Reviews and Syntheses: A trait-based approach to constrain controls on planktic foraminiferal ecology: key trade-offs and current knowledge gaps

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Abstract. Planktic foraminifera are a major contributor to global marine inorganic carbon production. They leave abundant calcium carbonate shells on the seafloor that serve as prime proxies for the physical and chemical attributes of past oceans. Despite their well-preserved fossil record and widespread use in palaeoceanography, our understanding of their ecology remains limited due to their low standing stocks in the modern ocean and the challenges in culturing multiple generations under laboratory conditions, even after decades of data collection. This limitation affects our ability to interpret their fossil remains to describe past ecosystems and predict their responses to ongoing environmental changes. Trait-based ecology offers a powerful framework to characterise how and why foraminifera interact with their environment. Here, we review the current state of knowledge on key planktic foraminifera traits, including morphological, physiological, behavioural and life history traits. Most spinose taxa are carnivorous, host to dinoflagellate photosymbionts, and are abundant and diverse in oligotrophic environments. In contrast, non-spinose taxa are typically herbivorous and most common in high-productivity regions. We highlight the potential of trait modelling to generate hypotheses testable in the field. Integration of trait-based modelling with metabarcoding, environmental DNA, and enhanced standardised data collection made openly available will help to fill critical gaps in our understanding of planktic foraminiferal ecology and allow us to use foraminifera as a key model organism for addressing fundamental ecological questions.

1 Introduction

Planktic foraminifera (heterotrophic marine protists, Fig. 1), along with phytoplankton coccolithophores and planktic snail pteropods, are the dominant calcifying plankton in the modern ocean (Deuser et al., 1981). Among these, planktic foraminifera constitute 23-56 % of the global $CaCO_3$ flux from the top 100 m of surface waters and between 32-80 % of the total deep-marine calcite budget, with their carbonate shells covering much of the seafloor (Neukermans et al., 2023). Thus, these

organisms have pronounced impacts on biogeochemical cycling, in particular the inorganic carbon cycle, by transferring carbon from surface to deep waters, and, over longer timescales, modulating ocean alkalinity, carbonate chemistry and ultimately climate (Ridgwell and Zeebe, 2005). Moreover, in part due to their calcareous shells that can be preserved in marine sediments for millions of years, planktic foraminifera have one of the best fossil records of all plankton groups (Aze et al., 2011; Fenton et al., 2021). This makes them a critical group for studying the influence of climate change in the past and improving our understanding of the possible impacts of future climate (Strack et al., 2024; Woodhouse et al., 2023; Fenton et al., 2023). Their relative abundances, biometry, and a wealth of geochemical proxies based on shell chemistry are extensively used to reconstruct past climates and oceans, including temperature and ocean chemistry (Kucera, 2007).

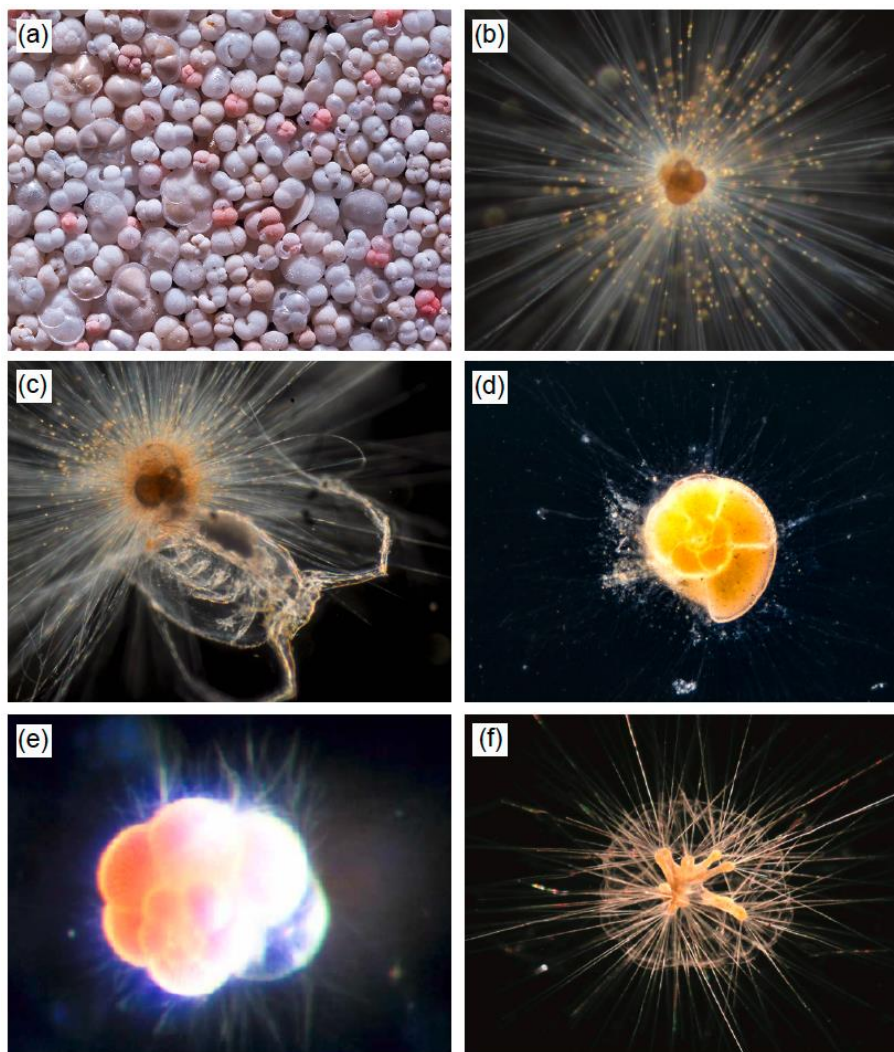



Figure 1. Selection of living and recent planktic foraminifera. (a) Assorted shells of planktic foraminifera from sea floor sediment (Image credit: Wilfried Rönnfeld). (b) *Orbulina universa* with symbionts attached along thin radial spines (Fig. 2 of Topa et al., 2017). (c) *Orbulina*

universa eating a small copepod (Image credit: Oscar Branson). (d) *Globorotalia truncatulinoides* in culture with pseudopodial network (a web-like structure formed of pseudopodia [see below] filaments, that interacts with the environment and provides physiological functions) extending from shell (https://www.usgs.gov/media/images/live-foraminifera-globorotalia-truncatulinoides). (e) *Neogloboquadrina dutertrei* suspended with pseudopodia (cytoplasmic projections that assist locomotion, feeding and other physiological functions) extending from shell (Image credit: Kate Darling). (f) *Hastigerinella digitata* with triradiate spines and bubble capsule (Fig. 1A of Hull et al., 2011).

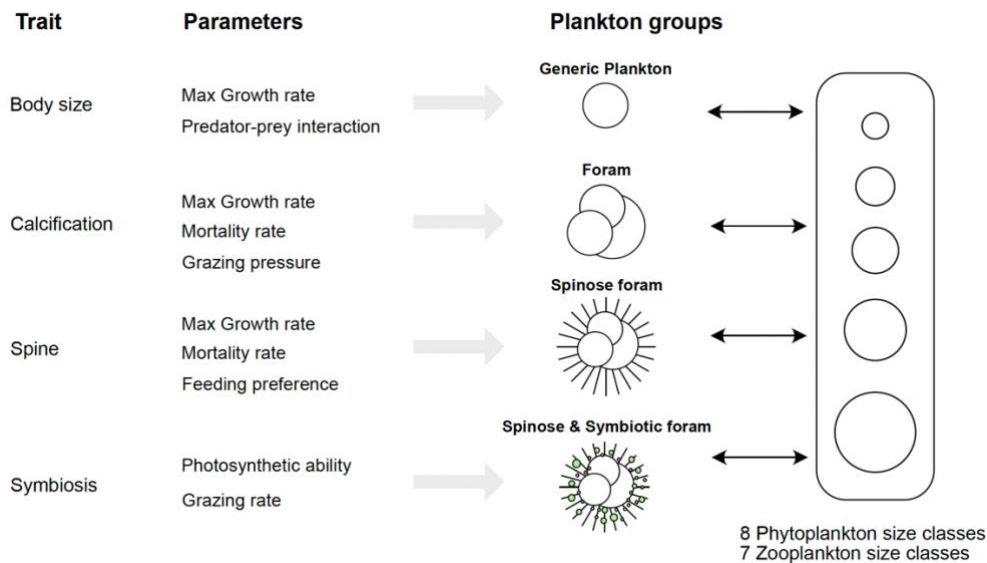
Despite their importance in understanding past oceans, planktic foraminifera ecology has received relatively little attention from modern ecologists due to their small contribution to the total plankton biomass (Michaels et al., 1995; Buitenhuis et al., 2013) and the challenges associated with culturing them (Del Campo et al., 2024; Meilland et al., 2024). Developing a mechanistic understanding of the controls on planktic foraminifera diversity and distribution is essential for generating accurate predictions of how changing environmental conditions will impact their communities and, ultimately, biogeochemical cycles (Dutkiewicz et al., 2020).

An improved mechanistic understanding can be supported by trait-based approaches (Dutkiewicz et al., 2020),which describe how species interact with each other and their environment based on measurable organismal characteristics or traits (e.g. size, resource acquisition mode and defence). Rather than focusing on individual species, these approaches group organisms with similar traits into functional groups, simplifying the characterisation of highly diverse ecosystems like plankton communities, where millions of specimens from thousands of species interact (De Vargas et al., 2015). This approach effectively links individual-level traits to larger ecosystem processes, helping to explain patterns of biodiversity, species distributions and how communities respond to environmental changes. However, a key challenge is to identify the trade-offs between traits (i.e., costs and benefits) (e.g., Litchman et al., 2013; Barton et al., 2013; Violle et al., 2007; Westoby, 2024). Trade-offs arise when the optimisation of one trait occurs at the expense of another (Kiørboe et al., 2018). Overall, trait-based approaches offer a mechanistic yet computationally efficient means of explaining large-scale patterns of diversity and abundance across microbial, planktic and nekton communities (e.g., Barton et al., 2013; Dutkiewicz et al., 2009; Follows et al., 2007; Grigoratou et al., 2019; Naidoo-Bagwell et al., 2024; Ying, 2024; Ward, 2013; Monteiro et al., 2016; Litchman et al., 2021).

Trait-based approaches are particularly promising for making predictions beyond the sampling domain and testing different (and often complex) hypotheses over longer timescales - both past and future (e.g., Barton et al., 2016; Grigoratou et al., 2022; Ying, 2024). This makes this approach particularly valuable in macroevolutionary studies spanning millions of years, where new traits evolve in response to changing environments and climates. By permitting functional groups with novel trait combinations, trait-based models can simulate emergent taxa that may not be present in the modern ocean but could have existed in the past or evolve in the future. For instance, the model of Knoll and Follows (2016) shows how the rise of the mixotrophy trait in the Mesozoic increases energy transfer efficiency to higher trophic levels in the food web. Similarly, Gibbs

et al. (2020) used trait-based modelling to explore ecological selectivity in marine plankton following the Cretaceous-Paleogene mass extinction.

While trait-based models have significant potential, they have inherent limitations. Like any models, they are a highly simplified version of natural systems. They may simplify complex ecological interactions and environmental influences, and the expression and importance of traits may vary by environment, impacting generalisation. Additionally, trade-offs between traits are not always well understood or quantified, as for example, the absence or presence of symbionts in foraminifera. The eco-evolutionary model used by Gibbs et al. (2020), for instance, resulted in modelled trait evolution at rates orders of magnitude faster than observed in the fossil dataset, highlighting the need for caution when interpreting these model results. Despite these caveats, trait-based approaches present an exciting opportunity to leverage the exceptional fossil record of foraminifera to test our understanding outside of the modern range of environmental conditions, assess the universal applicability of traits and trade-offs through time and ultimately improve our understanding of evolutionary processes.

Trait-based modelling has already provided novel insights into planktic foraminifera ecology and fitness. The first non-species specific trait-based planktic foraminifera modelling study by Grigoratou et al. (2019) highlighted the cost and benefits of calcification, and the influence of resource competition among planktic foraminifera and other zooplankton. Ying et al. (2023) further expanded this approach to characterise the main ecogroups of planktic foraminifera (Figs 1 and 2). In this study, we aim to present a comprehensive review of our current knowledge of planktic foraminifera traits and trade-offs, identify critical knowledge gaps and propose future research directions to advance the application of trait-based ecology in foraminifera research.

99 **Figure 2: Schematic representation of a trait-based ecosystem model incorporating planktic foraminifers.** Key functional traits include
100 size, calcification, spinosity and symbiosis, and are assumed to influence foraminiferal interactions within the food web by modifying
101 maximum growth rate, mortality rate, feeding strategy, and other predator-prey interactions.

2. Planktic foraminifera traits and trade-offs

Planktic foraminifera have been predominantly studied by geologists for their paleoecology and evolution, and as proxy carriers for paleoenvironmental studies, while most biological studies have, until recently, been from seminal papers by Allan Bé, and co-workers in the 1970s and '80s. Classification of planktic foraminifera is primarily based on adult morphology, with ~45 morphologically distinct species or 'morphospecies' in the modern ocean (Brummer and Kučera, 2022; Schiebel and Hemleben, 2017), many but not all of which consist of cryptic species (i.e., organisms that look identical but represent distinct evolutionary lineages; Morard et al., 2024; Morard et al., 2016).

Planktic foraminifera spend their lives in the open ocean, predominantly the upper ~200 m of the water column (Table 1), with very few individuals or species found below ~1 km water depth (Rebotim et al., 2019; Vincent, 1981). Planktic foraminifera are absent in shallow marine seas and on coastal shelves (Schiebel and Hemleben, 2017). Some taxa have unique ecologies, e.g. *Neogloboquadrina pachyderma* may spend parts of the year in sea ice (Dieckmann et al., 1991).

Table 1 Modern planktic foraminiferal species list and associated key traits. Species are listed alphabetically and correspond to those listed in the ForCenS database of Siccha and Kucera (2017) and underpin the trait distribution maps shown in Fig. 3. Summary of ecological information from Schiebel and Hemleben (2017), Takagi et al. (2019) and Aze et al. (2011). Obligate symbiosis=essential for optimal host fitness and observed in the majority of individuals of a species. Facultative symbiosis=not essential for host success and only associated with some individuals of the species (Table 1; Takagi et al., 2019). Determining whether symbiosis is obligate or facultative is challenging as photosymbiosis is a spectrum as proposed by Stoecker et al (2009) from non-symbiosis to robust symbiosis. *=bacterial endobionts *Synechococcus* reported by Bird et al. (2017) but unclear if symbionts.

SPECIES	SPINOSITY	SYMBIONT TYPE	SYMBIONT RELATIONSHIP
Beella digitata	Spinose	None	None
Berggrenia pumilio	Non-spinose	None	None
Candeina nitida	Non-spinose	Chrysophyte	Facultative
Dentigloborotalia anfracta	Non-spinose	None	None
Globigerina bulloides	Spinose	None*	None
Globigerina falconensis	Spinose	Chrysophyte	Facultative
Globigerinella adamsi	Spinose	None	None
Globigerinella calida	Spinose	Chrysophyte	Facultative
Globigerinella siphonifera	Spinose	Chrysophyte	Obligate
Globigerinita glutinata	Non-spinose	Chrysophyte	Facultative
Globigerinita minuta	Non-spinose	None	None
Globigerinita uvula	Non-spinose	Dinoflagellate	Obligate

Globigerinoides conglobatus	Spinose	Dinoflagellate	Obligate
Globigerinoides ruber	Spinose	Dinoflagellate	Obligate
Globigerinoides tenellus	Spinose	Dinoflagellate	Obligate
Globigerinoides white	Spinose	Dinoflagellate	Obligate
Globoconella inflata	Non-spinose	Chrysophyte	Facultative
Globoquadrina conglomerata	Non-spinose	None	None
Globorotalia cavernula	Non-spinose	None	None
Globorotalia crassaformis	Non-spinose	None	None
Globorotalia hirsuta	Non-spinose	None	None
Globorotalia menardii	Non-spinose	Chrysophyte/Prymensiophyte	Facultative
Globorotalia scitula	Non-spinose	None	None
Globorotalia theyeri	Non-spinose	None	None
Globorotalia truncatulinoides	Non-spinose	None	None
Globorotalia tumida	Non-spinose	None	None
Globorotalia ungulata	Non-spinose	None	None
Globorotaloides hexagonus	Spinose	None	None
Globoturborotalita rubescens	Spinose	Dinoflagellate	Obligate
Hastigerina pelagica	Spinose	None	None
Hastigerinella digitata	Spinose	None	None
Neogloboquadrina dutertrei	Non-spinose	Chrysophyte, Pelagophyte	Facultative
Neogloboquadrina incompta	Non-spinose	None	None
Neogloboquadrina pachyderma	Non-spinose	None	None
Orbulina universa	Spinose	Dinoflagellate	Obligate
Pulleniatina obliquiloculata	Non-spinose	Chrysophyte	Facultative
Sphaeroidinella dehiscens	Non-spinose	Dinoflagellate	Obligate
Tenuitella iota	Non-spinose	None	None
Trilobatus sacculifer	Spinose	Dinoflagellate	Obligate
		Chrysophyte, Haptophyte	
Turborotalita humilis	Spinose	Dinoflagellate	Obligate
Turborotalita quinqueloba	Spinose	None	None

123 Here we characterise planktic foraminiferal traits according to their type and function, following the approach of Litchman et

124 al. (2013) (Table 2). We discuss all identified key traits, along with their individual impacts on foraminiferal fitness, as well

125 as their main associated trade-offs. We recognise two levels of traits: (1) those that are common to all planktic foraminifera,

126 referred to as 'foraminiferal' traits and (2) those that are specific to individual species or groups of species as 'group/species-

127 specific' traits.

128

129 **Table 2. Summary of planktic foraminifera traits and associated trade-offs described in Sections 2.1-2.3.** Traits with '*' are

130 group/species specific traits, all other traits are common to all planktic foraminifera. Rhizopodia refers to the network of cytoplasmic strands

131 around the shell that help to capture, transport, and break-up prey items and carry waste out of the cell.

132

Trait Type	Trait	Cost(s)	Benefit(s)
Physiological /Morphological	Calcification (shell)	- Energy investment (~10-60% of energy budget) - Negative buoyancy	- Protection from predation and/or the environment
	Calcification (spines)*	- Energy investment (<60% of total energy budget) - Reduction in growth	- Tool for controlling active prey - Rhizopodial support - Increased prey capture area - Increased protection from predation - Positive buoyancy
Behavioural	Photosymbiotic host*	- Light limitation - Influenced by symbiont availability & health	- Nutrient exchange for calcification - Favorable ambient pH for calcification - Food for terminal, sick or starved hosts - Food for reproduction
	Immotility	- Reliant on surrounding available resources - Inability to actively escape predation - Sensitive to environmental conditions	- Energy conservation by not actively swimming - Reduced predator encounters
	Vertical migration (diel or seasonal)	- Sensitive to predation and environmental conditions	- Energy gain - Advantage of prey migration
	Passive feeding	- Reliant on availability of surrounding resources - Low feeding efficiency	- Energy conservation by not actively searching for food - Reduced predator encounters
Life History	Reproduction	- Dominantly sexual reproduction, once in life cycle	- Energy gain as not actively searching for mate - Reduced predator exposure by not actively searching for mate -Maintain higher genetic diversity
		- Number of gametes produced depends on shell size	

2.1 Physiological/Morphological traits

2.1.1 Body Size (foraminiferal trait)

Size is often considered as a master trait because it influences most relationships between organisms in an ecosystem, and how they respond to and influence their environment (Brown et al., 2004; Peters, 1983). Body size directly impacts physiological and ecological aspects like metabolic rates (e.g., growth), diet, predator-prey relationships, abundance, biomass and reproduction in organisms (e.g., Kiørboe et al., 2018; Mckinney, 1990). For instance, the primary mode of resource acquisition for organisms shifts from osmotrophy in the smallest single-celled organisms, to phototrophy, mixotrophy, and ultimately heterotrophy as body size increases (Andersen et al., 2016; Haldane, 1926). Body size also influences predator-prey relationships by impacting the range of prey sizes an organism can consume, with prey being typically smaller than the predator (Gaskell et al., 2019; Wirtz, 2012).

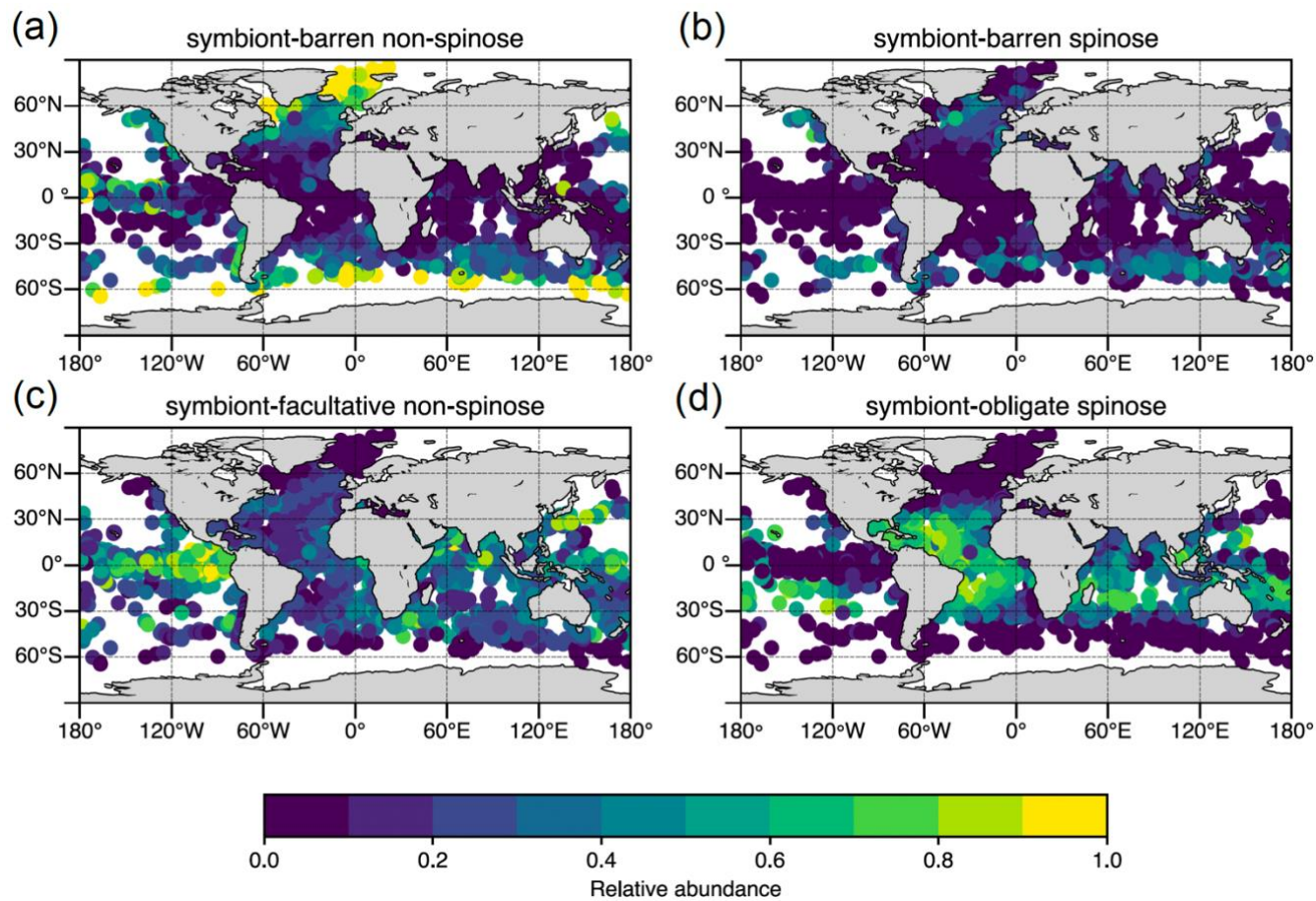
Planktic foraminifera grow their organic cell by adding multiple chambers in their calcite shell (Brummer et al., 1987; Caromel et al., 2016). Depending on the species, the shell size of adult individuals can vary from ~100 to 1500 µm (Schmidt et al., 2004). At the individual level, organisms typically reach their largest shell size under specific optimal environmental growth conditions (Chernihovsky et al., 2023; Schmidt et al., 2004), although some show no relationships between size and environments (Rillo et al., 2020). Temperature and suitable prey availability have been identified as the primary environmental factors influencing shell growth, followed by pH, salinity, and light conditions—particularly for species that maintain symbiotic relationships with algae. As a group, planktic foraminifera reach large sizes in the tropics, while smaller individuals dominate at the higher latitudes and in equatorial upwelling regions (Schmidt et al., 2004). This size distribution contrasts with most zooplankton species, which exhibit their largest sizes in polar regions (Brandão et al., 2021; Horne et al., 2017). The size distribution of foraminifera may reflect a combination of factors including higher temperatures and thus metabolic rates promoting growth, higher carbonate saturation and light intensity promoting calcification, more energy subsidy from algal photosymbionts, increased volume for prey encounter, or enhanced niche diversity through stratification (Schmidt et al., 2004; Burke et al., 2025). Shell size not only responds to environmental conditions but also directly reflects individual fitness and reproduction (Hemleben, 1989). Larger foraminifera have a greater amount of cytoplasm available to generate gametes and hence potentially higher reproductive success (Bé and Anderson, 1976; Weinkauf et al., 2022). In the open ocean, a semi lunar periodicity in shell fluxes (i.e. shells exported to the sea floor after death) of several species is interpreted as the presence of a circadian clock (Bijma et al., 1990; Jonkers and Kučera, 2015; Lončarić et al., 2005). This periodicity is modulated by seasonal changes in shell fluxes (Jonkers et al., 2015) with intervals characterised by smaller body sizes and extended life cycles during unfavourable conditions and food scarcity contrasting with times of high foraminiferal fluxes and larger shell

sizes (Chernihovsky et al., 2023). For organisms with a circadian clock and therefore a fixed life duration, large sizes may reflect increased growth rates (rather than prolonged growth), versus rapid reproduction and smaller body size as seen in many phytoplankton (Schmidt et al., 2006).

2.1.2 Calcification (foraminiferal trait)

The primary function of producing a calcite shell in planktic foraminifera is still debated. However, one potential advantage is that the shell and, to a lesser extent, the spines in spinose species provide the cytoplasm with support and protection, increasing the individual's potential to survive to reproductive maturity. This is achieved by (1) reducing their palatability to predators, (2) increasing their body size to reduce predation pressure, and (3) forming a potential barrier from environmental conditions such as harmful UV rays or pathogens (Armstrong, 2004).

The mineralised shell can comprise a significant proportion of an organism's total mass, making the construction and maintenance energetically expensive (Sanders et al., 2018). However, it is difficult to quantify the energetic costs of biomineralization, and foraminifera (as many organisms) can modulate their energy use between different activities depending on the environment. An unclear understanding of how biomineralization occurs for many groups further exacerbates the challenge (Gaylord et al., 2015). No laboratory assessments of the energy budget allotted to calcification in planktic foraminifera currently exist. However, theoretical trait-based models indicate a likely investment of ~10-60 % of foraminifera's total energy budget to calcification (Grigoratou et al., 2021; Grigoratou et al., 2022; Grigoratou et al., 2019).

A calcite shell reduces the buoyancy of foraminifera, i.e., it increases their tendency to sink through the water column (Armstrong, 2004; Caromel et al., 2014), although this is counterbalanced by low-density fibrillar bodies within the cytoplasm (Hemleben, 1989). Spinose foraminifera taxa have long calcite spines that may extend up to several centimetres from the shell surface (2-3x the shell size; Fig. 1b, c and f), which increases their drag and thus reduces their sinking rate (Takahashi and Be, 1984). Other benefits of spines include an increased capture area for prey acquisition, reduced palatability to predators, a rigid skeleton to anchor pseudopodia to enable acquisition of higher quality (active) prey, and a means of organising photosymbionts more effectively around the shell. Logically, the development of these compensatory features should increase the relative cost of calcification. However, trait-based modelling suggests similar calcification costs for both spinose and non-spinose foraminifera species (Grigoratou et al., 2021; Grigoratou et al., 2022; Grigoratou et al., 2019). This suggests that spine formation either does not significantly increase energy demand or is offset by nutritional benefits. Spinose species are predominantly carnivorous as adults, which provides more energy, and many also host algal photosymbionts providing an additional carbon subsidy. While non-spinose species are omnivorous, they prefer a herbivorous diet (Hemleben et al., 1985) (see Section 2.2).

209 **Figure 3. Modern distribution and relative abundance of planktic foraminifera by ecological group in surface**

210 **sediment samples.** Underlying data from ForCenS database (Siccha and Kucera, 2017) and traits coded as presented in

211 Table 1 (this study).

212

213 The range of estimated energetic calcification costs for foraminifera is broadly consistent with those of other calcifying groups

214 (although estimates vary dramatically), including: coccolithophores at ~30 % (Monteiro et al., 2016), marine benthic

215 gastropods at <60% (Palmer, 1992; Sanders et al., 2018), and <10% across gastropods and bivalves globally (Watson et al.,

216 2017). In the calcareous algae coccolithophores, the high energetic cost of calcification varies between species and

217 environments, and protection from predation may be the primary benefit (Monteiro et al., 2016). However, the role of predation

218 on foraminifera is unknown. Whilst adult foraminiferal shells have been found in pteropods, salps, shrimps and many other

219 metazooplankton, we do not know of any specialised predators (Berger, 1971). Nevertheless, the role of predation on

populations should not be underestimated, as many juveniles do not reach maturity (Schiebel et al., 1995) and are selectively found in faecal pellets of salp (Bé, 1977). Juvenile forms may have a higher palatability due to their higher ratio of cytoplasm to calcite (i.e., lack of numerous spines, thick calcite walls and gametogenic calcite) than adult forms (Meilland et al., 2016). In culture, damaged specimens or those undergoing gametogenesis were highly susceptible to digestion by other smaller protists (bacteria, sporozoans, and other parasitic organisms) that entered the foraminifera via the aperture (Hemleben, 1989).

Despite numerous data on the weight of foraminiferal shells (see Barrett et al., 2025 for a recent review), there are still large gaps in our understanding of the metabolic and energetic needs for calcification. However, it is clear that some specific traits within ecogroups, for example symbiosis (see Section 2.2.3), can positively impact calcification due to modification of the calcifying microenvironment and provision of an energy subsidy (e.g., Köhler-Rink and Kühl, 2005). Biomineralization pathways in planktic foraminifera are poorly known but are inferred to be extracellular, with calcification occurring predominantly via endocytosis, based on analogy to benthic foraminifera, e.g., *Amphistegina lobifera* (Bentov et al., 2009; Schiebel and Hemleben, 2007). Briefly, seawater is engulfed in vacuoles by the foraminiferal plasma membrane, modified in composition to become "alkalinized" via assorted biological and chemical processes, and transported to the site of calcification. Enhanced respiration near the site of calcification locally increases the CO_2 in the foraminiferal cytoplasm and ultimately the pool of total inorganic carbon available for calcification (Bentov et al., 2009). Alternative foraminiferal biomineralization pathways are suggested (Erez, 2003; de Nooijer et al., 2013; Bentov and Erz, 2006; Nehrke et al., 2013). This includes the benthic foraminiferal group, the miliolids, which precipitate an imperforate porcelaneous shell intracellularly, but this is very different in structure to planktic foraminifera shells (Hemleben et al., 1986). Many studies identify species-specific calcification responses and sensitivities associated with a range of environmental drivers (Barker and Elderfield, 2002; Béjard et al., 2024; Weinkauf, 2016; Pallacks et al., 2023). Understanding those drivers is complicated by differential environmental preferences of cryptic species (De Vargas et al., 2001), regional plasticity, and a lack of understanding of the controls on the thickness of gametogenic calcite or the biomineralization pathway (De Nooijer et al., 2023; Erez, 2003; Lekieffre et al., 2018; Nehrke et al., 2013). Furthermore, the variety of methods used to collect individuals for foraminifera weighing (i.e., the use of plankton tow, sediment trap and core-top data, as well as differences in the weighing technique itself) (Beer et al., 2010) and inadequate metadata reporting lead to further difficulty in understanding calcification. Our understanding of what drives calcification could be enhanced by resolving the aforementioned biological factors (i.e. resolving cryptic species, understanding regional plasticity, identifying what controls the thickness of gametogenic calcite, and determining the biomineralization pathway) and improving data collection and data management practices, e.g. by following FAIR principles (Wilkinson et al., 2016). In turn, this will result in better modelling of the potential changes in the pelagic carbonate production under future climate change (Barrett et al., 2025).

The cost of calcification increases under ocean acidification scenarios in a wide range of (though not all) marine calcifiers (Hoppit and Schmidt, 2022), e.g., corals, molluscs, coccolithophores (Leung et al., 2022). Impacted groups typically show

evidence of reduced growth, reduced calcification, muscle wastage or weakened shells (e.g., Alma et al., 2020; Hill and Hoogenboom, 2022; Swezey et al., 2020), supporting that the metabolic costs of calcification are at the expense of other life processes. While the allotment of the foraminifera energy budget to calcification is not well constrained, its cost is evidenced in the smaller terminal body sizes (e.g., maintaining calcification at the expense of growth) in field and laboratory studies (Schmidt et al., 2003; Russell et al., 2004; Lombard et al., 2010). This results in a reduced chance of individuals reaching sufficient size to obtain reproductive maturity (Bé et al., 1981) and potentially a smaller number of gametes based on the relationship between gamete number and body size, reducing reproductive success. This ultimately impacts the fitness of individuals' by increasing their vulnerability to further environmental change or predation etc., which may prove fatal.

2.2 Behavioural traits

2.2.1 Feeding (group-specific trait)

The biggest challenge faced by marine plankton is the acquisition of food from a very dilute suspension without being eaten, a challenge exacerbated in low prey density environments such as oligotrophic gyres. In these environments, organisms must maximize opportunities for finding food and capturing their prey. Marine plankton adopt a range of different feeding strategies to deal with the challenge, each with specific trade-offs that extend beyond an impact on feeding behaviour alone.

All planktic foraminifera are passive ambush feeders (Fenchel, 1986; Kiørboe, 2011). They do not actively detect or seek out their prey. Acquisition of food relies solely on the motility of their prey and the likelihood of direct interception, a function of prey density and foraminifera's ability to 'capture' prey (Kiørboe, 2011). The benefits of passive food capture are its low energy investment, as organisms do not need to move to acquire their prey, and reduced predation risk due to lower predator encounter rates. However, the cost of the passive ambush feeding strategy is a low feeding efficiency and potentially low mate encounter rate (Kiørboe, 2011). This trade-off is very well constrained in copepod populations, with passive ambush feeders having lower metabolic and mortality rates than their more active counterparts (Eiane and Ohman, 2004).

The importance of passive feeding as the main nutritional mode is supported by the correlation between growth rate and feeding frequency (Bé et al., 1981). Foraminifera are capable of digesting most organic materials, presumably a survival strategy for environments where one or more food sources may not be available and mitigating environmental change. They have an extensive network of thin, sticky strands of cytoplasm (rhizopodia) around their shell that are used to help capture, transport, and break-up prey items, as well as carry waste products out of the cell (Hemleben, 1989). During the early life stages (prolocular-juvenile, ~15-100 μm shell diameter (Spindler et al., 1984; Caron et al., 1987), foraminifera are omnivorous, although primarily consuming an herbivorous diet.

As some foraminiferal species transition from the juvenile to neanic stage (>100 µm shell diameter), they may become host to photosymbiotic algae and/or develop spines. Spines provide a rigid framework for rhizopodia to attach and increase foraminifera's capture area (Gaskell et al., 2019), allowing them to capture and hold active prey, facilitating a switch from a predominantly herbivorous to carnivorous diet (Fig. 1c; Anderson et al., 1979; Schiebel and Hemleben, 2017). For example, *O. universa* shifts from a herbivorous diet during its early and juvenile phase to a carnivorous diet in the spherical adult stage (Schiebel and Hemleben, 2017). A wide variety of animal prey can be consumed by spinose planktic foraminifera, including copepods, hyperiid amphipods, tunicates, ostracods, pteropods, gastropod larvae, ciliates, radiolarians, acanthurids and polychaete larvae (Anderson et al., 1979). Observational evidence suggests that copepods account for >40% of spinose taxa diets, with an additional ~20-30% from ciliates and the remainder made up of a variety of prey items (Schiebel and Hemleben, 2017). In a laboratory environment, spinose taxa exhibited higher acceptance rates of calanoid over cyclopoid copepods (Spindler et al., 1984), indicating some degree of prey selectivity. Spinose planktic foraminifera are capable of capturing and digesting prey items 2-3 times bigger than their body size (Schiebel and Hemleben, 2017). Carnivory is advantageous in a food-poor environment for organisms relying on chance encounters, because individual prey items have a higher calorific value relative to a similar sized phytoplankton (Boyd, 1971).

Non-spinose planktic foraminifera are omnivorous but prefer a herbivorous diet throughout their life cycle (Hemleben et al., 1985, Schiebel and Hemleben, 2017), preying on diatoms, dinoflagellates, and eukaryotic algae. Copepods (dead and alive) have been given in culture to several non-spinose species (*Globorotalia truncatulinoides, G. hirsuta, G. inflata, Globigerinita glutinata* and *Pulleniatina obliquiloculata*), but it was found these taxa are unable to capture and hold live zooplankton and are only able to consume zooplankton if they are immobilized or dead (Spindler et al., 1984; Anderson et al., 1979). In the ocean, non-spinose species such as *G. menardii* can capture and control small ciliates using their rhizopodia, as evidenced by muscle and other animal tissues in food vacuoles (Anderson et al., 1979). Metabarcoding studies have shown that the Arctic non-spinose species *Neogloboquadrina pachyderma* include animal tissue in their cytoplasm (Greco et al., 2021); however, it remains unclear whether this tissue comes from live or dead prey. Hence, the predominantly herbivorous diet may largely be because of their difficulty in capturing living zooplankton. Under laboratory conditions, non-spinose species exhibit cannibalism but whether they cannibalise in the natural habitat is unknown and considered unlikely due to the very low foraminiferal abundance (Schiebel and Hemleben, 2017; Westgård et al., 2023).

The temporal and spatial distribution of prey items is a major driver of the regional distribution of planktic foraminifera species, influencing their growth and fecundity in addition to sea surface temperature (Schiebel and Hemleben, 2017; Schmidt et al., 2004; Adebayo et al., 2017; Lombard et al., 2011). Spinose taxa are most abundant in (sub)tropical oligotrophic gyres (Fig. 3), where copepods are most abundant (Grice and Hart, 1962), whereas non-spinose species are most abundant in upwelling and coastal waters and at higher latitudes (>30°), which are rich in phytoplankton and small zooplankton (Grice and Hart, 1962).

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Model simulations of trophic dynamics requires data on prey preferences, e.g., prey acceptance rates, protein acquisition from zooplankton versus phytoplankton, and average digestion and capture times. Observational data can be collected by analysing feeding vacuoles and metabarcoding analyses of in-situ samples. For planktic foraminifera, this information is scarce and limited to a few taxa (e.g., the spinose species *Trilobatus sacculifer, Globigerinoides ruber* and *Orbulina universa*), which are most easily cultured in the laboratory. It is unclear, though, how representative laboratory environments are of natural feeding behaviours given the stress responses of some species, e.g., shortening or spine loss of *G. ruber* (Bijma et al., 1990). Furthermore, many critical parameters are known only from a single experiment. There is a clear need to capitalise on the recent success in culturing of a wider range of taxa, such as the eutrophic *G. bulloides* (Sykes et al., 2024) or the polar *N. pachyderma* (Meilland et al., 2022), to explore these questions across a wide range of foraminifera eco-groups. Multigenerational experiments would also allow closure of the important gap of quantitative data on the herbivory preferences or digestion rates of juveniles, or the role of bacteria and organic matter in foraminiferal diet.

There are many further gaps in knowledge about the costs and benefits of being a passive ambush feeder, competition with other foraminifera or their close relatives, the siliceous radiolarians, all of which impact our ability to consider interactions with zooplankton in trait models. To advance trait models, data is needed on prey preferences, prey-predator optimum length ratio, and encounter rates (successful and unsuccessful) to cover the energetic needs for calcification and other metabolic costs.

2.2.2 Starvation tolerance/dormancy (group-specific trait)

Feeding experiments indicate that when food is available at the optimum frequency, foraminifera reproduce quickly, but the reverse is also true. In culture, planktic foraminifera can survive and grow for 16-46 days with little or no food after initial capture, i.e., in some cases beyond their 'normal' lifespan in the ocean (Anderson et al., 1979; Bé et al., 1982). However, associated low growth leads ultimately to lower standing stocks and/or smaller body sizes, threatening their ability to undergo gametogenesis or, as volume is linked to the number of gametes, fewer gametes (Bé et al., 1981). The taxa that have survived longest in culture (>230 days) are asymbiotic herbivorous taxa such as *Neogloboquadrina pachyderma,* with growth optimised for low temperatures (Lombard et al., 2010) with presumably lower metabolic rates (Spindler, 1996).

N. pachyderma is the dominant planktic foraminifera at high latitudes and thrives in upwelling and (sub)polar oceans, able to survive low temperatures (-2 to +15°C) and a wider range of pH and salinities (Westgård et al., 2023). This is the only planktic foraminifera species for which dormancy is known. Specifically Antarctic genotype IV of *N. pachyderma* of Darling and Wade (2008) is observed to overwinter in brine channels and pockets within Antarctic sea ice (Spindler and Dieckmann, 1986; Dieckmann et al., 1991; Berberich, 1996; Spindler, 1996). This species can survive and grow in sea ice but does not reproduce. Brine pockets and channels can have salinities up to 177 psu and temperatures as low as -15°C. However, at >50 psu   ,

individuals grew more slowly and reached smaller overall body sizes and were unable to undergo gametogenesis. At >73 psu, pseudopodal activity and movement ceased, but they were able to survive for up to several weeks at up to ~82 psu without feeding (Spindler, 1996). This finding is supported by more recent culturing work suggesting tolerance to a wide range of salinities, but also that specimens are less active and less likely to add new chambers at very high or low salinities or reproduce (Bertlich et al., 2021, Westgård et al., 2023). Indeed, in culture, specimens that were inactive (e.g., no growth, limited/no rhizopodal activity) or dormant (appeared to have empty shells/decaying cytoplasm and did not feed) were able to recover as conditions became more favourable (Westgård et al., 2023). The same brine pockets and channels also contain dense populations of phytoplankton, predominantly diatoms, a rich potential food source for *N. pachyderma* (Spindler and Dieckmann, 1986; Dieckmann et al., 1991). Overwintering via dormancy is thus advantageous because it allows *N. pachyderma* to suppress metabolic activity to reduce energy consumption (e.g., buoyancy compensation, growth) and survive unfavourable environmental circumstances, but also provides rich food source for when conditions are favourable and protection from predators (Dieckmann et al., 1991). Dormancy ultimately means that taxa inhabiting sea ice can significantly extend their 'normal' lifespan, potentially surviving for up to one year from the formation of sea ice in the autumn until the following spring/summer (Spindler, 1996).

2.2.3 Photosymbioses (group-specific traits)

Symbiosis between different biological organisms is a common ecological strategy in the ocean from shallow benthic marine ecosystems (e.g., coral reefs) through to the nekton and plankton, a major source of evolutionary innovation and hence biodiversity (Decelle et al., 2015; Margulis, 1993). Planktic symbiotic relationships in the open ocean are relatively poorly constrained in contrast to the benthic shallow-water counterparts, however, symbiosis in planktic foraminifers appears to represent an adaptation to nutrient-poor, sunlit waters (Fig. 3d; Bé, 1971).

Many of the largest benthic and planktic foraminifera in the modern ocean tend to host algal photosymbionts (Kucera, 2007), highlighting the important role of symbiosis in providing additional energy to support the energetic costs of building a larger skeleton. In foraminifera, species that occupy the photic zone are commonly host to algal photoendosymbionts, either chrysophytes or dinoflagellates (Fig. 1b and c). Symbionts are acquired by juvenile foraminifera from the water column following sexual reproduction (Hemleben, 1989), but potentially also via the parent by direct vertical transmission during the more poorly known asexual reproductive cycle (Takagi et al., 2020). Whilst many spinose taxa are host to dinoflagellate photosymbionts, there are exceptions. For example, *G. bulloides* IId is associated with bacterial endobionts, e.g., *Synechococcus* in the eastern Pacific Ocean (Bird et al., 2017) or none, e.g., *Hastigerina pelagica* (Takagi et al., 2019). Some non-spinose taxa such as G. *glutinata* or *Globigerinella siphonifera* may also host photosymbionts, mostly chrysophytes (Takagi et al., 2019). However, whether these species have a truly symbiotic relationship with foraminifera, or just utilise waste products, is currently unknown (Hemleben, 1989). Available data suggest that the type of symbiont dictates

photophysiology rather than host size or spines (Hoadley et al., 2019; Takagi et al., 2019). This conclusion is supported by the likely evolution of dinoflagellate symbiosis in the Cretaceous before spines or spine-like structures evolved in the Palaeocene (Hoadley et al., 2019; Pearson et al., 2001; Bornemann and Norris, 2007), suggesting that whilst spines may help to optimise photosymbiont activities, they are not essential (and therefore, this is not the primary function of spines).

Symbiosis can be described as obligate (essential for optimal host fitness and observed in the majority of individuals of a species, making them functionally mixotrophic) or facultative (not essential to the host success and thus only associated with some individuals of the species) (Table 1; Takagi et al., 2019). Determining whether symbiosis is obligate or facultative is challenging as photosymbiosis is a spectrum, as proposed by Stoecker et al (2009), from non-symbiosis to robust symbiosis. We have direct observations of symbiotic presence or absence in more than 30 species (see Table 1), typically recognised via microscopic observations (Anderson and Be, 1976) and/or molecular work (Gast and Caron, 1996; Yonathan and Colomban De, 2006). However, it is difficult to clearly differentiate between digested and active symbiosis with these methods. Active chlorophyll fluorescence, a non-destructive and invasive approach that allows assessment of fluorescence through ontogeny, is a powerful technique helping to close this knowledge gap and advance modelling traits related to symbioses by enabling determination of the Chlorophyll-a content of specimens, health of symbionts and their light-level adaptation (Takagi et al., 2019; Takagi et al., 2016).

Within planktic foraminifera, taxa with obligate (dinoflagellate) photosymbionts tend to dominate oligotrophic regions with expanded mixed layers and high light penetration (Fig. 3). Symbionts are rarer at cold, low light high latitude areas, in deep waters >200 m and in eutrophic regions of the ocean, presumably where they are either unable to survive or unnecessary (Hemleben, 1989). No symbiont bearing-taxa are found at very high latitudes (>~50 degrees; Fig. 3).

Photosymbionts provide an important energy supplement to their host in the form of photosynthetically fixed carbon, aiding growth, longevity, calcification and reproductive potential (e.g., Lekieffre et al., 2018; Bé et al., 1982), but photosymbionts alone do not provide sufficient carbon subsidy to entirely support foraminiferal life processes. At the same time, symbionts preferentially use metabolites from the foraminifera for photosynthesis (Takagi et al., 2018). Algal photosymbionts also aid calcification by increasing the pH of the foraminifera's immediate microenvironment above ambient seawater by utilising CO_2 during photosynthesis and therefore potentially enhancing calcification (Rink et al., 1998; Kohler-Rink and Kuhl, 2005).

Photosymbionts are acquired as juveniles or, as new evidence suggests, provided to gametes during gametogenesis (Takagi et al. 2020) and are typically arranged in the external rhizopodial net during the day and brought into the shell at night (e.g., Anderson and Be, 1976; Lekieffre et al., 2018). Symbiont biomass rises and falls during the host's life (Takagi et al., 2016), with the symbionts eventually being consumed immediately prior to gametogenesis (Bé, 1983). Digestion of photosymbionts may help to meet the energy demands of gametogenesis or provide energy during periods of prolonged darkness (e.g., Spero

and Parker, 1985; Bé, 1983; Takagi et al., 2016). However, even under starvation, some symbionts are retained in culture until gametogenesis (Takagi et al., 2018).

Takagi et al. (2019) showed that photosynthetic activity in symbiont-facultative species tends to be weaker than in symbiont-obligate species and thus, nutritional benefit to the host may be smaller. However, the benefit of facultative symbiosis is still unclear. It may be opportunistic and may overall support a more flexible range of nutritional sources for the host. A lower reliance on symbiont activity in organisms might also allow these taxa to explore low-light eutrophic regions, including the deep-water layers and the turbulent upwelling regions. A recent study developing the ForamECOGEniE model to incorporate the different symbiosis types (Ying et al., 2023) replicated patterns of asymbiotic and obligate symbiotic global distributions but underestimated the abundance of the non-spinose symbiont-facultative group, particularly in the eastern equatorial Pacific. The challenge of modelling this group is the lack of information on what drives the symbiont-facultative group to acquire or lose their symbionts. Without a clear ecological/physiological understanding, trade-offs cannot be incorporated into the model. Intriguingly, if the abundances of the obligate and facultative symbiotic taxa are combined, there is a good fit between the model and observations (Ying et al., 2023). This may suggest that the facultative group overall exploits the same benefits from symbiosis. However, determining the mechanistic underpinning is critical to understand the data, particularly the environmental/biological conditions under which symbiosis is active or not, and the benefits of the relationship to the host. Thus, culture experiments and further observation of this phenomenon are still required.

The costs associated with hosting photosymbionts are that [1] they restrict foraminifera's depth habitat to the euphotic zone (generally <200 m water depth; Caron et al., 1987; Schiebel and Hemleben, 2017), and [2] the host is dependent on changes in the availability and health of the symbionts, which respond to environmental change. Studies suggest that foraminifera symbionts are not favoured in low pH waters (Henehan et al., 2017) or in eutrophic areas due to light limitation (Ortiz et al., 1995). Reduced photosynthetic activity results in smaller final body sizes and shorter survival times (Ortiz et al., 1995; Bé et al., 1981; Caron et al., 1982; Faber et al., 1989). During extreme temperatures in the geological record, planktic foraminiferal populations of 'bleached' individuals may have persisted for thousands of years with smaller sizes and lower population abundances (Edgar et al., 2013; Wade et al., 2008), which may have impacted fitness and increased their susceptibility to extinction (e.g., Wade et al., 2008).

The knowledge gap relating to symbioses, beyond the fundamental knowledge of which symbiont each species hosts, includes what triggers changes in symbiont activity and mode of symbiosis, the degree of energy subsidy symbionts provide to their host and further understanding of the use of symbionts as prey items. For *G. bulloides*, the nature of their association with bacterial endobionts also needs further exploration to understand how widespread the association is between genetic types and within the ocean. Without this understanding, and the ecological impact on the symbiont, the future fitness of planktic

foraminifera cannot be explored fully, nor can the importance of the loss of symbiosis in the fossil record after extinctions (Birch et al., 2016).

2.3 Reproduction

2.3.1 Sexual reproduction (foraminiferal trait)

Planktic foraminifera were traditionally observed to only reproduce sexually (e.g., Bé and Anderson, 1976, Ketten and Edmond, 1979, and references in Schiebel and Hemleben, 2017) differing from their benthic counterparts that can alternate between sexual and asexual reproductive modes (Goldstein, 1999). Most shallow dwelling planktic foraminifera reproduce on a semi-lunar or lunar synodic cycle (~2-4 weeks), whereas intermediate to deeper dwelling species may live for up to one year (Spindler, 1979; Hemleben, 1989). Foraminifera migrate to reproduce at depth close to the deep chlorophyll maximum, where there are optimum feeding and grazing protection opportunities for offspring (Hemleben, 1989). Notably, most observational work was on spinose species. During gametogenesis, foraminifera undergo a suite of morphological, physiological and ecological changes. They retract their rhizopodia, shorten and shed their spines by dissolution at the tips and resorption at the base, consume any photosymbionts and precipitate an additional outer layer of calcite (gametogenic calcite) over the shell (Schiebel and Hemleben, 2017). Gametogenesis ends with the conversion of all cytoplasm into gametes via vacuolisation, which are released directly into the water column (broadcast spawning). Gametogenesis takes ~1-3 days from the formation of the final chamber (Bé, 1983), resulting in an empty adult shell which sinks to the seafloor (Seibold, 1993).

Sexual reproduction allows populations to maintain higher genetic diversity and select for advantageous mutations or conversely eradicate unfavourable mutations (Otto and Lenormand, 2002). Therefore, sexual reproduction provides a definite (if though difficult to quantify) advantage for survival in the dynamic surface waters with constantly changing selective pressures (Lynch, 1991). In addition, the broadcast spawning strategy presumably confers energy savings compared to organisms actively searching for mates and reduced predator encounters. However, the typically low concentration of foraminifera in the water column (~1 specimen per m^3 in the open ocean) makes this a risky strategy. Further, any mismatches in the timing (or place) of reproduction between individuals would reduce the chance of fertilization.

Planktic foraminifera have developed a number of strategies to maximise the successful fertilization of gametes from different parents in the water column, including (1) the synchronization of the timing and depth of reproduction between multiple individuals of the same species, (2) the release of a large number of gametes (200,000-400,000 individuals; dependent on both shell and gamete size) from each adult, thereby increasing encounter and survival rates, and (3) the development of motile gametes (see Weinkauf et al., 2022a and references therein).

2.3.2 Asexual reproduction (species/group-specific traits)

Recent culture breakthroughs have shown that some non-spinose planktic foraminiferal species (*N. pachyderma, G. glutinata* and *G. uvula*) can reproduce both asexually and sexually (Davis et al., 2020; Kimoto and Tsychiya, 2006; Meilland et al., 2023; Meilland et al., 2024, Takagi et al., 2020). In *N. pachyderma*, precursors to asexual reproduction include feeding in large quantities, the development of bright red cytoplasm, and maintenance of the rhizopodial network, the latter in contrast to pre-gametogenic changes (Greco et al., 2023, Meilland et al., 2024). There also remains a positive relationship between the size of the foraminifera shell and the number of offspring under asexual reproduction, albeit with fewer offspring per individual (~80-300) than via sexual reproduction (Meilland et al., 2024). However, there is generally considered to be higher survival of offspring compared to sexual reproduction, hence, this reproductive mode supports rapid growth of planktic foraminifera populations when conditions are optimal. Asexual reproduction also provides a mechanism to explain the survival and rapid population growth of *N. pachyderma* at high latitudes (Davies et al., 2020, Meilland et al., 2024).

The ability of at least some species of planktic foraminifera to switch between sexual and asexual reproduction helps to reconcile rapid population growth in response to temporally and spatially optimal conditions and represents a distinct advantage for survival of polar species in particular (Davies et al., 2020). It is highly likely that future targeted experimental work will expand the evidence base for the number of planktic foraminifera species that can reproduce asexually.

Modelling the development of foraminifera in a way that resembles their accretionary growth has not been achieved to date. The main challenge is the lack of information on the different traits and trade- offs in their development, such as changes in metabolic rates, food uptake, etc. The new culturing breakthrough, which enables us to explore the full life cycle of planktic foraminifera, opens the door to explore these questions and close our knowledge gaps.

3. Suggestions for further research

Planktic foraminifera are an ideal target group for testing trait-based approaches, as a relatively small number of functional traits can define their ecological niches in the modern ocean. However, many of the traits identified here remain poorly qualified and quantitatively constrained, requiring further observational and experimental laboratory-based investigations.

A key trait requiring further study is calcification. Its trade-offs (Table 2), particularly its hypothesised benefit of protection against grazing, are fundamental to current trait-based models for calcifying plankton but still lack direct evidence (Barrett et al. 2025; Monteiro et al. 2016). We also require an understanding of the energetic costs of calcification and the mechanisms controlling biomineralization. This requires moving away from analogies largely based on physiological calcification studies of benthic foraminifera (e.g., De Nooijer et al 2009, De Nooijer et al 2014) to similar experiments on planktic foraminifera.

523 At present, the poorly constrained relationship between calcification and seawater carbonate chemistry limits our ability to
524 predict the impact of ocean acidification on foraminiferal growth and carbonate production. These knowledge gaps also hamper
525 accurate modelling of ocean alkalinity distribution and carbonate production in response to a changing climate.

526 In other organisms, food availability can support metabolism to reduce the impacts of anthropogenic climate change on other
527 physiological processes (Thomsen et al., 2013). Further understanding of foraminiferal predator-prey dynamics is therefore
528 urgently needed. For example, cultures and *in-situ* observations can improve our understanding of feeding by providing
529 quantitative data on (1) the role of bacteria, (2) the role of organic matter in foraminiferal diet - specifically protein acquisition
530 from zooplankton versus phytoplankton, (3) prey-predator optimum length ratio, (4) prey encounter rates (successful and
531 unsuccessful), and (5) average digestion and capture time of prey. These data could (in part) be collected by analysing feeding
532 vacuoles and metabarcoding analyses of samples.

533

534 Photosymbiosis, a major trait among symbiotic foraminifera, also requires further investigation. Culture and observational
535 studies should focus on the impacts of environmental change on symbiosis. These include understanding what triggers change
536 in symbiont hosting (e.g., bleaching, and hosting for symbiont-facultative species), which symbiont each species hosts
537 (facilitated by eDNA analyses), and the energy the symbiont provides to its host.

538 Experiments that exploit the new breakthrough in multigenerational planktic foraminifera culturing will improve our
539 knowledge of their life cycle through understanding the traits and trade-offs associated with their development, e.g., their
540 metabolic rates, food uptake, reproduction, and importantly, which species are capable of asexual reproduction and under what
541 conditions this mode dominates. All these new insights will contribute to better data for improved modelling of planktic
542 foraminifers.

543 Environmental DNA (eDNA) metabarcoding, which analyses the genetic material present in the environment, such as sediment
544 or water, is a powerful new tool for identifying and monitoring biodiversity, biogeography and reconstructing ecosystems and
545 ecologies (Ruppert et al., 2019). This technique can also provide insights into community composition over timescales
546 spanning several hundreds of thousands of years or longer, improving our understanding of the relationships between
547 biodiversity, environment and climate (e.g., Ambrecht et al., 2019). However, the bulk of eDNA foraminiferal studies to date
548 have focussed on benthic foraminifera. For instance, this technique has significantly increased the known diversity of organic
549 walled and "naked" foraminifera that are rarely observed, have few morphological characters for traditional species
550 delimitation, and don't preserve well in the fossil record (Pawlowski et al., 2014). Thus, eDNA holds great promise for
551 investigating marine plankton, as it has the potential to overcome many of the data limitations that we currently face in this
552 group with typically low standing stocks (de Vargas et al., 2015). It is a potentially more effective means of detecting species
553 presence in an environment than observations alone (Malviya et al., 2016; Ser-Giacomi et al., 2018; Barrenechea Angeles et
554 al., 2020), but can also contribute much more broadly, for instance, by providing insights into plankton population size (Andres

et al., 2023), response to environmental change (Cao et al., 2022) or predator-prey dynamics (Ruppert et al., 2019). A combination of molecular and microscopic approaches can also yield new insights, e.g., in benthic foraminifera it allowed rapid determination of multiple different feeding strategies driving diversity and abundance in several foraminiferal taxa (Schweizer et al., 2022), a question which is typically restricted to analysis of feeding vacuoles and laboratory experiments. However, further method development is still required as some groups are not as well represented by the eDNA technique as others, e.g., specimens may visually be present in sediments but not found in the eDNA analysis, likely because of limitations of the primer to detect certain groups, e.g., Prymnesiophyceae (Barrenechea Angeles et al., 2020, Hoshino and Inagaki, 2024).

In general, there is a need to improve data reporting practices in the aforementioned studies by following guidance on data publishing (e.g. FAIR principles) and developing standardized, community agreed protocols akin to other fields (e.g., Riebesell, et al., 2010) for measuring traits to enhance our understanding of planktic foraminifera and how they are best modelled.

Ultimately, dynamic trait-based models are a useful tool to create theoretical frameworks for assessing ecosystem functions of foraminiferal traits and explore questions at scales and beyond those possible in laboratory or natural environments. For instance, ecological parameters measured in laboratory environments could be used in trait-based models to assess their impacts on the global biomass and calcite production, which are both poorly constrained in the modern carbon cycle (Ying et al. 2023). In addition, paleoceanography models could help to elucidate the relationship between foraminiferal evolution (i.e., the emergence of new traits) and the background climate change, e.g., the evolution of deeper-water taxa as the oceans cooled over the past 15 Myrs (Boscolo-Galazzo 2021). For modern species with high mortality rates in laboratory culture or difficulties in maintaining multigenerational experiments (and high time and financial costs), trait-based models provide suitable setups to estimate potential physiological ecology in the absence of physical organisms (Grigoratou et al., 2019).

However, whilst a powerful tool, numerical models are ultimately just that, models. They are by necessity based on assumptions and simplifications of the natural world. Model reliability and performance is highly dependent on the specific research question asked and the observations available against which models can be validated. For planktic foraminifera, the most abundant data for model calibration is sediment core top data and most foraminiferal models can reproduce the observed global biogeography of main species/ecogroups in sediment cores. However, less empirical data can be used for foraminiferal physiological model parameterisation. The growth rate and temperature dependency data from Lombard et al. (2009) are adopted by most plankton functional type models to parameterise foraminiferal physiology (e.g., PLAFOM, FORAMCLIM, PLANKTOM). However, less constraint exists for food preference and grazing efficiency, hampering us to simulate the observed low foraminiferal biomass. Trait-based models can dynamically calculate grazing rate based on body size (allometric law) and temperature/food availability. However, a recent study shows that planktic foraminifera have lower allometric scaling of energetic needs compared to other plankton when considered in the context of organic density and catchment volume (Burke

588 et al. 2025). Therefore, key parameters needed to improve foraminiferal model performance include more quantitative data on

589 fundamental parameters such as: growth rate, respiration rate, half-saturation constant, and grazing preferences.

590

591 Despite existing data gaps and model challenges, distinct groupings of planktic foraminifera traits identified in the modern

592 ocean allow us to explore key drivers of past biogeography, changes in metabolic traits and trade-offs, and responses to extreme

593 environments with moderate confidence (e.g. Deutsch et al. 2020). Closer collaboration between modellers and data scientists

594 is essential to optimise the application of trait-based approaches to planktic foraminifera. Targeted data collection to fill

595 specific critical knowledge gaps via models, laboratory culturing, field observations, molecular techniques and more inclusive

596 reporting will improve confidence in predictions from trait-based models and help to realise the full potential of this approach.

597 Ultimately, understanding the associations of different traits and suites of traits with particular environments provides the basis

598 for understanding how environmental factors structure planktic foraminifera communities in the past and in the future. This

599 knowledge will be crucial for assessing the vulnerability of these communities to ongoing and future environmental changes.

600

601 **Code/Data availability**

602 All data referenced in the text is openly available and can be found in the cited sources.

603

604 **Author contribution**

605 DNS, FM and KME conceived the idea for the manuscript. KME and MG prepared the original draft of the manuscript. KME,

606 MG and RY created the figures and tables. All authors contributed to reviewing and editing of the manuscript. DNS supervised

607 the work.

608

609 **Competing Interests**

610 The authors declare that they have no conflict of interest

611

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618 **References**

619

620 Adebayo, M.B., Bolton, C.T., Marchant, R., Bassinot, F., Conrod, S and de Garidel-Thoron, T.: Environmental controls of

621 size distribution of modern planktonic foraminifera in the tropical Indian Ocean, Geochemistry, Geophysics, Geosystems,

622 24, e2022GC010586, 2023.

624 Alma, L., Kram, K. E., Holtgrieve, G. W., Barbarino, A., Fiamengo, C. J., and Padilla-Gamiño, J. L.: Ocean acidification

625 and warming effects on the physiology, skeletal properties, and microbiome of the purple-hinge rock scallop, Comparative

626 Biochemistry and Physiology Part A: Molecular & Integrative Physiology, 240, 110579,

627 https://doi.org/10.1016/j.cbpa.2019.110579, 2020.

629 Alve, E. and Goldstein, S. T.: Resting stage in benthic foraminiferal propagules: a key feature for dispersal? Evidence from

630 two shallow-water species, J. Micropalaeontol., 21, 95-96, 10.1144/jm.21.1.95, 2002.

632 Alve, E. and Goldstein, S. T.: Dispersal, survival and delayed growth of benthic foraminiferal propagules, Journal of Sea

633 Research, 63, 36-51, https://doi.org/10.1016/j.seares.2009.09.003, 2010.

635 Andersen, K. H., Blanchard, J. L., Fulton, E. A., Gislason, H., Jacobsen, N. S., and van Kooten, T.: Assumptions behind

636 size-based ecosystem models are realistic, ICES Journal of Marine Science, 73, 1651-1655, 10.1093/icesjms/fsv211, 2016.

638 Anderson, O. R. and Be, A. W. H.: The ultrastructure of a planktonic foraminifer, *Globigerinoides sacculifer* (Brady), and its

639 symbiotic dinoflagellates, Journal of Foraminiferal Research, 6, 1-21, 10.2113/gsjfr.6.1.1, 1976.

641 Anderson, O. R., Spindler, M., Bé, A. W. H., and Hemleben, C.: Trophic activity of planktonic foraminifera, Journal of the

642 Marine Biological Association of the United Kingdom, 59, 791-799, 10.1017/S002531540004577X, 1979.

644 Armbrecht, LH., Coolen, M.J.L., Lejzerowicz, F., George, S.C., Negandhi, K., Suzuki, Y., Young J., Foster N.R., Armand,

645 L.K., Cooper, A., Ostrowski, M., Focardi, A., Stat, M., Moreau, J.W., Weyrich L.S.: Ancient DNA from marine sediments:

646 precautions and considerations for seafloor coring, sample handling and data generation. Earth-Sci Rev 196:102887, 2019.

648 Armstrong, H. A. a. B., M.D.: Foraminifera, in: Microfossils, Blackwell Publishing, 142-187, 2004.

650 Aze, T., Ezard, T. H., Purvis, A., Coxall, H. K., Stewart, D. R., Wade, B. S., and Pearson, P. N.: A phylogeny of Cenozoic

651 macroperforate planktonic foraminifera from fossil data, Biol Rev Camb Philos Soc, 86, 900-927, 10.1111/j.1469-

652 185X.2011.00178.x, 2011.

654 Barker, S. and Elderfield, H.: Foraminiferal calcification response to glacial-interglacial changes in atmospheric CO2,
655 Science, 297, 833-836, 10.1126/science.1072815, 2002.

657 Barrett, R., de Vries, J., and Schmidt, D. N.: What controls planktic foraminiferal calcification?, Biogeosciences, 22, 791-
658 807, http:doi.org/10.5194/bg-22-791-2025-, 2025.

660 Barton, A. D., Irwin, A. J., Finkel, Z. V., and Stock, C. A.: Anthropogenic climate change drives shift and shuffle in North
661 Atlantic phytoplankton communities, Proceedings of the National Academy of Sciences, 113, 2964-2969,
662 doi:10.1073/pnas.1519080113, 2016.

664 Barton, A. D., Pershing, A. J., Litchman, E., Record, N. R., Edwards, K. F., Finkel, Z. V., Kiørboe, T., and Ward, B. A.: The
665 biogeography of marine plankton traits, Ecology Letters, 16, 522-534, https://doi.org/10.1111/ele.12063, 2013.

667 Beer, C. J., Schiebel, R., and Wilson, P. A.: Technical Note: On methodologies for determining the size-normalised weight
668 of planktic foraminifera, Biogeosciences, 7, 2193-2198, 10.5194/bg-7-2193-2010, 2010.

670 Berberich, D.: Die planktische Foraminifere Neogloboquadrina pachyderma (Ehrenberg) im Weddellmeer, Antarktis,
671 Berichte zur Polarfroschung, 195, 10.2312/BzP_0195_1996, 1996.

673 Berger, W. H.: Planktonic foraminifera; sediment production in an oceanic front, Journal of Foraminiferal Research, 1, 95-
674 118, 10.2113/gsjfr.1.3.95, 1971.

676 Bijma, J., Erez, J., and Hemleben, C.: Lunar and semi-lunar reproductive cycles in some spinose planktonic foraminifers,
677 Journal of Foraminiferal Research, 20, 117-127, 10.2113/gsjfr.20.2.117, 1990.

679 Birch, H. S., Coxall, H. K., Pearson, P. N., Kroon, D., and Schmidt, D. N.: Partial collapse of the marine carbon pump after
680 the Cretaceous-Paleogene boundary, Geology, 44, 287-290, 10.1130/g37581.1, 2016.

682 Bird, C., Darling, K.F., Russell, A.D., Davis, C.V., Fehrenbachers, J., Wyman, M. and Ngwenya, B.T. Cyanobacterial
683 endobionts within a major marine planktonic calcifier (*Globigerina bulloides*, Foraminifera) revealed by 16S rRNS
684 metabarcoding, Biogeosciences, 14, 901-920, 10.5194/bg-14-901-2017, 2017.

Bornemann, A. and Norris, R. D.: Size-related stable isotope changes in Late Cretaceous planktic foraminifera: Implications for paleoecology and photosymbiosis, Marine Micropaleontology, 65, 32-42, https://doi.org/10.1016/j.marmicro.2007.05.005, 2007.

Boyd, C. E. a. G., C.P.: Nutritive quality of food in ecological systems, Arch. Hydrobiol., 69, 256-270, 1971.

Brandão, M. C., Benedetti, F., Martini, S., Soviadan, Y. D., Irisson, J.-O., Romagnan, J.-B., Elineau, A., Desnos, C., Jalabert, L., Freire, A. S., Picheral, M., Guidi, L., Gorsky, G., Bowler, C., Karp-Boss, L., Henry, N., de Vargas, C., Sullivan, M. B., Acinas, S. G., ..., and Tara Oceans Consortium, C.: Macroscale patterns of oceanic zooplankton composition and size structure, Scientific Reports, 11, 15714, 10.1038/s41598-021-94615-5, 2021.

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., and West, G. B.: Toward a metabolic theory of ecology, Ecology, 85, 1771-1789, https://doi.org/10.1890/03-9000, 2004.

Brummer, G.-J. A., Hemleben, C., and Spindler, M.: Ontogeny of extant spinose planktonic foraminifera (Globigerinidae): A concept exemplified by *Globigerinoides sacculifer* (Brady) and *G. ruber* (d'Orbigny), Marine Micropaleontology, 12, 357-381, https://doi.org/10.1016/0377-8398(87)90028-4, 1987.

Brummer, G. J. A. and Kučera, M.: Taxonomic review of living planktonic foraminifera, J. Micropalaeontol., 41, 29-74, 10.5194/jm-41-29-2022, 2022.

Buitenhuis, E. T., Hashioka, T., and Quéré, C. L.: Combined constraints on global ocean primary production using observations and models, Global Biogeochemical Cycles, 27, 847-858, https://doi.org/10.1002/gbc.20074, 2013.

Bé, A. W. and Anderson, O. R.: Gametogenesis in planktonic foraminifera, Science, 192, 890-892, 10.1126/science.946914, 1976.

Bé, A. W. H.: An ecological, zoogeographic and taxonomic review of Recent planktonic foraminifera, in: Oceanic Micropaleontology, edited by: Ramsay, A. T. S., Academic Press, London, 1-100, 1977.

Bé, A. W. H., Caron, D. A., and Anderson, O. R.: Effects of feeding frequency on life processes of the planktonic foraminifer Globigerinoides sacculifer in laboratory culture, Journal of the Marine Biological Association of the United Kingdom, 61, 257-277, 10.1017/S002531540004604X, 1981.

720 Bé, A. W. H., Spero, H. J., and Anderson, O. R.: Effects of symbiont elimination and reinfection on the life processes of the
721 planktonic foraminifer Globigerinoides sacculifer, Marine Biology, 70, 73-86, 10.1007/BF00397298, 1982.
722

723 Bé, A. W. H., Anderson, O.R., Faber, W.W., Jr. and Caron, D.A.: Sequence of morphological and cytoplasmic changes
724 during gametogenesis in the planktonic foraminifer *Globigerinoides sacculifer* (Brady), Micropaleontology, 29, 310-325,
725 1983.
726

727 Bé, A. W. H. a. T., D.S.: Distribution and ecology of living planktonic foraminifera in surface waters of the Atlantic and
728 Indian oceans, in: Micropaleontology of marine bottom sediments, edited by: Riedel, B. M. F. a. W. R., Cambridge
729 University Press, Cambridge, 105-149, 1971.
730

731 Béjard, T. M., Rigual-Hernández, A. S., Tarruella, J. P., Flores, J. A., Sanchez-Vidal, A., Llamas-Cano, I., and Sierro, F. J.:
732 Planktonic foraminifera assemblage composition and flux dynamics inferred from an annual sediment trap record in the
733 central Mediterranean Sea, Biogeosciences, 21, 4051-4076, 10.5194/bg-21-4051-2024, 2024.
734

735 Cao, Y., Lei, Y., Fang, J.K.H. and Li, T., Molecular diversity of foraminiferal eDNA in sediments and their correlations with
736 environmental factors from the Yellow Sea. Ecological Indicators, 142: 109294, 2022.
737

738 Caromel, A. G. M., Schmidt, D. N., Fletcher, I., and Rayfield, E. J.: Morphological Change During The Ontogeny Of The
739 Planktic Foraminifera, J. Micropalaeontol., 35, 2-19, 10.1144/jmpaleo2014-017, 2016.
740

741 Caromel, A. G. M., Schmidt, D. N., Phillips, J. C., and Rayfield, E. J.: Hydrodynamic constraints on the evolution and
742 ecology of planktic foraminifera, Marine Micropaleontology, 106, 69-78, https://doi.org/10.1016/j.marmicro.2014.01.002,
743 2014.
744

745 Caron, D. A., Bé, A. W. H., and Anderson, O. R.: Effects of variations in light intensity on life processes of the planktonic
746 foraminifer *Globigerinoides sacculifer* in laboratory culture, Journal of the Marine Biological Association of the United
747 Kingdom, 62, 435-451, 10.1017/S0025315400057374, 1982.
748

749 Caron, D. A., Faber, W. W., and Bé, A. W. H.: Effects of temperature and salinity on the growth and survival of the
750 planktonic foraminifer *Globigerinoides sacculifer*, Journal of the Marine Biological Association of the United Kingdom, 67,
751 323-341, 10.1017/S0025315400026643, 1987.
752

753 Chernihovsky, N., Torfstein, A., and Almogi-Labin, A.: Daily timescale dynamics of planktonic foraminifera shell-size
754 distributions, Frontiers in Marine Science, 10, 10.3389/fmars.2023.1126398, 2023.
755
756 Darling, K. F. and Wade, C. M.: The genetic diversity of planktic foraminifera and the global distribution of ribosomal RNA
757 genotypes, Marine Micropaleontology, 67, 216-238, https://doi.org/10.1016/j.marmicro.2008.01.009, 2008.
758
759 Davis, C. V., Livsey, C. M., Palmer, H. M., Hull, P. M., Thomas, E., Hill, T. M., and Benitez-Nelson, C. R.: Extensive
760 morphological variability in asexually produced planktic foraminifera, Science Advances, 6, eabb8930,
761 doi:10.1126/sciadv.abb8930, 2020.
762
763 de Nooijer, L. J., Pacho Sampedro, L., Jorissen, F. J., Pawlowski, J., Rosenthal, Y., Dissard, D., and Reichart, G. J.: 500
764 million years of foraminiferal calcification, Earth-Science Reviews, 243, 104484,
765 https://doi.org/10.1016/j.earscirev.2023.104484, 2023.
766
767 de Vargas, C., Renaud, S., Hilbrecht, H., and Pawlowski, J.: Pleistocene adaptive radiation in *Globorotalia truncatulinoides*:
768 genetic, morphologic, and environmental evidence, Paleobiology, 27, 104-125, 10.1666/0094-
769 8373(2001)027<0104:PARIGT>2.0.CO;2, 2001.
770
771 de Vargas, C., Audic, S., Henry, N., Decelle, J., Mahé, F., Logares, R., Lara, E., Berney, C., Le Bescot, N., Probert, I.,
772 Carmichael, M., Poulain, J., Romac, S., Colin, S., Aury, J. M., Bittner, L., Chaffron, S., Dunthorn, M., Engelen, S., ..., and
773 Karsenti, E.: Ocean plankton. Eukaryotic plankton diversity in the sunlit ocean, Science, 348, 1261605,
774 10.1126/science.1261605, 2015.
775
776 Decelle, J., Romac, S., Stern, R. F., Bendif, E. M., Zingone, A., Audic, S., Guiry, M. D., Guillou, L., Tessier, D., Le Gall, F.,
777 Gourvil, P., Dos Santos, A. L., Probert, I., Vaulot, D., de Vargas, C., and Christen, R.: PhytoREF: a reference database of the
778 plastidial 16S rRNA gene of photosynthetic eukaryotes with curated taxonomy, Molecular Ecology Resources, 15, 1435-
779 1445, https://doi.org/10.1111/1755-0998.12401, 2015.
780
781 del Campo, J., Carlos-Oliveira, M., Čepička, I., Hehenberger, E., Horák, A., Karnkowska, A., Kolisko, M., Lara, E., Lukeš,
782 J., Pánek, T., Piwosz, K., Richter, D. J., Škaloud, P., Sutak, R., Tachezy, J., and Hampl, V.: The protist cultural renaissance,
783 Trends in Microbiology, 32, 128-131, https://doi.org/10.1016/j.tim.2023.11.010, 2024.
784

785 Deuser, W. G., Ross, E. H., Hemleben, C., and Spindler, M.: Seasonal changes in species composition, numbers, mass, size,

786 and isotopic composition of planktonic foraminifera settling into the deep sargasso sea, Palaeogeography,

787 Palaeoclimatology, Palaeoecology, 33, 103-127, https://doi.org/10.1016/0031-0182(81)90034-1, 1981.

788

789 Deutsch, C., Penn, J.L. and Seibel, B.: Metabolic trait diversity shapes marine biogeography. Nature, 585, 557-562, 2020.

790

791 Dieckmann, G. S., Spindler, M., Lange, M. A., Ackley, S. F., and Eicken, H.: Antarctic sea ice; a habitat for the foraminifer

792 Neogloboquadrina pachyderma, Journal of Foraminiferal Research, 21, 182-189, 10.2113/gsjfr.21.2.182, 1991.

793

794 Dutkiewicz, S., Follows, M. J., and Bragg, J. G.: Modeling the coupling of ocean ecology and biogeochemistry, Global

795 Biogeochemical Cycles, 23, https://doi.org/10.1029/2008GB003405, 2009.

796

797 Dutkiewicz, S., Cermeno, P., Jahn, O., Follows, M. J., Hickman, A. E., Taniguchi, D. A. A., and Ward, B. A.: Dimensions of

798 marine phytoplankton diversity, Biogeosciences, 17, 609-634, 10.5194/bg-17-609-2020, 2020.

799

800 Edgar, K. M., Bohaty, S. M., Gibbs, S. J., Sexton, P. F., Norris, R. D., and Wilson, P. A.: Symbiont 'bleaching' in planktic

801 foraminifera during the Middle Eocene Climatic Optimum, Geology, 41, 15-18, 10.1130/g33388.1, 2013.

802

803 Eiane, K. and Ohman, M., D.: Stage-specific mortality of Calanus finmarchicus, Pseudocalanus elongatus and Oithona

804 similis on Fladen Ground, North Sea, during a spring bloom, Marine Ecology Progress Series, 268, 183-193, 2004.

805

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

807 Reviews in Mineralogy and Geochemistry, 54, 115-149, 10.2113/0540115, 2003.

808

809 Faber, W. W., Anderson, O. R., and Caron, D. A.: Algal-foraminiferal symbiosis in the planktonic foraminifer

810 *Globigerinella aequilateralis*; II, Effects of two symbiont species on foraminiferal growth and longevity, Journal of

811 Foraminiferal Research, 19, 185-193, 10.2113/gsjfr.19.3.185, 1989.

812

813 Fenchel, T.: The Ecology of Heterotrophic Microflagellates, in: Advances in Microbial Ecology, edited by: Marshall, K. C.,

814 Springer US, Boston, MA, 57-97, 10.1007/978-1-4757-0611-6_2, 1986.

815

816 Fenton, I. S., Aze, T., Farnsworth, A., Valdes, P., and Saupe, E. E.: Origination of the modern-style diversity gradient 15

817 million years ago, Nature, 614, 708-712, 10.1038/s41586-023-05712-6, 2023.

818

819   Fenton, I. S., Woodhouse, A., Aze, T., Lazarus, D., Renaudie, J., Dunhill, A. M., Young, J. R., and Saupe, E. E.: Triton, a
820   new species-level database of Cenozoic planktonic foraminiferal occurrences, Sci Data, 8, 160, 10.1038/s41597-021-00942-
821   7, 2021.

823   Follows, M. J., Dutkiewicz, S., Grant, S., and Chisholm, S. W.: Emergent biogeography of microbial communities in a
824   model ocean, Science, 315, 1843-1846, 10.1126/science.1138544, 2007.

826   Gaskell, D. E., Ohman, M. D., and Hull, P. M.: Zooglider-Based Measurements of Planktonic Foraminifera in the California
827   Current System, Journal of Foraminiferal Research, 49, 390-404, 10.2113/gsjfr.49.4.390, 2019.

829   Gast, R. J. and Caron, D. A.: Molecular phylogeny of symbiotic dinoflagellates from planktonic foraminifera and radiolaria,
830   Molecular Biology and Evolution, 13, 1192-1197, 10.1093/oxfordjournals.molbev.a025684, 1996.

832   Gaylord, B., Kroeker, K. J., Sunday, J. M., Anderson, K. M., Barry, J. P., Brown, N. E., Connell, S. D., Dupont, S.,
833   Fabricius, K. E., Hall-Spencer, J. M., Klinger, T., Milazzo, M., Munday, P. L., Russell, B. D., Sanford, E., Schreiber, S. J.,
834   Thiyagarajan, V., Vaughan, M. L. H., Widdicombe, S., and Harley, C. D. G.: Ocean acidification through the lens of
835   ecological theory, Ecology, 96, 3-15, https://doi.org/10.1890/14-0802.1, 2015.

837   Gibbs, S. J., Bown, P. R., Ward, B. A., Alvarez, S. A., Kim, H., Archontikis, O. A., Sauterey, B., Poulton, A. J., Wilson, J.,
838   and Ridgwell, A.: Algal plankton turn to hunting to survive and recover from end-Cretaceous impact darkness, Sci Adv, 6,
839   10.1126/sciadv.abc9123, 2020.

841   Goldstein, S.T.: Foraminifera: A biological review in Modern Foraminifera, Sen Gupta, B.K. Eds., Kluwer Academic
842   Publishers, Dordrecht, 37-55, 1999.

844   Greco, M., Morard, R., and Kucera, M.: Single-cell metabarcoding reveals biotic interactions of the Arctic calcifier ^with the
845   eukaryotic pelagic community, Journal of Plankton Research, 43, 113-125, 10.1093/plankt/fbab015, 2021.

847   Grice, G. D. and Hart, A. D.: The Abundance, Seasonal Occurrence and Distribution of the Epizooplankton between New
848   York and Bermuda, Ecological Monographs, 32, 287-309, 10.2307/1942377, 1962.

850   Grigoratou, M., Monteiro, F. M., Ridgwell, A., and Schmidt, D. N.: Investigating the benefits and costs of spines and diet on
851   planktonic foraminifera distribution with a trait-based ecosystem model, Marine Micropaleontology, 166, 102004,
852   https://doi.org/10.1016/j.marmicro.2021.102004, 2021.

853

854 Grigoratou, M., Monteiro, F. M., Wilson, J. D., Ridgwell, A., and Schmidt, D. N.: Exploring the impact of climate change on
855 the global distribution of non-spinose planktonic foraminifera using a trait-based ecosystem model, Glob Chang Biol, 28,
856 1063-1076, 10.1111/gcb.15964, 2022.

857

858 Grigoratou, M., Monteiro, F. M., Schmidt, D. N., Wilson, J. D., Ward, B. A., and Ridgwell, A.: A trait-based modelling
859 approach to planktonic foraminifera ecology, Biogeosciences, 16, 1469-1492, 10.5194/bg-16-1469-2019, 2019.

860

861 Haldane, J. B. S.: On Being the Right Size, 1926.

862

863 Hemleben, C., Spindler, M., Breitinger, I., and Deuser, W.: Field and laboratory studies on the ontogeny and ecology of
864 some globorotaliid species from the Sargasso Sea off Bermuda, Journal of Foraminiferal Research, 15, 254-272,
865 10.2113/gsjfr.15.4.254, 1985.

866

867 Hemleben, C., Spindler, M., Anderson, R.O.: Modern Planktonic Foraminifera, Springer-Verlag, Ney York, Berlin,
868 Heidelberg, 363 pp. 1989.

869

870 Henehan, M. J., Evans, D., Shankle, M., Burke, J. E., Foster, G. L., Anagnostou, E., Chalk, T. B., Stewart, J. A., Alt, C. H.
871 S., Durrant, J., and Hull, P. M.: Size-dependent response of foraminiferal calcification to seawater carbonate chemistry,
872 Biogeosciences, 14, 3287-3308, 10.5194/bg-14-3287-2017, 2017.

873

874 Hill, T. S. and Hoogenboom, M. O.: The indirect effects of ocean acidification on corals and coral communities, Coral
875 Reefs, 41, 1557-1583, 10.1007/s00338-022-02286-z, 2022.

876

877 Hoadley, K. D., Lewis, A. M., Wham, D. C., Pettay, D. T., Grasso, C., Smith, R., Kemp, D. W., LaJeunesse, T. C., and
878 Warner, M. E.: Host–symbiont combinations dictate the photo-physiological response of reef-building corals to thermal
879 stress, Scientific Reports, 9, 9985, 10.1038/s41598-019-46412-4, 2019.

880

881 Hoppit, G. and Schmidt, D. N.: A Regional View of the Response to Climate Change: A Meta-Analysis of European Benthic
882 Organisms' Responses, Frontiers in Marine Science, 9, 10.3389/fmars.2022.896157, 2022.

883

884 Horne, C. R., Hirst, A. G., and Atkinson, D.: Seasonal body size reductions with warming covary with major body size
885 gradients in arthropod species, Proceedings of the Royal Society B: Biological Sciences, 284, 20170238,
886 doi:10.1098/rspb.2017.0238, 2017.

887

888 Hoshino, T. and Inagaki, F., Distribution of eukaryotic environmental DNA in global subseafloor sediments, Progress in

889 Earth and Planetary Science ,11, https://doi.10.1186/s40645-024000621-2, 2024.

890

891 Hull, P. M., Osborn, K. J., Norris, R. D., and Robison, B. H.: Seasonality and depth distribution of a mesopelagic

892 foraminifer, *Hastigerinella digitata*, in Monterey Bay, California, Limnology and Oceanography, 56, 562-576,

893 https://doi.org/10.4319/lo.2011.56.2.0562, 2011.

894

895 Jonkers, L. and Kučera, M.: Global analysis of seasonality in the shell flux of extant planktonic Foraminifera,

896 Biogeosciences, 12, 2207-2226, 10.5194/bg-12-2207-2015, 2015.

897

898 Jonkers, L., Reynolds, C. E., Richey, J., and Hall, I. R.: Lunar periodicity in the shell flux of planktonic foraminifera in the

899 Gulf of Mexico, Biogeosciences, 12, 3061-3070, 10.5194/bg-12-3061-2015, 2015.

900

901 Kimoto, K.: The" unusual" reproduction of planktonic foraminifera: an Asexual reproductive phase of *Neogloboquadrina*

902 *pachyderma* (Ehrenberg), Anuario do Instituto de Geociencias, Universidade Federal do Rio de Janeiro, 29, 461, 2006.

903

904 Kiørboe, T.: How zooplankton feed: mechanisms, traits and trade-offs, Biological Reviews, 86, 311-339,

905 https://doi.org/10.1111/j.1469-185X.2010.00148.x, 2011.

906

907 Kiørboe, T., Visser, A., and Andersen, K. H.: A trait-based approach to ocean ecology, ICES Journal of Marine Science, 75,

908 1849-1863, 10.1093/icesjms/fsy090, 2018.

909

910 Knoll, A. H. and Follows, M. J.: A bottom-up perspective on ecosystem change in Mesozoic oceans, Proceedings of the

911 Royal Society B: Biological Sciences, 283, 20161755, doi:10.1098/rspb.2016.1755, 2016.

912

913 Kucera, M.: Chapter Six Planktonic Foraminifera as Tracers of Past Oceanic Environments, Developments in Marine

914 Geology, Volume 1, 213-262, 10.1016/S1572-5480(07)01011-1, 2007.

915

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

917 Marine Biology Research, 1, 68-78, 10.1080/17451000510019015, 2005.

918

919   LeKieffre, C., Spero, H. J., Russell, A. D., Fehrenbacher, J. S., Geslin, E., and Meibom, A.: Assimilation, translocation, and
920   utilization of carbon between photosynthetic symbiotic dinoflagellates and their planktic foraminifera host, Marine Biology,
921   165, 104, 10.1007/s00227-018-3362-7, 2018.

922

923   Leung, J. Y. S., Zhang, S., and Connell, S. D.: Is Ocean Acidification Really a Threat to Marine Calcifiers? A Systematic
924   Review and Meta-Analysis of 980+ Studies Spanning Two Decades, Small, 18, 2107407,
925   https://doi.org/10.1002/smll.202107407, 2022.

926

927   Litchman, E., Edwards, K. F., and Boyd, P. W.: Toward trait-based food webs: Universal traits and trait matching in
928   planktonic predator–prey and host–parasite relationships, Limnology and Oceanography, 66, 3857-3872,
929   https://doi.org/10.1002/lno.11924, 2021.

930

931   Litchman, E., Ohman, M. D., and Kiørboe, T.: Trait-based approaches to zooplankton communities, Journal of Plankton
932   Research, 35, 473-484, 10.1093/plankt/fbt019, 2013.

933

934   Lombard, F. Labeyrie, L., Michel, E., Spero, H.J., and Lea, D.W.: Modelling the temperature dependent growth rates of
935   planktic foraminifera, Marine Micropaleontology, 70, 1-7, 2009.

936

937   Lombard, F., da Rocha, R. E., Bijma, J., and Gattuso, J. P.: Effect of carbonate ion concentration and irradiance on
938   calcification in planktonic foraminifera, Biogeosciences, 7, 247-255, 10.5194/bg-7-247-2010, 2010.
939   Lombard, F., Labeyrie, L., Michel, E., Bopp., L., Cortijo, E., Retailleau, S., Howa, H., and Jorissen, F.: Modelling planktic
940   foraminifer growth and distribution using an ecophysiological multi-species approach, Biogeosciences, 8, 853-873,
941   doi:10.5194/bg-8-853-2011, 2011.Lončarić, N., Brummer, G.-J. A., and Kroon, D.: Lunar cycles and seasonal variations in
942   deposition fluxes of planktic foraminiferal shell carbonate to the deep South Atlantic (central Walvis Ridge), Deep Sea
943   Research Part I: Oceanographic Research Papers, 52, 1178-1188, https://doi.org/10.1016/j.dsr.2005.02.003, 2005.

944

945   Lynch, M.: The Genetic interpretation of inbreeding depression and outbreeding depression, Evolution, 45, 622-629,
946   10.1111/j.1558-5646.1991.tb04333.x, 1991.

947

948   Malviya, S., Scalco, E., Audic, S., Vincent, F., Veluchamy, A., Poulain, J., Wincker, P., Iudicone, D., de Vargas, C., Bittner,
949   L., Zingone, A. and Bowler, C., Insights into global diatom distribution and diversity in the world's ocean. Proceedings of
950   the National Academy of Sciences, 113(11): E1516-E1525, 2016.

951

Margulis, L.: Origins of species: acquired genomes and individuality, Biosystems, 31, 121-125, https://doi.org/10.1016/0303-2647(93)90039-F, 1993.

McKinney, M. L.: Trends in body-size evolution, in: Evolutionary Trends, edited by: McNamara, K. J., Belhaven Press, London, 75-118, 1990.

Meilland, J., Howa, H., Lo Monaco, C., and Schiebel, R.: Individual planktic foraminifer protein-biomass affected by trophic conditions in the Southwest Indian Ocean, 30°S–60°S, Marine Micropaleontology, 124, 63-74, https://doi.org/10.1016/j.marmicro.2016.02.004, 2016.

Meilland, J., Siccha, M., Morard, R., and Kucera, M.: Continuous reproduction of planktonic foraminifera in laboratory culture, Journal of Eukaryotic Microbiology, 71, e13022, https://doi.org/10.1111/jeu.13022, 2024.

Meilland, J., Ezat, M. M., Westgård, A., Manno, C., Morard, R., Siccha, M., and Kucera, M.: Rare but persistent asexual reproduction explains the success of planktonic foraminifera in polar oceans, Journal of Plankton Research, 45, 15-32, 10.1093/plankt/fbac069, 2023   .

Michaels, A. F., Caron, D. A., Swanberg, N. R., Howse, F., and Michaels, C. M.: Planktonic sarcodines (Acantharia, Radiolaria, Foraminifera) in surface waters near Bermuda: abundance, biomass and vertical flux, Journal of Plankton Research, 17, 131-163, 1995.

Monteiro, F. M., Bach, L. T., Brownlee, C., Bown, P., Rickaby, R. E. M., Poulton, A. J., Tyrrell, T., Beaufort, L., Dutkiewicz, S., Gibbs, S., Gutowska, M. A., Lee, R., Riebesell, U., Young, J., and Ridgwell, A.: Why marine phytoplankton calcify, Science Advances, 2, e1501822, doi:10.1126/sciadv.1501822, 2016.

Morard, R., Escarguel, G., Weiner, A. K., André, A., Douady, C. J., Wade, C. M., Darling, K. F., Ujiié, Y., Seears, H. A., Quillévéré, F., de Garidel-Thoron, T., de Vargas, C., and Kucera, M.: Nomenclature for the Nameless: A Proposal for an Integrative Molecular Taxonomy of Cryptic Diversity Exemplified by Planktonic Foraminifera, Syst Biol, 65, 925-940, 10.1093/sysbio/syw031, 2016.

Morard, R., Darling, K. F., Weiner, A. K. M., Hassenrück, C., Vanni, C., Cordier, T., Henry, N., Greco, M., Vollmar, N. M., Milivojevic, T., Rahman, S. N., Siccha, M., Meilland, J., Jonkers, L., Quillévéré, F., Escarguel, G., Douady, C. J., de Garidel-Thoron, T., de Vargas, C., and Kucera, M.: The global genetic diversity of planktonic foraminifera reveals the structure of cryptic speciation in plankton, Biological Reviews, 99, 1218-1241, https://doi.org/10.1111/brv.13065, 2024.

986

987 Naidoo-Bagwell, A. A., Monteiro, F. M., Hendry, K. R., Burgan, S., Wilson, J. D., Ward, B. A., Ridgwell, A., and Conley,

988 D. J.: A diatom extension to the cGEnIE Earth system model – EcoGEnIE 1.1, Geosci. Model Dev., 17, 1729-1748,

989 10.5194/gmd-17-1729-2024, 2024.

990

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

992 element signatures of Foraminifera tests, Biogeosciences, 10, 6759-6767, 10.5194/bg-10-6759-2013, 2013.

993

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

995 understanding of the open ocean carbonate pump - perspectives for remote sensing and autonomous in situ observation,

996 Earth-Science Reviews, 239, 104359, https://doi.org/10.1016/j.earscirev.2023.104359, 2023.

997

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

999 California Current, Paleoceanography, 10, 987-1009, https://doi.org/10.1029/95PA02088, 1995.

1000

1001 Otto, S. P. and Lenormand, T.: Resolving the paradox of sex and recombination, Nature Reviews Genetics, 3, 252-261,

1002 10.1038/nrg761, 2002.

1003

1004 Pallacks, S., Ziveri, P., Schiebel, R., Vonhof, H., Rae, J. W. B., Littley, E., Garcia-Orellana, J., Langer, G., Grelaud, M., and

1005 Martrat, B.: Anthropogenic acidification of surface waters drives decreased biogenic calcification in the Mediterranean Sea,

1006 Communications Earth & Environment, 4, 301, 10.1038/s43247-023-00947-7, 2023.

1007

1008 Palmer, A. R.: Calcification in marine molluscs: how costly is it?, Proc Natl Acad Sci U   S   A, 89, 1379-1382,

1009 10.1073/pnas.89.4.1379, 1992.

1010

1011 Pawlowski, J., Lejzerowicz, F. and Esling, P.: Next-Generation Environmental Diversity Surveys of Foraminifera: Preparing

1012 the Future, The Biological Bulletin, 227(2): 93-106, 2014.

1013

1014 Pearson, P. N., Ditchfield, P. W., Singano, J., Harcourt-Brown, K. G., Nicholas, C. J., Olsson, R. K., Shackleton, N. J., and

1015 Hall, M. A.: Warm tropical sea surface temperatures in the Late Cretaceous and Eocene epochs, Nature, 413, 481-487,

1016 10.1038/35097000, 2001.

1017

1018 Peters, R. H.: The Ecological Implications of Body Size, Cambridge Studies in Ecology, Cambridge University Press,

1019 Cambridge, DOI: 10.1017/CBO9780511608551, 1983.

Rebotim, A., Voelker, A. H. L., Jonkers, L., Waniek, J. J., Schulz, M., and Kucera, M.: Calcification depth of deep-dwelling planktonic foraminifera from the eastern North Atlantic constrained by stable oxygen isotope ratios of shells from stratified plankton tows, J. Micropalaeontol., 38, 113-131, 10.5194/jm-38-113-2019, 2019.

Ridgwell, A. and Zeebe, R. E.: The role of the global carbonate cycle in the regulation and evolution of the Earth system, Earth and Planetary Science Letters, 234, 299-315, https://doi.org/10.1016/j.epsl.2005.03.006, 2005.

Riebesell, U., Fabry, V.J., Hansson, L. and Gattuso, J.-P. (Editors): Guide to best practices for ocean acidification research and data reporting. Publications Office of the European Union, Luxembourg, 260, 2010.

Rillo, M. C., Miller, C. G., Kucera, M., and Ezard, T. H. G.: Intraspecific size variation in planktonic foraminifera cannot be consistently predicted by the environment, Ecology and Evolution, 10, 11579-11590, https://doi.org/10.1002/ece3.6792, 2020.

Rink, S., Kühl, M., Bijma, J., and Spero, H. J.: Microsensor studies of photosynthesis and respiration in the symbiotic foraminifer Orbulina universa, Marine Biology, 131, 583-595, 10.1007/s002270050350, 1998.

Ruppert, K.M., Kline, R.J. and Rahman, M.S., Past, present, and future perspectives of environmental DNA (eDNA) metabarcoding: A systematic review in methods, monitoring, and applications of global eDNA. Global Ecology and Conservation, 17: e00547, 2019.

Russell, A. D., Hönisch, B., Spero, H. J., and Lea, D. W.: Effects of seawater carbonate ion concentration and temperature on shell U, Mg, and Sr in cultured planktonic foraminifera, Geochimica et Cosmochimica Acta, 68, 4347-4361, https://doi.org/10.1016/j.gca.2004.03.013, 2004.

Sanders, T., Schmittmann, L., Nascimento-Schulze, J. C., and Melzner, F.: High Calcification Costs Limit Mussel Growth at Low Salinity, Frontiers in Marine Science, 5, 10.3389/fmars.2018.00352, 2018.

Schiebel, R. and Hemleben, C.: Planktic Foraminifers in the Modern Ocean, Springer, Heidelberg 2017.

Schiebel, R., Hiller, B., and Hemleben, C.: Impacts of storms on Recent planktic foraminiferal test production and CaCO3 flux in the North Atlantic at 47 °N, 20 °W (JGOFS), Marine Micropaleontology, 26, 115-129, https://doi.org/10.1016/0377-8398(95)00035-6, 1995.

1054

Schmidt, D. N., Renaud, S., and Bollmann, J.: Response of planktic foraminiferal size to late Quaternary climate change, Paleoceanography, 18, https://doi.org/10.1029/2002PA000831, 2003.

Schmidt, D. N., Lazarus, D., Young, J. R., and Kucera, M.: Biogeography and evolution of body size in marine plankton, Earth-Science Reviews, 78, 239-266, https://doi.org/10.1016/j.earscirev.2006.05.004, 2006.

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

Schweizer, M., Jauffrais, T., Choquel, C., Méléder, V., Quinchard, S. and Geslin, E., Trophic strategies of intertidal foraminifera explored with single-cell microbiome metabarcoding and morphological methods: What is on the menu? Ecology and Evolution, 12(11): e9437, 2022.

Seibold, E. a. B., W.H.: The Sea Floor, Springer Verlag, Berlin, Heidelberg, New York, 356 pp.1993.

Siccha, M. and Kucera, M.: ForCenS, a curated database of planktonic foraminifera census counts in marine surface sediment samples, Scientific Data, 4, 170109, 10.1038/sdata.2017.109, 2017.

Ser-Giacomi, E., Zinger, L., Malviya, S., De Vargas, C., Karsenti, E., Bowler, C. and De Monte, S., Ubiquitous abundance distribution of non-dominant plankton across the global ocean. Nature Ecology & Evolution, 2(8): 1243-1249, 2018.

Spero, H. J. and Parker, S. L.: Photosynthesis in the symbiotic planktonic foraminifer *Orbulina universa*, and its potential contribution to oceanic primary productivity, Journal of Foraminiferal Research, 15, 273-281, 10.2113/gsjfr.15.4.273, 1985.

Spindler, M.: On the salinity tolerance of the planktonic foraminifer *Neogloboquadrina pachyderma* from Antarctic sea ice, Polar Biology, 9, 85-91, 1996.

Spindler, M. and Dieckmann, G. S.: Distribution and abundance of the planktic foraminifer *Neogloboquadrina pachyderma* in sea ice of the Weddell Sea (Antarctica), Polar Biology, 5, 185-191, 10.1007/BF00441699, 1986.

Spindler, M., Hemleben, C., Salomons, J. B., and Smit, L. P.: Feeding behavior of some planktonic foraminifers in laboratory cultures, Journal of Foraminiferal Research, 14, 237-249, 10.2113/gsjfr.14.4.237, 1984.

1088   Spindler, M., Hemleben, C., Bayer, U., Bé, A. W. H., Anderson, O.R.: Lunar Periodicity of Reproduction in the Planktonic

1089   Foraminifer *Hastigerina pelagica*, Marine Ecology Progress Series, 1, 61-64, 1979.

1090

1091   Stoecker, D. K., Johnson, M. D., deVargas, C., and Not, F.: Acquired phototrophy in aquatic protists, Aquatic Microbial

1092   Ecology, 57, 279-310, 2009.

1093

1094   Strack, T., Jonkers, L., C. Rillo, M., Baumann, K.-H., Hillebrand, H., and Kucera, M.: Coherent response of zoo- and

1095   phytoplankton assemblages to global warming since the Last Glacial Maximum, Global Ecology and Biogeography, 33,

1096   e13841, https://doi.org/10.1111/geb.13841, 2024.

1097

1098   Swezey, D. S., Boles, S. E., Aquilino, K. M., Stott, H. K., Bush, D., Whitehead, A., Rogers-Bennett, L., Hill, T. M., and

1099   Sanford, E.: Evolved differences in energy metabolism and growth dictate the impacts of ocean acidification on abalone

1100   aquaculture, Proc Natl Acad Sci U S A, 117, 26513-26519, 10.1073/pnas.2006910117, 2020.

1101

1102   Sykes, F. E., Meilland, J., Westgård, A., Chalk, T. B., Chierici, M., Foster, G. L., and Ezat, M. M.: Large-scale culturing of

1103   the subpolar foraminifera *Globigerina bulloides* reveals tolerance to a large range of environmental parameters associated to

1104   different life-strategies and an extended lifespan, Journal of Plankton Research, 46, 403-420, 10.1093/plankt/fbae029, 2024.

1105

1106   Takagi, H., Kurasawa, A., and Kimoto, K.: Observation of asexual reproduction with symbiont transmission in planktonic

1107   foraminifera, Journal of Plankton Research, 42, 403-410, 10.1093/plankt/fbaa033, 2020.

1108

1109   Takagi, H., Kimoto, K., Fujiki, T., and Moriya, K.: Effect of nutritional condition on photosymbiotic consortium of cultured

1110   *Globigerinoides sacculifer* (Rhizaria, Foraminifera), Symbiosis, 76, 25-39, 10.1007/s13199-017-0530-3, 2018.

1111

1112   Takagi, H., Kimoto, K., Fujiki, T., Kurasawa, A., Moriya, K., and Hirano, H.: Ontogenetic dynamics of photosymbiosis in

1113   cultured planktic foraminifers revealed by fast repetition rate fluorometry, Marine Micropaleontology, 122, 44-52,

1114   https://doi.org/10.1016/j.marmicro.2015.10.003, 2016.

1115

1116   Takagi, H., Kimoto, K., Fujiki, T., Saito, H., Schmidt, C., Kucera, M., and Moriya, K.: Characterizing photosymbiosis in

1117   modern planktonic foraminifera, Biogeosciences, 16, 3377-3396, 10.5194/bg-16-3377-2019, 2019.

1118

1119   Takahashi, K. and Bé, A. W. H.: Planktonic foraminifera: factors controlling sinking speeds, Deep Sea Research Part A.

1120   Oceanographic Research Papers, 31, 1477-1500, https://doi.org/10.1016/0198-0149(84)90083-9, 1984.

1121

Tang, Y. Z., Gu, H., Wang, Z., Liu, D., Wang, Y., Lu, D., Hu, Z., Deng, Y., Shang, L., and Qi, Y.: Exploration of resting cysts (stages) and their relevance for possibly HABs-causing species in China, Harmful Algae, 107, 102050, https://doi.org/10.1016/j.hal.2021.102050, 2021.

Thomsen, J., Casties, I., Pansch, C., Körtzinger, A. and Melzner, F.: Food availability outweighs ocean acidification effects in juvenile Mytilus edulis: laboratory and field experiments. Global Change Biology, 19(4): 1017-1027, 2013.

Topa, P., Faber, Ł., Tyszka, J., and Komosinski, M.: Modelling ecology and evolution of Foraminifera in the agent-oriented distributed platform, Journal of Computational Science, 18, 69-84, https://doi.org/10.1016/j.jocs.2016.07.009, 2017.

Vincent, E. a. B., W.H.: Planktonic foraminifera and their use in paleoceanography, in: The Sea, edited by: Emiliani, C., John Wiley & Sons, New York, 1035-1119, 1981.

Violle, C., Navas, M.-L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., and Garnier, E.: Let the concept of trait be functional!, Oikos, 116, 882-892, https://doi.org/10.1111/j.0030-1299.2007.15559.x, 2007.

Wade, B. S., Al-Sabouni, N., Hemleben, C., and Kroon, D.: Symbiont bleaching in fossil planktonic foraminifera, Evolutionary Ecology, 22, 253-265, 10.1007/s10682-007-9176-6, 2008.

Ward, B. B.: Oceans. How nitrogen is lost, Science, 341, 352-353, 10.1126/science.1240314, 2013.

Watson, S.-A., Morley, S. A., and Peck, L. S.: Latitudinal trends in shell production cost from the tropics to the poles, Science Advances, 3, e1701362, doi:10.1126/sciadv.1701362, 2017.

Weinkauf, M. F. G., Siccha, M., and Weiner, A. K. M.: Reproduction dynamics of planktonic microbial eukaryotes in the open ocean, Journal of The Royal Society Interface, 19, 20210860, doi:10.1098/rsif.2021.0860, 2022.

Weinkauf, M. F. G., Kunze, J.G., Waniek, J.J. and Kučera, M.: Seasonal Variation in Shell Calcification of Planktonic Foraminifera in the NE Atlantic Reveals Species-Specific Response to Temperature, Productivity, and Optimum Growth Conditions, PLOS ONE, 11, e0148363, 2016.

1153 Westgård, A., Ezat, M.E., Chalk, T.B., Chierici, M., Foster, G.L. and Meilland, J. Large-scale culturing of
1154 *Neogloboquadrina pachyderma*, its growth in, and tolerance of, variable environmental conditions, Journal of Plankton
1155 Research, 45, 732-745, 2023.

1156

1157 Westoby, M.: Trait-based ecology, trait-free ecology, and in between, New Phytol, 10.1111/nph.20197, 2024.

1158

1159 Wilkinson, M. D., Dumontier, M., Aalbersberg, I. J., Appleton, G., Axton, M., Baak, A., Blomberg, N., Boiten, J.-W., da
1160 Silva Santos, L. B., Bourne, P. E., Bouwman, J., Brookes, A. J., Clark, T., Crosas, M., Dillo, I., Dumon, O., Edmunds, S.,
1161 Evelo, C. T., Finkers, R., ..., and Mons, B.: The FAIR Guiding Principles for scientific data management and stewardship,
1162 Scientific Data, 3, 160018, 10.1038/sdata.2016.18, 2016.

1163

1164 Wirtz, K. W.: Who is eating whom? Morphology and feeding type determine the size relation between planktonic predators
1165 and their ideal prey, Marine Ecology Progress Series, 445, 1-12, 2012.

1166

1167 Woodhouse, A., Swain, A., Fagan, W. F., Fraass, A. J., and Lowery, C. M.: Late Cenozoic cooling restructured global
1168 marine plankton communities, Nature, 614, 713-718, 10.1038/s41586-023-05694-5, 2023.

1169

1170 Ying, R., Monteiro, F. M., Wilson, J. D., and Schmidt, D. N.: ForamEcoGEnIE 2.0: incorporating symbiosis and spine traits
1171 into a trait-based global planktic foraminiferal model, Geosci. Model Dev., 16, 813-832, 10.5194/gmd-16-813-2023, 2023.

1172

1173 Ying, R., Monteiro, F.M., Wilson, J.D., Ödalen, M. and Schmidt, D.N.: Past foraminiferal acclimation capacity is limited
1174 during future climate warming, Nature, 2024.

1175

1176 Yonathan, S. and Colomban de, V.: Pelagic photosymbiosis: rDNA assessment of diversity and evolution of dinoflagellate
1177 symbionts and planktonic foraminiferal hosts, Marine Ecology Progress Series, 325, 59-71, 2006.

1178