Changes in cavernicolous bivalve assemblages and environments within a submarine cave in the Okinawa Islands during the last 5,000 years

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Source: Paleontological Research, 11(2) : 163-182

Published By: The Palaeontological Society of Japan

URL: https://doi.org/10.2517/1342-8144(2007)11[163:CICBAA]2.0.CO;2

Paleontological Research, vol. 11, no. 2, pp. 163–182, June 30, 2007

Changes in cavernicolous bivalve assemblages and environments within a submarine cave in the Okinawa Islands during the last 5,000 years

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Received October 3, 2006; Revised manuscript accepted December 18, 2006

Abstract. Although many workers have investigated the ecological and evolutionary significance of cryptic organisms and short-term (seasonal to annuals) fluctuations in environments and fauna within submarine caves, no studies have examined millennia-scale variations in the organisms and environments. In this study, we analyzed the sedimentary characters and species composition of bivalves from surface and cored sediments within the Daidokutsu submarine limestone cave on the fore-reef slope of Ie Island, off the island of Okinawa, Japan. The sediments in the central and innermost area of the cave consist of carbonate mud. Their deposition indicates that a still-water environment prevailed over the past 5,000 years. Analysis of the spatial and temporal distribution of the bivalves shows that species living in the innermost area of the cave became dominant over at least the past 5,000 yrs, while species living near the entrance of the cave declined in abundance. This indicates that the environmental conditions of the innermost cave area gradually spread to the entrance of the cave. We believe that this phenomenon is explained by spreading nutritional deficiency within Daidokutsu cave.

Key words: cavernicolous bivalves, environmental changes, Ie Island, submarine cave deposits

Introduction

Sheltered, submarine limestone caves on reef slopes are inhabited by unique invertebrate communities that include ''living fossil'' species and relatives of deep-sea taxa. A number of workers have addressed the ecological and evolutionary significances of submarine cave communities (Jackson *et al*., 1971; Jackson and Winston, 1982; Kobluk, 1988, Hayami and Kase, 1992, 1993; Kase and Hayami, 1992, 1994; Kase and Kano, 2002; Reitner and Gautret, 1996; Wörheide, 1998; Tabuki and Hanai, 1999; Kano and Kase, 2000; Kano *et al*., 2002; Motchurova-Dekova *et al*., 2002; Lozouet, 2004) and seasonal to annual changes in fauna and environmental conditions in submarine caves (Gili *et al*., 1986; Fichez, 1990a, b, 1991; Harmelin, 1997; Lejeusne and Chevaldonné, 2005). For example, Kase and Hayami (1992) examined cavernicolous bivalves from many submarine caves of the Ryukyu Islands, southern Japan and reported the following common characteristics: 1) very small adult size (usually less than 5 mm in length), 2) unusually large prodissoconch I and absence of prodissoconch II in many species, indicating non-planktotrophic development, 3) persistent denticles of the provinculum are retained until the adult stage in many pteriomorph species, implying significant paedomorphosis by progenesis. According to Kase and Hayami (1992), these characteristics indicate that a relatively small number of larvae are produced, a predominantly *K*-selected reproductive strategy which is considered the optimal adaptation for living in stable or predictable environments. Although the evolutionary and ecological significance of cryptic organisms and seasonal/annual environmental fluctuations within submarine caves have been discussed, there is no published study of millennia-scale variations in the organisms and environments, excluding Kitamura *et al*. (2007). They examined a sediment layer (43 cm thick) in Daidokutsu cave and found that there were no remarkable tempo-

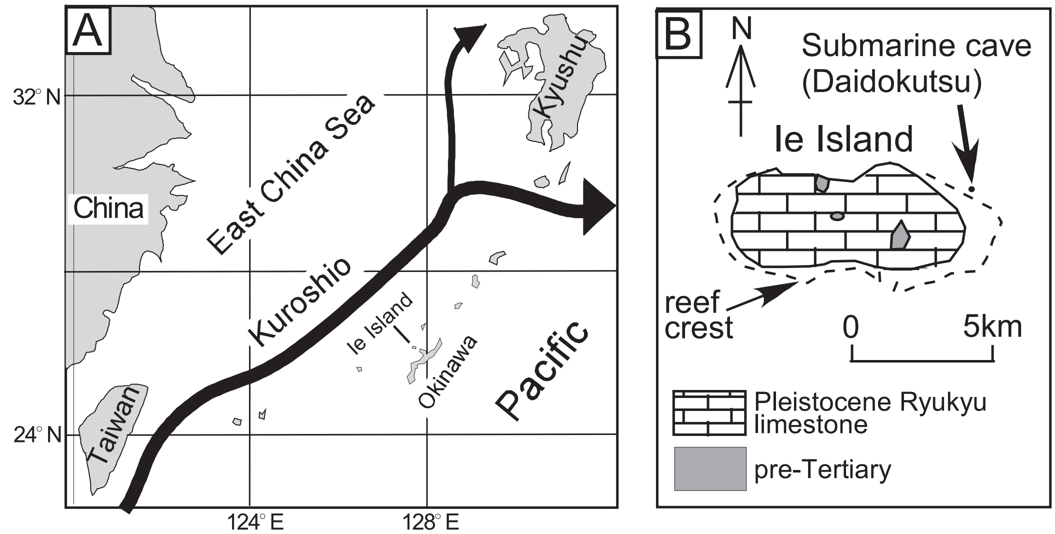

Figure 1. Location of Daidokutsu submarine cave on Ie Island, off Okinawa Island, Japan.

ral changes in grain-size distribution, in the components of the sediment, or in the species composition of the bivalve fauna during the past 2,000 years. In the present study, we collected surface and cored sediments from within Daidokutsu cave and examined the temporal and spatial distribution of both the sediments and cavernicolous bivalves during the last 5,000 years.

Study area

Daidokutsu cave is situated in the northeastern corner of Ie Island, which is located ca. 10 km west of the Motobu Peninsula on Okinawa Island (Figure 1). The cave's entrance lies about 20 m below sea level, and is about 1 m high and 2 m wide. Daidokutsu cave is 40 m long, very dark and deepens abruptly inward to its deepest point of 31 m. The floor is covered by more than 1.4-m-thick muddy deposits. Kitamura *et al*. (2003, 2007) reported that the deposits consist mainly of carbonate debris, benthic foraminifera and spicules of both sponges and didemnids. They documented a depositional rate that ranges between 20 cm/1,000 yrs and 40 cm/1,000 yrs. Water temperatures within the cave range from 30°C (August) to 20°C (February) and its seasonal pattern is similar to that at 30 m deep around Okinawa (Kitamura *et al*., 2007). In addition, the patterns of daily changes in temperature are synchronous with the tidal cycle. This indicates that the alternation of water masses within the cave is caused by the tidal cycle. Based on the sea-level curve of Fairbanks (1989), Bard *et al.* (1996) and Toscano and Macintyre (2003), the cave was submerged at ca 9,000 yr BP, and even the entrance might have been completely submerged at about 8,000 yr BP.

Methods

We collected surface sediments (5 cm thick) at six sites (a to f) situated at 5 m intervals along a transect (Figure 2). During sediment sampling, we found air bubbles rising from the sea floor (2 m depth) above Daidokutsu cave. The mud content was determined using standard sieves. All microbivalves were picked and counted from the > 0.5 mm fraction of each sample. The weight of whole sediment in each sample was 23–26 g. We also obtained cave sediment by hand with a coring tube 5 cm in diameter at two sites (cores 04 and 06) (Figure 2). The sediment cores were split and described. Each core was sliced into 1-cm-thick samples to measure the mud and carbonate content. We picked and counted all micro-bivalves from the > 0.5 mm fraction of each sample. The 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) discovered a sediment layer containing pumice grains (Daidokutsu pumice) which were deposited between BC 440 ± 40 and AD 640 ± 80. The pumice grains were transported to this area by the Kuroshio Current, since there are no active volcanoes around Ie Island or Okinawa. Kitamura *et al.* (2006) reported that the stratigraphic distribution of Daido-

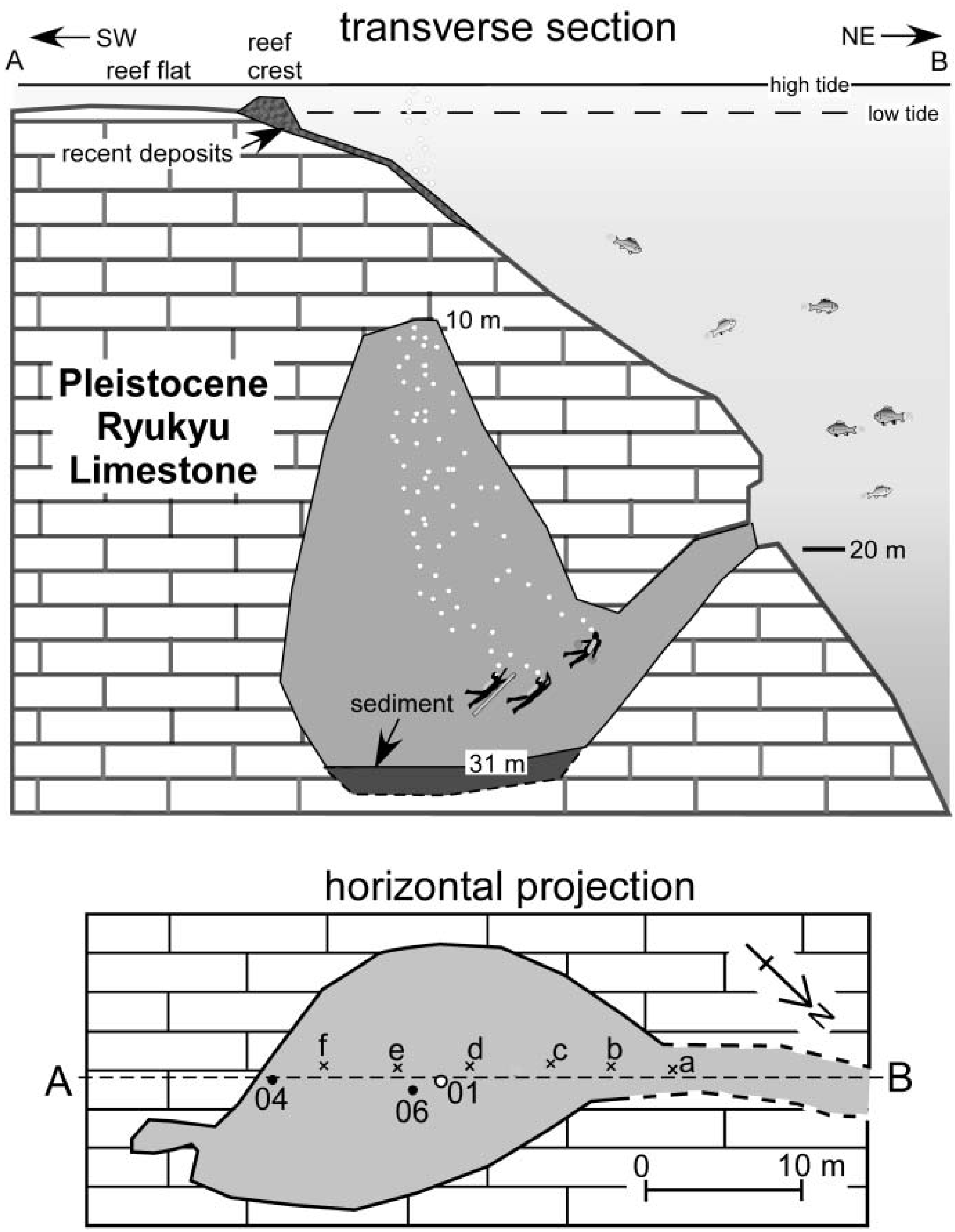

Figure 2. Simplified transverse section and horizontal projection of Daidokutsu cave. We observed air bubbles rising from the sea floor (2 m depth) above Daidokutsu cave during sediment sampling. Core 01 was examined by Kitamura *et al.* (2003, 2006, 2007).

Table 1. Results of mollusc ^{14}C-dating. All samples were analyzed with an accelerator mass spectrometry by Beta-Analytic Corporation.

core 04

depth (cm)	laboratory number	species	preservation	measured ^{14}C age (BP)	$\delta^{13}C$ (‰)	conventional ^{14}C age (BP)	Calibrated age Intercept* (cal)	Calibrated age age ranges (cal)
5	Beta-185227	*Ctenoides* sp.	partly broken	700 ± 40	1.2	1130 ± 40	AD 1300	AD 1270–AD 1320
18.5	Beta-185226	*Dimya filipina*	very good	840 ± 40	1.6	1280 ± 40	AD 1170	AD 1080–AD 1220
40	Beta-185225	*Arca ventricosa*	very good	1660 ± 40	3.5	2130 ± 40	AD 260	AD 220–AD 340
44	Beta-185224	*Ctenoides suavis*	very good	1600 ± 40	3.0	2060 ± 40	AD 360	AD 280–AD 420
68	Beta-185223	*Iniforis poecila*	very good	2060 ± 40	0.9	2480 ± 40	BC 150	BC 190–BC 70
83	Beta-185222	*Mimarcaria matsumotoi*	very good	2840 ± 40	2.9	3300 ± 40	BC 1150	BC 1220–BC 1070

core 06

depth (cm)	laboratory number	species	preservation	measured ^{14}C age (BP)	$\delta^{13}C$ (‰)	conventional ^{14}C age (BP)	Calibrated age Intercept* (cal)	Calibrated age age ranges (cal)
52	Beta-196807	*Indocrassatella oblongata*	very good	2440 ± 40	1.0	2870 ± 40	BC 710	BC 750–BC 550
52	Beta-196808	*Mimarcaria matsumotoi*	very good	2360 ± 40	2.7	2810 ± 40	BC 540	BC 690–BC 680 and BC 670–BC 450
79	Beta-196809	*Barbatia* sp.	very good	3460 ± 40	2.8	3920 ± 40	BC 1900	BC 1960–BC 1860
104	Beta-196810	*Indocrassatella oblongata*	very good	4370 ± 40	2.0	4810 ± 40	BC 3080	BC 3170–BC 3150 and BC 3130–BC 3010
126	Beta-196811	*Acar plicata*	very good	4600 ± 40	3.0	5060 ± 40	BC 3440, BC 3400, BC 3390	BC 3500–BC 3360
126	Beta-196812	*Ctenoides suavis*	very good	5200 ± 40	1.8	5640 ± 40	BC 4030	BC 4100–BC 3970
136	Beta-196813	*Mimarcaria matsumotoi*	very good	4390 ± 40	3.2	4850 ± 40	BC 3120	BC 3280–BC 3070
144	Beta-196814	*Mimarcaria matsumotoi*	very good	4690 ± 40	2.8	5150 ± 40	BC 3520	BC 3610–BC 3490

* Intercepts between the conventional ^{14}C age and the calibration curve of Stuiver *et al.* (1998).
All data shown with 1σ age range. All samples were measured by accelerator mass spectrometry and carried out through the Beta-Analytic corporation. Following Hideshima *et al.* (2001), a regional marine reservoir effect of $\Delta R = 35 \pm 25$ was adopted.

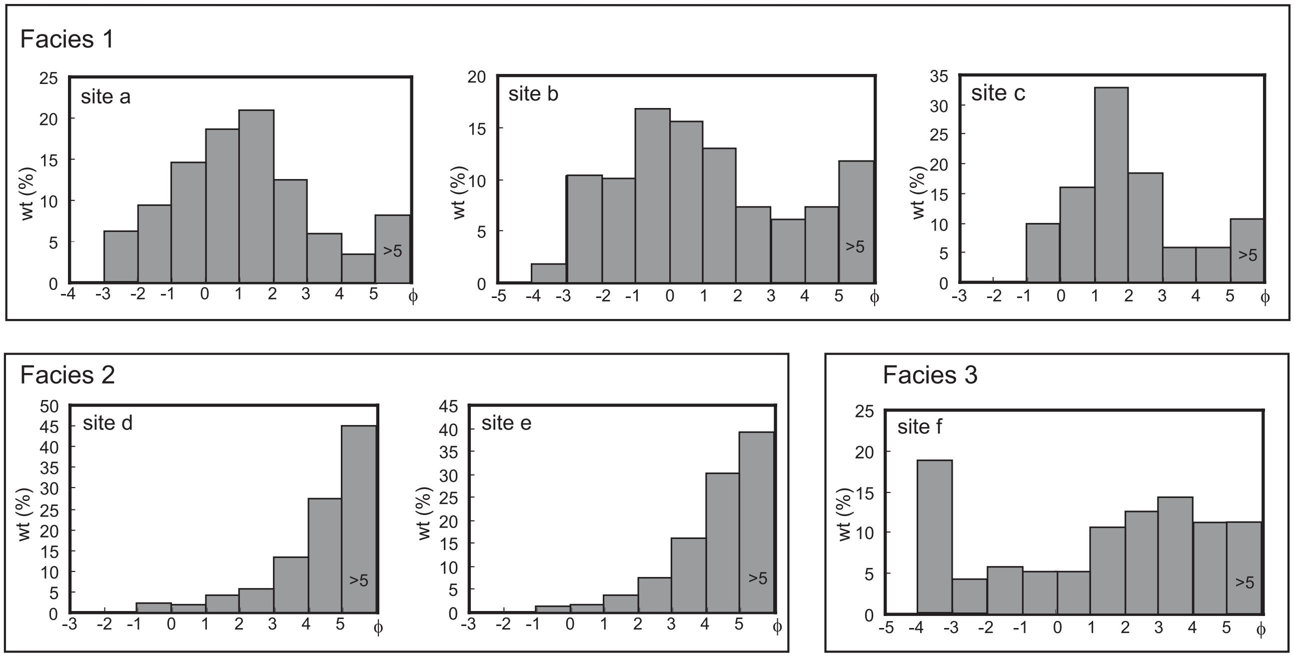

Figure 3. Histograms of grain distribution and facies at each site.

kutsu pumice can be identified by a low value in the carbonate content.

Bivalves from the surface and cored sediments exhibit excellent preservation despite being mostly disarticulated. The prodissoconch can be observed in many individuals. These factors imply 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 radiocarbon ages of 14 well preserved mollusc shells from two cores were conducted 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).

Results

Sediment and Bivalvia of the surface sediments

An analysis of grain distribution shows that three surface-sediment facies are present (Figure 3). Facies 1 is gray calcareous sand and occurs at sites a to c. Facies 2 is gray calcareous mud and occurs at sites d and e. Facies 3 is restricted to around site f and is calcareous sand with skeletons of partly encrusted coralline sponges, referred to as coralline sponge calcareous sand.

The dominant species are *Cosa kinjoi*, *Cosa waikikia*, *Parvamussium crypticum*, *Cyclopecten ryukyuensis*, *Chlamydella tenuissima*, *Malleus* sp., *Carditella iejimensis* and *Hiatella* sp. aff. *H. orientalis*. *Cosa waikikia*, *Malleus* sp. and *Hiatella* sp. aff. *H. orientalis* mainly inhabit the area near the entrance, while both *Cosa kinjoi* and *Parvamussium crypticum* mainly inhabit the innermost part of the cave (Figure 4, Table 2). The distributions of *Chlamydella tenuissima*, *Cyclopecten ryukyuensis* and *Carditella iejimensis* do not exhibit distinct patterns.

Sediment and Bivalvia of the cored sediments

Core 04.—The 84-cm-thick sediment consists of gray calcareous mud (Figure 5). The mud content of the sediment is $78.0 \pm 3.0\%$. Except for the horizon from 75 to 34 cm depth, the carbonate content is $93.4 \pm 2.2\%$ (Figure 5). However, the content decreases to 73.5% between 75 and 34 cm depth. This horizon corresponds to the layer containing Daidokutsu pumice. The sediment depth versus ^{14}C age diagram in Figure 5 implies that the average sedimentation rate is 26.5 cm/1,000 yrs and that the cored sediment covers 3,000 yrs. *Cosa kinjoi*, *Parvamussium crypticum* and *Carditella iejimensis* are predominant

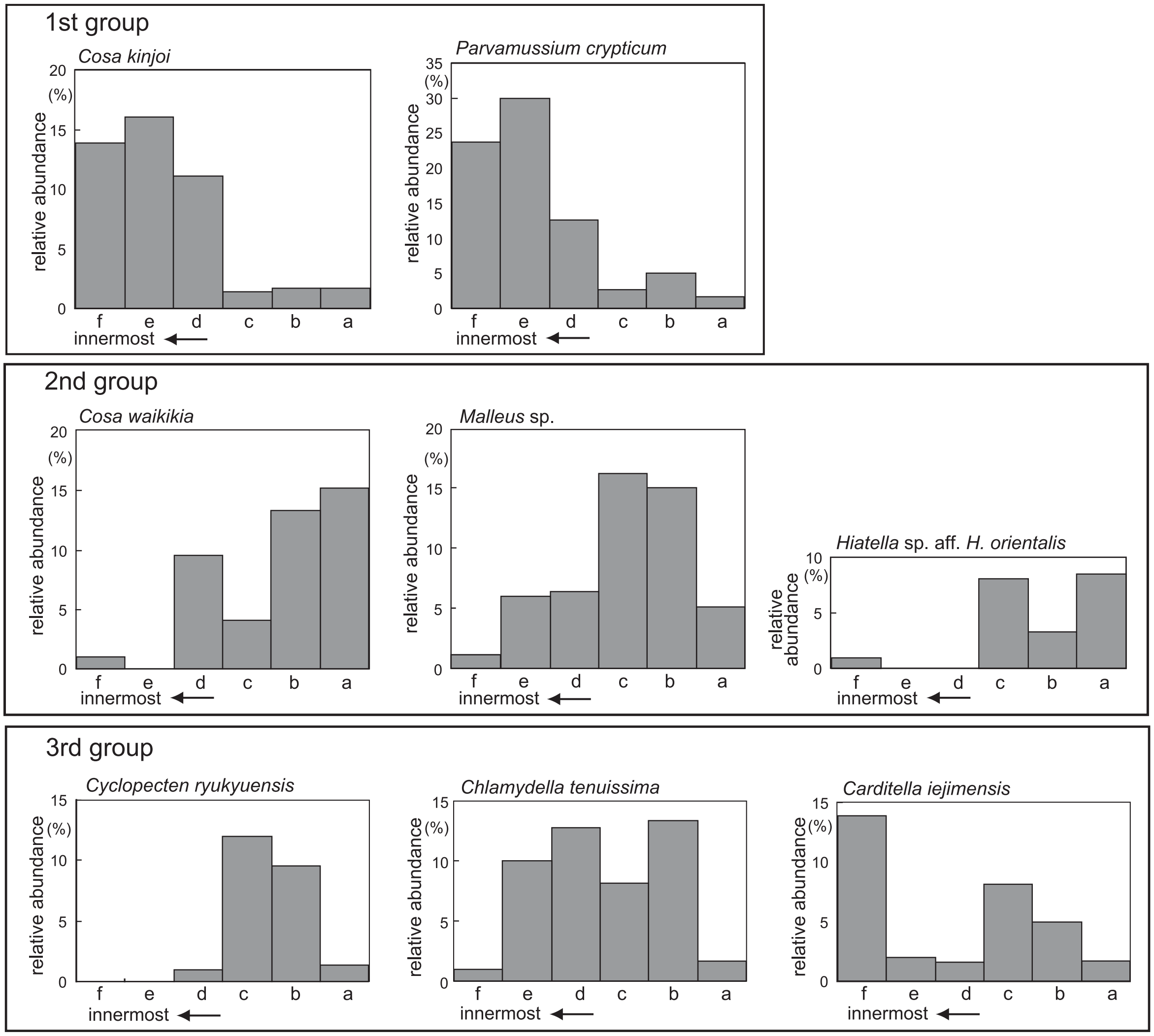

Figure 4. Spatial distributions of bivalve species in Daidokutsu cave. Percentage is given relative to total individuals of all bivalve species (Table 2).

and occur throughout the cored sediments (Figure 5, Table 3).

Core 06.—The 148-cm-thick sediment is divided into lower and upper parts. The lower part consists of yellow calcareous mud (148–126 cm depth) with a mud content of 60.1 ± 6.5%, while the upper part consists of gray calcareous mud (126–0 cm depth) with a mud content of 66.7 ± 4.4% (Figure 6). The boundary between the two parts is very sharp. The carbonate content of the yellow calcareous mud is consistent at 97.6 ± 0.6%. Except for the horizon from 37 to 21 cm depth, the carbonate content of the gray calcareous mud is consistent at 96.8 ± 0.6%. Between 37 and 21 cm depth, the carbonate content decreases to 82.3% (Figure 6). We regard this horizon as the deposit containing Daidokutsu pumice. The sediment depth versus ^{14}C age diagram in Figure 6 implies that the average sedimentation rate of the upper part is 21.1 cm/1,000 yrs in this part of the cave. Although the ^{14}C ages of all four samples from the lower part fall within a narrow range from BC 3,110 to 4,030, they exhibited a nonlinear relationship with depth. This may have resulted from bioturbation and/or a relatively high sedimentary rate such as sediment gravity flow processes. From these ^{14}C data, the boundary between the lower and upper parts is estimated to be about BC 3,500.

The bivalve fauna is dominated by *Bentharca tenuis*,

Table 2. List of bivalve species in surface sediments within Daidokutsu cave. A: articulated shells, R: right valve, L: left valve.

Species\Sample No.	a	b	c	d	e	f
Huxleyia cavernicola			L1/R1	L1/R2		L1
Pronucula insignis	R1					
Acar sp. aff. *A. plicata*	R1					
Bentharca tenuis	L1		L1	L1/R1		
Bentharca sp.	L2/R4	R2	L1/R2	L3/R1	R1	L2/R2
Bentharca excavata			L2			
Cosa waikikia	A1/L4/R4	A1/L3/R4	L3	L2/R4		R1
Cosa kinjoi	L1	R1	A1	A1/L3/R3	L3/R5	A1/L6/R7
Cosa sp.	R1		L1			
Cratis ohashii			R1			
Limopsoidea? gen. et sp. indet.		L1	R1			L1
Brachidontes sp.	L3/R2	L2			L1/R1	L1/R3
Septifer sp.	L1	L1/R1	L1			
Septifer rudis	L1		R1			
Crenella sp.	R1					
Dacrydium zebra	L1/R1		L1			
Malleus sp.	L1/R2	L6/R3	L7/R5	L4	L2/R1	R1
Parvamussium crypticum	R1	L2/R1	L1/R1	L3/R5	L6/R9	L9/R15
Cyclopecten ryukyuensis			L1	L6	L5/R1	R1
Chlamydella incubata	L1	L1	L1			
Chlamydella tenuissima	L1	L4/R4	L4/R2	L4/R4	L4/R1	L1
Lima sp.						L1
Divarilima elegans	L1		R1			L4/R2
Limaria sp.			L1		R1	
Cardita uruma		L2				L2/R3
Carditella iejimensis	R1	L2/R1	L4/R2	L1	L1	A1/L3/R10
Salaputium unicum	R1			R1		
Kelliella japonica						L1
Coralliophaga hyalina				R1		
Hiatella sp. aff. *H. orientalis*	L1/R4	L1/R1	L2/R4			R1
unidentified	15	16	17	12	8	21
total of individuals	59	60	74	63	50	101

Cosa kinjoi, *Cosa waikikia*, *Parvamussium crypticum*, *Cyclopecten ryukyuensis*, *Chlamydella tenuissima*, *Malleus* sp., *Carditella iejimensis* and *Hiatella* sp. aff. *H. orientalis* (Figure 6, Table 4). The relative abundances of *Cosa kinjoi* and *Parvamussium crypticum* increase rapidly just above the boundary, while *Bentharca tenuis*, *Cosa waikikia*, *Chlamydella tenuissima*, *Malleus* sp. and *Hiatella* sp. aff. *H. orientalis* decrease at about 47 cm depth, which corresponds to about BC 250. Since the sedimentation rate was constant throughout the upper part, the upward decrease in bivalve abundance implies that their population density dropped over time. Both *Cyclopecten ryukyuensis* and *Carditella iejimensis* occur continuously throughout the cored sediments (Figure 6). Kitamura *et al.* (2007) examined the stratigraphic distribution of bivalves in a core 01 collected close to core 06 (Figure 2). The result showed that *Parvamussium crypticum*, *Cosa kinjoi*, *Carditella iejimensis* and *Cyclopecten ryukyuensis* predominated during the last 2,000 years. This is consistent with our result.

Discussion and conclusion

Based on our analyses of sediments and bivalves, a generalized stratigraphic section of Daidokutsu sediments is shown in Figure 7. Isochronous lines were drawn in this section based upon the sedimentation rates. In terms of the surface sediments, calcareous mud occurs in the inner flat area, whereas calcareous sand occurs on a slope with a 45-degree angle. We therefore think that the distribution of surface sediment is mainly related to a combination of topographic features and the distance from the entrance. Encrustations observed on skeletons of coralline sponges suggest that sediment starvation occurred at site f. A companion study examining the grain composition of the sediments is underway and will docu-

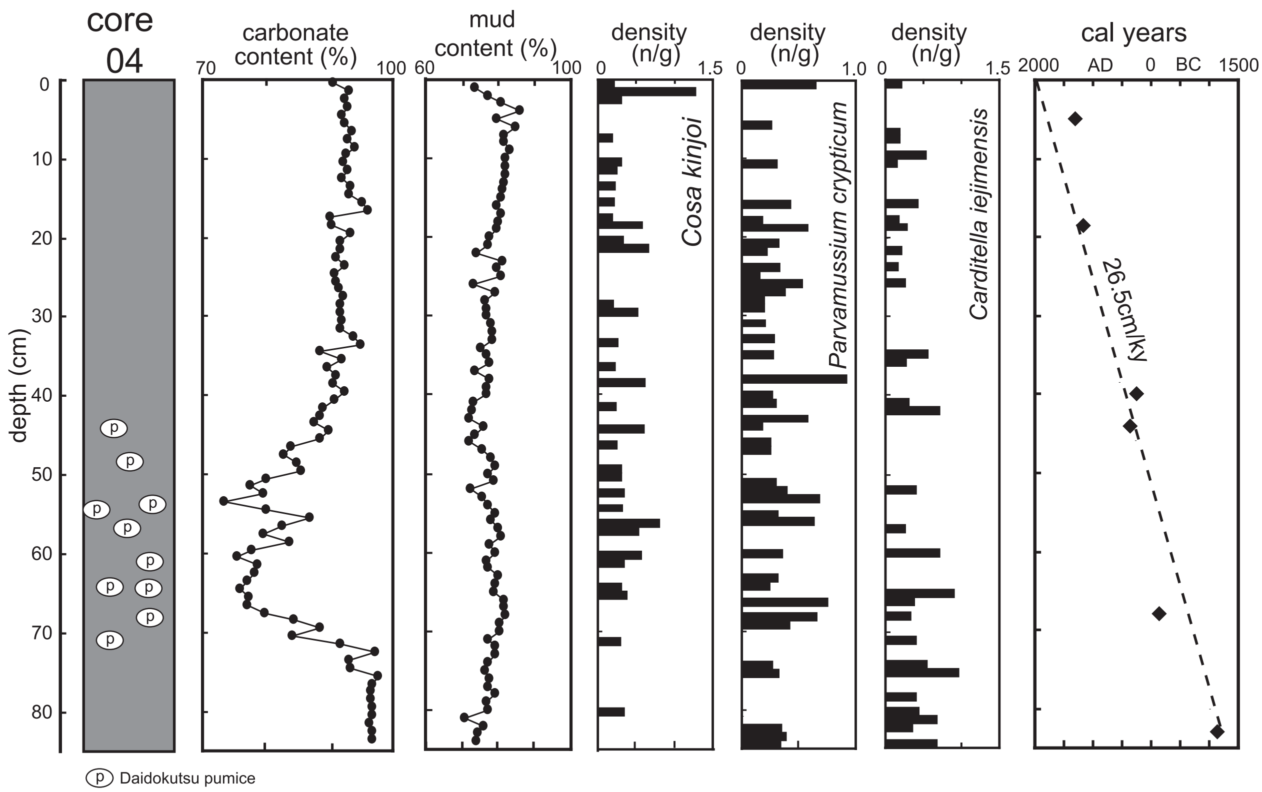

Figure 5. Columnar diagrams of submarine-cave sediment core 04, showing stratigraphic changes in mud and carbonate content and dominant bivalve species, with depositional rates inferred from ^{14}C ages of molluscs.

ment the detailed sedimentary environment and hydrodynamic conditions within the cave.

Except for the change in color between the lower and upper parts of core 06, there are no changes in sedimentary characters in the studied cores, such as sedimentary structure or mud and carbonate content. The continuous deposition of mud-sized particles implies that still-water conditions prevailed for at least 5,000 yrs.

Eight bivalve species are dominant in the surface sediments, and they are divided into three groups based on their horizontal distribution (Figure 4). The first group mainly inhabits the innermost cave area and includes *Cosa kinjoi* and *Parvamussium crypticum*. The second group dwells near the entrance and includes *Cosa waikikia*, *Malleus* sp. and *Hiatella* sp. aff. *H. orientalis*. The third group includes *Chlamydella tenuissima*, *Cyclopecten ryukyuensis* and *Carditella iejimensis* and does not exhibit a distinct distributional pattern. According to Kase and Hayami (1994), *Cosa kinjoi*, *Parvamussium crypticum* and *Carditella iejimensis* are dominant in the inner area, while *Cosa waikikia* and *Chlamydella tenuissima* are common in the area near the entrance of many caves. This pattern is consistent with our results.

The stratigraphic distribution of the bivalves shows that the first group increased rapidly just above the boundary between yellow and gray calcareous muds (ca. BC 3,500) in the central area (core 06) (Figure 7). This group occurs continuously throughout core 04, from the innermost cave area, and covers the past 3,000 yrs. The second group decreased at about BC 250 in the central area. The relative abundance of this group is very low throughout core 04. Except for *Chlamydella tenuissima*, there were no significant changes in either the temporal or spatial distribution of the third group (*Cyclopecten ryukyuensis* and *Carditella iejimensis*).

It is widely known that progressive reduction of the number of phyla, species, and biomass occurs towards the interior of submarine caves (e.g., Harmelin *et al*., 1985; Gili *et al*., 1986). This faunal pattern has been discussed by many authors. Gili *et al*. (1986) and Harmelin (1997) suggested that the diminution of food inputs below a critical level within the wall boundary layer may lead to decrease in the biomass of benthic

Table 3. List of bivalve species in core 04. A: articulated shells, R: right valve, L: left valve.

Species\Sample No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Depth (cm)	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	24–25	25–26	26–27	27–28	28–29	29–30
Acar sp. aff. *A. plicata*																														
Bentharca irregularis																														
Bentharca sp.																						L1								
Cosa waikikia					L1											R1														
Cosa kinjoi	R1	L2	L1					L1			L2	L1		L1		L1		L1	L2		R1	A1/R2							R1	L1/R1
Cosa uchimae																		L1			L1							L1	L1/R1	
Limopsoidea? gen. et sp. indet.																				R1										
Brachidontes sp.																														
Septifer sp.																														
Malleus sp.																						R1								
Parvamussium crypticum	L1/R2					L1					L2					R2		R1	L1/R1		R1	R1		L1/R1	R1	R2	L1/R1	R1	L1	
Cyclopecten ryukyuensis																		L1										L1		
Chlamydella incubata																											L1			
Chlamydella tenuissima																														
Divarilima elegans		L1						R1												R1						L1				L1
Ctenoides minimus																														
Cardita uruma																														
Cardita sp.																														
Carditella iejimensis	R1						L1	R1		L2	R1					R2		L1	L1			L1		R1		R1				
Salaputium unicum																														
Kelliella japonica																														
Hiatella sp. aff. *H. orientalis*																														
Halonympha asiatica																				R1							L1			
unidentified								1												2	2	2	1		1			5	1	1
total of individuals	5	3	1	0	1	1	1	4	0	2	5	1	0	1	0	6	0	5	5	5	5	9	1	3	2	4	4	8	5	4

Table 3. Continued

Species\Sample No.	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Depth (cm)	30–31	31–32	32–33	33–34	34–35	35–36	36–37	37–38	38–39	39–40	40–41	41–42	42–43	43–44	44–45	45–46	46–47	47–48	48–49	49–50	50–51	51–52	52–53	53–54	54–55	55–56	56–57	57–58	58–59	59–60
Acar sp. aff. *A. plicata*											L1																R1			
Bentharca irregularis	L1						R1																							
Bentharca sp.	R1					L1	R1							R1	L1							L1		L1	L1					
Cosa waikikia																					L1									
Cosa kinjoi				R1			R1		L2			R1			R2		L1			L1	L1		R1		R1		L1/R2	L1/R1		
Cosa uchimae			R1										R1																	
Limopsoidea? gen. et sp. indet.																														
Brachidontes sp.	R1			L1											L1															
Septifer sp.					R1																									
Malleus sp.																				R1										
Parvamussium crypticum	R1		R1		L1			L1/R2		L1	R1		R2	R1		R1	L1				R1	R1	R2		L1	L2				L1
Cyclopecten ryukyuensis												L1							L1					L1						
Chlamydella incubata																		R1												
Chlamydella tenuissima																														
Divarilima elegans	L1			L1		L1	R1	R1		L1			L1		R1	R1	L1				R1	L1				L1				
Ctenoides minimus																														
Cardita uruma						L1																								
Cardita sp.			R1																											
Carditella iejimensis					L1/R1	L1					L1	L1/R2										L1					R1			L2
Salaputium unicum																			L1				A1							
Kelliella japonica																														
Hiatella sp. aff. *H. orientalis*																														
Halonympha asiatica		R1																L1									L1			
unidentified	2			2	2	1			1	1	3	1		2	1		2	2	2			1		1				1		
total of individuals	7	1	3	5	6	5	4	4	3	3	6	6	4	4	6	2	5	4	4	2	4	5	4	3	3	3	6	3	0	3

Species\Sample No.	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84
Depth (cm)	60–61	61–62	62–63	63–64	64–65	65–66	66–67	67–68	68–69	69–70	70–71	71–72	72–73	73–74	74–75	75–76	76–77	77–78	78–79	79–80	80–81	81–82	82–83	83–84
Acar sp. aff. *A. plicata*																								
Bentharca irregularis			R1																			R2		L1
Bentharca sp.								R1																
Cosa waikikia																					R1			
Cosa kinjoi	L1	R1			L1	R1						R1									R1			
Cosa uchimae								R1			R1				R1		L1		R1					
Limopsoidea? gen. et sp. indet.																								
Brachidontes sp.		L1					L1																	
Septifer sp.							R1																	
Malleus sp.										L1							R1							
Parvamussium crypticum			R1	R1		R2		R2	L1					R1	L1							L1	L1	L1
Cyclopecten ryukyuensis					L1					L1													L1	
Chlamydella incubata																								
Chlamydella tenuissima		R1										R1												R1
Divarilima elegans					L1/R1								R1							L1				
Ctenoides minimus									L1															
Cardita uruma																								
Cardita sp.																								L1
Carditella iejimensis					R3	R1		R1			L1			L2	L2/R1			L1		L1	L1/R1	L1		L1/R1
Salaputium unicum																								
Kelliella japonica					L1	R1						L1				R1								
Hiatella sp. aff. *H. orientalis*				L1																				
Halonympha asiatica																								
unidentified							1		1	1	2									3	1		1	
total of individuals	1	3	2	2	8	5	3	5	3	3	4	3	1	3	5	1	2	1	1	5	5	4	3	6

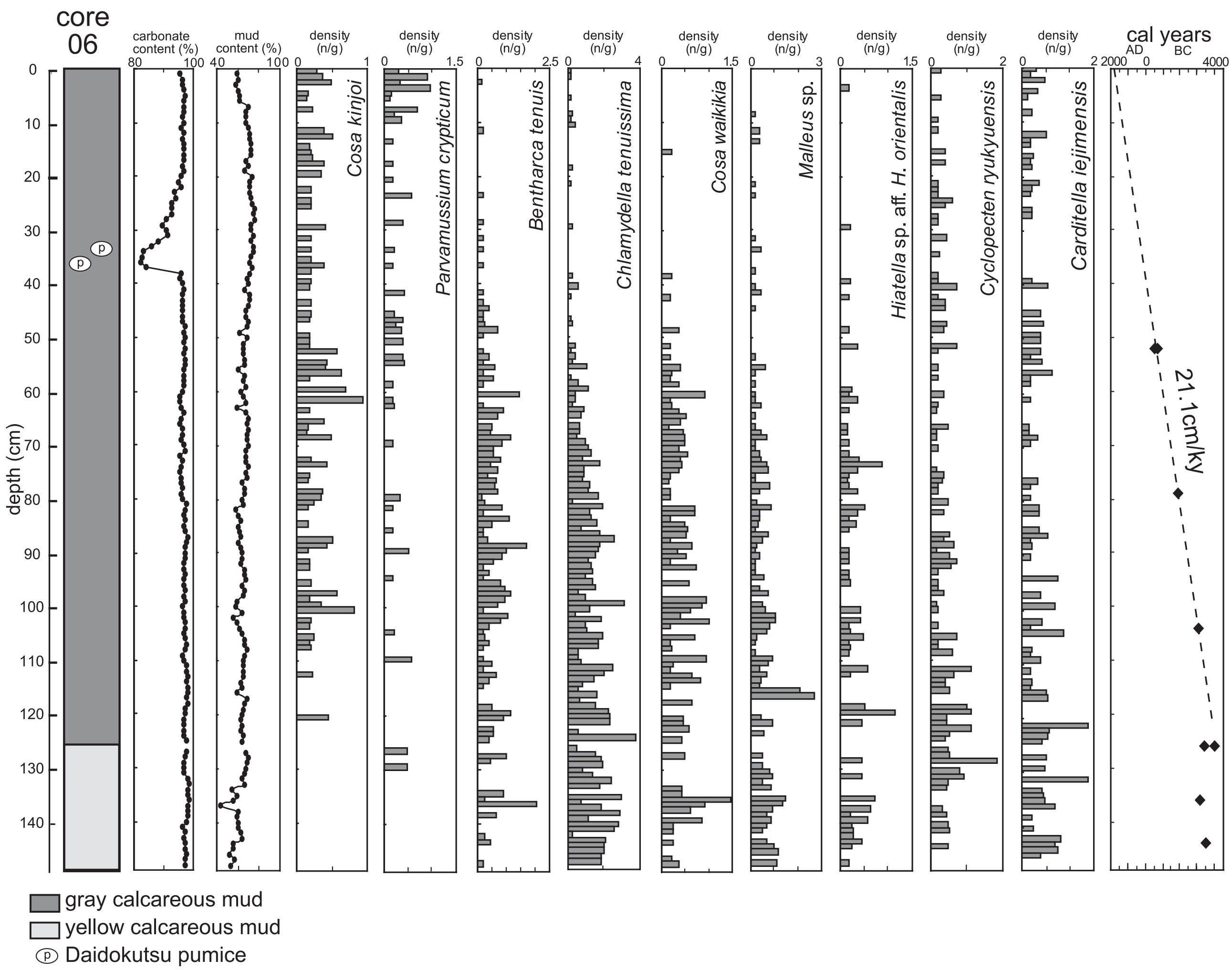

Figure 6. Columnar diagrams of submarine-cave sediment core 06, showing stratigraphic changes in mud and carbonate content and dominant bivalve species, with depositional rates inferred from ^{14}C ages of molluscs.

organisms. Fichez (1990a, b, 1991) measured suspended chloropigments and particulate organic matter and sedimentation rates in a submarine cave and concluded that the decrease in particulate organic matter input results in increasingly oligotorophic conditions with distance from the cave entrance. All of the eight species noted above are suspension feeders that are sustained by suspended nutrients which flow from the open sea into the cave. We therefore think that the zonation of the first and second groups in the fine surface deposits relates to nutrient levels, although there is no data showing that nutrient levels decline towards the innermost part of Daidokutsu cave. When this interpretation is applied to the spatial and temporal changes seen in the present bivalve samples, it is evident that the environmental conditions of the innermost cave area gradually spread to the entrance of the cave. In other words, a deficiency in nutrition has spread from the innermost cave to the area near the cave entrance over the past 5,000 yrs or more.

Temperature records show that the fluctuation of water masses within the cave is related to the tidal cycle (Kitamura *et al*., 2007). In addition, we found air bubbles rising from the sea floor above Daidokutsu cave during sediment sampling. These observations indicate that water exchange between inside and outside the cave takes place through the entrance and many small cavities. Kobluk (1988) noted that most cavities in reefs eventually fill up with surface-derived sediments, cement, debris, and in situ skeletons of cryptobionts. We believe that the infilling of cavities has caused a decrease in the exchange of water between

Table 4. List of bivalve species in core 06. A: articulated shells, R: right valve, L: left valve.

Species\Sample No.	1	2	3	4	5	6	7	10	9	10	11	12	13	14	15	16	17	110	19	20	21	22	23	24	25	26	27	28	29	30
Depth (cm)	0–1	1–2	2–3	3–4	4–5	5–6	6–7	7–8	8–9	9–10	10–11	11–12	12–13	13–14	14–15	15–16	16–17	17–18	18–19	19–20	20–21	21–22	22–23	23–24	24–25	25–26	26–27	27–28	28–29	29–30
Huxleyia cavernicola		L1						R1																						
Pronucula insignis																						1								
Mimarcaria matsumotoi																														
Acar plicata																														
Acar congenita																														
Acar sp. aff. *A. plicata*																														
Barbatia sp.																														
Bentharca tenuis			L1									L1												R1					L1	
Bentharca decorata																														
Bentharca excavata											R1							L1								L1				
Bentharca sp.	R3																R1				L1								2	
Vitracar albida																														
Cosa waikikia																L1														
Cosa kinjoi	L1/R1	L2	L3		L1	R1		L1				L1/R1	L2		L1	L1	R1	R2		L1/R1			R1		R1	L1				L2
Cosa uchimae			R1	L1																R1										
Cratis ohashii										R1																				
Limopsoidea? gen. et sp. indet.					R1				R1						L1															
Brachidontes sp.	L2							R1									R1													
Septifer excisus																														
Septifer sp.																														
Dacrydium zebra				L1																										
Malleus sp.									L1			L2		L2								R1		L1						
Parvamussium crypticum	L1/R1	L4/R1	R2	L2/R3	L1	R1		L2/R1	L1	R2				L1				L1			R1			L2/R1					L1/R1	
Parvamussium decoratum						L1																								
Cyclopecten ryukyuensis	L1/R1					L2				R1		L1				L2		L2				L1	L1	L1	L3	L2		L1	L1	
Chlamydella incubata													L1						L1											
Chlamydella tenuissima	R1	L1				L1			R1	R1	L2								R1			L1								R1
Lima sp.																														
Divarilima elegans			L1		L2						R1		R1																	
Ctenoides suavis																														
Ctenoides minimus																														
Limatula kinjoi																														
Limaria fragilis																														
Limaria sp.																							R1			L1				
Spondylus castus																														
Hyotissa chemnitzi																														
Epicodakia pygmaea					R1																									
Chama dunkeri																														
Cardita kyushuensis																														
Cardita uruma																														
Cardita sp.	L1				L1									R1								R1								
Indocrassatella oblongata																														
Carditella iejimensis	L1/R1	R1	L2/R1		R2	R1			L1				L2	L1	R1		R1	L1	L1			L2	R1	R1			L1	L1		
Salaputium unicum																														
Rochefortina sandwichensis							L1																							
Kelliella japonica																			R1											
Coralliophaga hyalina																					L1	R1								
Irus (*Irus*) sp.																														
Hiatella sp. aff. *H. orientalis*				R1																										R1
Haliris multicostata																														
unidentified	4	4	6	4	6	4	2	5	4	1		1	1		3	1	5		2			2	2	3		2	1			3
total of individuals	19	14	17	12	15	11	3	11	9	6	4	7	7	5	6	5	9	7	6	3	3	10	6	10	4	7	2	2	6	7

Table 4. Continued

Species\Sample No.	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Depth (cm)	30–31	31–32	32–33	33–34	34–35	35–36	36–37	37–38	38–39	39–40	40–41	41–42	42–43	43–44	44–45	45–46	46–47	47–48	48–49	49–50	50–51	51–52	52–53	53–54	54–55	55–56	56–57	57–58	58–59	59–60
Huxleyia cavernicola																			R1							L1				
Pronucula insignis																														
Mimarcaria matsumotoi																						R1								
Acar plicata																														
Acar congenita																						R1								
Acar sp. aff. *A. plicata*					L1				R1											R1						R1	R1			
Barbatia sp.																											L1			
Bentharca tenuis		R1		R1			L1					L1		R1	L2	R1	L1	L1	L2/R2	R1			L1	L1/R1	R1	L3	R1	L3	L1	
Bentharca decorata																														
Bentharca excavata							L1			L1				L1	L1															R1
Bentharca sp.														R1			L2			R1						L1/R1		R1	L2/R1	
Vitracar albida																						L1								
Cosa waikikia									R1				R1						L1/R1			L1		R1		R2	R1	L1	L2	
Cosa kinjoi		R1		R1		L1	L1/R1	L1		R1	L1			R1		L1	R1			R1	R1	L1	L2/R1		L2	L1/R1	L1/R2	R1		L1/R2
Cosa uchimae					R1																					L1				
Cratis ohashii																				L1										
Limopsoidea? gen. et sp. indet.																														
Brachidontes sp.											L1																			
Septifer excisus																														
Septifer sp.			R1																											
Dacrydium zebra									R1	R1																				
Malleus sp.		R1		L1/R1				R1			R1	L2			L1									L1		L3	R1		R1	
Parvamussium crypticum				R1			R1					L1/R1				R1	L1/R1	R1	R2		R2			R2	L2				R1	
Parvamussium decoratum																														
Cyclopecten ryukyuensis		L2			L1				L1	L1	L3/R1		L1	L2	L2			L2	R2			L3/R1	L1			L1		L1		
Chlamydella incubata								L1	L1	L1																				L1
Chlamydella tenuissima									L1		R3		R1				R1	L1				R1/L1	R1	L2	L1	L3/R2		L1	L2/R1	L3/R2
Lima sp.																														
Divarilima elegans																														
Ctenoides suavis																														
Ctenoides minimus																L1														
Limatula kinjoi															1															
Limaria fragilis																														
Limaria sp.																														
Spondylus castus																														A1
Hyotissa chemnitzi																														
Epicodakia pygmaea																												L1/R1		
Chama dunkeri																														
Cardita kyushuensis																														
Cardita uruma											R1																			
Cardita sp.														R1										L1						R1
Indocrassatella oblongata																						L1								
Carditella iejimensis										R1	L1/R2					L1/R1		L1/R1		L1/R1	L1/R1		L1/R1	R1	L1/R1		L1/R2	R1	L1	
Salaputium unicum															L1				R1									L1	L1	
Rochefortina sandwichensis																		L1												
Kelliella japonica																			R1											
Coralliophaga hyalina																														
Irus (*Irus*) sp.																														
Hiatella sp. aff. *H. orientalis*										R1			R1						L1			R2								R1
Haliris multicostata																														
unidentified	2		1	1	1	4		2	5	1	3	2	3	3	3	2	3	4			3	1	3	1	3	3	4	2	5	3
total of individuals	2	5	2	6	4	5	5	5	11	10	17	7	7	10	11	10	10	12	14	7	10	12	11	11	11	24	14	14	110	15

Species\Sample No.	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Depth (cm)	60–61	61–62	62–63	63–64	64–65	65–66	66–67	67–68	68–69	69–70	70–71	71–72	72–73	73–74	74–75	75–76	76–77	77–78	78–79	79–80	80–81	81–82	82–83	83–84	84–85	85–86	86–87	87–88	88–89	89–90
Huxleyia cavernicola			L1	R1	L1			R1				L1													L1				L1	
Pronucula insignis																														
Mimarcaria matsumotoi																														
Acar plicata																														
Acar congenita																														
Acar sp. aff. *A. plicata*	R1									R1		L1									R1	R1					L1		R1	
Barbatia sp.																			L1											
Bentharca tenuis	L4/R4		L1	L2/R3	L4		L3	L2/R1	L2/R5	L3/R2	L1/R2	L2/R1	L2/R2	L1/R1	L4	R2	L2/R2	R3	L3/R1	R1	R1	L3/R2	L1	A1/L4/R1	L2/R1	R1	L1	L2	L7/R1	A1/L4/R1
Bentharca decorata																														
Bentharca excavata					R1					L1										R1					L1					
Bentharca sp.			L2/R1		R1		L1/R2			1	R1		L1/R1			L2		L1				L1/R2	L1/R1	L1		L1				
Vitracar albida																														
Cosa waikikia	L3/R2	R1	R1	L1/R1	L1/R2	L1/R1	L1	R3	L2/R1	L2/R1	L2	L1/R2	L1/R1	R2	L1/R1	R1	L1		L1	R1		L1/R3	L3/R1	L1	L1/R2	L1/R2	L1/R2	L1	L1/R2	R1/L1
Cosa kinjoi		L3/R2		R1		L1/R1	R1	R1	L2/R1				L1	R2		R1	R1		R2	L2	L1	L1			A1			L2/R1	L1/R1	L1
Cosa uchimae							L1				L1											A1		L1		R1			L1	
Cratis ohashii																														
Limopsoidea? gen. et sp. indet.																													L1	
Brachidontes sp.			L1	L1				R1						L2/R1		L1	L1/R1	R1					R2	R1	L1				L2	
Septifer excisus																														
Septifer sp.														R1													L1			
Dacrydium zebra							L1					R1	R1																	
Malleus sp.	R1	R1	L2		L1		R1	L1/R2	L2/R2	L1	L1	L1/R1	R2	L1/R2	L3/R1	R1	R1	L3/R1	R2		R1	L2/R3	L2	R2	L2	R1	L3/R1	L3	L1	L1
Parvamussium crypticum		R1	R1							R1										R2		R1				R1				R3
Parvamussium decoratum																														
Cyclopecten ryukyuensis	L2		L1	L1			L3	L1	L1		L1				L1	L1/R1	L1/R1	L1	L1		L2		L2				L3	R2	L2/R1	L1
Chlamydella incubata					L1																									
Chlamydella tenuissima	R2	L2	L1	L2/R3	L1/R3		L3/R1	L2/R2	L1/R2	L1/R5	L6	L4/R3	L2/R2	L4/R4	L1/R4	L2/R3	L3/R2	L3/R3	L3/R3	L4/R6	L1	L9/R2	L3/R4	L5/R2	L7/R3	L4	L3/R7	L11/R4	L4/R4	L4/R6
Lima sp.									L1																					
Divarilima elegans			L1							L1				R1																R1
Ctenoides suavis																														
Ctenoides minimus																				L1										
Limatula kinjoi																														
Limaria fragilis																														
Limaria sp.	R1																													L1
Spondylus castus																														
Hyotissa chemnitzi																								L1						
Epicodakia pygmaea																														
Chama dunkeri							R1																							
Cardita kyushuensis													L1																	
Cardita uruma																														
Cardita sp.																														
Indocrassatella oblongata																														
Carditella iejimensis		R1					R1	R1	L2	R1							R2	L1		L1		L1/R1	R2			L1/R1	L1/R2	R1	R1	
Salaputium unicum		L1	R1											R1									R2							
Rochefortina sandwichensis																														
Kelliella japonica					L1																									
Coralliophaga hyalina																														
Irus (*Irus*) sp.																														
Hiatella sp. aff. *H. orientalis*	L1	R2		L1			R1	R1		L1		R1	R2	L2/R2	R2	L1	R1	L1	R2			L2/R1	L1/R1	R1	L1/R1	L1				L1
Haliris multicostata																														
unidentified	1	1	3	4	2		10	3	6	2	3	3	2	4	6	3	5	2	3		2	1	4	5	1	2	2	3	7	7
total of individuals	22	15	17	21	19	4	210	22	30	24	110	22	20	31	24	19	24	20	21	19	9	310	30	25	25	17	210	30	39	34

Table 4. Continued

Species\Sample No.	91	92	93	94	95	96	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113	114	115	116	117	118	119	120
Depth (cm)	90–91	91–92	92–93	93–94	94–95	95–96	96–97	97–98	98–99	99–100	100–101	101–102	102–103	103–104	104–105	105–106	106–107	107–108	108–109	109–110	110–111	111–112	112–113	113–114	114–115	115–116	116–117	117–118	118–119	119–120
Huxleyia cavernicola	L1	L1				R1				L1														R1			L1/R1			
Pronucula insignis				R1																										
Mimarcaria matsumotoi																														
Acar plicata																														
Acar congenita																														
Acar sp. aff. *A. plicata*			L1						L1								L1						R1		R1					
Barbatia sp.			L1																											
Bentharca tenuis	L4/R1	L1/R2	L1	L1/R1	L1	L2/R2	L3/R2	L3/R3	L4/R1	L2/R2	L1	L3/R2	A1/L2/R1	R2	L1	R1	R2	R1		L1	A1/L1	R1	L2/R1	L1/R1	L1				L1	R2
Bentharca decorata																								L1						
Bentharca excavata										L1/R1															R1					
Bentharca sp.		L1/R2				R1	L2	R1	L1/R1		R1	L2/R1	L1/R1			L2	R1		L1		R1			L1		R1	R1			
Vitracar albida																														
Cosa waikikia	A1/L1/R1	R1	L2/R2			R3			L4/R1	L2/R3	L1/R2	L2	L3/R2	L1		L1/R2	R1	R1		L5	L1	R1	R3	L2/R2	L1			R1		
Cosa kinjoi		L1	L1			R1		L1/R2	R1	R2	L1/R3		R1	R1		R1	L1	R1					L1							
Cosa uchimae												R1								L1										
Cratis ohashii																														
Limopsoidea? gen. et sp. indet.																														
Brachidontes sp.	L2	L1				R1			L1	L1/R1	L1/R1	L1	R1	L1/R1		R1					R1	R1		R1			L1/R1	R1		
Septifer excisus																														
Septifer sp.						R1																								
Dacrydium zebra																					L1						L1			
Malleus sp.	L2	L1	L1	L1	L2/R1		L2	L2/R2		L3	L2/R1	L3/R2	L4/R1	L3/R1	L2/R1	L1	L1		L1	L5	L1/R2	L2	L3	R1/L1	L1/R1	L4	L3/R2			
Parvamussium crypticum					R1										R1					R3										
Parvamussium decoratum																														
Cyclopecten ryukyuensis	L2/R1	L4	L1/R2	R1		L1	L1	L2		L1	L1			L1		L3	L1	L1	L1/R2			L2/R4	L1/R2	L2	L2	L1			L1/R1	L2
Chlamydella incubata													L1												L1					
Chlamydella tenuissima	L4/R5	L4/R2	L1/R6	L4/R3	L2/R3	L5/R2	L4/R4	L1/R2	L2/R3	L11/R7	L3/R3	L1/R1	L5/R4	L4/R1	L2/R3	L5/R3	L6/R3	L4/R4	L3	L2/R1	L1/R2	L6/R7	L5/R4	L4/R3	L2/R2	L1	L1/R2	R1	L2/R1	L1/R3
Lima sp.																														
Divarilima elegans																														
Ctenoides suavis																														
Ctenoides minimus			R1																											
Limatula kinjoi																														
Limaria fragilis																														
Limaria sp.			R1		R1	L1				L1					R1															
Spondylus castus																	R1													
Hyotissa chemnitzi													R1																	
Epicodakia pygmaea																														
Chama dunkeri																														
Cardita kyushuensis																														
Cardita uruma																														
Cardita sp.																														
Indocrassatella oblongata														L1																
Carditella iejimensis	L1				R2/L2			L1/R1		L2/R2			L2	L1	L2/R2			L1	R1	L1/R1		L1		R1	L1	R1	L1			
Salaputium unicum		L1						R1			L1	R1								R1	L1/R1					R1				
Rochefortina sandwichensis																														
Kelliella japonica																				L1										
Coralliophaga hyalina																														
Irus (*Irus*) sp.					R1										R1															
Hiatella sp. aff. *H. orientalis*	R1	L1		L1	L1	L1					L1/R1		L2	L1	L1	L2	L1	R1	L1			L2/R1	R1						L1	L2
Haliris multicostata																														
unidentified	3	10	5	10	5	4	9	1	5	15	6	3	2	3	5	3	2	10	3	4	3	10	3	6	3	1	3	1	5	
total of individuals	30	31	25	21	22	26	27	23	25	510	30	23	34	21	22	25	20	22	13	26	17	36	27	210	17	10	110	4	12	10

Species\Sample No.	121	122	123	124	125	126	127	128	129	130	131	132	133	134	135	136	137	138	139	140	141	142	143	144	145	146	147	148
Depth (cm)	120–121	121–122	122–123	123–124	124–125		126–127	127–128	128–129	129–130	130–131	131–132	132–133	133–134	134–135	135–136	136–137	137–138	138–139	139–140	140–141	141–142	142–143	143–144	144–145	145–146	146–147	147–148
Huxleyia cavernicola																			R1									
Pronucula insignis																												
Mimarcaria matsumotoi																L1								R1				
Acar plicata			L1																									
Acar congenita																												
Acar sp. aff. *A. plicata*												R1			L1/R1		R1											
Barbatia sp.															R1													
Bentharca tenuis	R2		L1	L1	L1			L1/R1	L1						L1/R1	R1	A1/L4/R4		L2/R1				L1	R2				A1
Bentharca decorata																R1												
Bentharca excavata					L1															L1								L1/R1
Bentharca sp.		R2							R1					R1		L1/R2		L2/R1			R2	L2		L2/R2			L1	L3/R1
Vitracar albida																												
Cosa waikikia	L1	R1	R1		R1			R1						R1	R1	L3/R3	L1/R3	L1/R1		L2/R1	L1	R1		R1			R1	L1/R1
Cosa kinjoi	L1																											
Cosa uchimae										L1																		
Cratis ohashii																												
Limopsoidea? gen. et sp. indet.																												
Brachidontes sp.	L1	L1	L2				L2				R1	R1			L1	L1	L1/R3	R2		R1				R1	R1		L1/R1	R1
Septifer excisus															L1													
Septifer sp.												L1							L1									
Dacrydium zebra			L1												R2												L1	
Malleus sp.	R1	L2		R1				L1		L1	L2	L1/R1	L1	L1/R1		L3/R3	L3/R3	L2/R1	L2/R1	L1/R2	L3	L1/R1		L1/R2	L3/R1	L1/R2		L5/R1
Parvamussium crypticum							R1			R1																		
Parvamussium decoratum																												
Cyclopecten ryukyuensis	L1	R1	L1/R1	R1	L1	**boundary**	L1	L1	L1/R3		L2	L1/R1	L1	L1				L1	L1/R1		L2	L1/R1			L2			
Chlamydella incubata																												
Chlamydella tenuissima	L2/R3	L1/R4		R1	L5/R4		L1/R2	L1/R2	L4	L2/R2	L2	L1/R2	L3/R2	L4		L6/R6	L2/R1	L4/R2	L10/R5	L1/R3	L7/R5	L4/R6	L1	L5/R4	L5/R3	L5	L5/R4	L6/R4
Lima sp.																					R1			R1				
Divarilima elegans																												
Ctenoides suavis					R1																							
Ctenoides minimus																				R1							R1	
Limatula kinjoi																												
Limaria fragilis																										A1		
Limaria sp.					R1											L1		L2			1							
Spondylus castus																								A1				
Hyotissa chemnitzi																L1										L2		
Epicodakia pygmaea	R1						R1							L1														
Chama dunkeri																												
Cardita kyushuensis																												
Cardita uruma																												L1
Cardita sp.																			R1									
Indocrassatella oblongata																												
Carditella iejimensis		L2/R1	L1	L1	L1			L1		L1		L1/R2		R1	L1	R2	L2/R1		R1		R1		L2/R1	L3	L1/R2	L1		
Salaputium unicum							R1																					
Rochefortina sandwichensis																				R1								
Kelliella japonica																							L1					
Coralliophaga hyalina																												
Irus (*Irus*) sp.																												
Hiatella sp. aff. *H. orientalis*		L1							R1			L1				L1/R2		L2	R1	R2	R1	R1	L1	L1/R1	R1			L1
Haliris multicostata																								L1				
unidentified	5	3	3		6		2		1		2		1	3		5	11	3		2	3	4	1	3		1	6	6
total of individuals	110	19	11	5	21		10	9	12	10	9	14	10	14	9	41	41	24	26	110	27	22	10	30	19	10	21	34

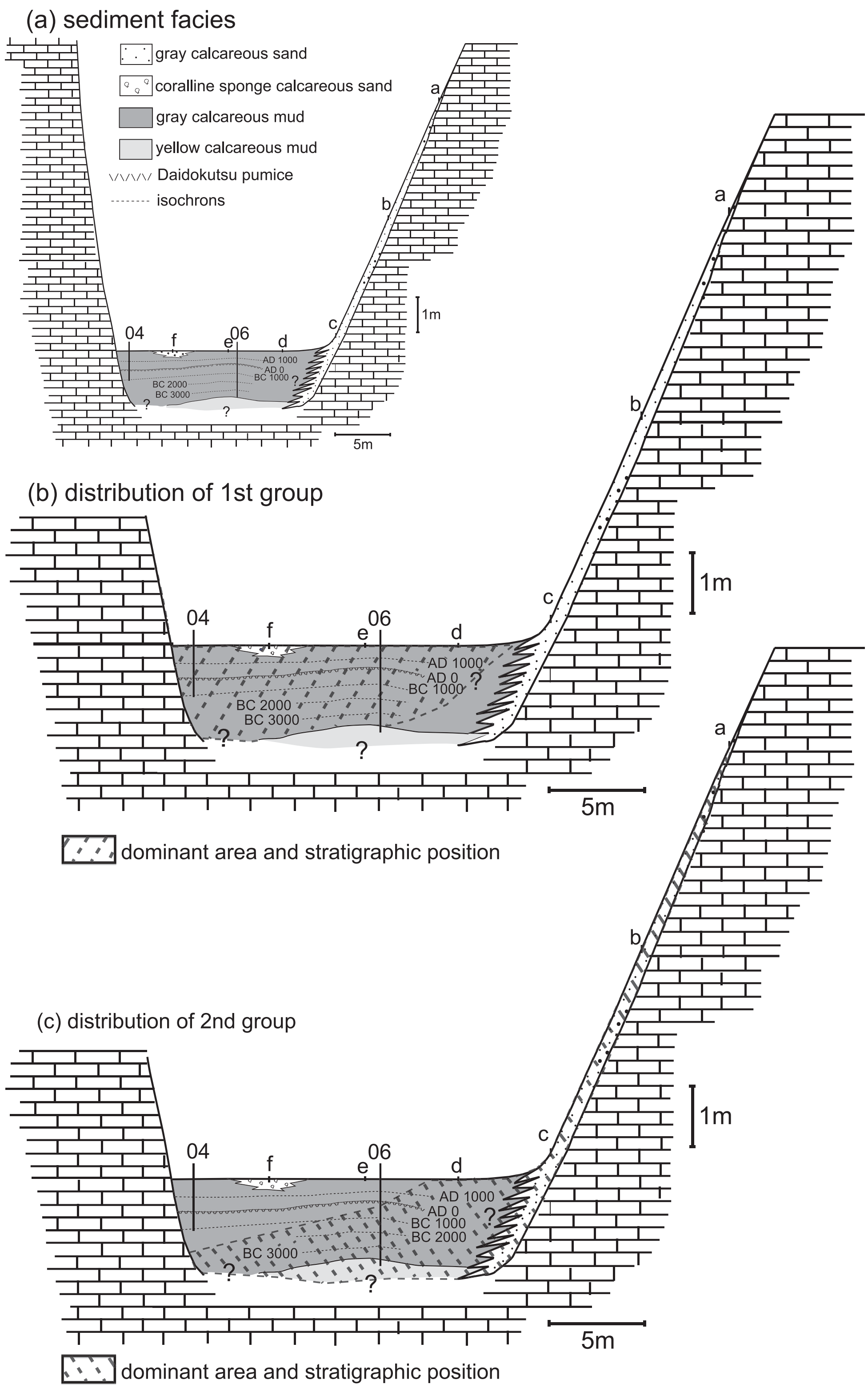

Figure 7. Stratigraphic sections of sediments in Daidokutsu cave, showing sediment facies and bivalves of 1st and 2nd groups.

the interior and the exterior of the cave, and consequently caused nutritional deficiency to spread within Daidokutsu cave. If this interpretation is correct, the long-term changes in the environments observed in Daidokutsu cave may be common to many submarine caves. An examination of the cause of the change in color of the sediments at ca. BC 3,500, will be the subject of future work.

Acknowledgments

We gratefully acknowledge I. Hayami, K. Konishi and T. Ubukata for their advice. Thanks are also due to Shigemitsu Kinjyo, Koushin Yasumura, Motoyuki Mato, Akifumi Tanabe, Yoshitaka Sakaguchi, Nanami Wakayama and Natsuko Wada for the preparation of samples. We also thank A. Beu and an anonymous reviewer, whose comments and suggestions improved the original manuscript. This study was funded by Grants-in-Aid 16340159, 111691106 and 11833018 from the Japan Society for Promotion of Science.

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