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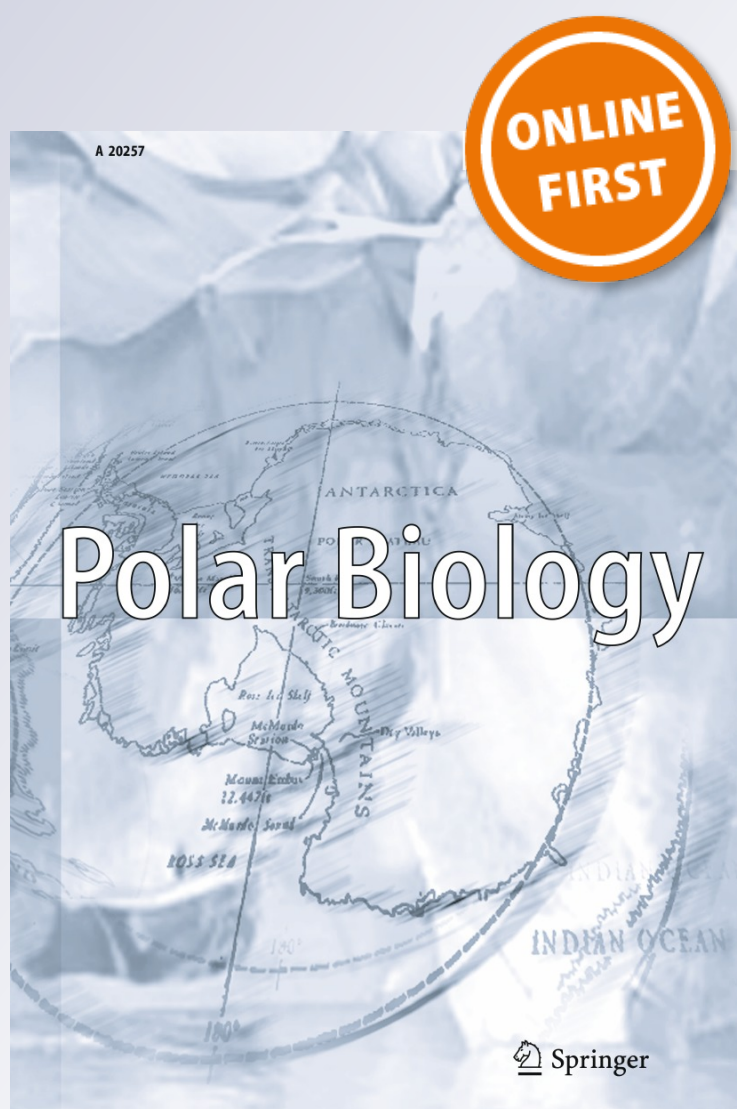
David K. Moss, Donna Surge & Vadim Khaitov

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Lifespan and growth of *Astarte borealis* (Bivalvia) from Kandalaksha Gulf, White Sea, Russia

David K. Moss¹ · Donna Surge¹ · Vadim Khaitov^{2,3}Received: 2 October 2017 / Revised: 13 February 2018 / Accepted: 21 February 2018
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Abstract

Marine bivalves are well known for their impressive lifespans. Like trees, bivalves grow by accretion and record age and size throughout ontogeny in their shell. Bivalves, however, can form growth increments at several different periodicities depending on their local environment. Thus, establishing lifespans and growth rates of marine bivalves requires a proper identification of annual growth increments. Here, we use isotope sclerochronology to decipher the accretionary growth record of modern *Astarte borealis* from the White Sea, Russia (N 67°05.70'; E 32°40.85'). Unlike winter growth increments observed in many other cold-temperate and boreal bivalve and limpet species, prominent growth increments in *A. borealis* corresponded to the most negative values in the oxygen isotope ($\delta^{18}\text{O}$) time series indicating that they formed during summer. Furthermore, summer growth increments do not coincide with the external concentric ridges on the shell making the latter feature an unreliable indicator of age. Similar to many other polar bivalves, *A. borealis* shows slow growth and long life. The von Bertalanffy growth equation for our sample is $H_t = 29.39 * (1 - e^{(-0.11(t - (-1.86))})}$. Lifespans of individuals examined here ($n = 18$) range from 16 to 48 years. Given its impressive longevity and widespread polar distribution, *A. borealis* may be a potentially valuable skeletal archive for monitoring environmental conditions in the Arctic Ocean and boreal seas in the face of changing climate.

Keywords *Astarte borealis* · Growth · Lifespan · Longevity · White Sea · von Bertalanffy

Introduction

Marine bivalves are some of the longest-lived non-colonial animals on the planet today. Several species attain lifespans in excess of a century (e.g., Turekian et al. 1975; Zolotarev 1980; Shaul and Goodwin 1982; Bureau et al. 2002; Sejr et al. 2002; Kilada et al. 2009; Ridgway et al. 2011a; Reynolds et al. 2013) and two, *Arctica islandica* and *Neopycnodonte zibrowii*, over five centuries (Thompson et al. 1980; Marchitto et al. 2000; Schöne et al. 2005; Wanamaker et al. 2008; Wisshak et al.

2009; Butler et al. 2013). Given their impressive longevity, bivalves have become targets of paleoclimate (e.g., Scourse et al. 2006; Butler et al. 2010; Winkelstern et al. 2013), water quality (e.g., Dunca et al. 2005; Gillikin et al. 2005; Black et al. 2017), macroevolutionary (Moss et al. 2016), and ageing studies (e.g., Abele et al. 2009; Philipp and Abele 2009; Buttemer et al. 2010). Akin to growth rings in trees, bivalves form growth increments in their shells throughout ontogeny. In bivalves, growth increments can form in response to changes in local environmental conditions. Thus, they can form at several periodicities: tidal, lunar, fortnightly, monthly, and annual (Weymouth 1923; Barker 1964; House and Farrow 1968; Pannella and MacClintock 1968; Evans 1972; Clark 1974; Pannella 1976; Goodwin et al. 2001). In addition, bivalves may form growth increments in response to biologic events like spawning (e.g., Jones et al. 1983). A single individual may form increments at all of these periodicities, so determining the lifespan and growth rate requires proper identification of annual increments. Fortunately, the techniques of isotope sclerochronology (the application of variations in stable isotope ratios corresponding to shell growth patterns) can help to

✉ David K. Moss
dkmoss@unc.edu

¹ Department of Geological Sciences, University of North Carolina, 104 South Road, CB #3315, Chapel Hill, NC 27599-3315, USA

² Department of Invertebrate Zoology, Saint-Petersburg State University, University Embankment 7-9, St. Petersburg 199034, Russia

³ Kandalaksha State Nature Reserve, Linejnaya Str., 35, Kandalaksha, Murmansk District 184040, Russia

identify annual growth lines. Oxygen isotope ratios ($^{18}\text{O}/^{16}\text{O}$; $\delta^{18}\text{O}$ values) are the most commonly employed geochemical proxy in carbonate hard parts, and because their values are in part a function of temperature, they show a sinusoidal pattern reflecting seasonal variation (Jones and Quitmyer 1996; Ivany 2012; Schöne and Surge 2012). This technique was applied in the early 1980s to the Atlantic surf clam, *Spisula solidissima* (Williams et al. 1982; Jones et al. 1983), and confirmed the presence of annual growth lines in the ventral shell margin. During the spring and summer, wide growth increments form reflecting fast growth in shells, and in the late summer narrow, dark lines form when growth slows or stops. Since then, isotope sclerochronology has been applied to many species from a range of habitats to document annual growth increments in both modern (e.g., Witbaard et al. 1994; Hallmann et al. 2008; Kubota et al. 2017) and pre-Holocene bivalves (e.g., Jones and Gould 1999; Buick and Ivany 2004; Mettam et al. 2014; Walliser et al. 2015).

Here, we use isotope sclerochronology to identify annual growth lines and document the season of their formation in a ubiquitous cold-temperate to polar bivalve, *Astarte borealis*, from a small population in the White Sea, Russia. Mueller-Lupp et al. (2003) sampled the external surface of *A. borealis* for oxygen isotope ratios to infer seasonal and interannual river discharge into the Laptev Sea, Russia. Their sampling was not guided by internal shell structure and thus provides no information on timing of growth line formation. Elsewhere, studies have reported lifespans from 8 to 10 years for *A. borealis* from the Baltic Sea (Gusev and Rudinskaya 2014), Sea of Okhotsk (Selin 2007, 2010), and the Eastern Siberian Sea (Gagayev 1989), but they primarily relied upon ridges on the external surface of shells to determine age, which are often unreliable (Krantz et al. 1984). Torres et al. (2011) used isotope sclerochronology on *A. borealis* from extreme northern Greenland and found individuals up to 150 years. In the White Sea, Skazina et al. 2013 tracked size cohorts through time and estimated *A. borealis* lifespans to be upwards of 20 years. In their study, length (anterior to posterior distance) was unimodal and ranged from 21.1 to 42.2 mm ($n = 676$). However, in high-latitude bivalves, growth tends to be slow (e.g., Sejr et al. 2009; Ambrose et al. 2012), and in particularly long-lived species, a few millimeters growth could potentially represent decades. Our results suggest that this may be the case for *A. borealis* as we document slow growing individuals with lifespans approaching 50 years.

Ecology

Astarte borealis is a major component of many Arctic and Boreal seas of the northern oceans (Zettler 2002), representing 15% or more of the total benthic biomass in some

regions (Schaefer et al. 1985). Populations are widespread and found in the Pacific Ocean from the Sea of Okhotsk to the Aleutian Islands, in the Arctic waters of Russia from the Barents Sea to the Chukchi Sea, and in the Atlantic Ocean from New Foundland to Greenland and Iceland, and in Europe in both the North and Baltic Seas (Zettler 2001). *Astarte borealis* is an infaunal suspension feeder found buried up to 2 mm below the sediment surface preferring muddy-sand containing gravel (Saleuddin 1965). In the White Sea, their main food source, phytoplankton, begin to bloom during the spring melt in April, but remain relatively low in abundance until the peak bloom in July and August (Vershinin et al. 2006). After ice formation in November, food is in low abundance until spring. Like other Astartids, *A. borealis* has large (150–200 μm) yolk-rich eggs with a sticky outer envelope causing populations to settle in clusters (Kauffman and Buddenhagen 1969; Von Oertzen 1972; Matveeva 1977). The timing of spawning varies by region. In Greenland and the North Atlantic Ocean, spawning occurs from October to December (Thorson 1936). In the Baltic Sea, individuals possess ripe eggs and sperm for almost the entire year and may portion spawn (takes place during several intervals) rather than at a certain period (von Oertzen 1972). Most populations of *A. borealis* are restricted to cold, marine/brackish waters, tolerating a salinity range of 8–35 psu (practical salinity units; Zettler 2002). In the White Sea, *A. borealis* is more or less evenly distributed throughout the depth range (2–100+ m; Naumov 2006). *Astarte borealis* have been the subject of several studies on anoxia within the Baltic Sea and has been found to be anoxia tolerant, although repeated extended exposures to anoxic conditions will eventually cause mortality (Theede et al. 1969; von Oertzen 1973; Oeschger 1990).

Materials and methods

Study area

The White Sea is a restricted body of water connected to the Arctic Ocean via the Barents Sea along the northwestern coast of Russia. It is comprised of four gulfs: Kandalaksha, Onega, Dvina, and Mezen. Kandalaksha Bay, located in the northwestern corner, is the deepest part of the White Sea reaching depths up to 343 m (Berger et al. 2001; Sukhotin and Berger 2013). Kandalaksha Bay is dominated by fjords and inlets along its coast and is ice covered for 5–7 months out of the year. The samples used here were collected from Illistaya Inlet, Gorey Island in the Kandalaksha State Nature Reserve Area (67°05.70' N; E 32°40.85' N) (Fig. 1). Bottom water temperature at the collection site is stable at approximately $-1\text{ }^{\circ}\text{C}$ during the winter months and averages $12.1\text{ }^{\circ}\text{C}$ during the summer months. Salinity

at the collection site varies with the seasons, ranging from 18.1 to 27.9 psu, with the lowest salinity occurring in April and May during the spring melt and the highest salinity from October to December (Skazina et al. 2013). Freshwater from river discharge accounts for 95% of the water budget in the White Sea (Berger et al. 2001) with most of this discharge due to late spring meltwater pulses. The Luvenga and Niva rivers (approximately 1 and 18 km away) provide most of the freshwater input for our sampling area. Most of this freshwater comes from major rivers in the southern region of the White Sea in Onega and Dvina Bays. Because of the significant seasonal freshwater input, $\delta^{18}\text{O}_{\text{water}}$ values in the White Sea are not constant temporally or spatially. During the summer, values are on average -3.0‰ VSMOW (Vienna-Standard Mean Ocean Water) near the mouth of the White Sea, but farther back into its bays values can drop to -10‰ (Nikolayev and Nikolayev 1988).

Shell collection and preparation

We used 18 shells collected during a previous study (Skazina et al. 2013) and now housed in collections at the University of North Carolina, Chapel Hill (UNC) to examine lifespan and growth rate. From this sample, three shells with a well-preserved ventral margin were selected for isotopic analysis

(UNC 16030, 16031, and 16032). Live specimens were harvested from late December 1999 to early January 2000 by taking four samples using a Petersen grab through a hole in the sea ice. Soft tissue was removed from the shells and not preserved. Water depth for the samples ranged from 3 to 7 m. Before processing, shell length (anterior to posterior) and maximum height (umbo to ventral margin) were measured using digital calipers to the nearest 0.01 mm to put our sample in context of the population.

To view internal growth increments, we first applied a layer of quick-dry metal epoxy resin (J-B KWIK WELD) along the axis of maximum growth from the umbo to ventral margin to prevent loss of shell material during cutting. Shells were then cut along this axis using a Gryphon diamond band saw. Thick sections were made of each shell using a Buehler Isomet low-speed saw (Fig. 2). Two thick sections were made of the shells selected for isotopic analysis. To remove saw marks and create a smooth surface for imaging, shell thick sections were polished on a Buehler MetaServ 2000 variable speed grinder polisher using silicon-carbide discs and finished with diamond suspension solutions with grit sizes of 6 and 1 μm . Polished thick sections were imaged using an Olympus SZX7 stereomicroscope system coupled with an Olympus DP71 12.5 megapixel digital camera and stitched together using Olympus Stream Essentials version

Fig. 1 Location of the study area in Kandalaksha Bay, White Sea, Russia, near the Luvenga archipelago (N 67°05.41', E 32°40.44'). Star indicates location of the shell collection site. Shells were collected at this location for a previous study (Skazina et al. 2013)

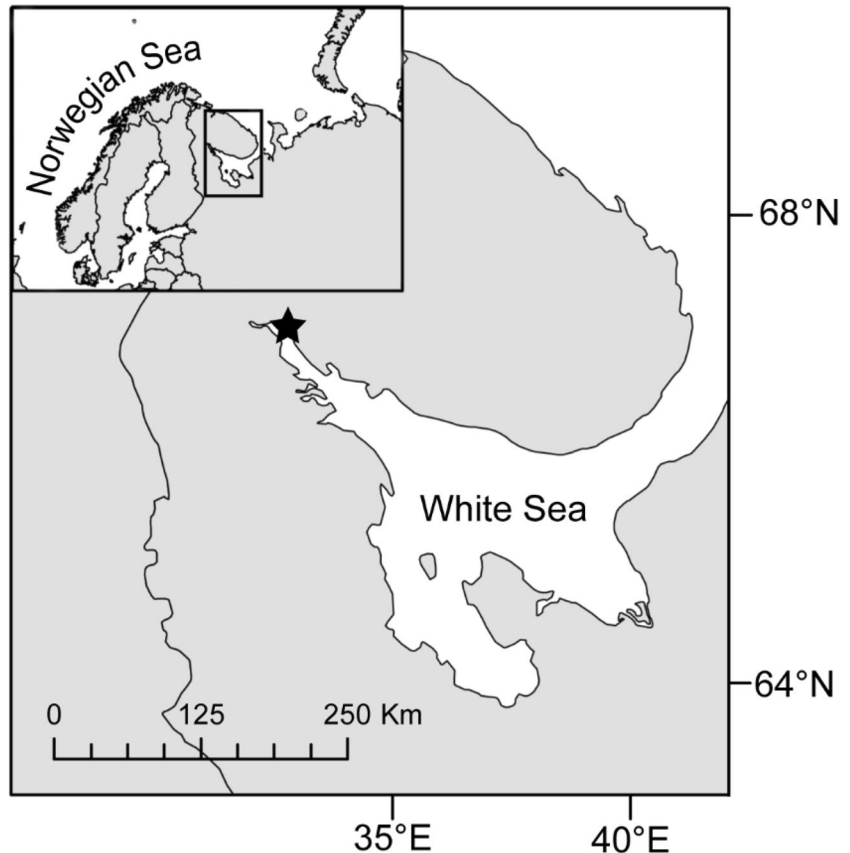
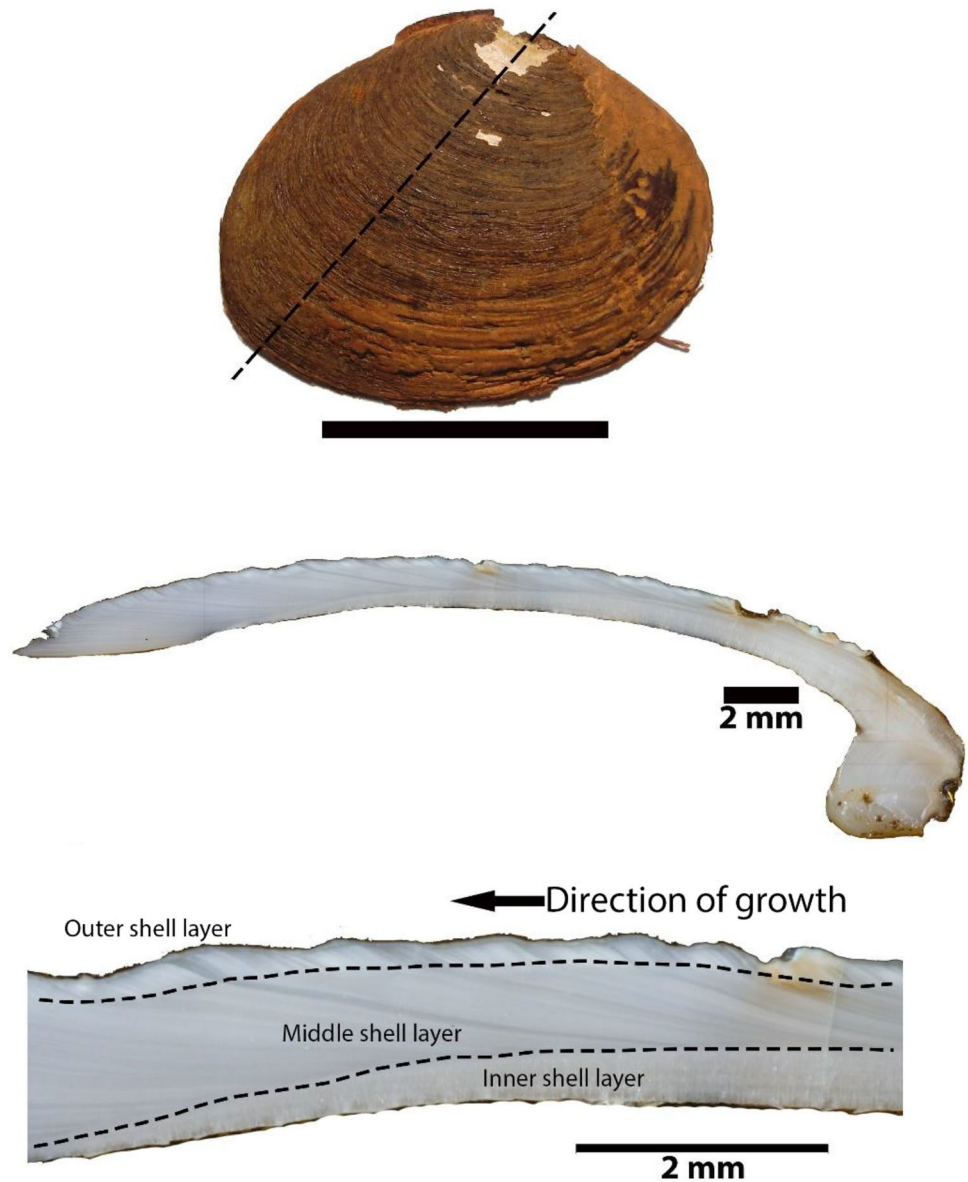


Fig. 2 Shell images of *A. borealis* illustrating sample preparation and measurements. Top panel: left valve with periostracum intact except near umbo. Dashed line indicates direction of sectioning along axis of maximum growth. Middle panel: thick section under reflected light with umbo on the right and ventral growth margin on the left. Bottom panel: enlarged reflected light image of polished shell cross section showing inner, middle, and outer microstructural layers; growth direction (black arrow); and prominent growth checks



2.2 to create a composite image of the entire shell from umbo to ventral margin.

The three shells selected to document periodicity of growth line formation were microsampled along the middle and outer crossed-lamellar microstructural layers for stable carbon and oxygen isotope analysis. Microsampling was performed using a Merchantek micromilling system fitted with a Brasseler tungsten carbide dental scriber point (part number H1621.11.008). Spacing between major growth lines is widest early in ontogeny, so we microsampled specimens UNC 16030 and UNC 16032 between sections of prominent lines in the first third of the shell to determine the season of annual growth line formation. Specimen UNC 16031 was sampled at a much higher resolution to distinguish between true annual growth checks and non-periodic disturbance lines. Aragonite microsamples were analyzed

at the Environmental Isotope Laboratory, University of Arizona. The samples were reacted with dehydrated phosphoric acid under vacuum at 70 °C for 1 h and liberated CO₂ gas was analyzed on a Finnigan MAT 252 mass spectrometer with an auto-carbonate reaction system (Kiel-III Device). Isotope ratios were calibrated based on repeated measurements of NBS-18 (National Bureau of Standard) and NBS-19. The precision is $\pm 0.1\text{‰}$ for $\delta^{18}\text{O}$ and $\pm 0.08\text{‰}$ for $\delta^{13}\text{C}$ (1 σ) based on repeated measurement of internal carbonate standards. Unknown samples were corrected with measured NBS-19 values, and no correction was applied based on mineralogy. Oxygen and carbon isotope ratios are reported relative to the VPDB (Vienna Pee Dee Belemnite) carbonate standard.

Once annual growth lines were identified in the ventral margin, we used the freeware ImageJ to count and measure

the cumulative distance between growth lines in all 18 specimens. We then fit the von Bertalanffy growth equation (von Bertalanffy 1938) (VBG) to the combined size-at-age data using the non-linear least squares (nls) procedure in the open source R language (cran.r-project.org). VBG has been used in many other bivalve studies (e.g., Brousseau 1979; Haag and Rypel 2011; Ridgway et al. 2012; Puljas et al. 2015) and describes the size of an individual at a given time (H_t):

$$H_t = H_{\infty}(1 - e^{-k(t-t_0)})$$

where H_{∞} = asymptotic size, t_0 = the time at which $H_t = 0$, and k = rate at which H_{∞} is attained.

Results

Oxygen and carbon isotope ratios

The $\delta^{18}\text{O}$ records of specimens UNC 16030, UNC 16031, and UNC 16032 (Figs. 3, 4) all form quasi-sinusoidal patterns. The most negative values correspond to prominent, dark growth lines originating from the middle shell layer and terminating in the outer shell layer, while the most positive values occur approximately half-way between two dark lines. We used these features to define the annual growth increments (couplets of dark lines and light increments) to age specimens. Not all dark growth lines correspond to valleys (i.e., most negative values) in the $\delta^{18}\text{O}$ time series, however

(Fig. 4). Such lines occur only in the outer shell layer and do not extend into the middle shell layer. External concentric ridges on the surface of the White Sea shells do not correlate with dark lines or light increments, nor do they occur at regular intervals along the $\delta^{18}\text{O}$ time series. They are, therefore, not reliable indicators of annual growth or lifespan.

Carbon isotope ratios do not covary with the oxygen isotope time series (Figs. 3, 4). Unlike the $\delta^{18}\text{O}$ time series, there is no consistent relationship between the $\delta^{13}\text{C}$ time series and growth features in the shell.

Size, lifespan, and growth

Lengths (anterior–posterior distance) of our specimens ranged from 28.2 to 35.5 mm, which covers a wide range of that observed by Skazina et al. (2013) over several decades of sampling on Gorely Island. Annual growth increments as documented by oxygen isotope ratios in the ventral shell margin allowed for determination of lifespan and characterization of growth using the VBG equation. Despite having a relatively small number of samples, we have captured a significant range of lifespans for this species with the shortest living individual reaching 16 years and the longest 48 years. Growth in our sample was well approximated by the VBG equation as all individuals showed an initial rapid increase in size to approximately 15 years followed by several years of slow growth (Fig. 5). The VBG for the pooled age-at-size data was $H_t = 29.39*(1 - e^{(-0.11(t-(-1.86))})}$.

Fig. 3 Values of shell $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$. Top panel: UNC 16032. Bottom panel: UNC 16030. Filled circles = $\delta^{18}\text{O}$ values. Open circles = $\delta^{13}\text{C}$ values. Vertical grey lines identify annual growth lines

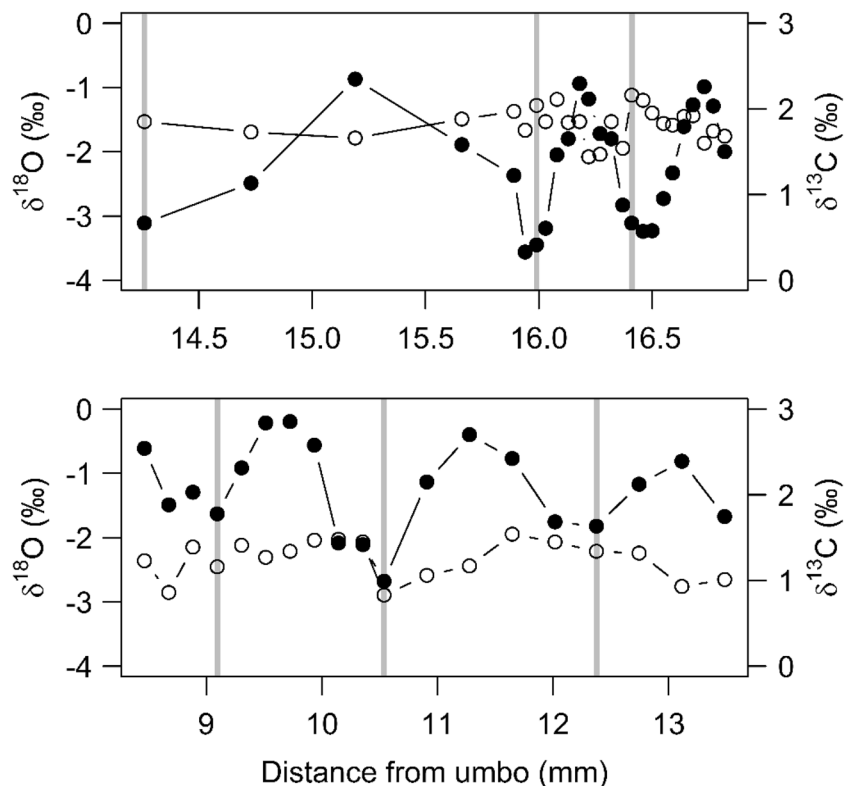
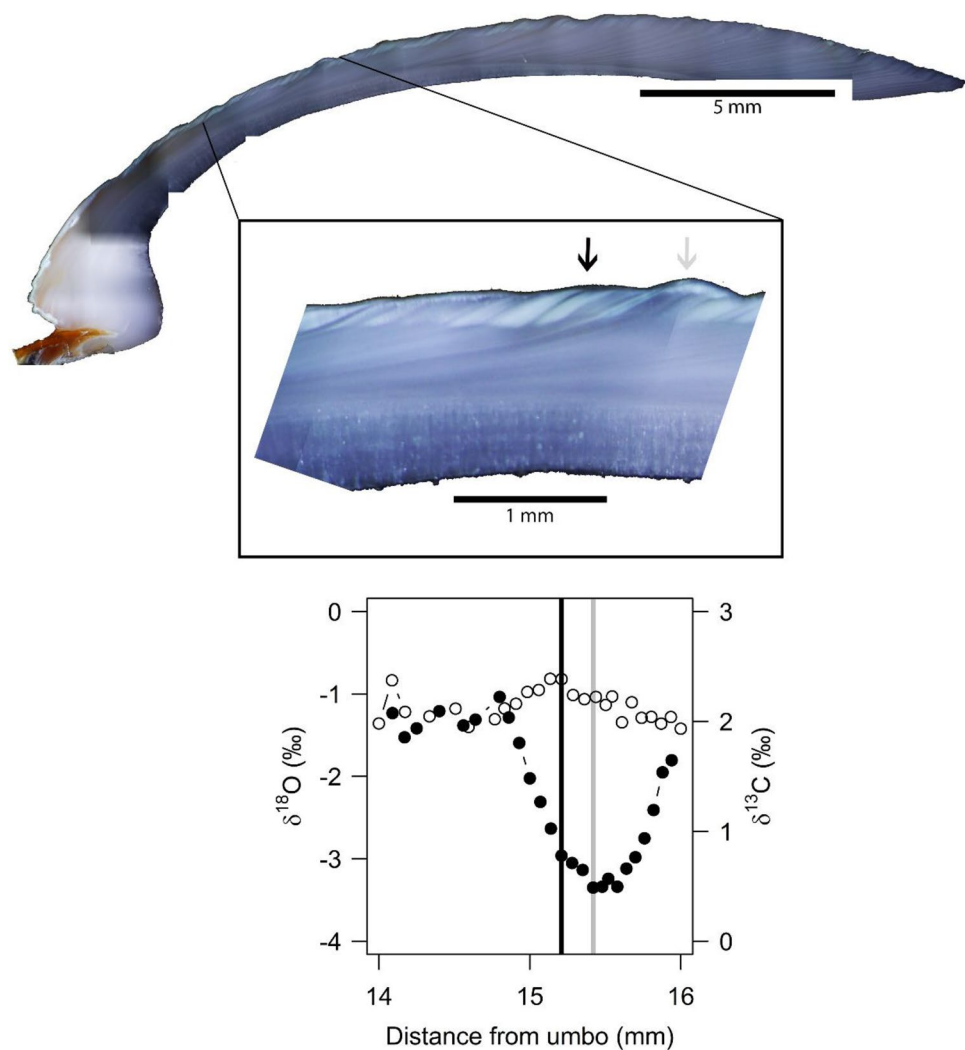


Fig. 4 Values of shell $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ and companion images illustrating locations of growth features in specimen UNC 16031. Top panel: shell cross section cut along maximum axis of growth with umbo on the left and ventral growth margin on the right. Middle panel: magnified area where high-resolution isotope sampling was completed. Black arrow points to “non-periodic” disturbance line. Grey arrow points to annual growth line. Note that the annual growth line continues through the middle and outer shell layers, whereas the disturbance line occurs in the outer shell layer only. Bottom panel: isotopic time series. Filled circles = $\delta^{18}\text{O}$ values. Open circles = $\delta^{13}\text{C}$ values. Vertical black and grey lines correspond to disturbance and annual growth lines, respectively, depicted in the middle panel



Discussion

Timing of annual growth line formation

Before the use of isotope sclerochronology, conventional wisdom was that bivalves would experience growth cessations in winter in response to cold temperature stress and lowered metabolic rates (Jones and Quitmyer 1996). However, a much more complicated picture involving not only environmental conditions, but also physiological conditions has emerged. Seasonal timing of growth increments in the hard clam, *Mercenaria mercenaria*, shows a latitudinal variation, where individuals from the United States Atlantic Coast from Florida to New York form dark annual increments in the summer and those in Rhode Island form dark increments in the winter (Jones et al. 1989; Quitmyer et al. 1997; Elliot et al. 2003). However, Henry and Cerrato (Henry and Cerrato 2007) studied more recent samples from Narragansett Bay, Rhode Island and showed that over more than two decades, *M. mercenaria* has switched from

a single dark increment in the winter to a more complicated pattern, where multiple dark increments can form in a single year, possibly in response to changing environmental conditions. The latitudinal differences in timing of annual growth line formation may be related to maximum and minimum temperature tolerances for growth of *M. mercenaria*. Similar to *M. mercenaria*, the extremely long-lived *A. islandica* forms an annual increment approximately 1 month after the maximum temperature, but the timing of this event depends on whether or not the individual in question lives above or below the thermocline: between September and November or December and February, respectively (Schöne 2013). More recently, though, growth in *A. islandica* has been shown to be controlled by the availability of food which is limited between the fall and spring (Ballesta-Artero et al. 2017). In addition to temperature, growth shutdowns for reproduction may also result in growth line formation. In *S. solidissima* from New Jersey, USA, dark increments form in late summer just before the annual spawning period (Jones et al. 1983). This is presumably a strategy for devoting

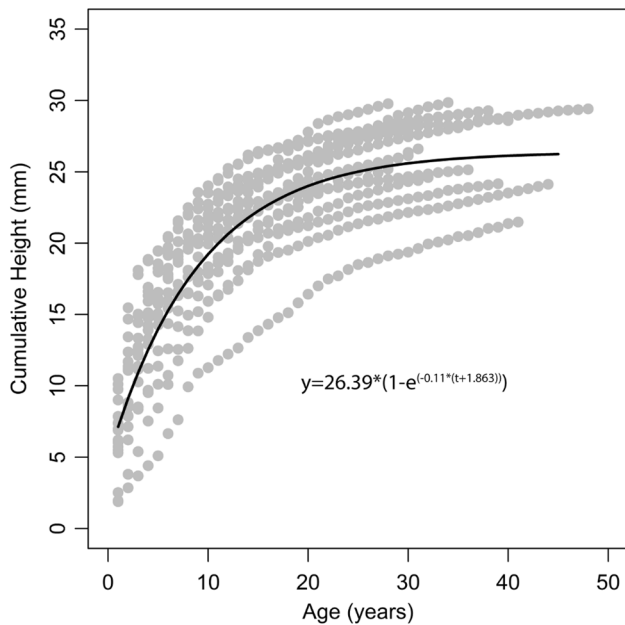


Fig. 5 von Bertalanffy growth curve fit to pooled age-at-size data for the White Sea shells. Black line represents best-fit VBG equation. Grey circles = cumulative width of annual growth lines of 18 individuals

resources to producing and releasing gametes rather than adding shell material at the most beneficial times of the year.

Quasi-sinusoidal trends of the $\delta^{18}\text{O}$ time series, like those seen here, can be produced by seasonal fluctuations in temperature, where the highest values correspond to winter and the lowest values correspond to summer. Because the $\delta^{18}\text{O}$ value of water in the Kandalaksha Bay is not constant due to spring melt water pulses and large influxes of freshwater from rivers, temperature cannot be accurately reconstructed using $\delta^{18}\text{O}$ values of shell carbonate. Moreover, estimating seasonal variations in growth temperature with minimal time-averaging biases requires submonthly resolution (Surge and Barrett 2012). Our sampling resolution was limited to a subseasonal scale given the narrow distance between dark annual growth lines and light growth increments. Nevertheless, coarser subseasonal sampling resolution is sufficient to determine cycles that identify the timing of annual growth line formation. In *A. borealis* from the White Sea, dark lines regularly occur near the most negative values on the $\delta^{18}\text{O}$ time series, indicating that the timing of slowed growth (dark increments) starts in late summer (Figs. 3, 4).

In addition to temperature and reproduction, changes in salinity are a stress to bivalve growth (Navarro 1988; Marsden 2004) and thus a potential mechanism of annual growth line formation. In the White Sea, salinity in the surface waters drops significantly during the spring melt period to 15 psu. At depths of 5–10 m, little mixing occurs between the cool, saline bottom waters, because the melting

freshwater is less dense. As a result, salinity is relatively constant throughout the year in shallow water averaging around 25 psu. *Astarte borealis* has a known salinity tolerance of 8–35 psu, and the spring melt period (April) does not correspond to the most negative $\delta^{18}\text{O}$ values (warmest temperatures); therefore, we do not favor salinity stress as an explanation for annual growth line formation in the White Sea population. Note though, that the disturbance line shown in Fig. 3 may have formed in the early spring and might be a temporary response to an influx of freshwater from ice melt.

The two most likely mechanisms for growth slowdown and growth line formation in summer for the White Sea are maximum temperature threshold or spawning. Stable populations of *A. borealis* exist in the more southern Baltic Sea (Zettler 2002), where summer water temperatures can reach 20+ °C (Pfeifer et al. 2005). In our sampling location in the White Sea, summer temperatures rarely exceed 15 °C (Skazina et al. 2013), so maximum thermal tolerance does not seem a likely explanation.

There are no direct observations on the reproductive cycle of *A. borealis* in the White Sea; however, some indirect observations do allow us to assess it. During the long-term observations of the Ilistaya inlet population (Skazina et al. 2013), all specimens found in January possessed matured, ripe gonads without any signs that spawning had taken place. The same was noted for mollusks from other populations in the White Sea during October, March, May, and July (Matveeva 1977). Additional investigation of *A. borealis* from the White Sea sampled in June–September revealed spent gonads (Kaufman 1977). Thus, annual growth line formation in *A. borealis* in the White Sea may correspond to the late summer spawning period.

Lifespan and growth rate comparisons

Identifying annual growth patterns in *A. borealis* allowed us to determine the lifespans of each of the 18 individuals in our sample. Today, most bivalve species are short-lived, with a modal lifespan of 3 years, but more than 25 species are known to attain lifespans in excess of 50 years. Moreover, Moss et al. (2016) have documented that long-lived bivalves are more often found at mid and high latitudes, and across the group, there is a tendency for lifespan to increase with latitude. *Astarte borealis* from northwest Greenland (78–82°N) can attain lifespans of 150 years (Torres et al. 2011). Though from a relatively small sample, we report lifespans of *A. borealis* up to 48 which fits the trend seen in other bivalves. We should note that all individuals studied here were collected alive, so they could have presumably lived for longer. As such, the lifespans reported should be regarded as maximum reported lifespans (MLSP) attained by *A. borealis* from the White Sea (i.e., with additional

sampling, the likelihood of finding an older individual than reported here increases).

To better conceptualize the impressive longevity of *A. borealis*, we compiled data for other species from the White Sea using a recently published global compilation of bivalve lifespans and growth rates (Moss et al. 2016) and from additional sources (Zotin and Ozernyuk 2004; Sukhotin et al. 2007; Gerasimova et al. 2016). Before our report, only two species of White Sea bivalve were known to live in excess of two decades, *Macoma balthica* (MLSP = 30 years; Gerasimova and Maximovich 2013), and *A. islandica* (MLSP = 44 years; Begum et al. 2010). However, it should be noted that the former used external ridges on the shell to determine lifespan, whereas the latter used isotope sclerochronology. In some short-lived species, external ridges are formed annually and can be used to determine lifespans, but their use is often fraught with difficulty (Krantz et al. 1984; Edie and Surge 2013). This is in part because external ridges can form in response to non-periodic disturbances (e.g., storm events) rather than annual events (e.g., spawning, minimum/maximum temperature tolerance). In the specimens of *A. borealis* we examined, external ridges do not match up with internal annual growth lines. We suggest caution when interpreting lifespans from external ridges rather than internal lines.

von Bertalanffy k values in marine bivalves range from 0.02 (*A. islandica*; Murawski et al. 1982) to 2.83 (*Ylistrum japonicum*; Williams and Dredge 1981) with lower values being indicative of slower growth and higher values indicating faster growth. Long-lived bivalves tend to display slow growth (e.g., Abele et al. 2008; Begum et al. 2010; Ridgway et al. 2011b; Moss et al. 2016), and *A. borealis* is no exception as it grows slow ($k = 0.11$) and lives for almost half a century (MLSP = 48). Data on von Bertalanffy growth parameters for other White Sea bivalves are sparse and are concentrated on three species *A. islandica* (Begum et al. 2010), *Mya arenaria* (Gerasimova et al. 2015, 2016), and *Mytilus edulis* (Sukhotin and Maximovich 1994; Sukhotin et al. 2007). *A. borealis* k value from the White Sea falls in the middle of those previously reported: *A. islandica*, 0.20; *Mya arenaria*, 0.03–0.16; and *Mytilus edulis* 0.02–0.26. Such similarity across several disparate bivalve families living in similar settings suggests a strong environmental influence on shell growth. Much has been written on the environmental factors that promote long lifespans, but recent work suggests that food availability—driven by the extremely seasonal light regime at high latitudes—may in part promote longer life through reduction of metabolic rates (Moss et al. 2016, 2017). Slow growth may be a necessary trait for White Sea bivalves, because sea ice and polar night during winter shut down primary productivity.

Oxygen isotope analysis reveals that *A. borealis* from the White Sea form annual growth lines in the late summer and

approach lifespans of 50 years. *A. borealis* is a widespread Panarctic species, but outside of one additional study (Torres et al. 2011), little is known about the timing of growth line formation. Further study is needed to confirm the presence of annual growth lines in other populations (e.g., Baltic Sea). In addition, while the taxonomy of *Astarte* is quite complicated (see Petersen 2001), it is a specious genus with several taxa warranting of sclerochronological study. In the White Sea, for example, *A. elliptica* and *A. montagui*, which co-occur with *A. borealis*, remain to be studied. Given its long Arctic history, *Astarte* may prove to be an effective tool for monitoring water quality, ecologic/environmental change, and consequences of global warming in boreal and Arctic seas.

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Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest associated with the publication of this article.

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