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Climate records from a bivalved Methuselah
(*Arctica islandica*, Mollusca; Iceland)

Bernd R. Schöne [a,*], Jens Fiebig [a], Miriam Pfeiffer [b], Renald Gleß [a], Jonathan Hickson [c],
Andrew L.A. Johnson [c], Wolfgang Dreyer [d], Wolfgang Oschmann [a]

[a]*Institute for Geology and Paleontology, INCREMENTS Research Group, J.W. Goethe University,
Senckenberganlage 32–34, 60325 Frankfurt / Main, Germany*
[b]*IFM-GEOMAR, Leibniz-Institute for Marine Sciences, Wischhofstr. 1–3, 24148 Kiel, Germany*
[c]*Division of Geography, Earth and Environmental Sciences, University of Derby, Kedleston Road, Derby DE22 1GB, U.K.*
[d]*Zoological Museum, Christian Albrechts University, Hegewischstr. 3, 24105 Kiel, Germany*

Abstract

We measured annual shell growth rates of a 374-year-old (radiometrically confirmed) bivalve mollusk specimen of *Arctica islandica* (Linnaeus). This bivalve represents the oldest ever reported individual animal. In addition, we analyzed 1051 individual powder samples from ontogenetic years two to 40 (=80% of the entire shell height) for isotope analyses. Oxygen and carbon isotopes exhibit clear intra-annual cycles. The highest measured carbon isotope values (on average +2.73‰) occurred during summer, i.e., during maximum primary productivity. The $\delta^{18}O_{aragonite}$-derived temperature time-series cover the period of AD 1496–1533. Temperatures calculated from oxygen isotopes ranged from 4.5 to 9.3 °C and exhibit a mean value of 6.2 °C. The latter coincides well with the 1854–2003 mean value of 6.81 °C for sea-surface temperature between February and September (=growing season of *A. islandica*). Neither oxygen nor carbon isotopes exhibit age-related, unidirectional trends. However, $\delta^{13}C_{aragonite}$ and $\delta^{18}O_{aragonite}$ values fluctuated at decadal periods of four, six and eight to nine years (NAO-type periods) as well as 12–14 years which may represent teleconnections to cycles in the tropical Atlantic. Annual shell growth is positively correlated to intra-annual $\delta^{18}O_{aragonite}$ minima, i.e., warm summer temperatures ($R^2=0.34$), and to intra-annual $\delta^{13}C_{aragonite}$ minima (higher food supply; $R^2=0.42$). Using a linear multiregression model, 65% of the variation in annual shell growth can be explained by summer temperature and food supply. The formation of extremely narrow annual increments coincides with major volcanic eruptions (e.g., Tambora 1815). A period of extremely variable growth occurred during the culmination of the Little Ice Age in Iceland between ca. AD 1550 and 1620. Shell growth during AD 1765–1780, however, was characterized by very little year-to-year variability, probably as the result of extremely mild climate near the end of the Little Ice Age. This study demonstrates that shells of *A. islandica* provide

* Corresponding author.
  E-mail address: B.R.Schoene@em.uni-frankfurt.de (B.R. Schöne).

subseasonal to multidecadal, precisely dated multi-proxies of environmental variables from marine, mid to high latitudes. Such data can be used to validate and complement climate models and further assess human impact on climate and ecosystems.

1. Introduction

Climate models require high-resolution and long-term records of environmental variables from many different settings including marine mid to high latitudes. Such data can be used, for example, to quantitatively assess the human impact on climate and ecosystems. However, observational records of temperature and other environmental parameters are spatiotemporally incomplete and extremely scarce prior to about AD 1860 (Hurrell and Trenberth, 1999; Smith and Reynolds, 2003; note: in what follows all years are 'AD'). Proxy data complement and significantly extend such records in space and back in time (Jones et al., 2001). For example, tree rings (Briffa et al., 1990; Schweingruber et al., 1991; Grudd et al., 2002) and stalagmites (McDermott et al., 1999; Frisia et al., 2003; Niggemann et al., 2003) have permitted reconstructions of summer air temperature and precipitation over the past centuries to millennia. However, these records do not provide information on environmental conditions of marine settings. This is partly achieved by using microfossils contained in oceanic sediments (Williams et al., 1979; Fairbanks and Wiebe, 1980; Jiang et al., 2001). The temporal resolution of laminated, microfossil-bearing sediments, however, is generally coarser than decades. In addition, marine microfossils cannot provide annually-resolved long-term records of seasonal environmental variables as their life-span is too short.

Shells of bivalve mollusks are now increasingly used for climate reconstructions. Mollusks combine virtually all the requirements for being perfect climate recorders.

(1) Bivalves sensitively record changes of ambient environmental conditions, in particular temperature (Henderson, 1929; Kennish and Olsson, 1975), food (Page and Hubbarrd, 1987; Sato, 1997), salinity (Davis and Calabrese, 1964; Marsden and Pilkington, 1995) and pollution (Mutvei et al., 1996).

(2) Environmental variables are recorded in the shells in multiple ways, i.e., as variable growth rates (Koike, 1980; Kennish and Olsson, 1975) and variable geochemical properties (Jones et al., 1986; Wefer and Berger, 1991; Owen et al., 2002). For example, shell oxygen isotope data have been used to infer changes of sea surface and bottom water temperatures on decadal to intra-annual time scales (Marsh et al., 1999; Ivany et al., 2004; Schöne et al., 2004).

(3) Bivalve shells function as calendars. Periodic accretion of calcium carbonate is controlled by biological clocks (Clark, 1975; Thompson, 1975; Richardson et al., 1979; Kim et al., 1999) and divides the growth pattern into time slices of approximately equal duration, i.e., growth lines and growth increments. Aside from annual growth patterns (Jones, 1980; Ropes et al., 1983), bivalves form daily growth increments and lines (Berry and Barker, 1968; Pannella and MacClintock, 1968).

(4) Some species are extremely long-lived and thus suited perfectly for long-term environmental reconstructions (Zolotarev, 1980; Mutvei et al., 1996; Marchitto et al., 2000). For example, up to 225 and 268 years have been reported for the Ocean Quahog *Arctica islandica* (Linnaeus) by Ropes and Murawski (1983) and Forsythe et al. (2003). It should be noted that the individual's life-span is not the limiting factor for long-term environmental reconstructions. Based on similar growth patterns, contemporaneous specimens with overlapping life-spans can be strung together to form mean and master chronologies, similar to tree-ring chronologies (Jones et al., 1989). Such multi-specimen records can stretch over centuries to millennia and contain precise environmental

data for the covered period (Marchitto et al., 2000; Schöne et al., 2003).

(5) Bivalves exhibit an extremely broad biogeographic distribution. They occur in shallow-water and deep-sea environments, in freshwater, marine and brackish settings, near the poles and the equator.

Some important questions still remain unanswered. It is unclear, for example, whether the growth period remains the same throughout life, in particular before and after maturity. Variations among annual growth rates and geochemical properties of pre-mature and mature or senescent shell portions can only be reliably interpreted if the time period contained in annual increments remains constant during life. It is also unclear whether the shell stable isotope composition of long-lived bivalve mollusks is really affected by ontogenetic trends (vital effects, biogenic fractionation; e.g., Jones et al., 1986). Short-lived bivalve mollusks (e.g., *Cerastoderma edule* (Linnaeus), *Mytilus edulis* (Linnaeus) and many pectinids, which usually live for less than ten years) apparently form their shell almost in carbon isotope equilibrium with the surrounding seawater. The dissolved inorganic carbon (DIC) of the ambient water is considered to be the primary source for the carbon isotope composition of the shells (Mook and Vogel, 1968; Hickson et al., 1999). If ontogenetic trends do not occur in long-lived bivalve mollusks, shell $\delta^{13}C$ values can be

used, for example, to precisely assess how the CO_2 budget of the oceans has changed on centennial to sub-annual time scales. A combined analysis of shell growth and stable carbon isotope values of the shell could also elucidate if and how increased CO_2 levels in the ocean affected the biomineralization.

Here, we study whether stable isotope values (C- and O-isotopes) of *A. islandica* from Iceland exhibit ontogenetic trends (vital effects). Seasonal ranges of oxygen and carbon isotope values are used to identify possible changes in the length of the growth period during life. We further address the question of whether well-known environmental extremes and climate oscillations can be recognized in the sclerochronological record (growth pattern). Results of our study are relevant for the interpretation of environmental proxy data derived from shells of the Ocean Quahog.

2. Material and methods

One specimen of *A. islandica* was collected alive during July 1868 near Iceland (Fig. 1) according to the attached tag and its shell has been stored at the museum since then. The shell belongs to the collection of Carl Möbius, biologist and founder of the Zoological Museum, University of Kiel, Germany. It is not known by whom the shell was collected or where exactly from Iceland it comes from. Despite
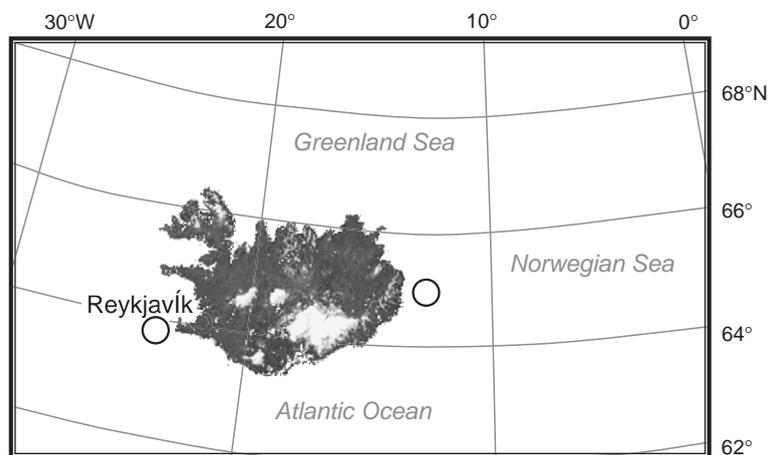

Fig. 1. Map showing approximate sample locality of the *A. islandica* specimen NE of Iceland or SW of Reykjavík (circles).

intensive studies of the correspondence between Möbius and colleagues, we were unable to find any more detailed locality data. The intra-annual oxygen isotope profile resembles that of shells from the upper mixed layer of the ocean (sinusoidal shape; Weidman et al., 1994; Schöne et al., 2005a). In addition, temperatures reconstructed from oxygen isotopes are consistent with measured (www.cdc.noaa.gov, www.ices.dk, www.hafro.is, all last checked on 16 December 2004) seasonal temperature profiles from NE Iceland or SW of Reykjavík. Because of this we feel confident that the shell was collected from less than about 30 m water depth. Remains of the soft parts (muscles) are still present in the shell and the periostracum partly preserved. The subfossil material enabled us to study how the shell grew under 'natural' conditions and whether isotope values of this long-lived bivalve mollusk exhibit ontogenetic trends. Burning of fossil fuels since industrialization has significantly changed the carbon isotope composition of the ocean DIC ($\delta^{13}C_{seawater}$) toward more negative values (Suess effect). Changes in the isotope composition of the water should have also affected the carbon isotope values of shells ($\delta^{13}C_{aragonite}$) that grew during this period. Using a shell from pre-industrial times (or at least the juvenile portion of the shell that formed during that time) enabled us to exclude human-induced changes of $\delta^{13}C_{seawater}$. According to Haugan and Drange (1996), enhanced sequestration of CO_2 has lead to a decrease in alkalinity of the seawater by approximately 0.1 pH-units since the beginning of the industrial revolution. The youth portion of the specimen used in the present study was laid down well before that time period.

2.1. Sample preparation

In preparation for sclerochronological and isotope analyses, one valve was mounted on a plexiglass block. A quick-drying metal epoxy resin (JB KWIK-Weld) was then applied to the valve surface. Two immediately adjacent, three-millimeter-thick sections (Fig. 2B) were cut from the valve (Fig. 2A) along the axis of maximum growth, and perpendicular to the annual growth lines, with a Buehler Isomet low-speed saw using a 0.3 mm thick diamond wafering blade. The 'mirroring' sections were subsequently mounted on glass slides, ground with 800 and 1200

SiC grit, polished with 1 μm Al_2O_3 powder and cleaned with dehydrated ethyl alcohol.

2.2. Radiocarbon dating

$^{14}C_{AMS}$ dating (performed by BetaAnalytics, Miami, FL, USA) was used to determine the approximate calendar ages of the umbonal shell portion (Table 1). After mechanically removing the periostracum and the outermost shell carbonate (ca. 50 μm), we carefully milled carbonate powder (about 100 mg per sample) from the outer shell layer. Two samples were taken from the shell, one stretching over the ontogenetic years one to five (second to sixth annual increment) and the other one from year twenty. Determination of the ontogenetic age was based on annual increment counts (Jones, 1980). Growth lines of *A. islandica* form on an annual basis as the result of a slowdown of growth during late summer and fall (Jones, 1983; Ropes et al., 1983). Calibrated ^{14}C ages (cal yr AD) were calculated using CALIB 4.4 (http://depts.washington.edu/qil/calib/calib.html) and the regional (Iceland and Faroe Islands) average value for the marine reservoir effect of $\Delta R = 49 \pm 19$ years (Broecker and Olson, 1961; Håkansson, 1983,1984; Krog and Tauber, 1974; Olsson, 1980). Calibration datasets are based upon Stuiver et al. (1998a).

2.3. Sclerochronological analyses

In order to resolve annual growth patterns (Fig. 2C,D) in the outer layer of the shell, a polished section was immersed in Mutvei's solution for 20 min at 37–40 °C (method described in detail by Schöne et al., 2005b). Immediately afterward, the etched section was rinsed with demineralized water and allowed to air-dry. Treatment with Mutvei' solution results in a very clear, three-dimensional display of growth patterns and reveals distinct annual growth lines (Fig. 2).

The growth patterns of the etched cross-section were then viewed under a reflected-light stereomicroscope (Leica Wild M2C) and digitized with a Nikon Coolpix 995 camera. Annual growth increment widths were measured to the nearest 1 μm with Scion/NIH version 4.0.2 beta image analysis software (available free at http://www.scioncorp.com). Measurements were conducted in the outer shell layer as shown in Fig. 2. The average annual growth increment width is 256 μm.
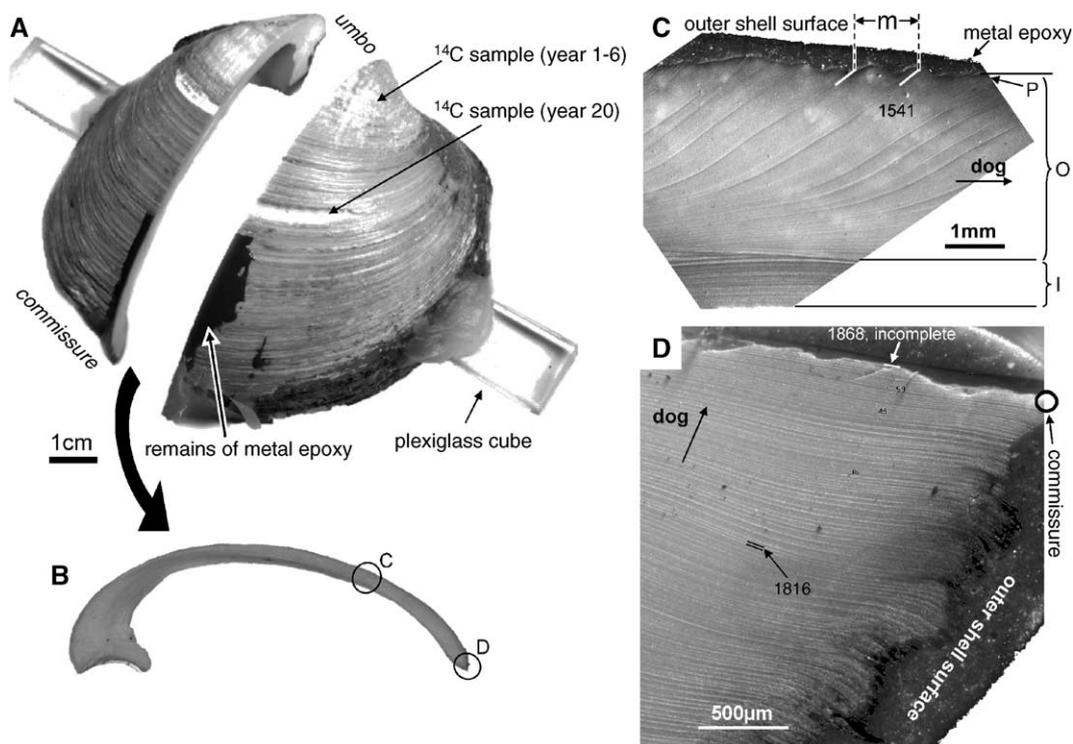
Fig. 2. Sample preparation and measurements. (A) Two powder samples were taken from the right valve of the *A. islandica* shell for radiocarbon analyses. Then, the shell was mounted on a plexiglass block, covered with epoxy and cut along the axis of maximum growth. (B) Two immediately adjacent slabs (two to three mm-thick) were obtained from the valve. After immersion in Mutvei's solution, annual growth patterns can be studied (C+D). Growth rates in older shell portions (D) are much slower than during earlier shell portions (C; AD 1541=age 47). Extreme environmental conditions (e.g., the volcanic eruption of Mount Tambora in AD 1815) resulted in strongly reduced shell growth rates. m=annual increment width (measured along the outer shell surface); p=periostracum; O=outer shell layer; I=inner shell layer; dog=direction of growth.

2.3.1. Detrending and standardization, mean chronologies

In order to isolate environmental signals from annual growth increment time-series ontogenetic trends must be removed. As the bivalve grows older, the rate at which carbonate is precipitated and the year-to-year variance of the increment widths decreases (Fig. 3). Such age-related trends were removed with statistical 'detrending' methods developed by dendrochronologists (see Cook and Kairiukstis, 1990; see Fig. 3).

The age-related growth trend can be adequately estimated with a running low-pass digital filter (filter length: 15 years; Fig. 3). We calculated growth indices (*GI*) by dividing measured by predicted (estimated) growth values for each year. Predicted growth values were derived from the low-pass filter, and hence the *GI* values measure the deviation of a

Table 1
Radiocarbon ages of the *A. islandica* shell (ID: M07_1868-A3R) used in the present study

Sample position (ontogenetic age)	Sclerochronological age (yr AD)	Uncalibrated ^{14}C age (yr BP)	ΔR		Calibrated 2σ ^{14}C age (cal yr AD)
1–5	1495–1499	950 ± 40			1364–1500
20	1513	920 ± 40	49 ± 19		1406–1520

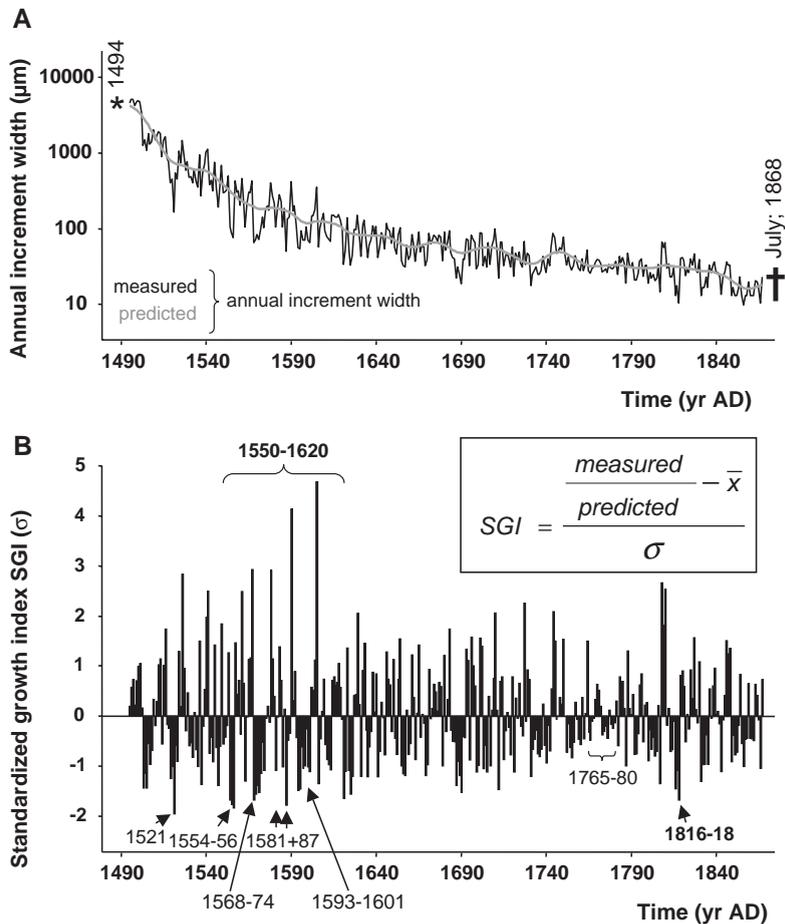Calibrated ^{14}C ages were calculated using CALIB 4.4 (see text).

Fig. 3. Annual shell growth of *A. islandica*. (A) Growth rates decreased with increasing ontogenetic age. Age-related growth trends were estimated with a low-pass digital filter (window length: 15 years; grey). (B) Dimensionless growth rates (*SGI*, standardized growth index) were calculated from the raw data by detrending (*GI*=m/p) and standardizing (*GI* values minus average divided by standard deviation; further explanation see text). Note individual years (AD 1521, 1581, 1587) and periods (1554–56, 1568–74, 1816–19) of strongly reduced shell growth. Some extremely negative *SGI* values coincide with major volcanic eruptions (e.g., Mount Tambora, AD 1815). Periods of strong (AD 1550–1620) and little (AD 1765–1780) growth variability coincide with the culmination period of the Little Ice Age and the mild climate near the end of the Little Ice Age, respectively.

year from the 15 year average on either side of it. Indexing removes age-related growth trends from the increment time-series. Then, the *GI* data were standardized by subtracting the mean and dividing by the standard deviation of the *GI* time series. Standardization removes the high correlation between the mean and variance from the data (i.e., the heteroscedasticity) and transforms the non-stationary *GI* values into a new series of stationary growth indices. Therefore the standardized growth index (*SGI*) is a dimensionless measure of how growth deviates from the average trend, i.e., the predicted growth. For

further details of detrending methods see Schöne (2003).

2.4. Stable isotope analyses

The remaining unetched, polished shell section was ultrasonically rinsed with demineralized water prior to the extraction of carbonate samples for oxygen and carbon isotope analyses. Following the shape of the microgrowth increments, $CaCO_3$ powder was milled from the outer shell layer (ontogenetic years one through 39) under a stereomicroscope at 10 to 20×

magnification (Fig. 4). We used a cylindrical diamond drill bit (1 mm diameter, Komet/Gebr. Brasseler GmbH and Co. KG model no. 835 104 010) mounted on a Rexim Minimo drill. An 'adaptive sampling technique' was applied: Sampling resolution (in milling perpendicular to the direction of growth) was coarser in fast-growing shell regions near the umbo (ca. 320 μm) and finer (ca. 20 μm) in slower growing, older shell portions (Fig. 4). This allowed us to compare extreme isotope values in younger and older shell portions with each other. The widths of the milling steps were constantly controlled during sampling using an eyepiece scale. Each milling yielded about

120 to 40 μg of carbonate (aragonite) powder. Samples were analyzed with a Finnigan MAT 253 continuous-flow mass spectrometer equipped with a Gas Bench II. Isotope values are reported relative to VPDB based on a NBS-19 calibrated Carrara marble value of $-1.76‰$ ($\delta^{18}O$) and $+2.02‰$ ($\delta^{13}C$). On average, replicated precision (1SD, multiple measurements of the Carrara standard) was better than $\pm 0.07‰$ for $\delta^{18}O$ and better than $\pm 0.05‰$ for $\delta^{13}C$.

Shell oxygen isotope ($\delta^{18}O_{aragonite}$) and carbon isotope ($\delta^{13}C_{aragonite}$) values provide important clues to environmental conditions during shell formation (Figs. 5, 6). The oxygen isotope composition of mol-
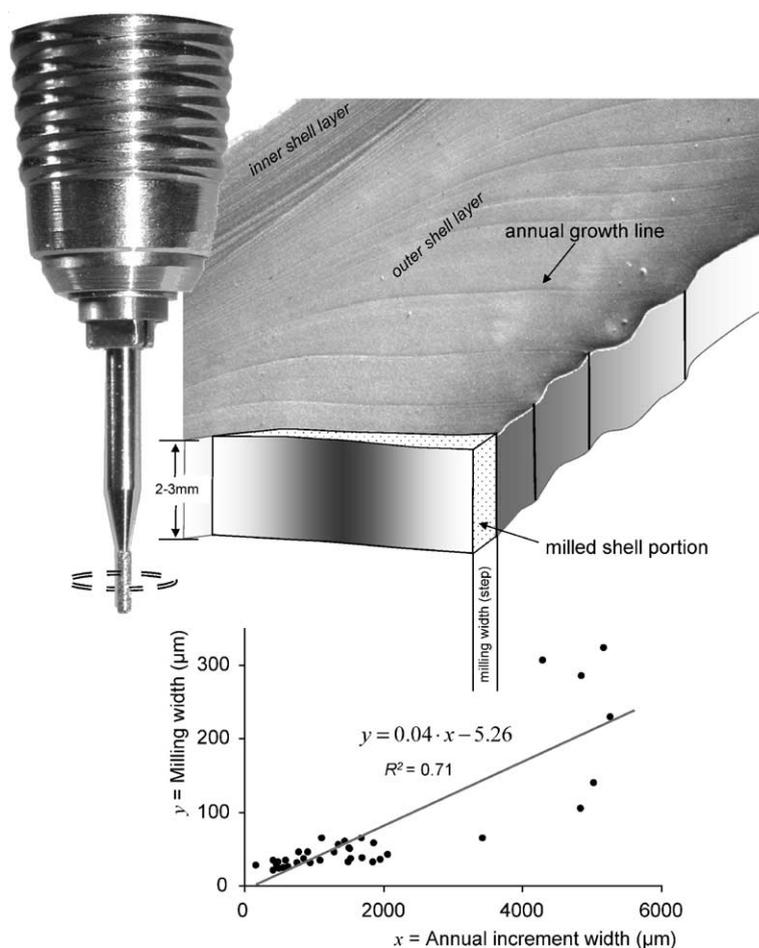

Fig. 4. Sampling of shell carbonate for isotope analyses. Carbonate powder was milled from the shell following the shape of the growth lines. An 'adaptive sampling strategy' was applied, i.e., low sampling resolution in fast-growing shell portions (broad annual increments), high sampling resolution in slow-growing shell portions (narrow annual increments). A strong positive correlation exists between annual increment width and milling width.

lusk shells is controlled by both the $^{18}O/^{16}O$ ratio ($\delta^{18}O_{seawater}$) and the temperature of the ambient seawater in which the animals live. Today's $\delta^{18}O_{seawater}$ value of the region where the animal lived is close to zero (Goddard Institute for Space Studies, http://www.giss.nasa.gov/cgi-bin/o18data/geto18.cgi). Changes of the $\delta^{18}O_{seawater}$ can occur as the result of freshwater influx of different $\delta^{18}O$ values or due to evaporation.

According to the empirically determined fractionation relationship of Grossman and Ku (1986), $\delta^{18}O_{aragnoite}$ ratios can be used to calculate water temperatures [$T_{\delta18O}$]. However, a small modification of their equation was required because they report water values in SMOW — 0.2‰ (Goodwin et al., 2001). The corrected function is as follows:

$$T_{\delta^{18}O}(^{\circ}C) = 20.60 - 4.34$$
$$\cdot \left(\delta^{18}O_{aragonite} - \left(\delta^{18}O_{seawater} - 0.20 \right) \right),$$

where $\delta^{18}O_{aragonite}$ is measured relative to the VPDB scale and $\delta^{18}O_{seawater}$ is relative to the SMOW scale. Thus, assuming no change in the $\delta^{18}O_{seawater}$, a shift in $\delta^{18}O_{aragonite}$ by 1‰ reflects a temperature change of the ambient seawater of 4.34 °C.

2.5. Statistical analyses

We conducted time series analyses of the *SGI* chronologies (Fig. 7). To ensure the stability of the spectral features, two independent techniques of spectral analysis were performed: the multitaper method (MTM; Thomson, 1982) and the singular spectrum analysis (SSA; Vautard and Ghil, 1989). MTM and SSA were computed with the SSA-MTM Toolkit written by Dettinger et al. (1995). MTM represents a refinement of the classical Fourier analysis with respect to resolution and spectral leakage. Mann and Lees (1996) developed techniques that allow robust signal detection against a red noise background. SSA enables the decomposition of a time series into trend, oscillating and noise components by analyzing its covariance matrix (Vautard and Ghil, 1989). Allen and Smith (1999) developed the so-called Monte Carlo
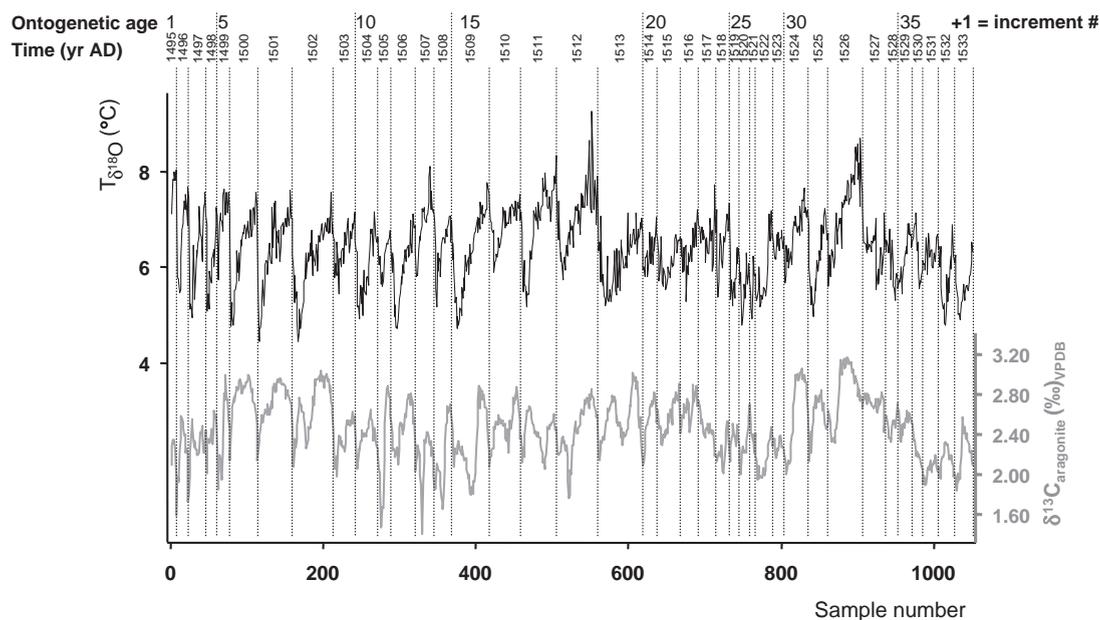

Fig. 5. Shell oxygen-isotope derived temperatures and carbon isotopes from 1051 powder samples taken from the first 39 years of growth. The unbroken time-series covers the period of AD 1495 to 1533. Distinct intra-annual cycles occur in $\delta^{13}C_{aragonite}$ and $\delta^{18}O_{aragonite}$ values. While no long-term trends exist in oxygen or carbon isotopes, decadal periods can be discerned (see Figs. 6, 8).
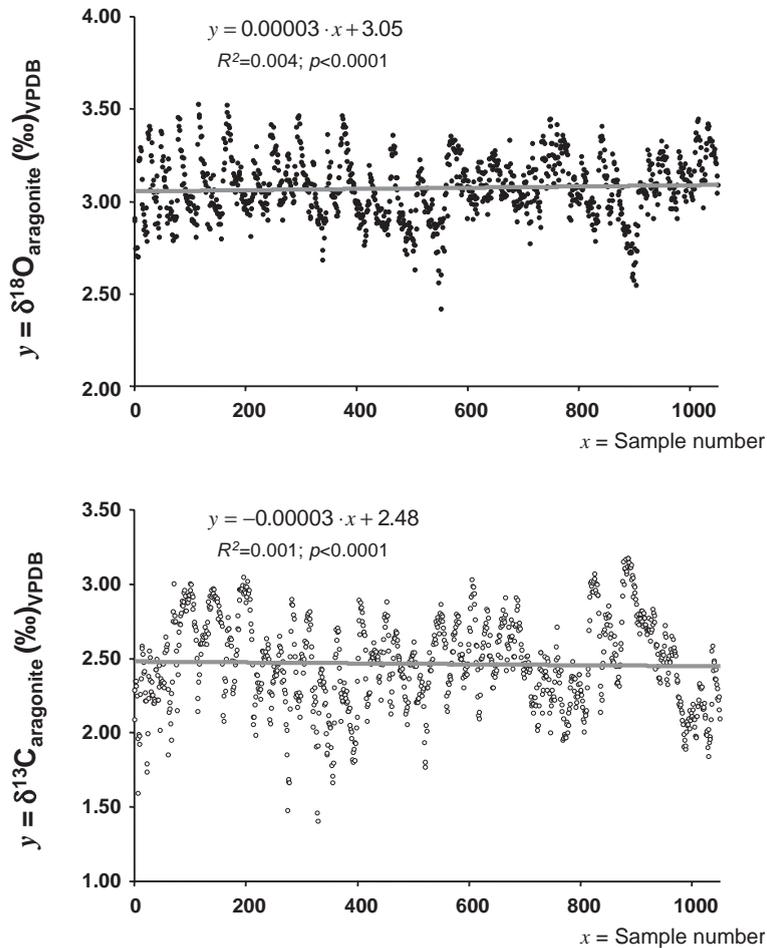
Fig. 6. Oxygen and carbon isotope chronologies over the first 39 years of growth (4/5 of the entire shell height) do not exhibit unidirectional growth trends.

SSA for calculating significance tests against a red noise background.

We also analyzed the stable isotope series for quasi-periodic components (Fig. 8), although the length of the chronology is not sufficient to perform statistical significance tests. We computed the arithmetic mean as well as minimum and maximum values of $T_{\delta 18O}$ and $\delta^{13}C_{aragonite}$ values for each complete year (between adjacent annual growth lines). Inherent cycles were determined by Fast Fourier Transform (FFT) of the low-pass filtered (Savitzky–Goley filter, window length: four years) chronologies. The agreement of year-to-year variability between *SGI* data and $T_{\delta 18O}$ and

$\delta^{13}C_{aragonite}$ values was quantified by linear regression analyses.

2.6. Observational water temperature data

Because no instrumental measurements are available for the time period during which the sampled shell portion was formed, shell oxygen isotope-derived temperature data were compared to today's sea surface temperatures in the region where the specimen was living (approx. 65 °N,14 °W). The extended reconstructed sea-surface temperature dataset ERSST (Smith and Reynolds, 2003; obtained from NOAA/NESDIS at http://
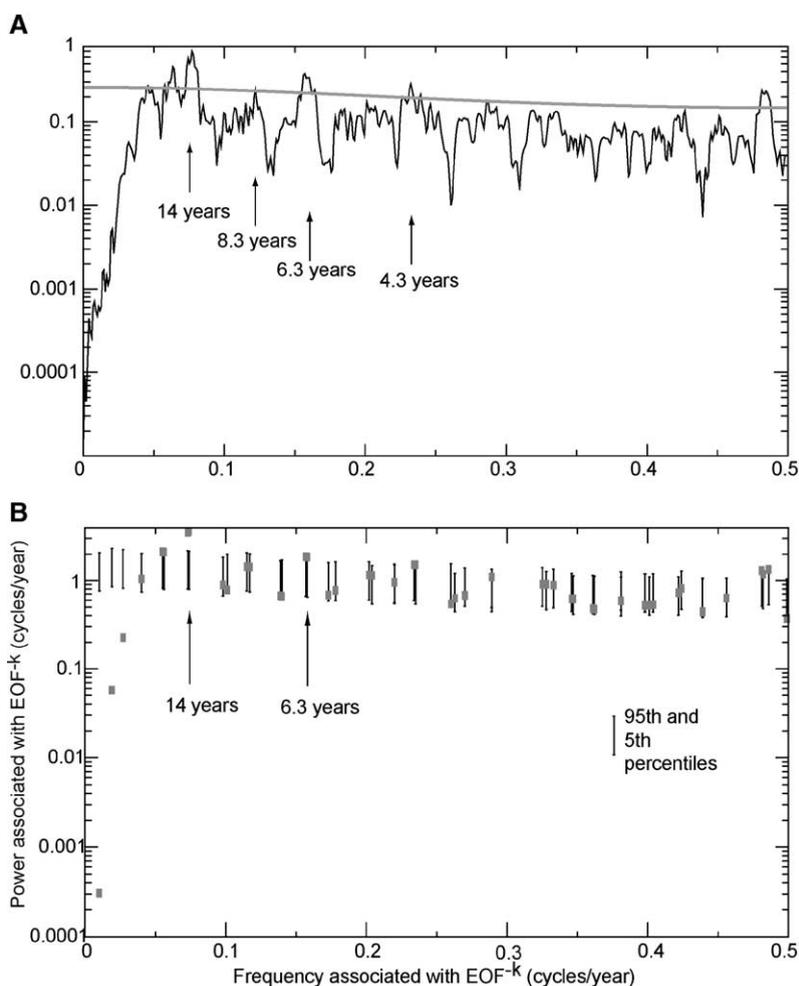
Fig. 7. Time series analysis of the *SGI* record. (A) MTM spectrum with 95% confidence levels (grey line). Periods (years) of significant spectral peaks are shown. (B) Monte Carlo SSA. Only the 14 and 6.3-year oscillations are significant at the 95th percentile.

www.cdc.noaa.gov) comprises the period 1854–2003. We calculated monthly mean temperatures over this period.

3. Results

We counted 375 annual increments (373 complete increments) in the shell of *A. islandica* collected alive during July 1868. Consequently, the shell started growing during fall (Jones, 1980; first annual increment) 1494 and was slightly more than 374 years old when sacrificed (Fig. 3). Radiometric age determinations strongly support the finding. The $^{14}C_{AMS}$ ages

(1364–1500 and 1406–1520 cal yr AD) encompass the sclerochronologically determined ages of 1495–99 and 1513, respectively (Table 1). Note that ontogenetic age is calculated as annual increment number minus one, e.g., age one was attained during 1495 when the second annual increment was laid down.

3.1. Shell oxygen and carbon isotopes

3.1.1. Intra-annual cycles

The 1051 carbon and oxygen isotope values determined over 39 years of growth (age one to 39; 1495–1533; 1495 was incompletely sampled) describe distinct annual cycles (Fig. 5). It should be noted that this
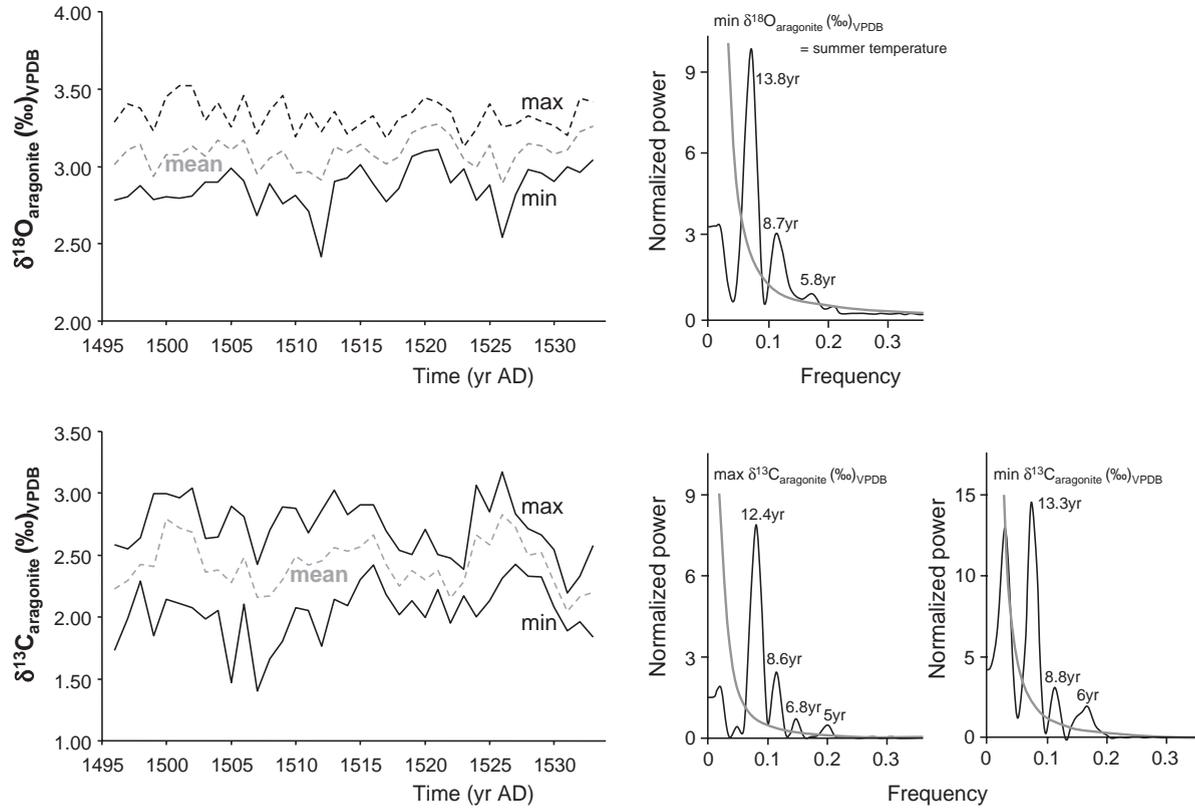
Fig. 8. Time-series of annual minimum, maximum and mean values of shell oxygen and carbon isotopes exhibit decadal periods. Fast Fourier Transforms are depicted for selected data (minimum $\delta^{18}O_{aragonite}$ and $\delta^{13}C_{aragonite}$ as well as maximum $\delta^{13}C_{aragonite}$ values; unbroken lines in left panel diagrams).

'juvenile' portion comprises almost 80% of the entire shell height (8.1 cm; distance between hinge and commissure measured along the outer shell surface is 10.7 cm). Limited by the sampling resolution of about 20 μm, we obtained between six (1521; age 27) and 58 (1513; age 19) isotope samples per annual increment, on average 27.4 samples per year (Figs. 4, 5). Assuming that the growth period was eight months (Schöne et al., 2005a,b) this translates into an average temporal resolution of less than nine days per isotope sample. The temporal resolution of the 28th annual increment was about 40 days and the resolution of increment number 20 ca. four days. Most positive intra-annual $\delta^{18}O$ values were measured shortly after the annual growth line and most negative values shortly before the following growth line (Fig. 5). This saw-tooth shaped (incomplete sinusoidal) pattern was observed throughout the entire studied shell portion.

3.1.2. Statistics

Over the interval from age one to 38, intra-annual $\delta^{18}O_{aragonite}$ values range – on average – between + 2.87‰ and +3.33‰. Assuming that the seawater oxygen isotope composition was always close to zero, this translates into temperatures of 7.3 and 5.3 °C, respectively. The most positive oxygen isotope values of +3.52‰ (=4.5 °C) were measured during 1501 and 1502 (ontogenetic ages seven and eight=annual increments eight and nine) and most negative values during 1512 (age 18; 2.41‰=9.3 °C; Fig. 5). Today's minimum and maximum temperatures occur during March (4.98 °C) and August (9.39 °C). The $\delta^{18}O_{aragonite}$-derived annual mean temperature of 6.2 °C averaged over the period of 1496–1533 corresponds well to the long-term (1854–2003) February–September (growth period of A. islandica; Schöne et al., 2005a,b) mean of 6.81 °C. Carbon isotopes showed a mean intra-annual range of 0.69‰ (2.04–2.73‰). Over years one to 39, the most enriched and depleted carbon isotope values occur during 1526 (age 32;+3.17‰) and 1506–1507 (age 13;+1.40‰), respectively (Fig. 5).

3.1.3. Trend analyses

We did not find trends in carbon or oxygen isotope values over the 39 year-long chronology (Fig. 6). The regression lines over the 1051 oxygen and carbon isotope datapoints are almost flat (Fig. 6). A slight positive trend (+0.25‰), however, appears to exist among the most depleted $\delta^{13}C_{aragonite}$ ratios (Fig. 6). Lowest $\delta^{13}C_{aragonite}$ values during ontogenetic years ten (1504) and twelve (1506) were near +1.5‰, while most depleted values during year 38 (1532) were about 0.3‰ higher.

3.1.4. Spectral analyses

The MTM-spectrum of the SGI chronology shows significant (95% confidence level) quasi-periodic oscillations centered at 14, 8.3, 6.3 and 4.3 years (Fig. 7A). Monte-Carlo SSA suggests that the 14 and 6.3 year components are the most robust spectral features of the SGI time-series (Fig. 7B). Similar spectral peaks are found in the annual isotope chronologies (maximum and minimum $\delta^{18}O_{aragonite}$ and $\delta^{13}C_{aragonite}$ values; Fig. 8).

3.2. Sclerochronology: annual shell growth rates

Annual increment widths decrease from the umbo toward the ventral margin (Fig. 3). The broadest annual increment measured 5108 μm (1497, age 3), and the narrowest increment was smaller than 10 μm (1856, age 362). Detrending and standardizing revealed a time interval of extremely variable growth between about 1550 and 1620. For example, SGI values fluctuate between 4.67 and −1.36 in consecutive years (1606 and 1607). Unusually narrow annual increments (SGI smaller than −1.7) formed, for example, during the following years: 1521, 1554–56, 1568–74, 1581, 1587, 1593–1601 and 1816–18. Little year-to-year variance was observed between about 1765 and 1780. SGI values exhibit decadal fluctuations. Spectral peaks (significant at the 95% confidence level) occur at periods of 6, 8.4 and 13 years (see above; Figs. 3, 7).

3.3. Relation between annual shell growth and shell isotope data

Regression analysis revealed a close relationship between SGI values and maximum $T_{\delta 18O}$ or maximum $\delta^{13}C_{aragonite}$ values, respectively (Fig. 9). About 34% ($r=0.58$, $p<0.0001$) of the variation in annual shell growth is explained by oxygen isotope-derived summer temperatures and 42% ($r=0.65$, $p<0.0001$) by the seasonal $\delta^{13}C_{aragonite}$ maximum values. The
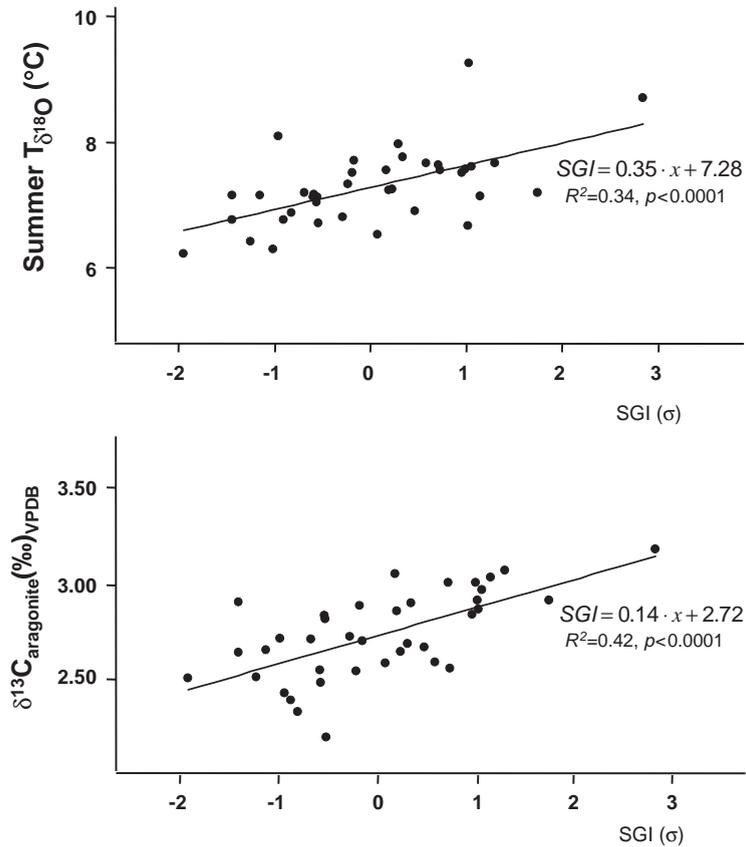
Fig. 9. Regression analyses between annual shell growth (*SGI*) and shell isotope data. Warmer temperatures (less positive $\delta^{18}O_{aragonite}$ values) and better food supply (^{13}C-enriched $\delta^{13}C_{aragonite}$ values) resulted in faster shell growth.

good agreement between isotope data and shell growth is depicted in Fig. 9. An even higher percentage (65%, $r = 0.81$; $p < 0.0001$) of variation in annual shell growth (*SGI*) can be explained by a combined model (linear multiregression analysis) including maximum $T_{\delta18O}$, maximum $\delta^{13}C_{aragonite}$ and minimum $\delta^{13}C_{aragonite}$ values as predictors (Fig. 9).

4. Discussion

4.1. Bivalved methuselahs

Aside from biblical myths, the 374 year-old *A. islandica* specimen from Iceland used in the present study is the oldest ever reported individual animal. Previous studies reported life spans of 225 (Ropes and Murawski, 1983) and 268 years (Forsythe et al., 2003) for the Ocean Quahog. In fact, bivalve mollusks lead the list of the longest-lived animals (Skrecky, 1996; Jones, 1983) with the Freshwater Pearl Mussel, *Margaritifera margaritifera* (Linnaeus) reaching 200 (Mutvei and Westermark, 2001) to over 280 years (E. Dunca, pers. comm., 2004), *Panopea abrupta* (Conrad) > 160 years (Strom et al., 2004) and *Crenomytilus grayanus* (Dunker) > 150 years (Zolotarev, 1980). Examples of other extremely long-lived individual animals include Bowhead Whales (*Balaena mysticetus* Linnaeus) which were estimated to be 211 ± 35 years old (George et al., 1999), Giant Turtles

(*Geochelone gigantean* (Schweigger)) 150 (Finch and Austad, 2001) to 180 years (Skrecky, 1996), and Rockfishes, *Sebastes* spp. 84 (Wilson and Boehlert, 1990) to 205 years (Cailliet et al., 2001). For comparison, the oldest human, the Frenchwoman Jeanna Calment died on August 4, 1997 at age 122 (Robine and Allard, 1998). Aside from prospects of better understanding why senescence in some animals is so much delayed and of developing methods to extend life-spans and slow-down the ageing process, *A. islandica* functions as an extraordinary climate archive as shown in the following and in previous studies (Marchitto et al., 2000; Marsh et al., 1999; Witbaard et al., 1997; Weidman et al., 1994; Thompson et al., 1980; Jones, 1980; Schöne et al., 2003, 2004).

In the following we discuss observations on growth rates and shell isotopes of *A. islandica* on different time-scales: annual, multi-decadal and over the shell's life span.

4.2. Annual cycles in the shell isotope record: temperature and food availability

The incomplete sinusoidal shape of the intra-annual oxygen isotope curve confirms previous findings on the annual periodicity of shell formation of *A. islandica* (Weidman et al., 1994; Schöne et al., 2005a,b). Shell growth starts before the winter minimum temperatures are attained and stops after the summer maximum has occurred (Fig. 5). It would seem that the summer temperature climax (see compilation in Skrecky, 1996) or decreasing water temperatures after this (see Schöne et al., 2005a) either directly trigger the retardation of shell growth or do so indirectly by stimulating the annual reproduction cycle, thus causing a diversion of resources to gonadal development. Note that *A. islandica* reaches maturity, on average, only at age thirteen (Rowell et al., 1990). However, pre-mature animals also produce an annual spawning break and interrupt or slow-down shell growth. Thompson et al. (1980) hypothesized that the shell mimics the reproductive cycle during youth. This kind of "foreshadowing" was also assumed for immature scallops (Fairbridge, 1953). Such findings suggest that the formation of the spawning break is controlled by some kind of a biological clock.

Temperatures reconstructed from $\delta^{18}O_{aragonite}$ values (Fig. 5) fall within the range of today's ob-served temperature ranges near Iceland. This finding supports previous observations that $\delta^{18}O_{aragonite}$ values of *A. islandica* provide a good proxy for temperatures if the $\delta^{18}O_{seawater}$ is known or can be accurately estimated (Marsh et al., 1999; Weidman et al., 1994; Schöne et al., 2004).

Carbon isotopes also show clear annual cycles (Fig. 5). During the spring and summer phytoplankton bloom, $\delta^{13}C_{aragonite}$ values become depleted (Krantz, 1990). Note that the specimen of *A. islandica* used in the present study lived in shallow waters. This is indicated by the intra-annual oxygen isotope-derived temperature curves which closely resemble today's SST data in the region from which the shell came from. The specimen used in the present study lived thus above the thermocline, so that changes in phytoplankton abundance and hence the $\delta^{13}C_{seawater}$ values are directly recorded by the shell. Seasonal change of $\delta^{13}C_{seawater}$ composition also depends on environmental factors such as river discharge (Khim et al., 2003).

4.3. Length of the annual growth period

Apparently, the growth period of *A. islandica* remains the same throughout life, at least during the first 39 years of growth. This interpretation is based on the following observations. First, the typical incomplete sinusoidal shape of the intra-annual $\delta^{18}O_{aragonite}$ curve was found in shell portions near the umbo and during later years of growth (Fig. 5), with the most positive oxygen isotope values shortly after the annual growth lines and most negative values slightly before the following line. Second, extreme $\delta^{18}O_{aragonite}$ and $\delta^{13}C_{aragonite}$ values in younger and older shell portions were approximately similar (Fig. 5). It has been barely studied in the past whether growth periods change through lifetime or not. However, this has important implications for the interpretation of geochemical data gathered from different positions across the shell. Such data include, for example, long-term trends of oxygen isotope-derived water temperatures or the shell carbon isotope record.

4.4. Shell isotopes on multi-decadal time scales

We did not observe ontogenetic trends, i.e., age-related 'vital effects' in the $\delta^{18}O_{aragonite}$ or $\delta^{13}C_{aragonite}$

record of *A. islandica* (Fig. 6). Previous results partly accord with this. Marsh et al. (1999) used the zδ^{18}O$_{aragonite}$ record of several *A. islandica* specimens with overlapping life spans to construct a century-long bottom water record. Ontogenetic trends were not observed in the δ^{18}O$_{aragonite}$ record of this species. However, the variability of oxygen isotope values decreased in later, slower-growing shell portions. Weidman et al. (1994) attributed this finding to lower sampling and hence reduced temporal resolution. The 'adaptive sampling strategy' utilized in the present study enabled us to capture summer and winter temperature extremes even in narrow increments in later ontogenetic stages.

As of yet, continuous δ^{13}C$_{aragonite}$ records from long-lived bivalves have only rarely been obtained. One case is the symbiont-bearing *Tridacna maxima* (Roeding) by Jones et al. (1986). Jones et al. (1986) showed that the carbon isotope composition measured across the first 28 years of growth becomes abruptly depleted at about age ten. However, many studies exist on carbon isotope values of relatively short-lived bivalves (life-spans of a few years to decades). Such studies demonstrate that carbon isotope values become more negative during lifetime (e.g., Krantz et al., 1987; Wefer and Berger, 1991; Kennedy et al., 2001; Elliot et al., 2003; Mueller-Lupp et al., 2003; Lorrain et al., 2004). Ontogenetic δ^{13}C$_{aragonite}$ trends have been interpreted as reflecting a greater respiratory CO_2 uptake as the shells become older and grow slower (Harrington, 1989).

We have no explanation why only short-lived bivalves show ontogenetic trends in shell carbon isotopes. Was the sampling strategy inappropriate in all such studies? Many studies sampled the shells with the same spatial resolution (drill bits of the same diameter, drilling instead of milling) in shell portions near the umbo and near the commissure. Hence, samples taken from later shell portions comprise longer time periods than samples from fast-growing juvenile portions of the shells. Is the growth period of short-lived bivalve mollusks changing during ontogeny, so that the isotope records of pre-mature and mature shell portions represent different proportions of the year? Furthermore, it seems likely that natural variations of carbon isotope values are misinterpreted as ontogenetic

trends. Trends in shell carbon isotopes of short-lived bivalves may in fact belong to decadal-scale swings in δ^{13}C$_{seawater}$. It is unclear whether our findings only apply to the Ocean Quahog or to other long-lived bivalve species as well. Additional studies are thus required.

4.5. Decadal cycles in the isotope and shell growth records

Although we did not find unidirectional, i.e., age-related trends in the δ^{18}O$_{aragonite}$ and δ^{13}C$_{aragonite}$ record of *A. islandica*, clear decadal cycles were observed (Fig. 8). Apparently, temperature and food supply have changed on decadal-scales. The statistical significance of these cycles was confirmed by the annual shell growth rates of *A. islandica* (Fig. 7) Annual shell growth rates show a strong linear relationship with δ^{18}O$_{aragonite}$ and δ^{13}C$_{aragonite}$, because temperature and food availability exerted a major control (65%) on the shell production of *A. islandica* (Fig. 9). Decadal cycles in food supply may result from changes in primary productivity or from increased resuspension of organic particles during positive NAO years (Schöne et al., 2003), i.e., during years of stronger current flow (Dickson, 1999).

Spectral analysis of the *SGI* chronology revealed four highly significant (95% confidence level) decadal-scale periodic components (Fig. 7). Similar periodic component are obvious in the shell isotope series (Fig. 8). The four, six and eight to nine-year-components probably represent NAO-type forcing. Previous studies have already demonstrated that variations in the North Atlantic Oscillation exert a major control on both the shell isotope record and on annual shell growth rates of *A. islandica* from the North Sea and the Norwegian Sea (Schöne et al., 2003, 2004). During positive stages of the NAO, winter temperatures and food levels are higher, supporting faster shell growth. Another strong spectral peak exists at frequencies corresponding to periods of about twelve to fourteen years. Currently, we do not have a clear-cut explanation of what this cycle means. The cycles in δ^{13}C$_{aragonite}$ may be attributed to the sunspot cycle and concurrent solar-induced variations in the δ^{13}C composition of the seawater (see Castagnoli et al., 2002). It is also hypothesized that the cycles in

$\delta^{18}O_{aragonite}$ and annual shell growth rates resemble the twelve to fourteen-year-periods that have been reported for North Atlantic SST (Sutton and Allen, 1997), which in turn might be teleconnected to the tropical Atlantic meridional SST gradient (TAMG; Mélice and Servain, 2003).

4.6. Variations in growth rates track climate extremes

Extremely low shell growth rates during 1816–18 (Fig. 3) are very likely the result of the environmental disturbances (cooling and reduced food supply) caused by volcanic eruptions of Mount Tambora (Sumbawa Island, Indonesia) during April 1815 (Robock, 2002). Large amounts of dust in the atmosphere caused a "year without a summer" (Stommel and Stommel, 1979) and a general cooling phase in the following years (Crowley et al., 1997). During 1816 and the following two years, tree growth in the northern hemisphere was strongly reduced (Briffa et al., 1998). The year 1816 also marks the midpoint of the Sun's extended period of low sunspot activity, the so-called Dalton Minimum (1795–1820).

Some other unusually narrow increments postdate major volcanic eruptions, e.g., 1581 and 1587 (Billy Mitchell, SW Pacific, 1580; Kelut, Java, 1586; Briffa et al., 1998) and 1593–1601 (Raung, Java, 1593; Huaynaputina, Peru, 1600; Briffa et al., 1998). On the other hand, the 1783 eruptions at Laki and Hekla did not result in significant growth reductions. Further analyses are required to analyze why some major volcanic eruptions were not recorded in the shell growth pattern.

The extreme interannual variability in shell growth during the 16th century, in particular between about 1550 and 1620 (Fig. 3) falls within a period of extraordinarily harsh and highly variable climate in Iceland (Ogilvie and Jónsson, 2001), also known as the culmination of the Little Ice Age (Lamb, 1965). More frequent shifts between temperature extremes during this period may have also influenced primary productivity. Extraordinarily mild climate during the early part of the 17th century near the end of the Little Ice Age (Ogilvie and Jónsson, 2001) coincides with a period of little growth variability (Fig. 3). It is likely that variations in temperature and food supply that occurred at the same time affected the shell growth of A. islandica.

5. Conclusion

The main results reported in the present study are as follows:

(1) A. islandica is the record-holder of longevity among individual animals. The specimen used here reached an ontogenetic age of 374 years.
(2) Variations in annual shell growth are closely correlated with summer temperatures (reconstructed from $\delta^{18}O_{aragonite}$) and food availability ($\delta^{13}C_{aragonite}$).
(3) Shell oxygen and carbon isotopes from ontogenetic age one to 39 do not exhibit age-related, unidirectional trends. Vital effects seem not to occur during the first 39 years of growth or 4/5 of the entire shell height.
(4) Four significant quasi-periodic oscillations were found in the shell record: a 12 to 14-year cycle and NAO-type periods of about four, six and eight to nine years.
(5) During the first 39 years of its life, the length of the growth period of A. islandica remained unchanged (probably February–September).
(6) Extreme environmental conditions are recorded in the shell as variable growth rates (e.g., volcanic eruptions, cold and mild climates).

Shells of A. islandica provide an extraordinarily high-resolution, long-term and multi-proxy archive of environmental variables for marine mid to high latitudes. Paleoenvironmental information inferred from shells of the Ocean Quahog may be very beneficial for improving climate models and for assessing human impact on climate and ecosystems.

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