The Effects of Climate Change on the Population Ecology of the Atlantic Surf Clam, Spisula solidissima, in the Middle Atlantic Bight

Adriana Picariello
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Adriana Picariello
THE EFFECTS OF CLIMATE CHANGE ON THE POPULATION ECOLOGY OF
THE ATLANTIC SURF CLAM, SPISULA SOLIDISSIMA, IN THE MIDDLE
ATLANTIC BIGHT

A Thesis
Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Science

By
Adriana Picariello
2006
APPROVAL SHEET

This thesis is submitted in partial fulfillment of
The requirements for the degree of
Master of Arts

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Approved, May 2006

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Abstract

The distribution of the Atlantic surf clam, *Spisula solidissima*, along the east coast of the USA has undergone a shift both northward and into deeper water since 1999. This observation is based on over 20 years of stock assessments by the National Oceanic and Atmospheric Administration/National Marine Fisheries Service/Northeast Fisheries Science Center (NOAA/NMFS/NEFSC). There has been a decline in biomass offshore of the Delmarva Peninsula at the southern limit of the species range coupled with this shift. This study addresses the age and growth of surf clams in different areas throughout the Middle Atlantic Bight (MAB) distribution by examining the growth of both individuals and populations, and relating the observed patterns to bottom water temperature in the MAB. Surf clams were sampled from four Northeast Fisheries Science Center (NEFSC) standard depth strata during the summer of 2005. These strata were offshore of the southern Delmarva Peninsula (9), offshore of the northern Delmarva Peninsula (13), offshore New Jersey (21), and inshore New Jersey (88). Age was estimated for 473 clams from 32 mm to 180 mm, using polished chondrophore cross-sections. A comparison of von Bertalanffy growth parameters show that the length-at-age relationships are significantly different between strata. The growth coefficient was highest in clams from offshore Delmarva (9) followed by inshore New Jersey (88), offshore New Jersey (21), and offshore Delmarva (13). While the growth coefficient was highest in surf clams from offshore Delmarva (9), these clams attained the smallest maximum lengths. Condition index, a measure of organic content calculated as the ratio of ash-free dry weight (g) to shell length (mm), was highest in surf clams from inshore New Jersey (88) followed by offshore New Jersey (21), offshore S. Delmarva (9), and offshore N. Delmarva (13).

Clams from each of the different strata were used to develop length-at-age curves by measuring the distances from the umbo to each growth line along a radial cross-section to determine the size of the clam at each age throughout its life. This technique allowed age-specific growth curves to be estimated for individuals and analyzed to determine whether changes have occurred in the length-at-age of surf clams over the past 20-30 years. Changes have occurred in the length-at-age of several year classes from Delmarva (strata 9 and 13). This change is not observed in the growth of clams from higher latitude (New Jersey, strata 21 and 88). Average annual bottom water temperatures in the Delmarva region have been warmer than the long-term (1970-2005) average for several consecutive years from 1995 to 2005. In addition, the average monthly summer bottom temperatures have been warmer than the long-term (1970-2005) average in the majority of years from 1995-2005. In the Delaware region September has had above average bottom water temperature in 10 of the past 11 years. Evidence presented here suggests that changes in surf clam length-at-age in this region might be related to increases in bottom water temperature over the past 10 years.
THE EFFECTS OF CLIMATE CHANGE ON THE POPULATION ECOLOGY OF THE ATLANTIC SURF CLAM, *SPISULA SOLIDISSIMA*, IN THE MIDDLE ATLANTIC BIGHT.
Introduction
Surf Clam Biology: An Overview

The Atlantic surf clam\(^1\), *Spisula solidissima* (Bivalvia: Mactridae) (Dillwyn 1917) (Figure 1) is a benthic bivalve inhabiting the continental shelf of the western North Atlantic Ocean, along the east coast of the United States of America and including the Middle Atlantic Bight (MAB). More specifically, the distribution of surf clams extends from Cape Hatteras, North Carolina to the Gulf of St. Lawrence, Canada and eastward to Georges Bank (Merrill and Ropes 1969, Abbott 1974, Franz and Merrill 1980) (Figure 2). The habitat of this infaunal suspension-feeding mollusc comprises mostly sandy substrate in the subtidal zone at depths from 10 to over 50 m (Jones et al. 1978, Ropes 1980, Cerrato and Keith 1992). Surf clams can attain maximum lengths of 226 mm (Ropes 1980) and longevity in excess of 30 years (Jones et al. 1978), with a maximum reported age of 37 years (Sephton and Bryan 1990). Spawning cycles differ depending on geographic location as spawning typically begins and ends earlier near the southern edge of the distribution (Virginia) (Ropes 1979) where two spawning events often occur per year (Ropes 1968).

The Atlantic surf clam is displaced in the north by the Stimpson surf clam, *Spisula polynyma* and in the south by the southern surf clam, *Spisula solidissima similis*. The range of *S.s. similis* extends from Cape Cod, Massachusetts to the Gulf of Mexico (Abbott 1974) in contrast to the distribution of *S. solidissima*. While there is an overlap in distribution between *S. solidissima* and *S.s. similis*, there are many distinctions between the life history strategies of these two clams (Walker and Heffernan 1994). *S.s. similis* has a shorter longevity, smaller maximum size, and a different gametogenic cycle

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\(^{1}\) While the nomenclature often varies in the literature ("surfclam" vs. "surf clam") I will use be using "surf clam" throughout this paper.
than *S. solidissima* (Walker and Heffernan 1994). In addition, *S.s. similis* can often occupy shallower estuarine waters as opposed to the predominantly oceanic habitats of *S. solidissima* (Walker and Heffernan 1994). Significant genetic differences have been found between *S. solidissima* and its subspecies *S.s. similis* that could potentially classify these as separate species (Hare and Weinberg 2005).

The Atlantic surf clam has supported a multi-million dollar per year fishery in New England and the MAB since the 1960’s (Ropes and Merrill 1969, Serchuk 1978). Surf clams historically have been harvested from the coastal waters of New York, New Jersey, Delaware, Maryland, and Virginia. Landings peaked around 40,100 metric tons per year in the mid-1970’s (NEFSC 1999) and were particularly high off the coast of Virginia. Intense fishing in the Delmarva Peninsula area up until 1980 rapidly depleted stocks, and for the past 17 years, the majority of surf clams and thus the majority of fishing effort has been concentrated off the coast of New Jersey (NEFSC 2003).

**Habitat and Role of Zoogeography**

Zoogeography reflects a distinct geographic distribution of flora and fauna that co-occur and are joined because of common environmental requirements (Franz and Merrill 1980). The MAB habitat is described by Franz and Merrill (1980) as a temperate zone supporting a mixed fauna including both northern/cold-water species (including the boreal surf clam) and southern/warm-water species. Mountain (2002) also describes the MAB region as the northern limit for warm-water species and the southern limit for cold-water species.
Figure 1. Line drawing of a surf clam, *Spisula solidissima* (not to scale). Drawing by Picariello.
Figure 2. Distribution of Atlantic surf clam, *S. solidissima*, indicated in grey along the east coast of the USA, from Cape Hatteras, North Carolina, to the Gulf of St. Lawrence, Canada. After Ropes and Merill (1969).
The environment in the MAB is one that is subject to seasonal variability in water temperatures (Mountain 2002). Coastal current systems generally follow a north-south flow and most of the region experiences stratification of the water column in the summer months due to increased surface heating in combination with increased river run-off (Mountain 2002). This seasonal thermocline often becomes an important factor in the reproductive cycle of surf clams, as a fall spawning event usually occurs with the breakdown of the thermocline during periods of increased mixing, bringing warmer water down to greater depths (Ropes 1968). The thermocline often serves as a boundary for other MAB species such as the ocean quahog, *Arctica islandica*, whose inshore distribution is below the thermocline (Franz and Merill 1980). Ocean quahogs are found along cold isotherms at greater depths, where temperatures do not exceed their thermal maximum. This concept is known as submergence (Franz and Merrill 1980). The circulation of ocean water in the MAB is also important. Periodic upwelling often occurs, and the relaxation in upwelling frequently relates to episodes of high recruitment of surf clams due to downwelling events (Chintala and Grassle 2001, Weissberger and Grassle 2003, Ma 2005).

Historically, several events have occurred within the MAB that have altered the surf clam habitat and shaped the modern distribution. In 1976 a hypoxic event occurred off the coast of New Jersey from June to August, effectively causing mass mortality in surf clams (Ropes 1979). Recruitment events followed the hypoxic event in New Jersey (1976) and Delmarva (1977) that may have led to intra-specific competition (Weinberg 1998) as well as size-selective harvesting by the fishery (Weinberg and Helser 1996) in these habitats. The closing of stratum 9 (NEFSC Delmarva offshore stratum, Figure 4)
to fishing from 1980-1991 is also of historic relevance. Weinberg (1998) found that length-at-age of surf clams sampled from this region during 1980 to 1991 was reduced in the absence of commercial harvesting, most likely the result of reduced growth rates due to density-dependent competition.

**Growth**

Surf clams are long-lived animals and like all shelled molluscs, they are capable of recording their entire life history, including both environmental (e.g. tidal cycles, temperatures) and physiological (e.g. spawning) events, in their calcium carbonate shells (Rhoads and Lutz 1980). Moreover, growth patterns within the bivalve shell represent complex interactions between the physiology of the animal and its environment, preserved as morphological, structural, or chemical changes contained within the shell (Rhoads and Lutz 1980). As molluscs undergo aerobic metabolism, calcium is taken in from the surrounding seawater or diet, and calcium carbonate is deposited from the mantle into the shell as a result of calcification (Gosling 2003). The cessation of this deposition due to a disturbance, whether physiological or environmental, results in a pause or slowing of growth, evident as dark growth lines as calcification ceases (Richardson 2001). These lines are often coincident with spawning, as shell deposition slows or stops while the clam distributes its energy into the production of gametes (Jones et al. 1978). While these external growth lines are apparent on the external shell to the naked eye (Figure 3), age and growth may be studied by microscopically examining bivalve internal shell growth lines (Ropes and O'Brien 1979) composed of alternating layers of calcium carbonate (calcite or aragonite) and organic material (conchiolin) (Rhoads and Lutz 1980). There is evidence from mark-recapture studies (Jones et al.
1978, Jones 1980) and stable isotope analyses (Jones et al. 1983) that these lines are deposited on an annual basis in surf clams, making age estimations possible by counting annual growth lines.

The growth rate in surf clams varies throughout their lives, as growth is very rapid up until approximately age 5 (Ambrose et al. 1980, Ivany et al. 2003, Cerrato and Keith 1992) and then slows until a maximum shell length is reached which reflects the environmental conditions and resources available within the surf clam habitat. This form of growth, found in all bivalves is described as allometric (Gosling 2003). As body size increases, the relative proportions of the shell dimensions progressively change, such that the size of one component (e.g. shell weight) increases in proportion to the size of another component (e.g. shell length) raised to a certain power. This form of growth is described by the equation:

$$y = ax^b$$

(equation 1)

where y and x represent different growth variables (e.g. shell length, shell height, shell weight) and a and b are constants. In addition, the body weight and size of clams has an allometric relationship with metabolism because the surface area available for oxygen diffusion limits metabolism (Gosling 2003). As the size of an animal increases, its weight specific physiological rates decrease so that biological processes proceed at favorable and sustainable rates with the decreasing surface to volume ratio (Gosling 2003). Younger/smaller clams thus grow much more rapidly than larger/older clams because they have a greater growth efficiency (Bayne 1985).
Figure 3. External growth lines (indicated by arrows) visible in a photograph of a surf clam valve. Photograph by Picariello.
Water temperature has been found to play an important role in surf clam growth and reproduction (Savage 1976, Goldberg 1980, Jones 1981, Sephton 1987, Sephton and Bryan 1990, Weissberger and Grassle 2003). Growth is most rapid during spring and summer when temperatures are warm (Jones et al. 1983, Weissberger and Grassle 2003); however, high temperatures have been found to be detrimental to growth and survival. Savage (1976) examined burrowing activity in surf clams and found that optimal temperature for burrowing was 20°C, and that burrowing activity decreased when temperatures rose beyond 20°C. Goldberg (1980) also found 20°C to be optimal for development and growth of embryos with a slowing of growth as temperatures exceeded 20°C. Temperatures above 28-30°C are lethal to all stages of surf clams (Walker and Heffernan 1994). Spawning is often stimulated by an acute increase in temperature reaching a threshold anywhere from 15°C at the northern edge of the distribution (Sephton 1987), to 20-23°C at more southern latitudes (Jones 1981, Chintala and Grassle 1995). High concentrations of larvae have been found in New England at temperatures of 14-18°C, with few found at temperatures greater than 19°C (Mann 1985).

As differences exist in temperature throughout the distribution, spawning cycles often vary and spawning typically begins and ends earlier near the southern edge of the distribution in the MAB (Ropes 1979). If temperatures are optimal, two spawning events can occur per year in these more southern locations (Ropes 1968): one in the early spring and another in late summer or fall associated with the breakdown of the thermocline bringing a pulse of warm water to greater depths (Ropes 1968).

Bottom temperatures in recent years (1998-present) in the Delmarva Peninsula have been exceptionally warm according to Weinberg (2005). This trend could
potentially alter the growth patterns of surf clams by changing the timing of spawning
events and also causing thermal stress if temperatures rise above optimal. Temperatures
greater than 20°C can initiate stress in surf clams enough that growth slows or ceases, as
well as affect certain vital behaviors such as burrowing which is a behavior that surf
clams use as an escape mechanism from predation.

Surf clams have an array of predators including naticid snails, sea stars, crabs, and
fishes including cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (NEFSC
1999), and the effects of predation have been studied as an important factor influencing
growth and recruitment of surf clams (Dietl and Alexander 1997, Franz 1997,
Weissberger and Grassle 2003). Some results show that smaller clams (<125 mm) are
often more susceptible to predation and predation can account for mortality in
approximately 5% to 8.6% of surf clam standing stock (Franz 1997, NEFSC 2003).

While temperature plays an important role in regulating the growth of surf clams,
Weinberg (1998) also found that intraspecific competition was important in structuring
the population of Delmarva surf clams from 1980 to 1994. This study examined an
increase in intraspecific competition following a period of population expansion in an
area that was recently closed to harvesting. Growth rates and tissue weights were found
to be lower in areas of higher density.

**Notes on the Population Ecology**

The National Oceanic and Atmospheric Administration/ National Marine Fisheries
Service/ Northeast Fisheries Science Center (NOAA NMFS / NEFSC) has surveyed
Atlantic surf clam stocks regularly for over two decades as part of the surf clam stock
assessment survey. These surveys provide data regarding the stock status and trends in
biomass along its distribution from Georges Bank to the southern portion of the
Delmarva Peninsula (Figure 2). These data have been used for many studies to analyze
the growth and distributional patterns of the species in differing geographic regions and
time intervals (Weinberg and Helser 1996, Weinberg 1998, Weinberg et al. 2005,
Weinberg 2005).

Weinberg and Helser (1996) showed that from 1980-1992 changes occurred in the
growth rates of surf clams from Delmarva, at the southern limit of their range, but not in
surf clams from Georges Bank at the northern limit (Figure 2). They related the
differences in growth rates of surf clams among geographic regions to differing bottom
water temperatures. They found that Delmarva surf clams in general have slower growth
than surf clams from higher latitudes. Bathymetric differences in the growth of inshore
(approximately 2-27 m) and offshore (approximately 27-46 m) clams also exist, as
inshore clams grow slower, reach smaller maximum sizes and have shorter lifespans,
trends are a result of clams being physiologically stressed by either extreme winter or
summer temperatures in inshore locations (Jones et al. 1978).

Recent data described by Weinberg et al. (2005) suggest that surf clam biomass in
the MAB has declined from 1997 to 2004, and that a noticeable shift in their distribution
has occurred. More specifically, biomass in southern New Jersey and southern Virginia
has declined significantly, with increased abundance observed in the offshore New Jersey
and Delmarva regions. Weinberg et al. (2005) found that in 2004, surf clams were most
abundant along the shelf of Northern New Jersey (~500,000 metric tons), and biomass
was low (~143,000 metric tons) in the Delmarva region. Weinberg (2005) established that in 1999 and 2002, some of the warmest years on record during the past few decades, surf clams were found in deeper water than in any other surveys during the previous 18 years indicating that mortality had occurred in the shallower locations. Similarly, off the Delmarva region during this time period proportions of dredge tows capturing at least one surf clam declined in stratum 9 (S. Delmarva, Figure 4) from 0.90 in 1994 to 0.64 in 2002. The data suggest that the recent distributional shift by this species has been northward and into deeper waters, a pattern expected if increasing temperatures were a driving force. In addition to Weinberg (2002b, 2005), Kim and Powell (2004) also suggested that shifts in temperature south of Delaware Bay in the MAB are a more important factor than disease (including parasites, nematodes, cestatodes) in determining the mortality rate of Delmarva surf clam populations in areas that recently suffered reductions in biomass.

**Objectives**

Recent reductions in biomass and shifts in the distribution of surf clams since 1999 provide the underlying premise to this study. The decline in Delmarva surf clams observed since 1999 appears to be related to above average water temperature conditions in the MAB as suggested by Weinberg et al. (2002a) and Weinberg (2005). In a study of *Macoma balthica*, another marine bivalve, Hummel et al. (1995) determined that animals living at the southern limit of their distribution are already living in stressful conditions, and are thus more susceptible to additional stress. Weinberg et al. (2002a) suggested that this could occur for surf clams by coupling already adverse environmental conditions in the Delmarva region with higher than optimal temperatures. As observed by Savage...
(1976) and Goldberg (1980), 20°C appears to be the optimal temperature for growth and
development. As Weinberg (2005) describes, seasonal bottom temperatures warmer than
20°C have occupied a larger portion of the Delmarva region seasonally since 1999. The
recent observed reduction in biomass (due to mortality) of surf clams since 1999 at the
southern limit of its distribution may be due to these warm temperatures as temperature
stress will be more pronounced in individuals from this region.

This study will 1) examine length-at-age of surf clams within and among
geographic regions over the past 20-30 years in relation to depth, latitude, and water
temperatures, and 2) relate observed patterns to ambient bottom water conditions.
Growth will be studied by utilizing shell length, biomass, and age data that are measured
from specimens collected from the 2005 NOAA NMFS/NEFSC surf clam stock
assessment survey. Additional analysis will include a comparison of two different
techniques used to estimate age. Two working hypotheses will be addressed for this
study.

H₁: Length-at-age are higher in surf clams in northern latitudes and offshore
waters, compared to those at southern latitudes and inshore waters.
H₀: No difference exists in the length-at-age of surf clams at different latitude and
depths.

H₂: Length-at-age in the past 25-30 years have changed in surf clams in the
southern MAB, so that a young clam in 2005 has a smaller length-at-age than an
older clam prior to 1995.
H₀: Length-at-age of surf clams from the southern MAB have not changed in the
past 30 years.

To determine whether length-at-age relationships are related to bottom water
temperatures, growth will be examined in conjunction with water temperature data
gathered over the last 35 years by NOAA buoys distributed throughout the MAB
(Harding et al. in review, Picariello et al. in preparation).
Materials and Methods
Field Methods

Sampling occurred in the summer of 2005 as part of the NOAA/NMFS/NEFSC surf clam/ ocean quahog stock assessment survey. The survey took place from 23 May 2005 to 30 June 2005 onboard the NOAA Research/Vessel (R/V) Delaware II, departing from Woods Hole, Massachusetts. Since 1982 these surveys have been conducted every three years in federal waters (> 5.5 km from shore). While collection methods and gear efficiency have changed slightly over the years, the sampling strata have remained fixed over this time interval (1982-2005). Surf clams and ocean quahogs are surveyed within a set of geographic regions along the east coast of the United States including Georges Bank, Long Island, New Jersey, and the Delmarva Peninsula; collectively known as the MAB (Figure 2). Using a stratified random sampling design within each of these regions, station locations were chosen randomly within a standard set of depth strata designated by NMFS (Figure 4). While the survey spans the latitudinal distribution of surf clams along the eastern USA from Georges Bank to North Carolina, it also includes the bathymetric range from inshore (9-27 m) to offshore (27-46 m). To address the stated hypotheses, six strata from the NMFS survey were targeted for this study. Two strata were chosen from each of the southern (Figure 4, southern Delmarva strata 9 and 84) and northern (Figure 4, New Jersey strata 21 and 88) areas of the MAB, and also from an intermediate location (Figure 4, northern Delmarva strata 13 and 85). In addition to the latitudinal distribution, strata were chosen to represent both inshore and offshore habitats.
Figure 4. Locations of NEFSC surf clam sampling along the MAB. White stars indicate targeted areas for this study. (Map from the NEFSC)
Sampling was performed with a hydraulic dredge, towed for five minutes at a speed of 1.5 knots along the sea floor as the R/V *Delaware II* moved in the direction of the next station. For descriptions of survey sampling gear, see Weinberg et al. (2002b). Dredging was done at each randomly selected location with a total of 426 stations sampled. After completion of each tow, the dredge was hauled back onto the ship, and the contents were released onto a large sorting table where the catch were separated by scientists and volunteers while the ship steamed toward the next station. At the sorting table, the biological catch was placed into either 5-gallon buckets or 2-bushel wire baskets by species. The most prominent catch was surf clams, ocean quahogs (*Arctica islandica*), and sea scallops (*Lactopecten magellanicus*). The volume of surf clams was recorded in numbers of full bushels as well as the weight of each bushel in kg. For more information on the 2005 stock assessment survey catch summary, see the *Resource Survey Report - Surfclam/Ocean Quahog* available on the Northeast Fisheries Science Center website.¹

Surf clam samples were processed onboard the R/V *Delaware II* and data was recorded using the Fishery Science Computer System (FSCS). Each surf clam was measured for a maximum shell length (mm) from anterior to posterior using Limnos electronic measuring boards wired to onboard computers (shell height from dorsal to ventral was later measured in the laboratory). These measuring boards along with digital scales directly input data into the FSCS system in an efficient manner. Using this system, one clam per every 10-mm shell length was processed. After a maximum length was recorded, the whole clam weight was taken in grams. Broken shells were omitted if an

１www.nefsc.noaa.gov/esb/Resource_Survey_Reports.htm
intact clam could be found in the same size class and substituted. Each clam was shucked with a stainless steel shucking knife at sea. The adductor muscles, which are the toughest part of the clam tissue, were cut first to facilitate the removal of the meat from the shells. Excess seawater was removed from the meat using paper towels. Sand stuck between the valves or in the mantle cavity was brushed or rinsed out. Valves were labeled in pencil with the station and identification number (Station-ID). The meat weight was then taken in grams and the meats were bagged with appropriate labels printed directly from the FSCS computer. These printed labels ensured that the correct identification number was assigned to each clam (both shell and meat) that was processed. Labels indicated the species, identification number of each shell, and station number. For each individual specimen, both shell valves and meats were labeled with the same identification number for cross-referencing of data. For each station, the shells were kept together in cloth bags and labeled appropriately including the number of shells per bag (a shell corresponding to both valves of the clam). This process was carried out at each of the stations where the catch included surf clams. At sea, samples were stored in the walk-in freezer onboard the R/V Delaware II. A total of 943 clams were collected for age estimation and 400 meats were collected for condition index. These animals represent a size range from 32 mm to 189 mm shell lengths (Figure 5), and cohorts from age 1 to age 30. In the shallow Delmarva region only 9 clams were caught from strata 83-86 collectively. These represent a size range of 43 mm to 101 mm. From the targeted strata, only 2 and 5 clams were caught in the inshore Delmarva strata (strata 84 and 85 respectively). Due to these low catch numbers and therefore insufficient data, these inshore Delmarva strata were eliminated from analysis, leaving four strata: offshore S.
Delmarva (9), offshore N. Delmarva (13), offshore New Jersey (21) and inshore New Jersey (88).

To ensure that no bias existed in using only live clams, a collection of live surf clams and clappers (dead surf clam shells still attached at the umbo, indicating clams that have died due to natural mortality) were also collected from two different locations (38°20’N 74°24’W, 39°40’N 73°26’W) (Figure 5) sampled on the commercial vessels F/V John N and Christy in March of 2006.

**Determination of Sample Size**

A total of 426 tows were completed on the NEFSC 2005 cruise. A power analysis was conducted in order to determine the appropriate number of samples (tows) needed to detect differences between strata for this study. The methods of Bros and Cowell (1987) were used for this analysis where a random number generator was used to assign the number of clams caught per tow (for each strata) in a Monte Carlo fashion. This provided replicates from which to plot the relationship of the number of samples and the standard error of the mean of all surf clams caught per tow, using all tow data from the 2005 stock assessment survey. Using these plots (Figure 7), sample sizes (# of tows) could be determined by following the plots to points of convergence. The sample sizes that minimized the standard error of the mean were optimal, and thus determined how many tows should be used for each stratum. See Table 1 for a summary of all sample sizes.
Figure 5. Map of the east coast of the USA, indicating locations of sampling on the F/V *John N* ("1") and *Christy* ("2") in March of 2006. Also indicated are locations of Chesapeake ("C", at 20 m) and Delaware ("D", at 30 m) buoys used to collect water temperature data. Historic Lightship stations for both Delaware and Chesapeake are in approximately the same locations as modern buoys. Range of *S. solidissima* is indicated in grey.
Figure 6. Shell dimensions of the Atlantic surf clam, shown on a right valve including the shell length (SL), shell height (SH) and chondrophore. U=umbo, AMS=anterior adductor muscle scar, PMS=posterior adductor muscle scar, PL=pallial line.
Table 1. Summary of sample sizes (number (#) of stations or tows) used for each strata. A total of 542 clams were processed from these four areas, providing sufficient data to address each hypothesis.

<table>
<thead>
<tr>
<th>Strata</th>
<th>Location</th>
<th># stations suggested</th>
<th># stations used</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>S. Delmarva offshore</td>
<td>15</td>
<td>29</td>
</tr>
<tr>
<td>13</td>
<td>N. Delmarva offshore</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>21</td>
<td>New Jersey offshore</td>
<td>25</td>
<td>27</td>
</tr>
<tr>
<td>88</td>
<td>New Jersey inshore</td>
<td>12</td>
<td>21</td>
</tr>
</tbody>
</table>
Figure 7. Standard error of the mean of the numbers of surf clams caught per tow, plotted versus sample size in order to determine appropriate sample sizes for this study per methods of Bros and Cowell (1987) for stratum 9 (A), 13 (B), 21 (C) and 88 (D). The region where the tail of the curve began to flatten or converge represents an appropriate sample size. A sample is equivalent to a station. Black arrows indicate the actual number of stations used. The differences between the scales in plots are a reflection of the differences between the standard error ranges among the strata examined.
B) Stratum 13

Standard Error

Sample Size (#stations)
C) Stratum 21

![Graph showing standard error vs. sample size for different categories A to E. The x-axis represents sample size (#stations) ranging from 1 to 65, and the y-axis represents standard error ranging from 0 to 50. The graph indicates a trend where the standard error decreases as the sample size increases, with a notable point at sample size 29 marked by an arrow.]
Laboratory Methods

Condition Index

A total of 238 individuals were selected for estimation of condition index to examine the relationship between tissue weight (g) and shell length (mm). Condition index is used as a tool to assess the general health of a population including resilience to stressors by observing the relationship between shell size and tissue weight (Mann 1978). For each animal, the meat was removed after shucking at sea, weighed fresh, and then labeled and frozen for later analyses. All material was transported from Woods Hole, Massachusetts to Gloucester Point, Virginia in September of 2006, where processing took place at the Virginia Institute of Marine Science (VIMS).

In the laboratory at VIMS, frozen clam tissue was thawed and weighed to obtain thawed wet weight (g). Tissue was then dried at 80-90 °C for 72 hours to obtain dry weight (g) and thenashed in a kiln at 450 °C to obtain the ash weight (g). The subtraction of ash weight from dry weight gives an estimation of ash-free organic weight, or ash-free dry weight, in grams. Ash-free dry weight (AFDW, g) was plotted against shell length (mm) in a regression for each stratum to estimate biomass versus shell length relationships in the form of a power curve:

\[ W = aL^b \]  

where \( W \) is weight (AFDW in grams), \( L \) is shell length (mm), and \( a \) and \( b \) are constants. Condition index was calculated following the method of Kim and Powell (2004), using AFDW instead of dry weight. This index of organic content was calculated as:
Equation 3:

\[
CI = \frac{AFDW (g)}{SL (mm)}
\]

Unless otherwise stated, all graphs and statistical analysis for this study were performed in Microsoft Excel X for The Macintosh.

**Shell Preparation for Age Estimation**

Immediately after collection at sea, surf clam valves were individually labeled and saved for age estimation (see page 25). At VIMS, the left valves were submerged in a 75% bleach solution for 10 minutes to remove any excess tissue, or mold that may have accumulated from storage. Valves were then rinsed and a target line was drawn on the exterior of the shell following the axis of maximum growth (Figure 8A). While still wet, valves were sectioned radially along this target line, from hinge to growth margin, making a clear section through the middle of the chondrophore (Figure 8B). Sectioning exposed growth lines in both the chondrophore and the valve cross-section (Figure 9). After valves were sectioned, both halves (a and b) were labeled with the corresponding station and identification number (Figure 8B). Small fragile shells, usually less than 90 mm in shell length, were embedded in Buehler Epoxicure resin to protect them during sectioning.
Figure 8. Location of sectioning along the axis of maximum growth on a left valve of an Atlantic surf clam, showing the exterior view (A) and the interior view (B). U=umbo. After the radial cross-section was made, each half was labeled (a and b).
A. Axis of maximum growth

B. axial

dorsal

Chondrophore

Anterior

Axis of maximum growth

ventral
Figure 9. Line drawing of radial cross-section of a surf clam from umbo to shell margin. Growth lines are visible in both the chondrophore and valve. Figure not to scale.
Outer shell layer

Annual Growth line

Shell margin

Exterior

Interior (body cavity)

umbo

chondrophore
Polishing

After valves were cut, the larger half (b) was polished (Figure 8). In situations where the “b” half was not intact, the “a” half was used. Halves were chosen based on the condition of the outer shell layer (eroded shells were not used) and completeness of the valve from hinge to the ventral growth edge, and the majority of valves chosen corresponded to the larger portions of the shell, the “b” half. Polishing was an important step, as it ensured that the cross-sections were analyzed on a clean and flat plane. Shells were polished using a Beuhler Metaserv 2000 Grinder/Polishing wheel at 115 Voltage following a set protocol (Table 2). The larger grit sizes of sandpaper were crucial to remove any unevenness or bumps after sectioning.

Age estimation using the chondrophore

Growth lines in surf clams can be found both externally on the shell, and in internal microstructures. While the external lines are visible to the naked eye, an element of caution should be applied if counting these lines to determine age. Previous studies have found that these external growth lines often overestimate the age of young animals and underestimate the age of older animals as the lines become very crowded on the edge of the shell (Jones et al. 1978, Ropes and Shepherd 1988). Since the accuracy in counting external lines is likely skewed, age estimation techniques often rely on the excision of a 2-mm section of the chondrophore from the right valve (Figure 10) per methods developed for the NEFSC by Ropes and O’Brien (1979) and later revised by Ropes and Shephard (1988). Under these methods, the sections are analyzed under a dual stereo microscope at ~25X and the dark lines are counted. The age-estimation technique
applied for this study was based on these original methods, where the entire valve was sectioned through the chondrophore from the umbo to edge of the growth margin. After polishing, an image of each chondrophore (Figure 11) was taken using an Olympus MagnaFire SP Mono digital camera fitted with a 55 mm Nikon Macro lens and/or bellows assembly, and analySIS Microsuite (version 3.2.6) software.

Terminology is important when describing patterns in the bivalve shell used for age estimation, and these patterns are often discussed in different ways. For the purpose of this study, I will adopt the terminology used by Richardson (2001). A **growth line**, according to Richardson (2001) is a dark line characterized as an annual deposition, whereas the **annual increment** is a lighter interval characterized as the distance separating growth lines. These increments represent the deposition of calcium carbonate as a product of calcification during shell growth. The annual periodicity of these lines in surf clams has been validated by both mark-recapture studies (Jones et al. 1978, Jones 1980) as well as work with stable isotopes (Jones et al. 1983).

When counting annual growth lines in the bivalve shell, the darker growth lines are not to be confused with **disturbance lines**, which are incomplete and less prominent than the annual growth lines. Ropes and Sheperd (1988) term these as **growth checks** and offer a description to aid in distinguishing these from growth lines when analyzing surf clam chondrophore patterns: growth checks do not fully extend to the edges of the chondrophore and are not considered as annual growth lines in comparison to the dark lines that are counted to estimate age. Age estimates (years) were obtained by counting the number of growth lines visible in each chondrophore for each of 463 chondrophores, using photographs taken at VIMS.
Table 2. Protocol for polishing cross-sections of surf clam shells. Grits 120-600 were Beuhler Carbimet PSA backed disks. 6 and 1 micron solutions were Beuhler Metadia Diamond solutions used in conjunction with Texmet 1000 Beuhler polishing cloths. For each grit size, shells were polished 1-4 times for the allotted number of seconds. RPM=revolutions per minute.

<table>
<thead>
<tr>
<th>Grit size</th>
<th>Duration (seconds)</th>
<th># times</th>
<th>RPM</th>
</tr>
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<tr>
<td>120*</td>
<td>20</td>
<td>1</td>
<td>200</td>
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<tr>
<td>240</td>
<td>30</td>
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<td>400</td>
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<td>4</td>
<td>150</td>
</tr>
<tr>
<td>600</td>
<td>20,30</td>
<td>2,2</td>
<td>150</td>
</tr>
<tr>
<td>6 micron</td>
<td>20</td>
<td>3</td>
<td>150</td>
</tr>
<tr>
<td>1 micron</td>
<td>20</td>
<td>4</td>
<td>150</td>
</tr>
</tbody>
</table>

*120 grit only used if shell was very uneven after cutting.
Figure 10. Location of sectioning on the right surf clam valve consistent with NEFSC protocol (Ropes and Shepherd 1988).
Dorsal

Site of NEFSC section

Anterior

Axis of maximum growth

Posterior

Ventral
Figure 11. Photograph of a surf clam chondrophore cross-section with scale bar. The oldest growth is near the umbo (right side of image), with the newest growth on the far left of the image towards the growth margin. Photograph by Picariello.
Estimates of age were plotted versus shell length to develop length (mm)-at-age (yr) curves for each of the four strata. Curves were generated using least squares methods, and parameters of the non-linear von Bertanaffy growth function (von Bertalanffy 1938) were estimated using the equation:

\[ L_t = L_\infty (1 - e^{-kt}) \]  

(equation 4)

Where \( L_t \) is the length at time \( t \), \( L_\infty \) is the maximum shell length, \( e \) is the natural logarithm, \( k \) is the growth coefficient which represents the rate at which the \( L_\infty \) is reached, and \( t_0 \) is the time at length 0. The von Bertalanffy growth curve has been used widely in studies of surf clam growth (Sephton and Bryan 1990, Cerrato and Keith 1992, Walker and Heffernan 1994, Weinberg and Helser 1996, Weinberg 1998)

Growth curves were compared between and within strata using an analysis of the residual sum of squares method (ARSS) developed by Chen et al. (1992) as described by Hadden (2001). This method was appropriate since the von Bertalanffy growth formula is nonlinear and thus a linear analysis of covariance (ANCOVA) model could not be used to test for differences. ARSS has been used often in growth studies to compare multiple non-linear growth curves such as the von Bertalanffy growth function (VBGF). The procedure as described in Chen et al. (1992) follows four main steps: 1) the residual sum of squares (RSS) and an associated degree of freedom (DF) of the VBGF were calculated for each strata, 2) the resultant RSS and DF of each strata were added to yield summed RSS and DF, 3) data of all strata were pooled to calculate the RSS and DF of a total VBGF and 4) the \( F \)-statistic was calculated per Chen (1992) as:
where \( RSS_p \) = RSS of each VBGF fitted by pooled growth data, \( RSS_s \) = the sum of the RSS of each VBGF fitted to growth data for each strata, \( N \) = total sample size, and \( K \) = the number of strata in the comparison (2 strata were compared at a time).

These methods were also used to compare curves between live surf clam shells and surf clam clappers collected in March 2006. Length measurements (mm) and estimates of age (years) were gathered on 74 clams from each location (37 live, 37 clappers) and a comparison of size at age was made between live (collected in 2005) versus clapper shells. For several age classes this comparison was made to determine if clappers and live shells had similar length-at-age, and to determine if there were differences in growth between the live clams, caught in 2005, and the clapper shells, which likely died prior to 2005.

Chondrophore: Valve Relationship

A representative size range of 25 individuals from each stratum was chosen to quantify the chondrophore-to-valve height relationship (Figure 9). This relationship was important to demonstrate that measurements taken on the chondrophore could be used to predict the height of the valve. Whereas this association has been supported in the past (Ropes and O’Brien 1979), it was imperative to determine whether the relationship held true in the samples examined for this study because as the chondrophore is located on the interior of the shell valve it is protected from environmental conditions and remains intact, thus providing a useful portion of the clam to take measurements. Individuals
used for this analysis had clearly identifiable external growth lines and/or internal annual growth signatures visible in radial cross section as well as an intact chondrophore. For each clam, measurements were taken on a radial cross section of the valve using a millimeter scale, held at the tip of the umbo and extending along the valve, measuring where each of the growth lines intersected the outer shell layer. To make measurements on the chondrophore, a digital image of each chondrophore was taken using an Olympus MagnaFire SP Mono digital camera fitted with a 55-mm Nikon Macro lens and/or bellows assembly, and analyzeIS Microsuite (version 3.2.6) software. A scale (mm) was included in the image to calibrate the length of the chondrophore in the image to mm. Images were analyzed with Image Pro Plus (version 4.5), and measurements were made on each image by using calibration tools included in the software. Marks were annotated into the image at the tip of the umbo and then at each subsequent growth line. The distance was then measured in mm from the umbo to each of the marked growth lines using the caliper tool (Image Pro v. 4.0) (Figure 12). This allowed a determination of the chondrophore size at each age throughout the life of the clam. The last growth line, where the final measurement was taken, represented the age of the clam at capture. For a subset of 25 animals within each stratum, chondrophore measurements were plotted against the measurements (mm) taken on the corresponding valve cross section. A linear regression was fitted to these data following the work of Ropes and O'Brien (1979).

**Age-specific growth in surf clams**

The chondrophore (Figures 6,11) provides an ideal tool for estimating growth of surf
Figure 12. Digital image of the cross-section of the chondrophore, showing annotations used for measurement. The oldest growth is near the umbo (right side of image), with the newest growth on the far left of the image towards the growth margin.
clams because it is an internal structure that is protected from environmental conditions and thus remains intact throughout the clam’s life (Richardson, 2001). Growth lines in the chondrophore are visible to the naked eye and even more discernable with digital imaging techniques. For each chondrophore, the distances from the umbo to each growth line were measured as described above and using the linear relationship for the chondrophore-to-valve height regression, the chondrophore height (mm) was converted to shell height (mm). Surf clam shell heights (mm) were then plotted with shell lengths (mm) for each stratum and a linear regression was used to find the relationship between the two shell dimensions. For all clams within each stratum, shell valve height could then be converted to shell valve length.

Age and length data gathered for each clam at each age throughout its life allowed length-at-age curves to be estimated by back-calculating the sizes they were at each age, using the increments in shell growth measured on the chondrophores. Age-specific shell lengths could then be compared across different time frames using the sizes of clams captured in 2005 and comparing these to older clams, also caught in 2005, where age-specific shell lengths were back-calculated to their sizes at younger ages. Any differences between length-at-age between time periods were examined in relation to trends in bottom water temperatures, described in Harding et al. (in review) and Picariello et al. (in preparation). Using the average back-calculated sizes for each age, yearly growth rates were then calculated for the two time periods in each region as the change in average shell length (mm) per year. This calculation was used to compare whether these rates have changed over time in either the Delmarva or New Jersey regions.
**Water Temperature Data**

Water temperature data from 1970-2005 were used to describe mean monthly bottom water temperatures (BT, °C) for two stations in the Mid-Atlantic Bight at the southern end of the latitudinal range of surf clam distribution (Figure 5, Table 3). The period 1970-2005 was chosen to incorporate the entire lifespan of the oldest surf clam observed (30 years, captured in 2005 at a SL of 160.0 mm). Harding et al. (In review) used daily sea surface and bottom water temperature data from the Delaware/Winter Quarter and Chesapeake lightship stations in the Mid-Atlantic Bight during the period 1956-1971 to calculate the average monthly observed difference between sea surface temperature (SST) and bottom water temperature (BT) on a site-specific basis. The observed average monthly SST-BT differences from the daily lightship data were used to estimate average monthly BT at these sites during years after 1971 when only SST was available (Harding et al. in review: Table 3).

Hourly air temperature (AT, °C) and SST data from NOAA buoys (1985-2002) were used to calculate the observed difference between average monthly AT and average monthly SST for Delaware (Feb-Apr 1991) and Chesapeake Light (Apr 1993-Feb 1994, Dec 1994-May 1995, Feb, Aug 1996, Aug 2003-Jul 2005; Harding et al., in review). The observed average monthly AT-SST differences from the buoy data were used to estimate hourly SST for these two sites during months after 1985 when only AT was available.

Average residuals for annual BT from the long-term (1970-2005) average annual BT were calculated for each site in which at least 9 months of data were available following the methods of Harding et al. (in review) (Picariello et al. in preparation). Monthly residuals from the long-term (1970-2005) average month-specific BT were
calculated for July, August, September and October for both sites (Picariello et al. in preparation). Monthly BT estimates from 1970 to 1983 (Delaware) and 1984 (Chesapeake) use a single published monthly average (Table 3) while monthly BT estimates from NOAA buoys (Table 3) are averages calculated from hourly readings with n values > 400 per month.

From stratum 9, in the S. Delmarva area, a predominant year class was 12 year-olds, which corresponds to a 1993 settlement event. Since these clams have been alive since 1995, a warming trend would likely have affected the growth of these individuals. From this stratum, a comparison of age-specific growth was made between the 12-year-olds captured in 2005, and the clams that are ages of 20 and older, also captured in 2005 but back-calculated to their estimated their shell lengths at 12 years of age during the 1980’s. This was possible by using the measurements taken on the first 12 growth lines for each of these clams. Von Bertalanffy growth parameters were estimated and an analysis of the residual sum of squares was used to determine whether the curves were statistically different. In order to relate these year classes to similar year classes from other regions, age-specific length-at-age was examined in each of the other three strata. When length-at-age was plotted for younger individuals prior to reaching their asymptote, the von Bertalanffy growth function could not be applied. The length-at-age of these younger clams was plotted using a linear regression and regression lines were compared using an analysis of variance (ANOVA).
Table 3: Summary of water temperature data sources from 1970-2005 for Delaware/Winter Quarter (1, Figure 5), and Chesapeake (2, Figure 5). Sea surface temperature (SST), bottom temperature (BT) and air temperature at the water surface (AT) were used. All temperatures were in degrees Celsius. From Harding et al. (in review), and Picariello et al. (in preparation).

<table>
<thead>
<tr>
<th>Station</th>
<th>Year(s)</th>
<th>Data</th>
<th>Station type</th>
<th>Depth</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delaware/Winter Quarter</td>
<td>1955-60</td>
<td>SST, BT</td>
<td>Winter Quarter lightship</td>
<td>24-29 m</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>1961-70</td>
<td>SST, BT</td>
<td>Delaware lightship</td>
<td>30 m</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>1970-74</td>
<td>SST</td>
<td>One degree quadrangles</td>
<td>NA</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1975-80</td>
<td>SST</td>
<td>One degree quadrangles</td>
<td>NA</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>1981-84</td>
<td>SST</td>
<td>One degree quadrangles</td>
<td>NA</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>1984-2005</td>
<td>AT, SST</td>
<td>NOAA buoy 44009</td>
<td>28 m</td>
<td>6</td>
</tr>
<tr>
<td>Chesapeake</td>
<td>1958-71</td>
<td>SST, BT</td>
<td>Chesapeake lightship</td>
<td>20 m</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>1971-74</td>
<td>SST</td>
<td>One degree quadrangles</td>
<td>NA</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>1975-80</td>
<td>SST</td>
<td>One degree quadrangles</td>
<td>NA</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>1981-84</td>
<td>SST</td>
<td>One degree quadrangles</td>
<td>NA</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>1985-2005</td>
<td>AT, SST</td>
<td>NOAA buoy CHLV2</td>
<td>11.6 m</td>
<td>8</td>
</tr>
</tbody>
</table>

Age estimation using the hinge region

A second age estimation technique was also applied for this study after the methods of Harding et al. (in review) developed for *Arctic islandica*. This technique utilizes a cross section of the hinge region, rather than the chondrophore. For each polished clam valve, the hinge was photographed using a bellows/macro lens assembly mounted on a Magnafire SP digital camera connected to a Windows based computer. Each specimen was positioned such that lines within the shell valve were oriented vertically or perpendicular to the width of the shell section in the resulting digital image. Monochrome images were captured using analySIS Microsuite (version 3.2.6) and analyzed using Image Pro Plus (version 4.5).

An intensity profile, which is a 1 pixel wide line, was drawn across the width of the hinge cross-section, and described for each hinge using the Line Profile tool in Image Pro Plus. Surf clams, like northern quahogs (*Mercenaria mercenaria*), grow more quickly early in life than in later years (Harding et al. in prep), and these differences in growth rates are reflected in patterns of shell deposition (see page 10). The areas of the valve cross-section that were deposited when the animal was young and experiencing faster growth contain obvious annual growth signatures. In areas of the shell that were deposited later in the animal’s life, growth signatures are compressed and difficult to identify with the naked eye. Edge filters in Image Pro Plus software were used to detect the transitions between seasonal periods of growth and shell deposition corresponding to annual growth lines within the recently deposited areas of the shell cross section.
Figure 13. Digital image of hinge structure of *S. solidissima*. The left side of the image is the interior of the hinge and the newest growth. The right side is the outer shell and the oldest growth. Dark annual growth lines are indicated with arrows.
A peak was defined as a trace on the intensity profile that intersected a predetermined intensity level while moving toward a maximum intensity (upper limit = 255) or while moving toward a baseline or 0 level representing an internal growth line within the shell cross section. Annual growth lines were identified from intensity profiles using the methods described by Harding et al. (in review) for *Arctica islandica*. These mathematical methods identify unique ranges of grayness in the grayness spectrum (0-255 intensity units), which correspond to annual growth lines by evaluating declination in the number of lines across intensity steps from intensities ranging from 20 to 210 for a sub-sample of 25 surf clams. After the intensity range corresponding to annual growth lines was established, using the methods of Harding et al. (in review), peaks (internal growth lines) in this range were counted yielding individual age estimates from intensity based line counts in the grayness range of 115-120.

Images of the hinge region were used in conjunction with the line profile tool in Image Pro to create intensity-based line counts for each of 25 surf clams at shell lengths of 107-160 mm. These intensity-based line counts were examined in 5-unit-grayness intensity intervals ($I_j$) from 25 to 185 units to determine a threshold level from which to count annual growth lines using methods described by Harding et al. (in review) for *Arctica islandica*. Annual growth lines should be darker than other lines and exist as a distinct group of uniform grayness within the available growth lines. Values for $I$ were defined as the incremental bin number across the grayness range (Harding et al. in review). The average rate of change in the line count (LC) was plotted as a function of change in intensity step ($I$), where the rate of change was calculated as:
With increasing grayness in the hinge image, the number of lines declines with progression from one intensity step to the next since the total number of lines counted decreases as the grayness level increases. A group of lines with a similar grayness, expected in annual growth lines, is reflected in Figure 14 by a local minimum in the average rate of change at the intensity interval of 115-120, where a sharp decline occurred.

As described in Harding et al. (in review), annual growth lines would be of sufficient strength, to separate these from other growth lines, as a high intensity grayness range. If a group of growth lines existed with a unique similarity in grayness, a high frequency of zero differences would be expected between the number of lines counted from one 5-intensity-unit level to the next.

The frequency of occurrences in which the difference in line counts between consecutive intensity levels was zero, was plotted for the 25 surf clams (Figure 15). A local maximum is depicted in the intensity range of 115-120, which is followed by a decline in the interval 120-125 intensity range. The rate of change in line counts was plotted in a regression against the incrementing grayness intensity (Figure 16) to yield the equation:

\[
\frac{dLC}{dl} = -0.0113537 + 2.3896
\]  

(equation 7)

A series of residuals was then determined using each of the 25 surf clam shells at a grayness intensity range of 25 to 185 grayness units. The mean residual was plotted
against the grayness intensity (Figure 17), and the most negative mean residual was observed in the grayness intensity of 115-120. This supports the observation from Figure 15, where for most shells, the rate of change in line count is lower in this grayness range than any other range. This would be expected with a yearly shift in growth, when shell deposition changes.

Fisher’s Least Significant Difference Multiple Comparison Test was used to compare the mean residuals within an intensity category across the range of intensity categories. The range of greatest intensities from 45 to 145 was focused on because it includes both the region for annuli deposition (115-120) as well as two intervals potentially correlated to spawning (50-55, 65-70). The number of times each set of residuals for the five unit grayness increment differed from all others within that increment was tallied from the multiple comparison test results. The maximum number of significant differences for any given set of residuals within an increment was 20. Figure 18 shows the results of these tallies as the frequency of the number of significant differences with regard to intensity interval. The Fisher’s test was run under a p-value of 0.01 following the methods of Harding et al. (in review).

A comparison of age estimation techniques

A comparison of the two different age estimation techniques (chondrophore and hinge methods) used for this study is of interest. Both methods rely on cross sections of the shell valve, yet two distinct portions of the shell are studied. Chondrophore-based methods rely on a cross-section of the chondrophore where growth lines are counted on a digital photograph, using the naked eye. The image-based technique utilizes the cross-
Figure 14. The rate of change in line count, dLC/dI, as a function of intensity level for 25 surf clams ranging from 107 to 160 mm in shell length, per methods of Harding et al. (in review).
Average rate of change vs. intensity range
Figure 15. Histogram depicting the frequency of occurrences where the difference in line counts between consecutive intensity levels was zero for the same 25 surf clams analyzed in Figure 14, per methods of Harding et al. (in review).
Number of zero differences

Intensity range

<table>
<thead>
<tr>
<th>Intensity Range</th>
<th>Bars</th>
</tr>
</thead>
<tbody>
<tr>
<td>25-30</td>
<td>3</td>
</tr>
<tr>
<td>30-35</td>
<td>4</td>
</tr>
<tr>
<td>35-40</td>
<td>4</td>
</tr>
<tr>
<td>40-45</td>
<td>6</td>
</tr>
<tr>
<td>45-50</td>
<td>5</td>
</tr>
<tr>
<td>50-55</td>
<td>3</td>
</tr>
<tr>
<td>55-60</td>
<td>5</td>
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<td>65-70</td>
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<td>70-75</td>
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<td>90-93</td>
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<td>110-115</td>
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<td>115-120</td>
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<tr>
<td>120-125</td>
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</tr>
<tr>
<td>125-130</td>
<td>1</td>
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<td>130-135</td>
<td>1</td>
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<td>135-140</td>
<td>1</td>
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<td>140-145</td>
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<td>155-160</td>
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<tr>
<td>160-165</td>
<td>1</td>
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<tr>
<td>165-170</td>
<td>1</td>
</tr>
<tr>
<td>170-175</td>
<td>1</td>
</tr>
</tbody>
</table>
Figure 16. Regression plot relating the rate of change in line count to increments of grayness intensities, per methods of Harding et al. (in review).
The graph shows the relationship between the average rate of change and the beginning value for the intensity interval. The equation of the line is given by

\[ y = 2.3896 - 0.011353x \]

with a coefficient of determination \( R^2 = 0.42606 \).
Figure 17. Mean and standard deviation of the residuals obtained from the expected rate of change per grayness intensity increment predicted from the regression line (Figure 38) and the observed rate of change per intensity increment for 25 surf clams, per methods of Harding et al. (in review).
Figure 18. The number of cases out of 20 possible in the grayness range of 45-145 where any one set of residuals from Figure 17 differed from all others.
Frequency of significant differences

Intensity Range

- 45-50
- 50-55
- 55-60
- 60-65
- 65-70
- 70-75
- 75-80
- 80-85
- 85-90
- 90-95
- 95-100
- 100-105
- 105-110
- 110-115
- 115-120
- 120-125
- 125-130
- 130-135
- 135-140
- 140-145
- 145-150
section of the hinge region using contemporary digital techniques from Harding et al. (in review) modified for the surf clam. Whereas the chondrophore-based method has been used for decades, and ensures that a large quantity of clams can be aged quite efficiently, the image-based methods supply a large amount of information, including both annual and sub-annual growth lines, but on a potentially lesser number of clams due to sample preparation time and costs. This method also avoids investigator error as it reduces the need to calibrate observer age estimations by performing blind tests.

Methods were compared by assigning the chondrophore age as the “observed age” and the hinge age as the “expected age.” The residual was calculated as the difference between the two (observed-expected). A Mann-Whitney nonparametric test was used to test the null hypothesis that for each stratum there were no differences between the ages estimated using the chondrophore and hinge methods. Using a nonparametric test implied that no assumptions were being made about the sample distribution. A dataset of 307 surf clams was used for this analysis, as ages were estimated on these clams using both techniques. To further the analysis, a Run’s Test (described in Zar 1999) was performed to determine whether the residuals for each stratum were distributed randomly, or whether a size bias existed which might indicate that there might be discrepancies between the age estimations of the two methods in clams of certain sizes. In situations where the Run’s Test was significant, a one-way analysis of variance (ANOVA) was performed using size class as the main effect and the residual as the response. In order to accommodate two clams in stratum 9 (S. Delmarva offshore) that were smaller than 80 mm, 20 mm size bins were used. MiniTab version 14 was used for all statistical methods in this analysis.
Results
Demographics

After ages were estimated, both age-frequency distributions (Figure 19) and length-frequency distributions (Figure 20) were constructed using all of the samples from each stratum in order to investigate the demographics of this species in the MAB in 2005. Based on the age-frequency distributions (Figure 19), dominant cohorts were observed in each of the four geographic areas studied. By counting backwards from the 2005 collection date, the dominant year classes were determined for each stratum, summarized in Table 4. Fewer surf clams over the age of 20 were found in the lower latitude strata off the Delmarva Peninsula (9 and 13), and a greater number of young clams (<3 years old) were found in stratum 9, in the S. Delmarva region.

Live surf clams and surf clam clapper shells collected from the F/V John N and Christy (Figure 5) were mostly larger specimens (> 100 mm). From the F/V Christy, which sampled in the region of the offshore New Jersey NEFSC stratum (21), larger and older clams were caught. This is different from samples collected by the F/V John N at a location corresponding to the NEFSC stratum 9 in the S. Delmarva region. These clams were smaller than those from New Jersey. [See the age and length-frequency distributions for F/V John N (Figure 21) and Christy (Figure 22).]
Table 4. Dominant year classes of surf clams collected in the summer of 2005 from four strata along the MAB.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Location</th>
<th>Dominant ages (yr)</th>
<th>Year Class</th>
</tr>
</thead>
<tbody>
<tr>
<td>13</td>
<td>N. Delmarva offshore</td>
<td>5, 8, 16</td>
<td>1979, 1997, 2000</td>
</tr>
<tr>
<td>21</td>
<td>NJ offshore</td>
<td>6, 7</td>
<td>1998, 1999</td>
</tr>
<tr>
<td>88</td>
<td>NJ inshore</td>
<td>4, 7</td>
<td>1998, 2001</td>
</tr>
</tbody>
</table>
Figure 19. Age-frequency distributions for surf clams collected from offshore S. Delmarva (stratum 9), offshore N. Delmarva (stratum 13), offshore New Jersey (stratum 21), and inshore New Jersey (stratum 88) in the summer of 2005 from the R/V Delaware II.
Figure 20. Length-frequency distributions for surf clams collected in the summer of 20005 onboard the R/V Delaware II from offshore S. Delmarva (stratum 9), offshore N. Delmarva (stratum 13), offshore New Jersey (stratum 21), and inshore New Jersey (stratum 88), grouped into 10 mm length classes (i.e. 30-39 mm, 40-49 mm, etc.).
Figure 21. Age-frequency (1) and length-frequency (2) distributions for live (A) and clapper (B) surf clams collected from Delmarva on the F/V John Henry in March 2006.
1.)

A) Delmarva (Live) Age-Frequency
n=37

B) Delmarva (Clappers) Age-Frequency
n=37

2.)

A) Delmarva (Live) Length-Frequency
n=37

B) Delmarva (Clappers) Length-Frequency
n=37
Figure 22. Age-frequency (1) and length-frequency (2) distributions for live (A) and clapper (B) surf clams collected from New Jersey on the F/V Christy in March 2006.
1.)

A) NJ (Live) Age-Frequency
n=37

B) NJ (Clappers) Age-Frequency
n=37

2.)

A) NJ (Live) Length-Frequency
n=37

B) NJ (Clappers) Length-Frequency
n=37
Condition Index

A total of 238 surf clam meats were processed for condition index. Condition index (equation 3, p.37) was highest in the inshore New Jersey surf clams (stratum 88), followed by offshore New Jersey (stratum 21), offshore S. Delmarva (stratum 9), and offshore N. Delmarva (stratum 13). The condition index, or organic content, was lower at the lowest latitudes (the Delmarva region) (Table 5). The power function (equation 2, p. 36) provided a good fit for all four strata (Regression, $p < 0.0001$) with most of the variation being explained by the regression ($R^2=0.98, 0.85, 0.95$ and $0.87$ for strata 9, 13, 21, and 88 respectively). The relationship between shell length (mm) and ash-free dry weight (g) is presented in Figures 23 and Figure 24 with regression parameters summarized in Table 6.

Length-at-Age

A total of 463 chondrophores were analyzed to determine length-at-age for surf clams collected in 2005. Fitted von Bertalanffy growth curves for each stratum are presented in Figure 25 and the predicted von Bertalanffy curves for all four strata are presented in Figure 26. Results show that of the four strata examined, clams from offshore S. Delmarva (stratum 9) and inshore New Jersey (stratum 88) had the highest growth coefficients and these coefficients were higher than those observed from the more northern strata, 21 and 88. Table 7 summarizes all von Bertalanffy growth parameter estimates. The lowest growth coefficient was found in stratum 13 in the N. Delmarva surf clams. The analysis of the residual sum of squares indicated that growth curves
differed between all strata combinations (ARSS, \( p<0.0001 \)) with the exception of offshore N. Delmarva, and offshore New Jersey (ARSS, \( p=0.14 \)) (Table 8).

Growth parameters for the live and clapper surf clam samples collected in March 2006 are summarized in Table 9. The parameters differed slightly, as live clam shells had higher growth coefficients than clappers from the F/V *John N* collection (Delmarva) and clappers had higher growth coefficients than live clam shells in the F/V *Christy* collection (New Jersey) (Table 10). These results may have been due to the absence of smaller clams in the collection, which would have filled out the curve at the younger end of the spectrum. However, no significant difference existed between the live and clapper growth curves (Figures 27 and 28) from clams collected on the F/V *John N* and *Christy* (ARSS results presented in Table 11). Thus no bias is apparent with using only live surf clam shells for growth analysis.

From the live and clapper surf clam shells in each location (Delmarva and New Jersey), several year classes were chosen to examine whether length-at-age was different in the live shells and the clapper shells. Age classes were examined that had at least two representatives for both live and clapper shells. No apparent patterns were found to indicate that any changes had occurred in growth between the live clams (caught in 2005) and the clapper shells (which died prior to 2005). The relationship between shell length (mm) and age (years) for live and clapper shells at selected ages is presented in Figure 24.
Table 5. Average Condition Index of surf clams in each strata, calculated as ash-free dry weight (g)/ shell length (mm), per methods of Kim and Powell (2004). CI=condition index with the standard error of the mean (SEM).

<table>
<thead>
<tr>
<th>Stratum</th>
<th>CI</th>
<th>SEM</th>
<th>Size range (SL, mm)</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>0.104</td>
<td>0.006</td>
<td>40-157</td>
<td>75</td>
</tr>
<tr>
<td>13</td>
<td>0.094</td>
<td>0.004</td>
<td>64-173</td>
<td>73</td>
</tr>
<tr>
<td>21</td>
<td>0.106</td>
<td>0.005</td>
<td>51-175</td>
<td>53</td>
</tr>
<tr>
<td>88</td>
<td>0.125</td>
<td>0.006</td>
<td>78-174</td>
<td>37</td>
</tr>
</tbody>
</table>
Figure 23. Power regression curves for shell length (mm) vs. ash-free dry weight (g) plotted for surf clams from four strata (9, 13, 21, 88) in the 2005 collection. Relationships were significant (Regression, $p<0.0001$) for all strata.
Stratum 9 (s. Delmarva offshore), n=75

\[ y = 0.00001x^{2.92547} \]
\[ R^2 = 0.977 \]

Stratum 13 (n. Delmarva offshore), n=73

\[ y = 0.00001x^{2.82652} \]
\[ R^2 = 0.852 \]

Stratum 21 (New Jersey offshore), n=53

\[ y = 0.00001x^{2.2172} \]
\[ R^2 = 0.946 \]

Stratum 88 (New Jersey inshore), n=37

\[ y = 0.00001x^{2.4927} \]
\[ R^2 = 0.865 \]
Figure 24. Fitted power regression trend lines for shell length (mm) versus ash-free dry weight (g) plotted for surf clams from the 2005 collection, collected from strata 9 (offshore S. Delmarva), 13 (offshore N. Delmarva), 21 (offshore New Jersey), and 88 (inshore New Jersey).
Table 6. Regression parameters for surf clam shell length (mm) versus ash-free dry weight (g). The equation corresponds to the power regression (equation 2, p. 23)

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Location</th>
<th>a</th>
<th>b</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>Offshore S. Delmarva</td>
<td>1.00E-05</td>
<td>2.926</td>
<td>0.978</td>
</tr>
<tr>
<td>13</td>
<td>Offshore N. Delmarva</td>
<td>2.00E-04</td>
<td>2.317</td>
<td>0.852</td>
</tr>
<tr>
<td>21</td>
<td>Offshore New Jersey</td>
<td>1.00E-05</td>
<td>2.825</td>
<td>0.946</td>
</tr>
<tr>
<td>88</td>
<td>Inshore New Jersey</td>
<td>2.00E-05</td>
<td>2.732</td>
<td>0.960</td>
</tr>
</tbody>
</table>
Chondrophore:Shell Valve Relationship

Linear regressions of chondrophore and shell valve measurements for each of the four strata demonstrate that a strong linear relationship exists between the height of the chondrophore and the height of the shell valve. Regressions yielded high coefficients of determination ($R^2$) that explain most of the variation in the data (Figure 30). The $p$-values (Regression, $p<0.0001$) indicate that this relationship is highly significant which is very important as the regression equations for each stratum allow a predictive relationship to be determined to relate the height of the chondrophore to the height of the valve. The high coefficients of determination and significant $p$ values ($p<0.0001$) in the shell length versus shell height regression (Figure 31) also allow another predictive relationship to be determined between these two shell dimensions, again by using the linear regression equation. This is important because the dimension obtained by taking a cross-section through the axis of maximum growth, for age-estimation, is the height of the clam, however the most common unit in the literature and for fisheries management purposes is the shell length. Using the regression equations, measurements made on the chondrophore for the age-specific growth analysis were converted to shell height, and eventually to shell length, which is the desired measurement. This allowed all measurements collected on chondrophores for age-specific growth analysis to be plotted as age (years) versus shell length (mm). See Table 12 for all conversion equations used.
Figure 25. Fitted von Bertalanffy growth curves for surf clams in each of the four strata (9, 13, 21, 88). Observed values were length-at-age (at capture), estimated by counting annual growth lines in the chondrophore, and predicted values were those predicted by the von Bertalanffy model. See Table 7 for estimates of growth parameters from von Bertalanffy model.
Figure 26. Predicted von Bertalanffy growth curves for four strata (9, 13, 21, and 88) plotted as age (yrs) versus predicted shell length (mm). See Table 7 for a summary of parameter estimates.
Age at length of surf clams from the MAB, 2005
Table 7. Estimated parameters of the von Bertalanffy growth equation, with the standard error of the mean (SEM) for each stratum, including sample sizes used in the analysis. (n = # of individual live surf clams examined).

<table>
<thead>
<tr>
<th>Location</th>
<th>Observed mean length in mm (SEM)</th>
<th>n</th>
<th>SL range (mm)</th>
<th>( L_{\infty} ) (SEM)</th>
<th>k (SEM)</th>
<th>t₀ (SEM)</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. Delmarva offshore</td>
<td>114.59 (3.25)</td>
<td>101</td>
<td>30-154</td>
<td>133.65 (1.55)</td>
<td>0.339 (0.039)</td>
<td>0.05 (0.21)</td>
<td>0.89</td>
</tr>
<tr>
<td>N. Delmarva offshore</td>
<td>119.97 (2.13)</td>
<td>140</td>
<td>64-173</td>
<td>176.45 (10.94)</td>
<td>0.096 (0.021)</td>
<td>2.90 (1.11)</td>
<td>0.79</td>
</tr>
<tr>
<td>NJ offshore</td>
<td>128.63 (2.46)</td>
<td>120</td>
<td>49-174</td>
<td>157.54 (3.59)</td>
<td>0.173 (0.023)</td>
<td>0.06 (0.02)</td>
<td>0.74</td>
</tr>
<tr>
<td>NJ inshore</td>
<td>143.46 (2.30)</td>
<td>102</td>
<td>76-189</td>
<td>158.57 (1.984)</td>
<td>0.327 (0.045)</td>
<td>0.43 (0.48)</td>
<td>0.71</td>
</tr>
</tbody>
</table>
Table 8. Results of the analysis of residual sum of squares (ARSS, Chen 1992)). Pairwise comparisons of all strata combinations are listed. All pairs yielded significant results (*) at p=0.05 with the exception of strata 13 and 21 (NS). (Del=Delmarva, O=offshore, I=inshore). Significant results indicate that there are statistical differences between the growth curves between the paired strata.

<table>
<thead>
<tr>
<th>Strata</th>
<th>Location</th>
<th>df</th>
<th>$F$-statistic</th>
<th>$p$-value</th>
<th>Pooled n</th>
</tr>
</thead>
<tbody>
<tr>
<td>9, 13</td>
<td>S. Del. O / N. Del. O</td>
<td>238</td>
<td>61.88</td>
<td>&lt;0.0001*</td>
<td>241</td>
</tr>
<tr>
<td>9, 21</td>
<td>S. Del. O / NJ O</td>
<td>218</td>
<td>19.22</td>
<td>&lt;0.0001*</td>
<td>221</td>
</tr>
<tr>
<td>9, 88</td>
<td>S. Del. O / NJ I</td>
<td>200</td>
<td>51.88</td>
<td>&lt;0.0001*</td>
<td>203</td>
</tr>
<tr>
<td>13, 21</td>
<td>N. Del. O / NJ O</td>
<td>257</td>
<td>1.83</td>
<td>0.14 NS</td>
<td>260</td>
</tr>
<tr>
<td>13, 88</td>
<td>N. Del. O / NJ I</td>
<td>239</td>
<td>67.97</td>
<td>&lt;0.0001*</td>
<td>242</td>
</tr>
<tr>
<td>21, 88</td>
<td>NJ O / NJ I</td>
<td>219</td>
<td>46.48</td>
<td>&lt;0.0001*</td>
<td>222</td>
</tr>
</tbody>
</table>
Figure 27. Fitted von Bertalanffy growth curves for clapper shells and live surf clams collected from the F/V John N (Delmarva) and Christy (New Jersey) in March of 2006.
Figure 28. Fitted Von Bertalanffy growth curves for live surf clams and clapper shells collected on the commercial fishing vessels, the John N (Delmarva) and Christy (New Jersey), March 2006. n = 37 for each collection. See Table 9 for summary of von Bertalanffy growth parameters.
Table 9. Von Bertalanffy growth parameter estimates with the standard error of the mean (SEM) for live and clapper surf clam shells collected on the F/V John N (Delmarva) and Christy (New Jersey) in March 2006.

<table>
<thead>
<tr>
<th>Latitude</th>
<th>Longitude</th>
<th>Location</th>
<th>Vessel</th>
<th>Status</th>
<th>n</th>
<th>$L_{\infty}$ (SEM)</th>
<th>K (SEM)</th>
<th>$t_0$ (SEM)</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>38°20' N</td>
<td>74°24' W</td>
<td>Delmarva</td>
<td>John N</td>
<td>Clapper</td>
<td>37</td>
<td>165.00 (7.661)</td>
<td>0.175 (0.076)</td>
<td>0.82 (3.09)</td>
<td>0.58</td>
</tr>
<tr>
<td>38°20' N</td>
<td>74°24' W</td>
<td>Delmarva</td>
<td>John N</td>
<td>Live</td>
<td>37</td>
<td>159.63 (3.603)</td>
<td>0.298 (0.170)</td>
<td>2.87 (3.648)</td>
<td>0.42</td>
</tr>
<tr>
<td>39°40' N</td>
<td>73°26' W</td>
<td>New Jersey</td>
<td>Christy</td>
<td>Clapper</td>
<td>37</td>
<td>161.08 (7.682)</td>
<td>0.192 (0.076)</td>
<td>1.74 (2.374)</td>
<td>0.61</td>
</tr>
<tr>
<td>39°40' N</td>
<td>73°26' W</td>
<td>New Jersey</td>
<td>Christy</td>
<td>Live</td>
<td>37</td>
<td>188.50 (5.46)</td>
<td>0.083 (0.089)</td>
<td>-3.48 (6.94)</td>
<td>0.63</td>
</tr>
</tbody>
</table>
Table 10. Results of the Analysis of Residual Sum of Squares (ARSS, Chen 1992) used to compare the pairs of growth curves of live surf clam shells and clappers from the F/V John N and Christy collections of March 2006. Both comparisons yielded non-significant (NS) results ($p > 0.05$).

<table>
<thead>
<tr>
<th>Pair</th>
<th>df</th>
<th>$F$-statistic</th>
<th>$p$</th>
</tr>
</thead>
<tbody>
<tr>
<td>F/V John N (Delmarva)</td>
<td>71</td>
<td>1.48</td>
<td>0.23  NS</td>
</tr>
<tr>
<td>F/V Christy (New Jersey)</td>
<td>71</td>
<td>0.38</td>
<td>0.77  NS</td>
</tr>
</tbody>
</table>
Figure 29. Relationship between shell length (means with 95% confidence intervals) and age for live surf clams and clapper shells collected from Delmarva (A) and New Jersey (B) in March of 2006. See Table 11 for sample sizes.
Table 11. Sample sizes (n) for live and clapper surf clams used to examine the relationship between mean shell length and age (Figure 29) for several age-classes of surf clams collected on the F/V John N (Delmarva) and Christy (New Jersey) in March of 2006.

<table>
<thead>
<tr>
<th>Area</th>
<th>Age (years)</th>
<th>n</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delmarva</td>
<td>11</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>16</td>
<td>3</td>
<td>5</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>4</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>18</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>19</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>New Jersey</td>
<td>8</td>
<td>3</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>9</td>
<td>3</td>
</tr>
<tr>
<td></td>
<td>12</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>
Figure 30. Relationship between the surf clam shell height (mm) (measured from umbo to each growth line in the cross section of the valve) and the chondrophore height (mm) (measured from umbo to each growth line in the cross section of the chondrophore), plotted as linear regressions for surf clams from the MAB collected in 2005.
Stratum 9 (S. Delmarva offshore), n=25

\[ y = 0.1671x - 1.0882 \]
\[ R^2 = 0.9797 \]

\[ P < 0.0001 \]

Stratum 13 (N. Delmarva offshore), n=25

\[ y = 0.173x - 1.592 \]
\[ R^2 = 0.9699 \]

\[ P < 0.0001 \]

Stratum 21 (New Jersey offshore), n=25

\[ y = 0.1628x - 0.6436 \]
\[ R^2 = 0.9684 \]

\[ P < 0.0001 \]

Stratum 88 (New Jersey inshore), n=25

\[ y = 0.1751x - 1.817 \]
\[ R^2 = 0.9672 \]

\[ P < 0.0001 \]
Figure 31. Relationship between surf clam shell length (mm) and shell height (mm), with fitted linear regressions for surf clams from the MAB.
Table 12. Linear regression equations used to predict surf clam shell dimensions. CH = chondrophore height (mm), SH=shell height (mm), SL=shell length (mm).

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Equation to predict surf clam shell height (mm) from chondrophore height (mm)</th>
<th>n</th>
<th>R²</th>
<th>Equation to predict shell length (mm) from shell height (mm)</th>
<th>n</th>
<th>R²</th>
</tr>
</thead>
<tbody>
<tr>
<td>9</td>
<td>CH = 0.1671(SH) - 1.0882</td>
<td>25</td>
<td>0.98</td>
<td>SH = 0.7159(SL) + 0.1014</td>
<td>112</td>
<td>0.98</td>
</tr>
<tr>
<td>13</td>
<td>CH = 0.173(SH) - 1.592</td>
<td>25</td>
<td>0.97</td>
<td>SH = 0.6808(SL) + 2.572</td>
<td>182</td>
<td>0.98</td>
</tr>
<tr>
<td>21</td>
<td>CH = 0.1628(SH) - 0.6436</td>
<td>25</td>
<td>0.97</td>
<td>SH = 0.6976(SL) + 1.9563</td>
<td>151</td>
<td>0.98</td>
</tr>
<tr>
<td>88</td>
<td>CH = 0.1751(SH) - 1.817</td>
<td>25</td>
<td>0.97</td>
<td>SH = 0.7162(SL) - 1.4793</td>
<td>112</td>
<td>0.96</td>
</tr>
</tbody>
</table>
Trends in Water Temperature

Average annual bottom water temperatures in the period 1970-2005 followed a latitudinal trend with Delaware (9.89 ± standard error of the mean 0.17°C) lower than Chesapeake (12.57 ± 0.24°C). The differences between SST and BT recorded by the lightships (approximately 1956-71) show the seasonal development of the thermocline beginning in April and persisting until October with the most pronounced differences between surface and bottom water temperatures occurring in July and August (Figure 32) when these stations experience surface temperatures that are at least 8-12° C higher than bottom temperatures (Harding et al. in review). Air temperatures recorded 1984-2002 by two NOAA buoys are 1-2° warmer than SST from April through July (Figure 33). For the rest of the year, air temperatures are colder than SST with the maximum difference (4-5° C) observed in December (Harding et al. in review).

Examination of annual average residual bottom water temperatures from the average long-term (1970-2005) bottom water temperatures (Figure 34) shows that both sites experienced above average water temperatures in multiple consecutive years between 1970-1980 and again in the period 1995-2005 (Harding et al. in review). Estimated bottom water temperatures for 2002 were among the highest observed during the period 1970-2005 at Delaware and Chesapeake (Harding et al. in review).

Examination of monthly average residual bottom water temperatures from the average long-term (1970-2005) bottom water temperatures at both Delaware and Chesapeake (See Figure 5 for locations of sampling) shows several trends. Based on these data, a warming trend began in the Delmarva region, near stratum 13, in 1995. More specifically, at Delaware September bottom temperatures have been above average
in 10 out of the past 11 years, and a similar trend exists in October, with 7 out of the past 9 years being above average (Figure 35). At Chesapeake (Figure 36), near stratum 9, monthly temperatures have shown several warming trends. Temperatures in July have been above average since 2002, with the exception of 2003. The highest temperatures on record in August for the period of 1970-2005, were from 1999, 2002, and 2005. October of 2002 had the highest bottom temperature between 1970 and 2005 for July, August, September, or October, for all years examined. The September and October long-term (1970-2005) averages at Chesapeake Light were already in a stressful range for surf clam (20.34°C, and 19.31°C respectively, Table 13), thus any temperatures above the long-term average are a reason for concern and this trend has been observed more often since the late 1990’s. While September and October at both sites show a very low residual in 1978, this cool year did not alter the long-term average significantly from 1970-2005. Data described in Harding et al. (in review) from 1930-2002 show similar means, even with the inclusion of 40 additional years (1930-2002 Chesapeake Light annual mean 9.67°C, ± 0.14°, in comparison to 1970-2005 annual mean 9.89°C, ± 0.17°; 1930-2002 Delaware Light annual mean 12.27°C, ± 0.014°, in comparison to 1970-2005 annual mean 12.57°C ± 0.24°).

**Age-Specific Growth**

Several comparisons were made in order to obtain a better understanding of the growth patterns over the last 20-30 years in the MAB and to test the hypothesis that growth has changed in stratum 9 (S. Delmarva offshore) over this time period. Results for this area show that 12-year-old surf clams (the from 1993 year class) have a smaller length-at-age in 2005 than they did in the late-1980’s through mid-1990’s (Figure 37a),
Figure 32. Average monthly difference between sea surface temperature (SST) and bottom water temperature (BT) from lightship data (Table 3) for Delaware (A) and Chesapeake (B) lightships from Harding et al. (in review). Error bars indicate standard error of the mean. N values (number of daily SST-BT pairs used to estimate monthly SST-BT differences) at each site are presented above the X axis in each panel.
A. Delaware
Feb 1961 - Dec 1970

B. Chesapeake
Jan 1958 - Dec 1971
Figure 33. Average monthly difference between air temperature (AT) and sea surface temperature (SST) from NOAA buoy data (1985-2002, Table 3) for Delaware (44009) and Chesapeake (CHLV2) buoys from Harding et al. (in review). Error bars indicate standard error of the mean. N values (number of hourly AT-SST pairs used to estimate monthly AT-SST differences) at each site are presented above the X axis in each panel.
A. Delaware (Buoy 44009)
Jan 1984 - Dec 2002

Average monthly AT-SST difference (°C)

B. Chesapeake (Buoy CHLV2)
Jan 1985 - Dec 2002
Figure 34. Annual average residual bottom temperatures (BT) from the long term (1970-2005) average bottom temperatures for Delaware (A) (long-term average = 9.89 ± 0.17°C) and Chesapeake (B) (long-term average = 12.57 ± 0.24°C) from Picariello et al. (in preparation). The error bars represent the standard error of the mean in °C.
Figure 35. Monthly average residual bottom temperatures (BT) from the long term (1970-2005) BT mean at Delaware for July (A), August (B), September (C), and October (D) from Picariello et al. (in preparation).
Figure 36. Monthly average residual bottom temperatures (BT) from the long term (1970-2005) BT mean at Chesapeake for July (A), August (B), September (C), and October (D) from Picariello et al. (in preparation).
Table 13. Summary of long-term (1970-2005) monthly bottom temperature (BT) data for Delaware (28 m) and Chesapeake (11.6 m) buoys (Table 3) for July, August, September and October from Picariello et al. (in preparation). SEM indicates standard error of the mean.

<table>
<thead>
<tr>
<th>Station</th>
<th>Month</th>
<th>n months</th>
<th>Long-term monthly average BT (°C)</th>
<th>SEM BT (°C)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Delaware</td>
<td>July</td>
<td>36</td>
<td>9.45</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>36</td>
<td>10.49</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>36</td>
<td>14.43</td>
<td>0.29</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>36</td>
<td>16.66</td>
<td>0.21</td>
</tr>
<tr>
<td>Chesapeake</td>
<td>July</td>
<td>36</td>
<td>15.25</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>August</td>
<td>36</td>
<td>16.76</td>
<td>0.18</td>
</tr>
<tr>
<td></td>
<td>September</td>
<td>36</td>
<td>20.35</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td>October</td>
<td>35</td>
<td>19.31</td>
<td>0.23</td>
</tr>
</tbody>
</table>
which might be related to density-dependent competition that was prominent in the 1980’s and 1990’s (Weinberg and Helser 1996). Curves are statistically different for both time frames examined (ARSS, \( p<0.0001 \)). With less biomass in the S. Delmarva area since 1997 (Weinberg et al. 2005), the decline in density-dependent competition for food may have been the cause for the larger sizes in 2005. As water temperatures have been warming, consistent with bottom water temperature data from Chesapeake Light, this 12-year-old age class would have been young at the onset of warming, and would have experienced temperatures exceeding the optimal limit for surf clam growth and physiology. Results for the S. Delmarva region (stratum 9) indicate that 12-year-old surf clams in 2005 experienced above average bottom water temperatures more often in July, September, and October than clams at age 12 in 1989-1994. Similarly, 11-year-old surf clams in stratum 13 experienced above average bottom water temperatures more often in all four summer months than 11-year-old surf clams in 1982-1998.

In stratum 13, in the N. Delmarva range, the differences in length-at-age were significant between past and present 11 year olds (ARSS, \( p<0.0001 \)) (Figure 38a). Whereas von Bertalanffy growth parameters are high for \( L_{\infty} \) (228 mm), clams as large as 220 mm have been reported in the past (Ropes 1980), and stratum 13 did have the highest \( L_{\infty} \) in the analysis of age-at-length by region. Similarly, the low growth coefficient for clams at age 11 are comparable to the low growth coefficient estimated for the region, which was the lowest of all four strata.

In comparison to the Delmarva region at southern latitudes (strata 9 and 13), the length-at-age of 14-year-old clams (1991 year class) from offshore New Jersey (stratum 21), at higher latitude, has not changed in comparison to surf clams that settled in the
1980’s. (Figure 39a). Von Bertalanffy growth curves are not statistically significant (ARSS, $p=0.89$) for this age class within this stratum. This year class was used for comparison because more samples were available than for the 1993 year class, and these clams coincided with roughly the same years as the 1993 cohorts. Results from stratum 88, the inshore New Jersey location, indicate that no changes have occurred in the length-at-age of 7-year-old clams, when compared to clams that are ages of 20 and older (settled from 1976-1985), back-calculated to when they were 7 (ANOVA, $p=0.86$) (Figure 40, Table 14). All von Bertalanffy growth parameters estimated for age-specific growth are summarized in Table 15. For each region, the average shell lengths (mm) for the same age classes (Figures 37b, 38b, 39b) were used to calculate the yearly growth rate, as the change in shell length (mm) per year (Table 16). These rates confirm that overall, the 12-year-old clams from stratum 9 (S. Delmarva offshore) grew more each year during the 1993-2005 time period than they did during the 1977-1989 time period. In stratum 13 (N. Delmarva Offshore) surf clams overall grew less during the 1994-2005 time period than they did during the 1982-1993 time period and in stratum 21 (New Jersey Offshore) surf clams did not show a trend toward either more or less growth during 1991-2005 in comparison to 1975-1988.

**Comparison of Age Estimation Methods**

Age estimations for surf clams using the hinge region for each stratum are presented in Figure 41 as von Bertalanffy growth curves. Chondrophore ages for the same surf clams are plotted along with the hinge ages for comparison of results.
A Mann-Whitney signed rank test resolved no significant differences between the ages estimated using the two techniques ($p>0.05$) for each of the four strata. These results were further analyzed by examining the residuals between the two methods (chondrophore age-hinge age) and searching for potential size bias. A Run’s test, which tests for auto correlation in the data, (Zar 1999) indicated that size bias did not exist in strata 13, 21, and 88; that is, residuals were randomly distributed across the size range (Figure 42). The exception was strata 9 (S. Delmarva offshore), from which the Run’s Test was significant. Additional analysis for this stratum confirmed that the unexpected number of runs were themselves randomly distributed (ANOVA, $p=0.804$).
Figure 37. (a) Von Bertalanffy growth curves for 12-year-old surf clams from stratum 9 (S. Delmarva, offshore) at different time periods: 1978-1989 and 1993-2005. Curves are statistically different (ARSS, $p<0.0001$) and (b) Average shell lengths of surf clams (mm) with 95% confidence intervals used to calculate the change in shell length (mm) per year (Table 16).
Stratum 9 (offshore S. Delmarva), AGE 12

a.

Predicted Shell Length (mm)

Age (years)

- 1993-2005 (n=15)
- 1978-1989 (n=8)

b.

Average Shell Length (mm)

Age (years)

- 1993-2005 (n=15)
- 1978-1989 (n=8)
Figure 38. (a) Von Bertalanffy growth curves for current (1994-2005) and past (1982-1993) 11-year-old clams from stratum 13 (N. Delmarva, offshore) and (b) average shell lengths of surf clams (mm) with 95% confidence intervals used to calculate the change in shell length (mm) per year (Table 16).
Stratum 13 (offshore N. Delmarva), AGE 11

![Graph of Predicted Shell Length vs. Age](image_a)

- 1982-1993 (n=7)
- 1994-2005 (n=6)

![Graph of Average Shell Length vs. Age](image_b)

- 1982-1993 (n=7)
- 1994-2005 (n=6)
Figure 39. (a) Von Bertalanffy growth curves for 14-year-old clams from stratum 21 (New Jersey, offshore) at different time periods. Curves are not statistically different (ARSS, $p<0.89$). See Table 15 for parameter estimates. (b) Average shell lengths of surf clams (mm) with 95% confidence intervals used to calculate the change in shell length (mm) per year (Table 16).
Stratum 21 (offshore New Jersey), AGE 14

(a)

Predicted Shell Length (mm)

Age (years)

1975-1988 (n=19)
1991-2005 (n=6)

(b)

Average Shell Length (mm)

Age (years)

1975-1988 (n=19)
1991-2005 (n=6)
Figure 40. Linear regression describing growth of current (1998-2005, $y=18.103X + 6.7068$, $R^2=0.93$) and past (1975-1982, $y=19.39X + 2.4433$, $R^2 = 0.90$) clams at age 7, collected from stratum 88 (New Jersey, inshore).
Stratum 88 (inshore New Jersey), AGE 7

\[ y = 19.39x + 2.4433 \]
\[ R^2 = 0.9029 \]

\[ y = 18.103x + 6.7068 \]
\[ R^2 = 0.9253 \]
Table 14. Stratum 88 parameters for the linear regression (equation \( y=ax+b \)) of growth of 7-year-old surf clams with sample sizes (n).

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Age (growth years)</th>
<th>n</th>
<th>a</th>
<th>b</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>88</td>
<td>7 (1998-2005)</td>
<td>15</td>
<td>19.39</td>
<td>2.44</td>
<td>0.90</td>
</tr>
<tr>
<td>88</td>
<td>7 (1975-1982)</td>
<td>24</td>
<td>18.10</td>
<td>6.71</td>
<td>0.93</td>
</tr>
</tbody>
</table>
Table 15. Von Bertalanffy growth parameter estimates with the standard error of the mean (SEM) and results of the analysis of residual sum of squares (ARSS, Chen 1992) for age-specific growth analysis for current and past clams from strata 9, 13, and 21. NS = not significant. Del=Delmarva. Sample sizes included (n).

<table>
<thead>
<tr>
<th>Location</th>
<th>Age (yr)</th>
<th>Growth Period</th>
<th>n</th>
<th>von Bertalanffy Parameter Estimates</th>
<th>ARSS Results</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>$L_\infty$ (SEM)</td>
<td>$k$ (SEM)</td>
</tr>
<tr>
<td>S. Del offshore</td>
<td>12</td>
<td>1993-2005</td>
<td>15</td>
<td>170.49 (4.648)</td>
<td>0.197 (0.014)</td>
</tr>
<tr>
<td>S. Del offshore</td>
<td>20+, when 12</td>
<td>1979-1989</td>
<td>8</td>
<td>127.89 (5.675)</td>
<td>0.252 (0.037)</td>
</tr>
<tr>
<td>N. Del offshore</td>
<td>11</td>
<td>1994-2005</td>
<td>7</td>
<td>211.75 (19.934)</td>
<td>0.119 (0.021)</td>
</tr>
<tr>
<td>N. Del offshore</td>
<td>18+, when 11</td>
<td>1882-1993</td>
<td>6</td>
<td>227.02 (18.787)</td>
<td>0.127 (0.197)</td>
</tr>
<tr>
<td>New Jersey offshore</td>
<td>14</td>
<td>1991-2005</td>
<td>19</td>
<td>177.16 (8.421)</td>
<td>0.172 (0.021)</td>
</tr>
<tr>
<td>New Jersey offshore</td>
<td>20+, when 14</td>
<td>1975-1988</td>
<td>6</td>
<td>186.77 (7.355)</td>
<td>0.153 (0.014)</td>
</tr>
</tbody>
</table>
Table 16. The average shell lengths (mm) for surf clams from Delmarva and New Jersey during different time periods and yearly growth rates calculated as the change in shell length (mm) per year.

<table>
<thead>
<tr>
<th>Stratum</th>
<th>Region</th>
<th>Age</th>
<th>Year</th>
<th>Growth (mm/yr)</th>
<th>Year</th>
<th>Growth (mm/yr)</th>
</tr>
</thead>
<tbody>
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Figure 41. Von Bertalanffy growth curves for surf clams from strata 9, 13, 21, and 88, presenting both hinge ages and chondrophore ages.
Figure 42. Residuals in years, calculated as hinge age subtracted from chondrophore age, plotted against surf clam shell length (mm) for (A) stratum 9 (S. Delmarva Offshore), (B) stratum 13 (N. Delmarva offshore), (C) stratum 21 (New Jersey Offshore), and (D) stratum 88 (New Jersey inshore). The plots represent the results of a Run’s test, which searched for potential size bias in the way the residuals were distributed across the size range.
(A) Stratum 9, n=53
(B) Stratum 13, n=103
(C) Stratum 21, n = 78
(D) Stratum 88, n=73
Discussion
This study investigated the age and length-at-age of surf clams at different geographic locations throughout their MAB distribution by testing the hypotheses that 1) length-at-age is larger at more northern latitudes and 2) length-at-age has changed over time in surf clams from the southern edge of the range. It is demonstrated in this study that both hypotheses were supported, suggesting that regional differences exist in the growth patterns of surf clams, and that growth and survival of surf clams has been and will continue to be influenced by increasing water temperatures associated with climate change.

Emphasis was placed on age-specific changes in length-at-age, which was used to examine growth at different time periods over the past 20-30 years. The results indicate that the Atlantic surf clam exhibits differences in age structure and growth patterns throughout the areas of the distribution that were sampled. Age-frequency distributions for the 2005 surf clam samples allow dominant year classes to be tracked since the previous stock assessment that was based on the 2002 NEFSC survey (NEFSC 2003).

The age-frequency distributions from this study are consistent with 2002 data. Dominant cohorts in New Jersey in 2002 included surf clams at ages 3, 4, 5, 10 and 11, which are consistent with the 2005 surf clams at age 6, 7, 8, 13 and 14. Similar trends are apparent in the Delmarva region. Dominant year classes at ages 2, 3, 4, and 10 in 2002 correspond to dominant 5, 6, 7, and 13 year-old surf clams in 2005. The use of age-frequency distributions such as these allows cohorts to be tracked over time, and this is a useful way to monitor the population.
Surf clam growth has previously been found to differ depending on geographic location. Weinberg and Helser (1996) and Weinberg (1998) found that growth rates at lower latitudes were slower than those at higher latitudes using the von Bertalanffy growth coefficient. In this study, the hypothesis that growth rates would be highest at higher latitudes was tested using the 2005 collection of surf clams. While differences did exist among the geographic regions, the highest growth coefficients from the 2005 collection were found in the most southern location (Delmarva, stratum 9). However, southern clams reached the smallest maximum size than the other three more northern locations and this is analogous to the findings of Weinberg (1998), suggesting there is an environmental control over the maximum size of the clams in this region.

Whereas Weinberg and Helser (1996) found growth coefficients in the Delmarva region to be on the order of 0.177 (Von Bertalanffy growth coefficient, k) for 1989 and 1992 samples, this study found growth coefficients of 0.339 (growth coefficient, k) (stratum 9) and 0.096 (k) (stratum 13) for the 2005 samples from this area. The growth curve for stratum 13 (N. Delmarva) suggested that more samples in the larger size classes might have been necessary, as the curve for this region did not seem to have reached its asymptote yet. This could have influenced the growth parameters and explain the very low k-coefficient as the lack of older animals in the analysis for stratum 13 may have skewed the estimated growth coefficient for this stratum, although this is probably not an issue as the growth coefficient is determined more by the initial slope of the line, representing the growth efficiency of the smaller individuals. Regardless of the value of the k-coefficient, the growth curve was statistically similar to stratum 21 (offshore New
Jersey), which also demonstrated lower growth coefficients in comparison to stratum 9 (offshore D. Delmarva) and 88 (inshore New Jersey).

There are several reasons why the growth parameters might have been different in this study in comparison to the growth parameters estimated by Weinberg and Helser (1996). Weinberg and Helser (1996) pooled all samples from strata 9 and 13 to examine the geographic region as a whole. In this study the two Delmarva strata were analyzed separately in order to address surf clam length-at-age at each location in relation to bottom water temperature. Since length-at-age seems to vary between strata, the predicted parameters from each stratum (9 and 13, Delmarva) would not have been comparable to parameters estimated by combining data from both strata. In addition, growth parameters predicted in Weinberg and Helser (1996) reflected growth of surf clams prior to 1992, whereas in this study the growth period extends until 2005, when the samples were collected. Surf clam length-at-age appears to undergo changes over time as observed in this study, as well as in Weinberg and Helser (1996). It is likely that this could explain the observed differences in the growth parameters between the two studies.

In regards to inshore versus offshore differences in growth, the findings of this study show that clams closest to shore (stratum 88) had higher growth rates than those offshore. This observation is comparable to some of the observations made by Chintala and Grassle (2001). These results are further interpreted by examining condition index in relation to length-at-age. Condition index was highest in stratum 88 followed by 21, 9, and 13, indicating that clams at higher latitudes are healthier than those at the southern limit of the distribution. The more northern areas (strata 21, 88) had the highest condition index, but condition index values for stratum 88 were higher than 21, which is unusual
given that 88 is a shallower location, usually indicative of a more stressful environment (Ambrose et al. 1981, Cerrato and Keith 1992, Jones et al. 1978). A possible explanation for this is that since condition index is often an indicator of nutritional status, a high condition in a shallower location might be the result of a greater availability of food closer to shore as a result of periodic cycles of upwelling and downwelling bringing nutrients to the sea floor. Both the condition index and von Bertalanffy growth coefficients were high in stratum 88 and clams attained the largest maximum size. These maximum sizes were comparable to those from offshore New Jersey clams also sampled in 2005. Chintala and Grassle (2001) found similar results in a study off of New Jersey as the largest clams were found within 1 mile of shore as opposed to the smaller clams 2 to 3 miles offshore.

Stratum 13, off the northern Delmarva Peninsula, is an area of concern due to the low growth rates, low condition index, and above average bottom water temperatures which have been occurring in the region more frequently since the 1990’s. Clams from this area had both a low average shell length and the lowest condition index. In the Delmarva region, the condition index was lower than that in New Jersey surf clams. Kim and Powell (2004) suggest that clams in the Delmarva region are malnourished as a result of temperatures that are too high to allow surf clams to efficiently feed on the available food. Trends in bottom water temperature show that in 10 out of the past 11 years, late summer and early fall temperatures have been above average in the Delmarva region. This is a likely indicator that clams are stressed and their poor condition might be a result of this.
Clams from the most inshore strata off of New Jersey (88) had similar growth patterns to those from the most southern location (9) in the Delmarva area. Both areas exhibited rapid growth until approximately age 10, when growth tapered off as the curves approached their asymptote. While the clams from stratum 9 grew rapidly at first and reached their maximum size faster than clams further offshore and north, these clams attained the smallest sizes and the third lowest condition index out of the four areas, which implies that they might not be the healthiest. While intraspecific competition was speculated to be prominent in stratum 9 during the time the area was closed to harvesting from 1980-1991 (Weinberg and Helser 1996, Weinberg 1998), the recent reduction in biomass since 1999 in this region (NEFSC 2003, Weinberg et al. 2005) might explain the rapid growth, as density dependent competition may no longer be a factor. Clams may be growing faster as there is less competition for food and space. However, these clams still remain smaller than clams from more northern latitudes. This may be a lingering effect of intraspecific competition that occurred in this area during the 11 years that the area was closed to harvesting because when these clams were younger, density-dependent competition was a factor influencing their growth (Weinberg 1998). However, evidence presented here suggests it is more likely that these clams are experiencing environmentally controlled growth patterns. With the proper environment these clams would be able to achieve sizes comparable to the New Jersey clams. While clams off of the New Jersey coast (strata 21 and 88) also may have experienced intraspecific competition during their rebound from the 1976 hypoxic event (Weinberg and Helser 1996), clams from this area are still considerably larger than clams from stratum 9. This
further suggests that there is an environmental control over the growth of clams from the southern range limit.

**Age-Specific Growth: Has Length-at-Age Changed?**

It was hypothesized that growth (length-at-age) has changed over time in the most southern area of the surf clam distribution, the Delmarva Peninsula, as a result of warming water temperatures in recent years. Based on the data presented in this study, changes have occurred in the growth patterns of clams from strata 9 and 13 in the Delmarva region, but the changes are not consistent between the two strata. From stratum 9 (S. Delmarva) the von Bertalanffy growth coefficient (k) is lower in 12 year-old clams captured in 2005 in relation to clams that were age 12 in 1989-1994. The decline in biomass since 1999 (Weinberg et al. 2005) could potentially explain why current clams are growing to larger sizes as there could have been a loss of unhealthy clams from the area, leaving more resources for the healthy clams to grow and thrive. In stratum 13, the area showing the lowest condition and growth rates, growth patterns also seem to have changed to some extent over the years. Current 11 year-olds are smaller than older clams in the first 11 years of their lives, back in 1982-1993. Current clams overall seem to be reaching smaller maximum sizes.

To investigate whether the changes in growth observed in these strata was only occurring in the Delmarva Peninsula, or whether this trend was more widespread, clams from strata 21 and 88 (offshore and inshore New Jersey), were also analyzed. The growth curves from current and past surf clams at age 7 were almost identical, as were
the growth curves of current and past 14 year olds. Statistically the current and past clams did not show any significant differences in growth, suggesting that changes in growth might be more localized to the Delmarva area; an area where fishing pressure once exhausted the surf clam stocks, and clams have struggled to recover as a result of environmental factors.

**Surf Clam Growth and Water Temperature**

Temperature has long been studied as an important influence on growth in surf clams. Among other studies, Jones et al. (1978) and Jones (1981) found temperature to be negatively correlated with growth in surf clams off the New Jersey coast, and Sephton and Bryan (1990) found similar results in their study of surf clam growth in the waters of Prince Edward Island, Canada. In a study of first-year growth, Weissberger and Grassle (1995) also concluded that inshore surf clam growth was temperature dependent in the waters off New Jersey.

An important part of this study was the investigation into the growth of different year classes in relation to trends in bottom water temperatures along the MAB during the time that these clams have been alive. This would date back to the late 1970’s for some of the oldest clams. An analysis of global ocean temperatures by Levitus et al. (2000) revealed that since the 1950’s the Atlantic Ocean has undergone a warming period. To take a closer look at what is happening locally in the MAB, water temperature data collected from NOAA buoys and described in Harding et al. (in review) and Picariello et al. (in preparation) was examined. Examination of the 1970 to 2005 record shows
multiple consecutive years of warm temperatures from 1970-1980, and again from 1995-2002. A closer look at monthly averages reveals that several months deviate positively from the long-term (1970-2005) mean monthly bottom water temperature more often since 1995 than prior to 1995. September and October, which often reflect the warmest ocean temperatures in the Delmarva region, are particularly noteworthy. Temperatures frequently warmer than the long-term average could affect the energetics of surf clams inhabiting these areas that are still undergoing summer growth and reproduction at this time. The waters off Delaware in particular show higher than average bottom temperatures with September being warmer than average for 10 of the past 11 years and October being warmer in 7 of the past 9 years. This observation is important because this time period coincides roughly with the findings of this study that growth is slower in 11-year-old clams from stratum 13 (N. Delmarva). Whereas above average temperatures do not always exceed 20°C (optimal for surf clam growth and development), if temperatures are above average more often than not, growth patterns would be affected as temperature and growth are negatively correlated. As temperatures increase above optimal, even small temperature increments can affect surf clam growth (Kim and Powell 2004). This would be more pronounced in larger individuals that have higher energy requirements than smaller clams (Bayne 1985). According to Cerrato and Keith (1992), surf clam energy intake and cost is a function of body size. Younger, smaller clams do not experience the same physiological demands from the environment as the larger clams do. This may be a reason why more small (and young) clams were caught in the S. Delmarva area, where temperatures are the highest. The physiology of these small clams ensures
that they have a higher energy efficiency and are more resistant to unfavorable conditions, which might affect larger clams.

Average long-term September bottom water temperatures from 1970-2005 from the Chesapeake, Virginia approach 21° C, high enough to initiate stress in surf clams. Any temperatures above this long-term average will continue to stress these animals. It is likely that surf clams from the southern edge of their distribution are experiencing this magnitude of temperatures during the late summer and early fall months, when growth otherwise would be expected to occur. This time frame would correspond to just before a growth line was deposited in their shells (Jones 1980). According to Jones (1980) shell growth is uniformly slow during the hottest and coldest months. As the mean monthly temperature in this region has been warmer than average since 1995, with the exception of 2003 which was slightly below average, high temperatures may be stunting summer growth, thus changes in growth of 11-year-olds from stratum 13 in the Delmarva region are likely a result of the above average bottom water temperatures in 10 of the past 11 years (for September). Overall, clams caught in 2005 have experienced a greater number of above average summer temperatures than clams that were growing in the late 1970’s and 1980’s. Changes in growth differ along a latitudinal gradient. Clams from the southern range limit have experienced changes in growth, which are evident in the different growth curves for clams from the 1970’s-1980’s in comparison to the 1990’s-2005. This change coincides with the onset of a warming trend that began in the mid 1990’s. In comparison, 2005 clams at higher latitudes (New Jersey) have the same growth curves as clams from the 1970’s and 1980’s.
Effects of Climate Change on Marine Species

As the effects of climate change continue to be a concern for those studying marine species and ecosystems, many speculations have arisen and much uncertainty abounds with regard to past, present, and future changes in climate. Undoubtedly, although some disagreement exists among climate model forecasts, the consensus is that temperature-related changes are occurring, and will continue to occur. The question is how will marine species adapt to these changes in temperature? Distributional shifts have been documented in fishes and squids in the form of poleward range extensions (Murawski 1993), likely as a result of warming of the continental shelf associated with climate change. Others, including Perry et al. (2005) and Rose (2005), have also documented northward range expansions in fishes as a response to warming waters. A similar shift in surf clams would not seem unusual, as suggested by Weinberg et al. (2002a) and Weinberg (2005).

Evidence presented here suggests that changes have already occurred in the growth of surf clams at the southern range limit, and that condition index is lower in these clams than clams from higher latitudes. The decrease in biomass (documented in Weinberg et al. 2005) in the absence of fishing or disease suggests an environmental affect on this species. The changes in length-at-age that have occurred in the Delmarva region, in an area currently experiencing more recent episodes of above average temperatures, are an indicator that temperature is influencing the growth of surf clams in this region and possibly shaping the present-day distribution, as suggested by Weinberg (2002a, 2005). The results of the age-specific growth analysis presented here are
indicative of changes in surf clam growth over the past 30 years at the southern limit of
the distribution. Continued warming in this area of the MAB has implications towards
future trends in stock supply for the fishery and also for ecosystem sustainability.

The surf clam co-occurs with many other marine species throughout its
distribution (Franz and Merrill 1980) and is dominant within its range, offering a benthic
substrate to other co-inhabitants, and also playing a pivotal role in community energy
flow and structure. If the distribution of clams is moving northward and into deeper
water, sampling in the future from an ecosystem perspective might prove valuable. The
population ecology and distributions of other organisms that coincide with surf clams in
their sandy habitats might reflect similar trends. From an ecosystem perspective, it might
imply that the distribution of these animals may also be shifting as a result of reduced
surf clam biomass that would otherwise provide substrate as well as food for other
inhabitants. Future studies should address the consequences of removing the surf clam
from its habitat, and the effects on other species that share a common territory. Similarly,
since the southern surf clam Spisula solidissima similis is known to tolerate warmer
temperatures (Walker and Heffernan 1994), it might be worthwhile to determine the
precise distribution of the southern surf clam in areas where overlap with S. solidissima
occurs, and regularly sample these areas to ascertain whether the southern surf clam
could potentially be shifting its own distribution into the MAB to take over a once
abundant Atlantic surf clam territory.

For this study, two different techniques were used to estimate surf clam ages.
Whereas the chondrophore-based method ensures that large numbers of clams can be
processed quite efficiently and an age can be estimated with little difficulty, the image-
based technique allows the entire life history of the clam to be deciphered. This technique is more time consuming, yet supplies a large amount of data for each clam. When utilizing the image-based technique it is essential to realize that surf clams exhibit a unique pattern of bi-phasic growth. This can only be properly observed when a precise cross-section of the shell has been taken, all scratches are removed by polishing, and when the digital image of the hinge region is captured with the proper lighting. If images are captured out of focus, the growth lines may not be distinguishable. If glare exists in the photograph the results may be skewed as the correct intensity is not captured and the technique relies on the intensity of the growth lines in the hinge. If these methods are properly implemented, the technique is an accurate method for estimating surf clam age. This is evident as a comparison of the two age-estimation techniques indicates that there is no statistical difference between the two methods.

The image-based method is an exceptional tool to explore the life histories of these animals. While the method was used in this study as an age-estimation tool, it also offers a promising future for meticulously examining the internal sub-annual growth lines in surf clams that are typically ignored by those who are seeking only annual lines to estimate age. Sub-annual signatures may provide extensive information about surf clams in relation to their environment, and this could be a feasible way to correlate exact environmental conditions with physiological responses, viewed within the microstructure of the shell. The techniques developed by Harding et al. (in review) will make this examination possible.

The results of this study indicate that the population ecology of surf clams is complex and highly dictated by environmental patterns. Between different geographic
regions, growth patterns can be remarkably different and this implies that viewing each
region as its own unique stock for management purposes might best preserve the future of
the surf clam along its distribution.
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Vita

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Born on August 17, 1981 in Newton, Massachusetts. Graduated in 1999 from Dover-Sherborn Regional High School. Graduated from Skidmore College (Saratoga Springs, NY) in 2003 with a B.A in Biology. Spent several summers as an intern with Wheaton College, working on a diamondback terrapin project based in Cape Cod, MA before entering the Masters program in the School of Marine Science, The College of William and Mary in August 2004.