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 have been influenced by 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 pCO_2 proxy), while others suggest that species optimum conditions, nutrient concentration, or temperature drive shell weight. To better understand this proxy, we investigate what drives SNW and whether discrepancies in the proposed control on weight are due to differing data collection methodologies and/or regionally different drivers. We integrate new and published SNW data with environmental hindcast data from the CMIP6 modelling suite. Using Bayesian regression modelling, we find that the environment alone does not 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 pCO_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 pCO_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.

1 Introduction

The unprecedented rise in CO_2 and temperature is altering our oceans and impacting marine ecosystems and their functioning (such as marine biogeochemical cycles). 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 pCO_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 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), optimum growth conditions (de Villiers, 2004) and seawater density (Zarkogiannis et al., 2019). Importantly, many studies identify multivariate environmental controls on foraminiferal calcification, such as surface ocean carbonate chemistry, temperature, productivity, nutrient availability, and 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 that have functional traits such as spines in common; Table 1; Aze et al., 2011) 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 that 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 does not 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 across species (i.e., all foraminifers in this study pooled together) and at the ecogroup and species 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 770 samples covering 11 species from 7 published datasets and a new dataset (*n* = 209; Fig. 1). The full article list is available in the supplementary material (Text S1) and the new SNW data can be found in the supplementary data.

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.

Data were only included if SNW was normalized by the measurement based weight (MBW) method as in equation 1 (Aldridge et al., 2012; Barker and Elderfield, 2002) using diameter or silhouette area (Béjard et al., 2023; Marshall et al., 2013). 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). *Globigerinoides ruber* white and *G. ruber* pink are combined to increase sample size.

Additionally, we included our own unpublished SNW measurements which significantly increased data coverage in high latitudes and the subtropical Atlantic (Fig. 1). For these new data, SNW measurements were collected from Atlantic core-tops and sediment cores for *G. truncatulinoides, G. ruber, O. universa, N. pachyderma, N. incompta* and *G. bulloides*. The former three were analysed from a 300-355 µm sieve size fraction, *G. bulloides* from 250-300 µm and the latter two from a 200-250 µm size fraction. SNW data were collected through the measurement-based approach (MBW; equation 1). Approximately 20-30 individuals were analysed per sample. Samples were weighed using a Mettler Toledo MT5 microbalance (error = ± 0.5 µg) and the mean weight calculated. Size measurements were taken for each individual foraminifera test at 125x magnification using a LEICA MZ12.5 microscope. Individual tests were aligned in the same orientation and the longest axis of the test (Feret's diameter) was measured using Fiji (Schindelin et al., 2012). The average Feret's diameter was calculated for each sample and tests were size normalised using equation 1.

For all data, samples were omitted if dissolution of foraminifera specimens was reported, or if the water depth was more than 4500m 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).

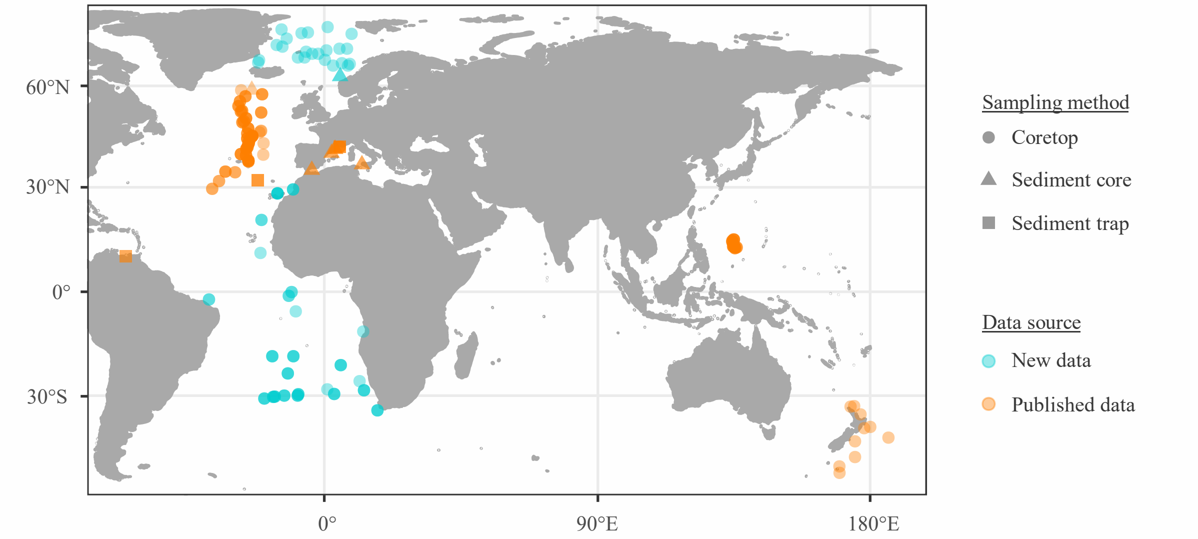

Figure 1 Location of SNW data. See Fig. S1 for sample count per datatype and Fig. S2 for a breakdown of species by location. $n_{samples} = 770$.

Table 1 Planktic foraminifera species and their features which determine their ecogroup (Aze et al., 2011). 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)

2.2 CMIP6 data extraction: compilation of environmental data

For all SNW data, corresponding environmental data were extracted from models in the CMIP6 ensemble for the modern and preindustrial. Using environmental data from Earth system models (ESMs) rather than the environmental output reported in publications enables us to fill data gaps and ensure harmonisation of environmental data. Environmental data includes 1° × 1° gridded decadal averages for seawater temperature, phosphate concentration, nitrate concentration, salinity, chlorophyll *a* concentration, net primary productivity (NPP), alkalinity, CO_3^{2-}, DIC, Calcite Ω and pH.

Although some species (e.g., *G. truncatulinoides, G. inflata, N. dutertrei, P. obliquiloculata*) in our analysis are considered deep dwelling (i.e., live at the thermocline), we use surface ocean environmental data (≤ 20 m depth). This approach is in part due to the challenges of estimating exact habitat depth given its variability. These challenges include (1) the habitat depth of a foraminifera changes through its life time, hence it would be difficult to determine the most suitable average depth; (2) even if an average habitat depth were determined, there is uncertainty about how much calcification happens at which depth; (3) thermocline depth, which is frequently used to describe habitats is different in different parts of the ocean (Mulitza et al., 1997) and (4) habitat depth can vary with the seasons (Waterson et al., 2017). For further discussion and analysis of habitat depth see Supplementary Text S3. In future SNW analysis we recommend that oxygen isotope values are measured on individual specimens and combined with SNW to calculate exact habitat depth.

Carbonate system, salinity and temperature data were derived from Jiang et al. (2023), in which 14 CMIP6 Earth system models (ESMs) were corrected for bias and model drift (see Table S1 and Jiang et al. 2023). Environmental data for the Mediterranean were not available from 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. S3) 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 were used to extract phosphate concentration, nitrate concentration, chlorophyll *a* concentration and net primary productivity (NPP) data to determine ‘optimum conditions’ (Table S1; Fig. S4). 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. Additionally, there is some evidence that phosphate can inhibit calcification in some other calcifiers (Demes et al., 2009; Kinsey and Davies, 1979; Lin and Singer, 2006; Paasche and Brubak, 1994). 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}. These data were not corrected to observational data as the data coverage is insufficient. The median of the non-corrected environmental outputs were calculated and the preindustrial (1750) values were assumed the same as in 1850. 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 (unless stated otherwise) this was used. These size fractions were chosen because of their large sample number, they are in the middle of the size range, and allow us to cover a wide environmental gradient (Fig. 2). This resulted in statistical analysis of 491 samples covering seven species from four published datasets and our data (Text S1).

Four of the initial ten environmental parameters were included in the analysis: 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. S5), 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, and a QR decomposition term added to models to reduce the effect of 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; Table S3). For the species *G. truncatulinoides, G. elongatus* and *N. incompta* VIF values suggested collinearity was problematic. As such, we decompose the data into non-correlated factors using principal component analysis (PCA; see Text S2) and use these principal components instead of individual environmental drivers in the Bayesian models. For all Bayesian analysis, outliers were checked for 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. S6). An R-hat value close to 1 (i.e., less than 1.1) indicates the chains have converged (Bürkner, 2017). All models had an R-hat of 1.01 or 1 and a Pareto’s k of less than 0.7.

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; $n_{samples} = 491$) 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; Table S3). 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. S7), we include the Gamma distribution shape term in the model which allows the variance between each species to vary.

The full model was compared to a 'null' model that included fixed environmental effects and sampling method but did not consider species. 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 247.5 ± 19.4, see details in results; Table S3). 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 S1) 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 (i.e., across species) model, data type was added as a fixed effect for each species-level model. *Globoconella inflata, T. sacculifer, N. dutertrei, P. obliquiloculata* and *O. universa* were not modelled because of their low number of observations (*n* = < 30). To remove the impact of collinearity for *G. truncatulinoides, G. elongatus* and *N. incompta,* PCs were used in place of the individual environmental variables (Text S2). Bayesian models were fitted to the remaining six species. To assess how much of the variability in foraminiferal SNW for different species can be explained by the environment and sampling method, the effect size and credible interval (i.e., Bayesian confidence interval) of coefficients (environmental variables) were extracted from each model.

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 negative correlation between carbonate ion concentration and SNW is unlikely, 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.

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] 7.96; 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. S8). 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 *G. truncatulinoides* 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.

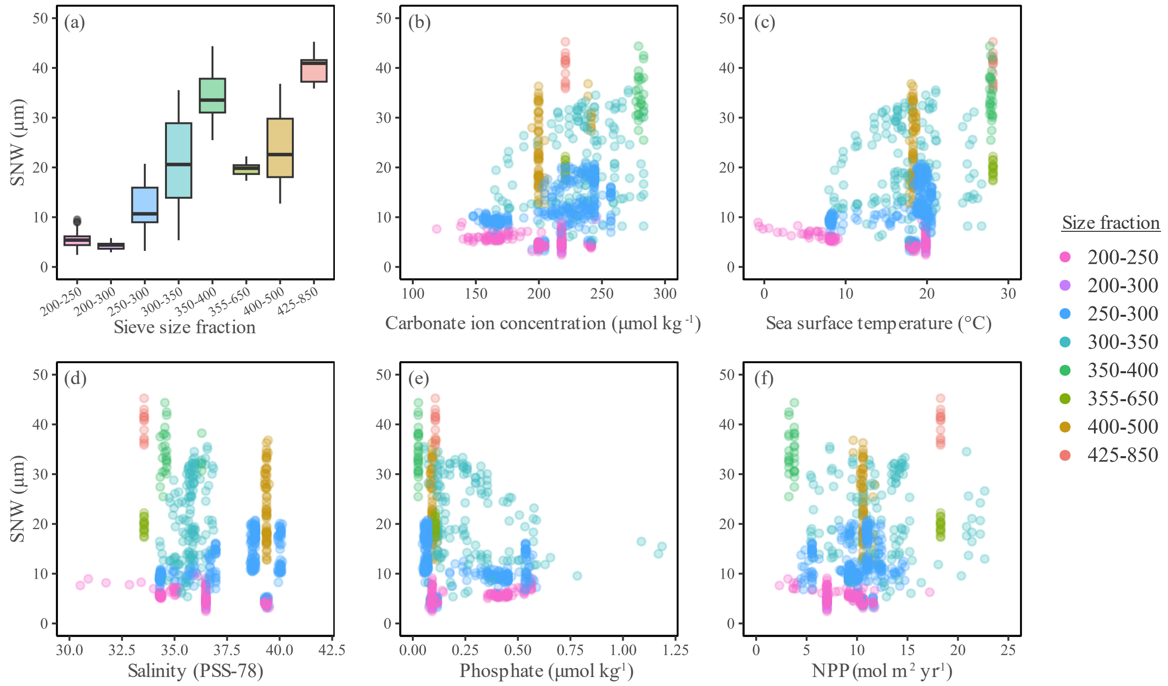

Figure 2 (a) Boxplot showing SNW distribution across sieve size fractions. (b-f) Planktic foraminiferal size-normalised weight (MBW) against environmental variables extracted from the CMIP6 modelling suite (see methods). Colour indicates the size-fraction foraminifers were initially sieved at before being normalised to their length or area. See Fig. S8 for planktic foraminiferal SNW separated by species, with sieve size fraction information and Fig. S9 for panel (a) separated by data type.

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. As such, although the smaller size fractions are meaningful in polar and subpolar areas (as foraminifers are smaller at the poles), they must be interpreted with caution in warm, high calcite saturation regions where including smaller size fractions might result in the selection of species which have not undergone a full developmental cycle and hence might miss final calcification such as the cortex or gametogenic calcite. 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 take out size fraction bias, all size fractions other than 250-300 µm and 300-350 µm have been removed and these two remaining size fractions have been merged to create a dataset sufficient for statistical analysis. Unless stated otherwise, the following statistics have been performed on this reduced dataset.

3.3 Is there an environmental control on SNW across species?

We use Bayesian regression to determine whether the there is an environmental control on SNW at the group-level" (i.e., across species). A model that is "environment only" explains 20% of the variability in SNW (Bayes R2; Table S3; Gelman et al., 2019). The addition of sampling method (i.e., the "null model") improves model performance ($\widehat{\mathrm{elpd}}_{\mathrm{loo}}$ improved by 114.4 [±23.7]) and explained variance increases to 60% (Table S3). The "full" model (i.e., environment, sampling method and species) performs better than the "null" model ($\widehat{\mathrm{elpd}}_{\mathrm{loo}}$ improved by 247.5 [±19.4]) and explained variance increases to 90% (Table S3). Together, this shows that the choice of sampling method can influence the SNW recorded and that species-specific responses are important in determining SNW. Results from the 'full' model highlight that higher SNWs are associated with a higher carbonate ion concentration (0.04 [0.01, 0.06]; effect size and 95% credible interval [lower, upper]; Fig. 3; Table S4) and lower phosphate concentration (−0.08 [−0.11, −0.06]; Fig. 3; Table S4), 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.

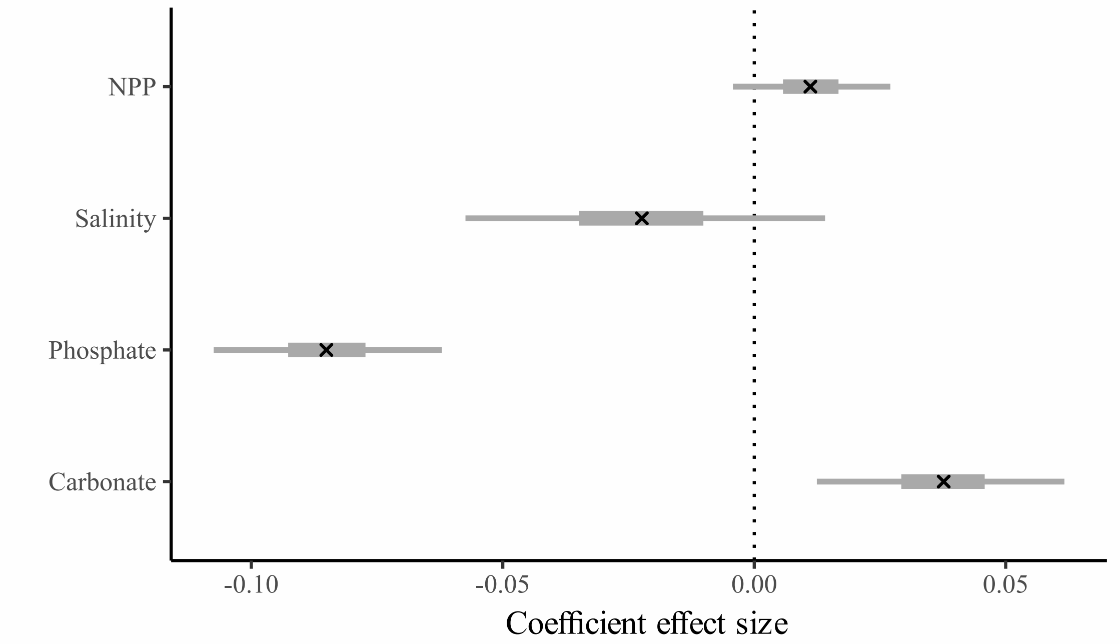

Figure 3 Effect size and credible intervals for the association between SNW and the environment for the group-level (across species, "full") model (see Table S4). A cross [x] represents the median value, the thicker line the 50% interval (i.e., where 50% of the posterior probability lies) and the thinner 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?

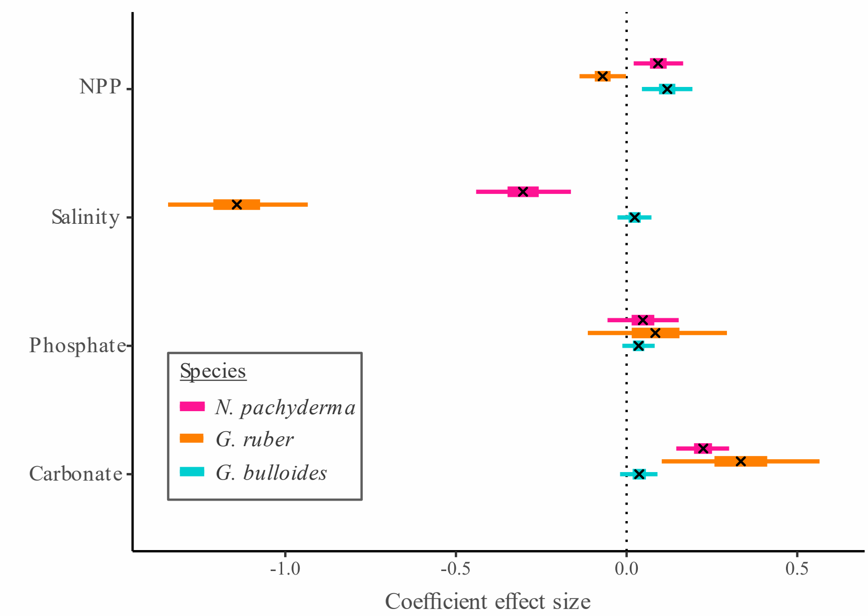

Figure 4 Effect size and credible intervals for the association between SNW and the environment for the species-level Bayesian modelling. A cross [x] represents the median value, the thicker line the 50% interval (i.e., where 50% of the posterior probability lies) and the thinner line the 95% interval. 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* is a symbiont-obligate, spinose species. *N. pachyderma* is a symbiont barren, non-spinose species.

Table 3 Summary of Bayesian model results for species that required and Principal Component Analysis to remove collinearity from models. The coefficient effect size and credible intervals (lower and upper 95% credible interval) for the association between SNW and the environment. Variance explained (%) indicate how well the principal component explains the environmental data. Percentage contribution show how well a particular environmental variable is represented in the principal component. Loadings (Eigenvectors) are indicative of the correlation between variables. Ecogroups are grouped by colour. *G. elongatus* is a symbiont-obligate, spinose species. *G. truncatulinoides* and *N. incompta* are symbiont barren, non-spinose species. See Text S2 for discussion of PCA results and Table S5 for extended data.

Model name and Principal components	**Bayesian model results**	**PCA results**				
	Coefficient effect size [lower 95%, upper 95%]	**Variance explained (%)**	**Quality of representation of variable in PC (% contribution) and *[Eigenvectors]***			
			Salinity	**PO$_4$**	**Carbonate**	**NPP**
G. truncatulinoides						
PC1	0.06 [0.00, 0.12]	59	34% *[0.58]*	28% *[−0.54]*	20% *[−0.45]*	17% *[−0.41]*
G. elongatus						
PC1	−0.06 [−0.08, −0.04]	62	27% *[−0.52]*	34% *[0.59]*	5% *[0.22]*	34% *[−0.58]*
PC2	−0.09 [−0.12, −0.06]	26	15% *[−0.39]*	2% *[−0.15]*	80% *[−0.90]*	2% *[−0.15]*
N. incompta						
PC1	0.08 [0.06, 0.09]	85	29% *[−0.53]*	28% *[0.53]*	23% *[−0.48]*	20% *[−0.45]*
PC2	0.01 [−0.02, 0.05]	12	1% *[−0.08]*	0% *[0.01]*	39% *[−0.62]*	60% *[0.78]*

Due to collinearity we are unable to assess the impact of sea surface temperature (SST) on SNW. 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 the 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).

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 S4). The relationship is not always positive though, with *G. bulloides* exhibiting no notable response to a change in carbonate ion concentration (0.04 [−0.01, 0.09]; Fig. 4; i.e., 95% interval crosses zero). PC1 for *G. truncatulinoides* is associated with a decrease in carbonate ion concentration (Eigenvector −0.45) that results in an increase in SNW (i.e., positive coefficient effect size; 0.06 [0.00, 0.12]; Table 3). Carbonate only contributes approximately one fifth to PC1 which only explains 59% of the variance in environmental data. Moreover, attributing the relative impact of environmental drivers is difficult given the contributions of salinity, PO_4 and NPP to PC1 (34%, 28% and 17%, respectively; Table 3). The positive eigenvector associated with *G.elongatus* PC1 for carbonate that contributes to a decrease in SNW (coefficient effect size −0.06 [−0.08, −0.04]; Table 3) should not be overinterpreted considering that carbonate only contributes 5% to PC1 in *G. elongatus.* Otherwise, the contributions of carbonate are as expected (i.e., a negative loading for carbonate in combination with the other environmental variables results in a negative coefficient effect size for SNW, i.e., a lower SNW).

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 a proxy for the HCO_3^-/ H^+ ratio, hence it is still important for calcification.

An increase in phosphate concentration is unlikely (<95% probability) to impact the SNW of *N. pachyderma, G. ruber* and *G. bulloides* (Fig. 4; Table S4; 95% interval crosses zero). Higher phosphate concentration is associated with lower SNWs for *G. truncatulinoides* and *G. elongatus.* For the former, weights are higher when phosphate concentration is lower (Eigenvector -0.54 and a positive coefficient effect size for PC1; Table 3), and for the latter weights are lower with increased phosphate (Eigenvector 0.59 and a negative coefficient effect size for PC1; Table 3). However, for both species phosphate only represents about a third of PC1, hence this impact cannot be separated from other environmental variables due to similar percent representations. Although *N. incompta* is also a symbiont barren non-spinose species, its response is different to *G.*

truncatulinoides. Increased phosphate (in combination with other environmental drivers; Eigenvector 0.53; Table 3) is associated with a higher SNW (a positive coefficient effect size for PC1).

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 a 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 taxon, 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). Though in our group-level model (i.e., all foraminifers) we observe a negative impact of phosphate on SNW (−0.08 [−0.11, −0.06]; Fig. 3; Table S4). This is unlikely an effect of sampling bias toward the Atlantic as the Atlantic has near-even sampling (*n* = 242) 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 (−1.14 [−1.35, −0.93]). *Neogloboquadrina pachyderma* has a similar but weaker response (−0.30 [−0.44, −0.16]; Fig. 4; Table S4) and *G. bulloides* shows no response (0.03 [−0.01, 0.08]; Fig. 4; Table S4). *Globorotalia truncatulinoides* and *G. elongatus* have the same direction of response to salinity, with SNWs being heavier when salinity is higher (Table 3). For *G. truncatulinoides*, this presents as higher salinity (Eigenvector 0.58) being associated with heavier weights, i.e., a positive coefficient effect size (0.06 [0.00, 0.12]) and for *G. elongatus*, as lighter weights (−0.06 [−0.08, −0.04] under lower salinity (Eigenvector −0.52; Table 3). The opposite is true for *N. incompta*, for which in combination with other drivers, weight increases (0.08 [0.06, 0.09]) under lower salinity (Eigenvector −0.53; Table 3).

Laboratory experiments that 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 the final test size was smaller. The difference in the *G. ruber* response here and in Bijma et al. (1990) 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 from 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.

A higher NPP (food availability) is associated with heavier SNWs for *N. pachyderma* and *G. bulloides* and is likely to be associated with a lighter SNW for *G. ruber* (Fig. 4; Table S4). Lower NPP is associated with heavier SNWs on PC1 for *G. truncatulinoides* and *N. incompta* (negative Eigenvectors associated with positive coefficient effect sizes; Table 3). Though it is important to note that the percent representation of NPP is one fifth or less of the total contribution to the PC. For *G. elongatus* SNW is lighter with lower NPP (Eigenvector −0.58 and coefficient effect size −0.06 [−0.08, −0.04]), though this interpretation is similarly limited by NPP being in combination with other environmental variables.

Given that *G. bulloides* and *G. ruber* have spines which could make it easier for them to capture prey therefore less reliant on NPP compared to non-spinose types, it is surprising that these species (though in opposite directions) are associated with NPP. For the asymbiotic non-spinose *N. pachyderma,* SNW increases with productivity (0.09 [0.02, 0.16]; Fig. 4, Table S4). 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. Given that asymbiotic species (*N. pachyderma* and *G. bulloides*) show a positive impact on SNW with increased food, while the opposite is true for the symbiont bearing *G. ruber*, this could hint at light attenuation due to high plankton standing stocks reducing symbiotic activity (Bijma et al., 1992; Ortiz et al., 1995) thereby reducing this additional energy source used to support growth and calcification (LeKieffre et al., 2018).

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).

Some tentative evaluation of ecogroup responses can be made despite the interpretation of PCA factors being limited. Interpretation is limited because PCA represents a gradient which includes multiple environmental drivers, hence the impact of a single driver cannot be separated from other environmental drivers. The SNW response to the environment is largely species specific and shows little evidence of an overriding ecological driven response. Although an increase in carbonate ion concentration is likely linked to heavier SNWs, this is true across all species and not ecogroup dependent. Otherwise, ecogroups do not have a unifying driver. For example, the symbiont barren, non-spinose species (*N. pachyderma,* and *G. truncatulinoides*) lack a unifying driver linked to their ecology and have the lowest Bayes R2 scores (55% and 33%, respectively). This could be because 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 Impact of sampling type

The choice of sampling method is important for the resulting weight of foraminifers. Despite attempting to minimise the impact of sampling method by removing (1) plankton tow data, (2) data for which dissolution is reported and (3) samples approaching the CCD, the impact of sampling method on SNW is still evident. In all models (excluding *N. pachyderma*, which only had one sampling method), the lightest SNWs were recorded from sediment traps (Fig. S10). Sediment core data are lighter than coretop data, hinting towards questions of preservation not visible externally, but are more similar to each other than to sediment trap data (Fig. S10). We additionally split data by location to check whether sediment trap data are still lighter when the ocean basin is explicitly accounted for (Fig. S11). This separation shows (1) no clear trends for *N. incompta*, a relatively thick specimen, (2) no clear trends in the two datasets for *G. bulloides* comparing the Mediterranean with the Atlantic, though overall for this reduced dataset SNW in sediment trap data is lighter than, or equal to seafloor (coretop and sediment core) data, (3) heavier *G. truncatulinoides* weight with coretop data. It is important to note that we have limited data from regions which have a very shallow CCD such as the Pacific, thereby limiting insight.

It is unlikely that dissolution in the water column (i.e., impact of intermediate and deep water) is the cause of lighter weights in sediment trap data (Fig. S10 and S11), because it would have impacted coretop and/or sediment core samples even more due to longer exposure. It is unlikely that diagenetic alteration (e.g. recrystallization in the pore water) has made the SNW of coretop and sediment core data comparatively heavier as relative to the weight of the entire test it would have little impact on overall weight. We speculate that sediment trap data are lighter as they reflect current environmental conditions, whereas sediment core and most coretop data are preindustrial, hence the lighter weights may be due to impacts of lower carbonate ion concentration due to ocean acidification (Moy et al., 2009; Pallacks et al., 2023).

4 Discussion

4.1 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 $p\text{CO}_2$.

Although there is a small but likely (i.e., >95% probability) effect of carbonate on a group level (i.e., across species; 0.04 [0.01, 0.06]), phosphate is also likely associated with SNW (−0.08 [−0.11, −0.06]; Fig. 3; Table S4). Hence, unless the impact of phosphate on SNW can be quantified and disentangled from the carbonate effect, SNW across species is not a reliable predictor for $p\text{CO}_2$. 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. S2) we find no correlation between SNW and carbonate ion concentration (Fig. 4). Hence we advocate for the regional calibration of $p\mathrm{CO}_2$ – SNW relationships, and caution against the extrapolation and global application of SNW as proxy for $p\mathrm{CO}_2$.

4.2 Current challenges and future outlook

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 environmental data were not available to determine drivers. Otherwise, SNW 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). It would also be useful for authors to report their foraminifera cleaning protocol, or even better the community agree on a standardised cleaning method as different methods can result in variable sedimentary contamination, which impacts the weight of specimens (Béjard et al., 2023; Zarkogiannis et al., 2020). Additionally, we still have important gaps in our understanding of foraminiferal ecology, for example the dynamics of the habitat throughout the year (including the depth of calcification; see Text S3), 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.

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.

5 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

An R markdown file has been uploaded as part of the supplement and is available at the University of Bristol Research Data Storage Facility (RDSF) DOIXXXXX

Data availability

All data used in this study are available at Pangaea 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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