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Response of large benthic foraminifera to climate and local changes: Implications for future carbonate production

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ABSTRACT

Large benthic foraminifera are major carbonate components in tropical carbonate platforms, important carbonate producers, stratigraphic tools and powerful bioindicators (proxies) of environmental change. The application of large benthic foraminifera in tropical coral reef environments has gained considerable momentum in recent years. These modern ecological assessments are often carried out by micropalaeontologists or ecologists with expertise in the identification of foraminifera. However, large benthic foraminifera have been under-represented in favour of macro reef-builders, for example, corals and calcareous algae. Large benthic foraminifera contribute about 5% to modern reef-scale carbonate sediment production. Their substantial size and abundance are reflected by their symbiotic association with the living algae inside their tests. When the foraminiferal holobiont (the combination between the large benthic foraminifera host and the microalgal photosymbiont) dies, the remaining calcareous test renourishes sediment supply, which maintains and stabilizes shorelines and low-lying islands. Geological records reveal episodes (i.e. late Palaeocene and early Eocene epochs) of prolific carbonate production in warmer oceans than today, and in the absence of corals. This begs for deeper consideration of how large benthic foraminifera will respond under future climatic scenarios of higher atmospheric carbon dioxide ($p\text{CO}_2$) and to warmer oceans. In addition, studies highlighting the complex evolutionary associations between large benthic foraminifera hosts and their algal photosymbionts, as well as to associated habitats, suggest the potential for increased tolerance to a wide range of conditions. However, the full range of environments where large benthic foraminifera currently dwell is not well-understood in terms of present and future carbonate production, and impact of stressors. The evidence for acclimatization, at least by a few species of well-studied large benthic foraminifera, under intensifying climate change and within degrading reef ecosystems, is a prelude to future host–symbiont resilience under different climatic regimes and habitats than today. This review also highlights knowledge gaps in current understanding of large benthic foraminifera as prolific calcium carbonate producers across shallow carbonate shelf and slope environments under changing ocean conditions.

Keywords Bioindicators, carbonate engineers, climate change, environmental stressors, ocean acidification, photosymbionts, sea-level rise, water quality.

INTRODUCTION

Symbiont-bearing large benthic foraminifera today and in the past

Globally, foraminifera play significant functional roles, from meiobenthic nutrient cycling (Enge *et al.*, 2016; Wukovits *et al.*, 2018) to global geochemical cycles (Hallock, 1981; Langer *et al.*, 1997; Langer, 2008). Their broad geographic, taxonomic and morphological diversity is evidence of their ability to adapt and prevail in almost all marine ecosystems (Förderer *et al.*, 2018). This aspect alone allows them to be used in interpretation and reconstruction of modern and palaeoenvironments (Duchemin *et al.*, 2005; Drinia, 2009; Reymond *et al.*, 2011b, 2013b; Narayan *et al.*, 2015; de Jesus *et al.*, 2020), thus lending themselves as ideal vessels of geochemical proxies (Curry & Matthews, 1981; Rae, 2018) and bioindicators of coastal pollution (Frontalini & Coccioni, 2011; Pati & Patra, 2012; Suokhrie *et al.*, 2017; Ben-Eliahu *et al.*, 2020). Specifically, the relative proportion of functional groups [large benthic foraminifera (LBF), small heterotrophic and opportunistic] of foraminifera has been established as a powerful bioindicator tool (for example, the FORAM Index) for monitoring the health of coral reefs in terms of nutrient loading (Hallock, 2000a, 2012; Prazeres *et al.*, 2020a). Similarly, the ecophenotypic characteristics (Boltovskoy *et al.*, 1991), i.e. in LBF *Amphistegina* spp., has been shown to alter its test curvature to optimise light exposure for photosymbionts and thereby indicate palaeowater depths (Mateu-Vicens *et al.*, 2009). Overall, foraminifera might appear microscopic on an individual scale compared to other marine calcifies, but their prolific abundance and significance is difficult to overlook.

Large benthic foraminifera are an informal taxonomic group of benthic foraminifera. Their highly adapted and diverse tests are characterized by high surface to volume ratios, complex, compartmentalization of chamber systems (Hohenegger, 2009), and morphological adaptations (for example, flattening and transparency) for optimal light penetration, CO_2 uptake and high hydrodynamic energy (spines and/or rounded margins) (Leutenegger, 1977; Lee & Hallock, 1987; Lee, 2004; Hohenegger, 2009). The LBF with lamellar-walled, perforate and hyaline tests (Order Rotaliida), house diatom symbionts (families Amphisteginidae, Calcarinidae, Nummulitidae), while those with non-lamellar, imperforate and porcelaneous tests (Order Miliolida), typically house dinoflagellates (Soritidae), rhodophytic (Peneroplidae), chlorophytic (Peneroplidae) or diatom (Alveolinidae) symbionts (Hottinger, 1982). These algal symbiont types differ in terms of the light spectrum range that they utilize, which then determines their preferred depth range (Lee & Hallock, 1987; Renema & Trolestra, 2001; Renema, 2018). Typically, diatom-bearing LBF have a broader depth distribution and are deeper-dwelling (Nummulitidae) compared to dinoflagellate-bearing taxa (Hottinger, 1983; Renema & Trolestra, 2001; Renema, 2018). In turn, energy provided through their mutual, symbiotic partnership allows these unicellular hosts to grow to relatively large test sizes, typically 10 to 20 mm (Hallock, 1985; Hallock & Seddighi, 2021). *Cycloclypeus carpenteri*, for example, is the largest (in diameter) and flattest, extant species dwelling in deep-water settings. It achieves an exceptionally large size of up to *ca* 70 mm (Hohenegger, 1994) or generally from 50 to 100 mm (Renema, 2018).

Throughout Earth's history, euphotic carbonate factories and areas of prolific carbonate production were influenced by global CO_2 levels and regional oceanographic change and nutrient inputs (Wilson, 2008; Pomar *et al.*, 2012a; Pomar, 2020). Distinctly warmer periods in Earth's history were associated with higher sea surface temperatures (SST) (Hottinger, 1983; Hallock, 1985; Zachos *et al.*, 2003; Scheibner *et al.*, 2005), atmospheric CO_2 concentrations (of up to 2000 μatm by the Palaeocene–Eocene Thermal Maximum) and sea levels, compared to today (Pearson & Palmer, 1999, 2000). The

Palaeogene 'reef gap', particularly in the Indo-West Pacific, is not an artefact of preservation but an actual record of disappearance (or drastic reduction) of scleractinian coral taxa (Wilson & Rosen, 1998), likely due to thermal stress and bleaching (Scheibner *et al.*, 2005; Speijer *et al.*, 2012).

The association of LBF with shallow water carbonate deposits, in the absence of corals, make them valuable biostratigraphic, palaeoenvironmental fossil indicators throughout the Cenozoic (Frost & Langenheim, 1974; Hallock & Glenn, 1986; Hallock & Seddighi, 2021). The size and shape (i.e. flattening) of their tests reflects succession with hydrodynamics, depth and substrates on carbonate shelves (Hottinger, 1983; Hallock & Glenn, 1986). During the early Palaeocene to mid-late Eocene epochs, of the Palaeogene Period, conditions supported radiation and diversification of several phyletic lineages of LBF, which persisted into the Miocene (Hallock & Glenn, 1986; Hottinger, 1998; Racey, 2001; Pomar & Hallock, 2008; Mateu-Vicens *et al.*, 2012). Adaptation to greenhouse conditions characterized by warm, stable, nutrient-deficient, transgressive, shallow seas resulted in progressive test size increases (Hallock & Seddighi, 2021) and possibly lifespan (Ferrández-Canadell *et al.*, 2014), which was accompanied by high test complexity and organization, over a period of 25 million years (Newell, 1949; Hallock, 1985). Some of these evolutionary, biological changes were driven by algal symbiosis (Haynes, 1965; Hottinger, 1983; Hallock, 1985; Lee *et al.*, 2010; Prazeres & Renema, 2019; Hallock & Seddighi, 2021). Under environmental stress, symbionts can either be 'shuffled' if a diverse symbiont pool exists (Schmidt *et al.*, 2018) or 'switched', which means the uptake of more thermally tolerant symbionts during early life stages of LBF, such as that suggested for corals (Buddemeier & Fautin, 1993; Buddemeier *et al.*, 2004). Indeed, LBF species were exceptionally large (Hallock & Seddighi, 2021) and prolific carbonate producers, compared to today, as evidenced by fossilized nummulitic limestones, for example, of the Egyptian pyramids (Hallock, 1985; Racey, 2001; Beavington-Penney & Racey, 2004; Lee *et al.*, 2010; Hallock & Seddighi, 2021), and by the formation of vast nummulitic carbonate banks (Hallock, 1981; Pomar & Hallock, 2008; Mateu-Vicens *et al.*, 2012; Papazzoni & Seddighi, 2018). These banks were interpreted to have occurred in relatively deep (mesophotic) water settings (Arni, 1965); however their origins are under debate (Mateu-Vicens *et al.*, 2012; Papazzoni & Seddighi, 2018).

These highly specialized assemblages were apparently poorly adapted to survive a shift to an 'icehouse' world of cooler, high-nutrient surface waters, upwelling and increased bottom circulation, and falling dissolved CO_2 (Ca^+ and Ca/Mg) levels, which resulted in a few genera surviving into the early–middle Miocene (Adams, 1983; Hallock, 1985; Hallock & Glenn, 1986; Renema & Trolestra, 2001; Renema *et al.*, 2008) to the present (for example, *Cycloclypeus*). The shift from LBF to coral-dominated carbonates occurred around the Oligo–Miocene boundary (Wilson, 2008). The early Miocene, for example, of SE Asia, saw the increased speciation of scleractinian corals and the build-up of reef framework carbonates consisting of corals and coralline algae, accompanied by benthic foraminifera (including LBF), echinoderms, molluscs and *Halimeda*, typical, for example, for modern Indo-West Pacific reefs (Wilson & Rosen, 1998; Wilson, 2008, 2012). Fewer and smaller sized LBF lineages (Hallock, 1981) continued to form along carbonate platforms and ramps in parts of the world (for example, Balearic Islands, Western Mediterranean) where warm, oligo-mesotrophic conditions prevailed into the Upper Miocene (Pomar *et al.*, 2004; Mateu-Vicens *et al.*, 2008, 2012). However, they never became the dominant producer in large-scale carbonate systems again.

During the Cenozoic period, global CO_2 levels and regional oceanographic change provide an appropriate analogue for the near-future climate change projections (Wilson, 2008). From these studies, the authors expect that certain modern LBF lineages that show signs of adaptation to differing conditions, for example, persistence in thermally polluted coastal waters of the Eastern Mediterranean and Gulf of Aqaba (Schmidt *et al.*, 2015, 2016), deep mesophotic (Renema, 2006a, 2018, 2019), or in turbid inner shelf (inshore) fringing patch reefs (Renema & Trolestra, 2001; Renema, 2006a, 2018; Uthicke & Nobes, 2008; Narayan & Pandolfi, 2010), may be able to withstand ongoing climatic upheavals in these potential climate refugia (Keppel *et al.*, 2012; Renema, 2019). However, in the context of current rapid increases in anthropogenic CO_2 levels, combined effects of stressors and increasing local impacts, it is speculative whether LBF could once again dominate carbonate production (Lee & Hallock, 1987; Hallock, 2005). The multiple dimensions of the ecological niche that shape LBF species distribution patterns and adaptation, including the diversity and stability of symbiotic partnerships with different algal groups, microbiome characteristics and genetic differentiation influencing high species dispersal, needs further consideration and research (Lee, 2004; Webster *et al.*, 2016; Prazeres *et al.*, 2017a, 2020b). Thus, the study of past and present LBF populations offers opportunities for integration and linkages between ecology and evolution or eco-evolutionary ('eco–evo') dynamics (Pelletier *et al.*, 2009) across multiple scales.

This review focuses on LBF, as a vital tropical, shallow-water $CaCO_3$-producing group (Zohary *et al.*, 1980; Hallock, 1981; Tudhope & Scoffin, 1988; Langer *et al.*, 1997; Hohenegger, 2002; Langer, 2008), that has seen underwhelming application and representation in global assessments of reef $CaCO_3$ budgets. While overwhelming 'coral-centric' approaches have been suggested (Vroom, 2011), it is important to note that corals and LBF occupy overlapping, but also different reef-associated environments, with reef framework production by corals mainly occurring in the reef flat, crest to reef slope (upper photic). Large benthic foraminifera production, on the other hand, is species-specific and generally occurs across broad carbonate environments (Hallock, 1984; Yamanouchi, 1998; Hohenegger *et al.*, 1999; Fujita *et al.*, 2009; Renema, 2018) (Figs 1 and 2). In light of increasing global stressors, including: (i) terrestrial inputs and eutrophication; (ii) thermal stress; (iii) ocean acidification (OA); and (iv) sea-level rise (SLR) (Fig. 2), there is strong interest in understanding reef carbonate dynamics, including the contribution and rates of $CaCO_3$ production by different producers to the global carbonate budget and how this budget may be altered (Lange *et al.*, 2020). Based on these stressors, the potential role of LBF in future reef carbonate production and stabilization, other possible functions, and the implications for further research directions on these ubiquitous reef $CaCO_3$ producers are discussed.

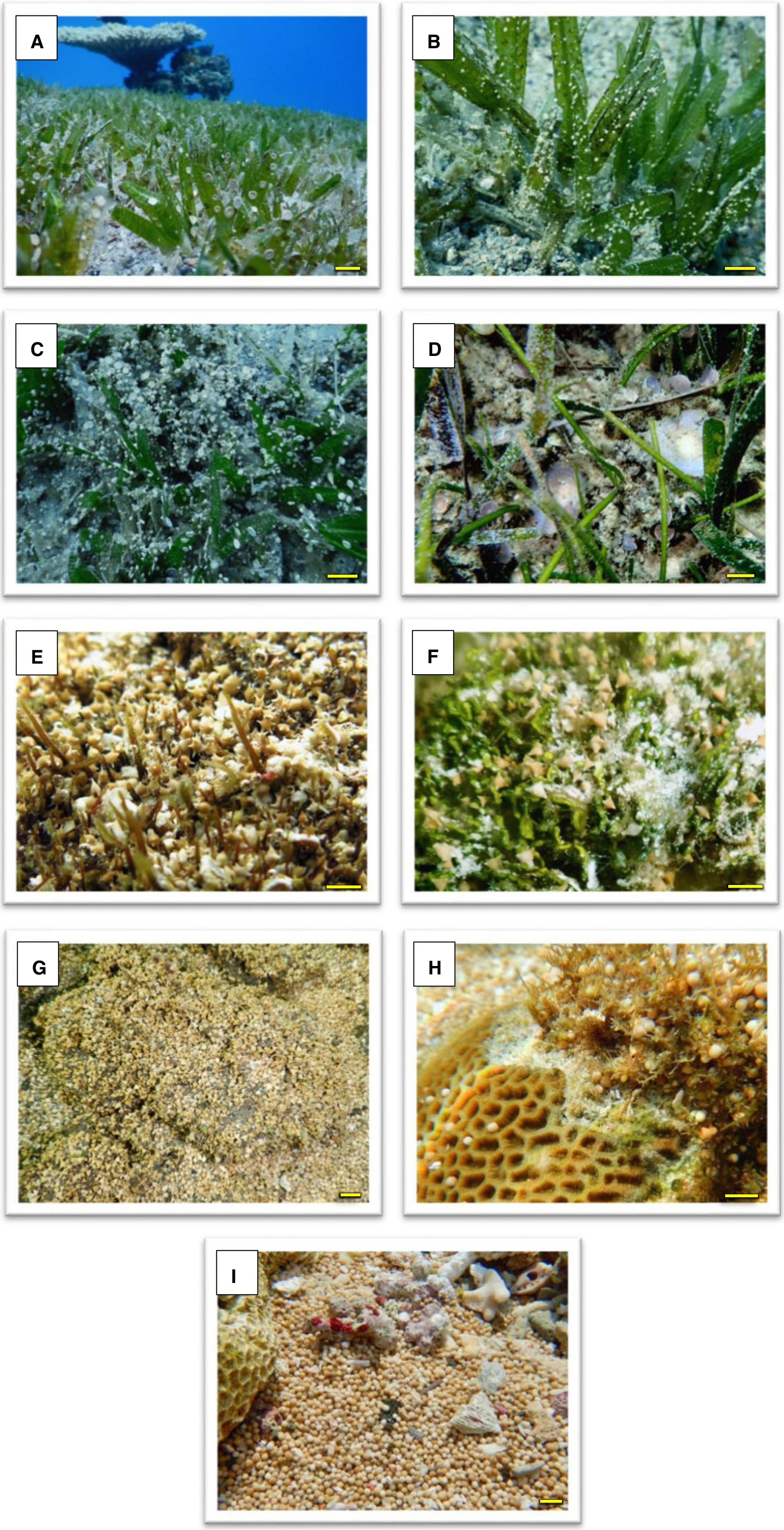
DISCUSSION

Tropical carbonate factories and the contribution of LBF to carbonate sediments and production

Tropical coral reefs are one of the most biologically diverse and productive (Odum & Odum, 1955; Connell, 1978; Reaka-Kudla, 1997) carbonate environments that form complex, three-dimensional, wave-resistant structures, typically dominated by hermatypic, scleractinian corals. As products of long-term accretionary processes, they are facilitated by several other calcium carbonate ($CaCO_3$) producing, functional groups. These carbonate 'engineers' are the skeletons of corals, coralline red algae, calcifying green algae (*Halimeda*), large benthic foraminifera (LBF) and other calcifiers, that can create, maintain or significantly modify habitats. In some environments they can be regarded as ecosystem engineers (Wilby, 2002). They contribute to reef sediment production, accretion, stabilization and maintenance (Wilson, 2008; Perry *et al.*, 2011; James & Jones, 2015; Janßsen *et al.*, 2017). Carbonate 'engineers' contribute to the $CaCO_3$ budget through a range of biological, physical and chemically-mediated production and erosion processes (Perry *et al.*, 2008, 2015; Montaggioni, 2009; Lange *et al.*, 2020).

After corals (primary) and coralline red algae (secondary), LBF have been considered as the third most prominent $CaCO_3$-producer and carbonate 'engineer' in coral reefs worldwide (Wells, 1957; Hallock, 1981; Harney *et al.*, 1999). Carbonate production rates by LBF are known to exceed that seen by coralline algae in the Great Barrier Reef (GBR) (Tudhope & Scoffin,

Fig. 1. Reef-dwelling, large benthic foraminifera (LBF), visible to the naked eye, in their natural field habitats. (A) Leaves of the Red Sea seagrass *Halophila stipulacea* covered by epiphytic LBF *Sorites orbiculus* in Eilat, Israel; (B) *Amphistegina* spp. or (C) both *Sorites* and *Amphistegina* on seagrass in Dahab, Egypt; (D) Large specimens of *Marginopora vertebralis* between seagrass shoots around (Changuu Island) Zanzibar, Tanzania (photograph: G. R. Narayan); (E) *Baculogypsina sphaerulata* on the intertidal algal reef flat of One Tree Island, Australian (photograph: S. S. Doo); (F) *Baculogypsinoides spinosus* and *Schlumbergerella neotetraedraon* on shallow *Halimeda* spp. on Gili Air, Indonesia; and (G) on volcanic substrates in Amed, Bali; (H) *Schlumbergerella floresiana* in intertidal pools growing in algal turfs, and accumulating as beach sediment; and (I) on Seger Beach near Kuta, Lombok, Indonesia (all other photographs: M. Stuhr). Scale bars (lower right) indicate *ca* 1 cm.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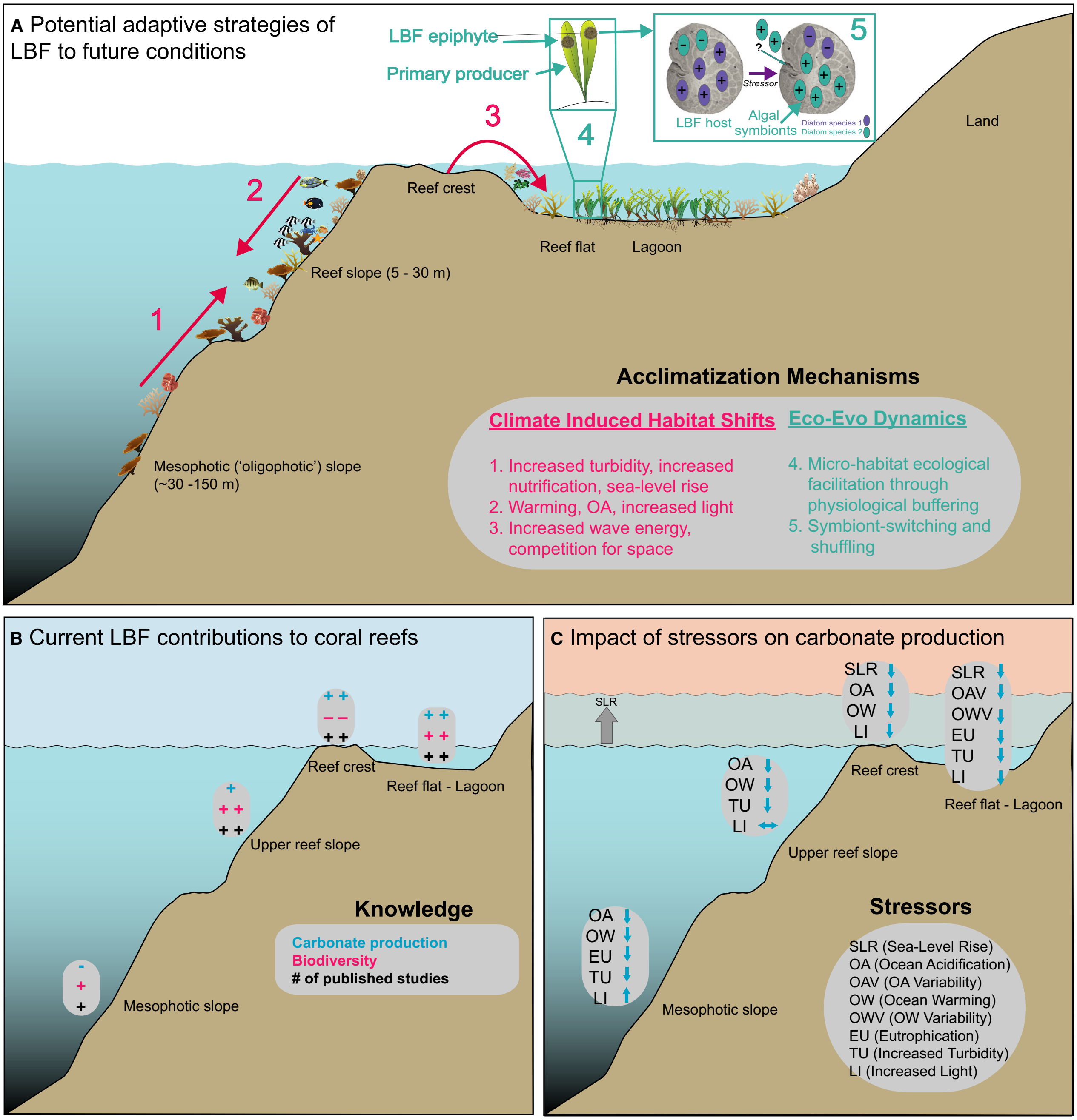

Fig. 2. A conceptual diagram of the current state of knowledge of large benthic foraminifera (LBF) (A) Potential adaptative strategies of LBF to future conditions are highlighted for the different reef zones that LBF can migrate to in response to changing physico-chemical conditions. Pink-coloured arrows and text indicate possible climate-induced habitat shifts. Blue-green arrows and text highlight the need for ecological-evolutionary (eco–evo) feedbacks (for example, the ability for LBF to modulate their evolutionary trajectory through ecological interactions), that need to be better understood. This study highlights the various methods to study these acclimatization mechanisms including: acclimatization potential through interspecies-interactions and symbiont shuffling/switching. (B) Current LBF contributions to reefs. The blue, positive/negative symbols indicate the importance of LBF for carbonate production in these particular reef zones; pink symbols indicate the known biodiversity of associated reef zones, and black symbols indicate the number of studies on LBF. (C) The impact of stressors on carbonate production. Primary stressors include: sea-level rise (SLR); ocean acidification (OA); ocean acidification variability (OAV); ocean warming (OW); ocean warming variability (OWV); eutrophication (EU); increased turbidity (TU); and increased light (LI). Blue arrows indicate the expected change in carbonate production in each reef zone, in response to the influence of these primary stressors.

1988). Although LBF themselves do not construct reef frameworks, accumulations of their tests support the stability and maintenance of carbonate habitats and structures (Sakai & Nishihira, 1981) by: filling in voids in the framework matrix; encrusting substrates; in large accumulations, baffling loose sediment; contributing carbonate detrital material to the formation of reef-associated landforms (Stearn *et al.*, 1977; Ford & Kench, 2012; Dawson *et al.*, 2014); as well as consolidating sediments into reef or beach rock (Jell *et al.*, 1965; Woodroffe & Morrison, 2001). Large, deep-dwelling taxa contribute to $CaCO_3$ accumulations on the outer carbonate shelf to seafloor, creating habitat, and often outweighing accumulation in shallow-water environments (Renema, 2018).

The relative contribution of carbonate producing taxa is important in determining which calcifier plays a key (primary to tertiary) role (Tudhope & Scoffin, 1988) in carbonate production. Carbonate component analysis is a tool for quantifying the relative percentage contribution to carbonate grains by the abundance of multiple, skeleton-building taxonomic groups in modern and palaeoecological studies (Tudhope & Scoffin, 1988; Lidz & Hallock, 2000; Pomar *et al.*, 2004; Chazottes *et al.*, 2008; Ford & Kench, 2012; Reijmer *et al.*, 2012; Perry *et al.*, 2014; Reymond *et al.*, 2014; Morgan & Kench, 2016; Janßsen *et al.*, 2017). The complementary use of carbonate component analysis has seen an upsurge of research in coral reef settings over the last decade (Renema, 2006b; Narayan & Pandolfi, 2010; Reymond *et al.*, 2013b; Fajemila *et al.*, 2015; Narayan *et al.*, 2015; Pisapia *et al.*, 2017; Fujita *et al.*, 2020; Prazeres *et al.*, 2020a). The LBF and other components derived from surface and sediment core samples, provide invaluable annual, decadal to millennial-scale records of benthic structure and stability in past reefs (Narayan & Pandolfi, 2011; Reymond *et al.*, 2013b; Narayan *et al.*, 2015; Johnson *et al.*, 2019; Fujita *et al.*, 2020). Test accumulations can outweigh the overall contribution of other, non-framework building carbonate components (Hallock, 1981, 2000a; Hallock *et al.*, 2003). In fact, a relatively small substrate sample (for example, algal turf) can yield a high density of individual specimens, greater than 1000 tests per 50 g sample (Hallock, 2012). The relative proportion of the total assemblage (non-LBF, LBF, living and empty tests) is, on average, *ca* 60 to 70% of the total sediment volume, relative to other carbonate components derived from the sand-sized (63 μm to 2 mm) fraction, but it can reach as high as 95% of the total sediment volume (Hohenegger, 2006; Langer, 2008; Dawson *et al.*, 2014).

While the role of benthic foraminifera as a major component of carbonate sands is well-established (Hallock, 1981; Langer *et al.*, 1997; Langer, 2008; Fujita *et al.*, 2009; Doo *et al.*, 2012, 2014, 2017; Dawson *et al.*, 2014), their overall contribution to reef $CaCO_3$ budgets relative to other carbonate components, remains largely unquantified (Harney & Fletcher, 2003; Vroom, 2011; Lange *et al.*, 2020), with the exception of the work of Reijmer *et al.* (2012) and Reymond *et al.* (2014), or it is considered to be relatively minor with respect to other macrocalcifiers (Andersson & Gledhill, 2013). In a recent review of carbonate budget estimates, as indicators of functional reef health, a call was made to incorporate the $CaCO_3$ contributions of different (non-framework building) reef communities into the global reef budget (Lange *et al.*, 2020). Yet, following extensive review of the literature on reef carbonate budgets, the authors made no mention of LBF contributions. In the light of increasing reef-scale research, LBF research is likely deprioritized by reef scientists for various reasons.

Current estimates suggest that LBF contribute approximately 3.9 to 5.4% to the global carbonate reef budget (Langer, 2008; Doo *et al.*, 2017), and generate an estimated 34 million tonnes of $CaCO_3$ annually (Langer, 2008). The estimated carbonate production by benthic foraminifera, including the contribution from small heterotrophic and opportunistic (non-symbiotic) taxa, ranges between 150 g and 2800 g $CaCO_3$ m^{-2} yr^{-1}, with LBF contributing amounts in excess of 1000 g $CaCO_3$ m^{-2} yr^{-1} (Hallock, 1981; Langer *et al.*, 1997; Langer, 2008). It is important to note that these budget estimates are very likely skewed by the over-representation of shallow-water reef habitats.

Calcium carbonate production by LBF has not been widely documented in reef budget estimates (Table 1). Complexities and inconsistencies in the methodologies for determining carbonate production rates, including standardized estimation methods, present a considerable problem. A common method of quantifying production rates is the census-based approach, which assesses population densities of individual species, the primary factor controlling production rates (Hallock *et al.*, 1986; Fujita *et al.*, 2016). Census-based estimates have been based

Table 1. Reported estimates for: standing crop (individuals/m^{-2}) – (unbolded); biomass (g m^{-2}) – (blue); and carbonate production rates (g m^{-2} yr^{-1}) – (bolded) for the known large benthic foraminifera (LBF) species from reef habitats. In studies where standing crop and turnover rates (τ) are specified (i.e. based on Hallock, 1981), the annual production rate was divided by τ to obtain the biomass. In reference to the test chemistry, high magnesium calcite (HMC) tests are considered to contain >4 mol % MgCO$_3$, while low magnesium calcite (LMC) <4 mol % MgCO$_3$. Biomass estimates were provided for studies that reported estimated production (by dividing reported τ by the estimated production rate).

Family	Species	Test chem. Mol % MgCO$_3$	Intertidal/ Lagoon (<5 m)	Reef flat to reef crest (<5 m)	Upper reef slope (5–20 m)	Reef slope (20–150 m) Reef margins Inter-reef areas	Location	Methods and references
	Peneroplis antillarum d'Orbigny, 1826 ($\tau = 12^{d}$)	15 – 18*	3.0 **36.4**^{d,5}		--	?	**a.** Eilat, Red Sea[1] **b.** West Caroline Island, Palau[2] **c.** Oahu, Hawaii[2,4] **d.** Okinawa, Japan[3,5] **e.** One Tree Island, GBR Australia[6,9] **f.** Raine Island, GBR Australia[7] **g.** Funafuti Atoll, Tuvalu[8]	**1** Growth and standing crop: Zohary *et al.*, 1980 **2** Standing crop: Hallock, 1981 **3** Biomass: Sakai & Nishihara, 1981 **4** Standing crop: Harney *et al.*, 1999 **5** Standing crop/biomass: Hohenegger, 2006 **6** Standing crop: Doo *et al.*, 2012 **7** Standing crop: Dawson *et al.*, 2014 **8** (i) Biomass; (ii) Standing crop (simple); (iii) Life tables; (iv) Growth increments; Fujita *et al.*, 2016 **9** Biomass: Doo *et al.*, 2017
	Peneroplis pertusus (Forsskål in Niebuhr 1775) ($\tau = 12^{d}$)	15–8*	1.6 **19.3**^{d,5}		--	?		
	Peneroplis planatus (Fichtel & Moll, 1798) ($\tau = 12^{d}$)	15–18*	34,000^{c,4} 9.6 **115.6**^{c,4} -------- 1.3 **16.0**^{d,5} -------- 1.7±0.3 (Oct)^{f,9} 3.7±0.6 (Feb)^{f,9} 22.1±3.3 (Jul)^{f,9}		11,000–26,000^{c,4} 3.1–7.3 **37.4–88.4**^{c,4}	?		
	Amphisorus hemprichii Ehrenberg, 1839 ($\tau = 1^{a}$)	16–8*	30,300^{a,1} 157.7 **157.7**^{a,1}	3500^{c,4} 11.9 **11.9**^{c,4}	3300–5000^{c,4} 11.2–17 **11.2–17**^{c,4}	?		
	Amphisorus kudakajimensis (Gudmundsson, 1994) ($\tau = 1^{a}$)	16–18*	84.6 **1015.1**^{d,5}	4.1 **48.6**^{d,5}	--	?		
	Marginopora vertebralis Quoy & Gaimard, 1830 ($\tau = 1^{f}, 16^{g}$)**	16–18*	4500±3710^{f,7} 11.3±9.3 **180±148**^{f,7} --------	7706±1400^{e,6} 71.7±1.4 **71.7±1.4**^{e,6} -------- 84.1±7.5 (Oct)^{e,9} 149.5±22.9 (Feb)^{e,9} 305.4±29.7 (Jul)^{e,9}	--	?		
	Amphistegina lessonii d'Orbigny, 1826 ($\tau = 16^{b}, 11^{c}$)	3–7*	12.5 **56.9–201**^{b,2}	0.09–2.11 **1.5–33.9**^{b,2} -------- 3.5 **12–40**^{c,2} -------- 31,000^{c,4} 9.7 **107**^{c,4}	1.3–30.7 **21.2–491**^{b,2} -------- 6.9 **76**^{c,2} -------- 62,000–123,000^{c,4} 19.2–38 **211–418**^{c,4}	?		
	Amphistegina lobifera Larsen, 1976 ($\tau = 13^{b}, 6^{c}, 13^{e}$)	3–7*	20.8 **39.7–269**^{b,2} -------- 22,000±11,100^{f,7} 1.5±0.8 **17±9**^{f,7}	5.3–23.6 **68.8–307**^{b,2} -------- 16.4 **25–103**^{c,2} -------- 30,000^{c,4} 17.2 **103**^{c,4} -------- 3.4 **41.3**^{d,5} -------- 15.5±1.5 (Feb)^{e,9} 15.9±1.8 (Oct)^{e,9} 17.5±2.1 (Jul)^{e,9}	33,000–70,000^{c,4} -------- 1.4–4.7 **18.7–60.7**^{b,2} -------- 4.1 **25**^{c,2} -------- 33,000–70,000^{c,4} 18.5–39.7 **111–238**^{c,4}	?		

Table 1. Continued

Family	Species	Test chem. Mol % $MgCO_3$	Intertidal/ Lagoon (<5 m)	Reef flat to reef crest (<5 m)	Upper reef slope (5–20 m)	Reef slope (20–150 m) Reef margins Inter-reef areas	Location	Methods and references
Order Rotaliida - Calcarinidae	*Baculogypsina sphaerulata* (Parker and Jones, 1860) (τ = 11[b,e,f] as *C. splengleri*)**	>21	487,000± 328,486[f,7] 146.1±98.5 **1607±1084**[f,7] -------- 210,000–1,430,000[g,8] 165±59[g,8-i)] **1818±648**[g,8-ii)] *669±138*[g,8-iii)] *400±83*[g,8-iv)]	5.5–34 **60.8–378**[b,2] -------- 2.3±0.5[d,3] **700**[d,3] -------- 7.1 **85.5**[d,5] -------- 455,000± 166,000[e,6] 260 **2860**[e,6] -------- 142.4±19.9 (Jul)[e,9] 169.5±21.3 (Oct)[e,9] 214.6±34.1 (Feb)[e,9]	--	?		
	Calcarina calcarinoides (Cheng & Zheng, 1978) (τ = 11[b,e] *C. splengleri*)**	17*	0.03–0.2 **0.3–1.7**[b,2]	0.2–8.1 **1.7–89.3**[b,2]	0.01 **0.1**[b,2]	?		
	Calcarina gaudichaudii d'Orbigny in Ehrenberg, 1840	17*	--	22.2 **266.2**[d,5]	--	?		
	Calcarina hispida Brady, 1876 (τ = 11[b,e] *C. splengleri*)**	17*	0.04–0.5 **0.5–5.5**[b,2]	0.2–0.5 **1.8–5.2**[b,2] -------- 6.3±1.2 (Oct)[e,9] 24.7±5.7 (Feb)[e,9] 27.7±4.5 (Jul)[e,9]	0.1–0.2 **0.9–1.9**[b,2]	?		
	Calcarina spengleri (Gmelin, 1791) (τ = 11[b,e])**	17*	0.2–15.5 **2.0–171**[b,2]	6.7–179.8 **73.6–1978**[b,2]	0.1–0.8 **0.6–9.1**[b,2]	?		
	Neorotalia calcar d'Orbigny in Deshayes, 1830	17–24*	--	4.2 **50.4**[d,5]	--	?		
	Heterostegina depressa d'Orbigny, 1826 (τ = 16[b] as *A. lessonii*)**	12–13*	0.2–1.0 **3.5–16.1**[b,2]	0.2–0.8 **2.9–13.4**[b,2] -------- 0.1 **2**[c,2] -------- 4000[c,4] 0.9 **13.6**[c,4]	0.3–0.9 **4.4–14.1**[b,2] -------- 0.6 **9**[c,2] -------- 4200–10,000[c,4] 0.9–2.1 **14.3–34**[c,4]	?		

*Species with unknown mol-% $MgCO_3$ have been allocated the family range noted by Blackmon & Todd (1959)
** is τ based on similar species (after Hallock ,1981)
Values as means ± SE

on: (i) life history tables, i.e. average population size, size-specific mortality, fecundity and average species life span (Muller, 1974; Zohary *et al.*, 1980; Hosono *et al.*, 2013; Fujita *et al.*, 2016); (ii) growth increment rates, i.e. daily growth rates of cultured individuals (g^3 $CaCO_3$ m^{-2} yr^{-1}) (Hosono *et al.*, 2013; Fujita *et al.*, 2016); (iii) monthly or biannual biomass estimates (g m^{-2}) (Fujita & Fujimura, 2008; Fujita *et al.*, 2016; Doo *et al.*, 2017); and (iv) standing crop estimates, i.e. test density (# per m^2) and turnover rates (Hallock, 1981).

Of these methods, the last approach listed (iv), also known as the 'simple method', has been the most common (Table 1) method used (Hallock, 1981; Doo *et al.*, 2012; Dawson *et al.*, 2014). In the simple method (iv), carbonate production rates are discussed in units of g $CaCO_3$ m^{-2} yr^{-1}, and carbonate production by a population is divided by the average standing crop ($\sum_i \overline{N}_i m_i$) to obtain the population turnover rate [$T = P/\sum_i \overline{N}_i m_i$, where $\overline{N}$ is the average number at size 'i' and m_i is the mass (g) at size i] (Hallock, 1981). Carbonate production rates of species are estimated using: $P = N\tau m$, where N is density (number of individuals m^2), τ is the turnover rate (yr^{-1}) and m is the mass (g) of a typical LBF individual (Hallock, 1981). A total standing crop of greater than 10^6 tests m^{-2} has been the benchmark for high productivity, whereas less than 10^4 tests m^{-2} is considered very low (Murray, 1967; Zohary *et al.*, 1980; Hallock, 1981). The simplicity of this method allows for quick production estimates, assuming that conditions are typically stable, and the effects of seasonality (i.e. length of day and amount of light) and physiochemical conditions are limited (Zohary *et al.*, 1980), as found in tropical coral reefs. Also, it is possible to estimate long-term carbonate production from time-averaged sedimentological data using this method (Dawson *et al.*, 2014).

Fujita *et al.* (2016) studied the carbonate production rate of *Baculogypsina sphaerulata* based on its population dynamics over a two-year period in an intertidal, turf algal zone in the Funafuti Atoll, South Pacific. Those authors estimated production rates using the four methods – (i) to (iv) – listed above (Table 1). In comparison, annual production rates of three – (i) to (iii) – of these four methods ranged between 165 and 669 g $CaCO_3$ $m^{-2}yr^{-2}$. Life history tables [method (i)] and growth increments [method (ii)] were three-fold to four-fold higher than that of monthly biomass estimates – method (iii). The simple method, on the other hand, showed an exceptionally high production rate of 1818 g $CaCO_3$ m^{-2} yr^{-2}. One reason for this is that, to date, knowledge of LBF species population dynamics is limited and based on studies of a few species in laboratory cultures (Muller, 1974; Hallock, 1981; Hallock *et al.*, 1986; Fujita *et al.*, 2000). Therefore, one caveat of the simple method is that it assumes the turnover rates of *B. sphaerulata* based on the population dynamics of similar, co-occurring species such as *Calcarina spengleri* (Hallock, 1981; Fujita *et al.*, 2016), as well as the assumption that species have similar turnover rates across their distribution range. Thus, the production rates of *B. sphaerulata* reported in literature (Table 1), including estimates of 378 g $CaCO_3$ m^{-2} yr^{-2} from Palau, in the West Pacific (Hallock, 1981); 144 ± 122 g $CaCO_3$ m^{-2} yr^{-2} from Green Island (Yamano *et al.*, 2000); *ca* 2860 g $CaCO_3$ m^{-2} yr^{-2} from One Tree Island (Doo *et al.*, 2012); and 1607 ± 1084 g $CaCO_3$ m^{-2} yr^{-2} from Raine Island in the GBR, are likely overestimated by an order of three-fold to ten-fold, due to the employment of the simple method (Fujita *et al.*, 2016). Population dynamic (i.e. life history tables) studies (Muller, 1974; Zohary *et al.*, 1980; Hosono *et al.*, 2013; Fujita *et al.*, 2016) are therefore suggested by Fujita *et al.* (2016) to provide the most reliable method for estimating annual carbonate production rates. Nonetheless, the lack of life history information is an important knowledge gap in estimating carbonate production. While more assessments of population dynamics and turnover rates, for a greater number of species are needed, it may not always be possible to collect life history information *in situ*, in which case, estimations that include at least two of the four methods may provide more robust estimates and a means for comparison.

Future estimates of carbonate production rates, in the least, should incorporate seasonal measurements (Zohary *et al.*, 1980; Fujita *et al.*, 2016; Doo *et al.*, 2017) to better understand the extent to which LBF physiology, algal–host symbiosis and population dynamics (growth, fecundity, life-span and population turnover rates) are being impacted by the effects of local environmental and global climate change. The few studies that have documented significant *in situ* population dynamics suggest seasonal fluctuations in densities and carbonate production rates among species living in different carbonate habitats, i.e. as epiphytes on seagrass or algal turf (Zohary *et al.*, 1980; Hohenegger, 2006; Baker *et al.*, 2009; Fujita *et al.*, 2016; Doo *et al.*, 2017). Also, it should not be assumed that areas of low nutrient and primary productivity conditions will result in high carbonate production rates, without knowledge of seasonal or long-term variability. Low carbonate production rates may reflect differences in species annual life stages/cycles, life-spans, turnover and growth rates, which may be due to mechanisms surrounding host–algal metabolism (Zohary *et al.*, 1980).

Large benthic foraminifera typically dwell in tropical, oligotrophic, euphotic, carbonate-dominated shelves, where photosymbiosis tends to be most efficient under good water quality conditions (Langer & Hottinger, 2000; Hallock, 2005). The LBF contributions to reef carbonate budgets, however, are not strictly reef-wide estimates. High LBF biomass has been recorded from the high energy reef crest, reef flat and lagoonal environments, both in the modern (Hallock, 1981; Tudhope & Scoffin, 1988; Hohenegger, 1994; Hohenegger *et al.*, 1999; Fujita *et al.*, 2009; Doo *et al.*, 2012, 2017; Mamo, 2016) and in historical settings (Reymond *et al.*, 2013b; Narayan *et al.*, 2015; Fujita *et al.*, 2020). The distribution of common shallow-water species (i.e. *Amphistegina spp.*, *Baculogypsina sphaerulata*, *Calcarina* spp. and *Marginopora vertebralis*) is controlled by light intensity, temperature, water energy, substrate type (including cryptic microhabitats), detrital input and nutrient availability (Hohenegger, 1994; Hohenegger *et al.*, 1999; Langer & Hottinger, 2000). A high proliferation of tests in these habitats largely contributes to beach sands, coral cay and reef island formation (Yamanouchi, 1998; Yamano, 2000; Yamano *et al.*, 2000; Hohenegger, 2002, 2006; Dawson *et al.*, 2014; Hosono *et al.*, 2014).

Hence, there is commonly under-representation in reef budget estimates of habitats peripheral to framework-building reef areas, including: reef margin areas, inter-reef areas, lower slope and the seafloor, where production by low-photic, deep-dwelling taxa occur (Hohenegger, 2002; Renema, 2006b, 2018). In areas where light attenuation in the water column becomes a limiting factor with increasing water depth, carbonate production by corals, and particularly certain diatom-bearing LBF (Nobes *et al.*, 2008; Uthicke & Nobes, 2008), tends to decrease (Hohenegger *et al.*, 1999; Langer & Hottinger, 2000; Renema, 2019) due to the limitation by photosynthetically active radiation (PAR) available for effective photosymbiosis (*ca* 1% PAR) (Huston, 1985; Renema, 2019). These areas have been termed the 'oligophotic' zone, which occurs below the fair-weather and storm-wave base (Pomar, 2001, 2020; Pomar *et al.*, 2017). At oligophotic depths, LBF distributions are partly controlled by low-light intensities and the spectral light requirements of the symbionts, low temperature, high water transparency, low hydraulic energy, extremely low nutrient concentrations and likely by the availability of calcium carbonate substrates (Hallock, 1987; Langer & Hottinger, 2000; Hohenegger, 2004; Renema, 2018, 2019).

Along the lower reef slope, down to the reef-base, and within inter-reef channels, below the storm-wave base (Renema, 2018), at water depths greater than 30 m, where corals do not typically occur (Bongaerts *et al.*, 2010), LBF can still occur down to depths of 50 m to *ca* 150 m in variable densities (Hohenegger *et al.*, 2000; Renema, 2006a, 2018). Low-light, nutrient depleted and depth-adapted assemblages possess large, flattened, paper-thin-walled tests, which reflect highly oligophotic conditions (Pomar et al., 2017). Some of the deepest dwelling extant taxa include: *Cyclocypeus carpentari*, *Heterostegina operculinoides*, *Nummulites venosus* and *Operculina heterosteginoides* (Tudhope & Scoffin, 1988; Hohenegger, 1994; Hohenegger *et al.*, 2000; Beavington-Penney & Racey, 2004; Renema, 2006a, 2018). Compressed depth ranges, due to a narrow range of low-light intensity, can result in variable densities and competition for space (Hallock, 1987; Hohenegger, 2004; Renema, 2006a). However, there is no available data on carbonate production by these species, and these habitats are not yet included in reef-scale carbonate budget estimates (Table 1). In the face of episodic environmental disturbances and large-scale climate change, the relatively stable lower photic, oceanic carbonate slope/ramp and seafloor habitats are potential areas for deep-reef refugia from bleaching and thermal stress experienced in shallow waters (Glynn, 1996; Bongaerts *et al.*, 2010; Keppel *et al.*, 2012; Renema, 2019).

In other low-photic environments, where water quality may be low, such as in turbid, mesotrophic inshore patch reefs that occur close to river deltas and within estuarine embayments, it is not uncommon to find low to moderate coral cover, diversity, and stress tolerant species of massive (favid) corals (Perry & Larcombe, 2003; Lybolt *et al.*, 2011) and proportionally low to high density accumulations of LBF (Renema & Trolestra, 2001; Renema, 2006b, 2008, 2018; Narayan & Pandolfi, 2010; Reymond *et al.*, 2013b; Fajemila *et al.*, 2015; Narayan *et al.*, 2015; Johnson *et al.*, 2017; Humphreys *et al.*, 2019). Higher LBF densities may occur in association with algal turf and seagrass species (Renema, 2006b; Narayan & Pandolfi, 2010; Dawson *et al.*, 2012). In these relatively degraded environments, LBF have shown persistence, consistently over millennial timescales (Reymond *et al.*, 2013b; Narayan *et al.*, 2015). Species composition and abundance are generally linked to long-term adaptation to low-photic conditions, as a result of variable but consistent terrestrial inputs over time, by both coral and LBF populations (Reymond *et al.*, 2013b; Narayan *et al.*, 2015; Johnson *et al.*, 2017). Similar to deep water, oligophotic habitats, these environments may also act as potential climate change (thermal) refugia for escape from bleaching and thermal stress (Cacciapaglia & van Woesik, 2016; Sully & van Woesik, 2020). Broad scale spatial studies across different carbonate environments are needed to account for the missing contribution of these LBF populations to reef-wide carbonate budget estimates.

Within a structurally complex reef-framework, the dynamic production of carbonate sands by LBF leads to the sustained formation, maintenance and stability of tropical low-lying islands, coral cays and carbonate beaches (Stoddart & Steers, 1977; Yamano *et al.*, 2005). The transport of empty foraminifera tests by strong and constant wave and current movement towards beaches have been known to lead to relatively high concentrations, particularly of one to two species of LBF (Yamanouchi, 1998; Harney *et al.*, 1999; Hohenegger, 2002). For example, it was found that 27% of the total volume of beach sands was composed of LBF components in Oahu, Hawaii (Moberly Jr. & Chamberlain, 1964; Harney *et al.*, 1999). Of this proportion, 80% consisted of *Amphistegina* spp. tests alone (Harney *et al.*, 1999). In Okinawa, Japan, the proportion of LBF in beach sands ranged between 20% and 95%, with species such as *Ampistegina lobifera*, *Baculogypsina spharerulata* and *Calcarina* spp. contributing significant proportions to beach deposits (Sakai & Nishihira, 1981; Hohenegger, 1994, 2002; Yamanouchi, 1998). Other examples of beaches that reflect deposition of high densities of monospecific LBF to low diversity foraminifera, are found in Palau (Hallock, 1981), Tuvalu (Collen & Garton, 2004; Hosono *et al.*, 2013), One Tree Island, GBR (Doo *et al.*, 2012), Raine Island, GBR (Dawson *et al.*, 2014) and the Bali–Gili–Lombok (Indonesian) islands (Hoeksema & Tuti, 2001).

The majority of tests produced in reef habitats likely do not accumulate on beaches (Resig, 2004). Furthermore, if test transport and deposition is disrupted by habitat destruction and/or by the diversion of water flow (for example, in the construction of a coastal seawall), test accumulation and abundances in beach deposits may change drastically (Hohenegger, 2006), even though *in situ* production may remain unchanged. Radiocarbon dates derived from *Amphistegina* spp. tests revealed ages of 1500 years or more for Hawaiian beach sands, indicating longer sand turnover rates (Resig, 2004). Whereas, in Raine Island, GBR, *B. sphaerulata* showed minimal storage time, rapid test transport (within 60 years or less) and persistence in deposits for a shorter (<100 years) period of time (Dawson *et al.*, 2012, 2014). This was likely due to the low durability of *B. sphaerulata* skeletal components (Ford & Kench, 2012). Also, the close proximity to highly productive ($>1 \times 10^6$ individual m^{-2}) algal turf-dominated substrates and lagoonal habitats, may result in higher beach and coral cay accumulations and indicate a critical source for sand replenishment (Hohenegger *et al.*, 1999; Fujita *et al.*, 2009; Dawson *et al.*, 2014). Consequently, some islands are likely only able to persist due to the constant supply and transport of LBF tests (Yamano, 2000; Collen & Garton, 2004; Fellowes *et al.*, 2016). These studies highlight the importance of preservation potential and diagenetic effects, because some species are more prone to mechanical abrasion and chemical dissolution, for example *B. sphaerulata* and *M. vertebralis*, than others, for example *Amphistegina* spp. and *Calcarina* spp. (Kotler *et al.*, 1992; Ford & Kench, 2012).

While the distribution of LBF tests is linked to *in situ* carbonate productivity (Dawson *et al.*, 2014), beach deposits (represented by high proportions of one to two species), do not necessarily reflect high *in situ* reef carbonate-production potential (Harney *et al.*, 1999), nor high coral cover (Renema, 2018). For example, algal and seagrass habitats that occur peripheral to reefs, have been found to promote high total carbonate storage potential for LBF (Borowitzka & Larkum, 1978), especially during the summer season, suggesting inter-annual (seasonal) and spatial variability in storage and redistribution in different reef-associated habitats (Dawson *et al.*, 2014; Doo *et al.*, 2017). Current understanding of the long-term, source to sink, continuum of autochthonous *in situ* carbonate production and allochthonous deposition and accumulation, still remains insufficient (Yamanouchi, 1998). As to whether beach accumulations reflect a healthy reef status (i.e. high coral productivity and cover) and active carbonate production potential of reefs is not well-quantified. These are topics that can benefit from further investigation, because they could have implications for interpreting how carbonate factories will be altered by coastal habitat destruction (Hohenegger, 2006) and/or climate change, resulting in implications for shoreline renourishment (Dawson & Smithers, 2010).

Large benthic foraminifera response to changing environmental conditions

Below, LBF response to four major groups of global stressors is discussed; water quality, temperature, ocean acidification and sea-level rise. This literature review includes a detailed look into the environmental conditions that have shaped LBF communities and their response to single or combined stressors. Extensive work done to date is summarized (in Tables 2 to 5) and the current trends observed from this review are outlined in conceptual Fig. 2.

Large benthic foraminifera response to reduced water quality from terrestrial inputs

Terrestrial inputs into coastal waters include various sources of pollution [toxic trace metals, effluent, agrochemical herbicides, polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs)] associated with land-use practices in catchment areas, coastal development, industrialization and generally rapid coastal population growth, which can have deleterious effects on carbonate producers. Over the last three decades, there has been extensive field-based and experimental research (and reviews) of the effects of trace element pollution – i.e. silver (Ag), cadmium (Cd), cobalt (Co), chromium (Cr), copper (Cu), mercury (Hg), manganese (Mn), nickel (Ni), lead (Pb) and zinc (Zn) – both historically and in modern sediments associated with nearshore environments, for example, in the Venice lagoon (Yamanouchi, 1998), and elsewhere in temperate to subtropical regions (Albani *et al.*, 2007; Coccioni *et al.*, 2009). Such past studies have mostly focused on mesotrophic–eutrophic environments and on populations of nearshore benthic foraminifera, particularly opportunistic taxa, for example *Ammonia* spp. (Schafer, 1973; Yanko *et al.*, 1994; Alve, 1995; Samir & El-Din, 2001; Saraswat *et al.*, 2004; Vilela *et al.*, 2004; Scott *et al.*, 2005; Nigram *et al.*, 2006; Frontalini & Coccioni, 2008, 2011; Carnahan *et al.*, 2009; Frontalini *et al.*, 2010, 2015, 2018; Pati & Patra, 2012; Suokhrie *et al.*, 2017; Teresa Losada Ros *et al.*, 2020), leaving out LBF. Morphological deformities of the test, stunted growth, changes to reproductive capacity, test dissolution and geochemistry (pyritization) of these non-LBF foraminifera have been linked to a number of environmental factors associated with both natural variations or high contamination by heavy metals and sewage (Vilela *et al.*, 2004; Frontalini *et al.*, 2015, 2018; Suokhrie *et al.*, 2017; Teresa Losada Ros *et al.*, 2020). These studies contributed to the recognition and application of non-LBF benthic foraminifera as sensitive bioindicators (Boltovskoy *et al.*, 1991; Yanko *et al.*, 1994; Alve, 1995; Nigram *et al.*, 2006; Frontalini *et al.*, 2015, 2018), with implications for monitoring coastal pollution (Coccioni, 2000; Suokhrie *et al.*, 2017).

In contrast, studies of the effects of coastal pollutants on tropical LBF ecology, morphology and physiology are relatively few (Prazeres *et al.*, 2012; van Dam *et al.*, 2012; Ross & Hallock, 2014; Youssef, 2015; Marques *et al.*, 2017; Akther *et al.*, 2020; Ben-Eliahu *et al.*, 2020). Chronic heavy metal contamination from anthropogenic sources has been associated with low population densities and high rates of bleaching, as seen in studies that reported on two amphisteginids (*Amphistegina gibbosa* and *A. lessoni*) from fringing reefs in north-eastern Brazil (Prazeres *et al.*, 2012; Marques *et al.*, 2017), two amphisteginids (*A. lessoni and A. lobifera*) and a soritid (*Sorites orbiculus*) from the eastern Mediterranean Sea (Ben-Eliahu *et al.*, 2020), and a soritid (*S. marginalis*) and peneroplid (*Peneroplis planatus*) from a sheltered Bay in the Red Sea, next to the major city of Jeddah, Saudi Arabia (Youssef, 2015). It was determined that the exposure (and addition) of the heavy metals Cd, Cu and Zn, over short or prolonged periods, inhibited Ca^{2+}-ATPase enzyme activity, which consequently weakened tests, making individuals more susceptible to threats arising from multiple stressors (Prazeres *et al.*, 2012; Marques *et al.*, 2017), and increased bleaching frequency when combined with OA effects (Marques *et al.*, 2017). The exposure to Cd, Cu and Pb resulted in: a species-specific and variable (up to 30%) decrease in growth rates; a negative, non-fatal, effect of Pb on algal symbionts (more than the host); a negative effect of Cu on both the host and symbionts; and a negative effect of Cu on growth, more so than Cd and Pb (Ben-Eliahu *et al.*, 2020). Concentrations of Cr, Fe, Mn, Ni, Zn, Cd, Pb and Cu were measured, and significantly high concentrations of Fe, Mn, Pb and Cu resulted in abnormalities in the shape of the chambers (for example, extreme compression and branched last chamber) and the apertures of *P. planatus* and *S. marginalis* (Youssef, 2015). The LBF were present in lagoonal environments. High percentages of opportunistic taxa (*Ammonium and Elphidium*) were recorded and high terrigenous sediments, in the port area, were noted. It appears that the test structure of miliolids (porcelaneous) is more susceptible to test deformations from environmental pollutants (Samir & El-Din, 2001; Youssef, 2015; Ben-Eliahu *et al.*, 2020) than that of rotalids.

Table 2. A summary of eight laboratory experimental and one field study highlighted in this review and the response of large benthic foraminifera (LBF) to terrestrial inputs and water quality (and combined effects) as discussed in this paper. The majority of the studies were conducted in laboratory-controlled aquariums or mesocosms using cultured LBF. References cited: **1**. Prazeres *et al.* (2012); **2**. Marques *et al.* (2017); **3**. Akther *et al.* (2020); **4**. Schmidt *et al.* (2011); **5**. van Dam *et al.* (2012); **6**. Reymond *et al.* (2011); **7**. Reymond *et al.* (2013); **8**. Youssef (2015); **9**. Prazeres *et al.* (2016).

Species studied	Brief description	Location	Response parameters	General response/effects (+) positive, (−) negative, (±) neutral/no effect
Alveolinella quoyi[5] *Amphistegina gibossa*[2] *A. lessonii*[1] *A. lobifera*[9] *A. radiata*[4] *Baculogypsina sphaerulata*[3] *Calcarina gaudichaudi*[3] *C. hispida*[4] *C. mayori*[4,5] *Heterostegina depressa*[4,5] *Marginopora rossi*[7] *M. vertebralis*[5,6] *Peneroplis planatus*[5,8] *Sorites marginalis*[8]	Effects of exposure to heavy metal contamination on Ca^{2+}-ATPase enzyme production	NE Brazil[1,2]	**1** Seawater Cd, Cu, Zn, +Zn addition on Ca^{2+}-ATPase enzyme activity; experiment on live-field and cultured specimen; Zn addition (9.53–93.37 μg L^{-1}); 48 hr;	**1** (−) Seawater metal concentrations strongly and negatively correlated to Ca^{2+}-ATPase activity, which increased at low Zn concentrations (>25 μg L^{-1}) and was inhibited at higher Zn concentration (>42 μg L^{-1}); resulting in weakened tests
			2 +Cu addition & OA; bleaching, growth, and mortality; mesocosm experiment; Cu addition (1.0, 1.6, 2.3, 3.2 μg L^{-1}); pH (8.1, 7.8, 7.5, 7.2); 10 and 25 d	**2** (−) Ca^{2+}-ATPase enzyme activity was inhibited with exposure to pH 7.2 and low Cu concentrations; bleaching frequency was higher with interaction of pH 7.2 and high Cu concentrations; there was no significant effect of **combined OA and Cu** on mortality
	Effects of (diluted) wastewater on photosynthesis activity	Okinawa, Japan[3]	**3** Fv:Fm; aquaria experiment of cultured specimen in 30 ml, capped, glass vials with 29 ml of diluted WW or seawater (control); 10 replicates; light intensity 250 lum/ft^2; diluted WW containing DOC (2.1 μM); NH$_4^+$ (2.0 μM); and PO$_4^{3-}$, 4 dilutions of WW (10x, 100x, 1000x, 1000x); 24 hr for 22 d	**3** (+)(−) Fv:Fm deteriorated in *C. gaudichaudii* after 3 d exposure to WW (at all dilutions); and within 1–2 days of exposure in *B. sphaerulata*. The latter showed an earlier response and greater sensitivity to WW and a higher epibiont infestation than *C. gaudichaudii*; even a 10,000x dilution of WW decreased active populations of both species, due to endosymbiont release
	Combined effects of terrestrial stressors with other stressors including: temperature and OA	Whitsunday islands[4], Orpheus and Lizard islands[5], Whitsunday islands[6], Palm islands[7],	**4** Flow-through experiment; specimen in six-well plates; nitrate levels 0.5, 1.0 and 1.4 μM; T 26, 29, 31°C; 30 d	**4** (+) Fv:Fm, chl-*a* and motility were reduced in specimens at 32°C and bleaching was observed Fv:Fm, chl-a and growth reduced at 31°C in *A. radiata* & *H. depressa*, but not in *C. mayorii*; no effect of nutrients or interaction with temperature on Fv/Fm, chl-*a* or growth; *H. depressa* symbionts more sensitive than *A. radiata*, because Fv/Fm decreased sooner, **nutrients had no effects**, thermal stress is species-specific, *C. mayorii* only showed insignificantly lower chl-a levels at 31°C
			5 Lab. experiment in beakers (500 ml); specimen collected from 2–9 m; herbicide diuron at 0, 1, 3 μg L^{-1} in 10 ml filtered seawater; T 26, 28, 30, 32, 34; Irradiance	

Table 2. (continued)

Species studied	Brief description	Location	Response parameters	General response/effects (+) positive, (–) negative, (±) neutral/no effect
		Jeddah, Red Sea, Saudi Arabia[8]	10 μmol quanta m^{-2} s^{-1} PAR; 96 hr (4 d)	**5** (–) Negative effects of elevated temperatures (>30°C) on Fv:Fm; more severe in presence of low levels of diuron; *M. vertebralis* slightly more sensitive to the negative effects of diuron than diatom-bearers; combined effects (>30°C) decreased photosynthetic and increased bleaching
		Lizard Island and northern GBR, Australia[9]	**6** Field and lab.; specimen collected at 5 m; T 22-28°C; DIP 0.2 μM; DIN 2.0 μM	**6** (–) Field and laboratory studies confirm a combined effect of enriched DIP or DIN with elevated temperatures (28°C) reduce growth rate by 51% and 37%, respectively
			7 Aquarium experiment; specimen (180 living), collected from 25–30 m depth; total nitrogen 7.5–12.5 μM and total phosphorus 0.18–0.38 μM); pH 7.6–8.1; 35 d	**7** (–)(+) Growth rates were inhibited by the interaction between eutrophication (flood plume) and OA (at threshold of 7.6); algal cells were more abundant per surface area suggesting release from nitrogen limitation; combined impacts of OA and eutrophication are dose dependent and interactive
			8 20 sediment samples; 33 species (15 genera) (live and dead) including LBF; ICP-MS for heavy metal analysis	**8** (–) Significantly high concentrations of Fe, Mn, Pb, Cu found in tests and abnormalities in shape of chambers and aperture
			9 Flow-through, outdoor aquaria; specimen collected at 6.0–9.5m depth; sites (inner, mid, outer reef populations); T 24, 26, 29°C; nitrate 0.45, 1.55, 4.5 μM; 30 d	**9** (–)(+) Significant interaction of site & temperature and site & nitrate on: bleaching frequency (outer at 29°C, mid at 4. μM); survivorship (mid and outer at 29°C and 4.5 μM nitrate); growth (outer at 29°C, mid at 4.5 μM); antioxidant capacity (not for nitrate; at 29°C, outer) and Ca-ATPase activity (at 29°C, outer); positive effects of nitrate (1.5 and 4.5 μM) on growth in inner and outer populations, but negative in mid (at 4.5 μM); mid- and outer shelf are more sensitive than inner-shelf populations

Abbreviations: ATP, adenosine triphosphate; Ca^{2+}, calcium ions; Cd, cadmium; chl-*a*, chlorophyll *a*; Cu, copper; d, day; DIN, dissolved inorganic nitrate; DIP, dissolved inorganic phosphate; DOC, dissolved organic carbon; Fe, iron; Fv:Fm, photosynthetic activity; g, grams; GBR, Great Barrier Reef; hr, hour; L, litres; m, metres; Mn, Manganese; NE, north-east; NH_4^+, ammonium; OA, ocean acidification; PAR, photosynthetically active radiation; Pb, lead; PO_4^{3-}, phosphate; T(°C), temperature; WW, wastewater; Zn, zinc; μM, micromoles;

Table 3. A summary of six laboratory experimental studies highlighted in this review and the response of large benthic foraminifera (LBF) to elevated temperature and the combined effects of other stressors (nutrients, herbicides). Temperature interactions with ocean acidification (OA) will be found under combined effects in Table 4. The majority of the studies were conducted in laboratory-controlled aquariums using cultured LBF. Only a few studies compared field (*in situ*) to laboratory studies. References cited: **1**. Fujita *et al.* (2014); **2**. Schmidt *et al.* (2016); **3**. Stuhr *et al.* (2018b); **4**. Pinko *et al.* (2020); **5**. Schmidt *et al.* (2011); **6**. van Dam *et al.* (2012).

Species studied	Brief description	Location	Response parameters (hr = hour; d = days)	General response/effects (+) positive, (−) negative, (±) neutral/no effect
Amphisorus kudakajimensis[1] *Amphistegina gibbosa*[3], *A. lessonii*[3] *A. lobifera*[2,4] *A. radiata*[5], *Baculogypsina sphaerulata*[1], *Calcarina gaudichaudii*[1], *Calcarina hispida*[5], *Calcarina mayori*[1,6], *Heterostegina depressa*[5,6], *Marginopora vertebralis*[7] *Pararotalia calcariformata*[2] *Peneroplis pertusus*[7] *Sorites orbiculus*[4]	Effects of thermal stress on photosynthesis activity and photochemical systems, growth and motility	Okinawa islands, Japan[1] Mediterranean coast of Israel[2] Florida Keys, USA (*A. gibbosa*) and Zanzibar, Tanzania (*A. lessonii*)[3]	**1** Aquarium incubator experiment; collected from 1 m depth; pooled *ca* 300 indiv. of *B. sphaerulata* or *C. gaudichaudii*, 10–25 indiv. of *A. kudakaj.*; T ranges 5–25°C, 15–35°C or 25–45°C; light *ca* 500 $\mu mol^{-2}\ s^{-1}$; DO_{dark_light} 2 hr incubations; <9 d **2** Aquarium experiment (x10, 18L), cultures in vials; cultures from thermally polluted site (+6°C); T 20–42°C (summer); T 20–36°C (winter); light (35–40 µmol m^2s^2); pH > 8.1; 2 weeks **3** Aquarium experiment; specimen collected from 18 m (*A. gibbosa)* and 5 m (*A. lessonii*) depth; T 25.5 to 32°C, single stress (1 × 3 days at 32°C), episodic stress (4 × 3 days at 32°C, intermittent by 6 days at 25.5°C), chronic stress (continuously 32°C) over 4 weeks, 30 d	**1** (−)(+) Net O_2 production and respiration rates peaked at *ca* 30°C, optimal temperature for a short exposure; very high temperatures (40°C) caused net O_2 production rates to decline (all 3 LBF) to less than zero and respiration rates slightly decreased, indicating that photosynthesis of symbionts was inactivated; longer time (days) required for recovery from damage to the photosystem by compared to the respiration system; oxygen metabolism of LBF holobionts can generally cope well with diurnal fluctuations **2** (−)(+) Reduced Fv:Fm (*A. lobifera*) occurred at 32°C, and photochemical stress in *P. calcariformata* first observed during exposure to 36°C; *P. calcariformata* survived all treatment conditions and grew under 36°C; has high bleaching threshold (36–42°C) **3** (−)(+) Chronic thermal stress (32°C for 30 days) reduced growth, motility, increased antioxidative capacities and resulted in extensive bleaching; *A. gibbosa* from different habitats had similar responses indicating marginally higher tolerance to thermal peaks in shallower sites; species-specific differences were stronger, with *A. lessonii* showing high tolerance to episodic stress and less pronounced impacts of chronic stress on motility, growth and photosymbiont performance

Table 3. (continued)

Species studied	Brief description	Location	Response parameters (hr = hour; d = days)	General response/effects (+) positive, (−) negative, (±) neutral/no effect
			4 Aquarium experiment; 10 d acclimation; T (25, 30, 32, 35°C); pH 8.0–8.1; salinity 38.4–39.2; alkalinity mol $CaCO_3$ measured per week	**4** Holobionts exhibited progressive loss-of-life functions between 32°C and 35°C. Species-specific response with calcification of *A. lobifera* drastically reduced compared with *S. orbiculus*; *A. lobifera* exhibited a synchronous response of calcification and net photosynthesis; symbionts in *S. orbiculus* decreased net photosynthesis prior to calcification.
	Combined effects of temperature with other stressors (nutrients) *Note*: additional examples found in Table 1 (Reymond *et al.*, 2011; Prazeres *et al.*, 2016)	Whitsunday islands, GBR[4], Orpheus and Lizard islands[7]	**5** Flow-through aquarium experiment; specimen in six-well plates; nitrate levels 0.5, 1.0, and 1.4 µM; T 26, 29, 31°C; 30 d	**5** (−)(+) Fv:Fm, chl-a and motility (a proxy for overall fitness) were reduced in specimens at 32°C and bleaching was observed; Fv:Fm, chl-a and growth reduced at 31°C in *A. radiata & H. depressa*, but not in *C. mayori*; no effect of nutrients or interaction with temperature on Fv/Fm, chl-a or growth; *H. depressa* symbionts more sensitive than *A. radiata*, because Fv:Fm decreased sooner, thermal stress was species-specific, *C. mayori* only showed insignificantly lower chl-a levels at 31°C; 2–3°C increase leads to rapid bleaching
			6 Lab. experiment in beakers (500 ml); specimen collected from 2–9 m; herbicide diuron at 0, 1, 3 µg L^{-1} in 10 ml filtered seawater; temp. 26, 28, 30, 32, 34; Irradiance 10 µmol quanta m^{-2} s^{-1} PAR; 96 hr (4 d)	**6** (−) Negative effects of elevated temperatures (>30°C) on Fv:Fm; was more severe in presence of low levels of diuron; *M. vertebralis* slightly more sensitive to the negative effects of diuron than diatom-bearers; combined effects (>30°C) decreased photosynthetic and increased bleaching

Abbreviations: chl-*a*, chlorophyll *a*; d, day; Fv:Fm, photosynthetic activity; g, grams; GBR, Great Barrier Reef; hr, hour; L, litres; m, metres; OA, ocean acidification; PAR, photosynthetically active radiation; T(°C), temperature; µM, micromoles.

Table 4. A summary of seven laboratory experimental studies highlighted in this review and the response of large benthic foraminifera (LBF) to ocean acidification (OA) and the combined effects of other stressors (eutrophication and temperature). The studies shown here were conducted in laboratory-controlled aquariums using cultured LBF. A broader review, including natural laboratory (field studies) can be found in the paper. References cited: **1**. Fujita *et al.* (2011); **2**. McIntyre-Wressig *et al.* (2011); **3**. Prazeres *et al.* (2015); **4**. Doo *et al.* (2020); **5**. Sinutok *et al.* (2011); **6**. Reymond *et al.* (2013); **7**. Schmidt *et al.* (2014).

Species studied	Brief description	Location	Response parameters	General response/effects (+) positive, (−) negative, (±) neutral/no effect
Amphisorus hemprichii[1], *A. kudakajimensis*, *Amphistegina gibbosa*[2], *A. lessonii*[3] *Baculogysina sphaerulata*[1], *Calcarina gaudichaudii*[1], *Heterostegina depressa*[7] *Marginopora rossi*[6] *Marginopora vertebralis*[4,3,5,7]	Variable and opposite trends with the effects of OA on growth/ calcification among different species	Okinawa islands, Japan[1], Florida Keys, USA[2], Heron Island and Green Island, GBR[3] Lizard Island, GBR, Australia[4]	**1** Aquarium experiment; 40 individuals; 5 $p\mathrm{CO_2}$ levels (260, 360, 580, 770, 970 µatm); temperature; 12 weeks **2** Aquarium experiment; 24 well plate; constant T (25°C); $p\mathrm{CO_2}$ levels (ambient 410 ± 30, 100, 2000 µatm); 6 weeks **3** Aquarium experiment; four $\mathrm{pH_{NBS}}$ levels of 8.1, 7.9, 7.7 and 7.6, representing 430 to 2000 µatm $p\mathrm{CO_2}$ **4** Flow-through aquarium, incubations; in association with *Laurencia intricata macro*algae; T ambient (26°C) and high (26°C); two pH units (8.0, 7.7); increase by 3°C and $p\mathrm{CO_2}$ to *ca* 1000 µatm; total 80 replicates; 15 d	**1** (−)(+) Hyaline diatom-bearing tests, show increased weights and net calcification at intermediate $p\mathrm{CO_2}$ levels (770 µatm), but reduced growth at highest $p\mathrm{CO_2}$ levels (970 µatm); net calcification in porcelaneous tests, with decrease at intermediate levels (580 to 770 µatm); intermediate levels favourable to hyaline tests but unfavourable to either hyaline or porcelaneous shells at higher (near 1000 µatm) $p\mathrm{CO_2}$ levels. **2** (−)(+) Fitness and survivorship were not directly affected by elevated $p\mathrm{CO_2}$; bleaching observed in all conditions was highest at elevated $p\mathrm{CO_2}$; growth was not affected; well-defined patch areas of dissolution (in hyaline tests up to 2000 µatm) were detected (area size increasing with decreasing calcite saturation state); dissolution also in offspring produced at 2000 µatm. **3** (−) *A. lessonii* showed significant decrease in buoyant weight, a reduction in the density of inner skeletal chambers, an increase of Ca-ATPase and Mg-ATPase activities at pH 7.6 when compared with ambient conditions of pH 8.1. **4** (+) *M. vertebralis* showed reduced growth when incubated in isolation; calcification rates were lowest in the high temp./low pH treatments; when incubated with marine algae *L. intricata*, growth

Table 4. (continued)

Species studied	Brief description	Location	Response parameters	General response/effects (+) positive, (−) negative, (±) neutral/no effect
				and calcification rates were similar to ambient; total chl-a decreased and maximum photochemical efficiency increased in ambient conditions; net production remained constant in isolated and associated; both production and respiration rates were significantly higher when associated
	Combined effects of OA with other stressors (eutrophication, temperature) often show the strongest stress responses	Heron Island, GBR[5,6], Orpheus Island, GBR, Australia[7]	**5** Aquarium experiment; specimen collected from 0.3 m depth; four temperatures (28, 30, 32 and 34°C); four CO_2 levels (39, 61, 101 and 203 Pa; pH 8.1, 7.9, 7.7 and 7.4, respectively)	**5** (−) Elevated $p\text{CO}_2$ caused a significant decline in Fv:Fm, oxygen production, calcification and growth; Fv:Fm decreased when exposed to elevated CO_2 (pH 7.4, in all temp. treatment) and temperature (32°C and 34°C in all pH treatments); elevated CO_2 and temperature reduced calcification (growth and crystal size) and oxygen production
			6 Aquarium experiment; specimen (180 living), collected between 25–30 m depth; total nitrogen 7.5–12.5 µM and total phosphorus 0.18–0.38 µM); pH 7.6–8.1; 35 d	**6** (−)(+) Growth rates were inhibited by the interaction between eutrophication (flood plume) and OA (at threshold of 7.6); algal cells were more abundant per surface area suggesting release from nitrogen limitation; impacts of OA and eutrophication are dose dependent and interactive
			7 Flow-through aquarium; specimen collected from 0–1 m (*M. vertebralis*), 8–12 m (*H. depressa*); $p\text{CO}^2$ levels *ca* 790 µatm (pH 7.9), *ca* 490 µatm (pH 8.1); T (28, 31°C); 53 d	**7** (−)(+) Increasing $p\text{CO}_2$, resulted in decreased chl-a content in *H. depressa* and increased chl-a in *M. vertebralis*; elevated $p\text{CO}_2$ had negative effects on growth and photosynthetic rate in *H. depressa* but a positive effect on effective quantum yield; elevated temperatures had negative effects on the physiology of both species

Abbreviations: chl-*a*, chlorophyll *a*; d, day; Fv:Fm, photosynthetic activity; g, grams; GBR, Great Barrier Reef; hr, hour; L, litres; m, metres; OA, ocean acidification; $p\text{CO}_2$, partial pressure of carbon dioxide; T(°C), temperature; µatm; micro-atmospheres; µM, micromoles.

Table 5. A summary of eleven studies highlighted in this review that discuss the relevance of large benthic foraminifera (LBF) carbonate production to low-lying reef islands and associated landforms, which may be impacted by sea-level rise/change. A broader discussion with additional references can be found in the paper. The key species studied are *Baculogypsina sphaerulata*, *Calcarina* spp. *Amphistegina lobifera* and *Marginopora vertebralis*. References cited: **1**. Hohenegger *et al.* (1999); **2**. Yamano (2000); **3**. Collen & Garton (2004); **4**. Hosono *et al.* (2014); **5**. Horton *et al.* (2007); **6**. Fujita *et al.* (2020); **7**. Fujita *et al.* (2000); **8**. Fujita *et al.* (2009); **9**. Doo *et al.* (2012); **10**. Doo *et al.* (2017); **11**. Dawson *et al.* (2014).

Species studied	Brief description	Location	General response/effects (+) positive, (−) negative, (±) neutral/no effect
Alveolinella quoyi[1] *Amphisorus hemprichii*[1] *Amphistegina lessonii*[1,3,5] *A. lobifera*[1,3,10,11] *A. radiata*[2] *Amphistegina* spp.[8] *Baculogypsina sphaerulata*[1,2,3,4,6,9,10,11] *Calcarina gaudichaudii*[3] *C. spengler*[7] *Calcarina* spp.[1,8,10] *Dendritina* spp.[1,5] *Heterostegina depressa*[2] *Marginopora kudakajimaensis*[7], *M. vertebralis*[3,9,10,11] *Neorotalia calcar*[2] *Nummulites venosus*[1] *Operculina ammonoides*[1] *O. complanata*[5] *Peneroplis pertusus*[1] *Peneroplis planatus*[1,10] *Peneroplis* spp.[1] *Parasorites orbitolitoides*[1] *Sorites marginalis*[1,3]	Implications for low-lying island formation, coastlines and reef growth patterns	Okinawa, Japan[1] Western Pacific[2] Funafuti Atoll, Tahiti[3] Tuvalu, South Pacific[4] Cleveland and Bowling Green Bay, GBR[5] Hydrographers Passage, GBR[6] Ryukyu Islands, NW Pacific[7] Majuro Atoll, Marshall Islands[8] One Tree Island, GBR[9,10] Raine Island, GBR[11]	**1** (±) Wide depth range of LBF facilitates potential production **2** (±)(−) Threshold rate of sea-level rise is 40 cm/100 yr, to 'keep-up' or 'give-up' the reef crest; the habitat of LBF would decrease as SLR; in a pessimistic scenario, *Halimeda* replace LBF **3** (±) *A. lobifera* and *M. vertebralis* are most abundant in shallow lagoonal sands where they comprise up to 77% of the sediment; landward, transport and dissolution causes preferential removal of weaker skeletal material (i.e. *Halimeda*), dissolution of aragonitic forms (coral, calcareous red algae, molluscs) and hence the concentration of calcitic LBF; a high, constant supply and transport of LBF tests may continue to maintain shorelines and low-lying reef islands **4** (+) Viable rearing through bioengineering supports high turnover and growth for sediment renourishment projects in low-lying islands **5** (+) Distributional patterns are depth related. LBF assemblage from the middle shelf zone showed strong, positive correlations, whereas inner shelf opportunistic and heterotrophic taxa showed strong negative correlations with water depth **6** (±) Rapid sea-level fall during the Last Glacial Maximum (LGM) resulted in sediment accumulation rates that were higher than or similar to those during the Holocene highstand, resulting in the formation of reef flat and back-reef environments and increased LBF production

Table 5. (continued)

Species studied	Brief description	Location	General response/effects (+) positive, (–) negative, (±) neutral/no effect
	Implications for reef sediment budgets and carbonate ($CaCO_3$) production rates		**7** (+) $CaCO_3$ production rates by *M. kudakjimaensis* populations are approximately 5000 g m^{-2} yr^{-1}, which is extremely high compared to other LBF; size-specific mortality rates were very low
			8 (+) High $CaCO_3$ production (>1000 g m^{-2} yr^{-1}) occurred in ORF, (windward) inter-islands, sparsely populated islands, and seaward reef flats with no reef islands; low production (<1000 g m^{-2} yr^{-1}) in nearshore zones of lagoonal reef flats, leeward ORFs, and a windward ORF near densely populated islands; water motion and depth influenced LBF distribution
			9 (+) An estimated total of 2800 metric tonnes of $CaCO_3$ is produced yearly by these two populations on the OTR flat, with *B. sphaerulata* having a greater contribution (*ca* 97%) to $CaCO_3$ production; estimates of production range between 3 to 72g m^{-2} yr^{-1}
			10 (+)(±) LBF contribute 3.9–5.4% to reef $CaCO_3$ budgets; further spatial and temporal (i.e. seasonal) studies are needed to assess $CaCO_3$ storage potential across multiple reef habitats (and microhabitats) using varied techniques such as remote sensing to provide reef-scale estimations
			11 (+) LBF contribute 55% of the sediment produced on the reef annually and a large proportion (54%) to net annual accretion of the island; standing stock data show high production rates (1800 g m^{-2} yr^{-1}); AMS ^{14}C dates of single LBF tests indicate rapid rates of sediment transport across reef

Abbreviations: AMS ^{14}C, accelerator mass spectrometry radiocarbon 14; $CaCO_3$, calcium carbonate; cm, centimetres; g, grams; GBR, Great Barrier Reef; ORF, ocean reef flat; yr, year.

Agricultural herbicides entering coral reefs through catchment areas are an increasing issue (Ben-Eliahu *et al.*, 2020). Van Dam *et al.* (2012) found that the combined effects of elevated temperature (>30°C) and herbicides (diuron) are generally higher than those caused by individual stressors in inhibiting the photosynthetic efficiency in different LBF species. There was a significant linear correlation between reduced photosynthetic efficiency and loss of chlorophyll-a (van Dam *et al.*, 2012). In addition, chemical pollutants derived from oil dispersants (propylene glycol and 2-buthoxyethanol) resulted in a significantly high incidence in bleaching in *A. gibbosa* over short-term (48-hours) exposure (Ross & Hallock, 2014). The study showed that some individuals recovered following exposure and removal into clean water. Short-term exposure to waste water was found to have beneficial components, such as temporarily enhanced photosynthetic efficiency, as well as harmful components, such as decreased LBF biodiversity and epibiont infestations, in two species of LBF (Akther *et al.*, 2020). Nonetheless, more morpho-physiological studies on the effects of agrochemical herbicides, chemical pollutants, trace elements and sewage effluent on LBF ecology and physiology are needed.

Foraminifera occur across a broad range of nearshore to offshore water quality gradients, including areas that experience natural eutrophication from seasonal upwelling and mesotrophic conditions (Richardson, 2006; Prazeres *et al.*, 2016; Humphreys *et al.*, 2019) from near river mouths, along populated, urban shorelines or sites close to sewage effluent (Renema & Troelstra, 2001; Renema, 2006b; Schueth & Frank, 2008; Narayan & Pandolfi, 2010). Water quality influences the sensitivity of photosymbiotic calcifiers to various environmental and climatic stressors (Schmidt *et al.*, 2011; Reymond *et al.*, 2013a; Prazeres *et al.*, 2016), mainly through the breakdown of the host–algal symbiosis, which disrupts photosynthetic activities of the algal endosymbionts (Fabricius, 2005).

Large benthic foraminifera persistence has also been recorded in long-term sedimentary archives from turbid inshore reefs, prior to and during early European settlement that saw intense changes in land-use practices in Eastern Australia (Lybolt *et al.*, 2011; Reymond *et al.*, 2013b; Narayan *et al.*, 2015; Johnson *et al.*, 2017, 2019; Fujita *et al.*, 2020).

The nutrient thresholds that are considered to promote macroalgal blooms, i.e. dissolved inorganic nitrogen (DIN) and phosphate (DIP), and that are associated with the onset of mesotrophic or eutrophic conditions in coral reefs are considered to be approximately 1.0 μM for DIN and about 0.2 to 0.3 μM for DIP (Hallock & Schlager, 1986; Bell, 1992; Lapointe *et al.*, 2004). High nutrient concentrations may release photosymbionts from nutrient limitation, which could decrease photosymbiont translocation of organic carbon (photosynthate) to the LBF host and thereby reduce energetically expensive mechanisms regulating test calcification (Muscatine *et al.*, 1984; Uthicke & Altenrath, 2010; Reymond *et al.*, 2013a). Hence, studies have shown that increasing concentrations of dissolved inorganic nutrients from pollution and runoff can impair reef growth (Uthicke & Altenrath, 2010; Reymond *et al.*, 2011b), particularly in inshore reefs, which are exposed to higher runoff than offshore reefs (Uthicke & Nobes, 2008; Uthicke & Altenrath, 2010). The interactive effects of OA and natural eutrophication (i.e. flood plume) inhibited growth rate at pH levels of 7.6; however, increased abundance of algal cells suggested release from nitrogen limitation in the dinoflagellate-bearing taxon *Marginopora* sp. (Reymond *et al.*, 2013a).

Differential tolerance to nutrients inputs (Lee & Hallock, 1987; Lee, 2006) can be found across a broad range of inner to outer-shelf gradients (Lee & Hallock, 1987; Lee, 2006; Prazeres *et al.*, 2016), including sites of seasonal upwelling (Renema, 2018) and mesotropic to eutrophic marginal reefs (Richardson, 2006; Prazeres *et al.*, 2016; Humphreys *et al.*, 2019). Prazeres *et al.* (2016), studied the potential influence of habitats on populations of diatom-bearing *Amphistegina lobifera* exposed to high nutrients (1.5 and 4.5 μM) and variable temperatures (26 and 29°C) in three different reef site locations (inner, mid and outer shelf) in the northern GBR. Here, the interaction between reef location with either elevated temperature or nutrient concentration, resulted in a greater negative effect on growth rate and survivorship, in the sensitive mid to outer shelf populations than in the more tolerant inner-shelf populations of *A. lobifera* (Prazeres *et al.*, 2016, 2017a). In contrast, Schmidt *et al.* (2011) did not find any effect of elevated nitrate concentrations (0.5 to 1.4 μM) on three LBF taxa. Nutrient concentrations alone (at least below threshold levels), do not strongly drive physiological changes in LBF populations. Overall, more studies are required to understand population variability across a broad range of LBF species and water pollution regimes to fully understand response thresholds.

In summary (Table 2), the effects of coastal pollution on LBF results in:

1 Inhibition of Ca^{2+}-ATPase enzyme activity, weakened tests (Prazeres *et al.*, 2012; van Dam *et al.*, 2012; Marques *et al.*, 2017), species-specific and variable changes in test growth (Ben-Eliahu *et al.*, 2020), and test abnormalities, the latter being more evident in miliolids with porcelaneous test structures (Youssef, 2015; Ben-Eliahu *et al.*, 2020).

2 Reduced photosynthetic efficiency, which is compounded by the combined effects with other stressors (i.e. elevated temperature) (van Dam *et al.*, 2012; Prazeres *et al.*, 2016, 2017a).

3 Reduced long-term adaptation in habitats with more sensitive and stable water quality (mid to outer shelf) conditions than in fluctuating inner-shelf conditions (Prazeres *et al.*, 2016).

4 Potentially beneficial, to no effects, from short-term exposure to high nutrients (Schmidt *et al.*, 2011; Akther *et al.*, 2020).

Large benthic foraminifera response to thermal stress

Globally, seawater temperatures are expected to rise by 1 to 3°C or more in the coming decades (Hughes *et al.*, 2017; McLachlan *et al.*, 2020). Thermal stress and bleaching from elevated temperature and light intensity (UV radiation) are strong drivers of adaptive physiology in photosymbiont-bearing calcifiers (Pandolfi *et al.*, 2011; Hoegh-Guldberg *et al.*, 2017; Kawahata *et al.*, 2019). Bleaching, a phenomenon that has occurred repeatedly in corals since 1979 (Hoegh-Guldberg *et al.*, 2007), also affects LBF (Hallock *et al.*, 2006a; Schmidt *et al.*, 2011). Unprecedented marine heatwaves recently resulted in three severe coral bleaching events (Hoegh-Guldberg *et al.*, 2017; Hughes *et al.*, 2017, 2018a; Eakin *et al.*, 2019), coinciding with the warmest decade on record (Hoegh-Guldberg *et al.*, 2017; Sully *et al.*, 2019). In parts of the world, such as the GBR, reef calcifiers are already experiencing prolonged thermal stress (Riegl, 2003; Riegl *et al.*, 2011; Coles *et al.*, 2018) and bleaching from accumulated heat exposure to temperatures 1 to 2°C above the normal summer maximum, and up to 6°C (Hughes *et al.*, 2017, 2018b). In other regions, calcifiers are showing growing resistance and an increase in species-specific temperature tolerance (Riegl, 2003; Riegl *et al.*, 2011; Carilli *et al.*, 2012; Coles *et al.*, 2018; Donner & Carilli, 2019).

Bleaching or a loss of photosymbionts or pigments, as a result of photo-oxidative stress, was first recorded in *Amphistegina gibbosa* from the Florida Keys (Hallock *et al.*, 1993, 2006b; Hallock, 2000b). When this species was experimentally exposed to elevated temperatures (>31°C) in the laboratory, cytological studies revealed temperature accelerated bleaching, deterioration and digestion of the diatom symbionts, and deterioration of the host cytoplasm, similar to that seen in field-stressed specimens (Talge & Hallock, 1995, 2003). An experimental study demonstrated that elevated temperatures (>30°C) resulted in bleaching, and decreased photosynthetic efficiency [measured with pulse amplitude modulated (PAM) fluorometry], chlorophyll-*a* concentration, an indicator of algal symbiont biomass, and growth in two diatom-bearing species (Schmidt *et al.*, 2011). However, two calcarinid diatom-bearing species originating from two different locations in the GBR showed greater but species-specific responses to thermal stress (Schmidt *et al.*, 2011). Stuhr *et al.* (2017) showed that exposure to chronic thermal stress (at 32°C for 30 days) had negative effects, causing reduced motility, reduced growth (by 50%), elevated antioxidant capacities and gradual bleaching. Single or pulsed thermal stress events in this experiment, in contrast, were associated with high motility and growth but potentially suppressed reproduction (Stuhr *et al.*, 2017).

Likewise, experimental studies in natural laboratory settings have demonstrated high thresholds of LBF to thermal stress in nearshore habitats, which experience variable conditions (Doo *et al.*, 2012; Engel *et al.*, 2015; Weinmann & Langer, 2017). Common and abundant *Baculogypsina sphaerulata* and *M. vertebralis* found in the intertidal reef flats of One Tree Reef, GBR, contribute greatly (97%) to local $CaCO_3$ production (Doo *et al.*, 2012). They commonly experience pulsed temperature increases of 2 to 4°C above the ambient SST (25 to 29°C) during low tides. In one study, both taxa demonstrated remarkable resilience to bear temperature increases of up to +4°C (Doo *et al.*, 2012). However, significant negative effects (dissolution) were recorded for growth rates in the latter species, when temperatures reached +6°C (Doo *et al.*, 2012). Similarly, a variety of small non-LBF and LBF, particularly perforate taxa (*Neorotalia calcar* and *Amphistegina* spp.), occurring in shallow tide pool samples in East Africa, showed the ability to withstand extreme ranges (35 to 40°C) in diurnal temperature fluctuations

(Weinmann & Langer, 2017). Short-term thermal tolerance of diatom-bearing species (*Calcarina defrancii* and *A. lessonii*) is indicated in a study where they were exposed to intermittent temperature extremes of up to 40° in shallow-water (10 m) habitats, associated with algal biofilms attached to volcanic rocks and exposed directly to hot vent CO_2 seeps in Papua New Guinea (Engel *et al*., 2015).

Latitudinal range expansions of amphisteginids from the northern Red Sea region demonstrate surprisingly high thermal tolerances, which were likely retained during their expansion from the Red Sea into the Eastern Mediterranean (Schmidt *et al*., 2016). *Amphistegina lobifera* showed reduced photosysnthetic and growth rates at 32°C which is above current summer maxima in both regions (Schmidt *et al*., 2016; Pinko *et al*., 2020). Corals from the Red Sea have extremely high bleaching thresholds when compared with other coral species worldwide and were described based on their invasive traits as positively ‘thermally filtered’ due to recolonization from the Indian Ocean over thousands of years (Fine *et al*., 2013). These temperature pre-conditioned populations maybe crucial for the survival of LBF under global warming, a hypothesis that remains to be tested also on other calcifying organisms. In summary, these studies demonstrate that extreme environments such as shallow tidal pools, intertidal flats and CO_2 seeps are areas for potential acclimatization and adaptation of foraminiferal populations (Prazeres *et al*., 2020b), which may become important sources and suppliers of resilient populations of marine calcifiers under future warmer ocean conditions.

Species Distribution Models (SDMs) suggest that areas of higher suitability will expand poleward, with increasing SSTs (Weinmann *et al*., 2013a). In turn, ranges of prolific LBF (*Amphistegina*, *Archaias* and *Calcarina*) are also expected to increase globally (Langer *et al*., 2013; Weinmann *et al*., 2013a; Prazeres *et al*., 2020b), thus, increasing the potential for $CaCO_3$ production in high-latitude shelf environments (Langer *et al*., 2012). For example, the northward range expansion of amphisteginids into the Mediterranean region has resulted in an increase in $CaCO_3$ production (Langer *et al*., 2012; Weinmann *et al*., 2013a,b; Schmidt *et al*., 2015). Also, their current, rapid expansion southward along the East African coastal waters into South Africa (30.84°S) is attributed to the influence of the warm surface waters of the Aguilas Current and the availability of suitable habitats there (Langer *et al*., 2013; Weinmann *et al*., 2013a).

Recently, there has been increased discussion on the influence of internal waves (IW) in shaping benthic carbonate communities (Pomar *et al*., 2012b; Wall *et al*., 2015; Reid *et al*., 2019; Pomar, 2020). Internal waves create strong, bottom-current pulses that influence nutrients and thermal variation by vertically displacing the thermocline (Garrett & Munk, 1979; Pomar *et al*., 2012b; Pomar, 2020). They travel long distances, transporting cool, nutrient-rich waters to coastal shelf habitats before breaking on beaches (Leichter *et al*., 1998; Alford *et al*., 2015; Reid *et al*., 2019). The occurrence of metazoan buildups in lower-photic, mid to outer carbonate ramp environments, throughout the Phanerozoic has been interpreted to be the result of IWs (Pomar *et al*., 2012b; Wall *et al*., 2015). Recent studies show that internal waves cooled SST beneficially during the summer months in the South China and Andaman seas (Wall *et al*., 2015; Reid *et al*., 2019). Thus, shoaling IWs may play a critical role in ameliorating metabolic and thermal stress in tropical, carbonate reefs, under changing climatic conditions (Roder *et al*., 2010; Wall *et al*., 2015; Reid *et al*., 2019).

In summary (Table 3), the effects of prolonged SST above a threshold of ≥31°C may:

- have a negative effect on growth and calcification (Schmidt *et al*., 2011, 2016; Doo *et al*., 2012; Stuhr *et al*., 2017, 2018b; Pinko *et al*., 2020) and photosynthetic efficiency in the LBF holobiont (Schmidt *et al*., 2011, 2016; Fujita *et al*., 2014; Stuhr *et al*., 2017);
- potentially change reproductive outputs (Prazeres *et al*., 2017b; Hohenegger *et al*., 2019); and
- be less detrimental under temporal, pulsed thermal stress, which allows for periods of recovery of the photosystems (Talge & Hallock *et al*., 1995, 2003; Schmidt *et al*., 2011; Fujita *et al*., 2014; Stuhr *et al*., 2017, 2018a,b).

These responses to thermal stressors are likely to vary due to:

- species-specific responses, which might be dependent on the type of photosymbionts housed, for example, as seen in the diversity and flexibility of the algal symbiont community in the globally distributed amphisteginids (Schmidt *et al*., 2011, 2016; Fujita *et al*., 2014; Stuhr *et al*., 2018b; Stuhr *et al*., 2021);
- differences in physico-chemical (local) conditions and the ability for acclimatization in

different cross-shelf habitats (for example, shallow tidal pools) (Doo *et al.*, 2014; Fujita *et al.*, 2014; Prazeres *et al.*, 2016, 2017a; Stuhr *et al.*, 2017); or

- evolutionarily high adaptation by their historical contingency and inherited traits (Schmidt *et al.*, 2016; Stuhr *et al.*, 2021).

Large benthic foraminifera test calcification and response to ocean acidification

Future predicted changes in seawater chemistry [pH, alkalinity and saturation state (Ω_{ARG})] are expected to decrease carbonate production in reef settings (Riegl, 2003; Harley *et al.*, 2006; Hoegh-Guldberg *et al.*, 2007, 2017; Carpenter *et al.*, 2008; Knowlton & Jackson, 2008; Pandolfi *et al.*, 2011; Graham *et al.*, 2015). Ocean acidification (OA) will negatively impact growth in carbonate producers in general (Kleypas *et al.*, 1999; Guinotte & Fabry, 2008; Hoffman *et al.*, 2010), in corals (Hoegh-Guldberg *et al.*, 2007; Pandolfi *et al.*, 2011; Doo *et al.*, 2019; Kline *et al.*, 2019), at least in combination with elevated temperatures (Guillermic *et al.*, 2021), and in LBF (Fujita *et al.*, 2011; Hikami *et al.*, 2011; Sinutok *et al.*, 2011; Uthicke *et al.*, 2013; Reymond *et al.*, 2013a; Knorr *et al.*, 2015; Prazeres *et al.*, 2015). It is predicted that reef framework accretion will diminish as the average Ω_{ARG} falls below the current level (Orr, 2005; Hoegh-Guldberg *et al.*, 2017). A decrease in Ω_{ARG} by 1 unit (or below Ω_{ARG} 3.3 to 2.3), as expected by the end of this century, will see the loss of coral dominated ecosystems (Hoegh-Guldberg *et al.*, 2007) through increased bioerosion and carbon-dioxide induced reef dissolution, especially in reefs that demonstrate low (<30%) coral cover (Kline *et al.*, 2019). The impending net-loss (erosion) may ultimately result in the loss of protective barriers, enhanced coastal erosion, and receding of carbonate beaches (Wong, 2003) and of low-lying reef islands (Stoddart & Steers, 1977; Yamano, 2000; Yamano *et al.*, 2007; Kench & Mann, 2017).

Calcification is dependent on the $CaCO_3$ saturation state Ω, but it is also influenced by the covarying parameters of light, temperature, water depth, pH, oxygenation, hydrodynamic energy and nutrient concentrations (Langer *et al.*, 2012, 2013; Weinmann *et al.*, 2013a; Schmidt *et al.*, 2015). Also, *in situ* concentrations of magnesium (Mg), calcium (Ca) and carbonate (CO_3) stoichiometry within the calcifying fluid, play a role (Reymond & Hohn, 2020). In reefs, calcifying marine organisms precipitate $CaCO_3$ skeletons composed of either: (i) aragonite (ARG, for example, corals, most molluscs and calcareous green algae, rare benthic foraminifera); (ii) high-magnesium calcite (HMC > 4 up to 13 mol% $MgCO_3$, for example, benthic foraminifera, calcareous red algae, sponges, crustaceans, echinoderms, serpulid worms and some bryozoans); or (iii) low-magnesium calcite [LMC < 4 mol% $MgCO_3$, for example, benthic foraminifera (Table 1), coccolithophores, molluscs and brachiopods] (Chave *et al.*, 1972; Lees & Buller, 1972; Lees, 1975; Flügel, 1982; Hallock & Schlager, 1986; Hallock, 1988; Halfar *et al.*, 2004; Wilson, 2008). Generally, there is a high degree of carbonate mineral stability in reefs with typical proportions of approximately 60% ARG, 25% HMC and 15% LMC mineralogies (Chave, 1962; Kinard, 1980; Stanley & Hardie, 1998; Raja *et al.*, 2005; Haese *et al.*, 2014). HMC shells are considered to be the most vulnerable to changes in Ω_{CaCO3} (Chave, 1967; Kleypas *et al.*, 1999; Morse *et al.*, 2006; Andersson & Gledhill, 2013). A reduction in the 5:1 Mg:Ca ratio (Morse *et al.*, 2006; Fabry *et al.*, 2008; Doney *et al.*, 2009, 2012; Yamamoto *et al.*, 2012) will favour precipitation of LMC over ARG, as the latter becomes 50% more soluble with undersaturation ($\Omega_{ARG} < 1$) (Stanley & Hardie, 1998).

Most LBF tests are composed of either low magnesium calcite (LMC) or high-magnesium calcite (HMC) (Kinard, 1980), with the latter having a higher solubility in seawater (Raja *et al.*, 2005). It is expected that LBF taxa possessing non-lamellar, porcelaneous-imperforate HMC tests will be more vulnerable to OA (Berner, 1975; Morse *et al.*, 2006). Porcelaneous taxa have a smooth, often translucent, outer test layer that extends over chambers and chamberlets to allow light penetration (Erez, 2003; Fujita *et al.*, 2011). If it dissolves, it leaves the chambers exposed (Cottey & Hallock, 1988; Engel *et al.*, 2015). Alternatively, taxa with hyaline, perforate, lamellar-walled LMC, are expected to show relatively greater resilience to dissolution in reduced pH conditions (Cottey & Hallock, 1988; Engel *et al.*, 2015). Moreover, hyaline taxa can secrete new layers of calcite over their test, thereby thickening the test and allowing for test repair following damage (Erez, 2003; Fujita *et al.*, 2011). The production of these two calcite polymorphs is primarily the result of the differential biomineralization pathways used by foraminifera. The HMC porcelaneous tests are a by-product of dissolved inorganic carbon (DIC) that is transported directly from seawater into the site of calcification, whereas LMC hyaline taxa benefit from pumping protons in exchange for calcium ions into large intracellular vacuoles, which increases the saturation states and thus facilitates calcification (ter Kuile & Erez, 1991; Glas *et al.*, 2012; de Nooijer *et al.*, 2014; Engel *et al.*, 2015; Toyofuku *et al.*, 2017).

The increase in atmospheric CO_2 concentrations is expected to increase dissolved inorganic carbon (DIC) availability, releasing algal symbionts from DIC limitation (Uthicke & Fabricius, 2012); hence, enhancing photosynthetic rates (Hanson & Dalberg, 1979; ter Kuile *et al.*, 1989). Such CO_2-fertilization of algal endosymbionts may increase the supply of energy-rich carbohydrates (photosynthate) to the host and enhance growth and calcification, or as is usually the case, is not sufficient enough to counter the need to remove protons from the site of calcification (Bentov *et al.*, 2009; de Nooijer *et al.*, 2009; Glas *et al.*, 2012; Uthicke & Fabricius, 2012; Martinez *et al.*, 2018). It is fundamental to also consider the diurnal changes in the biological activity of the algal symbionts and the host foraminifer, i.e. increased CO_2 induced by dark respiration (Köhler-Rink & Kühl, 2005) or diurnal recycling of carbon (Müller, 1978). Additionally, it is worth noting the ability of the photosymbiont to control its location, and not necessarily be at the site of calcification, for example as seen in planktonic species (*Hastigerina* sp., *Globigerinoides* sp. and *Orbulina* sp.), which create a rhizopodial network where the algae can be found during the day (Bé *et al.*, 1977), or the movement within the lacunary system amongst imperforated LBF (Leutenegger, 1977). The intracellular symbionts of *Marginopora vertebralis* show phototactic behaviour and are able to relocate (through host-mediated mechanisms) into deeper cavities within the test (Petrou *et al.*, 2017). Such behavioural studies demonstrate the importance of host photoprotection through host–symbiont signalling (Petrou *et al.*, 2017).

On local scales, the potential for studying the adverse effects of OA can be found in studies of natural systems such as shallow water CO_2-seeps (Dias *et al.*, 2010; Uthicke & Fabricius, 2012; Uthicke *et al.*, 2013; Engel *et al.*, 2015; Pettit *et al.*, 2015), groundwater springs (Martinez *et al.*, 2018) and/or in association with marine vegetation (Pettit *et al.*, 2015; Doo *et al.*, 2020). Uthicke *et al.* (2013) found a steep decline in calcifying foraminifer abundance, corrosion of test walls, an absence of carbonate accumulation and no shift to mixotrophy (Uthicke & Fabricius, 2012), in the vicinity of the CO_2-seeps ($pH < 7.9$ and $pCO_2 > 700$ μm) of Papua New Guinea (PNG). Variable symbiont colour was retained in specimens with limited test dissolution under extreme conditions (40 to 60°C, and pH between 5.9 and 7.4) near shallow CO_2-seeps in PNG (Engel *et al.*, 2015). Differences between these cases, possibly species-specific, linked shell structure and composition and likely substrates (i.e. surficial substrates in the former versus hard substrates in the latter). Martinez *et al.* (2018) found that total abundance of foraminifera was reduced (similar to Uthicke *et al.*, 2013). However, the relative abundance of LBF and agglutinated foraminifera was higher in the low pH, low calcite conditions compared to control sites, suggesting that the non-symbiont-bearing, heterotrophic calcareous foraminifera were more sensitive to the effects of OA in the submarine groundwater springs in the Caribbean.

Pettit *et al.* (2015) found that brown seaweed (*Padina pavonica*) associated with CO_2-seeps in the Mediterranean Sea, could not mitigate the effects of OA on epiphytic foraminifera. Instead, as the calcium carbonate saturation state fell, there was a reduction in the number of species, and the assemblage shifted from one dominated by calcareous taxa (pH *ca* 8.19) to one dominated by an agglutinated assemblage (pH *ca* 7.71); this is similar to other findings (Dias *et al.*, 2010). However, Doo *et al.* (2020) found that the stress effects of reduced growth and calcification rates (with increased warming), for the epiphytic *M. vertebralis* were mitigated when associated with non-calcifying macroalgae (*Laurencia intrica*), from the GBR, under end-of-century OA (pH 7.7) scenarios. It seems that, in certain regions, algal (Doo *et al.*, 2020) and seagrass (Martin *et al.*, 2008; Fabricius *et al.*, 2011) substrates may play a role in buffering seawater carbonate chemistry; however, varying results suggest different species-specific interactions between foraminifera and require further exploration.

Several experimental studies of cultured LBF have reported negative effects due to OA (Table 4), including:

1 Reduced test growth or net calcification below pH 7.6 (Lee & Anderson, 1991; Hikami *et al.*, 2011; Uthicke & Fabricius, 2012; Reymond *et al.*, 2013a).

2 Inhibited metabolic activities and enzyme (ATPase) production (Kuroyanagi *et al.*, 2009; Fujita *et al.*, 2011; McIntyre-Wressnig *et al.*, 2011; Uthicke & Fabricius, 2012; Reymond *et al.*, 2013a; Schmidt *et al.*, 2014; Knorr *et al.*, 2015; Prazeres *et al.*, 2015).

3 Reduced chlorophyll-*a* content and photosynthetic efficiency (ter Kuile *et al.*, 1989; Prazeres *et al.*, 2015).

4 Photosymbiont loss (bleaching) (Schmidt *et al.*, 2014).

5 Increased calcite dissolution of the test microfabric (McIntyre-Wressnig *et al.*, 2011; Glas *et al.*, 2012).

6 Inhibition of the enzymes that transport and regulate Ca^{2+} (Ca-ATPase) and Mg^{2+} (Mg-ATPase) in a dinoflagellate-bearing LBF (Prazeres *et al.*, 2015; Stuhr *et al.*, 2021).

Conversely, few studies have demonstrated either constant, or no change in growth or calcification rates (e.g. Fujita *et al.*, 2011; Reymond *et al.*, 2013a; Prazeres *et al.*, 2015), whereas others showed positive effects of OA on:

1 Growth (net calcification) in both diatom-bearing (Souder *et al.*, 2010; Hikami *et al.*, 2011; McIntyre-Wressnig *et al.*, 2011; Sinutok *et al.*, 2011; Uthicke *et al.*, 2013; Martinez *et al.*, 2018) and dinoflagellate-bearing taxa (Vogel & Uthicke, 2012; Schmidt *et al.*, 2014; Martinez *et al.*, 2018).

2 An increase in chlorophyll-*a* production and photosynthesis when combined with increased nutrient loads (Reymond *et al.*, 2013a).

3 In Ca^{2+}-ATPase and Mg^{2+}-ATPase in a diatom-bearing LBF (Prazeres *et al.*, 2015).

It was found that the strongest stress response occurred with the interaction of two stressors, i.e. warming and OA. Multi-stressors resulted in:

- reduced photosynthetic efficiency (Vogel & Uthicke, 2012; Schmidt *et al.*, 2014; Stuhr *et al.*, 2021);
- reduced chlorophyll-*a* and respiration rates (Schmidt *et al.*, 2014; Stuhr *et al.*, 2021); and
- micro-structural alterations to the test including decreased pore size and increased breakage frequency (Stuhr *et al.*, 2021).

Natural laboratories offer opportunities to examine the effect of elevated $p\text{CO}_2$, also in combination with elevated, or even extreme, temperature effects. Few studies have investigated the response of LBF in shallow water CO_2-vents (Hall-Spencer *et al.*, 2008; Dias *et al.*, 2010; Uthicke & Fabricius, 2012; Uthicke *et al.*, 2013; Engel *et al.*, 2015) or other *in situ* habitats (Martinez *et al.*, 2018; Doo *et al.*, 2020). Findings from these studies reveal:

1 Significant decreases in calcification rates and elevated respiration rates (net oxygen production) (Uthicke & Fabricius, 2012), i.e. in *M. vertebralis*.

2 Either signs of corrosion (pitting) of test walls (Uthicke *et al.*, 2013) or limited dissolution (Engel *et al.*, 2015).

3 Decline in the abundance of calcifying taxa (Uthicke *et al.*, 2013; Pettit *et al.*, 2015); and a shift to non-calcifying, agglutinated taxa (Dias *et al.*, 2010; Pettit *et al.*, 2015; Martinez *et al.*, 2018); or higher relative abundances of symbiont-bearing and agglutinated taxa, compared to non-symbiont-bearing, heterotrophic taxa (Martinez *et al.*, 2018).

4 Remarkable short-term tolerance of LBF exposed to low pH conditions and intermittent extremes in temperature, likely associated with substratum type (Engel *et al.*, 2015).

5 Either a reduction in the number of species and a shift from a calcareous to agglutinated-dominated assemblage in association with (non-calcareous) macroalgae (Dias *et al.*, 2010; Pettit *et al.*, 2015) or a positive mitigation against the negative of OA on growth and calcification rates with interaction with macroalgal substratum (Doo *et al.*, 2020).

In an attempt to evaluate the ubiquitous effect of OA on LBF, the authors came across a wide range of responses from: severely damaging (to the algal symbionts), to the opposite response of slightly positive effects. Further *in situ* and cultured studies are necessary to constrain these different trends among different species across broad spatial scales, and to determine how the influence of, for instance: life stages, biochemical pathways of test calcification and experimental parameters (dose levels), will affect LBF response to future impacts.

The impact of sea-level rise on LBF carbonate production

Global mean sea-level rise (SLR) has been occurring at an accelerated rate since the 1960s, due to thermal expansion (Dangendorf *et al.*, 2019), averaging at 3 mm yr^{-1} (Bamber *et al.*, 2019), with a projected rise of at least 0.3 m by 2100 (Bamber *et al.*, 2019; Lindsey, 2019). This is, at best, a conservative estimate, based on a newly defined sea-level sensitivity metric (Grinsted & Christensen, 2021). A very rapid rise in coastal seawater level is expected to increase turbidity and runoff (Rogers, 1990; Fabricius, 2005), drown-out shallow reefs with dire consequences for sessile, photosymbiont-bearing organisms dependent on algal photosynthesis (Edwards & Wright, 2015; Perry *et al.*, 2018). However, the effects of SLR may be mitigated in areas where reef growth and carbonate production rates 'keep-up' with SLR, (Buddemeier & Hopley, 1988; Woodroffe & Webster, 2014).

The use of intertidal benthic foraminifera taxa from post-glacial sedimentary deposits on carbonate shelves has been well-established as indicators of sea-level change in temperate regions (Scott & Medioli, 1978, 1986; Gehrels, 1994; Horton & Edwards, 2003; Cann *et al.*, 2006; Southall *et al.*, 2006; Sifat & Saha, 2019). Similarly, in the tropics, foraminifer taxa from nearshore mangrove and marsh (Horton *et al.*, 2003, 2007), as well as from reef habitats (Horton *et al.*, 2007; Reymond *et al.*, 2011a; Narayan *et al.*, 2015; Johnson *et al.*, 2017; Fujita *et al.*, 2020), show a strong, positive correlation with water depth, and have been used as tools for reconstructing Holocene sea-level change (Frost & Langenheim, 1974; Horton *et al.*, 2005). Such studies provide an analogue for assessing the effect of future predicted SLR on carbonate shelf and slope/ramp environments, including coral reef areas.

It has been suggested that predicted sea-level rise will impact habitats of LBF by reducing current populations to shallow reef crests, thereby reducing test accumulation in back-reef habitats and exacerbating shoreline erosion (Yamano, 2000; Yamano *et al.*, 2007). The impact of sea-level rise on LBF carbonate production dynamics has been assessed through reconstructing the initiation and development of reefs and reef islands, in the light of post-glacial, Holocene sea-level change (Reymond *et al.*, 2011a; Fujita *et al.*, 2020). However, there has been geographical variability of Holocene sea-level in equatorial basins, resulting from regional differences in the solid Earth response to water loading (Camoin & Webster, 2015; Horton *et al.*, 2018; Mann *et al.*, 2019a,b). Accordingly, reconstructions of Holocene LBF carbonate production and their importance for reef island development and maintenance are likely to differ between sites (Kayanne *et al.*, 2002; Fujita *et al.*, 2020).

A recent reconstruction of reef island formation in the Maldives shows that the onset of island formation occurred during a sea-level highstand in the Central Indian Ocean about 2.5 ka BP. During this early phase of island development, the sediment facies was coral dominated, pointing to coral reefs as the most important sediment source (Kench *et al.*, 2020). Following its incipient formation, the shoreline prograded rapidly over the reef flat between 2.1 to 1.5 ka BP, leading to a significant expansion of island size and volume. This major phase of island expansion coincided with a short-term sea-level drop that resulted in adjustments of the surrounding reef flat ecology and concurrent sediment production through a pronounced increase of LBF test accumulation along the shoreline. Consequently, the interplay between future sea-level rise and variable 'keep-up–catch-up' modes of reef platform development, might result in episodic shifts in reef flat ecology, related to water depth, and subsequent pulses of carbonate sediment production through the proliferation of LBF and other taxa (Woodroffe & Webster, 2014; Camoin & Webster, 2015; Yokoyama *et al.*, 2018; Fujita *et al.*, 2020).

A recent study by Fujita *et al.* (2020), found that LBF carbonate sediments accumulated at high rates during the last glacial lowstand, i.e. the Last Glacial Maximum (LGM), at rates similar to or even higher than those accumulated during the Holocene highstand. These deposits were associated with high proportions of fossil *Baculogypsina* and *Calcarina* tests, indicating an earlier development of geomorphically-mature fringing reefs on the modern shelf-edge of the GBR (Fujita *et al.*, 2020). Vertical reef accretion and subsequent development of reef flat and lagoon habitats followed LGM 'keep-up–catch-up' mode of rapid SLR. Thus, geological studies of LBF populations from fossil and submerged ('drowned') reefs, across broad carbonate shelf and ramp environments, can help to improve current understanding of how long-term sea-level fluctuations control the architecture and the potential for accumulation in carbonate depositional systems. The above observation of high accumulation rates during rising sea levels, for example, also corresponds with the behaviour of Miocene reef systems (Pomar, 1991; Pomar *et al.*, 2004; Mateu-Vicens *et al.*, 2012).

Detrimental effects of SLR may therefore be mitigated in areas where active reef growth and carbonate production will be maintained and stable, to allow the reef to keep-up with SLR (Buddemeier & Hopley, 1988; Webb & Kench, 2010; Woodroffe & Webster, 2014). This has been documented in reconstructions of post-glacial Holocene (transgressive) SLR, resulting in reef initiation, development and persistence of reef communities over time (Reymond *et al.*, 2011a, 2013b; Fujita *et al.*, 2020). It is evident that reef ecosystems and low-light adapted carbonate producers (Renema &

Trolestra, 2001; Mateu-Vicens *et al.*, 2012; Renema, 2019) can occur under mesophotic conditions and at greater depth ranges than previously thought (Beaman *et al.*, 1994; Woodroffe & Webster, 2014). However, a loss of functionality, due to chronic bleaching or anthropogenic degradation for instance, may not allow reef ecosystems as carbonate depositional systems to keep pace with SLR (Woodroffe & Webster, 2014).

The combination of sea-level rise and expanding subtropical climatic zones into higher latitudes, could also create additional, suitable shoreline habitats for carbonate deposition by LBF (Hallock, 2005). This could particularly be the case for a few taxa, such as *Amphistegina* spp., which show a wide depth range and temporal latitudinal range expansion (Langer *et al.*, 2012, 2013; Weinmann *et al.*, 2013a), and colonization of tropical species facilitated by increasing temperatures in regions such as the Mediterranean (Prazeres *et al.*, 2020b). Furthermore, increasing temperatures at higher latitudes and the availability of new habitats, could trigger radiation and diversification in LBF (Hallock *et al.*, 1991; Prazeres *et al.*, 2020b).

As a possible countermeasure against shoreline erosion on reef islands, and to enhance the self-sustaining mechanism in reef systems, researchers from Japan and the tropical South Pacific Island of Tuvalu have been mass-culturing *Baculogypsina sphaerulata* (Hosono *et al.*, 2013). This species typically lives in shallow waters (less than 5 m depth) and is thus adapted to the high light intensity and temperature conditions on exposed reef crests at low tide. Such efforts highlight the importance of ecosystem services provided by LBF and the potential for sustainable, high efficacy ecoengineering solutions with low environmental impacts (Hosono *et al.*, 2014; Fujita *et al.*, 2016).

FUTURE DIRECTIONS AND SUMMARY

Large benthic foraminifera (LBF) diversification and carbonate production have been intricately linked to ocean-climate conditions. In the ‘hothouse world’ of the early Cenozoic Era, vast nummulitic carbonate accumulations, consisting of exceptionally large, flattened and possibly long-lived (Ferrández-Canadell *et al.*, 2014; Hallock & Seddighi, 2021) LBF taxa, developed steadily over time, and were accompanied by warm temperatures, extremely depleted nutrients, reduced thermal stratification and ocean circulation, in possibly deep-water oligophotic settings (Racey, 2001; Hallock & Pomar, 2009; Pomar *et al.*, 2017; Hallock & Seddighi, 2021). Modern analogues are rare. The closest extant, largest and deepest-dwelling nummulitid LBF, *Cycloclypeus carpenteri*, is limited today to deep-waters in the Indo-west Pacific (Hohenegger, 1994; Beavington-Penney & Racey, 2004). It does not form similar carbonate deposits as in ancient times, largely due to dissimilarity in environmental conditions (Beavington-Penney & Racey, 2004; Hallock & Seddighi, 2021). Under rapidly changing ocean-climate conditions, the question remains as to whether LBF will have the capacity to acclimatize and maintain active carbonate production at current or higher production rates. In order to reduce under and/or overestimation, this review highlights the need for reef carbonate budget estimates, based on LBF, to encompass broader carbonate-producing reef habitats; and increase knowledge of life-history, growth and turnover rates, of a greater number of LBF species.

While LBF have had successful and widespread application in long-term, ecological studies, it appears that their underwhelming representation in modern coral reef studies lags, due to a lack of awareness of LBF relevance as carbonate producers and/or the impression that their application is too traditional and time-consuming. However, as greater collaborative efforts among reef scientists continue, it will encourage the application and further refinement of foraminifer bio-indicator tools, because they are cost-effective ways to sample, monitor and assess reef health, with a minimal environmental footprint (Hallock *et al.*, 2003; Prazeres *et al.*, 2020a). Prioritizing the use of comparative, comprehensive and complementary micropalaeontological and ecological research will benefit future pursuits in understanding carbonate ecosystems. As a way forward, greater inter-disciplinary approaches that integrate established, standardized protocols with relevant, new technologies, for example, remote sensing and habitat mapping (Doo *et al.*, 2017; Förderer *et al.*, 2018), and field-based ecological approaches, will provide valuable insights into the magnitude of species diversity and carbonate production across broader spatial and temporal scales. Such inter-disciplinary approaches may inspire increased cooperation among reef scientists, to draw a clearer picture of carbonate dynamics under changing conditions and potentially how to protect vital reef habitat areas.

Nearly 90% of the worlds coral reefs are expected to be threatened with environmental degradation by 2030 (Burke *et al.*, 2011) with only 10% remaining in suitable refugia by mid-century (Burke *et al.*, 2011; Hoegh-Guldberg *et al.*, 2017). Therefore, identification and protection of important, highly buffered calcification or climate refugia (Doo *et al.*, 2017; Förderer *et al.*, 2018) and areas of high species richness (Beckwith *et al.*, 2019; Kapsenberg & Cyronak, 2019; Doo *et al.*, 2020) is becoming increasingly critical. Refugia are areas where localized environmental conditions afford natural resilience (Glynn, 1996) to protect species from unfavourable or harmful conditions (Ashcroft, 2010; Kapsenberg & Cyronak, 2019) and/or reduce a species vulnerability to stressors by allowing persistence under changing conditions (Bongaerts *et al.*, 2010; Dawson *et al.*, 2011; Kapsenberg & Cyronak, 2019; Doo *et al.*, 2020). These areas promote high species richness influenced by oceanic current patterns (Förderer *et al.*, 2018), historical climatic stability (Riegl & Piller, 2003; Keppel *et al.*, 2012) and species persistence under changing conditions (Carter *et al.*, 2020). They can offer protection for biodiverse stocks of carbonate producers and help maximize genetic diversity necessary for adaptation and dispersal (Knowlton, 2012).

Globally, in addition to warmer ocean temperatures, increasing local anthropogenic impacts such as sewage effluents, oil spills and overharvesting, directly diminish the potentiality for the existence of such refugia. Therefore, the urgent identification and protection of carbonate/climate refugia (Riegl & Piller, 2003; Bongaerts *et al.*, 2010; Keppel *et al.*, 2012; Beckwith *et al.*, 2019) is an important first step to supporting and safeguarding current resilient stocks (Carter *et al.*, 2020). Reef ecosystems experiencing high anthropogenic or climatic pressures may still contain conditions (for example, exposure hotspots) to allow for adaptive behaviours and suitable microhabitats that support resilient LBF taxa. It is likely that suitable refugia for LBF may include environments that show: high alkalinity and seawater buffering potential, for example: among non-calcifying macroalgal (Doo *et al.*, 2020) and/or seagrass beds; high habitat connectivity; suitable hydrodynamics including vigorous water circulation (Riegl & Piller, 2003), currents, internal waves (Reid *et al.*, 2019) and low sedimentation rates. They may include areas where species show a capacity for natural acclimatization to high thermal tolerance thresholds or past bleaching events, such as in the high-latitude reefs of the Persian Gulf (Riegl, 2003; Riegl *et al.*, 2011), Caribbean (Castillo *et al.*, 2012), Kiribati (Carilli *et al.*, 2012) and Hawaii (Coles *et al.*, 2018). Further work is needed to better understand the eco–evo dynamics (Pelletier *et al.*, 2009), in which ecological (habitat) associations and interactions can affect evolutionary trajectories of species to promote adaptation (Fig. 2).

In summary, this review highlights key contributions to current understanding of how symbiont-bearing LBF may respond to current and future predicted environmental and climatic change, and its implications for carbonate production. Knowledge gaps exist, and the future of LBF research may benefit from: (i) understanding of the role that species-specific differences play in LBF resilience; (ii) refinement and standardization of the methods for estimating carbonate production rates; (iii) understanding the dynamic continuum between LBF from source to sink, and how this may be critically linked to the maintenance of coastal shorelines and landforms, as well as ecological reef (health) status; and (iv) increased assessment of LBF distribution and carbonate production in under-represented carbonate environments, LBF long-term persistence in these environments and their potential for acting as carbonate refugia.

Large benthic foraminifera appear to be an adaptive, robust and resilient group of $CaCO_3$-producers in the face of stressors in recent times. Several studies presented in this review provide support for the potential success of LBF, while others showed opposite and detrimental effects, under future predicted climate change scenarios. Overall, these studies support their circum-global distribution; latitudinal range expansions into high-latitude reefs (amphisteginids); flexibility in their host–diatom partnerships to suit different environmental conditions; persistence under varying conditions; and their relative tolerance for episodic thermal stress in nearshore environments. The studies that support the hypothesis that LBF have a high acclimatization capacity to short-term environmental stress, touch upon the idea that LBF may potentially thrive in a ‘hothouse world’ over other calcifiers such as corals and calcareous coralline algae. However, knowledge gaps that emerge suggest that further studies are needed in the understanding of: (i) host–symbiont acclimatization and multi-generational adaption potential, an area that is lacking or still in its infancy; and

(ii) the differences in responses across temporal and spatial scales amongst a wider variety of LBF taxa and across broader oligotrophic to mesotrophic, shelf to slope carbonate environments.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

Data sharing not applicable – no new data generated.

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