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High-latitude settings promote extreme longevity in fossil marine bivalves

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Abstract.—One of the longest-lived, noncolonial animals on the planet today is a bivalve that attains life spans in excess of 500 years and lives in a cold, seasonally food-limited setting. Separating the influence of temperature and food availability on life span in modern settings is difficult, as these two conditions covary. The life spans of fossil animals can provide insights into the role of environment in the evolution of extreme longevity that are not available from studies of modern taxa. We examine bivalves from the unique, nonanalogue, warm and high-latitude setting of Seymour Island, Antarctica, during the greenhouse intervals of the Late Cretaceous and Paleogene. Despite significant sampling limitations, we find that all 11 species examined are both slow growing and long-lived, especially when compared with modern bivalves living in similar temperature settings. While cool temperatures have long been thought to be a key factor in promoting longevity, our findings suggest an important role for caloric restriction brought about by the low and seasonal light regime of the high latitudes. Our life-history data, spanning three different families, emphasize that longevity is in part governed by environmental rather than solely phylogenetic or ecologic factors. Such findings have implications for both modern and ancient latitudinal diversity gradients, as a common correlate of slow growth and long life is delayed reproduction, which limits the potential for evolutionary change. While life spans of modern bivalves are well studied, data on life spans of fossil bivalves are sparse and largely anecdotal. Life histories of organisms from deep time can not only elucidate the controls on life span but also add a new dimension to our understanding of macroevolutionary patterns.

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Introduction

What controls life span? Today, one of the longest-lived, noncolonial animals on the planet is the ocean quahog, *Arctica islandica*, with a maximum reported life span of 507 years (Wanamaker et al. 2008; Butler et al. 2013). Along the Atlantic Coast of the United States, 200-year-old individuals of *Arctica* are common, but thus far, individuals 300 years of age or older have only been found off the coast of Iceland and northern Norway (Schöne et al. 2011; Butler et al. 2013; Mette et al. 2016). The pattern of longer life spans at higher latitudes is not only evident in the long-lived *Arctica* but is a feature consistent across the Bivalvia today (Moss et al. 2016). Such a strong pattern suggests that an environmental control may facilitate long life. Cool temperatures and caloric restriction are thought to be first-order controls on life span. Water temperature and food availability (driven by the extremely seasonal light regime in polar settings; Peck et al. 2006) covary with latitude, so separating their influences is difficult. Earth's history offers a range of conditions far broader than those that exist on the planet today, including nonanalogue settings that present opportunities to deconvolve these two factors and test hypotheses related to the role of environment in bringing about extreme longevity.

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Here, we use the skeletal archives of fossil bivalves from just such a nonanalogue setting, the warm, high-latitude, nearshore marine sediments of the Cretaceous and Paleogene on Seymour Island, Antarctica, to argue that high-latitude settings do indeed seem to be characterized by taxa exhibiting extreme longevity but that this effect is evidently not primarily brought about by cold temperatures. Rather, we argue that the seasonal availability of food resulting from extended periods of no sunlight may be the driving factor behind the link between latitude and life span. Our findings suggest that latitudinal patterns in life-history traits may be a persistent feature throughout the Phanerozoic and that they have significant consequences for macroevolution.

Background

Geologic Setting.—Seymour Island, off the Antarctic Peninsula (64°17′S, 56°45′W), has long been the subject of geologic investigation. The island is one of the very few places in the high southern latitudes where Meso-Cenozoic fossiliferous sediments are exposed, and the stratigraphy, paleontology, and paleoclimate history of its sedimentary record have been well studied (see sources in Feldmann and Woodburne [1988] and those cited in the following sentence). The Cretaceous and Paleogene marine section includes three formations consisting mostly of sands, muds, and shell beds. The Lopez de Bertodano and Sobral Formations crop out on the southern portion of the island and represent one of the most expanded Cretaceous and Paleogene sections currently known (Zinsmeister et al. 1989; Marshall 1995; Tobin et al. 2012; Witts et al. 2015, 2016). The Lopez de Bertodano Formation is a deepening-upward sequence from shallow-water deltaic/estuarine deposits to middle- to outer-shelf deposits, while the overlying Sobral Formation consists of progradational deltaic facies (Zinsmeister 1982; Macellari 1988). The Eocene La Meseta Formation is a shallow-marine succession that overlies the dominantly nonmarine Cross Valley Formation (Sadler 1988; Porebski 1995, 2000). A thorough investigation of Mesozoic and Cenozoic molluscan systematics has documented several hundred species (e.g., Macellari 1984, 1988; Zinsmeister 1984; Zinsmeister and Macellari 1988; Zinsmeister et al. 1989; Stilwell and Zinsmeister 1992; Beu 2009; Tobin et al. 2012; Tobin and Ward 2015; Witts et al. 2015, 2016).

Global greenhouse climates prevailed throughout the Cretaceous and Paleogene periods. Pole-to-equator temperature gradients were low (Huber and Sloan 2001; Hay and Floegel 2012), and the high latitudes were relatively warm and largely ice free until the Eocene–Oligocene transition (Zachos et al. 2001, 2008). Proxy data from Seymour Island suggest that the Antarctic Peninsula experienced cool-to-warm temperate conditions with mean annual temperatures similar to the mid-latitudes today, ranging from around 8 to 17°C (Dutton et al. 2002, 2007; Francis and Poole 2002, Ivany et al. 2008; Tobin et al. 2012; Douglas et al. 2014; Kemp et al. 2014). Thus, the Cretaceous and Paleogene bivalves of Seymour Island were living in an environment not currently represented anywhere on Earth—a high-latitude setting with near darkness for half the year where waters were comparatively warm and ice-free (Buick and Ivany 2004).

Determination of Bivalve Life Spans.—Bivalves have accretionary and indeterminate growth and, akin to trees, their skeletons record their size at each year of growth throughout their ontogeny and the environmental conditions in which they lived (Pannella and MacClintock 1968; Rhoads and Pannnella 1970; Lutz and Rhoads 1980; Rhoads and Lutz 1980; Jones 1983; Schöne and Gillikin 2013; Beierlein et al. 2015). As benthic organisms that are generally incapable of significant movement to track preferred conditions, bivalves are subject to changes in their local environment. Such changes result in temporary slowdowns or cessations in shell growth and lead to the formation of the two major classes of growth bands: disturbance and periodic. Disturbance lines result from events such as storms or predation attacks and form with no particular periodicity (i.e., they are random), whereas periodic lines form regularly at a known or detectable frequency (Clark 1974). Growth lines on the exterior surface of bivalve shells are often of the former type and were initially (and often erroneously) relied upon for estimates of age (e.g., as pointed out by Krantz et al. [1984] on scallops). Internal growth bands, revealed in cross section, are typically of the latter type and provide much more accurate age estimates if the periodicity of formation is known. At least five different types of periodic growth bands driven by tidal, lunar, and reproductive cycles have been documented in bivalves: semidaily, daily, fortnightly, monthly, and annual (e.g., Clark 1974; Pannella 1976; Richardson et al. 1980; Goodwin et al. 2001; Schöne et al. 2005b; Hallmann et al. 2008).

Desire for documenting the periodicity of formation of internal growth bands grew out of an emerging shellfish industry in the early 1900s (Belding 1910) and a post–World War II effort to supply a much-needed alternate source of protein (Neville 1945). One of the oldest methods for determining periodicity of formation in modern bivalves are mark-and-recapture experiments. In these studies, specimens are tagged or marked and in some cases caged and observed at set intervals of time (e.g., Jones et al. 1978; Jones 1980; MacDonald and Thomas 1980; Peterson et al. 1983; Sejr et al. 2002a). The operational requirement for frequent sampling to accurately determine periodicity of formation led to a drop-off in the use of mark-and-recapture studies. An alternative route is to sample ontogenetic variations in the oxygen isotope value of bivalve shell carbonate, which is particularly useful for fossil bivalves (Jones and Quitmyer 1996). Isotope profiles through growth increments that are annual in nature show variations that approximate the sinusoidal (seasonal) variation in environment (Ivany 2012). This phenomenon was first documented by Williams et al. (1982) and Jones et al. (1983) in shells of modern *Spisula solidissima* collected from New Jersey. These values showed that during the spring and summer, *S. solidissima* grows rapidly and deposits a wide, opaque growth band in transmitted light (white in reflected light), whereas a narrow, translucent (dark) band is deposited in late summer when growth slows or stops. Dark bands are typically associated with spawning periods and/or temperature extremes, which tend to be annual in nature (Jones et al. 1978; Thompson et al. 1980). These methods have been successfully applied to both modern (e.g., Jones et al. 1989; Hallmann et al. 2008) and fossil bivalves (e.g., Jones and Gould 1999; Buick and Ivany 2004).

The primary controls on growth-band formation are environmental parameters like temperature and food availability, and as a result bivalves living in highly seasonal environments today form unambiguous annual growth bands (e.g., Witbaard et al. 1994; Brey and Mackensen 1997; Lomovasky et al. 2002; Sejr et al. 2002b; Ambrose et al. 2011). The same is true of bivalves from the fossil record. Buick and Ivany (2004) and Ivany et al. (2008) documented annual growth bands in *Cucullaea raea* and *Eurhomaela antarctica* (now *Retrotapes antarcticus*, Alvarez et al. 2014) from the Eocene of Seymour Island, Antarctica, and Beard et al. (2015) and Ivany and Runnegar (2010) did the same with early Permian bivalves from SE Australia. In the past and today, the polar regions are characterized by extreme seasonality in light regime and hence phytoplankton production. Water temperatures are more consistently cold today, but become increasingly seasonal as climate warms. Given that the primary controls on growth-band formation are environmental, and that paleoenvironmental conditions were highly seasonal during the Cretaceous and Paleogene greenhouse, we presume the additional Seymour Island taxa studied here form annual bands as well.

Materials and Methods

Eleven species of infaunal marine bivalves were selected from the Cretaceous Lopez de Bertodano and Eocene La Meseta Formations on Seymour Island for investigation: *Cucullaea ellioti*, *C. antarctica*, *Cucullaea* sp., *Nordenskjoldia nordenskjoldia*, and *Lahillia larseni* from the Cretaceous, and *C. raea*, *C. donaldi*, *Retrotapes antarcticus*, *R. newtoni*, *R. robusta* (see Alvarez et al. [2014] for reassignment of *Eurhomalea* and *Eumarcia* to *Retrotapes*), and *L. wickensi* from the Eocene. These 11 were chosen because they are common in collections made by previous researchers (e.g., Macellari 1984; Stilwell and Zinsmeister 1992), their shell material is preserved sufficiently well to reveal internal growth bands, and they are well represented in archival research collections. While several additional common taxa are noted in field surveys, these were evidently smaller and not typically collected. Regardless, the 11 taxa examined here are dominant elements of assemblages both in the field and in collections, and hence they serve as representatives of the Seymour Island fossil bivalve fauna in general. Specimens used for analysis were drawn from collections at the Florida Museum of Natural History, the Paleontological Research Institution, and Syracuse University.

Life spans and growth rates are determined through examination of annual bands as revealed in cross section. To prevent damage to the shell (and loss of data) during cutting, individuals selected for sectioning were imbedded in an epoxy resin before being cross-sectioned along the maximum growth axis with a Buehler Iso-Met 1000 Precision Cutter run at low speed. We explored three successively more time-intensive methods as needed for visualizing annual bands in cross section. Thick sections were polished using silicon-carbide sanding disks and were finished with 1.0 and 0.05 μm aluminum-oxide powder to yield a smooth glassy surface. Specimens were observed with a Zeiss Discovery V.8 stereomicroscope at 1.25 × objective lens magnification, and images were captured under plane white light with an AxioCam ERc5s camera operated with Zeiss Zen software. One specimen of *R. antarcticus* was prepared by staining with Mutvei's solution, a procedure common in the field of sclerochronology and outlined in Schöne et al. (2005a). Images for this specimen were captured using a Nikon Coolpix 995 digital camera mounted to a Wild M3 stereomicroscope at 10 × magnification. Thin sections of *C. raea* were imaged using a petrographic microscope equipped with an AxioCam ERc5S camera. Up to 75 images were stitched together to create a complete montage of each shell using Photoshop.

Once adequate images were obtained, we used the open-source software ImageJ to count and measure growth bands to determine life span and growth rate of each individual. Because bivalve shells exhibit some degree of curvature, the length of cumulative growth-band widths measured in cross section will be greater than the umbo-to-commissure distance measured using calipers on an uncut individual. We therefore transformed cumulative growth-band widths to straight-line measured distances by dividing each band by the total cumulative size and multiplying that by the straight-line measured distance. This procedure allowed us to compare growth curves from cross sections with sizes of individuals previously measured using calipers in museum collections.

As the methodology for recovering life span and growth rate is deemed "destructive" by collections managers, we were limited in the subset of individuals available for sectioning. In most cases we were not permitted to section the largest specimens in collections, which hinders our ability to understand the full longevity potential of these taxa. To put our data into context within this population and get closer to our objective, we also measured the maximum height (dorsal to ventral distance) of all individuals present in the three collections. In total, we sectioned 31 individuals and measured 1058 intact shells from 11 different species. While it is tempting to draw inferences about population dynamics from size (or age) distributions, these specimens were collected by a number of individuals at a number of localities during field seasons spanning several decades. Some collecting was selective and opportunistic, including float specimens; some was systematically conducted to reflect the whole fauna; and some targeted large numbers of particular taxa. While some of our plotted distributions may in fact approximate those in the actual fossil assemblage, we use them here only to describe what is in collections and how our sectioned individuals compare with them in terms of size and age.

Growth rates of modern bivalves have been shown to correlate with longevity (Abele et al. 2008, 2009; Ridgway et al. 2011; Moss et al. 2016) through their relationship with metabolic rate (Speakman 2005; Camus et al. 2005). They are therefore a crucial component of any analysis of life span and life history. To determine growth rates for Seymour Island bivalves, growth curves for each sectioned individual were generated by plotting the cumulative distance between growth bands in the outer shell layer against the corresponding year of growth and fitting a von Bertalanffy (1938) growth equation (VBG):

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \tag{1}$$

where L_t is shell length at time t; L_∞ is asymptotic size, or the size at which growth rate is essentially zero; t_0 is the time at which $L_t = 0$; and k is the rate at which L_∞ is attained. Here, we report all VBG parameters for each of the cross-sectioned individuals, using k as a proxy for growth rate, and examine the relationship between k and life span for these fossil taxa. We also compute a best-fit curve for each taxon using the pooled age-at-size observations for all individuals of a species.

Finally, we compare k values of Seymour Island taxa to those of modern bivalves distributed across latitude and temperature from a global data set to identify where in the distribution of values from modern bivalves the Seymour fossil taxa best fall. The data set, published in Moss et al. (2016), includes maximum reported life spans drawn from 1148 observations of modern marine bivalves and more than 600 observations of von Bertalanffy k values, both of which are tabulated by latitude. The modern data set shows a pattern of decreasing k values and increasing life span as latitude increases. Despite a general decrease toward the poles, a wide range of k values is evident at any given latitude today. To determine the range of modern latitudes most consistent with observed Seymour Island data, we used resampling techniques that compare observed data with an equal number of k values drawn at random from the data set of modern global k values. As each observation in the modern data set represents a population value for a given taxon in a given place if more than one individual was sampled, we compare those data with the best-fit k values for all individuals of each species in the Seymour Island fauna from Table 1. We draw at random, without replacement, 11 observations from the available modern data within a 20° latitudinal band, calculate their mean, and repeat 1000 times, yielding a range of mean k values expected today for that window of latitude. We step the 20° latitude window by 1° of latitude from the equator through to the poles, each time drawing 11 k values and calculating their means 1000 times, then plot those means against latitude for comparison with the fossil data. For each draw of 11 values, we calculate the probability that our fossil mean k value is part of that distribution, and tally the number of comparisons with p-values greater than 0.05 in each latitudinal bin. The greater the number of insignificant comparisons, the more similar the fossil fauna is to the modern in that latitude range.

Results

Size Distributions.—In most cases, the individuals selected for "destructive" analysis were not the largest of any taxon in any collection (Fig. 1). Size distributions in collections reveal that sectioned individuals, for which life spans can be confidently assigned, range from 53% to 100% of the size of the largest measured specimen. For some species, like *C. raea*, we were able to section some of the largest individuals in the collections; for others, like *C. antarctica*, we were only able to section individuals near the median size in museum collections.

Longevities.—Annual growth bands in all species are well preserved, distinct, and virtually unambiguous (Fig. 2). Even though the most prominent growth bands are clearly annual in nature, several species (e.g., *L. larseni*, *C. raea*, and *R. antarcticus*) also reveal subannual growth banding, providing attractive prospects for high-resolution intra-annual studies (e.g., Goodwin et al. 2001) detailing shell growth under these unusual environmental conditions. Imaging techniques allow for discrimination of even the most closely spaced annual bands near the commissure of the shell.

All of the species examined reached ages greater than 20 years, and 10 of the 11 had life spans greater than 50 years (Table 1). *C. raea*, *C. antarctica*, and *N. nordenskjoldia* record maximum measured life spans of 120, 101, and 131 years, respectively, and Alvarez and Pérez (2016) recently reported ages of 93 and 96 years for *R. antarcticus*. Given restrictions on the number of individuals we were permitted to section and the fact that these shells did not typically include the largest individuals of any species in the collections, the life spans

TABLE 1. Life spans (LSP, years) and von Bertalanffy growth parameters of species examined (k = rate at which L_∞ is attained; L_∞ = asymptotic size in millimeters; t_0 = the time at which $L_t = 0$). Oldest individuals of each taxon are indicated in bold. The underlined rows mark the last entry for a species from the pooled best-fit von Bertalanffy equations. FMNH, Florida Museum of Natural History; PRI, the Paleontological Research Institution; SU, Syracuse University.

Family	Species	Period/epoch	Specimen no.	LSP	k	L_∞	t_0
Cucullaeidae	*Cucullaea antarctica*	Cretaceous	PRI 583113	**101**	0.06	58.17	−1.96
	Cucullaea donaldi	Eocene	SU 01-56-C2	**55**	0.11	48.66	−5.19
			SU 01-53-C3	50	0.16	35.61	−2.29
			SU 01-56-C1	36	0.22	44.20	−0.76
			SU 03-012	34	0.08	50.53	−0.03
			SU 01-85-C1	18	0.23	33.84	0.08
			SU 02-82-C1	15	0.15	52.68	−2.68
			Pooled age at size		0.14	43.19	−2.02
	Cucullaea ellioti	Cretaceous	PRI 58448	**36**	0.10	49.34	−4.81
			PRI 62371	35	0.09	41.29	−0.79
			Pooled age at size		0.09	45.70	−2.99
	Cucullaea raea	Eocene	UF 124613-I	**121**	0.05	78.90	−13.32
			SU 01-43-C3	118	0.04	88.82	−14.36
			SU 001-C2	108	0.05	84.59	−9.38
			SU 01-43-C2	102	0.03	89.93	−32.75
			UF 124605-I	90	0.11	88.77	−0.72
			SU 001-C1	73	0.07	86.08	−5.00
			SU 01-43-C1	65	0.06	94.59	−4.01
			SU 01-28-C1	43	0.08	98.91	−4.18
			UF 124605-III	38	0.16	78.52	0.94
			SU 01-42-C2	36	0.11	78.43	−1.09
			UF 124605-II	31	0.15	80.63	−3.57
			Pooled age at size		0.08	83.89	−4.67
	Cucullaea sp.	Eocene	SU 01-54-C2	**92**	0.09	38.89	−2.28
	Nodenskjoldia nodenskjoldia	Cretaceous	PRI 61339-B	**131**	0.05	61.76	−1.36
			PRI 61339-A	47	0.27	49.32	−0.22
			Pooled age at size		0.04	61.52	−7.38
Lahilliidae	*Lahillia larseni*	Cretaceous	PRI 58774	**58**	0.14	85.63	−0.51
			PRI 60667	42	0.11	85.31	−3.47
			Pooled age at size		0.13	85.45	−1.74
	Lahillia wilckensi	Eocene	PRI 59522	**71**	0.14	79.68	−2.04
			PRI 59425	55	0.09	99.75	−8.07
			Pooled age at size		0.14	87.05	−3.52
Veneridae	*Retrotapes antarcticus*	Eocene	SU 01-43-E3	**83**	0.04	35.71	−2.38
			UF 124959-II	35	0.09	60.75	−3.3
			UF 124961-I	31	0.11	68.42	−4.92
			PRI 59548	26	0.17	62.32	−0.98
			Pooled age at size		0.29	42.54	−0.52
	Retrotapes newtoni	Eocene	PRI 58961	**22**	0.12	49.79	−3.87
			PRI 59658	11	0.23	43.52	−0.12
			Pooled age at size		0.15	49.07	−1.80
	Retrotapes robusta	Eocene	PRI 62912	**38**	0.03	93.04	−2.04

documented here should be considered minimum estimates for those potentially attained by their taxa.

Growth Parameters.—Values for the parameter k (the growth constant) of the von Bertalanffy growth equation range from 0.03 to 0.23 (Table 1). There is a relationship between k and life span in the Seymour bivalves, such that slower-growing individuals live longer than faster-growing individuals (Fig. 3). While sample size is small, there is a tendency for this pattern to hold true within and across species. Mean growth curves for all species show rapid growth early in ontogeny followed by many years of much slower growth later in life (Fig. 4).

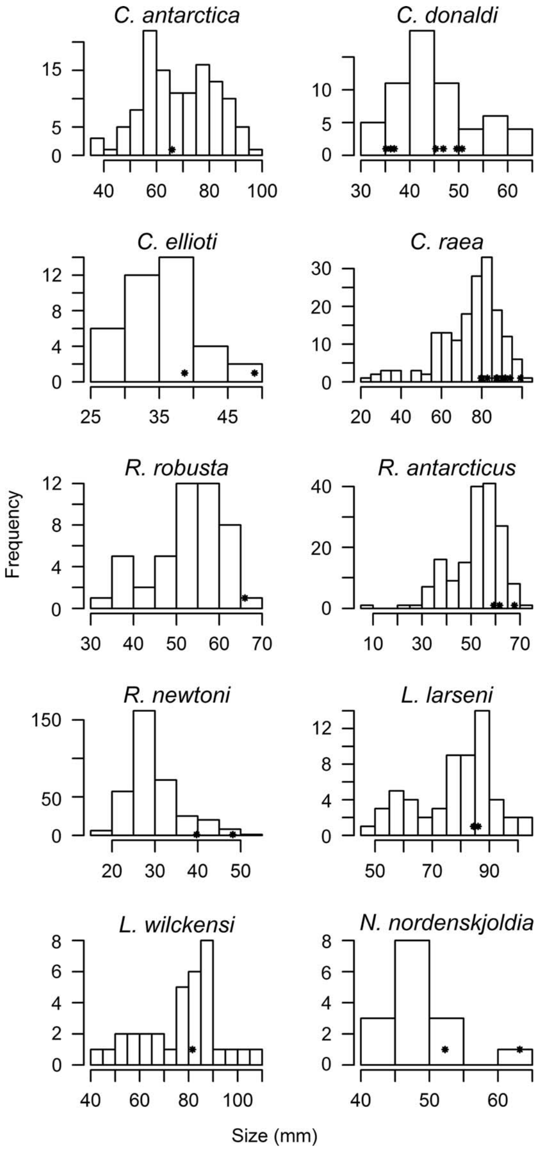

FIGURE 1. Umbo-to-commissure sizes of individuals measured in musuem collections. * = size of cross-sectioned individuals.

Comparison with Life Histories of Modern Bivalves.—The *k* values exhibited by Seymour Island bivalve taxa span a range generally consistent with those of modern high-latitude bivalves reported by Moss et al. (2016; Fig. 5A). The mean *k* value of all Seymour Island taxa (0.11) is on the low end of the means produced from resampling *k* values of populations in modern latitude bins (Fig. 5B). The probability that the observed fossil mean value is part of the distribution of modern mean resampled *k* values is near zero below about 60° latitude, and the number of insignificant tests rises steeply above that latitude (Fig. 5C). These results combined with observed longevities confirm that the life histories of fossil taxa are similar to those of modern high-latitude taxa, despite the substantial difference in the thermal environments in which they are each living.

Discussion

Limitations and Assumptions.—We face two nontrivial problems when using fossil (or modern) shells from existing collections to study life span and growth. The first is a limitation on the number of specimens permitted for “destructive” analysis. This is understandably an issue when working with museum collections, particularly when material is rare or comes from remote or no longer accessible field areas. This means that an understanding of the true life span potential for these taxa is not easily attainable. For example, some species, like *N. nordenskjoldia*, are rare in museum collections ($n = 15$), so the likelihood of finding a longer-lived individual than what is observed (here, 131 years) will increase significantly with more intensive sampling. In each respect, it is highly likely that individuals older than those reported are present in existing collections, and virtually certain that they are present in the field waiting to be discovered. Not only is this true of our understanding of life span, but it is also true of growth rate, as there is some intraspecific variation in von Bertalanffy *k* values in our sample of fossil bivalves. Finally, we were limited in this study not only to the number of individuals of a given species, but also to the number of species in total we were permitted to section, placing limits on our ability to reconstruct the full spectrum of life histories exhibited at this setting.

Even more difficult to circumvent is the problem of estimating life span demographics of a population, whether it be based on direct measurement from specimens or calculated from an age–size relationship. Life span for an individual is relatively easy to determine from shell cross sections, but the limitations on sample size and availability discussed above ensure that the largest and hence likely the oldest

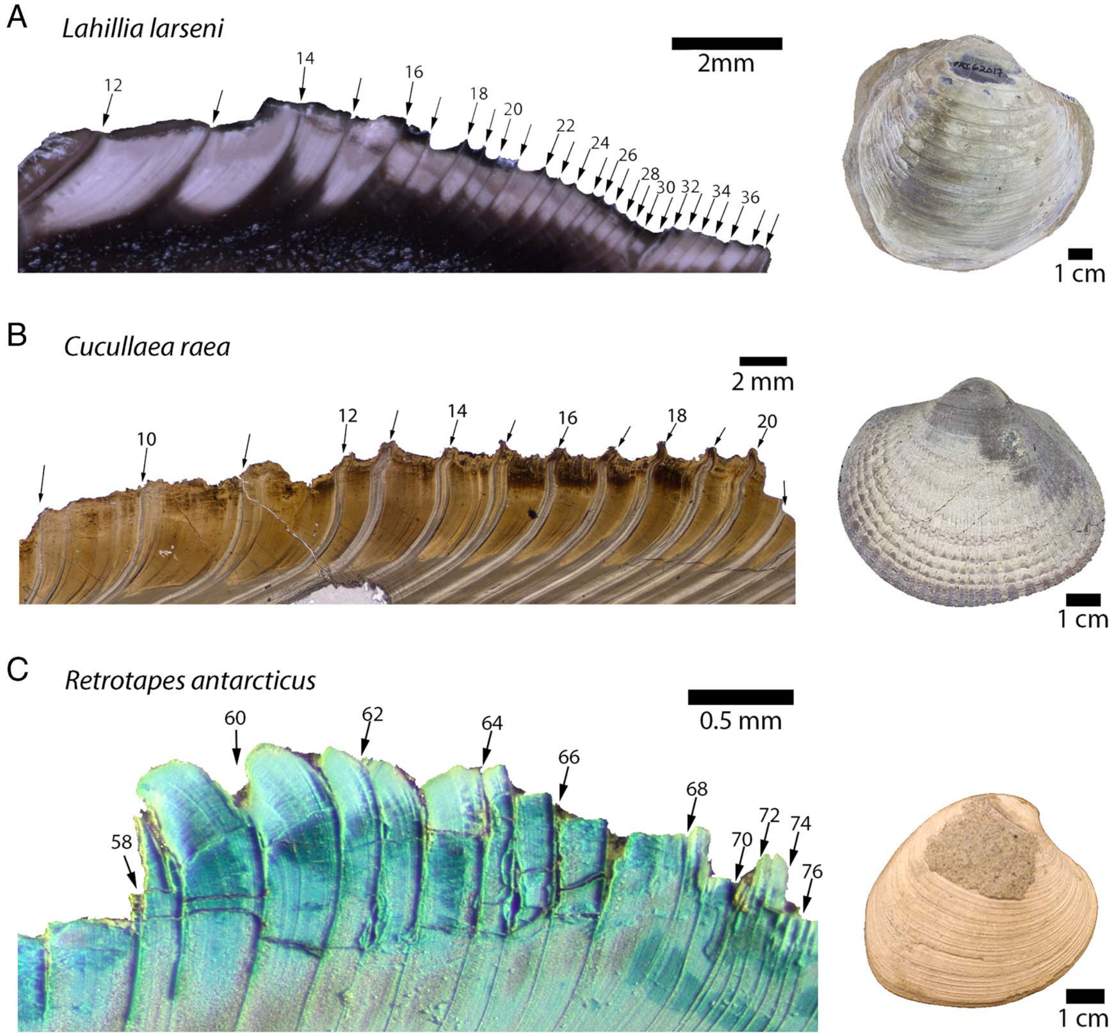

FIGURE 2. Annual growth banding in three species of Seymour Island bivalve. Shell cross sections encompass portions of their ontogenies, with years of growth indicated above the shell. Banding is illustrated using three different preparation techniques: A, polished thick section under reflected light (*Lahillia larseni*, Cretaceous); B, polished thin section under polarized light (*Cucullaea raea*, Eocene); C, thick section stained with Mutvei's solution (Schöne et al. 2005) (*Retrotapes antarcticus*, Eocene).

individuals will almost never be sectioned. One is therefore left with inferring ages based on the relationship between shell growth and age seen in one or a few sectioned specimens that may be a good deal smaller. While the von Bertalanffy growth equation can be algebraically rearranged such that age is calculated from a given size, two nontrivial issues arise when employing this approach. First, age predictions are deterministic—all ages predicted using the equation will necessarily fall on the line it establishes, and consequently any natural variation in age at size for the population is lost. Second, and perhaps more important for the issue at hand, the ages for measured shell sizes greater than L_∞ cannot be predicted, as the equation would call for taking the natural log of a negative number, a mathematically invalid operation. Though the bivalve aging community is well aware of these issues, no readily available solutions appear to exist. In most cases the "L_∞ problem" is acknowledged, but individuals of greater size (potentially the longest lived) are simply removed from analyses (e.g., Dexter and Kowalewski 2013), and age estimates for those of size less than L_∞ are

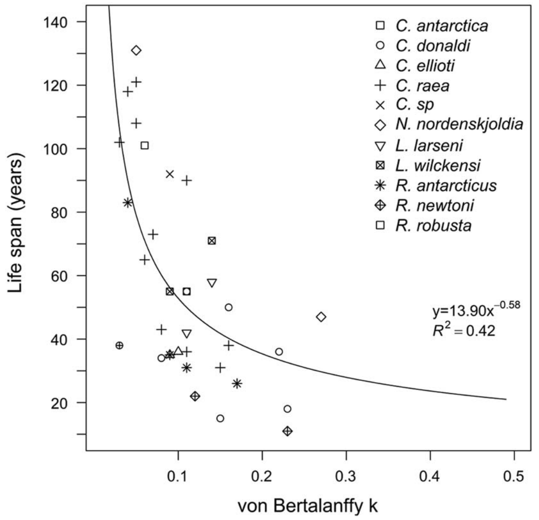

FIGURE 3. Relationship between growth rate (von Bertalanffy k) and life span for all Seymour Island taxa with best-fit equation. Slope of line is significantly different from 0 ($p < 0.01$).

recognized as "crude" (Ridgway et al. 2014) because of the failure to account for the natural variation in growth within the population. Both approaches are wholly unsatisfactory. We are exploring probabilistic approaches by which to circumvent these problems, but the slow growth over many years typical of the longest-lived taxa obfuscates the determination of age from size even more profoundly, for a few millimeters of growth near the commissural margin could represent many decades (e.g., in Fig. 2A, the last 5 mm of growth in *L. larseni* represent almost 20 of the 39 years of its full life span, and this is modest in comparison with the last 5 mm in taxa with much longer life spans). Fortunately for this study, accurate estimates of "maximum life span" for Seymour Island taxa are not required. Rather, as discussed in the following section, even our small sample of observed life spans (though all underestimate the "maximum" for their taxon to variable and unknown degrees) and k values offer firm constraint on the atypical nature of the fauna when compared with nearly all modern assemblages.

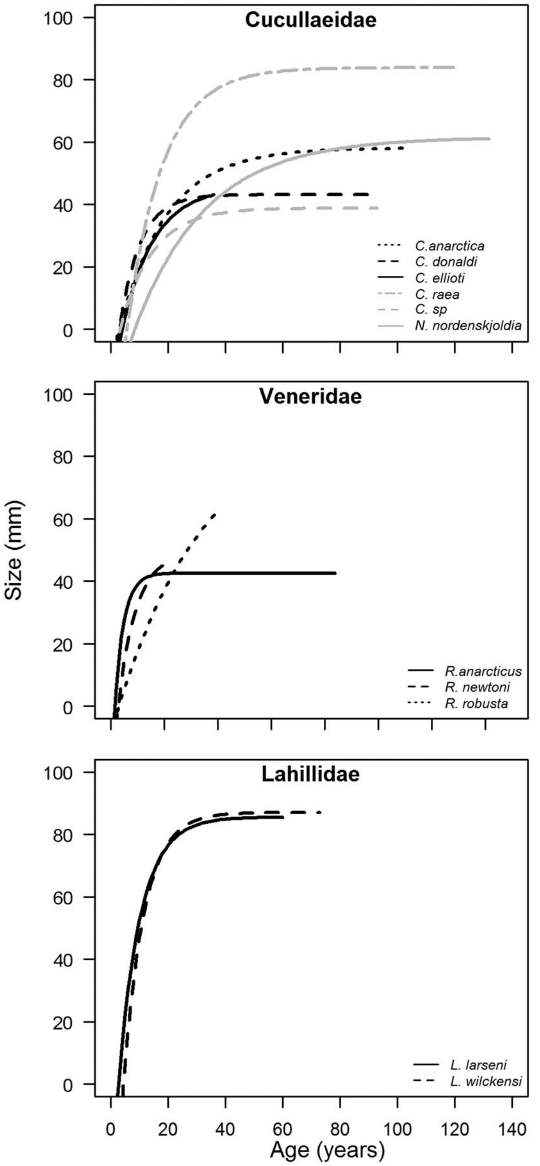

FIGURE 4. Best-fit growth curves for 11 taxa using the von Bertalanffy growth parameters based on the pooled size-at-age data from all individuals. Curves are extended to the maximum recorded age for the species.

Comparison with Living Bivalves.—When the life histories of these high-latitude fossil taxa are considered in comparison with living taxa, the unusual nature of the fauna becomes apparent. While a number of modern taxa can attain life spans in excess of 50 years, the modal value of maximum reported life span for bivalve species today is 3 years (Moss et al. 2016). The shortest-lived species measured from Seymour Island reached life spans of at least 22 years. The longevity of bivalves in this assemblage, even as established from such a restricted sample, is impressive. In addition, modern bivalves have k values that range as

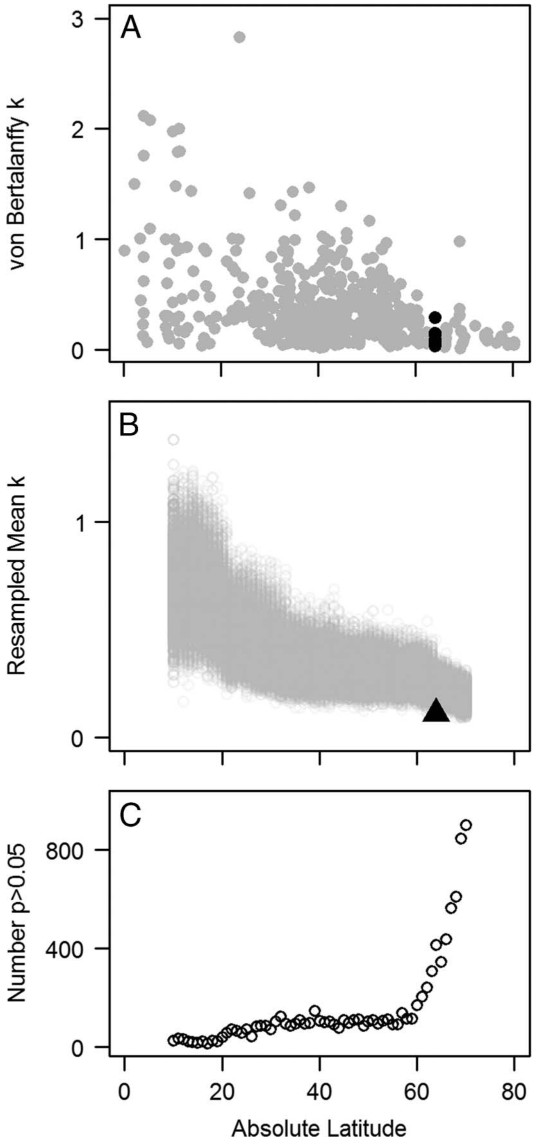

FIGURE 5. Growth rate of Seymour Island fossil bivalves in comparison with modern bivalves plotted by absolute (paleo)latitude. A, Growth rates (k) of modern bivalves (gray; Moss et al. 2016) and Seymour Island individuals (black). B, Mean of resampled k values for 20° bins with a 1° moving window for 1000 iterations (gray) and mean of Seymour Island k values (black). C, Number of t-tests (out of 1000) that fail to establish a significant difference between resampled k values and observed Seymour Island k values. Most tests are insignificant above about 60° of latitude.

high as 3, while the sectioned Seymour specimens all revealed k values less than 0.25 (Fig. 5A), on the lowest end of the modern distribution and representing extremely slow growth. Within this sample of slow-growing, long-lived fossil individuals, the relationship between k and life span seen in modern populations is also apparent: those exhibiting slower growth tend to have lived longer lives (Fig. 3).

When the life histories of modern taxa are considered in the context of latitude (Moss et al. 2016), however, the Seymour taxa become part of a general global pattern. Species living at tropical latitudes tend to be fast growing (k values range as high as 3) and short-lived (most <20 years). As latitude increases, the bivalve fauna includes progressively more taxa with much longer life spans, and growth universally slows until k values at high latitudes are nearly all less than 0.30. The range of life spans and k values from Seymour Island fossil taxa compare favorably with those exhibited by high-latitude bivalves today, much more so than those living at lower latitudes and what would be similar temperatures (Fig. 5). Slow growth and long life are consistent with a high-latitude position (64°S latitude) that has changed little if at all over the past 100 million years (e.g., Norton and Sclater 1979; Lawver et al. 1992; Torsvik et al. 2008), despite the substantial difference in thermal regimes between the modern and ancient polar faunas.

As noted earlier, the individuals sectioned for life-history analysis are generally not the largest individuals in collections for a given taxon; in some cases they are little more than half the maximum observed size. As a consequence, and to the degree that size and age are related, only a portion of the full life-history potential is available for von Bertalanffy parameterization. In such cases, L_∞ is likely to be underestimated, with the effect that k values are therefore overestimated. That species k values may be even lower than we report only further underscores the exceptional nature of the Seymour Island fauna in comparison with modern bivalves living in similarly temperate settings.

The bivalve fauna of Seymour Island is diverse and includes species with a range of ecologies. As modal life span in modern assemblages is still on the low side at any latitude, it is likely that short-lived species are present in the fossil fauna as well, although we have not sampled them here. In keeping with data from today's high-latitude bivalves, however, we would expect any short-lived fossil taxa discovered to nonetheless have relatively low *k* values.

In sum, bivalves today tend to grow more slowly and live longer as the latitude at which they live increases. High-latitude bivalves living during past intervals of polar warmth exhibit the same long life spans and slow growth as bivalves living in those regions today, suggesting a set of causes deriving from latitude but independent of large-scale swings in global climate.

What Influences Longevity?—From a physiological perspective, two of the most often cited mechanisms for long life are thermal stress (cold temperature) (e.g., Brey and Clarke 1993; Peck and Conway 2000; Sejr et al. 2002b) and caloric restriction (e.g., Masoro 2000), both of which vary systematically with latitude and work through a reduction in metabolic rate. In addition to physiology, ecology could also be a driver of long life span. Organisms living in areas where predation events are frequent would be expected to benefit from a life-history strategy characterized by fast growth and early reproduction. Given the demonstrated relationship between life span and growth rate (Moss et al. 2016; Fig. 3), those taxa would also likely have short life spans in comparison with those living where predation is rare. While there are data to suggest that predation frequency is high in the tropics and decreases with latitude (e.g., Bertness et al. 1981; Schemske et al. 2009; Freestone et al. 2011; Visaggi and Kelley 2015), the pattern may not be as clear as once thought (e.g., Vermeij et al. 1989; Dudley and Vermeij 1980; Kelley and Hansen 2007; Harper and Peck 2016). We elaborate here on these three factors and discuss their relative importance to the Seymour Island fauna.

A widely accepted principle in the research community studying the aging process is that individuals with low metabolic rates typically live longer than those with higher metabolic rates (Van Voorhies 2001). This relationship was first described over a century ago in mammals (Rubner 1908) and has since been expanded to include many animal groups. Metabolic activity results in the production of free radicals and reactive oxygen species, which are thought to promote cell damage and ultimately cell death. In modern bivalves, growth rate is correlated with metabolic rate (Lewis and Cerrato 1997), and there is a strong relationship between von Bertalanffy *k* (a proxy for growth rate) and life span (Moss et al. 2016). Seymour Island fossil bivalves (and living high-latitude bivalves) exhibit lower *k* values than most other living bivalves, thus their impressive longevities could be facilitated by slow growth and correspondingly low metabolic rates. In turn, metabolism within a given taxonomic group is affected by body size, temperature, and food supply (Brockington and Clarke 2001; Gillooly et al. 2001). While bivalve body size shows no systematic trend with latitude (Roy et al. 2000; Berke et al. 2013; Moss et al. 2016) temperature and food supply do.

Metabolic rates are the summation of chemical reactions in the body, and chemical reactions typically proceed faster at high temperatures where activation energies are lower. Consequently, the universal temperature dependence model for metabolism states that individuals living at higher temperatures typically have higher metabolic rates than those living at lower temperatures (Gillooly et al. 2001). Experimental work has shown that tropical bivalves have higher metabolic rates than mid- and high-latitude species (Vladimirova et al. 2003), a fact not unrelated to the high *k* values of tropical bivalves. Modern Antarctic organisms, living in water temperatures that hover around 0°C, typically have lower metabolic and growth rates than their mid- and low-latitude counterparts (Peck and Conway 2000; Vladimirova et al. 2003; Clarke et al. 2004; Peck et al. 2006; Sato-Okoshi and Okoshi 2007). Though the Seymour Island fossil taxa lived in relatively warm water, their *k* values are a good deal lower than those of midlatitude (comparably warm-water) taxa today, suggesting that temperature is not the driving factor behind their growth.

Research on caloric restriction suggests that limiting food intake lowers metabolic rate and brings about cellular changes that in turn decrease the accumulation of free radicals and reactive species. Studies spanning a range of invertebrate and vertebrate taxa show that caloric restriction can promote fewer age-related disorders and longer life spans (e.g., McKay et al. 1935; Fanestil and Barrows 1965; Klass 1977; Verdone-Smith and Enesco 1982;

Woodhead 1985; Austad 1989; Lakowski and Hekimi 1996; Colman et al. 2014; Brandhorst et al. 2015). For bivalves living on the seafloor, primary food sources are phytoplankton and suspended food particles in the water column. Because of the tilt of the Earth's axis, high-latitude settings are characterized by highly seasonal light regimes, with the majority of sunlight received during an approximately 4-month period. In the Antarctic today, phytoplankton and other suspended particles are only available in appreciable quantities during this 4-month period (Barnes and Clarke 1995; Smith et al. 2000; Peck et al. 2006; Arrigo et al. 2008).

The seasonal availability of food in the Antarctic has dramatic effects on the organisms that live there. Like those reported here, the von Bertalanffy *k* values for modern fish (e.g., Burchett et al. 1984; Brodte et al. 2006), brachiopods (e.g., Brey et al. 1995; Peck et al. 1997), gastropods (e.g., Picken 1980; Clarke et al. 2004), and bivalves (e.g., Brey and Hain 1992; Philipp et al. 2006; Brey et al. 2011) are all very low, suggesting a common environmental control. In the bivalve *Laternula elliptica*, Ahn et al. (2003) and Brockington (2001) both demonstrated dramatic decreases in metabolic rate associated with the austral winter food shortage. Additionally, in an experimental study, Brockington and Clarke (2001) showed that the significant increase in springtime metabolic activity seen in Antarctic sea urchins was primarily brought about by the increase in food availability rather than rising temperatures. The presence of food is evidently a primary driver of growth and metabolism in organisms living in Antarctica today, and this is controlled by the seasonal light regime. Without a Phanerozoic-scale vector in the seasonal insolation cycle, Cretaceous and Paleogene settings on Seymour Island would have experienced similarly extreme variation in the availability of food resources. Thus, limitations on primary production brought about by the high-latitude light regime are likely the more important factor promoting the slow growth and long life of the Seymour Island taxa.

While physiology affects life span through its influence on metabolism, ecological factors such as predation pressure could play a role as well. Shallow-burrowing infaunal bivalves like those studied here are largely sedentary and have only their shells to offer protection from predators. Today, predation frequencies in the Antarctic are low, and predation events often take much longer to complete than in more temperate waters. The modern gastropod *Trophon lonstaffi*, for example, takes 20–30 days to complete a drill hole, depending on the type of prey (Harper and Peck 2003). Drilling predation on Eocene Antarctic bivalves may have also been rare, as Aronson et al. (2009) found completed drill holes on only 5% of prey shells. In measuring sizes of museum specimens from both Cretaceous and Eocene samples, we also find predation to be rare, as only 2% of the more than 1000 individuals measured had drill holes. In combination with a slow metabolism due to food stress, low rates of predation may help to permit extreme longevity in modern and fossil Antarctic bivalves.

One plausible influence on longevity can be ruled out in the case of the Seymour Island fauna—that of taxonomic affinity. Members of at least one family of living bivalves, the Hiatellidae, may typically live longer for a given *k* value than other bivalves (Moss et al. 2016). This might be a correlate of their deep-burrowing habit, but one could argue that their unusually long life span is a life-history trait inherited from a common ancestor, regardless of the environment in which populations or species are found today. If the Seymour taxa belonged to such a group, the argument for an environmental driver would be less strong. However, the taxa exhibiting slow growth and long life in this fossil assemblage belong to three different families in three different orders (Table 1), and living taxa in these groups are dominantly shorter lived and faster growing (Moss et al. 2016). In addition, within both higher taxa and individual species, longer-lived individuals are found at higher latitudes today (Moss et al. 2016), suggesting that even if a taxon has an ecology generally pursuant to long life, a latitude-related variable nonetheless governs the life span typical of its populations. These observations make it clear that the primary variable associated with long life in these fossil bivalves as well as in living taxa is not phylogeny but rather is related to latitude.

The Latitudinal Driver of Life History.— Consistency of life-history parameters between Seymour Island fossil bivalves and those of modern species living at similar high latitudes, regardless of their taxonomic affinity, suggests that the set of factors influencing life span and growth at those latitudes today were operating in a similar way in the deep past, despite large differences in climate. In addition, the distinct relationships between latitude and life span and between latitude and growth rate exhibited on the modern Earth require a set of causes that vary systematically with latitude. As discussed earlier and by Moss et al. (2016), causal factors related to latitude might derive from some combination of physical variables such as temperature and insolation and/or ecological variables such as predation pressure, as all three of these correlate, to a greater or lesser degree, with latitude today.

The Seymour Island fossils offer an opportunity to evaluate the relative influence of each of these factors on the life histories of bivalves because, while latitude and insolation have not changed over time, temperature and predation pressure have. Estimated mean paleotemperatures on the Cretaceous and Eocene shelf at Seymour Island range from around 8°C (Tobin et al. 2012) to 17°C (Douglas et al. 2014), far warmer than similar latitudes today, at −0.5–1°C (Locarnini et al. 2013). In addition, Aronson et al. (1997, 2009) have argued that the Antarctic benthos during greenhouse times were functionally more similar to modern lower-latitude faunas and subject to higher durophagous predation pressure than they are today. If temperature and/or predation pressure were the dominant drivers behind the ancient data and modern latitudinal trend, we would expect the life histories of these ancient bivalves to be more similar to those at lower latitudes today. They are not. Instead, the data are more consistent with life histories exhibited above a latitude of approximately 60° today (Fig. 5). Given that the controls on extreme longevity in both modern and fossil high-latitude settings appear to derive more from food availability via insolation, these settings might be characterized by slow growth and extreme longevity throughout Earth's history. Today, the exceptionally long-lived bivalve *Arctica islandica* attains life spans in excess of five centuries and lives in cold, seasonally food-limited, high-latitude settings. Similarly, during the Cretaceous and Paleogene, several bivalves attained life spans in excess of 100 years, but in the warm, extremely seasonal, high-latitude settings of Antarctica. Slow growth characterizes bivalves in both settings and hence could be the variable through which long life is selected for at higher latitudes.

The slow pace of life in both modern and fossil high-latitude settings, coupled with much lower rates of predation, may also play a role in both modern and fossil latitudinal diversity gradients (LDG). The modern LDG is the most pervasive pattern of life on the planet; in almost all animal groups, in both marine and terrestrial settings, species diversity decreases with increasing latitude (Hillebrand 2004). Such a pattern is likely to have characterized life throughout the Phanerozoic (Alroy 2010). Though we currently have no clear way to detect the age at sexual maturity of fossil bivalves (but see Sato 1994, 1995, 1999), a correlate of long life is delayed reproduction (Ridgway et al. 2011). In a wide range of invertebrates, short generation times correlate with higher mutation rates (Thomas et al. 2010). Thus the higher speciation rates of low-latitude bivalves might be a side consequence of fast growth and early reproduction driven by a constant, year-round food supply. Limited food supply at high latitudes might therefore be a driver not only of longevity but of latitudinal diversity gradients today and in the past.

Conclusions

The petrographic and geochemical tools to study life spans and growth rates of modern bivalves have been developed over the past half century by the sclerochronological and paleoclimatological communities. Their application to the fossil record has already been tested by several studies, and methods for determination of periodicities of growth bands in the shells of fossil bivalves are now well understood and relatively easy to implement. Here, with a fairly small sample of bivalves from a nonanalogue, warm, high paleolatitude setting, we shed a bit more light on what is perhaps one of the most intriguing questions from a human perspective:

What controls life span? The life-history data from these fossil shells, in concert with a much larger database of bivalve life spans and growth rates, suggest that the pattern of increasing life span with latitude on the planet today is likely a result of seasonal food availability at high-latitude settings that results in slow growth and low metabolic rate. Given that insolation has varied little throughout Earth's history, we predict then that a similar latitudinal pattern of life-history parameters exists throughout the Phanerozoic. The shells of bivalved mollusks hold a wealth of information to address this and other fascinating questions. As the early paleontologists once produced copious volumes on the taxonomy of fossil mollusks from every corner of the globe, we now have the ability to do the same with molluscan life histories—both in space and through time. Modern paleobiologists have certainly profited from early taxonomic studies and their subsequent revisions—a good deal of the paleontological literature aims to answer questions about diversity through time and the rate and mode of evolution. Future paleobiologists will likely benefit from a comparable effort to document life spans and growth rates of fossil organisms and connect them to macroevolutionary studies.

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