REEF CORALS OF CANTON ATOLL: I. ZOOGEOGRAPHY

by

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ABSTRACT

Over 75 species and 36 genera and subgenera of reef corals were reported during recent surveys at Canton Atoll. When combined with the new records reported at McKean Atoll, these records nearly double the number of species and genera previously reported for the Phoenix Islands. Although the Phoenix Island coral fauna is considerably more diverse than previously estimated and more diverse than reported for island groups to the east, island groups to the west show much higher coral diversities. These findings are consistent with the overall trend, previously noted by Wells (1954) and others, of a decreasing number of coral species and genera from west to east across the tropical Pacific.

Investigations also reveal that significant dissimilarities exist between the species and generic lists of Canton and adjacent islands and island groups in the Central Pacific. Although some of the apparent discontinuities in the distribution of certain corals may be artifacts resulting from variable or incomplete sampling, some are apparently real. The causes for the local suppression of certain genera and species from some islands and their abundance on others nearby are unknown but are probably related to geographic isolation or variations in the local rates of immigration and extinction of coral species.

Comparison of the Phoenix data with previously reported coral distributions in the Indian Ocean seems to support the theory that the Indo-Pacific reef coral fauna shows a homogenous distribution.

ACKNOWLEDGMENTS

We would like to thank Leo Johnson for assistance in travel and diving arrangements; members of the Canton Diving Club for diving assistance; Dr. John W. Wells, who made available previous information on Canton Atoll corals and who generously identified many of our specimens; Dr. Tom Dana for providing access to his specimens and unpublished data on McKean corals; Dr. E. C. Evans III for providing economic support and laboratory space in Hawaii; and the Hawaii Institute of Marine Biology for clerical assistance. J. G. Grovhoug, R. S. Henderson, and Dr. Stephen V. Smith also provided assistance, and Dr. David R. Stoddart offered useful information on coral distributions.

INTRODUCTION

This paper describes the hermatypic and ahermatypic corals collected at Canton Atoll during visits by the authors in 1972 and 1973. An attempt is also made to compare the Canton reef coral fauna with those of other atolls and island groups in the Central Pacific. A companion paper (Jokiel and Maragos, this report) focuses on the abundance and distribution of corals in different environments at Canton and describes the probable factors controlling coral distribution on the atoll.

The results of this study are based upon corals collected during three separate visits to Canton. Jokiel visited Canton and Hull Atolls for one week during the summer of 1972 and acquired a collection of corals from lagoon and ocean reef environments. Maragos visited Canton for four weeks in September 1973 and also collected corals from lagoon and ocean reefs. Jokiel visited Canton and obtained additional coral specimens primarily from lagoon environments during a survey by the Naval Undersea Center and the Hawaii Institute of Biology for two weeks in November–December 1973.

Previous information on corals from the Phoenix Islands was obtained from John Wells (personal communication), who collected 20 genera and subgenera of reef corals from Canton lagoon. In addition, Dana (1975) made an extensive collection of corals from McKean Atoll, also in the Phoenix group, to the west of Canton (Frontispiece).

METHODS

Nearly 100 reef sites were surveyed during the three visits. Corals were collected by scuba divers operating from small skiffs or swimming out from shore. Information on location, water depth, reef morphology, and other environmental data was recorded for each site. Comprehensive water chemistry, biological, and physical data were also collected at some of the sites during the third visit (see other papers in this report). Locations of the collecting sites are found in the companion paper (Jokiel and Maragos, this report). Additional descriptive material on Canton is found in Henderson *et al.* (this report).

Coral identification was carried out at Canton and later in Hawaii.

Collected coral samples were immersed in a dilute sodium hypochlorite (Clorox) solution for 24 hours and then cleaned and dried. Tags showing the date, location,

depth of collection, and other information were attached to each coral skeleton sample. Some of the specimens were identified using published reference reports on coral systematics. Others were identified using the reference collections of Maragos, the Bishop Museum, and the Hawaii Institute of Marine Biology. Approximately 40 of the taxonomically difficult specimens were sent to Dr. John W. Wells (Cornell University), who kindly made the identifications.

Fortunately, it was possible to compare Dana's collections from McKean with ours from Canton and Hull before this paper was written. The comparisons provided a reliable basis for comparing the coral faunas of the respective localities and determining which of the differences in the species lists were real or artificial. Because of the problems associated with growth form variation in corals, systematic descriptions are frequently unreliable at the species level (Wells, 1954). Some of the discrepancies in the species assignments made for the two collections are probably the result of differences in source material, reference material, experience, and procedures of the different taxonomists making the identifications. In particular, there were inconsistent assignments for corals of the genera *Montipora*, *Pocillopora*, and *Porites*.

RESULTS

Canton is an oblong, roughly triangular atoll having a northeast-southwest axis about 17 km long. The width of the lagoon perpendicular to the long axis averages about 4 km (Henderson *et al.*, this report). The single deep passage through the atoll is located on the leeward (western) side of the atoll. Reefs in the lagoon were well sampled for corals. Ocean reefs within 2 km of the passage were also investigated. Time and logistic constraints did not permit surveys on ocean reefs farther from the passage.

A list of the corals collected at Canton Atoll is presented in Table 7. Only a few specimens were collected from the lagoon at Hull Atoll, and none of the species was unique to Hull. The coral list includes 82 species, of which 5 are ahermatypes and 77 are hermatypes (reef corals). Of the 40 genera and subgenera of corals collected, 36 are hermatypic. Only one hermatypic species and genus collected by Wells during an earlier visit was not collected during our later visits to Canton (*Podabacia crustacea*). The new records now raise the total number of reported reef coral genera and subgenera from 20 to 36. In addition, Dana (1975) has reported 24 genera and subgenera and 51 species of reef corals from McKean Atoll, also within the Phoenix Islands. Of the McKean corals, the genera *Plesiastrea* and *Porites (Synaraea)* were not reported at Canton. Thus, the total generic diversity (that is, number of genera and subgenera per island group) of reef corals from the Phoenix Islands has been increased to at least 38.

Table 7. Species list of reef corals collected from Canton Atoll by Jokiel and Maragos.

An "M" follows the names of species also reported at McKean by Dana (1975).

Acropora conigera (Dana)

Acropora sp. cf. A. corymbosa (Lam.)

Acropora cytherea (Dana) or A. hyacinthus var. cytherea (Dana)

Acropora formosa (Dana)

Acropora sp. cf. A. hyacinthus (Dana) - M

Acropora humilis (Dana) - M

Acropora sp. cf. A. nasuta (Dana)

Acropora palifera (Lam.)

Acropora sp. cf. A. polymorpha (Brook)

Acropora reticulata (Brook)

Acropora sp. cf. A. rotumana (Gardiner)

Acropora sp. cf. A. surculosa (Dana)

Acropora syringodes (Brook)

Agariciella sp.

Agariciella ponderosa (Gardiner)

Astreopora myriophthalma (Lam.)

Coscinaraea columna (Dana)

+☆Culicia sp. cf. C. rubeola (Quoy and Gaimard)

Cyphastrea serailia (Forskaal)

+☆ Distichopora violacea (Pallas)

Echinopora lamellosa (Esper) - M

Echinophyllia aspera Ellis & Solander

Favia pallida (Dana) - M

Favia sp. cf. F. rotumana (Gardiner)

Favia speciosa (Dana)

Favia stelligera (Dana) - M

Favites abdita (Ellis & Solander) - M

Favites pentagona (Esper) - M

Fungia (Danafungia) valida Verrill

Fungia (Fungia) fungites (Linn.)

Fungia (Pleuractis) paumotensis Stutchbury

Fungia (Pleuractis) scutaria Lam. - M

Fungia (Verrillofungia) concinna Verrill - M

Goniastrea pectinata (Ehrenberg) Halomitra philippinensis Studer – M

Herpolitha limax (Esper)

Hydnophora microconos (Lam.) - M

Hydnophora rigida (Dana) - M

Leptastrea purpurea (Dana) - M

Leptastrea transversa (Klunzinger) - M

Leptoria phrygia Ellis & Solander

Leptoseris mycetoseroides Wells - M

Leptoseris scabra Vaughan

Lobophyllia costata (Dana) - M

+Millepora platyphylla Hemprich and Ehrenberg - M

Montipora socialis Bernard - M

Montipora tuberculosa (Lam.)

Montipora verrilli Vaughan - M

Montipora verrucosa (Lam.)

Pachyseris speciosa (Dana)

Table 7. (Contd)

Parahalomitra robusta (Quelch) - M. Pavona clavus (Dana) - M Pavona gigantea Verrill - M Pavona praetorta (Dana) Pavona varians Verrill - M Pavona (Pseudocolumnastraea) pollicata Wells Pavona sp. - M Platygyra lamellina Ehrenberg var. rustica (Dana) - M Platygyra sinensis (Milne-Edwards and Haime) Plerogyra sinuosa (Dana) Pocillopora damicornis (Linn.) - M Pocillopora sp. cf. P. elegans - M Pocillopora eydouxi Milne-Edwards and Haime - M Pocillopora meandrina Dana - M? Pocillopora molokensis Vaughan Pocillopora verrucosa (Ellis and Solander) - M Podabacia crustacea (Pallas) Porites brighami Vaughan Porites sp. cf. P. ceylon Bernard or abnormal P. lichen (Dana) Porites lichen Dana – M Porites lobata Dana – M Porites lutea Milne-Edwards and Haime - M Porites pukoensis Vaughan Porites superfusa Gardiner - M Psammocora (Plesioseris) profundacella Gardiner Psammocora contigua (Esper) Psammocora nierstraszi Van der Horst - M Psammocora (Stephanaria) stellata Verrill +\times Stylaster sp. cf. S. elegans Verrill ☆ Tubastraea coccinea Lesson ☆ Tubastraea ciphans (Dana)

Among the most frequently encountered or common species observed at Canton are Acropora formosa, Echinopora lamellosa, Favia stelligera, F. pallida, Goniastrea pectinata, Halomitra philippinensis, Herpolitha limax, Hydnophora rigida, Millepora platyphylla, * Montipora verrilli, Pavona praetorta, Pocillopora meandrina, P. damicornis, and Porites lutea. Detailed information on the abundance and distribution of these and other corals at Canton may be found in Jokiel and Maragos (this report).

Turbinaria sp. cf. T. irregularis Bernard - M

[☆] Ahermatypes +Hydrozoan corals

^{*}There appears to be a complete growth-form series within the genus Millepora, between forms which could be described as M. platyphylla and M. tenera. This gradation is recognized at Canton, but all of the specimens of this genus are here included under the single name M. platyphylla.

DISCUSSION

Comparison of the Canton and McKean Coral Faunas

Dana's (1975) species list of reef corals from McKean includes 19 species which are absent from the Canton list (Table 8). This discrepancy principally appears to represent taxonomic vagaries rather than real differences. Comparisons of the actual specimens collected from both locations revealed that only eight of the McKean species were probably not reported from Canton (see footnotes, Table 8). In contrast, 41 of the 77 Canton reef coral species were not reported at McKean (Table 7). Table 9 lists 38 genera and subgenera from Canton and McKean; 2 of those genera are restricted to McKean, 15 are restricted to

Table 8. Reef coral species from McKean Atoll which were not reported from Canton or Hull Atolls.

Data from Dana (1975).

Acropora cymbicyathus (Brook) A. variabilis (Klunzinger) Cyphastrea microphthalma (Lamarck) Millepora murrayi Quelch1 Montipora aequi-tuberculata Bernard² M. granulata Bernard² M. informis Bernard M. venosa (Ehrenberg) Pavona clivosa Verrill3 P. minuta Wells P. (Polyastra) sp.4 Plesiastrea versipora (Lamarck) Platygyra daedalea (Ellis & Solander)5 Pocillopora elegans Dana⁶ P. setchelli Hoffmeister 7 Porites australiensis Vaughan8 P. fragosa Dana8 P. solida (Forskaal)8 P. (Synaraea) hawaiiensis Vaughan

¹We identified this form from Canton as a ramose variety of M. platyphylla.

²We identified all tuberculate *Montipora* from Canton as *M. verrilli* and thus this form may exist at Canton.

³We identified this form of Pavona from Canton as P. clavus.

⁴We identified this form of *Pavona* from Canton as *Pavona* sp.

⁵We identified this form of *Platygyra* from Canton as *P. lamellina*.

⁶We identified similar forms from Canton as P. meandrina or P. eydouxi.

⁷We identified all robust cespitose *Pocillopora* from Canton as *P. damicornis*, and thus this form may exist at Canton.

⁸We identified this form of *Porites* from Canton as *P. lobata*.

Canton, and 21 are found at both locations. If it is assumed that both atolls were equally sampled for corals, then these data indicate the McKean fauna to be considerably less diverse than those at Canton. The differences seem surprising, as McKean is located only 350 km to the west of Canton.

Table 9. Existing and new generic records of reef corals from Canton and McKean, Phoenix Islands. (Subgenera are in parentheses).

Existing	New
Acropora	+Agariciella
+Astreopora	+Coscinaraea
Cyphastrea	Favia
+(Danafungia)	Favites
Echinopora	+(Fungia)
+Echinophyllia	(Pleuractis)
+Goniastrea	(Verrillofungia)
Halomitra	+Leptoria
+Herpolitha	Leptoseris
Hydnophora	+Pachyseris
Leptastrea	Parahalomitra
Lobophyllia	++Plesiastrea
Millepora	+(Pseudocolumnastraea)
Montipora	+Plerogyra
Pavona	+(Plesioseris)
Platygyra	+(Stephanaria)
Pocillopora	++(Synaraea)
+Podabacia	Turbinaria
Porites	
Psammocora	

⁺⁺Recorded from McKean only (Dana, 1975).

The most likely causes of the lower diversity at McKean Atoll are geographic isolation and limitation both in amount and diversity of habitat. McKean is isolated from other islands of the Phoenix group. In addition, McKean is smaller than Canton and lacks a lagoon. Thus, potential coral colonizers may reach McKean in fewer numbers from nearby islands and would find proportionally fewer habitats in which to reside. Of the abundant species of Canton which are also present on McKean, only about half are also abundant at McKean. This further indicates potentially divergent colonization, extinction, and developmental patterns for coral communities on the two atolls. Dana (personal communication) also indicated that the sampling effort at McKean was only about one-third that of Canton. This may have, in part, contributed to the smaller number of recorded species from McKean.

⁺Recorded from Canton only (Wells, unpublished; this report).

Comparison of the Coral Faunas of the Phoenix and Other Central Pacific Island Groups

The Phoenix Islands are relatively isolated from other island groups in the Central Pacific, several of which have been well sampled for reef corals. Canton Atoll is the northernmost of the eight Phoenix Islands; the island group covers a 300 × 500 km section in the central equatorial Pacific (Frontispiece). Enderbury, the nearest atoll to Canton, is located about 75 km to the southwest. Howland and Baker atolls are outliers northwest of the Phoenix Islands. The Phoenix Islands lie approximately 1600 km southwest of the Line Islands, 3500 km southwest of Hawaii, 2500 km northwest of the Cook Islands and French Polynesia, 600 km north of the Tokelaus, 1200 km north of Samoa, 1000 km northeast of the Ellice Islands, 1200 km east-southeast of the Gilberts and 2200 km southeast of the Marshall Islands. There are also a number of isolated islands within 1500 km of Canton, including Swains, Nassau, Jarvis, and Danger Islands.

At least 85 species and 38 genera and subgenera of reef corals have now been reported from the Phoenix Islands, if our list is combined with those of Dana (1975) and Wells (unpublished). Recent studies in reef coral zoogeography are usually based on the distribution of genera and subgenera (Wells, 1954; Rosen, 1971; and other studies), because species may be inconsistently assigned.

Despite the augmented generic diversities for the Phoenix coral fauna, adequately sampled island groups to the northwest, west, and southwest show even higher generic diversities. For example, well over 50 genera and subgenera are now reported from the Marshall, Samoa, Fiji, and other groups (Wells, 1954; Stehli and Wells, 1971; and others). Although the Ellice Islands (including Funafuti Atoll and Rotuma Island) have only been superficially examined for corals (Gardiner, 1898; Whitelegge, 1898; and Finckh, 1904), at least six important genera (*Heliopora, Stylophora, Euphyllia, Symphyllia, Acanthastrea*, and *Oxypora*) present in that atoll group are apparently absent from the Phoenix Islands. Of special significance is the geological and ecological importance of the blue coral *Heliopora* at Funafuti (Finckh, 1904) and its absence from reefs in the Phoenix Islands.

Generic coral diversities are generally lower for island groups to the east of the Phoenix Islands. For example, only 14 genera and subgenera are present in Hawaii (Maragos, in press), and 35 have been reported in the Line Islands (Maragos, 1974). Generic diversities are still lower for island groups in the eastern Pacific (Stehli and Wells, 1971; Glynn *et al.*, 1972). These findings are consistent with the generally recognized trend, as discussed by Wells (1954) and others, of decreasing generic diversity from west to east across tropical oceans.

The studies of Stehli and Wells (1971) and Rosen (1971) provide convincing evidence for a positive correlation between seawater temperatures and generic diversities of corals. It seems safe to conclude that temperature conditions play an important role in controlling generic diversities on a broad oceanic scale, but may be less important at smaller distances, where differences in temperature conditions between adjacent island groups may not be significant. Other factors which may explain the greater diversities in the Western Pacific are the greater concentration of island groups (with a corresponding increase in the amount and diversity of habitat) and the predominant pattern of tropical ocean currents flowing from east to west (which would retain larvae in the western tropical Pacific or carry them westward).

Distributional Discontinuities of Some Genera

Although the total number of genera and subgenera generally decreases from west to east, the geographic distributions of particular genera are commonly discontinuous. Previous distributional discontinuities of reef corals were reported for certain coral genera among atolls of the Line Islands by Maragos (1974).

The Phoenix and Line Islands are relatively close to one another and exhibit similar generic diversities for corals, but the similarities are obscured because a number of the genera are not common to both regions. Future intensified field surveys may result in the discovery of some of the missing or rare genera but will not explain why some genera approach dominance at one locality, yet are insignificant at the other. For example, the genera *Stylophora*, *Plesiastrea*, and *Merulina* are very common at Fanning Atoll (Line Islands) but are not reported at Canton. Also, a dominant genus, *Astreopora*, at Fanning was only rarely observed at Canton. Conversely, the genera *Goniastrea*, *Halomitra*, and *Echinopora* are abundant on Canton but absent from Fanning.

It is of interest to note that some of these genera from one locality occupy habitats similar to those genera rare or absent at the other locality. Encrusting patches of *Merulina* were commonly noted growing in the shade under ledges in Fanning lagoon, while *Goniastrea* assumed a similar form in similar environments at Canton. Ramose colonies of *Stylophora* commonly occupy shallow lagoon reef flat habitats at Fanning, while finely ramose *Millepora* colonies dominate similar environments at Canton.

It is also interesting to note that an analogous form, ramose *Porites* (*P. compressa*), is generally the dominant form found in similar environments in Hawaii, a low diversity area; yet no species of ramose *Porites* has been reported from Canton or Fanning, which have much higher generic diversities. However, a ramose species of *Porites* (*P. andrewsi*) occurs commonly in Samoa, which lies adjacent to the Phoenix Islands to the south. Dr. David Stoddart

(personal communication) has also observed similar apparent distributional discontinuities of certain corals in his Pacific coral studies. He also remarked on the presence of the commonly distributed coral *Manicina areolata* in Honduras and Florida and its absence or scarcity nearby at Grand Cayman in the Atlantic. Stoddart has also pointed out that the anonymous review (later attributed to Henry Holland) of Darwin's (1842) book on coral reefs dealt in part with the problem of the presence or absence of coral reefs in certain ocean provinces.

The observed distributional discontinuities do not appear to be confined to corals of certain forms or taxonomic types. Otherwise, it could be concluded that these corals might show reduced larval dispersal potential and have colonized only some of the islands within specific coral ocean provinces.

Geographic isolation barriers, including large distances between adjacent islands, may inhibit the effective dispersal of many corals. Thus the sequence of species and genera that are successfully established over given time intervals may be determined by chance. If colonization rates are slow and incomplete for corals at certain isolated islands, then the process may be reflected as distributional discontinuities between these islands. If it is assumed that the colonization process has occurred continuously during the long tenure of scleractinian reef corals on Indo-Pacific reefs, then it would seem surprising that the discontinuities should still persist. Perhaps colonization and elimination of coral species and genera at specific islands are occurring simultaneously and at a sufficiently rapid rate to explain the observed distributional discontinuities.* Perhaps the colonization process cannot be assumed to have occurred without interruption over long geological time intervals and that periodic events, such as the ice ages, may have eliminated forms, requiring a renewal of the developmental colonization of coral communities at specific islands.

Sea level, temperature, and other factors associated with the late Pleistocene ice age may have resulted in the extinction of many coral genera and species at Canton so that recolonization may still be incomplete due to insufficient time. It is relevant to note that Smith and Jokiel (this report) postulate that the present Canton lagoon community reefs became established since the last glacial recession. Similarly, Ladd (1973) concluded that reefs above a 70-m depth on atolls in the Marshall Islands have developed since the last glacial recession. Newell (1972) also believed that some reefs have evolved since the last glacial recession. Thurber *et al.* (1965) remarked that "A hiatus in the development of coral between 6000 and 120,000 years ago on the Pacific

^{*}MacArthur and Wilson (1967) have proposed in an elaborate theory that colonization and extinction of island organism species are innate processes of insular biogeography.

Atoll of Eniwetok implies that conditions did not permit coral growth during this period." Furthermore, Goreau (1969) speculated that "Although the geologic record indicates reefs are among the oldest continually existing communities on earth, there is considerable evidence that the modern reefs are not stable and mature communities, but are undergoing successional changes typical of youthful assemblages." These studies may support the contention that environmental conditions during glacial epochs may be disruptive enough to cause the local extinction of certain genera which may not reestablish themselves until favorable conditions return and persist long enough for coral planulae to reach and colonize the island reefs. Analysis of the paleontological histories of certain species of corals on specific reefs may help resolve the causes for the discontinuous distribution of corals.

Homogeneity of the Indian and Pacific Ocean Coral Faunas

Rosen (1971) recently classified Indo-Pacific reef coral genera and subgenera on the basis of the frequency of which they have been reported on islands in the Indian Ocean. Class I genera are those occurring in more than 50% of the observed localities; Class II genera are found at 25–50% of the localities; Class III genera are found at less than 25% of the localities. The Phoenix Islands are far removed from the Indian Ocean but are well within the Indo-Pacific Biogeographic Province, so it is of interest to apply this scheme to the genera reported in the Phoenix Islands in order to estimate the level of homogeneity betwen the two regions within the Province.

Of the 12 Class I genera listed by Rosen (Acropora, Pocillopora, Porites, Favia, Favites, Montipora, Pavona, Galaxea, Platygyra, Fungia, Cycloseris, and Stylophora), at least nine (75%) have been reported in the Phoenix Islands. Of the 25 Class II genera listed by Rosen, at least 20 (80%) have now been observed in the Phoenix Islands; Class II genera not reported are Goniopora, Seriatopora, Alveopora, Acanthastrea, and Symphyllia. Of the 40 class III genera listed by Rosen, only nine (23%) have been reported in the Phoenix Islands. The genera reported are Plerogyra, (Synaraea), (Stephanaria), Podabacia, Echinophyllia, Halomitra, Parahalomitra, Agariciella, and (Pseudocolumnastraea). The discovery of the stinging bubble coral, *Plerogyra*, at Canton is particularly significant, because its known geographic distribution has now been extended 1000 km northeastward. Thus, the majority of the genera found in the Phoenix Islands may be considered common (Class I, II) while the "missing" genera are predominantly rare types (Class III). It is of interest to note that several of the Class I and II genera not reported in the Phoenix Islands are present on adjacent island groups in the Central Pacific; some may eventually be reported after more extensive surveys in deep water are conducted at Canton and elsewhere.

These comparisons tend to substantiate Wells' (1954) and Rosen's (1971) claims that the reef coral fauna of the Indo-Pacific is relatively homogenous. Most of the widespread Indian Ocean genera were also reported at Canton, while most of the rarer Indian Ocean genera were absent. Thus the observed reduction of generic diversity of the Phoenix Islands compared to more western localities is principally the result of the suppression of genera with relatively restricted distributions. These genera may be prevented from colonizing areas further eastward because of temperature limitations, short duration of larval stages relative to dispersal times established by ocean currents, or other factors.

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