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Pleistocene coral assemblages on Irabu-jima, South Ryukyu Islands, Japan

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Abstract. We identified 40 genera and 83 species of scleractinian corals from middle Pleistocene reef limestones on Irabu-jima, located in the South Ryukyu Islands (South Ryukyus); these data were then combined with previously published data sets on Pleistocene coral assemblages on Okinawa-jima (southern Central Ryukyus), and Kikai-jima (northern Central Ryukyus) to perform statistical analyses, including cluster analysis and multidimensional scaling (MDS) ordination of Bray–Curtis (BC) similarity coefficients applied to coral taxa (R-type analysis) and coral assemblages (Q-type analysis). Results of the analyses, combined with field descriptions of the coral assemblages, allowed interpretations of reef paleoenvironments. Outcrops of Quaternary reef deposits in the Ryukyus comprise both shallow- and deep-water coral assemblages. Generally, coral diversity increases southward along the island chain. The statistical analyses highlight differences in the taxonomic compositions of fossil coral assemblages in different geographic areas and in distinct reef environments. We report on the differences among assemblages on Irabu-jima, Okinawa-jima, and Kikai-jima. Upper reef slope coral assemblages on Irabu-jima, which are similar to those on Okinawa-jima, are dominated by acroporid corals, mainly *Isopora palifera* and branching *Acropora* spp., encrusting to platy *Porites* spp., and branching Pocilloporidae. *Porites* spp. and faviids, such as *Cyphastrea* spp. and *Favia pallida* gr., are more typical of the upper reef slope on Kikai-jima. Lower reef slope assemblages on Irabu-jima are dominated by thin laminar colonies of *Porites* and/or *Montipora* species. Associated coral taxa are *Stylocoeniella* sp., *Leptoseris* spp., small fungiid corals, *Trachyphyllia geoffroyi*, and *Montastrea valenciennesi*. Data from two large outcrops on Irabu-jima highlight the relatively large spatial homogeneity of community structures in lower reef slope coral assemblages as compared with their upper reef slope counterparts.

Key words: Coral assemblage, geographic distribution, paleoenvironment, Pleistocene, Ryukyu Islands

Introduction

The Ryukyu Islands (Ryukyus) consist of a chain of several tens of islands and islets stretching over a distance of 1100 km in a NE–SW direction between Kyushu and Taiwan (Figure 1). They are bordered to the northwest by the East China Sea and to the southeast by the Pacific Ocean. The Ryukyus are geographically and geologically divided into the South, Central and North Ryukyus by two major left-lateral faults beneath Tokara Strait and Kerama Gap, respectively (Figure 1). The Ryukyu Arc is formed by the subduction of the Philippine Sea Plate beneath the Eurasian Plate. A deep and narrow depression, the Ryukyu Trench, runs along the SE side of the Ryukyus. Extension along the NW side of the Ryukyus has created a large back-arc basin, the Okinawa Trough, which traps sediments derived from the Eurasian continent. The warm Kuroshio Current flows northeastward along the back-arc side of the Ryukyus, transporting heat and coral larvae from the tropics northwards (Figure 1). These environmental conditions are favorable for the development of coral reefs. Generally, coral diversity is controlled by sea surface temperature, and decreases with increasing latitude (Veron and Minchin, 1992).

The distribution of coral species in the Ryukyus has been the subject of a number of studies (Yabe *et al.*, 1936; Yabe and Sugiyama, 1941; Nakamori, 1986; Veron, 1992; Iryu *et al.*, 1995; Nishihira and Veron, 1995; Sugihara *et al.*, 2003; JCRS, 2004; Ikeda *et al.*, 2006; Sinniger *et al.*, 2013). The initiation of coral reefs in the Ryukyus dates to the earliest Calabrian (1.45–1.65 Ma; Yamamoto *et al.*, 2006). Uplifted Pleistocene reef

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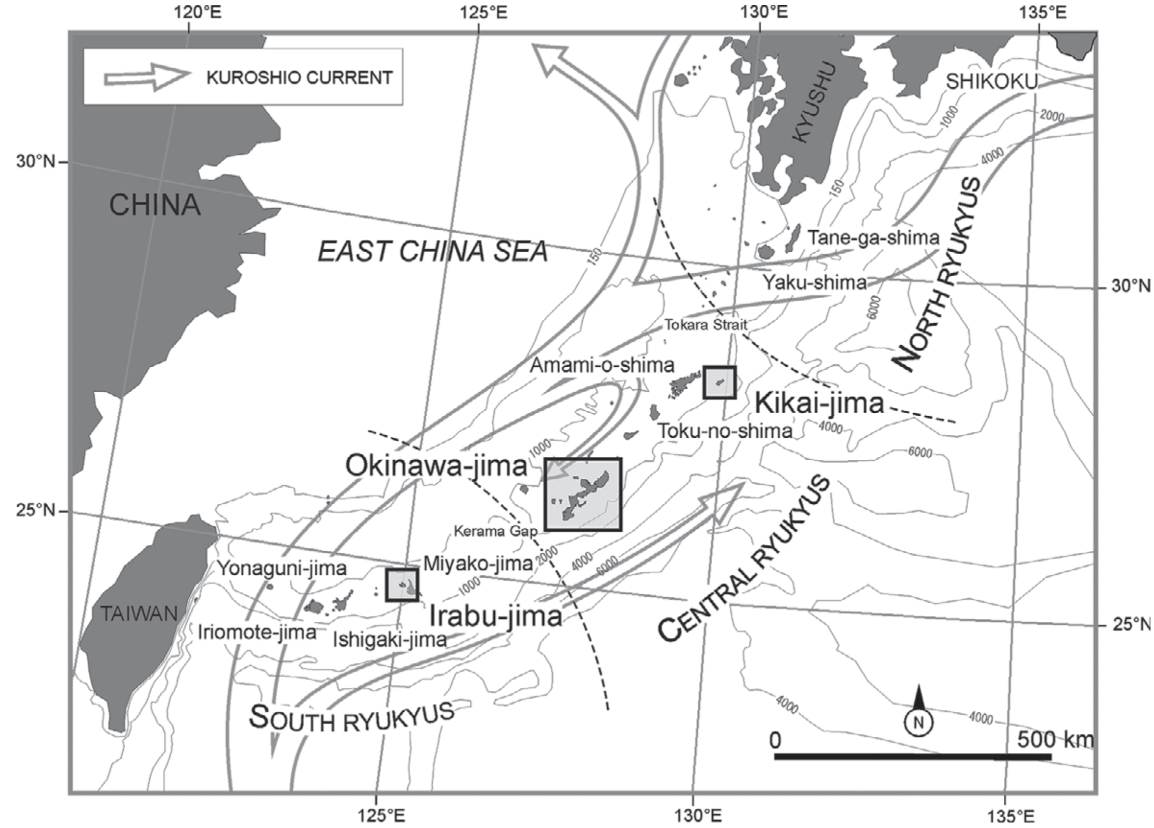

Figure 1. Map of the Ryukyu Islands showing the locations of Irabu-jima, Okinawa-jima, and Kikai-jima, situated in the South, southern Central, and northern Central Ryukyu Islands, respectively.

deposits and associated marine and nonmarine siliciclastic sediments (Ryukyu Group) are extensively distributed on most islands of the South and Central Ryukyus (Iryu *et al.*, 2006a), and the distribution and stacking patterns of sedimentary facies in the group are generally determined by changes in relative sea level. The Ryukyu Group can be subdivided into stratigraphic units deposited during successive cycles of sea-level change. Typically, each unit consists of a shallow-water coral limestone grading upward into deep-water shelf deposits (e.g. rhodoliths) overlain by shallow-water sediments (Iryu *et al.*, 2006b). The proportion of coral limestone and sediments from deeper depositional settings in each stratigraphic unit varies along a proximal–distal gradient.

Because fossil corals can be dated, and their community structures are a function of water depth and wave exposure, fossil coral assemblages have been used in the Ryukyus for paleoenvironmental and sea-level curve reconstructions (Holocene: Kan *et al.*, 1995; Kan *et al.*, 1997; Webster *et al.*, 1998; Yamano *et al.*, 2001; Sugihara *et al.*, 2003; Hongo and Kayanne, 2010) (Pleistocene: Nakamori *et al.*, 1995; Iryu *et al.*, 1998; Sagawa *et al.*, 2001). However, few studies have explored in detail spatio–temporal variations in the taxonomic compositions of Pleistocene coral assemblages. Humblet *et al.* (2009) analyzed the taxonomic and morphological compositions of Middle Pleistocene coral assemblages on Okinawa-jima and Kikai-jima in the southern and northern Central Ryukyus, respectively, and reported reef zonation and geographic differences in taxonomic compositions on the two islands. In addition, various types of coral succession were described, and possible controlling factors were discussed. The present work presents new data on the taxonomic compositions of Middle Pleistocene coral assemblages from Irabu-jima, South Ryukyus. This additional data set allows us to quantitatively analyze the distribution of Pleistocene coral taxa over a wider latitudinal range in the Ryukyus than was previously possible, from the South, southern Central and northern Central Ryukyus. The goals of the present study were: (1) to identify coral taxa associations (i.e., coexistence in the fossil record); (2) to compare the taxonomic compositions of coral assemblages within and between islands in the Ryukyus at different latitudes; (3) to study the

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detailed differences in taxonomic composition between upper and lower reef slope fossil coral assemblages, and their spatial variability over a few meters to several tens of meters; and (4) to explore the influence of sample size, distance between replicate samples, and type of data (abundance vs. presence–absence) on the detection of trends in community structure in the fossil record. Using this approach, we have developed a better understanding of the compositions of Pleistocene reefs in the Ryukyus, and of how different sampling methods influence our depiction of fossil coral assemblages. An understanding of how coral reef environments are preserved in the fossil record is important for paleoenvironmental interpretations. Moreover, detailed knowledge of the state of Pleistocene reefs can provide a useful baseline for distinguishing between natural trends in community structure and those induced by human disturbances.

Materials and methods

We studied the taxonomic compositions of Pleistocene coral assemblages from Irabu-jima (South Ryukyus), which in this study includes both Irabu-jima and the adjacent island of Shimoji-shima (Figure 2). Nine quadrats were established on Pleistocene coral limestone outcrops (Figure 2) and corals exposed within quadrat areas on vertical outcrops were sketched to describe the fossil assemblages (Figure 3). Species–area curves were established for each quadrat (Figure 4). We then combined the taxonomic data from Irabu-jima with data previously collected from southern and central Okinawa-jima (8 and 10 quadrats, respectively) and Kikai-jima (11 quadrats) and applied a statistical analysis to the data (Humblet *et al.*, 2009).

We investigated changes in taxonomic compositions between quadrats using the Bray–Curtis similarity coefficient (BC; Bray and Curtis, 1957), which is a reliable tool for quantifying differences in community structure (Faith *et al.*, 1987). A cluster analysis based on group-averaged linking of BC similarities was used to discriminate coral associations (R-mode analysis) and to segregate quadrats on the basis of their taxonomic compositions (Q-mode analysis). Ordination by non-metric multidimensional scaling (MDS) based on the ranked BC similarities provided an additional and useful picture of the relationships between data points. Analyses of similarity percentages (SIMPER) were performed to assess which taxa were primarily responsible for observed differences between groups of quadrats. We also evaluated the differences in taxonomic compositions between distinct geographic areas by conducting a one-way analysis of similarity (ANOSIM), which is a permutation test of the null hypothesis that there is no difference between sites. Statistical analyses were performed on 40 common individual taxa and morphogroups, i.e., those with a total number of colonies exceeding 8. The statistical methods follow Humblet *et al.* (2009). Two types of data were used: standardized untransformed abundance data and presence–absence data. Standardization was conducted to minimize the effects of size differences between quadrats. Statistical analyses were performed using PRIMER v5 (Clarke and Gorley, 2001). Further details about the statistical tools used in this study can be found in Clarke (1993) and Clarke and Ainsworth (1993).

We explored the variability in the taxonomic compositions of upper and lower reef slope coral assemblages at spatial scales of a few meters to several tens of meters. For this purpose, we selected two large outcrops on Irabu-jima. One outcrop is located along the western coast of Irabu-jima (site 20I), where a lower reef slope coral limestone is sharply overlain by a several-meter thick layer composed of rhodoliths, allochthonous shallow-water coral colonies, and poorly sorted coarse bioclasts (quadrat 20IQ3). The composition of the limestone suggests massive downslope transport of shallow-water corals on a fore reef slope. Three quadrats at the same stratigraphic level in a lower reef slope coral limestone (quadrats 20IQ1, 20IQ2, and 20IQ4) were established at distances of ~20 to ~90 m from one another. The second outcrop, located at an inland site on Irabu-jima (site 2I), exposes a large section (~5 m high) cutting through an upper reef slope coral limestone. The sediment is mostly coarse grained and composed of numerous fragments of corals, especially of branched colonies. Three quadrats were established at intervals of a few meters to ~100 m (quadrats 2IQ1, 2IQ2, and 2IQ3). Quadrat 2IQ1 is located in a stratigraphic layer approximately 2 m below the other two quadrats, but no major temporal (vertical) changes in the reef environment were observed at the scale of the outcrop. Therefore, we consider that the three quadrats at site 2I represent the same bathymetric conditions. The quadrats at both sites were subdivided into smaller areas of equal size, referred to as "replicates". Taxonomic data were compiled for replicates of increasing size, i.e., of 0.5 m^2, 1 m^2, 2 m^2, and 3 m^2.

Cluster analyses, MDS ordinations, and ANOSIM tests were performed to examine the influence of replicate size on the resolution of taxonomic differences between sites 20I and 2I, which represent, respectively, lower and upper reef slope settings. We compared the results of the statistical analyses performed on two different types of data: abundance data and presence–absence data. Finally, we looked at the within-reef-zone variability in taxonomic composition of the environments at the two sites at the scale of a large outcrop (~100 m wide and a few meters high). For this purpose, we compared pairwise BC similarities calculated

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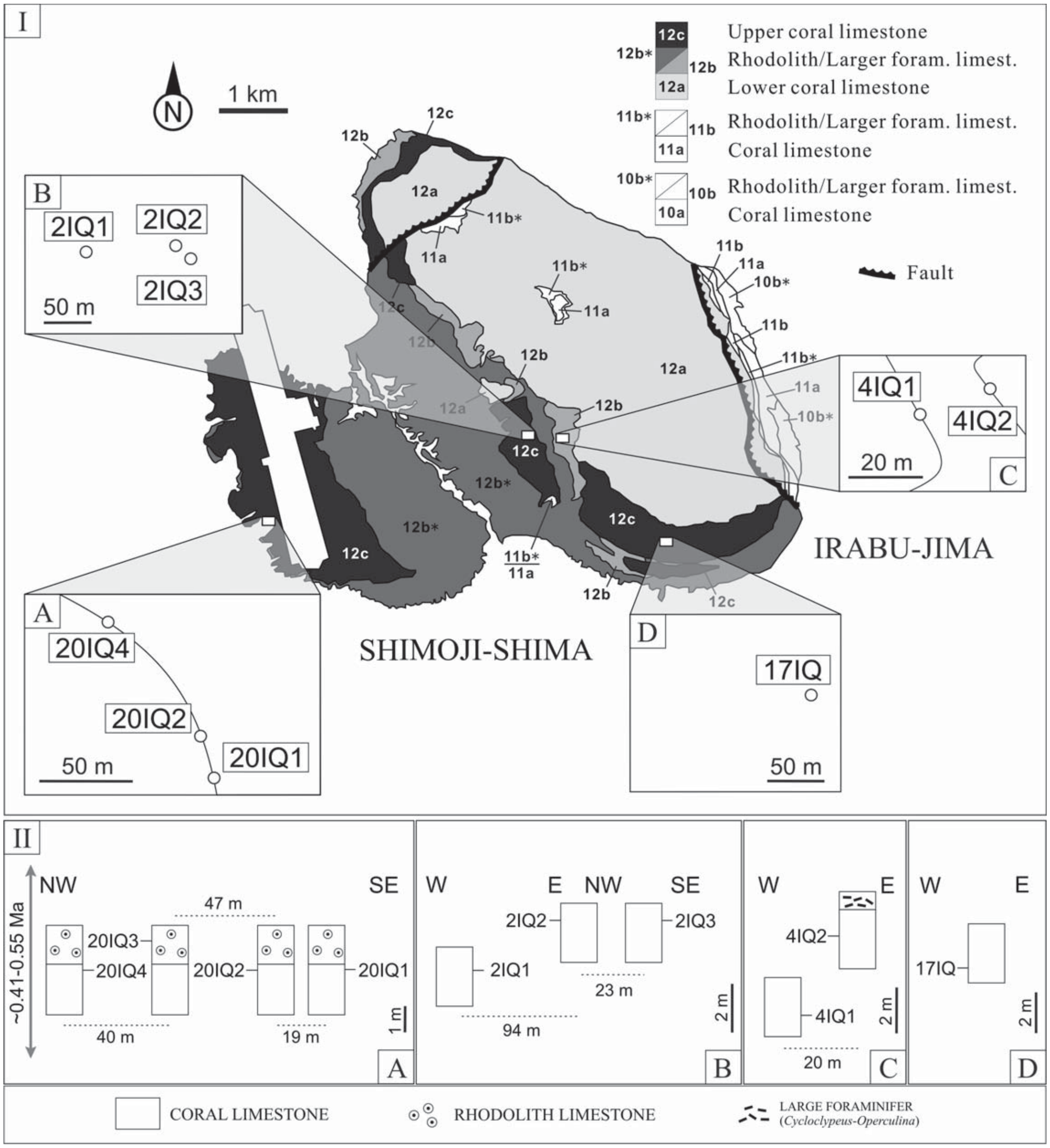

Figure 2. Geological map of Irabu-jima (including Shimoji-shima) showing the locations of quadrats established in Pleistocene coral limestones (I), and the stratigraphic relationships of the quadrats at each site (II).

between replicates obtained at distances of ~100 m, ~20 m, and <10 m from one another. We repeated the calculations for the three replicate sizes, i.e., 1 m^2, 2 m^2, and 3 m^2, to explore sample size effects.

In the present study, a coral association is a group of coral taxa that tend to coexist in the fossil record. The term “coral assemblage” represents all the coral taxa found within a particular quadrat or at a particular site. We divided the reef slope into upper (5–20 m depth), middle (20–30 m depth), and lower (>30 m) reef-slope zones (Sagawa *et al.*, 2001). The taxonomy of scleractinian corals follows Veron (2000), except for the taxonomy of *Isopora*, which is treated here as a genus (as per Wallace *et al*., 2007). Moreover, we did not distinguish between *Isopora palifera* and *I. cuneata*.

Geology of Irabu-jima

Studies of the calcareous nannofossil biostratigraphy of offshore and onshore drilled cores from Irabu-jima show that the Ryukyu Group in this region is composed

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Figure 3. Images of the study sites on Irabu-jima, including a general view of site 20I (A), quadrat 20IQ4 (B), quadrat 2IQ1 (C), quadrat 4IQ1 (D), and quadrat 17IQ (E). The frame displayed on the images is 1 × 1 m. The closeup image (C') shows a fragment of a fine *Acropora* branch found in the coral limestone at site 2I (scale bar, 4 mm).

of 13 units, ranging in age from 1.5 to 0.3 Ma (Sagawa *et al.*, 2001; Figure 2A). Units 1–4 are composed mainly of shallow-water coral limestones, with sedimentary features indicating frequent subaerial exposure (e.g. paleosols and reddish staining). Units 5–12 consist of a rhythmic succession of coral limestones, rhodoliths, and larger foraminiferal (= *Cycloclypeus-Operculina*) limestones deposited in response to relative sea-level changes. Unit 13 offlaps older units and likely represents a phase of uplift.

Overall, the paleobathymetry curve suggests that high-

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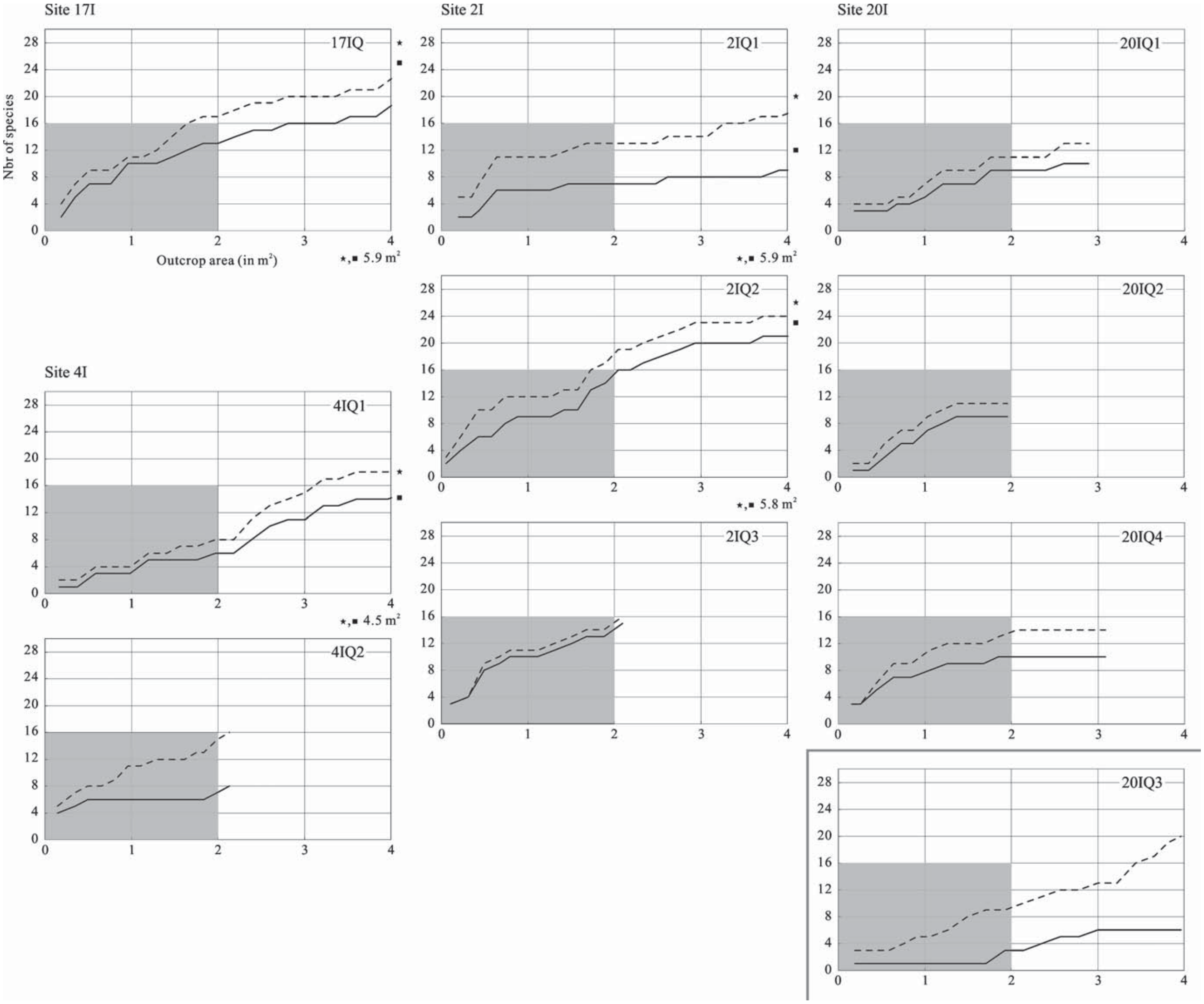

Figure 4. Species–area curves for the sites surveyed on Irabu-jima. The dashed line shows the total species richness derived from all corals (*in situ* or not *in situ*). The solid line shows the species richness determined on *in situ* corals only. All but one quadrat (20IQ3) was established in coral limestone.

frequency low-amplitude cycles of sea-level change are responsible for the deposition of units 1–4, whereas low-frequency high-amplitude cycles controlled the deposition of units 5–12 (Sagawa *et al.*, 2001). In this study, corals described at sites 20IQ (western coast of Irabu-jima) and 4IQ likely belong to the lower coral limestone of unit 12. At site 20IQ, the coral limestone is overlain by a rhodolith limestone, whereas at site 20IQ, the coral limestone is overlain by a larger foraminiferal limestone (Figure 2A, B). Coral assemblages studied at sites 2IQ and 17IQ belong to the upper coral limestone of unit 12 (Figure 2A, B). Unit 12 outcrops extensively on Irabu-jima, reaching a thickness of up to 23 m and ranging in age from ~0.41 to ~0.55 Ma (MIS11-13; Sagawa *et al.*, 2001). The geological setting of Okinawa-jima and Kikai-jima is described by Humblet *et al.* (2009).

Results

Coral associations

We identified 83 scleractinian coral species belonging to 40 genera from middle Pleistocene coral limestones on Irabu-jima (Tables 1 and 2), as well as the octocoral *Tubipora musica* and the remains of soft corals (fossilized

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Table 1. Abundances (numbers of individuals) of corals in Pleistocene reef limestones on Irabu-jima. All corals shown in this list are autochthonous, except for those described from quadrat 20IQ3 (designated by an asterisk), which are mostly allochthonous. Acroporid, poritid, and faviid corals are subdivided into morpho-groups. More details about this subdivision can be found in Humblet *et al.* (2009).

	2IQ1	2IQ2	2IQ3	4IQ1	4IQ2	17IQ	20IQ1	20IQ2	20IQ3*	20IQ4
SCLERACTINIAN CORALS										
1. ACROPORIDAE										
Acropora microphthalma gr. (arborescent)		7	4			2				
A. humilis gr. (corymbose)		1								
A. hyacinthus gr. (tabular)	1	1								
Isopora palifera (encrusting)	20	8	2			2				
Montipora spp. (encrusting/platy)	2	2				1			1	
M. digitata gr. (branching)	1	1								
2. POCILLOPORIDAE										
Stylophora pistillata?	1									
Seriatopora hystrix?		7	1							
Seriatopora sp.						1				
Seriatopora sp.?		4	3							
3. ASTROCOENIIDAE										
Stylocoeniella guentheri							6	3		7
Stylocoeniella sp.							3	5		
4. PORITIDAE										
Porites spp. (massive)	1	4		1	1	1				
Porites spp. (encrusting/platy)	13	23	10	6	3	6	14	6	10	7
Porites sp. (thick br./column.)						1				
Goniopora sp(p).						2				
Goniopora sp. (small c., thin walls)	1	1								
Goniopora sp. (small c., thick walls)						2				
Alveopora sp.	1	1								
A. fenestrata?						1				
Porites/*Mont.* spp. (encrusting)	19	28	3	9	11	24	20	19		29
Porites/*Mont.* sp(p). (massive)						1				
Porites/*Mont.* sp(p). (thick br./column.)						4				
5. FAVIIDAE										
Favia laxa gr. (small corallites)		1								
F. pallida gr.	3	2		1		3				
F. helianthoides		1								
F. rotumana					1					
Favia spp.				2	1	1				
Favites abdita gr.		1		1						
F. flexuosa						2				
F. styliphera					1	1				
F. pentagona						1				
Favites spp.			1			1				
Goniastrea pectinata				1		1				
Goniastrea spp. (submeandroid)				1						
G. edwardsi		1								
Montastrea annuligera gr.						1				
M. valenciennesi								2		2
Montastrea sp(p).				1	1		1			
Cyphastrea microphthalma?				1						
Cyphastrea spp.	2	1	1	6	3	1				
Leptastrea pruinosa gr.		1								
Plesiastrea versipora							3			
Barabattoia amicorun			1							
Platygyra daedalea gr.		3								
P. contorta						1				
P. ryukyuensis						1				
P. pini		1			1	1				
Platygyra spp.		1			1	1				
Oulophyllia crispa					1					
Oulophyllia sp.						1				
Echinopora sp(p).		1	1		1	1				
Caulastrea sp.?		1								
Faviidae	1	7	2	11	4	17		2	2	
6. MUSSIDAE										
Acanthastrea echinata gr.		1	1							
Acanthastrea spp.			1	1	1					
Lobophyllia corymbosa				1						
Lobophyllia spp.				1		1				
Symphyllia recta		1								
S. agaricia?				1						
Mussidae				2						1
7. TRACHYPHYLLIDAE										
Trachyphyllia geoffroyi							2	1		1
8. PECTINIIDAE										
Echinophyllia echinata								1	1	2
Echinophyllia sp(p).						1		3		2
Echinophyllid				1			1	1		1
9. FUNGIIDAE										
Fungia spp.				3	9				1	
Diaseris sp.?				1						
Cycloseris sp.							4		2	3
Cycloseris sp.?								4		
Halomitra pileus					1					
Fungiidae				3	10	3		1		
10. MERULINIDAE										
Hydnophora microconos?		1	1							
Hydnophora sp.?						1				
11. AGARICIIDAE										
Pavona clavus gr.				1						
Pavona sp.						1				
Leptoseris yabei gr.				1						
L. amitoriensis							1			
L. foliosa							1			
L. papyracea							2	2		
Pachyseris speciosa		2		2				1		
P. rugosa						2				
P. gemmae?						1				
Agariciidae				8		1				
12. SIDERASTREIDAE										
Coscinarea columna				6						
13. DENDROPHYLLIDAE										
Turbinaria reniformis	1	1					1			1
T. stellulata?								1		1
Turbinaria spp.	1	1	1			2		1		3
NON-SCLERACTINIAN CORALS										
OCTOCORALLINA										
Tubipora musica	13	14	4			2				
Soft corals						4				
? (scleractinians)	1	13	3	16	4	6	7	11	1	19
size of quadrat (in m²)	7.1	7.0	2.5	5.8	2.4	6.5	3.2	2.4	4.1	3.2

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Table 2. List of coral taxa recognized outside the quadrats set on Irabu-jima. Only the taxa marked with an asterisk were found *in situ*.

Irabu-jima	
1. ACROPORIDAE	5. MUSSIDAE
Acropora nasuta gr.	*Symphyllia radians*
2. POCILLOPORIDAE	6. AGARICIIDAE
Pocillopora sp.	*Leptoseris scabra* gr.
Palaustrea ramosa	
	7. SIDERASTREIDAE
3. PORITIDAE	*Psammocora* sp.
Alveopora excelsa	*Coscinarea exesa*
Alveopora verrilliana	
Goniopora sp. (with very large corallites)	8. OCULINIDAE *Galaxea horescens*
4. FAVIIDAE	9. DENDROPHYLLIDAE
Favia maxima	*Turbinaria mesenterina*
F. rotundata	*T.* aff. *peltata**
Favites russelli	
*Montastrea curta**	
M. magnistellata	
Cyphastrea serailia gr.	
Echinopora lamellosa	
E. lamellosa	

sclerites). We recognized 9 coral associations based on the cluster analysis (Figure 5). Five of the associations are composed of only two taxa and five isolated taxa (corresponding to single branches in the cluster diagram). The MDS graphic representation of coral associations shows a certain degree of overlap between the clusters, especially between associations A7, A8, and A9 (Figure 6). In addition, associations A7–A9 form a single cluster with association A6 and *Symphyllia* spp. at a similarity threshold of 20% (group Z in Figure 6). At this similarity level, two other clusters were recognized: group X (associations A3 and A4, *Leptoseris* spp., and *Pachyseris speciosa*) and group Y (association A5 and *Galaxea astreata*).

The five isolated taxa in the dendrogram are *Acropora monticulosa* gr., *Leptoseris* spp., *P. speciosa*, *G. astreata*, and *Symphyllia* spp. In the five associations composed of two taxa (A1, A2, A3, A4, and A6), *Stylophora* sp. (probably *Stylophora pistillata*), arborescent *Acropora* spp., encrusting *Montastrea* spp., *Stylocoeniella* sp. (probably *S. guentheri*), and *Platygyra contorta* are associated, respectively, with *Goniopora* spp., *Seriatopora* sp. (probably *Seriatopora hystrix*), fungiids, *Echinophyllia* sp., and *Pachyseris rugosa*. Association A5 is composed of encrusting to platy *Porites* spp. and *Montipora* spp., encrusting *I. palifera*, and encrusting to platy *Turbinaria* spp. Association A7 consists of various encrusting faviids, such as *Favia* spp., *Platygyra* spp., and *Leptastrea* spp. Other taxa present in this association are *Pavona* spp., *Lobophyllia* spp., and encrusting *Acanthastrea* spp. Association A8 is composed of submeandroid *Goniastrea* spp., massive *Acanthastrea* spp., and encrusting *Favites* spp. Association A9 consists primarily of massive and branching corals. Massive corals include *Porites* spp. and the faviid genera *Favites*, *Favia*, and *Cyphastrea*. Branching corals comprise tabular and corymbose *Acropora* spp.

Similarity among quadrats

Cluster analysis of the BC similarity among the 39 quadrats from the South and Central Ryukyus resulted in the discrimination of 8 groups and 5 isolated quadrats (Figures 5, 6). Of the five isolated quadrats, those from Okinawa-jima and Kikai-jima (RQ, 24HQ, GQ2, and 36HQ) were described by Humblet *et al.* (2009). Quadrat 2IQ3, located on Irabu-jima, is characterized by the presence of several colonies of arborescent *Acropora* spp., *Seriatopora* sp., and encrusting colonies of *I. palifera*.

With the exception of clusters Gr7 and Gr8, encrusting to platy *Porites* spp. are typical species and contribute to a large proportion of the average within-group similarity of all clusters (up to 54.44%; Table 3). Quadrats of group Gr1 are characterized by massive *Porites* spp. (Table 3). Massive to encrusting *Cyphastrea* spp. contribute to a large proportion of the average BC similarity (Table 3). Quadrats of Group Gr2 are distinguished from other clusters by the relatively high abundances of encrusting *I. palifera* (Table 3). Group Gr3 comprises quadrats with a high species diversity. Characteristic species of this group are *Favia* spp. (including *Favia pallida* gr.), *Lobophyllia* spp., *Platygyra sinensis* gr., and encrusting *P. rugosa* (Table 3). Group Gr4 is composed of only two quadrats, Oo1 and 4IQ2. Both quadrats are characterized by a very large proportion of fungiids (Table 3), but the species composition in the two quadrats differs: small *Cycloseris* sp(p). (and possibly *Diaseris* sp(p).) are dominant in quadrat Oo1 and larger Fungidae, including *Fungia* spp. and *Halomitra pileus*, are dominant in quadrat 4IQ2. Coral assemblages in group Gr5 are characterized by encrusting faviids, notably *Cyphastrea* spp. and *Favites* spp., and by fungiids (Table 3). The coral assemblage in quadrat Oo2 is composed of a large proportion of small fungiid corals, mainly *Cycloseris* sp(p)., whereas *Fungia* spp. are common in quadrats 5YOMQ1 and 4IQ1. Quadrats 4IQ1 and 4IQ2 (Gr4) represent two successive stratigraphic intervals. Fungiids, mainly *Fungia* spp., are present in both coral assemblages, and constitute an important component of the coral assemblage of quadrat 4IQ2. At a lower similarity level, Gr4 and Gr5 are grouped in the same cluster, characterized by fungiids.

The clustering of quadrats forming group Gr6 results from the very large proportion of encrusting to platy *Porites* and/or *Montipora* species in these quadrats

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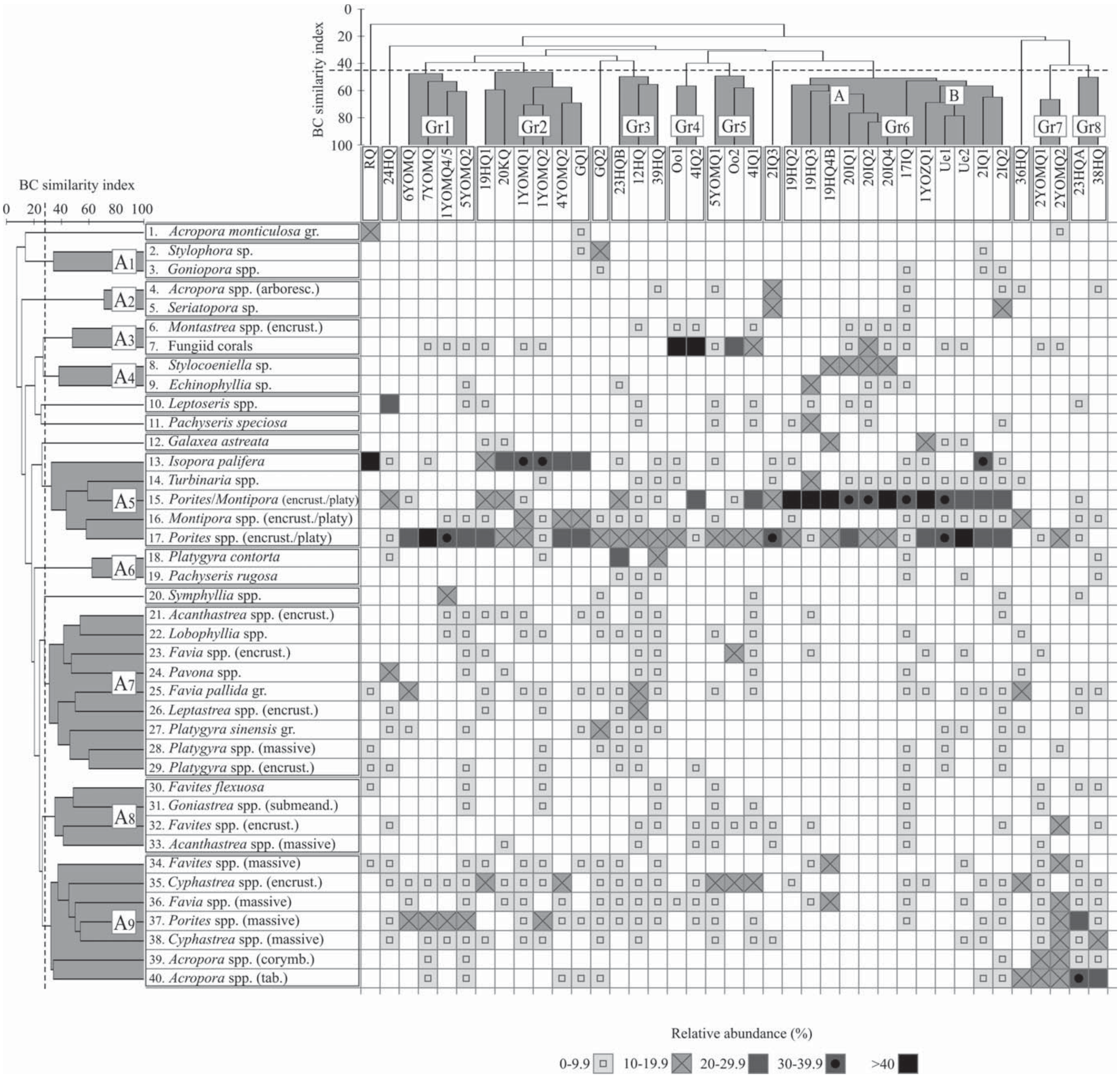

Figure 5. Group-averaged hierarchical clustering of coral taxa (R-mode) and quadrats (Q-mode) based on Bray–Curtis (BC) similarities calculated on standardized taxonomic abundance data (untransformed data) from Irabu-jima, Okinawa-jima, and Kikai-jima. Coral taxa are expressed at the species, morpho-group, and genus levels, except for fungiid corals, which are described at the family level. Morphologies are indicated in parentheses.

(Table 3). At a higher similarity threshold, this group can be divided into two subgroups showing distinct taxonomic compositions (A and B in Figure 5). Coral assemblages of subgroup Gr6A are characterized by a low diversity of faviids and the occurrence of species such as *Stylocoeniella* sp., *Echinophyllia* sp., and *P. speciosa*. Coral assemblages of subgroup Gr6B show a higher diversity of faviids, and include species such as *I. palifera*, arborescent *Acropora* spp., and *Stylophora* sp. (Figure 5). Quadrats of groups Gr7 and Gr8 display clear similarities in taxonomic composition: occurrences of platy and corymbose *Acropora* spp., massive *Porites* sp., and a high

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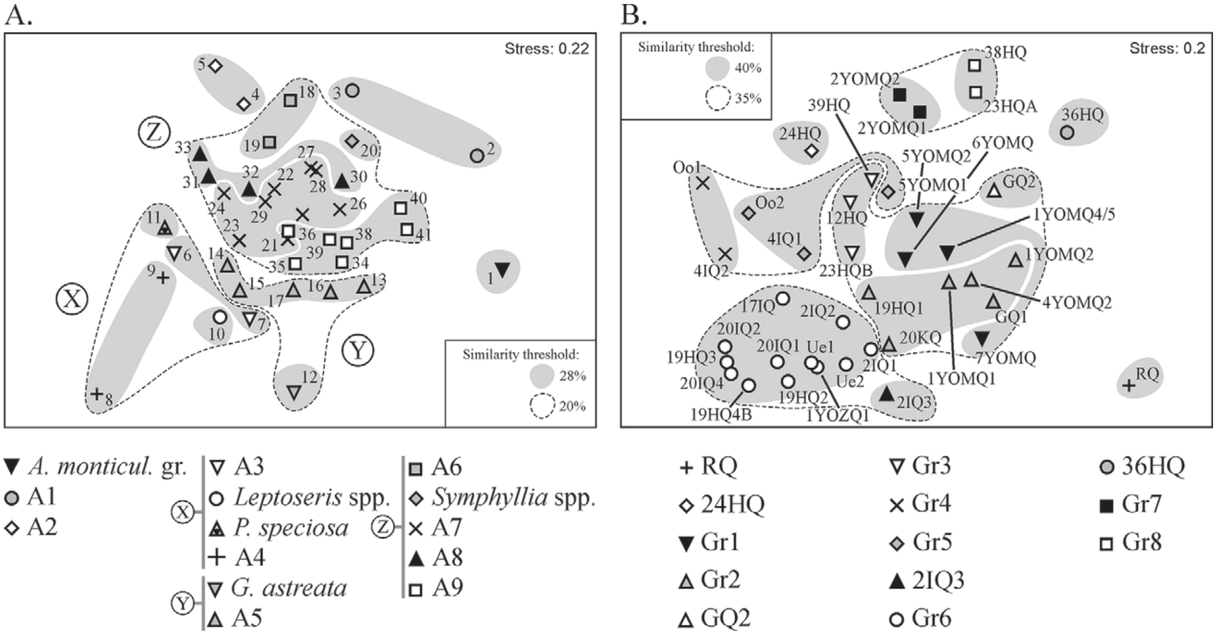

Figure 6. A 2-dimensional non-metric multidimensional scaling (MDS) ordination of coral taxa (A) and quadrats (B) obtained from the same BC similarities as in Figure 5. Grey zones and dashed lines indicate groups of coral taxa and quadrats identified in the cluster diagram of Figure 5 at different levels of similarity.

diversity of faviid species. However, the two quadrats of group Gr7 (2YOMQ1 and 2YOMQ2) are characterized by a larger proportion of massive corals and small corymbose *Acropora* spp., whereas large tabular *Acropora* spp. dominate in quadrats of group Gr8 (Table 3).

Discussion

Interpretation of coral associations

Taxa of association A1 (*Stylophora* sp. and *Goniopora* spp.) occur over a wide depth range (Kühlmann, 1983; Veron, 2000). However, *Stylophora* sp. (*S. pistillata*) may be dominant in shallow exposed reef environments (Veron, 2000; Sagawa *et al.*, 2001). Association A1 is found in quadrat GQ2, with *Pocillopora* sp. and massive faviids, and in 2IQ1, with large colonies of *I. palifera* (Figure 7A). Encrusting *I. palifera* is indicative of the upper reef slope in the Ryukyus (Nakamori, 1986; Iryu *et al.*, 1995; Sagawa *et al.*, 2001). Hence, in this study, association A1 suggests a shallow reef setting (shallower than 20 m). Association A2 (arborescent *Acropora* spp. and *Seriatopora* sp.) occurs in quadrats 17IQ, 2IQ2, and 2IQ3 (Figure 7A–C). Arborescent *Acropora* spp. and *Seriatopora* sp. are found in a wide range of environments. However, their association with *I. palifera* in these quadrats, as mentioned above, suggests an upper reef slope environment (<20 m). Association A3 (encrusting *Montastrea* spp. and fungiids) is an important constituent of the coral assemblage in quadrats of sites 20I (quadrats 20IQ1, 20IQ2, and 20IQ4) and 4I (quadrat 4IQ2). However, the taxonomic compositions of the coral assemblages at the two sites differ. Fungiids present in the three quadrats at site 20I are mainly *Cycloseris* sp(p)., and those found in quadrat 4IQ2 are mainly *Fungia* spp. The latter may form dense populations on unconsolidated substrates in shallow-water settings (Loya and Sakai, 2008). The presence of *Fungia* spp. and various faviids in quadrat 4IQ2 indicates a relatively shallow environment (<30 m). Corals of association A3 are also present in quadrat 4IQ1, but their abundances are limited (Figure 7F). The presence of *Coscinarea columna* and various faviids and mussids in quadrat 4IQ1 also points to a shallow reef setting (Veron, 2000).

Coral assemblages of quadrats 20IQ1, 20IQ2, and 20IQ4 are characterized by corals of group X: association A3 (encrusting *Montastrea* sp(p.), fungiids (mainly *Cycloseris* sp(p).)), association A4 (*Stylocoeniella* sp. and *Echinophyllia* sp.), *Leptoseris* spp., and *P. speciosa* (Figure 7D). Small fungiids, including *Cycloseris* spp., occur mainly on soft interreef substrates and on lower reef slopes (Veron, 2000). *Cycloseris* and *Diaseris* typically occur on the lower reef slope at depths of 30–50 m in the South Ryukyus (Sagawa *et al.*, 2001). Several flat encrusting colonies of *Montastrea valenciennesi* occur in

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Table 3. Results of a similarity percentage analysis (SIMPER) for taxa which primarily contribute to average within-group pairwise similarity (%avS(i)). Listed values are given for taxa which account for at least 90% of the average similarity. In the case of ungrouped quadrats, listed values correspond to relative abundances. The asterisks designate the four taxa which best typify the groups composed of more than 2 quadrats (i.e., taxa with the largest avS(i)/SD(i) ratios, in which SDi(i) is the standard deviation of their contribution, avS(i)). Underlined digits designate taxa with the largest avS(i)/SD(i) ratios.

	RQ % abund	24HQ % abund	Gr1 % avS(i)	Gr2 % avS(i)	GQ2 % abund	Gr3 % avS(i)	Gr4 % avS(i)	Gr5 % avS(i)	2IQ3 % abund	Gr6 % avS(i)	36HQ % abund	Gr7 % avS(i)	Gr8 % avS(i)	Upper reef-sl. Irabu-jima % avS(i)
Isopora palifera	63.2	3.7	–	37.04*	–	2.15	–	–	7.4	–	–	–	–	9.97*
Acropora monticulosa gr.	10.5	–	–	–	–	–	–	–	–	–	–	–	–	–
Acropora spp. (corymb.)	–	–	–	–	–	–	–	–	–	–	–	15.83	3.99	–
Acropora spp. (platy)	–	–	–	–	2.7	–	–	–	–	–	15.4	15.83	58.37	–
Acropora spp. (arborescent)	–	–	–	–	–	–	–	–	14.8	–	7.7	–	–	4.02
Montipora spp. (encrust./platy)	–	–	–	10.97*	5.4	–	–	–	–	–	15.4	–	3.99	–
Stylophora pistillata?	–	–	–	–	18.9	–	–	–	–	–	–	–	–	–
Seriatopora sp.	–	–	–	–	–	–	–	–	14.8	–	–	–	–	4.3
Stylocoeniella sp.	–	–	–	–	–	–	–	–	–	2.03*	–	–	–	–
Porites spp. (massive)	–	7.4	21.65*	5.91	2.7	4.48*	–	–	–	–	–	13.67	9.73	
Porites spp. (encrust./platy)	–	3.7	54.44*	26.21*	13.5	27.71*	11.79	26.17*	37.0	25.14*	–	13.67	–	28.19*
Porites/Montip. (encrust./platy)	–	14.8	–	3.64	–	6.73*	–	5.81	11.1	60.69*	–	–	–	36.89*
Goniopora spp.	–	–	–	–	5.4	–	–	–	–	–	–	–	–	–
Favia pallida gr.	5.3	–	–	2.28	2.7	10.04	–	–	–	–	15.4	–	–	2.64
Favia spp. (massive)	–	–	–	–	2.7	5.02	–	–	–	–	–	–	3.99	–
Favia spp. (encrust.)	–	–	–	–	–	2.15	–	2.84	–	–	–	–	–	–
F. flexuosa	5.3	–	–	–	–	–	–	–	–	–	–	–	–	–
Favites spp. (massive)	5.3	3.7	–	–	2.7	–	–	–	–	–	–	13.67	–	–
Favites spp. (encrust.)	–	3.7	–	–	–	2.42	–	5.88*	3.7	–	–	–	–	–
Goniastrea spp. (submeand.)	–	–	–	–	–	–	–	2.84	–	–	–	–	–	–
Montastrea spp. (encrust.)	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Cyphastrea spp. (massive)	–	3.7	3.98*	–	5.4	–	–	–	3.7	–	–	13.67	7.98	–
Cyphastrea spp. (encrust.)	–	7.4	10.99*	5.92*	2.7	4.48*	–	28.66*	–	–	15.4	–	3.99	–
Leptastrea spp. (encrust.)	–	7.4	–	–	–	–	–	–	–	–	–	–	–	–
Platygyra sinensis gr.	–	3.7	–	–	18.9	5.29	–	–	–	–	7.7	–	–	–
P. contorta	–	3.7	–	–	–	6.46	–	–	–	–	–	–	–	–
Platygyra spp. (massive)	5.3	–	–	–	8.1	–	–	–	–	–	–	–	–	–
Platygyra spp. (encrust.)	5.3	3.7	–	–	–	–	–	–	–	–	–	–	–	–
Acanthastrea spp. (massive)	–	–	–	–	–	–	–	–	3.7	–	–	–	–	–
Acanthastrea spp. (encrust.)	–	–	–	–	2.7	2.15	–	–	–	–	–	–	–	–
Lobophyllia spp.	–	–	–	–	2.7	5.38	–	–	–	–	7.7	–	–	–
Symphyllia spp.	–	–	–	–	2.7	–	–	–	–	–	–	–	–	–
Echinophyllia spp.	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Fungiid corals	–	–	–	–	–	–	78.58	19.07*	–	–	–	6.83	–	–
Pavona spp.	–	11.1	–	–	–	–	–	–	–	–	7.7	–	–	–
Leptoseris spp.	–	22.2	–	–	–	–	–	–	–	–	–	–	–	–
Pachyseris speciosa	–	–	–	–	–	–	–	–	–	–	–	–	–	–
P. rugosa	–	–	–	–	–	4.48	–	–	–	–	–	–	–	–
Galaxea astreata	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Turbinaria spp.	–	–	–	–	–	2.15	–	–	3.7	2.85*	7.7	–	–	4.69*

the three quadrats. This coral can inhabit a wide range of reef environments, including relatively deep reef habitats (observed at a depth of 28 m in Australia; Veron *et al.*, 1977). *Stylocoeniella guentheri*, which characterizes association A4, occurs mainly on outer reef slopes (Veron, 1992) and may be found to depths of 40–60 m (Kühlmann, 1983; data for the Central Pacific). Regarding the *Stylocoeniella* colonies identified on Irabu-jima, we would like to acknowledge the possibility that they were mistaken for a deep (mesophotic) *Montipora* species, which does not, however, change the paleoenvironmental interpretation. *Echinophyllia* spp., also characterizing association A4, commonly occurs at depths of 20–30 m in the South Ryukyus (Sagawa *et al.*, 2001). Coral assemblages in the three quadrats are also characterized by abundant thin encrusting colonies of *Porites* and/or *Montipora*. Kühlmann (1983) describes the corals *Leptoseris*, *Montipora*, *Porites*, and *P. speciosa* as the dominant characteristic taxa in the Central Pacific below 20 m. In the Ryukyus, *Leptoseris scabra* dominates the coral assemblage on the reef slope at depths greater than 25 m on Ishigaki-jima (Iryu *et al.*, 1995). *Leptoseris* is a typical coral genus in the mesophotic zone (30–150 m), and has been found at depths greater than

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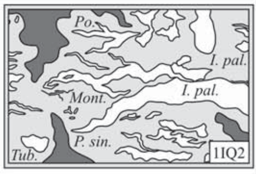
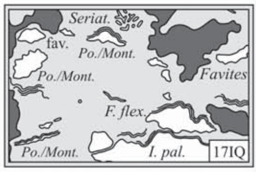
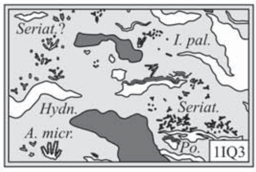
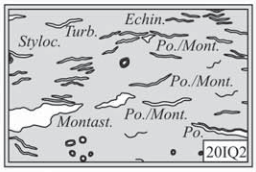
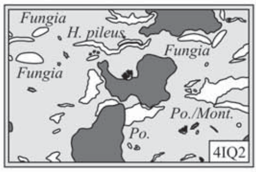
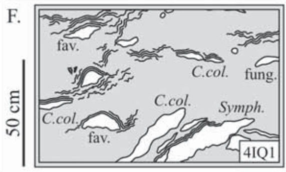
	QUADRATS	CHARACTERISTIC CORAL TAXA	ASSOCIATED CORAL TAXA	COMMON MORPHOLOGIES (+ LESS COMMON MORPHOLOGIES)	PALEOENVIRONM. INTERPRETATION
A. 	2IQ1/2IQ2 Gr6 (subgr. B)	***Isopora palifera*** *with small branching colonies becoming abundant in protected habitats*	*Porites/Mont.* sp(p). *A. microphthalma* gr. *Seriatopora* sp(p). *Goniopora* spp. various faviids	encrusting to thick encrusting, small branching arboresc. (+massive)	UPPER REEF SLOPE (protected to exposed habitat?) <20 m
B. 	17IQ Gr6 (subgr. B)				
C. 	2IQ3	***Acropora microphthalma* gr.**	*Porites* sp(p). *I. palifera* *Seriatopora* sp(p). various faviids	small branching arboresc., encrusting to thick encrusting, (+massive)	UPPER REEF SLOPE (protected habitat?) <20 m
D. 	20IQ1/20IQ2/20IQ4 Gr6 (subgr. A)	***Porites/ Montipora* sp(p).**	*Stylocoeniella* sp(p). *Leptoseris* spp. *Echinophyllia* sp(p). *Montastrea* sp(p) *Cycloseris* sp(p).	thin encrusting to platy, foliaceous, trocoid (+ encrusting)	LOWER REEF SLOPE >30 m
E. 	4IQ2 Gr5	***Fungia* spp.**	various faviidae *Montastrea* spp. *Porites* spp.	solitary encrusting/platy to thin encrusting	SHALLOW-WATER UNCONSOLIDATED BOTTOM SUBSTRATE <30 m
F. 	4IQ1 Gr4	***Coscinarea columna***	Agariciidae *Cyphastrea* sp(p). *Lobophyllia* sp. Fungiidae	encrusting (+ phacelloid and solitary)	SHALLOW ENVIRONM.? <30 m?

Figure 7. Coral assemblages and their paleoenvironmental interpretations based on their taxonomic and morphological characteristics. *A. micr.*, *Acropora microphthalma* gr.; *C. col.*, *Coscinarea columna*; *Echin.*, *Echinophyllia* sp.; fav., faviid coral; *F. flex.*, *Favites flexuosa*; fung., fungiid coral; *H. pileus*, *Halomitra pileus*; *Hydn.*, *Hydnophora* sp.; *I. pal.*, *Isopora palifera*; *Montast.*, *Montastrea* sp.; *Mont.*, *Montipora* sp.; *Po.*, *Porites* sp.; *Po./Mont.*, *Porites/Montipora* sp.; *P. sin.*, *Platygyra sinensis* gr.; *Seriat.*, *Seriatopora* sp.; *Styloc.*, *Stylocoeniella* sp.; *Symph.*, *Symphyllia* sp.; *Tub.*, *Tubipora musica*; *Turb.*, *Turbinaria* sp.

70 m in the Ryukyus (Yamazato, 1972), and as deep as 165 m in the Hawaiian Islands (Kahng and Maragos, 2006). *Leptoseris* is also associated with thin colonies of *Porites* and *Montipora* at depths greater than 40 m on the Great Barrier Reef of Australia (Bridge *et al*., 2012). Hence, corals of group X are indicative of middle to lower reef slope environments, if fungiids are composed of *Cycloseris* and/or *Diaseris* (>30 m).

Association A5 and *G. astreata* constitute group Y. This association includes *I. palifera*, which is characteristic of the upper reef slope. The distribution of *G. astreata*, unlike that of *G. fascicularis*, may extend to

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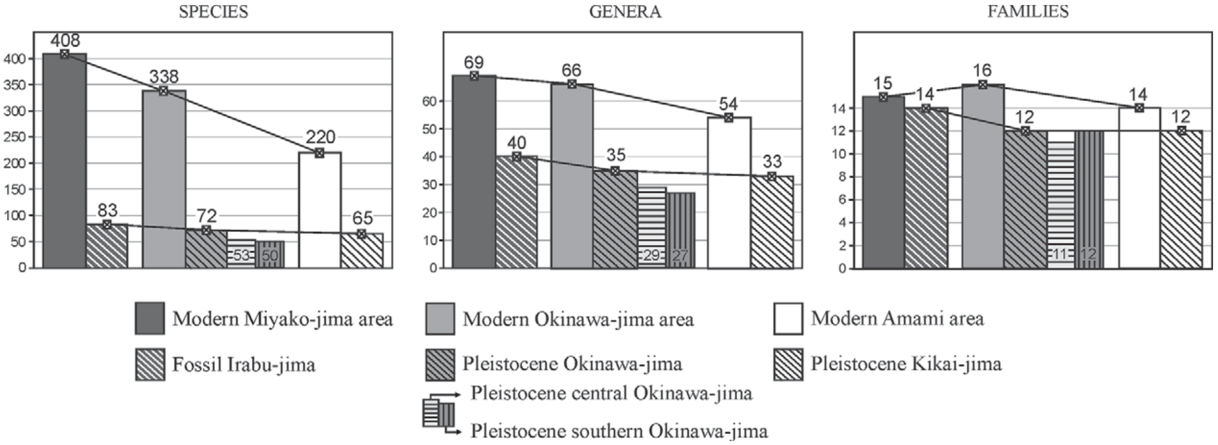

Figure 8. Comparison between the numbers of taxa recorded on modern reefs and the numbers of taxa recorded from Pleistocene reef limestones. Data for the Miyako-jima area, including Irabu-jima, are from JCRS (2004). Data for the Okinawa-jima and Amami areas are from Veron (1992) and Nishihira and Veron (1995). Note that the difference in the numbers of families from the Miyako-jima and Okinawa-jima areas on modern reefs is due to a difference in taxonomic classification schemes, and does not reflect a true difference in taxonomic richness.

depths of 30–40 m (see Kühlmann, 1983; data for the Central Pacific). Therefore, group Y indicates an upper to middle reef slope setting (<30 m). Taxa of group Y are best represented in quadrats 1YOZQ1, 19HQ1, and 20KQ (Figure 5). Group Z, which is much more diversified than groups X and Y, is composed of associations A6, A7, A8, A9, and *Symphyllia* spp. These associations are mainly characterized by faviid species. Association A6, composed of *Platygyra contorta* and *P. rugosa*, indicates a wide range of shallow reef settings (see Humblet *et al.*, 2009). Association A7, which is a highly diversified cluster composed of various mussids, faviids, and *Pavona* spp,, is an important component of the coral assemblage in quadrats of cluster Gr3 (Figure 5). These taxa often occur in association with *I. palifera*. Therefore, association A7 may represent an upper reef slope environment (<20 m). Taxa of association A8 do not indicate any particular environment. Association A9 is composed of tabular and corymbose *Acropora* spp., massive *Porites* sp., and massive to encrusting faviids. These taxa are particularly representative of quadrats in clusters Gr7 and Gr8 (Figure 5). Association A9 is equivalent to association A7 of Humblet *et al.* (2009) (with the exception of the occurrence of corymbose *Acropora* spp.) and indicates a reef edge to shallow upper reef slope or low-turbidity shallow lagoon environment (<10 m). Consequently, group Z is indicative of a wide range of shallow reef settings.

Variations in reef slope coral assemblages between and within islands

Variations between islands.—The Pleistocene reefs of the Ryukyus, like their modern counterparts, are characterized by a northward decrease in species and generic richness (Figure 8). The 3-dimensional (“3D”) MDS ordination of the BC similarity coefficients calculated for each pair of the 39 quadrats from Irabu-jima, Okinawa-jima, and Kikai-jima, reveals some dissimilarities in taxonomic compositions of quadrats from distinct geographic areas (Figure 9). The range of taxonomic differences (0.115 < *R* < 0.742) is greater than that obtained when data from Irabu-jima are excluded from the analysis (0.176 < *R* < 0.300; Humblet *et al.*, 2009). The distribution of the data in the 3D MDS delineates a rough trend from shallow (foreground) to deep (background) reef settings (Figure 9). This trend mainly reflects the proportion of encrusting to platy *Porites* and/or *Montipora* species in each quadrat. Thin laminar colonies of these taxa are particularly abundant in deeper middle to lower reef slope coral assemblages, but they may also have a high relative abundance in some shallow assemblages (2IQ1, 2IQ2, and 17IQ).

Middle Pleistocene upper reef slope assemblages on Irabu-jima are dominated by acroporid corals, mainly encrusting *I. palifera* and branching *Acropora* spp., encrusting to platy *Porites* spp., and branching Pocilloporidae (Table 3). *Turbinaria* spp. are also systematically present, although not abundant. As on Irabu-jima, *I. palifera*, *Porites* spp., and *Montipora* spp. dominate upper reef slope assemblages on Okinawa-jima. Branching *Acropora* spp. and *I. palifera* are dominant coral taxa on the reef crest to shallow upper reef slope on modern Pacific reefs (Montaggioni and Braithwaite, 2009). Our data also indicate that *Porites* spp. and faviids, such as *Cyphastrea* spp. and *F. pallida* gr., are typical

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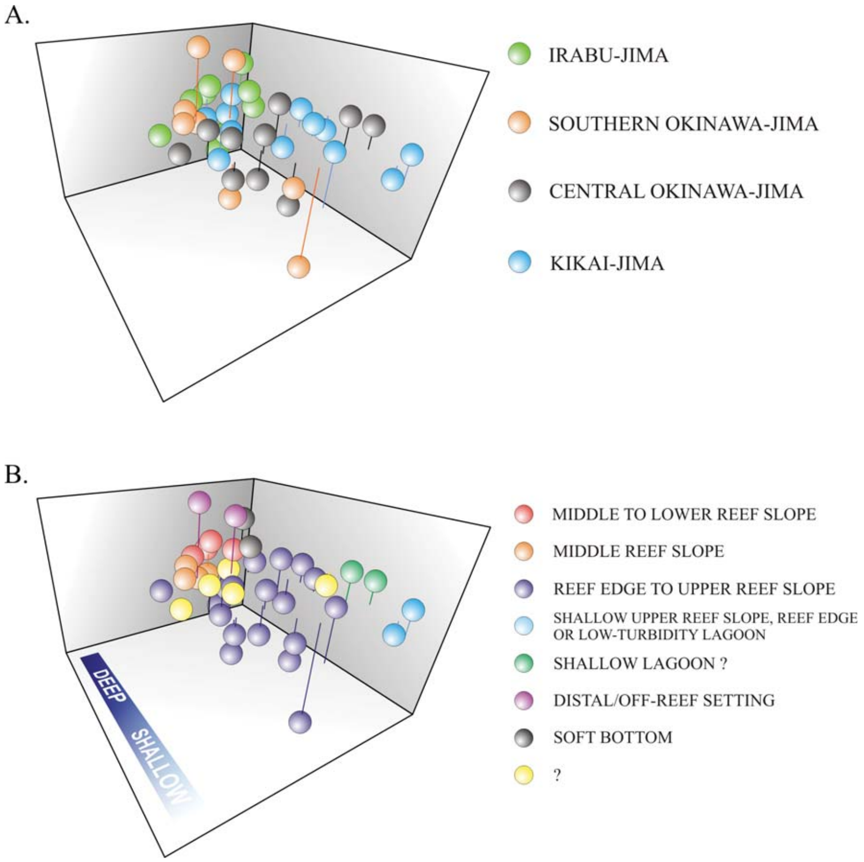

Figure 9. A 3-dimensional non-metric multidimensional scaling (MDS) ordination of quadrats based on BC similarities. Quadrats are labeled according to their geographic provenances (A) and their paleoenvironmental designations (B).

of the upper reef slope on Kikai-jima (Humblet *et al.*, 2009). The coverage of faviids and *Porites* on the modern reef slope on Kikai-jima increases at depths greater than 4 m, whereas that of *Acropora* declines rapidly (Dr. Kaoru Sugihara, pers. comm.). Therefore, we assigned the Pleistocene assemblages from Kikai-jima to an upper reef slope setting, that may reflect a slightly deeper bathymetry than that represented by the assemblages on Irabu-jima and Okinawa-jima.

When the ANOSIM test is performed on abundance data, the largest difference in taxonomic composition ($R = 0.750$) is between upper reef slope assemblages of Irabu-jima and central Okinawa-jima, and the smallest ($R = 0.157$) is between those of Irabu-jima and Kikai-jima (grey columns, Figure 10A). However, in the latter case, the number of quadrats involved is small, and trends are not statistically significant ($p >> 0.05$; Figure 10A). When the same test is performed on presence–absence data, the range of R values and most of the individual R values decrease ($0.115 < R < 0.426$; compare the grey and black columns in Figure 10A). Hence, variations in the relative abundances of taxa account for some of the observed variability in the upper reef slope coral community structures between distinct geographic areas. In particular, the relative abundances of encrusting and platy *Porites* spp. and *Montipora* spp. influence the extent of geographic differences in taxonomic composition between upper reef slope coral assemblages (Figure 10C). Correlation (R) values also indicate that within-island variations may be larger than latitudinal differences in species composition ($R_{(\mathrm{SO\ vs\ CO})} > R_{(\mathrm{K\ vs\ CO})}$; Figure 10A; see also Humblet *et al.*, 2009). Therefore, our data suggest that geographic proximity does not imply a greater similarity in taxonomic composition between upper reef slope assemblages in the studied area.

The R values for middle to lower reef slope assemblages are large, suggesting marked differences in the species compositions of distinct geographic areas. However, the limited number of quadrats involved in the analysis is not sufficient to ascertain the statistical significance of these results ($p >> 0.05$; Figure 10B, D). Unlike upper reef slope coral assemblages, removing

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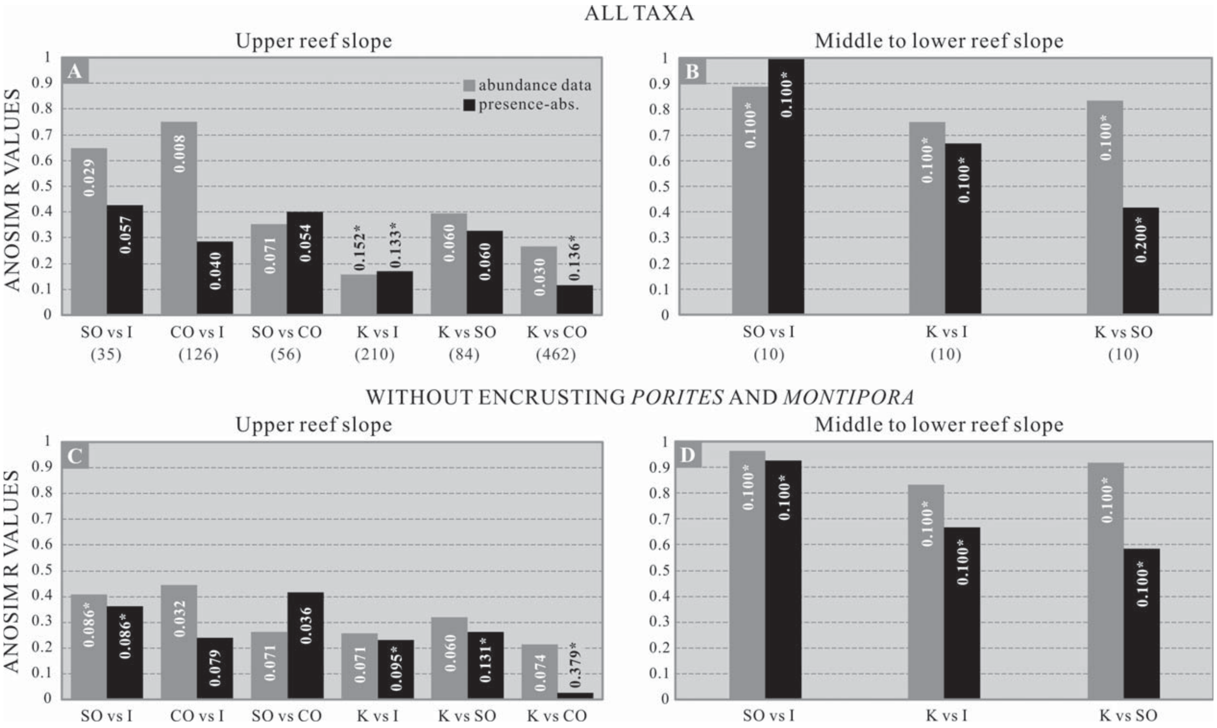

Figure 10. Bar chart showing the results of similarity tests (ANOSIM) between Irabu-jima, Okinawa-jima, and Kikai-jima, performed with standardized abundance data and presence–absence data. Analyses were conducted on upper (A) and middle to lower (B) reef slope coral assemblages separately. The same analyses were performed after removing encrusting *Porites* and *Montipora* species from the data set (C, D). Values of *R* closer to 1 indicate greater dissimilarities between geographic areas. Statistical significance is represented by $p \leq 0.05$. Asterisks designate results showing a high level of statistical uncertainty. The number of permutations performed for each of the tests is shown in brackets. I, Irabu-jima; SO, southern Okinawa-jima; CO, central Okinawa-jima, K, Kikai-jima.

encrusting to platy *Porites* spp. and *Montipora* spp. from the data set does not greatly affect the results of the ANOSIM test, as these taxa are an important component of all middle to lower reef slope assemblages (Figure 10D). Different species typify the deeper coral assemblages in different geographic areas: *G. astreata* on southern Okinawa-jima (1YOZQ1, Ue1, Ue2), *Pachyseris speciosa* on Kikai-jima (19HQ2, 19HQ3), and *Stylocoeniella* sp. on Irabu-jima (20IQ1, 20IQ2, 20IQ4). However, the number of replicate sites is not sufficient to tell whether these differences reflect local variations in community structure or large-scale geographic differences.

The differences in the taxonomic compositions observed between Pleistocene reef slope coral assemblages on Irabu-jima, Okinawa-jima, and Kikai-jima are not proportional to latitude. The observed geographic variability may result in part from local environmental factors, such as substrate type, wave energy, and turbidity, which may affect coral community structures within reef environments (Done, 1983). Our data stress the importance of understanding the influence of local factors on modern coral communities to interpret the fossil record.

Variations within islands.—The taxonomic compositions of upper reef slope assemblages on a given island are relatively uniform (Figure 11A). Removing encrusting *Porites* and *Montipora* species from abundance and presence–absence data results in a slight decrease in the average similarity between assemblages on the same island (Figure 11A, C). This can be explained by the fact that encrusting *Porites* and *Montipora* species are present in many upper reef slope assemblages.

Differences in the taxonomic compositions of upper reef slope assemblages on an island may be attributed to local environmental factors. Greater similarities in taxonomic composition are observed in lower reef slope settings on Irabu-jima, regardless of the type of data analyzed (the average BC similarity of all taxa between 20IQ1, 20IQ2, and 20IQ4 is greater than 75%; Figure 11B, D). A detailed description of the lower reef slope assemblages and a comparison with upper reef slope assemblages from the same island are presented in the next section. Similarities in the taxonomic compositions of middle reef slope setting assemblages on southern Okinawa-jima are also large (the average BC similarity between YOZQ1, Ue1,

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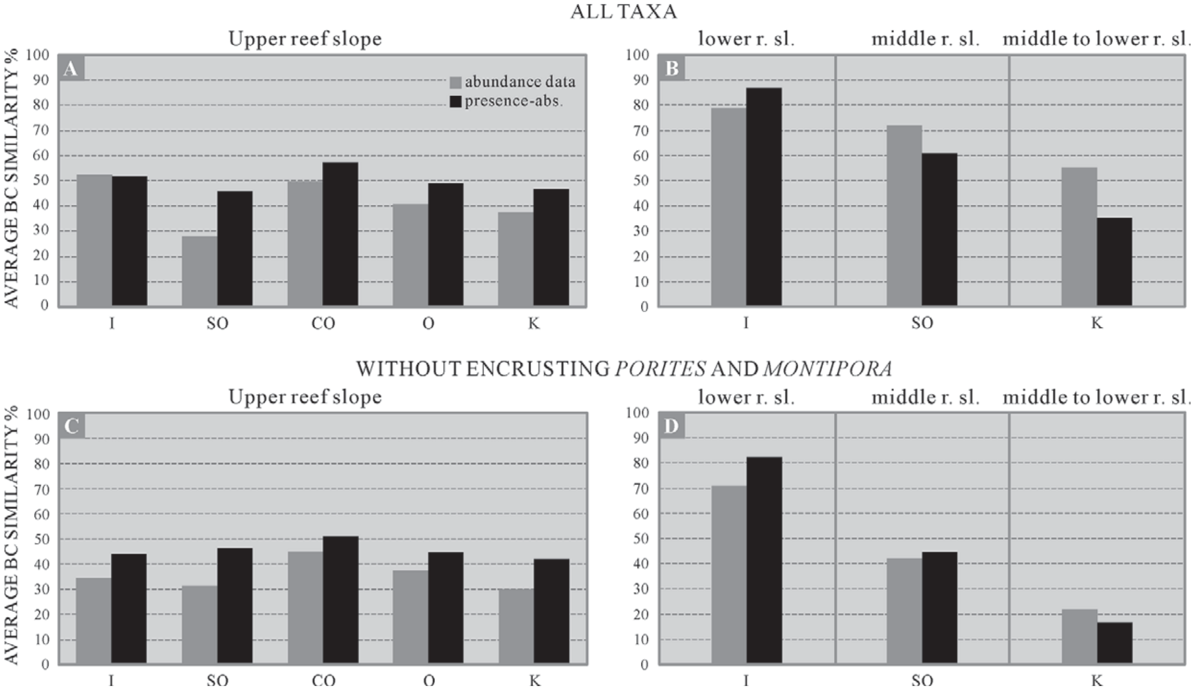

Figure 11. Bar chart showing the average BC similarity coefficient calculated between each pair of quadrats within a given geographic area on the basis of standardized abundance data and presence–absence data. Average BC similarity coefficients were calculated for upper (A) and middle to lower (B) reef slope coral assemblages, respectively. The same calculations were performed after removing encrusting *Porites* and *Montipora* species from the data set (C, D). I, Irabu-jima; SO, southern Okinawa-jima; CO, central Okinawa-jima; O, southern and central Okinawa-jima; K, Kikai-jima. Note that no middle or lower reef slope assemblages were described on central Okinawa-jima.

and Ue2 is greater than 70%; Figure 11B). However, the average similarity percentage is reduced when calculated on the basis of presence–absence data (average BC similarity of ~60%), and is reduced even further when encrusting *Porites* and *Montipora* species are removed from the data (average BC similarity of <50%; compare plates B and D, Figure 11).

The observation that similarities in taxonomic composition derived from abundance data are greater than those derived from presence–absence data results from the very large proportion of encrusting *Porites* and *Montipora* species reported in the three middle reef slope assemblages described for southern Okinawa-jima. The overall greater within-island similarity between middle to lower reef slope assemblages on Irabu-jima and southern Okinawa may result in part from the fact that all but one of these assemblages (YOZQ1) are from the same site (site 2I on Irabu-jima and site Ue on southern Okinawa-jima) and are in stratigraphic proximity. Hence, their similarities may reflect a uniformity in taxonomic composition at relatively small spatial and temporal scales. In the next section, we further explore the spatial variability in the taxonomic compositions of lower reef slope assemblages on Irabu-jima.

As compared with the assemblages on Irabu-jima and southern Okinawa, the differences between the species compositions of middle to lower reef slope assemblages on Kikai-jima (19HQ2, 19HQ3) are relatively large. The assemblages on Kikai-jima were from two distinct stratigraphic levels at the same outcrop, where the temporal trend in species composition suggests a deepening (Humblet *et al.*, 2009). Hence, these two assemblages probably represent distinct bathymetric settings.

Comparisons of community structures at sites 2I and 20I. In this section, we examine the extent of taxonomic variation at the scale of a large outcrop (~100 m wide and a few meters high) in two distinct reef environments: shallow upper reef slope (site 2I) and deep lower reef slope (site 20I). We address the important issues of the influence of replicate size, distance between replicates, and the type of data (abundance vs. presence–absence) on the detection of differences in community structures.

The relationship between species richness and outcrop area at site 2I indicates an overall high taxonomic diversity as compared with the diversity at site 20I (Figure 4). Cluster analysis of BC similarities performed on all quadrats shows that 20IQ1, 20IQ2, and 20IQ4 form a cluster at a particularly high level of similarity (>75%),

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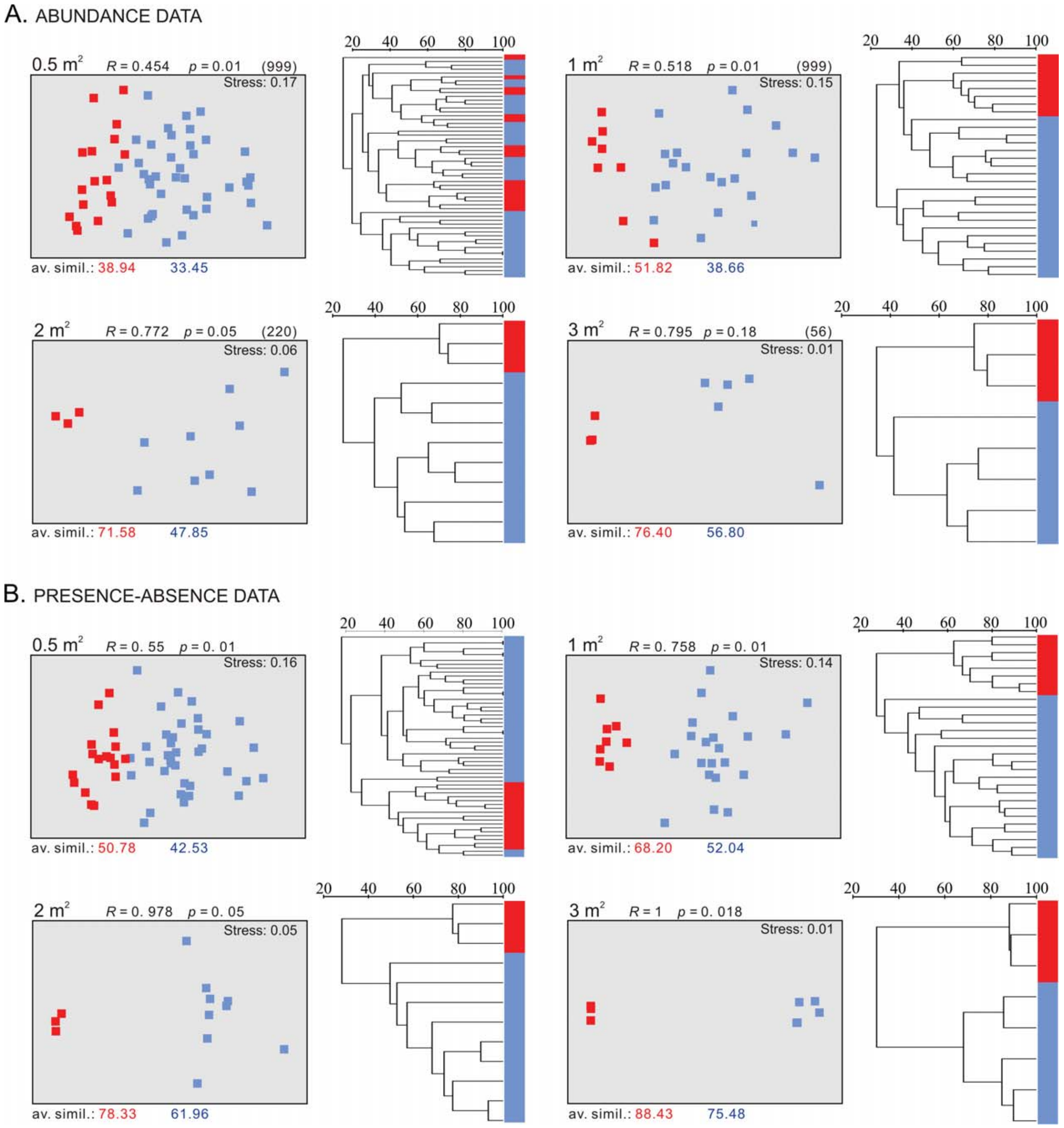

Figure 12. A 2-dimensional non-metric multidimensional scaling (MDS) ordination and clustering of upper reef slope coral assemblages (blue squares) and lower reef slope coral assemblages (red squares) based on similarities in their taxonomic compositions. The same statistical analysis was successively performed on taxonomic data derived from portions of outcrop with areas of 0.5 m^2, 1 m^2, 2 m^2, and 3 m^2. Two types of taxonomic data were compiled for the statistical analysis: abundance data (A) and presence–absence data (B). A similarity test between upper and lower reef slope assemblages (see *R* and *p* values indicated above each of the MDS plots) and the calculation of the average BC similarity coefficient for upper and lower reef slope assemblages (see values indicated below each MDS plots) were performed for each of the data sets. The number of permutations performed for each similarity test is indicated in brackets.

as compared with quadrats 2IQ1, 2IQ2, and 2IQ3 (Figure 4). The average within-reef-zone BC similarity increases steadily with increasing surface area (Figure 12). Lower reef slope assemblages (site 20I) are more similar to each other than upper reef slope assemblages (site 2I), regardless of the outcrop area (compare the average BC simi-

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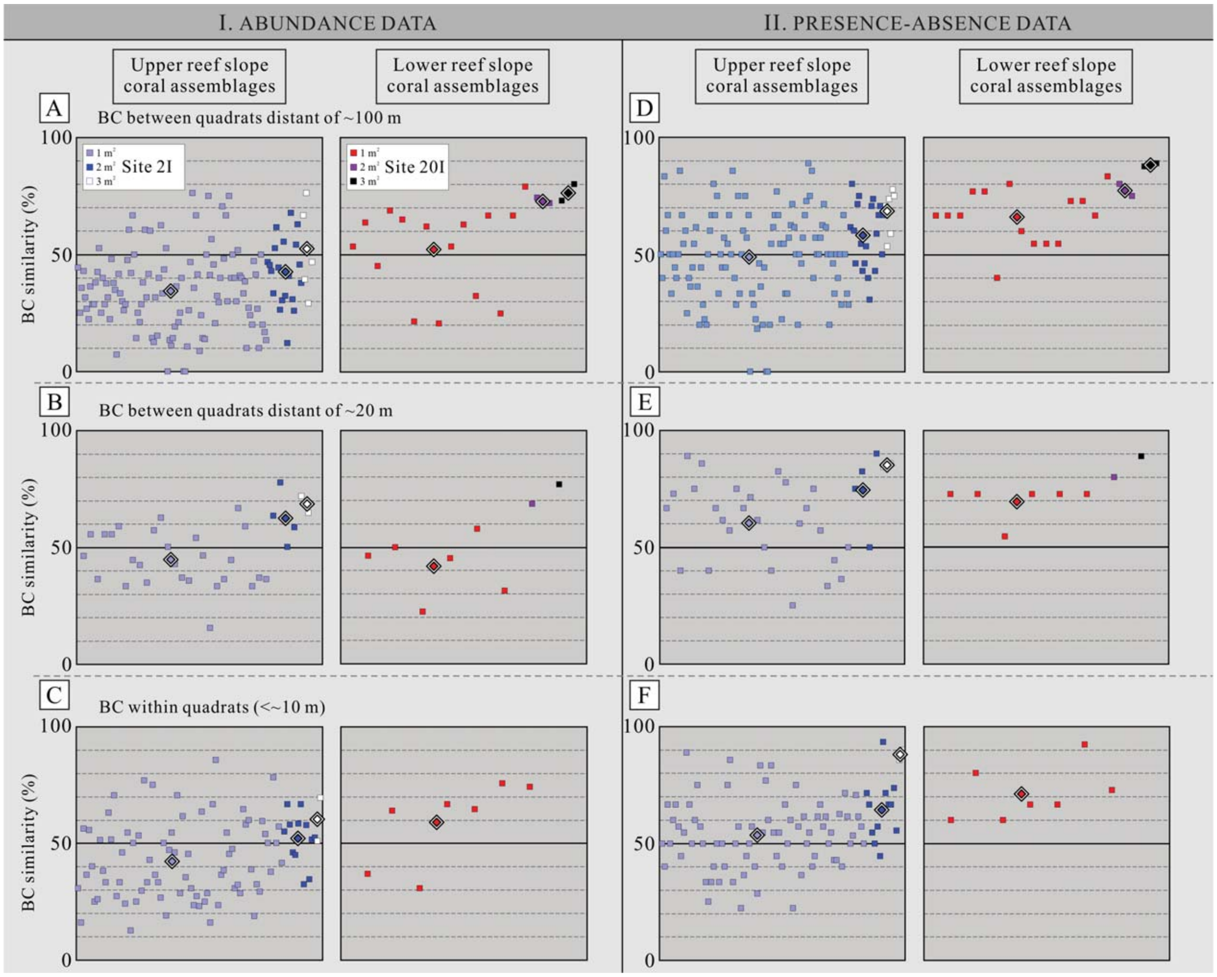

Figure 13. Bivariate plots of BC similarity coefficients calculated for pairs of coral assemblages as a function of distance between the assemblages, of ~100 m, ~20 m, and < ~10 m, at site 2I (upper reef slope setting) and site 20I (lower reef slope setting). Results are for the taxonomic data recorded from portions of the outcrop of different sizes (1 m^2, 2 m^2, and 3 m^2). Two types of taxonomic data were used for the calculation of BC similarities: abundance data (I) and presence–absence data (II). Average values for each data set are indicated with diamonds.

larity values of red and blue symbols in Figure 12). Similarly, taxonomic diversity seems more uniform across quadrats set in deeper reef settings (Figure 4). Calculations based on presence-absence data result in higher average BC similarity values (Figure 12B). The MDS ordinations and cluster analyses of BC similarity coefficients calculated for replicates of increasing size show that the minimum surface area needed to isolate all lower reef slope coral assemblages in a single cluster is 2 m^2 in the case of untransformed data ($R = 0.77$) and 1 m^2 in the case of presence–absence data ($R = 0.76$) (Figure 12). A larger area is thus needed to unambiguously distinguish two environments based on abundance data.

Examination of within-reef-zone variability in taxonomic composition as a function of distance between replicates (~100 m, ~20 m, and <10 m) and replicate size (1 m^2, 2 m^2, and 3 m^2) shows that replicates are, on average, more similar to one another as their sizes increase (Figure 13A–F). Conversely, the distance between replicates has a limited influence on within-reef-zone similarity. The average BC similarity among replicates at distances of less than 10 m is only slightly higher than for those at distances of ~100 m (Figure 13A, C). The taxonomic compositions of lower reef slope assemblages are less variable than those of upper reef slope assemblages for replicates at distances of ~100 m, and for those that are less than 10 m apart (Figure 13A, C). By contrast, no clear differences in average BC similarities are observed in either reef setting for replicates at distances of ~20 m from one another (Figure 13B). Using presence–absence data tends to increase the average BC similarities in both environments, and to narrow the

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range of BC similarity values of lower reef slope assemblages (Figure 13D–F).

Our data indicate that, at the scale of a large outcrop, lower reef slope assemblages are more consistently similar to one another than upper reef slope assemblages. Data on modern lower reef slope communities in the Ryukyus are lacking to verify whether this trend is also observed in modern reefs. However, lower reef slope (mesophotic) environments have been shown to be particularly stable, with relatively little change observed in coral community structures over decades, as compared with shallower coral communities (Bak *et al*., 2005). Conversely, shallower reef settings experience locally steep environmental gradients (e.g. wave energy, turbidity) and different disturbance regimes, which can result in highly variable coral community structures over relatively small temporal and spatial scales on a single reef (Connell *et al*., 1997). Consequently, our data may reflect the contrasting variability in taxonomic compositions of upper and lower reef slope communities at scales of 100 m or less. The spatial homogeneity of lower reef slope coral assemblages appears more pronounced when the sizes of replicates increase or the data set consists of presence–absence records rather than abundance counts.

Conclusions

We examined the taxonomic compositions of nine coral assemblages in middle Pleistocene limestones on Irabu-jima, South Ryukyus. These data were compiled along with other data sets formerly obtained from Okinawa-jima, southern Central Ryukyus, and Kikai-jima, northern Central Ryukyus. Cluster analyses of the resulting data set produced nine coral associations and eight groups of coral assemblages with similar taxonomic compositions. Quadrats grouped in the same cluster do not necessarily belong to a similar reef environment. The high relative abundances of encrusting to platy *Porites* and *Montipora* species in various coral assemblages may be responsible for the clustering of upper reef slope assemblages with middle to lower reef slope assemblages. The Pleistocene record reflects the complexity of reef ecosystems. A detailed knowledge of the distribution of modern reef communities is therefore important for providing accurate coral-based paleoenvironmental interpretations.

The taxonomic compositions of upper reef slope assemblages from different geographic areas exhibit significant differences, but the differences are not proportional to latitudinal distance. On Irabu-jima, acroporid corals (mainly *I. palifera*, branching *Acropora* spp., encrusting to platy *Porites* spp., and branching pocilloporids) dominate. Upper reef slope assemblages display high variability in the relative abundances of species, which is partly responsible for their groupings into various clusters.

Unlike their modern counterparts, fossil lower reef slope communities are readily accessible for study in uplifted Pleistocene coral limestones. Middle to lower reef slope assemblages of the South and Central Ryukyus are characterized by a large proportion of thin laminar colonies of *Porites* and *Montipora* species. However, the species associated with the middle to lower reef slope assemblages in the different regions vary: *Stylocoeniella* sp. on Irabu-jima, *Galaxea astreata* on southern Okinawa-jima, and *Pachyseris speciosa* on Kikai-jima. It is not possible in this study to know whether these differences are caused mainly by local environmental factors or large-scale latitudinal variations in community structure. Additional data on modern lower reef slope coral communities in the Ryukyus are needed to resolve this question.

A detailed analysis of the lateral variations in fossil coral community structures at the scale of a large outcrop (~100 m wide and a few meters high) on Irabu-jima showed that lower reef slope assemblages tend to have lower taxonomic richness values and higher average similarities in taxonomic compositions relative to those of upper reef slope assemblages. We conclude that a larger outcrop area is needed to fully integrate the lateral variability of upper reef slope assemblages. Moreover, we also point out the importance of the sampling method for accurate discrimination of paleoenvironments, as the distinction between lower and upper reef slope assemblages derived from statistical analyses of abundance data requires a relatively large outcrop (2 m^2) as compared with the same analysis performed on presence–absence data (1 m^2).

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