

MARINE ECOSYSTEMS

Latitudinal trends in shell production cost from the tropics to the poles

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The proportion of body mass devoted to skeleton in marine invertebrates decreases along latitudinal gradients from large proportions in the tropics to small proportions in polar regions. A historical hypothesis—that latitudinal differences in shell production costs explain these trends—remains untested. Using field-collected specimens spanning a 79°N to 68°S latitudinal gradient (16,300 km), we conducted a taxonomically controlled evaluation of energetic costs of shell production as a proportion of the total energy budget in mollusks. Shell production cost was fairly low across latitudes at <10% of the energy budget and predominately <5% in gastropods and <4% in bivalves. Throughout life, shell cost tended to be lower in tropical species and increased slightly toward the poles. However, shell cost also varied with life stage, with the greatest costs found in young tropical gastropods. Low shell production costs on the energy budget suggest that shell cost may play only a small role in influencing proportional skeleton size gradients across latitudes relative to other ecological factors, such as predation in present-day oceans. However, any increase in the cost of calcium carbonate (CaCO₃) deposition, including from ocean acidification, may lead to a projected ~50 to 70% increase in the proportion of the total energy budget required for shell production for a doubling of the CaCO₃ deposition cost. Changes in energy budget allocation to shell cost would likely alter ecological trade-offs between calcification and other drivers, such as predation, in marine ecosystems.

INTRODUCTION

The evolution of calcium carbonate (CaCO₃) shells and skeletons, and the rapid diversification and radiation of biomineralizing fauna, were pivotal events in the Cambrian explosion; today, calcifying invertebrates continue to play conspicuous and essential roles in the functioning of healthy marine ecosystems. Calcareous shells provide support for internal organs and structures for muscles to act upon. They also protect the occupant from predators, and because shell integrity determines survival, shell form is subject to strong selection pressure, with functional success or failure a fundamental evolutionary driving force. A major observed biogeographic pattern is the global pole-to-equatorward increase in proportional shell, or skeleton, size relative to total animal size (that is, the proportion of body mass as skeleton), in marine invertebrates (1). Polar species have proportionally smaller shells than tropical species. Studies describing shell size–latitude trends (2–6) date back nearly 50 years, but the question of “why proportional skeleton size increases with temperature across latitudes” (1) remains unanswered.

Here, we use a novel approach, based on energy budget calculations, to give new insight into the relative costs of making shells. Because energy trade-offs between shell and somatic tissue growth costs may be driven by the cost of shell production, we use data on the cost of shell production as a percentage of total energy budget and variation in proportional shell size across latitudes to examine the long-standing hypothesis that shell cost drives latitudinal gradients in proportional shell size (3, 7–10). This hypothesis is based on the theory that the cost of shell production as a proportion of the total energy budget is predicted to increase toward the poles. Carbon dioxide (CO₂) and CaCO₃ solubility increase as temperature decreases (11), causing poleward reductions in CaCO₃ saturation state (Ω_{CaCO_3}). Both increased solubility of CaCO₃ ions at lower temperatures (3, 7, 9, 10) and the poleward de-

crease in ectotherm metabolic rates (12–14) could be factors behind a potential increase in the proportion of the total energy budget an organism devotes to producing shell at higher latitudes.

Despite decades of interest, we know of no previous studies that have determined the energetic cost of shell production as a proportion of the entire energy budget, and there are no data sets containing the necessary physiological and biomineralization traits along tropical to polar latitudinal gradients required to test the shell cost hypothesis and its likely importance compared to other factors. Furthermore, rising CO₂ levels (15, 16) will make shell formation increasingly difficult for calcifying organisms (17–19). Ocean acidification is expected to increase the energetic cost of CaCO₃ production and reduce calcification (17–19), potentially altering the trade-off between shell cost and protection along latitudinal gradients. The effects of ocean acidification at high latitudes may be particularly pronounced especially in the Southern Ocean, where the amount of CO₂ absorbed is comparatively greater than in other oceans (20). Consequently, aragonite undersaturation in the Southern Ocean could occur by 2030 (21).

Using a specifically collected data set spanning 16,300 km along a 147° pole-to-pole latitudinal gradient from the Northern and Southern Hemispheres (79°N to 68°S), we adopted an energy budget approach to examine the relative importance of shell production cost on the evolution of shell size in closely related (intrageneric and intrafamilial) marine mollusks. We chose taxonomic groups that span a wide latitudinal range with very similar shell microstructure and CaCO₃ polymorphs, and used identical methods to assess both the physiological and biomineralization costs of each species. Along latitudinal gradients in temperature, we evaluated proportional shell size (the proportion of body mass as shell), growth rate, and age-specific shell production cost as a proportion of the total energy budget.

We also explore the potential effects of increasing CaCO₃ deposition cost on the energy budget. Ocean acidification is projected to decrease the saturation state of seawater (Ω) with respect to CaCO₃ mineral forms, such as aragonite and calcite, by nearly half (40.2 to 48.6%) across latitudes by 2095 (22). Because calcification can be driven by seawater pH, and Ω and pH are coupled under ocean acidification scenarios

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(23), these ~40 to 50% changes in Ω are expected to increase CaCO_3 deposition cost as calcification is strongly related to Ω (24). We therefore explore the effects on the energy budget of a potential doubling of costs associated with CaCO_3 deposition.

RESULTS

Growth coefficients [k , from von Bertalanffy growth functions (VBGFs)] were greater in tropical and warm-temperate mollusks than in their cold-water counterparts for both gastropods and bivalves (table S1). Growth coefficients (k) increased significantly with temperature along latitudinal gradients in gastropods ($F_{1,5} = 9.86, P = 0.026$; fig. S1), although a regression on the latitudinal trend in bivalve k was not significant ($F_{1,2} = 3.75, P = 0.192$; fig. S1). Larger-sized species in each group, such as *Buccinum undatum* and *Laternula elliptica*, predictably deposited greater absolute amounts of CaCO_3 compared with smaller-sized species, including tropical species (Fig. 1).

Our results indicate that shell production cost is a small component of the energy budget in the gastropod and bivalve mollusks studied. The relative annual cost of shell production as a percentage of the total annual energy budget (energy budget shell cost) varied with age and was

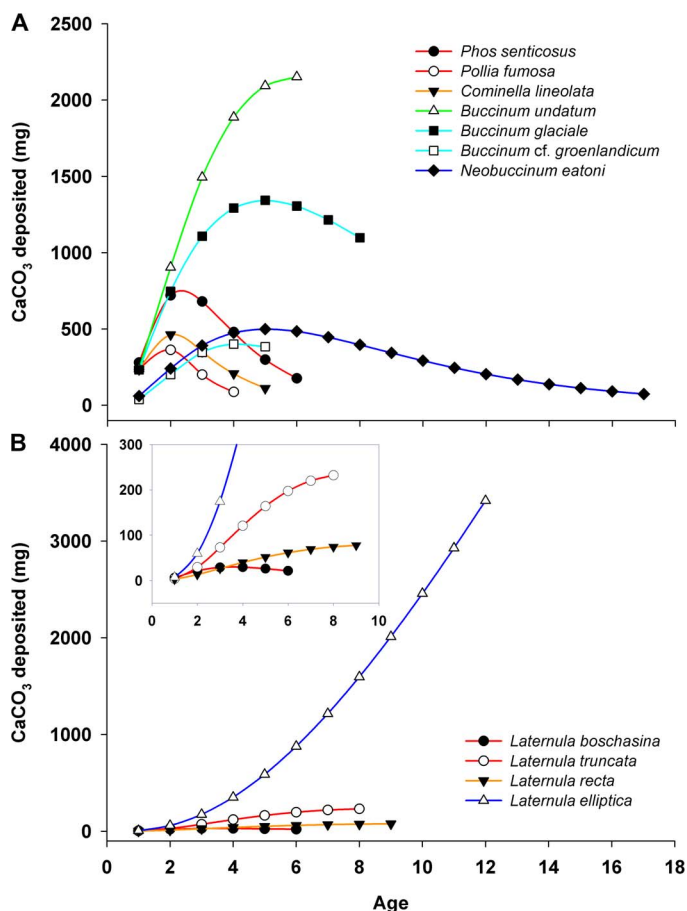


Fig. 1. Shell deposition. Amount of CaCO_3 deposited each year throughout the lifetime of species for (A) gastropods and (B) bivalves for all years of life up to the maximum age found in sample populations. Line colors denote species from tropical (red), warm-temperate (orange), cool-temperate (green), and polar (Arctic, light blue; Antarctic, dark blue) locations.

fairly low at <10% in gastropods (range, 0.3 to 9.7%) and very low at <4% in bivalves (range, 0.2 to 3.4%) across all ages (Fig. 2).

In gastropods, energy budget proportions allocated to shell cost ranged from 1.4 to 9.7% (mean \pm SE, $5.2 \pm 1.0\%$) in year 1, 3.3 to 7.5% (mean \pm SE, $5.0 \pm 0.5\%$) in year 2, and 0.3 to 4.6% at year 3 and older (Fig. 2A). In bivalves, energy budget shell cost was initially 0.2 to 3.4% (mean \pm SE, $1.5 \pm 0.7\%$) in year 1, 0.5 to 2.4% (mean \pm SE, $1.4 \pm 0.4\%$) in year 2, and 0.2 to 2.0% at year 3 and older (Fig. 2B).

For both gastropods and bivalves, shell cost varied with age (gastropods: $F_{1,25} = 38.14, P < 0.0001$; bivalves: $F_{1,14} = 101.10, P < 0.0001$; Fig. 2) and latitudinal zone (tropical, temperate, or polar; gastropods: $F_{2,4} = 15.73, P = 0.0127$; bivalves: $F_{2,1} = 1016.30, P = 0.0222$; Fig. 2 and fig. S2). Moreover, the pattern of change with age differed between latitudinal zones (gastropods: $F_{2,25} = 4.032, P = 0.0304$; bivalves: $F_{2,14} = 4.077, P = 0.0402$; Fig. 2 and fig. S2). Gastropod energy budget allocation to shell cost tended to either decrease poleward or remain constant across latitudinal zones in the early-life stages (years 1 and 2), but for subsequent life stages (year 3 onward), this cost tended to increase with

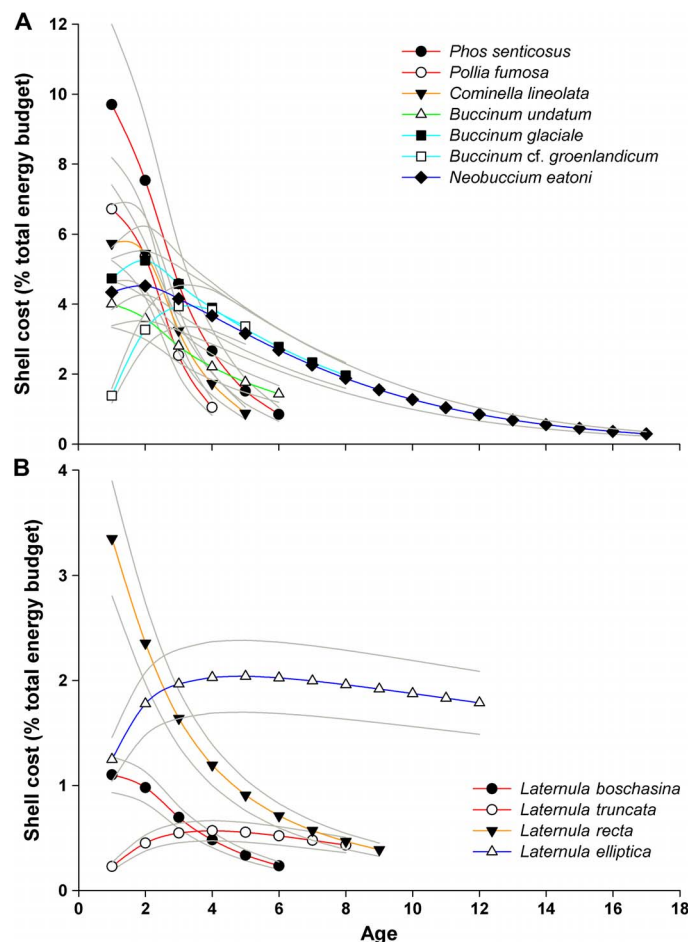


Fig. 2. Energy budget shell cost throughout the lifetime of species. Percentage of the total annual energy budget devoted to shell production for (A) gastropods and (B) bivalves for all years of life up to the maximum age found in sample populations. Line colors denote species from tropical (red), warm-temperate (orange), cool-temperate (green), and polar (Arctic, light blue; Antarctic, dark blue) locations and were calculated using the mean CaCO_3 deposition cost of 1.5 J mg^{-1} . Gray lines indicate the range of values of energy budget cost calculated using CaCO_3 deposition costs of 1 to 2 J mg^{-1} .

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latitude toward the poles. Energy budget shell cost in polar gastropods remained greater than in tropical and temperate species throughout life from year 3 (Fig. 2A). For bivalves, energy budget allocation to shell cost tended to increase with latitude, and the polar species sustained the greatest energy budget shell cost from year 3 (Fig. 2B).

Energy budget allocation to shell cost, averaged over the first 6 years of life, was low overall at $\leq 4.2\%$ in gastropods and $\leq 1.8\%$ in bivalves across latitudinal zones (Fig. 3). Doubling CaCO_3 deposition cost to 3 J mg^{-1} increased annual energy budget allocation to shell cost by 54 to 69% in gastropods ($F_{1,68} = 38.04$, $P < 0.0001$; Fig. 3A) and 48 to 50% in bivalves ($F_{1,43} = 13.85$, $P = 0.0006$; Fig. 3B) to a mean average for the first 6 years of life of $\leq 7.2\%$ in gastropods and $\leq 2.8\%$ in bivalves across latitudinal zones.

Along planetary temperature gradients, proportional shell size (the proportion of body mass as shell, measured by total animal inorganic mass/total animal dry mass) increased with increasing seawater temperature from the poles to the tropics (gastropods: $F_{1,5} = 12.92$, $P = 0.0156$; Fig. 4A; bivalves: $F_{2,1} = 225.2$, $P = 0.0471$; polar versus temperate: $t_1 = 16.81$, $P = 0.0378$; polar versus tropical: $t_1 = 21.17$, $P = 0.0301$; Fig. 4B). In contrast to proportional shell size, mean energy budget shell cost for the first 6 years of life for each species did not show a strong

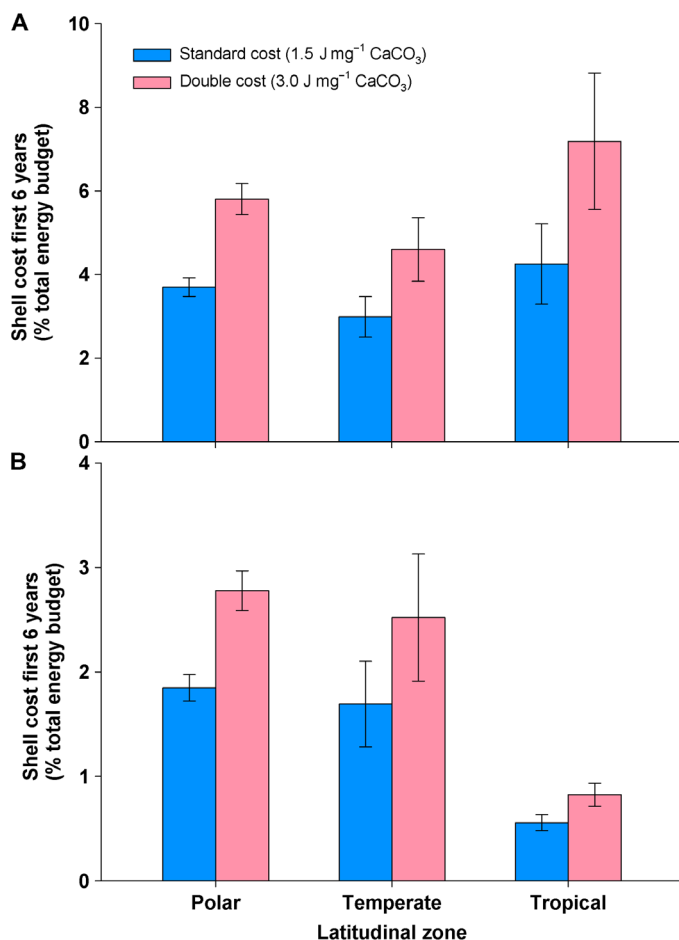


Fig. 3. Shell cost by latitudinal zone. Mean energy budget shell cost across latitudinal zones for (A) gastropods and (B) bivalves during the first 6 years of life. Data show the standard CaCO_3 deposition cost of $1.5 \text{ J mg}^{-1} \text{ CaCO}_3$ and the effect of a hypothetical doubling of CaCO_3 cost to 3 J mg^{-1} on the energy budget. Error bars are $\pm 1 \text{ SE}$.

latitudinal pattern; gastropod shell cost tended to remain fairly constant or increase slightly toward the tropics, and bivalve shell cost tended to increase toward the poles, but neither of these trends with temperature were significant (gastropods: $F_{1,5} = 0.0918$, $P = 0.7741$; bivalves: $F_{2,1} = 46.85$, $P = 0.1028$; Fig. 4).

DISCUSSION

Overall, along latitudinal gradients, as temperature decreased toward the poles, proportional shell size (proportion of body mass as shell) decreased, and gastropods and bivalves tended to grow more slowly to maximum size.

Our results suggest that shell production generally represents a small energetic cost at $<10\%$, and predominately $<5\%$, of the total energy budget in gastropods and $<4\%$ in bivalves (Figs. 2 and 3). These findings support those from a previous study on two temperate gastropods, which showed that CaCO_3 biomineralization cost was low compared to other metabolic costs (25). Here, our results show that shell production cost is a low proportion of the total energy budget and that energy budget allocation to shell cost varies with life stage (Fig. 2), and was greater in gastropods than in bivalves in early to mid-life, most likely as a function of the relatively greater amount of new shell produced per year in gastropods due to rapid shell growth relative to their soft tissues. In the tropics, the greater cost of new shell for young gastropods (years 1 and 2) (Fig. 2) may be a necessary response to high predation pressure on these individuals, and reaching a size refuge from predation (26, 27) could be the reason why warmer-water mollusks grew faster to maximum size. For burrowing bivalves, reaching an early size refuge may be less critical because the infaunal habitat offers a degree of protection from predators.

Across latitudinal zones, energy budget shell cost tended to increase toward the poles in bivalves but was more variable in gastropods. Excluding early-life stages (years 1 and 2), gastropod shell costs tended to increase toward the poles (Fig. 2). Mean energy budget shell costs for gastropods are driven by greater tropical species' costs in early life (years 1 and 2) and their potentially shorter life spans.

Although shell calcification cost is currently a fairly small proportion of the total energy budget, anthropogenic processes such as ocean acidification may increase CaCO_3 cost. A doubling in CaCO_3 mineralization cost is projected to increase energy budget allocation to shell cost by ~ 50 to 70% . As a consequence of any increasing shell cost, calcifiers have some options. They may divert energy from other components of the energy budget, consume more food, or decrease shell production. For polar species, which also experience greater seasonality of food availability (28), increasing shell costs could be more difficult to compensate because of seasonal limitations. Conditions of increased CaCO_3 cost would likely therefore alter the ecological trade-off and relative importance of shell production costs versus other abiotic and biotic factors, such as the ecological effects of predation.

While there are latitudinal trends in proportional shell size (inorganic content; Fig. 4) (1), latitudinal gradients in shell costs are less clear (Fig. 4). Because shell cost is a fairly small component of the energy budget, it may be expected to play a smaller role in explaining latitudinal gradients in proportional shell size compared with other ecological factors such as predation. From temperate to tropical latitudes, the number of carnivores in rocky intertidal systems increases (29), fish predation on gastropods increases (30, 31), and repaired gastropod shell injuries increase (8, 32). In contrast, in the Antarctic, shell-breaking predators are rare or absent from shallow-shelf habitats (33–35). However, as ocean temperatures rise, durophagous (shell-breaking) predators

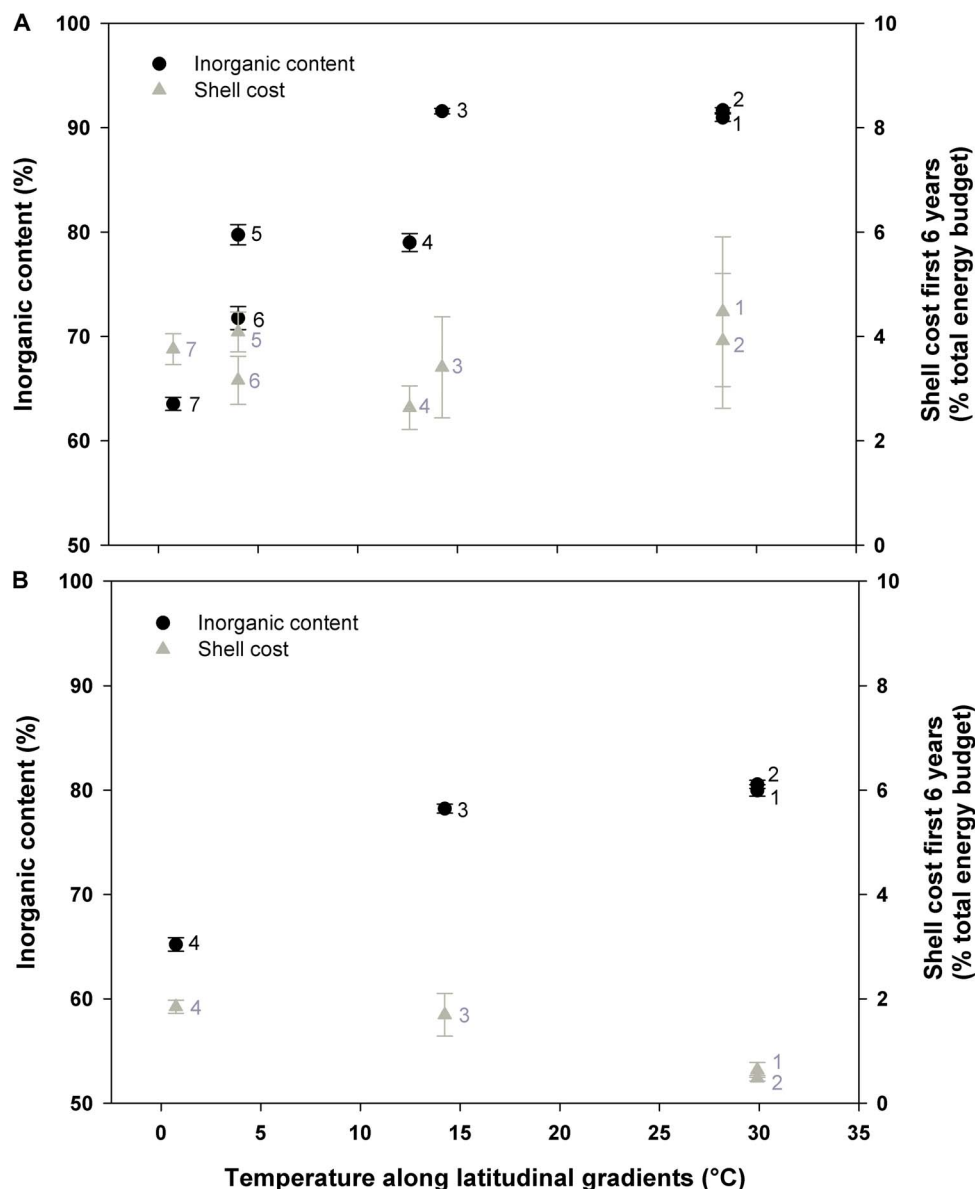


Fig. 4. Proportional shell size and cost along global temperature gradients. Latitudinal trends plotted by temperature for inorganic content (shell size) and shell cost in (A) gastropods and (B) bivalves. For gastropods (A), numbers represent species: (1) *Phos senticosus* (tropical), (2) *Pollia fumosa* (tropical), (3) *Cominella lineolata* (warm-temperate), (4) *Buccinum undatum* (cool-temperate), (5) *B. glaciale* (polar, Arctic), (6) *B. cf. groenlandicum* (polar, Arctic), and (7) *Neobuccinum eatoni* (polar, Antarctic). For bivalves (B), numbers represent species: (1) *Laternula boschasina* (tropical), (2) *L. truncata* (tropical), (3) *L. recta* (temperate), and (4) *L. elliptica* (polar). Data are means \pm 1 SE.

could expand their ranges into polar shallow waters (35, 36). The potential invasion of shell-crushing predators into Antarctic benthic ecosystems with warming (35, 36), the weak calcification of Antarctic marine invertebrates (1), and the rapidly declining saturation state of the Southern Ocean (20) may mean that shell cost is particularly important for Southern Ocean marine calcifiers. The combination of any potential increases in shell production cost and predation pressure means that ancient Antarctic calcifying communities may be particularly at risk from global change. However, ocean acidification could impair predator, as well as prey calcification, reducing the integrity of shell-breaking predatory structures and therefore predator effectiveness, and also change predator-prey behaviors in marine calcifiers (37, 38).

This study focused on taxonomically related groups (genus or family) that had representative species across a broad latitudinal range and could be field-collected live for analyses. Consequently, we used two mollusk groups as models for field studies within which 11 shelled mollusk species were analyzed comprehensively for growth, metabolic, and skeletal content data. This forms a valuable and indicative data set, but not an exhaustive one, and care should be taken not to overgeneralize these findings. Echinoderm endoskeletons, for example, are made from high-magnesium calcite ($>4\%$ mol $MgCO_3$), a more soluble $CaCO_3$ polymorph compared to the calcite and aragonite exoskeletons of mollusks. Magnesium content in echinoderm skeletons decreases with increasing latitude, and this may reduce their solubility but increase their

vulnerability to predation because echinoderm skeletons with less MgCO_3 are weaker (39). Because synthesis costs of CaCO_3 (40) and proteins for organic matrix (41), however, vary little for a wide range of calcified structures, these findings could apply broadly to other marine calcifiers. Potential uncertainties in this study include the estimation of annual energy budgets and growth. Growth rates in gastropods may be less precise because they are determined from operculum striae compared with bivalves where growth is determined from shell growth bands, and consequently, there may be a greater uncertainty in cost calculations in gastropods than in bivalves. Other aspects of the energy budget, such as mucus output and nitrogen excretion, were not evaluated, and these may vary in different patterns to growth and metabolic costs, although this is not likely. They are also relatively small fractions of the energy budget and are unlikely to markedly affect the trends identified here. Future work building on these shell cost projections could collect additional data across latitudes to project the effect of warming temperatures and associated changes in metabolic rates on shell cost along global temperature gradients.

Our taxonomically controlled analyses demonstrate that shell cost is a relatively small component of molluscan energy budgets across latitudes for the tropical to polar calcifiers examined. We find that proportions of the energy budget allocated to shell cost tend to increase in bivalves or remain relatively constant in gastropods from the tropics to the poles. However, any future shell cost increases, such as those likely to be caused by rising CO_2 , could lead to an increase in the relative importance of shell cost on the energy budget, which may be particularly important for Southern Ocean calcareous invertebrates. In future oceans, shell cost may play a greater role in dictating shell size and thus the consequent evolutionary success or failure of marine calcifiers.

MATERIALS AND METHODS

Study species

Two groups of closely related gastropod and bivalve marine mollusks that occur naturally over wide tropical to polar latitudinal gradients (147° latitude) along a natural seawater temperature range of 0.7° to 29.9°C were specifically chosen for this study. Eight sites were investigated across tropical, temperate, and polar latitudes (table S1). From low to high latitudes, these sites, species, and sample sizes [for inorganic content and ash-free dry mass (AFDM), growth, metabolic rate, and shell organic content] included (i) Singapore (*L. boschasina*, $n = 30$, 66, 19, 13; *L. truncata*, $n = 45$, 48, 30, 32); (ii) Lucinda, Queensland, Australia (*Phos senticosus*, $n = 30$, 34, 30, 30); (iii) Townsville, Queensland, Australia (*Pollia fumosa*, $n = 32$, 21, 33, 33); (iv) Port Phillip Bay, Victoria, Australia (*L. recta*, $n = 21$, 72, 22, 18); (v) Barwon Heads, Victoria, Australia (*C. lineolata*, $n = 33$, 32, 21, n/a); (vi) Southampton, UK (*B. undatum*, $n = 37$, 43, 28, 37); (vii) Rothera Point, Adelaide Island, Antarctic Peninsula (*N. eatoni*, $n = 30$, 23, 30, 29; *L. elliptica*, $n = 32$, 127, 32, 55); and (viii) Ny-Ålesund, Spitsbergen, Svalbard in the Arctic (*B. glaciale*, $n = 12$, 9, 12, 10; *B. cf. groenlandicum*, $n = 21$, 13, 21, 20) [further details of sites are provided by Watson *et al.* (1, 14)]. Specimens were collected live by hand either from the low intertidal or by SCUBA diving subtidal sites ≤ 30 m in depth. Seven confamilial gastropod species (family: Buccinidae) and four congeneric burrowing bivalve species (genus: *Laternula*) were sampled, and for each species, individuals comprising a range of sizes were collected for the analysis of shell morphological features. Before analysis, any epibionts and sediment on the shell surface were gently removed. For each species, identical methods were used to determine total animal inorganic content (proportional

shell size), growth rate, metabolism, energy budget modeling, and calcification cost of individuals.

Proportional shell size determination

For each species, shell morphology (shell length and height) was measured (to 0.01 mm) using digital calipers, and whole-animal (shell + soft tissues) dry mass, AFDM, and inorganic content were recorded (to 0.001 g). Shell terminology for gastropods was taken from Cox (42) and terminology for bivalves was taken from Cox *et al.* (43). Here, shell length and height refer to the maximum linear dimensions. Whole-animal wet weight was measured after gently blotting to remove excess water. Dry mass was measured after drying to constant mass at 60°C. AFDM was determined by loss on ignition at 475°C for 24 hours and was measured after cooling samples in a desiccator for 24 hours. Inorganic content was determined by the material remaining after ignition at 475°C for 24 hours. Proportional shell size, which is the proportion of body mass as shell, was determined from total animal inorganic content as a percentage of total animal dry mass, a proxy for shell CaCO_3 . This metric (proportional shell size) was used to provide a standardized measure of shell content and thus compare relative shell sizes among species that may have different absolute shell sizes (that is, smaller species versus larger species).

Growth and age determination

Growth rates were determined from bivalve shell increments and gastropod operculum striae. Bivalve growth increments form annually (44–47) and were measured along the growth axis of the shell (shell height) from the hinge to the growth band (43). Coiled gastropods were aged from annual operculum growth striae (48–50), and these data were plotted against shell height (42). Shell size was measured along the growth axis (that is, shell height for bivalves and gastropods), and growth was modeled by VBGFs (table S1).

Cost of shell production

We developed a new approach to determine the energetic cost of shell production as a proportion of the organism's total energy budget. Cost of shell production was determined from the amount of shell deposited each year, the absolute cost of this new shell, and the cost of new shell as a proportion of the total energy budget of the animal, as described below.

Absolute cost of shell

Annual new shell deposition was calculated from the size of each annual growth increment. The mass of new shell growth was determined by total inorganic content as above. Palmer (25) calculated the cost of CaCO_3 biomineralization by measuring the additional food consumed by thick-shelled individuals among populations of two temperate congeneric gastropods. Here, we determined the cost of new shell by adding the cost of CaCO_3 and shell organic matrix production (1 to 2 J mg^{-1} and 29 J mg^{-1} , respectively), including metabolic synthesis [after the study of Palmer (25)]. Because there is only a very small effect of a wide range of temperatures on the kinetics of crystallization (40), and crystal size has little effect on energy costs (51), the mean of 1.5 J mg^{-1} for the cost of CaCO_3 was taken for calculations in this study, and the range of 1 to 2 J mg^{-1} is also shown in Fig. 2. The synthesis cost of proteins varies little in energetic terms across latitudes and temperatures (41), so 29 J mg^{-1} was used for shell organic matrix production. Shell organic content data were taken from Watson *et al.* (1). Shell organic content was not measured for *C. lineolata*, and the mean of all other buccinid gastropods [$3.66 \pm 0.61\%$ (1 SE)] was used. Closely related species had very similar

shell microstructure and CaCO₃ polymorphs (predominately aragonite) across latitudes (52).

$$\begin{aligned} \text{Total cost of shell (J)} = & [\text{Shell CaCO}_3 \text{ mass (mg)} \\ & \times \text{Cost of CaCO}_3 \text{ at 1.5 (J mg}^{-1})] + \\ & [\text{Shell organic mass (mg)} \\ & \times \text{Cost of protein at 29 (J mg}^{-1})] \end{aligned}$$

Annual routine metabolic rate expenditure

Maintenance metabolic costs for each species were calculated by converting measured oxygen consumption [standard metabolic rates (SMRs)] for each species [data are from Watson *et al.* (14)] to energy (J year⁻¹) for each age using size and SMR data. Briefly, individuals of each species were fasted and gently transferred to respirometers underwater, and SMR was determined using a fiber-optic, temperature-compensated oxygen meter (PreSens). The commonly used oxycalorific coefficient 4.8 cal·ml O₂⁻¹ (53) was used to convert oxygen consumption to power expenditure (metabolic energy expenditure). Annual metabolic rates were calculated from measured metabolic rates using published seasonal correction factors (table S2). SMR was converted to routine metabolic rate by multiplying SMR by the postprandial rise in metabolism following feeding, the specific dynamic action (SDA), using the mean of 2.2 (table S3).

Somatic growth per year

Annual somatic growth (P_g) increments were calculated and added to values of respiration (R) to produce an estimate of energy use as the main components of the energy budget. Energy used as somatic growth (P_g) was determined from annual organic content increases determined from AFDM for each species. Soft tissue (organic content) energy content was calculated by multiplying AFDM by the tissue energy content for each taxon (gastropods, 23.27 J mg⁻¹; bivalves, 22.79 J mg⁻¹) from Brey *et al.* (54).

Annual energy budget estimation

The annual energy budget for each species was estimated using the energy equation

$$I = E + P_g + P_r + R + U + M$$

where I is ingestion, E is egestion, P_g is somatic growth, P_r is reproductive investment, R is respiration, U is excretion, and M is mucus production (55). Energy budgets were estimated from respiration (R) and somatic growth (P_g)—the components that usually comprise the largest proportion of the energy budget and were scaled up to the total energy budget from published values. The percentage of the energy budget accounted for by R and P_g was sourced from mollusk energy budget data summarized by Bayne and Newell (56). Values used for the combined proportions of the energy budget accounted for by R and P_g were 52.5% ($n = 11$) and 45.3% ($n = 14$) for gastropods and bivalves, respectively. The total age-specific energy budget for each year of life was calculated by

$$\begin{aligned} \text{Total energy budget (J)} = & [\text{Energy (J) from } R + P_g] * 100 / \\ & [(R + P_g)\% \text{ of total energy budget}] \end{aligned}$$

Cost of shell as a percentage of the energy budget

For each year of life, shell size, shell mass deposited, cost of shell mass deposited, and the estimated total annual energy budget were used to calculate the cost of shell as a percentage of the estimated total annual energy budget across the age and size range measured for each species

$$\begin{aligned} \text{Annual cost of shell as a percentage of the} \\ \text{total energy budget (\%)} = & \text{Energy required to} \\ & \text{build shell mass deposited per year (J year}^{-1}) / \\ & \text{Annual total energy budget (J year}^{-1}) * 100\% \end{aligned}$$

Annual energy budget shell costs among species were compared. Mean costs of shell production (percentage of the total annual energy budget) for the first 6 years of life were calculated for species from each latitudinal zone (tropical, temperate, and polar).

Effect of increasing CaCO₃ cost

The cost of CaCO₃ deposition may increase in future oceans, for example, with increasing anthropogenic CO₂ uptake and associated ocean acidification. Although some calcifiers can up-regulate pH at the site of calcification (57), ocean acidification generally reduces calcification in marine organisms (58). To explore the potential effect of increased CaCO₃ biomineralization cost on shell production cost as a proportion of the total energy budget, we explored the effect of a potential doubling of CaCO₃ cost, to 3.0 J mg⁻¹ CaCO₃, on the energy budget.

Statistical analysis

Latitudinal data were analyzed using mean annual temperature for each location rather than latitude because of slight differences in ocean thermodynamics at high latitudes (for example, the Northern Hemisphere Gulf Stream). We used linear mixed-effects modeling to analyze species traits along latitudinal temperature gradients including growth coefficients (k), inorganic content, and energy budget shell costs. In the models, species was included as a random effect, and heterogeneity of variance was included to improve model fit where appropriate. The energy budget shell cost modeled for all ages had a nonlinear relationship with age, modeled as a quadratic polynomial. The fixed effects were therefore latitudinal zone (tropical, temperate, and polar), age and age², as well as zone:age and zone:age² interactions. Species was included as a random effect, and a random slopes model was fitted so that the coefficients of age and age² were allowed to vary among species within a zone. Factorial analyses were conducted on multiple observation data with three independent factor levels. TIBCO Spotfire S+ 8.2 and SigmaPlot 11.0 were used for statistical analyses. Akaike information criterion, likelihood ratio tests, and residual analysis were used to examine model fit and assumptions of analyses.

SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/3/9/e1701362/DC1>

table S1. Species, locations of collection sites, and VBGF parameters.

table S2. Scaling factors used to convert metabolism into annual metabolism for species from seasonal locations.

table S3. Specific dynamic action.

fig. S1. Growth coefficients (k) from VBGFs for gastropods and bivalves along latitudinal temperature gradients.

fig. S2. Shell production cost as a percentage of the total annual energy budget displayed for each latitudinal zone.

References (59–66)

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