- 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
- 4 N. Yamamoto<sup>a</sup>, A. Kitamura<sup>a,\*</sup>, A. Ohmori<sup>a</sup>, Y. Morishima<sup>a</sup>, T. Toyofuku<sup>b</sup>, S. Ohashi<sup>c</sup>
- 5 <sup>a</sup> Institute of Geosciences, Shizuoka University, Shizuoka 422-8529, Japan
- 6 *E-mail:* seakita@ipc.shizuoka.ac.jp
- 7 <sup>b</sup> Japan Agency for Marine-Earth Science and Technology, Yokosuka 237-0061, Japan

1

8 <sup>c</sup> Kaiyo Planning Co. Ltd., 1732-12, Maeda, Urasoe, Okinawa, 901-2102, Japan

Abstract We analyzed sediments and cavernicolous bivalve assemblages within cored 9 10sediments recovered from the Daidokutsu submarine limestone cave, which occurs in Pleistocene limestone on the fore-reef slope of Ie Island, off Okinawa, Japan. We found 11 sand-sized brown grains within sediments aged 7,000-6,000 cal BP, and identified them 12the grains as debris derived from a red soil layer developed in coastal zones around the 13Island. Temporal changes in the abundance of the debris suggest that water flow in the 14cave weakened at about 6,500 cal BP. Temporal changes in the cevernicolous bivalve 1516assemblages indicate that the environmental conditions of the innermost cave area have 17gradually spread to the cave entrance over the past 5,000 years. These findings indicate 18that the filling of cavities within the reefal foundations of the cave has continued over time, resulting in a progressive decrease in the flux of water between the interior and 1920exterior parts of the cave during at least the past 6,500 years. This indicates in turn a long-term decline in the functioning of the cryptic community within the reef as a 2122source of the nutrients that support coral reef growth. Our findings regarding the 23distribution of debris from the red soil layer strongly supports the occurrence of a mid-Holocene high-energy window, which represents a period of high wave energy 24prior to the formation of a reefal barrier. 25

26

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

29

### 30 Introduction

### 31

Cavities in coral reefs are produced in a number of ways, including reef framework 32growth and the dissolution of limestone (Kobluk 1988). Such cavities constitute 33between 30 and 75% of the bulk volume of coral reefs (Garret et al. 1971; Ginsburg 341983) and between 60 and 75% of the total available reef surface (Jackson et al. 1971; 35Logan et al. 1984). The large area of reef made up of cavities is inhabited by sponges, 36bryozoans, brachiopods and other organismss. The biomass of the cryptic communities 37 38has the potential to extend beyond the reef surface (Hutchings 1974; Brock and Brock 391977; Meesters et al. 1991).

Previous studies have addressed the evolutionary significance of cryptic 4041 communities (Jackson et al. 1971; Jackson and Winston 1982; Gili et al. 1986; Harmelin 1997; Wörheide 1998; Kano and Kase 2000, 2008; Kano et al. 2002; 4243Motchurova-Dekova et al. 2002; Ubukata et al. 2009) and the fluxes of various materials (e.g., dissolved oxygen, dissolved inorganic matter, dissolved organic matter, 44and bacterioplankton) in reef cavities (Fichez 1990a, 1990b, 1991; Richter et al. 2001; 45Scheffers et al. 2004; Van Duyl et al. 2006; De Goeij and Van Duyl 2007). However, we 46are unaware of any published studies that have searched for millennia-scale variations 47in the community of organisms in reef cavities, with the exception of Kitamura et al. 4849(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 living in the innermost area of the cave have become increasingly dominant over the past 5,000 years, while those living near the entrance of the cave have declined in abundance over this period (Kitamura et al. 2007a). This finding indicates that the environmental conditions of the innermost cave area have progressively extended to the entrance of the cave.

According to Kobluk (1988), most cavities in reefs are eventually filled with 60surface-derived sediments, cement, debris, and in situ skeletons of the cryptic 6162community. 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 64between the interior and exterior parts of **Daidokutsu-the** cave, leading in turn to an increase in the spatial extent of the zone of nutritional deficiency. However, the 6566stratigraphic distribution of cavernicolous bivalve assemblages within the cave requires additional consideration, as the possibility exists that the lowest part of the cored 6768sediments consists of sediment gravity flow deposits (22 cm thick), which would have 69 modified the species composition in the sediments (see below). To extend Kitamura et 70al.'s (2007a) study, we examined the temporal distribution of both cavernicolous bivalves and sediment within Daidokutsu cave during the past 7,000 years, based on an 7172examination of newly obtained sediment cores.

73

### 74 Study area-

75

# 76 Cave conditions and sediments

Ie island is approximately 23 km<sup>2</sup> in area and <u>is\_covered by the Pleistocene Ryukyu</u>
Limestone, with a fringing reef close to Pleistocene limestone sea cliffs that have
beenare undercut at the mean high-water level (Fig. 1). The surface of the fringing reef

is largely flat and <u>is\_exposed</u> at ebb tide (mean tidal range, 1.8 m). The reef crest is
located roughly 200 m from the shoreline, and 20 m from the entrance to Daidokutsu
cave.

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

Based on the sea-level curves of Fairbanks (1989), Bard et al. (1996), and Toscano
and Macintyre (2003), Daidokutsu cave is considered to have become submerged at ca.
9,000 yr BP, with the entrance having become completely submerged at about 8,000 yr
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.

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

Core 06 (148 cm thick) can be divided into a lower part, consisting of yellow 105106 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 is estimated to represent an age of 5,450 cal BP (Kitamura et al. 2007a). Based on the 108relationship between sediment depth and <sup>14</sup>C data, the gray calcareous mud is 109 110 interpreted to have been deposited continuously at a sedimentation rate of 21.1 cm/1,000 years. The <sup>14</sup>C ages of samples obtained from the lower part of the core fall 111 112within a narrow range from 5,980 to 5,060 cal BP, showing a non-linear relationship with depth (Fig. 3). Accordingly, Kitamura et al. (2007a) considered the possibility that 113114the sediment in the lower part originated as a sediment gravity flow. Although there exist differences in color and sedimentation rate between the yellow and gray 115116calcareous muds, the continuous deposition of mud-sized particles throughout the sequence indicates that still-water conditions prevailed for 5,000 years. 117

118

119 Bivalve assemblages

Hayami and Kase (1992, 1993, 1996) and Kase and Hayami (1992) studied 120121cavernicolous bivalves in tropical west-Pacific coral reefs, including Daidokutsu cave. 122The authors reported about 60 species of cavernicolous bivalves that share the following-common characteristics: 1) reduced adult size (usually less than 5 mm in 123length); 2) unusually large prodissoconch I and absence of prodissoconch II in many 124species, indicating non-planktotrophic development; and 3) persistent denticles of the 125126provinculum are retained until the adult stage in many pteriomorph species, indicating 127significant paedomorphosis by progenesis. According to Kase and Hayami (1992) and 128Hayami and Kase (1996), these features are regarded to reflect a common adaptive 129strategy toward the oligotrophic condition and low predation pressure of cave habitats.

Eight bivalve species are dominant in the surface sediments within Daidokutsu cave. 130131 Kitamura et al. (2007a) divided these species into three groups based on their spatial 132distribution (Fig. 4). The first group (Cosa kinjoi and Parvamussium crypticum) mainly 133inhabits the innermost cave area, whereas the second group (Cosa waikikia and Hiatella sp. aff. H. orientalis) is found near the entrance, and the third group (Chlamydella 134135tenuissima, Cyclopecten ryukyuensis, and Carditella iejimensis) shows no distinct distribution pattern. Carditella iejimensis appears to be endemic to caves of Ie Island, 136137while the others are found on many isolated islands in tropical west-Pacific coral reefs (Hayami and Kase 1996). 138

139The first group showed a rapid increase in abundance immediately above the boundary between the yellow and gray calcareous muds (ca. 5,450 cal BP) in the 140141 central area (core 06; Fig. 3). It is possible that the stratigraphic distribution of this group was influenced by the mixing of shells transported by a sediment gravity flow. 142143The species of the second- group, along with *Chlamydella tenuissima*, show a decrease in abundance at about 2,200 cal BP in the central part of the cave (core 06), and the 144145relative abundances of these species are very low in the innermost part of the cave (core 04; Fig. 3) over the past 3,000 years. We observed no significant changes in the 146temporal or spatial distribution of Cyclopecten ryukyuensis and Carditella iejimensis. 147These findings indicate that the cave environment has remained largely unchanged for 148149the past 5,000 years.

- 150
- 151 Methods

152

We sampled the cave sediment by hand using a coring tube of 6 cm in diameter and 233 cm in length (core 19; Figs. 2, 5). The core did not reach basement. The sediment core was first split and described, and then sliced into 1 cm thick samples for the measurement of mud and carbonate content. We picked and counted all micro-bivalves from the >0.5 mm fraction of each sample. Mud content was determined using standard sieves. The carbonate content of 500 mg of sediment was determined by gentle removal with 10% acetic acid.

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

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

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

In this study, we discovered sand-sized brown grains (debris <u>derived</u> from <u>a</u> red soil layer; see below) in the lower portion of core 19. We observed these grains in thin sections viewed under a polarizing microscope, and analyzed their mineral composition by powder X-ray diffractometry (XRD) using a Rigaku RINT2500 V housed at 180 Shizuoka University, Japan. The major element compositions of ten-10 brown grains 181 were analyzed byusing a non-destructive energy dispersive type-X-ray fluorescence (XRF) analyzer; (TATSCAN-F1) housed at the Japan Agency for Marine-Earth Science 182and Technology (JAMSTEC). The chemical compositions were determined at a tube 183 voltage of 30kV and the diameter of the collimater was 400µm. We picked and counted 184all brown grains from the 0.5-1.0 mm and 1.0-2.0 mm fractions of samples collected at 1851 cm thick-intervals from-within core 19. In the same way, we determined the 186187 stratigraphic distribution of brown grains in cores 04 and 06. We also picked and counted brown grains from the 0.5-1.0 mm and 1.0-2.0 mm fractions of a sample of 188 189reef-slope sediment and six samples of surface sediment from within the cave (Figs. 1, 190 2).

191

### 192 Results

193

The sediment in core 19 shows a fining-upward trend, and is divided into a lower gray 194195calcareous sand (233-178 cm depth) and an upper gray calcareous mud (178-0 cm depth) (Fig. 5). Between 233 and 192 cm depth, the carbonate content increases upward 196197 from 88 to 94%. Except for the horizon from 52 to 28 cm depth, the carbonate content between 192 and 0 cm depth is consistent at 95-97%. Between 52 and 28 cm depth, the 198199carbonate content decreases to 84% (Fig. 5). We regard this horizon to represent the 200 deposit containing the Daidokutsu pumice (deposited between 1,990 and 1,710 cal BP). Table 1 lists the radiocarbon ages obtained for mollusc shells; <sup>14</sup>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 <sup>14</sup>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 150 and 233 cm depth, and <u>a rate of 29.8 cm/1,000</u> years between 0 and 150 cm depth (Fig. 5). This change in sedimentation rate at 150 cm depth was synchronous with the change in deposition from calcareous sand to calcareous mud. An age-depth model presented in this study reveals that pale yellow calcareous mud <u>of in</u> the lower part of core 6 is heteropic with gray calcareous mud <u>of in</u> core 19 (Figs. 3, 5), although we cannot explain the cause of the change in sediment color at ca. 5,450 cal BP.

212Observations of thin sections reveal that the sand-sized brown grains are also brown internally (Supplementary Fig. 1). The grains were not dissolved by 10% acetic acid, 213214and XRD analysis reveals that they contain quartz (Fig. 6). XRF analysis reveals that the grains consist mainly of Si, Al, and Fe (Table 2). Based on these observations, we 215interpret that the brown grains are to be detritus derived from a red soil layer that are is 216widely distributed across Ie Island (Tokashiki 1993; Vuai et al. 2003; Mkadam et al. 2172182006). The dDebris with a diameter of 1.0-2.0 mm in diameter was only found from in 219the lower part of core 19 (Fig. 5). The number density of these grains (numbers per 220gram) decreases upward from 0.6/g at 233 cm depth to 0-0.1/g at 203 cm depth. The 221number density of debris with a diameter of 0.5-1.0 mm shows an upward in diameter 222decreases upward from 10/g at 233 cm depth to 0-1/g at 180 cm depth (Fig. 5). This upper stratigraphic limit of small-sized debris (0.5-1.0 mm in diameter) derived from 223224the red soil layer coincides with the boundary between calcareous sand and calcareous 225mud (178 cm depth), and coincides with an upward increase in carbonate content over 226the interval between 233 and 192 cm depth. The debris from the red soil layer is 227 recognized within surface sediment at three sites (d-f) of the six sites analyzed in the cave, although at number densities less than 0.08/g (Table 3). We found no the debris at 228229the other three sites (a-c) in the cave, in the reef-slope sample (Table 3), or in core 04.

230 The debris occurs sporadically in core 06 (Fig. 3).

231The cavernicolous bivalve fauna within core 19 is dominated by Huxleyia 232cavernicola, Bentharca tenuis, Cosa kinjoi, Cosa waikikia, Parvamussium crypticum, Cyclopecten ryukyuensis, Chlamydella tenuissima, Carditella iejimensis, and Hiatella 233234sp. aff. H. orientalis (Fig. 5, Supplementary Table 1). Species of the first-group (Cosa 235kinjoi and Parvamussium crypticum) occur continuously above 158 and 130 cm depth, 236respectively. In contrast, species of the second-group (Cosa waikikia and Hiatella sp. 237aff. H. orientalis) show an upward decrease in abundance at from about 72 cm depth. 238The stratigraphic distribution of Chlamydella tenuissima and Bentharca tenuis is 239similar to that of the second group. Huxleyia cavernicola showed shows an upward decrease in abundance at from about 150 cm depth. Both Cyclopecten ryukyuensis and 240241Carditella iejimensis occur continuously throughout the cored sediments (Fig. 5).

242

### 243 Discussion

244 Debris from <u>the</u> red soil layer

245In this studycore 19, we found that debris from the red soil layer is commonly observed in the horizon from the bottom of the core <del>19</del> to about 180 cm depth. The age range of 246247this interval is estimated to be between 7,000 and to 6,000 cal BP, based on our age model (Fig. 5). In contrast, the debris was-is only rarely observed in the younger 248249sediments of-within core 19, in other cores (04 and 06), and in surface sediments sampled from within the cave, and was-is absent from reef-slope sediments (Table 3). 250251Consequently, we consider that the stratigraphic distribution of debris from the red soil 252layer indicates that the washing of debris from coastal paleosols became weaker, and nearly terminated, during the period leading up to 6,000 cal BP. 253

254

Kawana and Kan (2002) reconstructed the Holocene development of coral reefs

around southern Okinawa Island, located about 70 km south of the present study area, 255256based on an analysis of drilling cores. The authors documented that reef began to grow upward upon basement at about 7,600 yr BP, under 10-20 m water depth, and reached 257the present sea surface at 6,000-5,500 yr BP, and then developed seaward by via 258accretion of the forereef. At the time when a similar pattern of coral reef development 259260occurred around Ie Island, the termination of the supply of debris from the red soil layer coincided with the establishment of the reef crest/flat zones (when the reef reached the 261262present sea level). The observed changes in supply of debris from the red soil layer are therefore considered to be consistent with the existence of a high-energy window-a 263264concept first proposed by Neumann (1972) and revisited by Hopley (1984). During the mid-Holocene, in areas where the rate of sea-level rise outstripped the ability of newly 265266settled coral communities to grow vertically, a period of high wave energy may have occurred prior to the formation of a reefal barrier. The high-energy window may have 267268remained open from the first complete submergence of the antecedent foundations until the moment at which modern reef flats began to develop, between about 8,000 and 269270 6,000 yr BP (Neumann<sub>7</sub> -1972; Hopley<sub>7</sub> 1984; Montaggioni<sub>7</sub> 2005). Under such conditions, the enhanced hydrodynamic energy may have helped-resulted in the rapid 271272winnowing of finer particles from paleosols and terrigenous sediments deposited on inner shelves and coastal zones. From 6,000 yr BP, the window progressively closed as 273274reef tops reached the sea level, which stabilized around its present position, and reef 275flats became sufficiently extended laterally. Consequently, the supply of detritus was 276terminated. It appears that the stratigraphic distribution of debris from the red soil layer provides direct evidence of the occurrence of athe mid-Holocene high-energy window. 277It is noteworthy that the decline in the abundance of larger debris (1.0-2.0 mm in 278

diameter) preceded that of smaller debris (0.5-1.0 mm in diameter) by 550 years (Fig.

280 5). This difference is well explained by <u>a</u> weakening in water flow within the cave,
rather than changes in sorting processes outside the cave.

282

283 Long-term changes in cavernicolous bivalve assemblages

The continuous occurrence of Cyclopecten ryukyuensis and Carditella iejimensis 284indicates that the cave environment in Daidokutsu has persisted for the past 7,000 years. 285The progressive decrease in abundance of species of the second-group (Cosa waikikia 286287and Hiatella sp. aff. H. orientalis), as well as Chlamydella tenuissima and Bentharca tenuis, is consistent with the findings of Kitamura et al. (2007a). Our data indicate that 288289species of the first\_group (Cosa kinjoi and Parvamussium crypticum) were absent from core 19 at depths between 223 and 160 cm, although other species occurred 290 291continuously throughout this interval. This finding confirms Kitamura et al's (2007a) tentative conclusion that spiecies of the first\_group species living in the innermost part 292293of the cave became dominant over the past 5,000 years. In addition, we found that Huxleyia cavernicola shows an upward decrease in abundance fromat a depth of about 294295150 cm, corresponding to about 5,130 cal BP. The bivalve species described above are suspension feeders, whereas Huxleyia cavernicola is thought to be a deposit feeder 296(Hayami and Kase 1993). This species is very rare in the surface sediments in the cave 297298(Fig. 4). Thus, the temporal changes in species abundance reveal that a decrease in the 299amount of organic matter in cave sediment-decreased at about 5,130 cal BP.

As noted above, our new data indicate that the water flow in the cave weakened at about 6,500 cal BP, suggesting in turn a decrease in the exchange of water between the interior and exterior of the cave, and <u>a</u>\_consequent<del>ly a</del> decline in nutrient levels within the cave. However, the observed changes in cavernicolous bivalve assemblages occurred after termination of the supply of debris from <u>the</u> red soil layer, at about 6,000 cal BP. This finding indicates that the population dynamics of *Cosa waikikia*, *Hiatella*sp. aff. *H. orientalis*, *Chlamydella tenuissima*, *Bentharca tenuis* and *Huxleyia cavernicola* were not significantly influenced by the decline in nutrient supply at about
6,500 cal BP. However, it <u>seems-appears</u> that the ongoing decline in nutrient supply
resulted in an expansion of the distribution of *Cosa kinjoi* and *Parvamussium crypticum*,
thereby preventing the five species listed above from inhabiting the inner part of the
cave.

312The large extent of the cryptic habitat and extensive cover of encrusting organisms within reef cavities provide a potentially important interface in the exchange of material 313 between cavities and the overlying water column (e.g., Tribble et al. 1988; Richter and 314Wunsch 1999). Coral cavities are sinks of bacterioplankton and dissolved organic 315carbon, and a source of NO<sub>x</sub> and PO<sub>4</sub><sup>3-</sup> (Van Duyl et al. 2006; De Goeij and Van Duyl 3162007; De Goeij et al. 2008). Our results show that, at least in terms of the coral cryptic 317318 community within cavities developed in the reefal foundations, the a decline in the functioning of the cryptic community as a source of nutrients to the coral reef has 319320 continued over at least the past 6,500 years.

322Acknowledgments We gratefully acknowledge K. Konishi, T. Kase and T. Ubukata for 323their advice. Thanks are also due to Shigemitsu Kinjyo, Koushin Yasumura for the 324preparation of samples. We thank A. Beu and an anonymous reviewer, whose comments 325and suggestions improved the original manuscript. We thank A. Stallard for improving 326the English in the manuscript. This study was funded by Grants-in-Aid 16340159 and 327 19540492 awarded by the Japan Society for Promotion of Science, The Japan Science Society, a Sasakawa Scientific Research Grant, and a Grants-in-Aid from the Fukada 328 329 Geological Institute.

321

## 331 References

- 332 Bard E, Hamelin B, Fairbanks RG, Zindler A (1996) Deglacial sea-level record from
- Tahiti corals and the timing of global meltwater discharge. Nature 382:241-244
- Brock RE, Brock JH (1977) A method for quantitatively assessing the infaunal
  community in coral rock. Limnol. Oceanogr 22:948-951
- De Goeij JM, Van Duyl FC (2007) Coral cavities are sinks of dissolved organic carbon
   (DOC) Limnol Oceanogr 52(6):2608–2617
- 338 De Goeij JM, Van den Berg H, Van Oostveen MM, Epping EHG, Van Duyl FC (2008)
- Major bulk dissolved organic carbon (DOC) removal by encrusting coral reef cavity
   sponges. Mar Ecol Prog Ser 357:139–151.
- Fairbanks RG (1989) A 17,000-year glacio-eustatic sea level record: influence of
  glacial melting rates on the Younger Dryas event and deep-ocean circulation. Nature
  342:637-642
- Fichez R (1990a) Les pigments chlorophylliens : indices d'oligotrophie dans les grottes
  sous-marines. Compte Rendus Académie des Sciences de Paris, Série III 310:
  255-261
- Fichez R (1990b) Decrease in allochtonous organic inputs in dark submarine caves,
   connection with lowering in benthic community richness. Hydrobiologia 207:61-69
- Fichez R (1991) Suspended particulate organic matter in a Mediterranean submarine
   cave. Mar Bio 108:167-174
- Garret P, Smith DL, Wilson AO, Patrquin D (1971) Physiography, ecology, and
  sediments of two Bermuda patch reefs. J. Geol 79:647-668
- 353 Gili JM, Riera T, Zabala M (1986) Physical and biological gradients in a submarine
- 354 cave on the Western Mediterranean coast (north-east Spain). Mar Bio 90:291-297

Ginsburg RN (1983) Geological and biological roles of cavities in coral reefs. In:
 Barnes DJ (ed) Perspectives on coral reefs. Australian Institute of Marine Science,

357 Townsville, Australia (pp 148-153)

- Harmelin JG (1997) Diversity of bryozoans in a Mediterranean sublittoral cave with
  bathyal-like conditions: role of dispersal processes and local factors. Mar Ecol Prog
  Ser 153:139-152
- Hayami I, Kase T (1992) A new cryptic species of *Pycnodonte* from Ryukyu Islands: A
  living fossil oyster. Trans Proc Palaeontol Soc Jpn NS 165:1070-1089
- Hayami I, Kase T (1993) Submarine cave bivalvia from the Ryukyu Islands:
  systematics and evolutionary significance. Bull Univ Mus Univ Tokyo 35:1-133
- Hayami I, Kase T (1996) Characteristics of submarine cave bivalves in the
  northwestern Pacific. Am Malacol Bull 12(1/2):59-65
- Hideshima S, Matsumoto E, Abe O, Kitagawa H (2001) Northwest Pacific marine
  reservoir correction estimated from annually banded coral from Ishigaki Island,
  southern Japan. Radiocarbon 43:473-476
- 370 Hopley D (1984) The Holocene high-energy window on the Central Great Barrier Reef.
- In: Thom BG. (Ed.), Coastal Geomorphology in Australia. Academic Press, Sydney,
  135–150
- Hutchings PA (1974) A preliminary report on the density and distribution of
  invertebrates living on coral reefs. In Proc 2nd Int Coral Reef Symp, Australia,
  1:285-296
- Jackson JBC, Goreau TF, Hartman WD (1971) Recent brachiopod-coralline sponge
   communities and their paleoecological significance. Science 173:623-625
- 378 Jackson JBC, Winston JE (1982) Ecology of cryptic coral reef communities. 1.
- 379 Distribution and abundance of major groups of encrusting organisms. J Exp Mar

- 380 Biol Ecol 57:135-147
- 381 Kano Y, Chiba S, Kase T (2002) Major adaptive radiation in neritopsine gastropods
- estimated from 28S rRNA sequences and fossil records. Proc Royal Soc London Ser
  B, Bio Sci 269:2457-2465
- Kano Y, Kase T (2000) Taxonomic revision of *Pisulina* (Gastropoda: Neritopsina) from
  submarine caves in the tropical Indo-Pacific. Paleontol Res 4:107-129
- Kano Y, Kase T (2008) Diversity and distributions of the submarine-cave Neritiliidae in
  the Indo-Pacific (Gastropoda: Neritimorpha). Org Divers Evol 8:22–43
- Kase T, Hayami I (1992) Unique submarine cave mollusc fauna: composition, origin
  and adaptation. J Mollus Stud 58:446-449
- Kawana T, Kan H (2002) Description of the new drilling cores through the Holocene
   coral reefs at the Gushichan coast in the southern Okinawa Island, the Ryukyus,
- Japan. Bull Coll Edu Univ Ryukyus 60:235-244 (in Japanese with English abstract)
- 393 Kitamura A, Kase T, Ohashi S, Hiramoto M, Sakaguchi Y, Tanabe A, Matou M (2003)
- Sedimentary facies and depositional rates of submarine cave sediment in coral reef
   of Okinawa Islands. The Quat Res (Daiyonki-Kenkyu) 42:99-104 (in Japanese with
- 396 English abstract)
- 397 Kitamura A, Kase T, Umino S, Yamamoto N, Ohashi S, Hiramoto M, Wakayama N,
- Amemiya M (2006) Discovery of sediment layer containing pumice grains in
   submarine cave sediment in coral reef of Okinawa Islands. The Quat Res
   (Daiyonki-Kenkyu) 45:141-144 (in Japanese with English abstract)
- Kitamura A, Hiramoto M, Kase T, Yamamoto N, Amemiya M, Ohashi S (2007a)
  Changes in cavernicolous bivalve assemblages and environments within a
  submarine cave in Okinawa Islands during the last 5,000 years. Paleontol Res
  11:161-180

405	Kitamura A, Yamamoto N, Kase T, Ohashi S, Hiramoto M, Fukusawa H, Watanabe T,
406	Irino T, Kojitani H, Shimamura M, Kawakami I, (2007b) Potential of
407	submarine-cave sediments and oxygen isotope composition of cavernicolous
408	micro-bivalve as a late Holocene paleoenvironmental record. Glob Planet Change
409	55:301-316

- 410 Kobluk DR (1988) Cryptic faunas in reefs: ecology and geologic importance. Palaios 3:
  411 379-390
- Logan A, Mathers SM, Thomas MLH (1984) Sessile invertebrate coelobite
  communities from reefs of Bermuda: Species composition and distribution. Coral
  Reefs 2:205-213
- Mkadam KM, Yonaha T, Ali VS, Tokuyama A (2006) Dissolved aluminum and silica
  release on the interaction of Okinawan subtropical red soil and seawater at different
  salinities: Experimental and field observations. Geoch Jour 40:333-343
- 418 Meesters E, Knijn R, Willemsen P, Pennartz R, Roebers G, Soest RWM (1991)
  419 Sub-rubble communities of Curaçao and Bonaire coral reefs. Coral Reefs
  420 10:189-197
- 421 Montaggioni LF (2005) History of Indo-Pacific coral reef systems since the last 422 glaciation: Development patterns and controlling factors. Earth-Sci Rev 71:1 –75
- 423 Motchurova-Dekova N, Saito M, Endo K (2002) The recent rhynchonellide brachiopod
- 424 Parasphenarina cavernicola gen. et sp. nov. from the submarine caves of Okinawa,
  425 Japan. Paleontol Res 6:299-319
- 426 Neumann AC (1972) Quaternary sea level history of Bermuda and the Bahamas. Am
  427 Quatern Assoc Second Nat Conf Abstracts, 41–44
- 428 Richter C, Wunsch M (1999) Cavity-dwelling suspension feeders in coral reefs-a new
- 429 link in reef trophodynamics. Mar Ecol Prog Ser 188:105-116

430	Richter C, Wunsch M, Rasheed M, Koötter I, Badran M (2001) Endoscopic exploration
431	of Red Sea coral reefs reveals dense populations of cavity-dwelling sponges. Nature

- 432 413:726-731
- 433 Scheffers SR, Nieuwland G, Bak RPM, Van Duyl FC (2004) Removal of bacteria and
  434 nutrient dynamics within the coral reef framework of Curaçao (Netherlands Antilles).
  435 Coral Reefs 23:413-422
- 436 Stuiver M, Reimer PJ, Bard E, Beck JW, Burr GS, Hughen KA, Kromer B, McCormac
- 437 G, Van der Plicht J, Spurk M (1998) INTCAL 98 radiocarbon age calibration,
  438 24,000–0 cal B.P. Radiocarbon 40:1041–1083
- 439 Tokashiki Y (1993) Soil survey; Jahgaru, Shimajiri Mahji, Feichisya, Kunigami Mahji
- Japanese society of pedology. In: Hirayama R, Yamada I (eds). Soil and Nature of
  Okinawa Island. 63-88 (in Japanese)
- 442 Toscano MA, Macintyre IG (2003) Corrected western Atlantic sea-level curve for the
- last 11,000 years based on calibrated <sup>14</sup>C dates from *Acropora palmata* framework
  and intertidal mangrove peat. Coral Reefs 22:257-270
- 445 Tribble GW, Sansoné FJ, Li Y-H, Smith SV, Buddemeier RW (1988) Material fluxes
- from a reef framework. In: Proceeding of 6th INt Coral Reef Symp, Australia,2:577-582
- 448 Ubukata T, Kitamura A, Hiramoto M, Kase T (2009) A 5,000-year fossil record of
  449 larval shell morphology of submarine cave microshells. Evolution 63:295-300
- 450 Van Duyl FC, Scheffers SR, Thomas FIM, Driscoll M (2006) The effect of water
- exchange on bacterioplankton depletion and inorganic nutrient dynamics in coral
   reef cavities. Coral Reefs 25:23–36
- 453 Vuai SA, Ishiki M. Tokuyama A (2003) Acidification of fresh waters by red soil in a
- 454 subtropical silicate rock area, Okinawa. Limnology 4:63-71

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

457

458	Figure captions
459 Fig	ure 1 Location map of the submarine Daidokutsu cave on Ie Island, off Okinawa
460	Island, Japan.
461	
462 Fig	ure 2 Map showing water depth and the locations of sampling points of surface
463 \$	sediments (a-f) and cored sediments. Also shown is the distribution of surface
464 5	sediment facies (see text for details).
465	
466 Figu	ure 3 Columnar sections of submarine-cave sediment within cores 04 and 06,
467 5	showing stratigraphic changes in mud and carbonate content, abundance of debris
468 9	derived from a red soil layer, the dominant cavernicolous bivalve species, and
469 0	depositional rates, as inferred from the ${}^{14}C$ ages of molluscs (modified after
470	Kitamura et al. 2007a).
471	
472 Fig	ure 4 Spatial distributions of selected cavernicolous bivalve species in Daidokutsu
473 0	cave (modified after Kitamura et al. 2007a). Percentages are given relative to the
474 t	total number of individuals of all bivalve species. The locations of a-f are shown in
475 l	Fig. 2.
476	
477 Fig	ure 5 Columnar sections of submarine-cave sediment within core 19, showing
478 5	stratigraphic changes in mud and carbonate content, abundance of debris <u>derived</u>
479 1	from <u>a</u> red soil layer, <u>the</u> dominant cavernicolous bivalve species, and depositional
480 i	rates, as inferred from the <sup>14</sup> C ages of mollusks.
481	
482 Fig	ure 6 Diffractograms of brown grains (debris <u>derived</u> from <u>a</u> red soil layer) found

483	within sediments from Daidokutsu cave. Peaks labelled "1" correspond to those					
484	<del>peaks</del> -for quartz.					
485						
486	Table 1 Results of <sup>14</sup> Cdating of molluscs. All samples were analyzed by accelerator					
487	mass spectrometry.					
488						
489	Table 2 Concentrations of major elements (wt%) within 10 grains of debris derived	4-		<b>書式変更:</b> インデント ら下げインデント : -1.5 字	:左: 1.5 字,	0 mm, ぶ 最初の行 :
490	from <u>a</u> red—_soil layer, as measured by non-destructive X-ray fluorescence.		C	1.0 ]		
491						
492	Table 3 Grain distribution (wt%) and number density of debris <u>derived</u> from <u>a</u> red soil	4-		<b>書式変更:</b> インデント ら下げインデント : -1 5 字	:左: 1.5 字,	0 mm, ぶ 最初の行 :
493	layer (number/g)—_in a sample of reef-slope sediment and six samples of surface		C			
494	sediment from within —Daidokutsu cave.					
495						
496	Electronic Supplementary Material Figure 1 Photomicrographs of debris derived from a	4-		<b>書式変更:</b> インデント ら下げインデント : -1 5 字	:左: 1.5 字, :	0 mm, ぶ 最初の行 :
497	red soillayer (plane-polarized light).		Ĺ	1.0 丁		
498						
499	Electronic Supplementary Material Table 1 List of cavernicolous bivalve species in					
500	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. 4



Yamamoto et al. Fig 5

denth	laboratory			measure		conventional	Calibrated age		
(cm)	number	sample	preservation	d <sup>14</sup> C age (BP)	δ <sup>13</sup> C	<sup>14</sup> C age* (BP)	intercept** (cal BP)	age ranges (cal BP)	
153	Beta-241526	Acar congenita	articulated shell very good	4430 ± 40	+3.3	4890 ± 40	5220	5270-5060	
211	Beta-236980	Barbatia cometa	disarticulated shell very good	5590 ± 40	+2.2	6040 ± 40	6400	6460-6370	
233	Beta-236979	Indocrassatella oblongata	disarticulated shell very good	6240 ± 40	+1.7	6680 ± 40	7170	7230-7140	
*reserv	voir correction v	was not applied							

\*reservoir correction was not applied.

\*\*intercepts between the conventional <sup>14</sup>C age and the calibration curve of Stuiver *et al*. (1998).

All errors are  $1\sigma.$ 



Yamamoto et al. Fig 6

Sample no.	1	2	3	4	5	6	7	8	9	10
Mg	3.5	4.9	6.2	5.8	9.4	7.8	5.0	3.3	5.9	7.3
Al	19.5	18.4	22.5	18.3	17.5	21.6	17.5	24.6	18.2	20.5
Si	51.2	51.1	41.6	40.6	33.6	39.0	43.7	37.7	38.5	38.3
K	6.8	6.5	7.0	5.3	4.7	5.5	6.4	5.9	4.6	5.3
Ca	2.0	0.8	1.8	3.7	4.2	0.9	5.0	1.8	0.7	1.5
Ti	2.5	2.2	1.8	1.9	1.2	1.3	2.3	2.1	1.3	1.6
Fe	14.0	15.7	18.7	22.5	27.6	22.8	19.5	23.4	29.9	24.7
others	0.5	0.4	0.4	1.9	1.8	1.1	0.6	1.2	0.9	0.8

Sample					grain c	listribut	ion $(\phi)$					lateritized
	<-4	-4~-3	-3~-2	-2~-1	-1~0	0~1	1~2	2~3	3~4	4 <b>~</b> 5	>5	debris
reef slope	0.0	0.0	0.0	0.0	2.1	7.0	39.3	36.7	10.6	0.9	3.4	0.00
а	0.0	0.0	6.2	9.4	14.6	18.6	21.0	12.4	5.9	3.4	8.3	0.00
b	0.0	1.7	10.5	10.0	16.7	15.5	13.0	7.3	6.1	7.3	11.7	0.00
С	0.0	0.0	0.0	0.0	10.0	16.0	32.9	18.4	5.9	5.9	10.8	0.00
d	0.0	0.0	0.0	0.0	2.3	1.9	4.0	5.6	13.3	27.6	45.2	0.04
е	0.0	0.0	0.0	0.0	1.4	1.7	3.6	7.5	16.0	30.3	39.3	0.04
f	0.0	19.0	4.7	5.7	5.1	5.3	10.6	12.6	14.3	11.3	11.3	0.08









Yamamoto et al, Suplpementary Material Figure 1