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What controls planktic foraminiferal calcification?

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Abstract. Planktic foraminifera are key producers of pelagic carbonate, and their shell weight is suggested to represent the environment in which they calcify. However, there is debate about the use of size-normalised weight (SNW) as a proxy, as some authors invoke a carbonate system control on calcification (and by extension SNW as a $p\text{CO}_2$ proxy), while others suggest that species optimum conditions, nutrient concentration, or temperature drive shell weight. To better understand its use as a proxy, we investigate what drives SNW and whether discrepancies in the proposed control on weight is due to differing data collection methodologies and/or regionally different drivers. We integrate new and published SNW data with environmental hindcast data extracted from the CMIP6 modelling suite. Using Bayesian regression modelling, we find that the environment alone cannot explain the variability in SNW across species. Although physiology likely modulates the response to the environment, we find little evidence of a unifying driver at the ecogroup-level. Instead, we identify species-specific responses associated with drivers including (but not limited to) the carbonate system, which are likely different between ocean basins. We hypothesise that this is partly influenced by cryptic species and regional phenotypic plasticity in not well understood changes to shell weight, such as the thickness of calcite deposited during some species' reproductive phase. Consequently, which species to use as a $p\text{CO}_2$ proxy or whether multiple species should be used in parallel to reduce uncertainty should be carefully considered. We strongly encourage the regional testing and calibration of $p\text{CO}_2$ – SNW relationships.

Short summary. Planktic foraminifers are a plankton whose fossilised shell weight is used to reconstruct past environmental conditions such as seawater CO_2. However, there is debate about whether other environmental drivers impact shell weight. Here we use a global data compilation and statistics to analyse what controls their weight. We find that the response varies between species and ocean basin, making it important to use regional calibrations and consider which species should be used to reconstruct CO_2.

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1 Introduction

The unprecedented rise in CO_2 and temperature is altering our oceans and impacting marine ecosystems and their services. In the case of planktic foraminifera (a calcifying zooplankton which lives in the surface ocean), ocean acidification, sea surface warming and changing nutrient availability are all projected to impact their calcification (IPCC, 2022; Leung et al., 2022). Currently, these zooplankton contribute approximately a quarter of modern pelagic carbonate production (Buitenhuis et al., 2019; Langer, 2008) and 23–56% of total carbonate flux (Neukermans et al., 2023; Schiebel, 2002). The amount of carbonate produced by individual planktic foraminifers in the first order determines this flux to depth and is a function of their abundance, size and weight (Barrett et al., 2023). While research generally agrees on what drives foraminiferal size (Schmidt et al., 2004; c.f. Rillo et al., 2020) and abundance (Bé and Tolderlund, 1971), the controls on the size-normalized weight (SNW) of planktic foraminifers is debated (e.g. Aldridge et al., 2012; Barker & Elderfield, 2002; de Villiers, 2004; Lombard et al., 2010; Table 2).

As well as resolving what controls SNW to understand how carbonate production could be impacted by environmental change, it is also important for the interpretation of SNW as a proxy for past ocean conditions. That is whether SNW should be used to reconstruct carbonate saturation from bottom waters (Lohmann, 1995), and/or as proxy for surface ocean carbonate, and by extension atmospheric $p\mathrm{CO}_2$ (Barker and Elderfield, 2002). The former stipulates that SNW records dissolution post deposition rather than environmental conditions during life. The latter supports the opposite – that SNW is controlled by carbonate ion concentration $[CO_3^{2-}]$ and records changes in the environment during life and the impact of post depositional processes are minimal (Russell et al., 2004). If variables other than the carbonate system control SNW, the use of this proxy should be reassessed.

There is contradicting evidence of a carbonate system control on foraminiferal calcification, with some studies showing a positive relationship between SNW and $[CO_3^{2-}]$, pH, and calcite saturation (Ω) (Barker & Elderfield, 2002; Beer et al., 2010b; Bijma et al., 2002; Bijma et al., 1999; Broecker & Clark, 2001; Davis et al., 2017; de Moel et al., 2009; Dong et al., 2022; Lombard et al., 2010; Manno et al., 2012; Moy et al., 2009; Russell et al., 2004; Weinkauf et al., 2013). However, this response is not uniform between or even within species, with some studies reporting no response to $[CO_3^{2-}]$ (Béjard et al., 2023; Gonzalez-Mora et al., 2008; Henehan et al., 2017; Mallo et al., 2017; Naik et al., 2011; Pak et al., 2018; Song et al., 2022; Weinkauf et al., 2016). Others suggest that different environmental parameters are the primary control on SNW, such as temperature (Marr et al., 2011; Pak et al., 2018; Qin et al., 2020; Song et al., 2022), nutrient concentration (Aldridge et al., 2012), and optimum growth conditions (de Villiers, 2004). Importantly, many studies identify multivariate environmental controls on foraminiferal calcification, such as surface ocean carbonate chemistry, temperature, productivity, nutrient availability, salinity, (Béjard et al., 2023; Mallo et al., 2017; Marshall et al., 2013; Pallacks et al., 2023; Weinkauf et al., 2016), which can be species-specific and vary between and within ocean basins.

Physiology and ecological mechanisms such as biogeography or symbiosis may modulate the environmental response. Hence different ecogroups (i.e. species grouped by their ecology which have functional traits such as

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spines in common; Table 1) may respond differently to the environment. For example, in symbiont bearing species the negative impact of low carbonate ion concentration could be reduced due to CO_2 uptake by symbionts in the foraminifer's microenvironment (Jørgensen et al., 1985; Köhler-Rink and Kühl, 2005; Rink et al., 1998). Species with spines may better capture food than non-spinose species (Gaskell et al., 2019; Spindler et al., 1984), providing energy for metabolic processes which support calcification.

SNW could additionally be variable between species due to potential differences in biomineralization pathways. Models suggest different biological controls, such as the intracellular storage of inorganic carbon and calcium ions (Erez, 2003), pH regulation (Lastam et al., 2023; de Nooijer et al., 2009; Toyofuku et al., 2017), and active transport of calcium and/or magnesium pumping (Bentov and Erez, 2006; Nehrke et al., 2013). These different pathways could have different sensitivities to environmental change. Furthermore, SNW measurements taken at the morphospecies level (i.e. a species designated based on morphological features) could mask differences in the individual genotypes within cryptic species (i.e. organisms that look identical but represent distinct evolutionary lineages) if these have different environmental preferences (Darling et al., 2000; Morard et al., 2024).

Furthermore, the SNW response may vary spatially. For example, at higher latitudes where carbonate saturation is close to undersaturation (Mikis et al., 2019), a foraminifera may be at its limit of tolerance and therefore more vulnerable to small changes in carbonate ion concentration than low latitudes dwellers, akin to observations of coralline algae species responses to temperature changes at the trailing and leading edges of their distribution (Kolzenburg et al., 2023).

Additionally, the wide range in methodology used to collect weight measurements could also complicate our understanding of what drives SNW. Results are either generated with a sieved-based approach (SBW), in which planktic foraminifers are sieved through a narrow size fraction then the average specimen weight is taken, or through the measurement-based approach (MBW), where the additional step of normalizing to a measured size parameter (diameter or area) is taken (equation 1). MBW is a more rigorous approach as the use of sieve fractions (SBW) can be unreliable due to size variability within the sieve fraction itself (Aldridge et al., 2012; Beer et al., 2010a; Béjard et al., 2023)

$$MBW = \frac{Mean\ SBW_{sample} * Mean\ parameter_{size\ fraction}}{Mean\ parameter_{sample}} \tag{1}$$

Finally, different sample collection methodologies (i.e. whether results are derived from culture, plankton tow, core-top, or sediment trap samples) could further complicate our understanding of what drives calcification. Some authors have analysed foraminiferal SNW from plankton tow samples (Aldridge et al., 2012; Beer et al., 2010b; Mallo et al., 2017). However, foraminifers living in the water column are likely juvenile and have not completed calcification, meaning that anomalously light tests could be measured in comparison to the same size class derived from sediments. The SNW of sediment trap or core-top samples could be impacted by dissolution as foraminifera fall through the water column, however this can be largely accounted for if samples are derived from above the lysocline. Culture experiments are useful in circumventing these limitations, but they do not reflect real-world conditions as many are grown in artificial seawater, and the meta-data collected is variable between publications limiting aggregation of studies.

Here, we apply Bayesian regression to statistically infer what drives SNW (measurement-based). We hypothesise that (1) the environment alone cannot explain variability in foraminiferal SNW across species. Instead, (2) physiology modulates the foraminiferal SNW response to the environment, hence the SNW response will be similar within ecogroups. (3) Species-specific SNW sensitivities may overprint the ecogroup response

2 Methods

To infer which environmental variables drive SNW at both a species and group level, we conducted an exhaustive literature review, pre-processed our data to ensure data quality, and then statistically analysed our data using Bayesian regression modelling. Details for each step are provided below.

2.1 Compilation of planktic foraminiferal SNW data

This study gathers articles on foraminiferal SNW published until the 31st October 2023, and includes 790 samples covering 11 species from 7 published datasets and a new dataset (*n* = 229; Fig. 1; Text S1 and S2). A literature search for planktic foraminiferal SNW was conducted on Google Scholar. Publications with the key words ‘planktic foraminifera’ with ‘size normalized weight’, ‘weight’, ‘calcification’ were included. The results were expanded by exploring citations of key papers and identifying additional studies from the reference list of review articles. Articles were initially screened considering title relevance, then abstract content, and finally full-text content. Additionally, we included our own unpublished SNW which significantly increased data coverage in high latitudes and the subtropical Atlantic (Fig 1, see Text S1 for methodology). The full article list is available in the supplementary material and the new SNW data can be found in the supplementary data.

Data were only included if SNW was normalized by the measurement based weight (MBW) method as in equation 1 (Barker & Elderfield, 2002) using diameter or silhouette area. (Aldridge et al., 2012; Beer et al., 2010a; Béjard et al., 2023). Because the count of foraminifera collected can be low in sediment traps, selecting narrow size classes was not always possible for this data type as restricting sieve size would have resulted in a very small number of specimens. Data from plankton tows were removed from analysis as these may contain juvenile foraminifers. Given typical sedimentation rates in the open ocean and bioturbation, core-top data were considered preindustrial (unless the publication stated otherwise). Core samples were considered preindustrial if dated between 1000 AD and 1900 AD as CO_2 remained fairly stable over the Holocene (IPCC, 2021). *G. ruber* white and *G. ruber* pink are combined to increase sample size.

Samples were omitted if dissolution of foraminifera specimens was reported, or if the water depth was more than 4000m thereby approaching the CCD (Carbonate compensation depth; Broecker & Clark, 2009). Due to sampling effort and preservation (i.e. the CCD being shallower in the pacific), data are focused in the Atlantic with only some Pacific data. Measurements span a wide latitudinal gradient (54°S to 78°N; Fig. 1). Planktic foraminifers were assigned to one of three ecogroups following Aze et al. (2011) (Table 1).

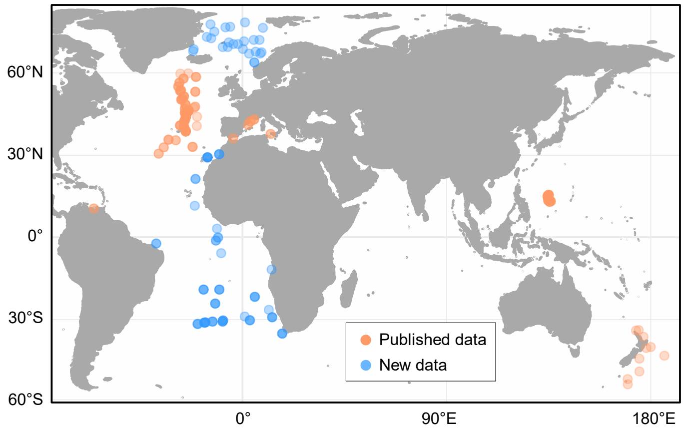

Figure 1 Location of SNW data. See Fig. S1 for a breakdown of species by location. $n_{samples}$ = 790

Table 1 Planktic foraminifera species and their features which determine their ecogroup. The number in brackets indicate the genotype counts from Morard et al. (2024).

Species	**Ecogroup**	**Habitat depth**	**Cryptic diversification**
G. bulloides	symbiont-barren, spinose	mixed layer	High (10)
G. inflata	symbiont-barren, non-spinose	thermocline	Low (2)
N. pachyderma	symbiont-barren, non-spinose	mixed layer	High (8)
G. truncatulinoides	symbiont-barren, non-spinose	sub-thermocline	Moderate (5)
N. incompta	symbiont-barren, non-spinose	mixed layer	Low (2)
G. ruber	symbiont-obligate, spinose	mixed layer	Moderate (4)
O. universa	symbiont-obligate, spinose	mixed layer	Low (2)
T. sacculifer	symbiont-obligate, spinose	mixed layer	None (1)
G. elongatus	symbiont-obligate, spinose	mixed layer	None (1)
N. dutertrei	symbiont-facultative, non-spinose	thermocline	None (1)
P. obliquiloculata	symbiont-facultative, non-spinose	thermocline	Low (2)

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2.2 CMIP6 data extraction: compilation of environmental data

For all SNW data, corresponding surface ocean environmental data were extracted from models in the CMIP6 ensemble for the modern and preindustrial. Environmental data includes sea surface temperature, phosphate concentration, nitrate concentration, salinity, chlorophyll *a* concentration, net primary productivity (NPP), alkalinity, CO_3^{2-}, DIC, Calcite Ω and pH.

Carbonate system, salinity and temperature data were derived from Jiang et al. (2023), in which 14 CMIP6 ESMs were corrected for bias and model drift (see Table S1 and Jiang et al. 2023). Environmental data for the Mediterranean was not available from the Jiang et al. (2023) . For this region, sea surface temperature (SST), sea surface salinity (SSS), dissolved inorganic carbon (DIC) and total alkalinity (TA) were extracted from CESM2 (Danabasoglu et al., 2020) (Fig. S2) as the carbonate system output from CESM2 was closest to the median of the global average for the 14 ESMs (see Table S4 and S5 in Jiang et al. 2023).

The CESM2 data used in this manuscript were manipulated the same as other ESMs in Jiang et al. (2023). For consistency with other models, CESM2 outputs were converted from mol m^{-3} to µmol kg^{-1} using a density function calculated from the Thermodynamic Equation of Seawater (TEOS-10; IOC et al., 2010; McDougall & Barker, 2011). Interannual variability was reduced by calculating a 10 year average for each decade. Model bias was removed by correcting to DIVA gridded (Troupin et al., 2012) GLODAP (Lauvset et al., 2022) observational data and model drift was removed using the relevant CESM2 preindustrial control (piControl). The adjusted SST, SSS, DIC and TA were then used to calculate the rest of the OA indicators (CO_3^{2-}, Calcite Ω and pH) using CO2System (van Heuven et al., 2011; Lewis and Wallace, 1998). Ice core-based atmospheric CO_2 data (Etheridge et al., 1996; MacFarling Meure et al., 2006) were used to approximate the oceanic fCO_2 change from 1750 to 1850, thereby enabling estimation of the carbonate system for the preindustrial (1750) assuming that all locations are in equilibrium with the atmosphere (Takahashi et al., 2014).

Five Earth System Models (ESMs) were used to extract phosphate concentration, nitrate concentration, chlorophyll *a* concentration and net primary productivity (NPP) data to determine 'optimum conditions' (Table S1; Fig.S3). NPP and chlorophyll are indicators of the algal biomass concentration, which is a large part of some foraminifera species' diet (Schiebel and Hemleben, 2017). Nutrient concentration is a step detached from this, and represents the food available for their prey. There is some evidence that phosphate can inhibits calcification in some other calcifiers. Decadal averages were calculated for these variables. For comparison to existing data and to improve data readability phosphate and nitrate were converted from mol m^{-3} to µmol kg^{-1}, and chlorophyll *a* from kg m^{-3} to mg m^{-3}. The median of the non-corrected environmental outputs were calculated and the preindustrial (1750) values were assumed the same as in 1850. These data were not corrected to observational data as the data coverage is insufficient. Although species' abundance is also often used to inform optimum conditions, these data were not available for the same locations.

2.3 Statistical modelling

2.3.1 Data cleaning: addressing size fraction bias and collinearity in environmental data

All statistical analyses were carried out using R version 4.2.1 (R Core Team, 2018). To remove size fraction bias in SNW, the size fractions 250-300 and 300-350 were merged into one size fraction and this used. These size fractions were chosen because of their large sample number, they are in the middle of the size range, and allow us cover a wide environmental gradient (Fig. 2). This resulted in statistical analysis of 512 samples covering seven species from four published datasets and our data (Text S2).

Four of the initial ten environmental parameters were analysed: phosphate concentration, salinity, NPP, and CO_3^{2-}. We were unable to analyse the impact of sea surface temperature due to collinearity, which would inflate the variance and standard error of coefficient estimates (Dormann et al., 2013). Nitrate was excluded as phosphate and nitrate concentration are highly correlated (*rho* = 0.83, *p* = <.000). We chose to keep phosphate as it is more commonly assessed in the literature. Similarly, the carbonate system parameters are highly correlated (Fig. S4), but as carbonate ion concentration is often used in the literature we use this to represent the carbonate system. Because NPP is more directly linked with plankton biomass than chlorophyll *a* concentration, the former is analysed here. Due to this data cleaning, it is important to note that while in the following we emphasise the parameter we analysed, the impacts on SNW could also be driven by the highly correlated driver.

2.3.2 Model Specification

All models were fitted using the Bayesian regression model package, brms (Bürkner, 2017) which uses the probabilistic programming language Stan (Carpenter et al., 2017). The models were specified to be Gamma distributed and were fitted using the NUTS (Hoffman and Gelman, 2014) sampler with 4 chains and 2000 iterations, each of which the first 1000 are warmup to calibrate the sampler, thus leading to 4000 posterior samples.

All models were checked with appropriate tests before interpretation to ensure model assumptions were not violated. Variables were centred and standardised to reduce structural collinearity, and a QR decomposition term added to models to reduce correlation between variables. To check for any remaining collinearity pairs plots were visually assessed, and variance inflation factors (VIF) were verified using the package 'performance' which passes the brms model to its frequentist counterpart. A VIF of ten or less indicates that collinearity is not problematic (Marcoulides & Raykov, 2019). Outliers were detected using Pareto's k, for which a value of 0.7 or higher indicated an unduly influential observation. Visual posterior predictive checks were carried out to assess model fit and chain mixing (Fig. S5). An Rhat value close to 1 (i.e. less than 1.1) indicates the chains have converged (Bürkner, 2017).

2.3.3 Modelling: Can the environment explain foraminiferal SNW across species?

To assess whether there is a universal driver and how much variability in SNW across all foraminifers can be explained by the environment, a "group-level" (i.e. foraminifera species pooled together; $n_{samples} = 512$) Bayesian multi-level model was fitted (Bürkner, 2018). The full model included carbonate ion concentration (CO_3^{2-}), salinity, phosphate concentration, and net primary productivity (NPP) as fixed environmental effects and species as a random effect (intercept only). Data type (i.e. sediment trap, sediment core and core-top) was added as a fixed effect (not a random effect because data type had less than five levels (Harrison et al., 2018). Because the range of variance was unequal ("heteroscedastic") between species (Fig. S6), we add a shape term to the model which allows the variance between each species to vary.

The full model was compared to a 'null' model which did not consider species and included fixed environmental effects only (the impact of data type as a fixed effect was removed from bayes R2 values to ensure it was environmental effect only that was measured). Both models were compared using leave-one-out cross-validation ('LOO'; Vehtari et al., 2017), a measure which informs which model is performing best.

LOO indicated that adding species as a random effect improved model fit ($\widehat{\mathrm{elpd}}_{\mathrm{loo}}$ improved by 261.3 ± 18.6, see details in results). As such, we fit models for individual species to assess their association with the environment.

2.3.4 Modelling: Is the SNW response to the environment similar between ecogroups or species specific?

The size fraction restriction imposed for analysis of SNW across species (250-350 µm only) was relaxed (Text S2) as it is less relevant at the species-level which recognises the size ranges of taxa. Only sieve size fractions that are 50 µm in range were used (unless data were from sediment traps). Similar to the group-level model, data type was added as a fixed effect for each species-level model. *G. inflata, T. sacculifer, N. dutertrei, P. obliquiloculata* and *O. universa* were not modelled because of their low number of observations (*n* = < 30). *N. incompta* was excluded from analysis because of significant multi-collinearity that prevented meaningful inference of environmental effects. Bayesian models were fitted to the remaining five species. To assess how much of the variability in foraminiferal SNW for different species can be explained by the environment, the effect size and credible interval (i.e. Bayesian confidence interval) of coefficients (environmental variables) were extracted from each model. Results were clustered by ecogroup to assess whether there were differences in the SNW response to the environment between ecogroups (Fig. 4).

3 Results

3.1 Qualitative assessment of existing data

Assessing the available SNW data and their suggested drivers in the literature, there is no single environmental control on foraminiferal size normalised weight across species (Table 2). Although this summary suggests that a low carbonate ion concentration does not reduce foraminiferal SNW, it is inconclusive as to whether an increase in carbonate ion concentration has no impact on shell weight or increases it. For other environmental variables, it is either a mixed response or there is too little information to determine a direction of response. However, it is important to note that where no significant effect is reported in Table 2, this could possibly reflect the lack of statistical power rather than no response. Using environmental data from earth system models allows us to reanalyse the data and determine whether any environmental drivers emerge for SNW across all species.

Table 2 Compilation of results from previous studies assessing the relationship between planktonic foraminiferal size-normalized weight (SNW) and the environment. + = positive correlation, − = negative correlation, ~ = no response. This table summarizes information from measurement based SNW (i.e. silhouette area, or diameter normalised) studies only and omits those which only normalised to size by sieving (i.e. sieve-based weights; SBW) or use plankton tow data. See supplementary Table S2 for detail on SNW measurement method. [1] Barker & Elderfield (2002); [2] Béjard et al. (2023); [3] Marr et al. (2011); [4] Marshall et al. (2013); [5] Osborne et al. (2016); [6] Pallacks et al. (2023); [7] Weinkauf et al. (2016).

Species	**Data type**	**Biogeozone**	**Carbonate ion**	**pH**	**CO_2**	**Temperature**	**Productivity**	**Phosphate**	**Nitrate**	**Salinity**	**Optimum conditions**
symbiont-barren, spinose											
G. bulloides[6]	Core	Subtropical	+		−	−					
G. bulloides[1]	Core-top	Temperate	+			~					
G. bulloides[3]	Core-top	Subtropical				−					
G. bulloides[5]	Trap/Core	Tropical	+			~		~			
G. bulloides[2]	Trap	Subtropical	~	~	~	~	~	~	~	~	~
G. bulloides[7]	Trap	Subtropical	~			~	~				−
symbiont-obligate, spinose											
G. elongatus[6]	Core	Subtropical	+		−	−					
G. elongatus[7]	Trap	Subtropical	~			+	−				+
G. ruber[7]	Trap	Subtropical	~			+	−				~
G. ruber[4]	Trap	Tropical	+			+					
G. sacculifer[4]	Trap	Tropical	+			+					
symbiont-barren, non-spinose											
G. inflata[1]	Core-top	Temperate	+			~					
G. trunc[1]	Core-top	Temperate	+			~					
G. trunc[2]	Trap	Subtropical	+	~	~	+	−	~	~	~	−
N. incompta[2]	Trap	Subtropical	~	~	~	+	~	~	~	~	~
N. incompta[1]	Core-top	Temperate	+			~					

3.2 Qualitative assessment of reanalysed data

Here we qualitatively assess the integrated published SNW and new SNW dataset alongside the environmental output from the CMIP6 modelling suite. Generally, larger foraminifers (e.g. 425-850 µm) have heavier tests (average 40.14 µg) and smaller foraminifers (e.g. 200-250 µm) have lighter tests (average 5.49 µg; (Fig. 2a). The 300-350 µm size fraction shows greatest variability in weight (standard deviation [σ] 9.32; Fig. 2a), likely as it has a higher species diversity (*n* = 5) compared to other size fractions (*n* = 1 to 4). Interestingly, the second highest variability in weight is for the 400-500 µm size fraction (σ 6.77; Fig. 2a) and is linked to only one species, *G. truncatulinoides,* from one publication (Béjard et al., 2023; Fig. S7). The species is atypical as a very large proportion of the weight is in the gametogenic calcite covering the entire test (Schmidt et al., 2008) whose thickness might be driven by environmental parameters as well. Furthermore, the species has a year-long life cycle (whilst other species analysed here have lunar cycles and peak in a specific season), meaning that this species is exposed to greater environmental variability throughout the year. The lack of environmental variability shown here for these samples likely reflects averaging of the seasons in this annual environmental record.

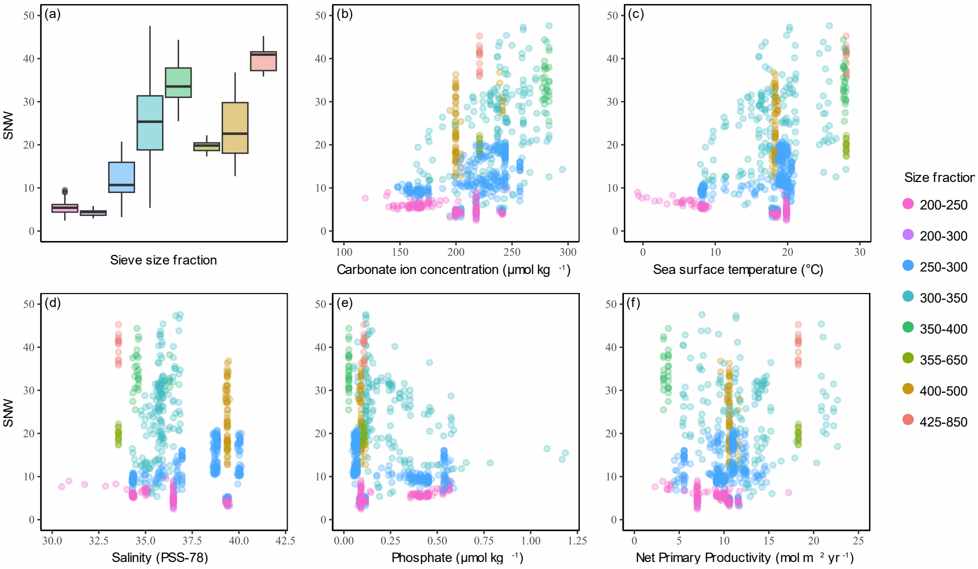

Figure 2 (a) Boxplot showing SNW distribution across sieve size fractions. (b-f) Planktic foraminiferal size-normalised weight (MBW) against environmental variables extracted from the CMIP6 modelling suite (see methods). Colour indicates the size-fraction foraminifers were initially sieved at before being normalised to their length or area. See Fig. S7 for planktic foraminiferal SNW separated by species, with sieve size fraction information.

The smallest size fractions must be interpreted with caution (Fig. 2) as they have not been systematically assessed in warm regions (where carbonate ion concentration is higher) due to a preference for using larger sieve size fractions in these regions. Although the smaller size fractions are meaningful in polar and subpolar areas (as foraminifers are smaller at the poles), there are data missing for small sizes in warm, high calcite environments. The absence of heavy foraminifer in low carbonate ion saturation (Fig. 2b) and cool (Fig. 2c) environments suggest that these environments limit foraminiferal weight. To remove size fraction bias, the size fractions 250-300 and 300-350 have been merged to create a 250-350 size fraction and (unless stated otherwise) the following statistics has been performed on this reduced dataset.

3.3 Is there an environmental control on SNW at the group-level?

We use Bayesian regression to determine whether the there is an environmental control on SNW across species. An 'environment only' model explains 23% of the variability in SNW (Bayes R2; Gelman et al., 2019), whilst a model which additionally includes species as a random effect explains 86% of the variability in SNW, indicating that species-specific differences are more important than environmental effects for SNW at the group-level. Higher SNWs are associated with a higher carbonate ion concentration (0.05 [0.02, 0.07]; effect size and 95% credible interval [lower, upper]; Fig. 3) and lower phosphate concentration (−0.09 [−0.11, −0.07]; Fig. 3; Table S3), though the effect size is small. To dive deeper into the link between SNW and the environment, Bayesian models were fitted at the species level.

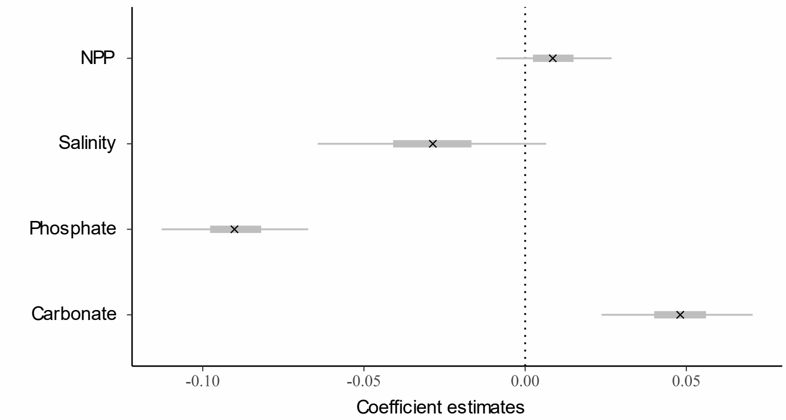

Figure 3 Effect size and credible intervals for the association between SNW and the environment for the group-level model. A cross [x] represents the median value, the thicker line the 50% interval (i.e. where 50% of the posterior probability lies) and the thinner line the 95% interval. If the 95% interval does not cross zero, then there is a 95% probability there is an effect of the environmental variable. A negative value represents a negative correlation between SNW and the coefficient. Note that the modelled dataset is slightly different to the species-level dataset. The group-level model dataset includes species which were omitted from species-level models due to their low sample size, and the size fraction ranges are more restricted for the group-level model due to a bias against larger size fractions in cooler environments (see methods).

3.4 Is there a species specific or an ecogroup response?

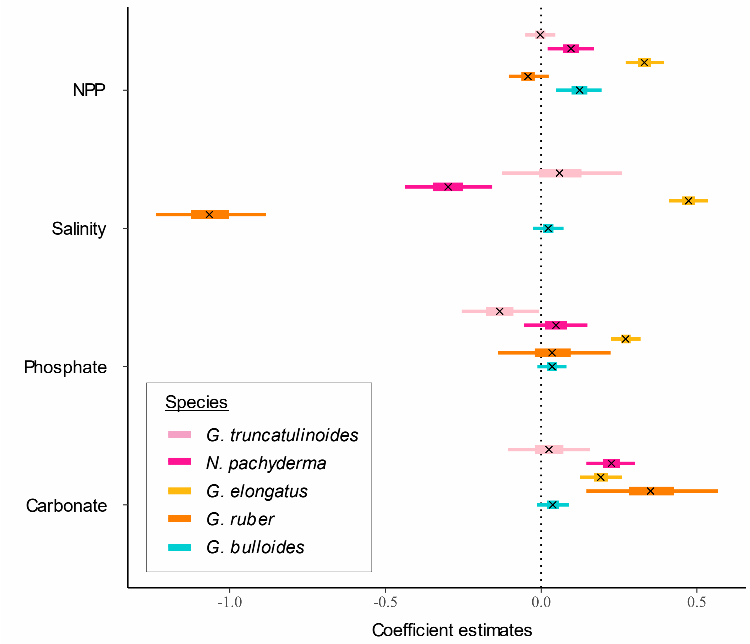

Figure 4 Effect size and credible intervals for the association between SNW and the environment for the species-level Bayesian modelling. A cross [x] represents the median value, the thicker line the 50% interval (i.e. where 50% of the posterior probability lies) and the thinner line the 95% interval. If the 95% interval does not cross zero then there is a 95% probability there is an effect of the environmental variable. A negative value represents a negative correlation between SNW and the environmental variable. Ecogroups are grouped by colour. *G. bulloides* is a symbiont barren, spinose species. *G. ruber* and *G. elongatus* are symbiont-obligate, spinose species. *N. pachyderma* and *G. truncatulinoides* are symbiont barren, non-spinose species.

In agreement with published literature (Aldridge et al., 2012; Barker and Elderfield, 2002; Béjard et al., 2023; Marshall et al., 2013; Osborne et al., 2016; Pallacks et al., 2023), an increase in carbonate ion concentration does not negatively impact SNW (Fig. 4; Table S3). The relationship is not always positive though, with *G. bulloides* (0.04 [−0.02, 0.09]) and *G. truncatulinoides* (0.03 [−0.11, 0.16]) exhibiting no notable response to a change in carbonate ion concentration (i.e. 95% interval crosses zero).

It remains up for debate which part of the carbonate system exerts control on calcification. It has been suggested that the HCO_3^-/ H^+ ratio (where HCO_3^- [bicarbonate ions] are the inorganic carbon substrate and H^+ [protons] are a calcification inhibitor) controls calcification and that CO_3^{2-} correlates because of a proportionality between CO_3^{2-} and this ratio (Bach, 2015). Yet even if this is the case, this implies that CO_3^{2-} can be proxy for the HCO_3^-/ H^+ ratio hence it is still important for calcification.

An increase in phosphate concentration is unlikely (<95% probability and <50% probability for *G. ruber*) to impact SNW other than for *G. truncatulinoides* (−0.13 [−0.26, −0.01]), and *G. elongatus* (0.27 [0.22, 0.32]). For the former, increased phosphate may reduce SNW and for the latter, SNW increases with phosphate concentration (Fig. 4; Table S3). Given the evidence for calcification inhibition in high phosphate conditions (Lin and Singer, 2006) for other calcifiers, such as corals (Kinsey and Davies, 1979), coccolithophores (Paasche and Brubak, 1994), and calcifying green algae (Demes et al., 2009), it is interesting that we do not observe stronger detrimental effect of phosphate on these foraminiferal species. However, this disparity could be explained by the different calcification mechanisms. For example, foraminifers biomineralize extracellularly by engulfing calcite-forming materials through seawater vacuolisation (potentially assisted by transmembrane ion transport; Bentov et al., 2009; de Nooijer et al., 2014; Erez, 2003; Nehrke et al., 2013). In contrast, coccolithophores biomineralize by forming coccoliths in intracellular organelles called 'coccolith forming vesicles' (Brownlee and Taylor, 2004).

There is no consensus on the impact of phosphate on calcification even within a taxa, with a recent study on coccolithophores not showing calcification inhibition but instead showing decreased calcification with phosphate limitation (Gerecht et al., 2018). Hence pointing to other taxa exhibiting similar response to our species-level modelling. Our *G. bulloides* result conflicts with a study of North Atlantic *G. bulloides,* in which a decrease in SNW with increased phosphate was recorded (Aldridge et al., 2012), though Béjard (2023) and Mallo et al. (2017) did not observe this in the Mediterranean. This disparity could be due to the use of shallow plankton tows in Aldridge et al. (2012) which is likely to complicate the SNW signal as juveniles which had not completed their development may have been measured. Additionally, *G. bulloides* has several cryptic species (Morard et al., 2024) which have their own ecological adaptation and spatial variability. Hence the geographic difference might further complicate the interpretation of data in these studies (Fig. S2). In our group-level model though we observe a negative impact of phosphate on SNW across species (−0.09 [−0.11, −0.07]; Fig. 3; Table S3). This is unlikely an effect of sampling bias toward the Atlantic as the Atlantic has near-even sampling (n = 263) to the Mediterranean (n = 239). Instead, as the group-level model contains some different species than the species-level modelling, we suggest that this difference reflects that certain species of foraminifera are sensitive to phosphate, while others are not.

Salinity has a mixed impact on foraminiferal SNW. For *G. ruber* SNW is lighter at high salinity (−1.06 [−1.24, −0.88), and *N. pachyderma* has a similar but weaker response (−0.30 [−0.44, −0.16]; Fig. 4; Table S3). Meanwhile, the SNW of *G. elongatus,* closely related to *G. ruber* and by some assumed to be an ecotype, increases with salinity (0.47 [0.41, 0.54]). Laboratory experiments which exposed foraminifers to a wider salinity range than observed under normal ocean conditions concluded that *G. ruber* was most tolerant to changes in salinity out of the seven species analysed (Bijma et al., 1990). For other foraminiferal species, they found that under low salinity growth rate reduced and final size was smaller. This difference could be because salinity values reported by Bijma et al. (1990) were more extreme than normal ocean conditions, or that growth rate and size are impacted differently to weight, i.e. foraminifers could be smaller but have a thicker test. Unfortunately, weight was not recorded in the study so this cannot be tested.

Similar to carbonate ion concentration, it is unlikely (<95% probability) that an increase in NPP decreases SNW. Instead, for *N. pachyderma, G. elongatus* and *G. bulloides,* increasing NPP (food availability) results in a heavier SNW (Fig. 4; Table S3). For *G. elongatus,* their symbionts should make the species less dependent on productivity due to cross transfer of sugars (LeKieffre et al., 2018), and for *G. bulloides* the presence of spines should make it easier for them to capture prey therefore should similarly be less associated with NPP. Yet, both SNWs increase with food availability (*G. bulloides:* 0.12 [0.05, 0.19]; *G. elongatus:* 0.33 [0.27, 0.40]). Even in the asymbiotic, non-spinose ecogroup, *N. pachyderma* and *G. truncatulinoides* there is no clear pattern, with the former's SNW increasing with productivity (0.09 [0.02, 0.17]) and the latter showing no response (−0.00 [−0.05, 0.05]). It is interesting that despite constructing a secondary calcite crust (which could overprint the primary SNW signal), *N. pachyderma* (Kohfeld et al., 1996) still exhibits a response to the environment.

Due to collinearity we are unable to assess the impact of SST on SNW for the species-level models. However, we could expect an increase in SNW with warming as warmer water decreases the solubility of atmospheric CO_2, which elevates surface water carbonate ion concentration, and also increases enzymatic activity which promotes growth and calcification rate (Lombard et al., 2009; Spero et al., 1991). Although some past research has identified an increase in SNW with warming (Béjard et al., 2023; Davis et al., 2013; Gonzalez-Mora et al., 2008; Marshall et al., 2013; Osborne et al., 2016; Qin et al., 2020; Song et al., 2022; Weinkauf et al., 2016), there is also evidence for the reverse (Mallo et al., 2017; Naik et al., 2010, 2011; Pallacks et al., 2023). This dichotomy has been attributed to overriding effect of decreasing carbonate ion concentration on SNW due to ocean carbon input (Naik et al., 2010; Pallacks et al., 2023), temperature induced sea surface stratification and lower food availability (Mallo et al., 2017).

Due to limited shell flux data, we were unable to investigate how optimum growth conditions (OGC) impacted SNW. Although NPP may facilitate OGC by making food available for growth, we cannot assume that high NPP results in optimum conditions as it also hinders photosynthesis and excludes species (Ortiz et al., 1995). There is some evidence of SNW increasing where a species is at its OGC (i.e. where shell flux for that species is high; de Villiers, 2004), but there is no consensus in the data (Table 2) with some observing a negative correlation between OGC and SNW (Béjard et al., 2023; Weinkauf et al., 2016).

The SNW response to the environment is largely species specific and shows little evidence of an overriding ecological driven response. For some taxa, similar responses can be found, e.g. the symbiont-obligate, spinose species *G. ruber* and *G. elongatus* show the same direction of response to carbonate, though the strength of response is variable (0.35 [0.14, 0.56] and 0.19 [0.12, 0.26], respectively; Fig. 4; Table S3). The symbiont barren, non-spinose species (*N. pachyderma,* and *G. truncatulinoides*) lack a unifying driver linked to their ecology. Though it is important to note that the SNWs of these species are likely to be more heavily impacted the production of a secondary calcite crust than other species analysed here (Kohfeld et al., 1996; Schmidt et al., 2008).

3.5 Should SNW be used as proxy for CO_2?

Disentangling the controls on SNW is important for understanding the use of SNW as a proxy for interpreting past ocean conditions. This paper cautions the use of planktic foraminiferal SNW as a reliable proxy for the surface ocean carbonate system and palaeo pCO_2.

Although there is a small but likely (i.e. >95% probability) effect of carbonate on a group level (i.e. across species; 0.05 [0.02, 0.07]), phosphate is also likely associated with SNW (−0.09 [−0.11, −0.07]; Fig. S3; Table S3). Hence, unless the impact of phosphate on SNW can be quantified and disentangled from the carbonate effect, SNW is not a reliable predictor for pCO_2. As SNW is variable on a species level, there is a need to consider which species to use for paleo proxies, or a need to consider multiple species in parallel to reduce uncertainty from species-specific differences.

Although the use of SNW to inform past CO_2 has been shown to work regionally with certain species, e.g. *G. bulloides* in the North Atlantic (Barker and Elderfield, 2002), the relationship between SNW and carbonate ion concentration seems to break down when taken out of its calibration region. When expanding the *G. bulloides* dataset to include Pacific, Mediterranean and higher latitude North Atlantic samples (Fig. S1) we find no correlation between SNW and carbonate ion concentration. Hence we advocate for the regional calibration of pCO_2 – SNW relationships, and caution against the extrapolation and global application of SNW as proxy for pCO_2.

One of the challenges in assessing a unifying calcification response is unequal methodologies and data reporting. In this paper 57 publications were screened for their SNW data, but only 7 publications (and our data) could be used for the species-level modelling. Around half were omitted as they were older than preindustrial and therefore could not be used to determine drivers. Otherwise, data were often not freely available (or at all available) and if deposited, only provided processed data with different methods of normalising weight to size. We strongly encourage the community to deposit raw data to make the legacy of data longer. 28 publications were omitted because shell weights were reported using the sieve-based weight (SBW) methodology and not normalised to size or area (MBW). Although there is some debate as to whether this additional step of normalising weight to measurement-based size is necessary, some publications (Aldridge et al., 2012; Beer et al., 2010a; Béjard et al., 2023) indicate that MBW SNW is more robust than SBW. It would be a step forward for the community to derive protocols for SNW akin to trace element analysis e.g. Hathorne et al. (2013) and Rosenthal et al. (2004). Additionally, it is important to acknowledge the different developmental stages in plankton tow samples compared to sediment trap and core-top samples. Post-depositional dissolution will reduce weights, while infilling and diagenesis increase weight and both need to be carefully monitored (Bassinot et al., 1994; Broecker & Clark, 2001). Additionally, we still have important gaps in our understanding of foraminiferal ecology, for example the dynamics of the habitat throughout the year, the peak times of biomass production in different regions and the drivers of thickness of gametogenic calcite. All of these factors limit the use of the proxy.

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Importantly, our analyses lack data from the Indian Ocean, Southern high latitudes and large parts of the Pacific - highlighting challenges of preservation in deep sea sediments, logistics of reaching remote areas, and bias due to the traditional areas of sampling of sea going nations. As analyses expand to ocean regions below the lysocline, authors should provide a measure of dissolution and/or high resolution images of specimens which can help assess the impact of post-diagenetic alteration. Although such images can also support morphological assessment of cryptic species, these images are still not systematically implemented in palaeoceanographic studies.

4 Conclusions

Although higher carbonate ion concentration and lower phosphate concentration are associated with heavier SNWs at the group-level (i.e. across species), the environment alone explains relatively little of the variability in SNW at the group-level. Instead, we identify species-specific SNW responses that better explain variability in weight. Although physiology is likely to modulate the foraminiferal response to the environment, we find limited evidence of an ecogroup-level response.

The species-specific SNW response to the environment is complex, with each species responding to a different combination of environmental drivers. We hypothesise that this is in part influenced by cryptic species and our limited understanding of what drives the thickness of gametogenic calcite. The SNW response being species-specific and responding to drivers other than carbonate implies there is a need to consider which species to use as a $p\mathrm{CO}_2$ proxy, or a need to consider multiple species in parallel to reduce uncertainty from species-specific differences. Furthermore, due to differences in the published response of *G. bulloides* in the North Atlantic and our more global dataset of *G. bulloides* SNW, we advocate for the regional calibration of $p\mathrm{CO}_2$ – SNW relationships.

Our understanding of SNW as a proxy would be greatly improved with some community efforts to solve some of the above questions including (1) making raw SNW data freely available, (2) community agreed protocols, i.e. whether SBW or MBW should be used in such analyses, (3) improving our understanding of the calcification process itself and how the environment drives the thickness of gametogenic calcite, and (4) resolving the impact that cryptic species have on SNW measurements.

Code availability

The code (R script) supporting this article has been uploaded as part of the supplement and is available at DOIXXXXX

Data availability

All data used in this study are available at DOIXXXX

Supplement

The supplement related to this article is available at: DOIXXXX

Author contribution

R.B. and D.N.S. conceptualised the study. R.B. collated existing SNW data and processed CMIP6 model data, and conducted analysis of these data. J.V. contributed to the methodological design and statistical analysis. R.B. prepared the manuscript with contributions from all co-authors.

Competing interests

The authors declare that they have no conflict of interest.

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