What controls planktic foraminiferal calcification?

Ruby Barrett[1], Joost de Vries[2], Daniela N. Schmidt[1]

[1] School of Earth Sciences, University of Bristol, UK

[2] BRIDGE, School of Geography, University of Bristol, UK

RB 0000-0002-6805-1707

JDV 0000-0003-3427-6921

DNS 0000-0001-8419-2721

Correspondence to: Ruby Barret, ruby.barrett@bristol.ac.uk

Abstract. Planktic foraminifera are key producers of pelagic carbonate, and their shell weight is suggested to ~~represent~~ 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 $p\text{CO}_2$ proxy), while others suggest that species optimum conditions, nutrient concentration, or temperature drive shell weight. To better understand ~~its use as a~~this proxy, we investigate what drives SNW and whether discrepancies in the proposed control on weight ~~is~~ are 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~~ 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 $p\text{CO}_2$ 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.

1 Introduction

The unprecedented rise in CO₂ and temperature is altering our oceans and impacting marine ecosystems and their ~~services~~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 pCO₂ (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 [CO₃²⁻] 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 [CO₃²⁻], 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 [CO₃²⁻] (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) and seawater density (Zarkogiannis et al., 2019). (Schiebel and Hemleben, 2005)(Zarkogiannis et al., 2022)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.

69   Physiology and ecological mechanisms such as biogeography or symbiosis may modulate the environmental

70   response. Hence different ecogroups (i.e., species grouped by their ecology ~~which~~ that have functional traits

71   such as spines in common; Table 1; ~~(~~Aze et al., 2011)~~)~~ may respond differently to the environment. For

72   example, in symbiont bearing species the negative impact of low carbonate ion concentration could be reduced

73   due to CO_2 uptake by symbionts in the foraminifer's microenvironment (Jørgensen et al., 1985; Köhler-Rink and

74   Kühl, 2005; Rink et al., 1998). Species with spines may better capture food than non-spinose species (Gaskell et

75   al., 2019; Spindler et al., 1984), providing energy for metabolic processes ~~which~~ that support calcification.

76   SNW could additionally be variable between species due to potential differences in biomineralization

77   pathways. Models suggest different biological controls, such as the intracellular storage of inorganic carbon and

78   calcium ions (Erez, 2003), pH regulation (Lastam et al., 2023; de Nooijer et al., 2009; Toyofuku et al., 2017), and

79   active transport of calcium and/or magnesium pumping (Bentov and Erez, 2006; Nehrke et al., 2013). These

80   different pathways could have different sensitivities to environmental change. Furthermore, SNW

81   measurements taken at the morphospecies level (i.e., a species designated based on morphological features)

82   could mask differences in the individual genotypes within cryptic species (i.e., organisms that look identical but

83   represent distinct evolutionary lineages) if these have different environmental preferences (Darling et al., 2000;

84   Morard et al., 2024).

85   Furthermore, the SNW response may vary spatially. For example, at higher latitudes where carbonate

86   saturation is close to undersaturation (Mikis et al., 2019), a foraminifera may be at its limit of tolerance and

87   therefore more vulnerable to small changes in carbonate ion concentration than low latitudes dwellers, akin to

88   observations of coralline algae species responses to temperature changes at the trailing and leading edges of

89   their distribution (Kolzenburg et al., 2023).

90   Additionally, the wide range in methodology used to collect weight measurements could also complicate our

91   understanding of what drives SNW. Results are either generated with a sieved-based approach (SBW), in which

92   planktic foraminifers are sieved through a narrow size fraction then the average specimen weight is taken, or

93   through the measurement-based approach (MBW), where the additional step of normalizing to a measured

94   size parameter (diameter or area) is taken (equation 1). MBW is a more rigorous approach as the use of sieve

95   fractions (SBW) can be unreliable due to size variability within the sieve fraction itself (Aldridge et al., 2012;

96   Beer et al., 2010a; Béjard et al., 2023)

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

97

98   Finally, different sample collection methodologies (i.e., whether results are derived from culture, plankton tow,

99   core-top, or sediment trap samples) could further complicate our understanding of what drives calcification.

100   Some authors have analysed foraminiferal SNW from plankton tow samples (Aldridge et al., 2012; Beer et al.,

101   2010b; Mallo et al., 2017). However, foraminifers living in the water column are likely juvenile and have not

102   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~~ 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 ~~at both a~~across species (i.e., all foraminifers in this study pooled together) and ~~group~~ 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 7~~7~~90 samples covering 11 species from 7 published datasets and a new dataset (n = 2~~20~~09; Fig. 1~~; Text S1 and S2~~). 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. ~~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,~~ (Aldridge et al., 2012; Barker and Elderfield, 2002) using diameter or silhouette area (Béjard et al., 2023; Marshall et al., 2013). ~~(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). *Globigerinoides G. 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, S samples were omitted if dissolution of foraminifera specimens was reported, or if the water depth was more than 4̶0̶500m 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).

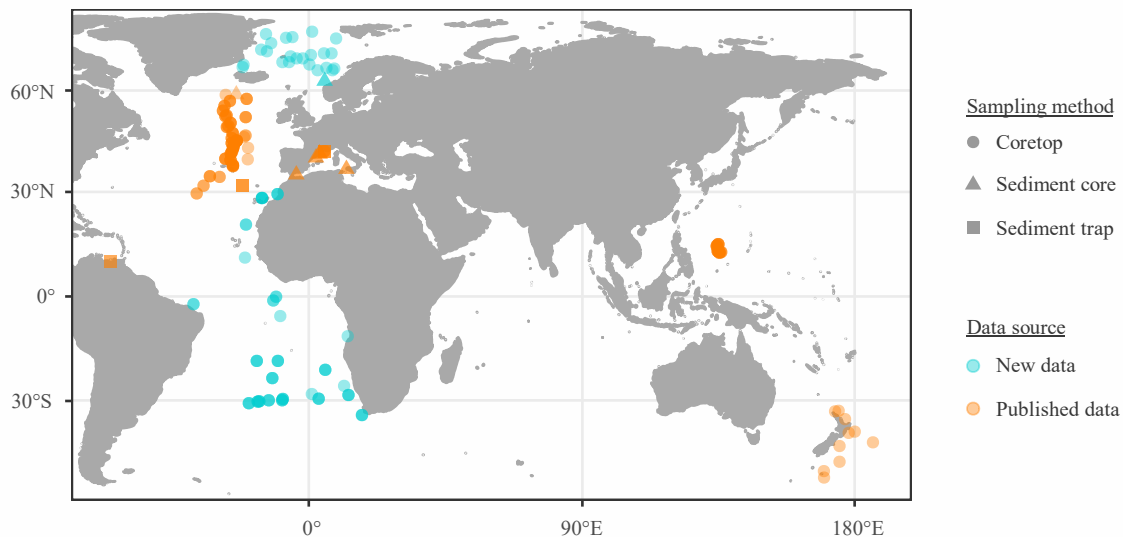



Figure 1 Location of SNW data. See Fig. S1 for sample count per datatype and Fig. S2 for a breakdown of species by location. $n_{samples}$ = 7̶7̶9̶0.

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 ~~surface ocean~~ 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

182 habitat depth see Supplementary Text S3. In future SNW analysis we recommend that oxygen isotope values

183 are measured on individual specimens and combined with SNW to calculate exact habitat depth.

184 Carbonate system, salinity and temperature data were derived from Jiang et al. (2023), in which 14 CMIP6

185 Earth system models (ESMs) were corrected for bias and model drift (see Table S1 and Jiang et al. 2023).

186 Environmental data for the Mediterranean was were not available from the Jiang et al. (2023). For this region,

187 sea surface temperature (SST), sea surface salinity (SSS), dissolved inorganic carbon (DIC) and total alkalinity

188 (TA) were extracted from CESM2 (Danabasoglu et al., 2020) (Fig. S32) as the carbonate system output from

189 CESM2 was closest to the median of the global average for the 14 ESMs (see Table S4 and S5 in Jiang et al.

190 2023).

191 The CESM2 data used in this manuscript were manipulated the same as other ESMs in Jiang et al. (2023). For

192 consistency with other models, CESM2 outputs were converted from mol m^{-3} to µmol kg^{-1} using a density

193 function calculated from the Thermodynamic Equation of Seawater (TEOS-10; IOC et al., 2010; McDougall &

194 Barker, 2011). Interannual variability was reduced by calculating a 10 year average for each decade. Model bias

195 was removed by correcting to DIVA gridded (Troupin et al., 2012) GLODAP (Lauvset et al., 2022) observational

196 data and model drift was removed using the relevant CESM2 preindustrial control (piControl). The adjusted SST,

197 SSS, DIC and TA were then used to calculate the rest of the OA indicators (CO$_3^{2-}$, Calcite Ω and pH) using

198 CO2System (van Heuven et al., 2011; Lewis and Wallace, 1998). Ice core-based atmospheric CO$_2$ data

199 (Etheridge et al., 1996; MacFarling Meure et al., 2006) were used to approximate the oceanic fCO$_2$ change from

200 1750 to 1850, thereby enabling estimation of the carbonate system for the preindustrial (1750) assuming that

201 all locations are in equilibrium with the atmosphere (Takahashi et al., 2014).

202 Five Earth Ssystem Mmodels (ESMs) were used to extract phosphate concentration, nitrate concentration,

203 chlorophyll a concentration and net primary productivity (NPP) data to determine 'optimum conditions' (Table

204 S1; Fig. S43). NPP and chlorophyll are indicators of the algal biomass concentration, which is a large part of

205 some foraminifera species' diet (Schiebel and Hemleben, 2017). Nutrient concentration is a step detached from

206 this, and represents the food available for their prey. Additionally, tThere is some evidence that phosphate can

207 inhibits calcification in some other calcifiers (Demes et al., 2009; Kinsey and Davies, 1979; Lin and Singer, 2006;

208 Paasche and Brubak, 1994). Decadal averages were calculated for these variables. For comparison to existing

209 data and to improve data readability phosphate and nitrate were converted from mol m^{-3} to µmol kg^{-1}, and

210 chlorophyll a from kg m^{-3} to mg m^{-3}. The median of the non-corrected environmental outputs were calculated

211 and the preindustrial (1750) values were assumed the same as in 1850. These data were not corrected to

212 observational data as the data coverage is insufficient. The median of the non-corrected environmental outputs

213 were calculated and the preindustrial (1750) values were assumed the same as in 1850. Although species'

214 abundance is also often used to inform optimum conditions, these data were not available for the same

215 locations.

216

217 **2.3 Statistical modelling**

218 **2.3.1 Data cleaning: addressing size fraction bias and collinearity in environmental data**

219 All statistical analyses were carried out using R version 4.2.1 (R Core Team, 2018). To remove size fraction bias

220 in SNW, the size fractions 250-300 and 300-350 were merged into one size fraction and (unless stated

221 otherwise) this was used. These size fractions were chosen because of their large sample number, they are in

222 the middle of the size range, and allow us to cover a wide environmental gradient (Fig. 2). This resulted in

223 statistical analysis of 491~~512~~ samples covering seven species from four published datasets and our data (Text

224 S1~~2~~).

225 Four of the initial ten environmental parameters were included in the analysis: phosphate concentration,

226 salinity, NPP, and CO_3^{2-}. We were unable to analyse the impact of sea surface temperature due to collinearity,

227 which would inflate the variance and standard error of coefficient estimates (Dormann et al., 2013). Nitrate

228 was excluded as phosphate and nitrate concentration are highly correlated (*rho* = 0.83, *p* = <.000). We chose to

229 keep phosphate as it is more commonly assessed in the literature. Similarly, the carbonate system parameters

230 are highly correlated (Fig. S5~~4~~), but as carbonate ion concentration is often used in the literature we use this to

231 represent the carbonate system. Because NPP is more directly linked with plankton biomass than chlorophyll *a*

232 concentration, the former is analysed here. Due to this data cleaning, it is important to note that while in the

233 following we emphasise the parameter we analysed, the impacts on SNW could also be driven by the highly

234 correlated driver.

235 **2.3.2 Model Specification**

236 All models were fitted using the Bayesian regression model package, brms (Bürkner, 2017) which uses the

237 probabilistic programming language Stan (Carpenter et al., 2017). The models were specified to be Gamma

238 distributed and were fitted using the NUTS (Hoffman and Gelman, 2014) sampler with 4 chains and 2000

239 iterations, each of which the first 1000 are warmup to calibrate the sampler, thus leading to 4000 posterior

240 samples.

241 All models were checked with appropriate tests before interpretation to ensure model assumptions were not

242 violated. Variables were centred and standardised ~~to reduce structural collinearity~~, and a QR decomposition

243 term added to models to reduce the effect of correlation between variables. To check for any remaining

244 collinearity, pairs plots were visually assessed, and variance inflation factors (VIF) were verified using the

245 package 'performance' which passes the brms model to its frequentist counterpart. A VIF of ten or less

246 indicates that collinearity is not problematic (Marcoulides & Raykov, 2019; Table S3). For the species *G.*

247 *truncatulinoides, G. elongatus* and *N. incompta* VIF values suggested collinearity was problematic. As such, we

248 decompose the data into non-correlated factors using principal component analysis (PCA; see Text S2) and use

249 these principal components instead of individual environmental drivers in the Bayesian models. For all

250 Bayesian analysis, ~~O~~outliers were ~~detected~~ checked for using Pareto's k, for which a value of 0.7 or higher

251 indicated an unduly influential observation. Visual posterior predictive checks were carried out to assess model

fit and chain mixing (Fig. S65). 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; $n_{samples}$ = 491512) 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. S76), 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 which that included fixed environmental effects and sampling method but 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 ($\widehat{elpd}_{loo}$ improved by 261.347.5 ± 18.619.4, 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 S12) 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. *GloboconellaG. 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). *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 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. 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~~ negative correlation between carbonate ion concentration ~~does not reduce foraminiferal~~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. ~~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.~~

Species	Data type	Biogeozone	Carbonate ion	pH	CO₂	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	+			~					

305 **Table 2** Compilation of results from previous studies assessing the relationship between planktonic
306 foraminiferal size-normalized weight (SNW) and the environment. + = positive correlation, − = negative
307 correlation, ~ = no response. This table summarizes information from measurement based SNW (i.e., silhouette
308 area, or diameter normalised) studies only and omits those which only normalised to size by sieving (i.e., sieve-
309 based weights; SBW) or use plankton tow data. See supplementary Table S2 for detail on SNW measurement
310 method. [1] Barker & Elderfield (2002); [2] Béjard et al. (2023); [3] Marr et al. (2011); [4] Marshall et al. (2013);
311 [5] Osborne et al. (2016); [6] Pallacks et al. (2023); [7] Weinkauf et al. (2016).

312

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~~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~~7~~). 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* ~~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.

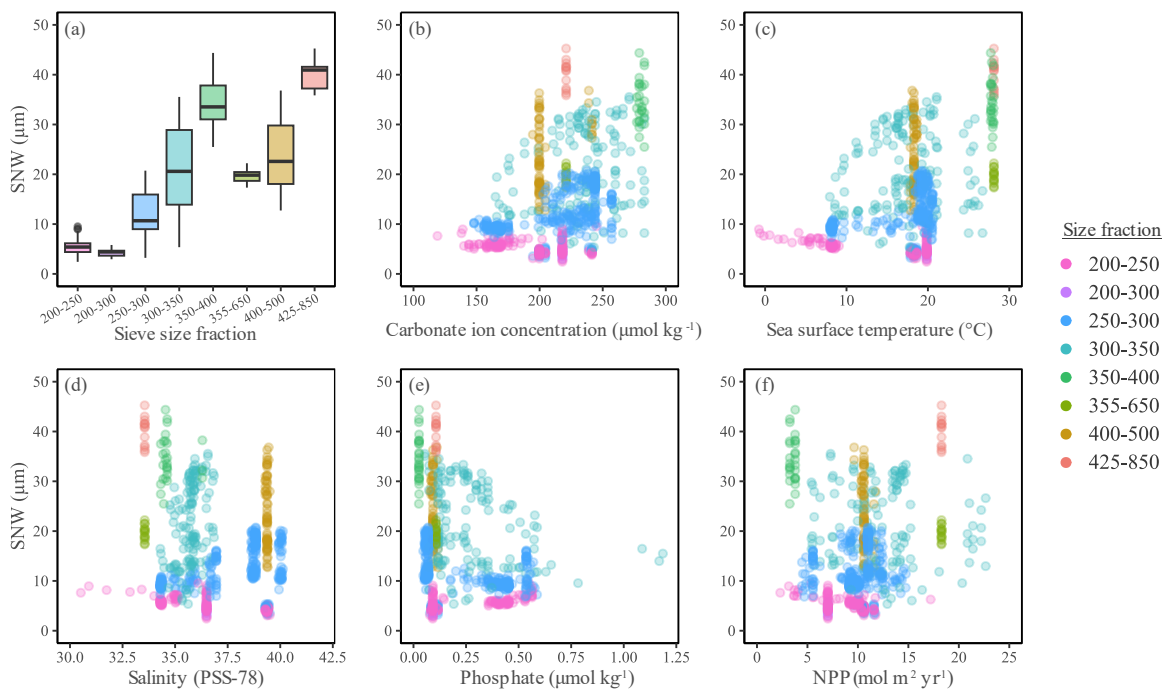
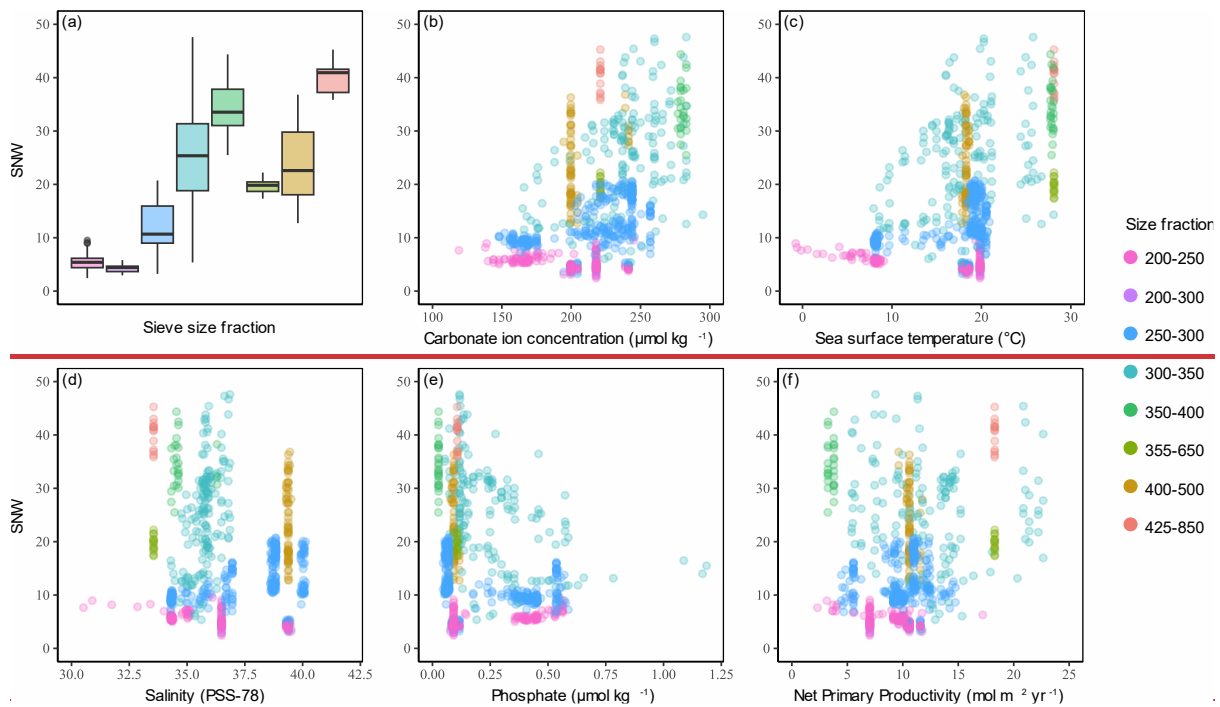



Figure 2 (a) Boxplot showing SNW distribution across sieve size fractions. (b-f) Planktic foraminiferal size-normalised weight (MBW) against environmental variables extracted from the CMIP6 modelling suite (see methods). Colour indicates the size-fraction foraminifers were initially sieved at before being normalised to their length or area. See Fig. S87 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, Aalthough 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.the size fractions 250-300 and 300-350 have been merged to create a 250-350 size fraction and (u Unless stated otherwise), the following statistics has have been performed on this reduced dataset.

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

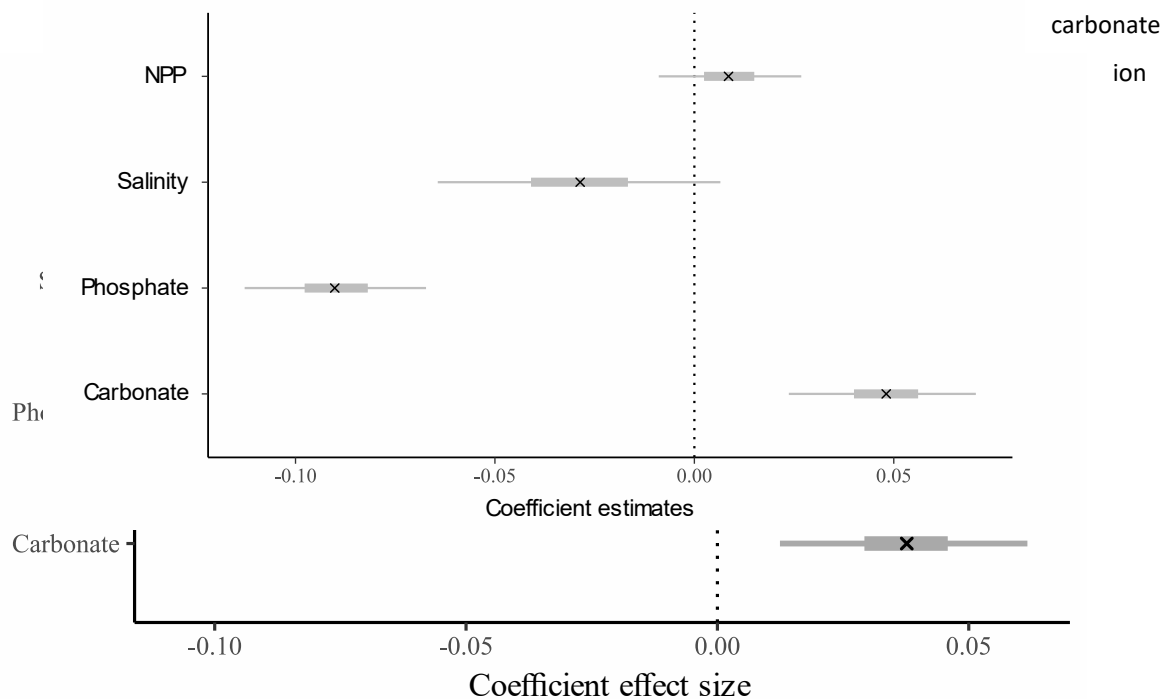
We use Bayesian regression to determine whether the there is an environmental control on SNW at the group-level" (i.e., across species). A model that is "environment only" explains 20% of the variability in SNW (Bayes R2; Table S3; Gelman et al., 2019). The addition of sampling method (i.e., the "null model") improves model performance ($\widehat{elpd}_{loo}$ 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 ($\widehat{elpd}_{loo}$ 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 ~~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. H~~higher SNWs are associated with a higher carbonate ion

concentration (0.0~~45~~ [0.0~~12~~, 0.0~~76~~]; effect size and 95% credible interval [lower, upper]; Fig. 3; Table S4) and lower phosphate concentration (−0.0~~98~~ [−0.11, −0.0~~76~~]; Fig. 3; Table S~~3~~4), 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

373 restricted for the group-level model due to a bias against larger size fractions in cooler environments (see
374 methods).

375

3.4 Is there a species specific or an ecogroup response?

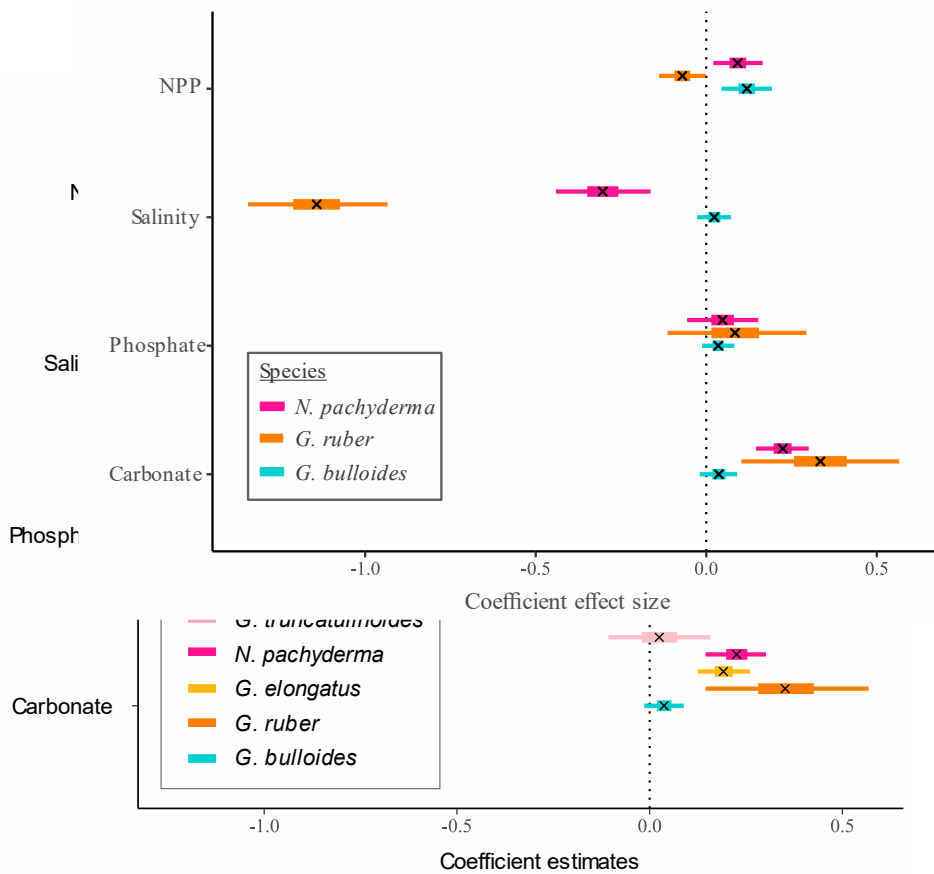



Figure 4 Effect size and credible intervals for the association between SNW and the environment for the species-level Bayesian modelling. A cross [x] represents the median value, the thicker line the 50% interval (i.e., where 50% of the posterior probability lies) and the thinner line the 95% interval. 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~~is a symbiont-obligate, spinose species. *N. pachyderma* ~~and *G. truncatulinoides* are~~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	PO₄	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]

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

394 could expect an increase in SNW with warming as warmer water decreases the solubility of atmospheric CO_2,

395 which elevates surface water carbonate ion concentration, and also increases enzymatic activity which

396 promotes growth and calcification rate (Lombard et al., 2009; Spero et al., 1991). Although some past research

397 has identified an increase in SNW with warming (Béjard et al., 2023; Davis et al., 2013; Gonzalez-Mora et al.,

398 2008; Marshall et al., 2013; Osborne et al., 2016; Qin et al., 2020; Song et al., 2022; Weinkauf et al., 2016),

399 there is also evidence for the reverse (Mallo et al., 2017; Naik et al., 2010, 2011; Pallacks et al., 2023). This

400 dichotomy has been attributed to the overriding effect of decreasing carbonate ion concentration on SNW due

401 to ocean carbon input (Naik et al., 2010; Pallacks et al., 2023), temperature induced sea surface stratification

402 and lower food availability (Mallo et al., 2017).

403

404 In agreement with published literature (Aldridge et al., 2012; Barker and Elderfield, 2002; Béjard et al., 2023;

405 Marshall et al., 2013; Osborne et al., 2016; Pallacks et al., 2023), an increase in carbonate ion concentration

406 does not negatively impact SNW (Fig. 4; Table S43). The relationship is not always positive though, with *G.*

407 *bulloides* (0.04 [−0.02, 0.09]) and *G. truncatulinoides* (0.03 [−0.11, 0.16]) exhibiting no notable response to a

408 change in carbonate ion concentration (0.04 [−0.01, 0.09]; Fig. 4; i.e., 95% interval crosses zero). PC1 for *G.*

409 *truncatulinoides* is associated with a decrease in carbonate ion concentration (Eigenvector −0.45) that results in

410 an increase in SNW (i.e., positive coefficient effect size; 0.06 [0.00, 0.12]; Table 3). Carbonate only contributes

411 approximately one fifth to PC1 which only explains 59% of the variance in environmental data. Moreover,

412 attributing the relative impact of environmental drivers is difficult given the contributions of salinity, PO_4 and

413 NPP to PC1 (34%, 28% and 17%, respectively; Table 3). The positive eigenvector associated with *G.elongatus*

414 PC1 for carbonate that contributes to a decrease in SNW (coefficient effect size −0.06 [−0.08, −0.04]; Table 3)

415 should not be overinterpreted considering that carbonate only contributes 5% to PC1 in *G. elongatus.*

416 Otherwise, the contributions of carbonate are as expected (i.e., a negative loading for carbonate in

417 combination with the other environmental variables results in a negative coefficient effect size for SNW, i.e., a

418 lower SNW).

419 It remains up for debate which part of the carbonate system exerts control on calcification. It has been

420 suggested that the HCO_3^- / H^+ ratio (where HCO_3^- [bicarbonate ions] are the inorganic carbon substrate and H^+

421 [protons] are a calcification inhibitor) controls calcification and that CO_3^{2-} correlates because of a

422 proportionality between CO_3^{2-} and this ratio (Bach, 2015). Yet even if this is the case, this implies that CO_3^{2-} can

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

424 An increase in phosphate concentration is unlikely (<95% probability ~~and <50% probability for *G. ruber*~~) to

425 impact the SNW ~~other than for *G. truncatulinoides* (−0.13 [−0.26, −0.01]), and *G. elongatus* (0.27 [0.22, 0.32])of~~

426 ~~*N. pachyderma*, *G. ruber* and *G. bulloides* (Fig. 4; Table S4; 95% interval crosses zero).~~ Higher phosphate

427 concentration is associated with lower SNWs for *G. truncatulinoides* and *G. elongatus.* For the former, weights

428 are higher when phosphate concentration is lower (Eigenvector -0.54 and a positive coefficient effect size for

429 PC1; Table 3), and for the latter weights are lower with increased phosphate (Eigenvector 0.59 and a negative

430 coefficient effect size for PC1; Table 3). However, for both species phosphate only represents about a third of

431 PC1, hence this impact cannot be separated from other environmental variables due to similar percent

432 representations. Although *N. incompta* is also a symbiont barren non-spinose species, its response is different

433 to *G. truncatulinoides*. Increased phosphate (in combination with other environmental drivers; Eigenvector

434 0.53; Table 3) is associated with a higher SNW (a positive coefficient effect size for PC1).

435 ~~For the former, increased phosphate may reduce SNW and for the latter, SNW increases with phosphate~~

436 ~~concentration (Fig. 4; Table S3).~~ Given the evidence for calcification inhibition in high phosphate conditions (Lin

437 and Singer, 2006) for other calcifiers, such as corals (Kinsey and Davies, 1979), coccolithophores (Paasche and

438 Brubak, 1994), and calcifying green algae (Demes et al., 2009), it is interesting that we do not observe a

439 stronger detrimental effect of phosphate on these foraminiferal species. However, this disparity could be

440 explained by the different calcification mechanisms. For example, foraminifers biomineralize extracellularly by

441 engulfing calcite-forming materials through seawater vacuolisation (potentially assisted by transmembrane ion

442 transport; Bentov et al., 2009; de Nooijer et al., 2014; Erez, 2003; Nehrke et al., 2013). In contrast,

443 coccolithophores biomineralize by forming coccoliths in intracellular organelles called 'coccolith forming

444 vesicles' (Brownlee and Taylor, 2004).

445 There is no consensus on the impact of phosphate on calcification even within a tax~~a~~on, with a recent study on

446 coccolithophores not showing calcification inhibition but instead showing decreased calcification with

447 phosphate limitation (Gerecht et al., 2018)~~.~~, ~~H~~ hence pointing to other taxa exhibiting similar response to our

448 species-level modelling. Our *G. bulloides* result conflicts with a study of North Atlantic *G. bulloides,* in which a

449 decrease in SNW with increased phosphate was recorded (Aldridge et al., 2012), though Béjard (2023) and

450 Mallo et al. (2017) did not observe this in the Mediterranean. This disparity could be due to the use of shallow

451 plankton tows in Aldridge et al. (2012), which is likely to complicate the SNW signal as juveniles which had not

452 completed their development may have been measured. Additionally, *G. bulloides* has several cryptic species

453 (Morard et al., 2024) which have their own ecological adaptation and spatial variability. Hence the geographic

454 difference might further complicate the interpretation of data in these studies (Fig. S2). Though ~~I~~ in our group-

455 level model (i.e., all foraminifers) ~~though~~ we observe a negative impact of phosphate on SNW ~~across species~~

456 (−0.0~~8~~9 [−0.11, −0.0~~6~~7]; Fig. 3; Table S~~3~~4). This is unlikely an effect of sampling bias toward the Atlantic as the

457 Atlantic has near-even sampling (*n* = 2~~63~~42) 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~~06 [−1.~~24~~35, −0.~~88~~93])~~., and~~ *~~Neogloboquadrina~~N.* pachyderma has a similar but weaker response (−0.30 [−0.44, −0.16]; Fig. 4; Table S~~3~~4) 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).

~~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~~ 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. Th~~is~~e 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 ~~to~~ 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.

~~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~~A higher NPP (food availability) ~~results~~ is associated with~~in a~~ heavier SNW~~s~~ for *N. pachyderma* and *G. bulloides* ~~(Fig. 4; Table S3)~~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.

~~For *G. elongatus,* their symbionts should make the species less dependent on productivity due to cross transfer of sugars (LeKieffre et al., 2018), and fo~~Given that~~r~~ *G. bulloides* ~~and *G. ruber* ~~the presence of~~have spines ~~should~~ which could make it easier for them to capture prey therefore less reliant on NPP compared to non-spinose types, ~~therefore~~it ~~should similarly be~~is surprising that these species (though in opposite directions) are~~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~~For the asymbiotic~~,~~ non-spinose ~~ecogroup,~~ *N. pachyderma*~~, and *G. truncatulinoides* there is no clear pattern, with the former's~~ SNW ~~increasing~~ increases with productivity (0.09

494 [0.02, 0.1~~6~~7]; Fig. 4, Table S4). ~~and the latter showing no response (−0.00 [−0.05, 0.05]).~~ It is interesting that

495 despite constructing a secondary calcite crust (which could overprint the primary SNW signal), *N. pachyderma*

496 (Kohfeld et al., 1996) still exhibits a response to the environment. Given that asymbiotic species (*N.*

497 *pachyderma* and *G. bulloides*) show a positive impact on SNW with increased food, while the opposite is true

498 for the symbiont bearing *G. ruber*, this could hint at light attenuation due to high plankton standing stocks

499 reducing symbiotic activity (Bijma et al., 1992; Ortiz et al., 1995) thereby reducing this additional energy source

500 used to support growth and calcification (LeKieffre et al., 2018).

501 ~~Due to collinearity we are unable to assess the impact of SST on SNW for the species-level models. However,~~

502 ~~we could expect an increase in SNW with warming as warmer water decreases the solubility of atmospheric~~

503 ~~CO₂, which elevates surface water carbonate ion concentration, and also increases enzymatic activity which~~

504 ~~promotes growth and calcification rate (Lombard et al., 2009; Spero et al., 1991). Although some past research~~

505 ~~has identified an increase in SNW with warming (Béjard et al., 2023; Davis et al., 2013; Gonzalez-Mora et al.,~~

506 ~~2008; Marshall et al., 2013; Osborne et al., 2016; Qin et al., 2020; Song et al., 2022; Weinkauf et al., 2016),~~

507 ~~there is also evidence for the reverse (Mallo et al., 2017; Naik et al., 2010, 2011; Pallacks et al., 2023). This~~

508 ~~dichotomy has been attributed to overriding effect of decreasing carbonate ion concentration on SNW due to~~

509 ~~ocean carbon input (Naik et al., 2010; Pallacks et al., 2023), temperature induced sea surface stratification and~~

510 ~~lower food availability (Mallo et al., 2017).~~

511 Due to limited shell flux data, we were unable to investigate how optimum growth conditions (OGC) impacted

512 SNW. Although NPP may facilitate OGC by making food available for growth, we cannot assume that high NPP

513 results in optimum conditions as it also hinders photosynthesis and excludes species (Ortiz et al., 1995). There

514 is some evidence of SNW increasing where a species is at its OGC (i.e., where shell flux for that species is high;

515 de Villiers, 2004), but there is no consensus in the data (Table 2) with some observing a negative correlation

516 between OGC and SNW (Béjard et al., 2023; Weinkauf et al., 2016).

517 Some tentative evaluation of ecogroup responses can be made despite the interpretation of PCA factors being

518 limited. Interpretation is limited because PCA represents a gradient ~~which~~ includes multiple environmental

519 drivers, hence the impact of a single driver cannot be separated from other environmental drivers. The SNW

520 response to the environment is largely species specific and shows little evidence of an overriding ecological

521 driven response. Although an increase in carbonate ion concentration is likely linked to heavier SNWs, this is

522 true across all species and not ecogroup dependent~~For some taxa, similar responses can be found, e.g. the~~

523 ~~symbiont-obligate, spinose species G. ruber and G. elongatus show the same direction of response to~~

524 ~~carbonate, though the strength of response is variable (0.35 [0.14, 0.56] and 0.19 [0.12, 0.26], respectively; Fig.~~

525 ~~4; Table S3).~~. Otherwise, ecogroups do not have a unifying driver. For example, ~~Tt~~he symbiont barren, non-

526 spinose species (*N. pachyderma,* and *G. truncatulinoides*) lack a unifying driver linked to their ecology and have

527 the lowest Bayes R2 scores (55% and 33%, respectively). ~~Though it is important to note that~~This could be

528 because the SNWs of these species are likely to be more heavily impacted the production of a secondary calcite

529 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 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

3.5 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 pCO_2.

Although there is a small but likely (i.e., >95% probability) effect of carbonate on a group level (i.e., across species; 0.045 [0.012, 0.067]), phosphate is also likely associated with SNW (−0.098 [−0.11, −0.067]; Fig. S3; Table S34). 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 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. S21) we find no correlation between SNW and carbonate ion concentration (Fig. 4). 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.

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 therefore could not be used to determine drivers.

576 Otherwise, SNW data were often not freely available (or at all available) and if deposited, only provided

577 processed data with different methods of normalising weight to size. We strongly encourage the community to

578 deposit raw data to make the legacy of data longer. 28 publications were omitted because shell weights were

579 reported using the sieve-based weight (SBW) methodology and not normalised to size or area (MBW).

580 Although there is some debate as to whether this additional step of normalising weight to measurement-

581 based size is necessary, some publications (Aldridge et al., 2012; Beer et al., 2010a; Béjard et al., 2023) indicate

582 that MBW SNW is more robust than SBW. It would be a step forward for the community to derive protocols for

583 SNW akin to trace element analysis e.g. Hathorne et al. (2013) and Rosenthal et al. (2004). Additionally, it is

584 important to acknowledge the different developmental stages in plankton tow samples compared to sediment

585 trap and core-top samples. Post-depositional dissolution will reduce weights, while infilling and diagenesis

586 increase weight and both need to be carefully monitored (Bassinot et al., 1994; Broecker & Clark, 2001). It

587 would also be useful for authors to report their foraminifera cleaning protocol, or even better, the community

588 agree on a standardised cleaning method as different methods can result in variable sedimentary

589 contamination, which impacts the weight of specimens (Béjard et al., 2023; Zarkogiannis et al., 2020). A

590 Additionally, we still have important gaps in our understanding of foraminiferal ecology, for example the

591 dynamics of the habitat throughout the year (including the depth of calcification; see Text S3), the peak times

592 of biomass production in different regions and the drivers of thickness of gametogenic calcite. All of these

593 factors limit the use of the proxy.

594 Importantly, our analyses lack data from the Indian Ocean, sSouthern high latitudes and large parts of the

595 Pacific - highlighting challenges of preservation in deep sea sediments, logistics of reaching remote areas, and

596 bias due to the traditional areas of sampling of sea going nations. As analyses expand to ocean regions below

597 the lysocline, authors should provide a measure of dissolution and/or high resolution images of specimens

598 which can help assess the impact of post-diagenetic alteration. Although such images can also support

599 morphological assessment of cryptic species, these images are still not systematically implemented in

600 palaeoceanographic studies.

601 **54 Conclusions**

602 Although higher carbonate ion concentration and lower phosphate concentration are associated with heavier

603 SNWs at the group-level (i.e., across species), the environment alone explains relatively little of the variability in

604 SNW at the group-level. Instead, we identify species-specific SNW responses that better explain variability in

605 weight. Although physiology is likely to modulate the foraminiferal response to the environment, we find

606 limited evidence of an ecogroup-level response.

607 The species-specific SNW response to the environment is complex, with each species responding to a different

608 combination of environmental drivers. We hypothesise that this is in part influenced by cryptic species and our

609 limited understanding of what drives the thickness of gametogenic calcite. The SNW response being species-

610 specific and responding to drivers other than carbonate implies there is a need to consider which species to

611   use as a pCO$_2$ proxy, or a need to consider multiple species in parallel to reduce uncertainty from species-

612   specific differences. Furthermore, due to differences in the published response of *G. bulloides* in the North

613   Atlantic and our more global dataset of *G. bulloides* SNW, we advocate for the regional calibration of pCO$_2$ –

614   SNW relationships.

615   Our understanding of SNW as a proxy would be greatly improved with some community efforts to solve some

616   of the above questions including (1) making raw SNW data freely available, (2) community agreed protocols,

617   i.e., whether SBW or MBW should be used in such analyses, (3) improving our understanding of the

618   calcification process itself and how the environment drives the thickness of gametogenic calcite, and (4)

619   resolving the impact that cryptic species have on SNW measurements.

620

Code availability

~~The code (R script) supporting this article~~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.

~~**Disclaimer**~~

~~[for journal to fill out?]~~

Acknowledgements

This work would not have been possible without the efforts of the ODP and IODP programs. We acknowledge the University of Bremen, Dr Barbara Donner and Dr KH Baumann for sharing samples. We would like to thank Dale Thompson and Dr Maricel Williams for processing samples to produce these new SNW data. Thank you to Dr Li-Qing Jiang for providing support early on in the study design, and for sharing their processed CMIP6 data.

Financial support

R.B. was funded by NERC GW4+ DTP grant NE/S007504/1
D.N.S. was funded by NERC grant NE/P019439/1
J.V. was funded by NERC grant NE/X001261/1

Review statement

~~This paper was reviewed~~Thank you to ~~by XXXX~~Brian Huber, Pincelli Hull and an anonymous reviewer for their feedback on an earlier version of this manuscript.

649 **References**

650 Aldridge, D., Beer, C. J., and Purdie, D. A.: Calcification in the planktonic foraminifera *Globigerina bulloides*

651 linked to phosphate concentrations in surface waters of the North Atlantic Ocean, Biogeosciences, 9, 1725–

652 1739, https://doi.org/10.5194/bg-9-1725-2012, 2012.

653 Aze, T., Ezard, T. H. G., Purvis, A., Coxall, H. K., Stewart, D. R. M., Wade, B. S., and Pearson, P. N.: A phylogeny

654 of Cenozoic macroperforate planktonic foraminifera from fossil data, Biol. Rev. Camb. Philos. Soc., 86, 900–

655 927, https://doi.org/10.1111/J.1469-185X.2011.00178.X, 2011.

656 Bach, L. T.: Reconsidering the role of carbonate ion concentration in calcification by marine organisms,

657 Biogeosciences, 12, 4939–4951, https://doi.org/10.5194/BG-12-4939-2015, 2015.

658 Barker, S. and Elderfield, H.: Foraminiferal calcification response to glacial-interglacial changes in atmospheric

659 CO2, Science (80-.)., 297, 833–836, https://doi.org/10.1126/science.1072815, 2002.

660 Barrett, R., Adebowale, M., Birch, H., Wilson, J. D., and Schmidt, D. N.: Planktic Foraminiferal Resilience to

661 Environmental Change Associated With the PETM, Paleoceanogr. Paleoclimatology, 38,

662 https://doi.org/10.1029/2022PA004534, 2023.

663 Bassinot, F. C., Beaufort, L., Vincent, E., Labeyrie, L. D., Rostek, F., Müller, P. J., Quidelleur, X., and Lancelot, Y.:

664 Coarse fraction fluctuations in pelagic carbonate sediments from the tropical Indian Ocean: A 1500-kyr record

665 of carbonate dissolution, Paleoceanography, 9, 579–600, https://doi.org/10.1029/94PA00860, 1994.

666 Bé, A. W. H. and Tolderlund, D. S.: Distribution and ecology of living planktonic foraminifera in surface waters

667 of the Atlantic and Indian Oceans, in: The Micropalaeontology of Oceans, Cambridge University Press, 105–

668 149, 1971.

669 Beer, C. J., Schiebel, R., and Wilson, P. A.: On methodologies for determining the size-normalised weight of

670 planktic foraminifera, Biogeosciences, 7, 2193–2198, https://doi.org/10.5194/bg-7-2193-2010, 2010a.

671 Beer, C. J., Schiebel, R., and Wilson, P. A.: Testing planktic foraminiferal shell weight as a surface water [CO2-3]

672 proxy using plankton net samples, Geology, 38, 103–106, https://doi.org/10.1130/G30150.1, 2010b.

673 Béjard, T. M., Rigual-Hernández, A. S., Flores, J. A., Tarruella, J. P., Durrieu De Madron, X., Cacho, I., Haghipour,

674 N., Hunter, A., and Sierro, F. J.: Calcification response of planktic foraminifera to environmental change in the

675 western Mediterranean Sea during the industrial era, Biogeosciences, 20, 1505–1528,

676 https://doi.org/10.5194/BG-20-1505-2023, 2023.

677 Bentov, S. and Erez, J.: Impact of biomineralization processes on the Mg content of foraminiferal shells: A

678 biological perspective, Geochemistry, Geophys. Geosystems, 7, 8, https://doi.org/10.1029/2005GC001015,

679 2006.

680 Bentov, S., Brownlee, C., and Erez, J.: The role of seawater endocytosis in the biomineralization process in

681 calcareous foraminifera, Proc. Natl. Acad. Sci., 106, 21500–21504, https://doi.org/10.1073/PNAS.0906636106,

682   2009.

683   Bijma, J., Faber, W. W., and Hemleben, C.: Temperature and salinity limits for growth and survival of some

684   planktonic foraminifers in laboratory cultures, J. Foraminifer. Res., 20, 95–116, 1990.

685   Bijma, J., Hemleben, C., Oberhänsli, H., and Spindler, M.: The effects of increased water fertility on tropical

686   spinose planktonic foraminifers in laboratory cultures, J. Foraminifer. Res., 22, 242–256, 1992.

687   Bijma, J., Spero, H. J., and Lea, D. W.: Reassessing Foraminiferal Stable Isotope Geochemistry: Impact of the

688   Oceanic Carbonate System (Experimental Results), Use Proxies Paleoceanogr., 489–512,

689   https://doi.org/10.1007/978-3-642-58646-0_20, 1999.

690   Bijma, J., Hönisch, B., and Zeebe, R. E.: Impact of the ocean carbonate chemistry on living foraminiferal shell

691   weight: Comment on "Carbonate ion concentration in glacial-age deep waters of the Caribbean Sea" by W. S.

692   Broecker and E. Clark, Geochemistry, Geophys. Geosystems, 3, 1–7, https://doi.org/10.1029/2002GC000388,

693   2002.

694   Broecker, W. and Clark, E.: An evaluation of Lohmann's foraminifera weight dissolution index,

695   Paleoceanography, 16, 531–534, https://doi.org/10.1029/2000PA000600, 2001a.

696   Broecker, W. and Clark, E.: Reevaluation of the CaCO3 size index paleocarbonate ion proxy, Paleoceanography,

697   16, 669–671, https://doi.org/10.1029/2001PA000660, 2001b.

698   Broecker, W. and Clark, E.: Ratio of coccolith CaCO3 to foraminifera CaCO3 in late Holocene deep sea

699   sediments, Paleoceanography, 24, https://doi.org/10.1029/2009PA001731, 2009.

700   Brownlee, C. and Taylor, A.: Calcification in coccolithophores: A cellular perspective, in: Coccolithophores,

701   Springer, Berlin, 31–49, https://doi.org/10.1007/978-3-662-06278-4_2, 2004.

702   Buitenhuis, E. T., Le Quéré, C., Bednaršek, N., and Schiebel, R.: Large Contribution of Pteropods to Shallow

703   CaCO3 Export, Global Biogeochem. Cycles, 33, 458–468, https://doi.org/10.1029/2018GB006110, 2019.

704   Bürkner, P. C.: brms: An R Package for Bayesian Multilevel Models Using Stan, J. Stat. Softw., 80, 1–28,

705   https://doi.org/10.18637/JSS.V080.I01, 2017.

706   Bürkner, P. C.: Advanced Bayesian multilevel modeling with the R package brms, R J., 10, 395–411,

707   https://doi.org/10.32614/RJ-2018-017, 2018.

708   Carpenter, B., Gelman, A., Hoffman, M. D., Lee, D., Goodrich, B., Betancourt, M., Brubaker, M. A., Guo, J., Li, P.,

709   and Riddell, A.: Stan: A Probabilistic Programming Language, J. Stat. Softw., 76,

710   https://doi.org/10.18637/JSS.V076.I01, 2017.

711   Danabasoglu, G., Lamarque, J. F., Bacmeister, J., Bailey, D. A., DuVivier, A. K., Edwards, J., Emmons, L. K.,

712   Fasullo, J., Garcia, R., Gettelman, A., Hannay, C., Holland, M. M., Large, W. G., Lauritzen, P. H., Lawrence, D. M.,

713   Lenaerts, J. T. M., Lindsay, K., Lipscomb, W. H., Mills, M. J., Neale, R., Oleson, K. W., Otto-Bliesner, B., Phillips,

714 A. S., Sacks, W., Tilmes, S., van Kampenhout, L., Vertenstein, M., Bertini, A., Dennis, J., Deser, C., Fischer, C.,

715 Fox-Kemper, B., Kay, J. E., Kinnison, D., Kushner, P. J., Larson, V. E., Long, M. C., Mickelson, S., Moore, J. K.,

716 Nienhouse, E., Polvani, L., Rasch, P. J., and Strand, W. G.: The Community Earth System Model Version 2

717 (CESM2), J. Adv. Model. Earth Syst., 12, https://doi.org/10.1029/2019MS001916, 2020.

718 Darling, K. F., Wade, C. M., Stewart, I. A., Kroon, D., Dingle, R., and Leigh Brown, A. J.: Molecular evidence for

719 genetic mixing of Arctic and Antarctic subpolar populations of planktonic foraminifers, Nature, 405, 43–47,

720 https://doi.org/10.1038/35011002, 2000.

721 Davis, C. V., Badger, M. P. S., Bown, P. R., and Schmidt, D. N.: The response of calcifying plankton to climate

722 change in the Pliocene, Biogeosciences, 10, 6131–6139, https://doi.org/10.5194/bg-10-6131-2013, 2013.

723 Davis, C. V., Rivest, E. B., Hill, T. M., Gaylord, B., Russell, A. D., and Sanford, E.: Ocean acidification

724 compromises a planktic calcifier with implications for global carbon cycling, Sci. Rep., 7, 1–8,

725 https://doi.org/10.1038/s41598-017-01530-9, 2017.

726 Demes, K. W., Bell, S. S., and Dawes, C. J.: The effects of phosphate on the biomineralization of the green alga,

727 Halimeda incrassata (Ellis) Lam., J. Exp. Mar. Bio. Ecol., 374, 123–127,

728 https://doi.org/10.1016/J.JEMBE.2009.04.013, 2009.

729 Dong, S., Lei, Y., Bi, H., Xu, K., Li, T., and Jian, Z.: Biological Response of Planktic Foraminifera to Decline in

730 Seawater pH, Biology (Basel)., 11, https://doi.org/10.3390/BIOLOGY11010098/S1, 2022.

731 Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade,

732 B., Leitão, P. J., Münkemüller, T., Mcclean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell,

733 D., and Lautenbach, S.: Collinearity: a review of methods to deal with it and a simulation study evaluating their

734 performance, Ecography (Cop.)., 36, 27–46, https://doi.org/10.1111/J.1600-0587.2012.07348.X, 2013.

735 Erez, J.: The Source of Ions for Biomineralization in Foraminifera and Their Implications for Paleoceanographic

736 Proxies, Rev. Mineral. Geochemistry, 54, 115–149, https://doi.org/10.2113/0540115, 2003.

737 Etheridge, D. M., Steele, L. P., Langenfelds, R. L., Francey, R. J., Barnola, J. M., and Morgan, V. I.: Natural and

738 anthropogenic changes in atmospheric CO2 over the last 1000 years from air in Antarctic ice and firn, J.

739 Geophys. Res. Atmos., 101, 4115–4128, https://doi.org/10.1029/95JD03410, 1996.

740 Gaskell, D. E., Ohman, M. D., and Hull, P. M.: Zooglider-Based Measurements of Planktonic Foraminifera in the

741 California Current System, J. Foraminifer. Res., 49, 390–404, https://doi.org/10.2113/GSJFR.49.4.390, 2019.

742 Gelman, A., Goodrich, B., Gabry, J., and Vehtari, A.: R-squared for Bayesian Regression Models, Am. Stat., 73,

743 307–309, https://doi.org/10.1080/00031305.2018.1549100, 2019.

744 Gerecht, A. C., Šupraha, L., Langer, G., and Henderiks, J.: Phosphorus limitation and heat stress decrease

745 calcification in Emiliania huxleyi, Biogeosciences, 15, 833–845, https://doi.org/10.5194/BG-15-833-2018, 2018.

746 Gonzalez-Mora, B., Sierro, F. J., and Flores, J. A.: Controls of shell calcification in planktonic foraminifers, Quat.

747   Sci. Rev., 27, 956–961, https://doi.org/10.1016/j.quascirev.2008.01.008, 2008.

748   Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. D., Robinson, B. S.,

749   Hodgson, D. J., and Inger, R.: A brief introduction to mixed effects modelling and multi-model inference in

750   ecology, PeerJ, 2018, https://doi.org/10.7717/PEERJ.4794/FIG-3, 2018.

751   Hathorne, E. C., Gagnon, A., Felis, T., Adkins, J., Asami, R., Boer, W., Caillon, N., Case, D., Cobb, K. M., Douville,

752   E., Demenocal, P., Eisenhauer, A., Garbe-Schönberg, D., Geibert, W., Goldstein, S., Hughen, K., Inoue, M.,

753   Kawahata, H., Kölling, M., Cornec, F. L., Linsley, B. K., McGregor, H. V., Montagna, P., Nurhati, I. S., Quinn, T.

754   M., Raddatz, J., Rebaubier, H., Robinson, L., Sadekov, A., Sherrell, R., Sinclair, D., Tudhope, A. W., Wei, G.,

755   Wong, H., Wu, H. C., and You, C. F.: Interlaboratory study for coral Sr/Ca and other element/Ca ratio

756   measurements, Geochemistry, Geophys. Geosystems, 14, 3730–3750, https://doi.org/10.1002/GGGE.20230,

757   2013.

758   Henehan, M. J., Evans, D., Shankle, M., Burke, J. E., Foster, G. L., Anagnostou, E., Chalk, T. B., Stewart, J. A., Alt,

759   C. H. S., Durrant, J., and Hull, P. M.: Size-dependent response of foraminiferal calcification to seawater

760   carbonate chemistry, Biogeosciences, 14, 3287–3308, https://doi.org/10.5194/bg-14-3287-2017, 2017.

761   van Heuven, S., Pierrot, D., Rae, J. W. B., Lewis, E., and Wallace, D. W. R.: MATLAB Program Developed for CO2

762   System Calculations, https://doi.org/https://doi.org/10.3334/CDIAC/otg.CO2SYS_MATLAB_v1.1, 2011.

763   Hoffman, M. D. and Gelman, A.: The No-U-Turn Sampler: Adaptively Setting Path Lengths in Hamiltonian

764   Monte Carlo, J. Mach. Learn. Res., 15, 1593–1623, 2014.

765   IOC, SCOR, and IAPSO: The International Thermodynamic Equation of Seawater - 2010: Calculation and use of

766   thermodynamic properties, ntergovernmental Oceanogr. Comm. Manuals Guid. No. 56. UNESCO.196., 2010.

767   IPCC: Summary for Policymakers. In: Climate Change 2021: The Physical Science Basis. Contribution of Working

768   Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Masson-

769   Delmotte, V., Zhai, P., Pirani, A., Connors, S. L., Péan, C., Berger, S., Caud, N., Chen, Y., Goldfarb, L., Gomis, M.

770   I., Huang, M., Leitzell, K., Lonnoy, E., Matthews, J. B. R., Maycock, T. K., Waterfield, T., Yelekçi, O., Yu, R., and

771   Zhou, B., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

772   https://doi.org/10.1017/9781009157896, 2021.

773   IPCC: Climate Change 2022: Impacts, Adaptation, and Vulnerability. Contribution of Working Group II to the

774   Sixth Assessment Report of the Intergovernmental Panel on Climate Change, edited by: Pörtner, H. O., Roberts,

775   D. C., Tignor, M., Poloczanska, E. S., Mintenbeck, K., Alegría, A., Craig, M., Langsdorf, S., Löschke, S., Möller, V.,

776   Okem, A., and Rama, B., Cambridge, UK and New York, NY, USA, https://doi.org/10.1017/9781009325844,

777   2022.

778   Jiang, L. Q., Dunne, J., Carter, B. R., Tjiputra, J. F., Terhaar, J., Sharp, J. D., Olsen, A., Alin, S., Bakker, D. C. E.,

779   Feely, R. A., Gattuso, J. P., Hogan, P., Ilyina, T., Lange, N., Lauvset, S. K., Lewis, E. R., Lovato, T., Palmieri, J.,

780   Santana-Falcón, Y., Schwinger, J., Séférian, R., Strand, G., Swart, N., Tanhua, T., Tsujino, H., Wanninkhof, R.,

781   Watanabe, M., Yamamoto, A., and Ziehn, T.: Global Surface Ocean Acidification Indicators From 1750 to 2100,

782   J. Adv. Model. Earth Syst., 15, https://doi.org/10.1029/2022MS003563, 2023.

783   Jørgensen, B. B., Erez, J., Revsbech, P., and Cohen, Y.: Symbiotic photosynthesis in a planktonic foraminiferan,

784   Globigerinoides sacculifer (Brady), studied with microelectrodes1, Limnol. Oceanogr., 30, 1253–1267,

785   https://doi.org/10.4319/LO.1985.30.6.1253, 1985.

786   Kinsey, D. W. and Davies, P. J.: Effects of elevated nitrogen and phosphorus on coral reef growth, Limnol.

787   Oceanogr., 24, 935–940, https://doi.org/10.4319/LO.1979.24.5.0935, 1979.

788   Kohfeld, K. E., Fairbanks, R. G., Smith, S. L., and Walsh, I. D.: Neogloboquadrina pachyderma (sinistral coiling)

789   as paleoceanographic tracers in polar oceans: Evidence from northeast water polynya plankton tows, sediment

790   traps, and surface sediments, Paleoceanography, 11, 679–699, https://doi.org/10.1029/96PA02617, 1996.

791   Köhler-Rink, S. and Kühl, M.: The chemical microenvironment of the symbiotic planktonic foraminifer Orbulina

792   universa, Mar. Biol. Res., 1, 68–78, https://doi.org/10.1080/17451000510019015, 2005.

793   Kolzenburg, R., Moreira, H., Storey, C., and Ragazzola, F.: Structural integrity and skeletal trace elements in

794   intertidal coralline algae across the Northeast Atlantic reveal a distinct separation of the leading and the

795   trailing edge populations, Mar. Environ. Res., 190, https://doi.org/10.1016/J.MARENVRES.2023.106086, 2023.

796   Langer, M. R.: Assessing the contribution of foraminiferan protists to global ocean carbonate production, J.

797   Eukaryot. Microbiol., 55, 163–169, https://doi.org/10.1111/J.1550-7408.2008.00321.X, 2008.

798   Lastam, J., Griesshaber, E., Yin, X., Rupp, U., Sánchez-Almazo, I., Heß, M., Walther, P., Checa, A., and Schmahl,

799   W. W.: The unique fibrilar to platy nano- and microstructure of twinned rotaliid foraminiferal shell calcite, Sci.

800   Reports 2023 131, 13, 1–19, https://doi.org/10.1038/s41598-022-25082-9, 2023.

801   Lauvset, S. K., Lange, N., Tanhua, T., Bittig, H. C., Olsen, A., Kozyr, A., Alin, S., Álvarez, M., Azetsu-Scott, K.,

802   Barbero, L., Becker, S., Brown, P. J., Carter, B. R., Da Cunha, L. C., Feely, R. A., Hoppema, M., Humphreys, M. P.,

803   Ishii, M., Jeansson, E., Jiang, L. Q., Jones, S. D., Lo Monaco, C., Murata, A., Müller, J. D., Pérez, F. F., Pfeil, B.,

804   Schirnick, C., Steinfeldt, R., Suzuki, T., Tilbrook, B., Ulfsbo, A., Velo, A., Woosley, R. J., and Key, R. M.:

805   GLODAPv2.2022: the latest version of the global interior ocean biogeochemical data product, Earth Syst. Sci.

806   Data, 14, 5543–5572, https://doi.org/10.5194/ESSD-14-5543-2022, 2022.

807   LeKieffre, C., Spero, H. J., Russell, A. D., Fehrenbacher, J. S., Geslin, E., and Meibom, A.: Assimilation,

808   translocation, and utilization of carbon between photosynthetic symbiotic dinoflagellates and their planktic

809   foraminifera host, Mar. Biol., 165, 1–15, https://doi.org/10.1007/S00227-018-3362-7/FIGURES/9, 2018.

810   Leung, J. Y. S., Zhang, S., Connell, S. D., Leung, J. Y. S., Zhang, S., and Connell, S. D.: Is Ocean Acidification Really

811   a Threat to Marine Calcifiers? A Systematic Review and Meta-Analysis of 980+ Studies Spanning Two Decades,

812   Small, 18, https://doi.org/10.1002/SMLL.202107407, 2022.

813   Lewis, E. and Wallace, D. W. R.: Program Developed for CO2 System Calculations, 1998.

814 Lin, Y. P. and Singer, P. C.: Inhibition of calcite precipitation by orthophosphate: Speciation and thermodynamic

815 considerations, Geochim. Cosmochim. Acta, 70, 2530–2539, https://doi.org/10.1016/J.GCA.2006.03.002, 2006.

816 Lohmann, G. P.: A model for variation in the chemistry of planktonic foraminifera due to secondary

817 calcification and selective dissolution, Paleoceanography, 10, 445–457, https://doi.org/10.1029/95PA00059,

818 1995.

819 Lombard, F., Labeyrie, L., Michel, E., Spero, H. J., and Lea, D. W.: Modelling the temperature dependent growth

820 rates of planktic foraminifera, Mar. Micropaleontol., 70, 1–7, https://doi.org/10.1016/j.marmicro.2008.09.004,

821 2009.

822 Lombard, F., da Rocha, R. E., Bijma, J., and Gattuso, J. P.: Effect of carbonate ion concentration and irradiance

823 on calcification in planktonic foraminifera, Biogeosciences, 7, 247–255, https://doi.org/10.5194/BG-7-247-

824 2010, 2010.

825 MacFarling Meure, C., Etheridge, D., Trudinger, C., Steele, P., Langenfelds, R., Van Ommen, T., Smith, A., and

826 Elkins, J.: Law Dome CO2, CH4 and N2O ice core records extended to 2000 years BP, Geophys. Res. Lett., 33,

827 https://doi.org/10.1029/2006GL026152, 2006.

828 Mallo, M., Ziveri, P., Graham Mortyn, P., Schiebel, R., and Grelaud, M.: Low planktic foraminiferal diversity and

829 abundance observed in a spring 2013 west-east Mediterranean Sea plankton tow transect, Biogeosciences, 14,

830 2245–2266, https://doi.org/10.5194/BG-14-2245-2017, 2017.

831 Manno, C., Morata, N., and Bellerby, R.: Effect of ocean acidification and temperature increase on the

832 planktonic foraminifer Neogloboquadrina pachyderma (sinistral), Polar Biol., 35, 1311–1319,

833 https://doi.org/10.1007/s00300-012-1174-7, 2012.

834 Marcoulides, K. M. and Raykov, T.: Evaluation of Variance Inflation Factors in Regression Models Using Latent

835 Variable Modeling Methods, Educ. Psychol. Meas., 79, 874, https://doi.org/10.1177/0013164418817803,

836 2019.

837 Marr, J. P., Baker, J. A., Carter, L., Allan, A. S. R., Dunbar, G. B., and Bostock, H. C.: Ecological and temperature

838 controls on Mg/Ca ratios of Globigerina bulloides from the southwest Pacific Ocean, Paleoceanography, 26,

839 https://doi.org/10.1029/2010PA002059, 2011.

840 Marshall, B. J., Thunell, R. C., Henehan, M. J., Astor, Y., and Wejnert, K. E.: Planktonic foraminiferal area density

841 as a proxy for carbonate ion concentration: A calibration study using the Cariaco Basin ocean time series,

842 Paleoceanography, 28, 363–376, https://doi.org/10.1002/palo.20034, 2013.

843 Getting started with TEOS-10 and the Gibbs seawater (GSW) oceanographic toolbox: https://www.teos-

844 10.org/pubs/Getting_Started.pdf.

845 Mikis, A., Hendry, K. R., Pike, J., Schmidt, D. N., Edgar, K. M., Peck, V., Peeters, F. J. C., Leng, M. J., Meredith, M.

846 P., Jones, C. L. C., Stammerjohn, S., and Ducklow, H.: Temporal variability in foraminiferal morphology and

847   geochemistry at the West Antarctic Peninsula: A sediment trap study, Biogeosciences, 16, 3267–3282,

848   https://doi.org/10.5194/BG-16-3267-2019, 2019.

849   de Moel, H., Ganssen, G. M., Peeters, F. J. C., Jung, S. J. A., Kroon, D., Brummer, G. J. A., and Zeebe, R. E.:

850   Planktic foraminiferal shell thinning in the arabian sea due to anthropogenic ocean acidification?,

851   Biogeosciences, 6, 1917–1925, https://doi.org/10.5194/bg-6-1917-2009, 2009.

852   Morard, R., Darling, K. F., Weiner, A. K. M., Hassenrück, C., Vanni, C., Cordier, T., Henry, N., Greco, M., Vollmar,

853   N. M., Milivojevic, T., Rahman, S. N., Siccha, M., Meilland, J., Jonkers, L., Quillévéré, F., Escarguel, G., Douady,

854   C. J., Garidel-Thoron, T. de, Vargas, C. de, and Kucera, M.: The global genetic diversity of planktonic

855   foraminifera reveals the structure of cryptic speciation in plankton, Biol. Rev.,

856   https://doi.org/10.1111/BRV.13065, 2024.

857   Moy, A. D., Howard, W. R., Bray, S. G., and Trull, T. W.: Reduced calcification in modern Southern Ocean

858   planktonic foraminifera, Nat. Geosci., 2, 276–280, https://doi.org/10.1038/ngeo460, 2009.

859   Mulitza, S., Dürkoop, A., Hale, W., Wefer, G., and Niebler, H. S.: Planktonic foraminifera as recorders of past

860   surface-water stratification, Geology, 25, 1997.

861   Naik, S. S., Naidu, P. D., Govil, P., and Godad, S.: Relationship between weights of planktonic foraminifer shell

862   and surface water $CO_3=$ concentration during the Holocene and Last Glacial Period, Mar. Geol., 275, 278–282,

863   https://doi.org/10.1016/j.margeo.2010.05.004, 2010.

864   Naik, S. S., Godad, S. P., and Naidu, D. P.: Does carbonate ion control planktonic foraminifera shell calcification

865   in upwelling regions?, Curr. Sci., 101, 1370–1375, 2011.

866   Nehrke, G., Keul, N., Langer, G., de Nooijer, L. J., Bijma, J., and Meibom, A.: A new model for biomineralization

867   and trace-element signatures of Foraminifera tests, Biogeosciences, 10, 6759–6767,

868   https://doi.org/10.5194/bg-10-6759-2013, 2013.

869   Neukermans, G., Bach, L. T., Butterley, A., Sun, Q., Claustre, H., and Fournier, G. R.: Quantitative and

870   mechanistic understanding of the open ocean carbonate pump - perspectives for remote sensing and

871   autonomous in situ observation, Earth-Science Rev., 239, 104359,

872   https://doi.org/10.1016/J.EARSCIREV.2023.104359, 2023.

873   de Nooijer, L. J., Toyofuku, T., Kitazato, H., and Stanley, S. M.: Foraminifera promote calcification by elevating

874   their intracellular pH, PNAS, 106, 15374–15378, 2009.

875   de Nooijer, L. J., Spero, H. J., Erez, J., Bijma, J., and Reichart, G. J.: Biomineralization in perforate foraminifera,

876   https://doi.org/10.1016/j.earscirev.2014.03.013, 1 August 2014.

877   Ortiz, J. D., Mix, A. C., and Collier, R. W.: Environmental control of living symbiotic and asymbiotic foraminifera

878   of the California Current, Paleoceanography, 10, 987–1009, https://doi.org/10.1029/95PA02088, 1995.

879   Osborne, E. B., Thunell, R. C., Marshall, B. J., Holm, J. A., Tappa, E. J., Benitez-Nelson, C., Cai, W. J., and Chen,

880 B.: Calcification of the planktonic foraminifera Globigerina bulloides and carbonate ion concentration: Results

881 from the Santa Barbara Basin, Paleoceanography, 31, 1083–1102, https://doi.org/10.1002/2016PA002933,

882 2016.

883 Paasche, E. and Brubak, S.: Enhanced calcification in the coccolithophorid Emiliania huxleyi (Haptophyceae)

884 under phosphorus limitation, Phycologia, 33, 324–330, https://doi.org/10.2216/I0031-8884-33-5-324.1, 1994.

885 Pak, D. K., Hendy, I. L., Weaver, J. C., Schimmelmann, A., and Clayman, L.: Foraminiferal proxy response to

886 ocean temperature variability and acidification over the last 150 years in the Santa Barbara Basin (California),

887 Quat. Int., 469, 141–150, https://doi.org/10.1016/J.QUAINT.2016.07.049, 2018.

888 Pallacks, S., Ziveri, P., Schiebel, R., Vonhof, H., Rae, J. W. B., Littley, E., Garcia-Orellana, J., Langer, G., Grelaud,

889 M., and Martrat, B.: Anthropogenic acidification of surface waters drives decreased biogenic calcification in the

890 Mediterranean Sea, Commun. Earth Environ., 4, 1–10, https://doi.org/10.1038/s43247-023-00947-7, 2023.

891 Qin, B., Li, T., Xiong, Z., Algeo, T. J., and Jia, Q.: Calcification of planktonic foraminifer Pulleniatina

892 obliquiloculata controlled by seawater temperature rather than ocean acidification, Glob. Planet. Change, 193,

893 103256, https://doi.org/10.1016/J.GLOPLACHA.2020.103256, 2020.

894 R Core Team: R: A language and environment for statistical computing. R Foundation for Statistical Computing.,

895 https://www.r-project.org/, 2018.

896 Rillo, M. C., Miller, C. G., Kučera, M., and Ezard, T. H. G.: Intraspecific size variation in planktonic foraminifera

897 cannot be consistently predicted by the environment, Ecol. Evol., 10, 11579–11590,

898 https://doi.org/10.1002/ECE3.6792, 2020.

899 Rink, S., Kühl, M., Bijma, J., and Spero, H. J.: Microsensor studies of photosynthesis and respiration in the

900 symbiotic foraminifer Orbulina universa, Mar. Biol., 131, 583–595, https://doi.org/10.1007/s002270050350,

901 1998.

902 Rosenthal, Y., Perron-Cashman, S., Lear, C. H., Bard, E., Barker, S., Billups, K., Bryan, M., Delaney, M. L.,

903 DeMenocal, P. B., Dwyer, G. S., Elderfield, H., German, C. R., Greaves, M., Lea, D. W., Marchitto, T. M., Pak, D.

904 K., Paradis, G. L., Russell, A. D., Schneider, R. R., Scheiderich, K., Stott, L., Tachikawa, K., Tappa, E., Thunell, R.,

905 Wara, M., Weldeab, S., and Wilson, P. A.: Interlaboratory comparison study of Mg/Ca and Sr/Ca measurements

906 in planktonic foraminifera for paleoceanographic research, Geochemistry, Geophys. Geosystems, 5, 4–09,

907 https://doi.org/10.1029/2003GC000650, 2004.

908 Russell, A. D., Hönisch, B., Spero, H. J., and Lea, D. W.: Effects of seawater carbonate ion concentration and

909 temperature on shell U, Mg, and Sr in cultured planktonic foraminifera, Geochim. Cosmochim. Acta, 68, 4347–

910 4361, https://doi.org/10.1016/j.gca.2004.03.013, 2004.

911 Schiebel, R.: Planktic foraminiferal sedimentation and the marine calcite budget, Global Biogeochem. Cycles,

912 16, https://doi.org/10.1029/2001gb001459, 2002.

913 Schiebel, R. and Hemleben, C.: Modern planktic foraminifera, Paläontologische Zeitschrift, 79, 135–148,
914 https://doi.org/10.1007/bf03021758, 2005.

915 Schiebel, R. and Hemleben, C.: Planktic Foraminifers in the Modern Ocean, Springer, Berlin, 154 pp.,
916 https://doi.org/10.1007/978-3-662-50297-6_1, 2017.

917 Schindelin, J., Arganda-Carreras, I., Frise, E., Kaynig, V., Longair, M., Pietzsch, T., Preibisch, S., Rueden, C.,
918 Saalfeld, S., Schmid, B., Tinevez, J. Y., White, D. J., Hartenstein, V., Eliceiri, K., Tomancak, P., and Cardona, A.:
919 Fiji: an open-source platform for biological-image analysis, Nat. Methods, 9, 676–682,
920 https://doi.org/10.1038/nmeth.2019, 2012.

921 Schmidt, D. N., Renaud, S., Bollmann, J., Schiebel, R., and Thierstein, H. R.: Size distribution of Holocene
922 planktic foraminifer assemblages: Biogeography, ecology and adaptation, Mar. Micropaleontol., 50, 319–338,
923 https://doi.org/10.1016/S0377-8398(03)00098-7, 2004.

924 Schmidt, D. N., Elliott, T., and Kasemann, S. A.: The influences of growth rates on planktic foraminifers as
925 proxies for palaeostudies - A review, Geol. Soc. Spec. Publ., 303, 73–85, https://doi.org/10.1144/SP303.6,
926 2008.

927 Song, Q., Qin, B., Tang, Z., Liu, Y., Chen, Z., Guo, J., Xiong, Z., and Li, T.: Calcification of planktonic foraminifer
928 Neogloboquadrina pachyderma (sinistral) controlled by seawater temperature rather than ocean acidification
929 in the Antarctic Zone of modern Sothern Ocean, Sci. China Earth Sci., 65, 1824–1836,
930 https://doi.org/10.1007/S11430-021-9924-7/METRICS, 2022.

931 Spero, H. J., Lerche, I., and Williams, D. F.: Opening the carbon isotope "vital effect" black box, 2, Quantitative
932 model for interpreting foraminiferal carbon isotope data, Paleoceanography, 6, 639–655,
933 https://doi.org/10.1029/91PA02022, 1991.

934 Spindler, M., Hemleben, C., Salomons, J. B., and Smit, L. P.: Feeding behavior of some planktonic foraminifers
935 in laboratory cultures, J. Foraminifer. Res., 14, 237–249, https://doi.org/10.2113/GSJFR.14.4.237, 1984.

936 Takahashi, T., Sutherland, S. C., Chipman, D. W., Goddard, J. G., and Ho, C.: Climatological distributions of pH,
937 pCO2, total CO2, alkalinity, and CaCO3 saturation in the global surface ocean, and temporal changes at
938 selected locations, Mar. Chem., 164, 95–125, https://doi.org/10.1016/J.MARCHEM.2014.06.004, 2014.

939 Toyofuku, T., Matsuo, M. Y., De Nooijer, L. J., Nagai, Y., Kawada, S., Fujita, K., Reichart, G. J., Nomaki, H.,
940 Tsuchiya, M., Sakaguchi, H., and Kitazato, H.: Proton pumping accompanies calcification in foraminifera, Nat.
941 Commun., 8, 1–6, https://doi.org/10.1038/ncomms14145, 2017.

942 Troupin, C., Barth, A., Sirjacobs, D., Ouberdous, M., Brankart, J. M., Brasseur, P., Rixen, M., Alvera-Azcárate, A.,
943 Belounis, M., Capet, A., Lenartz, F., Toussaint, M. E., and Beckers, J. M.: Generation of analysis and consistent
944 error fields using the Data Interpolating Variational Analysis (DIVA), Ocean Model., 52–53, 90–101,
945 https://doi.org/10.1016/J.OCEMOD.2012.05.002, 2012.

946 Vehtari, A., Gelman, A., and Gabry, J.: loo: Efficient Leave-One-Out Cross-Validation and WAIC for Bayesian
947 Models. R Package Version 1.1.0, https://github.com/stan-dev/loo, 2017.

948 de Villiers, S.: Optimum growth conditions as opposed to calcite saturation as a control on the calcification rate
949 and shell-weight of marine foraminifera, Mar. Biol., 144, 45–49, https://doi.org/10.1007/s00227-003-1183-8,
950 2004.

951 Waterson, A. M., Edgar, K. M., Schmidt, D. N., and Valdes, P. J.: Quantifying the stability of planktic
952 foraminiferal physical niches between the Holocene and Last Glacial Maximum, Paleoceanography, 32, 74–89,
953 https://doi.org/10.1002/2016PA002964, 2017.

954 Weinkauf, M. F. G., Moller, T., Koch, M. C., and Kučera, M.: Calcification intensity in planktonic Foraminifera
955 reflects ambient conditions irrespective of environmental stress, Biogeosciences, 10, 6639–6655,
956 https://doi.org/10.5194/bg-10-6639-2013, 2013.

957 Weinkauf, M. F. G., Kunze, J. G., Waniek, J. J., and Kučera, M.: Seasonal Variation in Shell Calcification of
958 Planktonic Foraminifera in the NE Atlantic Reveals Species-Specific Response to Temperature, Productivity, and
959 Optimum Growth Conditions, PLoS One, 11, e0148363, https://doi.org/10.1371/journal.pone.0148363, 2016.

960 Zarkogiannis, S. D., Antonarakou, A., Tripati, A., Kontakiotis, G., Mortyn, P. G., Drinia, H., and Greaves, M.:
961 Influence of surface ocean density on planktonic foraminifera calcification, Sci. Rep., 9, 1–10,
962 https://doi.org/10.1038/s41598-018-36935-7, 2019.

963 Zarkogiannis, S. D., Kontakiotis, G., Gkaniatsa, G., Kuppili, V. S. C., Marathe, S., Wanelik, K., Lianou, V., Besiou,
964 E., Makri, P., and Antonarakou, A.: An Improved Cleaning Protocol for Foraminiferal Calcite from
965 Unconsolidated Core Sediments: HyPerCal—A New Practice for Micropaleontological and Paleoclimatic
966 Proxies, J. Mar. Sci. Eng., 8, 998, https://doi.org/10.3390/JMSE8120998, 2020.

967 Zarkogiannis, S. D., Iwasaki, S., Rae, J. W. B., Schmidt, M. W., Mortyn, P. G., Kontakiotis, G., Hertzberg, J. E., and
968 Rickaby, R. E. M.: Calcification, Dissolution and Test Properties of Modern Planktonic Foraminifera From the
969 Central Atlantic Ocean, Front. Mar. Sci., 9, 864801, https://doi.org/10.3389/FMARS.2022.864801/BIBTEX,
970 2022.

971

972

973 Supplementary reference list

974 Barker, S.: Planktonic foraminiferal proxies for temperature and pCO2, University of Cambridge, 2002.

975 Barker, S. and Elderfield, H.: Foraminiferal calcification response to glacial-interglacial changes in atmospheric
976 CO2, Science (80-.)., 297, 833–836, https://doi.org/10.1126/science.1072815, 2002.

977 Béjard, T. M., Rigual-Hernández, A. S., Flores, J. A., Tarruella, J. P., Durrieu De Madron, X., Cacho, I., Haghipour,
978 N., Hunter, A., and Sierro, F. J.: Calcification response of planktic foraminifera to environmental change in the
979 western Mediterranean Sea during the industrial era, Biogeosciences, 20, 1505–1528,
980 https://doi.org/10.5194/BG-20-1505-2023, 2023.

981 van Heuven, S., Pierrot, D., Rae, J. W. B., Lewis, E., and Wallace, D. W. R.: MATLAB Program Developed for CO2
982 System Calculations, https://doi.org/https://doi.org/10.3334/CDIAC/otg.CO2SYS_MATLAB_v1.1, 2011.

983 Jiang, L. Q., Dunne, J., Carter, B. R., Tjiputra, J. F., Terhaar, J., Sharp, J. D., Olsen, A., Alin, S., Bakker, D. C. E.,
984 Feely, R. A., Gattuso, J. P., Hogan, P., Ilyina, T., Lange, N., Lauvset, S. K., Lewis, E. R., Lovato, T., Palmieri, J.,
985 Santana-Falcón, Y., Schwinger, J., Séférian, R., Strand, G., Swart, N., Tanhua, T., Tsujino, H., Wanninkhof, R.,
986 Watanabe, M., Yamamoto, A., and Ziehn, T.: Global Surface Ocean Acidification Indicators From 1750 to 2100, J.
987 Adv. Model. Earth Syst., 15, https://doi.org/10.1029/2022MS003563, 2023.

988 Marcoulides, K. M. and Raykov, T.: Evaluation of Variance Inflation Factors in Regression Models Using Latent
989 Variable Modeling Methods, Educ. Psychol. Meas., 79, 874, https://doi.org/10.1177/0013164418817803, 2019.

990 Marr, J. P., Baker, J. A., Carter, L., Allan, A. S. R., Dunbar, G. B., and Bostock, H. C.: Ecological and temperature
991 controls on Mg/Ca ratios of Globigerina bulloides from the southwest Pacific Ocean, Paleoceanography, 26,
992 https://doi.org/10.1029/2010PA002059, 2011.

993 Marshall, B. J., Thunell, R. C., Henehan, M. J., Astor, Y., and Wejnert, K. E.: Planktonic foraminiferal area density
994 as a proxy for carbonate ion concentration: A calibration study using the Cariaco Basin ocean time series,
995 Paleoceanography, 28, 363–376, https://doi.org/10.1002/palo.20034, 2013.

996 Getting started with TEOS-10 and the Gibbs seawater (GSW) oceanographic toolbox: https://www.teos-
997 10.org/pubs/Getting_Started.pdf.

998 Osborne, E. B., Thunell, R. C., Marshall, B. J., Holm, J. A., Tappa, E. J., Benitez-Nelson, C., Cai, W. J., and Chen, B.:
999 Calcification of the planktonic foraminifera Globigerina bulloides and carbonate ion concentration: Results from
1000 the Santa Barbara Basin, Paleoceanography, 31, 1083–1102, https://doi.org/10.1002/2016PA002933, 2016.

1001 Pallacks, S., Ziveri, P., Schiebel, R., Vonhof, H., Rae, J. W. B., Littley, E., Garcia-Orellana, J., Langer, G., Grelaud,
1002 M., and Martrat, B.: Anthropogenic acidification of surface waters drives decreased biogenic calcification in the
1003 Mediterranean Sea, Commun. Earth Environ., 4, 1–10, https://doi.org/10.1038/s43247-023-00947-7, 2023.

1004 Qin, B., Li, T., Xiong, Z., Algeo, T. J., and Chang, F.: Deepwater carbonate ion concentrations in the western
1005 tropical Pacific since 250 ka: Evidence for oceanic carbon storage and global climate influence,
1006 Paleoceanography, 32, 351–370, https://doi.org/10.1002/2016PA003039, 2017.

1007 van Sebille, E., Scussolini, P., Durgadoo, J. V., Peeters, F. J. C., Biastoch, A., Weijer, W., Turney, C., Paris, C. B., and
1008 Zahn, R.: Ocean currents generate large footprints in marine palaeoclimate proxies, Nat. Commun., 6, 1–8,
1009 https://doi.org/10.1038/ncomms7521, 2015.

1010 Waterson, A. M., Edgar, K. M., Schmidt, D. N., and Valdes, P. J.: Quantifying the stability of planktic foraminiferal
1011 physical niches between the Holocene and Last Glacial Maximum, Paleoceanography, 32, 74–89,
1012 https://doi.org/10.1002/2016PA002964, 2017.

1013 Weinkauf, M. F. G., Kunze, J. G., Waniek, J. J., and Kučera, M.: Seasonal Variation in Shell Calcification of
1014 Planktonic Foraminifera in the NE Atlantic Reveals Species-Specific Response to Temperature, Productivity, and
1015 Optimum Growth Conditions, PLoS One, 11, e0148363, https://doi.org/10.1371/journal.pone.0148363, 2016.

1016