A Retrospective Analysis of Atlantic Surfclam (*Spisula solidissima*) Growth and Distribution in the Context of a Changing Ocean

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ABSTRACT

Climate change is one of the greatest challenges the natural world currently faces, particularly in marine ecosystems, as many marine organisms are sensitive to warming water temperatures and other aspects of climate change. The Mid Atlantic Bight region is warming rapidly in comparison to the rest of the world's oceans. In the face of climate change, organisms must either adapt to altered environmental conditions or shift their distribution to avoid extinction. One such example of the latter is the Atlantic Surfclam (*Spisula solidissima*), whose range has exhibited a shift over the past 4 decades, recorded in both stock assessments and fishing industry activity. This organism supports a substantial fishery, worth approximately \$30 million annually. The surfclam's optimal temperature range is relatively narrow, with thermal stress occurring around 20°C and death occurring with sustained temperatures beyond 24°C. This organism's sensitivity and exposure to climate change make it likely that this species will exhibit a climate-driven range shift, which may be incorrectly interpreted as a response to fishing pressure in an otherwise well managed stock. This study used growth data stored in archived Atlantic Surfclam shell hinges to investigate the relationship between climate drivers and the historic range shift of this species.

Shells used in this analysis came from federal survey collections performed by the Northeast Fisheries Science Center in the years of 1986, 2008, and 2011-2016. A random 10% sample was imaged and aged to fit von Bertalanffy growth curves to individual clams. Parameters from the von Bertalanffy growth model (maximum size and the growth coefficient, k, used as a proxy for growth rate) were used to summarize clam growth. Linear models were constructed to use individual and environmental variables (location, station depth, temperature, time, and age at collection) to predict indices of clam growth. Results found that depth had a negative effect on maximum size; clams grew smaller in deeper water and larger in shallower water. The most useful temperature metric was number of extreme warm days (days above 20°C). Temperature had a negative effect on maximum size, but a positive effect on growth rate; clams grew faster but to smaller maximum sizes with higher occurrence of extreme warm events, likely reflective of respiratory and physiological demands not being met by feeding ability at high temperatures in large clams. Over time, clams in the south decreased in size while clams in the north increased in size, suggesting a northward movement of optimal range, potentially explained by increased food abundance in northern areas of this region. Over time, growth rate in deeper depths increased, but did not match the earlier reversed pattern in magnitude of higher growth rates in shallower waters, suggesting that an offshore movement is occurring but may be limited by decreased light penetration, benthic primary production, and food availability at increasing depths. These results describe a relationship between environmental variables and surfclam growth, supporting the occurrence of a historical range shift driven by climate change. These results may be useful in future studies predicting continued effects of climate change on this species growth and distribution.

A Retrospective Analysis of Atlantic Surfclam (*Spisula solidissima*) Growth and Distribution in the Context of a Changing Ocean

Statement of the problem

Climate change and species distributions

Climate change is arguably the greatest challenge that the world currently faces, and marine systems are not unaffected. The US Northeast continental shelf in particular has exhibited high rates of ocean warming, warming at rates significantly faster than most of the rest of the world's oceans (Pershing *et al.* 2015; Saba *et al.* 2015). The Mid-Atlantic Bight (MAB) has been warming at a rate of 0.5°C per decade for at least the past four decades (Wallace *et al.* 2018). This region of the Northeast shelf is expected to continue warming in the upcoming decades by +3oC (Saba *et al.* 2015).

As climate changes, species must either acclimate to altered environmental conditions or shift their range to more suitable habitat in order to survive. Examples of the latter are profuse in both terrestrial and marine literature, with examples found in insects (Williams and Liebhold 2002; Karban and Strauss 2004; Bentz et al. 2010), birds (Benning *et al.* 2002), plants (Lenoir *et al.* 2008), fishes (Bell *et al.* 2015; Kleisner *et al.* 2016), benthic invertebrates (Hale *et al.* 2017), macroalgae (Wernberg *et al.* 2011), and marine bivalves (Roy *et al.* 2001), including the Atlantic surfclam (Timbs *et al.* 2019; Weinberg 2005). Exposure and sensitivity to climate change combine to determine a species' vulnerability to range shifts (Hare *et al.* 2016; McHenry *et al.* 2019). These range shifts and effects of climate change are not necessarily negative (Hare *et al.* 2016). McHenry *et al.* (2019) demonstrated the importance of incorporating more than just temperature in models predicting species' range shifts; temperature alone can result in masked vulnerability as species' abilities to expand or shift their range may be restricted by other environmental factors such as ocean circulation.

The Atlantic Surfclam, *Spisula solidissima* (Dillwyn 1817), is a benthic dominant species in the MAB. This thesis examines growth and distribution of the surfclam over the past four decades in relation to changing ocean conditions with particular emphasis on water temperature.

The Mid-Atlantic Bight: the physical setting.

Waters of the MAB originate from both the Labrador Sea to the north and, arguably, in the Gulf of Mexico to the south, with minor volumes originating from the major estuaries of the U.S east coast. The northerly element crosses the Scotian Shelf into the Gulf of Maine, and hence to the MAB via the Great South Channel and Southern New England Shelf. The MAB shelf is broad, relatively shallow, and exhibits only a modest gradient in an offshore direction. Sediment in the MAB is primarily composed of quartz sand originating in the Appalachians and transported via major riverways (*e.g.*, Hudson River, Delaware River, Susquehanna River, etc.), where it is then subsequently reworked by hydrodynamic processes on the continental shelf (Miller *et al.* 2014). Georges Bank (GB) at the northeastern extreme of the MAB is the extension of a terminal moraine from the most recent glaciation, and though larger boulders can be found across the bottom in that region, the majority of hard substrate in these regions is biogenic carbonate. The late Holocene history of the Mid-Atlantic shelf encompasses a period of substantial sea level rise (Milliman and Emery 1968). Thus, the spatial distribution of resident species will have moved shoreward over the past 15,000 years.

The seasonal stratification of the water column enclosing the Cold Pool of the southern New England shelf and Mid-Atlantic was originally described by Henry Bryant Bigelow (1933) based upon sailings on the *R/V Atlantis* from Woods Hole, Massachusetts. The feature has been the subject of much interest since that time (Bigelow 1933, Ketchum & Corwin 1964, Beardsley

& Boicourt 1981, Houghton et al 1982, Wallace et al. 2018, Friedland et al. 2020). In the MAB and GB regions, a cold and relatively fresh band of water dubbed "the Cold Pool" forms each year as remnant winter water persists through warm months (Lentz 2017; Chen et al. 2018). The Cold Pool appears in the spring with the development of the seasonal thermocline and disappears in the fall with the storm-driven destruction of the thermocline (Ketchum and Corwin 1964; Houghton et al. 1982; Lentz 2017). Although the primary source of this Cold Pool is remnant winter water, it is supplemented with an upstream source on the southwest flank of GB (Chen et al. 2018). The seasonal warming of the Cold Pool occurs primarily due to vertical mixing (Lentz 2017). The Cold Pool is an important component of the MAB's ecosystem, as it acts as a reservoir of nutrient-rich water supporting primary production in the MAB and allows arcticboreal species to extend their ranges farther south than would be expected (Lenz 2017). Spatiotemporal variability in the Cold Pool influences the recruitment and settlement of multiple marine species (Chen et al. 2018), and many species depend on the existence of the Cold Pool for spawning and nursery grounds (Lentz 2017). Over time, the Cold Pool has been warming and shrinking in area (Gaichas et al. 2020).

Clams as recorders of environmental change

Bivalves store a complete record of their growth in their valves. As bivalves grow, their mantle epithelium synthesizes a protein matrix onto which calcium carbonate crystallizes to form a hard shell. Due to the bidirectionality of the process of calcium carbonate synthesis, bivalve shells can also dissolve during periods of anaerobic respiration to neutralize acidic byproducts and avoid harmful reductions in pH. This balance between shell formation and shell dissolution for pH buffering is the explanation for the formation of growth lines. The Lutz-Rhoads

Hypothesis (1977) of shell growth line formation proposes that as the mollusc undergoes anaerobic metabolic pathways and neutralizes resulting acids, the ratio of acid-insoluble organic material to calcium carbonate at the interface between the mantle epithelium and inner shell surface increases. When aerobic metabolism is again possible and shell formation resumes, the deposition of calcium carbonate and organic material in that localized area will have an increased proportion of organic material being deposited in the shell, resulting in a difference in shell structure at that point. In addition to periods of shell dissolution, the same result can occur if calcium carbonate deposition ceases, but the deposition of organic material continues (e.g., during extreme cold temperatures). Growth signatures can be formed annually (annuli), monthly, daily, and even on tidal cycles (Jones 1980; Richardson 2001) as well as in response to suboptimal temperature conditions and spawning events (Richardson, 2001). Such records have been used successfully as proxies for long-term environmental conditions using sclerochronology (Richardson 2001; Schöne and Gillikin 2012; Mann et al. 2013). Included under the sclerochronology umbrella is a range from simple growth increment studies where, for example, variations in increment width between annual growth lines (annuli) can yield information on past climate conditions (Richardson 2001; Schöne and Gillikin 2012), through more complex isotope studies that build on known incorporation rates of ¹⁶O and ¹⁸O oxygen isotopes into shell carbonate to elucidate both absolute values and seasonal variation in water temperature.

Bivalve growth is temperature dependent; differences in growth rates recorded in shells can yield information about the conditions in which individual bivalves grew. In a study on the Greenland Cockle (*Serripes groenlandicus*), Ambrose *et al.* (2006) found that variation in individual growth rates corresponded to the Arctic Climate Regime Index (ACRI), with high

growth during positive ACRI periods (warmer and wetter climate). Reynolds *et al.* (2013) used *Glycymeris glycymeris* sclerochronology and δ^{18} O data in foraminifera to create a multiproxy series with significant correlations between both series and sea surface temperatures. Additionally, radiocarbon dating allows for the use of long-dead shells from archaeological sources to expand records even further back in time (Mann *et al.* 2013). Studies like these demonstrate the potential use of sclerochronology as the marine equivalent to dendrochronology in terrestrial systems for both reconstruction of past climate records and predictions of future bivalve productivity.

Surfclams as benthic dominants and barometers of climate change

The Atlantic surfclam (genus Spisula, Family Mactridae, Order Veneroida, Subclass Heterodonta, Class Bivalvia, Phylum Mollusca) is the largest member of the Mactridae, and one of the largest clams without symbiotic bacteria (Munroe *et al.* 2013). A brief description of the Mactridae in general is given as an appendix to this thesis. The Atlantic surfclam is a benthic dominant on the Mid-Atlantic shelf from Cape Hatteras to a northern limit on Georges Bank and the southern Gulf of Maine (Merrill and Ropes 1969, Franz and Merrill 1980). It occupies depths from 10-60 m (Franz and Merrill 1980, Merrill and Ropes 1969). It is considered to be part of the endemic Mid-Atlantic fauna as described by Franz and Merrill (1980). The endemic range would therefore appear to be defined by a mix of environmental variables such as high summer temperature to the south, and substrates where the sedimentary bottom types of the Mid-Atlantic and Georges Bank grade into the harder bottom types of the Gulf of Maine to the north. The presence of a similar species, *Mactromeris polynyma*, off the coast of Nova Scotia (Franz and Merrill 1980) suggests that substrate of this area would be suitable for *S. solidissima* if

temperature conditions warmed. The Atlantic surfclam supports a major fishery, is well documented with respect to population biology and growth dynamics (Jacobsen and Weinberg 2006, NEFC 2010), and is a major indicator of species response to ongoing climate change over its distribution (Weinberg 2005, McCay et al 2011).

The Atlantic surfclam is a filter feeder with a diet of phytoplankton secured mostly from the water column; however, benthic algal production may be a substantial dietary component with benthic food source supplements of 20% needed in simulations to support surfclams of observed size and biomass (Munroe *et al.* 2013). Surfclam spawning ranges from late spring to fall and is greatest from late summer to early fall (Jones 1980; Zhang *et al.* 2016). Annual growth line formation coincides with spawning (Jones 1980), suggesting that, at least in surfclams, the growth line is a result of cessation of growth due to the physiological demands of spawning. Generally, larvae are transported downcoast from the Northeast to the Southwest (Munroe *et al.* 2016) with a net inshore shift, but Zhang *et al.* (2015, 2016) note periodic reversals in transit with upcoast and offshore trajectories. Larval settlement occurs in large pulses from June to July, but can occur as late as December, and varies in intensity depending on upwelling/downwelling circulation (Weissberger and Grassle 2003; Ma *et al.* 2006; Munroe *et al.* 2016).

The Atlantic surfclam has a narrow optimal temperature range, with thermal stress above 20°C, growth cessation around 24°C, and death occurring beyond 24°C (Hofmann *et al.* 2018), making them sensitive to climate change. Thus far, studies have found that the maximum shell length for this species has decreased since 1982, driven by a combination of warming bottom water temperatures and fishing pressure (Munroe *et al.* 2016). In addition to high sensitivity, this species exhibits high exposure to climate change, resulting in a high potential for a distribution

shift in response to changing climate (Hare *et al.* 2016). A range shift has already been observed in this species by both stock assessment surveys and the gradual movement of harvest activity (NEFSC 2016). This range shift has been found to be temperature driven, via increased mortality to extreme warm waters (Weinberg 2005). Surfclams have no easily-resolvable stock recruit relationship, with recruitment instead influenced by other factors such as environmental variability and habitat suitability (Timbs *et al.* 2018). This makes forecasting abundance challenging when based on survey recruitment indices (Timbs *et al.* 2018). This project seeks to reconcile this observed range shift in surfclams with ocean temperature records, allowing for a prediction of future productivity of surfclams based on predicted temperature changes due to climate change.

The Atlantic surfclam supports a substantial commercial fishery in the Eastern United States, with 2019 landings approximating 34.3 million pounds with a value of \$29.3 million. A comprehensive history is provided in NEFSC (2016). Earlier fishery efforts, pre-2000, were focused between Hudson Canyon and as far south as offshore of the Chesapeake Bay with substantial landings in New Jersey ports and Norfolk VA (figure 13 in NEFSC 2016). Since that time, the focus of fishing effort and landings has moved progressively northwards with the current fishery focused from New Jersey through Georges Bank.

Hypotheses and Objective:

General Objective

The range of surfclams in the MAB and GB regions is moving north and east by tens of kilometers per decade as warming waters shift where the optimal habitat for this species is located. Through a retrospective analysis of surfclam growth in an archive dating back to 1986,

this chapter seeks to identify the optimal ranges for surfclams as these movements continue relevant to predicting future spatial limitations to the surfclam stock and, hence, the fishery.

Hypotheses: L-infinity

H₀₁: The maximum size of Atlantic surfclams does not vary spatiotemporally

 H_{A1} : The maximum size of Atlantic surfclams is a function of space and time, such that location, depth, time, and temperature can be used to predict the maximum size of any given clam:

i at shallowest depths, maximum size should be small; as depth increases, maximum size increases until optimal depth is reached, after which, with increasing depth, maximum size should decrease.

ii maximum size should be smallest at most southerly locations and should increase as distance along the arc of the MAB toward GB increases.

iii maximum size should be largest in earlier years of the study period and

decrease through time

iv maximum size should be related to temperature in that maximum size should increase with increasing average number of degree days per year, and maximum size should decrease with increasing number of extreme warm days per year (>20°C)

Hypotheses: Growth rate (k)

H₀₁: The growth rate of Atlantic surfclams does not vary spatiotemporallyH_{A1}: The growth rate of Atlantic surfclams is a function of space and time, such that location,depth, time, and temperature can be used to predict the maximum size of any given clam:

i at shallowest depths, growth rate should be low; as depth increases, growth rate increases until optimal depth is reached, after which, with increasing depth, growth rate size should decrease.

ii growth rate should be smallest at most southerly locations and should increase as distance along the arc of the MAB toward GB increases.

iii growth rate should be largest in earlier years of the study period and decrease through time

iv growth rate should be related to temperature in that growth rate should increase with increasing average number of degree days per year, and growth rate should decrease with increasing number of extreme warm days per year (>20°C)

Methods

Data collection

Clams as source material for the current study were collected as part of the regular surfclam stock assessment surveys completed by the Northeast Fisheries Science Center, National Marine Fisheries Service (NEFSC NMFS) laboratory in Woods Hole MA. For surveys through 2015, the survey vessel was the *R/V Delaware II* using a towed hydraulic dredge with a 60-inch width and 2.5-inch bar spacing. Sampling protocol included a standard 5-minute tow (nominal distance based on Doppler sensors of 0.2-0.25 nautical miles) at 1.5 km at stations located by stratified random selection in defined strata based on latitude and bathymetry (see NEFSC 2007 – SAW 44). Dredge manifold pressure was usually 35-40 psi to assist liberation of the clams from the substrate before collection by the dredge knife. For the 2016 survey, the *F/V Pursuit* was used with a towed hydraulic dredge with 156-inch width and 2.5-inch bar spacing.

Sampling protocol follows that of prior surveys on the *R/V Delaware II*. All surfclams collected at each station were measured and subsamples taken in predetermined size ranges for estimation of live weight and wet tissue weight after shucking. Valves from each shucked sample were retained for subsequent sectioning to estimate age for the individual and contribute to development of age-at-length plots for the population. All hinges examined were retained in an archive at NEFSC Woods Hole and made available for the current study.

The NEFSC archive collection contains 4930 surfclam hinges spanning 30+ years of surveys from the region of interest (Fig. 1). Surveys occurred in the summers of 1986, 2008, 2011, 2012, 2013, 2014, 2015, and 2016. Shells had previously been sectioned to remove the hinge region and polished for annuli counts. A stratified random sampling design was used to select 10% of hinges from each year (sampling years being the strata).

All selected hinges were imaged using a high-definition Olympus DP73 digital microscope camera using the Olympus cellSens imaging software. When more than one image was required to view the entire hinge with resolution adequate to discriminate all annuli, images were automatically stitched together by the imaging software. Each hinge image was then analyzed using the ObjectJ plugin of the software ImageJ, allowing individual annuli to be marked by users. This software automatically calculated distances between annuli (Fig. 2). Hinges that were broken or younger than age 4 were not imaged, as growth curves extrapolated from specimens younger than 4 years of age were highly variable. A total of 458 hinges were imaged and aged.



Figure 1. NEFSC Atlantic surfclam survey range (1986-2016) with stations marked where surfclams were collected.



Figure 2. Sectioned surfclam hinge with annual growth lines (annuli, dark) marked with squares. This specimen was collected in 1986, with an estimated age of 21 years, making the birth year 1965.

To ensure accurate age estimation through annuli counting an initial reader error study was conducted. A selection (n=50) of images was distributed to lab members at the Virginia Institute of Marine Science (VIMS) and NEFSC who were familiar with bivalve aging methods. Each participant independently marked all annuli on each imaged hinge. The results were then compared through discussion to ensure consistency in aging techniques going forward. Participants determined that the first small growth line near the origin should be counted to be consistent with NEFSC methods (Jacobsen *et al.* 2006), though this may not represent a full year of growth. Each annulus is counted. Annuli can be determined by following line signatures back to the origin; a line is annual if it does not diverge from another line. Only one of each set of diverging lines should be counted as one year, with the line furthest from the origin used as the annual line. Discrepancies among readers was minimal (qualitative) and differences easily resolved to a consistent reader protocol.

Output from ImageJ was in the form of distance between each annulus, which could be summed to yield cumulative hinge lengths at any given age throughout a clam's life. These length-at-age data were then added to a dataset containing, for each clam, information on birth year, collection year, age at collection, station location (latitude and longitude), station depth, and length of the hinge at each year of life. Traditional growth studies use the total shell lengthat-age. In this study, hinge length can be used as a suitable proxy for total shell length because surfclam hinges grow in proportion to the entire shell length (Picariello 2006).

A von Bertalanffy growth curve (von Bertalanffy 1938) was fitted to each individual clam's set of length-at-age data. Despite the sigmoidal shape of the beginning part of each growth curve, indicating that the von Bertalanffy growth model may not be the best fit for this species, the von Bertalanffy growth model was chosen to be consistent with precedent set in

prior literature for ease of comparison. Estimation of von Bertalanffy parameters was often less accurate for individuals of young ages (Age <5), yielding impossibly large maximum size (L-infinity) and growth parameter (k) values (Picariello 2006). A maximum shell length of 200 mm was used as a cut-off, based on the largest observed shell lengths in this region, with a corresponding hinge length of 34 mm (Picariello 2006). Individuals with estimations of L-infinity hinge lengths greater than 34 mm were removed from the dataset. Additionally, clams with unusually high estimates of k (> 0.5) were removed (Picariello 2006). The spatiotemporal distribution of removed samples showed no pattern; remaining data represent a random sample. Resulting sample size was n = 383 individuals.

Location

A continuous variable for location was desirable in addition to the traditional use of a regional approach. The regions employed in prior stock assessments are based on bathymetry and major geological features (e.g., canyons and channels) rather than any prior knowledge that bounadries would correspond to separate stocks or populations. Additionally, environmental conditions associated with areas in space vary across time, making fixed regional definitions of limited value in determining spatiotemporal variation in surfclam growth. Latitude and longitude in the study region are correlated, making them difficult to use simultaneously in linear models. A novel continuous descriptor of location was defined; the angle θ . An origin was defined as having a latitude of 35° 15' 14'' N (derived from latitude of Cape Hatteras Lighthouse when it was erected) and a longitude of 65° 41' 59'' W (derived from the westernmost longitude of the Hague Line on Georges Bank). No station in this dataset is farther east or south compared to this origin (Fig. 3).



Figure 3. Example (not to scale) of how each station's angle θ was calculated. An origin at 5° 15' 14'' N (derived from latitude of Cape Hatteras Lighthouse when it was erected) and 65° 41' 59'' W was defined from which horizontal and direct distance to the station of interest (red arrow) are calculated. These vectors form the adjacent and hypotenuse sides of a right triangle. Those distances are used within a trigonometry (inverse cosine) function to calculate the angel (θ)

To calculate θ , the horizontal distance (difference in longitude) and the straight distance between the origin and each station was calculated using the distVincentyEllipsoid function in the geosphere package of R (a highly accurate calculation of the shortest distance between two locations on Earth) (Hijmans, 2021). These lengths form the adjacent and hypotenuse sides of a right triangle respective to the angle of interest, θ , which was calculated in degrees using the inverse cosine function (Fig. 3). Each station can then be described uniquely with respect to location in terms of a latitude, angle, and depth. A summary of descriptive variables for each individual clam associated growth curve is given in Table 1.

Region

For an initial descriptive analysis, region was used to visualize data in spatial units. There were two iterations of region used. The first was a broad scale approach defining three regions based on notable geographic features (Fig .4): region i was defined as north and east of the Hudson Canyon; region ii was defined as between the Hudson Canyon and the Delaware Bay; Region iii was defined as south of the Delaware Bay. The second iteration was a smaller scale approach defining five regions based on the surfclam fishery and federal survey (Fig. 5). They were, from north to south: Georges Bank (GB), Long Island (LI), New Jersey (NJ), DelMarVa (DMV), and Southern Virginia (SVA). Descriptive figures used for data exploration note where either of these regional definitions were used. All modeling and statistical analysis used Theta as a location variable.

Variable	Description (units)	
Station	Station ID	
Collection Year	Year of collection	
Age	Age of the clam at collection (years)	
Birth Year	Calculated from collection year and age	
Latitude		
Longitude		
Theta (θ^{o})	Angle from a marked location (degrees)	
Depth	Station depth (m)	
Depth2	Station depth squared (m^2)	
k	Growth parameter from von Bertalanffy model (no units)	
L-inf	Maximum size parameter from von Bertalanffy model (mm)	
DD_avg	Average degree days per year of individual's life (days)	
Temp_over_20_avg	Average count of days above 20 degrees C per year of individual's life (days)	

Table 1. Descriptions of variables used in analysis of Atlantic surfclam growth



Figure 4. Broad scale region definition. Region i was defined as north and east of the Hudson Canyon; region ii was defined as between the Hudson Canyon and the Delaware Bay; region iii was defined as south of the Delaware Bay.



Figure 5. Fine scale region definition, from north to south: Georges Bank (GB), Long Island (LI), New Jersey (NJ) DelMarVa (DMV), and Southern Virginia (SVA).

Temperature

Daily bottom temperature estimates for each clam were obtained from the Global Ocean Physics Reanalysis (Glorys reanalysis) of a numerical simulation of the North West Atlantic Ocean performed with the Regional Ocean Modelling System (ROMS). Two temperature metrics were then summarized from this dataset. First, an average degree day estimate was calculated by dividing the number of degree days an individual clam experienced over its lifetime (lifetime degree days defined as the difference over 9°C summed over the clam's life) by the age of each clam, yielding an average number of degree days experienced by a clam per year (Fig. 6). Second, a raw count of the number of days over 20°C, a temperature considered to be the onset of significant stress in growth models by Munroe et al (2016), was calculated for each clam and averaged per year, yielding an average number of extreme warm days experienced by a clam per year.

Depth

Both the linear and quadratic relationships between depth and the response variables (maximum size and growth rate) were considered due to the expected non-linear effect of depth on growth; shallow depths are expected to be associated with smaller maximum sizes and smaller k values. As depth increases toward an optimum depth (likely related to variable temperature and food availability at differing depths and dependent on location), maximum size and growth rate (k) are expected to increase. Once beyond that optimum depth, maximum size and k are expected to decrease again. Depth plotted against maximum size and k show loosely dome-shaped relationships and figures of Depth2 against maximum size and k show more linear relationships, though considerable variation exists (Fig. 7). The squared term of depth (Depth2)



Figure 6. Box and whisker plot separated by fine scale region definitions of degree days above 9°C per year for Georges Bank (GB), Long Island (LI), New Jersey (NJ) DelMarVa (DMV), and Southern Virginia (SVA). Degree day temperature estimates summarized from Global Ocean Physics Reanalysis (Glorys reanalysis) of a numerical simulation of the NWA Ocean performed with the Regional Ocean Modelling System (ROMS).



Figure 7. Relationship of Depth and depth – squared (Depth2) to maximum size (top left and top right, respectively) and growth rate, k, (bottom left and bottom right respectively).

was chosen in all models because of the expected role of temperature and food availability on the relationship between depth and growth, resulting in a non-linear relationship.

Interaction terms

For models with maximum size as the response variable, one 2-way interaction term was considered between Theta and Birth Year (Fig. 8) For models with growth rate as the response variable, three 2-way interaction terms between Depth2 and Theta, Birth Year and Theta, and Birth Year and Depth2 were considered (Fig. 9-11)

Modeling

A series of mixed effects models was developed to examine predictors of surfclam growth in terms of maximum size and growth rate. Analyses were performed in R (R Core Team, 2021) using the package nlme (Pinheiro *et al.* 2021).

Error structure and random Age component

For each fixed-effects model structure, 4 models were considered, increasing in complexity: simple fixed effects model, mixed effects model with random Age component, fixed effects model with spatially correlated errors (fit using an exponential covariance structure), and mixed effects model with random Age component and spatially correlated errors. Akaike's Information Criterion (AIC) was used to identify the model with the appropriate structure For each set of 4 models, the simplest model within 10 \triangle AIC points of the favored model was chosen as the best model. Those best models were then compared using AIC to determine which overall model structure was the best at predicting growth parameters.



Figure 8. Interaction between Birth Year and Theta. The relationship between Birth Year and Maximum size is plotted in each panel. Panels represent 20% quantiles of Theta values (which do not correspond to previously defined regions). The relationship between Birth Year and maximum size depends on location (Theta), supporting the inclusion of this interaction term.



Figure 9. Interaction between Depth – squared (Depth2) and Theta. The relationship between Depth2 and growth rate (k) is plotted in each panel. Panels represent 20% quantiles of Theta values (which do not correspond to previously defined regions). The relationship between Depth2 and k depends on location (Theta), supporting the inclusion of this interaction term.



Figure 10. Interaction between Birth Year and Theta (growth rate). The relationship between Birth Year and growth rate (k) is plotted in each panel. Panels represent 20% quantiles of Theta values (which do not correspond to previously defined regions). The relationship between Birth Year and k depends on location (Theta), supporting the inclusion of this interaction term.



Figure 11. Interaction between Depth – squared (Depth2) and Birth Year. The relationship between Depth2 and growth rate (k) is plotted in each panel. Panels represent 20% quantiles of Birth Year values. The relationship between Depth2 and k depends on time (Birth Year), supporting the inclusion of this interaction term.

Model formula

The model formula for the most complicated of the 4 models (mixed effects model with random Age and spatially correlated errors) below:

$$Y \sim MVN(\mu, \Sigma)$$
$$\mu = X\beta + Zb$$
$$\Sigma = \sigma^2 e^{\frac{-D}{\phi}}$$

Y – Response variables (maximum size (L-inf) and growth rate (k))

 μ – Mean response structure

 $X\beta$ – Fixed effects matrix where X is the fixed effects design matrix and β is a vector of fixed effects

Zb – Random effects matrix where Z is the random effects design matrix and b is a vector of the random effects

 Σ – Random errors with spatial exponential covariance structure

 σ^2 – Variance

- ϕ Range; controls how quickly spatial dependency decays with increasing distance
- D Distance matrix, calculated from latitude and longitude of observations

Results

Descriptive plots


Figure 12. Descriptive plots of variation in Atlantic surfclam growth by region and time. All six graphs in this figure show a growth curve of hinge length (mm) at age (years). The top two graphs are of clams collected from north of the Hudson Canyon, which includes Georges Bank. The middle two graphs are of clams collected from south of the Hudson Canyon to the Delaware Bay. The bottom two graphs are of clams collected from south of the Delaware Bay to the southernmost station, just south of an extension of the VA/NC state line, which includes Delmarva. Clams born in different years are denoted using a color gradient, where darker colors are indicative of earlier years.



Figure 13. Descriptive plots of Atlantic surfclam growth by region and time. In each graph, growth curves for individual surfclams are plotted as hinge length by year. Graphs from top to bottom are regions i (north of the Hudson Canyon) ii (south of the Hudson Canyon to the Delaware Bay) and iii (south of the Delaware Bay).





Figure 14. Descriptive plots of Atlantic surfclam growth over time. In each graph, individual surfclam growth curves have been simplified to a single point representative of the period of quickest growth: hinge length at age 4. This metric is plotted against clam birth year. A trendline is fitted to each graph to signify trend in growth rate over time (qualitative). Graphs from top to bottom are regions i (north of the Hudson Canyon) ii (south of the Hudson Canyon to the Delaware Bay) and iii (south of the Delaware Bay).

Modeling

Maximum size

There were complete data (including temperature) for n = 373 individuals. The best model structure for predicting maximum size was the most complex (Model_6b; Table 2) and included Birth Year, Theta, Depth2, Temp_over_20_avg, an interaction term between Birth Year and Theta, and Age as a random variable. 17% of the residual variance was explained by the random Age term, suggesting that it is a useful parameter to include when modeling maximum size. The interaction term suggests that at low Theta values (more southerly locations), maximum size decreased through time, and at high Theta values (more northerly locations), maximum size increased through time (Fig. 15). The square of station depth had a negative relationship to maximum size (Fig. 16), as did temperature (Table 3). Model residuals showed no concern for autocorrelation, heteroscedasticity, or outliers.

Two other models (Model_6 and Model_6a) were also supported (delta AIC < 10), differing in what temperature metric they used.

Table 2. Selected models with L-infinity (Linf; maximum size) as the response variable, with their corresponding predictor structures. AIC values listed as well as the delta AIC values in reference to the best fitting model. Weights (W), inclusion of Age as a random term, and Structure of the covariance matrix noted. The best supported model is in bold.

Model	AIC	Predictors	Delta AIC	W	Random Age	Exponential Covariance Structure
Model_0	2163.43	Linf ~ 1	57.63	0	No	Yes
Model_1	2153.19	$Linf \sim log(DD_avg)$	47.39	0	No	Yes
Model_1a	2152.63	Linf ~ log(Temp_over_20_avg + 1)	46.83	0	No	Yes
Model_1b	2148.21	Linf ~ (Temp_over_20_avg)	42.41	0	No	Yes
Model_2	2130.62	$Linf \sim Depth2 + log(DD_avg)$	24.82	0	Yes	No
Model_2a	2125.56	Linf ~ Depth2 + log(Temp_over_20_avg + 1)	19.76	0.00003	Yes	No
Model_2b	0 2119.93	Linf ~ Depth2 + (Temp_over_20_avg)	14.13	0.00053	Yes	No
Model_3	2128.4	Linf ~ Depth2 + log(DD_avg) + Birth Year	-22.6	0.00001	Yes	No
Model_3a	2124.64	Linf ~ Depth2 + log(Temp_over_20_avg + 1) + Birth Year	18.84	0.00005	Yes	No
Model_3b	2119.44	Linf ~ Depth2 + (Temp_over_20_avg) + Birth Year	13.64	0.00068	Yes	No
Model_4	2131.84	$Linf \sim Depth2 + log(DD_avg) + Theta$	-26.04	0	Yes	No

Model	AIC	Predictors	Delta AIC	W	Random Age	Exponential Covariance Structure
Model_4a	2126.16	Linf ~ Depth2 + log(Temp_over_20_avg + 1) + Theta	20.36	0.00002	Yes	No
Model_4b	2120.78	Linf ~ Depth2 + (Temp_over_20_avg) + Theta	14.98	0.00035	Yes	No
Model_5	2130.16	Linf ~ Birth Year + Theta + Depth2 + log(DD_avg)	24.36	0	Yes	No
Model_5a	2125.85	Linf ~ Birth Year + Theta + Depth2 + log(Temp_over_20_avg + 1)	20.05	0.00003	Yes	No
Model_5b	2120.68	Linf ~ Birth Year + Theta + Depth2 + (Temp_over_20_avg)	14.88	0.00037	Yes	No
Model_6	2109.46	Linf ~ Birth Year + Theta + Depth2 + log(DD_avg) + Birth Year * Theta	3.66	0.10041	Yes	No
Model_6a	2107.47	Linf ~ Birth Year + Theta + Depth2 + log(Temp_over_20_avg + 1) + Birth Year * Theta	1.67	0.27158	Yes	No
Model_6b	2105.8	Linf ~ Birth Year + Theta + Depth2 + (Temp_over_20_avg) + Birth Year * Theta	0	0.62593	Yes	No



Figure 15. Effect of interaction between Theta and Birth Year on Atlantic surfclam maximum size. Outputs from the best model (Model_6b) were used to predict expected L-infinity values at different values of Theta and Birth Year. In earlier years of the time period, Theta had a negative effect on the maximum size of Atlantic Surfclams, which reached larger sizes at lower Theta values (southern locations). In later years of the study, this trend was opposite: Theta had a positive effect on the maximum size of Atlantic Surfclams, which reached larger sizes at higher Theta values (northern locations).



Figure 16. Effect of station depth (m) on Atlantic surfclam maximum size. Depth was included as a quadratic term in the best fitting model (Model_6b). As depth increases, the expected maximum size of the clam decreases in a non-linear fashion.

Variable	Value	Std.Error	DF	t-value	p-value
(Intercept)	314.8132	67.7765	340	4.644874	< 0.0001
Birth Year	-0.14601	0.03414	340	-4.276934	< 0.0001
Theta	-6.63173	1.60371	340	-4.135251	< 0.0001
Depth2	-0.00163	0.00029	340	-5.554547	< 0.0001
Temp_over_20_avg	-0.03011	0.01325	340	-2.271979	0.0237
Birth Year * Theta	0.00333	0.00081	340	4.128645	< 0.0001

Table 3. Parameter estimates (value), standard errors, and p-values for each predictor in Model_6b (Linf ~ Birth
Year + Theta + Depth2 + (Temp_over_20_avg) + Birth Year * Theta).

Growth Rate

The best model structure for predicting k was the most complex (Model_6c; Table 4) and included Birth Year, Theta, Depth2, Temp_over_20_avg, and an interaction term between Birth Year and Depth2. No model with k as the response variable included Age as a random variable and no model structure favored an exponential covariance structure. There was a significant interaction term between Depth2 and Birth Year, where in earlier years of the study, depth had a negative effect on growth rate and in later years of the study, depth had a positive effect on growth rate (Fig. 17). Theta and Temperature (as the log of Temp_over_20_avg) had positive relationships with k (Table 5). Model residuals showed no concern for autocorrelation, heteroscedasticity, or outliers.

Table 4. Selected models with k (growth rate) as the response variable, with their corresponding predictor structures. AIC values listed as well as the Delta AIC values in reference to the best fitting model. Weights (W) noted. No selected model included Age as a random variable, and no selected model had an exponential covariance matrix. The best supported model is in bold.

Model	AIC	Predictors	Delta AIC	W
Model_k0	-770.45	k ~ 1	22.69	0.00001
Model_k1	-770.5	$k \sim log(DD_avg)$	22.64	0.00001
Model_k1a	-772.32	$k \sim log(Temp_over_20_avg + 1)$	20.82	0.00002
Model_k2	-770.27	$k \sim log(DD_avg) + Depth2$	22.87	0.00001
Model_k2a	-771.46	$k \sim log(Temp_over_20_avg+1) + Depth2$	21.68	0.00002
Model_k3	-771.54	$k \sim log(DD_avg) + Theta$	21.6	0.00002
Model_k3a	-774.07	$k \sim log(Temp_over_20_avg + 1) + Theta$	19.07	0.00006
Model_k4	-770.69	$k \sim log(DD_avg) + Birth \ Year$	22.45	0.00001
Model_k4a	-772.48	$k \sim log(Temp_over_20_avg + 1) + Birth$ Year	20.66	0.00003
Model_k5	-773.99	$k \sim log(DD_avg) + Depth2 + Theta$	19.15	0.00006

Model	AIC	Predictors	Delta AIC	W
Model_k5a	-775.48	$k \sim log(Temp_over_20_avg + 1) + Depth2 + Theta$	17.66	0.00012
Model_k6	-774.42	$k \sim log(DD_avg) + Depth2 + Theta + Birth$ Year	18.72	0.00007
Model_k6a	-776.03	$k \sim log(Temp_over_20_avg + 1) + Depth2 + Theta + Birth Year$	17.11	0.00016
Model_k7	-786.2	$k \sim log(DD_avg) + Depth2 + Theta + Birth$ Year + Depth2 * Theta	6.94	0.02551
Model_k7a	-784.08	$k \sim log(Temp_over_20_avg + 1) + Depth2 +$ Theta + Birth Year + Depth2 * Theta	9.06	0.00884
Model_k8	-777.49	$k \sim log(DD_avg) + Depth2 + Theta + Birth$ Year + Birth Year * Theta	15.65	0.00033
Model_k8a	-781.04	k ~ log(Temp_over_20_avg + 1) + Depth2 + Theta + Birth Year + Birth Year * Theta	12.1	0.00193
Model_k9	-789.65	k ~ log(DD_avg) + Depth2 + Theta + Birth Year + Birth Year * Depth2	3.49	0.14315
Model_k9a	-793.14	k ~ log(Temp_over_20_avg + 1) + Depth2 + Theta + Birth Year + Birth Year * Depth2	0	0.81966



Figure 17. Effect of interaction between Depth and Birth Year on Atlantic surfclam growth rate. Outputs from the best model (Model_k9a) were used to predict expected growth rate (k) values at different values of Depth and Birth Year. In earlier years of the time period, Depth had a negative effect on the growth rate of Atlantic surfclams, which exhibited faster growth rates at shallower depths. In later years of the study, this trend was opposite: Depth had a positive effect on the growth rate of Atlantic surfclams exhibited faster growth rates at deeper depths.

Table 5.	Parameter	estimates	(value),	, standard	errors,	and p-v	values	for e	each	predictor	in Model	k9a ((k ~
log(Tem	o over 20	avg + 1)	+ Depth	2 + Theta	ı + Birt	h Year	+ Birtl	h Ye	ar *	Depth2).			

Predictor	Value	Std.Error	t-value	p-value
(Intercept)	6.138013	3 1.2991242	4.724731	< 0.0001
$log(Temp_over_20_avg + 1)$	0.018292	0.0048088	3.803791	0.0002
Depth2	-0.003925	5 0.0008919	-4.400925	< 0.0001
Theta	0.000798	0.0002392	3.335497	0.0009
Birth Year	-0.002976	6 0.000655	-4.543032	< 0.0001
Depth2 * Birth Year	0.000002	2 0.0000004	4.392508	< 0.0001

Discussion

Maximum size hypothesis (H_{A1})

The square of station depth was a useful predictor of maximum size and station depth had a negative relationship with the response variable (Fig. 16). This suggests that as depth increased, the maximum size of surfclams was likely to be smaller, which supports part i of H_{A1}. This was expected and is likely due to a combination of temperature and food availability at varying depths.

The interaction term between location (Theta) and time (Birth Year) was significant, indicating that the effects of location and time are dependent on each other. In the earlier years of the study, Theta had a negative relationship with maximum size: southern locations had larger clams. As the study progressed, this negative relationship diminished and eventually reversed. In later years of the study, Theta had a positive relationship to maximum size, where northern locations had larger clams. This supports parts ii and iii of H_{A1} and supports the occurrence of a northeasterly shift in optimal range for Atlantic surfclams since the mid 1960s.

Temperature represented by the yearly number extreme warm days demonstrated a negative relationship with maximum size, as expected. As clam size increases, respiration scales as a cube and filtration as a square, and as temperature increases, respiration continues to increase, whereas filtration rate decreases. Larger clams are increasingly impacted by warm temperatures because the differential in energy intake versus use in respiration is larger (*i.e.*, their scope for growth is less, see Munroe *et al.* 2013). This supports part iv of H_{A1} .

These results supported H_{A1} , and suggests an ongoing range shift as represented by where large surfclams can be found. Based on these data, this shift has been northeasterly and offshore

and is driven by increasing instances of extreme warm temperatures outside of the surfclam's optimal temperature range.

Growth rate hypothesis (H_{A2})

The significant interaction between depth and time (Birth Year) in the favored model indicates that the effects of these two variables are dependent on one another. In earlier years of the study, depth had a negative relationship to growth rate and clams grew at slower rates in deeper water, likely driven by warmer water conditions, as surfclam growth is temperature dependent and increases with increasing temperature until a maximum threshold is reached (likely around 20°C, Hofman *et al.* 2018). In earlier years with less frequent occurrence of extreme warm events above this threshold, growth rate was expected to be higher in warmer, shallower water. In later years of the study, this relationship reversed and clams in deeper waters exhibited faster growth rates, indicating a gradual offshore movement of the optimal range for this species, though the difference in growth rate between shallow and deep depths is less in later years than in early years. One hypothesis is that food supply may be more limiting at depths beyond light penetration, limiting maximum size at such depths, as large surfclams may support their diet by up to 20% with benthic algal production (Munroe *et al.* 2013). These results support parts i and iii of H_{A2} .

Theta was a useful predictor of growth rate (k) and had a positive relationship. Clams growing in more northerly locations had a faster growth rate than conspecifics growing at more southerly locations. This is counterintuitive, as growth rate should be related to temperature in that they are positively related, and it would be expected that more southern locations should have higher temperatures on average and be more favorable to high growth rates. However, other

aspects of more northerly locations (such as increased food availability due to high mixing on Georges Bank) may allow for faster growth. Additionally, increased occurrence of extreme temperature events above 20°C (Hoffmann *et al.* 2018) over the course of the study may also limit growth rates in the southern locations. As temperature exceeds 20°C, scope for growth declines at a given food content. High food availability spares the effect of high temperature. This supports the part ii of H_{A2} .

Temperature represented by both the yearly number of extreme warm days and the yearly average degree day count was a useful predictor of growth rate (k); it had a positive relationship to k. This was expected, as surfclam growth is temperature-dependent. This supports part iv of H_{A1} .

A comprehensive description of spatial and temporal migration of the footprint

While the moving range boundaries for the surfclam in the MAB have been described in an earlier publication by Weinberg (2005) and the continuing series of NEFSC stock assessment reports (NEFSC 2007, NEFSC 2010, NEFSC 2016), this is the first report to examine variability of response to warming trends within the populations. Whole population length-at-age relationships employed in assessments and setting of catch quotas submerge spatial variation as identified herein. While these whole population estimates serve the needs of stock management, the stock is notably robust and far from being overfished or subject to overfishing, and finer scale examination illustrates the value of longer-lived bivalves as barometers of changing ocean conditions.

Timbs *et al.* (2018, 2019) examined the stock-recruit relationship (S/R) across a spatial gradient from the Georges Bank to the Virginia portions of the surfclam exploited stock. A S/R

relationship was lacking, suggesting that, in any one year, recruitment occurred over a wide area with population structure subsequently being determined by post settlement mortality. This is consistent with a proposal of "larval rain or deluge" in larval ecology where larval supply to a community is not limiting as opposed to larval supply being limited and thus being instrumental in determining subsequent population structure. The widespread opportunity to recruit in any one year also ensures that as oceanic conditions change, there will be recruits in regions that move from a sub-optimal status to an optimal status, thereby facilitating relatively rapid range expansion into new habitat. These observations of Timbs et al. (2018, 2019) and the observed temporal - spatial variation in surfclam growth of the present study are consistent with the progressive discussion of BIDE models (Birth, Immigration, Death, and Emigration) and Ecologically and Evolutionary Stable (ESS evolutionary stable) strategy concept as discussed in a series of contributions by Pulliam (1988), Morris (1991), Hanski (1994), and Dias (1996). Also notable in this general discussion is that whereas retreat of the range southern edge is observed in relation to temperature, the northern range edge remains limited by the geology of the Georges Bank grading into the depths of the Gulf of Maine, leaving offshore or downslope (for Georges Bank) expansion as the primary response.

The role of benthic production in food supply to explain large terminal size in surfclams has been discussed by Munroe *et al.* (2013) and briefly mentioned earlier in this text. In the context of long-term warming trends and stability of the seasonal thermocline that effectively sets the offshore bathymetric distribution limit for surfclams, the question arises as to the future bathymetric distribution of the species with warming. The descriptions of surfclam population size structure east of Nantucket by Powell *et al.* (2018) are informative. Whereas shallower populations are exemplified by very large individual clams, often exceeding 180 mm shell

length), deeper populations are notably smaller and more recent in recruitment. The population center is deepening as warming occurs and progresses. The Nantucket study site is dynamic and well mixed. Nonetheless it is suggestive that mixing depth and the supply of nutrient to benthic production may contribute to determining the limit of expansion of extent surfclam population into deeper water throughout the MAB, which is further supported by these data (Fig. 17).

Given the observed changes in surfclam growth rates and terminal size over the time course of the current study, will these populations ever reach the equivalent of the climax communities observed in, for example, boreal hardwood forests? The answer is probably not, especially so as climate continues to warm and a multitude of species in the MAB are considered vulnerable (Hare et al. 2008), and, at least for finfish, substantial range movements are both observed (see annual state of the ecosystem reports to New England Fishery Management Council and Mid-Atlantic Fishery Management Council) and predicted (Kleisner et al. 2017). If continued migration of species boundaries are expected, then can we develop estimators of these boundaries over time? The current study suggest this goal tractable providing estimates of the temperature field are available. Fortunately, the continuing focus of the physical oceanographic research community continues to produce temperature simulations of ever increasing fidelity. The temperature data employed in the current study is such an example, as is the ROMS DOPPIO model of Lopez et al (2020). While these models offer intriguing tools for exploration, the need also exist to refine the biological portion of the "question." The current study employs a degree day estimator to model surfclam growth with a chosen critical value of 20°C as a transition to debilitating conditions when respiratory and physiological demands are not met by feeding ability – the constraints of allometry that limit size and scope for growth (see Mann et al. 2013 for example). A clear need exists for an improved understanding of this temperature-

affected transitional period of bioenergetic in surfclams and other sedentary benthic species if realistic projections of future distributions and productivity are to be achieved. What are the thermal tolerances of sedentary benthos, and how does the combination of high temperature and exposure period act in concert to limit survival? What is the ability of species to recover from extended periods of thermal stress, and how does this compare to future projections of temperature as provide by ROMS type models? Forward projections of biology will improve iteratively as this knowledge base expands.

The records of commercial effort and landings since the mid 1980's reflect the migration of the range boundaries of surfclams in the Mid-Atlantic over that period. This is but a small part of the longer term consideration of range boundary movements of benthic communities in that same footprint. The Mactridae have origins in the Cretaceous (Sall 1973), that is 145-66 mya. By contrast the northwestern margin of the Atlantic Basin has experienced glacial expansion and retreat in the late Holocene with substantial fall and rise in sea levels (Milliman and Emery 1968), necessitating both the offshore and onshore migration of species ranges. Within this relatively recent time frame of sea level rise have been periods of warming a cooling. These are recorded in pollen records of the Chesapeake and Mid-Atlantic shoreline (Brush 1986) that reflect periodic regional oscillations of warm and cold linking meteorological and regional shelf conditions. Indeed, the story of pollen as a wider indicator of atmospheric climate change, supportive of the findings of Brush (1986) have recently been reviewed by Sanchez-Goni et al. (2018). Ongoing studies by LeClaire and co-workers (pers. communication) are examining onshore and offshore movement of the distribution of Arctica islandica offshore of the DelMarVa employing Carbon-14 dating of fossil shell representing the past 4500 years. A pattern is emerging of periods of both onshore and offshore boundary migrations, presumably

associated with increase and decreased influence of cold water from the north. The aforementioned report of Moore et al (2017) notes a statistically significant change in the Labrador Sea algal time series, that extends from 1365 through 2007, around 1825 associated with human industrial development. Nixon et al (2004) review one hundred and seventeen years of coastal water temperature records for Woods Hole, MA. Gradual cooling occurred through the first 60 years of this record; however, this was followed by a notable warming trend between 1970 and 2002. Nixon et al. (2004) note a weak positive correlation between annual and winter water temperature and the annual and winter North Atlantic Oscillation index during the period of study. Historical records also describe anomalies in the Labrador Sea originating contribution to the Mid-Atlantic. Fisher et al (2014) describe mass mortality of tilefish (Lopholatilus chamaeleonticeps) off the New England coast associated with an intrusion of lethally cold sub-Artic water into their habitat in 1882. Again, the North Atlantic Oscillation was implicated in the event, and continued to influence the landings of tilefish throughout most the early 20th century prior to overfishing in the 1970s. Dynamic range shifts of species in the Mid-Atlantic are, as noted earlier, not limited to surfclams, and continue over varying time frames and with varying intensities in response to environmental change.

Bivalve molluses maintain a complete history of their individual life in their shells (valves). The shell structure is a time-based integrator of growth in the seasonally and otherwise oscillating environment that each individual occupies. Shell formation is a process of calcification over a protein matrix affected by the underlying soft tissue mantle, with each layer adding as a laminate to the internal surface of the intact shell (Rhoads and Lutz 1980, Richardson 2001). The carbonate form and crystallography may vary at a species-specific level, as may the presence of an external proteinaceous periostracum. Carbonate dissolution from the internal

valve surface can occur during periods of anaerobic respiration to maintain pH balance (Crenshaw and Neff 1969, Wilkes and Crenshaw 1979, Rhoads and Lutz 1980), but this is transitory in terms of longer-term deposition patterns. The overall result is a shell structure inclusive of multiple growth signatures – the challenge is to discriminate the time base and/or the physiological and environmental events that correspond to each signature (review in Richardson 2001; see Schöne *et al.* 2005 for an interesting example).

Growth signatures in individual valves are typically visualized by sectioning from the hinge (dorsal) to the ventral margin and polishing the exposed surface (height of the shell dorsal to ventral). The laminate structure of the individual layers is thus exposed, with each more recent layer being exposed at the growing edge beyond that of the immediately preceding layer. This shingle like structure results in the concentric growth signatures on the external valve surface. These are subject to erosion over time, thus external signatures are often absent near the hinge region in older individuals, even where an overlaying periostracum may have once been present (for example Arctica islandica). Even though external signatures may have been lost, the laminate structure of the valve retains the internal signatures and is thus available for reconstruction of the individual life history. Described signatures correspond to annual, spawning, tidal, and disturbance events (Richardson 1988, 2001). At a species-specific level, polished edges of sectioned valves may reveal considerable structure by direct visual examination. The exposed edge can be acid etched and an acetate sheet applied. Upon careful removal, the acetate peel provides a "negative" record that can be examined to reveal fine structure with transmission light microscopy (Rhoads and Lutz 1980, Ropes 1984, Richardson 2001). Alternatively high-definition imaging can be used directly on the polished edge (Harding et al. 2008a). Image analysis using scanning densitometry to discriminate junctions of growth

form that characterize signatures can be used with either approach (Richardson 2005, Harding *et al.* 2008a). The proverbial "bottom line" is a highly defined chronology of signatures corresponding to the hinge to ventral margin growth axis that encompass the entire individual life span that can be quantified.

Visual signatures are widely used to generate length-at-age relationships, typically by von Bertalanffy fits (for examples see Sasaki 1981, Jones et al. 1989, Ramón and Richardson 1992). Where species support capture fisheries, the age-at-length curve is a central component, together with mortality estimators from population demographics, size versus fecundity descriptors, and yield estimators (weight at length/age) in development of sustainable fisheries management plans (for example see Thorarinsdóttir and Jacobsen 2005). Isotope techniques offer resolution to the question of the temporal basis of the sequence of signatures. Bivalve shells are in situ bathythermographs in that the incorporation of oxygen isotopes into carbonate is temperature and salinity dependent, thus in coastal shelf systems the O16/O18 ratio provides a now well calibrated record of temperature. The cyclical nature of the ratio identifies seasonal periodicity. The absolute values of the ratio provide environmental temperature proxies from short term (Kirby et al. 1998, Harding et al. 2010, Chute et al. 2012) to very long-term situations (Schöne et al. 2004, 2005). Additionally, cyclical variation in elemental ratios in molluscan shell growth provide tools for investigating seasonal growth (see Richardson 2003 for example with Pinna nobilis), while bomb radiocarbon signatures can provide absolute temporal reference points for long lived species - see Kilada et al. (2009) for application in age verification of the propeller clam (Cyrtodaria siliqua) in Eastern Canada.

The products of this work provide retrospective quantitative descriptors of growth of surfclams over time and space in the Mid-Atlantic and Georges Bank regions. The increasing

fidelity of physical oceanographic models describing these regions, notably that providing the temperature data used herein, and such examples as the Doppio model of Lopez et al. (2020), proffer the option to generate prospective values of the seasonal temperatures and thus the development of prospective maps of species distribution. While such maps have utility in examining the direct interaction of species distribution and climate change, they also contribute to the ongoing societal debates addressing development of wind farms on the continental shelf, many of which either partially overlap with current surfclam distribution or will overlap based on projected continued expansion of the windfarm footprints through build-out over the coming decades. An entire volume of a peer journal (Oceanography 33(4), 2020, Special Issue on Understanding the Effects of Offshore Wind Energy Development on Fisheries) presents a discussion of state of the art of knowledge of impacts of wind farm development on fisheries, yet the very dynamic nature of wind farm development ensures that state of the art knowledge is almost out of date by the time of publication. Placement of multiple foundation structures in optimally formatted arrays to capture wind energy also disturbs water column structure and hence stratification, thermal and nutrient mixing, and productivity in terms of magnitude and temporal signal, all with implications for reproductive periodicity and early life history of both benthic and water column species of ecological and economic importance. The long-heralded contributions of Hjort (1914) on match-mismatch in relation to recruitment success may no longer apply as we enter a phase wherein massive engineering development on the continental shelf threatens to destabilize biological relationships that are the foundation of community structure in this biome. Mann (2021) addresses the need for balanced consideration of societal needs where the economic values of the fishing industry are dwarfed by that of projected wind farm economies. Movement of wind farm design from fixed monopole construction to moored

but floating windmills will allow expansion into deeper water in yet further locations from shore, thus threatening yet more footprint of fishing activity. The magnitude of this development is reflected in the recent auction of wind leases in offshore New York and New Jersey – on February 25 2022 sales for six leases by the federal Bureau of Energy Management totaled a staggering \$4.37 billion with a footprint of 488,000 acres and projected energy production of 7 gigawatts or enough energy to power nearly 2 million homes, this is over half of all the homes in New York city. To place this lease sale in context, a discussion paper by King (2017) estimated economic impact of all fisheries, inclusive of both commercial and recreational, in the Mid-Atlantic in 2015 at \$5.68 billion.

The recognition of ongoing climate change as a driver of change in ecosystems worldwide represents a stimulus to explore both the factors determining extant and projected ranges of all species, especially where projections drive major displacement of industries that support local economies that have historical focus and leave little option for rapid diversification. The centers of the fishing industry in the Mid-Atlantic are such a case with the ports of New Bedford and Atlantic City being prime home port examples. This study represents an extension of prior focus on finfish species (see for example Klesiner *et al.* 2017) to benthic dominants, and encourages future examination of allied fisheries targeting ocean quahogs (*Arctica islandica*) and scallops (*Placopecten magellanicus*) with implications for the economies that they support in mid Atlantic fishing ports and societies.

Appendix: A brief description of the surfclam and the Mactridae

Spisula solidissima Dillwyn 1817

Genus *Spisula* Gray, J.E. (1837). A synoptical catalogue of the species of certain tribes or genera of shells contained in the collection of the British Museum and the author's cabinet. Magazine of Natural History N.S. 1: 370-376. Family Mactridae Lamarck 1809 Superfamily Mactroidea Order Cardiida Class Bivalvia Phylum Mollusca

Common description: *Spisula* is a genus of medium-sized to large marine bivalve mollusc or clams in the family Mactridae, commonly known as surf clams, bar clams, hen clams skimmer, sea clam, trough shells.

Other members of the genus Spisula acquilateralis (Deshayes, 1854) – Triangle shell Spisula elliptica Spisula ovalis (J. Sowerby, 1817) Spisula solida (Linnaeus, 1758) Spisula solidissima (Dillwyn, 1817) – Atlantic surfclam Spisula subtruncata (da Costa, 1778) Spisula sachalinensis Spisula polynyma is now Mactromeris polynyma

On the status of S. solidissima similis (Say 1822):

Museum type specimens are lacking in the National Museum of Natural History collection at the Smithsonian Institution (Dr. Michael Vecchione, National Systematics Laboratory, personal communication), and the Academy of Natural Sciences of Philadelphia (Jacobsen and Old1966). Abbott (1974) suggests that *S. raveneli* may be a synonym of *S. s. similis*; however, Jacobsen and Old (1966) and Porter and Schwartz (1981) suggest the use of *S. raveneli* to be more appropriate and that the distinction be at the species, rather than subspecies level. Neither Theroux and Wigley (1983), nor Turgeon *et al.* (1988) recognize *S. raveneli* or *S. s. similis*. Abbott (1974) suggests that *S. s. similis* is found from Cape Cod to Texas including both sides of the Florida peninsula - a range that would warrant inclusion in Theroux and Wigley (1983). Descriptions of either *S. s. similis* or *S. raveneli* south of Cape Hatteras are limited (Kanti *et al.* 1993, Walker and Heffernan 1993). Growth and age data indicate more rapid growth in the southern species with a smaller maximum size and age (76mm and 4 years in Georgia, 135mm and 5.5 years in Florida) than *S. solidissima* (up to 226mm and 37 years). The taxonomic status of *Spisula solidissima* is currently under review by M. Hare.

Mactrid clams are long lived benthic dominant species found on inner continental shelves throughout the northern hemisphere where they variously support major fisheries (*Spisula solidissima* in the Mid-Atlantic Bight, *Mactromeris polynyma* in eastern Canada, *Spisula sachalinensis* in Japan), recreational fisheries (*M. polynyma* in Alaska), and serve as dietary

items for charismatic species such as bearded seals (*Erignathus barbatus*) and walrus (*Odobenus rosmarus divergens*). Ongoing studies, employing both sophisticated adult growth and larval dispersal models, of the response of *Spisula solidissima* to climate change in the Mid-Atlantic Bight suggest the general use of Mactrids as barometers of climate change over broader geographic footprints.

To the south of S. *solidissima* is the limited shallow-water distribution of *S. solidissima similis* (Say 1822), also described as *Spisula raveneli*, Conrad, 1831, a species limited in terminal size, arguably driven by seasonal higher water temperatures and the allometric discord between energy budget functions as described earlier.

In the southern New England to northern rim of the Georges Bank, the dominant Mactrid grades from S. solidissima to Mactromeris polynyma with the latter continuing along the northeastern Atlantic shoreline through the Canadian Maritimes and Labrador Straits (also known as the Straits of Belle Isle) to a pan-Arctic distribution with a western component extending from the Juan de Fuca Straits to Point Barrow, Alaska and Sakhalin Island, Russia (Chamberlin and Sterns 1963, DFO 2007). For completeness, the continuum of species progresses west with Spisula sachalinensis into the Sea of Japan (Golikov and Scarlato 1970), a species for which Sasaki (1981,1982) provides both a von Bertalanffy growth descriptor and size versus fecundity estimator. To the east the northern European shelf from the Iberian Peninsula to Norway is habitat for Spisula solida (Linnaeus 1758) (Conchological Society of Great Britain and Ireland, 2011). The smaller Spisula subtruncata (da Costa) (50mm versus 26 mm maximum length) occupies the corresponding shallow subtidal depths, in addition to extending into the northwestern Mediterranean Sea, where Fraschetti et al. (1997) address population level dynamics in the Ligurian Sea. Population structure and dynamics of S. solida have been examined in support of fishery management and aquaculture (Fahey et al. 2003, Dolbeth et al. 2006, Joaquim et al. 2008a). The resource has arguably been over-exploited in part of the range (Gaspar et al. 2003, Joaquim et al. 2008b). Reuda and Smaal (2002, 2004) provide data on the physiological energetics of individual S. subtruncata.

A rich quantitative literature on the life history, population dynamics and bioenergetics exists for the genus *Spisula* from three continental margins. Indeed, in the manner that Ambrose *et al.* (2006) and Carroll *et al.* (2009) reported the record of climate change in the shells of the Greenland smooth cockle, *Serripes groenlandicus* in the Barents Sea, there are also records of response of *S. solidissima* to climate change in the Mid-Atlantic Bight. Weinberg (2005), based on long-term stock assessment survey data, notes a bathymetric shift in distribution in response to warmer ocean temperature wherein the southern range limit is moving north while simultaneously moving to deeper water. Picariello (2006) noted changes in growth rate within a generational time frame at locations in this southern transitioning zone. In combination with current bioenergetics model of Munroe *et al.* (2013), the proposal to employ the genus *Spisula* as a continental shelf sentinel species as describe earlier is supported.

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Alexis Hunter Hollander was born in Madison, Wisconsin on October 14, 1996. Alexis grew up with her sister and cousin exploring the woods of Wisconsin and the beaches of South Carolina, where her interest in biology and marine science began. She completed her secondary education at Portage High School, in Portage, Wisconsin where she participated in a study abroad program in Germany and graduated as salutatorian. Alexis attended the University of Wisconsin-Stevens Point in 2015 and pursued a B.S. majoring in biology and minoring in chemistry and German. She was heavily involved in research in paleontology and archaeology and did research projects on algae and snails. In 2018 she completed a competitive Research Experience for Undergraduates program working with the NOAA Alaska Fisheries Science Center in Seattle, Washington. There, she conducted research on larval fish development. In 2019, Alexis was awarded the prestigious Albertson Medallion award from UWSP for her achievements in academia, leadership, and community service during her undergraduate program. A degree of Bachelor of Science was awarded in 2019.

Alexis began graduate training in 2019 at the Virginia Institute of Marine Science and has held membership with the National Shellfisheries Association and the American Fisheries Society. During her graduate education, she has taken one trip to sea aboard the F/V ESS Pursuit. After completion of her Master of Science degree, Alexis will continue her education with a doctoral program at the University of Wyoming focused on sage grouse.