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Abstract: The factors involved in promoting long life are extremely intriguing from a human perspective. In part by confronting our own mortality, we have a desire to understand why some organisms live for centuries and others only a matter of days or weeks. What are the factors involved in promoting long life? Not only are questions of lifespan significant from a human perspective, but they are also important from a paleontological one. Most studies of evolution in the fossil record examine changes in the size and the shape of organisms through time. Size and shape are in part a function of life history parameters like lifespan and growth rate, but so far little work has been done on either in the fossil record. The shells of bivalved mollusks may provide an avenue to do just that. Bivalves, much like trees, record their size at each year of life in their shells. In other words, bivalve shells record not only lifespan, but also growth rate. Being abundant both on the surface of the planet today, and in the geologic record, bivalves provide a vessel by which we can explore the factors that influence lifespan from two different perspectives.

Mean body size in marine animals has increased more than 100 fold since the Cambrian. Associated with this increase in body size is thought to be an overall shift in the metabolic rates of organisms as well. Both factors bring attention to the key life history parameters of lifespan and growth rate. Variation in these parameters is not well understood among modern taxa, much less in deep time. Therefore, in Chapter 1, I present a global database of modern bivalve lifespans and growth rates in order to understand if latitudinal patterns exist in life history parameters in today's oceans. The database consists of over 1,000 entries from 297 species compiled by latitude. The data indicate that 1) lifespan increases, and growth rate decreases, with latitude, both across the group as a whole and within well-sampled species, 2) growth

rate, and hence metabolic rate, correlates inversely with lifespan, and 3) opposing trends in lifespan and growth combined with high variance obviate any demonstrable pattern in body size with latitude. These observations suggest that the proposed increase in metabolic activity and demonstrated increase in body size of organisms over the Phanerozoic, should be accompanied by a concomitant shift towards faster growth and/or shorter lifespan in marine bivalves.

Clear latitudinal patterns in both lifespan and growth rate documented in Chapter 1 suggest a role for some environmental factors in promoting lifespan. From a physiological perspective, cool temperatures and low/seasonal food availability are thought to promote long lifespan. However, on the planet today, these two factors covary with latitude so separating their influence using modern organisms is difficult. Fortunately, Earth's fossil record offers a chance to tease apart these factors. In Chapter 2, I turn to fossils from the Cretaceous and Eocene of Seymour Island, Antarctica. During these times, Antarctica was situated in almost the same latitude as today, but temperatures resembled those of modern day mid-latitude environments (e.g, North Carolina). In this unique setting, I found several co-occurring, unrelated, slow growing, long-lived species of bivalve. Cool temperatures cannot explain these impressive longevities. However, the high latitude setting would have resulted in extended periods of no sunlight and suggests that caloric restriction may be the driving factor in extreme longevity.

Chapters 1 and 2 suggest that growth rate could be the factor through which long-life is selected in the evolution of extreme longevity. Studies of growth rates of bivalves living at similar latitudes, under similar environmental conditions through long spans of geologic time,

could help shed light on this question. However, determining growth rates and lifespans of bivalves requires cross-sectioning individuals to reveal internal growth bands. Such methods are time intensive and destructive sampling is often not permitted by museum curators. An alternative method could be to determine age by simply measuring the size of individuals without cross-sectioning, but the nature of growth in bivalves (long-lived in particular) is such that a few millimeters of growth could equate to several decades and introduces a large degree of error. In Chapter 3 then, I explore probabilistic methods for determining age from size in order to constrain population growth parameters without cutting large numbers of individuals. From a small original sample size, I use the relationship between parameters of the von Bertalanffy growth equation to constrain the theoretical age/size distributions of a population of modern *Spisula solidissima*. From these distributions, age can be assigned to an individual of any given size by drawing at random from the corresponding age/size distribution. This method works extremely well in reconstructing population growth parameters in a modern bivalve and should be applicable to the fossil record as well.

With the three chapters presented here, the foundation has been laid to study life history parameters in the fossil record. Currently, life history data are missing from studies of body size and energetics of organisms through time. The growth rate parameter k of the von Bertalanffy growth equation is the variable that will add a new dimension to our understanding of these fundamental patterns in the history of life on Earth. The conclusions from Chapter 1 predict that the temporal trend in body size is driven by an increase in k through time. The methods in Chapter 3 allow for study of k values through time in the fossil record. Chapter 2 examines lifespans and growth rates of fossil bivalves and provides significant revelations into

the factors that influence extreme longevity. Though bivalves have been on the planet for over 500 million years, only a handful of studies have examined their life histories in the fossil record. Besides those presented, other fascinating areas where life history information is needed include studies of survival at mass extinction events and the transitions associated with the Mesozoic Marine Revolution. Incorporation of life history data into paleontological studies can and will provide fascinating insights in the evolution of life on Earth.

THE EVOLUTION OF EXTREME LONGEVITY IN MODERN AND FOSSIL BIVALVES

by

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A dissertation, submitted in partial fulfillment of the requirements for the degree of
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Finally, I must thank my family for their continued support and encouragement. A long time ago now, my mom and dad supported me without question when I made the decision to form a one man swim team in high school. This decision ultimately sent me to a little college in Louisiana where I not only discovered my passion for geology, but also met my future wife. Their support sent me down a road less traveled and that has made all the difference.

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Chapter 1:

Lifespan, growth rate, and body size across latitude in marine Bivalvia, with implications for Phanerozoic evolution

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Abstract

Mean body size in marine animals has increased more than 100 fold since the Cambrian, a discovery that brings to attention the key life history parameters of lifespan and growth rate that ultimately determine size. Variation in these parameters is not well understood on the planet today, much less in deep time. Here, we present a new global database of maximum reported lifespan (MLSP) and shell growth coupled with body size data for 1,148 populations of marine bivalves and show that 1) lifespan increases, and growth rate decreases, with latitude, both across the group as a whole and within well-sampled species, 2) growth rate, and hence metabolic rate, correlates inversely with lifespan, and 3) opposing trends in lifespan and growth combined with high variance obviate any demonstrable pattern in body size with latitude. Our observations suggest that the proposed increase in metabolic activity and demonstrated increase in body size of organisms over the Phanerozoic, should be accompanied by a concomitant shift towards faster growth and/or shorter lifespan in marine bivalves. This prediction, testable from the fossil record, may help to explain one of the more fundamental patterns in the evolutionary and ecological history of animal life on this planet.

Introduction

Animals living at high latitudes have long been suspected to live longer and grow more slowly than those in the tropics, but this contention is based on sparse and largely anecdotal data, and virtually nothing is known of how these parameters have changed over time. Bivalve molluscs are distributed pole to pole, are abundant in the fossil record, and their accretionary shells typically preserve records of age-at-size for every year of an animal's life. As such, they offer an ideal vessel by which to constrain these parameters for marine ectotherms over Earth's

surface today. Faster growth and longer life offer two avenues by which to attain larger size, but they have contrasting implications for the metabolic and ecologic changes hypothesized to drive a mean size increase over time (Bambach 1993, Finnegan et al. 2011, Heim et al. 2015, Payne et al. 2009, Smith et al. 2016). In addition, ‘faster’ life histories allow for more rapid evolutionary change, and so any documented trend with latitude will have implications for gradients in diversity and ecology. An examination of spatial variation in life history parameters may therefore provide insight into modern biodiversity patterns as well as lay the groundwork for interpreting trends through time.

Our dataset (available online at Proceedings B website) derives from an exhaustive search of the peer-reviewed literature and consists of measures of maximum reported lifespan (MLSP), growth, and maximum body size from 1,148 local populations of living marine bivalves spanning the tropics to the polar regions. Data encompass 297 species in 158 genera and include members of nearly half (45) of all extant marine bivalve families (97). Not surprisingly, families that serve as fisheries targets (e.g., Veneridae, Pectinidae, Mytilidae) are represented by greater numbers of populations in the published literature. Fewer populations are recorded from low latitudes; however, these observations account for over 140,000 individuals. Only data from “wild” populations are included; aquacultural and experimental studies were omitted. Growth is approximated by k , the von Bertalanffy growth coefficient, a measure of how fast maximum adult size is attained and a consistent proxy for shell growth across disparate taxa. Maximum body size of individuals within populations is approximated by L_{∞} , the asymptotic size derived from the von Bertalanffy growth equation. See the Supplement for details on the dataset and the von Bertalanffy growth equation (von Bertalanffy 1938).

Results

The data reveal that most bivalves are short lived and that there is a pattern in the distribution of lifespan and growth, but not body size, with latitude.

Maximum reported lifespans for populations of the Bivalvia are exponentially distributed; in more than half the sampled populations, the oldest individuals live for fewer than 11 years (Fig. 1). While most bivalves by far are short-lived (the modal lifespan of species is 3 years), a not insignificant number of species have MLSPs that exceed 20 years, and at least 9 centenarian taxa are documented, including the record-holding *Arctica islandica*, at 507 years (Butler et al. 2013) (Table S1). Note that “maximum” lifespan is in part a function of sampling effort, and reported values should be treated as estimates.

Population-level data plotted by latitude reinforce the preponderance of short-lived bivalves but also demonstrate a strong tendency for populations with longer-lived individuals to be found at higher latitudes (Fig. 2A). Because frequency distributions of population MLSPs, both for the whole dataset (Fig. 1) and for subsets of populations divided by latitude (Fig. S1), are exponentially distributed, standard parametric descriptive statistics can be used to compare population variables across latitude. The mean and standard deviation of MLSPs reported for populations increase with increasing latitude. Populations of tropical (< 30°) bivalves record a mean MLSP of 7.9 years, whereas those in the mid- to high-latitudes have a mean MLSP of 24.7 years. Outliers for low latitudes include the photosymbiotic giant clams (*Tridacna*) and the chemosymbiotic vent clam *Bathymodiolus*. No other low-latitude species have populations with MLSPs longer than 30 years. Individual taxa represented by at least 15 sampled populations spanning >10° of latitude show a similar pattern of increasing lifespan with latitude

(Fig. S2), suggesting a cause that acts both within and across species. Growth (k) shows a similar, but inverse, relationship with latitude (Fig. 2B). Low-latitude bivalves are characterized by significantly higher and more variable growth coefficients than those in the mid and high latitudes.

The potential for these observed patterns to arise simply from uneven sampling with latitude is evaluated by comparing observed data to modeled distributions where lifespan and k in fact have no relationship to latitude. For each variable, we generate exponential distributions using a rate term (slope on a log plot) equal to $1/\text{mean}$ of all observed values (a better approximation of the actual distribution than the best-fit to the discretized histogram), draw values from the modeled distributions at random, and randomly assign them to each of our sampled-population latitudes, thus eliminating any preferred tendency with latitude. We then bin modeled data by latitude and calculate the mean and standard deviation of lifespan and k in each bin. After 1000 trials, we compare the distributions of modeled lifespans and k values in each bin, where there is no relation with latitude but sampling is still non-uniform, to the observed data. Despite being undersampled, observed lifespans are significantly shorter and less variable in the tropics, and higher and more variable near the poles, than seen in the randomized trials (Fig. 3A,B). Likewise, the observed mean and standard deviation of growth/metabolic rate are significantly higher in the tropics and lower toward the poles (Fig. 3C,D).

Plotting k versus lifespan reveals a significant log-log relationship ($p < 0.001$) such that slower growing bivalves tend to have longer lifespans than fast growing forms (Fig. 4), corroborating a relationship suggested earlier from a limited dataset (Ridgway et al. 2011a).

Data grouped by order (Fig. 4) or family exhibit the same negative lifespan-growth relationship, suggesting that causal factors act universally across taxa, rather than the pattern being merely an epiphenomenon of specialization for distinct physiologies or habitats. Because shell growth, more-so than soft-tissue growth, provides a strong proxy for metabolic rate (Lewis and Cerrato 1997), these data also indicate that short-lived (tropical) bivalves have faster metabolisms than long-lived (polar) species, an inference supported by oxygen consumption data for bivalves across a range of habitats (Vladimirova et al. 2003).

The exponential fits to frequency distributions of population MLSPs grouped into 16° latitudinal bands (Fig. S1) illustrate the increasing proportion of populations with longer-lived individuals as latitude increases. Such a pattern requires a systematic decrease in the exponent of the exponential equation (slope on a log scale) with latitude (Fig. S1F). This value corresponds to the probability of death; higher slopes at low latitudes reflect higher overall rates of bivalve mortality (Fig. 5). This pattern is evident whether grouping data into bins of equal latitude or equal numbers of observations.

While lifespan and growth rate demonstrate clear trends with latitude, the combined result of these two variables, body size, does not. Using the von Bertalanffy parameter L_{∞} as a proxy for maximum size within populations reveals no significant relationship between body size and latitude (Fig. 2C, Fig. 3E, F), lifespan, or growth rate (Fig. S3A, B). Populations of slower growing, longer lived, high latitude species show a similar range of sizes overall to those of faster growing, short-lived, tropical species. This lack of a consistent pattern in bivalve body size with latitude, within or across taxa, is supported by earlier work and has been discussed at some length (e.g., Berke et al. 2013, Roy et al. 2000).

Note that R^2 values for the relationships described above are low; latitude alone is a poor predictor of lifespan and growth. To be sure, the lifespans and growth rates exhibited within a population are controlled by a myriad of factors (e.g., see the discussion below), and this complexity contributes to the high variance exhibited in these relationships. Nevertheless, highly significant p values indicate that, despite the variance, latitude and its correlates contribute in a substantive way to an explanation of lifespan and growth across marine Bivalvia today, and hence can be expected to have done so in the past as well.

Potential Causal Factors

Strong trends in lifespan and growth coefficient with latitude, both within and across taxa, require an explanation consistent with factors that vary systematically with latitude. Environmental variables such as temperature and light (and hence primary production, or food availability) are perhaps the most obvious – both have strong impacts on physiology through their influence on metabolism, and metabolic rate is widely suspected to relate causally to lifespan (Speakman 2005, Van Voorhies 2001). Indeed, our documentation of the relationship between lifespan and growth coefficient in bivalves lends further support to that hypothesis. The decrease in temperature that accompanies increasing latitude has a profound influence on biology; as temperature decreases, so too does metabolic rate in both plants and animals (Gillooly et al. 2001). Metabolic rate is also influenced by the availability of food. For the dominantly filter-feeding bivalves, food constitutes phytoplankton and other suspended particles, and phytoplankton production is strongly tied to solar insolation. Studies on a range of animals have shown that caloric restriction increases lifespan, likely through a reduction in

metabolic rate (Fontana et al. 2010). Today, high-latitude bivalves like *Arctica islandica* experience not only cold temperatures but also a limited and highly seasonal supply of food. Deconvolving their influence is difficult, but work with austral sea urchins demonstrates that the effect on metabolism of starvation in winter is far more significant than that of cold temperature (Brockington and Clarke 2001). In either case, long lifespan might simply be a side consequence of limited metabolism rather than a true adaptation to high-latitude environments. Alternatively, if trophic constraints are severe enough that successful reproduction in any given year is unlikely, then long life would be adaptive for organisms that spawn only once per year.

A decrease in disturbance frequency with latitude might also play a role in growth/lifespan trends because long-lived bivalves tend to delay the onset of reproduction for years or even decades (Ridgway et al. 2011a), not a viable life history strategy when an early death due to some calamity is probable. While physical/environmental disturbances such as storms or sediment gravity flows are unlikely to show a consistent relationship with latitude, ecological disturbances like predation could. Such has been postulated (Vermeij 1978), and, while not observed everywhere (Kelley and Hansen 2007, Vermeij et al. 1989), studies have demonstrated a decrease in both drilling (Visaggi and Kelley 2015) and skeleton-crushing (Bertness et al. 1981) predation on bivalves with increasing latitude and extremely low predation in shallow Antarctic ecosystems (Aronson et al. 2007, Harper and Peck 2003, Harper and Peck 2016, Martinelli et al. 2013). Our data are consistent with the hypothesis that fast growth, and consequently shorter life, in the tropics is an adaptation to higher predation frequency. A general, though not universal, decrease in predation with latitude would allow for

increasing variation in life history strategies. While diversity and ecological interactions have a strong influence on local trophic structure (e.g., Hairston and Hairston 1993), a putative latitudinal trend in predation intensity may itself also derive in part from the distribution of temperature and light over Earth's surface.

Note that temperature and food supply in the oceans decrease not only with latitude, but also with water depth. There is evidence, too, that predation pressure decreases with increasing depth (Harper and Peck 2003, Oji 1996). While not the focus of our study, water depth was reported for 425 of the populations in our dataset. Data are sparse, strongly skewed to shallow shelf depths, and often reported as ranges of values, but a tendency toward longer lifespan with increasing water depth is suggested (Fig. S4A). There does not appear to be a relationship with growth rate or, perhaps less surprising given the lack of a latitudinal pattern as well, body size (Fig. S4B,C). Nevertheless, the limitations of the available data require caution when interpreting pattern (see discussion in SI). Additional targeted sampling might help to clarify the nature of these relationships.

Implications for Phanerozoic Evolution

We document a clear global pattern in the latitudinal distribution of life history parameters in today's oceans for a pervasive marine ectotherm, animals that also dominate the post-Paleozoic fossil record and range back to the Cambrian. Is there a temporal trend in the expression of this pattern, and what might it mean for the evolution and ecology of marine ecosystems over the deep history of life? Despite the relative ease with which bivalve lifespans and growth rates can be determined from their shells, the longevities of fossil bivalves have

only been reported in a handful of studies. Anecdotal data are consistent with today's broad latitudinal pattern persisting back through the Phanerozoic: subtropical mollusks live only a few years in the Eocene (Haveles and Ivany 2010), mid-latitude ($\sim 40^\circ\text{N}$) Jurassic gryphaeid bivalves live upwards of 20 years, and early Permian high-latitude faunas contain bivalves with lifespans of several to many decades (Ivany and Runnegar 2010), all consistent with the modern trend. The degree to which temperature is driving this pattern will determine how sensitive the gradient is to global climate change over time. Early in the Cenozoic, for example, the poles were a good deal warmer than today, yet bivalve centenarians are still present in austral polar faunas (Buick and Ivany 2004). Such non-analog settings, where temperature and light/food limitation are not as tightly correlated as they are today, can offer critical tests of their relative causal roles.

The pace of life – growth rate and life span – has significant implications for the interpretation of macroevolutionary trends. Not only is this at the heart of resolving modes of heterochronic change in the evolution of individual lineages (Jones 1988, Jones and Gould 1999), but there are potential connections to global Phanerozoic trends in body size, energetics and diversity. Causal hypotheses for aspects of each of these can be tested using life history data from the fossil record now that patterns in Modern oceans are understood.

An increase in the mean body size of animals through time is now well documented (Heim et al. 2015, Payne et al. 2014), a trend manifest within bivalves as well (Fig. S5). Today, consistent relationships between body size and latitude (Fig 2), body size and lifespan (Fig S3A) or body size and growth rate (Fig. S3B) cannot be demonstrated in marine bivalves, obfuscating the driving factor behind a temporal increase in body size using a space-for-time

substitution argument. However, the relationship between lifespan and growth rate predicts that even limited new data on one variable or the other can bring greater clarity on how a trend toward larger body size comes about. The scenarios of increasing lifespan or growth rate bear rather different implications for the macroecological history of bivalves, hence these types of data are critical complements to existing data on body size evolution.

An increase in the metabolic rate of marine organisms is an inherent prediction of broad ecological hypotheses such as Seafood through Time and escalation during the Mesozoic Marine Revolution (Bambach 1993, Vermeij 1977). This prediction is supported by Finnegan et al. (Finnegan et al. 2011), who use the metabolic model of Gillooly et al. (Gillooly et al. 2001) to relate increasing body size in post-Paleozoic gastropods to faster metabolic rates through time and provide the first quantitative test of the energetics hypothesis. A subsequent analysis by Payne et al. (2014) using size data of bivalves over the Phanerozoic suggests a similar increase in metabolic rates. The necessary assumptions that accompany the application of this model to extinct organisms in deep time call for some caution in interpreting the results. However, because shell growth correlates with both metabolic rate and lifespan, one could validate the Finnegan et al. (Finnegan et al. 2011) and Payne et al. (2014) results, and hypotheses about energetics through time, with a targeted study of von Bertalanffy k values and/or lifespans of shells sampled from similar paleolatitudes over time. To the degree that lifespan/growth gradients are sensitive to temperature, our data also predict that polar faunas may become more 'escalated' during times of global warmth. Antarctic faunas during the warm Eocene are ecologically more similar to low latitude assemblages than they become once temperature

begins to fall (Aronson et al. 2009). Comparison of Eocene life history traits with those from more recent cooler times could test this prediction.

Another fundamental biological pattern, the latitudinal diversity gradient, may not be unrelated to the distribution of life history parameters with latitude. Speciation rates are in part dependent upon the rates of mutation, and taxa with shorter generation times have the potential to accumulate more variation in a given interval of time (Thomas et al. 2010). Because slow-growing bivalves also tend to delay the onset of sexual maturity (Ridgway et al. 2011a), polar taxa might be less likely to spin off new species than are fast-growing tropical taxa. It is therefore not unreasonable to suggest that life history parameters in fact contribute to the maintenance of the latitudinal diversity gradient. Such is consistent with observations of preferential bivalve origination in the tropics during the Neogene (Jablonski et al. 2006). Furthermore, a connection might be made with the modest rise in sample-standardized diversity seen over the Phanerozoic (Alroy et al. 2008).

While the potential for testing hypotheses about relationships between life history traits and spatio-temporal macroevolutionary trends using the modern and fossil record is high, little work has thus far been done. This may be the next frontier of paleobiological research.

Figures

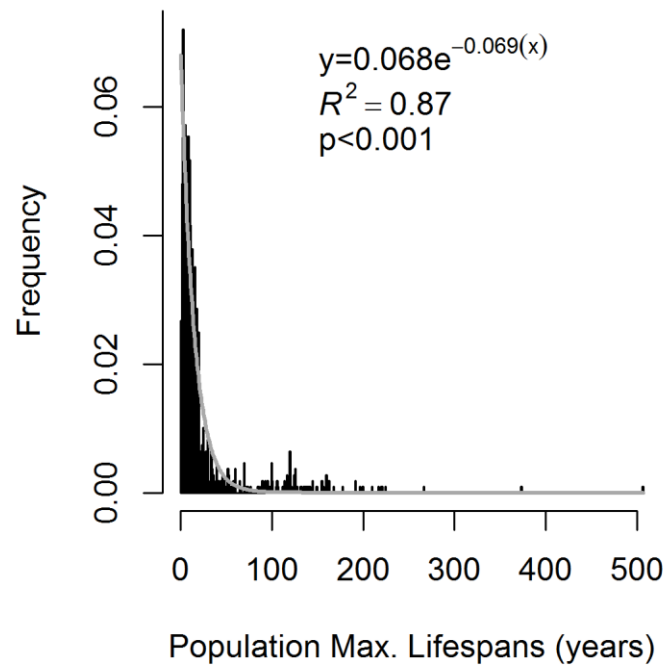


Figure 1. Distribution of maximum reported lifespans of individuals within all populations of the Bivalvia in the database. Minimum = 0.25 yrs (*Donax variabilis*), maximum = 507 yrs (*Arctica islandica*). Dataset provided in the Supplement. N = 1,084.

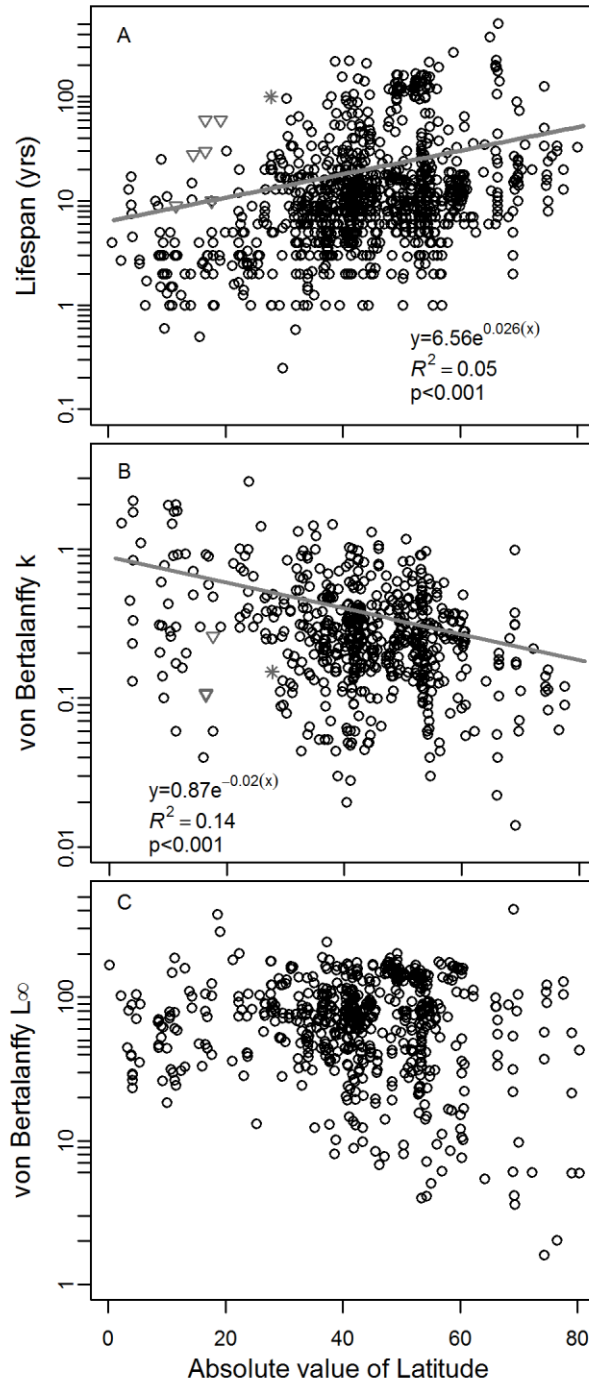


Figure 2. Relationships between latitude and life history parameters in local populations of marine bivalves. A) Maximum lifespan; N=1077. B) Growth as measured by the von Bertalanffy growth parameter, k ; N=613. C) Body size as measured by the von Bertalanffy L_{∞} parameter;

N=636. ▽ = *Tridacna*, a photosymbiotic taxon; * = *Bathymodiolus*, a chemosymbiotic taxon from a hydrothermal vent setting.

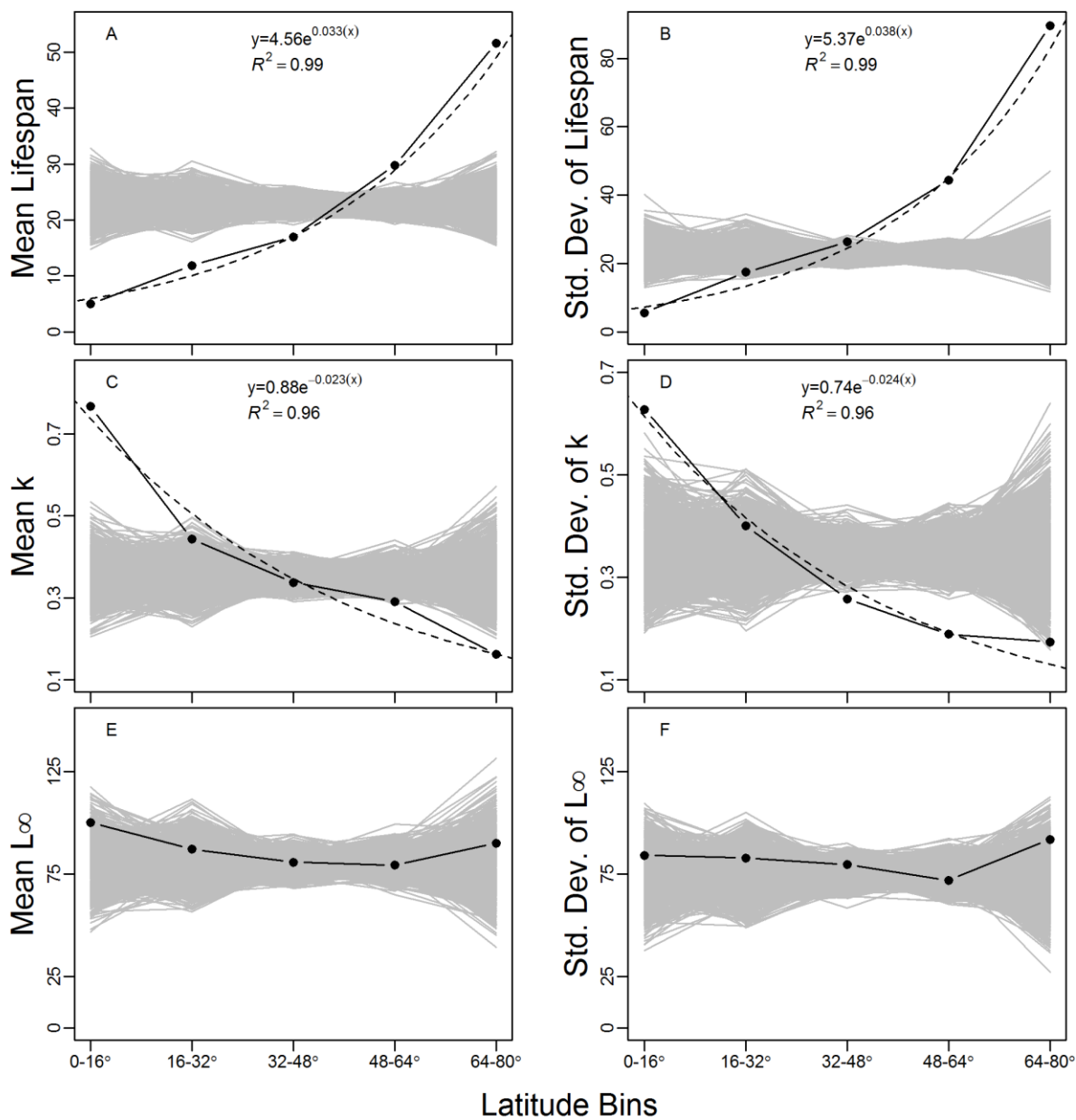


Figure 3. Results of resampling procedures to evaluate statistical significance of relationships between latitude and life history parameters. Gray lines connect resampled values assuming no relationship with latitude. Black lines are the observed trends in values and their best-fit lines. A) Mean and B) standard deviation of maximum lifespan vs. latitude. Mean observed lifespan = 22.47 for entire database. C) Mean and D) standard deviation of von Bertalanffy k

values vs. latitude. Mean observed $k = 0.35$ for entire database. Tropical and polar bivalves fall well outside the range of randomized trials for both lifespan and k . E) Mean and F) standard deviation of L_{∞} . Observed values fall within the range of randomized trials suggesting no significant relationship.

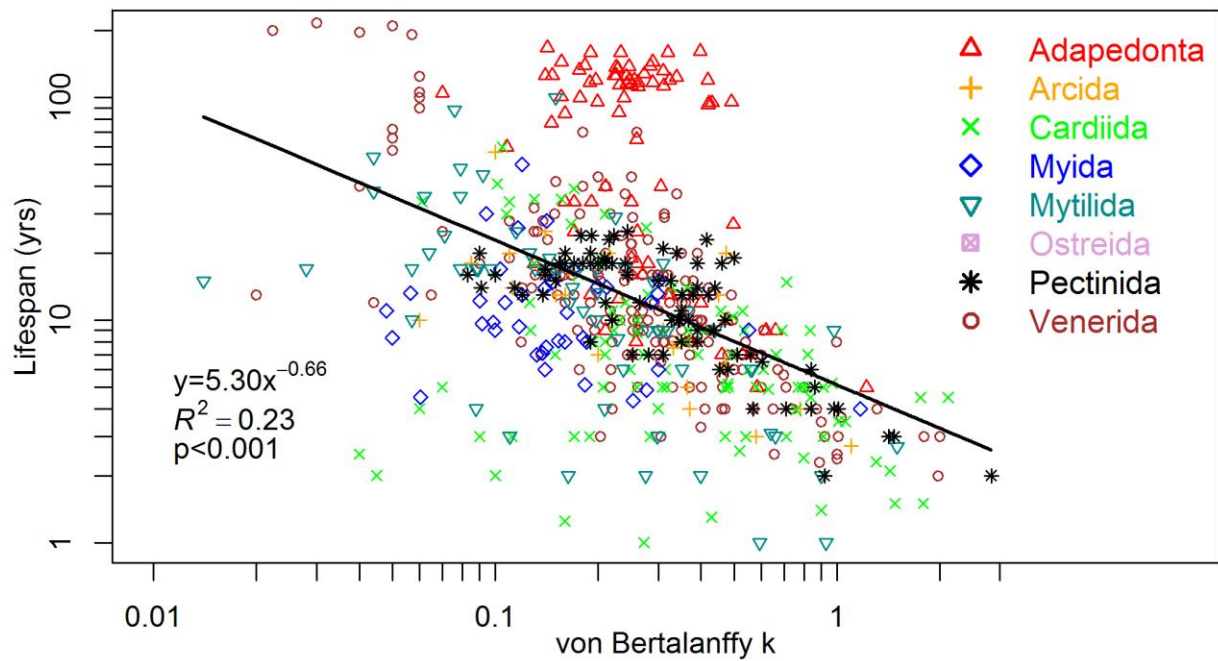


Figure 4. Relationship between the von Bertalanffy k growth coefficient and lifespan, with data points coded by Order within the Bivalvia. Only orders with >20 observations are included. Six-hundred and thirteen populations contain data on both lifespan and growth rate.

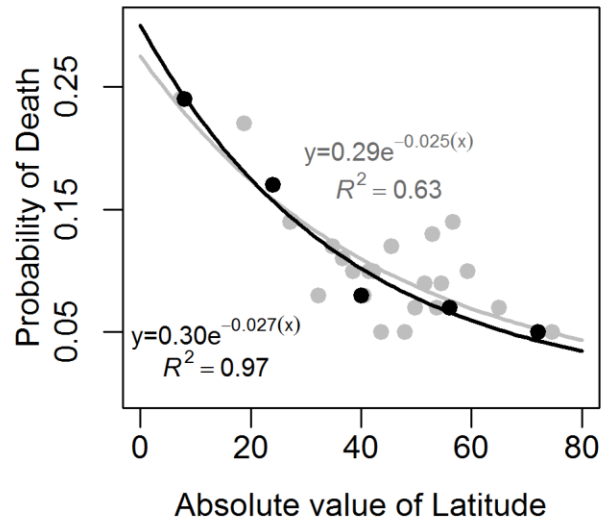


Figure 5. Probability of death versus latitude based on exponential fits to frequency distributions of populations MLSPs (Fig. S1). Lifespan observations are binned by equal latitude (in black, 16° bins) or by equal number of observations (in grey, 50 lifespans per bin except last with 26). Total number of observations on lifespan =1078. Absolute value of latitude is plotted as the midpoint of each bin. Note that both approaches yield essentially the same relationship ($p<0.01$).

Supplementary Material for Chapter 1:

Methods

We identified and searched the entire publication runs of 30 peer-reviewed journals (Table S2) likely to contain articles reporting lifespan and/or growth rate data on marine bivalves. We tracked down additional references cited therein, and also retrieved articles cited in previous molluscan lifespan compilations (Comfort 1957, Heller 1990, Kidwell and Rothfus 2010, Powell and Stanton 1985, Robertson 1979). A full list of references is provided at the end of this Supplement. Our database differs from previous attempts in that all entries are derived solely from primary sources, based on natural populations, and we record not only maximum reported lifespan (MLSP), but also von Bertalanffy growth parameters and latitude and longitude of the population sampled. Water depth was also tabulated if provided, along with other population metadata (Table S3). The database consists of observations derived from 1,148 populations. Not all variables are recorded for all populations, but 1,084 report maximum lifespan, 673 report von Bertalanffy k values, and 613 report both of these.

Parameters from the von Bertalanffy growth equation (von Bertalanffy 1938) can be used to describe the growth of many marine invertebrates. The standard form of the von Bertalanffy growth equation can be written as:

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

where L_t = shell length at time t , L_∞ = asymptotic size, or the size at which growth rate is essentially zero, k = rate at which L_∞ is attained, and t_0 = age at which the bivalve has a size of zero (the x intercept on a plot of size as a function of age). In organisms with indeterminate growth, such as bivalves, a maximum size may not be biologically appropriate, though L_∞ is often treated as

such in the literature. Where only age-size data were provided but not curve-fit, we calculated von Bertalanffy growth parameters using the nls procedure in R.

Taxonomy for all entries in the database was verified using the World Online Register of Marine Species (<http://www.marinespecies.org/>). Representatives from 45 bivalve families are included in the database (Table S4), accounting for nearly half of all described families. The most numerous are the Veneridae (n=223), Mytilidae (n=121), Pectinidae (n=116), and Hiatellidae (n=70).

Results and Discussion

Lifespan and growth within taxa

An examination of lifespan versus latitude in species with at least 15 observations spanning more than 10° of latitude (Fig. S2) makes apparent that the pattern in Fig. 2A is not driven by one or a few taxa, but rather is a feature present across the Bivalvia, both within and across taxa. In 11 of 12 well-sampled species spanning 9 families, the slope of the relationship between maximum within-population lifespan and absolute latitude exceeds zero at a significance of $p < 0.10$. The lower slope of the best-fit line for *Mercenaria* may be an artifact of sampling mainly shallow-water populations along the U.S. Atlantic Coast, which have historically been heavily harvested (Quitmyer and Jones 1997, Rice 1992). The oldest specimen of *Mercenaria mercenaria*, a 106-year-old individual, was collected in water deeper (15m) than had

been investigated before (Ridgway et al. 2011b), suggesting the potential for a different age-latitude relationship in less impacted, deeper-water populations. See discussion on depth below.

Depth versus lifespan, growth rate, and size

Nutrient availability and temperature decrease with depth as they do with latitude, and thus the depth at which an organism lives may also relate to its longevity and growth. In addition, deep-water ecosystems have been described as ecologically distinct from those on the shelf due in part to different evolutionary histories (Jablonski et al. 1983), and this could be reflected in differences in lifespan and growth (e.g., Koslow 2000 for fishes). Sources report depths for fewer than half of all populations (N = 425), and those are often given as approximations or broad ranges. It is possible, therefore, that water depth could introduce variation that is unaccounted for and obscures patterns in lifespan and growth with latitude. Reported data, however, are strongly skewed toward shallow shelf settings (modal depth = 10 m; only 7 populations are recorded from ≥ 200 meters), and there is no reason to believe the remainder to be any different, particularly given that most come from fisheries targets harvested on the shelf. Patterns we report are therefore likely to characterize shallow shelf faunas – there is no systematic bias associated with including a large number of slope or deep sea taxa from particular regions that could color our results.

While the vast majority of our data come from shelf settings, it is nonetheless possible that effects associated with water depth could be present in the data. Jones et al. (Jones et al. 1978a), e.g., presented data suggesting differences in longevity, growth, and body size between shallow and deep populations of *Spisula solidissima* off New Jersey, but few other systematic

studies exist. We restricted our analysis to the well-sampled mid-latitudes (30-60° N and S) so as to minimize conflation with covariates of latitude as much as possible. The relationship between depth and lifespan is positive and significant, but there is no demonstrable relationship between depth and either growth rate or body size (Fig. S4). These results should be treated with caution. Observations from many more populations along broad depth transects at constant latitude are needed to establish the presence or absence of pattern with confidence.

Supplementary Figures

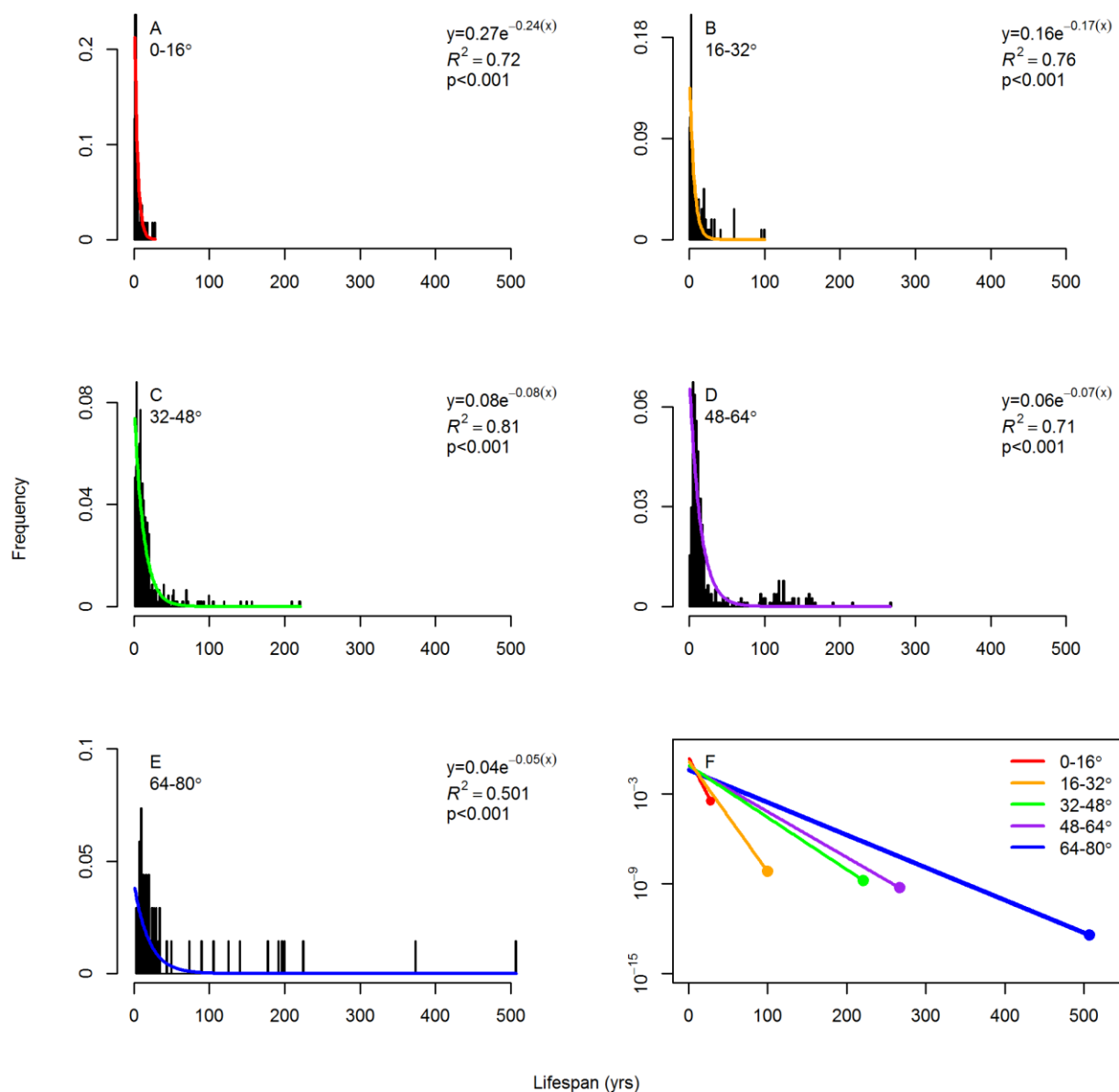


Figure S1. Histograms of population-level maximum lifespans for each 16° latitude bin. Curves are best fit exponential equations. Y-axes vary to best show fits to distribution. Panel F shows all 5 regressions on a log scale, truncated at the observed maximum lifespan for that bin, to illustrate differences in slope (probability of death) with latitude and maximum lifespan. See main text for more discussion.

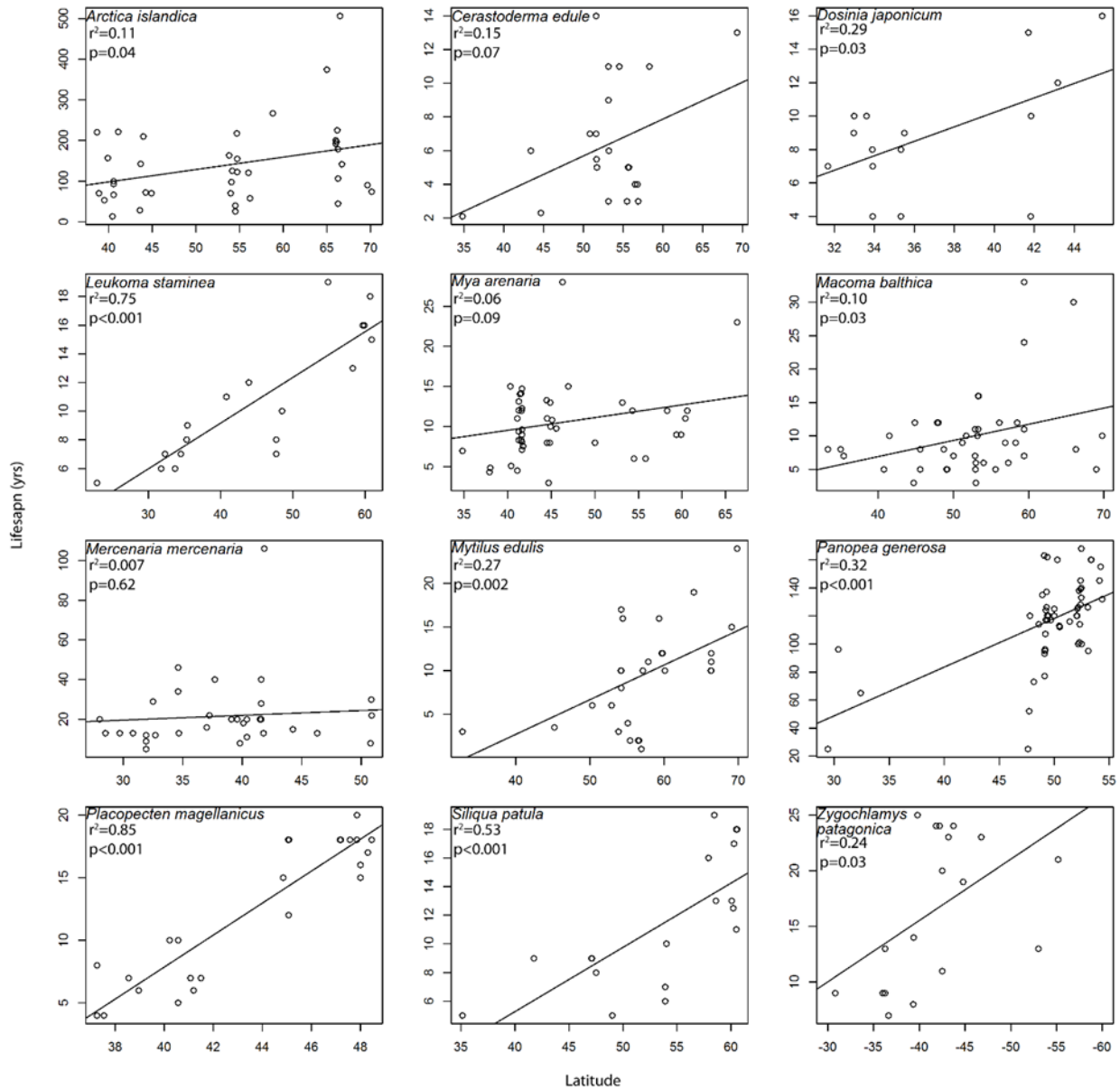


Figure S2. Relationship between latitude and lifespan in 12 species with at least 15 populations spanning $>10^\circ$ of latitude. All but one of the regressions (*Mercenaria*) are significant at the 0.01 level.

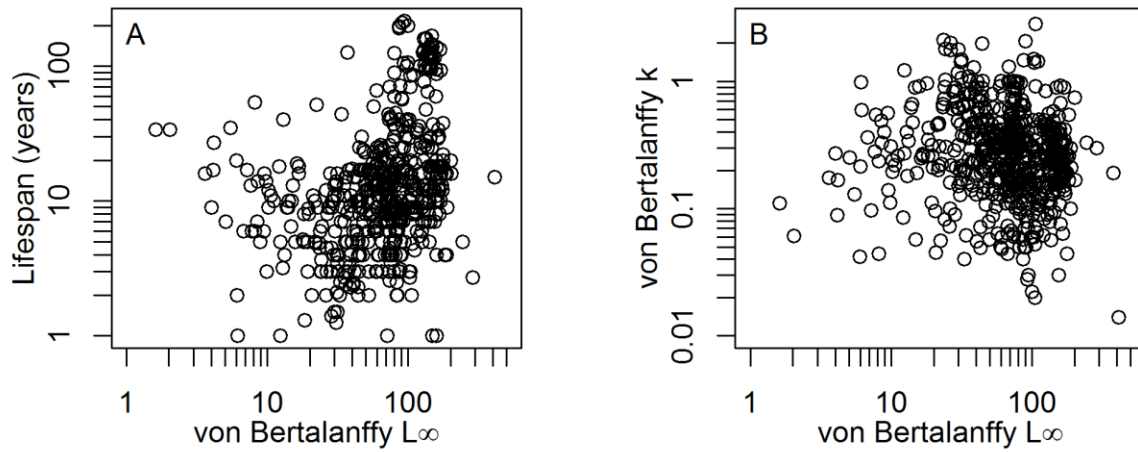


Figure S3. Relationships between maximum body size (approximated by L_{∞}) and lifespan (A) and growth rate (B). Neither of the relationships are statistically significant.

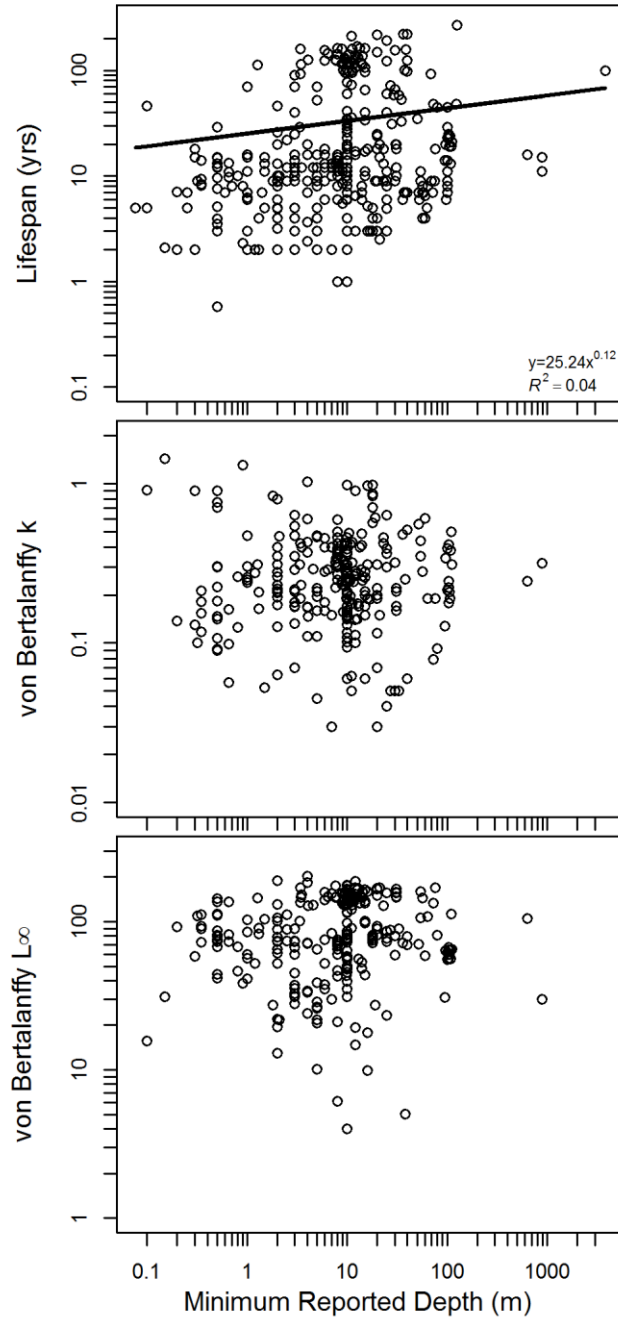


Figure S4. Relationship between water depth and A) maximum lifespan, N=411 observations, B) growth rate, N=278 observations, and C) body size, N=278 observations, for populations between 30° and 60° N and S latitude. Only the trend with lifespan is significant ($p \leq 0.01$).

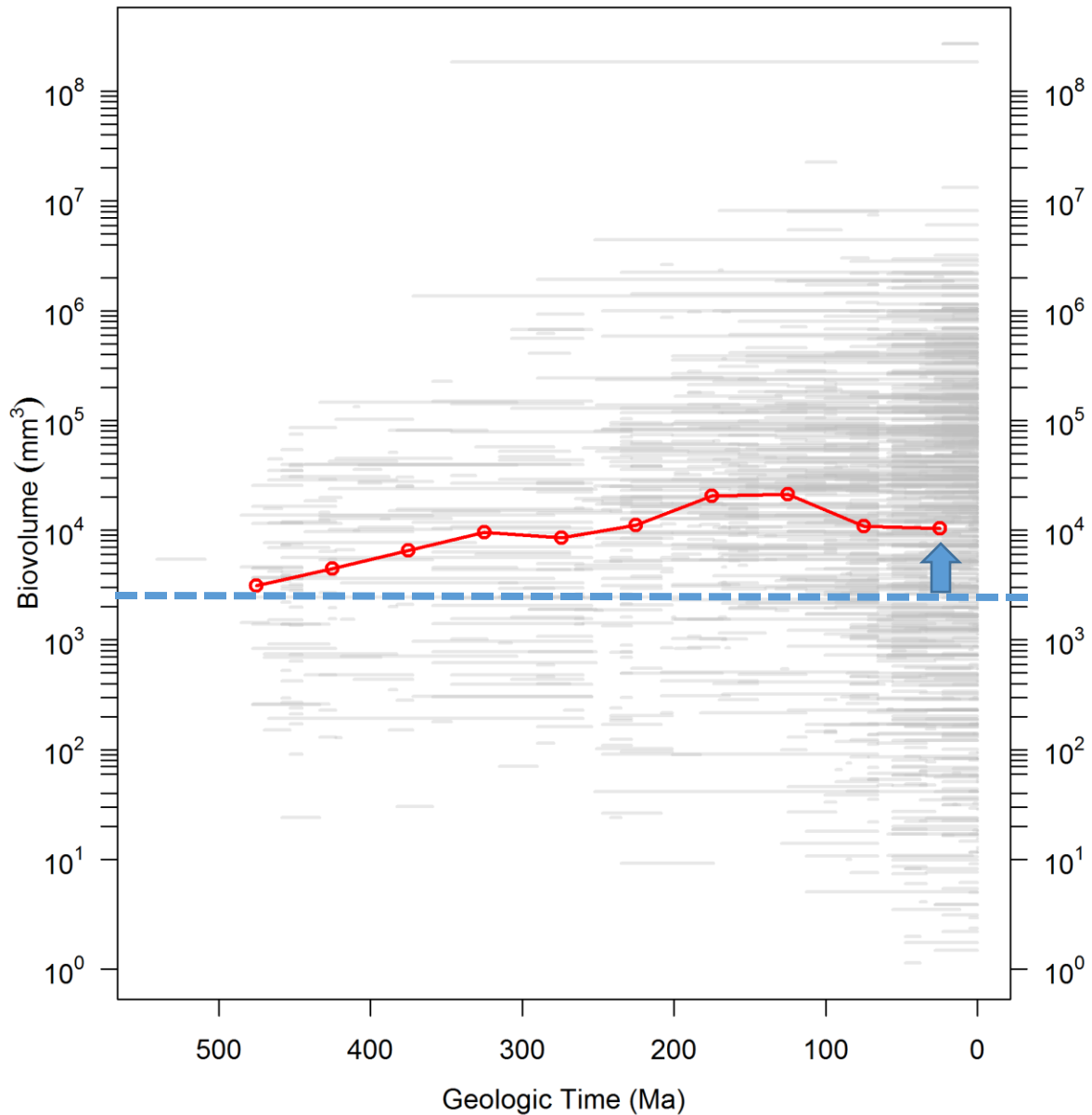


Figure S5. Biovolume of bivalve genera through the Phanerozoic derived from Heim et al. (Heim et al. 2015), plotted as body size of the largest measured species within each genus over the geologic range of the entire genus. Gray bars are geologic ranges. Red line shows the trend in mean biovolume towards the Recent for 50-million-year time bins, an increase perhaps first noticed by Runnegar (Runnegar 1985).

Supplementary Tables

Table S1. Maximum reported lifespans (MLSP) for species represented in database. References provided in Appendix 1.

Species	MLSP (yrs.)	Species	MLSP (yrs.)
<i>Abra alba</i>	4	<i>Barnea parva</i>	6
<i>Abra nitida</i>	8.8	<i>Bathymodiolus childressi</i>	100
<i>Abra prismatica</i>	1.8	<i>Brachidontes variabilis</i>	5
<i>Abra tenuis</i>	2.5	<i>Callista chione</i>	18
<i>Adacnarca nitens</i>	20	<i>Calyptogena magnifica</i>	4
<i>Adamussium colbecki</i>	20	<i>Carditamera affinis</i>	17.25
<i>Aequipecten opercularis</i>	8	<i>Cavatidens omissa</i>	1
<i>Aligena elevata</i>	7	<i>Cerastoderma edule</i>	14
<i>Amarilladesma mactroides</i>	8	<i>Cerastoderma glaucum</i>	6
<i>Amiantis purpurata</i>	25	<i>Chamelea gallina</i>	12
<i>Amusium pleuronectes</i>	2	<i>Chamelea striatula</i>	11
<i>Amygdalum glaberrimum</i>	1	<i>Chione cancellata</i>	6
<i>Anadara broughtonii</i>	20	<i>Chione cortezi</i>	8
<i>Anadara cornea</i>	4	<i>Chione elevata</i>	11
<i>Anadara inaequalis</i>	7	<i>Chione undatella</i>	2
<i>Anadara nobilis</i>	4	<i>Chionista fulctifraga</i>	16
<i>Anadara tuberculosa</i>	25	<i>Chlamys islandica</i>	35
<i>Anodontia alba</i>	2	<i>Chlamys tehuelcha</i>	5
<i>Anomalocardia flexuosa</i>	2.6	<i>Choromytilus chorus</i>	1.25
<i>Anomalodiscus squamosus</i>	3	<i>Choromytilus meridionalis</i>	9
<i>Arca noae</i>	16	<i>Ciliatocardium ciliatum</i>	35
<i>Arca ventricosa</i>	10	<i>Clinocardium nuttallii</i>	16
<i>Arca zebra</i>	10	<i>Corbicula fluminea</i>	4
<i>Arctica islandica</i>	507	<i>Corbula gibba</i>	2
<i>Arcuatula arcuatula</i>	1.5	<i>Crassostrea ariakensis</i>	5
<i>Arcuatula senhousia</i>	2	<i>Crassostrea bilineata</i>	4
<i>Argopecten irradians</i>	2	<i>Crassostrea gigas</i>	7
<i>Argopecten irradians concentricus</i>	2	<i>Crassostrea glomerata</i>	1.25
<i>Argopecten purpuratus</i>	6	<i>Crassostrea rhizophorae</i>	1
<i>Arvella manshurica</i>	9	<i>Crassostrea virginica</i>	6
<i>Asaphis deflorata</i>	7	<i>Crassula aequilatera</i>	5
<i>Astarte arctica</i>	9	<i>Crenella decussata</i>	7
<i>Astarte borealis</i>	10	<i>Crenomytilus grayanus</i>	150
<i>Astarte elliptica</i>	20	<i>Cumingia tellinoides</i>	4
<i>Astarte warhami</i>	3	<i>Cyclocardia ventricosa</i>	12
<i>Atrina vexillum</i>	11	<i>Cyrtodaria siliqua</i>	105
<i>Aulacomya atra</i>	18	<i>Cyrtodaria kurriana</i>	19
<i>Austrovenus stutchburyi</i>	9	<i>Decatopecten radula</i>	8
<i>Barbatia trapezina</i>	6.29	<i>Diplodon chilensis patagonicus</i>	90
<i>Barnea candida</i>	4	<i>Diplodonta aleutica</i>	6

Table S1 cont.

Species	MLSP (yrs.)	Species	MLSP (yrs.)
<i>Divaricella irpex</i>	1	<i>Hiatella arctica</i>	126
<i>Donax cuneatus</i>	3	<i>Katelysia opima</i>	3
<i>Donax denticulatus</i>	1.5	<i>Keenocardium californiense</i>	9
<i>Donax dentifer</i>	4.5	<i>Kurtiella bidentata</i>	7
<i>Donax faba</i>	2	<i>Lasaea adansoni</i>	4
<i>Donax gouldi</i>	3	<i>Laternula elliptica</i>	36
<i>Donax hanleyanus</i>	5.18	<i>Leiosolenus patagonicus</i>	15
<i>Donax incarnatus</i>	2	<i>Leukoma antiqua</i>	16
<i>Donax serra</i>	2	<i>Leukoma grata</i>	14
<i>Donax sordidus</i>	1.4	<i>Leukoma jedoensis</i>	6
<i>Donax spiculum</i>	0.6	<i>Leukoma staminea</i>	19
<i>Donax striatus</i>	2.4	<i>Leukoma thaca</i>	9
<i>Donax trunculus</i>	5	<i>Liocyma fluctuosa</i>	23
<i>Donax variabilis</i>	1	<i>Lissarca miliaris</i>	7
<i>Donax vittatus</i>	8	<i>Lissarca notorcadensis</i>	18
<i>Dosinia concentrica</i>	3	<i>Lithophaga lithophaga</i>	54
<i>Dosinia elegans</i>	6	<i>Loripes lucinalis</i>	4.9
<i>Dosinia exoleta</i>	12	<i>Lunarca ovalis</i>	3
<i>Dosinia hepatica</i>	9	<i>Lyonsia arenosa</i>	7
<i>Dosinia japonicum</i>	16	<i>Lyonsia vniroi</i>	10
<i>Dosinia lupinus</i>	15	<i>Macoma balthica</i>	33
<i>Ensis directus</i>	8.5	<i>Macoma calcarea</i>	18
<i>Ensis macha</i>	9	<i>Macoma lama</i>	8
<i>Ensis magnus</i>	18	<i>Macoma loveni</i>	11
<i>Ensis siliqua</i>	10	<i>Macoma middendorffi</i>	19
<i>Eontia ponderosa</i>	15	<i>Macoma nobilis</i>	3
<i>Equichlamys bifrons</i>	13	<i>Mactra chinensis</i>	12
<i>Eurhomalea exalbida</i>	70	<i>Mactromeris polynyma</i>	60
<i>Eurhomalea rufa</i>	2.5	<i>Megapitaria maculata</i>	10
<i>Ezocallista brevisiphonata</i>	52	<i>Megapitaria squalida</i>	2.5
<i>Fragum fragum</i>	5	<i>Megayoldia thraciaeformis</i>	15
<i>Gafrarium pectinatum</i>	3	<i>Mercenaria campechiensis</i>	28
<i>Gaimardia trapesina</i>	5	<i>Mercenaria mercenaria</i>	106
<i>Gari solida</i>	14.83	<i>Meretrix casta</i>	3
<i>Gemma gemma</i>	6	<i>Mesodesma arctatum</i>	24
<i>Geukensia demissa</i>	24	<i>Mimachlamys gloriosa</i>	4
<i>Glossocardia obesa</i>	8	<i>Mimachlamys varia</i>	6
<i>Glycymeris bimaculata</i>	57	<i>Mizuhopecten yessoensis</i>	15
<i>Glycymeris glycymeris</i>	192	<i>Modiolus modiolus</i>	48
<i>Glycymeris nummaria</i>	20	<i>Mulinia edulis</i>	7

Table S1 cont.

Species	MLSP (yrs.)	Species	MLSP (yrs.)
<i>Mulinia lateralis</i>	0.58	<i>Pholas dactylus</i>	14
<i>Musculus discors</i>	9	<i>Phreagena kilmeri</i>	16
<i>Musculus niger</i>	19	<i>Pillucina neglecta</i>	1.5
<i>Mya arenaria</i>	28	<i>Pinctada imbricata</i>	7
<i>Mya baxteri</i>	30	<i>Pinctada imbricata fucata</i>	6
<i>Mya pseudoarenaria</i>	26	<i>Pinctada imbricata radiata</i>	4
<i>Mya truncata</i>	50	<i>Pinctada margaritifera</i>	5
<i>Mysella cuneata</i>	4	<i>Pinctada maxima</i>	20
<i>Mysella kurilensis</i>	9	<i>Pinna bicolor</i>	12
<i>Mysella planulata</i>	4	<i>Pinna nobilis</i>	26
<i>Mytilus californianus</i>	6	<i>Placopecten magellanicus</i>	20
<i>Mytilus coruscus</i>	29	<i>Politapes aureus</i>	5
<i>Mytilus edulis</i>	24	<i>Politapes rhomboides</i>	11
<i>Mytilus edulis planulatus</i>	3	<i>Portlandia arctica</i>	7
<i>Mytilus galloprovincialis</i>	20	<i>Potamocorbula adusta</i>	1.71
<i>Mytilus trossulus</i>	13	<i>Protapes gallus</i>	3
<i>Nucula paulula</i>	1	<i>Protothaca euglypta</i>	15
<i>Nucula turgida</i>	10	<i>Pteria colymbus</i>	1
<i>Nuculana minuta</i>	9	<i>Pteria penguin</i>	2.7
<i>Nuculana pernula</i>	11	<i>Ptericolaria pholadiformis</i>	10
<i>Ostrea chilensis</i>	8	<i>Rangia cuneata</i>	8
<i>Ostrea edulis</i>	16	<i>Reloncavia chilencia</i>	1
<i>Ostrea puelchana</i>	6.5	<i>Ruditapes decussatus</i>	8
<i>Panomya ampla</i>	11	<i>Ruditapes philippinarum</i>	16
<i>Panopea abbreviata</i>	86	<i>Saxidomus gigantea</i>	20
<i>Panopea generosa</i>	168	<i>Saxidomus purpurata</i>	9
<i>Panopea globosa</i>	60	<i>Scrobicularia plana</i>	18
<i>Panopea zelandica</i>	85	<i>Semele lenticularis</i>	13
<i>Paphia laterisulca</i>	3	<i>Semele solida</i>	9
<i>Paphia undulata</i>	3	<i>Senilia senilis</i>	30
<i>Paphies donacina</i>	5	<i>Septifer virgatus</i>	12
<i>Paphies ventricosa</i>	7	<i>Serripes groenlandicus</i>	39
<i>Parvicardium exiguum</i>	1	<i>Siliqua alta</i>	18
<i>Patinopecten caurinus</i>	19	<i>Siliqua patula</i>	19
<i>Pecten albus</i>	3	<i>Siliqua pulchella</i>	2
<i>Pecten fumatus</i>	16	<i>Solemya sp.</i>	1
<i>Pecten jacobaeus</i>	13	<i>Sphenia sincera</i>	3
<i>Pecten maximus</i>	22	<i>Spisula discors</i>	9
<i>Perna perna</i>	9.03	<i>Spisula murchisoni</i>	7
<i>Perna viridis</i>	3	<i>Spisula sachalinensis</i>	70

Table S1 cont.

Species	MLSP (yrs.)	Species	MLSP (yrs.)
<i>Spisula solida</i>	13	<i>Timoclea micra</i>	1
<i>Spisula solidissima</i>	37	<i>Tindaria callistiformis</i>	100
<i>Spisula solidissima similis</i>	5.5	<i>Tivela mactroides</i>	3.3
<i>Spisula subtruncata</i>	4	<i>Tivela stultorum</i>	53
<i>Spisula voyi</i>	52	<i>Tresus capax</i>	16
<i>Spondylus limbatus</i>	16	<i>Tresus nuttallii</i>	16
<i>Tagelus divisus</i>	2.5	<i>Tridacna crocea</i>	60
<i>Tagelus dombeii</i>	10	<i>Tridacna darsa</i>	30
<i>Tawera elliptica</i>	23	<i>Tridacna gigas</i>	60
<i>Tawera mawsoni</i>	14	<i>Tridacna maxima</i>	28
<i>Tawera sphaericula</i>	9	<i>Venerupis bruguieri</i>	6.5
<i>Tegillarca granosa</i>	7.5	<i>Venerupis corrugata</i>	10
<i>Tellina capsoides</i>	3	<i>Venerupis japonica</i>	10
<i>Tellina cuspis</i>	4	<i>Venus verrucosa</i>	16
<i>Tellina exotica</i>	1	<i>Xenostrobus pulex</i>	3
<i>Tellina fabula</i>	6	<i>Ylistrum balloti</i>	3
<i>Tellina liliana</i>	1	<i>Ylistrum japonicum</i>	2
<i>Tellina lutea</i>	41	<i>Yoldia amygdalea hyperborea</i>	9
<i>Tellina martinicensis</i>	2	<i>Yoldia eightsi</i>	65
<i>Tellina piratica</i>	2	<i>Yoldia limatula</i>	4
<i>Tellina tenuis</i>	7	<i>Yoldia myalis</i>	11
<i>Teredo navalis</i>	2	<i>Yoldia notabilis</i>	17
<i>Theora lubrica</i>	1.8	<i>Yoldia seminuda</i>	14
<i>Thracia septentrionalis</i>	11	<i>Zirfaea pilsbryi</i>	7
<i>Thyasira flexuosa</i>	3.2	<i>Zygochlamys patagonica</i>	25
<i>Thyasira gouldi</i>	2		

Table S2. List of journals and years for which exhaustive searches were completed.

Journal	Years Searched	Journal	Years Searched	Journal	Years Searched
Advances in Marine Biology	1963-present	U.S. Fisheries Bulletin	1881-present	Journal of the Marine Biological Association of the U.K.	1888-present
Aquatic Biology	2007-present	Fisheries Research	1982-present	Marine Biology	1967-present
Australian Journal of Marine and Freshwater Research	1950-present	Helgoland Marine Research	1937-present	Marine Ecology	1980-present
Bulletin of Marine Science	1951-present	Indian Journal of Fisheries	1965-present	Marine Ecology Progress Series	1979-present
Canadian Journal of Zoology	1929-present	Indian Journal of Marine Science	2001-2014	Marine Fisheries Review	1971-2014
Chesapeake Science	1960-1977	Journal of Experimental Marine Biology and Ecology	1967-present	Netherlands Journal of Sea Research	1961-1995
Estuaries	1977-2005	Journal of Marine Science	1903-present	New Zealand Journal of Marine and Freshwater Research	1967-present
Estuaries and Coasts	2006-2013	Journal of Molluscan Studies	1893-present	Polar Biology	1983-present
Estuarine and Coastal Marine Science	1973-1980	Journal of Sea Research	1996-present	Proceedings of the National Shellfisheries Association	1954-1980
Estuarine, Coastal and Shelf Science	1981-present	Journal of Shellfish Research	1981-present	The Biological Bulletin	1897-present

Table S3. Parameters recorded in the lifespan database (see Proceedings B website), as provided by the authors.

Family- Accepted family

Given genus – Genus supplied in text

Given species –Species supplied in text

Accepted genus – Genus according to WoRMS

Accepted species –Species according to WoRMS

MLSP – Maximum lifespan of each population presented in source

IP- Scale of study, I=Individual, P=population

N- number of individuals if population

Location – Geographic name

Latitude – Decimal degrees

Longitude – Decimal degrees

Minimum depth - meters

Maximum depth - meters

Linf – Parameter of von Bertalanffy growth equation

K – Parameter of von Bertalanffy growth equation

t_0 - Parameter of von Bertalanffy growth equation

Vbmethod – Method of estimating von Bertalanffy growth equation; L=length frequency analysis,

M=growth bands produced at shell margin, H=growth bands in hinge, R=mark and recapture

Author

Year

Paper title

Journal

Comments – from enterer

Table S4. Number of observations for each family recorded in the database.

Family	n	Family	n	Family	n
Veneridae	223	Astartidae	10	Vesicomyidae	2
Mytilidae	121	Philobryidae	10	Lasaeidae	1
Pectinidae	116	Yoldiidae	9	Nassariidae	1
Cardiidae	73	Glycymerididae	7	Nuculidae	1
Hiatellidae	70	Montacutidae	7	Solemyidae	1
Mactridae	70	Pholadidae	5	Spondylidae	1
Tellinidae	68	Nuculanidae	5	Teredinidae	1
Myidae	51	Psammobiidae	4	Thraciidae	1
Donacidae	42	Carditidae	3	Tindariidae	1
Arcticidae	39	Corbulidae	3	Trapezidae	1
Arcidae	28	Thyasiridae	3	Undulinidae	1
Semelidae	28	Latemulidae	3		
Pharidae	24	Ungulinidae	3		
Ostreidae	24	Cyamiidae	2		
Pinnidae	22	Cyrenidae	2		
Pteriidae	14	Lucinidae	2		
Mesodesmatidae	12	Lyonsiidae	2		
Solenidae	11	Solecurtidae	2		

Chapter 2:

High latitude settings promote extreme longevity in fossil bivalves

Chapter 2 has been prepared in the format of the journal *Paleobiology*. It will be submitted with co-authors Linda C. Ivany, John Schnue, Robert B. Silver, and Emily Artruc.

Abstract

The longest lived, non-colonial animal on the planet today is a bivalve that can attain lifespans in excess of 500 years and lives in a cold, seasonally nutrient limited setting. Separating the influence of temperature and food availability on lifespan in modern settings is difficult, as the two covary. Fortunately, the lifespans 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. Earth's deep past encompasses a range and combination of environmental conditions not currently represented on the surface today, thus providing opportunities to test hypotheses about how particular variables might relate to life history. Here we examine bivalves from the unique, non-analog, warm and high-latitude setting of Seymour Island, Antarctica, during the greenhouse intervals of the late Cretaceous and Eocene. All ten species we examine here are both slow growing and long-lived, especially when compared to modern bivalves living in similar temperature settings. Cool temperatures have long been thought to be a key factor in promoting long lifespan, but our findings suggest an important role for caloric restriction driven by the low and extremely seasonal food availability at high latitude settings. Our life history data, from multiple species across three different families of the Bivalvia that otherwise do not typically exhibit long life, emphasize that longevity is at least in part governed by environment, rather than phylogenetic or ecologic factors particular to a given taxon. 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 and longer generation times that limit the potential for evolutionary change. While lifespans of modern bivalves are well studied, data on lifespans of fossil bivalves are sparse and largely anecdotal, although

methods for ontogenetic age determination have been in practice for over half a century. Life histories of organisms from deep time can not only elucidate the controls on lifespan, but will also add a new dimension to our understanding of macroevolutionary patterns.

Introduction

What controls lifespan? Today, the longest-lived, non-colonial animal on the planet is the ocean quahog, *Arctica islandica*, with a maximum reported lifespan of 507 years (Butler et al. 2013, Wanamaker et al. 2008). Along the Atlantic Coast of the United States, 200-year-old individuals of *Arctica* are common, but thus far, individuals of 300 years or older have only been found off the coast of Iceland and northern Norway (Butler et al. 2013, Mette et al. 2016, Schöne et al. 2011). The pattern of longer lifespans 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 lifespan. Water temperature and food availability (driven by the extremely seasonal light regime in polar settings) covary with latitude so separating their influence is difficult. Fortunately, Earth's history offers a range of conditions far broader than those that exist on the planet today, including non-analog settings that present opportunities to deconvolve these two factors and test hypotheses related to the role of environment in bringing about extreme longevity.

Here, we use the skeletal archives of fossil bivalves from just such a non-analog 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 low and seasonal availability of food resulting from extended periods of no sunlight may be the driving factor behind the link between latitude and lifespan. Our findings suggest that latitudinal patterns in life history traits may be a persistent feature throughout the Phanerozoic, and that they have 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. Being one of the very few places in the high southern latitudes where Meso-Cenozoic fossiliferous sediments are exposed, the stratigraphy, paleontology, and paleoclimate history of the island's sedimentary record have been well studied (see sources in Feldmann and Woodburne 1988 and those cited below). The Cretaceous and Paleogene marine section includes three formations consisting mostly of sands, muds, and shell beds. The Lopez de Bertodano and Sobral Formations are exposed on the southern portion of the island and represent one of the most expanded K-Pg sections currently known (Marshall 1995, Tobin et al. 2012, Witts et al. 2015, Witts et al. 2016, Zinsmeister et al. 1989). 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 (Macellari 1988, Zinsmeister 1982). The Eocene La Meseta Formation is a shallow-marine succession that overlies the dominantly non-marine Cross Valley

Formation (Porebski 1995, 2000, Sadler 1988). A thorough investigation of Mesozoic and Cenozoic molluscan systematics has documented several hundred species (e.g., Beu 2009, Macellari 1984, 1988, Stilwell and Zinsmeister 1992, Tobin and Ward 2015, Tobin et al. 2012, Witts et al. 2015, Zinsmeister 1984, Zinsmeister et al. 1989, Zinsmeister and Macellari 1988).

Global greenhouse climates prevailed throughout the Cretaceous and Paleogene periods. Pole to equator temperature gradients were low (Hay and Floegel 2012, Huber and Sloan 2001) and the high latitudes were relatively warm and largely ice free until the Eocene-Oligocene transition (Zachos et al. 2001, Zachos et al. 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 5-17 °C (Douglas et al. 2014, Dutton et al. 2007, Dutton et al. 2002, Francis and Poole 2002, Ivany et al. 2008, Kemp et al. 2014, Tobin et al. 2012). 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, but where waters were comparatively warm and ice-free (Buick and Ivany 2004).

Determination of bivalve lifespans

Bivalves have accretionary and indeterminate growth and, akin to trees, record not only their size at each year of growth throughout their ontogeny, but also the environmental conditions in which they lived (e.g., Beierlein et al. 2015, Jones 1983, Lutz and Rhoads 1980, Pannella and MacClintock 1968, Rhoads and Lutz 1980, Rhoads and Pannella 1970, Schöne and Gillikin 2013). 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 slow- or shut-downs 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 and provide much more accurate age estimates if the periodicity of formation is known. At least five different types of periodic growth bands have been documented: semi-daily, daily, fortnightly, monthly, and annual (e.g., Clark 1974, Goodwin et al. 2001, Pannella 1976, Richardson et al. 1980, Schone et al. 2005).

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 1980, Jones et al. 1978b, MacDonald and Thomas 1980, Peterson et al. 1983, Sejr et al. 2002a). The downfall of mark and recapture studies is that frequent sampling is required in order to accurately determine periodicity of formation and the limit to constraining the timing of formation is directly related to the interval between observations. An alternative route, which is particularly useful for fossil bivalves, is to sample

ontogenetic variations in the oxygen isotope value of bivalve shell carbonate (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. 1978b, Thompson et al. 1980). These methods have been successfully applied to not only modern (just to name a few Hallmann et al. 2008, Jones et al. 1989), but also fossil bivalves (e.g., Buick and Ivany 2004, Ivany and Runnegar 2010, Jones and Gould 1999).

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., Ambrose et al. 2011, Brey and Mackensen 1997, Lomovasky et al. 2002, Sejr et al. 2002b, Witbaard et al. 1994). 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* from the Eocene of Seymour Island, Antarctica, and Beard et al. (2015) and Ivany and Runnegar (2010) do 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 formed annual bands as well.

Materials and Methods

Ten 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*, *Nodenskjoldia nodenskjoldia*, and *Lahillia larseni* from the Cretaceous, and *C. raea*, *C. donaldi*, *Eurhomalea antarctica*, *E. newtoni*, *Eumarcia robusta*, and *L. wickensi* from the Eocene. These ten 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 10 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 bivalve fauna in general. Specimens used for analysis were drawn from collections at the Florida Museum of Natural History (FMNH), the Paleontological Research Institution (PRI), and Syracuse University (SU).

Lifespans and growth rates are determined through examination of annual bands as revealed in cross section. In order to prevent damage to the shell (and loss of data) during cutting, individuals selected for sectioning were imbedded in an epoxy resin before cross-

sectioning along the maximum growth axis with a Buehler Iso-Met 1000 low speed saw. 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 discs and finished with 1.0 and 0.05 micron aluminum oxide powder to yield a smooth glassy surface, and images were captured under plane white light with an AxioCam ERc5s camera coupled to a Zeiss Discovery V.8 stereomicroscope at 1.25x magnification. One specimen of *E. antarctica* was prepared by staining with Mutvei's solution, a procedure common in the field of sclerochronology and outlined in Schöne et al. (2005). Images for this specimen were captured using a Nikon Coolpix 995 digital camera mounted to a Wild M3 stereomicroscope at 10x 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 lifespan and growth rate of each individual. Because bivalve shells have some degree of curvature in their thickness, 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 allows us to compare growth curves from cross-sections with sizes of individuals measured using calipers in museum collections.

As the methodology for recovering lifespan 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 estimate 'maximum' longevity for these taxa. In order to put our data into context of the population and get closer to this objective, we also measured the maximum height (dorsal to ventral distance) of all individuals present in the three collections. In total, we sectioned 34 individuals and measured 1,058 intact shells from 10 different species. Care should be taken not to over interpret size distributions. While 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 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 to them in terms of size.

Growth rates of modern bivalves have been shown to correlate with longevity (Moss et al. 2016, Ridgway et al. 2011a) through their relationship with metabolic rate (Camus et al. 2005, Speakman 2005). They are therefore a crucial component of any analysis of lifespan 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 modified von Bertalanffy growth equation (MVBG):

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

where L_t = shell length at time t , L_∞ = asymptotic size, or the size at which growth rate is essentially zero, and k = rate at which L_∞ is attained. The standard form of the von Bertalanffy growth equation (von Bertalanffy 1938) contains an additional term, t_0 , which is the size of the organism at age 0, or in other words, where the growth curve crosses the x-axis. For organisms such as whales with substantial size at birth, this term is appropriate, but bivalve size at 'birth' is essentially zero, hence the term is unnecessary. There is little difference in parameter values of the modified and standard form of the equation fitted to individuals in our samples. Here, we report all MVBG parameters for each of the cross-sectioned individuals and examine the relationship between k and lifespan for these fossil taxa. We compute mean growth curves for each taxon by averaging von Bertalanffy parameters for all individuals. Finally, we compare k values of Seymour Island taxa to those of modern bivalves distributed across latitude and temperature as compiled by Moss et al. (2016) so as to identify where in the distribution of values from modern bivalves the Seymour fossil taxa best fall.

Because methods for precisely determining the age of bivalves require cross-sectioning to reveal internal growth bands, we explore methods of estimating age from size measured with calipers. The von Bertalanffy growth equation is typically written with age as the dependent variable and size as the independent variable. However, the equation can be solved algebraically such that size (L_t) is the predictor and age (t) is the response variable:

$$t = (-1/k) * (\ln(1 - (L_t / L_\infty)))$$

Thus, given a von Bertalanffy growth equation established from some sample of individuals, age can be estimated from a simple size measurement of un-sectioned individuals. However, a few non-trivial issues arise when using this approach. First, predictions from the von Bertalanffy

growth equation are deterministic. That is, all ages predicted using the equation will necessarily fall on the line it establishes. As a result, any natural variation in age at size in the original population is lost. Second, and perhaps most important, is that for sizes (L_t) that are greater than L_∞ , age cannot be predicted, as the equation would call for taking the natural log of a negative number, a mathematically invalid operation. This could result in significant numbers of individuals for which age cannot be estimated from size. 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 typically removed from analyses (e.g., Dexter and Kowalewski 2013) and age estimates for those less than L_∞ are recognized as "crude" (Ridgway et al. 2014). Both approaches are wholly unsatisfactory.

We explore two alternative methods for aging shells by size alone using both cross-sectioned and measured individuals of *Cucullaea raea*, the species for which we have the greatest number of cross-sectioned individuals. In the first method to avoid issues created by L_∞ , we use three different von Bertalanffy growth curves derived from age-size relations in sectioned individuals to predict ages for measured museum specimens: the mean of parameters from all 11 individuals and the parameter values from the individuals with the largest and smallest L_∞ value. The three curves were then used to predict ages for individuals less than or equal to their L_∞ values. Our second approach avoids the deterministic nature of von Bertalanffy growth equations and instead uses a probabilistic approach to the age-at-size problem. We model the theoretical age/size distribution for *C. raea* using the linear relationship between logged values of k and L_∞ from sectioned individuals. From these

modeled values, we 'grew' 50,000 individuals of *C. raea* to the maximum lifespan reported here and then constrained the age distributions for each size in the population. Finally, we assigned ages to each measured individual by selecting at random an observation from the appropriate age/size distribution. We compare the resulting age histograms for measured individuals using the two approaches.

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 lifespans 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 *E. antarctica*) also reveal sub-annual growth banding, providing attractive prospects for high resolution intra-annual studies (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 (Fig. 2).

All of the species examined reached ages greater than 20 years, and nine of the ten had lifespans greater than 50 years (Table 1). *C. raea*, *C. antarctica*, and *N. nodesnkjoldia* record maximum measured lifespans of 120, 101, and 131 years, respectively. 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 lifespans documented here should be considered minimum estimates for that potentially attained by their taxa.

Growth Parameters

Values for the parameter k (the growth constant) of the MVBG equation range from 0.05 to 0.37 (Table 1). There is a relationship between k and lifespan in the Seymour bivalves, with slower growing individuals living longer than faster growing individuals (Fig. 3). While sample size is small, there is a tendency for this pattern to hold true within species as well as across. 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).

Age from size in C. raea

Using the three different modified von Bertalanffy growth equations, 10 of the 163 measured individuals were unable to be assigned an age because their lengths were greater than the maximum L_{∞} value. For those that could be assigned, their ages were constrained to each of

the three curves (Fig. 5A). The maximum age that can be predicted for each curve is that at which the curve essentially reaches L_{∞} . Predicted ages from measured individuals are significantly less than the actual ages of sectioned individuals of almost identical size. The resulting age distribution of all measured individuals using this approach predicts a large number of very young *C. raea*, with only one individual greater than 40 years old (Fig. 5C), highly unlikely given that some sectioned shells demonstrably attained ages of over 100 years.

The probabilistic approach yields more satisfactory results. Because age predictions here are not constrained by the L_{∞} of any of the three curves, there is much more variation in predicted ages at any given size in the population (Fig. 5B). This variation also approximates the natural shape expected in the age-size relationships of *C. raea*. In addition, this approach avoids the ‘ L_{∞} problem’ and all measured individuals are able to be assigned an age. The distribution of predicted ages here shows fewer short-lived individuals and is more right skewed than that using only the three modified von Bertalanffy growth curves (Fig. 5D).

Discussion

Limitations and Assumptions

We face two non-trivial problems when using fossil (or modern) shells from existing collections to study lifespan and growth. 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 the maximum observed lifespans for the ten species examined here are surely underestimates. In addition, some species, like *N. nodenskjoldia*, 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 lifespan, but it is also true of growth rate, as even in our small samples there is a significant variation in von Bertalanffy k values. 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 'maximum lifespan' itself, whether it be based on direct measurement from specimens or calculated from an age-size relationship. Lifespan 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 oldest individuals will almost never be sectioned. One is therefore left with inferring an age for the largest available specimens based on the relationship between shell growth and age seen in one or a few sectioned specimens. Slow growth over many years though, as is typical of the longest-lived taxa, obfuscates the determination of age from size, for a few millimeters of growth near the margin could represent many decades (e.g., in Figure 2A, the last 5 millimeters of growth in *L. larseni* represent almost 20 of the 39 years of its full lifespan). Maximum age cannot be estimated simply by using the von Bertalanffy growth equation either because, as discussed above, the ' L_{∞} problem' combined with restrictions on destructive sampling nearly always prevents age predictions for the largest individuals. However, the probabilistic methods

for estimating age from size described here may provide some relief. Modeling a significant number of values for growth parameters should ensure that the entire theoretical age/size distribution is captured and thus age can be predicted for any size. Note though, that predicted ages are probabilistic and change with each iteration such that a range of ages is produced for any individual. Using the probabilistic approach with *C. raea* reveals an age distribution that suggests the common occurrence of 'old' individuals. In other words, the individuals we selected for cross-sectioning were not outliers in the population, and it is likely that shells in that size range routinely attain ages well over 50 years.

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 Recent taxa can attain lifespans in excess of 50 years, the modal value of maximum reported lifespan for bivalve species today is three years (Moss et al. 2016). The shortest-lived species from Seymour Island reached lifespans 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 high as 3, while the sectioned Seymour specimens all revealed k values <0.4 , 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 lifespan seen in modern populations is also apparent: those exhibiting slower growth tend to have lived longer lives.

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 lifespans, and growth universally slows until k values at high latitudes are nearly all less than 0.5. The Seymour Island taxa examined here plot within the range of lifespans and k values exhibited at high latitudes today (Fig. 6A), consistent with a high-latitude position (64° S) that has changed little if at all over the past 100 million years (e.g., Lawver et al. 1992, Norton and Sclater 1979, Torsvik et al. 2008).

Despite a general decrease toward the poles, a wide range of k values is evident at any 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 a modern global dataset of k values published elsewhere (Moss et al. 2016). We draw at random, without replacement, 34 observations from the available data within a twenty-degree 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 twenty-degree latitude window by 1° of latitude from equator through to the poles, each time drawing k values and calculating means 1000 times, then plot those means against latitude for comparison to the fossil data (Fig. 6B). For each random draw, we also assess the significance of the difference between the fossil versus modern k values in that latitude bin using a t-test for independent samples. Results from the t-tests show that insignificant tests (no difference between the means of randomly sampled and Seymour Island k values)

predominate in latitude bins with midpoints greater than 60° (Fig. 6C). These results confirm that the life histories of fossil taxa are consistent with those of modern high-latitude taxa, despite the substantial difference in the thermal environment in which they are each living.

The bivalve fauna of Seymour Island is diverse and includes species with a range of ecologies. As modal lifespan 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 slower 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 lifespans 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 (see below). In addition to physiology, ecology could also be a driver of long lifespan. 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 lifespan and growth rate (Moss et al. 2016; Fig 3), those taxa would also likely have short lifespans in

comparison to those 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, Freestone et al. 2011, Schemske et al. 2009, Visaggi and Kelley 2015), the pattern may not be as clear as once thought (e.g., Dudley and Vermeij 1980, Harper and Peck 2016, Kelley and Hansen 2007, Vermeij et al. 1989). We elaborate below 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 numerous 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 lifespan (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 longevity could be facilitated by slow growth and correspondingly low metabolic rates. Metabolism, in turn, 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 (Berke et al. 2013, Moss et al. 2016, Roy et al. 2000) 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 (Clarke et al. 2004, Peck et al. 2006, Sato-Okoshi and Okoshi 2007, Vladimirova et al. 2003). Though the Seymour Island fossil taxa lived in relatively warm water, their k values are a good deal lower than those of mid latitude (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 lifespans (e.g., Austad 1989, Brandhorst et al. 2015, Colman et al. 2014, Fanestil and Barrows 1965, Klass 1977, Lakowski and Hekimi 1996, McKay et al. 1935, Verdone-Smith and Enesco 1982, Woodhead 1985). For bivalves living on the seafloor, their primary food sources come from phytoplankton and suspended food particles in the water column. Because of the tilt of the Earth's axis, high latitude settings are characterized by extremely seasonal light regimes, with the majority of their sunlight received during an approximately four month period. In the Antarctic today,

phytoplankton and other suspended particles are only available in appreciable quantities during this four month period (Peck et al. 2006).

The low and extremely 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., Brodte et al. 2006, Burchett et al. 1984), brachiopods (e.g., Brey et al. 1995, Peck et al. 1997), gastropods (e.g., Clarke et al. 2004, Picken 1980), and bivalves (e.g., Brey and Hain 1992, Brey et al. 2011, Philipp et al. 2006) are all extremely 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 extremely 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 is likely the more important factor promoting the slow growth and long life of the Seymour Island taxa.

While physiology affects lifespan 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 shell to offer protection from

predators. Today, predation frequencies in the Antarctic are extremely low and predation events often take much longer to complete than in more temperate waters. The 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 1,000 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 Hiatellidea, 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 lifespan 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 lifespan typical of its populations. These

observations make 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 lifespan 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 relationship between latitude and lifespan, and latitude and growth rate, exhibited on the modern Earth requires a set of causes that vary systematically with latitude. As discussed above 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° to 1° C (Locarnini et al. 2013). In addition, Aronson et al. (1997) and Aronson et al. (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. 6). 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 may be characterized by slow growth and extreme longevity throughout Earth's history. Today, the longest lived bivalve on the planet attains lifespans in excess of five centuries and lives in cold, seasonally food limited, high latitude settings. Similarly, during the Cretaceous and Eocene, several bivalves attained lifespans 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 one of the most pervasive patterns of life on the planet; in almost all animal groups, in both marine and terrestrial settings, species diversity decreases with increasing latitude (Hillbebrand 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, Sato 1999 for a possibility), a correlate of long life is delayed reproduction (Ridgway et al. 2011a). 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 geochemical tools to study lifespans 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 non-analog, 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 lifespan? The life history data from these fossil shells, in concert with a much larger database of bivalve lifespans and growth rates, suggest that the pattern of increasing lifespan with latitude on the planet today is likely a result of low and 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 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 their 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 lifespans and growth rates of fossil organisms and connect them to macroevolutionary studies.

Tables

Table 1. Lifespans (LSP, years) and von Bertalanffy growth parameters of species examined.

Oldest individuals of each taxon are indicated in bold.

Family	Species	Period/Epoch	Specimen #	LSP	k	L_{∞}
Cucullaeidae	<i>Cucullaea antarctica</i>	Cretaceous	PRI 583113	101	0.07	57.52
	<i>Cucullaea donaldi</i>	Eocene	SU 01-56-C2	55	0.26	47.05
			SU 01-53-C3	50	0.26	34.97
			SU 01-56-C1	36	0.27	43.78
			SU 03-012	34	0.08	50.47
			SU 01-85-C1	18	0.22	33.98
			<u>SU 02-82-C1</u>	<u>15</u>	<u>0.39</u>	<u>45.95</u>
			Mean		0.25	42.70
	<i>Cucullaea ellioti</i>	Cretaceous	PRI 58448	36	0.22	46.21
			<u>PRI 62371</u>	<u>35</u>	<u>0.10</u>	<u>40.45</u>
			Mean		0.16	43.33
	<i>Cucullaea raea</i>	Eocene	UF 124613-I	121	0.15	75.62
			SU 01-43-C3	118	0.10	84.29
			SU 001-C2	108	0.09	81.16
			SU 01-43-C2	102	0.20	79.83
			UF 124605-I	90	0.12	88.44
			SU 001-C1	73	0.13	83.51
			SU 01-43-C1	65	0.08	90.59
			SU 01-28-C1	43	0.15	93.27
			UF 124605-III	38	0.20	77.52
			SU 01-42-C2	36	0.13	76.54
<u>UF 124605-II</u>			<u>31</u>	<u>0.33</u>	<u>77.33</u>	
Mean				0.15	82.55	
<i>Cucullaea</i> sp.	Eocene	SU 01-54-C2	92	0.11	35.51	
<i>Nodenskjoldia nodenskjoldia</i>	Cretaceous	PRI 61339-B	131	0.05	61.41	
		<u>PRI 61339-A</u>	<u>47</u>	<u>0.29</u>	<u>49.22</u>	
		Mean		0.17	55.32	

Table 1. Cont'd.

Family	Species	Period/Epoch	Specimen #	LSP	k	L_{∞}
Lahilliidae	<i>Lahillia larseni</i>	Cretaceous	PRI 58774	58	0.16	85.35
			<u>PRI 60667</u>	<u>39</u>	<u>0.18</u>	<u>82.16</u>
			Mean		0.17	83.76
	<i>Lahillia wilckensi</i>	Eocene	PRI 59522	71	0.19	78.85
			<u>PRI 59425</u>	<u>55</u>	<u>0.29</u>	<u>95.05</u>
			Mean		0.24	86.95
Veneridae	<i>Eumarcia robusta</i>	Eocene	PRI 62912	38	0.05	80.55
	<i>Eurhomalea antarctica</i>	Eocene	SU 01-43-E3	83	0.04	34.76
			UF 124959-II	35	0.15	56.83
			UF 124961-I	31	0.30	63.39
			<u>PRI 59548</u>	<u>26</u>	<u>0.21</u>	<u>60.81</u>
			Mean	43.75	0.18	53.95
	<i>Eurhomalea newtoni</i>	Eocene	PRI 58961	22	0.33	45.19
			<u>PRI 59658</u>	<u>11</u>	<u>0.24</u>	<u>42.85</u>
			Mean		0.29	44.02

Figures

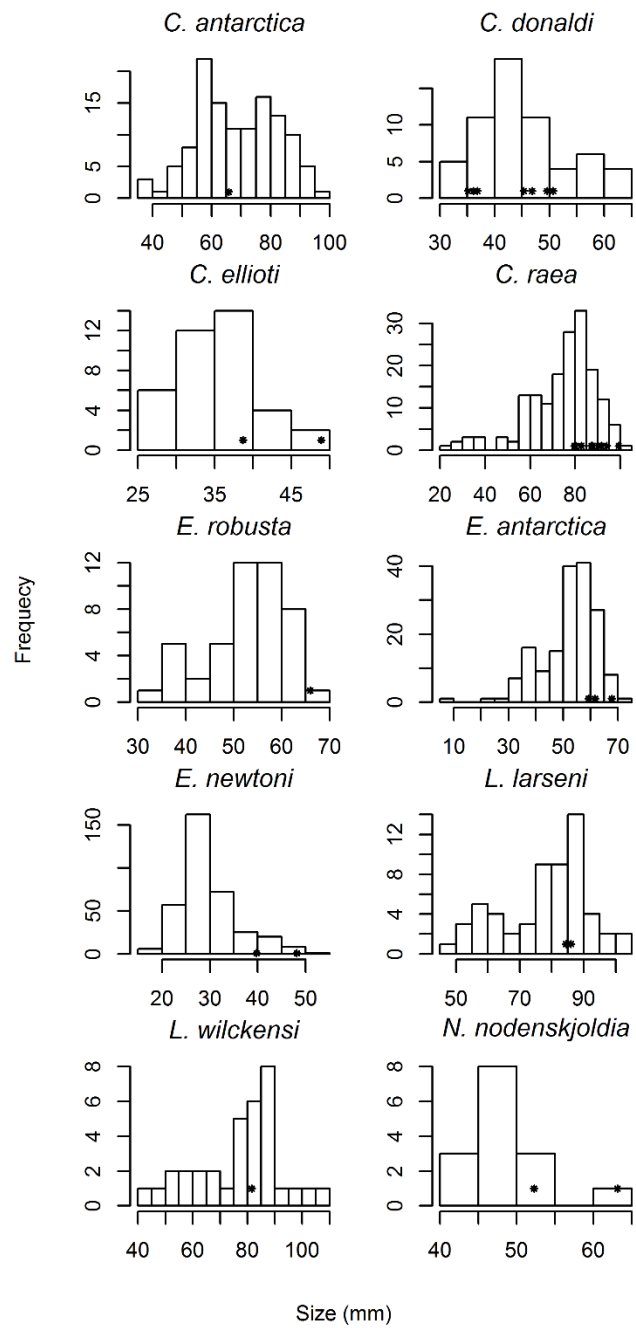


Figure 1. Umbo-to-commissure sizes of individuals measured in museum collections. * = size of cross-sectioned individuals.

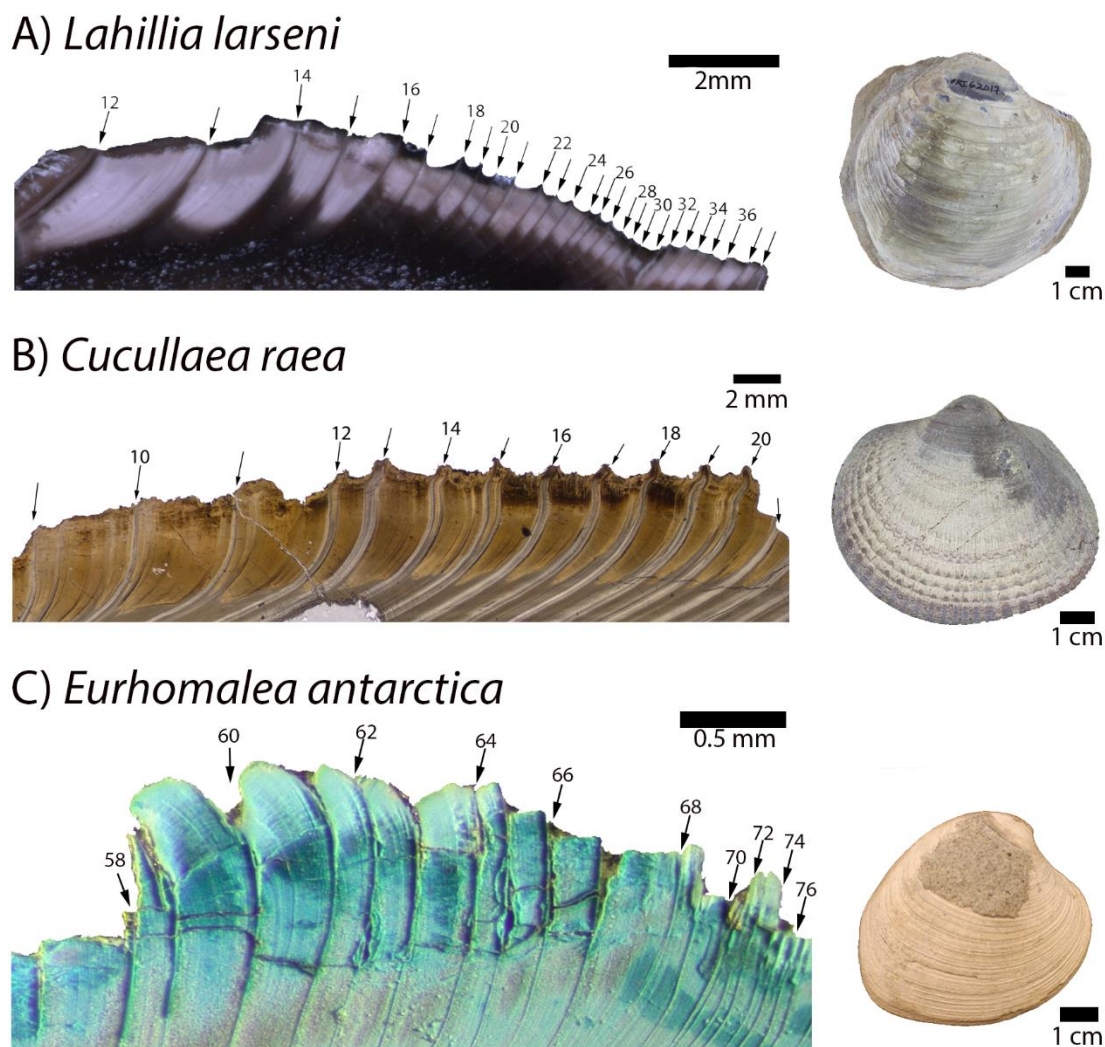


Figure 2. Annual growth banding in three species of Seymour Island bivalve. Shell cross sections encompass portions of their ontogenies, with years of growth indicated above the shell.

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) (*Eurhomalea antarctica*, Eocene).

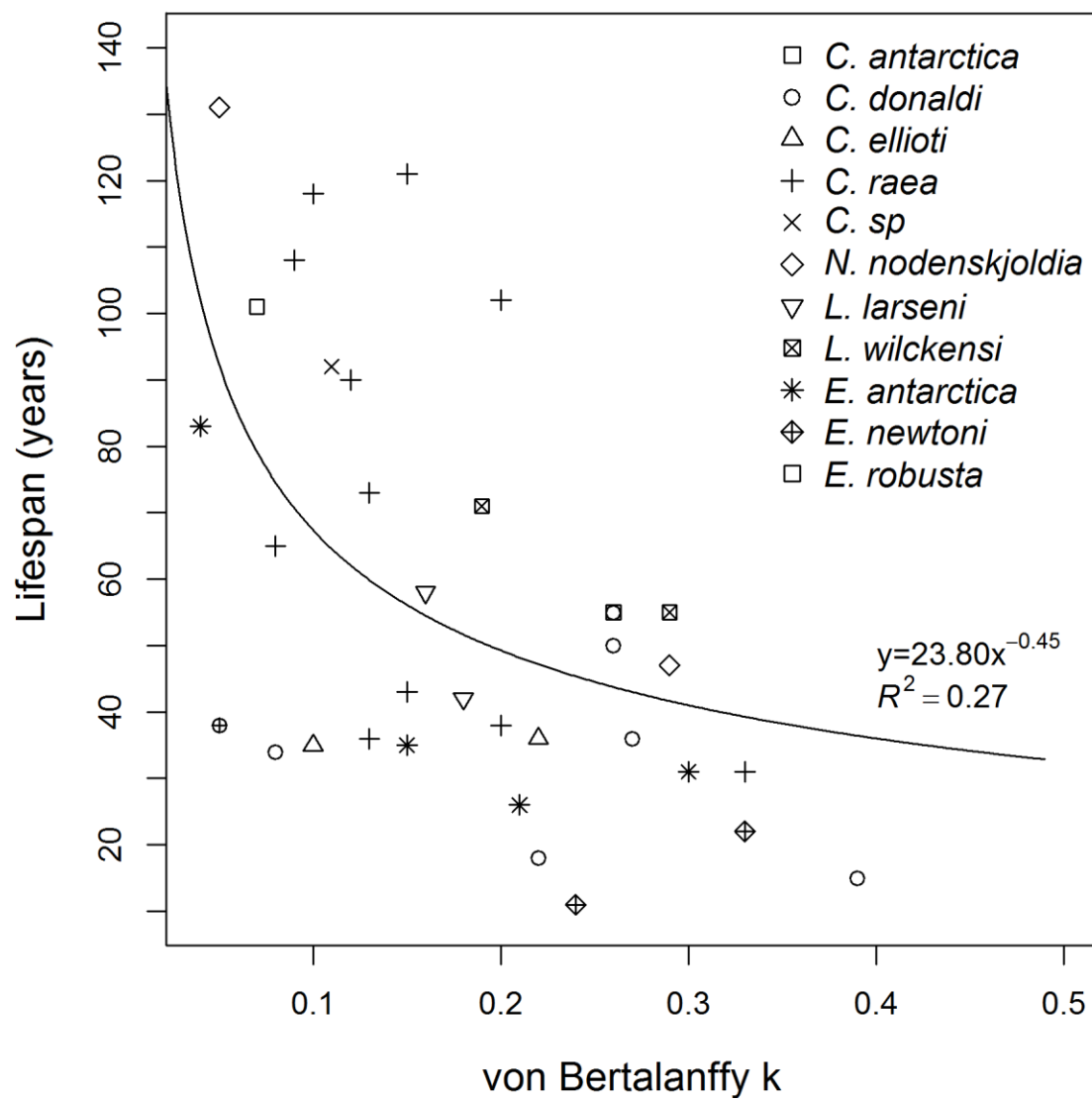


Figure 3. Relationship between growth rate (k) and lifespan in Seymour Island taxa ($p < 0.01$).

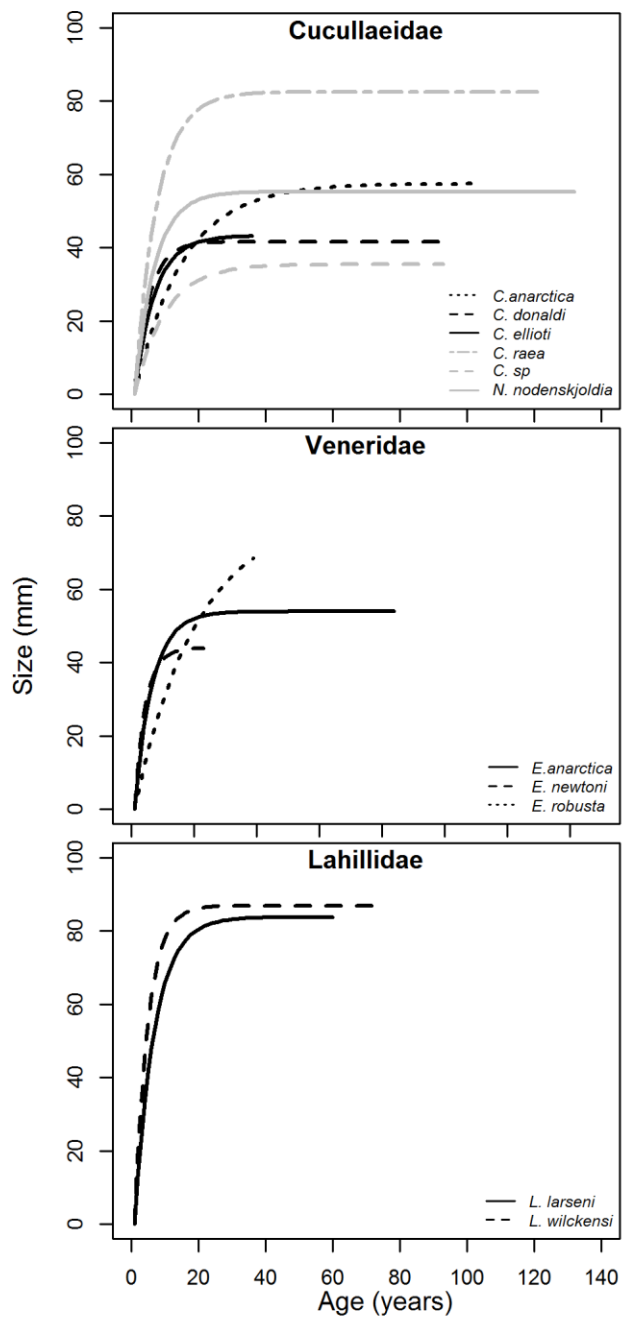


Figure 4. Growth curves for eleven taxa using the mean von Bertalanffy growth parameters in Table 1. Growth curves are extended to the maximum recorded age for species.

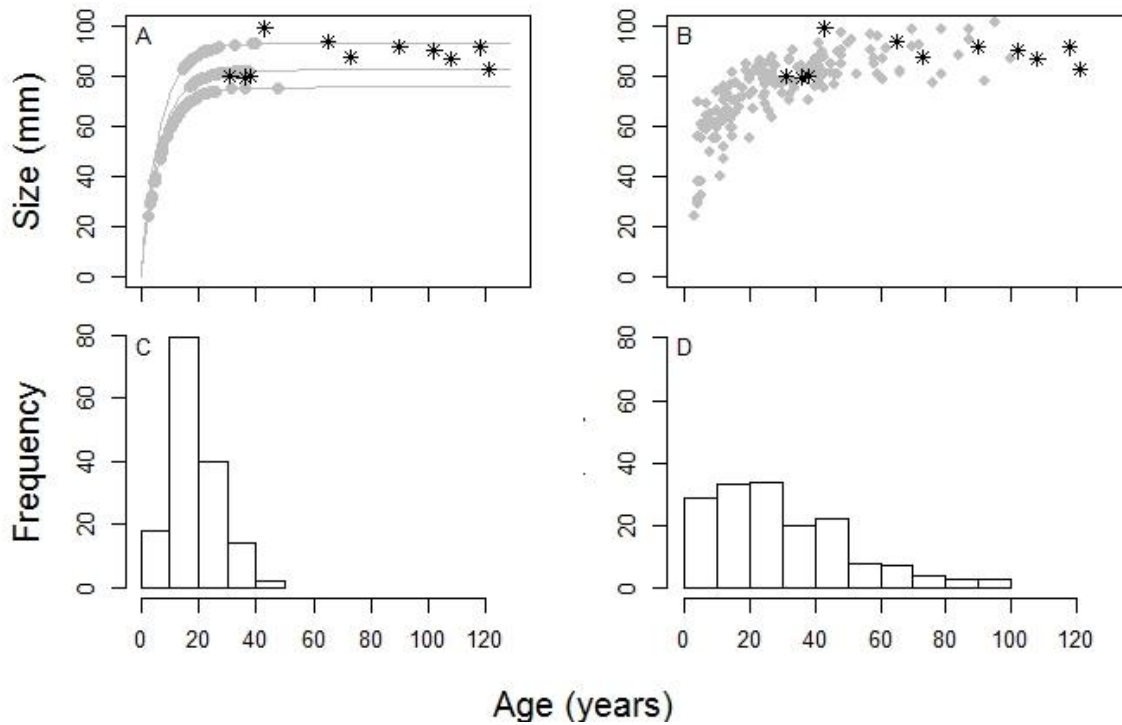


Figure 5. Results of two different methods of predicting age from size in measured individuals of *Cucullaea raea* (see Fig. 1 for size distribution). A) and C) predictions from three von Bertalanffy growth curves. B) and D) predictions from probabilistic method. * = actual age size relationships from cross sectioned individuals. ● = predicted ages from sizes of specimens measured in museum collections.

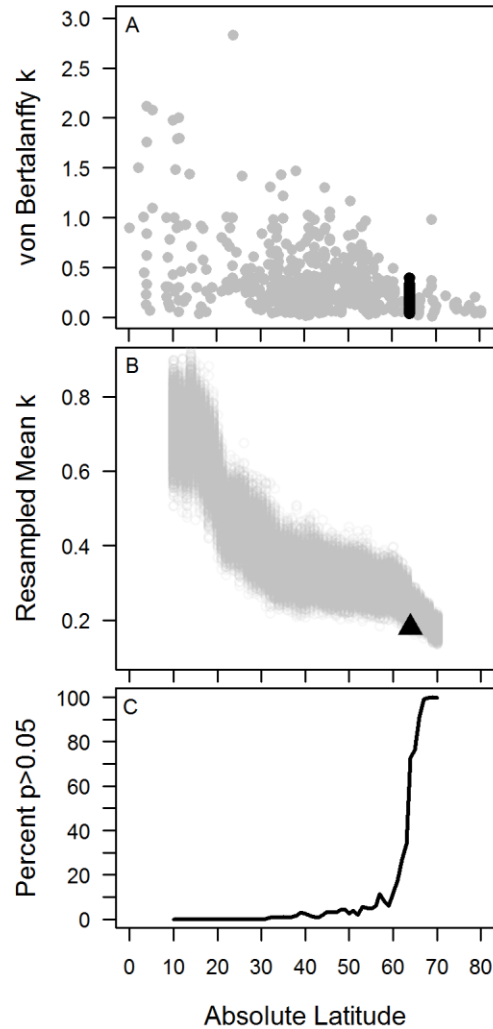


Figure 6. Growth rate of Seymour Island fossil bivalves in comparison to modern bivalves plotted by absolute (paleo)latitude. A) Growth rates (k) of modern bivalves (gray; Moss et al. 2016) and Seymour Island individuals (black) B) Mean of resampled k values for 20° bins with a 1 degree moving window for 1000 iterations (grey) 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 degrees of latitude.

Chapter 3:

Estimating von Bertalanffy growth parameters using a probabilistic approach to the age-size relationship in *Spisula solidissima*

Abstract

Obtaining population life history parameters such as lifespan and growth rate from bivalves requires cross-sectioning large numbers of individuals to reveal internal growth bands. Such methods are often time intensive and not possible with species that are endangered or with specimens from hard to access locations. One of the most common equations for describing bivalve growth, the von Bertalanffy growth equation, has significant limitations when predicting age from size and typically results in the largest specimens in a population being excluded from analysis. To circumvent this problem, we develop probabilistic methods to determine age from size using a modern data set of *Spisula solidissima*. Our model uses the relationship between parameters of a modified von Bertalanffy growth equation to constrain the theoretical age/size distributions for a population. From these distributions, ages are assigned by drawing at random from the appropriate age/size distribution. The resulting age/size predictions can then be used to determine population growth rates from a large number of measured individuals.

Introduction

Accurate characterization of life history parameters, such as growth rate and lifespan, in bivalves is vital for both modern resource management and the newly-emerging field of study of life histories in the fossil record (Moss et al. 2016). The former represents a multi-billion dollar industry in the United States, whereas the latter represents a largely untapped field of research in paleobiology. Bivalves record in their shells their size at each year of their life and methods for determining life history parameters of both modern and fossil bivalves are well understood and relatively straight forward to implement (e.g., Ivany 2012, Jones 1983, Jones

and Quitmyer 1996, Pannella and MacClintock 1968). Unfortunately, revealing internal growth bands is a time intensive process and may also require sacrificing live and/or potentially rare individuals. In endangered species (e.g., Hastie 2006) or fossil organisms from localities that are either difficult and/or expensive to access, or are no longer accessible due to anthropogenic influences, such “destructive” sampling is often not feasible or permitted by museum curators. Thus a non-destructive method for determining age from size is needed.

Here we develop a probabilistic approach to estimate age from size using a dataset of modern *Spisula solidissima*. Our approach can be used to approximate growth parameters on a population level without cross-sectioning and counting growth bands of the entire population. We presume that at each size in a population there is a knowable distribution of ages that changes in a predictable manner throughout ontogeny. For example, at small sizes, it is more likely that an individual is of a ‘young’ age than it is an ‘old’ age. The converse is true as well; at larger sizes it is more likely that an individual is of an ‘old’ age than a ‘young’ age. In order to constrain these age/size distributions we first fit a modified von Bertalanffy growth equation (MVBG, see methods) to plots of age versus cumulative growth band width to individuals in our dataset. We then use the relationship between these parameters to model growth in 50,000 *S. solidissima* in order to constrain theoretical age/size distributions. From these distributions, we then assign an age to a specimen of any given size by drawing at random from its corresponding age distribution. We compare the MVBG parameters estimated when using the entire known dataset to that of the predicted age/size relationships. In addition, because our ultimate goal is to only cross-section a small number of individuals and use probabilistic methods to assign age

to specimens measured with calipers, we also explore these methods using sampling procedures with subsets of 5, 15, and 30 individuals from the original dataset.

Background

Determining annual nature of growth bands

While not at the heart of this paper, a brief review of the methods for determining periodicity of bivalve growth band formation is warranted. Though for a much more detailed review, the reader is referred to Pannella and MacClintock (1968), Jones and Quitmyer (1996), Ivany (2012), Schöne and Gillikin (2013) and the references therein. 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). Mark and recapture experiments are one of the oldest methods for determining periodicity of growth band formation. In these studies, specimens are tagged or marked and in some cases caged and observed at set intervals of time (e.g., Jones 1980, Jones et al. 1978b, MacDonald and Thomas 1980, Sejr et al. 2002a). The downfall of mark and recapture studies is that frequent sampling is required in order to accurately determine periodicity of formation as many species record growth bands at a wide range of periodicities (e.g., daily, tidally, annually), and the limit to constraining the timing of formation is directly related to the interval between observations. Recapture rates are often quite low and in one example from the ocean quahog, *Arctica islandica*, of 41,000 marked specimens, only 60 were recovered the following year (Jones 1983). Furthermore, there is also some suggestion that the act of marking and releasing can often result in a disturbance line that

can obfuscate the perceived signal (Clark 1974). Fortunately though, the carbonate in bivalve shells records variation in oxygen isotopes which can be used to determine periodicity of formation. Clear sinusoidal variations in oxygen isotope values between growth bands can indicate annual formation. This phenomenon was first documented in bivalve shells by Williams et al. (1982) and Jones et al. (1983) using the surf-clam, *Spisula solidissima*, from New Jersey. There the authors found that the striking, alternating pattern of opaque and translucent bands revealed in cross-section corresponded to oxygen isotope variations recording seasonal temperatures. In addition, they were also able to understand that shell growth is most rapid in the spring and slows considerably in the winter months. Such studies can confirm the annual periodicity of growth band formation in both modern and fossil bivalves and should be undertaken before the methods described below are implemented.

Spisula solidissima

The data used here come from *Spisula solidissima*, which is commonly referred to as the “surf clam.” This species is a conspicuous component of waters of the northeast Atlantic Coast of the United States and is a large, infaunal, suspension feeder. It is found from the Gulf of Saint Lawrence, Canada to Cape Hatteras, North Carolina in shallow subtidal water depths down to approximately 70 meters in depth (Ropes 1979). While Native Americans and colonials likely consumed surf clams, fishing in earnest began in the late 1800’s and the “modern” industry developed on Long Island, NY with the introduction of power dredging in the 1920’s. Today, an extensive industry exists from the Delmarva Peninsula to Massachusetts with the heaviest fishing off the coast of New Jersey.

Given the existence of an extensive and profitable fishery today, much work has been done on the lifespans and growth rates of *S. solidissima* throughout its geographic range. Twenty year old surf clams are common throughout its distribution. As with other bivalves, there appears to be a latitudinal cline in lifespan (Moss et al. 2016) as individuals from southern waters have maximum reported lifespans around 30 years (e.g., Cerrato and Keith 1991, Jones 1980, Jones et al. 1978a, Weingber 1999), while at the northern limit off Prince Edward Island, the maximum reported lifespan is 37 years (Sephton and Bryan 1990). Such a pattern, however, may not be present in growth rates of *S. solidissima* as it has been heavily impacted by the intense fishing activity off the Delmarva Peninsula (Weinberg and Helser 1996)

Age length keys in fish

Over 70 years ago, Fridriksson (1934) developed Age-length keys (ALKs) to estimate age from size in fish. ALKs are constructed by first taking a subsample of a fish population, recording their size, and determining their ages using growth increments recorded in internal otoliths (see Campana 2001 for review). The proportion of different ages in each length-group (usually 5 mm categories) of the subsample are used to assign ages to all fish in each length-group of the unknown sample (Bettoli and Miranda 2001). There are various methods by which to do this and even within the literature there is debate on which method is most appropriate (Bartoo and Parker 1983, Kimura 1977, Westrheim and Ricker 1978). However, there are several factors which limit the use of ALKs for our purpose here. First, they rely on a large number of initial samples to characterize the age/size relationships of an entire population, which would not avoid the issue of destructive sampling and significant amounts of time.

Second, if there is significant overlap in size among age groups, ALKs tend to be biased and yield unreliable results (Westrheim and Ricker 1978). Finally, the range of sizes for which age can be approximated using an ALK is determined by the original subsample. This means that an individual larger than any length category in the subsample either cannot be assigned an age or is sometimes assigned the age of the largest subsampled specimen. Our goal here is to be able to approximate the age of any individual in a population of bivalves based on a small subsample. Once we have age/size relationships for a large number of individuals, we should be better able to constrain population life history parameters like growth rate. While a simple application of ALKs will not solve our problems, we can borrow some of their methods. Though assignment of age in ALKs is constrained by the original proportions of the subsample, the actual assignment of age to an individual of a given size is stochastic. We must first develop a way to describe the theoretical age distributions at each size that is not limited by the original subsample.

The age at size problem in bivalves

In marine bivalves, one of the most common representations of relations between size and age is the von Bertalanffy growth equation (VBG) (von Bertalanffy 1938):

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

where L_t = shell length at time t ; L_∞ = maximum or asymptotic size, the size at which growth rate is essentially zero; k = rate at which L_∞ is attained; and t_0 = age at which the bivalve has a

size of zero (the x intercept on a plot of size as a function of age). Equation 1 can be applied both at the individual and population levels. For an individual, plots of age versus cumulative growth band width can be fitted for a single individual throughout its ontogeny, whereas for a population, the final age and size of a number of individuals is fit using non-linear least squares regression. Given a VBG for a population Equation (1) can be rearranged such that a prediction of age can be made for an individual of a given size:

$$t = t_0 - (1/k) * \ln(1 - L_t/L_\infty) \quad (2)$$

Equation (2) is deterministic in that there is only one age predicted for a given size. This means that any natural variation around the best fit equation is lost in such predictions. Furthermore, when the length of a measured individual (L_t) is greater than L_∞ the right side of Equation (2) calls for taking the natural log of a negative number which is a mathematically invalid operation. This could result in a large number of individuals which VBG cannot be used to predict age from size (e.g., Bartoo and Parker 1983, Dexter and Kowalewski 2013, Ridgway et al. 2014) and does not alleviate issues caused by ALKs. However, if we can determine the relationship between parameters of the VBG, we should be able to use those to model growth in a large number of individuals to constrain the potential age/size relationships.

Methods

Assigning Age from Size using MVBG

The dataset contains a total of 321 individuals of *Spisula solidissima* collected near Barneat Light and Point Pleasant New Jersey in the late 1970s from commercial fishing vessels. The data are divided into inshore (n=149) and offshore (n=172) populations based on their distance from shore and have been published elsewhere (Jones et al. 1978a, Jones et al. 1983). For each population, a modified form of the von Bertalanffy growth equation (MVBG) is used to approximate growth:

$$L_t = L_\infty(1 - e^{-k(t)}) \quad (3)$$

thus omitting the t_0 parameter found in the standard form (1). This parameter essentially controls where the curve intercepts the x-axis and can be thought of as the size at birth. In organisms like fish and whales that have a meaningful size at birth its use is appropriate, but for bivalves, whose size at settlement is extremely small, this is a numerically-meaningless term.

Our first step was to fit a modified MVBG to the cumulative growth band widths of all individuals using non-linear least squares regression in R. Despite not having the extra parameter (t_0) R^2 values for both populations are extremely high (mean inshore = 0.97, mean offshore = 0.98) and the MVBG describes individual growth quite well. Our dataset, though containing a significant number of individuals, does not represent the entire age/size distribution theoretically possible for *S. solidissima*. Values of k and L_∞ are lognormally distributed, so in order to model that potential distribution we first determined the best fit linear relationship between logged values of k and L_∞ . To model L_∞ values we use the equation:

$$mL^{\infty} = \left(\sum_{n=0}^1 i = 12 \right) - 6 * (\sigma (\log(L^{\infty})) + \mu (\log(L^{\infty}))) \quad (4)$$

which creates a log normal distribution by adding Gaussian noise to a distribution with a mean and standard deviation of the distribution of L^{∞} values in the dataset. A similar process is used to model values of k but here, in addition to Gaussian noise, we use the best fit linear relationship between logged k and L^{∞} values:

$$mk = \left(\sum_{n=0}^1 i = 12 \right) - 6 * (\sigma (\text{residuals}(k)) + ((-1.15 * (mL^{\infty}) + 1.74))) \quad (5)$$

From these values we modeled clam growth to the maximum age reported for *S. solidissima* from New Jersey (31 years). These curves are somewhat unnatural for *S. solidissima* as the species does not tend to add multiple increments less than 1 mm for a significant portion of its lifespan and are also unrealistic in that 30+ year old individuals of the species are not common (Weinberg and Helser 1996, Weingber 1999). We therefore, introduce a “kill coefficient” to terminate growth of modeled clams. This coefficient terminates the growth of an individual when the addition of an increment results in less than a predetermined amount of growth. As this number could somewhat be construed as arbitrary, we compare results using kill coefficients of 1, 0.5, and 0.25 mm.

The large number of modeled clams gives us a sufficient sample size to examine age distributions of *S. solidissima* throughout its entire theoretical size range. From these distributions, we produced a matrix of ages at every size (rounded to 0 digits) represented in the modeled curves that can be used when assigning age to an individual of any size.

The known dataset of inshore and offshore clam sizes and ages provided an opportunity to test the ability of our method to reconstruct growth parameters for the population from

probabilistic assignments of age from size. To the size of each individual in the original dataset, we assigned an age by sampling at random from the modeled age distribution for that size, which results in new age size relationships. Because this process is probabilistic, the predicted age-size relationships will vary with each iteration. Therefore, we repeated the process of assigning ages for 1000 iterations of both inshore and offshore populations and each time we fit a MVBG to the predicted age-size relationships. We evaluate the ability of our approach to faithfully reconstruct population level MVBG parameters by comparing the mean and standard deviation of predicted k and L_{∞} values to the observed original MVBG values.

How many individuals are needed?

The procedures outlined above use all of the individuals from both inshore and offshore populations ($N=321$) to constrain the theoretical age size distributions for each population of *S. solidissima*. Such a large sample is extremely time intensive to collect and would not be practical for large scale studies of von Bertalanffy growth parameters through time. Therefore we test the robustness of our method by repeating the procedure above with sample sizes of 5, 15, and 30 individuals from the inshore population. For each sample size, we selected at random the number of individuals and then determined the relationship between their logged k and L_{∞} values and used Equations (4) and (5) to model growth of 50,000 clams from which an age at size matrix was produced. Using this matrix, we then assign ages to the sizes of inshore individuals and fit a MVBG to the predicted age-size relationship. After 100 iterations for each sample size we used an ANOVA to compare the means of the predicted distributions of k values using the entire dataset and the sampled runs.

Results

Actual k and L_{∞} values for individuals in the known dataset are lognormally distributed (Figure 1) and there is a significant relationship between the two parameters (Figure 2). Offshore individuals grow slower (have lower k values) and attain larger sizes (have higher L_{∞} values) than inshore individuals. Modeled growth curves with a kill coefficient of 1, approximate the shape of the growth curves for both populations (Figure 3). Most importantly though, they span a significantly wider range of values in sizes at every age in the population. Though not applied directly here, it would allow for us to approximate the age of an individual larger than any in the original sample. As expected, age distributions of this species (and presumably others) change shape with increasing size from right to left skewed. This conforms to the assumption that at small sizes, it is more likely than an individual is of a young than an old age.

While inherent in our model design, but not the ultimate goal, each iteration of our model results in a predicted age distribution. Our sample size in the original dataset is actually relatively small to get a complete picture of an age distribution, but because we run our model for 1000 iterations, we can get a sense of what a population age distributions might look like (Figure 4). The average age predicted for inshore clams is 8.7 years, which is slightly lower than the actual average age of 11.4 years, while the maximum predicted age of 20 years is slightly higher than the actual maximum age of 18 years. Offshore predicted ages on the other hand are more widely distributed than those for inshore individuals. The average age predicted for offshore clams is 12.8 years, which is less than the actual mean of 18.4 years, while the maximum predicted age of 29 years is almost identical to the actual maximum age of 28 years.

Our model then, seems to slightly over predict ages for inshore clams but under predicts for offshore clams.

Though there is some discrepancy in actual and predicted ages for both populations, the predicted k and L_{∞} values for 1000 iterations of assigning age based on size are extremely close to the actual growth curve for each population (Figure 5). In fact, for both inshore and offshore simulated k values, there is a difference of only 0.01 in the mean predicted and the actual k value (Figure 6). Changing the kill coefficient to 0.5, and 0.25 mm resulted in little difference between the predicted and observed k and L_{∞} values. This indicates that our approach to estimating age from size and approximating population growth parameters is robust.

When we repeated our procedure with samples of 5, 15, and 30 individuals and compared distributions of k values from 100 iterations, we found no significant difference between the means of each distribution. However, the standard deviation of each distribution decreased with increasing sample size from 0.10 with 5 samples, to 0.05 with 30 samples (Figure 7). This suggests that a remarkably small sample size can on average predict accurate MVBG parameters for an entire population, but that as expected, with larger sample sizes the range of predicted k values decreases significantly.

Discussion

Much more complex models for approximating von Bertalanffy growth parameters exist but their application to the fossil record would be extremely difficult. Models developed by Hofmann et al. (2006), Hart and Chute (2009), Narváez et al. (2015), and Munroe et al. (2016), and many others account for a wide range of environmental parameters to characterize

growth of bivalve populations. However, the benefit of our model is that it is simplistic. It can be applied to both modern and fossil bivalves independent of any environmental knowledge. Though it is simplistic, results presented here show that our model works remarkably well when predicting von Bertalanffy growth parameters for both populations of *Spisula solidissima*. In both inshore and offshore populations the mean of our k values from age size relationships predicted using probabilistic methods are within 0.01 of the actual value for each population. Previous workers had suggested that offshore *S. solidissima* from New Jersey and elsewhere along the Atlantic Coast grow faster than inshore individuals (Ambrose et al. 1980, Jones et al. 1978a), but our results do not support this claim. The k values, a proxy for how fast L_{∞} is attained, are much higher on average for inshore than offshore clams. Across the bivalvia, k is inversely related to lifespan in that bivalves with higher k values tend to live shorter than those with lower k values. Thus, the much larger sizes attained by offshore *Spisula* are likely a result of their longer lifespans (28 versus 18 years).

One important aspect of our model is that it requires a relatively small number (15-30) of individuals to reproduce accurate von Bertalanffy growth parameters for a population. Not only is this important for studies of modern organisms that are threatened or endangered, such as many of the long-lived freshwater species, but it is also important for studies of life history parameters of bivalves in deep time. Heim et al. (2015) document an increase in the mean body size of marine animals over the Phanerozoic, a trend manifest in bivalves as well. However, no work has been done on the life history parameters, lifespan and growth rate, that ultimately determine body size, though the capabilities to determine the periodicity of bivalve growth bands in the fossil record have existed for quite some time. Other authors have

suggested an increase in organism energetics since the Mesozoic (Bambach 1993, Finnegan et al. 2011, Vermeij 1977), which implies that faster growth may be driving the observed trends in body size. If that is true, then we would expect to see an increase in the von Bertalanffy k values of marine bivalves over this time interval. Our method, in concert with geochemical techniques to determine annual periodicity of growth bands makes a study of k values of this magnitude possible. With only a moderate number of samples from each species and quick size measurements in the field of large numbers of individuals, application of our method can provide not only a mean and standard deviation of k , but also a reasonable approximation of the age distribution.

Though the model works remarkably well for predicting growth parameters, it is not without limitations. One drawback is that a reasonable estimate of the maximum lifespan for a population of species is needed. Today, clear latitudinal patterns in the increasing lifespan and decreasing growth rate both across the bivalvia and within species have been documented (Moss et al 2016). Thus for our model to work with any certainty, a reasonable estimate of the maximum lifespan of the population in question must be known. For modern species that are fisheries targets where population demographics are reasonably known this is not an issue. However, when dealing with fossil species the problem becomes more complex. For more recent intervals in geologic time (e.g., Pleistocene), lifespan estimates from modern taxa could be used but for much older intervals, such estimates may not be useful as lifespan could be a trait that evolves over time.

Conclusions

Determining age from size in large numbers of bivalves using internal growth bands is a time intensive process. Here we have developed a model that uses a small subsample of a population to create theoretical distributions of age for each possible size. In combination with a probabilistic method of assigning age from size, our methods work remarkably well when approximating von Bertalanffy growth parameters for two distinct populations of *S. solidissima*. We have only used our methods on a single species, but the same procedure should be applicable to other species whose growth is described by the von Bertalanffy growth equation as well. Our methods should be of significant use to not only study of endangered species, but also study of growth rate and lifespan of fossil bivalves as well.

Figures

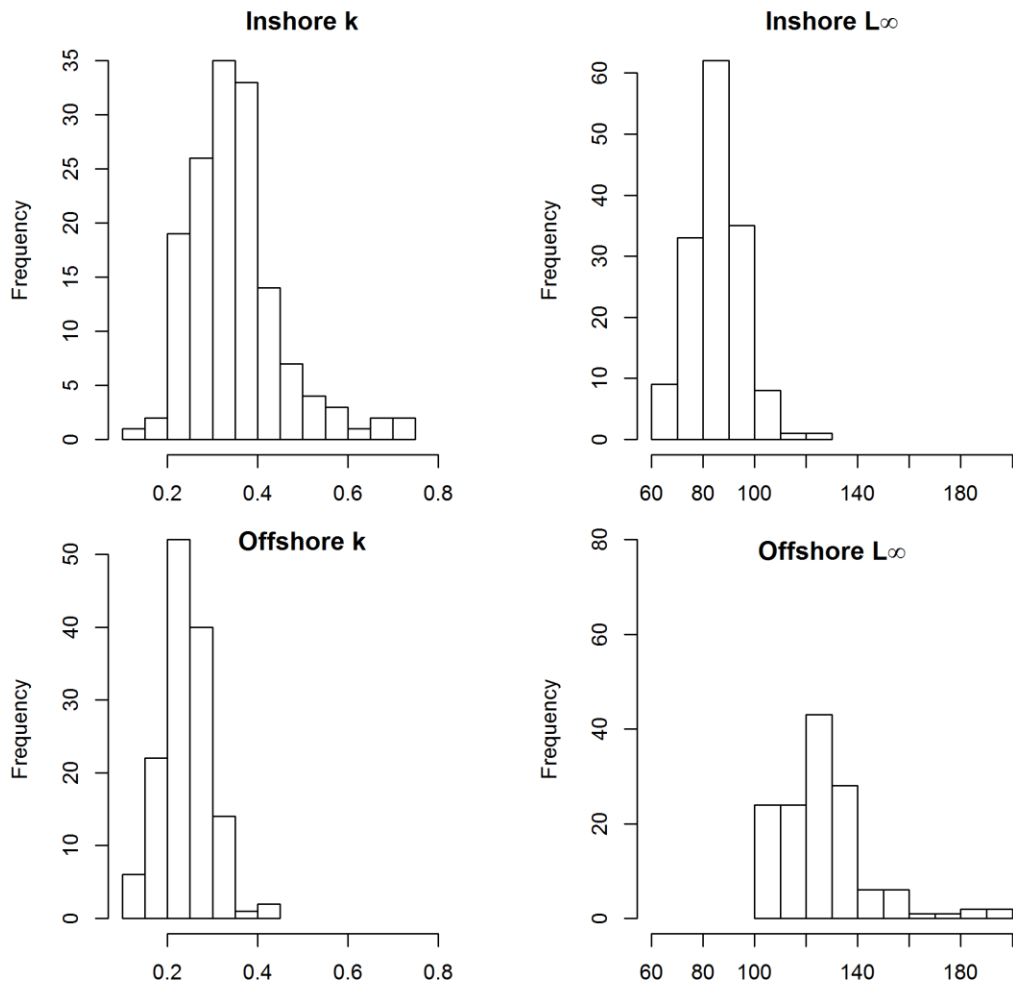


Figure 1. Parameters of the MVBG for inshore and offshore populations of *Spisula solidissima* from New Jersey.

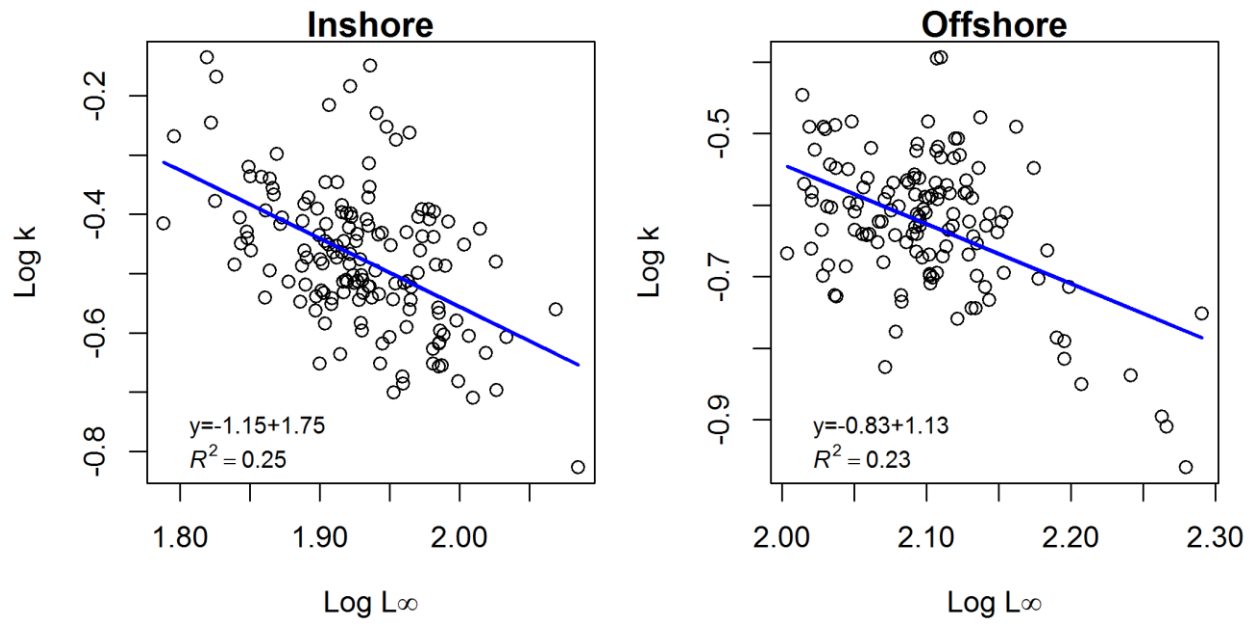


Figure 2. Log-log relationship between k and L_∞ used to model additional MVBG parameters.

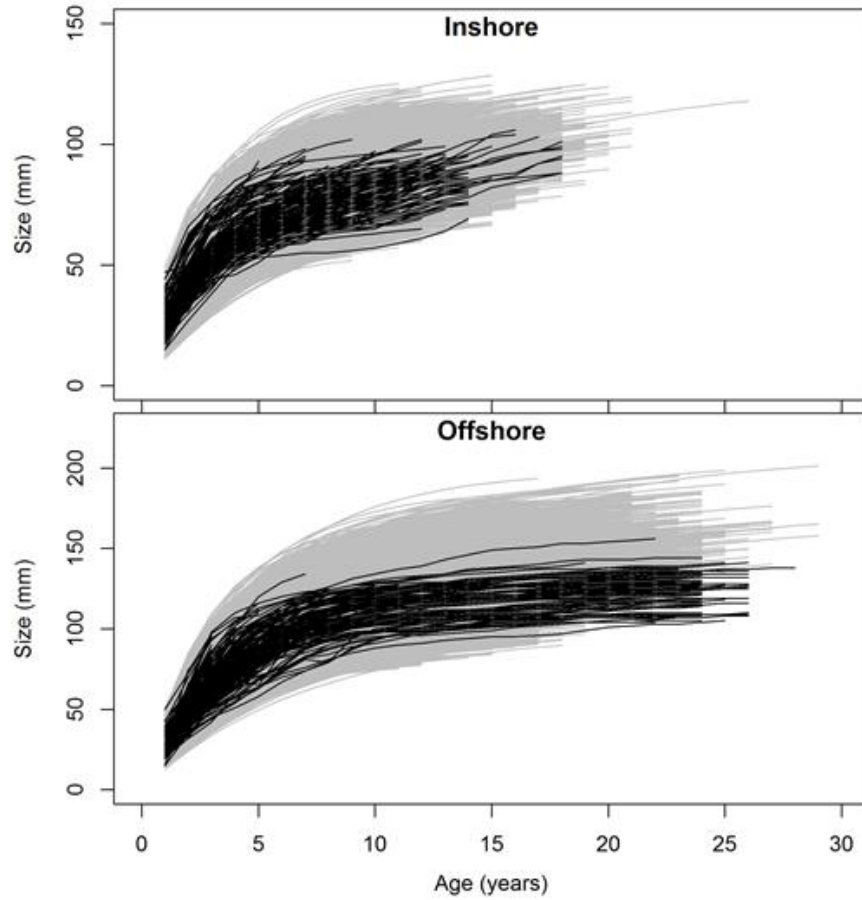


Figure 3. Actual (black) and 50,000 modeled (grey) growth curves for inshore and offshore populations of *S. solidissima*.

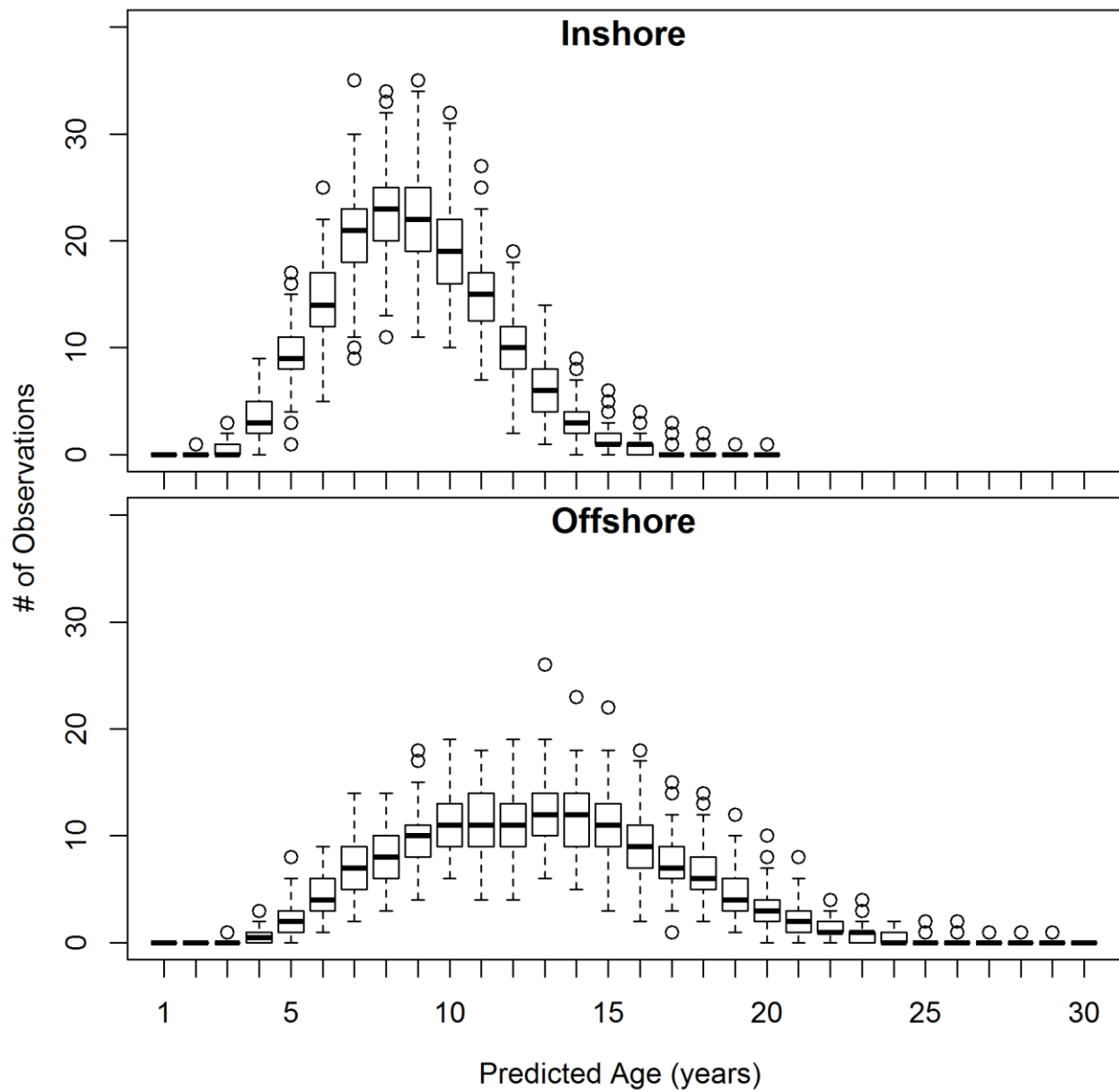


Figure 4. Range of ages predicted for sizes of both inshore and offshore clams from 1000 iterations of the model.

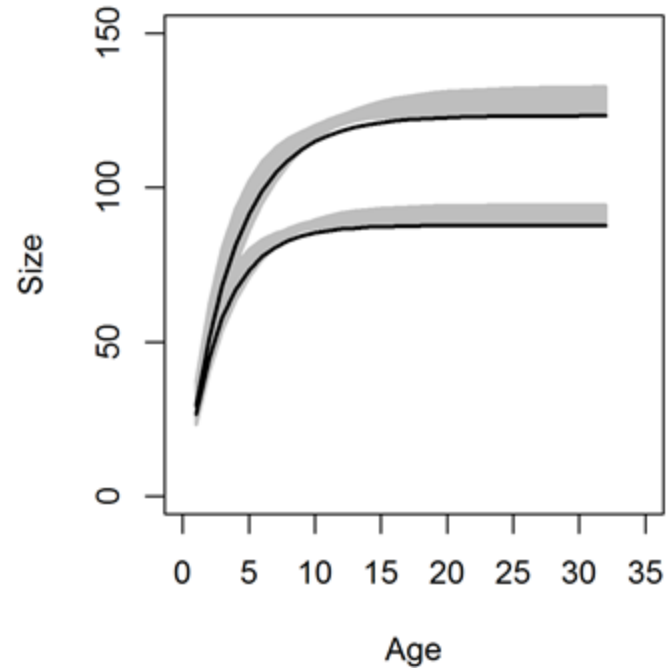


Figure 5. Range of predicted MVBG curves for 1000 iterations of age from size for Inshore (lower curve) and Offshore (upper curve). Black is actual MVBG for population, grey is predicted values.

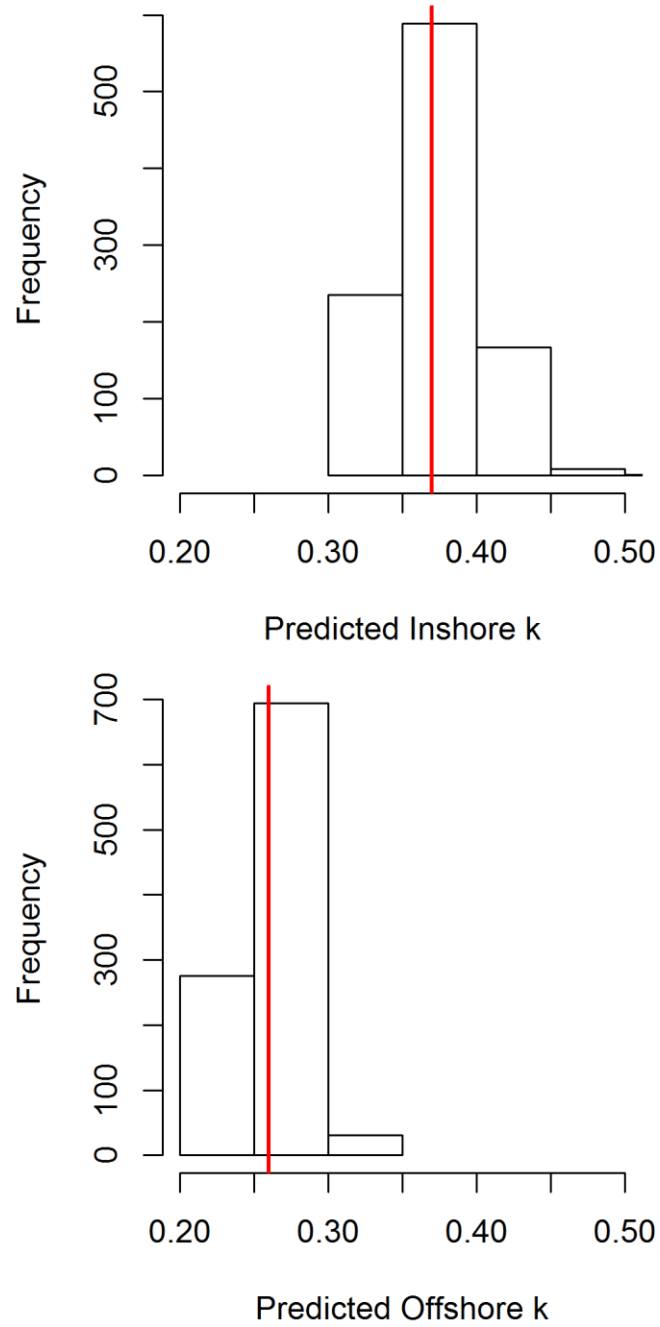


Figure 6. MVBG k values predicted from 1000 iterations of age from size. Red lines are the actual k values for each population.

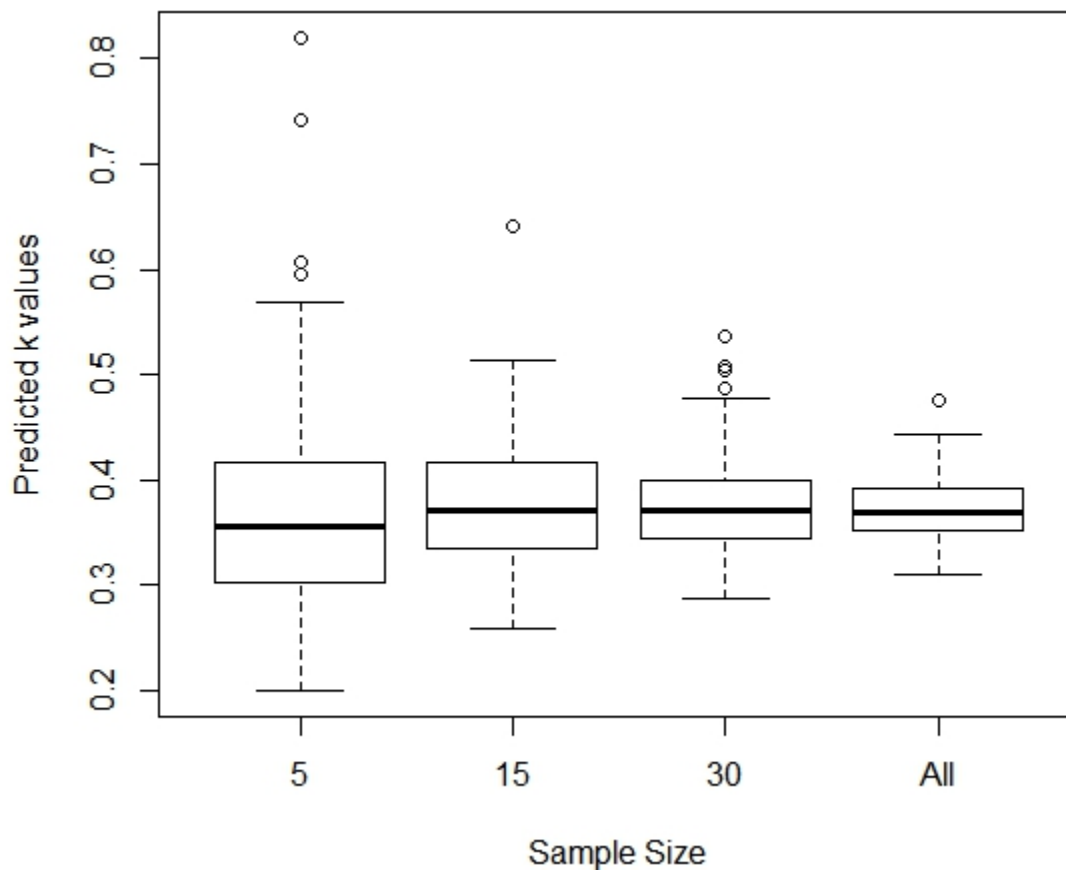


Figure 7. MVBG k values predicted from differing sample sizes for 100 iterations. There is no significant difference between the means of 15, 30 and all samples.

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DAVID MOSSEDUCATION

Syracuse University, Syracuse, NY

Ph.D. Earth Sciences**2016**

Dissertation: The evolution of extreme longevity in modern and fossil bivalves

University of Oklahoma, Norman, OK

M.S. Geology**2012**

Thesis: Trilobite faunas and facies of the Upper Ordovician (Sandbian) Lebanon Limestone, Nashville Dome Tennessee

Centenary College of Louisiana, Shreveport, LA

B.S. Geology with Honors**2010**

Honors Thesis: Pliocene development of great white shark serrations

AWARDS

Certificate in University Teaching, Syracuse University

20163 Minute Thesis, Syracuse University, 1st place**2016**

Outstanding Teaching Assistant Award, National Association of Geoscience Teachers

2015

Outstanding Teaching Assistant, Syracuse University

2014

Department of Earth Sciences Publication Award, Syracuse University

2014

Outstanding Senior Geology Major, Centenary College

2010TEACHING EXPERIENCE*INSTRUCTOR*

Syracuse University, Syracuse, NY

Summer 2015**Earth Science (EAR 105)**

Introductory course in physical geology intended for non-majors, summer session enrolls ≈25 students

State University of New York, Oswego, NY

Spring 2015**Historical Geology Laboratory (GEO 201)**

Laboratory for majors and non-majors (mostly education), enrolls ≈20 Students

TEACHING ASSISTANT

Syracuse University, Syracuse, NY

2012-present**Introduction to Paleobiology (EAR 325)**

Laboratory section enrolls ≈15 students commonly majors and biology majors, developed new material and taught lab, guest lectured for lecture section

Oceanography (EAR 117)*

Four recitation sections of ≈30 students, primarily non-majors, helped develop assignments

Dynamic Earth (EAR 110)*

Three labs of 20 science majors, helped develop assignments

Earth Science (EAR 105)*

Four recitation sections of ≈30 students, intended for non-majors, helped develop assignments

Volcanoes and Earthquakes (EAR 225)

Two recitation sections of ≈30 students, intended to fulfill science requirements

*Served as TA coordinator

University of Oklahoma, Norman, OK

2010-2012**The Dynamic Earth (GEOL 1104)**

Two lab sections for non-science majors of ≈20 students

Physical Geology for Science and Engineering Majors (GEOL 114)

Two lab sections for science majors of ≈20 students

The History of Earth and Life (GEOL 1024)

One lab section of ≈20 students, developed material

TEACHER DEVELOPMENT

Teaching Controversial Issues-Climate & Energy (GSA)	November 2015
Teaching Controversial Issues-Evolution of Life & Earth (GSA)	
Syracuse University Project Advance (SUPA)	April 2014
Invited speaker to workshop for high school Earth Science teachers teaching courses for Syracuse University credit - Syracuse & New York City	

UNDERGRADUATE RESEARCH SUPERVISED

Steve Harris, Syracuse University Lifespan and growth rate of Pliocene <i>Glycymeris subovata</i> from the Atlantic Coastal Plain	Fall 14-Spring 15
Lauren Williamson, Colorado College Latitude and growth rate in Pliocene <i>Glycymeris americana</i>	Summer 2015
Emily Artruc, SUNY College of Environmental Science and Forestry Lifespans of Eocene Antarctic bivalves. Literature search of lifespans and growth rates in modern bivalves	Fall 14-Spring 15

RESEARCH GRANTS

Paleontological Society Allison R. "Pete" Palmer Award <i>"The role of phylogeny in the evolution of extreme longevity in bivalves"</i> (\$800)	2014
Graduate Student Organization Research Grant, Syracuse University <i>"The role of phylogeny in the evolution of extreme longevity in bivalves"</i> (\$500)	2014
Geological Society of America Graduate Student Research Grant <i>"The role of phylogeny in the evolution of extreme longevity in bivalves"</i> (\$900)	2014
<i>"The evolution of extreme longevity in bivalves"</i> (\$2125)	2013

TRAVEL GRANTS

Syracuse University Earth Sciences Department travel funding to Fossilworks Workshop (\$1500)	2014
Syracuse University Graduate Student Organization Travel Grant (\$900)	2012, 2013, 2015, 2016
Syracuse University Prucha Research Fund (\$300)	2013
Geological Society of America Northeastern section Student Travel Grant (\$100, \$200, \$100)	2012, 2013, 2015
Geological Society of America Central section Student Travel Grant (\$250)	2011

PUBLICATIONS

Moss, David K., Ivany, Linda C., Judd, Emily J., Cummings, Partrick W., Bearden, Claire E., Kim, Woo-Jun, Artruc, Emily G., and Driscoll, Jeremy R. Latitudinal patterns in lifespan and growth rate across modern marine bivalves with implications for Phanerozoic evolution. *Proceedings of the Royal Society B*, 238.

Moss, David K. and Westrop, Stephen R. 2014. Systematics of some Late Ordovician encrinurid trilobites from North America. *Journal of Paleontology*, v. 88, p. 1095-1119.

PUBLISHED ABSTRACTS

Moss, David K., Ivany, Linda C., Judd, Emily J., Cummings, Partrick W., Bearden, Claire E., Kim, Woo-Jun, Artruc, Emily G., and Driscoll, Jeremy R. 2015. Latitudinal patterns in lifespan and growth rate across modern marine bivalves. *Geological Society of American Abstracts with Programs*. v. 47, p. 668.

Moss, David K. and Ivany, Linda C. 2014. Environmental controls on extreme longevity in modern and fossil bivalves. *North American Paleontological Convention. The Paleontological Society Special Publications*, v. 13, p.26.

Moss, David K. And Ivany, Linda, C. 2013. The role of the environment in the evolution of extreme longevity in bivalves. *Geological Society of America Abstracts with Programs, Annual Meeting*. Vol. 45, no. 7, p.320.

Moss, David K. and Westrop, Stephen R. 2012. Sorting through a paraphyletic garbage can: A phylogenetic analysis of Middle and Upper Ordovician "*Encrinuoides*" (Trilobita)

species from Laurentian North America. Geological Society of America, Abstracts with Programs, v. 44, no. 7, p. 233.

Moss, David K. And Westrop, Stephen R. 2011. Trilobite Biofacies and Lithofacies of the Upper Ordovician (Sandbian) Lebanon Limestone, Nashville Dome, Tennessee. Geological Society of America, Abstracts with Programs, v. 43, no. 5, p.83.

PRESENTATIONS

Geological Society of America	November 2015
Central NY Paleo Group (<i>Invited</i>)	October 2015
Central NY Earth Sciences Student Symposium	April 2015
Rochester Academy of Science, Fossil Division (<i>Invited</i>)	December 2014
Paleontological Research Institution Summer Symposium	August 2014,
2015	
Syracuse University Project Advance (<i>Invited</i>)	April 2014
North American Paleontological Convention	February 2014
Central NY Paleo Group (<i>Invited</i>)	Feb 2014

WORKSHOPS

Fossilworks Intensive Workshop in Analytical Paleobiology Macquarie University, Sydney, Australia Analytical methods in paleoecology, diversity, morphometrics, and phylogenetics using R	Summer 2014
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OUTREACH ACTIVITIES

Syracuse University Frontiers of Science Program Instructor for Earth Sciences day, activities have included "Fossils of New York", "Sediments of Hyde Park Mammoth Site", "Reconstructing human ancestry", "Evolution of great white sharks"	Fall 2012-2015
National Fossil Day Jamesville-Dewitt Middle School Visited four classrooms, "what can fossils tell us?"	Fall 2012-2014
Liverpool High School department visit day Research topics in geosciences for 9 th grade students, helped organize and presented	Fall 2012, 2014
Little Luke's Preschool Dewitt, NY Visited four classrooms, "what is a fossil?"	Spring 2014, 2015

Syracuse University Orange Scholars Summer Program **2013**
Assisted lead instructor with activities and ran evolution of great white sharks exercise

LEADERSHIP ROLES

Geology Graduate Organization (GeoGO) Chair **Spring 2014-2016**
Founding member, run meetings and set organizational goals, serve as primary graduate student-faculty liaison

PROFESSIONAL MEMBERSHIPS

National Association of Geoscience Teachers
Geological Society of America
Paleontological Society
Sigma Xi