

Reconstruction of light conditions within a submarine cave during the past 7000 years based on the temporal and spatial distribution of algal symbiont-bearing large benthic foraminifers

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ABSTRACT

Coral reef cavities, crevasses, and caves are inhabited by cryptic communities. The sediments within the submarine Daidokutsu Cave (29 m water depth) on the fore-reef slope of Ie Island, Okinawa, Japan, preserve a fossil record of cryptic bivalve species over the past 7000 years. The record suggests that infilling of cavities caused a progressive decrease in the exchange of water between the interior and exterior of the cave, resulting in a decline in food supply to the cave. To test this hypothesis, the light conditions within the cave were reconstructed from the spatial and temporal distributions of algal symbiont-bearing large benthic foraminifers, based on the assumption that infilling of reef cavities would have resulted in reduced light intensity within the cave. The results show that progressive darkening of the cave occurred by about 5130 yr BP, synchronous with a weakening in water flow within the cave. This synchronicity indicates that infilling of cavities and narrowing of the cave entrance might cause declines in the exchange of water between the interior and exterior of the cave, as well as in light intensity within the cave. These resulted in a deficiency in food in the cave, thereby affecting the species composition of cavernicolous bivalves.

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1. Introduction

Cavities and caves are estimated to constitute between 60% and 75% of the total available surface of a coral reef (Jackson et al., 1971; Buss and Jackson, 1979; Logan et al., 1984) and between 30% and 75% of the bulk volume (Garrett et al., 1971; Ginsburg, 1983; Kobluk and van Soest, 1989). Such spaces are occupied by unique invertebrate communities (Jackson et al., 1971). Many workers have investigated the ecological and evolutionary significance of such communities (Jackson and Winston, 1982; Kobluk, 1988; Reitner and Gautret, 1996; Wörheide, 1998; Tabuki and Hanai, 1999; Kano and Kase, 2000; Kano et al., 2002; Kase and Kano, 2002; Ubukata et al., 2009) and seasonal to annual changes in environmental conditions within reef cavities (Gili et al., 1986; Fichez, 1990a,b, 1991; Harmelin, 1997; Lejeusne and Chevaldonné, 2005). In addition, several studies have examined the fluxes of various materials (e.g., dissolved oxygen, dissolved inorganic matter, dissolved organic matter, and bacterioplankton) in reef cavities (e.g., Ayukai, 1995; Yahel et al., 1998; Van Duyl et al., 2002; Scheffers et al., 2004; Van Duyl et al., 2002, 2006). For example, de Goeij and Van Duyl (2007) documented that coral cavities are a sink of dissolved organic carbon (DOC) which is

produced by reefs and reef overlying waters, and possibly supplied from land-based sources. According to de Goeij et al. (2008), encrusting cryptic sponges are of quantitative importance in the removal of DOC in coral reef cavities.

Hayami and Kase (1992, 1993, 1996) and Kase and Hayami (1992) reported about 60 species of cavernicolous bivalves in tropical west-Pacific coral reefs, including Daidokutsu Cave, which is the focus of the present report. Most species are epifaunal or semi-infaunal suspension feeders, with no photosymbiotic or chemosymbiotic species being reported. However, no previous studies have investigated millennia-scale variations in the community of these organisms or their environment, with the exception of Kitamura et al. (2007a) and Yamamoto et al. (2009).

Kitamura et al. (2007a) examined the species composition of cavernicolous bivalves from the surface and two sediment cores (Cores 04 and 06) within Daidokutsu Cave of Ie Island, northwest of the main island of Okinawa, Japan (Figs. 1 and 2). The results showed that species living in the innermost area of the cave (the 1st group) became dominant in the past 5000 yr, whereas species living near the cave entrance (the 2nd group) declined in abundance during this time (Figs. 3 and 4). This finding indicates that the environmental conditions typically seen in the innermost cave area gradually spread across the cave. It is well known that the number of species and biomass show a progressive reduction toward the cave interior (e.g., Harmelin et al., 1985; Gili et al., 1986). This pattern has been

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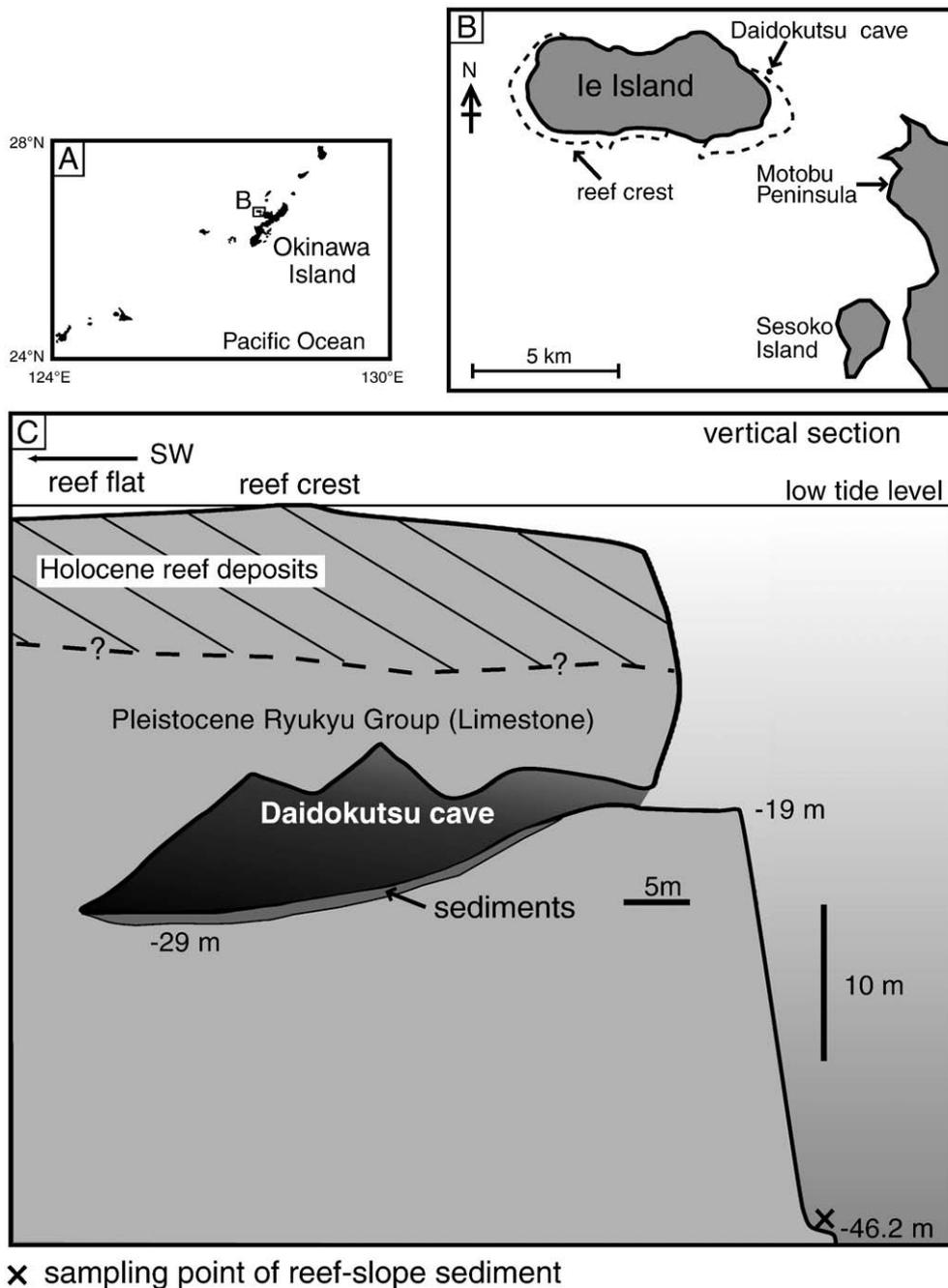


Fig. 1. Location map of the submarine Daidokutsu Cave on Ie Island, west of Motobu Peninsula, Okinawa Island, Japan (A, B), and simplified transverse section through the cave (C).

explained by a decrease in the amount of organic matters provided by water flow from the open sea into the cave, with increasing distance from the cave entrance (Gili et al., 1986; Fichez, 1990a,b, 1991; Harmelin, 1997). Thus, Kitamura et al. (2007a) concluded that in the case of Daidokutsu Cave, faunal changes in the bivalve assemblage suggest a gradual increase in extent, over the past 5000 yr or more, of the cave area deficient in foods. In addition, the authors interpreted that the infilling of cavities had led to reduced exchange of water between the interior and exterior of the cave, resulting in a progressive decline in food supply.

Yamamoto et al. (2009) extended the record of the distribution of bivalves and sediment within Daidokutsu Cave up to 7000 years BP, based on an analysis of a sediment core (Core 19; Fig. 5). The authors found brown sand-sized grains within sediments corresponding to the period 7000–6000 cal BP, and identified them as debris derived

from a red soil layer formed in coastal zones around Ie Island. Moreover, the authors showed that the decline in abundance of very coarse sand-sized debris (1.0–2.0 mm in diameter; VCS debris) preceded that of coarse sand-sized debris (0.5–1.0 mm in diameter; CS debris) by about 550 years (Fig. 5), and regarded this difference as direct evidence of a weakening in water flow within the cave. The disappearance of VCS debris at about 6500 cal BP was not accompanied by a change in bivalve assemblage, although the observed expansion of the 1st group coincided with the termination of CS debris at about 6000 cal BP. Thus, an examination of the cause of the termination of CS debris would provide information that could be used to test the validity of Kitamura et al.'s (2007a) hypothesis that millennia-scale variations in cavernicolous bivalve assemblages were strongly influenced by a decline in food supply associated with the infilling of reef cavities.

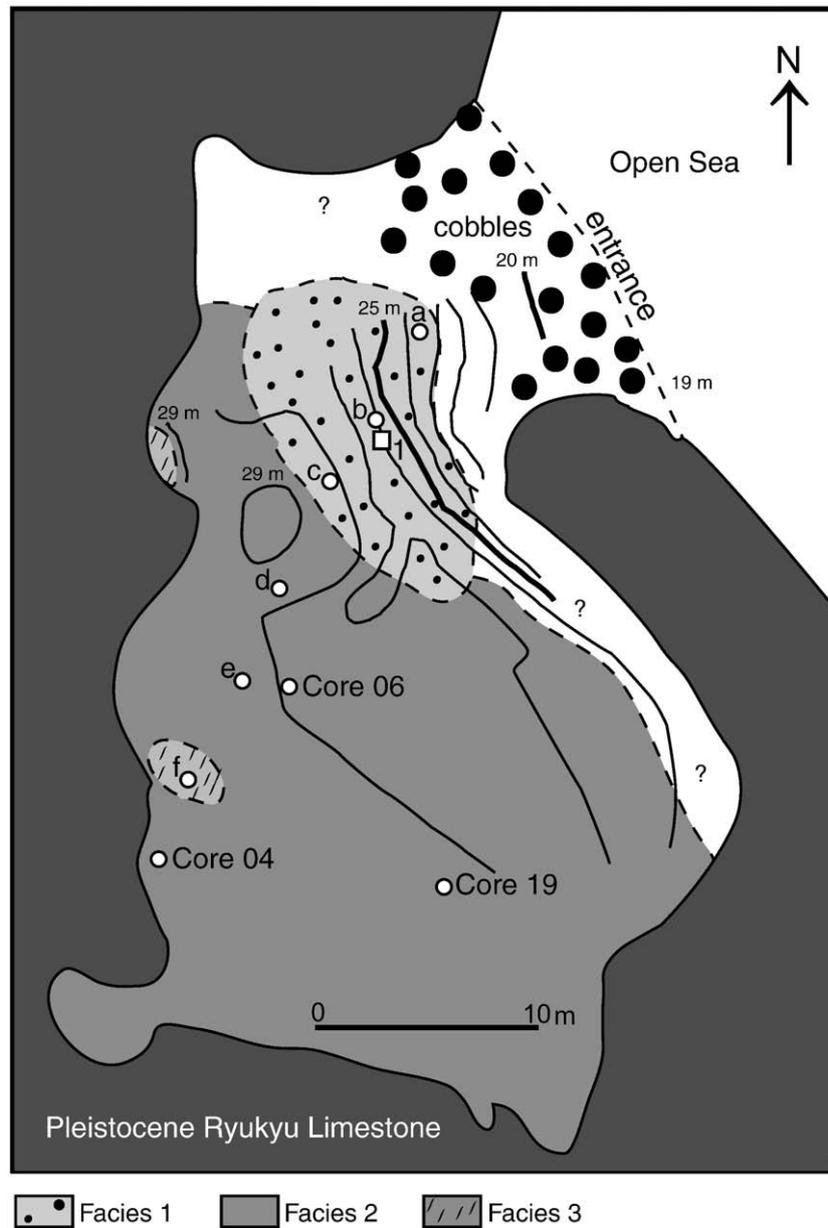


Fig. 2. Bathymetric map showing the locations of sampling points for surface sediments (a–f, 1) and cored sediments. Also shown is the distribution of surface sediment facies (see text for details).

However, there are two possible explanations of the termination of CS debris. The first interpretation assumes that the development of reef flats protected the coastal zones and thereby prevented erosion and transport of the red soil layer by high wave energy (Neumann, 1972; Hopley, 1984; Montaggioni, 2005). A second interpretation assumes that the infilling of cavities and narrowing of the cave entrance resulted in reduced water flow within the cave.

To evaluate the above interpretations, this study reconstructed temporal trends in light conditions within Daidokutsu Cave based on an analysis of the distributions of algal symbiont-bearing large benthic foraminifers (LBF) recovered from the surface and cored sediments within the cave. With infilling of the cavities and narrowing of the entrance, the interior of the cave would have become progressively darker. Distributions of living algal symbiont-bearing LBF are mainly controlled by temperature, light, water motions, substrate types, and nutrient levels (Hallock, 1999; Hohenegger, 2004; Renema, 2006; Uthicke et al., 2010). Of these parameters, light is the most important factor affecting depth distributions of algal symbiont-bearing LBF (e.g., Hallock, 1999; Hohenegger, 2004). Previous studies have provided a

detailed account of the depth distribution of LBF around Sesoko Island, which is located 10 km southeast of Ie Island (Fig. 1; Hohenegger, 1994; Hohenegger et al., 1999; Yordanova and Hohenegger, 2002). This database in the same physico-chemical oceanographic setting enables us to reconstruct the light conditions within the cave.

Although many studies have examined the species compositions of benthic foraminifers within littoral and anchialine caves (Denitto et al., 2007; van Hengstum et al., 2008, 2009a,b), we are unaware of any published studies that have searched for millennia-scale variations in the species composition of LBF in completely submerged marine caves. This study is the first to describe the taxonomic composition and temporal-spatial distribution of algal symbiont-bearing LBF in submarine caves.

2. Study area

Daidokutsu Cave is located on the northeastern coast of Ie Island, Okinawa, Ryukyu Island Arc (Fig. 1A, B). The cave's entrance lies in about 19 m water depth on the fore-reef slope, and is roughly 18 m

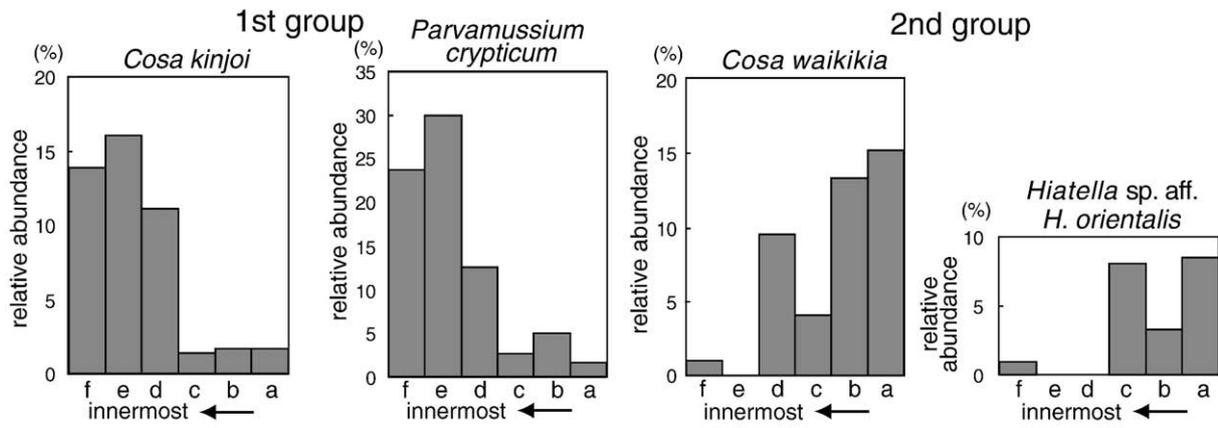


Fig. 3. Spatial distributions of selected cavernicolous bivalve species in Daidokutsu cave (modified after Yamamoto et al., 2009). Percentages are given relative to the total number of individuals of all bivalve species. The locations of sites a–f are shown in Fig. 2.

wide and 2 m high. The interior of the cave is very dark, 40 m long, and deepens abruptly inward to a maximum depth of 29 m (Fig. 1C). The floor near the cave entrance is covered with cobbles and boulders, while the floor of the interior is covered by calcareous sand and mud (Fig. 2). Kitamura et al. (2007a) divided the surface sediments in the interior into three facies (Fig. 2); Facies 1 is gray calcareous sand that occurs close to the entrance, Facies 2 is gray calcareous mud that occurs in the inner part of the cave, and Facies 3 is calcareous sand

containing the skeletons of partly encrusted coralline sponges, which occurs in patches within Facies 2.

Water temperature inside the cave ranges from 29 °C (August) to 21 °C (February), showing similar seasonal variations to that observed at 30 m depth in the open sea around Okinawa (Kitamura et al., 2007b; Kitamura and Yamamoto, 2009). If we accept the sea-level curve proposed by Fairbanks (1989), Bard et al. (1996), and Toscano and Macintyre (2003), the cave was possibly completely submerged

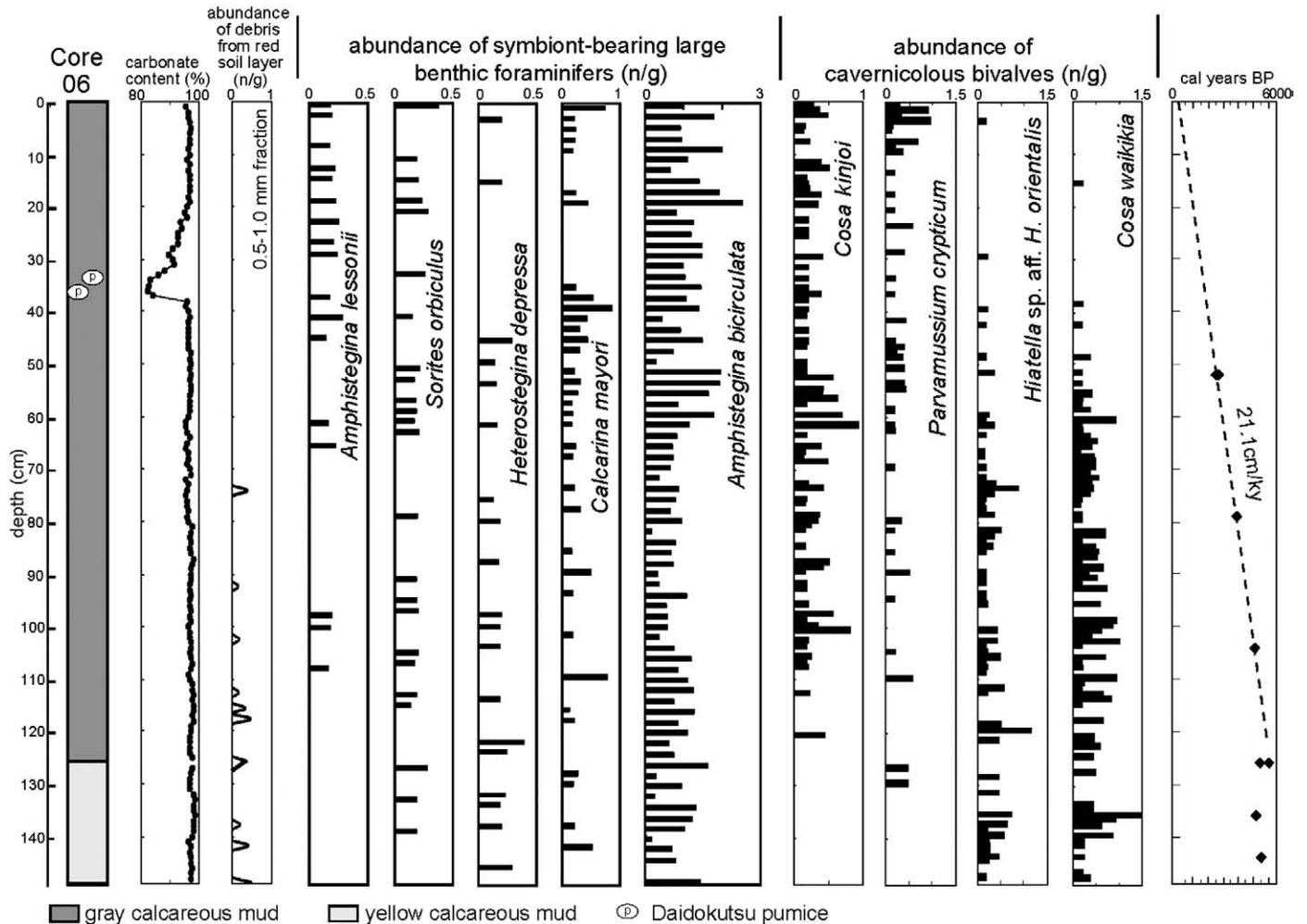


Fig. 4. Columnar sections of submarine-cave sediment within Core 06, showing stratigraphic changes in lithology and carbonate content, and abundances of debris, dominant large benthic foraminifer species and cavernicolous bivalve species, along with depositional rates inferred from the ¹⁴C ages of molluscs (modified after Yamamoto et al., 2009).

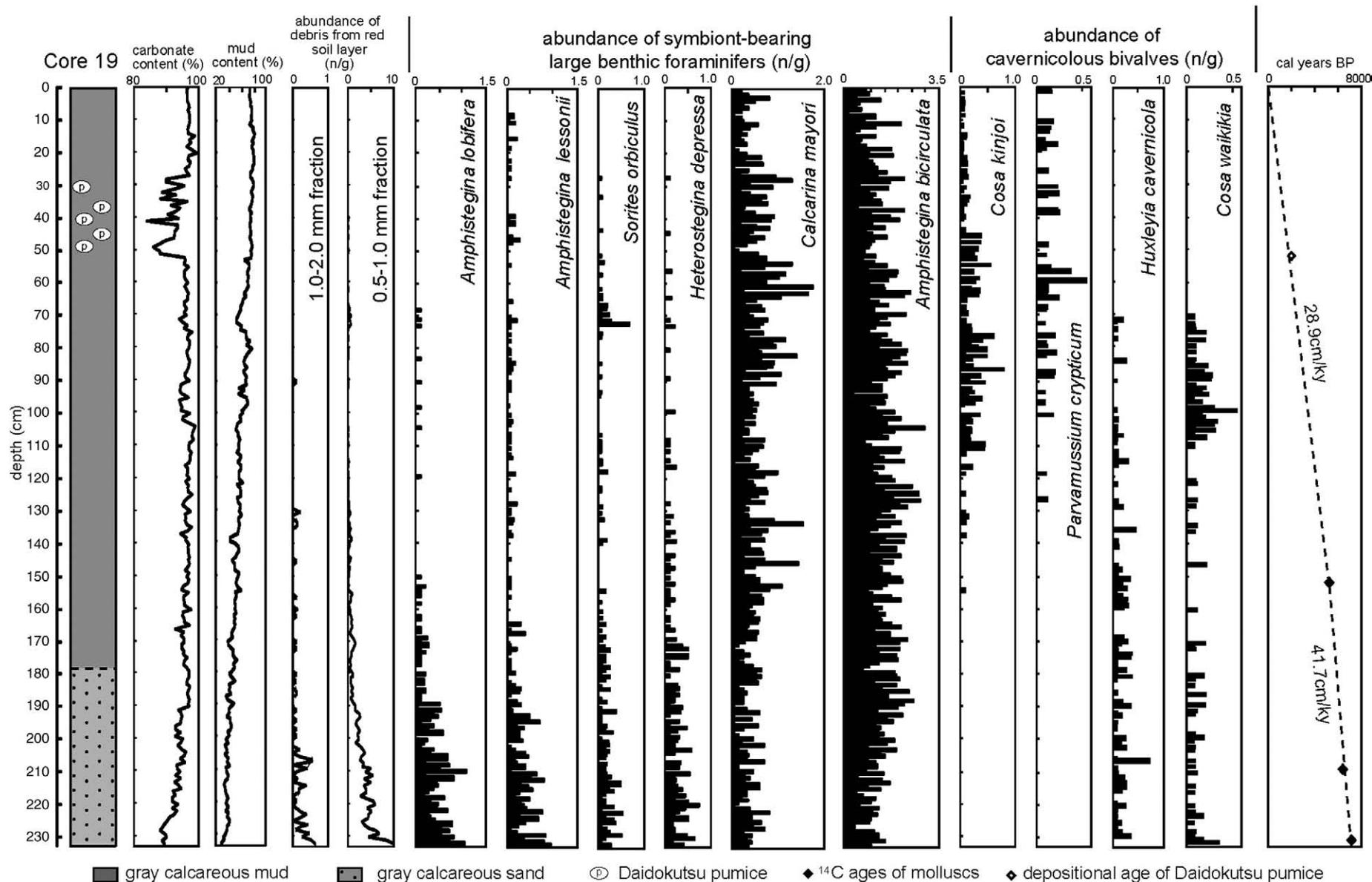


Fig. 5. Columnar sections of submarine-cave sediment within Core 19, showing stratigraphic changes in lithology, carbonate and mud contents and abundances of debris, dominant large benthic foraminifer species, and cavernicolous bivalve species, along with depositional rates inferred from the ¹⁴C ages of molluscs (modified after Yamamoto et al., 2009).

by about 8000 yr BP. Sea level has remained at its present height during the past 7000 yr (Montaggioni, 2005).

3. Materials

3.1. Sediments from the cave floor and reef slope

Kitamura et al. (2007a) examined the cavernicolous bivalve assemblage in surface sediments (uppermost 5 cm) collected at six sites within Daidokutsu Cave (a–f; Fig. 2). In the present study, we documented the LBF assemblage in these samples, as well as in the uppermost 5 cm of cored sediments (Core 04) collected from the innermost cave area (Fig. 2). For comparison, we also analyzed the LBF assemblage in a surface sediment sample collected from the reef slope (46.2 m below sea level; Fig. 1) and a living LBF assemblage in the surface sediment sample (70 g in weight) from site 1, which was located close to site b (Fig. 2).

The cavernicolous bivalves *Cosa kinjoi* and *Parvamussium crypticum* (1st group) are found within surface sediments at three sites (d–f) in the innermost cave area, while *Cosa waikikia* and *Hiatella* sp. aff. *H. orientalis* (2nd group) are observed within surface sediments at four sites (a–d) near the cave entrance (Kitamura et al., 2007a) (Fig. 3). According to Yamamoto et al. (2009), a very small amount of debris (less than one grain per 12.5 g) from the red soil layer is recognized in surface sediments at three sites in the cave (d–f), but is not found in surface sediments at the other three sites (a–c) in the cave and on the reef slope.

3.2. Cored sediments

As noted above, Kitamura et al. (2007a) and Yamamoto et al. (2009) investigated temporal changes in the cavernicolous bivalve assemblage within three sediment cores. In the present study, we examined the LBF assemblage in Cores 06 and 19.

Core 06 (148 cm length) can be divided into a lower part, consisting of yellow calcareous mud (>22 cm length), and an upper part consisting of gray calcareous mud (approximately 126 cm length) (Kitamura et al., 2007a) (Fig. 4). The sharp boundary between the two parts is estimated to represent an age of about 5450 cal BP. The gray calcareous mud is interpreted to have been deposited continuously at a sedimentation rate of ca. 21.1 cm/kyr. The ^{14}C ages of samples obtained from the lower part of the core fall within a narrow range from 5980 to 5060 cal BP, showing a non-linear relationship with depth (Fig. 4). Accordingly, Kitamura et al. (2007a) considered the possibility that the sediment in the lower part originated as a sediment gravity flow. CS debris occurs sporadically in Core 06, while VCS debris is not found (Fig. 4). Molluscs of the 1st group show a rapid increase in abundance immediately above the boundary between the yellow and gray calcareous muds. The species of the 2nd mollusc group show a decrease in abundance at about 2200 cal BP.

Core 19 preserves a record of fossils and sedimentation over the past 7000 years (Yamamoto et al., 2009). The sediment in the core shows a fining-upward trend, and is divided into an underlying gray calcareous sand (233–178 cm depth) and an overlying gray calcareous mud (178–0 cm depth) (Fig. 5). The sedimentation rate is estimated to be 41.7 cm/kyr between 233 and 153 cm depth, and 28.9 cm/kyr between 153 and 0 cm depth (Fig. 5). The VCS debris from the red soil layer is only found in the lower part of Core 19 (Fig. 5), and the abundance of the debris (the number of grains per gram of sediment) decreases upward from 0.6/g at 233 cm depth to <0.1/g at 203 cm depth. The abundance of CS debris decreases upward from 10/g at 233 cm depth to <1/g at 180 cm depth. Two species of the 1st mollusc group (*Cosa kinjoi* and *Parvamussium crypticum*) occur almost continuously after the termination of CS debris at about 6000 cal BP (Fig. 5), while two species of the 2nd mollusc group (*Cosa waikikia* and *Hiatella* sp. aff. *H. orientalis*) show an upward decrease in abundance from about 72 cm depth.

4. Methods

Foraminifer tests were picked from the >0.5 mm size-fraction of surface and cored sediment samples. For Core 06, we analyzed foraminifer tests from samples collected at 1 cm intervals. The surface sediment sample from site 1 was stained with a rose Bengal solution (1 g L^{-1} of water), washed three times to remove surplus stain, and dried at 60 °C. From >0.5-mm size fraction of the residue, all stained foraminifer specimens with well-preserved test surfaces were identified as alive when collected, and isolated.

Foraminifer tests were identified to the lowest taxonomic level and the number of individuals was counted for each taxon. Taxonomic identifications were based on Hatta and Ujiie (1992a, b), Yordanova and Hohenegger (2002), and Renema and Hohenegger (2005).

We calculated the relative abundance (%) of foraminifer species in surface sediment samples. The stratigraphic distribution of each species in the cored sediments is expressed as abundance (the number of specimens per gram of sediment) (Supplemental Tables 1 and 2).

To find sediment sample groups with similar taxonomic composition, Q-mode cluster analysis was performed on log-transformed, relative abundance data of foraminifer taxa using a group-average linking method. For Cores 06 and 19, the top 25-most common taxa were used for analysis, to exclude occurrence of rare species from the data matrix. A Bray–Curtis dissimilarity coefficient was used to calculate a similarity matrix of taxonomic composition among samples. The multivariate analysis and the Bray–Curtis dissimilarity coefficient were computed using the software PRIMER Ver. 5 (PRIMER-E Ltd., England).

5. Results

A total of 61 taxa were identified from surface sediments in the submarine cave and on the fore-reef slope (Fig. 6; Table 1). Q-mode cluster analysis demonstrated that living LBF assemblage was clearly distinct from the dead assemblages in surface sediments (Supplemental Fig. 1). The dead assemblages could be divided into two subassemblages. One subassemblage was found in the innermost cave area (sites d–f, and Core 04). The sub-assemblage is dominated by *Amphistegina bicirculata*, *Calcarina mayori*, *Eponides repandus*, *Siphoniferoides siphonifera*, and *Rosalina petasiformis*. Another subassemblage was found near the cave entrance and on the fore-reef slope (sites a–c, and fore-reef slope). The subassemblage was dominated by *Amphistegina lessonii*, *A. bicirculata*, *E. repandus*, *S. siphonifera*, and *Planorbulina mediterraneanensis*. Most symbiont-bearing species in the dead assemblages such as *Amphistegina lobifera*, *A. lessonii*, *Heterostegina depressa*, and *Sorites orbiculus* were found mainly near the cave entrance and the fore-reef slope, whereas *A. bicirculata* and *C. mayori* occupied the innermost part of the cave (Fig. 7).

The living LBF assemblage in surface sediments from site 1 was dominated by non-symbiotic *E. repandus* and *Lenticulina* spp. (Fig. 6; Table 1). Many individuals of *A. bicirculata* and a few individuals of *C. mayori* and *H. depressa* were found as living in surface sediments from site 1. We found no stained individuals of *A. lessonii*, *A. lobifera*, and *S. orbiculus*.

A total of 38 and 78 taxa were identified from Cores 06 and 19, respectively. LBF assemblages from the two cores were dominated by *Amphistegina bicirculata*, *E. repandus*, *Quinqueloculina lamarckiana*, and *S. siphonifera*. Results of Q-mode cluster analysis demonstrated only one large cluster for the Core 06 data (Supplemental Fig. 2), suggesting that LBF assemblages in the vicinity of Core 06 were generally stable over time. *A. bicirculata* was commonly found throughout Core 06, whereas *A. lessonii*, *H. depressa*, *Calcarina mayori*, and *Sorites orbiculus* occurred sporadically (Fig. 4; Supplemental Table 1). We did not find *Amphistegina lobifera* in Core 06. In contrast, three major clusters could be recognized for the Core 19 data, being correlated to samples from the lower (149–233 cm),

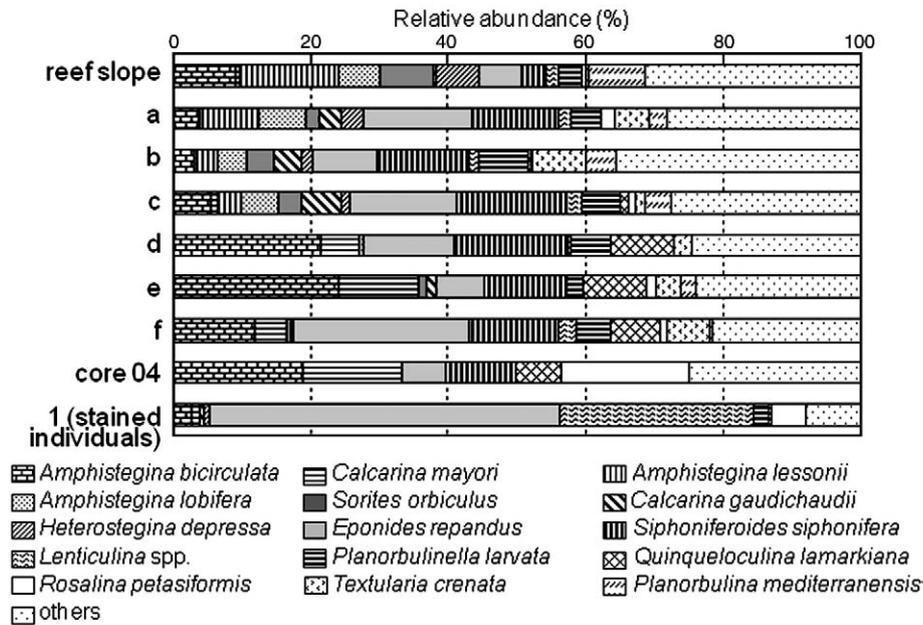


Fig. 6. Relative abundances of dominant benthic foraminifer species (those that make up >3% of the total count in each sample; dead specimens except for site 1) in Daidokutsu Cave. The locations of sites a–f, 1, Core 4, and the fore-reef samples are shown in Figs. 1 and 2.

middle (70–187 cm) and upper (0–135 cm) parts of the core (Supplemental Fig. 3). *A. lobifera*, *A. lessonii*, *H. depressa*, and *S. orbiculus* were commonly found in the lower part (233–151 cm depth), but were rare in the upper 150 cm, which was deposited after around 5130 cal BP (Fig. 5; Supplemental Table 2). *Sorites orbiculus* was abundant within the horizon from 73 to 68 cm depth, and *C. mayori* was relatively rare between 233 and 170 cm depth. *A. bicirculata* showed a gradual increase in abundance between 233 and 210 cm depth, and was predominant throughout the interval between 210 and 60 cm depth before showing a gradual upward decrease in abundance from 60 cm depth.

6. Discussion

Large benthic foraminiferal assemblages from surface and cored sediments inside the cave are composed of diverse heterotrophic and algal symbiont-bearing mixotrophic taxa. Algal symbiont-bearing mixotrophic taxa are characterized by species adapted to hard substrates in a low-light condition (e.g., the deeper part of the euphotic depths). It is notable that species adapted to soft (sandy) substrates in the low-light condition such as *Dendritina* spp., *Parasorites orbitolitoides*, *Amphistegina radiata*, *Amphistegina papillosa*, *Nummulites venosus*, and *Operculina complanata* (Hohenegger, 2004) were rare or absent. This was possibly because of the lack of sandy area particularly in the inner part of the cave and of relatively high-light conditions near the cave entrance.

In Core 19, *Amphistegina lobifera*, *A. lessonii*, *H. depressa*, and *S. orbiculus* show a decrease in abundance from at least 7000 cal BP and occur only sporadically after about 5130 cal BP, which corresponds to the upper 150 cm in the core (Fig. 5). *A. lobifera* inhabits turf algae that grow on high-energy reef crests throughout the Ryukyu Islands (Hohenegger, 1994; Iryu et al., 1995; Fujita, 2004), but rapidly decreases in abundance down to 20 m water depth, and is not found below 30 m depth (Hohenegger et al., 1999; Yordanova and Hohenegger, 2002; Hohenegger, 2004). Therefore, favorable water depths for this species are shallower than 15 m (Yordanova and Hohenegger, 2002). The optimal conditions for *A. lessonii* are found in water depths of 15–20 m with no substrate preference (Hohenegger, 2004; Renema, 2006): it is rare at the reef edge and is not found at

water depths exceeding 75–80 m (Yordanova and Hohenegger, 2002). The maximum abundance of *S. orbiculus* occurs on hard substrates (in particular, macroalgae; Hohenegger, 2004; Renema, 2006) of reef slopes at 15 m depth; after a strong decrease in abundance down to 40 m depth, individuals are extremely rare at 50 m (Yordanova and Hohenegger, 2002).

Given that the present sea level has remained approximately constant for the past 7000 years, the interior of Daidokutsu Cave (29 m depth) during this period has been much darker than 30 m water depth in the open sea. Therefore, there is no doubt that the interior of cave has been an unsuitable environment for *A. lobifera*, *A. lessonii*, and *S. orbiculus*. This is consistent with the absence of living individuals of these species from surface sediments at site 1 (Fig. 6; Table 1). However, many of their well-preserved empty tests occur in surface sediments within the cave at sites near the entrance (sites a–c) (Fig. 7) as well as in Core 19 (Fig. 5). Since this preservational state indicates short transport distances from the habitats of *A. lobifera*, *A. lessonii*, and *S. orbiculus*, these species are interpreted to live on hard substrates of cobbles and walls near the entrance of the cave at 19 m depth. Thus the upward decreasing trend in *A. lobifera*, *A. lessonii*, and *S. orbiculus* within Core 19 is explained by a decline in light intensity and/or weakening of water flow within the cave. The similar stratigraphic distributions of these species and CS debris (Fig. 5) indicates that termination of the supply of debris was caused mainly by a weakening of water flow within the cave, rather than a reduction in sediment supply from paleosols and terrigenous sediments deposited in coastal zones. Both *S. orbiculus* and CS debris are abundant in the horizon from 73 to 68 cm depth, implying that sediment reworking, although not significant, occurred at about 2530 cal BP.

There exists a clear difference in the spatial and stratigraphic distributions of *H. depressa* and *C. mayori* within Daidokutsu Cave. The distribution of *H. depressa* is similar to that of *A. lobifera*, whereas the distribution of *C. mayori* is similar to that of *A. bicirculata* in Core 19, as shown below (Figs. 5 and 7). The two species show similar distributions around Sesoko Island (Yordanova and Hohenegger, 2002) as well as other area in the Ryukyus (Fujita, 2004), Indonesia (Renema, 2006) and inshore reefs of the Great Barrier Reef (Uthicke et al., 2010). *Heterostegina depressa* is rare near the reef edge, but its abundance shows a sudden increase at 10 m depth. The maximum

Table 1

Census data of large benthic foraminifer species in surface sediments.

Species/site	Reef slope	a	b	c	d	e	f	Core 04	Stained individuals (site 1)
<i>Amphistegina bicirculata</i>	29	15	8	14	34	20	41	9	5
<i>Amphistegina lessonii</i>	45	35	10	9			1		
<i>Amphistegina lobifera</i>	20	27	11	13	1		1		
<i>Amphistegina papillosa</i>	11	9	2						
<i>Amphistegina radiata</i>	17	10	7	2					
<i>Amphistegina</i> sp.	21	1	6	4			2		
<i>Anomalinella rostrata</i>	3	5	5	5			4		
<i>Baculogypsina sphaerulata</i>	2	4	6	10			1		
<i>Baculogypsinoidea spinosus</i>	1		1						
<i>Calcarina defranci</i>	3	5	4	4	1	2	3		2
<i>Calcarina gaudichaudii</i>	1	13	10	15		1			1
<i>Calcarina hispida</i>	1	2	1						
<i>Calcarina mayori</i>	2	1		2	9	10	16	7	2
<i>Calcarina</i> sp.	2	2	1						
<i>Cibicides lobatulus</i>	1	1			1	1			
<i>Cibicidoides</i> sp.				1	3		3		
<i>Criboeponides cribrorepaudus</i>				2	5	3	5	1	
<i>Cymbaloporetta squamosa</i>		3	3	1					
<i>Cymbaloporetta tabellaeformis</i>									1
<i>Cymbaloporetta</i> sp.	1	6	7	2					
Elphidiidae		1	2						
<i>Eponides repandus</i>	20	66	26	40	21	6	91	3	92
<i>Glandulina ovula</i>									3
<i>Heterostegina depressa</i>	20	13	5	3					1
<i>Lenticulina</i> spp.	5	8	4	5	1		10		51
<i>Lingulinopsis</i> sp.									1
<i>Neoeponides</i> sp.					1		2		
<i>Neorotalina calcar</i>				1	1		1		
<i>Operculina ammonoides</i>	1		1						
<i>Pegidia dubia</i>	4	5	3	2	6	2	15	2	4
<i>Planorbulina larvata</i>	11	17	20	15	9	2	17		4
<i>Planorbulina mediterraneensis</i>	26	12	12	9		2	2		
<i>Planostegina operculinoides</i>		2	1	2					
<i>Rosalina petasiformis</i>	3	8	1	2		1	4	9	9
<i>Sphaerogypsina globulus</i>		6	6	4	6	7	7		
Rotaliida				1		1	6	4	1
<i>Amphisorus hemprichii</i>	4	2	1	3					
<i>Dendritina</i> sp.			1						
<i>Peneroplis pertusus</i>		1					1		
<i>Peneroplis planatus</i>	2								
<i>Peneroplis</i> sp.	2								
<i>Pyrgo denticulata</i>					1				1
<i>Pyrgo</i> sp.		3	6	5	2				
<i>Quinqueloculina bicarinata</i>		1	1	1	1				
<i>Quinqueloculina lamarkiana</i>			1	3	15	8	26	3	1
<i>Quinqueloculina parkeri</i>	3		1						
<i>Quinqueloculina rugosa</i>	1								
<i>Quinqueloculina</i> sp.		1						1	
<i>Sorites orbiculus</i>	25	8	12	9		1	1		
<i>Spiroloculina</i> sp.	3	5	3		2	2	3		1
<i>Triloculina kerimbatica</i>			1		1				
Miliolida	1	2		1				2	
<i>Siphoniferoides siphonifera</i>	11	50	37	40	26	10	45	5	
<i>Textularia agglutinans</i>		7	6	3	3		13	1	
<i>Textularia crenata</i>	1	20	21	4	4	3	21		
<i>Textularia dulpa</i>		9	3	3	1		5		
<i>Textularia foliacea</i>			5	2		2			
Textulariida		5	2	2			1		
Acervulinidae	13	11	12	10	3		1		
Globigerinida		1					1		
<i>Spirillina</i> ? sp.		1						1	
Unidentified	3	3			1		1		
Total	319	407	276	253	159	84	351	48	180

abundance is found at 25 m depth, below which a gradual decrease in abundance occurs to 50 m depth; the deepest individuals occur at 95 m (Yordanova and Hohenecker, 2002). *Calcarina mayori* also lives in a wide range of water depths (10–70 m), although its optimal depth is around 30 m (Hohenecker, 2004).

The above findings indicate that the difference between the two species in terms of their temporal and spatial distributions within the cave cannot be explained by light intensity alone. One possible interpretation is microhabitat differences between the two species. Although the two species prefer hard (macroalgae and reef rubble)

substrates (Hohenecker, 2004; Renema, 2006), *Heterostegina depressa* is also found on sand (Hohenecker et al., 1999). *Heterostegina depressa* is characterized by weaker attachment than *C. mayori*. Thus, *H. depressa* avoids settling in exposed smooth surfaces to resist entrainment by hydrodynamics (Fujita, 2004), whereas *C. mayori* can attach to the smooth surface of hard substrates (Hohenecker et al., 1999). *H. depressa* also shows a clear preference for horizontal or oblique surfaces, and tends to avoid vertical surfaces (Renema, 2006). These observations suggest that *H. depressa* can live on reef rubble and calcareous sands on gentle slopes near the cave entrance, while *C.*

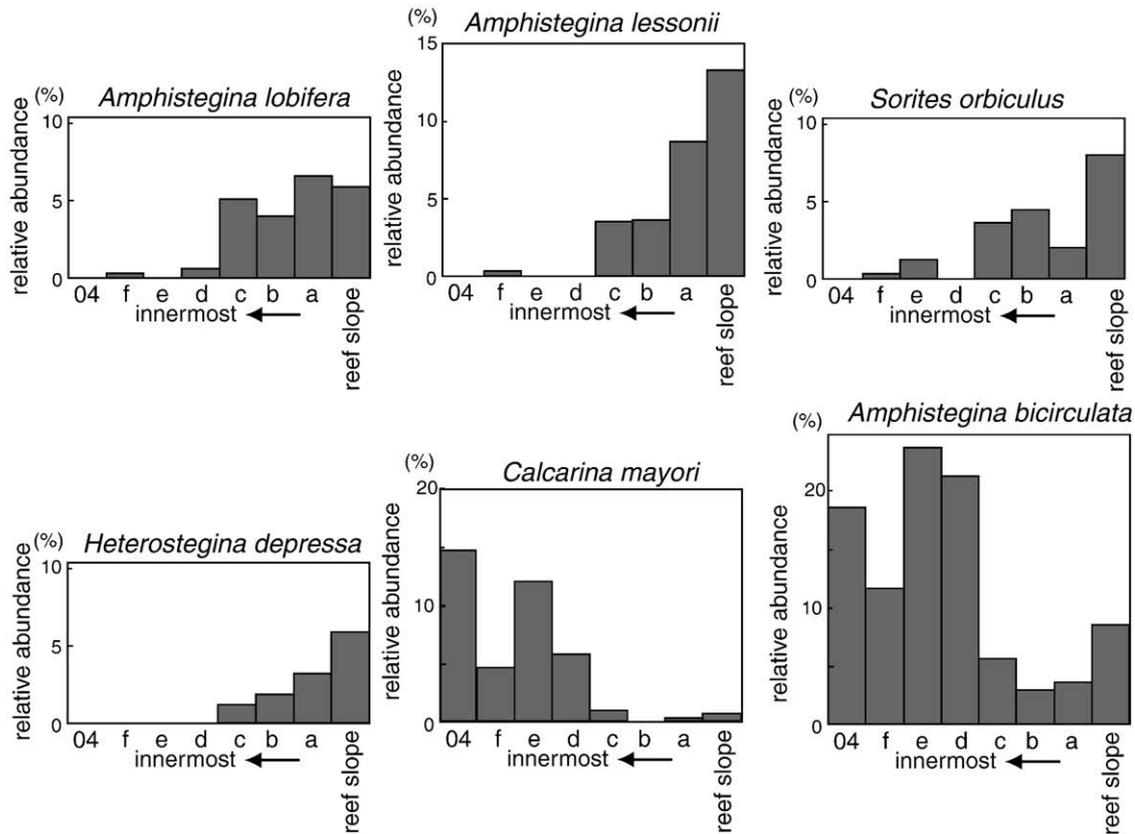


Fig. 7. Spatial distributions of algal symbiont-bearing large benthic foraminifer species in Daidokutsu Cave. The locations of sites a–f, Core 4, and fore-reef samples are shown in Figs. 1 and 2.

mayori can live attached to roofs and vertical walls inside the cave. Another possible interpretation is space competition proposed by Hohenegger (2004), which showed that the density of *H. depressa* was suppressed by the co-occurrence of *C. mayori*.

Amphistegina bicirculata occurs continuously within the sediment from both the central part of Daidokutsu Cave (Core 06) and the innermost part (Core 19) (Figs. 4 and 5). The species lives on hard, gravel and coarse sand substrates in water depths of 30–130 m (Yordanova and Hohenegger, 2002; Hohenegger, 2004), particularly favoring the lower part of the euphotic zone (optimal depth of 80 m; Yordanova and Hohenegger, 2002). Tests of *A. bicirculata* are found in the innermost part of the cave (Fig. 7), and five living individuals were found within the surface sediment at site 1 (Table 1). These findings suggest that the specimens of this species are indigenous, living on calcareous sand, skeletal remains of macroinvertebrates, roofs and walls inside the cave, and that the innermost part of the present-day cave is a favorable environment for survival of the species. The abundance of *A. bicirculata* in sediment from the inner area of the cave (Core 19) shows a gradual increase until 5000 yr BP (Fig. 5). Considering a gradual increase in abundance of *A. bicirculata* and *C. mayori*, as well as decreases in abundance of LBF species commonly found near the cave entrance discussed above, the interior of the cave is considered to have become darker during the period leading up to 5130 yr BP. The darkness corresponds to the light intensity at 50–70 m water depth in the open sea, which is based on the overlap range between the depth distributions of *A. bicirculata* and *C. mayori*.

Because the gradual darkening of the cave was synchronous with reduced inflow of material from the open sea (debris from the red soil layer), it is likely that the infilling of cavities and narrowing of the cave entrance occurred up to 5130 yr BP, which were probably caused by the development of reef-front and fore-reef zones and the transport of cobbles and boulders to the entrance. The decline in light intensity led to a decrease in photosynthetic production within the cave. In

addition, the reduction in water exchange between the interior and exterior of the cave appears to have resulted in a reduction in the supply of various materials into the cave (e.g., dissolved inorganic and organic matter, and bacterioplankton) that are essential for both heterotrophs and autotrophs. Therefore, the findings of this study support Kitamura et al.'s (2007a) hypothesis that the infilling of cavities and narrowing of the cave entrance caused a millennia-scale decline in food supply within the cave, thereby affecting the species compositions of cavernicolous bivalves.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at [doi:10.1016/j.palaeo.2010.04.004](https://doi.org/10.1016/j.palaeo.2010.04.004).

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