

1 **Long-term changes in sediment type and cavernicolous bivalve assemblages in**
2 **Daidokutsu submarine cave, Okinawa Islands: evidence from a new core extending**
3 **over the past 7,000 years**

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9 **Abstract** We analyzed sediments and cavernicolous bivalve assemblages within cored
10 sediments recovered from the Daidokutsu submarine limestone cave, which occurs in
11 Pleistocene limestone on the fore-reef slope of Ie Island, off Okinawa, Japan. We found
12 sand-sized brown grains within sediments aged 7,000-6,000 cal BP, and identified the
13 grains as debris derived from a red soil layer developed in coastal zones around the
14 Island. Temporal changes in the abundance of the debris suggest that water flow in the
15 cave weakened at about 6,500 cal BP. Temporal changes in the cavernicolous bivalve
16 assemblages indicate that the environmental conditions of the innermost cave area have
17 gradually spread to the cave entrance over the past 5,000 years. These findings indicate
18 that the filling of cavities within the reefal foundations of the cave has continued over
19 time, resulting in a progressive decrease in the flux of water between the interior and
20 exterior parts of the cave during at least the past 6,500 years. This indicates in turn a
21 long-term decline in the functioning of the cryptic community within the reef as a
22 source of the nutrients that support coral reef growth. Our findings regarding the
23 distribution of debris from the red soil layer strongly support the occurrence of a
24 mid-Holocene high-energy window, which represents a period of high wave energy
25 prior to the formation of a reefal barrier.

26

27 **Keywords** Coral reef • Submarine cave sediments • Cavernicolous bivalves • Soil •
28 Environmental change

29

30 **Introduction**

31

32 Cavities in coral reefs are produced in a number of ways, including reef framework
33 growth and the dissolution of limestone (Kobluk 1988). Such cavities constitute
34 between 30 and 75% of the bulk volume of coral reefs (Garret et al. 1971; Ginsburg
35 1983) and between 60 and 75% of the total available reef surface (Jackson et al. 1971;
36 Logan et al. 1984). The large area of reef made up of cavities is inhabited by sponges,
37 bryozoans, brachiopods and other organisms. The biomass of the cryptic communities
38 has the potential to extend beyond the reef surface (Hutchings 1974; Brock and Brock
39 1977; Meesters et al. 1991).

40 Previous studies have addressed the evolutionary significance of cryptic
41 communities (Jackson et al. 1971; Jackson and Winston 1982; Gili et al. 1986;
42 Harmelin 1997; Wörheide 1998; Kano and Kase 2000, 2008; Kano et al. 2002;
43 Motchurova-Dekova et al. 2002; Ubukata et al. 2009) and the fluxes of various
44 materials (e.g., dissolved oxygen, dissolved inorganic matter, dissolved organic matter,
45 and bacterioplankton) in reef cavities (Fichez 1990a, 1990b, 1991; Richter et al. 2001;
46 Scheffers et al. 2004; Van Duyl et al. 2006; De Goeij and Van Duyl 2007). However, we
47 are unaware of any published studies that have searched for millennia-scale variations
48 in the community of organisms in reef cavities, with the exception of Kitamura et al.
49 (2007a).

50 Kitamura et al. (2007a) examined cavernicolous bivalve assemblages in surface and
51 cored sediments within Daidokutsu submarine cave (29 m water depth) on the fore-reef
52 slope of Ie Island (26°43'N, 127°50'E) (Fig. 1), Okinawa, Japan. The cave is developed
53 in Pleistocene Ryukyu Limestone, having formed by the movement of underground
54 water during periods of low sea level (Hayami and Kase 1993). The bivalve species

55 living in the innermost area of the cave have become increasingly dominant over the
56 past 5,000 years, while those living near the entrance of the cave have declined in
57 abundance over this period (Kitamura et al. 2007a). This finding indicates that the
58 environmental conditions of the innermost cave area have progressively extended to the
59 entrance of the cave.

60 According to Kobluk (1988), most cavities in reefs are eventually filled with
61 surface-derived sediments, cement, debris, and *in situ* skeletons of the cryptic
62 community. On this basis, Kitamura et al. (2007a) concluded that the progressive
63 infilling of cavities at Daidokutsu cave has resulted in a decrease in the flux of water
64 between the interior and exterior parts of the cave, leading in turn to an increase in the
65 spatial extent of the zone of nutritional deficiency. However, the stratigraphic
66 distribution of cavernicolous bivalve assemblages within the cave requires additional
67 consideration, as the possibility exists that the lowest part of the cored sediments
68 consists of sediment gravity flow deposits (22 cm thick), which would have modified
69 the species composition in the sediments (see below). To extend Kitamura et al.'s
70 (2007a) study, we examined the temporal distribution of both cavernicolous bivalves
71 and sediment within Daidokutsu cave during the past 7,000 years, based on an
72 examination of newly obtained sediment cores.

73

74 **Study area**

75

76 Cave conditions and sediments

77 Ie island is approximately 23 km² in area and is covered by the Pleistocene Ryukyu
78 Limestone, with a fringing reef close to Pleistocene limestone sea cliffs that are
79 undercut at the mean high-water level (Fig. 1). The surface of the fringing reef is

80 largely flat and is exposed at ebb tide (mean tidal range, 1.8 m). The reef crest is
81 located roughly 200 m from the shoreline, and 20 m from the entrance to Daidokutsu
82 cave.

83 Daidokutsu cave is situated on the northeastern coast of Ie Island. The cave's
84 entrance lies at approximately 19 m below sea level (Fig. 1), and is roughly 2 m high
85 and 18 m wide (Hayami and Kase 1992). The cave is 40 m long, dark inside, and
86 deepens abruptly inward to its deepest point at 29 m below sea level. Water temperature
87 within the cave ranges from 30°C (August) to 20°C (February), and seasonal trends in
88 water temperature are similar to those at 30 m water depth in the open ocean around
89 Okinawa (Kitamura et al. 2007b). During sediment sampling, we found air bubbles
90 rising from the sea floor above the cave, indicating that water is exchanged between the
91 water masses inside and outside the cave via the cave entrance and via numerous
92 passages in the surrounding porous substrates.

93 Based on the sea-level curves of Fairbanks (1989), Bard et al. (1996), and Toscano
94 and Macintyre (2003), Daidokutsu cave is considered to have become submerged at ca.
95 9,000 yr BP, with the entrance having become completely submerged at about 8,000 yr
96 BP. Sea level had attained its present level by about 7,000 yr BP.

97 The floor of the cave is covered by calcareous sediments (Kitamura et al. 2003).
98 Kitamura et al. (2007a) divided the surface sediments in the cave into three facies (Fig.
99 2): Facies 1 is gray calcareous sand that occurs at sites close to the entrance, Facies 2 is
100 gray calcareous mud that occurs in the inner part of the cave, and Facies 3 is calcareous
101 sand containing the skeletons of partly encrusted coralline sponges, which occurs in
102 patches within Facies 2.

103 Kitamura et al. (2007a) collected and examined cored sediment samples from the
104 central part (core 06) and the innermost part (core 04) of Daidokutsu cave (Figs. 2, 3).

105 Core 06 (148 cm thick) can be divided into a lower part, consisting of yellow
106 calcareous mud (> 22 cm long), and an upper part consisting of gray calcareous mud
107 (approximately 126 cm thick) (Fig. 3). The sharp boundary that separates the two parts
108 is estimated to represent an age of 5,450 cal BP (Kitamura et al. 2007a). Based on the
109 relationship between sediment depth and ^{14}C data, the gray calcareous mud is
110 interpreted to have been deposited continuously at a sedimentation rate of 21.1
111 cm/1,000 years. The ^{14}C ages of samples obtained from the lower part of the core fall
112 within a narrow range from 5,980 to 5,060 cal BP, showing a non-linear relationship
113 with depth (Fig. 3). Accordingly, Kitamura et al. (2007a) considered the possibility that
114 the sediment in the lower part originated as a sediment gravity flow. Although there
115 exist differences in color and sedimentation rate between the yellow and gray
116 calcareous muds, the continuous deposition of mud-sized particles throughout the
117 sequence indicates that still-water conditions prevailed for 5,000 years.

118

119 Bivalve assemblages

120 Hayami and Kase (1992, 1993, 1996) and Kase and Hayami (1992) studied
121 cavernicolous bivalves in tropical west-Pacific coral reefs, including Daidokutsu cave.
122 The authors reported about 60 species of cavernicolous bivalves that share the
123 following characteristics: 1) reduced adult size (usually less than 5 mm in length); 2)
124 unusually large prodissoconch I and absence of prodissoconch II in many species,
125 indicating non-planktotrophic development; and 3) persistent denticles of the
126 provinculum are retained until the adult stage in many pteriomorph species, indicating
127 significant paedomorphosis by progenesis. According to Kase and Hayami (1992) and
128 Hayami and Kase (1996), these features reflect a common adaptive strategy toward the
129 oligotrophic condition and low predation pressure of cave habitats.

130 Eight bivalve species are dominant in the surface sediments within Daidokutsu cave.
131 Kitamura et al. (2007a) divided these species into three groups based on their spatial
132 distribution (Fig. 4). The first group (*Cosa kinjoi* and *Parvamussium crypticum*) mainly
133 inhabits the innermost cave area, whereas the second group (*Cosa waikikia* and *Hiatella*
134 sp. aff. *H. orientalis*) is found near the entrance, and the third group (*Chlamydella*
135 *tenuissima*, *Cyclopecten ryukyuensis*, and *Carditella iejimensis*) shows no distinct
136 distribution pattern. *Carditella iejimensis* appears to be endemic to caves of Ie Island,
137 while the others are found on many isolated islands in tropical west-Pacific coral reefs
138 (Hayami and Kase 1996).

139 The first group showed a rapid increase in abundance immediately above the
140 boundary between the yellow and gray calcareous muds (ca. 5,450 cal BP) in the
141 central area (core 06; Fig. 3). It is possible that the stratigraphic distribution of this
142 group was influenced by the mixing of shells transported by a sediment gravity flow.
143 The species of the second group, along with *Chlamydella tenuissima*, show a decrease
144 in abundance at about 2,200 cal BP in the central part of the cave (core 06), and the
145 relative abundances of these species are very low in the innermost part of the cave (core
146 04; Fig. 3) over the past 3,000 years. We observed no significant changes in the
147 temporal or spatial distribution of *Cyclopecten ryukyuensis* and *Carditella iejimensis*.
148 These findings indicate that the cave environment has remained largely unchanged for
149 the past 5,000 years.

150

151 **Methods**

152

153 We sampled the cave sediment by hand using a coring tube of 6 cm in diameter and
154 233 cm in length (core 19; Figs. 2, 5). The core did not reach basement. The sediment

155 core was first split and described, and then sliced into 1 cm thick samples for the
156 measurement of mud and carbonate content. We picked and counted all micro-bivalves
157 from the >0.5 mm fraction of each sample. Mud content was determined using
158 standard sieves. The carbonate content of 500 mg of sediment was determined by
159 gentle removal with 10% acetic acid.

160 Kitamura et al. (2006) reported a pumice-bearing sediment layer (Daidokutsu
161 pumice) within the gray calcareous mud. The main period of deposition of this layer is
162 estimated to have occurred from 1,990 to 1,710 cal BP (Kitamura et al. 2006). The
163 pumice layer can be identified by its relatively low carbonate content, thereby enabling
164 its use as a reference time surface.

165 The obtained bivalves show excellent preservation despite most being
166 disarticulated: the prodissoconch can be observed in many individuals. These factors
167 indicate that the shells represent a life assemblage. Taxonomic identifications are based
168 on Hayami and Kase (1993). For disarticulated shells, a separate valve was counted as
169 one individual. The stratigraphic distribution of each species is expressed as the density
170 of individuals (numbers per gram).

171 The radiocarbon ages of three well-preserved mollusc shells were determined by
172 Beta Analytic Inc., using accelerator mass spectrometry (Table 1). Calibrated age
173 ranges were calculated according to Method A of Stuiver et al. (1998) after applying a
174 local correction for the northwestern Pacific of 355 years ($\Delta R = 35 \pm 25$) (Hideshima et
175 al. 2001).

176 In this study, we discovered sand-sized brown grains (debris derived from a red soil
177 layer; see below) in the lower portion of core 19. We observed these grains in thin
178 sections viewed under a polarizing microscope, and analyzed their mineral composition
179 by powder X-ray diffractometry (XRD) using a Rigaku RINT2500 V housed at

180 Shizuoka University, Japan. The major element compositions of 10 brown grains were
181 analyzed using a non-destructive energy dispersive X-ray fluorescence (XRF) analyzer
182 (TATSCAN-F1) housed at the Japan Agency for Marine-Earth Science and Technology
183 (JAMSTEC). The chemical compositions were determined at a tube voltage of 30kV
184 and the diameter of the collimator was 400 μ m. We picked and counted all brown grains
185 from the 0.5-1.0 mm and 1.0-2.0 mm fractions of samples collected at 1 cm intervals
186 within core 19. In the same way, we determined the stratigraphic distribution of brown
187 grains in cores 04 and 06. We also picked and counted brown grains from the 0.5-1.0
188 mm and 1.0-2.0 mm fractions of a sample of reef-slope sediment and six samples of
189 surface sediment from within the cave (Figs. 1, 2).

190

191 **Results**

192

193 The sediment in core 19 shows a fining-upward trend, and is divided into a lower gray
194 calcareous sand (233-178 cm depth) and an upper gray calcareous mud (178-0 cm
195 depth) (Fig. 5). Between 233 and 192 cm depth, the carbonate content increases upward
196 from 88 to 94%. Except for the horizon from 52 to 28 cm depth, the carbonate content
197 between 192 and 0 cm depth is consistent at 95-97%. Between 52 and 28 cm depth, the
198 carbonate content decreases to 84% (Fig. 5). We regard this horizon to represent the
199 deposit containing the Daidokutsu pumice (deposited between 1,990 and 1,710 cal BP).

200 Table 1 lists the radiocarbon ages obtained for mollusc shells; ^{14}C ages are plotted
201 in Fig. 5. The age of a bivalve shell from the base of core 19 is $7,170 \pm 45$ cal BP,
202 indicating that the cored sediments preserve a record of fossils and sedimentation over
203 the past 7,000 years. Based on ^{14}C age data and the stratigraphic position of the
204 Daidokutsu pumice, we estimate a sedimentation rate of 41.7 cm/1,000 years between

205 150 and 233 cm depth, and a rate of 29.8 cm/1,000 years between 0 and 150 cm depth
206 (Fig. 5). This change in sedimentation rate at 150 cm depth was synchronous with the
207 change in deposition from calcareous sand to calcareous mud. An age-depth model
208 presented in this study reveals that pale yellow calcareous mud in the lower part of core
209 6 is heteropic with gray calcareous mud in core 19 (Figs. 3, 5), although we cannot
210 explain the cause of the change in sediment color at ca. 5,450 cal BP.

211 Observations of thin sections reveal that the sand-sized brown grains are also brown
212 internally (Supplementary Fig. 1). The grains were not dissolved by 10% acetic acid,
213 and XRD analysis reveals that they contain quartz (Fig. 6). XRF analysis reveals that
214 the grains consist mainly of Si, Al, and Fe (Table 2). Based on these observations, we
215 interpret the brown grains to be detritus derived from a red soil layer that is widely
216 distributed across Ie Island (Tokashiki 1993; Vuai et al. 2003; Mkadam et al. 2006).
217 Debris with a diameter of 1.0-2.0 mm was only found in the lower part of core 19 (Fig.
218 5). The number density of these grains (numbers per gram) decreases upward from
219 0.6/g at 233 cm depth to 0-0.1/g at 203 cm depth. The number density of debris with a
220 diameter of 0.5-1.0 mm shows an upward decrease from 10/g at 233 cm depth to 0-1/g
221 at 180 cm depth (Fig. 5). This upper stratigraphic limit of small-sized debris (0.5-1.0
222 mm in diameter) derived from the red soil layer coincides with the boundary between
223 calcareous sand and calcareous mud (178 cm depth), and coincides with an upward
224 increase in carbonate content over the interval between 233 and 192 cm depth. The
225 debris from the red soil layer is recognized within surface sediment at three sites (d-f)
226 of the six sites analyzed in the cave, although at number densities less than 0.08/g
227 (Table 3). We found no debris at the other three sites (a-c) in the cave, in the reef-slope
228 sample (Table 3), or in core 04. The debris occurs sporadically in core 06 (Fig. 3).

229 The cavernicolous bivalve fauna within core 19 is dominated by *Huxleyia*

230 *cavernicola*, *Bentharca tenuis*, *Cosa kinjoi*, *Cosa waikikia*, *Parvamussium crypticum*,
231 *Cyclopecten ryukyuensis*, *Chlamydella tenuissima*, *Carditella iejimensis*, and *Hiatella*
232 sp. aff. *H. orientalis* (Fig. 5, Supplementary Table 1). Species of the first group (*Cosa*
233 *kinjoi* and *Parvamussium crypticum*) occur continuously above 158 and 130 cm depth,
234 respectively. In contrast, species of the second group (*Cosa waikikia* and *Hiatella* sp.
235 aff. *H. orientalis*) show an upward decrease in abundance from about 72 cm depth. The
236 stratigraphic distribution of *Chlamydella tenuissima* and *Bentharca tenuis* is similar to
237 that of the second group. *Huxleyia cavernicola* shows an upward decrease in abundance
238 from about 150 cm depth. Both *Cyclopecten ryukyuensis* and *Carditella iejimensis*
239 occur continuously throughout the cored sediments (Fig. 5).

240

241 **Discussion**

242 Debris from the red soil layer

243 In core 19, debris from the red soil layer is commonly observed in the horizon from the
244 bottom of the core to about 180 cm depth. The age range of this interval is estimated to
245 be 7,000 to 6,000 cal BP, based on our age model (Fig. 5). In contrast, the debris is only
246 rarely observed in the younger sediments within core 19, in other cores (04 and 06), and
247 in surface sediments sampled from within the cave, and is absent from reef-slope
248 sediments (Table 3). Consequently, we consider that the stratigraphic distribution of
249 debris from the red soil layer indicates that the washing of debris from coastal paleosols
250 became weaker, and nearly terminated, during the period leading up to 6,000 cal BP.

251 Kawana and Kan (2002) reconstructed the Holocene development of coral reefs
252 around southern Okinawa Island, located about 70 km south of the present study area,
253 based on an analysis of drill cores. The authors documented that reef began to grow
254 upward upon basement at about 7,600 yr BP, under 10-20 m water depth, and reached

255 the present sea surface at 6,000-5,500 yr BP, and then developed seaward via accretion
256 of the forereef. At the time when a similar pattern of coral reef development occurred
257 around Ie Island, termination of the supply of debris from the red soil layer coincided
258 with the establishment of the reef crest/flat zones (when the reef reached the present sea
259 level). The observed changes in supply of debris from the red soil layer are therefore
260 considered to be consistent with the existence of a high-energy window—a concept first
261 proposed by Neumann (1972) and revisited by Hopley (1984). During the
262 mid-Holocene, in areas where the rate of sea-level rise outstripped the ability of newly
263 settled coral communities to grow vertically, a period of high wave energy may have
264 occurred prior to the formation of a reefal barrier. The high-energy window may have
265 remained open from the first complete submergence of the antecedent foundations until
266 the moment at which modern reef flats began to develop, between about 8,000 and
267 6,000 yr BP (Neumann 1972; Hopley 1984; Montaggioni 2005). Under such conditions,
268 the enhanced hydrodynamic energy may have resulted in the rapid winnowing of finer
269 particles from paleosols and terrigenous sediments deposited on inner shelves and
270 coastal zones. From 6,000 yr BP, the window progressively closed as reef tops reached
271 sea level, which stabilized around its present position, and reef flats became sufficiently
272 extended laterally. Consequently, the supply of detritus was terminated. It appears that
273 the stratigraphic distribution of debris from the red soil layer provides direct evidence
274 of the occurrence of a mid-Holocene high-energy window.

275 It is noteworthy that the decline in the abundance of larger debris (1.0-2.0 mm in
276 diameter) preceded that of smaller debris (0.5-1.0 mm in diameter) by 550 years (Fig.
277 5). This difference is well explained by a weakening in water flow within the cave,
278 rather than changes in sorting processes outside the cave.

279

280 Long-term changes in cavernicolous bivalve assemblages

281 The continuous occurrence of *Cyclopecten ryukyuensis* and *Carditella iejimensis*
282 indicates that the cave environment in Daidokutsu has persisted for the past 7,000 years.
283 The progressive decrease in abundance of species of the second group (*Cosa waikikia*
284 and *Hiatella* sp. aff. *H. orientalis*), as well as *Chlamydella tenuissima* and *Bentharca*
285 *tenuis*, is consistent with the findings of Kitamura et al. (2007a). Our data indicate that
286 species of the first group (*Cosa kinjoi* and *Parvamussium crypticum*) were absent from
287 core 19 at depths between 223 and 160 cm, although other species occurred
288 continuously throughout this interval. This finding confirms Kitamura et al.'s (2007a)
289 tentative conclusion that species of the first group living in the innermost part of the
290 cave became dominant over the past 5,000 years. In addition, we found that *Huxleyia*
291 *cavernicola* shows an upward decrease in abundance from a depth of about 150 cm,
292 corresponding to about 5,130 cal BP. The bivalve species described above are
293 suspension feeders, whereas *Huxleyia cavernicola* is thought to be a deposit feeder
294 (Hayami and Kase 1993). This species is very rare in the surface sediments in the cave
295 (Fig. 4). Thus, the temporal changes in species abundance reveal a decrease in the
296 amount of organic matter in cave sediment at about 5,130 cal BP.

297 As noted above, our new data indicate that the water flow in the cave weakened at
298 about 6,500 cal BP, suggesting in turn a decrease in the exchange of water between the
299 interior and exterior of the cave, and a consequent decline in nutrient levels within the
300 cave. However, the observed changes in cavernicolous bivalve assemblages occurred
301 after termination of the supply of debris from the red soil layer, at about 6,000 cal BP.
302 This finding indicates that the population dynamics of *Cosa waikikia*, *Hiatella* sp. aff.
303 *H. orientalis*, *Chlamydella tenuissima*, *Bentharca tenuis* and *Huxleyia cavernicola* were
304 not significantly influenced by the decline in nutrient supply at about 6,500 cal BP.

305 However, it appears that the ongoing decline in nutrient supply resulted in an expansion
306 of the distribution of *Cosa kinjoi* and *Parvamussium crypticum*, thereby preventing the
307 five species listed above from inhabiting the inner part of the cave.

308 The large extent of the cryptic habitat and extensive cover of encrusting organisms
309 within reef cavities provide a potentially important interface in the exchange of material
310 between cavities and the overlying water column (e.g., Tribble et al. 1988; Richter and
311 Wunsch 1999). Coral cavities are sinks of bacterioplankton and dissolved organic
312 carbon, and a source of NO_x and PO_4^{3-} (Van Duyl et al. 2006; De Goeij and Van Duyl
313 2007; De Goeij et al. 2008). Our results show that, at least in terms of the coral cryptic
314 community within cavities developed in the reefal foundations, a decline in the
315 functioning of the cryptic community as a source of nutrients to the coral reef over at
316 least the past 6,500 years.

317

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326

327 **References**

328 Bard E, Hamelin B, Fairbanks RG, Zindler A (1996) Deglacial sea-level record from
329 Tahiti corals and the timing of global meltwater discharge. *Nature* 382:241-244

330 Brock RE, Brock JH (1977) A method for quantitatively assessing the infaunal
331 community in coral rock. *Limnol. Oceanogr* 22:948-951

332 De Goeij JM, Van Duyl FC (2007) Coral cavities are sinks of dissolved organic carbon
333 (DOC) *Limnol Oceanogr* 52(6):2608–2617

334 De Goeij JM, Van den Berg H, Van Oostveen MM, Epping EHG, Van Duyl FC (2008)
335 Major bulk dissolved organic carbon (DOC) removal by encrusting coral reef cavity
336 sponges. *Mar Ecol Prog Ser* 357:139–151.

337 Fairbanks RG (1989) A 17,000-year glacio-eustatic sea level record: influence of
338 glacial melting rates on the Younger Dryas event and deep-ocean circulation. *Nature*
339 342:637-642

340 Fichez R (1990a) Les pigments chlorophylliens : indices d'oligotrophie dans les grottes
341 sous-marines. *Compte Rendus Académie des Sciences de Paris, Série III* 310:
342 255-261

343 Fichez R (1990b) Decrease in allochthonous organic inputs in dark submarine caves,
344 connection with lowering in benthic community richness. *Hydrobiologia* 207:61-69

345 Fichez R (1991) Suspended particulate organic matter in a Mediterranean submarine
346 cave. *Mar Bio* 108:167-174

347 Garret P, Smith DL, Wilson AO, Patruquin D (1971) Physiography, ecology, and
348 sediments of two Bermuda patch reefs. *J. Geol* 79:647-668

349 Gili JM, Riera T, Zabala M (1986) Physical and biological gradients in a submarine
350 cave on the Western Mediterranean coast (north-east Spain). *Mar Bio* 90:291-297

351 Ginsburg RN (1983) Geological and biological roles of cavities in coral reefs. In:
352 Barnes DJ (ed) *Perspectives on coral reefs*. Australian Institute of Marine Science,
353 Townsville, Australia (pp 148-153)

354 Harmelin JG (1997) Diversity of bryozoans in a Mediterranean sublittoral cave with

355 bathyal-like conditions: role of dispersal processes and local factors. Mar Ecol Prog
356 Ser 153:139-152

357 Hayami I, Kase T (1992) A new cryptic species of *Pycnodonte* from Ryukyu Islands: A
358 living fossil oyster. Trans Proc Palaeontol Soc Jpn NS 165:1070-1089

359 Hayami I, Kase T (1993) Submarine cave bivalvia from the Ryukyu Islands:
360 systematics and evolutionary significance. Bull Univ Mus Univ Tokyo 35:1-133

361 Hayami I, Kase T (1996) Characteristics of submarine cave bivalves in the
362 northwestern Pacific. Am Malacol Bull 12(1/2):59-65

363 Hideshima S, Matsumoto E, Abe O, Kitagawa H (2001) Northwest Pacific marine
364 reservoir correction estimated from annually banded coral from Ishigaki Island,
365 southern Japan. Radiocarbon 43:473-476

366 Hopley D (1984) The Holocene high-energy window on the Central Great Barrier Reef.
367 In: Thom BG. (Ed.), Coastal Geomorphology in Australia. Academic Press, Sydney,
368 135–150

369 Hutchings PA (1974) A preliminary report on the density and distribution of
370 invertebrates living on coral reefs. In Proc 2nd Int Coral Reef Symp, Australia,
371 1:285-296

372 Jackson JBC, Goreau TF, Hartman WD (1971) Recent brachiopod-coralline sponge
373 communities and their paleoecological significance. Science 173:623-625

374 Jackson JBC, Winston JE (1982) Ecology of cryptic coral reef communities. 1.
375 Distribution and abundance of major groups of encrusting organisms. J Exp Mar
376 Biol Ecol 57:135-147

377 Kano Y, Chiba S, Kase T (2002) Major adaptive radiation in neritopsine gastropods
378 estimated from 28S rRNA sequences and fossil records. Proc Royal Soc London Ser
379 B, Bio Sci 269:2457-2465

- 380 Kano Y, Kase T (2000) Taxonomic revision of *Pisulina* (Gastropoda: Neritopsina) from
381 submarine caves in the tropical Indo-Pacific. *Paleontol Res* 4:107-129
- 382 Kano Y, Kase T (2008) Diversity and distributions of the submarine-cave Neritiliidae in
383 the Indo-Pacific (Gastropoda: Neritimorpha). *Org Divers Evol* 8:22–43
- 384 Kase T, Hayami I (1992) Unique submarine cave mollusc fauna: composition, origin
385 and adaptation. *J Mollus Stud* 58:446-449
- 386 Kawana T, Kan H (2002) Description of the new drilling cores through the Holocene
387 coral reefs at the Gushichan coast in the southern Okinawa Island, the Ryukyus,
388 Japan. *Bull Coll Edu Univ Ryukyus* 60:235-244 (in Japanese with English abstract)
- 389 Kitamura A, Kase T, Ohashi S, Hiramoto M, Sakaguchi Y, Tanabe A, Matou M (2003)
390 Sedimentary facies and depositional rates of submarine cave sediment in coral reef
391 of Okinawa Islands. *The Quat Res (Daiyonki-Kenkyu)* 42:99-104 (in Japanese with
392 English abstract)
- 393 Kitamura A, Kase T, Umino S, Yamamoto N, Ohashi S, Hiramoto M, Wakayama N,
394 Amemiya M (2006) Discovery of sediment layer containing pumice grains in
395 submarine cave sediment in coral reef of Okinawa Islands. *The Quat Res*
396 (Daiyonki-Kenkyu) 45:141-144 (in Japanese with English abstract)
- 397 Kitamura A, Hiramoto M, Kase T, Yamamoto N, Amemiya M, Ohashi S (2007a)
398 Changes in cavernicolous bivalve assemblages and environments within a
399 submarine cave in Okinawa Islands during the last 5,000 years. *Paleontol Res*
400 11:161-180
- 401 Kitamura A, Yamamoto N, Kase T, Ohashi S, Hiramoto M, Fukusawa H, Watanabe T,
402 Irino T, Kojitani H, Shimamura M, Kawakami I, (2007b) Potential of
403 submarine-cave sediments and oxygen isotope composition of cavernicolous
404 micro-bivalve as a late Holocene paleoenvironmental record. *Glob Planet Change*

405 55:301-316

406 Kobluk DR (1988) Cryptic faunas in reefs: ecology and geologic importance. *Palaios* 3:
407 379-390

408 Logan A, Mathers SM, Thomas MLH (1984) Sessile invertebrate coelobite
409 communities from reefs of Bermuda: Species composition and distribution. *Coral*
410 *Reefs* 2:205-213

411 Mkadam KM, Yonaha T, Ali VS, Tokuyama A (2006) Dissolved aluminum and silica
412 release on the interaction of Okinawan subtropical red soil and seawater at different
413 salinities: Experimental and field observations. *Geoch Jour* 40:333-343

414 Meesters E, Knijn R, Willemsen P, Pennartz R, Roebers G, Soest RWM (1991)
415 Sub-rubble communities of Curaçao and Bonaire coral reefs. *Coral Reefs*
416 10:189-197

417 Montaggioni LF (2005) History of Indo-Pacific coral reef systems since the last
418 glaciation: Development patterns and controlling factors. *Earth-Sci Rev* 71:1 –75

419 Motchurova-Dekova N, Saito M, Endo K (2002) The recent rhynchonellide brachiopod
420 *Parasphenarina cavernicola* gen. et sp. nov. from the submarine caves of Okinawa,
421 Japan. *Paleontol Res* 6:299-319

422 Neumann AC (1972) Quaternary sea level history of Bermuda and the Bahamas. *Am*
423 *Quatern Assoc Second Nat Conf Abstracts*, 41– 44

424 Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs-a new
425 link in reef trophodynamics. *Mar Ecol Prog Ser* 188:105-116

426 Richter C, Wunsch M, Rasheed M, Koötter I, Badran M (2001) Endoscopic exploration
427 of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. *Nature*
428 413:726-731

429 Scheffers SR, Nieuwland G, Bak RPM, Van Duyl FC (2004) Removal of bacteria and

430 nutrient dynamics within the coral reef framework of Curaçao (Netherlands Antilles).
431 Coral Reefs 23:413-422

432 Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac
433 G, Van der Plicht J, Spurk M (1998) INTCAL 98 radiocarbon age calibration,
434 24,000–0 cal B.P. Radiocarbon 40:1041–1083

435 Tokashiki Y (1993) Soil survey; Jahgaru, Shimajiri Mahji, Feichisya, Kunigami Mahji
436 Japanese society of pedology. In: Hirayama R, Yamada I (eds). Soil and Nature of
437 Okinawa Island. 63-88 (in Japanese)

438 Toscano MA, Macintyre IG (2003) Corrected western Atlantic sea-level curve for the
439 last 11,000 years based on calibrated ¹⁴C dates from *Acropora palmata* framework
440 and intertidal mangrove peat. Coral Reefs 22:257-270

441 Tribble GW, Sansoné FJ, Li Y-H, Smith SV, Buddemeier RW (1988) Material fluxes
442 from a reef framework. In: Proceeding of 6th Int Coral Reef Symp, Australia,
443 2:577-582

444 Ubukata T, Kitamura A, Hiramoto M, Kase T (2009) A 5,000-year fossil record of
445 larval shell morphology of submarine cave microshells. Evolution 63:295-300

446 Van Duyl FC, Scheffers SR, Thomas FIM, Driscoll M (2006) The effect of water
447 exchange on bacterioplankton depletion and inorganic nutrient dynamics in coral
448 reef cavities. Coral Reefs 25:23–36

449 Vuai SA, Ishiki M, Tokuyama A (2003) Acidification of fresh waters by red soil in a
450 subtropical silicate rock area, Okinawa. Limnology 4:63-71

451 Wörheide G (1998) The reef cave dwelling ultraconservative coralline demosponge
452 *Astrosclera willeyana* Lister 1900 from the Indo-Pacific. Facies 38:1-88

453

454 Figure captions

455 Figure 1 Location map of the submarine Daidokutsu cave on Ie Island, off Okinawa
456 Island, Japan.

457

458 Figure 2 Map showing water depth and the locations of sampling points of surface
459 sediments (a-f) and cored sediments. Also shown is the distribution of surface
460 sediment facies (see text for details).

461

462 Figure 3 Columnar sections of submarine-cave sediment within cores 04 and 06,
463 showing stratigraphic changes in mud and carbonate content, abundance of debris
464 derived from a red soil layer, the dominant cavernicolous bivalve species, and
465 depositional rates, as inferred from the ^{14}C ages of molluscs (modified after
466 Kitamura et al. 2007a).

467

468 Figure 4 Spatial distributions of selected cavernicolous bivalve species in Daidokutsu
469 cave (modified after Kitamura et al. 2007a). Percentages are given relative to the
470 total number of individuals of all bivalve species. The locations of a-f are shown in
471 Fig. 2.

472

473 Figure 5 Columnar sections of submarine-cave sediment within core 19, showing
474 stratigraphic changes in mud and carbonate content, abundance of debris derived
475 from a red soil layer, the dominant cavernicolous bivalve species, and depositional
476 rates, as inferred from the ^{14}C ages of mollusks.

477

478 Figure 6 Diffractograms of brown grains (debris derived from a red soil layer) found

479 within sediment from Daidokutsu cave. Peaks labelled “1” correspond to those for
480 quartz.

481

482 Table 1 Results of ^{14}C dating of molluscs. All samples were analyzed by accelerator
483 mass spectrometry.

484

485 Table 2 Concentrations of major elements (wt%) within 10 grains of debris derived
486 from a red soil layer, as measured by non-destructive X-ray fluorescence.

487

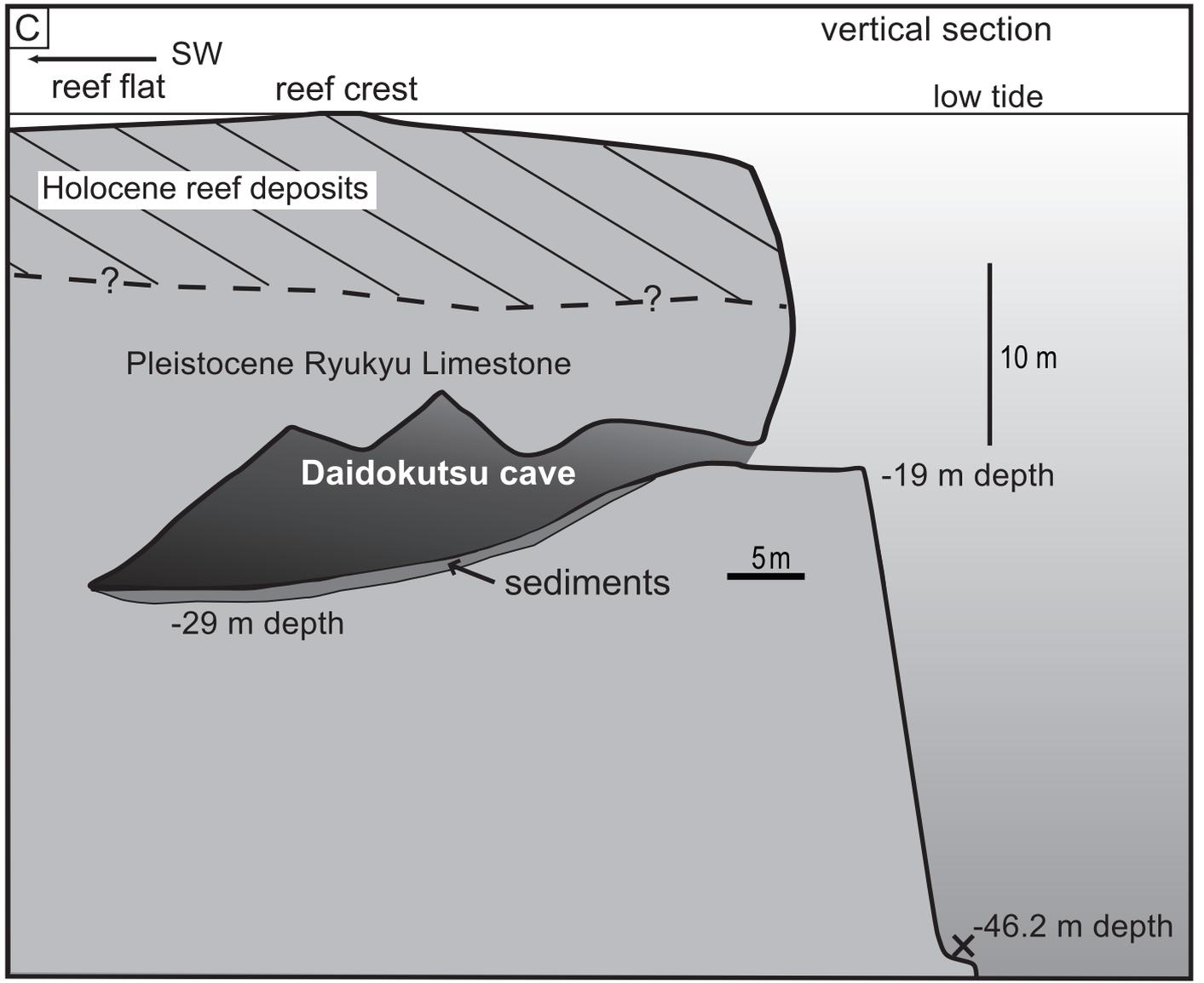
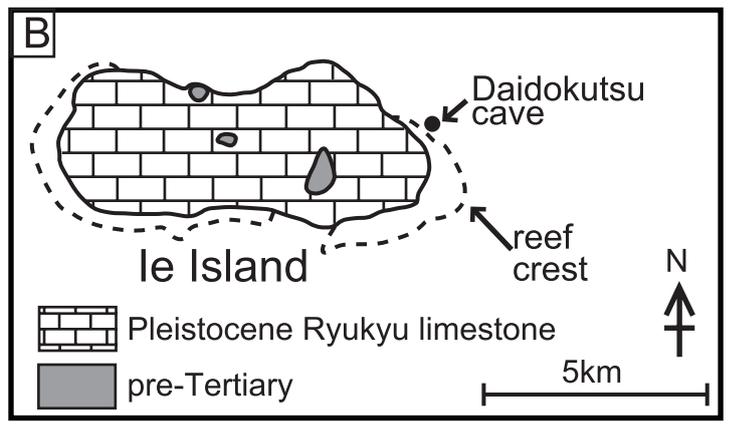
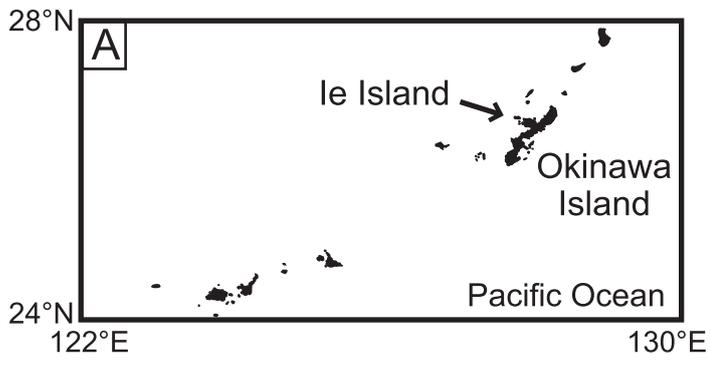
488 Table 3 Grain distribution (wt%) and number density of debris derived from a red soil
489 layer (number/g) in a sample of reef-slope sediment and six samples of surface
490 sediment from within Daidokutsu cave.

491

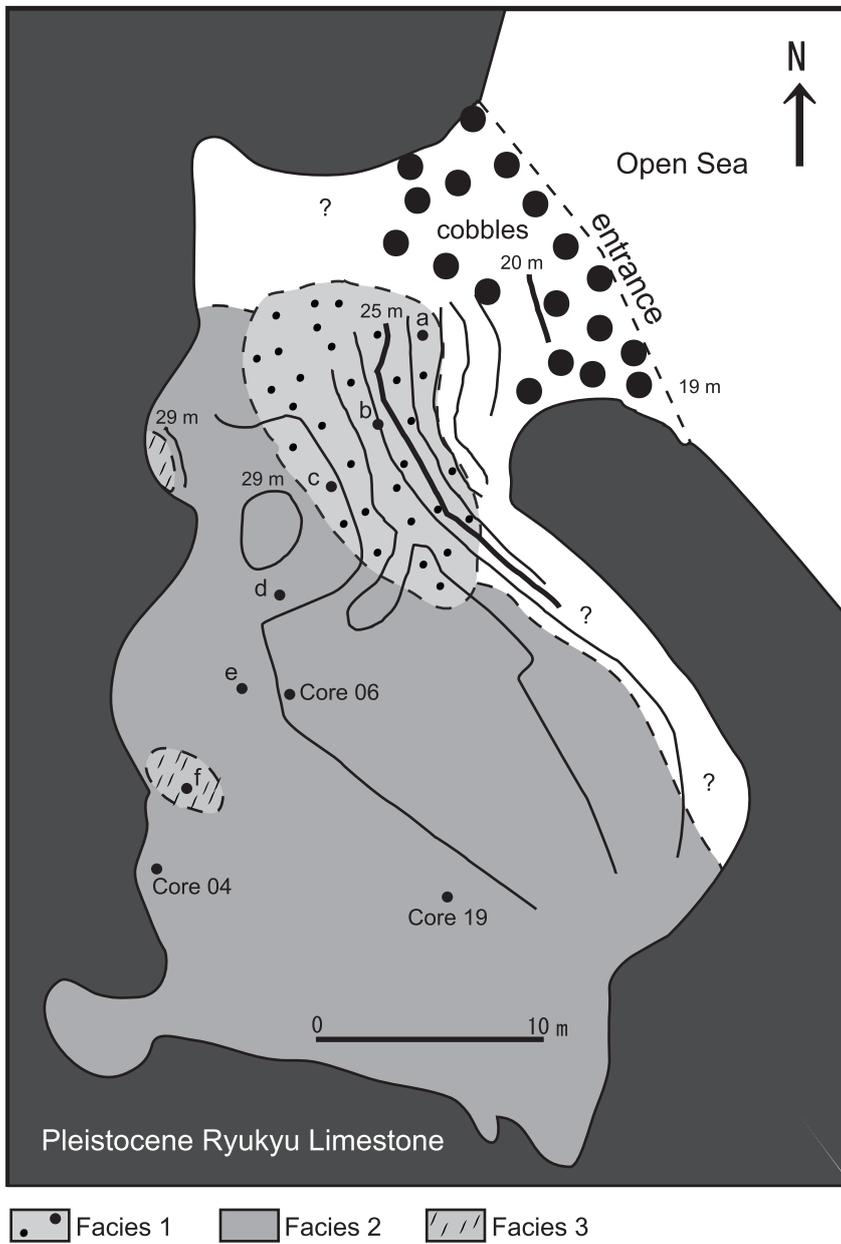
492 Electronic Supplementary Material Figure 1 Photomicrographs of debris derived from a
493 red soil layer (plane-polarized light).

494

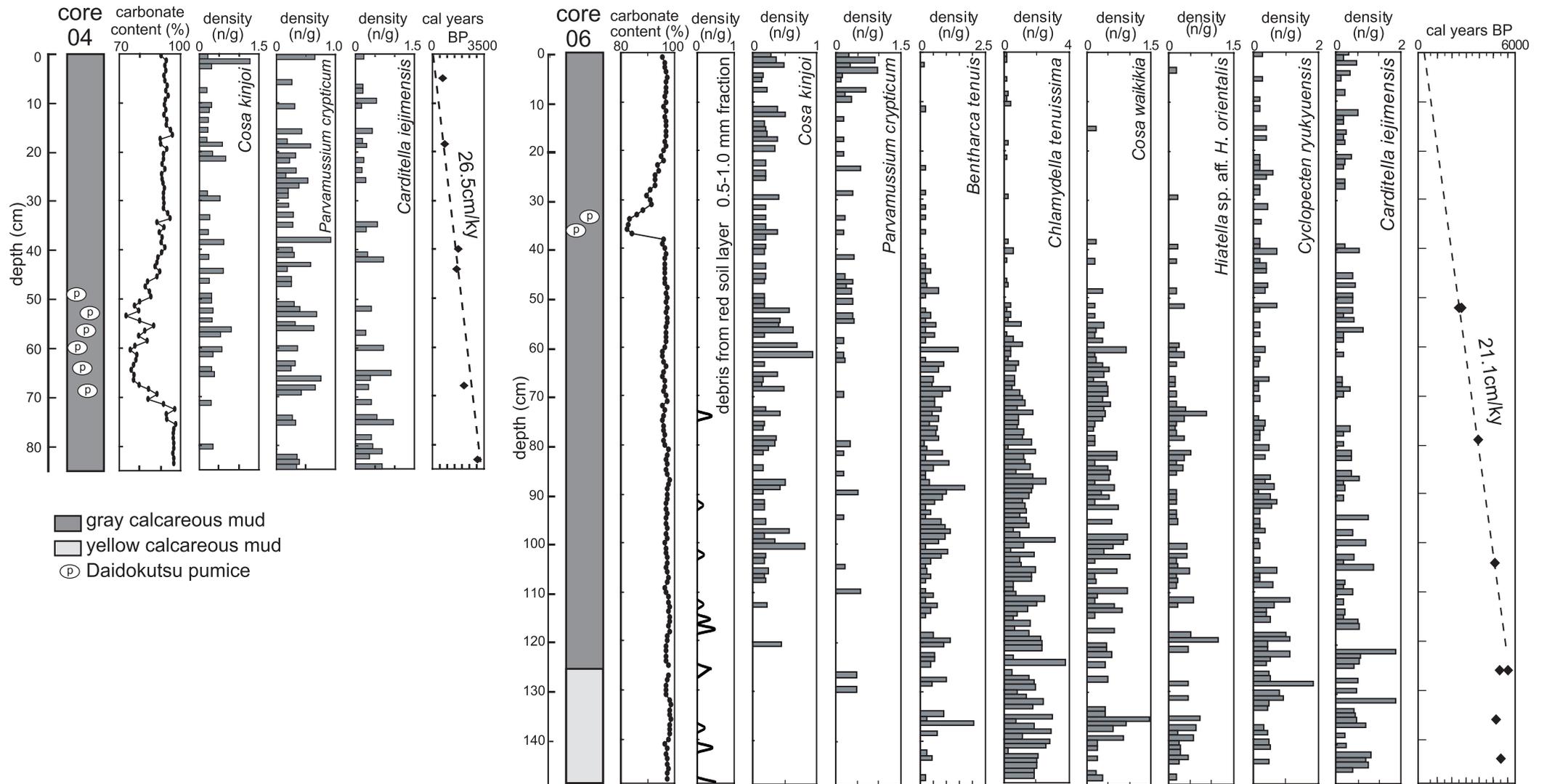
495 Electronic Supplementary Material Table 1 List of cavernicolous bivalve species in
496 core 19. A: articulated shells, R: right valve, L: left valve.



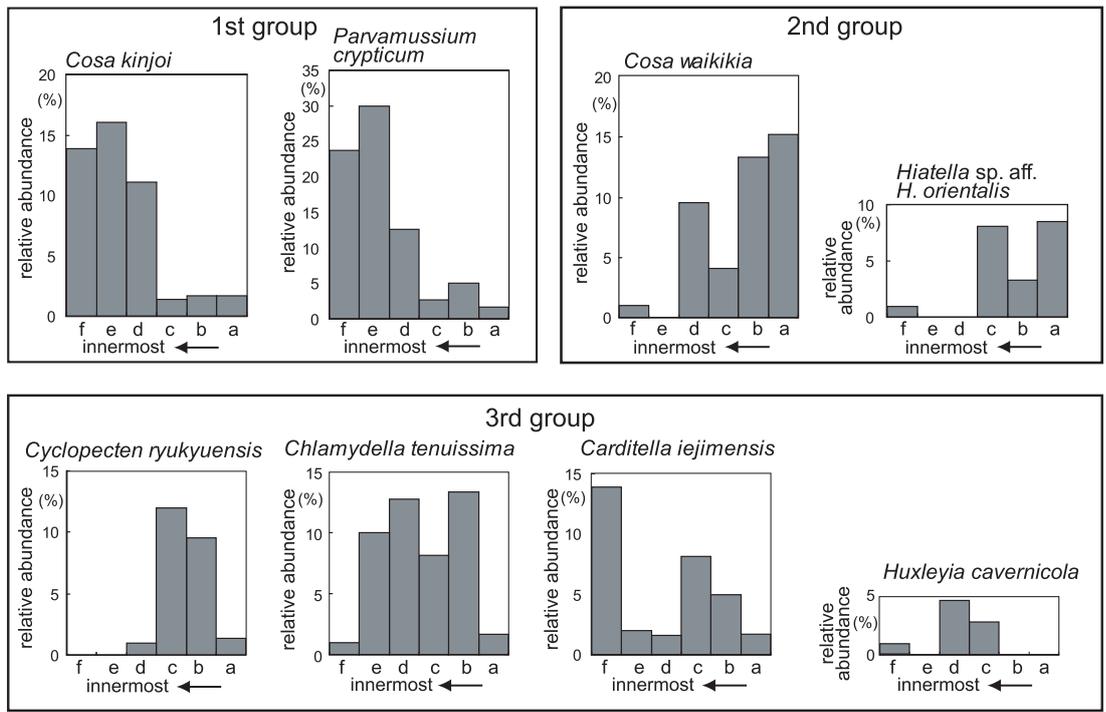
× sampling point of reef slope sediment



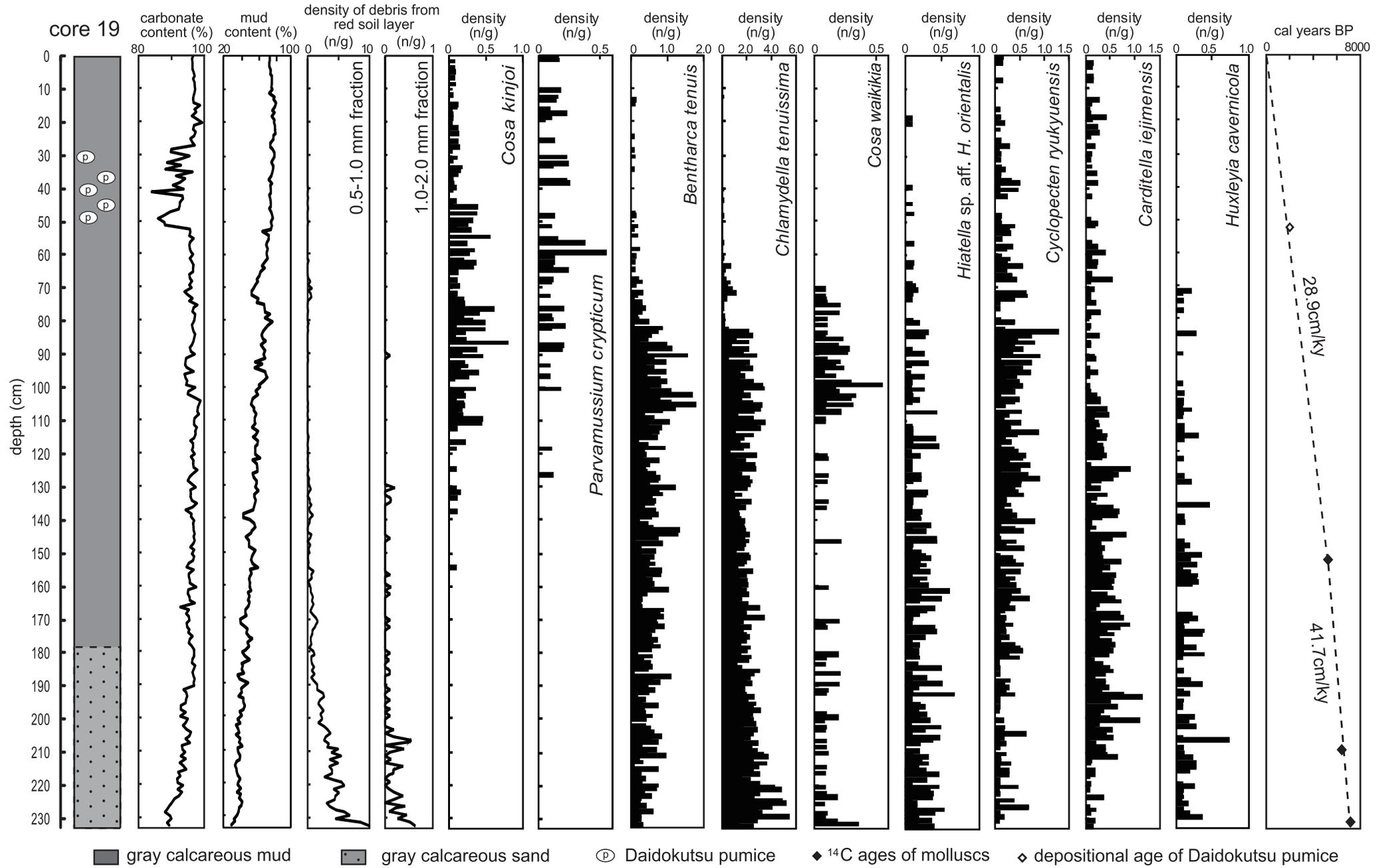
Yamamoto et al. Figure 2



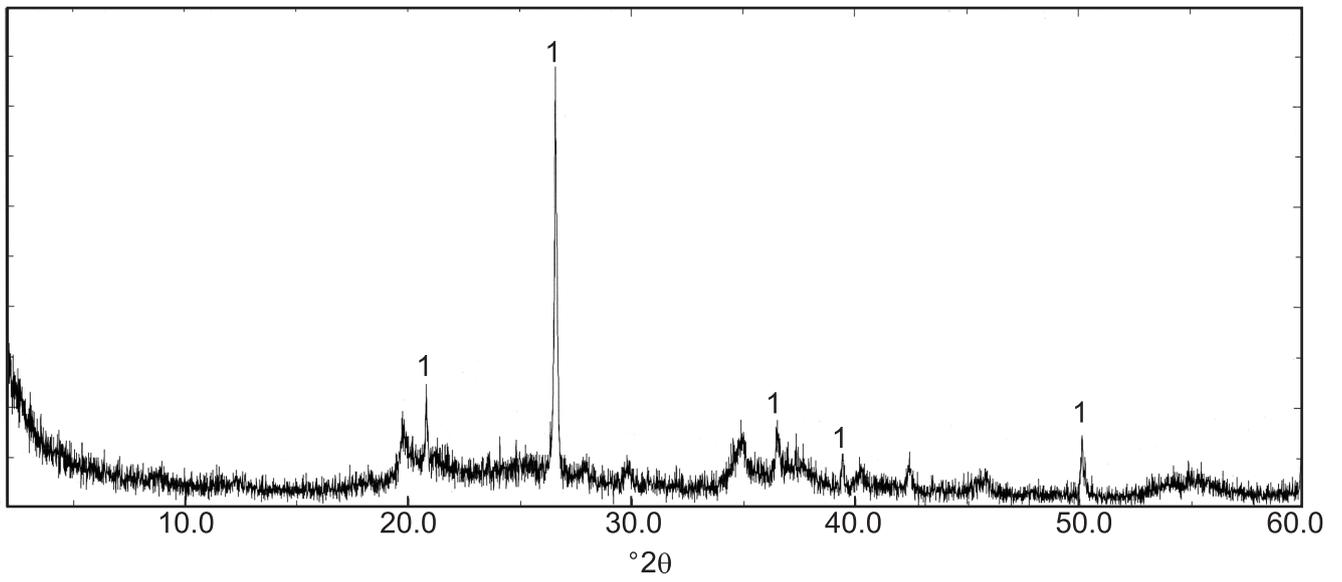
Yamamoto et al. Fig. 3



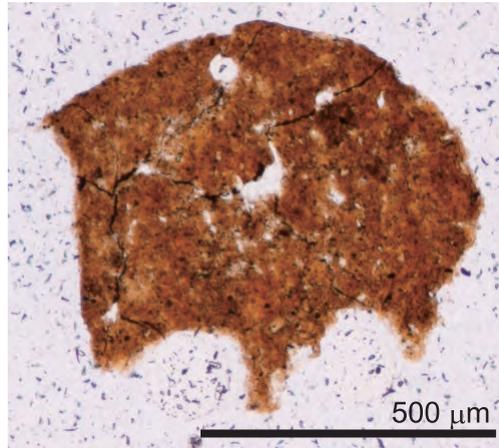
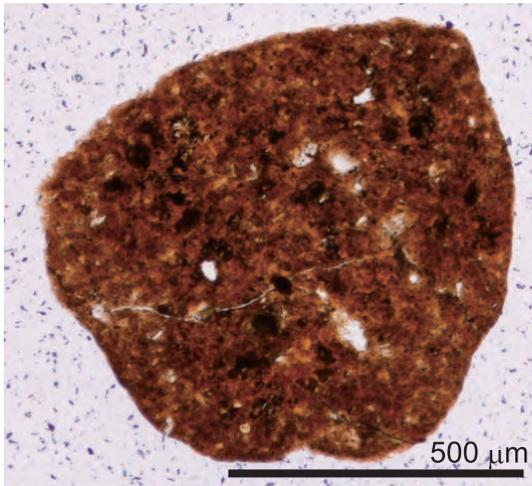
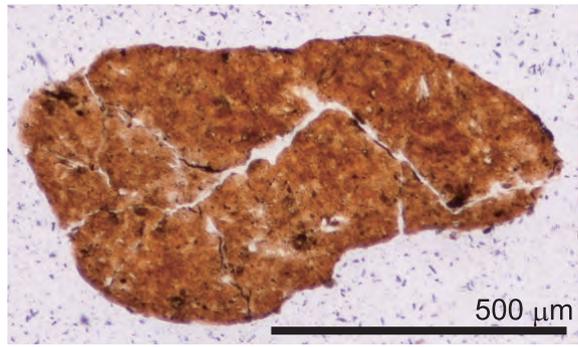
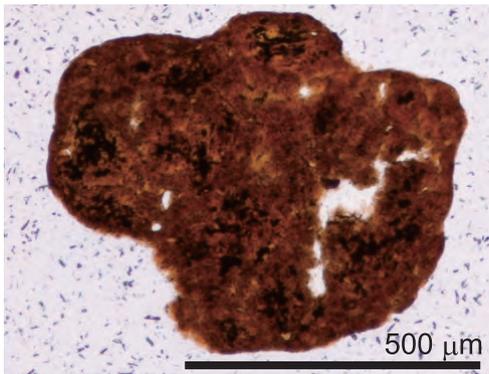
Yamamoto et al. Fig. 4



Yamamoto et al. Fig 5



Yamamoto et al. Fig 6



Yamamoto et al, Suplplementary Material Figure 1