Reviews and Syntheses: 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 marine inorganic carbon production. They leave abundant calcium carbonate shells on the sea floor, which serve as prime proxies for the physical and chemical attributes of past oceans. Despite a well-preserved fossil record and wide use in palaeoceanography, our understanding of their ecology is limited due to their low-standing stocks in the modern surface ocean and the challenges in culturing multiple generations under laboratory conditions, even after decades of data collection. This limitation affects our ability to use their fossil remains to describe past ecosystems and predict their responses to modern environmental changes. Trait-based ecology can be particularly useful at characterising how and why foraminifera might interact with their environment. Here, we review the state of knowledge of planktic foraminifera key 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. We propose that trait modelling, metabarcoding, eDNA, and enhanced standardised data collection, released in open data, can help fill critical gaps in our understanding of planktic foraminiferal trait-based ecology and allow us to use foraminifera as a key model organism for 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). Of 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, 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 provide one of the best plankton fossil records of any group (Aze et al., 2011; Fenton et al., 2021), making them a critical group for studying the influence of climate change in the past and improving our understanding for the future (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 climate, including temperature and ocean chemistry (Kucera, 2007).
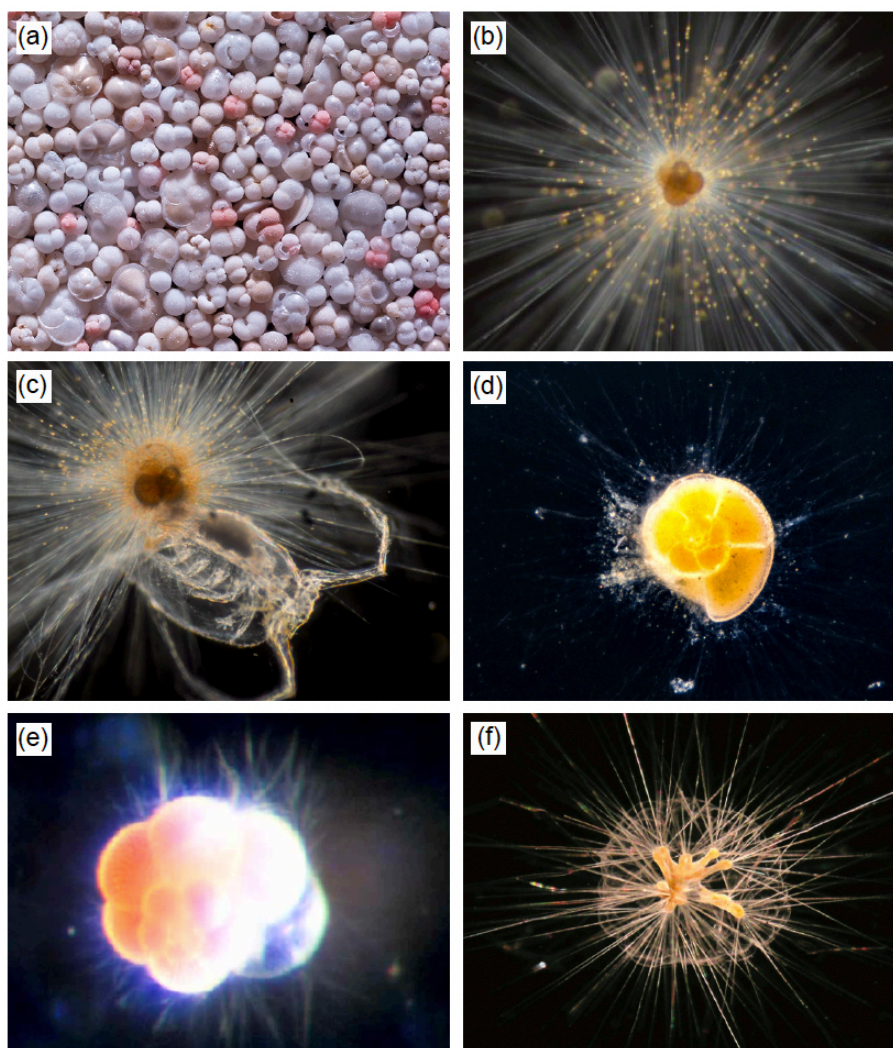
Figure 1. Selection of living and recent planktic foraminifera. (a) Assorted shells of planktic foraminifera from sea floor sediment (Image credit: Wilfried Rönnfeld). (b) *Orbulina universa* with symbionts attached along thin radial spines (Fig. 2 of Topa et al., 2017). (c) *Orbulina universa* eating a small copepod (Image credit: Oscar Branson). (d) *Globorotalia truncatulinoides* in culture with pseudopodial network

extending from shell (https://www.usgs.gov/media/images/live-foraminifera-globorotalia-truncatulinoides). (e) *Neogloboquadrina dutertrei*

45   suspended with pseudopodia 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 little attention from modern
ecologists due to their small contribution to the total plankton biomass (Michaels et al., 1995; Buitenhuis et al., 2013) and

50   challenges 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 to generating accurate predictions of how changing
environmental conditions will impact planktic foraminifera communities and ultimately biogeochemical cycles (Dutkiewicz
et al., 2020).

55   Trait-based approaches (Dutkiewicz et al., 2020) allow to describe species and their interactions without the need to
realistically designate each specimen in a plankton community where millions of specimens of thousands of species interact
(De Vargas et al., 2015). Trait-theory provides a theoretical framework, as it mechanistically links organismal traits (e.g. size,
resource acquisition mode and defence) with their trade-offs (costs and benefits) (e.g., Litchman et al., 2013; Barton et al.,
2013; Violle et al., 2007; Westoby, 2024). Trade-offs arise where the optimisation of one trait is often to the detriment of

60   another (Kiørboe et al., 2018). Therefore, trait-based approaches offer a mechanistic but computationally efficient means of
explaining large-scale patterns of diversity and abundance of microbial, planktonic and nekton organisms (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).

65   Trait-based approaches are a promising tool for making predictions beyond the sampling domain and to test different (and
often complex) hypotheses over longer timescales - past and future (e.g., Barton et al., 2016; Grigoratou et al., 2022; Ying,
2024). This approach is particularly promising in macroevolutionary studies over millions of years where new traits evolve to
facilitate adaptation the novel climate and environments as it permits 'species' or functional groups (i.e., species with similar
traits) with novel combinations of traits to emerge as an environment evolves that may not be present in the modern ocean.

70   For instance, Knoll and Follows (2016) model shows that the rise of the mixotrophy trait in the Mesozoic increases the energy
transfer efficiency upward to higher trophic levels in the food web. Using similar trait processes, Gibbs et al. (2020) explored
ecological selectivity in the aftermath of the Cretaceous-Paleogene mass extinction in marine plankton. Therefore, trait-based
approaches offer exciting opportunities to use the excellent fossil record of foraminifera to test model predictions outside of
the modern range of environmental conditions, the universal applicability of traits/trade-offs through time and ultimately for

75   understanding evolutionary processes.

Trait-based modelling has the potential to vastly improve our understanding of the driver(s) of planktic foraminifera ecology and fitness. For example, the first trait-based modelling study by Grigoratou et al. (2019) provided novel insights regarding the cost and benefits of calcification, and the influence of resource competition among planktic foraminifera and other

80   zooplankton. This approach was expanded by Ying et al. (2023) to characterise the main ecogroups of foraminifera (Figs 1 and 2). In this study, we aim to [1] present a review of our current knowledge of planktic foraminifera traits and trade-offs, and [2] identify key gaps in our understanding, to facilitate future studies.
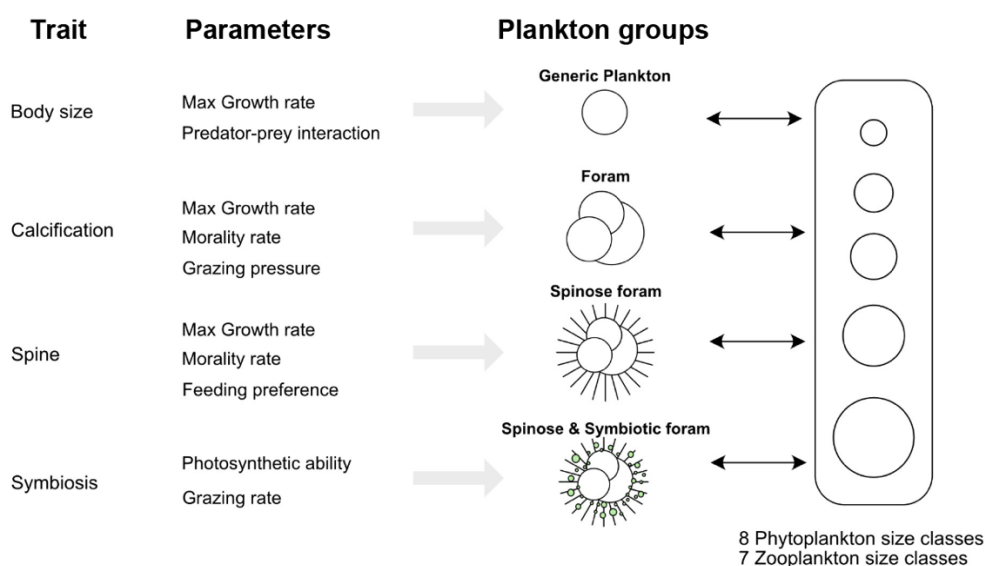
85   **Figure 2: Schematic representation of a trait-based ecosystem model incorporating foraminifers.** Key functional traits: size, calcification, spinosity and symbiosis are assumed to influence foraminiferal biotic interactions with other components in the food web through modifying maximum growth rate, mortality rate, feeding strategy, and other predator-prey interactions.

2. Planktic foraminifera traits and trade-offs

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Planktic foraminifera have been predominantly studied by geologists for their paleoecology and evolution, and as proxy carriers for paleoenvironmental studies, while most biological studies until relatively recently were 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

95   Hemleben, 2017) many but not all of which consist of cryptic species (Morard et al., 2024; Morard et al., 2016).

Planktic foraminifera spend their lives in the surface 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),which results in

their absence in shallow marine seas and on coastal shelves (Schiebel and Hemleben, 2017). Some taxa have unique ecologies,

100 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 listed here 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 ecology information from Schiebel and Hemleben (2017), Takagi et al. (2019) and Aze et al. (2011).

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SPECIES	SPINOSITY	SYMBIONT TYPE	SYMBIONT RELATIONSHIP	DEPTH HABITAT
Beella digitata	spinose	none	none	sub-thermocline
Berggrenia pumilio	non-spinose	none	none	sub-thermocline
Candeina nitida	non-spinose	chrysophyte	facultative	thermocline
Dentigloborotalia anfracta	non-spinose	none	none	surface
Globigerina bulloides	spinose	none	none	surface
Globigerina falconensis	spinose	chrysophyte	facultative	surface
Globigerinella adamsi	spinose	none	none	sub-thermocline
Globigerinella calida	spinose	chrysophyte	facultative	thermocline
Globigerinella siphonifera	spinose	chrysophyte	obligate	thermocline
Globigerinita glutinata	non-spinose	chrysophyte	facultative	surface
Globigerinita minuta	non-spinose	none	none	surface
Globigerinita uvula	non-spinose	dinoflagellate	obligate	surface
Globigerinoides conglobatus	spinose	dinoflagellate	obligate	surface
Globigerinoides ruber	spinose	dinoflagellate	obligate	surface
Globigerinoides tenellus	spinose	dinoflagellate	obligate	surface
Globigerinoides white	spinose	dinoflagellate	obligate	surface
Globoconella inflata	non-spinose	chrysophyte	facultative	thermocline
Globoquadrina conglomerata	non-spinose	none	none	surface
Globorotalia cavernula	non-spinose	none	none	sub-thermocline
Globorotalia crassaformis	non-spinose	none	none	thermocline
Globorotalia hirsuta	non-spinose	none	none	sub-thermocline
Globorotalia menardii	non-spinose	chrysophyte/prymensiophyte	facultative	thermocline
Globorotalia scitula	non-spinose	none	none	sub-thermocline
Globorotalia theyeri	non-spinose	none	none	surface
Globorotalia truncatulinoides	non-spinose	none	none	sub-thermocline
Globorotalia tumida	non-spinose	none	none	thermocline
Globorotalia ungulata	non-spinose	none	none	thermocline
Globorotaloides hexagonus	spinose	none	none	sub-thermocline
Globoturborotalita rubescens	spinose	dinoflagellate	obligate	surface
Hastigerina pelagica	spinose	none	none	sub-thermocline
Hastigerinella digitata	spinose	none	none	sub-thermocline
Neogloboquadrina dutertrei	non-spinose	chrysophyte, pelagophyte	facultative	thermocline
Neogloboquadrina incompta	non-spinose	none	none	thermocline
Neogloboquadrina pachyderma	non-spinose	none	none	thermocline
Orbulina universa	spinose	dinoflagellate	obligate	thermocline
Pulleniatina obliquiloculata	non-spinose	chrysophyte	facultative	surface
Sphaeroidinella dehiscens	non-spinose	dinoflagellate	obligate	thermocline
Tenuitella iota	non-spinose	none	none	surface
Trilobatus sacculifer	spinose	dinoflagellate	obligate	surface
Turborotalita humilis	spinose	chrysophyte, haptophyte, dinoflagellate	obligate	surface
Turborotalita quinqueloba	spinose	none	none	surface

Here we characterise planktic foraminiferal traits according to their type and function, following the approach of Litchman et al. (2013) (Table 2). We discuss each identified key traits, along with their individual impacts on foraminiferal fitness, as well

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110   as their main associated trade-offs. We recognise two levels of traits: (1) those that are common to all planktic foraminifera, referred to as 'foraminiferal' traits and (2) those that are specific to individual species or groups of species as 'Group/Species-specific' traits.

Table 2. Summary of planktic foraminifera traits and associated trade-offs described in Sections 2.1-2.3. Traits with '*' are
115   group/species specific traits, all other traits are common to all planktic foraminifera.

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)*	- Energetic investment (<60% of total energy budget) - Reduction in growth	- Tool for controlling active prey - Rhizopodial support - Increased surface area to volume - 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	- Only reproduce once during their life cycle - Number of gametes produced depends on shell size	- Energy gain as not actively searching for mate - Reduced predator exposure

2.1 Physiological/Morphological traits

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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
125   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
130   (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
135   conditions (Chernihovsky et al., 2023; Schmidt et al., 2004), though some show no relationships between size and environments (Rillo et al., 2020). Temperature and 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 or upwelling regions (Schmidt et al., 2004). This size distribution contrasts with most
140   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 or enhanced niche diversity through stratification (Schmidt et al., 2004). Shell size not only responds to environmental conditions but also directly reflects individual fitness and reproduction (Hemleben, 1989). Larger foraminifera
145   have a greater amount of cytoplasm available to generate gametes and hence reproductive success (Bé and Anderson, 1976; Weinkauf et al., 2022). In the open ocean, a (semi)lunar periodicity in shell fluxes 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
150   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)

155   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).

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The skeleton can comprise a significant proportion of an organism's total mass making the construction and maintenance of a mineralised skeleton energetically expensive (Sanders et al., 2018). However, it is difficult to quantify the energetic costs of biomineralisation and foraminifera (as with many organisms) can modulate their energy use between different activities depending on the environment. Lack of a mechanistic understanding of how biomineralization occurs for many groups further

165 exacerbates the challenge (Gaylord et al., 2015). No laboratory assessments of the energy budget allotted to calcification in planktic foraminifera currently exists. However, theoretical trait-based models indicate a likely investment of ~10-60 % of foraminifera's total energy budget is apportioned to calcification (Grigoratou et al., 2021; Grigoratou et al., 2022; Grigoratou et al., 2019).

170 A calcite shell increases the negative buoyancy of foraminifera, i.e., it increases their tendency to sink through the water column (Armstrong, 2004; Caromel et al., 2014) though 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 cm from the shell surface (2-3x the shell size; Fig. 1b, c and f), which increases their drag and thus, sinking rate (Takahashi and Be, 1984). Other benefits of spines include increased capture area for prey acquisition, including reduced palatability to predators, a rigid

175 skeleton to anchor pseudopodia to enable acquisition of higher quality (active) prey and a means of organising photosymbionts more effectively around the shell. Logically, development of these compensatory features should increase the relative cost of calcification. However, trait-based modelling suggest 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

180 carnivorous which provides more energy, and many also host algal photosymbionts providing an additional carbon subsidy, while non-spinose species are mainly herbivorous (see Section 2.2).
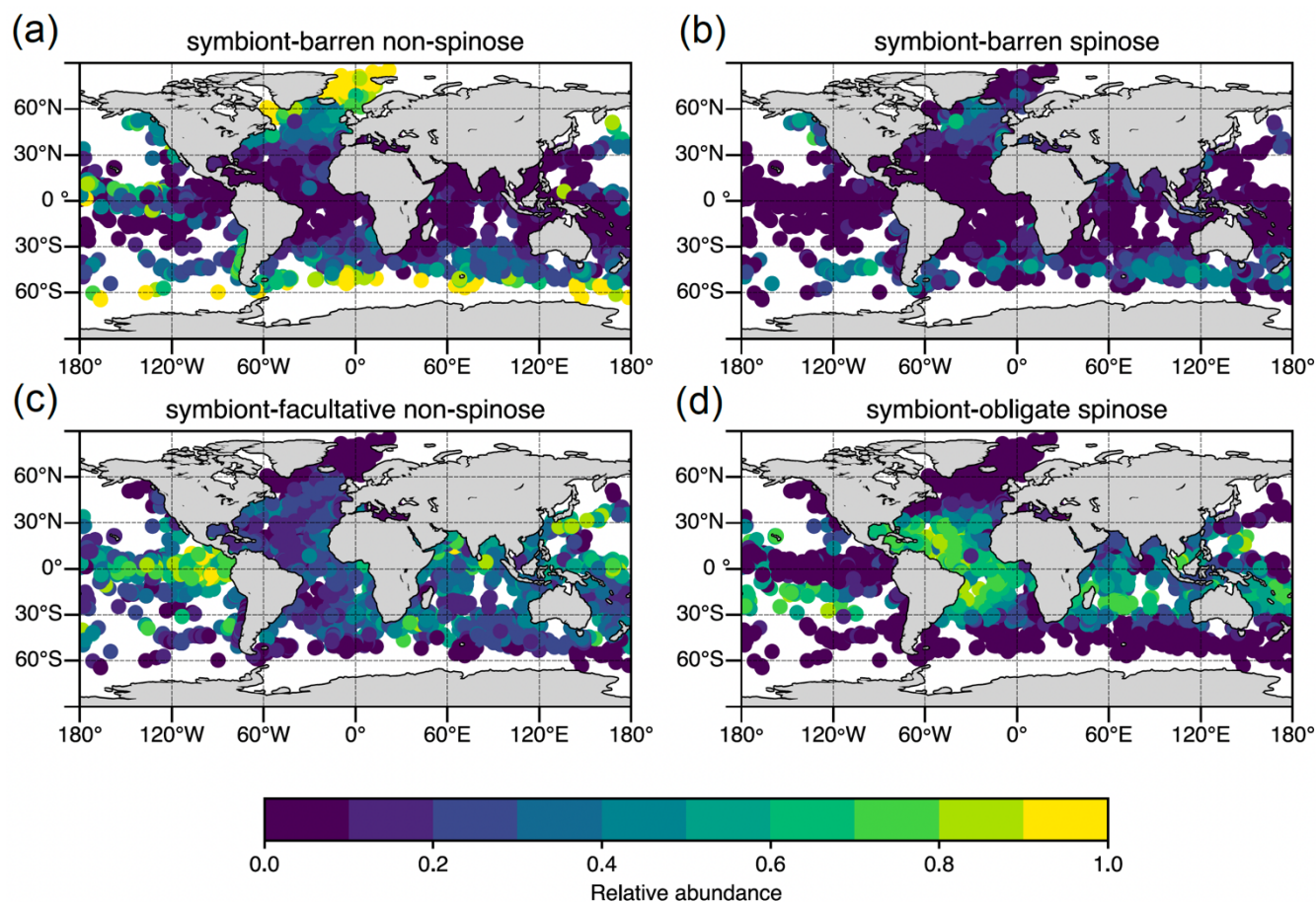
Figure 3. Modern distribution and relative abundance of planktic foraminifera by ecological group in surface sediment samples. Underlying data from ForCenS database (Siccha and Kucera, 2017) and traits coded as presented in Table 1 (this study).

The range of estimated energetic calcification cost for foraminifera is broadly consistent with those of other calcifying groups (although estimates vary dramatically) including: coccolithophores at ~30 % (Monteiro et al., 2016), marine benthic gastropods at <60% (Palmer, 1992; Sanders et al., 2018), and <10% across gastropods and bivalves globally (Watson et al., 2017). In the calcareous algae coccolithophores, the high energetic cost of calcification varies between species and environments, and protection from predation may be the primary benefit (Monteiro et al., 2016). However, the role of predation on foraminifera is unknown. Whilst adult foraminiferal shells have been found in pteropods, salps, shrimps and many other 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 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,
200   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., 2024 for a recent review), there are still large
gaps in our understanding of the metabolic and energetic needs for calcification. It is clear that specific traits within ecogroups,
for example symbiosis, impact the calcification response due to alterations of the environment at a group level (e.g., Köhler-
205   Rink and Kühl, 2005). Many studies though identify a species-specific 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
drivers is complicated by differential environmental preferences of cryptic species (De Vargas et al., 2001), regional plasticity,
and lack of understanding of controls of thickness of gametogenic calcite, or 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
210   for foraminifera weight (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 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 to the pelagic carbonate production under future climate change
215   (Barrett et al., 2024).

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), which typically show evidence of
reduced growth, calcification, muscle wastage or weakened shells (e.g., Alma et al., 2020; Hill and Hoogenboom, 2022;
220   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). In the short-term, this results in a reduced chance of individuals reaching sufficient
size to obtain reproductive maturity (Bé et al., 1981), potentially a smaller number of gametes based on the relationship
225   between gamete number and body size reducing reproductive success, and ultimately impacts individuals fitness by increasing
their vulnerability to further environmental change or predation etc. that may prove fatal.

2.2 Behavioural traits

2.2.1 Feeding (group-specific traits)

The biggest challenge facing 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

235 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

240 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 lowered metabolic and mortality rates than their more active counterparts (Eiane and Ohman, 2004).

245 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

250 (prolocular-juvenile, ~15-100 µm shell diameter (Spindler et al., 1984; Caron et al., 1987) foraminifera are omnivorous, 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 develop spines. Spines provide a rigid framework for rhizopodia to attach and increase foraminifera's capture area (Gaskell et al., 2019) allow them to capture and hold active prey and switch from a predominantly herbivorous to carnivorous diet (Fig. 1c; Anderson et al., 1979; Schiebel and Hemleben,

255 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).

260 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. Notably, compared to most zooplankton, 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).

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Non-spinose planktic foraminifera are primarily herbivorous throughout their life cycle (Schiebel and Hemleben, 2017) preying on diatoms, dinoflagellates, and eukaryote 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 these taxa are unable to capture and hold live zooplankton, and 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 rhizpodia 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 show cannibalism but is unknown if they cannibalise in a natural habitat and is not considered likely due to very low foraminifera standing stocks.

The temporal and spatial distribution of prey items is a major cause of the regional distribution of foraminifera species influencing growth and fecundity after temperature (Schiebel and Hemleben, 2017). 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).

To simulate trophic dynamics with mathematical models (especially dynamic mechanistic models), observational data on prey preferences such as prey acceptance rates, protein acquisition from zooplankton versus phytoplankton, and average digestion and capture times are needed. Observational data can be collected by analysing feeding vacuoles and metabarcoding analyses of in-situ samples. For planktic foraminifera, this information is scare, 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. Such 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 of around the cost and benefits of being a passive ambush feeder, competition with other foraminifera or their close relative the siliceous radiolarians, all of which impact our ability to consider interactions between zooplankton in trait models. To advance trait models, data is needed on prey preferences, prey-predator optimum

300   length ratio, and encounter rates (successful and unsuccessful) to cover the energetic needs for calcification and other metabolic costs.

2.2.2 Starvation tolerance (group-specific traits)

305   Feeding experiments indicate that when food is available at the optimum frequency, foraminifera reproduce quickly but the reverse is also true. There is no evidence at present for a specialist adaptation in planktic foraminifera that enables certain groups to tolerate food deprivation for longer, e.g., lipid acquisition or diapause as evident in benthic foraminifera (Alve and Goldstein, 2002; Alve and Goldstein, 2010) or dinoflagellates (Tang et al., 2021). These resting stages are also associated with bloom formation when conditions become favourable again. In culture, planktic foraminifera can survive and grow for 16-46

310   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, 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 number of gametes, fewer gametes (Bé et al., 1981). The taxa that have survived longest in culture (>230 days) are asymbiotic herbivorous taxa with growth optimised for low temperatures (Lombard et al., 2010) with presumably lower metabolic rates (Spindler, 1996).

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An extreme example of a species with periods of low metabolism is the overwintering in sea ice of non-spinose non-symbiotic *Neogloboquadrina pachyderma* (specifically Antarctic genotype IV of Darling and Wade (2008), which dominates polar planktic foraminifera assemblages. This species can survive the lack of algal biomass on which to feed during the austral winter by surviving and growing (but not reproducing) within Antarctic sea ice (Spindler and Dieckmann, 1986; Dieckmann

320   et al., 1991; Berberich, 1996) in brine channels and pockets within the ice with salinities up to 177 psu and temperatures as low as -15°C. At >50 psu though individuals 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 ~82 psu (Spindler, 1996). The same habitats also contain dense populations of phytoplankton, predominantly diatoms, a rich food source (Spindler and Dieckmann, 1986; Dieckmann et al., 1991). Overwintering via dormancy is thus advantageous because of the rich food source, protection from

325   predators, and/or a means of conserving energy by reducing the need for buoyancy compensation (Dieckmann et al., 1991).

2.2.3 Photosymbioses (group-specific traits)

Symbiosis between different biological organisms is a common ecological strategy in the ocean from shallow benthic marine

330   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 benthic shallow-water counterparts, however, symbiosis in planktic foraminifers appears to represent an adaptation to nutrient-poor, sunlit waters (Fig. 3d; Bé, 1971).

335 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
chrysophycophytes or dinoflagellates (Fig. 1b and c) which are acquired by juvenile foraminifera from the water column
(Hemleben, 1989). Whilst many spinose taxa are host to dinoflagellate photosymbionts there are exceptions (e.g., *Hastigerina*
340 *pelagica* and *G. bulloides*). 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 evolution of dinoflagellate symbiosis in the Cretaceous before spines or spine like structures evolved in the
345 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 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
350 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
355 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 chlorophyll a content of specimens, health of symbionts and their light-level adaptation (Takagi et al., 2019;
Takagi et al., 2016).

360 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).

365 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. Photosymbionts provide an

additional energy source (Lekieffre et al., 2018), aiding foraminifera growth and calcification (Bé et al., 1982). At the same time, symbionts preferentially use metabolites from the foraminifera for photosynthesis (Takagi et al., 2018). Algal

370   photosymbionts also aid calcification by modifying the pH of the foraminifera's immediate microenvironment above ambient seawater by utilising CO_2 during photosynthesis (Rink et al., 1998).

Photosymbionts are acquired as juveniles, or as new evidence suggest 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.,

375   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 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). Even under starvation, some symbionts are retained in culture until gametogenesis (Takagi et al., 2018).

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It is unclear what triggers the need to change from asymbiotic to symbiotic in these facultatively symbiont bearing taxa, making it impossible to model these as the costs and benefits cannot be determined sufficiently. Takagi et al. (2019) showed that photosynthetic activity in symbiont-facultative species tends to be weaker than in symbiont-obligate species. However, the benefit of this facultative trait is still unclear. A lower reliance on symbiont activity in organisms might allow the symbiont-

385   facultative foraminifera to explore more low-light eutrophic regions including the deep-water layers and the turbulent upwelling regions. However, determining the facultative symbiosis trait, its trait-offs and the environmental conditions for the transition need detailed culture experiments including variable environmental conditions and resulting physiological changes.

There are several costs associated with hosting photosymbionts [1] they restrict foraminifera's depth habitat to the euphotic

390   zone (generally <200 m water depth; Caron et al., 1987; Schiebel and Hemleben, 2017) and [2] the host is dependent to changes in the availability and health of the symbionts which responds to environmental change. Studies suggesting that foraminifera symbionts are not favoured in low pH waters (Henehan et al., 2017) or in eutrophic areas due to light limitations (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

395   populations of 'bleached' individuals may persist 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

400   what triggers changes in symbiont hosting, the degree of energy subsidy symbionts provide to their host and further understanding of the use of symbionts as prey items. Without this understanding, and the ecological impact on the symbiont,

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

2.3 Reproduction

2.3.1 Sexual reproduction (foraminiferal/group-specific traits)

Planktic foraminifera were traditionally considered to reproduce sexually only but recent culture breakthroughs have shown that non-spinose foraminiferal species (*N. pachyderma* and *G. glutinata*) can generate via both asexual and sexual reproduction (Davis et al., 2020; Kimoto, 2006; Meilland et al., 2022). 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).

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). As they only grow for short periods and typically undergo reproduction without producing viable offspring, multi-generational experiments of planktic foraminifera have only recently been achieved (Meilland et al., 2024; Sykes et al., 2024).

Being able to change reproductive strategies is consistent with the ability to respond to short lived optimal conditions in the ocean (Davis et al., 2020). 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 production provides a definite (if 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 low concentration of foraminifera in the water column (~1 specimen per m^3 in blue waters) makes this a risky strategy. Delayed reproduction potentially reduced the chance of fertilization by putting individuals out-of-sync with the rest of the population and/or because the organism is smaller and thus, produces fewer gametes.

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As such, 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

440   motile gametes (see Weinkauf et al., 2022a and references therein).

Modelling development in foraminifera, resembling their accretionary growth has not been achieved to date. The main challenge is the lack of information of the different trades and trait offs in their development such as changes in metabolic rates, food uptake, etc. The new culturing breakthrough enabling us to explore the full life cycle of planktic foraminifera opens

445   to door to explore these questions and close our knowledge gaps.

The multigenerational experiments were achieved with *N. pachyderma* which as discussed above can overwinter in sea ice. After overwintering in sea ice *N. pachyderma* either return to the water column by migrating towards the base of the ice (Berberich, 1996) and/or as the ice melts are released to seed a new population (Spindler and Dieckmann, 1986). This

450   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) and ability to change between asexual and sexual reproduction might be the way of achieving this unique life cycle and need for rapid blooms under optimal environmental conditions in the short Antarctic summer. However, specimens grown under high salinity conditions are small resulting in reduced gamete production.

455   **3. Conclusions**

A relatively small number of functional traits are necessary to define the ecological niches of planktic foraminifera in the modern ocean and they are thus, an ideal target group for testing trait-based approaches. Unfortunately, many of the traits identified here remain poorly qualified and quantitatively constrained requiring new observational and/or laboratory/experimental work. Further there is a need to improve data reporting practices by following guidance on data

460   publishing (e.g. FAIR principles) and developing standardized, community agreed protocols for measuring traits to enhance our understanding of planktic foraminifera and how they are best modelled.

Despite a lack of comprehensive datasets there are clear groupings of traits in the modern ocean allowing us to explore drivers of past biogeography, changes in metabolic traits and trade-offs and response to extreme environments. Understanding the

465   association of different traits and suites of traits with particular environments provides the basis to understand how environmental factors structure planktic foraminifera communities in the past and in the future and thereby the vulnerability of pelagic carbonate production.

470 A key trait needing further constraint is calcification. Its trade-off, particularly the benefit of protection from grazing, is the fundamental assumption of current trait-based models for calcifying plankton but still lacks direct evidence. Fundamentally, the relationships between calcification and seawater carbon chemistry is unclear limiting our ability to predict the impact of acidification on foraminiferal growth and carbonate production. The challenge of modelling calcification hampers the accurate simulation of the distribution of ocean alkalinity and carbonate production in response to a changing climate.

475 In other organisms, food availability can support metabolism to reduce the impacts of anthropogenic climate change on other physiological processes. Further understanding of foraminiferal predator-prey dynamics is therefore urgently needed. Metabarcoding, eDNA, and eRNA studies offer valuable insights into distribution patterns and predator-prey dynamics. Dynamic ecosystem models, such as trait-based models, can create theoretical frameworks akin to laboratory experiments and explore various 'what if' scenarios. For foraminifera, these models can address laboratory limitations, such as high mortality
480 rates in multispecies experiments (and high time and financial costs) and provide realistic setups even in the absence of physical organisms. Beyond utilizing existing observational data, trait-based models are a powerful tool to generate new data that enhance our mechanistic understanding of the observations we gather, allowing us to move beyond correlation to uncover the underlying causative relationships.

485 **Author contribution**

DNS, FM and KME conceived the idea for the manuscript. KME and MG prepared the original draft of the manuscript. KME, MG and RY created the figures and tables. All authors contributed to reviewing and editing of the manuscript. DNS supervised the work.

490 **Competing Interests**

The authors declare that they have no conflict of interest

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