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Temperature Effects on the Distribution of Aragonitic and Calcite-Secreting Epifaunal Bivalves

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ABSTRACT

Aim: To test if temperature significantly influences the global biogeographic distribution of marine epifaunal bivalves via their skeletal mineralogy.

Location: Global.

Taxa: Marine, epifaunal bivalves.

Methods: The skeletal mineralogy of 45,789 epifaunal bivalve occurrences from 669 species from the Ocean Biodiversity Information System (OBIS) was related to sea surface temperatures from Bio-ORACLE. Binomial regression was used to assess the influence of temperature and seasonality on the distribution of aragonitic and calcite-secreting bivalve occurrences, aggregated in equal-area grid cells.

Results: The proportion of aragonitic bivalve occurrences significantly increases with mean annual temperature in our global analysis and most marine biogeographic realms. A greater prevalence of calcite-secreting bivalves in seasonal climates could be shown at low mean annual temperatures at the global scale but not within biogeographic realms.

Main Conclusions: The global biogeographic distribution of epifaunal bivalves is significantly influenced by water temperature via their skeletal mineralogy. The mechanism driving this pattern is best explained by the temperature modulation of the effect of Mg^{2+} on calcite growth. Although this Mg^{2+} effect predicts an advantage for aragonite secretion at higher temperatures, poleward migration in response to higher temperature extremes will expose tropical taxa to cooler temperatures in the cold season, which may impede aragonite secretion in taxa not adapted to these climates.

Significance: Our results suggest that skeletal mineralogy is likely to influence ocean warming-induced migration patterns.

1 | Introduction

With increasing ocean warming and acidification (OWA) (IPCC 2019, 2021), great efforts are undertaken to understand how marine organisms respond to anthropogenic climate change (Poloczanska et al. 2016). Ocean acidification particularly threatens calcifying organisms, as the rising pCO_2 and falling pH increase the solubility of their calcium carbonate ($CaCO_3$) skeletons (Orr et al. 2005), and the effect of ocean warming can either compound or mitigate the negative impact of ocean acidification (Harvey, Gwynn-Jones, and Moore 2013; Knights et al. 2020). A key aspect of marine calcifiers that is likely to influence the vulnerability to OWA is their skeletal $CaCO_3$ mineralogy (Andersson, Mackenzie, and Bates 2008; Ries 2011; Figuerola et al. 2021) as aragonite is more soluble than calcite (Morse, Arvidson, and Lüttge 2007).

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Temperature change, too, may differentially impact aragonitic and calcitic taxa as it impacts the saturation state of aragonite and calcite and modulates the effect of naturally abundant Mg^{2+} ions on $CaCO_3$ mineral formation. While the abiotic formation of calcite is thermodynamically favoured, Mg^{2+} ions kinetically inhibit calcite growth but not aragonite (Davis, Dove, and De Yoreo 2000; Morse, Arvidson, and Lüttge 2007), thus providing a mechanism explaining why $CaCO_3$ precipitates as aragonite or calcite. The high Mg/Ca ratio (~5) in modern seawater generally favours inorganic aragonite precipitation at temperatures above 15°C (Balthasar and Cusack 2015), whereas calcite formation is favoured in cooler waters. Conventionally, the prominence of calcitic taxa in cooler or brackish waters is generally attributed to the low $CaCO_3$ saturation state in these conditions and its impact on the more soluble aragonite (e.g., Ramajo et al. 2015; Taylor and Reid 1990). However, decreasing saturation state should not favour one polymorph over another unless seawater is undersaturated for aragonite while remaining oversaturated for calcite.

Although genetic controls generally determine skeletal mineralogy (Lowenstam and Weiner 1989), geographic patterns of increased calcite secretion at lower temperatures, analogous to abiotic patterns of $CaCO_3$ mineralisation, have been reported for a number of calcifying taxa including gastropods (Cohen and Branch 1992; Ramajo et al. 2015), bivalves (Lowenstam 1954a, 1954b; Dodd 1963, 1964; Waller 1972), serpulids (Lowenstam 1954a, 1954b) and bryozoans (Figuerola et al. 2022; Piwoni-Piorewicz et al. 2024; Lombardi et al. 2008; Kuklinski and Taylor 2009).

In bivalves, the aragonite proportion in the shells of several bimineralic species has been shown to increase with the average water temperature (Lowenstam 1954a, 1954b, Dodd 1963, 1964, Waller 1972). The temperature influence on biomineralisation appears to affect the geographical distribution of mytilid bivalves, with aragonitic mytilid species having more often a tropical affinity and bimineralic species preferentially occurring in temperate climates (Carter 1980). For other bivalves, the global biogeographical distribution of shell mineralogy and possible factors governing such a distribution are unknown.

For most bivalve species, it remains unknown to what extent shell composition can be adjusted to match differing environmental constraints. Biomineralisation plasticity may be inferred indirectly via the environmental occupancy of bivalve taxa. For example, if bivalves with calcitic and aragonitic shell layers are generally able to adjust their shell aragonite: calcite ratio in response to seasonal temperature change, they may be better adapted to changes in seasonal temperature variation than purely aragonitic bivalves. Revealing patterns in the environmental occupancy of aragonitic and calcitic bivalves may therefore facilitate predicting the responses of marine bivalves to future climate change.

2 | Methods

2.1 | Data

Bivalve occurrence data from the Ocean Biodiversity Information System (OBIS, https://obis.org/) were downloaded on 26 October 2020. The initial download comprised 1,339,903 occurrences of marine bivalves. Several taxonomic corrections and exclusions of taxa were manually implemented using information from the World Register of Marine Species (WoRMS, http://www.marinespecies.org/), keeping only occurrences from valid, extant species (Table S1). Bivalve taxa were sorted into two mineralogical categories: aragonitic, and calcite-secreting. 'Aragonitic' denotes all bivalves that lack calcitic shell layers, although some aragonitic bivalves may exhibit patchy calcite within an aragonitic shell layer (Carter, Barrera, and Tevesz 1998). Aragonitic bivalves are contrasted with bivalves that (1) secrete one or more distinct calcitic shell layers in addition to an aragonitic shell layer, as, e.g., many species of *Mytilus* or (2) secrete an entirely calcitic adult shell such as members of the superfamily Ostreoidea (Kennedy, Taylor, and Hall 1969). Because even wholly calcitic bivalves secrete aragonite as juveniles, we grouped calcitic species with bimineralic species. Our assignments of bivalve mineralogy are largely based on Carter, Barrera, and Tevesz (1998), with additional information from other publications (Taylor 1969, 1973; Hautmann 2001; Dijkstra and Maestrati 2012; Waller 2012). As the mineralogy of Mytilidae is highly variable at the genus and species level, Mytilidae species for which no information on skeletal mineralogy could be obtained were excluded from the data set.

All infaunal bivalves are aragonitic and therefore do not change mineralogy with temperature; they were excluded from our data set (Table S1).

The environmental data were retrieved from Bio-ORACLE (Tyberghein et al. 2012; Assis et al. 2018). Data layers of modelled mean annual temperature, mean annual temperature range (seasonality, i.e., the difference in mean temperatures of the coldest and the warmest months) and mean salinity of the sea surface (as practical salinity units) of each grid cell were downloaded via the R package 'sdmpredictors' (Bosch, Tyberghein, and De Clerck 2017). Underlying the climate and salinity models are monthly averages from the years 2000 to 2014. The resolution of the modelled data sets is 0.083° longitude and latitude, which translates to cells of ca. 9×9 km at the equator. These environmental data were assigned to every bivalve occurrence falling into the same grid cell. Occurrences for which Bio-ORACLE records no information were excluded. Salinity has been shown to differentially affect aragonite and calcite secretion in *Mytilus* living under salinities of 5.4–34.8 (Telesca et al. 2019). The resolution of environmental data in Bio-ORACLE is, however, too coarse to reliably capture salinity variations in estuaries. To reduce the potential conflation of temperature trends with salinity effects, occurrences from waters of salinity < 30 and the few occurrences associated with salinity > 40 were excluded. As temperature and $CaCO_3$ saturation change with water depth, we restricted the analyses to bivalves from depths ≤ 100 m.

The spatial coverage of bivalve occurrences in OBIS is uneven, with the majority being recorded in Europe, eastern North America, Australia and New Zealand. Aggregating data into grids tends to lower the dominance of the strongly sampled region, as a large share of samples originates from a small area. We aggregated the data into pentahexagonal, equal-area grid cells in three different resolutions (cell diameters of 139, 247 and 555 km) with the R package *icosa* (Kocsis 2017). The sea surface temperatures of the occurrences of a grid cell are more homogenous at finer resolutions, whereas the distribution of the cells between biogeographic realms (see below) becomes more even with increasing cell size (Figure S1). For the analyses, we chose the grid with the intermediate resolution, with a diameter of 247 km and 12,962 faces, with a cell area of ca. 39,000 km^2. The mean annual sea surface temperatures and seasonalities of all occurrences of a grid cell were averaged for the analyses. To gauge the impact of the grid resolution on the results, the global-scale analysis was repeated with a coarser and a finer grid.

A total of 493 grid cells contained bivalve occurrences from at least two bivalve species. Cells with only one species and cells that were strongly dominated by one or two species were excluded from the analyses, as those likely represent sampling artefacts, e.g., *Mytilus edulis* in the North Atlantic or *Pecten novaezelandiae* in New Zealand. Therefore, we excluded cells with a Shannon evenness below 0.5, resulting in the removal of 38 cells. An alternative cutoff point, excluding cells with a Berger–Parker dominance >0.75, led to similar results in the global analysis. The main analyses were carried out with 454 cells, containing a total of 45,789 occurrences from 669 species. The distribution of data among the biogeographic realms is shown in the Table S2.

2.2 | Analyses

To assess whether the environmental variables (mean annual water temperature and seasonality) predict the occurrence of aragonitic and calcite-secreting bivalves (including bivalves with both aragonitic and calcitic shell layers), we carried out binomial regressions, with mineralogy (aragonitic or calcite-secreting) as the dependent variable. Environmental predictors were standardised to zero mean and unit variance to permit a direct comparison of regression coefficients (effect sizes).

The number of aragonitic occurrences (a_i) in grid cell i is modelled as a binomial distribution,

$$a_i = \text{Binomial}(n_i, p_i), \qquad i = 1, \dots N, \tag{1}$$

with n_i denoting the number of all occurrences in cell i and p_i denoting the probability of an occurrence being purely aragonitic (i.e., lacks the ability to secrete calcite). N denotes the total number of grid cells across which bivalve occurrences are distributed. The log-odds (logit) of p are regressed against mean temperature (T), seasonality (S) and against the interaction term of temperature and seasonality (TS), with α denoting the intercept and β denoting the slopes:

$$\text{logit}(p_i) = \alpha + \beta_T T_i + \beta_S S_i + \beta_{TS} T_i S_i \tag{2}$$

This regression was implemented with the GLM function in R, version 4.0.2 (R Core Team 2020). Analogous regressions were implemented with seasonality (S) instead of T and with both T and S as predictors. Model selection was carried out with the Akaike information criterion (AIC). As a goodness-of-fit measure, the deviance-squared (D^2) was calculated with the R package *modEvA* (Barbosa et al. 2020).

In addition to these global-scale analyses, we implemented hierarchical regression with partial pooling (Kruschke 2014; McElreath 2016) at the scale of marine, biogeographic realms defined by Spalding et al. (2007). Here, the temperature values of realms were standardised separately, ensuring that the regression coefficients of different realms can be readily compared. Four realms with little data (8–10 grid cells) were excluded, restricting the analysis to the eight realms with good sampling (16–112 grid cells).

The binomial regression shown above is modified to:

$$a_i = \text{Binomial}(n_i, p_i) \tag{3}$$

$$\begin{gathered} \text{logit}(p_i) = \alpha_j + \beta_{T,j} T_i + \beta_{S,j} S_i + \beta_{TS,j} T_i S_i \\ i = 1, \dots N_j, \qquad j = 1, \dots 8 \end{gathered} \tag{4}$$

This model estimates an individual intercept α_j and slope β_j for each realm j. N_j denotes the number of grid cells in realm j. α_j, $\beta_{T,j}$, $\beta_{S,j}$ and $\beta_{TS,j}$ are assumed to stem from a common normal distribution each, with mean μ and precision τ.

The slopes of realm j are informed by the relationship of skeletal mineralogy and temperature and seasonality within realm j and by the overall mean relationship across all eight realms. The influence of $\mu_{T\beta}$ on $\beta_{T,j}$ depends on the amount of data in realm j and decreases with N_j. The same holds true for α_j and the other slope parameters.

The hierarchical regression was fitted in the Bayesian framework, which was preferred over a frequentist approach due to allowing better uncertainty quantification, providing full posterior distributions rather than point estimates (Gelman et al. 2013). The analysis was implemented using the jags program (Plummer 2012), accessed in R through the R2jags package (Su and Yajima 2015). The inference is based on three chains, each with 15,000 iterations of a Markov chain Monte Carlo algorithm, the first 5000 of each were discarded as burn-in. Normal distributed priors with mean zero and a standard deviation of 10 were placed on μ_α, $\mu_{\beta T}$, $\mu_{\beta S}$, $\mu_{\beta TS}$. Changing the standard deviation of these priors to 1 or 100 did not substantially affect the results. For τ_α, $\tau_{\beta T}$, $\tau_{\beta S}$, $\tau_{\beta TS}$, log-normal distributed priors with mean zero and a standard deviation of 10 were used.

An analogous regression was implemented for only temperature (T), seasonality (S) and with T and S without the interaction term. The deviance information criterion (DIC) was used for model selection.

To assess the significance of regression parameters, 95% confidence intervals were used for the global-scale generalised linear models, and 95% credible intervals were used for the Bayesian analyses at the scale of biogeographic realms. For simplicity, both are abbreviated as '95% CI'.

The effect of global warming on the temperatures experienced by migrating organisms was estimated using projections from the Coupled Model Intercomparison Project Phase 6 (CMIP6). We downloaded long-term (2081–2100) sea surface temperature projections from the SSP3.7 scenario at a grid resolution of 1° longitude and latitude from the IPCC AR6-WWG Interactive Atlas (https://interactive-atlas.ipcc.ch). The relationship between the mean annual temperatures (and cold season temperatures) and the temperatures of the warm season was estimated with a LOESS regression with a span of 0.1. This LOESS regression was carried out separately for the baseline temperatures (1981–2010) and for the long-term projections.

3 | Results

The geographical distribution of epifaunal bivalve occurrences shows no universal latitudinal trend in skeletal mineralogy (Figure 1a). Although the proportion of aragonitic bivalves decreases with increasing latitude in some regions (e.g., along the East coast of North America), aragonitic bivalves are also common in temperate and polar regions. Cross-plots of temperature and seasonality indicate that cells with many aragonitic occurrences are concentrated in polar and warm temperate regions (Figure 1b,c). The relationship between the proportion of aragonitic occurrences (*P. arag.*) and mean annual temperature (*T*) and seasonality (*S*) was assessed with multiple binomial regression. Model selection resulted in a model with *T*, *S* and the interaction *TS* as predictors ($D^2 = 0.15$, Figure 2a–c-3). Globally, the proportion of aragonitic occurrences (*P. arag.*) generally increases with annual mean temperature ($\beta_T = 0.41$, 95% CI = 0.38–0.44). The slope of *S* is not significant ($\beta_S = 0.02$, 95% CI = −0.01 to 0.04), but the slope of the interaction term (*TS*) is significant ($\beta_{TS} = 0.30$, 95% CI = 0.27–0.32) and substantially moderates the

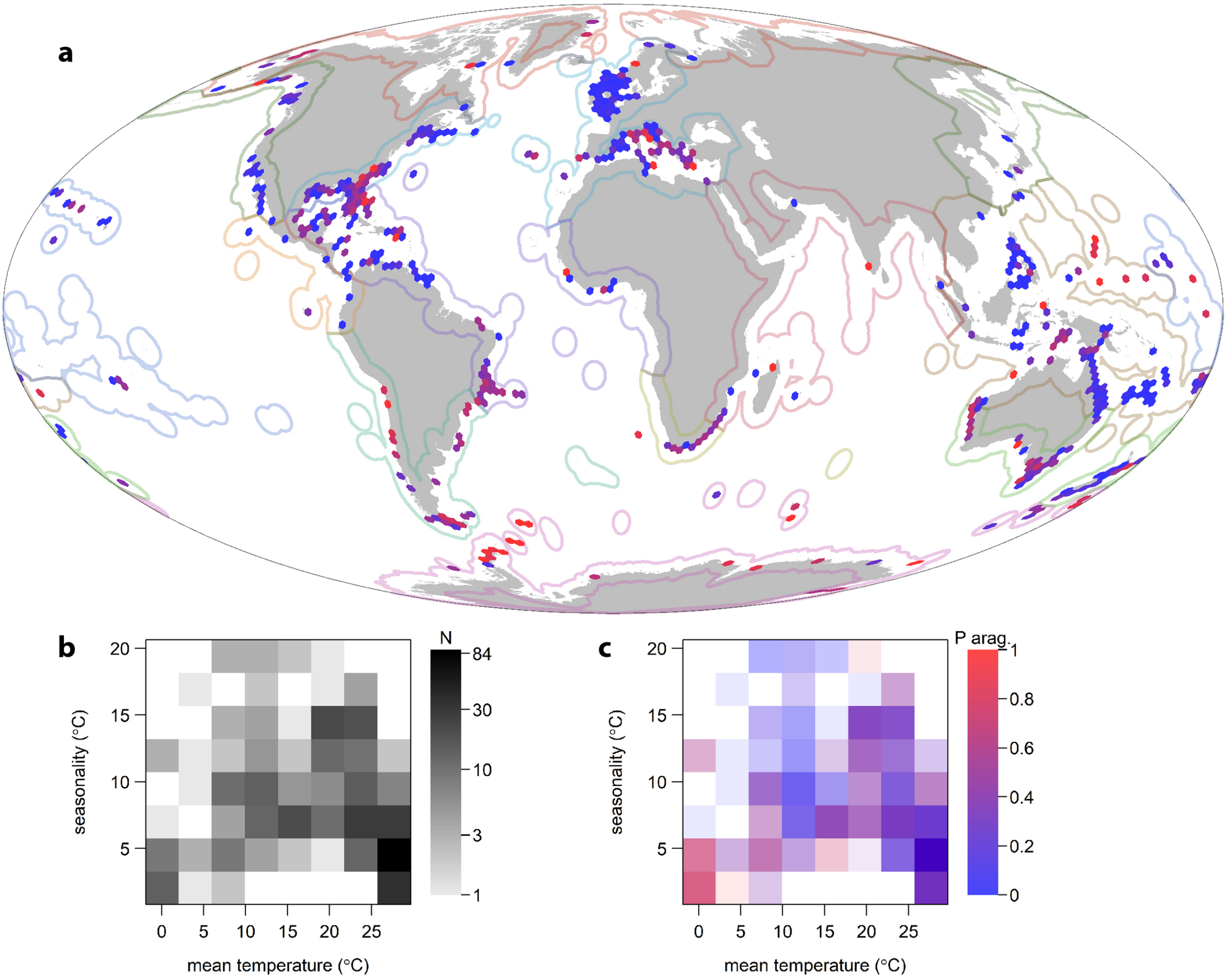

FIGURE 1 | Skeletal mineralogy and environmental occupancy of epifaunal bivalve occurrences from OBIS. (a) Bivalve occurrences are shown aggregated in an equal-area hexagonal grid (cell diameter = 247 km, cell size ~39,000 km^2). Colours indicate the proportion of aragonitic occurrences in each grid cell, ranging from red (aragonitic taxa only) to blue (calcite-secreting taxa only). Only cells with at least two species and a Shannon evenness ≥0.5 are shown here and in (b, c). Faint, coloured outlines indicate the marine, biogeographic realms shown in Figure 3. (b) Two-dimensional density plot of the average mean annual sea surface temperature and seasonality of the grid cells occupied by bivalves, shown in (a). Shading indicates the number (*N*) of grid cells in each square of the raster, with darker shades indicating more occurrences. (c) Skeletal mineralogy of bivalve occurrences superimposed on the 2D density plot from (b). Colours indicate the average proportion of aragonitic bivalve occurrences in the grid cells falling into each square of the raster.

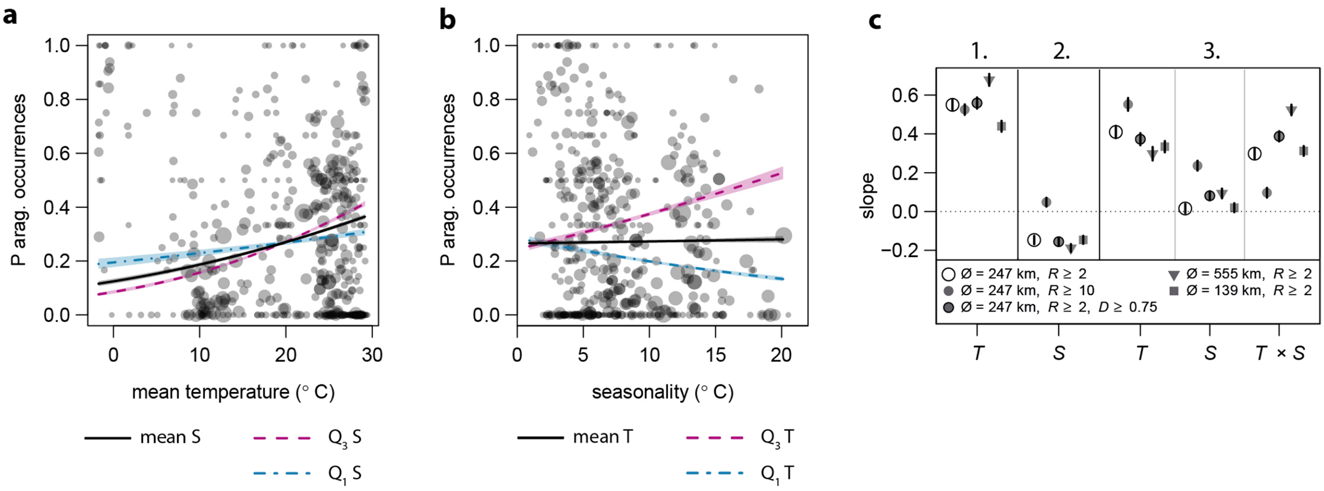

FIGURE 2 | Environmental patterns in the mineralogy of bivalve occurrences. (a, b) Multiple binomial regression of the probability that occurrences from a grid cell are aragonitic (*P. arag.*), against the averaged annual mean temperature (T) and seasonality (S) of the occurrences of that grid cell, including the interaction term $T \times S$ as a predictor. The Pearson correlation of T and S is −0.18. Regression coefficients and associated statistics are reported in the Table S1. (a) Predicted relationship between *P. arag.* and T, with S being fixed at the mean value (7.6°C, black, solid line), 1st quartile (4.4°C, blue, dash-dotted line) and 3rd quartile (10.2°C, purple, dashed line). Shadings here and in (b) denote 95% CI around the regression lines. (b) Predicted relationship between *P. arag.* and S, with T being fixed at the mean value (20.1°C, black, solid line), 1st quartile (14.0°C, blue, dash-dotted line) and 3rd quartile (27.0°C, purple, dashed line). (c) Slopes (effect sizes) of regressions of *P. arag.* against T (1.), against S (2.) and against $T+S+T \times S$ (3.). The open circles denote the slopes of regressions with the data aggregated at the grid resolution used throughout this study, a cell diameter (Ø) of 247 km, with regression 3. Being visualised in (a, b). The grey, filled circles denote the slopes of regressions with the same grid resolution but with only cells with a species richness (R) of 10 or more. The grey, filled circles with a black outline denote the slopes of regressions with the same grid resolution with a species richness (R) of 2 or more, but including only cells with a Berger–Parker dominance ≤0.75, instead of the evenness threshold of 0.5 applied in the other analyses. The triangle and the square show the slopes of regressions with a finer and coarser grid resolution, respectively.

predicted relationship of *P. arag.* with T and S. The relationship of *P. arag.* with T remains positive at most values of S, although the strength of the relationship increases with S (Figure 2a). The predicted relationship of *P. arag.* and S is insignificant at mean T but is positive at high temperatures and negative at low temperatures (Figure 2b). For comparison, the regression coefficients of the models with only T and S, respectively, are shown in Figure 2c. The regression coefficient of T changes relatively little when omitting S and remains significantly positive, and D^2 decreases to 0.11. The regression with only S has a negative slope and a very low goodness of fit ($D^2 = 0.01$). Varying the resolution of the spatial grid in which the data were aggregated, or the diversity thresholds for excluding poorly sampled cells, differentially affects the regression coefficients. The slope of T varies the least (0.30–0.56), whereas the slopes of S and TS and are more sensitive to changes in the analytical protocol, although the slope of TS remains significantly positive (Figure 2c).

To test whether a salinity effect on bivalve mineralogy remains, despite excluding occurrences from brackish and hypersaline water (salinity < 30 and > 40, respectively), salinity was included in an additional regression with T, S and TS. Salinity negatively predicts aragonitic occurrences ($\beta_{\text{salinity}} = -0.22$, 95% CI = −0.18 to −0.25), but the regression coefficients of T, S and TS change little (Figure S2).

At the scale of marine, biogeographic realms, model selection also resulted in a model with T, S and TS being favoured (Figure 3, Tables S4 and S5). The overall mean relationship of *P. arag.* and T, estimated with this hierarchical regression, is positive but not significant ($\mu_{\beta T} = 0.56$, 95% CI = −0.27 to 1.40) and is positive in five out of the eight realms included in the regression (Figure 3d). Significantly negative relationships are predicted in the Tropical Atlantic and in the Southern Ocean (Figure 3), although the relationship in the Tropical Atlantic switches sign when not including S. A significantly positive relationship of *P. arag.* and S ($\mu_{\beta S} = 0.56$, 95% CI = 0.17 to 0.96) emerges in the hierarchical regression. The interaction of T and S is not significant ($\mu_{\beta TS} = -0.14$, 95% CI = −0.48 to 0.19) and has only a moderate effect on their predicted relationships with *P. arag.* (Figure 3b,c). The regression coefficients in a regression with only T are mostly similar to those in the full regression (Figure 3d), whereas the regression coefficients in an analysis with only S change substantially, particularly in those realms in which T and S are strongly correlated (Figure 3).

4 | Discussion

4.1 | Temperature as a Driver

The results of this study support our hypothesis that the relative abundance of aragonitic bivalves increases, on average, with the mean annual water temperature, and calcite-secreting bivalves in turn occur more commonly in cooler water. This trend is evident at the global scale and in most biogeographic realms (Figures 2 and 3), suggesting that water temperature differentially affects bivalves with different shell compositions. As the mineralogy of shell layers is evolutionarily conservative (Harper, Palmer, and Alphey 1997) and uniform within most families (Carter, Barrera, and Tevesz 1998), bivalves cannot change their skeletal mineralogy to adapt to changing environmental conditions. Temperature impacts skeletal mineralogy by modulating the effect of Mg^{2+} as a calcite-specific growth inhibitor (Davis, Dove, and De Yoreo 2000; Balthasar and Cusack 2015), which has significantly shaped the biogeographic distribution of marine calcifiers throughout much of the Phanerozoic (Eichenseer et al. 2019). Although the strength of this influence strongly decreased since the mid-Jurassic, laboratory experiments suggest that the Mg^{2+} effect (Checa et al. 2007; Ries 2010) and its temperature modulation (Higuchi et al. 2017) still impact modern marine calcifiers.

The seawater Mg/Ca ratio can be considered the main driver of the Mg^{2+} effect, but insufficient data at an appropriate spatial resolution do not currently allow a direct test of this hypothesis. Existing data show that Mg/Ca varies between 4.1 and 6.6 in shallow water (<100 m) coastal settings of the salinity range of 30–40 (Figure S3) and is dependent on local factors such as riverine input, coastal upwelling or glacial runoff (Lebrato et al. 2020). While these Mg/Ca strongly favour aragonite precipitation at temperatures above 15°C in inorganic systems (Balthasar and Cusack 2015), experimental data suggest that skeletal mineralogy of marine invertebrates can be impacted by Mg/Ca ratios within this range (Ries 2010). This variability in local Mg/Ca has the potential to considerably mask the temperature signal on skeletal mineralogy in our global and regional analyses.

Calcite and aragonite saturation state also influences the Mg^{2+} effect as the calcite inhibition by Mg^{2+} is somewhat mitigated by higher saturation states (De Choudens-Sánchez and González 2009). Biogenically, shell secretion becomes metabolically more costly at a lower saturation state (Watson, Morley, and Peck 2017), which is likely to increase selection for metabolically cheaper skeletal materials in the context of environmental conditions. As both aragonite and calcite saturation state decrease with decreasing temperature and with decreasing salinity, stronger selection for the environmentally favoured skeletal mineralogy should generally be expected for cooler and less saline waters, but local variability in saturation state (e.g., Robbins et al. 2018) would also mask the temperature signal on skeletal mineralogy in our data set.

A similar biogeographic pattern of an increasing proportion of calcite-secreting species with cooler temperatures has been noted for bryozoans (Figuerola et al. 2022; Piwoni-Piorewicz et al. 2024), and together with various case studies on bimineralic species that show increasing calcite deposition with cooler temperatures in gastropods (Cohen and Branch 1992; Ramajo et al. 2015), serpulids (Lowenstam 1954a, 1954b) and bivalves (Lowenstam 1954a, 1954b; Dodd 1963, 1964; Waller 1972), it seems likely that this is a fundamental biogeographic pattern of calcifying clades with aragonite and calcite-secreting species.

Our analyses do not indicate a consistent relationship of seasonality with shell mineralogy. Globally, a greater prevalence of calcite-secreting bivalves at high seasonalities is supported for cool annual temperatures (Figure 2), but this trend is reversed in tropical climates, where seasonality tends to be low. At regional scales, a greater prevalence of aragonitic bivalves is predicted at high seasonality when accounting for mean annual temperature, although this association is complicated by the strong collinearity of temperature and seasonality within most realms.

4.2 | Outlook for the Future

The observed association of aragonitic bivalves and warm temperatures provokes the exploration of how the current and projected warming of the oceans (IPCC 2019, 2021) may affect the distribution of aragonitic and calcite-secreting bivalves. A straightforward prediction would be that warming favours aragonitic bivalves over calcite-secreting bivalves analogous to the temperature-related aragonite expansion in the shells of *Mytilus* and other bimineralic taxa. Yet, skeletal mineralogy may play a more subtle role in shaping the response of bivalves to warming oceans.

Tropical, marine ectotherms tend to live relatively close to their upper thermal limits (Nguyen et al. 2011; Pinsky et al. 2019), and ocean warming has caused local extirpations and range shifts (Poloczanska et al. 2013; Wiens 2016). More than annual mean temperatures, higher temperature extremes affect the fitness of organisms (Clusella-Trullas, Blackburn, and Chown 2011; Ma, Rudolf, and Ma 2015). Recent climate models predict substantially higher mean temperatures and greater seasonal temperature amplitudes for the surface ocean across most of the globe (Kwiatkowski et al. 2020). Due to the increasing seasonality towards the temperate zones, tropical organisms that migrate polewards to track tolerable summer temperatures are likely to encounter lower annual mean temperatures, especially colder winter temperatures than in their current environments (Figure 4). This effect is most pronounced in the tropics, where organisms are moving towards the more variable temperate zones (Figure 4c). For calcifiers moving poleward due to equatorial warming, cooler winter temperatures may make calcification more costly, and this may especially pertain to the secretion of aragonite (see Ramajo et al. 2015). In higher latitudes, bivalves commonly react to unfavourably cold winter temperatures with a cessation of growth and are therefore likely to tolerate moderate changes in winter temperatures. Most tropical and subtropical species, however, lack this response (Killam and Clapham 2018). Low temperatures of the cold season may thus represent an overlooked impediment for bivalves that shift their range poleward in response to climate change, and the warming of the ocean may have conflicting effects on the distribution of bivalves with regards to their skeletal mineralogy. While warming per se would be expected to favour aragonite secretion, calcite-secreting bivalve species may be more apt at tracking poleward-shifting climates than aragonitic bivalves.

Skeletal mineralogy has additional importance for the future distribution and ecological success of marine calcifiers in the context of ocean acidification. The surface water pH is decreasing by about 0.002 units per year, on average (Stocker et al. 2014), with detrimental effects for many marine calcifiers (Gazeau et al. 2013; Kroeker et al. 2013). It is sometimes suggested that aragonitic calcifiers may be more vulnerable to ocean acidification than organisms with a calcitic skeleton. Experimental evidence is, however, ambiguous, with most, but not all, aragonitic and calcitic bivalves responding negatively to ocean acidification (Ries, Cohen, and McCorkle 2009; Parker et al. 2013). An

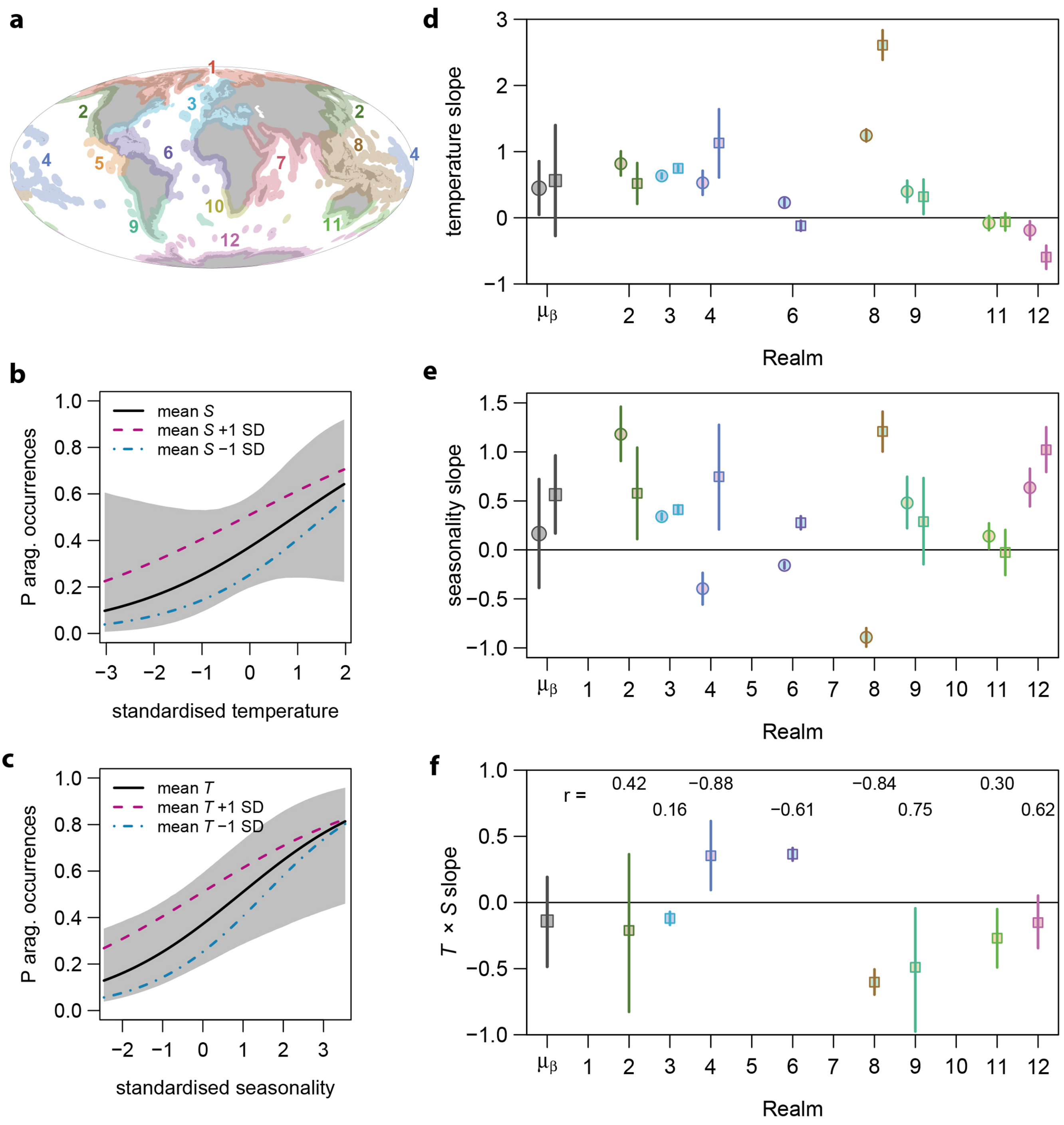

FIGURE 3 | Regression coefficients of temperature and seasonality within marine, biogeographic realms. (a) Twelve marine, biogeographic realms from Spalding et al. (2007). 1 = Arctic, 2 = Temperate Northern Pacific, 3 = Temperate Northern Atlantic, 4 = Eastern Indo-Pacific, 5 = Tropical Eastern Pacific, 6 = Tropical Atlantic, 7 = Western Indo-Pacific, 8 = Central Indo-Pacific, 9 = Temperate South America, 10 = Temperate Southern Africa, 11 = Temperate Australasia, 12 = Southern Ocean (b) Predicted relationship between *P. arag.* and temperature in the hierarchical binomial regression, with T, S and $T \times S$ as independent variables, across the eight biogeographic realms with sufficient data. The predicted relationship is shown at mean seasonality (black, solid line, shading denotes 95% CI) and at seasonalities 1 standard deviation below (blue, dash-dotted line) and above (purple, dashed line) mean seasonality. As T and S were standardised separately within each realm, the mean (0) and standard deviation cannot be transformed back onto the original scales. (c) As (b), but showing the predicted relationship between *P. arag.* and seasonality. (d–f) Slopes (effect sizes) of the hierarchical, binomial regression of *P. arag.* against T, S and $T \times S$ (squares) and against just T (circles, d) or just S (circles, e). The overall mean effect sizes (μ_β) are shown in grey. The coloured symbols show the individual effect sizes for the eight realms included in the analyses. Bars denote 95% CI. The correlation coefficients (r) in (f) denote the correlation of T and S in the eight realms. Regression coefficients and associated statistics are reported in the Tables S4 and S5.

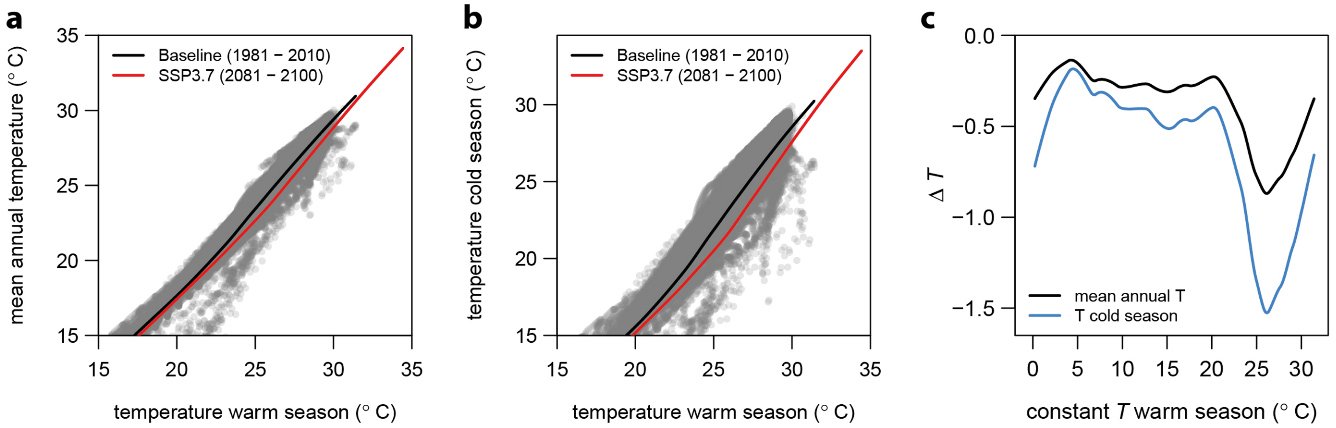

FIGURE 4 | Shifting temperature windows in a warming scenario. (a) Average sea surface temperature of the warm season (mean summer temperatures) and annual mean temperatures from grid cells with a resolution of 1° longitude and latitude (grey points), with a local regression (LOESS fit, black curve), averaged across 1981–2010 (baseline). The red line shows an analogous LOESS fit with temperatures from the SSP3.7 long-term warming scenario (2081–2100) from the CMIP6 (see Section 2). Only temperatures > 15°C are shown to highlight the temperature range in which differences are most substantial. (b) As (a), but with temperature averages of the cold season (mean winter temperatures) instead of mean annual temperatures. The gap between the warming scenario and the baseline has widened relative to (a). (c) The difference between the warming scenario and the average expected mean annual temperature of the baseline at a given (constant) temperature of the warm season is shown in black. The same difference, but with the temperature of the cold season instead of mean annual temperature, is shown in blue. A region in the warming scenario, which has the same warm season temperature as another region in the baseline, has lower mean annual and cold season temperatures, on average. This is especially pronounced for warm season temperatures of ~23 to 30°C, as comparable temperatures in the warming scenario correspond to more poleward, seasonal climates.

accurate comparison of the responses of bivalve species to ocean acidification is impaired by differences in exposure time, pH and $p\text{CO}_2$ levels and measured response variables in different studies. Blue mussels (*Mytilus edulis*) have been found to secrete thinner shells with relatively more calcite and less aragonite in ocean acidification experiments (Fitzer et al. 2015), which may be an advantageous compensatory mechanism for bimineralic species, and explain their low extinction risk inferred from the fossil record (Reddin et al. 2020), but responses to ocean acidification differ between experimental studies (Ries, Cohen, and McCorkle 2009; Parker et al. 2013). Additional compensatory mechanisms of *Mytilus* that require further research are the secretion of thinner shells with higher organic contents and a thicker periostracum, as observed in cold water and brackish water populations (Telesca et al. 2019, see also Hahn et al. 2012).

In conclusion, we have shown that aragonitic bivalves are more common in warm water both globally and within most biogeographic realms. Whereas the role of skeletal mineralogy in the context of ocean acidification has elicited a considerable amount of research, direct implications of warming on skeletal mineralogy are rarely discussed. Our study reveals previously undetected, potential interactions of climate warming with skeletal mineralogy. Warming may favour aragonite secretion, but tropical, calcite-secreting bivalves may have a greater capacity to move poleward into temperate climates.

Author Contributions

K.E., U.B. and W.K. conceived the idea; K.E. conducted the data analysis with inputs from U.B. and W.K.; K.E. and U.B. led the writing with assistance from W.K. and C.W.S.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and the R code supporting the results are available on Zenodo (https://doi.org/10.5281/zenodo.5494452).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.