



Genetics, Age Demographics, and Shell Size of Atlantic Surfclams from the Southern Edge of Their Range

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Received: 18 June 2023 / Revised: 5 September 2023 / Accepted: 13 September 2023 / Published online: 26 October 2023
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Abstract

The Atlantic surfclam (*Spisula solidissima solidissima*) is an economically valuable clam species that supports a major US fishery. Until recently, fishery efforts along the southern edge of the surfclam range were low due to clam mortalities there in the 1990s. Recent surfclam fishing efforts off Virginia raised questions of whether the surfclam population has returned in the southern region or if a single cohort is supporting the fishery there. Questions have also arisen about whether *S. s. similis* is among the population fished off the coast of VA. *Spisula solidissima similis* is a warm-water cryptic subspecies of the Atlantic surfclam. Although morphologically indistinguishable, *S. s. similis* grows to a smaller size and is genetically distinct. Atlantic surfclams ($n = 103$) were collected from the fishing grounds off the coast of VA. Each surfclam was aged, and shell length and tissue weight recorded for comparison to surfclams of the same age from the center of the population. Analyses of mitochondrial (mtCOI) sequences suggests that the two groups sampled off VA are genetically homogeneous, both groups contain two divergent mitochondrial lineages, and one surfclam sampled shares the *S. s. similis* mtCOI sequence. There are multiple cohorts of surfclams, suggesting that environmental conditions may have improved for surfclams in the south, or that this population has acclimated to altered conditions. Further research should investigate the potential for subspecies hybridization.

Keywords Atlantic surfclam · Edge populations · Cryptic subspecies · Age cohorts · Mitochondrial COI

Introduction

Atlantic surfclams (*Spisula solidissima*) are a large, long-lived cold-water clam species living on the continental shelf from South VA to Canada (Hofmann et al. 2018; Jones et al. 1978; Narváez et al. 2015). The species supports one of the largest bivalve fisheries in the USA and generates around 30 million USD each year in revenue from landings alone (Scheld et al. 2022). Optimal temperatures for Atlantic surfclams range from 16 to 22 °C (Narváez et al. 2015), and elevated bottom temperatures can result in increased stress levels, starvation, and ultimately death (Loosanoff and Davis

1963; Narváez et al. 2015). In the early 1990s, warm water temperatures resulted in a major mortality event of Atlantic surfclams along the southern end of the range, off the coast of VA (Weinberg 2005), and low population numbers remaining after the mortality event have continued to limit Atlantic surfclam fishing efforts in the southern region. The cryptic subspecies (*Spisula solidissima similis*), though genetically distinct from Atlantic surfclams, are morphologically indistinguishable with the possible exception of one small hinge process or cardinal tooth (Hare et al. 2010).

Compared to *S. s. solidissima*, *S. s. similis* tends to live in warmer shallower waters and is not a commercially targeted species. The presence of *S. s. similis* among the Atlantic surfclam population could indicate a possible range shift for *S. s. similis* into deeper waters. Previous studies have shown *S. s. similis* to have shifted to northern and inshore waters (Hare and Weinberg 2005; Hare et al. 2010). A range shift for *S. s. similis* into deeper waters may lead to overlap with the Atlantic surfclam stock which could result in changes to fishery composition or other federal fishery management challenges (Reiss et al. 2009).

Communicated by John Carroll

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Recently, Atlantic surfclams have once again been fished along the southern edge of the range, raising the question about whether the Atlantic surfclam (*S. s. solidissima*) population has returned or if a single cohort has survived the warmer temperatures. A recent study found that juvenile Atlantic surfclams exposed to long periods of higher-than-normal water temperatures are better able to withstand thermal stress as adults (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 adaptation to high temperatures is possible (Acquafredda et al. 2021). The presence of multiple cohorts along the southern edge of the range could indicate population recovery since the 1990s mortality events and possible adaptation to the warmer bottom temperatures.

To better understand the circumstances underlying the resurgence of the commercial fishery along the southern edge of the Atlantic surfclam range, tissue and shell samples were collected to genetically and morphometrically determine if *S. s. similis* is present within the Atlantic surfclam population of the southern edge and if growth differs from Atlantic surfclams in the middle of their range. Results from

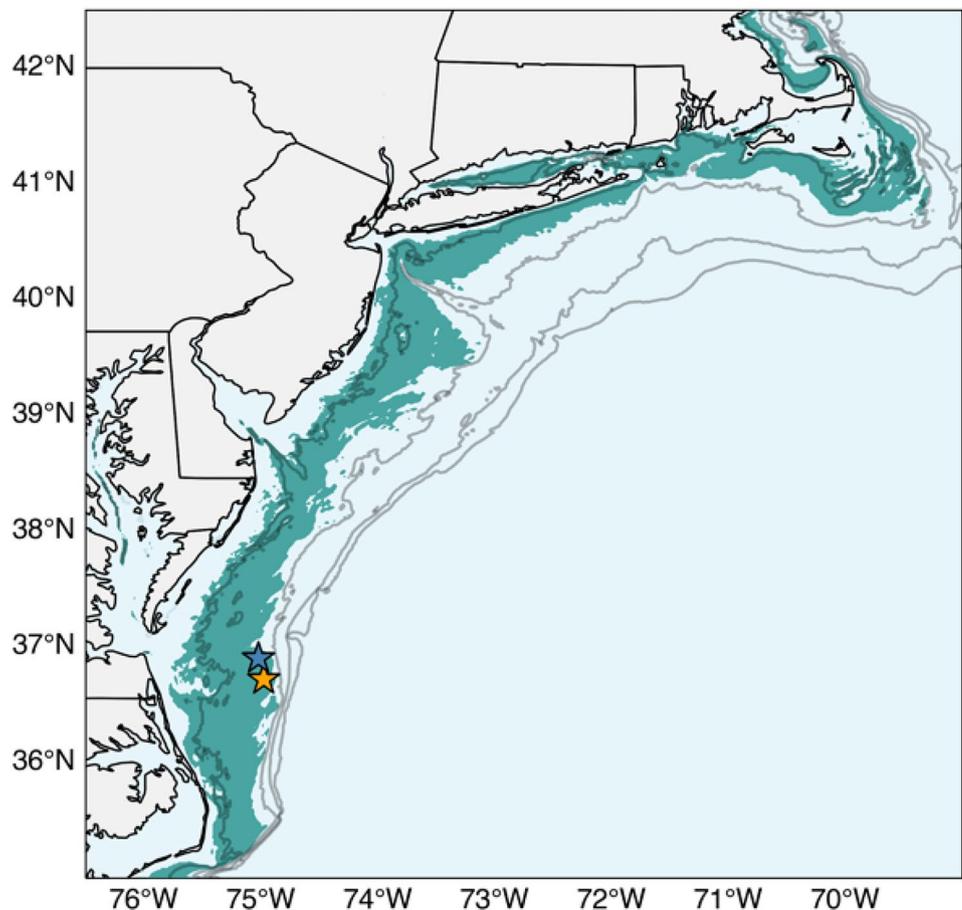
this study will help determine the health and genetic composition of the Atlantic surfclams on the southern edge.

Materials and Methods

Atlantic surfclams were caught on November 17, 2021, from the southern fishing grounds by two commercial fishing vessels *F. V. Betty C* (BC) and *F. V. Cristy Caroline* (CC). Fishing grounds occupied by the *F. V. Betty C* (BC) were located at 36.7191°N, –74.9774°W in 32 m water depth, and by the *F. V. Cristy Caroline* (CC) at 36.8994°N, –75.0233°W in 38 m water depth (Fig. 1). Samples of live, fully intact Atlantic 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.

Shell length, height, and width were measured for each Atlantic surfclam using electronic calipers. Each Atlantic surfclam was shucked and both wet and dry whole meat weights were measured. Mantle tissue samples (< 1 g tissue) were collected from each individual and preserved in ethanol for genetic testing. The left cardinal tooth was extracted, and the top and bottom processes of the cardinal tooth were photographed under a microscope with $\times 10$ magnification

Fig. 1 Atlantic surfclam range from Cape Cod and below highlighted in teal. Location of the two fishing sites where samples were obtained is indicated with stars (BC in blue and CC in orange). Isobaths depths of 25, 50, 75, and 100 m are shown with gray lines, and land is represented in gray



and measured using the computer software imageJ. The ratio of the length of the top and bottom processes of the left cardinal tooth was calculated. After shucking, shells were cleaned, labeled, and retained for aging.

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 c oxidase I (mtCOI) gene containing ~710 bp was amplified with PCR using primers LCO1490, 5'-GGTCAACAAATCATAAAGATATTGG-3' and HCO2198, 5'-TAAACTTCAGGGTGACCAAAAAATCA-3' (Folmer et al. 1994), and following protocols in Cui et al. (2021). Resulting PCR products were checked using horizontal electrophoresis. PCR products from forty-eight samples, one of which was a negative control, were sent from each group (BC and CC) to Azenta Life Sciences (NJ, USA) for two-directional Sanger sequencing. Consensus sequences from forward and reverse reads were assembled and trimmed using MEGA 11 software (Tamura et al. 2021). The merged and trimmed sequences for each sample were used to construct maximum likelihood (ML) and neighbor-joining (NJ) trees with reference sequences for *S. s. solidissima* and *S. s. similis* from the National Center for Biotechnology Information website using MEGA 11. Haplotypes in the mtCOI sequences were identified, and haplotype-based statistics (Hst) (Hudson et al. 1992) was estimated to characterize differentiation between the two populations using DnaSP 6 Software (Rozas et al. 2017). Pairwise Kimura 2-parameter (K2P) genetic distances were calculated between sequences using MEGA 11 (Tamura et al. 2021).

The left valve from each sampled Atlantic surfclam was cut from umbo to growing edge (Fig. 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 produced an even, smooth, reflective quality. Polished hinges were imaged under a dissecting microscope at $\times 10$ magnification.

Photographs of polished chondrophores (Fig. 2) were aged by counting annual lines, identified as a band across the hinge, using the software ImageJ. Atlantic surfclam sizes at age for the sampled clams were compared to maximum and minimum sizes at age observed in Atlantic surfclams collected in the 2015 Northeast regional stock assessment from the central part of the Atlantic surfclam range (NJ).

Results

Of the 48 samples sequenced from each sampled location, 46 and 43 high-quality sequences ranging from 569 to 632 bp were obtained from BC and CC populations, respectively. During alignment, several shorter sequences were excluded resulting in 43 BC and 40 CC sequences trimmed to 593 bp for phylogenetic analysis. Among all 83 sequences, 22 haplotypes were identified, and one haplotype represented by clam CC4 showed 100% sequence identity with the reference sequence of the Atlantic surfclam subspecies (*S. s. similis*). Phylogenetic analysis with ML and NJ models produced trees with the same topology, and only the NJ tree is presented. All clam samples other than CC4 clustered with *S. s. solidissima* with a large distance away from *S. s. similis* on the NJ tree (Fig. 3). Although all *S. s. solidissima* samples formed a large cluster, a small set of nine clams formed a distinctive subclade. The K2P genetic distances between *S. s. solidissima* and *S. s. similis* haplotypes were large, ranging from 0.127 to 0.135, suggesting they are different species. The K2P distance between *S. s. solidissima* haplotypes of the main clade was smaller and ranged from 0.0016 to 0.0085. The K2P distance between the subclade of nine Atlantic surfclams and the *S. s. solidissima* reference was 0.021–0.035, which is high for within species divergence (Habib et al. 2021; Guo et al. 2018; Wang et al. 2010). The mtCOI sequences of *S. s. solidissima* were dominated by three common haplotypes, and the haplotypes showed no

Fig. 2 On the left Atlantic surf clam shell cut from umbo to growing edge and on the right a polished chondrophore with annual rings under $\times 10$ magnification



Table 1 Distribution of 22 mtCOI haplotypes in two geographic populations (BC and CC) of Atlantic surfclam. Clam IDs are listed for each haplotype, and haplotypes belonging to *S. s. similis* or a subclade of *S. s. solidissima* are noted in parenthesis

Haplotype	N	BC	CC	Clam IDs
1	22	12	10	BC2/3/5/22/24/25/31/32/46/49/50/53; CC11/12/16/19/25/26/27/38/39/42
2	21	10	11	BC1/4/6/18/30/33/39/40/42/44; CC5/6/8/18/21/23/24/36/44/47/50
3	15	8	7	BC7/14/20/26/34/36/41/47; CC3/13/29/30/35/41/46
4	3	1	2	BC12; CC28/45 (subclade)
5	3	1	2	BC38; CC15/20
6	2	2		BC28/37 (subclade)
7	2	1	1	BC29; CC40 (subclade)
8	1	1		BC8
9	1	1		BC9
10	1	1		BC11
11	1	1		BC19
12	1	1		BC27
13	1	1		BC35
14	1	1		BC43
15	1	1		BC51
16	1		1	CC1
17	1		1	CC33 (subclade)
18	1		1	CC37
19	1		1	CC43
20	1		1	CC48 (subclade)
21	1		1	CC49
22	1		1	CC4 (<i>S. s. similis</i>)
Total	83	43	40	83

Genetic analysis of the mtCOI sequences found no significant differentiation between the two populations (BC and CC) sampled. Within each geographic population, two

genetically distinct groups were detected. The genetic distance in mtCOI between the two groups (0.021 to 0.035) was high for within species divergence, suggesting they

Fig. 4 Cardinal tooth ratios for individual Atlantic surfclams with blue circles representing BC samples and orange circles represent CC samples. The lower gray 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. The cardinal tooth for sample CC4 was damaged and is not present in the figure

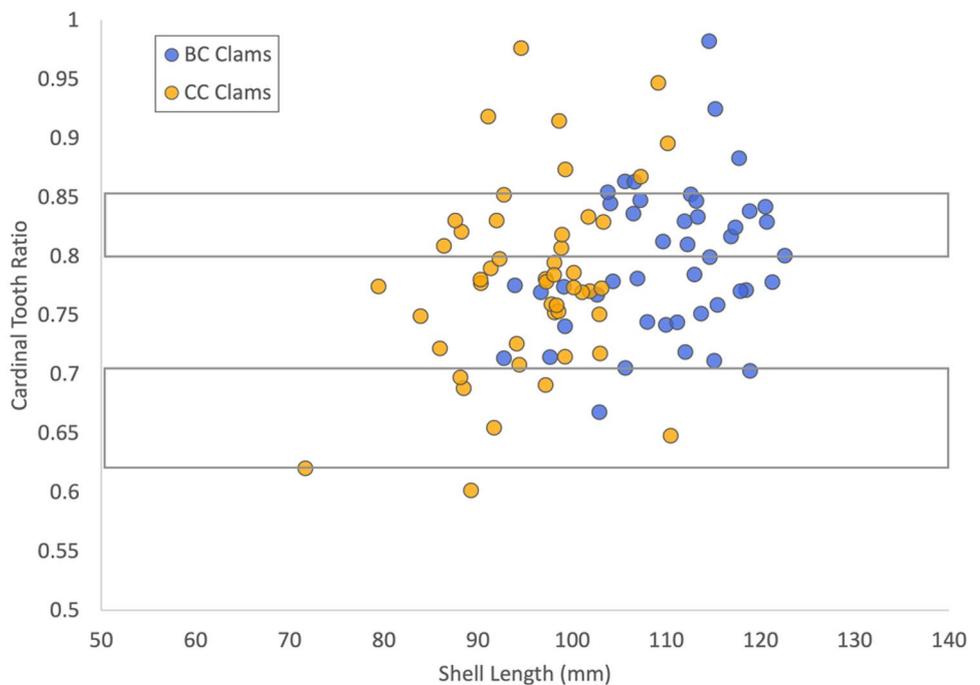
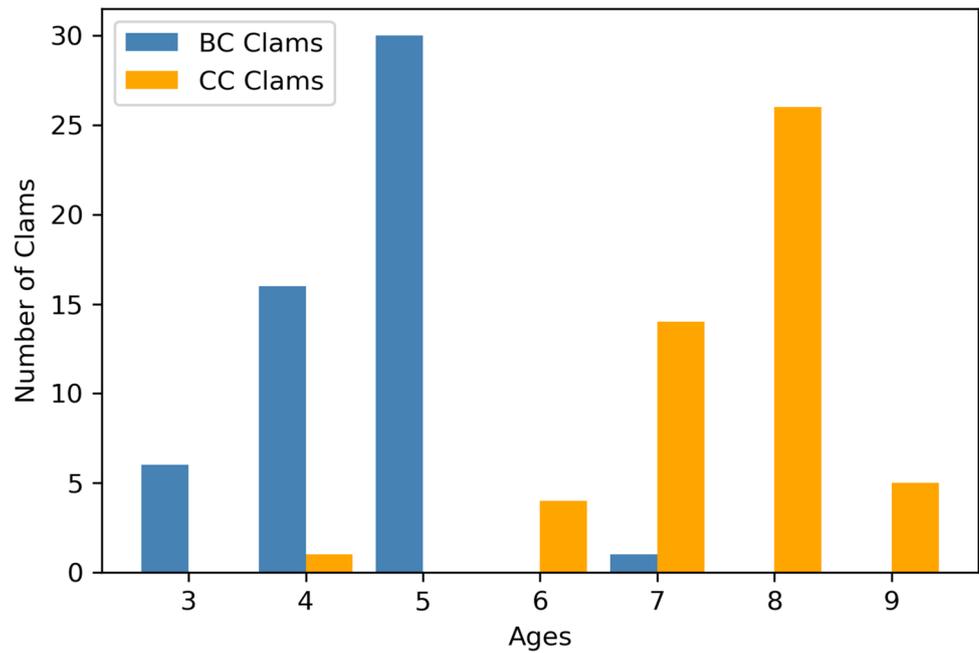


Fig. 5 Number of Atlantic surfclams within each age cohort collected on the southern edge of the Atlantic surfclam range off VA. CC clams (orange bars) were collected slightly farther south than the BC clams (blue bars)



are highly divergent or close to subspecies levels. In comparison, the K2P genetic distance in mtCOI is 0.022–0.034 between *Crassostrea gigas gigas* and *Crassostrea gigas angulata*, 0.013–0.029 between *Ostrea edulis* and *Ostrea angasi*, and 0.020–0.022 between Atlantic and Gulf populations of *Crassostrea virginica* (Wang et al. 2010; Guo et al. 2018). As a reference, the divergence time between *C. g. gigas* and *C. g. angulata* is estimated to be 2–3.6 million years (Ren et al. 2010). These findings suggest that there are two highly divergent mitochondrial lineages of *S. s. solidissima* which are well mixed in the two populations sampled. Two hypotheses may account for the observed mixing of the two mitochondrial lineages. First, it is possible that

there are currently two distinct populations located elsewhere that larval transport to the two sampled locations has led to mixing. Alternatively, it is possible that there were historically two divergent populations, which had become fully mixed throughout its range; the two mitochondrial lineages remained distinctive due to maternal inheritance, while nuclear genomes of the two might be fully mixed. This study did not examine nuclear genes and therefore cannot distinguish from the two alternatives. Further studies with nuclear genes or markers may distinguish these two hypotheses. Besides genetics differentiating the two Atlantic surfclam groups, no morphological differences could be found. The nine individuals from the subclade spanned a range of

Fig. 6 Size at age of BC Atlantic surfclams (blue circles) and CC Atlantic surfclams (orange circles). The surfclam matching the cryptic subspecies (*S. s. similis*) mtDNA (CC4, Fig. 3) is shown as a pink star. Gray lines represent the range of sizes at each age for surfclams observed off NJ (NEFSC 2017)

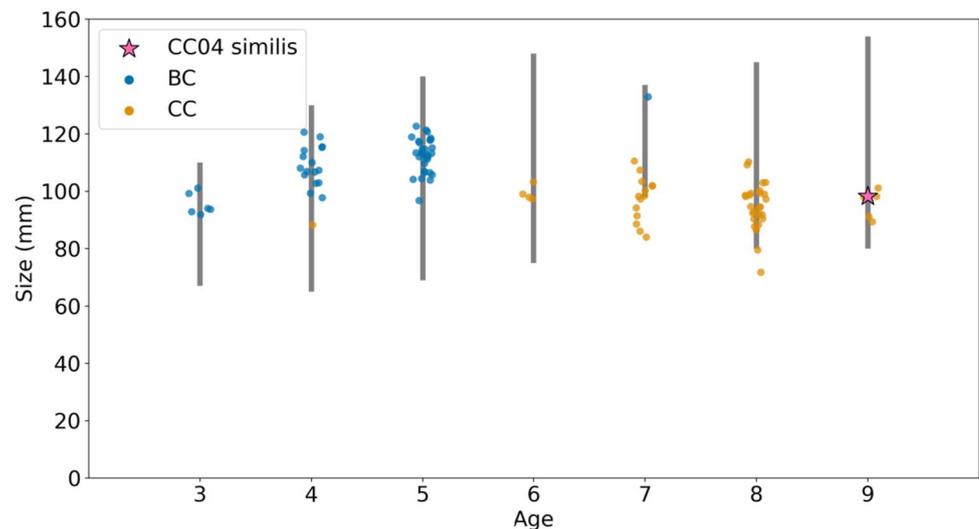
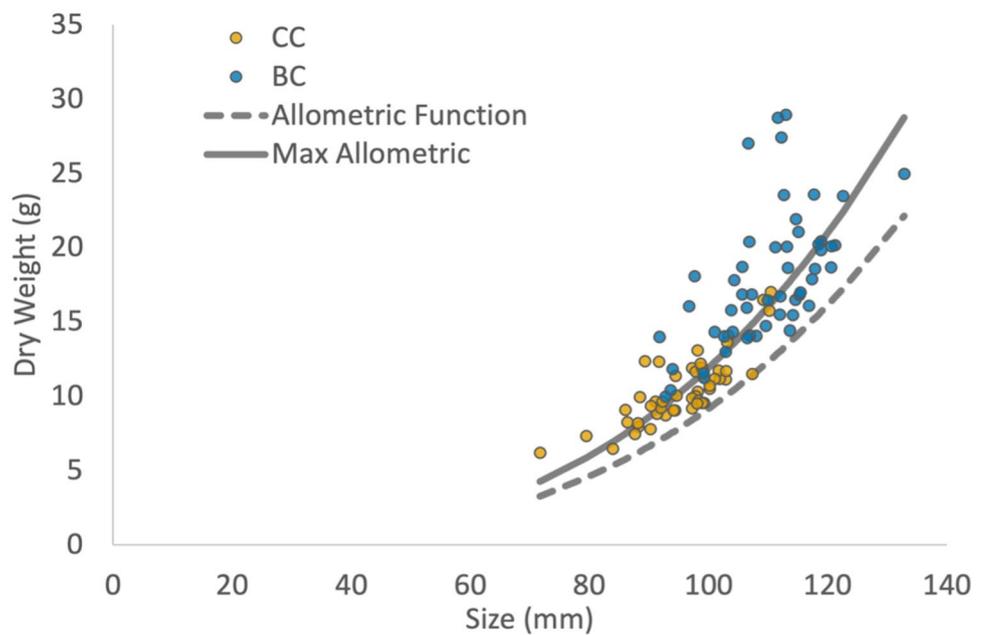


Fig. 7 Mass (g) for a given shell length (mm) of all Atlantic surfclams sampled. Blue circles represent BC sample and orange circles represent CC sample. Known allometric function (Marzec et al. 2010) is shown with the dashed gray line and the high biomass allometric function (Marzec et al. 2010) is shown with the solid gray line



sizes and ages (data not shown) similar to that of other *S. s. solidissima*, suggesting that the two mitochondrial lineages are well mixed in all year classes.

In addition to two mitochondrial lineages within *S. s. solidissima*, the mtCOI sequence from one surfclam (CC4) matched that of the cryptic subspecies (*S. s. similis*) with 100% identity, indicating it belongs to the mitochondrial lineage of *S. s. similis*. The K2P genetic distances in mtCOI sequence between *S. s. solidissima* and *S. s. similis* haplotypes (0.127–0.135) are surprisingly high, and much higher than what is expected for subspecies level divergence (Wang et al. 2010; Guo et al. 2018). Subspecies divergence in mtCOI is typically around 0.02–0.03, and the large genetic distances observed in this study strongly support that *S. s. solidissima* and *S. s. similis* should be classified as two species, *S. solidissima* and *S. similis*. As this study did not examine any nuclear genes, the possibility that the CC4 is a hybrid between the two subspecies cannot be ruled out. Previous research indicated that *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 *S. s. similis* was found within the habitat of the Atlantic surfclam population. A population shift to cooler waters farther offshore may also explain *S. s. similis* within the Atlantic surfclam region. During the warmer water conditions in the 1990s and early 2000s, Atlantic surfclams were found in deeper waters than they had been previously, suggesting a bathymetric shift to deeper, cooler waters (Weinberg 2005). A similar situation may have occurred

within *S. s. similis* as they have been shown to shift their range toward colder waters in the past with the population being found farther north than previously reported (Hare and Weinberg 2005).

Ratios of the cardinal tooth processes also spanned a wider range than has been previously reported (Hare et al. 2010). Prior studies suggested there were different cardinal tooth ratios for the Atlantic surfclam and the *S. s. similis* (Hare et al. 2010), with *S. s. similis* having a cardinal tooth ratio between 0.63 and 0.68, and a greater ratio (0.79 to 0.84) indicative of the Atlantic surfclam (*S. s. solidissima*). The results presented in this study show a range of cardinal tooth ratios from *S. s. solidissima* spanning that previously identified for the subspecies (*S. s. similis*). The cardinal tooth for specimen CC4, the cryptic subspecies (*S. s. similis*), was damaged and was not usable for a cardinal tooth ratio. Even so, the results spanning both ratios for the Atlantic surfclam suggest that this morphological feature is more varied than previously reported, and that this structure may not be a means by which the cryptic subspecies can be identified.

Of the two areas sampled in this study, the samples taken further south (CC group) contained Atlantic surfclams that appear to be slightly smaller at a given age compared to the BC group and Atlantic surfclams from the center of the range (NJ). However, a limited size range for 7-year-old New Jersey surfclams may be making the CC group appear smaller than they are. Past research has found that warmer temperatures result in slower growth rates for Atlantic surfclams (Jones 1981) and an inverse relationship between temperature and body size (Weinberg 1998; Angilletta 2004; Narváez et al. 2015). Larger clams have higher metabolic demands and are therefore impacted more by warmer water temperatures

(Munroe et al. 2016). Slower growth rates could generate smaller individuals with lower energy expenditure that would be beneficial in the warmer water temperatures of 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. 2021; Wilkin et al. 2018). Modeled bottom water timeseries over the past decade at these two locations show temperatures are similar among the locations, with BC experiencing slightly higher (~ 2 °C) temperatures during the summer months (Levin et al. 2021; Wilkin et al. 2018), suggesting that if slower growth is occurring for the CC Atlantic surfclams, the slower growth may be related to factors other than bottom temperature.

In summary, the contemporary Atlantic 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 suggesting good health. Two well-mixed populations of Atlantic surfclams exist and a small portion ($\sim 1\%$) of the population match the cryptic subspecies *S. s. similis* or are hybrids between the subspecies and Atlantic surfclams. Further research should investigate the potential for hybridization and 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 may not be suitable as an indicator of the cryptic subspecies or species.

Acknowledgements 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. Z.W. and X.G. were partly supported by National Oceanic and Atmospheric Administration award NA18OAR4170357 and USDA NIFA Hatch/Animal Health project 1004475/NJ30401, and D.M. was partly supported by USDA NIFA Hatch project 1020831/NJ33140. We are indebted to the captain and crew of the fishing vessels Betty C and Cristy Caroline for collecting samples, and H. Tanaka, B. Horowitz, and S. Borsetti for help with sample processing and data analysis.

Funding Funding for this research was supported by the National Science Foundation Industry/University Cooperative Research Center SCeMFis (Science Center for Marine Fisheries) NSF award #1841112. B.W. was supported by the National Science Foundation Grant No. OCE-1831625. Z.W. and X.G. were partly supported by National Oceanic and Atmospheric Administration award NA18OAR4170357 and USDA NIFA Hatch/Animal Health project 1004475/NJ30401. D.M. was partly supported by USDA NIFA Hatch project 1020831/NJ33140.

Data Availability Raw data was generated at the Haskin Shellfish Research Laboratory. Derived data supporting the findings of this study are available from the authors (DM and XG) on request.

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