptic subspecies has not been confirmed, yet could explain mixing of the cryptic subspecies within the Atlantic surfclam southern range population.

Recently, Atlantic surfclams have once again been caught on the southern end of the range raising the question of whether the Atlantic surfclam population has recovered in that area or if a single cohort has survived to support recent fishing effort. If multiple cohorts are present, that could suggest that the Atlantic surfclam population has recovered along the range edge and possibly adapted to the warmer bottom temperatures. A recent study has shown that juvenile Atlantic surfclams exposed to sustained periods of higher-than-normal water temperatures and survive to adulthood are able to withstand thermal stress longer than surfclams that were not exposed to high water temperatures (Acquafredda et al., 2021). Further, there is evidence that the progeny from Atlantic surfclams that survived a thermal stress event have improved capacity to survive high temperature events, suggesting that thermal tolerance is a heritable trait and adaptation to high temperatures is possible (Acquafredda, 2021)

To better understand the circumstances underlying the resurgence of the commercial fishery along the southern edge of the Atlantic surfclams range, samples were collected to evaluate the genetics, age demographics, and morphology of Atlantic surfclams from the southern edge of their range.

## Materials and Methods

Surfclams were caught on November 17<sup>th</sup>, 2021, from the southern fishing grounds by two commercial fishing vessels *F. V. Betty C* (BC) and *F. V. Cristi-Caroline* (CC). Fishing locations for the *F. V. Betty C* (BC) was 36.7191°N, -74.9774°W at 32m depth, and for *F. V. Cristi-Caroline* (CC) 36.8994 °N, -75.0233°W at 38m depth (Figure 1). Samples of live, fully intact surfclams (n=53 from BC, n=50 from CC) from the catch were collected as they arrived at the clam processing facility the next day.

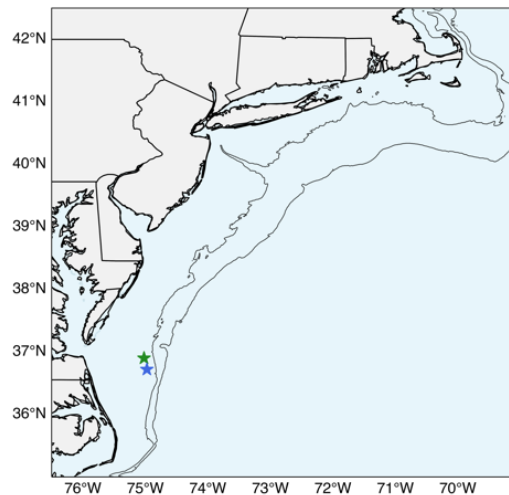


Figure 1. Location of the fishing sites where samples from which samples were obtained are indicated with stars (BC green and CC blue). The 50m and 100m isobaths are shown with black lines, and land is represented in grey.

Shell length, height, and width were measured for each surfclam using electronic calipers. Each surfclam was shucked and both wet and dry whole meat weights were measured. Small mantle tissue samples (<1g tissue) were collected and preserved in ethanol for genetic testing. Upon shucking, the sex of each clam was also identified and recorded. The left cardinal tooth was extracted, and the top and bottom process of the cardinal tooth were photographed under a microscope with 10x magnification and measured using the computer software ImageJ. The ratio of the length of the top and the bottom process of the left cardinal tooth was calculated. After shucking, shells were cleaned, labeled, and retained for aging.

The left valve from each sampled surfclam was cut from umbo to growing edge (Figure 2), through the center of the chondrophore using a diamond blade saw. Cut shells were ground and polished using an Eco-met 30 variable speed grinder-polisher until the chondrophore has an even, smooth, reflective quality. Polished hinges were imaged under a dissecting microscope with 10x magnification. Photographs of polished chondrophores were aged by counting annual lines, identified as a thick band laying across the hinge, using the software ImageJ.



Figure 2. Atlantic surf clam shell cut from umbo to growing edge.

Atlantic surfclam sizes at each age were compared to maximum and minimum sizes at age of Atlantic surfclams caught off New Jersey in the 2015 federal survey (NEFSC, 2017). Surfclams from New Jersey are from the central part of the range and would provide insight onto whether surfclams from the southern edge were noticeably different in size compared to their central counterparts.

DNA was extracted from preserved mantle tissue using an E.Z.N.A mollusc DNA kit and extracted DNA was quality checked using a nanodrop spectrophotometer. A fragment of the mitochondrial cytochrome oxidase I (mtCOI) gene was amplified with PCR using primers LCO1490 for the forward sequencing and HCO2198 for the reverse sequencing. The resulting PCR products were tested using a horizontal electrophoresis system to detect and amplify the extracted DNA. Forty-eight samples one of which was a negative control were sent from each group (BC and CC) to an external lab for Sanger sequencing. Of the samples sent only forty-six BC sequences and forty-three CC sequences were of high enough quality to be used for phylogenetic analysis. The sequences were trimmed in the software MEGA and unidentified bases in the forward sequences were filled using bases in the aligned reverse sequences. The merged sequences for the 89 samples were used to construct a maximum likelihood tree with reference sequences for *S. s. solidissima* and *S. s. similis* from the National Center for Biotechnology Information website. The maximum likelihood method built multiple variants of the phylogenetic tree morphology until no tree topology remained that had a greater likelihood than the previously created tree.

## Results

Surfclams from 3 to 7 years of age were observed in the BC sample group with age 5 being the most common. The CC sample contained older surfclams with ages 4 to 9 years observed, and age 9 being the most common (Figure 3).

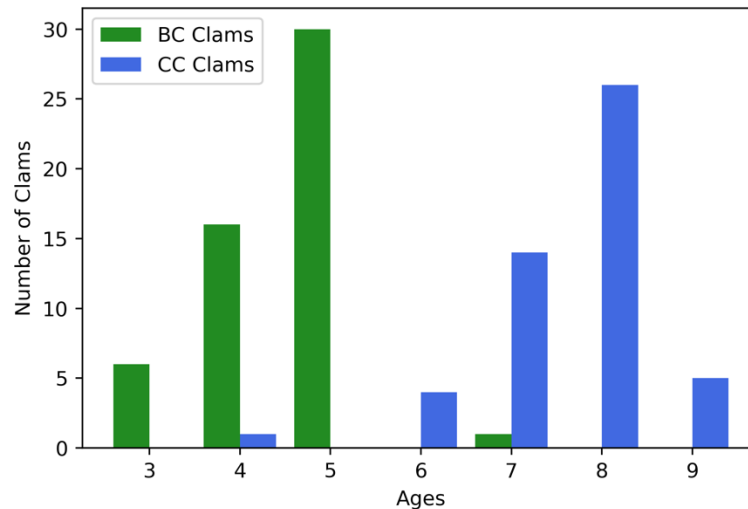


Figure 3: Number of surfclams within each age cohort.

Surfclams from the BC sample were similar in shell size (length) for a given age compared to surfclams from off New Jersey (NEFSC, 2017). However, surfclams in the CC group were distinctly smaller in shell length at a given age than New Jersey surfclams of the same age (Figure 4). Both surfclam sample groups had a meat weight for their size reflective of an established allometric relationship for the species (Marzec et al., 2010), and their weight at size matches most closely to a maximum biomass for size (Figure 5).

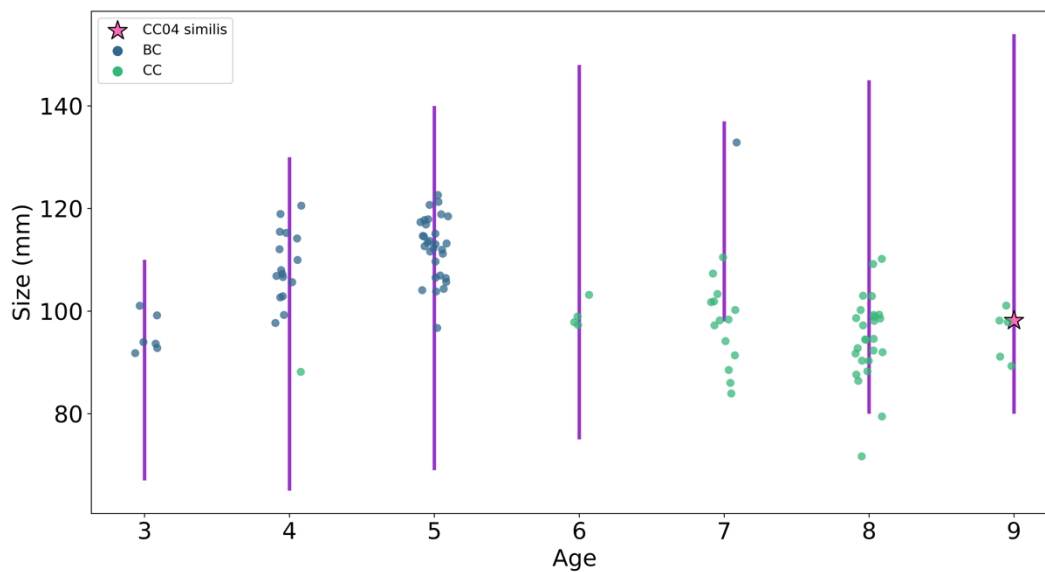


Figure 4: Size-at-age of BC surfclams (green circles) and CC surfclams (blue circles). The surfclam matching the cryptic subspecies mtDNA (CC04, Figure 6) is shown as a pink star. Purple lines represent the size range of sizes at each age for surfclams observed off New Jersey and Delmarva (NEFSC, 2017).

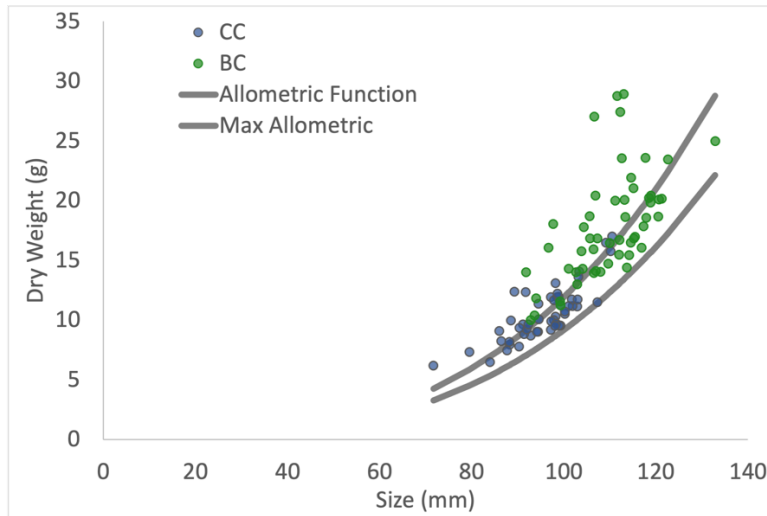


Figure 5: Mass (g) for a given shell length (mm) of all surfclams sampled. Green circles represent BC sample and blue circles represent CC sample. Known allometric functions (Marzec et al. 2010) are shown with the black lines.

All but one of the surfclams mtCOI sequence statistically matched the genetic sequence of the Atlantic surfclam (*S. s. solidissima*). One surfclam sample matched the mtCOI sequence of the cryptic subspecies (*S. s. similis*) (Figure 6). The ratio of cardinal teeth recovered from the clams range from 0.60 to 0.98 (Figure 7), a wider range than that reported by Hare and colleagues (2010). The cardinal tooth for the sample (CC04) that matched mtCOI of the cryptic subspecies was damaged on shucking and is not included in Figure 7.

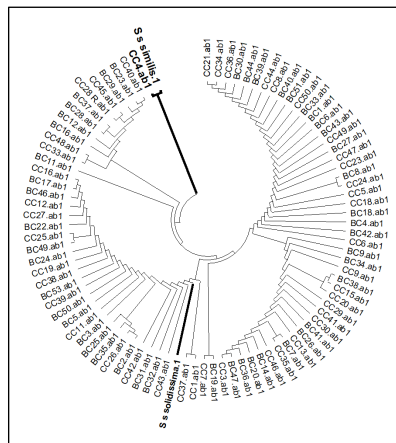


Figure 6. Maximum likelihood phylogenetic tree of surfclam mtCOI sequence. Surfclam CC04 matched the cryptic subspecies *S. s. similis*, whereas all other samples matched the Atlantic surfclam *S. s. solidissima*. The reference sequences for *S. s. solidissima* and *S. s. similis* are indicated in bold text.

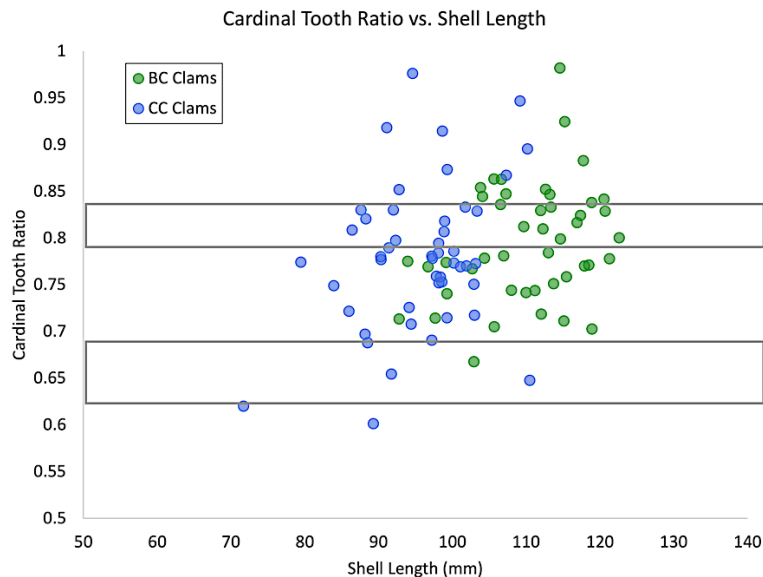


Figure 7. Cardinal tooth ratios for clams from which tooth was recovered. Green circles represent BC sample and blue circles represent CC sample. The lower grey box bounds the cardinal tooth ratio reported in Hare et al. (2010) as indicative of the cryptic subspecies (*S.s.similis*), the upper box bounds the cardinal tooth ratio reported as indicative of Atlantic surfclams.

## Discussion

The Atlantic surfclam fishery has resumed fishing on ground that are near the southern edge of the species range. Warmer water temperatures in the past have caused Atlantic surfclam mortality in this region that resulted in the fishery abandoning effort there because of low clam abundances (Weinberg and Helser, 1996). Results from this study demonstrate that today, the population in this southern edge population includes a number of age cohorts and that the surfclams are of a normal to high weight for their size, although one of the groups sampled appear to be growing slightly slower than expected. Observation of multiple cohorts over the past decade suggests that environmental conditions such as bottom water temperatures or other factors may have become more favorable for Atlantic surfclams in the area since the 1990s mortality events, or that this clam population has acclimated to altered environmental conditions and are able to survive in this southern range.

Of the two areas sampled in this study, the more southerly sample location (CC Group) had surfclams that were slightly smaller at age compared to sizes in the BC group and Atlantic surfclams from New Jersey. Reduced maximum sizes have been reported for surfclams in recent decades along the south of the range (Hollander, 2022) and past research has found that warmer temperatures resulted in slower growth rates for Atlantic surfclams (Jones, 1981). Other studies have found a negative relationship between warmer temperatures and smaller body size which may explain the stunted growth from the CC group (Weinberg 1998; Angilletta, Steury, & Sears, 2004; Narvaez et al. 2015). Larger clams have higher metabolic demands and are therefore more impacted by warmer water temperatures (Munroe et al. 2016). Slower growth rates could result in smaller individuals with lower energy expenditure that could be beneficial in the warmer water temperatures in the southern region. Although no observations of bottom



temperature are available for the two locations sampled, data-assimilative oceanographic model timeseries for the bottom waters at these locations are available (Levin et al., 2019; Wilkin et al., 2018). The modeled bottom water timeseries over the past decade at these two locations show that the temperatures are similar among the locations, with BC having slightly higher ( $\sim 2^{\circ}\text{C}$ ) temperatures during the summer months which may indicate that the smaller CC condition may be related to conditions other than bottom temperature (for example food supply, as suggested in Hollander, 2022).

Genetic material from one surfclam matched that of the cryptic subspecies (*S.s.similis*). Past research indicated that the cryptic subspecies (*S.s.similis*) and Atlantic surfclams are genetically distinct and reproductively isolated; however, little research has been done on the possibility of hybridization between the subspecies (Hare et al. 2010). Due to the lack of research on hybridization between the two, introgression cannot be ruled out and could explain how the genetic signature of the cryptic subspecies was found within the habitat of the Atlantic surfclam population. A range shift of the cryptic subspecies to cooler waters farther offshore may also explain the presence of the subspecies within the Atlantic surfclam region. During the warmer water temperatures in the 1990s and early 2000s Atlantic surfclams were found in deeper waters than they had been previously, suggesting a bathymetric shift to cooler waters (Weinberg 2005). A similar situation may have occurred in the cryptic subspecies as the cryptic subspecies has been shown to shift its range towards colder waters in the past with the population being found farther north than previously thought (Hare et al. 2005).

Ratios of the cardinal tooth processes spanned a much wider range than has been previously reported (Hare et al., 2010). Prior studies suggested that a cardinal tooth ratio between 0.63 to 0.68 is indicative of the cryptic subspecies (*S.s.similis*), whereas a greater ratio (0.79 to 0.84) is indicative of the Atlantic surfclam (*S.s.solidissima*). The results presented in this study show a wide range of cardinal tooth ratios for surfclams that are genetic matches of the Atlantic surfclam, suggesting that this morphological feature is more varied than previously reported, and that this structure is not a means by which the cryptic subspecies can be identified.

In summary, the contemporary surfclam population at the southern edge of its range is composed of multiple cohorts, some of which may be growing more slowly than other portions of the stock. Regardless of size-at-age, these clams have high mass for their size and appear healthy. There is a small number ( $\sim 1\%$ ) of the population that matches the genotype of the cryptic subspecies, or are hybrids among the subspecies and Atlantic surfclams, in these samples. Further research should be conducted to investigate the potential for hybridization and the extent to which this introgression may exist in other regions of the stock. Finally, our observations show that the ratio of the cardinal tooth processes is a highly varied morphological character and is not suitable as an indicator of the cryptic subspecies.

## Acknowledgments

Brynne Wisner was supported by the National Science Foundation Grant No. OCE-1831625, and this research was supported by the National Science Foundation Industry/University Cooperative Research Center SCeMFIS (Science Center for Marine Fisheries) NSF award #1841112. WE are indebted to the captain and crew of the fishing vessels



Betty C and Cristi-Caroline for collecting samples, and Ximing Guo, Zhenwei Wang, Hails Tanaka, Becca Horowitz, and Sarah Borsetti for help with sample processing and data analysis.

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