

Precise Temporal Correlation of Holocene Mollusk Shells Using Sclerochronology

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Annual growth bands of mollusk shells record several types of paleoenvironmental information, including geochemical proxies for water properties and morphological characteristics of growth and mortality. Sclerochronology, the marine counterpart of dendrochronology, offers a way to link individual shells together to form long continuous records of such parameters. It also allows for precise dating of recent shells and identification of contemporaneous fossil individuals. The longevity of the ocean quahog *Arctica islandica* (commonly >100 yr) makes this species well suited for sclerochronology. Band width records of contemporaneous *A. islandica* specimens from the same region exhibit high correlations ($\rho = 0.60$ – 0.80 for spans of ≥ 30 bands), indicating some common environmental influences on shell growth. By adopting several strict criteria, fossil (dead-collected) shells can be linked into composite sclerochronologies. A seven-shell 154-yr chronology was constructed for Georges Bank using three live-collected and four dead-collected shells. Band width matching indicates that the dead-collected individuals died in A.D. 1950, 1971, 1978, and 1989. Sclerochronological age assignments were verified using aspartic acid racemization dating. Construction of a 1000-yr sclerochronology is judged to be feasible using the described methods. © 2000 University of Washington.

INTRODUCTION

Biologists and paleontologists have long been intrigued by growth banding in mollusk shells. The periodicity of

these increments ranges from semidiurnal to annual, and they generally result from interactions between the environment and the organism's physiology (see Lutz and Rhoads, 1980, for a review). Although genetic factors can influence initial growth rates and other fitness-related traits (David *et al.*, 1995), year-to-year variability is mainly caused by external factors. Variations in growth banding (both mineralogical and structural) are thus potential recorders of various environmental parameters, including temperature, salinity, nutrients, and dissolved oxygen (Carter, 1980). Growth bands are also useful as temporal frameworks for interpreting within-shell time series of geochemical proxies such as $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Several mollusk species have been used to obtain continuous (subannual to decadal) isotopic records, including the California mussel *Mytilus californianus* (Killingley and Berger, 1979), the Atlantic surf clam *Spisula solidissima* (Williams *et al.*, 1982; Arthur *et al.*, 1983; Krantz *et al.*, 1987), and the hard clam (quahog) *Mercenaria mercenaria* (Jones *et al.*, 1989). Finally, patterns of growth banding are valuable tools for population studies, offering information about life spans, growth rates (including genetic influences), and seasonalities of recruitment (survival of larvae) and mortality (e.g., Rhoads and Pannella, 1970; Tevesz, 1972; Kennish, 1980; David *et al.*, 1995).

Given that molluscan growth band characteristics are influenced by the environment, individuals from within a population can be expected to share similar growth records. For example, each member of a population might form a thick annual band during a "good" year and thin bands during

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subsequent "bad" years. Theoretically, then, records of these band widths from different individuals could be correlated and spliced together to produce long sclerochronologies, in analogy to tree ring dendrochronologies. Specimens from within a living population may often be matched in this way (Jones, 1980, 1981, 1983; Thompson *et al.*, 1980; Jones *et al.*, 1989; Witbaard and Duineveld, 1990), but we are not aware of any previous attempts to patch back in time using dead-collected shells.

The main purpose of the present study was to build the first such composite mollusk sclerochronology. Composite sclerochronologies would offer long records of growth/environmental variations and also provide extended temporal frameworks for geochemical measurements. In addition, exactly contemporaneous individuals from within a fossil population could be identified, potentially revealing such important events as successful recruitments and mass mortalities.

SUITABILITY OF *ARCTICA ISLANDICA*

The ocean quahog *Arctica islandica* (range commonly 35–70°N and 10–280 m depth in the North Atlantic; Nicol, 1951) is an ideal species with which to build composite sclerochronologies. It forms easily identified annual growth bands and has a very long lifespan, frequently living over 100 yr (Jones, 1980; Thompson *et al.*, 1980; Murawski *et al.*, 1982), with one specimen reported at 220 yr (Jones, 1983). This longevity means that, relative to shorter-lived taxa, fewer specimens are required to span a given interval of time. In addition, longer overlapping series of years allow for more robust tests of correlation between individuals.

Arctica islandica has also been shown to be a useful isotopic recorder. Weidman *et al.* (1994) adapted the microsampling techniques of Dettman and Lohmann (1993) to produce a high-resolution $\delta^{18}\text{O}$ record from an *A. islandica* shell collected alive from 60 m depth on Nantucket Shoals. This record spanned A.D. 1956–1957 and 1961–1970, with up to 50 samples per annual band. Comparison to nearby instrumental measurements of bottom water temperature and salinity over the same interval showed that the oxygen of *A. islandica* shell carbonate is in isotopic equilibrium with ambient seawater. This allowed Weidman (1995) to construct a 109-yr (A.D. 1875–1983) record of Nantucket Shoals bottom temperatures, using $\delta^{18}\text{O}$ measurements from four live-collected individuals. Weidman and Jones (1993a, 1993b) also constructed a 52-yr (A.D. 1939–1990) $\Delta^{14}\text{C}$ time history using an *A. islandica* shell collected alive from southeastern Georges Bank. The timing of the bomb pulse (^{14}C increase from thermonuclear testing) agreed very well with Druffel's (1989) coral records from Florida and Bermuda. Similar shell-derived $\Delta^{14}\text{C}$ records have been obtained from Iceland, Norway, and the North Sea (Weidman, 1995). Such high-resolution records of $\delta^{18}\text{O}$ and $\Delta^{14}\text{C}$ are unprecedented for middle and high latitudes, and the

potential exists to extend them much further back in time using sclerochronology.

MATERIALS AND METHODS

Both live and dead *A. islandica* specimens were dredged from a number of sites southeast of New England and north of Iceland between 1982 and 1994 (see Table 1). Relatively long-lived individuals (mean age of 85 yr) were chosen for this study to maximize the length of growth band records. Shells were prepared for band analysis by making thin-sections, following the methods of Weidman and Jones (1993a, 1993b). A 2-mm-thick radial slice was cut from one valve of each individual, along the axis of maximum linear growth (umbo to ventral margin; Fig. 1) using a low-speed lapidary saw with diamond wafer blades. This slice was mounted on a glass petrographic slide with epoxy and ground down to a shell thickness of 50–150 μm . The thin-section was then viewed with a transmitting light microscope at 35 \times magnification, using plane-polarized light. Starting at the ventral margin, band widths were measured using a morphometrics computer program. The first 20–25 bands of each individual's life were not analyzed because they were too wide to be clearly imaged. Although bands can also be examined at the hinge plate (e.g., Thompson *et al.*, 1980; Jones, 1980; Ropes, 1985), they are often too thin and crowded in this area to be accurately measured.

A plot of band width vs band number (or year, if known) shows a strong growth curve, with widths decreasing asymptotically as the animal ages (Fig. 2). This trend was removed by fitting the data with a smooth spline that preserves decadal-scale band width fluctuations which are unrelated to the growth curve. Tree ring width series are usually treated in a similar manner (see Cook *et al.*, 1995, for a review). The specific curve equation used is not important, as long as it is fairly stiff and fits the data reasonably well (see Fig. 2). The residuals of this spline fit were then standardized by dividing by the standard deviation of the residual population. Standardized band widths are thus expressed as the number of standard deviations away from zero, with wider bands being positive and thinner bands being negative. Although the standardized band widths tend to exhibit slightly greater variance in the earlier years of shell growth, removal of this second trend did not improve correlations between shells and was not performed. Individual shells were compared via the correlation coefficient, ρ . A Matlab script was used to calculate the correlation coefficient for every possible alignment of two individual records, to find the most likely match. Significance was assessed in terms of significance probability (p), which is the probability that a higher correlation coefficient (ρ) could arise by chance over a given number of bands (n). It is calculated (SAS Institute Inc., 1990) by assuming that the statistic $P = \rho(n - 2)^{1/2} / (1 - \rho^2)^{1/2}$ has a two-tailed t distribution with $n - 2$ degrees of freedom.

Samples for aspartic acid (Asp) analyses were cut from halved or sliced shells using a Dremel hand tool with a diamond wafer blade. Each sample represented 1 to 7 yr of

TABLE 1

Shells Analyzed during This Study

Shell ID	No. of bands	Site coordinates	Depth (m)	Region	Analyses
I1-1	82	66°10'N, 18°53'W	22	Iceland	s
I1-3	36	66°10'N, 18°53'W	22	Iceland	s
I1-5	35	66°10'N, 18°53'W	22	Iceland	s
I1-9	40	66°10'N, 18°53'W	22	Iceland	s
I1-10	40	66°10'N, 18°53'W	22	Iceland	s
82-381-1	100	41°05'N, 66°56'W	67	Georges Bank	c
82-381-3	61	41°05'N, 66°56'W	67	Georges Bank	c
82-381-4	66	41°05'N, 66°56'W	67	Georges Bank	c
92-315-3	105	40°28'N, 69°29'W	66	Nantucket Shoals	o, a
92-315-4	30	40°28'N, 69°29'W	66	Nantucket Shoals	a
92-315-7	87	40°28'N, 69°29'W	66	Nantucket Shoals	d, o
92-315-10	*	40°28'N, 69°29'W	66	Nantucket Shoals	a
92-315-12	*	40°28'N, 69°29'W	66	Nantucket Shoals	a
92-315-13	30	40°28'N, 69°29'W	66	Nantucket Shoals	d, o
92-315-28	*	40°28'N, 69°29'W	66	Nantucket Shoals	a
92-333-1	80	41°08'N, 67°27'W	57	Georges Bank	d
92-333-2	31	41°08'N, 67°27'W	57	Georges Bank	d
92-333-3	31	41°08'N, 67°27'W	57	Georges Bank	d
92-334-1	60	41°03'N, 67°18'W	67	Georges Bank	d
92-334-2	37	41°03'N, 67°18'W	67	Georges Bank	d
92-334-3	58	41°03'N, 67°18'W	67	Georges Bank	d
92-335-f1	55	41°01'N, 67°10'W	72	Georges Bank	c
92-335-f2	65	41°01'N, 67°10'W	72	Georges Bank	c
92-335-f3	54	41°01'N, 67°10'W	72	Georges Bank	c
92-335-f4	36	41°01'N, 67°10'W	72	Georges Bank	c
92-336-1	51	41°01'N, 67°05'W	70	Georges Bank	d
92-336-2	66	41°01'N, 67°05'W	70	Georges Bank	d
92-336-3	31	41°01'N, 67°05'W	70	Georges Bank	d
92-336-f3	30	41°01'N, 67°05'W	70	Georges Bank	c
92-336-f4	31	41°01'N, 67°05'W	70	Georges Bank	c
92-337-f1	87	41°04'N, 66°51'W	79	Georges Bank	c
92-337-f2	57	41°04'N, 66°51'W	79	Georges Bank	c
92-337-f3	35	41°04'N, 66°51'W	79	Georges Bank	c, a
92-337-f4	125	41°04'N, 66°51'W	79	Georges Bank	c
92-337-f5	37	41°04'N, 66°51'W	79	Georges Bank	c
92-339-1	59	41°06'N, 66°56'W	73	Georges Bank	d, c
92-339-2	57	41°06'N, 66°56'W	73	Georges Bank	d, c
92-339-3	50	41°06'N, 66°56'W	73	Georges Bank	d, c, a
92-339-f1	86	41°06'N, 66°56'W	73	Georges Bank	c, a
92-339-f2	30	41°06'N, 66°56'W	73	Georges Bank	c
92-339-f3	67	41°06'N, 66°56'W	73	Georges Bank	c, a
92-339-f4	85	41°06'N, 66°56'W	73	Georges Bank	c
92-339-f5	60	41°06'N, 66°56'W	73	Georges Bank	c
94-441-1	51	41°03'N, 66°53'W	74	Georges Bank	d, c
94-441-2	47	41°03'N, 66°53'W	74	Georges Bank	d, c
94-441-3	60	41°03'N, 66°53'W	74	Georges Bank	d, c

Note. Shell ID notation for Georges Bank and Nantucket Shoals is as follows: (year of collection)-(NMFS site no.)-(shell no., with “f” indicating fossil). No. of bands is the number of measured bands; asterisks indicate that bands were not measured, only counted. Analyses performed were: s, synchronization test; d, distance test; c, composite sclerochronology; o, comparison to $\delta^{18}\text{O}$ record; a, Asp measurement.

growth, depending on band widths. The inner shell layer (nonsynchronous material) and periostracum (organic outer covering) were not used. Aspartic acid D/L ratios were measured by gas chromatography at the Carnegie Institution of Washington, following the methods of Goodfriend (1991).

RESULTS AND DISCUSSION

Band Width Synchronization

The first step in developing a composite sclerochronology for *A. islandica* was verifying that growth band widths vary in parallel among members of a population. Thompson *et al.*

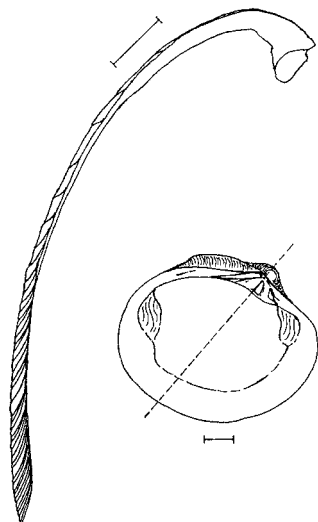


FIG. 1. (right) Interior of left valve of *A. islandica*, showing the direction of cut for growth band analysis (dashed line). (left) Radial slice along that line, revealing about 43 annual growth bands. The concave surface is the valve's interior, and the lower end is the ventral growth margin. Scale bars are 1 cm. After Ropes (1985) and Weidman and Jones (1993).

(1980) demonstrated qualitative band width synchronization among 10 young *A. islandica* individuals collected off of Long Island, over a span of nine bands. Similarly, Witbaard and Duineveld (1990) found qualitative synchronization of growth among seven young specimens from the northern North Sea, over a span of 10 yr. To quantitatively verify this synchronization over longer periods, five shells collected alive in 1992 from a single site off northern Iceland were examined (all specimen identification and collection site information is listed in Table 1). These individuals range in age from 54 to 135 yr, and a span of 35 measurable bands (A.D. 1957–1991) is shared by all of them.

Comparison of standardized band widths over this interval yields excellent correlations for four of the five records (I1-1, I1-5, I1-9, and I1-10; Fig. 3). Among these four, the lowest correlation coefficient is 0.58, the highest is 0.79, and the mean is 0.70; all significance probabilities are <0.00005 except one (0.0003). The fifth shell (I1-3) correlates to the others with ρ between 0.27 and 0.66 ($p = 0.12$ to <0.00005). These results indicate that band widths are synchronized within a population over periods longer than a decade, making the creation of long, composite sclerochronologies theoretically possible. In addition, correlation appears to be independent of the lifespan of the individuals; I1-1, which is ~ 40 – 50 yr older than the other specimens, is highly correlated with I1-5, I1-9, and I1-10 (all $\rho > 0.70$, $p < 0.00005$). Thus band widths in *A. islandica* must indeed be influenced by some external environmental factor(s), as will be discussed later.

Another important step was to determine the geographical distance over which this band width synchronization holds. Are band widths controlled by very localized environmental

factors, such that two clams must be from the same trawl to correlate well? Or is growth controlled by regional factors, producing synchronization in individuals hundreds of kilometers apart? To answer these questions, shells were examined from a transect of five stations on Georges Bank (stations 333, 334, 336, 339, and 441 in Fig. 4). These sites range from 7 to 48 km apart, with water depth differences of 1–17 m. For each station three live-collected individuals were analyzed, and the two whose band widths correlated best were chosen for inter-site comparison, yielding a data set of 10 shells. Figure 5 shows a graph of correlation coefficients vs distance between the different sites. Mean correlations tend to decrease with increasing distance, to a value near 0.20 at 50 km. Although occasional p values >0.60 can be found at intersite distances >30 km, sclerochronology is probably only practical within ~ 20 km on Georges Bank. The difference between site depths (vertical distance) may also be an important factor, but no trend was found within the narrow depth range of this study (1–17 m difference). Two additional shells from station 315 (186–228 km away from the above sites) have generally low correlations with the 10 shells (mean $\rho = 0.26$), but five of the 20 correlations are >0.40 (p as low as 0.0001). This suggests that significant similarities can persist over long distances, implying some regional influence on shell growth.

Composite Sclerochronology

The southeastern flank of Georges Bank was chosen as the region in which to build a composite sclerochronology. Band measurement was first performed on nine live-collected shells: three collected in 1994, three collected in 1992, and three collected in 1982. All three sites are within 7 km of each other

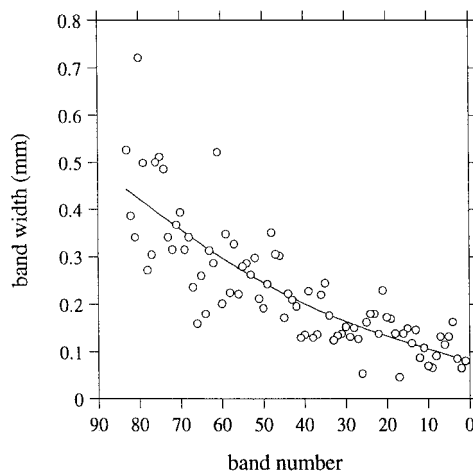


FIG. 2. Annual growth band widths for shell 92-339-f4 from Georges Bank, showing the decrease of shell extension as the animal ages (band number 1 is the most recent band). The ontogenetic trend is removed by fitting the data with a smooth spline and calculating the residuals. Each shell has its own unique curve, but the spline shown is very typical of the individuals in this study.

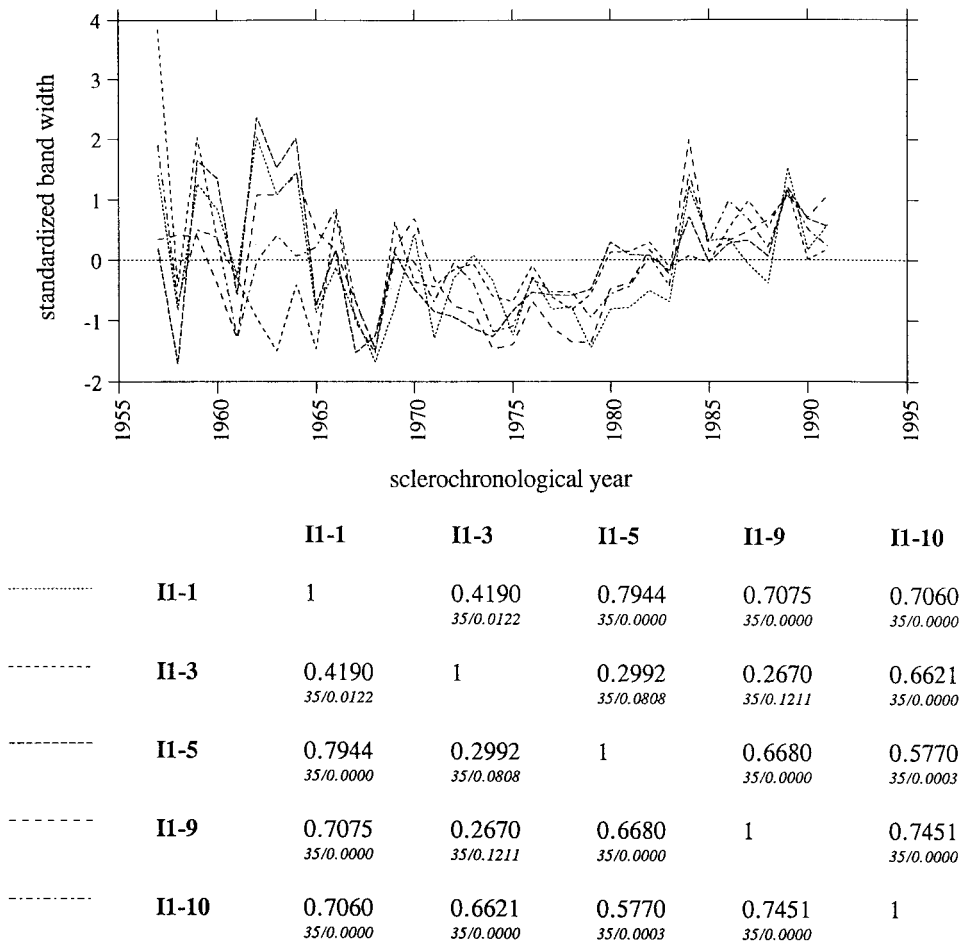


FIG. 3. Band width records of five shells from northern Iceland, showing synchronization of growth. The matrix lists correlation coefficients (ρ) between shells; italicized numbers indicate how many bands each correlation is measured over ($n = 35$ in all cases here), followed by the significance probability (p). The figure 0.0000 indicates a value of <0.00005 .

(stations 441, 339, and 381, respectively, in Fig. 4). Of these nine shells, one was chosen from each site such that correlations were maximized (lowest group of three p values), and these three shells served as the “base” for the chronology, spanning the years 1917 to 1994 (Fig. 6). The correlation coefficients between these records are 0.62, 0.66, and 0.72 (all $p < 0.00005$).

Next, 10 dead-collected shells which appeared to have died fairly recently, based on the preservation states of the periostracum, ligament, inner layer, and hinge dentition, were chosen from material collected in 1992 in the same area (stations 337 and 339). Since the year of death of a dead-collected shell is not known *a priori*, care must be taken to ensure that apparent correlations between individuals represent true synchronousness, not just coincidental mismatches. The following three criteria for adding shells to a sclerochronology give good results: (1) the shell in question must correlate to at least one shell in the chronology with $p \leq 0.0010$, over a span of ≥ 20 bands; (2) the shell in question must correlate to all other shells

in the chronology with $p \leq 0.0500$, over a span of ≥ 20 bands; and (3) any correlations on spans of < 20 bands are insignificant and can be ignored. The first criterion corresponds to $\rho \geq 0.68$ for 20 bands and $\rho \geq 0.57$ for 30 bands; the second criterion corresponds to $\rho \geq 0.44$ for 20 bands and $\rho \geq 0.36$ for 30 bands.

Using these criteria, the 10 dead-collected shell band width records were compared to the base sclerochronology, and four shells were added to the record (Fig. 6). Their placement indicates that these four individuals died in A.D. 1989, 1978, 1971, and 1950, and they extend the composite record back to A.D. 1840, the approximate birth-year of the 1950 shell. Note that the actual band width data only reach back to A.D. 1865, since the early years of shell growth are not measured. The correlation coefficients which admitted these dead-collected shells into the chronology are 0.62, 0.73, 0.78, and 0.71, respectively (all $p < 0.00005$), and the mean ρ among all seven shells (for spans of ≥ 20 bands) is 0.61. Six additional dead-collected shells (from sites 335 and 336) that had a

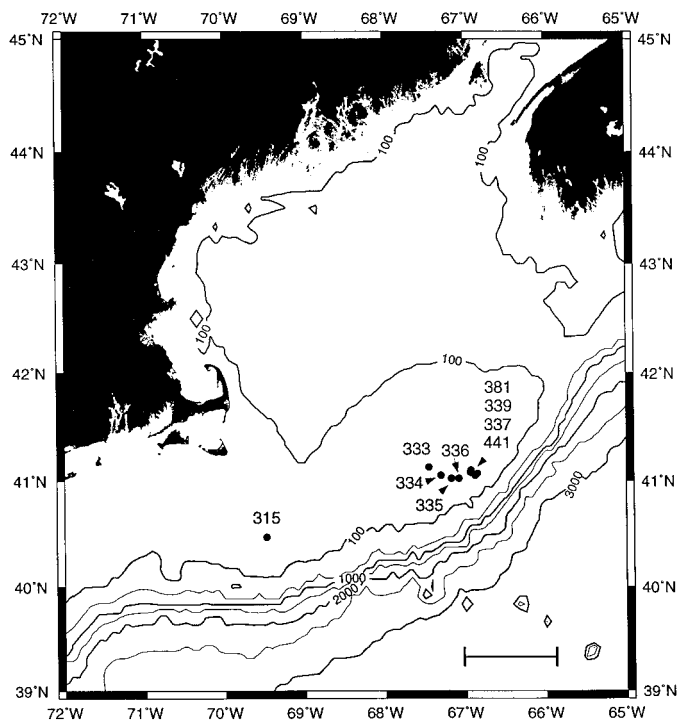


FIG. 4. Site locations on Nantucket Shoals (315) and Georges Bank. Coordinates are listed in Table 1. Bathymetry contours are in meters, and the scale bar is approximately 100 km.

slightly older appearance than most of the previous 10 were also examined. None of these could be added to the chronology, perhaps because these sites are too far from the others (15–27 km) or because these clams died before the late 19th century. Although the length of the final composite record (154 yr) could be spanned by a single, exceptionally long-lived individual, its successful construction suggests that much longer sclerochronologies could be extended back in time.

Aspartic Acid Racemization Dating

To validate our composite sclerochronology, dead-collected shell ages can be checked by two independent means, radiocarbon dating and amino acid racemization dating. Radiocarbon is useful for assigning approximate ages to fossil shells, but it is relatively insensitive during certain periods, particularly over the last few centuries. This insensitivity is due to large variations in the ^{14}C content of the atmospheric reservoir that can produce multiple calendar age solutions for a given radiocarbon age (Stuiver and Becker, 1993). Uncertainties in the ^{14}C age of the surface marine reservoir, which varies globally over a range of ~ 1000 years (Stuiver and Braziunas, 1993), also make precise dating difficult.

Aspartic acid racemization is a promising alternative for mollusk dating over recent centuries (Goodfriend, 1991, 1992; Goodfriend and Rollins, 1998). In shell proteins laid down during growth, all aspartic acid (Asp) residues are initially in

the L-isomer form, but they gradually convert (racemize) to the D-isomer. The ratio D/L can thus be used as a measure of time since the formation of a growth band, once the racemization rate (which varies with temperature and between species) is determined by calibration. This calibration is performed by plotting D/L versus sample age, which may be determined independently by radiocarbon dating (Goodfriend, 1991, 1992; Goodfriend and Rollins, 1998) by using known-collection-date museum specimens (Goodfriend, 1992) or by growth band counting (this study). This yields an equation for age as a function of D/L; such Asp-derived dates can be used to verify a shell's placement within a sclerochronology, or they can be used to predetermine approximately where the shell might fit into an existing sclerochronology.

A total of 40 samples were used for the *A. islandica* Asp calibration, 16 from five individuals collected alive at station 315 (Nantucket Shoals), five from a shell collected alive at station 339 (southeastern Georges Bank), and 19 from three dead-collected shells from the composite sclerochronology (92-337-f3, 92-339-f1, and 92-339-f3). Samples consisted of one to seven growth bands each and spanned the interval A.D. 1873–1992. Figure 7 is a plot of their D/L values versus year. A simple linear fit ($r^2 = 0.90$, $p < 0.00005$) yields the equation

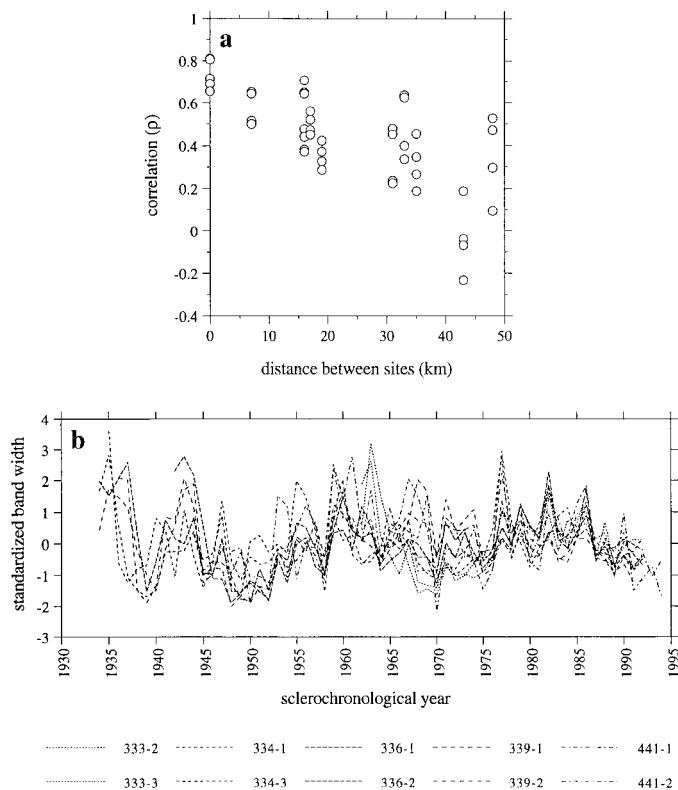
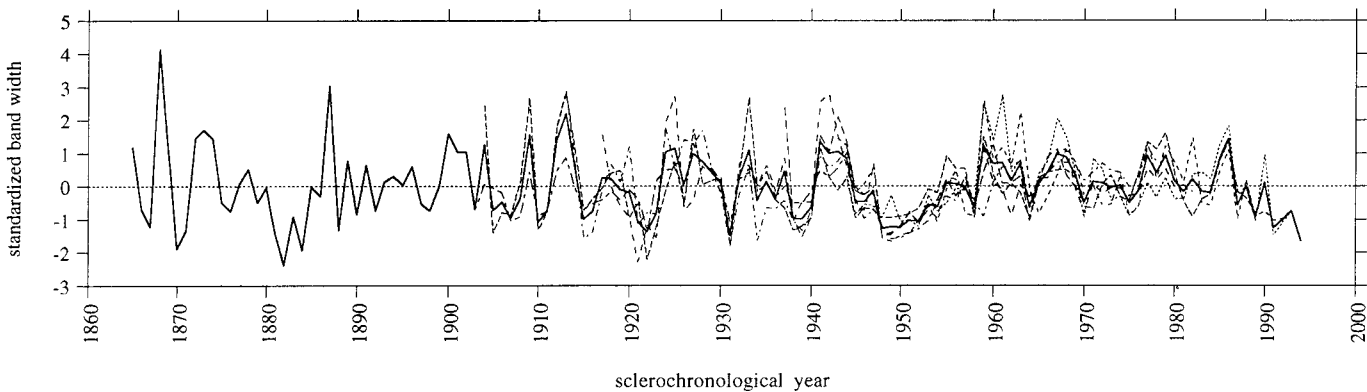


FIG. 5. (a) Band width correlations between individual shells as a function of the distance between collection sites, Georges Bank. (b) Band width records for the 10 shells used in the distance analysis.



	94-441-1 (1944-1994)	92-339-3 (1943-1992)	92-339-f1-c (1904-1989)	82-381-4-a (1917-1982)	92-339-f3 (1912-1978)	92-337-f3 (1937-1971)	92-339-f4 (1865-1947)
----- 94-441-1 (1944-1994)	1	0.6579 <i>49/0.0000</i>	0.5109 <i>46/0.0003</i>	0.6240 <i>39/0.0000</i>	0.4686 <i>35/0.0045</i>	0.6735 <i>28/0.0001</i>	0.9111 <i>4/0.0889</i>
----- 92-339-3 (1943-1992)	0.6579 <i>49/0.0000</i>	1	0.5159 <i>47/0.0002</i>	0.7222 <i>40/0.0000</i>	0.5604 <i>36/0.0004</i>	0.6768 <i>29/0.0001</i>	0.8316 <i>5/0.0808</i>
----- 92-339-f1-c (1904-1989)	0.5109 <i>46/0.0003</i>	0.5159 <i>47/0.0002</i>	1	0.5392 <i>66/0.0000</i>	0.6246 <i>67/0.0000</i>	0.5994 <i>35/0.0001</i>	0.6471 <i>44/0.0000</i>
----- 82-381-4-a (1917-1982)	0.6240 <i>39/0.0000</i>	0.7222 <i>40/0.0000</i>	0.5392 <i>66/0.0000</i>	1	0.5085 <i>62/0.0000</i>	0.7781 <i>35/0.0000</i>	0.5130 <i>31/0.0032</i>
----- 92-339-f3 (1912-1978)	0.4686 <i>35/0.0045</i>	0.5604 <i>36/0.0004</i>	0.6246 <i>67/0.0000</i>	0.5085 <i>62/0.0000</i>	1	0.7267 <i>35/0.0000</i>	0.7071 <i>36/0.0000</i>
----- 92-337-f3 (1937-1971)	0.6735 <i>28/0.0001</i>	0.6768 <i>29/0.0001</i>	0.5994 <i>35/0.0001</i>	0.7781 <i>35/0.0000</i>	0.7267 <i>35/0.0000</i>	1	0.7412 <i>11/0.0091</i>
----- 92-339-f4 (1865-1947)	0.9111 <i>4/0.0889</i>	0.8316 <i>5/0.0808</i>	0.6471 <i>44/0.0000</i>	0.5130 <i>31/0.0032</i>	0.7071 <i>36/0.0000</i>	0.7412 <i>11/0.0091</i>	1

FIG. 6. Seven-shell composite sclerochronology for southeastern Georges Bank. Solid line is the mean of all records. Shell identification notation is described in Table 1. Years in parentheses are the intervals of growth bands measured; the earliest bands on each shell are not measured, nor are the latest few bands on some fossil shells, so these intervals do not represent the entire lifespan of each individual. The ages of the fossil shells are derived from their fit within the sclerochronology. The matrix lists correlation coefficients (*p*) between shells; italicized numbers indicate how many bands each correlation is measured over (*n*, or the amount of overlap), followed by the significance probability (*p*). The figure 0.0000 indicates a value of <0.00005.

year = -4666(D/L) + 2159.

The root mean square error of this equation, which gives the average deviation of data from the regression line, is 12 yr. The fact that the live-collected and dead-collected shells plot on the same line supports the sclerochronological age assignments of the latter. The precision of the equation indicates that Asp dating is potentially very useful for building sclerochronologies. One complication of Asp dating arises from the fact that the racemization rate eventually decreases with time, producing a nonlinear relationship between D/L and age (Goodfriend, 1991; Collines *et al.*, 1999). In *A. islandica*, this relationship is linear over the past 125 yr and may remain so for centuries. However, a longer calibration, perhaps incorporating

radiocarbon ages, is needed for precise Asp dating of significantly older samples.

Controls on Band Widths

The synchronization of band widths within a population indicates that shell growth is influenced by some environmental parameter(s). One strong possibility is water temperature. Shell growth in *A. islandica* ceases during the coldest months, typically from January through April on Georges Bank (Weidman *et al.*, 1994). If the growing season were extended by warmer winter or spring temperatures, wider growth bands would likely result. Temperatures may also influence the rate of shell extension; growth in *Mercenaria mercenaria* slows dramatically below 10°C and above 30°C (Kennish, 1980). In

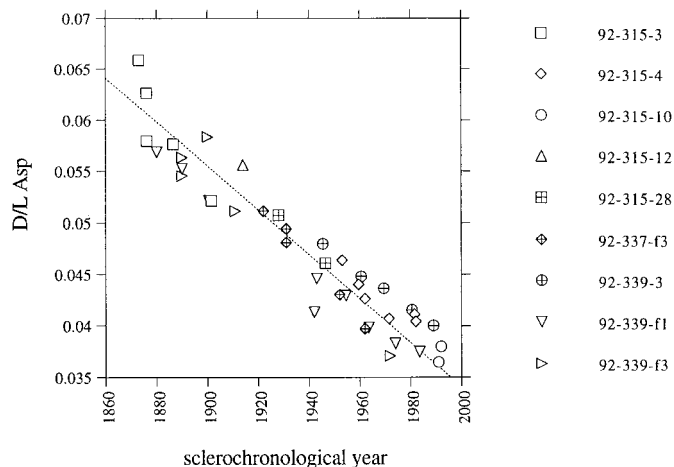


FIG. 7. Aspartic acid D/L ratio vs sclerochronological year for various Georges Bank shells, with the best linear fit ($r^2 = 0.90$) through all the data. The age assignments of the fossil shells (based on the seven-shell composite sclerochronology) are verified by their agreement with the D/L vs age trend of the live-collected shells.

Narragansett Bay, *M. mercenaria* band widths are positively correlated with mean annual water temperature (Jones *et al.*, 1989). However, band widths in *Spisula solidissima* from off the coast of New Jersey are inversely correlated with sea surface temperature (Jones, 1981). It is thus unclear what response *A. islandica* would have to changing water temperatures. The response may vary by region, depending on whether the habitat is nearer the cold end or the warm end of the clam's tolerance range.

Simple comparisons of *A. islandica* band width records from Georges Bank to historical sea surface temperature (SST) records are of limited use because of the considerable depths (57–74 m) from which these clams were collected. Since the upper water column is typically stratified during the warmer months, temperature changes in bottom waters can become decoupled from, or can be the inverse of, SST changes (Weidman, 1995). A comparison of gross features might be informative, however. The longest continuous SST record on the United States east coast comes from Boothbay Harbor, Maine (A.D. 1906 to present; Lazzari, 1995). Since long-term trends in band width are removed by detrending and standardization, the SSTs must be treated in the same way. Unfortunately, this necessary disposal of information decreases the likelihood of identifying a strong relationship. There is a very weak inverse correlation ($\rho = -0.19$, $p = 0.088$) between Boothbay mean annual SSTs and the mean of the composite Georges Bank sclerochronology (Fig. 8). Perhaps more significantly, the most conspicuous feature of the SST record, an extreme warming in the late 1940s to early 1950s, coincides with the longest episode of low shell growth. A possible interpretation of this short-term inverse relationship is that warm SSTs caused increased water column stratification, colder bottom waters, and narrower growth bands.

A much better comparison would be between band widths and bottom water temperatures, or some proxy of bottom water temperatures. Weidman's (1995) 109-yr $\delta^{18}\text{O}$ temperature record from site 315 on the Nantucket Shoals can be compared to *A. islandica* band widths from the same site. Three live-collected shells form a miniature composite sclerochronology at this site. The mean of this sclerochronology has very weak positive correlations with mean and maximum shell-derived annual bottom temperatures ($\rho = 0.14$, $p = 0.14$; and $\rho = 0.14$, $p = 0.16$, respectively) (Fig. 9a). Although year-to-year correspondence is poor, there are some gross similarities between growth and temperature in terms of decadal trends. This suggests that temperature has an influence on band width but also that other factors such as food supply cause some additional variability. Correlation increases by calculating 5- and 11-yr running means, especially for mean annual bottom temperature ($\rho = 0.35$ and 0.38 , respectively; Figs. 9b and 9c). Decadal and multidecadal trends are quite similar between A.D. 1900 and 1960 but show little agreement after 1960. This recent decoupling could indicate an increased influence of nontemperature growth factors, perhaps due to some new environmental stress.

Kennish (1980) described various processes that are known to interrupt molluscan shell growth, such as heat shock, abrasion, spawning, and storms. Other possibilities include predation (natural or anthropogenic), turbidity, and disease. Off northern Iceland, band widths seem to correlate with a combination of temperature and salinity, properties which depend mainly on the varying influences of Arctic vs Atlantic waters (Weidman, unpublished data). These competing water masses might also supply varying amounts of food and oxygen, which may be important controls on shell growth. It may therefore be difficult to interpret band width records as recording only a single environmental parameter.

FEASIBILITY AND APPLICATIONS

The results presented above suggest that a composite *A. islandica* sclerochronology could theoretically be extended as far back in time as the ages of fossil shells collected. On Georges Bank this could be at least 5000 yr, based on radiocarbon dating (G. Jones, unpublished data). Clearly, however, this task may be limited by the availability of fossil material. For example, preferential breakage and decay of older shells would likely make extension of a sclerochronology more difficult as it reaches back in time. There may also be gaps in the sclerochronological record, perhaps due to periods of time when *A. islandica* was rare or absent because of environmental stress. Thus as a sclerochronology is built there will be "floating" sections that may be made up of numerous shells but that have not been connected to the base (live-collected) chronology. Presumably these sections could be linked together as more shells are collected, as long as there are no intervals of time that are actually barren of *A. islandica*. If there are barren

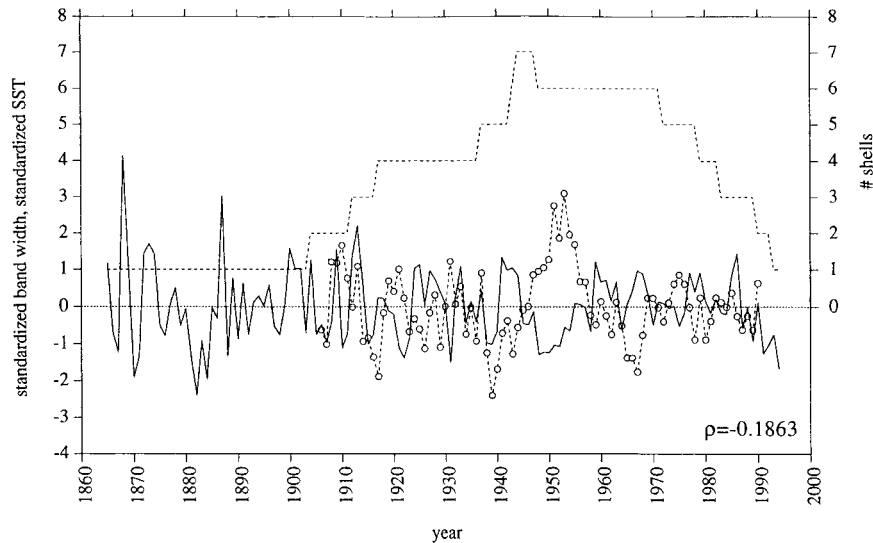


FIG. 8. Mean of the Georges Bank composite sclerochronology (solid line) compared to Boothbay Harbor standardized mean annual sea surface temperatures (dashed line with circles; warm is positive). Note that period of warmest SSTs (~1947–1955) is coincident with the most prolonged period of decreased shell growth. Dashed step function shows the number of shells that make up the mean band width record in a given year.

periods, the floating sclerochronologies could be assigned approximate ages by radiocarbon or aspartic acid dating. In addition, these two dating tools could be used to identify shells (prior to band analysis) that are most likely to fill in the gaps. In this way, we believe that one could construct a continuous or near-continuous 1000-yr composite sclerochronology.

With such a framework, one could construct continuous records of $\delta^{18}\text{O}$ and $\Delta^{14}\text{C}$ with unprecedented resolution for mid- to high latitudes. A shallow-water site would produce records of SST and atmospheric/surface ocean radiocarbon variability, while a deeper site might reflect variations in ventilation, upwelling, and the thermal signature of the North Atlantic Oscillation (Dickson *et al.*, 1996). Other chemical proxies could also be measured, such as Cd, Sr, and Ba (e.g., Reichart *et al.*, 1998). Further, a long record of band widths may contain paleoceanographic information independent of any chemical analyses. Although long-term trends in band width (longer than ~30 yr) are lost during the growth curve correction, shorter-term fluctuations may record significant environmental changes. This can be manifested in periods of increased or decreased growth (such as the late 1940s to early 1950s on Georges Bank) or in a change in the frequency of band width variation. The latter could potentially reflect long-term climatic shifts. However, interpretation of such changes requires a better understanding of the controls on shell growth in *A. islandica*.

Patterns of death within a population of *A. islandica* may offer additional paleoceanographic information. For example, a mass mortality could result from a large temperature anomaly, an anoxic event, or a marked decrease in food supply. With sufficient sampling, such an event could be recognized using sclerochronology, since a disproportionate number of fossil

individuals would share the same year of death. Likewise, patterns of spawning and recruitment could be analyzed by charting the birth-years of individuals, both living and dead, in a particular area. Mass recruitments might be further linked to advantageous oceanographic conditions such as warm water temperatures, favorable currents, abundant food supplies, or reduced predation. Although the results presented in this paper are specific to *A. islandica*, our methods could theoretically be modified and applied to various mollusk taxa, both extant and extinct.

CONCLUSIONS

The widths of annual growth bands in *A. islandica* vary synchronously among members of a population. This relationship weakens as the distance between individuals increases, but strong correlations persist up to ~20 km on Georges Bank. By adopting several strict criteria for matching band width records, clams that died at different times can be linked together in a composite sclerochronology. On Georges Bank, seven shells were connected to span the interval from A.D. 1840 to 1994. It is likely that band widths are influenced by water temperature, although the weak correlations between band width and $\delta^{18}\text{O}$ suggest that other factors are also at work.

The D/L ratio of aspartic acid in *A. islandica* shells increases with time, offering another way to date annual bands. A calibration suggests that band age can be predicted to within ± 12 yr (over the past 125 yr) using D/L. This independent dating method verifies the Georges Bank composite sclerochronology and will aid in developing long sclerochronologies in the future. Long sclerochronologies can be used as temporal frameworks for isotopic records, with resolution and duration

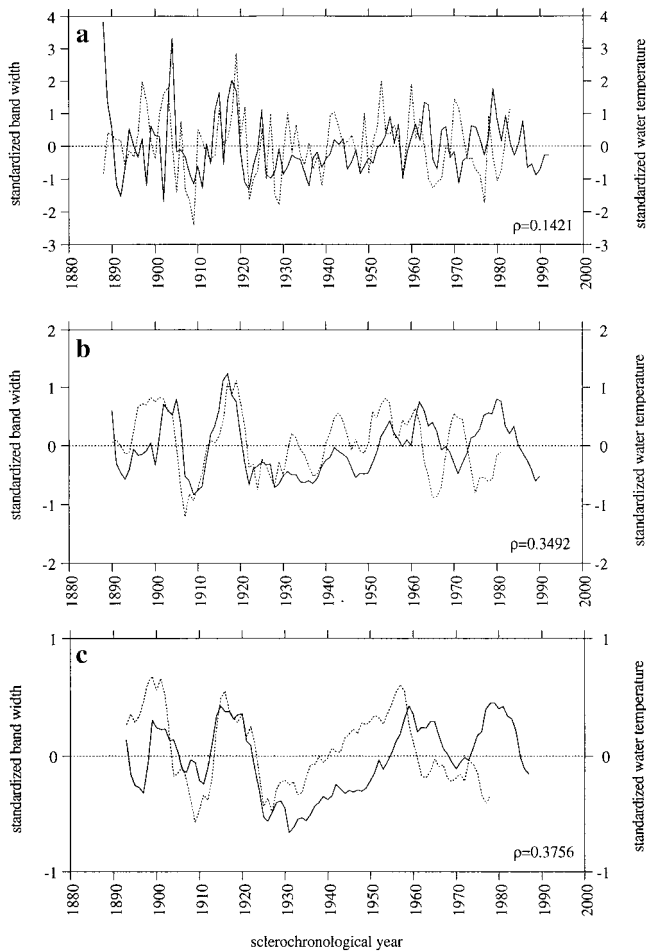


FIG. 9. Mean of a three-shell composite sclerochronology from site 315 on the Nantucket Shoals (solid line) compared to the site 315 standardized mean annual bottom temperature record derived from shell $\delta^{18}\text{O}$ (dashed line; warm is positive; Weidman, 1995): (a) direct comparison; (b) 5-yr running means; (c) 11-yr running means.

unprecedented for middle to high latitudes. In addition, band width records may offer paleoceanographic information independent of isotopes, as well as insights into molluscan population dynamics. Sclerochronology promises to be a very useful paleoenvironmental tool by enabling the exact temporal correlation of fossil mollusk shells.

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