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

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Abstract We analyzed sediments and cavernicolous bivalve assemblages within cored sediments 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 sand-sized brown grains within sediments aged 7,000-6,000 cal BP, and identified the grains as debris derived from a red soil layer developed in coastal zones around the Island. Temporal changes in the abundance of the debris suggest that water flow in the cave weakened at about 6,500 cal BP. Temporal changes in the cavernicolous bivalve assemblages indicate that the environmental conditions of the innermost cave area have gradually spread to the cave entrance over the past 5,000 years. These findings indicate that 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 exterior 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 source of the nutrients that support coral reef growth. Our findings regarding the distribution of debris from the red soil layer strongly support the occurrence of a mid-Holocene high-energy window, which represents a period of high wave energy prior to the formation of a reefal barrier.

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

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

Previous studies have addressed the evolutionary significance of cryptic 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; Motchurova-Dekova et al. 2002; Ubukata et al. 2009) and the fluxes of various materials (e.g., dissolved oxygen, dissolved inorganic matter, dissolved organic matter, and bacterioplankton) in reef cavities (Fichez 1990a, 1990b, 1991; Richter et al. 2001; Scheffers et al. 2004; Van Duyl et al. 2006; De Goeij and Van Duyl 2007). However, we are unaware of any published studies that have searched for millennia-scale variations in the community of organisms in reef cavities, with the exception of Kitamura et al. (2007a).

Kitamura et al. (2007a) examined cavernicolous bivalve assemblages in surface and cored sediments within Daidokutsu submarine cave (29 m water depth) on the fore-reef slope of Ie Island (26°43’N, 127°50’E) (Fig. 1), Okinawa, Japan. The cave is developed in Pleistocene Ryukyu Limestone, having formed by the movement of underground 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
surface-derived sediments, cement, debris, and *in situ* skeletons of the cryptic
community. On this basis, Kitamura et al. (2007a) concluded that the progressive
infilling of cavities at Daidokutsu cave has resulted in a decrease in the flux of water
between the interior and exterior parts of the cave, leading in turn to an increase in the
spatial extent of the zone of nutritional deficiency. However, the stratigraphic
distribution of cavernicolous bivalve assemblages within the cave requires additional
consideration, as the possibility exists that the lowest part of the cored sediments
consists of sediment gravity flow deposits (22 cm thick), which would have modified
the species composition in the sediments (see below). To extend Kitamura et al.’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
examination of newly obtained sediment cores.

**Study area**

**Cave conditions and sediments**

Ie island is approximately 23 km² in area and is covered by the Pleistocene Ryukyu
Limestone, with a fringing reef close to Pleistocene limestone sea cliffs that are
undercut at the mean high-water level (Fig. 1). The surface of the fringing reef is
largely flat and is exposed 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 entrance lies at approximately 19 m below sea level (Fig. 1), and is roughly 2 m high and 18 m wide (Hayami and Kase 1992). The cave is 40 m long, dark inside, and deepens abruptly inward to its deepest point at 29 m below sea level. Water temperature 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 Okinawa (Kitamura et al. 2007b). During sediment sampling, we found air bubbles rising from the sea floor above the cave, indicating that water is exchanged between the water masses inside and outside the cave via the cave entrance and via numerous passages in the surrounding porous substrates.

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.

The floor of the cave is covered by calcareous sediments (Kitamura et al. 2003). Kitamura et al. (2007a) divided the surface sediments in the cave into three facies (Fig. 2): Facies 1 is gray calcareous sand that occurs at sites 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.

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 calcareous mud (> 22 cm long), and an upper part consisting of gray calcareous mud (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 relationship between sediment depth and $^{14}$C data, the gray calcareous mud is interpreted to have been deposited continuously at a sedimentation rate of 21.1 cm/1,000 years. The $^{14}$C ages of samples obtained from the lower part of the core fall within 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 the 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 calcareous muds, the continuous deposition of mud-sized particles throughout the sequence indicates that still-water conditions prevailed for 5,000 years.

Bivalve assemblages

Hayami and Kase (1992, 1993, 1996) and Kase and Hayami (1992) studied cavernicolous bivalves in tropical west-Pacific coral reefs, including Daidokutsu cave. The authors reported about 60 species of cavernicolous bivalves that share the following characteristics: 1) reduced 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; and 3) persistent denticles of the provinculum are retained until the adult stage in many pteriomorph species, indicating significant paedomorphosis by progenesis. According to Kase and Hayami (1992) and Hayami and Kase (1996), these features reflect a common adaptive strategy toward the oligotrophic condition and low predation pressure of cave habitats.
Eight bivalve species are dominant in the surface sediments within Daidokutsu cave. Kitamura et al. (2007a) divided these species into three groups based on their spatial distribution (Fig. 4). The first group (Cosa kinjoi and Parvamussium crypticum) mainly inhabits 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 tenuissima, Cyclopecten ryukyuensis, and Carditella iejimensis) shows no distinct distribution pattern. Carditella iejimensis appears to be endemic to caves of Ie Island, while the others are found on many isolated islands in tropical west-Pacific coral reefs (Hayami and Kase 1996).

The 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 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. The 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 relative 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 temporal or spatial distribution of Cyclopecten ryukyuensis and Carditella iejimensis. These findings indicate that the cave environment has remained largely unchanged for the past 5,000 years.

**Methods**

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 prodissocoanchn 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 derived from a 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
Shizuoka University, Japan. The major element compositions of 10 brown grains were analyzed using a non-destructive energy dispersive X-ray fluorescence (XRF) analyzer (TATSCAN-F1) housed at the Japan Agency for Marine-Earth Science and Technology (JAMSTEC). The chemical compositions were determined at a tube voltage of 30kV and the diameter of the collimater was 400µm. We picked and counted all brown grains from the 0.5-1.0 mm and 1.0-2.0 mm fractions of samples collected at 1 cm intervals within core 19. In the same way, we determined the 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 reef-slope sediment and six samples of surface sediment from within the cave (Figs. 1, 2).

Results

The sediment in core 19 shows a fining-upward trend, and is divided into a lower gray calcareous 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 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 carbonate content decreases to 84% (Fig. 5). We regard this horizon to represent the deposit containing the Daidokutsu pumice (deposited between 1,990 and 1,710 cal BP).

Table 1 lists the radiocarbon ages obtained for mollusc shells; $^{14}$C ages are plotted in Fig. 5. The age of a bivalve shell from the base of core 19 is 7,170 ± 45 cal BP, indicating that the cored sediments preserve a record of fossils and sedimentation over the past 7,000 years. Based on $^{14}$C age data and the stratigraphic position of the Daidokutsu pumice, we estimate a sedimentation rate of 41.7 cm/1,000 years between
150 and 233 cm depth, and a rate of 29.8 cm/1,000 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 in the lower part of core 6 is heteropic with gray calcareous mud in core 19 (Figs. 3, 5), although we cannot explain the cause of the change in sediment color at ca. 5,450 cal BP.

Observations 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, and 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 interpret the brown grains to be detritus derived from a red soil layer that is widely distributed across Ie Island (Tokashiki 1993; Vuai et al. 2003; Mkadam et al. 2006). Debris with a diameter of 1.0-2.0 mm was only found in the lower part of core 19 (Fig. 5). The number density of these grains (numbers per gram) decreases upward from 0.6/g at 233 cm depth to 0-0.1/g at 203 cm depth. The number density of debris with a diameter of 0.5-1.0 mm shows an upward decrease 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 the red soil layer coincides with the boundary between calcareous sand and calcareous mud (178 cm depth), and coincides with an upward increase in carbonate content over the interval between 233 and 192 cm depth. The debris from the red soil layer is 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 debris at the other three sites (a-c) in the cave, in the reef-slope sample (Table 3), or in core 04. The debris occurs sporadically in core 06 (Fig. 3).

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

Discussion

Debris from the red soil layer

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

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,
based on an analysis of drill 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
the present sea surface at 6,000-5,500 yr BP, and then developed seaward via accretion
of the forereef. At the time when a similar pattern of coral reef development occurred
around Ie Island, 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 present 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 concept 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
settled 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
remained 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
6,000 yr BP (Neumann 1972; Hopley 1984; Montaggioni 2005). Under such conditions,
the enhanced hydrodynamic energy may have resulted in the rapid winnowing 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 reef tops reached
sea level, which stabilized around its present position, and reef flats became sufficiently
extended laterally. Consequently, the supply of detritus was terminated. It appears that
the stratigraphic distribution of debris from the red soil layer provides direct evidence
of the occurrence of a mid-Holocene high-energy window.

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

The continuous occurrence of *Cyclopecten ryukyuensis* and *Carditella iejimensis* indicates that the cave environment in Daidokutsu has persisted for the past 7,000 years.

The progressive decrease in abundance of species of the second group (*Cosa waikikia* and *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 species 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 continuously throughout this interval. This finding confirms Kitamura et al.’s (2007a) tentative conclusion that species of the first group living in the innermost part of the cave became dominant over the past 5,000 years. In addition, we found that *Huxleyia cavernicola* shows an upward decrease in abundance from a depth of about 150 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 (Hayami and Kase 1993). This species is very rare in the surface sediments in the cave (Fig. 4). Thus, the temporal changes in species abundance reveal a decrease in the amount of organic matter in cave sediment 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 a consequent decline in nutrient levels within the cave. However, the observed changes in cavernicolous bivalve assemblages occurred after termination of the supply of debris from the 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 appears 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.

The 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 between cavities and the overlying water column (e.g., Tribble et al. 1988; Richter and Wunsch 1999). Coral cavities are sinks of bacterioplankton and dissolved organic carbon, and a source of NO$_x$ and PO$_4^{3-}$ (Van Duyl et al. 2006; De Goeij and Van Duyl 2007; De Goeij et al. 2008). Our results show that, at least in terms of the coral cryptic community within cavities developed in the reefal foundations, a decline in the functioning of the cryptic community as a source of nutrients to the coral reef over at least the past 6,500 years.

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Figure captions

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

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

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

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

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

Figure 6 Diffractograms of brown grains (debris derived from a red soil layer) found
within sediment from Daidokutsu cave. Peaks labelled “1” correspond to those for quartz.

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

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

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

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

Electronic Supplementary Material Table 1 List of cavernicolous bivalve species in core 19. A: articulated shells, R: right valve, L: left valve.
A: Map of Le Island and Okinawa Island.
B: Map of Le Island showing Daidokutsu cave and reef crest.
C: Vertical section showing Holocene reef deposits, Pleistocene Ryukyu Limestone, Daidokutsu cave, sediments, and sampling point of reef slope sediment.

Yamamoto et al. Fig. 1
Yamamoto et al. Figure 2
Yamamoto et al., Supplementary Material Figure 1