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IDENTIFYING THE TICKS OF BIVALVE SHELL CLOCKS: SEASONAL GROWTH IN
RELATION TO TEMPERATURE AND FOOD SUPPLY

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ABSTRACT: Sclerochronology uses shell growth lines or bands for the construction of environmental time-series and the measurement of organism growth, but more study is needed to constrain the triggers of the dark cessation bands observed in many bivalve groups. We constructed a database of direct observations of modern growth seasonality across the class Bivalvia and compared the occurrence of seasonal growth bands to environmental data including latitude, temperature, and chlorophyll-a concentration. Bivalves with cold-season (winter) cessations are more common towards the poles, with logistic regression showing that temperature, followed by latitude of occurrence, displays the strongest relationship with occurrence of winter cessation. Remotely sensed and directly measured chlorophyll-a concentration show no significant relationship. Summer cessations are sparse and only weakly associated with environmental controls but are concentrated at the subtropical latitudes among temperate bivalves at their equatorial extremes. The rarity of summer cessations can be explained by the limited annual ranges of temperature in the tropics, combined with the exponential relationship of metabolic rate to temperature leading to a narrow window between normal functioning and mortality at high temperatures. This data suggests that, unless annual temperatures have low variability like in equatorial or polar regions, the season of growth cessation across bivalves is primarily a function of temperature tolerance through restriction of scope for growth. At most latitudes, growth bands can be interpreted as being primarily triggered by temperature stress, rather than seasonal starvation.

INTRODUCTION

Bivalves secrete their shells at varying rates throughout the year, often forming white opaque increments correlating to optimal growth conditions and dark translucent growth lines or bands during adverse conditions when viewed under transmitted light (Schöne, 2008). These bands are useful for the identification of growth seasonality of extinct organisms (Stevenson and Dickie 1954; Richardson 1993; Jones and Quitmyer 1996; Veinott and Cornett 1996), and by extension their environmental preferences and thresholds of stress. The seasonal allocation of energy to shell growth within and between species has been proposed to be controlled primarily by temperature (Beukema et al. 1985, Jones and Quitmyer 1996), food supply (Incze et al. 1980; Pilditch et al. 1999), or spawning (Sato 1995), and is moderated by ontogeny (Ivany et al. 2003). While many workers are in agreement that water temperature is an important determinant of seasonal skeletal growth in bivalves (Wefer and Berger 1991), it is less certain whether dark growth bands can be ascribed primarily to temperature stress rather than being a function integrating food supply, seasonal spawning, or other factors across species.

Previous attempts to relate overall annual shell growth to latitude usually focused on total growth or growth rate rather than the seasonal distribution of growth band formation (Weymouth

et al. 1931; Ansell 1968; Bachelet 1980; Watson et al. 2012). Bivalves live longer and grow more slowly at higher latitudes (Moss et al. 2016), and specimens at lower latitudes within their range reach greater maximum sizes and shell thicknesses than high latitude counterparts (Watson et al. 2012). Past work often modeled growth of bivalves using a Von Bertalanffy growth curve fitted with a seasonally varying coefficient (Cloern and Nichols 1978), or used principal component analysis to quantify the influence of different environmental variables on growth within a species (Witbaard et al. 1999). However, a cross-species attempt to relate growth to latitude was inconclusive, largely because of the confounding effects of relative shell shape (Vakily 1992). Other studies uncovered a strong seasonal relationship between metabolic rate and soft tissue growth with both temperature and food supply, but seasonal variability in growth of hard parts, while investigated intensively from the standpoint of individual species, has not been aggregated across taxa (Brockington and Clarke 2001). However, there is some evidence that the seasonal timing of growth band formation may also switch across the latitudinal range of a species. Pleistocene and modern oysters experience warm-season (summer) cessations in shell extension at the equatorial end of their range and cold-season (winter) cessations at the polar end (Kirby et al. 1998), as do quahogs (Ansell 1968; Surge and Walker 2006) and other mollusks such as limpets (Surge et al. 2013), but it is not clear whether these patterns can be generalized across bivalves.

Bivalves have a limited energy budget and experience constricted aerobic scope for growth when adverse stresses such as extreme temperatures, low food availability, or excess turbidity increase the energy expenditure required for survival (Schöne 2008). Metabolic oxygen supply and demand become increasingly mismatched at temperature extremes because of the temperature-dependence of metabolic rate and the increasing need for cellular protection and damage repair (Pörtner 2012; Sokolova 2013). Likewise, limited food supplies reduce total energy production such that less is available for growth, reproduction, or other activities once basal metabolic and maintenance needs are met (Sokolova 2013). In addition, gametogenesis represents a significant energy investment for bivalves and occurs on seasonal scales (Newell and Bayne 1980; Sato 1995; Gaspar et al. 1999).

These dynamics affect bivalve populations in response to climate change (Pörtner et al. 2005), while acute stresses may cause mortality during extreme conditions such as El Niño warming events (Urban 1994), but the influence on seasonal scales is still poorly understood. Seasonally moderated sources of physiological stress are distinct from acute environmental stresses because they are periodic and gradual. Many organisms are more susceptible to temperature changes, and therefore suffer proportionally larger restriction of scope for growth, when such stresses occur over a long period, a concept known as “thermal inertia” (Peck et al. 2009; Lah et al. 2017). These chronic sources of stress and their impacts on scope for growth represent a gap in knowledge, largely due to the difficulty in simulating realistic environmental variation at population scale in an experimental setting. Because metabolic rate and temperature follow an exponential relationship (Martin and Huey 2008; Payne and Smith 2017), it can be difficult to conduct cross-species comparisons of physiological tolerance at the narrow interval between normal seasonal stress and mortality. Bivalves inhabit environments with widely differing degrees of environmental variation, from the relatively stable deep subtidal to the extreme intertidal, exacerbating the difficulty of simulating cross-species responses with experimental designs capturing the true diversity of habitats. Shell formation has been found to represent a relatively small proportion of bivalve energy budgets and could be precisely the type of minor energy allocation that would be mediated by sublethal seasonal stress (Watson et al.

2017). Annual band formation could therefore be a marker of this inertial response across species and environments, because the bands indicate a slowdown in growth potentially leading up to complete seasonal cessation in response to sustained environmental stress.

We focused on formation of shell bands potentially visible in fossil specimens to ground-truth paleobiological studies where we inherently lack direct observations of growth in extinct organisms. We coded seasonal growth as a binary variable, which can be related to continuous variables such as latitude, temperature, productivity, and depth using logistic regression. This cross-species analysis will assist in determining the most likely environmental constraints on the triggers of growth band formation and the physiology of extinct bivalve species.

MATERIALS AND METHODS

We surveyed the existing literature of bivalve growth, gathering 294 direct observations of marine or brackish estuarine bivalve growth for 115 species from 183 publications in ecology, earth science and aquaculture journals (Fig. 1) (see Online Supplemental File, data set 1). These observations included absolute latitude and season of growth cessation if one was present. We focused on direct observations of cessation through mark-recapture, internal growth band or population length-frequency studies because other techniques, such as post-hoc observations of external growth bands, are believed to be confounded by tidal, reproductive and other intermittent growth cessations (Schöne, 2008). We coded cessation as 1 and continuous growth as 0 by season; for example, a species growing year-round at a location at winter and summer would have values of [0, 0]. Because fall and spring are less certain in their comparative definition in differing climate zones, we use 'winter' and 'summer' to refer to cold-season and warm-season cessations, respectively. We recorded a shutdown when the researchers made mention of 'cessation,' 'shutdown,' 'negligible growth' or other similar keywords in reference to specific months or seasons (climatological season rather than calendar season). We avoided observations of juvenile or senescent individuals, which are more likely to experience year-round growth or constricted growth seasons, respectively (Ivany et al. 2003). If juvenile or senescent status were unclear (keywords such as "spat", "juvenile", "post-reproductive," etc.), we only integrated observations with an explicit age falling in the mid-range of its species' respective growth curve, avoiding those at the indeterminate rapid juvenile stage or flattened senescent state. Authors varied in their terminology, sometimes noting 'slowdowns' with unclear criteria behind their meaning, as opposed to clearer terminology such as 'shutdown' or 'cessation.' Where these occurred, we noted that they were slowdowns, rather than complete cessations and ran analyses to confirm that trends were consistent with and without these slowdown cases. Among our collected data, too few sources noted the occurrence of a cessation specifically corresponding to gametogenesis or reproduction to conduct a global analysis of their occurrence.

Some publications also recorded local temperature range based on high and low temperatures, which we recorded when provided. To control for possible methodological differences in temperature measurement between studies (depth and temporal resolution), we also downloaded daily remotely sensed sea surface temperature for the years 2004–2014 from the NOAA OI SST V2 Dataset (see Online Supplemental File, data set 4). This 0.25-degree gridded data allowed us to determine the influence of true daily high and low temperature on the occurrence among the bivalves in our dataset.

We also recorded chlorophyll-a (chl-a) concentration when reported in the study, which can be used as a proxy for productivity. While bivalves have flexibility in their food supply, we settled on chl-a and therefore phytoplankton abundance as the best measure of food availability

because phytoplankton, as primary producers, represent the greatest proportional amount of biomass and are the most seasonally variable in abundance, often blooming at the end of the winter months and outmassing higher trophic levels of plankton by several orders of magnitude (Harris 1986). Grazing zooplankton, by contrast, often lag phytoplankton in their appearance and thus display weaker seasonality. Because chl-a was not reported in all papers, we also downloaded monthly average 4.6 km grid chl-a concentration data output from the VGPM global productivity model as a proxy for food supply (growth data with appended satellite productivity data in Online Supplemental File, data set 2). This model aggregates remote spectrometry data from the MODIS satellite observatory and uses a model-based approach to control for environmental confounding variables such as coastal turbidity and cloud cover (Behrenfeld and Falkowski 1997). We correlated each of our observation sites to the nearest pixel in the dataset using BEAM remote sensing visualization software and found average monthly chl-a results for the period 2003–2014. While satellite ocean color data has been used to study temporal variability in coastal productivity, we sought to corroborate these results with an independent set of *in situ* direct observations of productivity from our sites, as coastal productivity can sometimes be subject to localized trends (D’Ortenzio et al. 2002; Lavender et al. 2004; Yamada et al. 2005; Hyde et al. 2007). To this end, we also aggregated direct chl-a-based measurements of productivity from various data sources collected within the same satellite grid cell and at similar depths to the observed bivalves (these independent chl-a sources are included in the Online Supplemental File, data set 3). These data were then averaged to monthly resolution for easier comparison to the remote sensing output.

We compiled and analyzed the relative contribution of environmental factors including absolute latitude, low/high seasonal temperature (lowest and highest daily values reported), low/high seasonal monthly mean productivity and local temperature range via principal components analysis (PCA) on a correlation matrix. Visual analysis of these four environmental variables on paired PCA plots allowed us to identify patterns in occurrence of cessation types in bivalves in relation to their local environmental conditions.

RESULTS

Cessation Related to Latitude and Temperature

Winter cessations are prevalent in bivalves above 25 degrees latitude, becoming increasingly common at higher latitudes, whereas summer cessations are concentrated in the subtropical zone between 15–30 degrees (Fig. 2). A small subset of populations, many of which are constricted at the polar end of their range including the Gulf of California, Gulf of Mexico, and Adriatic (Quitmyer et al. 1985; Arneri et al. 1998; Schöne et al. 2002) (Fig. 1), have both winter and summer cessations. In our data, populations with no recorded seasonal cessation (growing year-round) are common at the equatorial latitudes (Fig. 2).

We first separated cessation type by season and related each binary variable to absolute latitude. There is a significant positive relationship between latitude and the occurrence of winter cessation (Fig. 3A) (log-odds ratio 0.055, $p < 0.0001$), with the odds of winter cessation increasing by 5.6% per degree latitude (95% CI: 3.4–8.2%). This association, as well as all others following (for winter cessation events), hold regardless of whether “slowdown” events are excluded (log-odds ratio 0.059, $p < 0.0001$).

Summer cessation also has a significant relationship with latitude, with a one degree increase in latitude leading to 3% decrease in probability of shutting down in the summer months (log-odds ratio -0.029, $p = 0.0114$). However, the relationship is a much weaker fit to the data

(Fig. 3B) compared to the winter cessation model (Fig. 3A), with a predicted summer cessation probability of only 50% at equatorial latitudes. The predicted summer cessation probabilities fail to converge towards 1 at the lower, high-temperature latitudes largely because the occurrences of summer cessation are concentrated at the lower temperate latitudes rather than in the equatorial zone where bivalves tend to grow year-round.

Winter cessation is significantly associated with minimum local seasonal temperature, with a stronger relationship than that of latitude alone. The odds of winter cessation increased by 14.7% for each degree Celsius decrease in temperature (log-odds ratio = -0.13, $p < 0.0001$, 95% CI: 8.1–21.4%) (Fig. 3C). Populations with winter cessations also experience a significantly wider temperature range (mean 15.27°C) than species without such a cessation (mean 11.25°C) (Welch's t-test: $t = 3.82$, $df = 87.64$, $p < 0.0001$). A multiple logistic regression (Table 1) showed that this relationship is significant, independent of the influence of latitude (temperature range is known to increase with latitude within the range of our data). There is no significant difference in mean temperature range between species with a summer cessation and those without. Summer cessation displays no significant relationship with summer maximum locally recorded temperature (log-odds ratio 0.009, $p = 0.7$). However, summer cessation does relate significantly to highest mean remotely sensed daily sea-surface temperature (log-odds ratio 0.106, $p = 0.0015$). Among the recorded temperatures in our database, there was great variability in methodology of temperature data collection and reporting, in terms of frequency, depth, and method of collection, which necessitated using a more standardized remote sensing data source to see whether true annual maxima were being excluded. This relationship is slightly stronger when only temperate bivalves occurring above 20 degrees latitude are included, which experience more annual variability in temperature (log-odds ratio 0.153, p -value < 0.001).

Effects of Food Supply

There is no significant relationship between the occurrence of winter cessation and remote-sensed winter minimum chl-a concentration, which we set as the lowest monthly mean chl-a from October to March in the Northern hemisphere, and April to September in the Southern hemisphere (log-odds ratio: -0.005, $p = 0.27$). The majority of observation sites instead experience a productivity maximum in the late winter or early spring months according to the chl-a data. While phytoplankton productivity is dependent on insolation that is seasonally modulated, it is also limited by nutrient scarcity during times of thermal stratification. Shelf phytoplankton in the temperate zone typically thrive during the period when insolation is increasing but upwelling from deeper-nutrient rich waters has not been disrupted by the formation of a thermocline (Legendre 1981). Direct observations of monthly chl-a concentration were available for 34 stations, and corroborate the results observed from the remote-sensing sourced data (Online Supplemental File, data set 3). A logistic regression showed no significant relationship between occurrence of a winter cessation and the directly measured low winter productivity of the study sites (lowest monthly mean from winter months), even when normalized by the sites' annual average to remove significant inter-site variability (log-odds ratio: 0.101, $p = 0.52$).

Combined Effects of Multiple Stressors

We can also interpret the relationship of winter cessation to multiple environmental variables using principal component analysis (Fig. 4A). PC1 explains 52% of the variance and reflects the effects of minimum temperature and latitude. PC2 explains 26% of the variance, associated with winter minimum chl-a and annual temperature range. Bivalves with winter cessations tend to occur at low values on PC1, indicating higher latitude and colder annual

minimum temperatures, whereas bivalves that grow throughout the winter tend to cluster at higher values of PC1 with warmer annual minimum temperatures. In contrast, observations of winter cessations are distributed along the PC2 axis, indicating a weaker relationship with minimum chl-a or annual temperature range. A similar PCA plot showing the distribution of summer cessations relating to summer maximum temperature, latitude, temperature range, and summer minimum chl-a shows little grouping or correspondence of cessation in relation to the environmental variables (Fig. 4B).

For a quantitative test of the relative significance of the different variables, we used a multiple logistic regression. When integrating latitude, winter minimum chl-a concentration, temperature range, and minimum local temperature into the equation predicting winter cessation, minimum local temperature and temperature range are the only coefficients with p-values indicating significance (Table 1). Quantitatively and qualitatively, food supply has little correspondence to the data, and temperature has the strongest influence on cessation occurrence, followed by latitude.

DISCUSSION

Latitude and Temperature

The most powerful predictor of growth seasonality in bivalves, and thus the formation of a dark growth line in the shells, is temperature. Winter cessation is the most prevalent growth pattern among our recorded observations, especially above 25° latitude, where seasonality is more extreme. Among these individuals, the most important variable explaining cessation is low annual temperature, followed by the observed range of temperature. Latitude also explains a significant amount of the variance, because it is a proxy for temperature that approximately decreases from equator to pole. This result is consistent with laboratory studies of single bivalve species, which also find temperature to be a hard constraint on bivalve scope for growth, independent of food supply (Laing 2000). Despite the presence of strong winter productivity at some of our study locations, winter cessations may dominate because very low temperature can prevent bivalves from filter feeding and/or metabolizing ingested material to fuel shell growth.

Although cold temperatures are a reliable trigger of winter cessation among bivalves, summer cessations are not as closely linked to high temperature and are not as widespread. Logistic regression plots of summer cessation do not converge near 1 for the highest temperatures experienced by bivalves in our dataset, unlike winter cessations in response to low temperature. This is largely because summer cessations are rare near the equator; growth cessations display a stronger relationship with daily remote sensed temperature data when equatorial observations are excluded. The spatial patterns of summer cessations, concentrated in the subtropical latitudes around 15–30 degrees, likely arises from a combination of unusually stable temperatures in equatorial regions, as well as from physiological limitations and adaptations in bivalves.

Subtropical latitudes are distinguished by large seasonal temperature ranges and warm summer maximum temperatures. Bivalves experiencing summer cessation in this band of latitudes may experience true high temperature-triggered shell growth cessation, as they may be under temperature stress at both extremes and cannot merely adapt to the warmest temperatures. Equatorial habitats have low annual temperature variability, so summer temperatures are typically not high enough in comparison to the annual average to place most bivalves under regular metabolic stress (Conover 1992). Though some equatorial species experience interruptions in shell formation during times of acute heat stress, such as on the coast of South

America during El Niño warming events (Lazareth et al. 2006), these interruptions are a sign of near-mortality due to low-frequency extremes, rather than an encoded response of the organism to annual temperature fluctuations.

High-temperature cessations may be rare in general due to the effects of temperature on ectotherm physiology. The exponential relationship between temperature and metabolic rate leads to an asymmetrical thermal performance curve in many species, with a sharp transition between warm-water optimum and declining performance (Martin and Huey 2008; Payne and Smith 2017). As a result, some mollusks show a sigmoidal relationship between shell formation rate and temperature, with a similarly sharp transition from temperature-accelerated growth to mortality (Irie and Morimoto 2016). The abrupt decline in fitness and shell formation rate near the high-temperature extreme leads to a narrow window for inducing a heat stress-related growth band, while still remaining below the threshold temperature that would trigger mortality. Furthermore, equatorial bivalves can adapt their entire metabolic regime to ensure survival at these extremes, prioritizing growth at higher temperatures at the expense of efficiency at lower normal seasonal temperatures (Riascos et al. 2012), and can also reschedule their growth to prioritize growth during cooler summer nights (Schöne et al. 2006). Bivalves therefore may maintain a greater safety margin in their thermal physiology (Martin and Huey 2008), minimizing the likelihood of high-temperature growth band formation to avoid the risk of mortality, potentially explaining the comparative rarity of summer cessations in our dataset.

With temperature exerting a strong control on the overall metabolic rate of bivalves, the allocation of energy to shell extension may be one of the first expenditures to be curtailed during times of extreme temperature. This aligns with the results of a lab culture study, which confirmed that temperatures outside of a normative range experienced by the pearl oyster *Pinctada margaritifera* influences the expression of genes related to biomineralization (Joubert et al. 2014). Bivalve shell growth is consistent with an energy balance between metabolic costs and available energy supply dictating scope for growth in invertebrate organisms (Sokolova 2013). Bivalves grow their shells during times of favorable temperature, but not when temperatures fall outside certain seasonal thresholds (Schöne 2008). This suggests that the constricted scope for growth resulting from low, or less commonly high, ambient temperature results in the bivalve reducing energy allocated for shell extension.

Food Supply

Although food availability can influence growth rate, especially of soft tissue mass (Thompson and Nichols 1988), chl-a has a limited relationship with the occurrence of winter cessations at a global scale in our dataset. While some previous observations of winter cessation have been proposed to be due to starvation resulting from low seasonal productivity (Incze et al. 1980), in our collected observations we observed no significant relationship between seasonal chl-a availability and the occurrence of a cessation. A majority of stations have winter minimum chl-a concentration between the months of February and April, yet most of our recorded cessations begin at the start of winter. While we anticipated phytoplankton to exhibit high seasonal variability due to the impact of seasonal insolation and temperature on photosynthetic output, our dataset shows no such clear patterns in seasonal phytoplankton abundance across latitudes, confirming other prior attempts to find such trends (Winder and Cloern 2010). In many regions of the world, phytoplankton experience complex seasonal variability deviating from the 12-month period that would be expected if seasonal insolation and temperatures were the major controlling variables, and many experienced no seasonal regularity at all (Winder and Cloern 2010). Other experimental attempts to determine timing of bivalve shell growth in relation to

peak food availability have had varying levels of success across species, with some finding a poor or mixed relationship (Schöne et al. 2006) but others arguing for a stronger link (Joubert et al. 2014). In general, we assert that while productivity may influence bivalve growth, at most latitudes it does not experience the seasonality needed to explain the occurrences of annual growth cessation observed in our dataset.

It is possible that limitations in the coverage or resolution of remotely sensed chl-a productivity may have obscured a relationship between food supply and growth cessations. Remote-sensing sourced chl-a models are calibrated from observational data (D'Ortenzio et al. 2002; Lavender et al. 2004; Yamada et al. 2005; Hyde et al. 2007) and have been widely used to assess productivity (Halfar et al. 2004), but the models may be less accurate in oceanographically complex coastal regions. Nevertheless, to rule out the possibility of inaccuracies in the coastal productivity proxy, we also compared the occurrence of growth cessations to direct measurements made at the same locations (see Online Supplemental File, data set 3). The use of direct chl-a measurements did not strengthen the relationship with growth cessation, suggesting an overall limited effect of food supplies on growth band formation.

Many bivalve species also exhibit great flexibility in their food sources outside of phytoplankton, consuming particulate organic matter, detritus, and bacteria (Stephenson and Lyon 1982; Langdon and Newell 1989; Kang et al. 1999), but these other food sources are less likely to exhibit annual seasonality relating to insolation or temperature in a manner that is consistent between sites. Zooplankton, for example, usually lag behind in abundance following spring phytoplankton blooms due to their longer generation time, and also have been found to exhibit great interannual plasticity in their phenology (Mackas et al. 2012). The other food sources, due to a comparative lack of seasonality, could represent another potential explanation for the lack of a seasonal relationship between chl-a and growth. A significant proportion of the species in our dataset may be calling upon alternate food sources during times of seasonal food stress.

Polar and high-latitude bivalves may represent an exception to the trends seen in our dataset. *Arctica islandica* and other high-latitude bivalves can experience winter cessations at times of low non-phytoplankton food availability in locations with almost no annual variability in temperature (Witbaard 1996; Sejr et al. 2002; Schöne et al. 2005; Butler et al. 2013). For example, the northernmost populations of *A. islandica* open their valves more widely when chl-a is high, with the gaping in turn correlating to faster shell growth (Ballesta-Artero et al. 2017). Our dataset lacks the coverage in polar regions necessary to identify significant predictive relationships between the occurrence of winter cessations and food supply in these localities. These extreme environments, where food supply displays stronger seasonal signatures than temperature, could be an exception to the temperature-growth relationship we observed across bivalves at subtropical to subpolar latitudes. Polar environments, with low temperature variability but extreme seasonal variations in food quantity, could represent an energetic regime that requires true annual starvation-related cessations in growth for bivalves.

Other Cessation Triggers

Although temperature is a key overarching control on bivalve growth, and food supply may be important where temperature is extremely stable, other factors can locally be significant. For example, salinity stresses often affect species in intertidal zones exposed to monsoonal influxes of freshwater, such as the coasts of India. Bivalves in these regions are exposed to frequent reductions of salinity during the rainy season which trigger them to close their shells to maintain homeostatic osmotic pressure (Nayar and Rao 1985). Many bivalves also experience

short cessations during spawning times when energy is dedicated to gonadal development rather than shell growth (Sato 1995). These interruptions are usually distinguished by thin, well-defined dark growth lines of uneven periodicity rather than the thick, periodic bands which match up to seasonal temperature trends, or may not result in the formation of a growth line at all, particularly for the bivalves whose gametogenic period coincides with improving condition indices (Newell and Bayne 1980; Gaspar et al. 1999). Such growth bands can nevertheless make it difficult to discern the start or end of growth seasons, particularly when trying to identify growth from external rather than internal growth bands (Clark 1974). In general, across the bivalves recorded in our dataset, reproductive events are not a consistently recorded trigger of growth bands useful for diagnosing periodicity of samples along the growth axis in a shell, though additional study of the latitudinal and environmental factors determining bivalve spawning time may help shed more light on the interactive effects of spawning time and annual shell growth cessation. Further work could identify whether there are phylogenetic or spatial associations influencing the occurrence of reproductive interruptions and the biases they introduce to estimates of life history based on annual bands.

Implications for Sclerochronology

Sclerochronology, the study of sequential growth bands in calcifying organisms, has been broadly applied to help answer paleoclimatological and paleophysiological questions. Because shell-growth patterns provide unique utility to reconstruct seasonality due to their higher resolution in comparison to sedimentological records, it is important to understand the seasonal controls on shell deposition. Bivalves with a winter cessation will record warmer average annual temperatures but, as the climate warms, that cessation might disappear or even switch seasons, necessitating a correction between paleoclimate proxy records from populations at different times, and also corrections between taxa (Schöne et al. 2006). If that cessation was due more to food supply than temperature, its seasonality could be altered through time if the nutrient regime at that location changed, also influencing the fidelity and comparability of proxy records. These questions can only be addressed if the dominant cause of bivalve growth cessation is known, and we propose that these annual bands are primarily a function of temperature related stress, rather than starvation.

A study of the cessation temperatures of bivalves during a past climate change would help shed light on whether bivalves are able to evolve their thermal tolerance in response to changing temperatures. Shifts in the seasonality of growth cessations (from winter to summer, or the reverse) in response to changing temperature may imply limited adaptability in thermal tolerance. Bivalves may instead be forced to migrate or may suffer stunted growth or local extinction. In contrast, shifts in the onset temperature of growth cessation would indicate that the species can, at least partially if not totally, adapt to changing temperatures by adjusting its thermal tolerance window.

CONCLUSIONS

The formation of dark growth lines or bands in bivalves from subtropical to subpolar latitudes is primarily triggered by low temperature exposure rather than seasonal food deprivation. This suggests that temperature-linked metabolic constraints, manifesting as reduced scope for growth, are the primary control on bivalve shell growth across most latitudes. Conversely, high-temperature restrictions across bivalve species are less widespread. Summer cessations may be infrequent because warm equatorial oceans have limited temperature variability. In addition, thermal performance curves are asymmetrical, with a narrow window

between optimum and mortality at high temperatures, so the range of temperatures over which growth bands can form is limited. Bivalves may also need to maintain a greater safety margin at high temperatures because of the risk of mortality with small temperature increases. At equatorial latitudes, cessations are likely caused by non-temperature related local factors, but the majority of bivalves grow almost year-round. Bivalves with summer cessations may be constricted outside of their ideal temperature regime by geographic or other factors.

Food supply is not a primary control on the seasonal timing of growth cessation but may become locally important in regions of low temperature variability and high productivity variability, such as in polar areas. Although nutrition may be important in certain situations, such as in polar environments where temperature is stable, food supply does not vary systematically or predictably with time or space, as bivalves have flexibility to use different food sources, and temperature may have a stronger influence on aerobic scope for growth. Other environmental stresses, such as reduced salinity, can also trigger growth band formation, but only in unusual local circumstances.

The primary importance of temperature in the formation of growth bands provides opportunities for assessing the impacts of climate changes on marine organisms. Studies of growth band timing in fossil populations across ancient climate change events can constrain whether bivalves are able to adapt their physiological thermal tolerances to temperature change by shifting the onset temperature of growth cessation. More investigation is needed into whether seasonal cessation is a deeply conserved or more adaptable response to changing environmental conditions.

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SUPPLEMENTAL MATERIAL

Data are available from the PALAIOS Data Archive:
<http://www.sepm.org/pages.aspx?pageid=332>.

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FIGURES

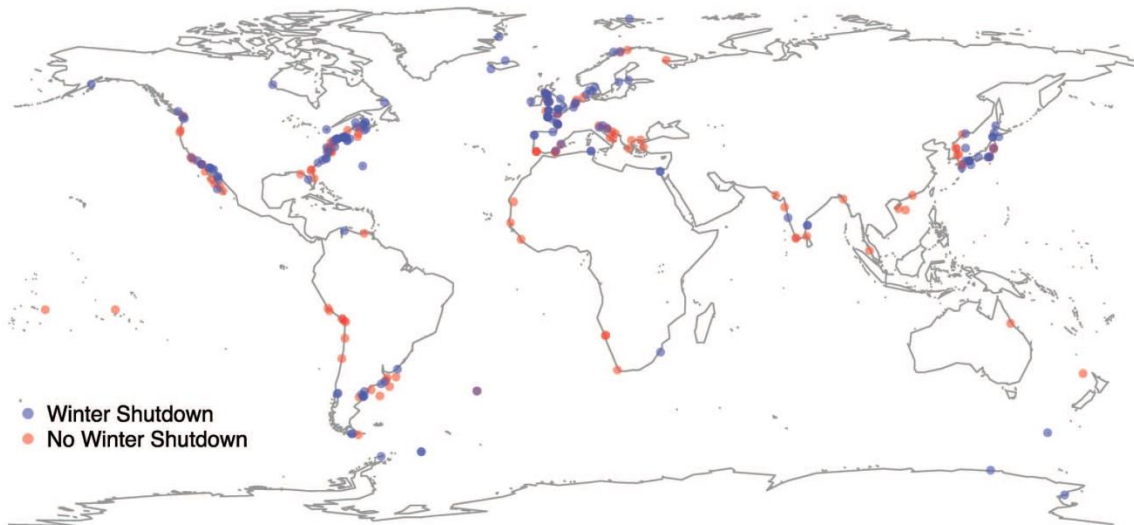


FIG. 1.—Map of occurrences, with blue representing winter cessations and red representing no winter cessation. Points are semi-transparent, so purple indicates summer and winter cessation observations at the same locality.

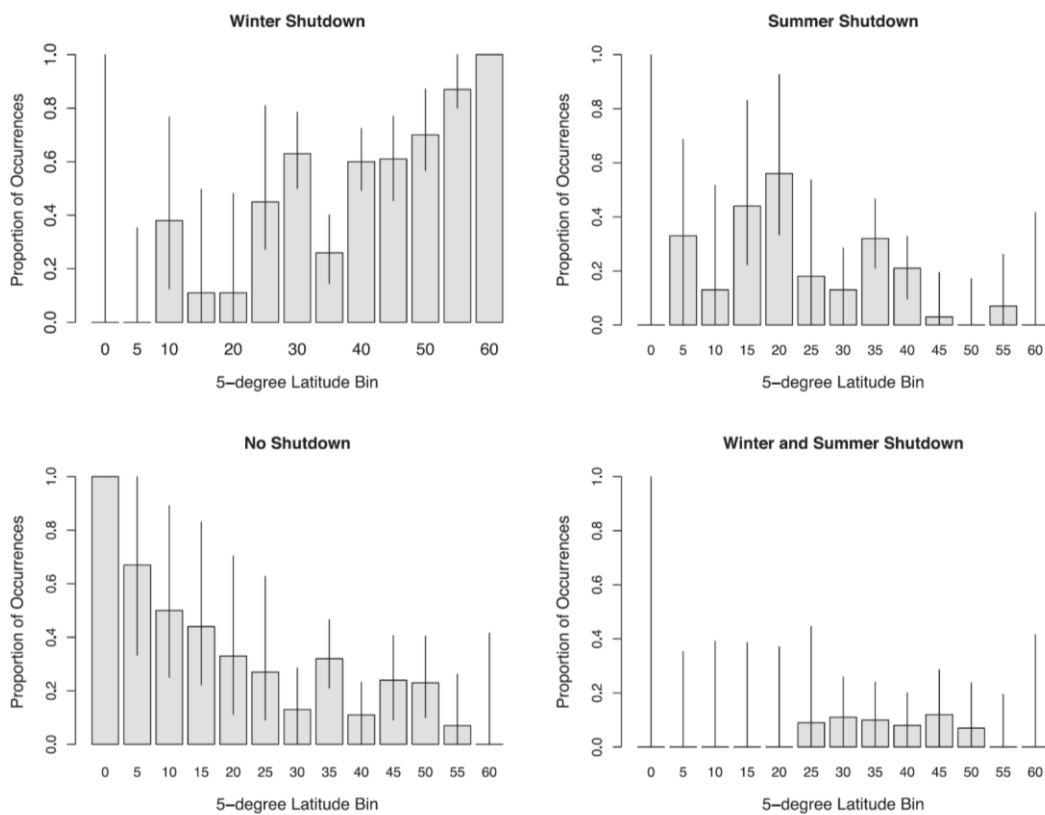


FIG. 2.—Proportion of occurrences of cessation types within 5° latitude bins, showing the comparative distributions of growth seasonalities for bivalves displaying respective cessations. **A)** Winter cessation. **B)** Summer cessation. **C)** Those that grow year-round. **D)** Those with both winter and summer cessations. Error bars represent multinomial confidence intervals with $\alpha = 0.05$ (Sison and Glaz 1995).

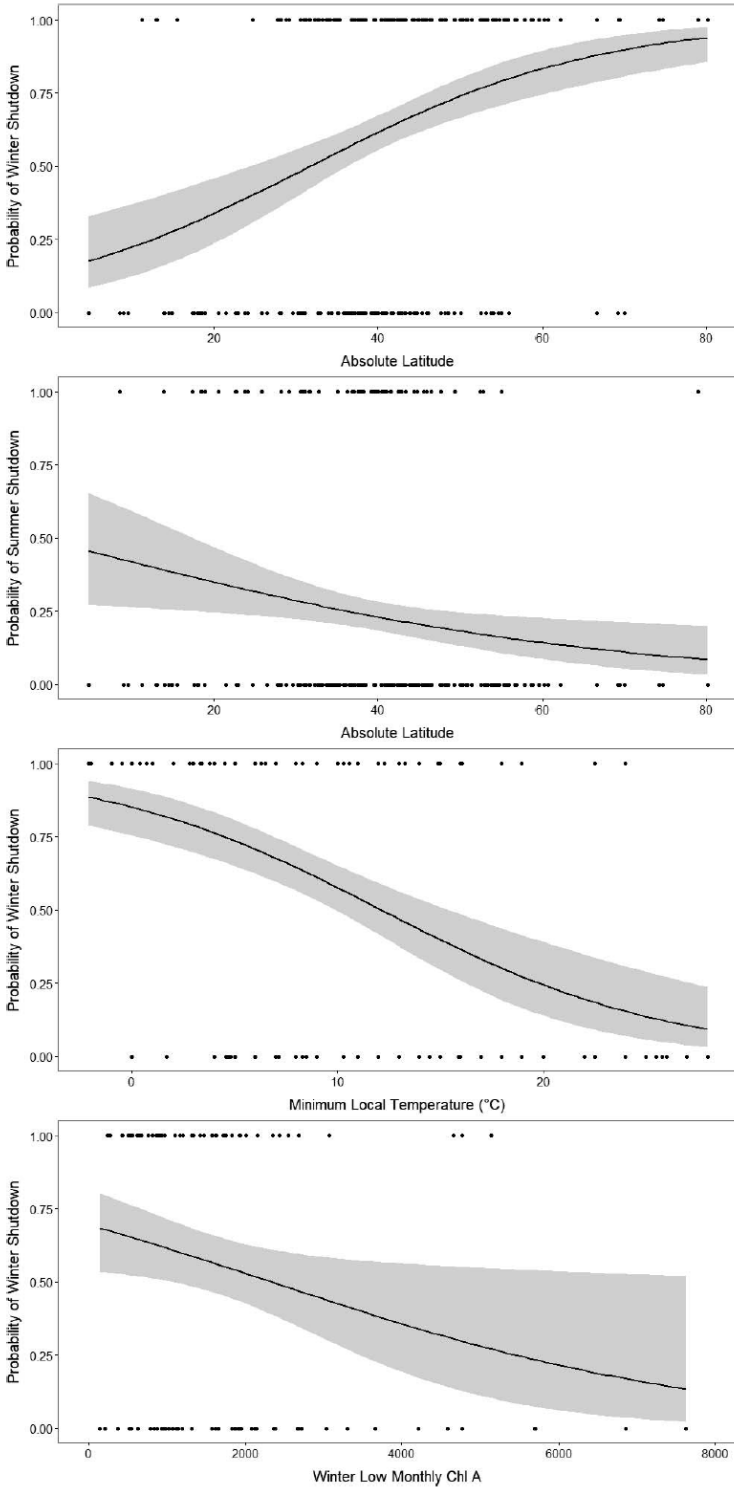


FIG. 3.—Logistic regression analyses comparing growth cessation to environmental variables. **A)** Relationship between absolute latitude and the probability of winter cessation. **B)** Relationship between absolute latitude and the probability of summer cessation. **C)** Relationship between winter minimum recorded temperature and the probability of winter cessation. **D)** Relationship between winter low monthly mean chlorophyll-a (mg/m^3) concentration and the probability of winter cessation.

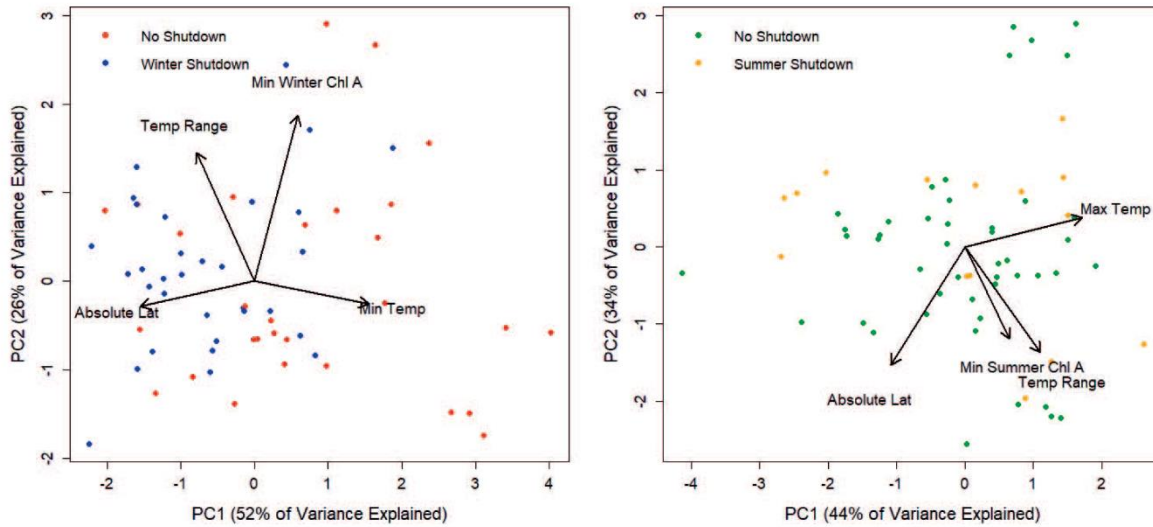


FIG. 4.—Principal component analysis plots of bivalve occurrences. **A)** Occurrence of winter cessation (blue) with lack of winter cessation (red) as related to absolute latitude, temperature range, minimum winter chlorophyll-a and minimum temperature. The blue winter cessations are largely grouped to the left of the plot, defined by high latitude and low minimum temperature, which follow the dominant principal component, PC1. Bivalves lacking a winter cessation primarily occur in conditions of high minimum temperature and low latitude. Minimum winter chlorophyll-a is orthogonal to this dominant axis, explaining less of the resulting grouping. **B)** PCA results for summer growth cessations, substituting maximum temperature and minimum summer chlorophyll-a. The occurrences of summer cessations appear well intermixed throughout the plot with little correspondence to any particular environmental variable.

| | Estimate | Std. error | z value | Pr(> z) | Significant? |
|-----------------------|----------|------------|---------|----------|--------------|
| Intercept | 0.706 | 1.74 | 0.406 | 0.685 | |
| Absolute latitude | -0.0083 | 0.0274 | -0.303 | 0.7617 | |
| Minimum local temp | -0.145 | 0.0573 | -2.53 | 0.0114 | * |
| Temp. range | 0.102 | 0.0338 | 3.02 | 0.00256 | ** |
| Chlorophyll A minimum | 0.00053 | 0.0003 | 1.77 | 0.0767 | |

TABLE 1.—Results for multiple logistic regression of environmental variables with winter cessation.