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DECADAL TRENDS IN AGE STRUCTURE AND RECRUITMENT PATTERNS OF OCEAN QUAHOGS *ARCTICA ISLANDICA* FROM THE MID-ATLANTIC BIGHT IN RELATION TO WATER TEMPERATURE

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ABSTRACT Ocean quahogs (*Arctica islandica*) are long-lived bivalves. Distribution patterns and biology of ocean quahogs in the Mid-Atlantic Bight (MAB) off the east coast of North America are directly related to bottom water temperatures. We examined long term recruitment patterns for ocean quahogs across temporal (decadal) and spatial (latitudinal, bathymetric) scales using a spatially defined (Long Island Sound to Chesapeake Bay mouth) population encompassing a broad size (age) range of animals that had not yet recruited to the commercial fishery [<80 mm shell length (SL)]. An age-at-length relationship for quahogs less than 80 mm SL is described using a power function. Quahog age did not vary significantly with depth or region, nor were any interaction terms between age and length with depth or region significant. An age-length key was developed for ocean quahogs to generate age frequencies for each station. Principal components analysis (PCA) on the resulting age-frequency distributions standardized per tow enabled construction of characteristic age-frequency distributions for similar stations identified by the PCA factor scores. These characteristic age-frequency distributions identified quahog cohorts with modal ages corresponding to recruitment during the 1948–1950, 1954–1959, 1972–1980, and 1978–1983 time periods. Observed recruitment patterns in MAB ocean quahogs are strongly related to bottom water temperature patterns. Years in which the number of months with water temperatures averaging 6°C to 10°C exceeds the number of months with water temperatures less than 6°C by at least two months are also years that contribute strongly to the modal year classes in the population age-frequency distributions. In general, years with above average bottom water temperatures during January, February, and March tend to produce year classes that are distinct in the age-frequency distributions from the MAB quahog populations. The observed time series of quahog recruitment operates at a different time scale than stock surveys and most estimates of fishery dynamics. The 50–60-y lag between quahog recruitment to the benthos and recruitment to the fishery presents challenges for fishery forecasting in that changes in adult biomass and subsequent effects on stock-recruit relationships will only become evident on this time scale.

KEY WORDS: ocean quahog, *Arctica islandica*, Mid-Atlantic Bight, water temperature, climate change, zoogeography, age estimation

INTRODUCTION

Ocean quahogs or mahogany clams (*Arctica islandica*, Linnaeus 1767) are an ecologically and commercially important species off the east coast of North America, notably in the Virginian subprovince of the Mid-Atlantic Bight (MAB, Franz & Merrill 1980a). This sessile amphiatlantic boreal species is long lived (150–375 y; Thompson et al. 1980a, Murawski et al. 1982, Ropes & Murawski 1983, Ropes et al. 1984, Fritz 1991, Schone et al. 2005) and provides a permanent record of its life history in its shell valves. Environmental fluctuations and seasonal changes in biology and physiology are recorded in the valves as external rings, internal lines and growth increments, or both (e.g., Pannella & MacClintock 1968, Lutz & Rhoads 1980, Ropes 1985, Weidman et al. 1994, Richardson 2001). Using the terminology of Richardson (2001), a growth line is an internal line deposited once a year (annually), whereas the annual growth increment is the distance separating adjacent growth lines. Ocean quahogs deposit a single growth line each year (Thompson et al. 1980b, Jones 1980, Ropes et al. 1984, Schone et al. 2005, Epple et al. 2006) typically in the late summer or fall (Thompson et al. 1980b). Growth rates of these clams in the MAB have been described (e.g., Jones 1980, Murawski et al. 1982, Fritz 1991, Kennish et al. 1994) with latitudinal variation observed (Ropes 1984).

The distribution and biology of adult ocean quahogs in the MAB have been well documented (Merrill & Ropes 1969, Ropes 1979, Franz & Merrill 1980a) since the 1970s, given the continuing interest in and economic importance of the commercial fishery for this animal (Cargnelli et al. 1999) and its ecological role as a dominant benthic species. Ocean quahog recruitment patterns in the MAB are poorly understood (Murawski & Serchuck 1979, Mann 1985, Powell & Mann 2005). The latitudinal and bathymetric range occupied by ocean quahogs in the MAB (Ropes 1979, Franz & Merrill 1980, Dahlgren et al. 2000), combined with the longevity and life history of these animals, make them an ideal target species for examination of long term ecological patterns within habitats.

Distributional patterns and biology of ocean quahogs in the MAB are directly related to bottom water temperatures (Franz & Merrill 1980a, Franz & Merrill 1980b, Dahlgren et al. 2000). The presence of an intense seasonal thermocline facilitates the creation of a colder lens of water (on the order of meters to 10s of meters thick depending on location) on the bottom from approximately May–October (Bigelow 1933, Parr 1933, Ketchum & Corwin 1964). Although the upper thermal maximum for adult ocean quahogs is approximately 20°C (Lewis et al. 2001), a strong relationship exists between the 16°C bottom isotherm and the inshore distribution limit of ocean quahogs (Mann 1982) inferring that a practical thermal maximum is on the order of 16°C for adult quahogs in the MAB. Spawning typically occurs between 10°C to 16°C (Loosanoff

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1953, Jones 1981, Mann 1982) although gametogenesis begins in early February at water temperatures $<6^{\circ}\text{C}$ for males and females (Mann 1982). Shell growth in ocean quahogs does not occur at water temperatures below 6°C (Weidman et al. 1994) although filtration continues down to water temperatures of 4°C (Winter 1969). Gonad development proceeds from February through May at water temperatures of 6°C to 10°C (Jones 1981, Mann 1982) with ripe males and females observed from May through October (Jones 1981, Mann 1982). Egg development, larval growth, and time to metamorphosis for ocean quahogs are fastest at temperatures in the range 10°C to 16°C (Landers 1976, Lutz et al. 1982, Mann 1986). Ocean quahog veligers typically are found below the 16°C isotherm (Mann & Wolf 1983, Mann 1985) although older veligers may survive modest periods of exposure to temperatures 20°C to 23°C (Mann & Wolf 1983).

Ocean quahog recruitment events occur once or twice every 20–40 y (Powell & Mann 2005). In ecological time, given the quahog's 200+ year life span, recruitment at the observed time scale is actually frequent. Fishery and management processes operate at shorter time scales. The ability to hindcast recruitment processes on the basis of observed bottom water temperature patterns would facilitate temporal and spatial fidelity for management processes for this long-lived species.

Ocean quahogs present an opportunity to examine the impact of changing environmental conditions, notably temperature, on the population biology of a dominant member of the MAB benthic community because of its longevity, sessile habit, and ability to store a complete record of its life history in its shell. There are several prerequisites to achieving this goal. The first is a representative sampling of the population both latitudinally and bathymetrically, and over a time frame of decades. We provide this through a stock assessment survey focused on submarket size animals (<80 mm SL) with expected age ranging as high as 70 y. Secondly, an unambiguous method of age determination is required to allow hindcasting of recruitment patterns by year. We address this challenge by using a novel image analysis based method of discriminating annual signatures in the shell. To date the method of choice for counting internal signatures has been a sequence of sectioning and polishing followed by preparation of an acetate peel "negative" of the section (e.g., Jones 1980, Thompson et al. 1980a, Thompson et al. 1980b, Ropes et al. 1984, Ropes 1985). The peel is then examined by eye with subjective counting of annual signatures. Whereas well used, this approach inevitably incurs error associated with both peel preparation and discrimination of annual *versus* other signatures in the final peel. We use a computer-based system that acquires images of the polished section, thereby eliminating peels, and quantifies the signatures as a density profile from the outer to inner shell surface. The quantitative data allow consistent discrimination of signatures to categories that can be defensibly assigned as annual or any other time base eliminating subjective operator, and, more importantly, between operator inconsistencies in age estimation. The third requirement is high frequency but long-term temperature records of the local environment. We have developed these for *Arctica* collection sites in the MAB from both direct records using U.S. Coast Guard lightship data and other sources, and where these are absent, from surface records in concert with surface to bottom relationships developed where both data are available simultaneously. In the present manu-

script we describe each of the earlier mentioned, namely the sampled population, age determination in the collected material and generated long term bottom water temperature data, and from these explore emergent patterns of temporal and spatial recruitment of *Arctica islandica* in the MAB for the period 1930–2002.

MATERIALS AND METHODS

Collection Sites

A sample of clams (328 ocean quahogs, shell length range of 12–84 mm) collected in September 2002 (Powell & Mann 2005) was grouped into five regions corresponding to sampling locations (A) nearshore shallow Long Island habitats, (B) on the edge of the continental shelf south of Long Island in deeper water, (C) on the northern edge of the Hudson canyon, (D) north of Cape May, New Jersey and south of the Hudson canyon, and (E) north of the Virginia capes (Norfolk Canyon) and south of Cape May, New Jersey (Fig. 1). Within each region, individuals were sorted by shell length (maximum dimension perpendicular to the hinge, mm) to determine the available size range. Individual clams were randomly selected from all stations within a region to correspond to 1–2 mm size intervals within the available size range for a particular region. A minimum of 60 quahogs from each region were selected for age analyses to describe the population age structure of that region.

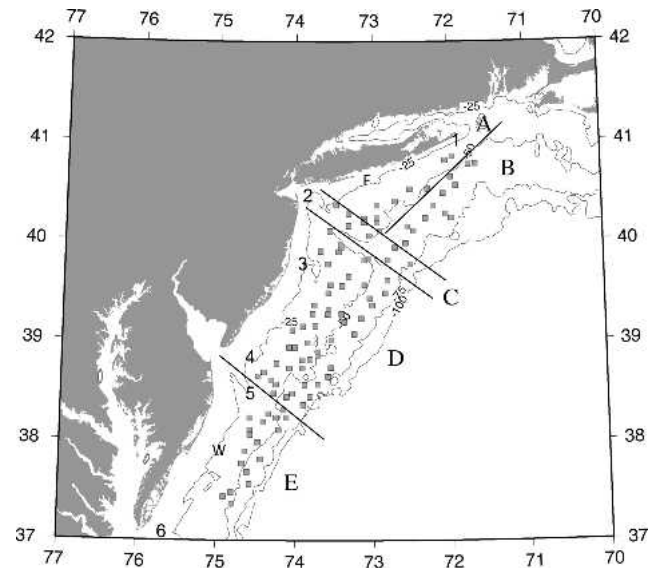


Figure 1. Map of Mid-Atlantic Bight showing the locations of stations (squares) from which ocean quahogs were sampled for these analyses from Powell and Mann (2005) and the locations designated by number of the 6 stations for which long term bottom water temperatures were available (1) Montauk Point, (2) Ambrose Channel, (3) Barnegat, (4) Five Fathom Bank, (5) Delaware, and (6) Chesapeake. Data from Fire Island (F) and Winter Quarter (W) lightships were used to supplement the data record for Ambrose Channel and Delaware lightships, respectively. Stations were initially grouped by regions: (A) nearshore shallow Long Island, (B) on the edge of the continental shelf south of Long Island in deeper water, (C) on the northern edge of the Hudson canyon, (D) north of Cape May, NJ and south of the Hudson canyon, and (E) north of the Virginia capes (Norfolk canyon) and south of Cape May, NJ. Contour depths are in m.

Sample Preparation for Age Estimation

Individuals were shucked, dipped in bleach, and then the intact valves were individually labeled. The right valve of each animal was sectioned through the cardinal tooth (Ropes 1985) along the axis of maximum growth and polished to 1 micron (Buehler Carbimet disks and Metadai suspension). If the right valve was not intact, the left valve was substituted. The periostracum of each shell valve was intact establishing an external boundary for the specimen's growth lines. A cross section of the hinge region for each polished clam valve 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 (v. 3.2.6) and analyzed using Image Pro Plus (ver 4.5).

Age Estimation

An intensity profile, a single line 1 pixel wide drawn across the width of the shell section, was described for each hinge cross section using the Line Profile tool in Image Pro Plus. 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. A peak representing an internal growth line within the shell cross section was defined as a location on the intensity profile that intersected a predetermined intensity level.

Evaluation of the 95–105 Sequences of Intensities as the Proper Intensity Range for Counting Yearly Bands

The data set is composed of the quahog shell length and a series of intensity-based line counts. These counts result from enumeration of the peaks (described earlier) in the intensity profiles at grayness intensities of 25–140 for 24 ocean quahogs from 22.7–78.3 mm shell length.

Because intensity varies across the grayness spectrum, line counts decrement from a large number, when even the lightest growth lines are counted, to a small number when just the darkest growth lines are counted. Significant line types, such as annual growth bands should be distinctly darker than other growth lines (Thompson et al. 1980b) and should exist as a distinctive group of uniform grayness within the array of growth lines observed from the lightest to the darkest grayness level. Thus, the decrement in line count as line darkness increases should not proceed uniformly from the lightest to the darkest grayness intensity. To identify yearly growth bands, therefore, we first test the hypothesis that some groups of growth lines are distinctly more uniform in darkness than other growth lines. We expect that the decrement rate in line count as line darkness increments should proceed in a stepped pattern, rather than a continuous one, across the range of grayness scales as the uniformly intense groups of lines are passed.

Line counts were first evaluated in 5-intensity-unit intervals (I_i) from 25–140 grayness units for a subsample of 24 individuals in the size range 22.7–78.3 mm shell length. Intensity levels outside this range were either too sensitive and thus produced unreasonably high line counts or not sensitive enough and thus

produced unreasonably low line counts. Hereafter, values of I used for statistical analysis are defined as the incremental bin number across this range of grayness units: thus, intensity range 25–30 = I_1 ; intensity range 135–140 = I_{23} . Figure 2A plots the average rate of change in line count (LC) as a function of change in intensity step (I), where the rate of change is calculated as:

$$\frac{dLC}{dI} = \frac{LC_{i-1} - LC_i}{I_{i-1} - I_i} \quad (1)$$

The decrement in the number of lines from one intensity step to another declines in magnitude with increasing grayness, as expected. This occurs because the total number of lines counted is large at the lightest grayness level and small at the darkest grayness level and, so, more lines are likely to be lost per intensity increment at light intensity levels of grayness. If a group of lines has similar grayness, as might be expected for yearly bands, this group of lines should manifest themselves in Figure 2A by a local minimum in the average rate of change. In what is otherwise a constantly decreasing relationship, two local minima stand out in Figure 2A, at intensities of 60–65 and 95–100. Fewer lines are lost in incrementing across these two ranges of grayness than anticipated from the overall rate at which line count decrements across the wider range of grayness levels.

One might expect that annual bands would be of sufficient strength in comparison with other growth lines that a step in grayness intensity would not change the line count. That is, a high frequency of zero differences between the numbers of lines counted from one 5-intensity-unit level to the next would be expected if a group of growth lines existed with a unique similarity in grayness. In Figure 2B, we tally the number of cases in which an increment of 5 grayness units produced the same line count for these 24 quahogs. Overall, the number of cases of zero decrement with a 5-unit increment in grayness rises at the higher end of the grayness scale, as the total number of growth lines counted declines (Fig. 2B). Nevertheless, local maxima are observed at grayness intensities of 55–60 and 95–100 (Fig. 2B) and, as importantly, these are succeeded by minima at 65–70 and 100–105.

The regression equation for Figure 2A relating the rate of change in line count with incrementing grayness intensity is:

$$\frac{dLC}{dI} = -0.1015I + 3.510 \quad (2)$$

This regression was used to obtain a series of residuals for each of the 24 shells and grayness intensities in the range of 25–140 grayness units and the mean residual was plotted against grayness intensity (Fig. 2C). The most negative mean residuals are encountered at the 60–65 and 95–100 grayness intensities, as anticipated from Figures 2A and 2B, indicating that, for most shells, the rate of change in line count is distinctly lower in these two grayness ranges than elsewhere in the grayness spectrum. This is anticipated if growth lines in this grayness range are associated with significant life history events, such as yearly shifts in growth.

The residuals comprising Figure 2C were ranked and a least-square means multiple comparison test was used to test the null hypothesis that the means of the residuals were equal across a range of grayness intensities. We would anticipate that the two intensity ranges characterized by highly negative residuals would differ significantly from the residuals for other intensity ranges more frequently than expected by chance. In this and all

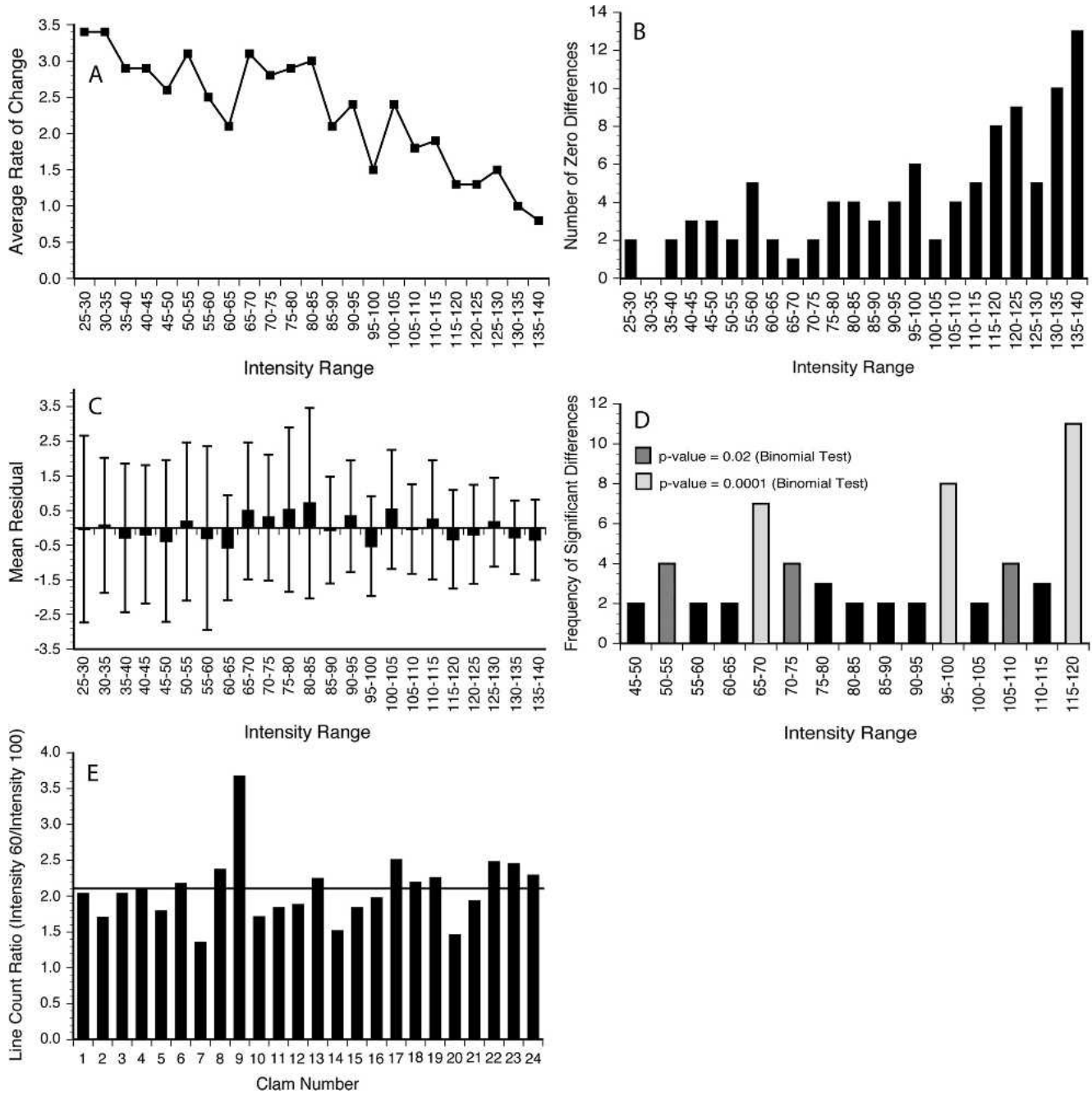


Figure 2. A: The rate of change in line count, dLC/dI , as a function of intensity level, for 24 ocean quahogs spanning a range in size from 22.7–78.3 mm. B: The number of cases in which the difference in line counts between consecutive 5-unit intensity levels was zero for the 24 ocean quahogs analyzed in C. Mean and standard deviation of the residuals obtained from the expected rate of change per grayness intensity increment predicted from the regression line and the observed rate of change per grayness intensity increment for the 24 measured ocean quahogs, D: The number of cases out of 14 possible in the grayness intensity range of 45–120 in which any one set of residuals from Figure 4 differed from all others, E: The ratio of the number of growth bands at grayness scale 60 to the number of growth bands at grayness scale 100 for the 24 ocean quahogs examined in detail. The average ratio is 2.1 (dark line).

subsequent analyses, we focused on a range of grayness intensities, 45–120, encompassing these two potentially unique regions. We tallied, from the results of the multiple comparison test the number of times each set of residuals for each 5-unit grayness increment differed from all others. As the reduced range of grayness intensities encompassed 15 five-unit intensity increments, the maximum number of significant differences for

any given set of residuals was 14. Figure 2D reports the results of these tallies by recording how frequently one set of residuals differed significantly from another at $\alpha \leq 0.10$. We used the binomial test to assess the likelihood that each tally might have occurred by chance. Results showed significant divergences from chance at grayness intensities of 65–70 and 95–100 ($P < 0.0001$, Fig. 2D).

Collectively, the analyses shown in Figures 2A through 2D identify two unique ranges of grayness in the grayness spectrum summarized by Figure 2A, in the range 60–70 and 95–105. The average line count for the lower grayness intensity is about double that of the higher grayness intensity (Fig. 2E), suggesting that annual bands are detected at intensities of 95–105 and that seasonal bands or spawning breaks are detected at intensities of 60–70 (Fig. 2E).

Development of an Age-length Key

The data set is composed of the shell length and age (years) from a series of intensity-based line counts in the grayness range 95–105 for 328 ocean quahogs from 12–84 mm (Fig. 3). Development of an age-length key using these 328 ocean quahogs that were aged first requires that the growth rates are approximately equal over the range of latitudes and depths from which they came. These animals were obtained from Mid-Atlantic Bight waters south and west of Montauk, NY (Fig. 1). Higher growth rates have been reported east of this area on Georges Bank (Lewis et al. 2001). Hence, we first evaluated the estimated age as a function of shell length for 328 quahogs with respect to depth and latitude by nonparametric ANCOVA. For ease of analysis, we combined all ocean quahogs into 5-mm length bins. We further transformed depth and latitude into polytomous main effects after Powell and Mann (2005). Stations were allocated to one of three depth zones: <43 m, 43–55 m, and >55 m. Stations were allocated to 4 geographic zones based on degree of north latitude: >40°, 39–40°, 38–39°, <38°. Length was included as the covariate. Age varied as expected with length ($P < 0.0001$). Age did not vary significantly with depth or geographic zone, nor were any interaction terms between age and length with depth or geographic zone significant. Accordingly, the assumption of growth uniformity over the region sampled by these collections is supported by statistical analysis.

The first step in creation of an age-length key is to establish the uncertainty in known age for an individual. Line counts, and therefore apparent age, vary from grayness intensity 95–100 and thence to 105. We examined the variation in apparent age across the 100-unit grayness boundary by calculating the change in line count between grayness intensities of 95 and 100 and grayness intensities of 100 and 105 as a function of shell length (SL):

$$\Delta LC = \frac{LC_{100} - LC_{95}}{SL} \quad \text{and} \quad \Delta LC = \frac{LC_{100} - LC_{95}}{SL} \quad (3)$$

The distribution of these deviations did not diverge significantly from that expected from a normal distribution (Shapiro-Wilk test, $P = 0.54$; Fig. 4). As a consequence, the uncertainty in age for an individual shell was modeled as Gaussian using the three line counts at grayness intensities of 95, 100, and 105 to calculate a mean and variance.

Calculation of the mean and variance in age from the age estimates derived from line counts at 95, 100, and 105 intensity units for the 24 ocean quahogs examined in detail yields a set of mean ages and variances. For some individuals, the variance was unusually large or small. The variance should expand with the mean according to Taylor's Power Law (Elliott 1977, Elliott 1983, Green 1989). Because the number of ocean quahogs examined at this level of detail is too few to compensate for the variation in the uncertainty of the determination of age within individuals of the same mean age, data for the 24 quahogs were fit to Taylor's Power Law. This yields:

$$\delta^2 = 0.146x^{0.824}; R^2 = 0.72 \quad (4)$$

The final variances in age for each mean age were obtained from this relationship.

The age-length key was obtained by first establishing the age probability spectrum for each of the 328 aged individuals of known length obtained from Eq. (4) (Fig. 5). In cases where individuals of several mean ages had the same length, the total probability was expressed as the standardized sum of the individual probabilities for each of the animals of that length. This step, in essence, assumes that the age spectrum for a given length can be expressed as a cumulative density function. That is, the probability of a given mean age for any length is determined by the probability of that age for all individuals of that length in the input data set.

An alternative would be to assume a normal distribution of ages at each length. We examined the likelihood that the distribution of mean ages at length was normally distributed. Combining the lengths into 5-mm size classes yielded 14 length classes. In no case were the distribution of ages significantly different from normal (Shapiro-Wilk test, $\alpha = 0.05$); however, in only three cases did the probability of normality exceed $P = 0.95$,

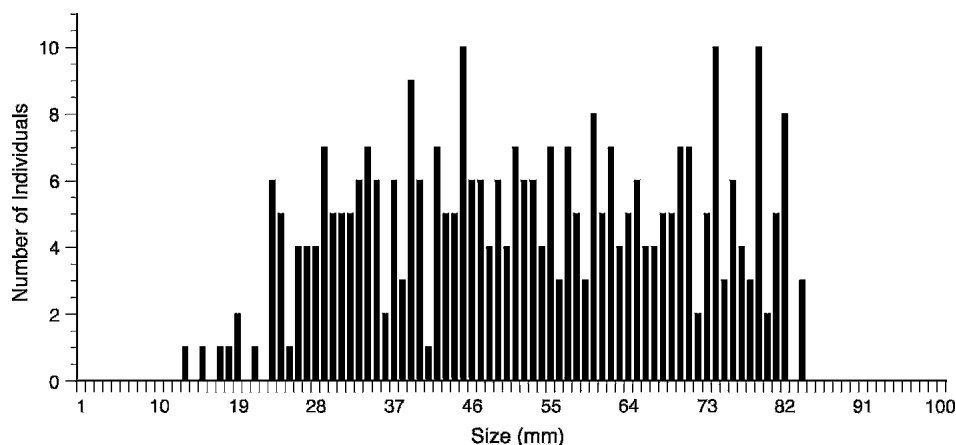


Figure 3. The size-frequency distribution of small ocean quahogs used for aging.

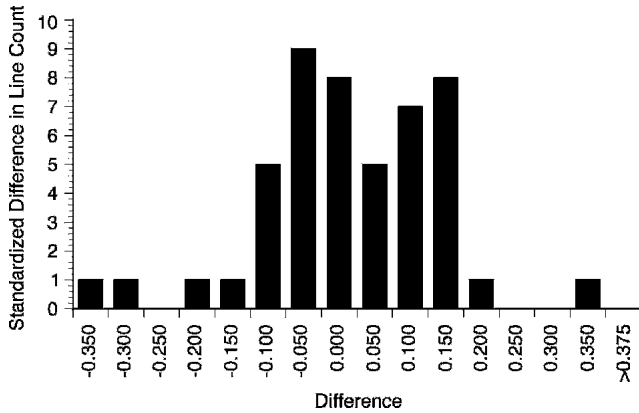


Figure 4. Difference in line counts between grayness intensities of 95 and 100 (negative abscissa values) and between 100 and 105 (positive abscissa values) standardized by shell length for the 24 ocean quahogs examined in detail.

an unlikely event by chance (binomial test, $P = 0.017$). The median was $P = 0.35$. Thus, the data support an assumption of normality but not strongly so. Recent theoretical work by Hofmann et al. (2006) suggests that the age-length distributions in populations are unlikely to be described by a simple Gaussian model, as, in fact, we observe. Thus, the conservative approach is the use of a cumulative density function to describe the probability of mean age for a given length. The age-length key is thusly obtained (Fig. 6, Table 1).

The age-length key was then applied to generate age frequencies in the standard way:

$$P(\hat{A}|\hat{L}) * P(L) = P(A) \tag{5}$$

where \hat{A} and \hat{L} represent the set of probabilities of a given age for a given length obtained from the age-length key in Figure 6, L represents the length frequencies obtained from the 104 survey samples (see Powell & Mann 2005), and A represent the 104 age frequencies derived therefrom.

PCA Analysis of Age Frequencies for the Mid-Atlantic Bight

The data consist of age-frequency distributions for the 104 stations described in Powell and Mann (2005) as size-frequency distributions. Approximately five dominant year classes are represented in the 104 age frequencies (Fig. 7) and these are remarkably consistent across stations. Note that the age axis has been truncated at 63 y; the right-hand extension of the age-frequency spectrum is artificial, because animals greater than 80 mm were poorly represented in this data set ($n = 17$ in the size range 80–84 mm SL). This study targeted small (<80 mm SL) ocean quahogs and, thus, poorly sampled animals of commercial shell length (>80 mm SL). As a consequence animals greater than 63 y old have thus been excluded from further analyses.

To examine the relationships in age-frequency distribution between sites, a PCA (principal component analysis) was run. For convenience, in this case, ocean quahogs were lumped into 3-y categories from age 4–63 y. This yielded 20 three-year age

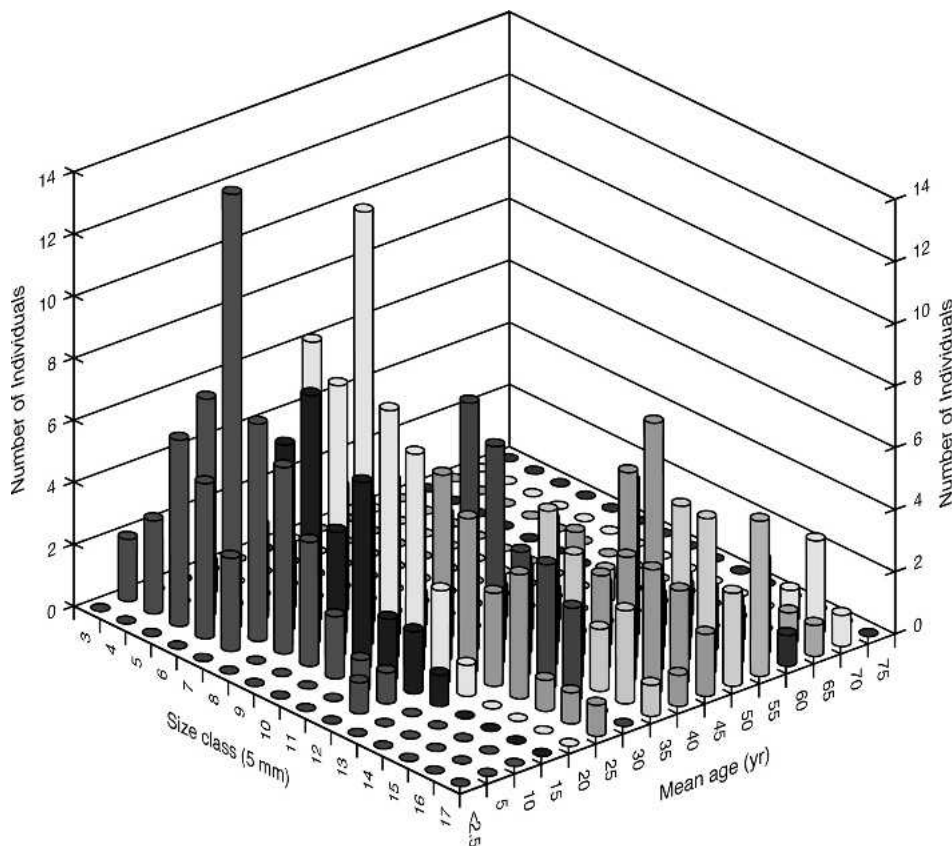


Figure 5. Distribution of mean ages (years) by shell length (mm) class for the 328 ocean quahogs that were aged.

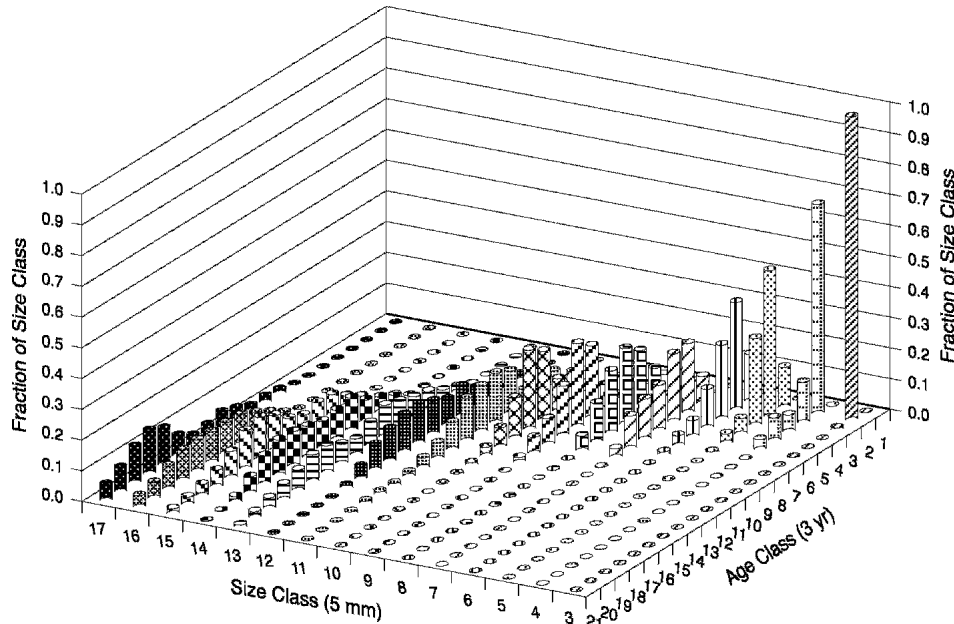


Figure 6. The probability of age (years) for a given shell length (mm) for young ocean quahogs in the Mid-Atlantic Bight as indicated by the fraction of a size class within an age class. Size classes are in 5 mm increments and describe animals ranging from 15 through 85 mm shell length. Age classes are in three-year increments and describe animals from 1 through 63 y of age.

classes. Age-frequencies were then standardized to the number in each 3-y age class per 100 individuals caught in the tow (sample), thereby giving each sample equal weight. PCA was conducted with orthogonal rotation on data further standardized to mean = 0 and variance = 1.

Statistical analyses focused on ANOVA using factor scores as the dependent variables, and depth zone and latitudinal zone as main effects. Sampled depths were allocated to one of three depth zones for these analyses: <43 m (29 stations), 43–55 m (30 stations), and >55 m (45 stations). Stations were also allocated to 4 geographic zones based on degree of north latitude: >40° (27 stations), 39–40° (32 stations), 38–39° (34 stations), <38° (11 stations). The most southern geographic zone was somewhat underrepresented, but was important to be maintained separate as it encompasses an area off the Delmarva Peninsula that received significant fishing pressure early in the fishery's history, during the mid-1980s, and as it marks the southernmost extension of the geographic range (Dahlgren et al. 2000). *A posteriori* least-square means tests were used to identify significant components within the ANOVA.

Characteristic age-frequency distributions were constructed by cumulating the age-frequency distributions for ocean quahog assemblages from stations with PCA factor scores exceeding 1.0. PCA factors determining the four principal characteristic size-frequency distributions accounted for 98% of the total variation, with most of the variation (90%) explained by the first two factors.

Water Temperature Data

Water temperature data from 1930–2002 were used to describe mean monthly bottom water temperatures (BT, °C) for six stations in the Mid-Atlantic Bight spanning the latitudinal range of ocean quahog distribution (Fig. 1, Table 2). The

period 1930–2002 was chosen to incorporate the entire lifespan of the oldest quahog observed (71 y, captured in 2002 at a SL of 76.5 mm). Daily sea surface and bottom water temperature data from 6 lightship stations in the Mid-Atlantic Bight during the period 1956–1971 were used to calculate the average monthly observed difference between sea surface temperature (SST) and bottom water temperature (BT) on a site-specific basis. Data from the Fire Island lightship (1930–1940, Fig. 1) were used to supplement the Ambrose Channel lightship (1941–1972, Fig. 1) data record in the period 1930–1940 before the Ambrose Channel lightship took up station and these data are referred to as Ambrose Channel for these analyses. Data from the Winter Quarter lightship (1955–1961, Fig. 1), which was discontinued in 1961 when the Delaware lightship took up station (1961–1972, Fig. 1) were used to supplement the Delaware lightship record and are referred to as Delaware herein. The observed average monthly SST-BT differences from the daily lightship data were used to estimate average monthly BT at these five sites during years before 1956 and after 1971 when only SST was available (Table 2). The Ambrose Channel SST-BT estimators were used to estimate average monthly bottom temperatures at Montauk Point (Table 2). The NOAA buoy at Five Fathom Bank (44012, Fig. 1) was discontinued at the end of 1992. SST data from Delaware buoy (44009, Fig. 1) was used with the Five Fathom Bank SST-BT estimators to estimate hourly BT for Five Fathom Bank from 1993–2002.

Hourly air temperature (AT) and SST data from NOAA buoys (1985–2002) were used to calculate the observed difference between average monthly AT and average monthly SST for Ambrose Channel (Mar 1985 to Nov 1986), Five Fathom Bank (Mar, Apr 1987), Delaware (Feb to Apr 1991), and Chesapeake (Apr 1993 to Feb 1994, Dec 1994 to May 1995, Feb, Aug 1996). The observed average monthly AT-SST differences from the buoy data were used to estimate hourly SST for

TABLE 1.

Age-length key derived from the 328 ocean quahogs from the Mid-Atlantic Bight <80 mm SL that were aged. Ages are in 3-y year classes with the first age represented in that age class given in the column heading (age class = "AC"). Sizes are in 5-mm shell length classes with the first size represented in a size class given in the row heading. The values given are the frequencies with which a quahog of an age occurs within a size class.

Size Class (5mm)	1	4	7	10	13	16	19	22	25	28	31	34	37	40	43	46	49	52	55	58	61	
15	0	0.992	0.008	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	0	0.686	0.136	0.059	0.079	0.038	0.002	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0.136	0.479	0.288	0.056	0.035	0.006	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	0	0.156	0.355	0.245	0.131	0.058	0.038	0.014	0.003	0	0	0	0	0	0	0	0	0	0	0	0	0
35	0	0.019	0.093	0.230	0.225	0.152	0.136	0.110	0.033	0.001	0	0	0	0	0	0	0	0	0	0	0	0
40	0	0	0.012	0.128	0.215	0.250	0.207	0.131	0.053	0.005	0	0	0	0	0	0	0	0	0	0	0	0
45	0	0	0.043	0.023	0.085	0.239	0.275	0.166	0.088	0.058	0.021	0.003	0	0	0	0	0	0	0	0	0	0
50	0	0	0	0.039	0.104	0.110	0.230	0.262	0.136	0.068	0.033	0.012	0.005	0.002	0	0	0	0	0	0	0	0
55	0	0	0.003	0.057	0.031	0.055	0.144	0.166	0.154	0.142	0.093	0.056	0.036	0.019	0.012	0.014	0.012	0.006	0.002	0	0	0
60	0	0	0.020	0.027	0.012	0.045	0.071	0.105	0.091	0.113	0.133	0.127	0.111	0.088	0.046	0.013	0	0	0	0	0	0
65	0	0	0	0	0.002	0.024	0.041	0.066	0.077	0.092	0.108	0.081	0.057	0.068	0.093	0.092	0.072	0.054	0.039	0.023	0.009	0.009

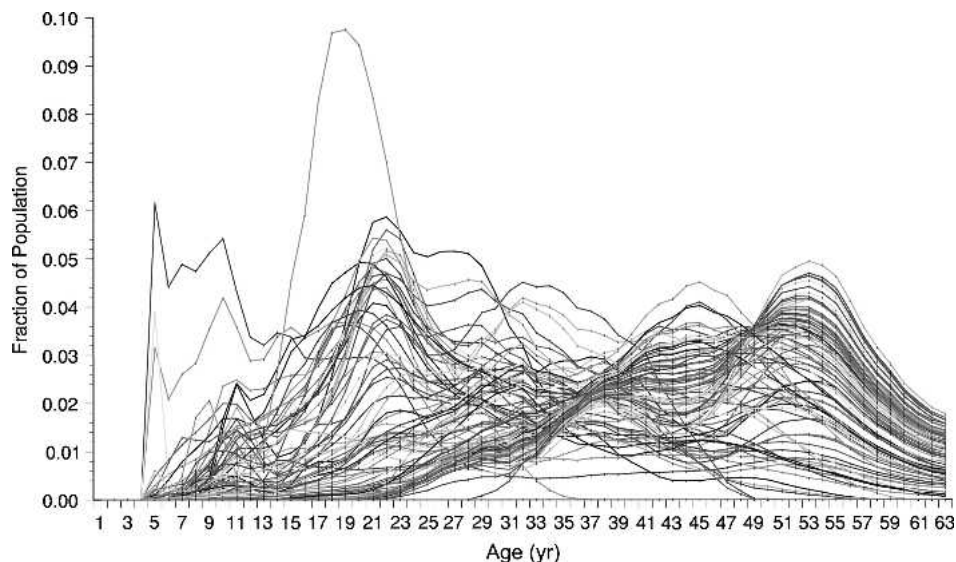


Figure 7. Age frequency for each of the 104 stations. Note that the age axis has been truncated at 63 y. The righthand extension of the age frequency spectrum is artificial because animals greater than 80 mm were not targeted by the survey used for this study (Powell & Mann 2005).

these four sites during months after 1985 when only AT was available.

Four bottom water temperature categories were established to characterize average monthly bottom water temperatures within a given year based on ocean quahog biology. The categories of cold ($<6^{\circ}\text{C}$), mild (6°C to 10°C), warm (10°C to 16°C), and hot ($>16^{\circ}\text{C}$) correspond to reported temperature ranges for ocean quahog gametogenesis and growth cessation, gonad development, adult and larval growth, and rapid progression toward metamorphosis. Average monthly bottom temperatures were categorized within a year for years with 9 or more months of available temperature data. The mild temperature category corresponds to water temperatures that encourage growth and gametogenesis for ocean quahogs (Mann 1982). Mild water temperatures also correspond to a thermal predation refuge for quahogs in that these temperatures set periods when quahog predators that rely on isotherms to determine their distribution (starfish *Astropecten americanus*, and *Sclerasteria tanneri* Franz et al. 1981) do not typically use quahog habitat. Predators that co-occur with quahogs display reduced activity at mild temperatures (starfish e.g., *Asterias forbesi*, MacKenzie 1969, Franz et al. 1981, *Asterias vulgaris*, *Leptasterias tenera*, Franz et al. 1981, winter flounder *Pleuronectes americanus*, Steimle et al. 1994) also reducing predation pressure.

Years in which there were at least 2 more cold months than mild months were identified for each station from 1940–1994. This time period was identified by the PCA analyses of age-frequencies as years of interest. These years are referred to hereafter as having a “mild > cold” temperature pattern. For each PCA factor and station, the number of years identified by the PCA factor with and without the mild > cold temperature pattern were compared with the number of years between 1940–1994 at that station with and without the pattern. Chi Square analyses were used to test the hypothesis that the proportion of years in which the mild > cold temperature pattern occurs is the same at a site in years identified by PCA analyses and in the period 1940–1994.

Average residuals for annual BT from the long-term (1930–2002) average BT temperature were calculated for each site in which at least 9 mo of data were available. For each station, the number of years with annual BT residuals above and below the long term BT average was counted. Two-tailed binomial tests were used to compare the number of years with above or below average BT and the number of years with strong recruitment potential as indicated by at least 2 more months of mild > cold BT. A two-tailed binomial test was used to assess the likelihood that each count might have occurred by chance.

Pearson correlation coefficients were used to compare the station specific (Fig. 1) monthly average bottom water temperatures in each year ($^{\circ}\text{C}$) with the observed percentage of quahogs within each PCA specific age class for that year (earlier, see Figs. 9–13 later) at that location. The percentage of quahogs within PCA specific age classes describes the strength of the recruitment signal within any given year. The residuals of the average monthly bottom water temperatures during the years where the majority of recruitment described by each PCA (see Figs. 9–13 later) was observed in relation to the long-term (1930–2002) average monthly bottom water temperatures were calculated.

RESULTS

Age-at-length Relationship

The relationship between age (y) and shell length (mm) for 311 ocean quahogs <80 mm shell length from the MAB (Fig. 8) was described with a power equation:

$$\text{Shell length (mm)} = 10.132 * \text{Age}(\text{yr})^{0.498}, R^2 = 0.73 \quad (6)$$

The least squares regression from this model is significant ($F = 811.8, P < 0.001$). Linear, Von Bertalanffy, and logarithmic models were also fit to this data set but the coefficients of determination (0.69, 0.69, and 0.63, respectively) for these models were lower than that for the power function. A power

TABLE 2.

Summary of water temperature data sources from 1930–2002 for the Mid-Atlantic Bight stations shown in Figure 1: Montauk Point (1), Ambrose Channel (2), Barnegat (3), Five Fathom Bank (4), Delaware (5), and Chesapeake (6). Sea surface temperature (SST), bottom temperature (BT) and air temperature at the water surface (AT) were used. All temperatures were in degrees Celsius.

Station	Year(s)	Data	Station Type	Depth	Source
Montauk Point	1947–1971	SST	Tide	NA	1, 2, 3, 4
	1972–2002	SST	One degree quadrangles	NA	5, 6, 7, 8
Ambrose Channel/Fire Island	1930–1940	SST	Fire Island lightship	NA	9
	1947–1955	SST	Ambrose Channel lightship	29 m	10
	1956–1970	SST, BT	Ambrose Channel lightship	29 m	10
	1971–1984	SST	One degree quadrangles	NA	5, 6, 7
	1985–2002	AT, SST	NOAA buoy ALSN 6	NA	11
Barnegat	1947–1955	SST	Barnegat lightship	NA	9
	1956–1970	SST, BT	Barnegat lightship	24 m	12
	1970–2002	SST	One degree quadrangles	NA	5, 6, 7, 8
Five Fathom Bank	1930–1955	SST	Five Fathom Bank lightship	NA	9
	1956–1970	SST, BT	Five Fathom Bank lightship	24 m	13
	1970–1984	SST	One degree quadrangles	NA	5, 6, 7
	1984–1992	AT, SST	NOAA buoy 44012	NA	14
	1993–2002	BT	Data estimated from Delaware SST with Five Fathom bank SST-BT estimators (see text).		
Delaware/Winter Quarter	1930–1940	SST	Winter Quarter lightship	NA	9
	1955–1960	SST, BT	Winter Quarter lightship	24–29 m	15
	1961–1970	SST, BT	Delaware lightship	30 m	16
	1970–1984	SST	One degree quadrangles	NA	5, 6, 7
Chesapeake	1984–2002	AT, SST	NOAA buoy 44009	NA	17
	1930–1955	SST	Chesapeake lightship	NA	8
	1956	BT	Chesapeake lightship	NA	18
	1957	BT	Chesapeake lightship	NA	19
	1958–1971	SST, BT	Chesapeake lightship	20 m	20
	1971–1984	SST	One degree quadrangles	NA	5, 6, 7
	1985–2002	AT, SST	NOAA buoy CHLVZ	NA	21

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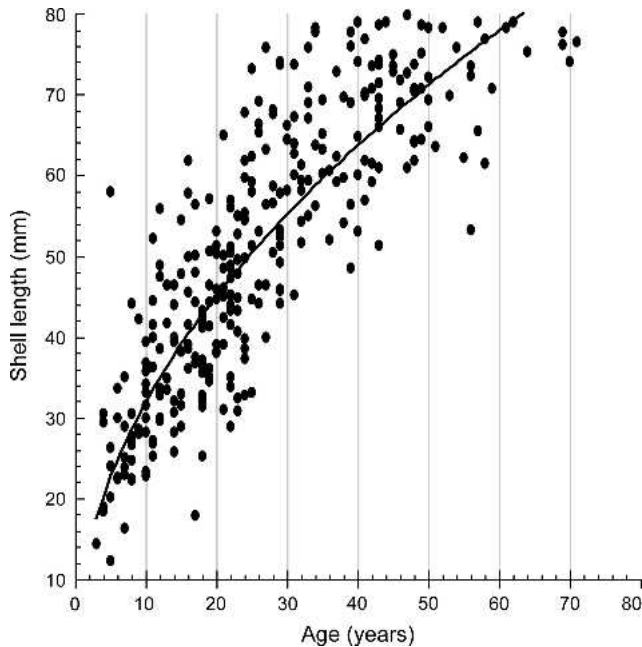


Figure 8. Length-at-age curve for ocean quahogs <80 mm shell length from this study.

function was used to describe the age-at-length relationship for small ocean quahogs because animals <80-mm shell length still have an increasing growth trajectory (Fig. 8). Kraus et al. (1992) also found the power model to be the best descriptor of growth for quahogs <80 mm SL in both field and laboratory settings.

Results of PCA Analysis for Age-frequency Distribution Relationships Between Sites

PCA Factor 1 represented ocean quahogs with a modal age of 52–54 y, with most ages between 46 and 60 y (Fig. 9A). Stations with this age-frequency distribution were widely distributed in the Mid-Atlantic Bight, but most noticeably inshore in the southern half of the region and offshore and along the northern edge of Hudson Canyon (Fig. 9B).

PCA Factor 2 represented ocean quahogs with a modal age of 43–48 y, with most ages between 37 and 54 y (Fig. 10A). Stations with age-frequency distributions of this type were widely distributed in the Mid-Atlantic Bight, but most noticeably off southernmost New Jersey and the Delmarva Peninsula and northeast of Hudson Canyon (Fig. 10B).

PCA Factor 3 represented ocean quahogs with a modal age of 22–30 y, with most ages between 19 and 36 y (Fig. 11A). Stations with this age-frequency distribution were localized inshore and south of Hudson Canyon (Fig. 11B).

PCA Factor 4 represented ocean quahogs with a modal age of 19–24 y, with most ages between 10 and 30 y (Fig. 12A). Stations with this age-frequency distribution were concentrated in the most southern reach of the ocean quahog range, off Delmarva Peninsula (Fig. 12B).

ANOVA analyses (Table 3) showed that latitude was a significant determinant of the spatial distributions of ocean quahogs in age classes described by Factors 1, 2, and 4. These

are the youngest and the two oldest modal size classes. Depth only influenced the youngest age classes described by Factor 4. *A posteriori* tests support the visual conclusions from Figures 9B, 10B, and 12B that the younger ocean quahogs were principally distributed in the southern Mid-Atlantic Bight, that the oldest ocean quahogs are unusually rare northeast of Hudson Canyon, and that ocean quahogs of somewhat lesser age, described by Factor 2, are most abundant at the northernmost and southern portions of the study area. Significant interactions between depth and latitude were also present for Factors 1, 2, and 4, suggesting that processes more complex than simply the cross-shelf depth gradient or latitude are responsible for the distributional patterns observed.

Water Temperature Data

Average annual bottom water temperatures in the period 1930–2002 followed a latitudinal trend with the lowest (8.68°C) observed at Montauk Point and the highest (12.27°C) observed at Chesapeake (Table 4). The differences between SST and BT recorded by the lightships (approximately 1956–1971) 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 (Fig. 13) when these stations experience surface temperatures that are at least 8°C to 12°C higher than bottom temperatures. Air temperatures recorded for 1984–2002 by three NOAA buoys are 1° to 2° warmer than SST from April through July (Fig. 14). For the rest of the year, air temperatures are colder than SST with the maximum difference (–4°C to 5°C) observed in December (all three stations) and January (Ambrose Channel only, Fig. 14).

The number of years highlighted by PCA Factors 1 and 2 in which the mild > cold pattern occurred did not differ significantly from the total number of years in which the pattern occurred between 1940–1994 (time period of recruitment corresponding to the age range of quahogs predicted by the age-length key) at all sites (Table 5). However, at Five Fathom Bank and Chesapeake, the years corresponding to PCA 3 modal ages (1972–1980) with the mild > cold pattern were significantly more common than expected based on the number of years in which the pattern occurred at these sites between 1940–1994 (Table 5). The occurrence of the mild > cold pattern between 1972–1992, corresponding to the majority of ages indicated by PCA factor 4 in the vicinity of Chesapeake, was also significantly higher than the occurrence of this pattern between 1940–1994 at this site.

Examination of the deviation of annual average bottom water temperatures from the average long-term (1930–2002) bottom water temperatures (Fig. 15) shows that most sites experienced above average water temperatures in multiple consecutive years between 1970–1980 and again in the period 1995–2002. Estimated bottom water temperatures for 2002 were among the highest observed during the period 1930–2002 for the three southernmost sites (Five Fathom Bank, DE, Chesapeake). Although Montauk Point did not experience multiple consecutive years of above average temperatures in the 1970–80 period, the period 1984–1992 included 8 out of 9 y with above average water temperatures (Fig. 15A). Below average water temperatures prevailed for most of the period 1950–1970 as well as 1930–1940 at sites for which data are available.

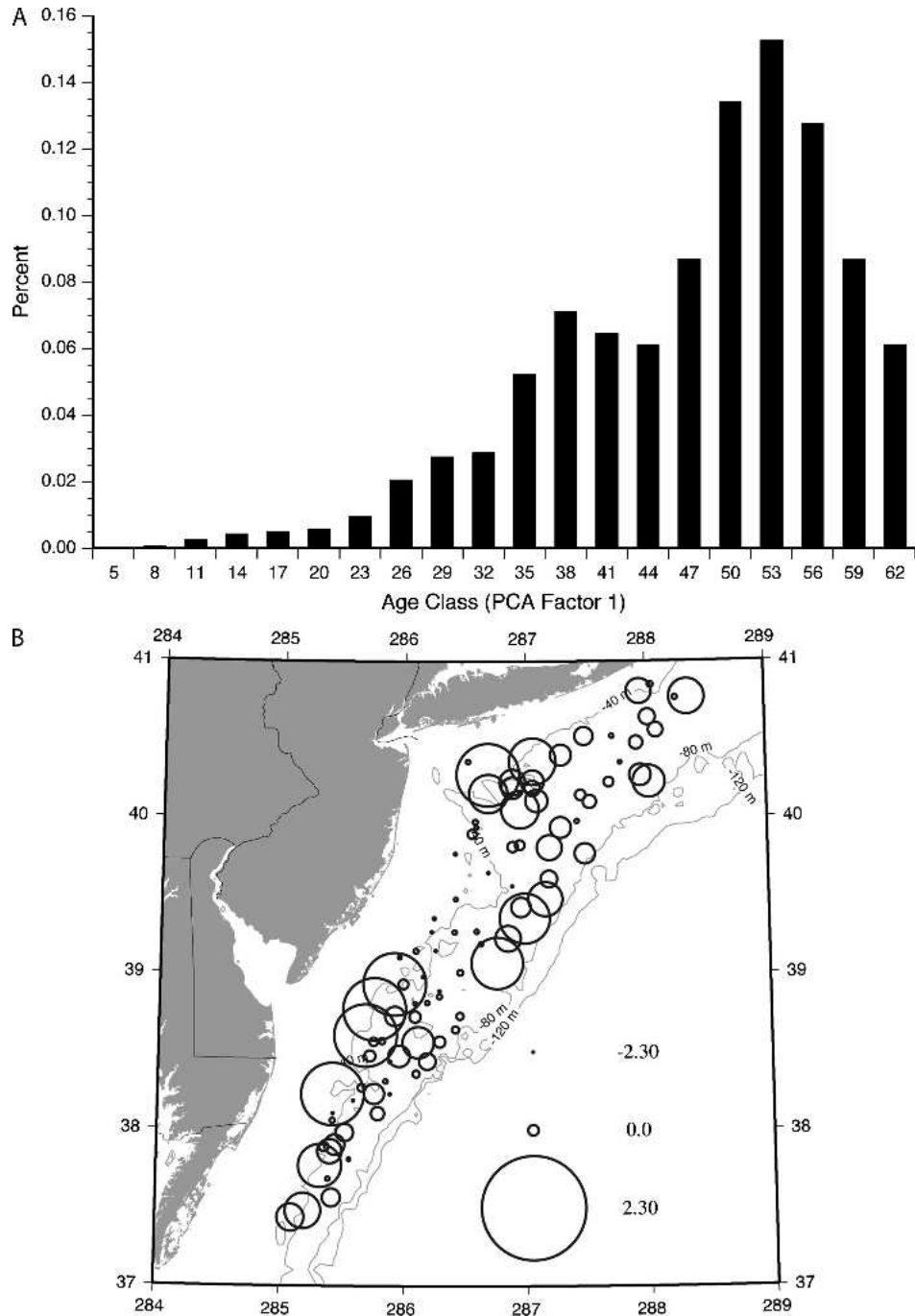


Figure 9. A: Summary age-frequency distribution for all stations with factor scores above 1.0 for Factor 1. Age classes are in 3-y increments with the midpoint of the age class used as the x-axis label. B: The geographic distribution of stations with high Factor 1 scores. Factor 1 is weighted most heavily by the oldest ocean quahogs in the study. Circle diameter is nonlinearly proportional to factor score. Circle diameter is calculated as $e^{(factor1)}/10$. The legend shows the size of circles with factor scores of -2.3 , 0.0 , and $+2.3$.

Binomial tests comparing the number of years with the mild > cold pattern and above average temperatures with the number of years with above average temperatures were significantly different from the hypothesized value of 0.5 for Five Fathom Bank and Delaware for the period 1940–1994 indicating that years with the mild > cold pattern years occurred more frequently than would be expected by chance at these sites ($P < 0.05$, Fig. 15). In contrast, Montauk Point, Ambrose

Channel, Barnegat, and Five Fathom Bank all had significantly fewer years in the 1940–1994 period with below normal temperatures and incidence of the mild > cold pattern than would be expected by chance (Binomial tests, $P < 0.05$, Fig. 15). At these sites, the mild > cold pattern occurred in below average temperature years less than 19% of the time.

Significant negative Pearson correlations between monthly bottom water temperatures during January, February, or

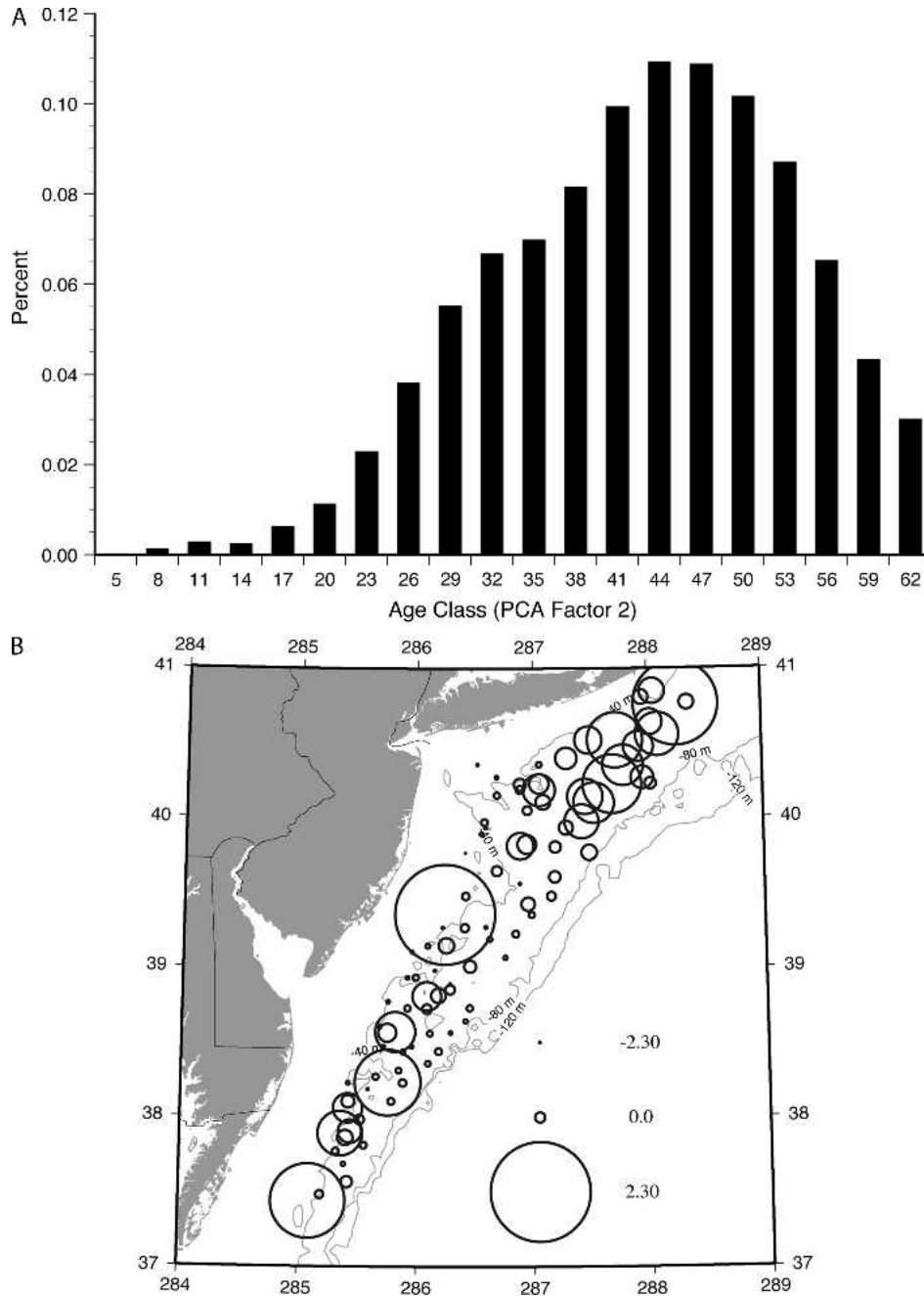


Figure 10. A. Summary age-frequency distribution for all stations with factor scores above 1.0 for Factor 2. Age classes are in 3-y increments with the midpoint of the age class used as the x axis label (B). The geographic distribution of stations with high Factor 2 scores. Factor 2 is weighted most heavily by ocean quahogs between 37 and 54 y old. Circle diameter is nonlinearly proportional to factor score. Circle diameter is calculated as $e^{(factor2)/10}$. The legend shows the size of circles with factor scores of -2.3, 0.0, and +2.3.

March, and quahog recruitment within a year as described by PCAs 1 and 2 (Figs. 9 and 10) were observed at Montauk Point and Ambrose Channel (Table 6). Recruitment described by PCA 1 and 2 (Figs. 9 and 10) at Montauk Point was also significantly and negatively correlated with below average bottom water temperatures during December (Table 6, 7). Pearson correlations between year specific bottom water temperatures during winter months and quahog recruitment as described by PCAs 3 and 4 (Figs. 11 and 12) were positive and significant at Montauk Point, Ambrose Channel, Five Fathoms, and Dela-

ware (Table 6). These periods correspond to above average monthly bottom water temperatures during January, February, and March and below average September bottom water temperatures (Table 7).

Years in which strong year classes/recruitment signals were identified by the PCA analyses were also typically characterized by a sequence of bottom water temperatures that were above average in at least two out of three months during January, February, or March (Table 7). The modal age classes indicated by PCA Factor 1 (Fig. 9A) correspond spatially to Montauk

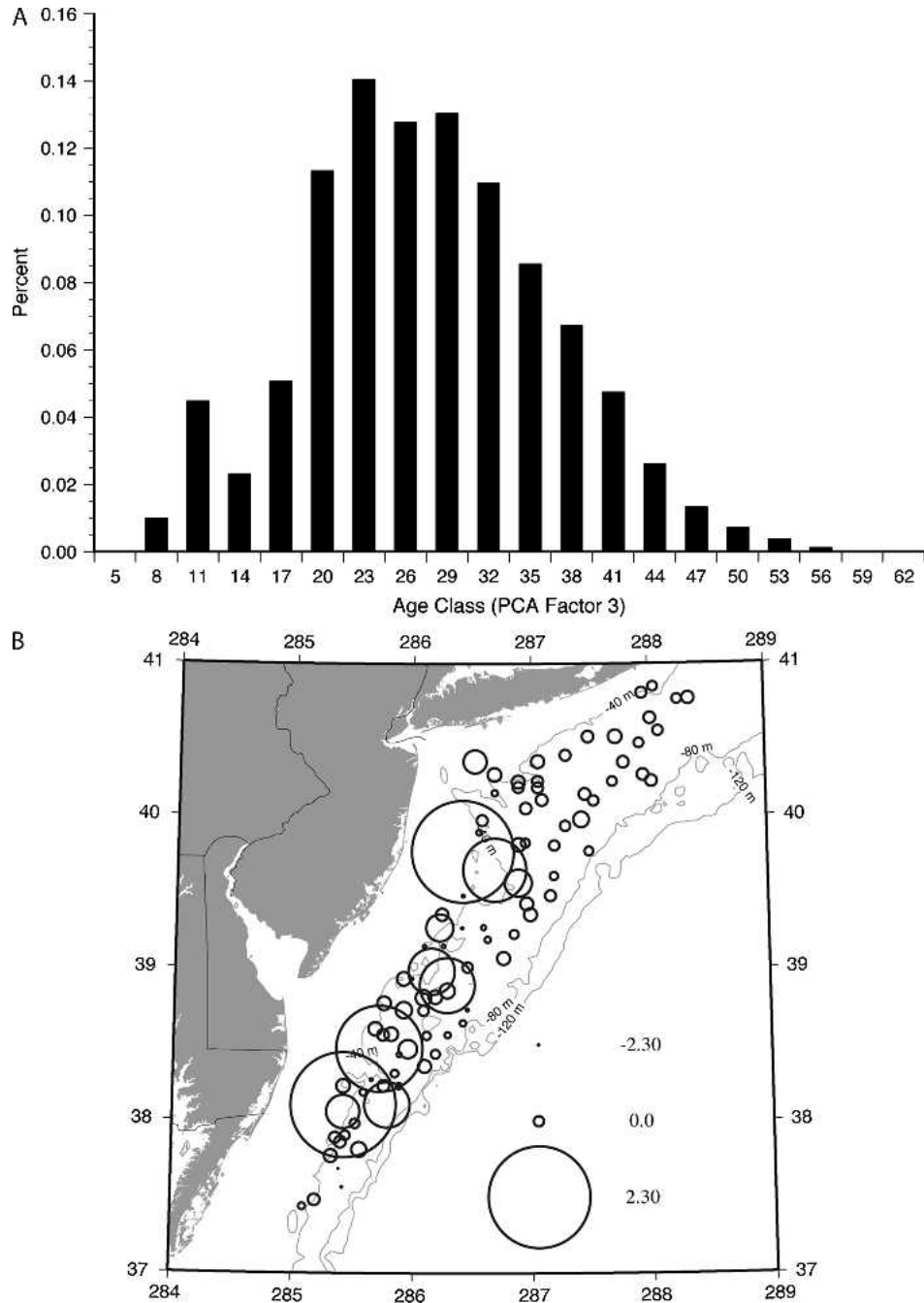


Figure 11. A: Summary age-frequency distribution for all stations with factor scores above 1.0 for Factor 3. Age classes are in 3-y increments with the midpoint of the age class used as the x axis label, B: The geographic distribution of stations with high Factor 3 scores. Factor 3 is weighted most heavily by the young ocean quahogs between 22 and 30 y of age. Circle diameter is nonlinearly proportional to factor score. Circle diameter is calculated as $e^{(\text{factor}^3)}/10$. Legend shows the size of circles with factor scores of -2.3, 0.0, and +2.3.

Point, Ambrose Channel, Five Fathom Bank, and Delaware (Fig. 9B) and temporally to the year 1949, a year characterized by above average bottom water temperatures from January to August (Table 7). Water temperatures during 1954–1959, the modal years described by PCA 2, were characterized by below average temperatures in January, February, and March at all sites. The distribution of quahogs described by PCA 2 is at or below the 40-m contour in offshore areas

(Fig. 10B). A latitudinal gradient of recruitment in relation to bottom temperature is indicated by PCA 4 where warmer temperatures in November and December at Montauk Point and Ambrose Channel are correlated with increased recruitment (Tables 6, 7, Fig. 9B). Recruitment at sites south of Ambrose Channel described by PCA 4 occurred when water temperatures were below average in September and October (Table 7, Fig. 13B).

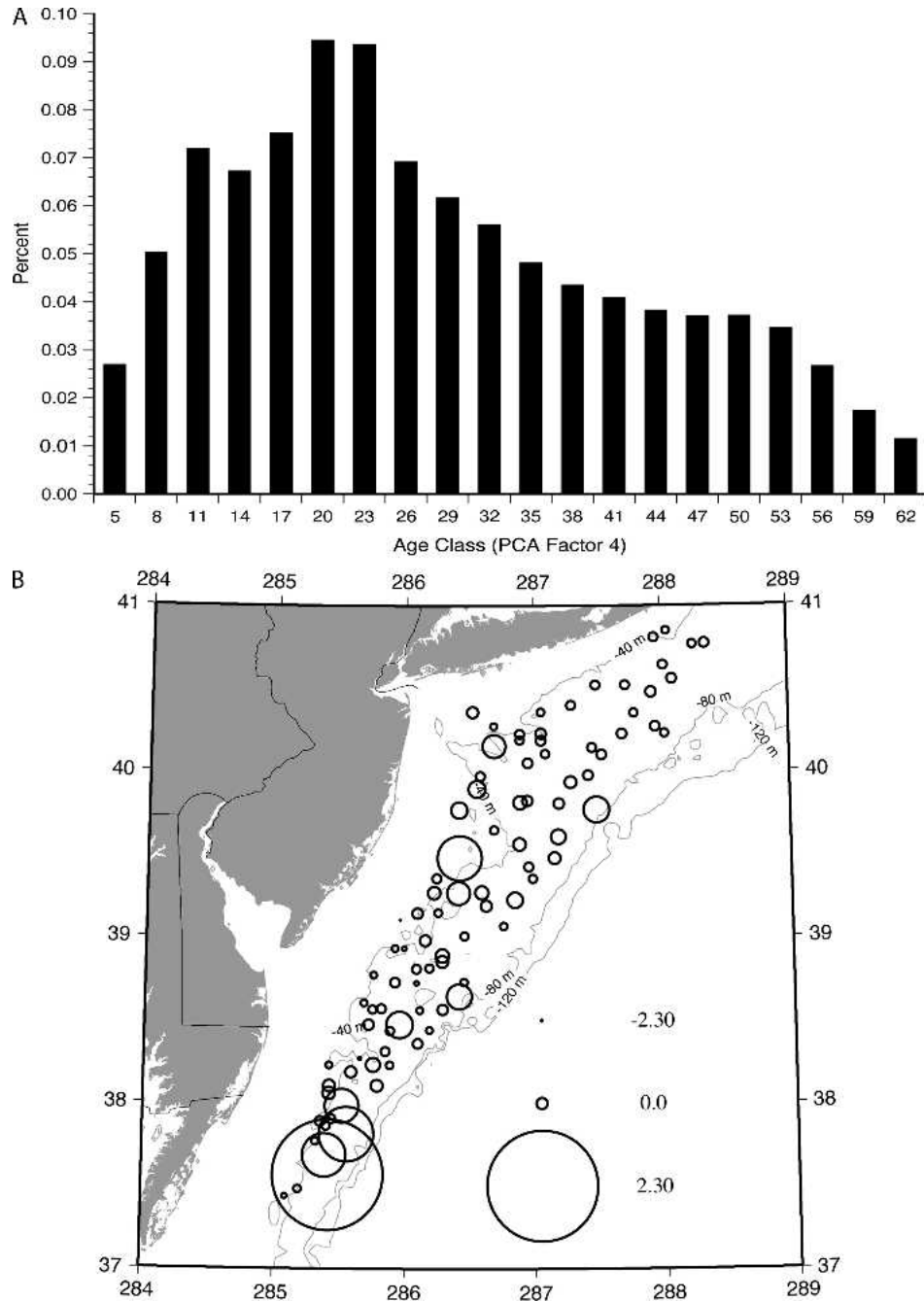


Figure 12. A: Summary age-frequency distribution for all stations with factor scores above 1.0 for Factor 4. Age classes are in 3-y increments with the midpoint of the age class used as the x axis label; B: The geographic distribution of stations with high Factor 4 scores. Factor 4 is weighted most heavily by the youngest ocean quahog age classes in the study. Circle diameter is nonlinearly proportional to factor score. Circle diameter is calculated as $e^{(factor^4)}/10$. Legend shows the size of circles with factor scores of -2.3, 0.0, and +2.3.

DISCUSSION

Bottom water temperature patterns are strongly related to observed recruitment patterns in MAB ocean quahogs. Years in which the number of months with water temperatures 6°C to 10°C (mild) exceed the number of months with water temperatures less than 6°C (cold) by at least two months are also years that contribute strongly to the modal year classes in the population age-frequency distributions. In general, years with above

average monthly bottom water temperatures during January, February, or March have water temperatures in the 6°C to 10°C range instead of the average 4°C to 6°C (depending on latitude) and these years tend to produce year classes that are distinct in the age-frequency distributions from the MAB ocean quahog populations. The persistence of the recruitment signal through time depends on larval and adult biological processes that are driven by ambient water temperatures. Ambient water temperatures influence adult conditioning for spawning (Jones 1981,

TABLE 3.

Results of ANOVA analysis on PCA factor scores. Significance levels given for $\alpha = 0.05$. NS = not significant. Results of *a posteriori* least-square means tests (1–4) provided, where appropriate as defined by superscript annotations in the ANOVA table.

ANOVA Factor	PCA Factor 1	PCA Factor 2	PCA Factor 3	PCA Factor 4
Latitudinal region	0.0077 ¹	0.0001 ²	NS	0.0001 ³
Depth	NS	NS	NS	0.0001 ⁴
Region \times Depth	0.0002	0.0093	NS	0.0005
(1)				
Latitudinal zone	39–40°	38–39°	<38°	
>40°	0.0012	0.0074	NS	
39–40°		NS	NS	
38–39°			NS	
(2)				
Latitudinal zone	39–40°	38–39°	<38°	
>40°	0.0005	0.0001	NS	
39–40°		NS	0.024	
38–39°			0.0048	
(3)				
Latitudinal zone	39–40°	38–39°	<38°	
>40°	NS	NS	0.0001	
39–40°		NS	0.0001	
38–39°			0.0001	
(4)				
Depth zone	43–55 m	> 55 m		
<43 m	0.0007	0.0001		
43–55 m		NS		

Mann 1982), timing of gamete release (Jones 1981, Mann 1982), egg development time (Landers 1976, Lutz et al. 1982, Mann 1986), larval development time (Mann & Wolf 1983), larval distribution in the water column in relation to the thermocline (Mann 1985), and growth postsettlement (Weidman et al. 1994) as well as the distribution of predators (Franz et al. 1981).

Bottom water temperatures on the order of 6°C to 10°C in the period January through March could enhance the observed recruitment signal in several ways. Above average temperatures in January through March would facilitate development of the recruits from the previous season, particularly if warmer temperatures encouraged spring blooms earlier than normal. Warmer spring temperatures may also enhance recruitment associated with that same year in that ocean quahogs in the MAB typically begin gametogenesis in February and March at water temperatures of 6°C to 10°C (Jones 1981, Mann 1982). Earlier onset of suitable temperatures would lengthen the period for optimal gametogenesis and feeding, whereas avoiding exposure to temperatures >10°C that encourage spawning (Mann 1982) and may be more stressful physiologically. Additional gonad development time prior to the seasonal return of predators might translate into increased fecundity early in the spawning season and, subsequently, increased recruitment relative to available broodstock.

TABLE 4.

Long term average annual bottom water temperature (BT) data with standard error of the mean (SEM) for the six stations of interest within the Mid-Atlantic Bight shown in Figure 1.

Station	Average Annual BT 1930–2002 (°C)	SEM	n Months of Data	Years for Which No Data Were Available
Montauk Point	8.68	0.158	641	1930–1946, 1959
Ambrose Channel	9.3	0.153	726	1942, 1945, 1950, 1953
Barnegat	9.22	0.161	648	1930–1946
Five Fathom Bank	10.10	0.145	781	1941–1946
Delaware	9.67	0.141	685	1941–1955
Chesapeake	12.27	0.014	758	1941–1946

Ocean quahogs have been fished commercially since the early 1980s (Cargnelli et al. 1999). Recruitment of this long-lived species is rare throughout most of its MAB habitat with the exception of the southern end of its range where recruitment seems to have been regular in recent years (Powell & Mann 2005). Ironically, the onset of quahog fishery activity followed the 1970s, a decade with multiple consecutive years of above average water temperatures and more frequent periods of good recruitment than previously observed. The relative absence of a recruitment signal since the early 1990s indicated by the age frequencies described herein should be interpreted carefully. Ocean quahogs that were 12–15 y old during sampling in 2002 were between 30–40 mm in shell length and at the lower size limit of what the dredge, even lined with 2.54 cm mesh (see Powell & Mann 2005 for sampling methods), could effectively sample. Animals that recruited after 1990 were certainly under sampled. Accordingly, the strength of year classes since 1990 remains unknown although water temperature data from the late 1990s through 2002 suggest that at least some of these years would have been suitable for good recruitment of ocean quahogs at a level to be discernible when these animals recruit to the fishery at shell lengths of approximately 80 mm.

We examined annual growth increment (mm yr⁻¹) patterns for quahogs 60–70 mm SL from this study by using the power relationship for age-at-length (Eq. 6, Fig. 12). The 60–72 mm SL interval was chosen because it overlaps with the shell lengths examined by Murawski et al. (1982) for calculation of growth increments from mark and recapture studies off Long Island during 1978–1979 and is well represented in collections from this study ($n = 62$). Ocean quahogs 60–72 mm SL captured in 2002 were ages 36–50 y and had growth increments between 0.70 and 0.85 mm yr⁻¹ and were described with a linear model:

$$\text{Annual growth increment mm yr}^{-1} = 1.562 - 0.012\text{SL}, \quad (7)$$

$$R^2 = 0.99$$

Annual growth increments calculated by Murawski et al. (1982) from mark (1978) and recapture (1979 and 1980) data for 60–72 mm SL quahogs range from 0.30–1.40 mm yr⁻¹ (Fig. 2, Murawski et al. 1982). The linear model used by Murawski

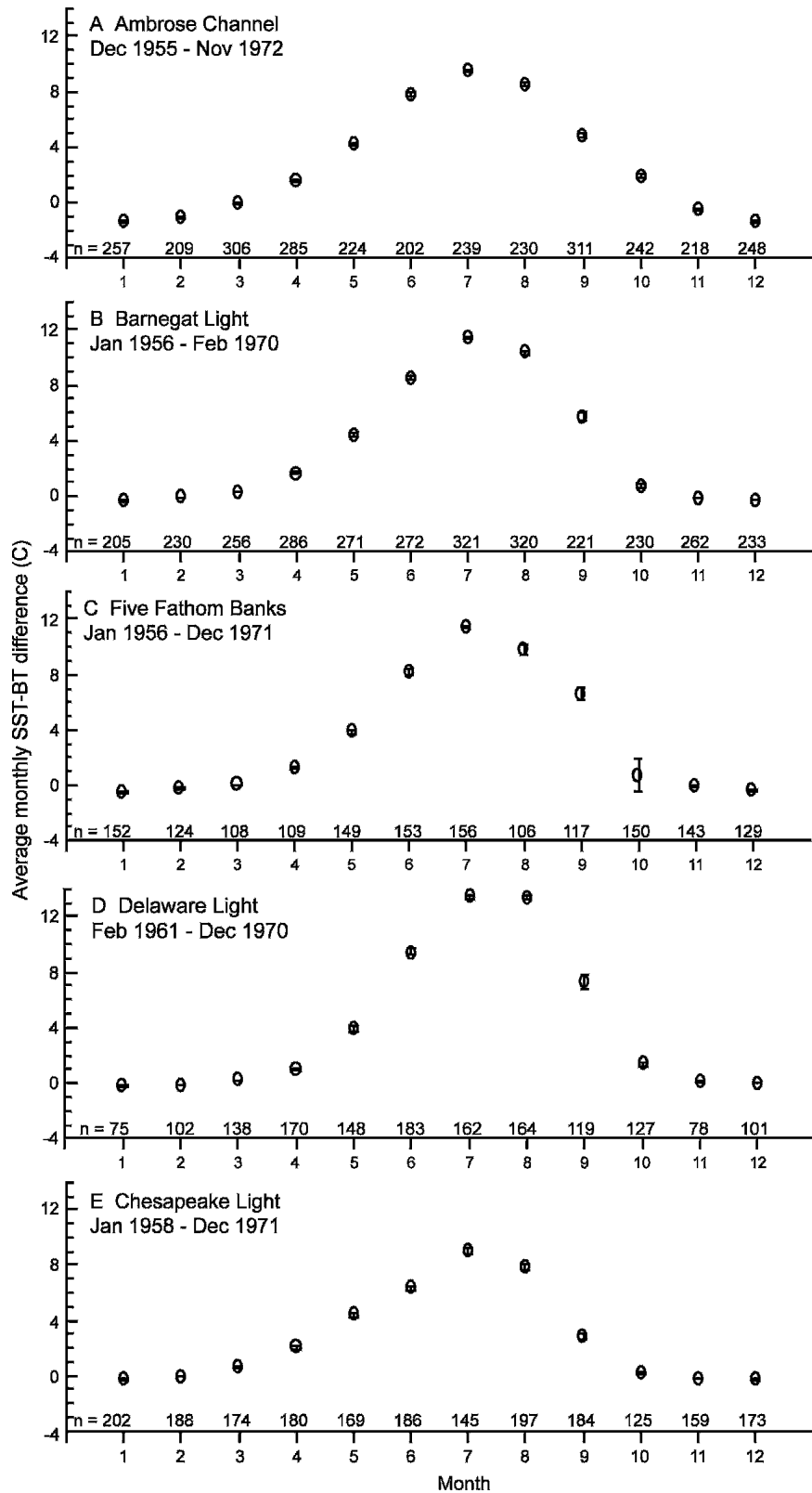


Figure 13. Average monthly difference between sea surface temperature (SST) and bottom water temperature (BT) from lightship data (Table 2) for Ambrose Channel (A), Barnegat (B), Five Fathom Bank (C), Delaware (D), and Chesapeake (E) lightships. Error bars indicate standard error of the mean. The number of daily SST-BT pairs used to estimate monthly SST-BT differences (*n* values) at each site are presented above the X axis in each panel.

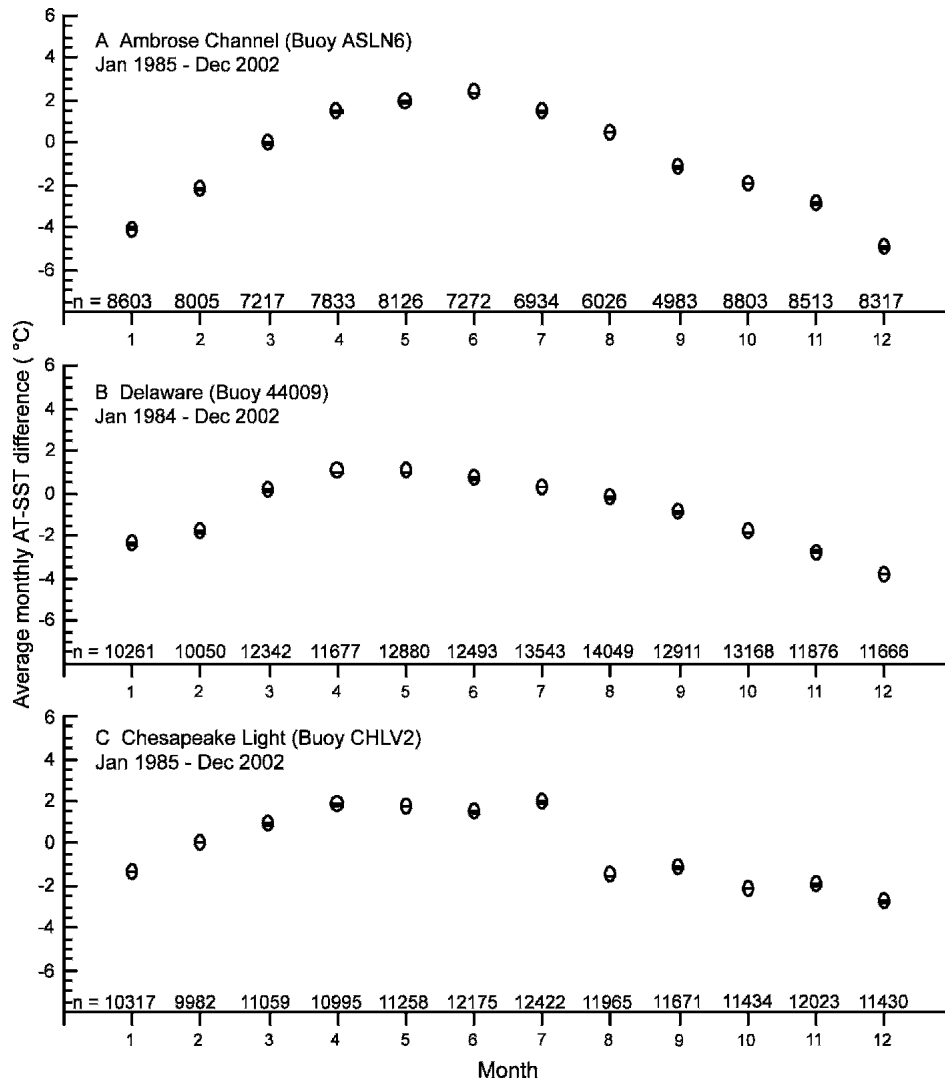


Figure 14. Average monthly difference between air temperature (AT) and sea surface temperature (SST) from NOAA buoy data (Table 2) for Ambrose Channel (ASLN6, A), Delaware (44009, B), and Chesapeake (CHLV2, C) buoys. Error bars indicate standard error of the mean. The number of hourly AT-SST pairs used to estimate monthly AT-SST differences (n values) at each site are presented above the X axis in each panel.

et al. (1982) to describe quahog growth increments from 60–100 mm SL ($n = 67$) is:

$$\begin{aligned} \text{Annual growth increment mm yr}^{-1} &= 2.0811 - 0.019\text{SL}, \\ R^2 &= 0.77 \end{aligned} \quad (8)$$

This model is in close agreement with the linear model from this study. The yearly increment for a 50-mm clam, for example, would be 0.962 by Eq. (7) and 1.131 by Eq. (8), a difference of only 8%. Thus, the empirical data from the mark-recapture study done by Murawski et al. (1982) parallel the age-at-length relationships described herein.

The age-at-length data derived by Murawski et al. (1982) from visual counts of growth bands disagree with the growth-increment data from Murawski et al. (1982) and this study. This disagreement is probably caused by the heavier yearly bands that ocean quahogs deposit every few years. These heavier yearly bands remain identifiable in the 115–120 intensity range (Fig. 5) and are the most apparent growth lines on the shell

surface. Murawski et al. (1982) estimated that 52-mm shell length (SL) ocean quahogs in 1970 were age 12 and 65-mm SL animals in 1980 were age 21. Age-at-length relationships from this study reflect older ages at similar lengths (52 mm SL = age 26, 65 mm SL = age 41, Fig. 12). Examination of bottom water temperatures for 1958 at either Ambrose Channel or Montauk Point shows below average water temperatures at both sites. It is probable, given the observed overall strength of the 1949 y class at the northern edge of ocean quahog distribution in 2002 (Figs. 14, 24–26), that the 1958–1959 y class described by Murawski et al. (1982) was really the 1949 y class, which still persisted in the 2002 samples.

A warming trend has been evident since the 1970s for the southern three temperature stations (Five Fathom Bank, DE, Chesapeake), which also overlap with the area fished extensively for ocean quahogs during much of the 1980s and 1990s (NEFSC 2004). The fact that depth was a significant factor for PCA Factor 4, which represented the most southern stations near Chesapeake, which also experiences the warmest annual

TABLE 5.

Summary of years highlighted by the age-frequency PCA analyses (modal and majority) with regard to the number of months in which mild bottom water temperatures were mild exceeded the number of months categorized as cold per year (mild > cold) by at least two months at each site. The percentage of the number of years identified by the PCA (modal and majority, PCA 1 through 4) was compared with the percentage of years that this mild > cold month pattern occurred at each site between 1940–1994. Site locations are given in Figure 1. Asterisks indicate significance at the $P = 0.05$ level as indicated by Chi Square tests. The abbreviation “Nd” designates years in which no data were available.

PCA 1																			
Relevant Stations	Modal y (52–54 y)		# Years		Years When Mild > Cold		Majority y (46–60 y)		# Years		Years When Mild > Cold		Modal y (52–54 y)		Majority y (46–60 y)		Site %		
	Mild > Cold (#)	#	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold	Mild > Cold	Mild > Cold	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold (%)	Mild > Cold (%)	30–02	30–02	40–94	40–94
Montauk Point	1	3	3	3	1949	1949	1	15	9	1949	1949	33	11	11	11	13			
Ambrose Channel	Nd						0	15	2						25	24			
Barnegat	2	3	3	3	1949, 1950	1949, 50, 52, 53, 54	5	15	9	1949, 50, 52, 53, 54	1949, 50, 52, 53, 54	67	56	56	27	30			
Five Fathom Bank	2	3	3	3	1949, 1950	1949, 50, 52, 53, 54	5	15	9	1949, 50, 52, 53, 54	1949, 50, 52, 53, 54	67	56	56	49	45			
Delaware	Nd														77	77			
Chesapeake	1	3	3	3	1950	1950, 54, 55	3	15	6	1950, 54, 55	1950, 54, 55	33	50	50	49	50			
PCA 2																			
Relevant Stations	Modal y (43–48 y)		# Years		Years When Mild > Cold		Majority y (37–54 y)		# Years		Years When Mild > Cold		Modal y (43–48 y)		Majority y (37–54 y)		Site %		
	mild > cold (#)	#	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold	Mild > Cold	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold (%)	Mild > Cold (%)	30–02	30–02	40–94	40–94	
Montauk Point	0	6	5	6	1954, 58	1949	1	18	17	1949	1949	0	6	11	13				
Barnegat	2	6	6	6	1954, 58	1949, 50, 52, 53, 54, 58	6	18	18	1949, 50, 52, 53, 54, 58	1949, 50, 52, 53, 54, 58	33	33	27	30				
Five Fathom Bank	2	6	6	6	1954, 58	1949, 50, 52, 53, 54, 58	6	18	18	1949, 50, 52, 53, 54, 58	1949, 50, 52, 53, 54, 58	33	33	49	45				
Delaware	3	6	4	6	1957, 58, 59	1957–62, 64, 65	8	18	10	1957–62, 64, 65	1957–62, 64, 65	75	80	77	77				
Chesapeake	3	6	6	6	1954, 55, 57	1950, 54, 55, 57	4	18	16	1950, 54, 55, 57	1950, 54, 55, 57	50	25	49	50				
PCA 3																			
Relevant Stations	Modal y (22–30 y)		# Years		Years When Mild > Cold		Majority y (19–36 y)		# Years		Years When Mild > Cold		Modal y (22–30 y)		Majority y (19–36 y)		Site %		
	Mild > Cold (#)	#	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold	Mild > Cold	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold (%)	Mild > Cold (%)	30–02	30–02	40–94	40–94	
Montauk Point	2	9	9	9	1974, 76	1974, 76, 83	3	19	19	1974, 76, 83	1974, 76, 83	22	16	11	13				
Ambrose Channel	4	9	9	9	1974, 76, 78, 80	1974, 76, 78, 80	4	19	19	1974, 76, 78, 80	1974, 76, 78, 80	44	21	25	24				
Barnegat	4	9	9	9	1972, 74, 76, 80	1966, 72, 74, 76, 80, 83	6	19	19	1966, 72, 74, 76, 80, 83	1966, 72, 74, 76, 80, 83	44	32	27	30				
Five Fathom Bank	8	9	9	9	1972–77, 79, 80	1972–77, 79, 80–83	11	19	19	1972–77, 79, 80–83	1972–77, 79, 80–83	89*	58	49	45				
Delaware	8	9	9	9	1972–77, 79, 80	1966, 68, 72–77, 79–83	13	19	19	1966, 68, 72–77, 79–83	1966, 68, 72–77, 79–83	89	68	77	77				
Chesapeake	8	9	9	9	1972–77, 79, 80	1966, 72–77, 79–81, 83	11	19	19	1966, 72–77, 79–81, 83	1966, 72–77, 79–81, 83	89*	58	49	50				
PCA 4																			
Relevant Stations	Modal y (19–24 y)		# Years		Years when Mild > Cold		Majority y (10–30 y)		# Years		Years When Mild > Cold		Modal y (19–24 y)		Majority y (10–30 y)		Site %		
	Mild > Cold (#)	#	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold	Mild > Cold	#	w Data	Mild > Cold	Mild > Cold	Mild > Cold (%)	Mild > Cold (%)	30–02	30–02	40–94	40–94	
Chesapeake	4	6	6	6	1979, 80, 81, 83	1972–77, 79–81, 83–85, 88–92	17	21	21	1972–77, 79–81, 83–85, 88–92	1972–77, 79–81, 83–85, 88–92	67	81*	49	50				

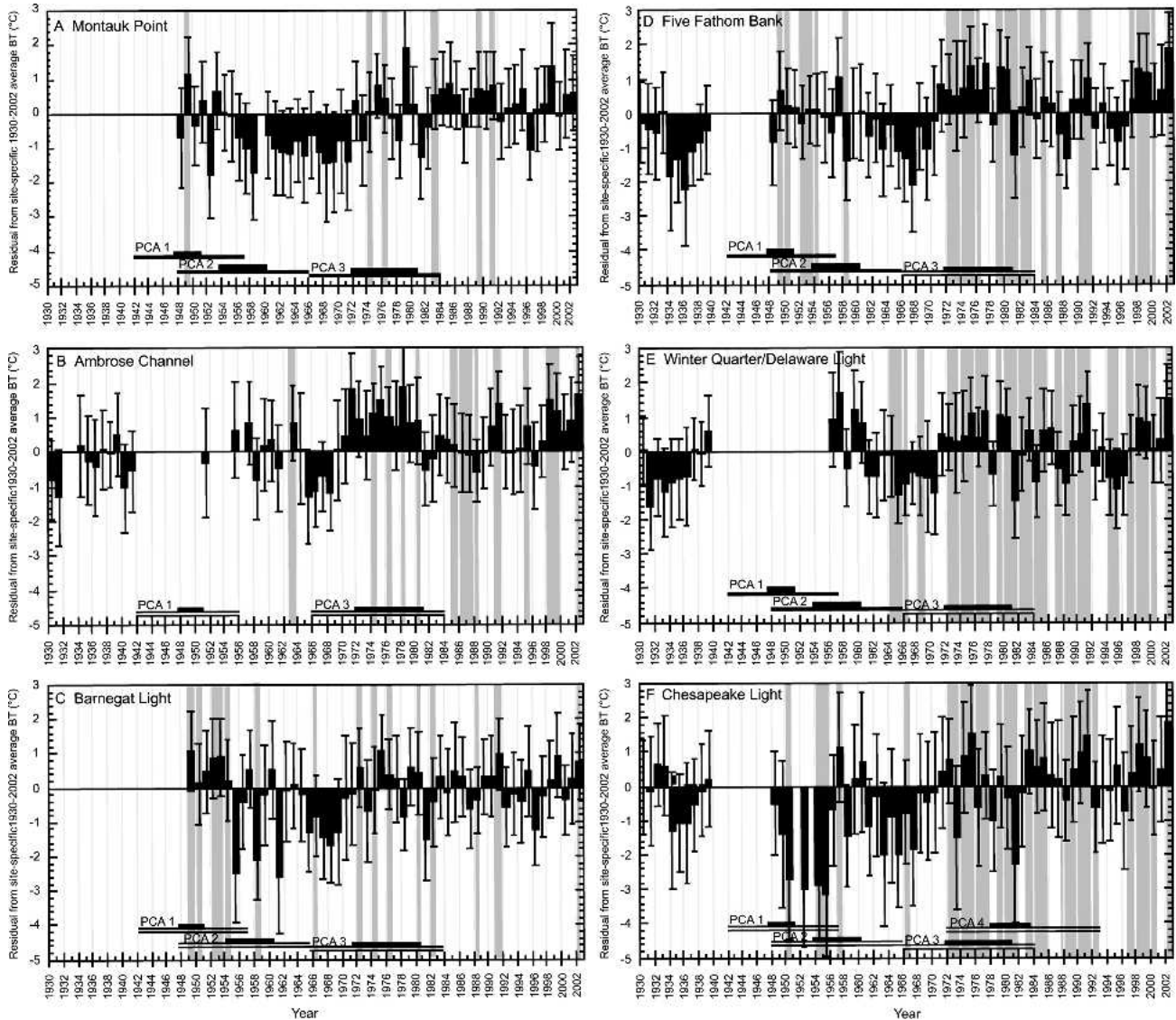


Figure 15. Annual average deviations of bottom temperatures (BT) from the long-term (1930–2002) average bottom temperatures for Montauk Point (A), Ambrose Channel (B), Barnegat (C), Five Fathom Bank (D), Delaware (E), and Chesapeake (F). The error bars represent the standard error of the mean in °C. The grey vertical bars highlight years in which the number of mild months (BT 6–10°C) exceeded the number of cold months (BT <6°C) by 2 or more. Thick black horizontal bars delineate the years that correspond to the years indicated as modal years by the PCA analyses of age frequencies for ocean quahogs (Figures 9–12, Table 5). Double black horizontal bars delineate the years that correspond to the years indicated as majority years by the PCA analyses of age frequencies for ocean quahogs (Figures 9–12, Table 5).

temperature cycle, may indicate that quahogs in this region rely on burrowing as a means to tolerate or ameliorate seasonal periods of warmer bottom water temperatures. Ocean quahog habitat is three-dimensional and quahogs can burrow and survive anoxia for extended periods of time (Taylor 1976a, 1976b) taking advantage of differential burial depths in relation to ambient bottom water temperatures. Burrowing to avoid warm temperatures may also offer quahogs a depth-based refuge from fishing gear if burial depths are below the maximum gear penetration depth.

Changes in the seasonal periodicity and increased duration of periods of warmer bottom water temperatures have the potential to affect the distribution and composition of faunal assemblages on local and regional scales as well as the biology

and functional relationships of one particular species. At the species level, water temperatures directly affect physiological rates (feeding, respiration) as well as timing and duration of reproductive seasons and, in the case of mobile demersal species, seasonal migrations into and out of suitable feeding habitat as defined by bottom water isotherms. For ocean quahogs, increased frequency of water temperatures 6°C to 8°C probably would not increase predator contact time and foraging efficiency. However these periods of 6°C to 8°C temperatures might delay the arrival of water temperatures >8°C and the predators that are restricted by this isotherm. The temporal and spatial delay in foraging habitat availability for predators may provide a thermal refuge to facilitate an early-enhanced growth period.

TABLE 6.

Summary of Pearson correlation P values. Correlations were made between monthly bottom water temperatures from each site during the years included in the PCA age frequency distributions (Figs. 9A-13A) and the percentage of quahogs observed in each age class for each of the four PCA age frequency distributions (Figs. 9A-13A). Nonsignificant P values are indicated by "ns". Site/month combinations for which there are no available water temperature data are indicated by "x". The year(s) in parentheses after each PCA are the modal year(s) for each distribution (Table 5, Figs. 9-13A).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
PCA 1: 1949												
Five Fathoms	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Delaware	x	x	x	x	x	x	x	x	x	x	x	x
Chesapeake	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
PCA 2: 1954-59												
Montauk Point	<0.01	<0.01	0.01	ns	ns	ns	ns	ns	ns	ns	0.02	<0.01
Ambrose Channel	0.03	ns	0.03	0.05	0.05	ns	0.04	ns	ns	ns	ns	ns
Barnegat Light	ns	ns	ns	ns	ns	ns	0.04	ns	ns	ns	ns	ns
Five Fathoms	ns	ns	0.02	ns	ns	ns	0.02	ns	ns	ns	ns	ns
Delaware	ns	ns	ns	ns	ns	ns	ns	<0.01	ns	ns	ns	ns
Chesapeake	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
PCA 3: 1972-80												
Montauk Point	ns	ns	ns	0.01	ns	<0.01	0.03	ns	ns	ns	ns	ns
Ambrose Channel	0.01	0.04	0.02	ns	ns	ns	0.04	ns	ns	ns	ns	<0.01
Barnegat Light	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Five Fathoms	ns	0.03	<0.01	ns	ns	ns	ns	<0.01	ns	ns	ns	0
Delaware	ns	0.02	0.03	ns	ns	ns	ns	ns	ns	ns	ns	0.02
Chesapeake	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
PCA 4: 1978-83												
Montauk Point	<0.01	<0.01	0.05	ns	ns	ns	ns	ns	ns	ns	0.01	<0.01
Ambrose Channel	0.02	ns	ns	ns	ns	ns	0.05	ns	ns	ns	0.04	ns
Barnegat Light	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Five Fathoms	ns	0.03	<0.01	ns	ns	ns	ns	ns	ns	ns	ns	0.03
Delaware	ns	0.03	0.03	ns	ns	ns	ns	ns	ns	ns	ns	ns
Chesapeake	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns

Seasonally warmer temperatures may facilitate quahog recruitment, but consistently warmer temperatures year round have the potential to shift the observed distribution of sessile benthic animals (ocean quahogs and surf clams) to deeper water and more northerly areas so as to take advantage of cooler (suitable) habitat (Weinberg 2005). Franz and Merrill (1980a, 1980b) and Dahlgren et al. (2000) describe the role that submergence has played in allowing ocean quahogs to invade and maintain populations along the MAB. Habitats occupied by ocean quahogs where submergence may occur would shift to deeper or more northern regions with gradual trends toward warmer bottom water temperatures. The possibility exists that the distribution of Atlantic surf clams *Spisula solidissima* and other members of the faunal assemblages would follow this trend according to thermal tolerances. Weinberg (2005) reported a shift in distribution of Atlantic surf clams in the Delmarva region of the southern MAB toward deeper and more northern regions in relation to warmer water temperatures observed in the late 1990s. A gradual transition from one MAB benthic dominant species (ocean quahogs) to another MAB species that is more tolerant of warmer temperatures (surf clams) may already be in progress at the southern end of the MAB. Reinvasion of these southern habitats by ocean quahogs would be less likely if water temperatures in the area continue to rise. Faunal communities in these continental shelf habitats, predators as well as prey, that rely on the

seasonal progression of isotherms to set habitat boundaries may be gradually forced into more northern and eastern (deeper) habitats. These changes will set the stage for gradual shifts of faunal assemblages along the United States east coast with one possible outcome being the northern extension of ranges and communities that formerly were restricted south of Cape Hatteras as well as south of Cape Cod by water temperatures.

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TABLE 7.

Summary of monthly bottom water temperatures at each site in relation to the long term (1930–2002) monthly average (A) for the modal year(s) described by each of the four PCA age frequency distributions (B to E; Figs. 9A–13A). Site/month combinations for which there are no available water temperature data are indicated by “x”. The year(s) in parentheses after each PCA are the modal year(s) for each distribution (Table 5, Figs. 9–13A).

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
A. Average 1930–2002												
Montauk Pt	5.69	4.24	3.69	4.61	6.17	7.80	10.55	12.55	14.45	13.84	12.12	8.60
Ambrose Ch	6.44	4.60	3.96	5.25	7.27	8.98	11.36	13.34	15.55	14.39	12.03	9.62
Barnegat	5.79	4.22	4.26	5.44	7.26	8.85	10.22	12.10	15.18	15.90	12.67	8.76
Five Fathoms	6.44	4.85	5.11	6.58	8.78	9.98	10.92	13.51	14.96	16.91	13.60	9.83
Delaware	7.00	5.25	5.29	6.83	8.72	9.19	9.21	10.46	14.47	16.52	13.54	9.95
Chesapeake	7.13	5.55	6.03	8.11	10.95	14.27	14.82	16.53	20.25	19.14	14.82	10.41
B. PCA 1: 1949												
Montauk Pt	0.93	0.73	0.44	1.88	2.50	2.82	1.73	1.03	0.63	1.07	0.10	–0.58
Ambrose Ch	1.24	x	x	x	x	x	x	x	x	x	x	x
Barnegat	0.93	1.43	0.75	1.03	1.57	2.12	1.88	1.66	–0.53	1.24	0.99	–0.28
Five Fathoms	–0.11	1.58	0.46	0.08	0.73	1.61	1.48	1.07	–0.57	0.46	0.57	0.28
Delaware	x	x	x	x	x	x	x	x	x	x	x	x
Chesapeake	0.72	x	x	x	0.53	0.18	1.49	–0.64	–1.61	0.98	0.59	–0.05
C. PCA 2: 1954–59												
Montauk Pt	–1.82	–1.50	–0.11	0.35	0.75	0.56	0.11	–0.10	0.01	0.18	–0.54	–2.14
Ambrose Ch	–0.88	–0.09	0.02	–0.36	–1.01	–0.95	–0.79	0.68	–0.68	0.85	0.30	–0.27
Barnegat	–0.95	–0.58	–0.17	0.15	0.52	0.18	–0.79	–0.31	0.12	0.59	–0.17	–0.39
Five Fathoms	–0.12	–0.54	–0.48	0.12	–0.12	–0.06	–0.64	–0.25	–0.36	0.32	0.24	–0.23
Delaware	–0.20	–0.45	–0.10	0.38	0.62	1.73	0.77	2.92	1.54	0.99	0.44	0.53
Chesapeake	–1.02	–0.56	0.25	0.12	–0.01	0.06	–0.58	0.55	0.37	–0.64	–0.57	–0.38
D. PCA 3: 1972–80												
Montauk Pt	2.32	1.87	0.70	–0.47	–0.55	–0.98	–0.47	0.15	–0.63	0.10	0.89	1.70
Ambrose Ch	2.44	1.60	1.54	0.69	–0.11	0.18	1.21	0.95	0.48	–0.43	0.90	1.64
Barnegat	1.52	1.25	1.07	–0.08	–0.36	0.01	–0.20	0.32	–0.19	–0.01	0.42	0.74
Five Fathoms	1.79	1.88	2.11	0.85	0.49	0.34	0.56	0.99	0.45	0.67	0.41	1.93
Delaware	1.41	1.40	1.78	0.76	0.47	–0.14	0.28	0.51	0.24	0.34	0.19	1.49
Chesapeake	1.40	1.03	1.17	0.26	0.38	–0.28	0.38	0.20	–0.24	0.16	0.62	1.45
E. PCA 4: 1978–83												
Montauk Pt	1.48	0.80	0.08	–0.60	–0.22	–0.68	0.06	–0.28	–0.82	0.18	1.26	1.20
Ambrose Ch	1.36	1.00	0.41	0.08	–0.19	–0.32	1.11	0.47	1.44	0.62	0.74	0.87
Barnegat	0.72	0.62	0.06	–0.46	–0.12	–0.42	–0.07	0.20	–0.59	–0.06	0.02	–0.29
Five Fathoms	1.20	1.61	1.18	0.42	0.37	0.00	0.66	0.56	–0.41	–0.20	–0.06	1.06
Delaware	0.72	1.13	0.86	0.34	0.36	–0.47	0.38	0.08	–0.62	–0.53	–0.30	0.62
Chesapeake	0.52	–0.34	–0.63	–0.61	–0.17	–0.42	0.14	0.59	–0.89	–0.41	–0.37	0.00

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Data Appendix 1.

The fraction of a size class (SC, 5 mm bins) within an age class (AC, 3 y bins) for young ocean quahogs from the MidAtlantic Bight. These data are plotted Figure 6.

	SC 3	SC 4	SC 5	SC 6	SC 7	SC 8	SC 9	SC 10	SC 11	SC 12	SC 13	SC 14	SC 15	SC 16	SC 17
AC 1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
AC 2	0.9917	0.6861	0.1355	0.1564	0.0193	0	0	0	0	0	0	0	0	0	0
AC 3	0.0083	0.1363	0.4790	0.3550	0.0932	0.0121	0.0426	0	0.0025	0.0199	0	0	0	0	0
AC 4	0	0.0592	0.2877	0.2453	0.2295	0.1279	0.0232	0.0385	0.0574	0.0269	0	0	0	0	0
AC 5	0	0.0787	0.0559	0.1307	0.2254	0.2146	0.0845	0.1044	0.0310	0.0118	0.0021	0	0	0	0
AC 6	0	0.0377	0.0353	0.0580	0.1522	0.2503	0.2386	0.1104	0.0546	0.0448	0.0236	0	0	0	0
AC 7	0	0.0020	0.0064	0.0378	0.1361	0.2064	0.2754	0.2300	0.1438	0.0705	0.0412	0.0023	0.0002	0	0.0002
AC 8	0	0	0	0.0141	0.1101	0.1307	0.1662	0.2616	0.1658	0.1046	0.0653	0.0331	0.0092	0	0.0046
AC 9	0	0	0	0.0025	0.0328	0.0531	0.0884	0.1359	0.1535	0.0912	0.0774	0.0560	0.0394	0	0.0177
AC 10	0	0	0	0	0.0012	0.0046	0.0575	0.0677	0.1424	0.1133	0.0917	0.0754	0.0721	0.0028	0.0248
AC 11	0	0	0	0	0	0	0.0208	0.0327	0.0931	0.1326	0.1083	0.1112	0.0752	0.0224	0.0231
AC 12	0	0	0	0	0	0	0.0029	0.012	0.0556	0.1271	0.0807	0.1000	0.0635	0.0533	0.0446
AC 13	0	0	0	0	0	0	0	0.0050	0.0359	0.1108	0.0566	0.0930	0.0819	0.0795	0.0604
AC 14	0	0	0	0	0	0	0	0.0016	0.0189	0.0875	0.0684	0.1063	0.1202	0.1019	0.0484
AC 15	0	0	0	0	0	0	0	0.0002	0.0119	0.0458	0.0926	0.1186	0.1438	0.1054	0.0432
AC 16	0	0	0	0	0	0	0	0	0.0135	0.0128	0.0922	0.1204	0.1293	0.1047	0.0718
AC 17	0	0	0	0	0	0	0	0	0.0120	0.0004	0.0717	0.0980	0.0909	0.1074	0.1242
AC 18	0	0	0	0	0	0	0	0	0.0064	0	0.0544	0.0581	0.0583	0.1038	0.1463
AC 19	0	0	0	0	0	0	0	0	0.0019	0	0.0394	0.0230	0.0415	0.0808	0.1236
AC 20	0	0	0	0	0	0	0	0	0.0001	0	0.0233	0.0045	0.0294	0.0565	0.0838
AC 21	0	0	0	0	0	0	0	0	0	0	0.0094	0.0003	0.0207	0.0424	0.0585