1 Title: Mass culturing of living sands (*Baculogypsinasphaerulata*) to protect island coasts against
2 sea-level rise
3
4 Running title: Mass culturing of *Baculogypsinasphaerulata*
5
6
7 Takashi Hosono^{*a)}, PaeniuLopati^{b)}, Filipino Makolo^{b)}, Hajime Kayanne^{a)}
8
9 ^{a)}Department of Earth and Planetary Science, Graduate School of Science, The University of Tokyo, 7-3-1
10 Hongo, Bunkyo-ku, Tokyo 113-8654, Japan
11 ^{b)}Fisheries Department, Teone Funafuti, Tuvalu
12
13 Corresponding author: Takashi Hosono
14 E-mail: usujiri3@gmail.com
15 Telephone number: +81-3-5841-4021
16
17

18 **Abstract**

19 Coral reef islands have a self-sustaining mechanism that expands and maintains the islands
20 through the deposition of calcium carbonate (CaCO₃) by marine organisms. However, the human
21 societies established on such low-lying coral reef islands are vulnerable to rapid sea-level rises.
22 Enhancing the self-sustaining mechanism of coral reefs will become one of the required sustainable
23 countermeasures against sea-level rise. We examined the feasibility of mass culturing the large benthic
24 foraminifera *Baculogypsina sphaerulata*, which is known as “living sand.” We developed a rearing
25 system with the key components of an artificial lawn as a habitat and a stirring device to create vertical
26 water currents. Batches of *B. sphaerulata* in two different size groups were reared to examine size
27 growth and reproduction under the culture conditions. All culture batches reproduced asexually
28 following generations over 6 months in culture. The small-sized group exhibited steady growth, whereas
29 the large-sized group underwent a reduction in mean size because large individuals (>1.5 mm²) died off.
30 Similar traits of size structure between the culture batches and natural populations indicate that our
31 culturing conditions can successfully reproduce environments similar to the habitat of
32 this species. Reproduction, consistent size growth, and size structure similar to the natural population
33 indicate that the examined rearing system is viable for culturing Foraminifera at a large scale.

34

35 **Keywords:** *Baculogypsina sphaerulata*, coral reef island, aquaculture, mass culturing, sea-level rise

36

37

38 **1. Introduction**

39 Global sea-level rise is widely recognized as one of the consequences of anthropogenic
40 climate change. To protect coastal lines against sea-level rise, countries located in low-lying areas, such
41 as the Netherlands, are working on coastal protection by means of beach nourishment as an

eco-engineering approach to flood management along the coast (Delta Commission, 2008; Kabat et al., 2009). Similarly, low-lying reef islands on coral reefs are also threatened by anticipated sea-level rise (Nicholls et al., 2007; Perry et al., 2011; Woodroffe, 2008; Yamano et al., 2000). Coral reef islands are originally established by the natural process of sedimentation of calcium carbonate (CaCO_3) produced by marine organisms such as corals, shells and calcareous algae (Kench et al. 2005, 2009; Perry et al., 2011; Yamano et al., 2007). This means that coral reef islands have a land-forming and -expanding mechanism (Kench et al., 2005; 2009). If it is possible to promote such a self-sustaining mechanism, it can be used as an effective and sustainable countermeasure against sea-level rise with a low environmental load.

The algal symbiont-bearing large benthic Foraminifera (LBF) known as “living sand” are unicellular animals with a hard calcium carbonate shell. Because they are widely distributed around coral reefs and often form high-density populations on reef flats, LBFs play a major role in CaCO_3 production in coral reef ecosystems (Fujita and Fujimura, 2008; Hallock, 1981a; Kayanne et al., 2011; Langer, 2008; Langer et al., 2013; Thissen et al., 2013). In some Indo-Pacific coral reefs, LBF CaCO_3 production can contribute 30-90% of the reef deposits (Chapman, 1901; Langer et al., 1997; Yamano et al. 2007). Among LBFs, several species, such as *Marginopora* spp., *Calcarina* spp., *Baculogypsina sphaerulata*, and *Amphistegina* spp., which are distributed in shallower areas and largely contribute to coastal sediments, are potential candidates for mass culturing. Rearing these LBFs would not be very difficult on a small scale. Previously, these species have been cultured within Petri dishes or small bottles for several days, several months or approximately 1 year to investigate their life histories or to examine their responses to degradation in coastal environments (Hallock, 1981b, 1986; Lee et al., 1991; Schmidt et al., 2011; Talge and Hallock, 2003; Uthicke et al., 2012; van Dam et al., 2012a, 2012b). A case report regarding the incidental formation of benthic Foraminifera assemblages in an artificial coral reef in an aquarium (Ernst et al., 2011) also indicated the ease of

66 rearing these animals. However, Ernst et al. (2011) mentioned that calcarinids, which dominate
67 the Indonesian natural coastal habitat, did not occur in the aquarium assemblages. This indicates that
68 some type of management is required for mass culturing of the calcarinids that play a major role as sand
69 producers in shallower areas. To establish culturing methods for LBFs as reliable countermeasures
70 against sea-level rise, it is essential to quantify suitable rearing conditions for these
71 organisms and confirm whether generation exchange is possible under those conditions to enable
72 the rearing of these organisms on a large scale.

73 *Baculogypsina sphaerulata* (Foraminifera, Calcarinidae) dominates the sediments of some
74 Indo-western Pacific coral reefs (Collen and Garton, 2004; Dawson et al., 2012; Yamano et al., 2007).
75 The species is distributed mainly in the reef crest (shallower than 5 m depth), which is the most exposed
76 habitat for LBFs (Hallock, 1984; Hohenegger, 1994, 2004, 2006; Hohenegger et al., 1999). Because its
77 habitat is characterized by emersion, high light intensity and high temperatures at low tide in tropical
78 environments, the species is considered to have high tolerance to environmental changes.
79 This tolerance could make it easy to culture and handle the species in artificial conditions. However,
80 there are only a few studies reporting rearing experiments of the species, for example,
81 photo-physiological experiments conducted over a few days (Fujita and Fujimura, 2008; Hosono et al.,
82 2012; Ziegler and Uthicke, 2011) or rearing experiments to describe its growth patterns over 2 months
83 (Hosono et al., 2013). In the present study, we examined whether it is possible to rear *B. sphaerulata*
84 for a long period on a large scale. Specifically, we focused on the following points to evaluate the
85 feasibility of culturing: (1) steady growth in culture conditions and (2) a new generation reproduced by
86 the rearing batches under the culture conditions.

87

88

89 **2. Materials and methods**

90 A plastic tank (187 cm³; length × width × depth: 136.4 × 90.2 × 20.7 cm) was prepared for the
 91 culturing. It is known that the growth of *Amphistegina* spp., which are algaesymbiont-bearing LBFs,
 92 largely depends on light availability (Hallock, 1986). Therefore, the tank was placed in an outdoor
 93 location at the Fisheries Department in Tuvalu to imitate a shallow reef-flat, the natural habitat for
 94 *Baculogypsina*. The tank was divided into four blocks, and artificial lawns (15 × 21 cm) were installed
 95 as a habitat substrate in each block. In its natural habitat, *Baculogypsina* attaches with their pseudopod
 96 to turf algae growing in a thin sediment layer of coral sand (Fig. 1A). To imitate the natural habitat of
 97 the species, the artificial lawns were arranged in a manner such that the leaves (thickness: 0.5 mm;
 98 green projection in Fig. 1B) stood erect from the bottom surface, and the leaves were trimmed to
 99 approximately 0.7 cm high. Under high light intensity, the substrate and *B. sphaerulata* are easily
 100 covered with microalgae such as diatoms or cyanobacteria. This competition was a major cause of
 101 failure in our preliminary culturing. However, constant disturbance with sand and water currents
 102 inhibits cyanobacterial overgrowth and allows a high survival rate (> 90%) of *Baculogypsina* within a
 103 small floating chamber (Hosono et al., 2013). Therefore, we attempted to create constant disturbance
 104 using a combination of fine sands and current (Fig. 2). Aeration nozzles were arranged in a grid-like
 105 array with a spacing of 6 cm on the artificial lawn, and the openings of the nozzles were positioned near
 106 the lawn surface and oriented downward. The artificial lawns were covered with coral sands (< 500 μm
 107 sieve-size) to a depth of 0.5 cm. Aeration was used to create vertical currents to stir the sand particles
 108 throughout the experiment. Depending on the status of algae overgrowth, we removed the algae from
 109 the surface of the artificial lawn with a hand brush every 2 weeks. Seawater in the tank was exchanged
 110 at a rate of approximately 1000 ml/min. During the experiment, the water temperature and light
 111 intensity were monitored every 10 min using a temperature logger (Hobo UA-002-64, Onset Corp.,
 112 USA) and a light logger (MDS-MkV/L, JFE Advantech Co. Ltd., Japan). The mean water temperature
 113 was 28.7°C (±1.39 SD), and the maximum temperature reached 40.9°C in the daytime (Fig. 3A). The

114 mean maximum light intensity in the daytime was $1588 \mu\text{mol photons m}^{-2} \text{ s}^{-1}$ (± 765.3 SD) (Fig. 3B).

115 To evaluate the growth of cultured *B. sphaerulata*, size-controlled batches were prepared.
116 Animals were collected from an intertidal area on the ocean side of a causeway in Fongafale Island,
117 Tuvalu, on March 25, 2012. The collected specimens were sorted using sieves with openings of 0.5
118 and 1 mm under water; the specimens in the fraction >1 mm were categorized as the large-sized group,
119 whereas the specimens in the fraction within 0.5-1 mm were categorized as the small-sized group. At
120 the beginning of the experiment, approximately 200-400 individuals were randomly collected from
121 each fraction, and their sizes were measured based on the area of a two-dimensional projection to
122 determine the size structures of the two groups. Each size group was randomly divided into two rearing
123 groups for a total of four rearing groups introduced into each rearing block. Specimens were retrieved
124 on 29 September 2012, 182 days after the start of the experiments, and their size structure was
125 examined. The specimens were also checked for their reproductive types (sexual or asexual). Röttger
126 et al. (1990) reported that the proloculus size (a cell-like CaCO_3 framework within a shell)
127 in individuals (agamonts) that reproduced asexually by multiple fission is smaller than that in
128 individuals (gamonts) produced by sexual reproduction. The size of the proloculus of newly born
129 individuals measuring less than approximately 0.2 mm^2 was checked under a microscope.

130 The size structures of the cultured populations were compared with that of a natural
131 population. Samples of a natural population were obtained on 17 March and 30 September 2012 in the
132 areas where we collected the culturing specimens. We randomly selected four sampling areas
133 (each 8.64 cm^2) from the habitat, collected the foraminifera with their substrate (algae and sediments),
134 and then measured their sizes to determine the size structure.

135 Densities of *Baculogypsina* in the culturing tank were checked after the experiments. To
136 estimate the LBF densities in the experiments, we photographed each rearing block of the large-sized
137 group. The number of visible individuals larger than 1 mm^2 was counted. Then, we compared the

138 densities with the number of individuals in the same size range ($>1 \text{ mm}^2$) of a natural population.

139

140

141 **3. Results**

142 The mean initial size was 1.48 mm^2 in the large-sized group (Fig. 4A) and 0.78 mm^2 in the
143 small-sized group (Fig. 4C). The size distribution pattern changed from unimodal to bimodal,
144 indicating reproduction during the rearing period of 182 days (Figs. 4B, D). In the large-sized group,
145 small individuals less than 1.0 mm^2 were excluded before rearing, but many individuals less than 1.0
146 mm^2 were observed after rearing. Similarly, in the small-sized group small individuals less than 0.4
147 mm^2 were excluded before rearing, but after rearing, individuals less than 0.4 mm^2 were observed.
148 These changes in size structure before and after rearing indicate that newly born individuals reached up
149 to 1.0 mm^2 and 0.4 mm^2 in the large-sized and small-sized groups, respectively. No individual with a
150 small proloculus was confirmed, indicating that the newly born individuals were produced by asexual
151 reproduction.

152 To evaluate growth in the cultured batches, the mean sizes of the groups were compared,
153 excluding the newly generated individuals. The mean size of the large-sized group after rearing (1.34
154 mm^2 , Fig. 4B) was significantly smaller than the same group before rearing (Kolmogorov-Smirnov
155 test, $p < 0.001$; Fig. 4A, B). The mean size of the small-sized group increased significantly after
156 rearing (mean size: 0.97 mm^2 ; Fig. 4D) compared to before rearing (K-S test, $p < 0.001$; Fig. 4C). The
157 rate of occurrence of individuals over 1 mm^2 was 17.7% before rearing (Fig. 4C) but increased to
158 35.7% after rearing (Fig. 4D). The maximum size also changed from 1.4 mm^2 to 2.0 mm^2 (Fig. 4C, D).
159 The size range of the small-sized group was larger after rearing than before rearing (from 0.39 - 1.15
160 mm^2 to 0.49 - 1.45 mm^2 in the 5-95% quantile range), which suggests that individual growth rates were
161 not homogeneous but varied among individuals.

162 The natural population of *B. sphaerulata* in a tropical habitat had a flat size structure up to
163 1.5 mm² on both sampling dates, except for the size mode of 0-0.5 mm² in the population of September
164 30 (Figs. 4B, D). The frequency of large size classes decreased beyond 1.5 mm² and dropped to almost
165 zero at approximately 2.0 mm² for both sampling dates. These traits corresponded to those in the small-
166 and large-sized culturing groups after the rearing period (Figs. 4B, D).

167 The densities of individuals larger than 1.0 mm² in the natural population at the study site of
168 Fongafale Island were 36.5 cm⁻² (± 28.5 SD) and 16.3 cm⁻² (± 6.03 SD) in March and September,
169 respectively. The rearing densities of visible individuals (> 1.0 mm²) were 15.1 cm⁻² (± 4.2 SD) at the
170 beginning and 8.5 cm⁻² (± 1.5 SD) at the end of the experiments.

171

172

173 **4. Discussion**

174 *4.1 Growth and reproduction in mass culturing*

175 In both the large- and small-sized groups, the individuals smaller than the original
176 individuals were newly born. This is the first successful report of asexual reproduction of the
177 *Baculogypsina* foraminifer in mass culturing conditions. In the large-sized group, the newly born
178 generation could grow up to the size of 1.0 mm². In the small-sized group, the original individual itself
179 grew to a larger size and then produced a second generation. The observed growth and reproduction
180 indicate that it is possible to create net CaCO₃ production within a culture tank.

181 Growth in culturing conditions can be evaluated through a comparison with the known
182 growth patterns of the species or with the size structure of a natural population. Hosono et al. (2013)
183 estimated the growth pattern of the species under experimental conditions as a logistic
184 equation: $G = 0.0065S(2.66 - S) / 2.66$, where G is the growth rate (mm²/day) and S is the size in area
185 (mm²). Based on this equation, the mean sizes of cultured batches after 182 days are predicted to

186 be 1.09 and 1.95 mm² in the small- and large-sized groups, respectively. However, the actual mean
 187 sizes of the small- and large-sized groups (0.97 and 1.34 mm², respectively) were both smaller than the
 188 predictions. In the large-sized group, individuals did not grow much beyond 2.0 mm², and the
 189 proportion of large individuals (> 1.5 mm²) was decreased. The decrease in number of larger
 190 individuals can be partly explained by the generation exchange, where large mature individuals
 191 (agamonts) died after reproduction. A decreased occurrence of larger individuals (> 1.5 mm²) was also
 192 observed in the natural population (Figs. 4B, D). Annual changes in the population structure of the
 193 species have been studied in a sub-tropical area of Okinawa Island by Sakai & Nishihara (1981) and
 194 by Hohenegger (2006). From the size histograms reported in those two papers, it can be recognized
 195 that the frequency of large-sized individuals decreased rapidly beyond the size of approximately 1.4 or
 196 1.5 mm² [originally 1.3 mm in diameter, Sakai & Nishihara (1981); 1.0 mg^{1/3} in weight, Hohenegger
 197 (2006), respectively]. These size structural traits suggest a possibility of decreased growth rates and/or
 198 increased natural mortalities at sizes over approximately 1.5 mm². Therefore, it is thought that the
 199 decrease in mean size observed in the culturing of the large-sized group is due to size-dependent
 200 mortality and/or growth limitation over 1.5 mm², similarly to the natural population. In the small-sized
 201 group, individuals could grow up to a larger size, but the mean size (0.97 mm²) was smaller than
 202 predicted by the growth equation of Hosono et al. (2013). The mean growth rate in the small-sized
 203 group was reduced by the occurrence of individuals with a restricted growth rate. This low growth rate
 204 appears to be caused by rearing conditions peculiar to mass culturing. In the present study, we used an
 205 artificial lawn with a three-dimensional structure and coral sands to create disturbance (Figs. 1B; 2); as
 206 a result, individual microenvironments were heterogeneous due to the uneven sand distribution and
 207 substrate structures.

208 A large variability in growth rate due to heterogeneous micro-environments could lead to a
 209 decreased growth rate of the whole culture population and thus reduce sand production. The

210 attachment mechanism via the pseudopodia of *B. sphaerulata* is considered to be one cause of the large
 211 variability in growth rate among individuals. Algal symbiont-bearing LBFs, including *B. sphaerulata*,
 212 obtain nutrients by filter feeding and concurrently obtain photosynthesis products from their symbiotic
 213 algae (Lee, 1980; Lee and Anderson, 1991). Hallock (1986) reported that the growth rate of
 214 *Amphistegina lobifera* varied significantly depending on light levels, from 0.3 $\mu\text{g/day}$ at 1.6 $\mu\text{E s}^{-1}$
 215 m^{-2} to 6.6 $\mu\text{g/day}$ at 40 $\mu\text{E s}^{-1} \text{m}^{-2}$. Another LBF, *Marginopora vertebralis*, exhibits diel motility to
 216 select habitat in response to changes in light conditions (Sinutok et al., 2013). Fujita et al. (2000)
 217 investigated the population dynamics of *M. kudakajimensis* throughout the year and observed that
 218 natural mortality increased in July to September, with increased crowding caused by its sessile
 219 attachment pattern and overlap between large individuals. These studies indicate that the motility
 220 pattern, attachment pattern, and/or individual interactions of each LBF can strongly affect light
 221 availability for individuals. Regarding *B. sphaerulata*, Röttger and Krüger (1990) described a durable
 222 attachment mechanism in the species that allows it to thrive in high-energy environments of intertidal
 223 areas facing the ocean. This attachment mechanism indicates that *Baculogypsina* have less motility.
 224 Therefore, once *Baculogypsina* individuals attach to their substrate, their capacity for behavioral
 225 modification against subsequent environmental changes is considered to be relatively low, similar to
 226 the case of *M. kudakajimensis* described by Fujita et al. (2000). This low responsiveness could enhance
 227 the difference in light availability caused by the heterogeneity of microenvironments under culture
 228 conditions. In addition to the heterogeneity of culture conditions similar to the field, the specific
 229 responsiveness of *B. sphaerulata* to this heterogeneity may result in larger variability in growth
 230 rates. This study demonstrated that it is possible to reproduce habitable environments in culture tanks.
 231 However, it has also revealed the tradeoff between culturing at a high density and heterogeneous
 232 growth of the species, which must be taken into consideration for more efficient CaCO_3 production.
 233 Aside from heterogeneous microenvironments, there is another possible mechanism that

234 explains the restricted growth rates observed under the artificial environments. Respiration and
235 photosynthesis of the species as a holobiont peaks at approximately 30°C, and physiological
236 metabolisms are drastically restricted at 35°C (Fujita et al. in press). In the present study, we set culture
237 tanks in an outdoor location to imitate the natural habitat of *Baculogypsina*. However, this
238 environment caused a rapid increase of water temperature in daytime (Fig. 3A). During the study
239 period, the water temperature in the culture tanks frequently reached 35-40°C in daytime.
240 Therefore, the high temperature condition might have had a negative influence on the growth of the
241 species in the culture tanks. However, because high temperature conditions also usually occur in the
242 natural intertidal habitat during low tide in spring tides under the tropical climate of Tuvalu with strong
243 solar radiation (see electrical supplement, Fig. ES), the species occasionally experiences similar
244 temperature changes in its natural habitat. Further investigation of the optimum temperature conditions
245 or temperature fluctuation pattern needed to promote its growth rate in prolonged culturing is needed to
246 promote efficient sand production.

247

248 4.2 Culturing foraminifera

249 To apply a reliable countermeasure against sea-level rise, it is essential not only to develop
250 culturing techniques but also to keep the culturing cost at a practical level. Our culturing method
251 requires only commercially available materials, such as a plastic tank and an artificial lawn, which are
252 not expensive technical equipment. However, our method also requires aeration and seawater intake,
253 which represent a major portion of the overall running cost (i.e., electricity expenses). From the
254 perspective of practicality in an electrical-resource-limited island country, a culturing method that
255 requires little electrical power should be developed as a next step.

256 There are significant merits to culturing Foraminifera as a countermeasure against sea level
257 rise, although technical issues still remain to be resolved. The first is that culturing Foraminifera (sand

258 production) and sand consumption (usage of sand for beach nourishment) can both occur within a
259 local region. This linkage indicates a low environmental risk of physically or biologically disturbing
260 coastal ecosystems due to transport between the source and destination. Defeo et al. (2009) reviewed
261 the ecological impacts of beach nourishment and summarized their management recommendations as
262 follows: (1) avoid sediment compaction; (2) carefully time the operations to minimize biotic impacts
263 and to enhance recovery; (3) select locally appropriate techniques; (4) implement several small projects
264 rather than a single large project, including repeated application of sediment in shallow layers (<30 cm)
265 rather than in single pulses that kill the fauna by deep burial; (5) intersperse nourished beach sections
266 with unaffected areas; and (6) import sediments and create beach profiles that match the original beach
267 conditions as closely as possible. The combination of Foraminifera culturing and beach nourishment
268 by enhancing natural mechanisms such as sand transportation and sedimentation by coastal currents
269 along coral reef islands would fulfill recommendations (1)-(4) and can create beach profiles closely
270 similar to the original one, as suggested in recommendation (6). Additionally, Foraminifera can
271 potentially be raised as ornamental species. *Baculogypsina sphaerulata* and its processed goods are
272 known as high-profile goods for souvenirs in Japan. An analysis of the financial feasibility of culturing
273 Foraminifera will reveal whether these species can become target species for culturing, along with
274 pearl oysters, giant clams and corals, for export for the hobby aquarium industry.

275

276 4.3. Conclusions

277 This study reveals that it is possible to reproduce a habitable environment for *B.*
278 *sphaerulata* on a large scale. Mass culturing of the species indicates a possibility of promoting sand
279 production to protect the coastal zone of coral reef islands as one of the sustainable countermeasures
280 against sea-level rise.

281

282

283 **5. Acknowledgements**

284 We extend our sincerest thanks to Mochida Takeo (JICA) and Semese Alefaio for their
285 coordination of our project and to Yoichi Ide (Ocean Planning Co., Ltd.) for assistance with the field work.
286 We also extend our thanks to three anonymous reviewers for their helpful comments and suggestions to
287 improve the manuscript. This study was supported by JST/JICA's Science and Technology Research
288 Partnership for Sustainable Development (SATREPS, 0808918) and by the Adaptable and Seamless
289 Technology Transfer Program through target-driven R&D, JST (AS242Z01815N). The authors declare that
290 they have no conflict of interest.
291

292 **References**

- 293 Chapman, F., 1901. Foraminifera from the Lagoon at Funafuti. J. Linn. Soc. Lond. Zool. 28, 161-210.
- 294 Collen, J.D., Garton, D.W., 2004. Larger foraminifera and sedimentation around Fongafale Island,
- 295 Funafuti Atoll, Tuvalu. Coral Reefs 23, 445-454.
- 296 Dawson, J.L., Hua, Q., Smithers, S.G., 2012. Benthic foraminifera: Their importance to future reef
- 297 island resilience, in: Yellowlees, D., Hughes, T.P. (Eds.), Proceedings of the 12th
- 298 International Coral Reef Symposium. James Cook University, Townsville, Cairns, Australia,
- 299 p. 7.
- 300 Defeo, O., McLachlan, A., Schoeman, D.S., Schlacher, T.A., Dugan, J., Jones, A., Lastra, M., Scapini,
- 301 F., 2009. Threats to sandy beach ecosystems: A review. Estuar. Coast. Shelf Sci. 81, 1-12.
- 302 Delta Commission, 2008. Working together with water. A living land builds for its future, Findings of
- 303 the Deltacommissie, p. 134.
- 304 Ernst, S., Janse, M., Renema, W., Kouwenhoven, T., Goudeau, M.-L., Reichart, G.-J., 2011. Benthic
- 305 foraminifera in a Large Indo-Pacific coral reef aquarium. J. Foraminifer. Res. 41, 101-113.
- 306 Fujita, K., Fujimura, H., 2008. Organic and inorganic carbon production by algal symbiont-bearing
- 307 foraminifera on northwest Pacific Coral-Reef Flats. J. Foraminifer. Res. 38, 117-126.
- 308 Fujita, K., Nishi, H., Saito, T., 2000. Population dynamics of
- 309 *Marginopora kudakajimensis* Gudmundsson (Foraminifera: Soritidae) in the Ryukyu Islands,
- 310 the subtropical northwest Pacific. Mar. Micropaleontol. 38, 267-284.
- 311 Fujita, K., Okai, T., Hosono, T., in press. Oxygen metabolic responses of three species of large benthic
- 312 foraminifers with algal symbionts to temperature stress. Plos One.
- 313 Hallock, P., 1984. Distribution of selected species of living algal symbiont-bearing foraminifera on
- 314 two pacific coral reefs. J. Foraminifer. Res. 14, 250-261.
- 315 Hallock, P., 1986. Influence of environment on the test shape of *Amphistegina*. J. Foraminifer. Res. 16,

316 224-231.

317 Hallock, P., 1981b. Light dependence in *Amphistegina* J. Foraminifer. Res. 11, 40-46.

318 Hallock, P., 1981a. Production of carbonate sediments by selected large benthic foraminifera on two

319 Pacific coral reefs. Journal of Sedimentary Research 51, 467-474.

320 Hohenegger, J., 1994. Distribution of Living Larger Foraminifera NW of Sesoko-Jima, Okinawa,

321 Japan. Mar. Ecol. 15, 291-334.

322 Hohenegger, J., 2004. Depth coenoclines and environmental considerations of Western Pacific larger

323 foraminifera. J. Foraminifer. Res. 34, 9-33.

324 Hohenegger, J., 2006. The importance of symbiont-bearing benthic foraminifera for West Pacific

325 carbonate beach environments. Mar. Micropaleontol. 61, 4-39.

326 Hohenegger, J., Yordanova, E., Nakano, Y., Tatzreiter, F., 1999. Habitats of larger foraminifera on the

327 upper reef slope of Sesoko Island, Okinawa, Japan. Mar. Micropaleontol. 36, 109-168.

328 Hosono, T., Fujita, K., Kayanne, H., 2012. Estimating photophysiological condition of

329 endosymbiont-bearing *Baculogypsina sphaerulata* based on the holobiont color represented

330 in CIE L*a*b* color space. Mar. Biol. 159, 2663-2673.

331 Hosono, T., Lopati, P., Kayanne, H., 2013. Estimation of the growth pattern of *Baculogypsina*

332 *sphaerulata* (Foraminifera) in a tropical environment using a floating chamber method. J.

333 Exp. Mar. Biol. Ecol. 448, 156-161.

334 Kabat, P., Fresco, L.O., Stive, M.J.F., Veerman, C.P., Alphen, J.S.L.J.v., Parmet, B.W.A.H., Hazeleger,

335 W., Katsman, C.A., 2009. Dutch coasts in transition. Nature Geoscience 2, 450-452.

336 Kayanne, H., Yasukochi, T., Yamaguchi, T., Yamano, H., Yoneda, M., 2011. Rapid settlement of

337 Majuro Atoll, central Pacific, following its emergence at 2000 years CalBP. Geophys. Res.

338 Lett. 38, L20405.

339 Kench, P., Perry, C.T., Spencer, T., 2009. Coral Reefs, in: Slaymaker, O., Spencer, T.,

340 Embleton-Hamelin, C. (Eds.), *Geomorphology and Global Environmental Change:*
341 *Landscape Scale Implications*. Cambridge University Press, Cambridge, pp. 180-213.

342 Kench, P.S., McLean, R.F., Nichol, S.L., 2005. New model of reef-island evolution: Maldives, Indian
343 Ocean. *Geology* 33, 145-148.

344 Langer, M.R., 2008. Assessing the Contribution of Foraminiferan Protists to Global Ocean Carbonate
345 Production. *J. Eukaryot. Microbiol.* 55, 163-169.

346 Langer, M.R., Silk, M.T., Lipps, J.H., 1997. Global ocean carbonate and carbon dioxide production;
347 the role of reef Foraminifera. *J. Foraminifer. Res.* 27, 271-277.

348 Langer, M.R., Weinmann, A.E., Lötters, S., Bernhard, J.M., Rödder, D., 2013. Climate-driven range
349 extension of *Amphistegina* (protista, foraminiferida): models of current and predicted future
350 ranges. *PLoS ONE* 8, e54443.

351 Lee, J.J., 1980. Experimental studies of larger foraminifera and their symbionts from the Gulf of Elat
352 on the Red Sea. *J. Foraminifer. Res.* 10, 31-47.

353 Lee, J.J., Anderson, O.R., 1991. *Biology of foraminifera*. Academic Press, London, p. 368.

354 Lee, J.J., Sang, K., terKuile, B., Strauss, E., Lee, P.J., Faber, W.W., 1991. Nutritional and related
355 experiments on laboratory maintenance of three species of symbiont-bearing, large
356 foraminifera. *Mar. Biol.* 109, 417-425.

357 Nicholls, R., Wong, P., Burkett, V., Codignotto, J., Hay, J., McLean, R., Ragoonaden, S., Woodroffe,
358 C., 2007. Coastal systems and low-lying areas, in: Parry, M., Canziani, O., Palutikof, J., van
359 der Linden, P., CE, H. (Eds.), *Climate change 2007: impacts, adaptation and vulnerability*.
360 Contribution of Working Group II to the Fourth Assessment Report of the
361 Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp.
362 315-357.

363 Perry, C.T., Kench, P.S., Smithers, S.G., Riegl, B., Yamano, H., O'Leary, M.J., 2011. Implications of

reef ecosystem change for the stability and maintenance of coral reef islands. Global
Change Biol. 17, 3679-3696.

Röttger, R., Krüger, R., 1990. Observations on the biology of Calearinidae (Foraminiferida). Mar. Biol.
106, 419-425.

Röttger, R., Krüger, R., Rijk, S.d., 1990. Larger foraminifera: Variation in outer morphology and
prolocular size in *Calcarinagaudichaudii*. J. Foraminifer.Res. 20, 170-174.

Sakai, K., Nishihira, M., 1981. Population study of the benthic foraminifer *Baculogypsina sphaerulata*
on the Okinawa reef flat and preliminary estimation of its annual production. Proceedings of
the Fourth International Coral Reef Symposium, Manila 2, 763-766.

Schmidt, C., Heinz, P., Kucera, M., Uthicke, S., 2011. Temperature-induced stress leads to bleaching
in larger benthic foraminifera hosting endosymbiotic diatoms. Limnol.Oceanorg. 56,
1587-1602.

Sinutok, S., Hill, R., Doblin, M.A., Ralph, P.J., 2013. Diurnal photosynthetic response of the motile
symbiotic benthic foraminifer *Marginoporavertebralis*. Mar. Ecol. Prog. Ser. 478,
127-138.

Talge, H.K., Hallock, P., 2003. Ultrastructural responses in field-bleached and experimentally stressed
Amphisteginagibbosa (Class Foraminifera). J. Eukaryot. Microbiol. 50, 324-333.

Thissen, J.M., Langer, M.R., 2013. Foraminifera as ecosystem engineers in shallow-water reef
habitats from the Zanzibar Archipelago (Tanzania), in: Pichler, T., Häusler, S., Tsounis, G.
(Eds.), 3rd International Workshop " Research in Shallow Marine and Fresh Water Systems".
Berichte, Marum, Bremen, pp. 28-32.

Uthicke, S., Vogel, N., Doyle, J., Schmidt, C., Humphrey, C., 2012. Interactive effects of climate
change and eutrophication on the dinoflagellate-bearing benthic foraminifer
Marginoporavertebralis. Coral Reefs 31, 401-414.

388 van Dam, J.W., Negri, A.P., Mueller, J.F., Altenburger, R., Uthicke, S., 2012a. Additive Pressures of
 389 Elevated Sea Surface Temperatures and Herbicides on Symbiont-Bearing
 390 Foraminifera. PLoS ONE 7, e33900.
 391 van Dam, J.W., Negri, A.P., Mueller, J.F., Uthicke, S., 2012b. Symbiont-specific responses in
 392 foraminifera to the herbicide diuron. Mar. Pollut. Bull. 65, 373-383.
 393 Woodroffe, C.D., 2008. Reef-island topography and the vulnerability of atolls to sea-level
 394 rise. Glob. Planet. Change 62, 77-96.
 395 Yamano, H., Kayanne, H., Yamaguchi, T., Kuwahara, Y., Yokoki, H., Shimazaki, H., Chikamori, M.,
 396 2007. Atoll island vulnerability to flooding and inundation revealed by historical
 397 reconstruction: Fongafale Islet, Funafuti Atoll, Tuvalu. Global Planet. Change 57, 407-416.
 398 Yamano, H., Miyajima, T., Koike, I., 2000. Importance of foraminifera for the formation and
 399 maintenance of a coral sand cay: Green Island, Australia. Coral Reefs 19, 51-58.
 400 Ziegler, M., Uthicke, S., 2011. Photosynthetic plasticity of endosymbionts in larger benthic coral reef
 401 Foraminifera. J. Exp. Mar. Biol. Ecol. 407, 70-80.
 402
 403

404 **Figure captions**

405 Figure 1. Photographs of *Baculogypsina sphaerulata* in (A) its natural habitat and (B) a culture tank. The
406 bar in each photograph measures approximately 1 cm.

407

408 Figure 2. Cross section diagram of the mass culturing system for *Baculogypsina*.

409

410 Figure 3. Environmental conditions in a culture tank; (A) temperature and (B) light intensity. "x"
411 indicates draining of the batteries.

412

413 Figure 4. Size histograms of *Baculogypsina sphaerulata* before (A and C) and after (B and D) the
414 experiments. A and B indicate the large-sized group and C and D the small-sized group. The gray
415 transparent bars indicate the size structure of *Baculogypsina sphaerulata* in its natural habitat on the
416 open ocean side of Fongafale Island on March 17 (A, C, n = 2401) and September 30, 2011 (B, D, n =
417 700).

418

419

420 Figure ES. Water temperature change in the natural habitat from May 16, 2011 to March 23 2012 in
421 Fuakea Island (Fig. 3A). Water temperature was monitored every hour using a temperature logger
422 (Hobo UA-002-64, Onset Corp., USA) fixed to the surface of intertidal reef flat.

Fig1

fig2

fig3

fig4