Spatial and Temporal Variations in Pleistocene Coral Assemblages in the South and Central Ryukyu Islands

氏名・(本籍)	Humblet (ハンブレ) Marc (マーク) André (アンドレ)
学位の種類	博　士(理　学)
学位記番号	理博第2384号
学位授与年月日	平成19年9月12日
学位授与の要件	学位規則第4条第1項該当
研究科，専攻	東北大学大学院理学研究科(博士課程)地学専攻
学位論文題目	Spatial and Temporal Variations in Pleistocene Coral Assemblages in the South and Central Ryukyu Islands (南琉球および中琉球における更新世サンゴ群集の時空変化)
論文審査委員	(主査)　准教授　井龍康文 教授　尾田太良，箕浦幸治，海保邦夫 教授　永広昌之 准教授　中森亨

論　文　目　次

論 文 内 容 要 旨

The first part of this thesis consists of a review of studies on paleoecology and taphonomy of coral communities. Taxonomic similarity between modern and fossil coral communities is useful to investigate past environments based on our knowledge of the present-day coral species distribution. However, using fossil coral communities for paleoenvironmental reconstructions requires that the fossil record accurately

preserves the original structure of coral communities prior to their fossilization. The taxonomic compositions of life and co-occurring dead coral communities are averaged over time and provide the material that will be fossilized. Paleoecologists and paleontologists have shown that various degrees of similarity exist between life and corresponding fossil assemblages. These differences result from processes acting over multiple spatial scales. Environmental parameters such as the energy regime, related to the bathymetry and the reef topography, and the distance from sediment sources control the amount of allochthonous fragments imported. On the other hand, low energy regime may promote longer post-mortem residence times on the sea floor and longer exposure to taphonomic processes. Bioerosion rates are positively correlated with nutrient concentrations and the density of coral skeleton, both of which show a tendency to increase with increasing water depth. The activity of fishes feeding on bioeroding organisms may also potentially influence the rate of bioerosion. Turbidity affects the size of coral colonies and consequently modifies their resistance to physical and biological alterations. Intrinsic factors such as the morphology of corals and the microstructure of their skeleton are important for their resistance to physical stress and diagenetic processes. On larger scales, the frequency and intensity of disturbances are of fundamental importance. Hurricanes cause mass-breakage and colony dislodgement, whereas temperature anomalies raise the rate of mortality, which increase the amount of dead skeletons that can be colonized by bioeroding organisms. In the course of the geological history, sea-level changes have a great influence on the mode of preservation of coral assemblages. Rapid regressions may result in fast burials due to higher sedimentation rates, and hence increase the similarity between life and fossil assemblages. On the other hand, continuous increase in sea level accompanied by a "keep up" reef growth may hinder burial-exhumation cycles and limit the extent of the sedimentological time-averaging. In this condition, ecological time-averaging, which works on a timescale of$\sim 10^3$ years or less, prevails. All these processes acting at different scales influence the reliability with which fossil assemblages reflect the ecological structure of the life assemblages they originate from.

Using fossil coral communities for paleoenvironmental reconstructions also requires to understand the dynamics of coral communities in space and time. Previous paleoecological studies of Pleistocene coral assemblages in the Caribbean and the Indo-Pacific provinces have shown that fossil coral assemblages are potentially reliable indicators of paleoenvironments. The coral reef zonation is preserved in the fossil record, unless high frequency, high intensity hurricanes prevent the *in-situ* preservation of the coral framework and promote spatial mixing. In the Ryukyu Islands, coral reef zones very similar to those of present-day reefs have been identified in several studies, including the present one. Previous studies have identified patterns of consistency in coral community structure reflecting associations of species sharing similar niches over km-scale areas across the Caribbean Province in Pleistocene limestones. However, the spatial scale at which these patterns of consistency are observed is not well defined. The within reef-zone distribution of coral species in modern reefs across the Indo-Pacific Province appears to be more variable than in the Pleistocene record across the Caribbean, which may be due in part to the lower taxonomic diversity of Caribbean reefs. Conversely, the smallest temporal (years, tens of years) and spatial scales (a few meters) yield the highest variations in coral community structure due to highly variable disturbance conditions, caused by storms and disease. At very large spatial scales (hundreds of kilometers or more), the variability of community structure is also high due to factors such as the geological history, the oceanographic setting and variations in SST. At low latitudes, coral assemblages seem to retain the same taxonomic composition over tens of thousands of years throughout repeated sea-level changes and varying SSTs. This supports the hypothesis of limited

species membership in Pleistocene coral assemblages. In the case of high-latitude coral communities, lower species diversity and lower ecological complexity might lead to less predictable species associations during Quaternary climate and oceanographic changes. The Ryukyu Islands are a perfect field to test this hypothesis.

The second part of the thesis presents the results of a paleoecological study of Pleistocene coral assemblages in the Ryukyu Islands, Japan. The taxonomic composition and colony morphologies were studied using the quadrat method in Irabu-jima (South Ryukyus), Okinawa-jima (southern Central Ryukyus) and Kikai-jima (northern Central Ryukyus). A total of 84 species and 40 genera were found in Irabu-jima. A total of 72 species belonging to 35 genera were identified in Okinawa-jima, whereas 65 species coming under 33 genera were recorded in Kikai-jima. The cluster analysis of the Bray-Curtis similarity coefficient produced 4 coral associations in Irabu-jima, 6 in Okinawa-jima and 4 in Kikai-jima. Some of these coral associations contain taxa indicative of a specific depth range, while others, composed exclusively of cosmopolitan taxa, do not point to any particular reef zone. Within-reef-zone variability in taxonomic and morphological compositions is high on various scales, from a few meters to several kilometers, in shallow reef slope-environments. This is well illustrated by the *Acropora palifera*-bearing association. In the present-day reefs of the Ryukyu Islan ds, *Acropora palifera* occurs mainly on exposed upper reef slopes between 0 and 20 m of water depth. The composition of associated taxa varies significantly from place to place resulting in distinctive coral assemblages. Moreover, the thickness of *A. palifera* is highly variable and is likely to be correlated with the degree of exposure to wave action. Within areas of a few meters, distinctive coral assemblages belonging to the same reef zone may co-exist, reflecting local variations in disturbance regime. This contrasts well with the low variability in taxonomic and morphological compositions of middle to lower reef-slope assemblages on a scale of tens of meters. Greater homogeneity of community structure in deeper reef settings is likely to be related to relatively high environmental stability. The present study on vertical coral sequences in Pleistocene limestones reveal a wide range of taxonomic and morphological variations. Minor to moderate taxonomic and morphological changes may be related to within-reef-zone variability recorded in reef limestones over thousands of years. Major changes, i.e. transitions from one reef zone to another, are likely to result from sea-level fluctuations. The coral assemblages in these coral successions are similar to those living in present-day reefs. However, the present study points out possible variations in the geographic distribution of specific taxa in the Pleistocene. The limited presence of *Acropora palifera* in the present-day southern and central Okinawa-jima contrasts with its common occurrence in Pleistocene limestones in both regions. Bleaching events related to temperature anomalies, to which acroporids are particularly sensitive, may be responsible for changes in geographic patterns of abundance of *A. palifera.* Human activities may also play a role. Another species, *Platygyra contorta*, is abundant in Pleistocene limestones on the Hyakunodai terrace of Kikai-jima, although its present-day range of high abundance is limited to the mainland of Japan. Increased abundance of this species to the south may reflect lower SSTs than present in the Pleistocene. However, at the present stage, we cannot confirm the existence of large-scale variations in species distribution without further investigations in other locations of the Ryukyu Islands. Nevertheless, this may give a first piece of evidence of the existence of mixed high-latitude and low-latitude coral populations in the Quaternary in the northern Central Ryukyus. The resulting taxonomic composition of these mixed populations may result in species assemblages that are different from those living in modern reefs.

The latitudinal attenuation of taxonomic richness characteristic of modern reefs in the Ryukyu Islands is not clearly reflected by the taxonomic census of coral taxa in the Pleistocene limestones. The latitudinal

attenuation of taxonomic richness in Pleistocene reefs may be hard to detect due to the difficulty to accurately record the number of uncommon taxa in the fossil record and taphonomic processes which prevent from identifying species assigned to common genera. Hence, latitudinal variations in the bulk taxonomic richness in the Quaternary may be very difficult to trace in the Ryukyu Islands. Specific taxa with a high preservation potential and abundant in modern reefs may be a better tool than the bulk taxonomic data to delineate latitudinal changes in distribution patterns.

Taphonomic processes affect coral assemblages at various scales. Morphological and microstructural characteristics influence the preservation state of corals. Branching colonies have a greater chance to be entirely dissolved during the process of meteoric diagenesis than massive colonies. Conversely, faviid species are less susceptible to diagenetic alteration due to the low porosity of their skeleton, and a relatively high proportion of faviid species can be identified in the fossil record compared with the species of other families. Branching species are also exposed to breakage during storms and typhoons. However, exposed shallow reef settings may yield a higher preservation potential of *in-situ* coral framework, including branching colonies. Corals which are likely to be preserved *in situ* are not only those adapted to high energy regime, but also more fragile species inhabiting locally sheltered areas which have a chance to be buried rapidly and encrusted by coralline algae.

The quality of outcrops, the size and density of coral colonies show a wide range of variations. Therefore, when the taxonomic richness of reef-slope assemblages is plotted against the size of quadrats, the resulting dots show a large dispersion. Conversely, the relation between the taxonomic richness and the number of *in-situ* corals is much more linear. In addition, the number of species and genera increases more slowly in deeper reef environments as the number of *in-situ* corals becomes larger, which may reflects the higher homogeneity in taxonomic composition of deeper reef-slope assemblages. Consequently, the number of *in-situ* corals required for an accurate description of the taxonomic composition of a fossil reef-slope assemblage needs not to be as high in deeper reef-slope settings. Another difference between shallow and deep reef-slope assemblages is the higher discrepancy between the number of species and genera in shallower reef-slope settings. This may reflects the higher diversity of faviid species with a high preservation potential living on upper to middle reef slopes. It may also be related to the shallower depth limit of many species compared with the depth range of their respective genus.

Scleractinian corals offer the possibility to compare modern communities to fossil assemblages at multiple spatial and temporal scales. Fossil assemblages reflect the complexity of modern reefs and provide a promising way to gain insight into the dynamics of coral communities in space and time. However, taphonomic biases should always be considered since ecological information is inevitably lost as a consequence of factors acting at various scales. This study highlights the great complexity of coral successions which reflect the spatial heterogeneity of shallow reef-slope assemblages and the influence of large scale environmental changes. The spatial heterogeneity of shallow-water coral communities should be taken into account in paleoenvironmental reconstructions. This is particularly important for studies based on drilled cores, in which the lateral continuity of coral assemblages cannot be easily assessed. As shown by this study, the fossil record is also very useful to understand the ecological differences between shallow and deep coral communities. This study takes the first steps towards future paleoecological studies in the Ryukyu Islands aiming to provide a better understanding of the response of high-latitude coral communities to environmental changes.

論文審査の結果の要旨

琉球列島に分布する第四紀更新世のサンゴ礁堆積物である琉球層群には造礁サンゴ化石が多く含まれ，古環境，特に古水深の指標として用いられてきた。しかし，造礁サンゴ化石群集の変化を引き起こす原因として水深（海水準）の変化以外の要因が想定されるにもかかわらず，それらは十分に考察されてこなかった。

提出者は方形区法を用いて，伊良部島で40属84種，沖縄本島で35属72種，喜界島で33属65種の造礁サンゴ化石を見出した。クラスター解析により，伊良部島で4つの，沖縄本島で6つの，喜界島で4つの群集が識別され，これらの群集には，特定の環境を指示するサンゴが含まれるものと，様々な礁内環境で生育するサンゴ（cosmopolitan）から構成され，特定の環境を示さないものとが認められることが明らかにされた。方形区間の類似度のクラスター解析により，伊良部島で2つの，沖縄本島で5つの，喜界島で4つのグループが識別された。この解析では，同様の礁内環境に生息していたと思われる造礁サンゴ化石群集が複数のグループに区分される場合が認められた。これは，同一礁内環境内でも造礁サンゴ群集の組成は多様で変化に富むという“within-reef zone variability”が化石群集に反映されているためと解釈された。

次いで，提出者は造礁サンゴ化石群集の時空変化を詳細に検討した。その結果，垂直方向の変化には，新旧の群集組成の差異が，ある礁内環境から別の礁内環境へという大きな変化を示す場合と，そのような変化が認められない（推定される新旧の礁内環境が重複する）場合があることを明らかにし，前者の要因は海水準変動などの地球規模の環境変化であり，後者の要因は生物・非生物擾乱作用による地域的環境変化であるとした。また，現在の琉球列島における造礁サンゴの多様性は高緯度ほど小さくなるにもかかわらず，この傾向は更新世の造礁サンゴ化石群集では明瞭ではないことが示され，その理由として，(1) 現世サンゴ礁内の稀産属・種が，化石としてはほとんど産しないこと，(2) 現世造礁サンゴ礁内の多産属・種であっても，化石化の過程で同定に重要な形質が失われる等の理由により，造礁サンゴ化石群集の正確な属数や種数が把握し難いことが指摘された。

以上の成果は，造礁サンゴ化石を用いた古環境解析により厳密さを与え，信頼性を向上させた点で特筆すべき業績として評価され，提出者が自立して研究活動を行うに必要な高度の研究能力と学識を有することを示している。よって，Humblet Marc André 提出の博士論文は，博士（理学）の学位論文として合格と認める。