REEF CORALS OF CANTON ATOLL: II. LOCAL DISTRIBUTION

by

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and

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ABSTRACT

Although undoubtedly of great importance as reef-formers, corals occupy only a few percent of the total bottom area at Canton Atoll. Distribution and abundance of the 77 reported species of reef corals at Canton appear to be controlled largely by biological interactions (that is, competition for space) at intermediate depths on the ocean reef slope and largely by physical factors (increased salinity, sedimentation, and turbidity; decreased water motion; and possibly available nutrients) in the lagoon. Coral coverage and number of species present in the lagoon decrease with increasing distance from the single passage where lagoon water exchanges with the open ocean.

Canton is geographically isolated from atolls having extensive lagoon systems. Furthermore, exchange of lagoon water with the open ocean is confined to one passage along the atoll rim. Consequently, the lagoon fauna lacks "exclusively lagoon" species of corals. Apparently the lagoon reefs have been colonized by a few of the abundant ocean-reef species.

Widespread Indo-Pacific species belonging to the genera *Pocillopora, Acropora, Montipora,* and *Millepora* account for much of the coral coverage. In addition, several species uncommon elsewhere (including *Hydnophora rigida* and *Halomitra philippinensis*) account for an unusually large portion of the total coverage in some habitats. An abundance of fungiid species (eight genera and subgenera) is one of the most striking and unusual features of the coral fauna, along with an extensive lagoon line reef system dominated by *Millepora.*

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INTRODUCTION

The physiography of Canton Atoll, with its large enclosed lagoon water mass connected to the ocean by only one passage (Henderson *et al.*, this report), results in the formation of a strong environmental gradient ranging from the clear, turbulent open ocean to the calm, high-salinity, silt-laden waters of the back lagoon. The observed biogeochemical gradients in the water column (Smith and Jokiel, this report), gradients in fish fauna (Grovhoug and Henderson, this report), gradients in micromollusk distribution (Kay, this report), as well as other biological gradients, are reflected (and to a large extent determined) by the coral fauna. The reef corals are very conspicuous members of this ecosystem, and they have played an important structural role in the formation and maintenance of the atoll as a persistent geological feature. The interaction of the coral species present at Canton (Maragos and Jokiel, this report) with the strong gradients of physical and chemical factors has resulted in a unique and previously undescribed coral community. The purpose of this study was to describe the diversity and abundance of living reef corals in various environments at Canton Atoll and to identify, insofar as possible, the factors controlling these distributions.

METHODS

The extensive area of the atoll (approximately 50 km^2) made it necessary to employ qualitative sampling techniques to assess the overall distribution of corals, followed by detailed quantitative analysis of representative areas. Study locations are shown in Fig. 26.

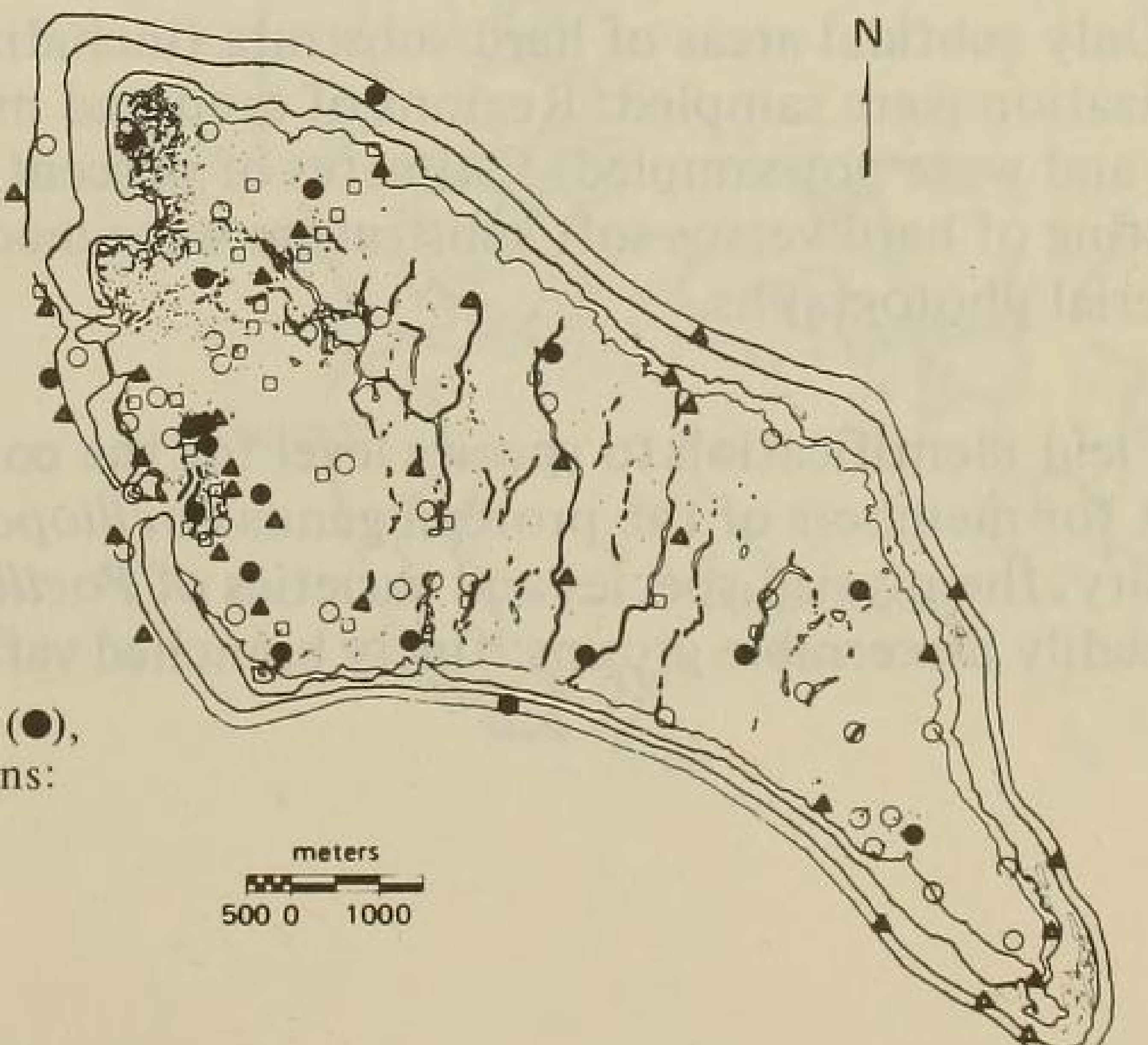


Figure 26. Coral survey stations. Qualitative inventory and specimen collections: June 1972 (●), Sept. 1973 (▲), Dec. 1973 (○). Transect locations: Sept. - Dec. 1973 (□).

Approximately 200 man-hours of field observations were devoted to the qualitative appraisal. This portion of the survey included making intensive scuba and snorkel dives throughout the lagoon and leeward ocean reefs, making observations from a glass-bottom boat, viewing the reefs with look-boxes from skiffs, making aerial observations from a low-flying helicopter, examining aerial photographs (recent to pre-World War II, on file at Bishop Museum), and consulting with members of the local Canton Diving Club. During the qualitative survey, notes were taken on the condition of the reefs. Also, samples of the various coral species encountered were collected for later taxonomic identification (Maragos and Jokiel, this report).

The quantitative survey was divided into two discrete studies: (1) an atoll-wide survey covering all types of reef environments and (2) a detailed study of structurally similar patch reefs in line with the main channel at various distances from the lagoon entrance. The atoll-wide survey was designed to include all the various reef environments; the more detailed study of patch reefs was intended to examine relationships between coral distribution and physical factors, exclusive of the complicating effects of differing reef morphology.

The atoll-wide survey was carried out by contiguous quadrat transects across representative reefs throughout the region. A 1-m^2 quadrat frame divided into 100 equal squares was laid on the bottom and used to estimate areal coverage by each species of coral to the nearest square decimeter (one-hundredth of a frame). The lower limit of measurement for the quadrat so used is 1 dm^2, or one subdivision of the frame. Corals occupying less than half of a grid square were not counted, but individual colonies were generally sufficiently large so that such a procedure apparently did not underestimate the area of significant species. If individual coral heads had been smaller, the technique could have been adapted to allow estimates of fractions of square decimeters. In general, each transect extended from the deeper limit of coral coverage on a reef structure to shallow water. The transect data were grouped into 135 samples, each consisting of five contiguous quadrats, for a total of 67,500 bits of information for later analysis.

Only subtidal areas of hard substrata (including rubble) suitable for coral colonization were sampled. Regions of sand and mud were practically devoid of corals and were not sampled. Estimates of percent coverage of lagoon bottom consisting of hard versus soft substratum were made using survey data, charts, and aerial photographs.

Field identification to species level for the common corals was not difficult except for members of the protean genus *Pocillopora.* As an operational necessity, the myriad species and varieties of *Pocillopora* were subdivided into two readily discernible groups: finely branched varieties (*Pocillopora damicornis* and homeomorphs) and coarsely branched varieties (*Pocillopora meandrina* and homeomorphs). Septal structure cannot be discerned underwater, placing *Pocillopora eydouxi* into the *P. meandrina* group.

Many of the species and their intergrading growth forms in this genus seem to be present at Canton. Large areas of *Pocillopora* could not be identified underwater in a reasonable time and (even if successful) probably would have little biological meaning due to the present taxonomic confusion of the group. As pointed out by Vaughan (1907, 1918) and Crossland (1952), specimens of numerous species of this genus can be found forming an unbroken intergrading series which might represent growth forms of one or only a few true biological species. It was therefore difficult to justify any other field identification procedure. Only a few readily discernible species of *Acropora, Porites,* and *Montipora* were common at Canton, thus eliminating the potential taxonomic problems presented by these diverse genera and simplifying sampling problems.

During the course of the lagoon survey, it became apparent that a strong gradient in coral cover (from about 50% to 0% in 3 km) exists along the main ship channel. This area was therefore chosen for a more detailed study. Two ship navigation range markers were chosen for the alignment of eight transect stations that constituted the "range transect" (Fig. 27). Station 1 was located at the edge of the shallow reef flat on the northeastern lagoon side of the atoll rim. The other seven stations were located on patch reefs selected to be as similar to one another as possible in size and morphology, thus minimizing biological differences due to specific reef morphology. Most of these patch reef structures exhibit the basic shape of a truncated cone: steep sides and flat circular tops which are 10–20 m across and which reach to within 0.5 to 1.0 m of the surface at low tide.

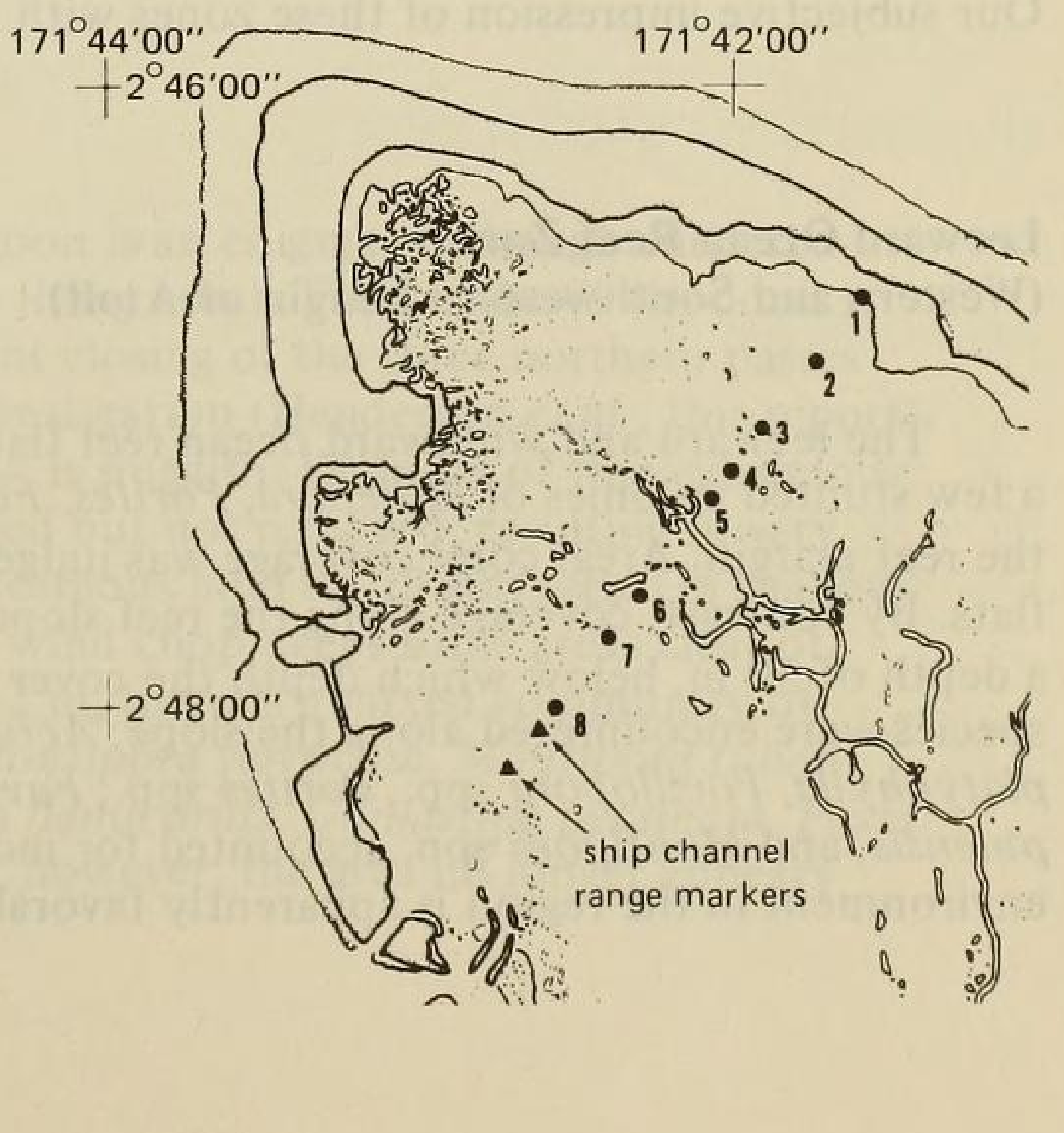


Figure 27. Coral, water chemistry and substratum stations along the range transect.

Sediment quantity and quality varied along the transect and appeared to be important environmental parameters. At each station, divers collected sediment samples from various depths for later analysis. Maximum depth of living coral coverage, coral genera present on the patch reef, and maximum depth of the surrounding area were also recorded. The patch reefs selected were small enough to allow sampling across virtually the entire extent of living coral (hard substrata) by a point-line method. Coral coverage was estimated by point-sampling along a 21-m line marked with lead weights at 0.5-m intervals. The lines were laid across the reef top and down the slope to the edge of the living coral zone. This process was repeated at least six times at each station (252 points), giving good spatial sampling of the entire patch reef.

Size analyses of the sediment were carried out according to standard settling techniques (Folk, 1974). Percent aragonite and percent magnesium in calcite were determined by x-ray diffraction by means of calibration curves from Smith (1970).

QUALITATIVE ANALYSIS

During qualitative appraisal of the atoll (Henderson *et al.*, this report), four major intergrading lagoon biotic provinces were recognized; the present analysis includes a fifth province, the leeward ocean reef in the vicinity of the pass (Frontispiece). This zonation scheme is based on the variety of information available, including assessment of the macrobiotic and physiochemical data. Our subjective impression of these zones with respect to corals is as follows:

Leeward Ocean Reef Zone (Western and Southwestern Margin of Atoll)

The leeward and windward ocean reef flats are devoid of coral, except for a few stunted colonies of *Millepora, Porites, Favia,* and *Pocillopora,* mostly near the reef margin. Areal coral coverage was judged to be less than 0.1% on the reef flats. By contrast, coverage along the reef slope is high (approximately 50%) to a depth of 30 m, below which depth the cover decreases. A large number of coral species were encountered along the slope; *Acropora formosa, Millepora platyphylla, Pocillopora* spp., *Porites* spp., *Favia stelligera, Halomitra philippinensis*, and *Montipora* spp. accounted for most of the cover. The physical environment in the region is apparently favorable for the development of a rich coral fauna. Water clarity is high, water motion and circulation strong, sedimentation rate low; and suitable hard substratum is available for coral settlement.

Pass Zone

This zone consists of the lagoon area within 2 km of the inlet and is characterized by coral knolls, pinnacles, and patch reefs which rise from the relatively shallow (5–15 m) lagoon floor. Except during slack tide, the reefs near the pass are subjected to strong and reversing currents of up to several meters per second; the currents are generated by tidal exchange between the ocean and the enclosed lagoon. The floor of the main channel consists of current-scoured cobble and little living coral. Farther inside the pass, water motion prevents the buildup of fine sediments on available hard substrata, but not the accumulation of shifting sand on the lagoon floor. Many coral species are present; *Acropora formosa, Pocillopora* spp., *Hydnophora rigida*, and *Millepora platyphylla* account for most of the coral cover. One of the most striking aspects for the coral community is the abundance of Fungiidae, including four species of *Fungia* (mostly *Fungia* (*Verrillofungia*) *concinna*), *Herpolitha limax*, and *Halomitra philippinensis*. A specimen of the coral *Podabacia* has also been collected in this region of the lagoon (Wells, personal communication). Areas near the pass dredged 35 years before this survey (for example, the turning basin) have become recolonized by corals (mostly *Pocillopora*). By contrast, lagoon areas farther from the pass (the dredged seaplane runways) do not show signs of recovery. The Pass Zone includes the two most beautiful and diverse lagoon reefs, known locally as Coral Gardens and Thornet Reef (Frontispiece).

Altered Zone

The northwest portion of the lagoon is an enigma. Although cluttered with reef structures, the area has little living coral. The demise of the coral is probably related to the relatively recent closing of the three northern passes approximately 35 years before this investigation (Henderson *et al.*, this report). Presently, water exchange in the region is sluggish. Deposits of fine calcareous sediment are apparently being generated but not removed, resulting in very turbid water and accumulations of calcareous mud on all surfaces. On shallow patch reefs, water motion induced by wind chop keeps some areas clear of sediment. In depths shallower than 1–2 m, there is a mixed community of sediment-tolerant species, including *Montipora verrucosa, Montipora tuberculosa, Acropora formosa, Pocillopora damicornis, Goniastrea pectinata, Favia speciosa,* and *Porites lutea.* In general, however, the area no longer appears suitable for coral reef development.

Line Reef Zone

Most of the central lagoon is characterized by linear reef formations dominated by highly branched *Millepora platyphylla*. On the line reefs, the *Millepora* fits Morton's (1974) growth form classification "*Millepora* 1." Corals are present only on the shallow crests of the reefs. Little or no coral is found below depths of 2–3 m. In the deeper water between the line reefs, the lack of water motion and the constant deposition of sediments apparently prevent coral colonization and growth. On the shallow reef flats, water motion is enhanced by small wind-driven waves and tide-induced currents which flow over the dam-like line reefs. This water motion probably promotes the development of fairly high coral coverage localized on the line reef shallows.

Back Lagoon Zone

The southeast portion of the lagoon and the intertidal flats along the north and south margins of the lagoon are typified by extensive deposits of carbonate mud and by a general lack of reef structures. Living corals are present but are quite rare; coverage is low (less than 0.1%). The coral fauna consists of heads of *Favia speciosa, Goniastrea pectinata, Porites lutea, Favia stelligera, Pocillopora damicornis*, and *Millepora platyphylla*.

One of the most conspicuous features of the lagoon coral community is that the maximum depth where living corals are found decreases with increasing distance from the pass. Near the pass, living coral can be found to the maximum depth of the lagoon. In the Line Reef, Altered, and Back Lagoon Zones coral growth is generally restricted to depths of less than 2–3 m.

QUANTITATIVE ANALYSIS

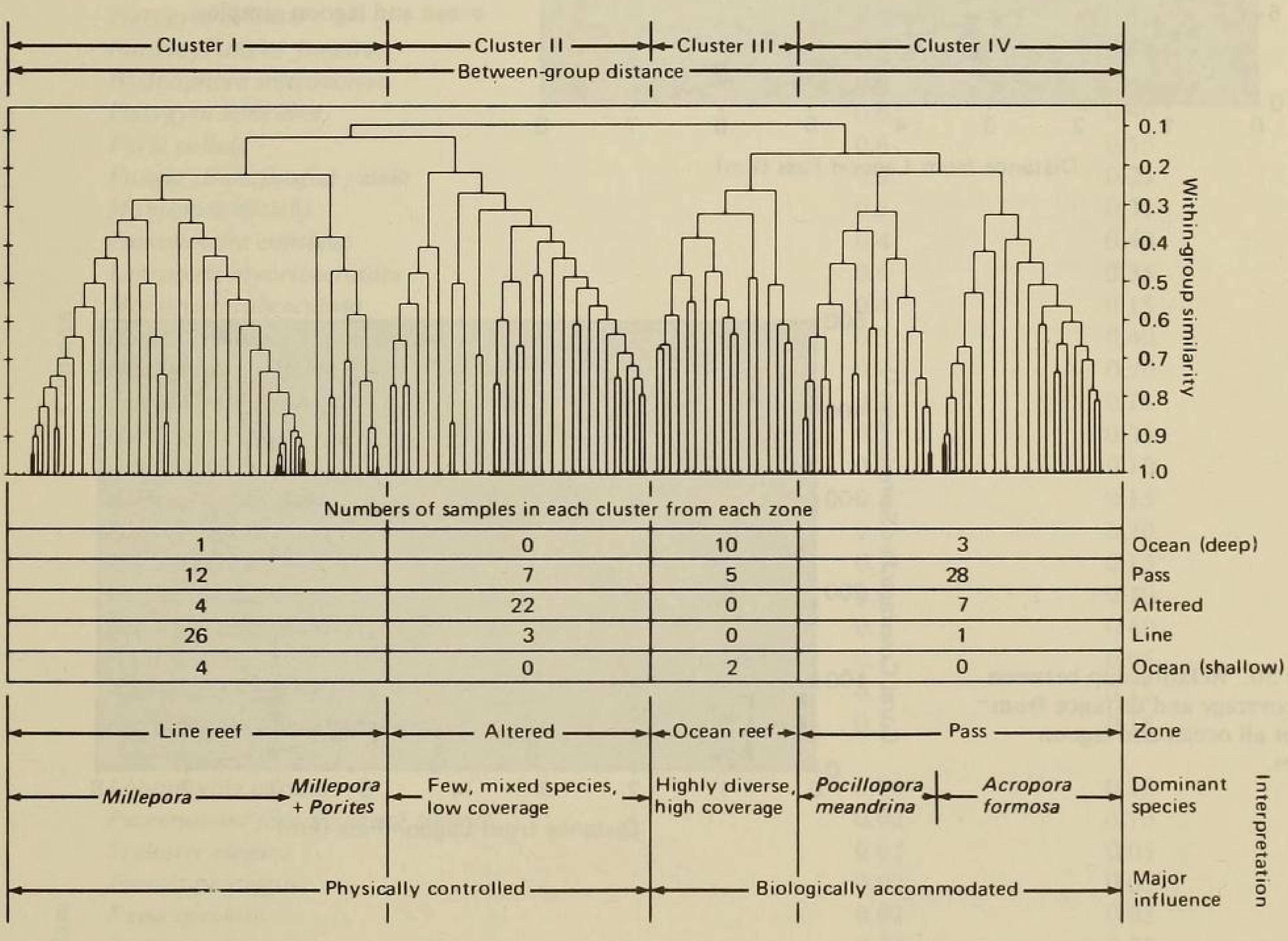
Atoll-Wide Survey

Similarity indices (I) were computed for all sample pairs by using a quantitative modification (Motyka *et al.*, 1950) of the Sϕrensen Similarity Index (Sϕrensen, 1948); this modification is described by the formula:

$$I = \frac{2M_W}{M_A + M_B} \qquad (13)$$

where M_B is the sum of the smaller abundance values of each species encountered in the sample pair AB; M_A is the sum of the abundance values of each species in sample A; and M_B is the sum of the abundance values of each species in sample B.

The resulting similarity matrix is reduced (after the technique of McCammon, 1968; McCammon and Wenninger, 1970) to the dendrograph shown as Fig. 28. The distance between any two adjacent samples on the horizontal axis of the dendrograph is proportional to their dissimilarity. Similarity within groups or clusters is represented as distance along the vertical scale. Major clusters corresponding to four of the zones previously described are apparent and are indicated on the figure.



Cluster I	Cluster II	Cluster III	Cluster IV	
1	0	10	3	Ocean (deep)
12	7	5	28	Pass
4	22	0	7	Altered
26	3	0	1	Line
4	0	2	0	Ocean (shallow)

Figure 28. Dendrograph based on Sørenson's Similarity Indices computed for all sample pairs.

The number of coral species encountered per sample and the coverage by living coral are plotted in Fig. 29 and 30, respectively, against distance from the lagoon pass. Samples taken outside of the lagoon on the leeward ocean reef are assigned a distance of 0, because they represent an environment free from any lagoon effect and serve as the baseline for comparison with the lagoon.

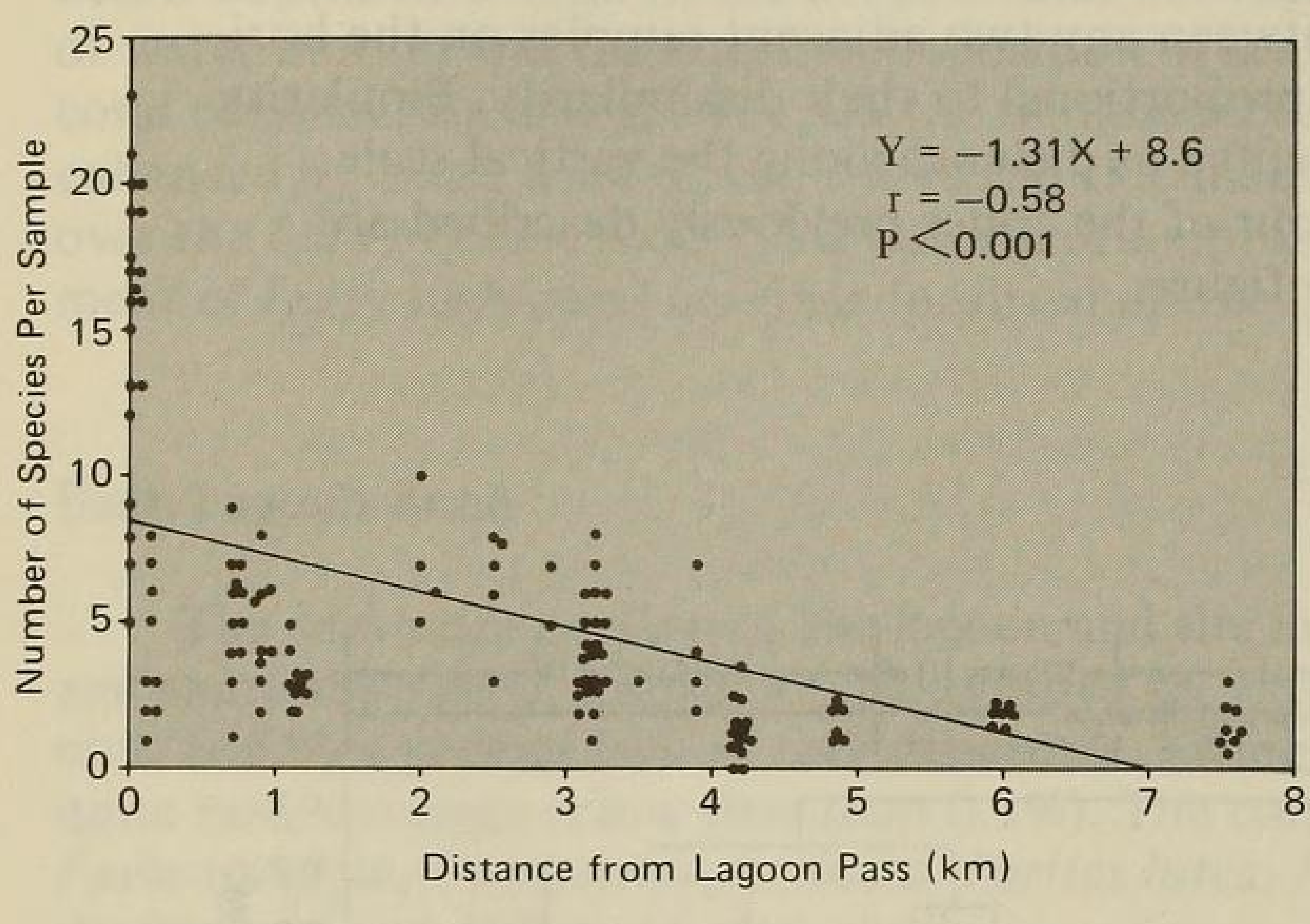


Figure 29. Relationship between number of coral species per sample and distance from pass for all ocean and lagoon samples.

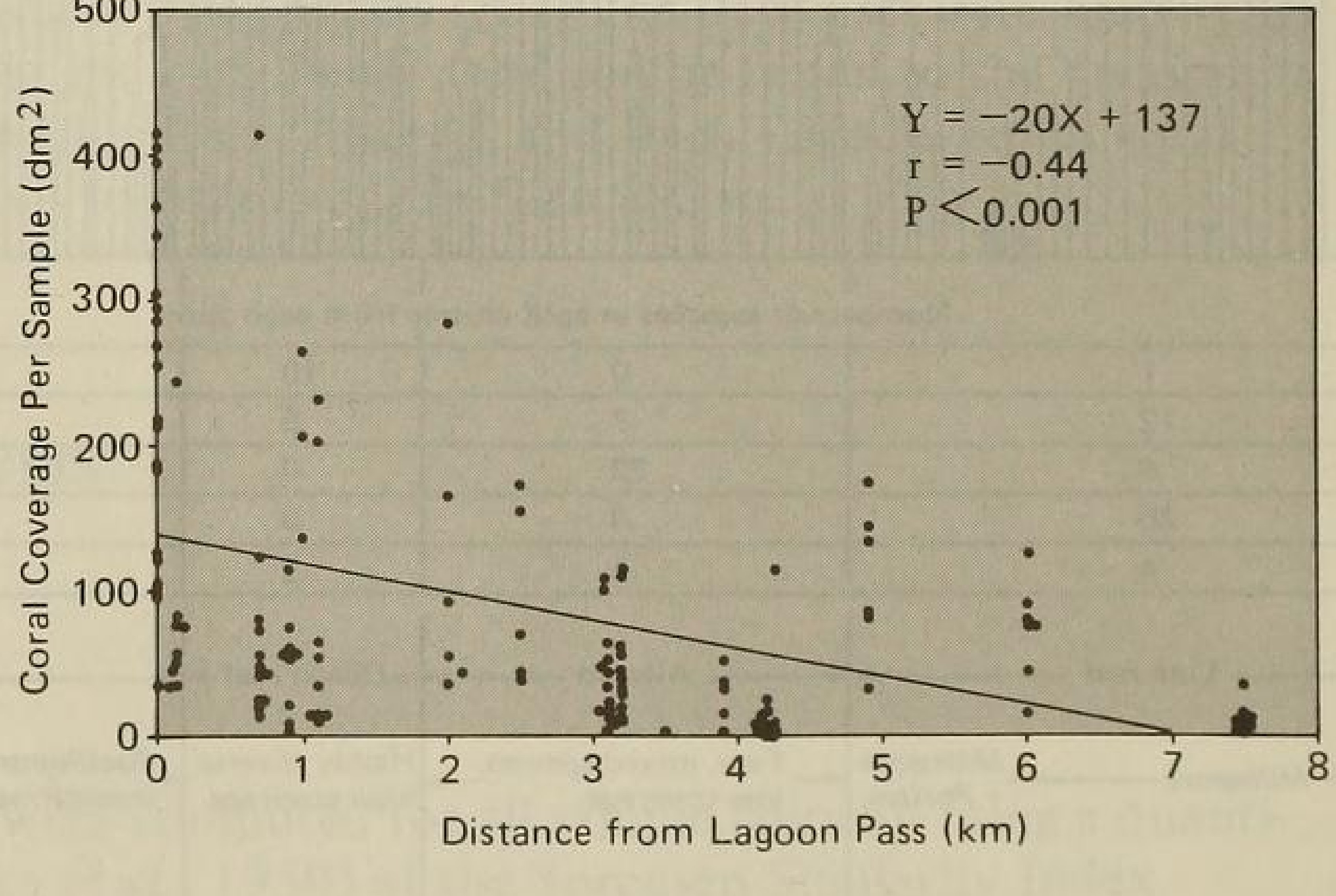


Figure 30. Relationship between coral coverage and distance from pass for all ocean and lagoon samples.

Results of the similarity analysis support the validity of the previously established qualitative zonation (Frontispiece) and justify the discussion of coral abundance according to zone. Percent cover and frequency of occurrence in each 5-m^2 sample from each zone are presented in Tables 10–14. Based on

Table 10. Ocean reef slope samples (20 stations).

	Species	Percent coverage	Frequency of occurrence
Abundant	*Pocillopora meandrina* and homeomorphs	5.8	0.85
	Montipora verrilli	4.8	0.70
	Millepora platyphylla	4.2	0.35
	Halomitra philippinensis	4.1	0.60
	Favia stelligera	4.1	0.85
	Echinopora lamellosa	3.7	0.80
	Pavona varians	3.0	0.90
	Leptastrea purpurea	2.8	0.75
	Acropora formosa	2.6	0.60
	Porites lobata	1.6	0.45
	Hydnophora rigida	1.2	0.40
	Pavona clavus	1.2	0.50
Common	*Platygyra sinensis*	0.8	0.55
	Fungia (Fungia) fungites	0.8	0.40
	Hydnophora microconos	0.6	0.40
	Platygyra lamellina	0.6	0.40
	Favia pallida	0.6	0.55
	Fungia (Danafungia) valida	0.5	0.25
	Montipora socialis	0.5	0.35
	Psammocora contigua	0.4	0.40
	Leptoseris mycetoseroides	0.4	0.35
	Montipora tuberculosa	0.4	0.15
	Fungia (Pleuractis) paumotensis	0.3	0.40
	Goniastrea pectinata	0.2	0.50
	Parahalomitra robusta	0.2	0.15
	Herpolitha limax	0.2	0.35
	Acropora humilis	0.2	0.10
	Acropora reticulata	0.2	0.15
	Pavona gigantea	0.1	0.20
	Favites abdita	0.1	0.15
	Cyphastrea serailia	0.1	0.10
	Pavona (Pseudocolumnastraea) pollicata	0.1	0.40
	Porites lichen	0.1	0.05
	Agariciella ponderosa	0.1	0.15
	Psammocora (Plesioseris) profundacella	0.1	0.15
Rare	*Lobophyllia costata*	0.04	0.15
	Psammocora (Stephanaria) stellata	0.02	0.10
	Stylaster elegans	0.02	0.05
	Favites pentagona	0.02	0.05
	Favia speciosa	0.02	0.05
	Porites pukoensis	0.02	0.05
	Porites brighami	0.001	0.05
	Astreopora myriophthalma	0.001	0.05
	Acropora palifera	0.001	0.05
	Echinophyllia aspera	0.001	0.05
	Porites superfusa	0.001	0.05

Table 11. Pass Zone samples (52 stations).

	Species	Percent coverage	Frequency of occurrence
Abundant	*Acropora formosa*	4.4	0.35
	Pocillopora meandrina and homeomorphs	3.7	0.56
	Hydnophora rigida	2.3	0.27
	Millepora platyphylla	1.1	0.27
Common	*Halomitra philippinensis*	0.8	0.40
	Fungia (Verrillofungia) concinna	0.7	0.44
	Pocillopora damicornis and homeomorphs	0.6	0.46
	Echinopora lamellosa	0.6	0.31
	Montipora verrilli	0.5	0.31
	Pavona praetorta	0.5	0.23
	Montipora tuberculosa	0.3	0.27
	Goniastrea pectinata	0.3	0.19
	Favia speciosa	0.2	0.23
	Leptastrea purpurea	0.1	0.11
	Montipora verrucosa	0.1	0.04
	Acropora syringodes	0.1	0.04
	Favia stelligera	0.1	0.10
	Porites lutea	0.1	0.02
	Herpolitha limax	0.1	0.08
Rare	*Pavona varians*	0.04	0.06
	Cyphastrea serailia	0.04	0.04
	Pavona gigantea	0.02	0.04
	Agariciella ponderosa	0.02	0.04
	Hydnophora microconos	0.02	0.04
	Acropora reticulata	0.02	0.02

Table 12. Altered Zone samples (33 stations).

	Species	Percent coverage	Frequency of occurrence
Abundant	*Montipora verrucosa*	1.4	0.39
	Acropora formosa	1.2	0.18
	Goniastrea pectinata	1.1	0.51
Common	*Pocillopora damicornis* and homeomorphs	0.7	0.55
	Acropora conigera	0.5	0.09
	Favia speciosa	0.5	0.51
	Porites lutea	0.3	0.12
	Cyphastrea serailia	0.2	0.27
	Echinopora lamellosa	0.1	0.39
	Fungia (Verrillofungia) concinna	0.1	0.21
Rare	*Favia stelligera*	0.04	0.06
	Hydnophora rigida	0.04	0.03
	Montipora tuberculosa	0.02	0.03
	Halomitra philippinensis	0.02	0.03

Table 13. Line Reef Zone samples (30 stations).

	Species	Percent coverage	Frequency of occurrence
Abundant	*Millepora platyphylla*	10.1	0.73
	Porites lutea	1.4	0.53
Common	*Goniastrea pectinata*	0.2	0.13
	Favia speciosa	0.1	0.17
Rare	*Favia stelligera*	0.04	0.03
	Psammocora (Stephanaria) stellata	0.01	0.07
	Pocillopora damicornis and homeomorphs	0.01	0.07
	Montipora tuberculosa	0.01	0.03
	Cyphastrea serailia	0.006	0.03
	Montipora verrucosa	0.006	0.03
	Echinopora lamellosa	0.006	0.03

Table 14. Very rare species.
(Collected at Canton Atoll but not found in quantitative samples.)

Acropora nasuta
Acropora polymorpha
Acropora surculosa
Acropora hyacinthus
Acropora cytherea
Acropora rotumana
Agariciella sp.
Coscinaraea columna
Distichopora violacea
Favia rotumana
Fungia (Pleuractis) scutaria
Leptastrea transversa
Leptoria phrygia
Leptoseris scabra
Pachyseris speciosa
Plerogyra sinuosa
Porites ceylon
Psammocora nierstraszi
Tubastraea coccinea
Turbinaria irregularis

mean percent coverage of available hard substrata, corals are classified by powers of ten as "abundant" (greater than 1% coverage), "common" (0.1 to 1.0% coverage), or "rare" (less than 0.1% coverage). "Very rare" species (Table 14) are defined as species collected at Canton but not occuring in any quantitative sample.

Estimates of area and percent coral cover are summarized in Table 15. Areal estimates of the zones were calculated from maps and aerial photographs. Estimated percent coral coverage represents the mean of all samples taken in each particular zone. The standard errors of the means suggest that percent coverage on hard substrata has probably been estimated to well within 50% of its true value. The areal estimates for each zone were derived from the hydrographic chart of Canton and are probably more reliable than the percent cover estimate.

For the ocean reefs, most of the living reef coral was assumed to occupy a band 100 m wide, or extending from the edge of the reef flat to a depth of 40 m. Estimates given in Table 15 are probably well within a factor or two of the listed value.

Living coral coverage accounts for only 1 to 2% of the total lagoon floor. Less than 5% of the total bottom coverage (lagoon plus all ocean reefs to a depth of 40 m) is living coral. Although the ocean reef slopes occupy less than one-tenth of the lagoon area, they apparently account for 80% of the living coral on the atoll. This figure may be somewhat biased by ocean reef sampling being limited to the leeward side of the atoll.

Table 15. Estimated coral coverage on Canton Atoll.

Zone	Total substrata area (km^2)	Estimated percent coral coverage (mean plus or minus standard error)	Estimated total coral coverage (km^2)
Ocean			
Reef face (38.5 km circumference to depth of 40 m, sloping band 100 m wide)	3.9	47.0 (±5.0)	1.80
Reef flat	7.2	0.1	0.007
Total ocean	11.1	16.0	1.81
Lagoon			
Reef flat	5.9	0.1	0.006
Altered Zone			
Hard substrata	1.0	6.4 (±2.5)	0.064
Sand and mud	4.6	0	0
Line Reef Zone			
Hard substrata	1.0	11.9 (±2.0)	0.119
Sand and mud	24.6	0	0
Back Lagoon Zone			
Hard substrata	0.1	0.1	0.0001
Sand and mud	5.1	0	0
Pass Zone			
Hard substrata	2.0	16.8 (±2.3)	0.336
Sand and mud	5.3	0	0
Total lagoon	49.6	1.2	0.53
Total ocean + lagoon	60.7	3.9	2.3

Estimates of total areal coverage for each of the most important lagoon species are listed in Table 16. In the lagoon, *Acropora formosa, Millepora platyphylla, Pocillopora* spp., and *Hydnophora rigida* account for over 60% of the living coral cover; all are highly branched species which have a tissue surface many times their areal coverage. Another 20% is attributable to *Halomitra philippinensis, Fungia (Verrillofungia) concinna, Echinopora lamellosa, Porites lutea,* and *Goniastrea pectinata.*

Table 16. Total coverage by dominant lagoon corals.

Zone	Species	Total estimated areal coverage (km^2)
Pass	*Acropora formosa*	0.09
	Pocillopora meandrina and homeomorphs	0.07
	Hydnophora rigida	0.05
	Millepora platyphylla	0.02
	Halomitra philippinensis	0.02
	Fungia (Verrillofungia) concinna	0.01
	Pocillopora damicornis and homeomorphs	0.01
	Echinopora lamellosa	0.01
	All other species	0.06
Altered	*Montipora verrucosa*	0.01
	Acropora formosa	0.01
	Goniastrea pectinata	0.01
	All other species	0.03
Line Reef	*Millepora platyphylla*	0.10
	Porites lutea	0.01
	All other species	0.01
Back	None	–

NOTE:
Dominant is defined as corals covering at least 0.01 km^2.
Lagoon area is approximately 50 km^2.

The Shannon-Weaver diversity index (Shannon and Weaver, 1948) was calculated from coverage data for each sample by using the formula

$$H_c = -\sum_{i=1}^{s} P_i \ln P_i$$

where P_i is the proportion of total area coverage of species i ($i = 1, 2, \ldots s$). Diversity is plotted against distance from the pass in Fig. 31.

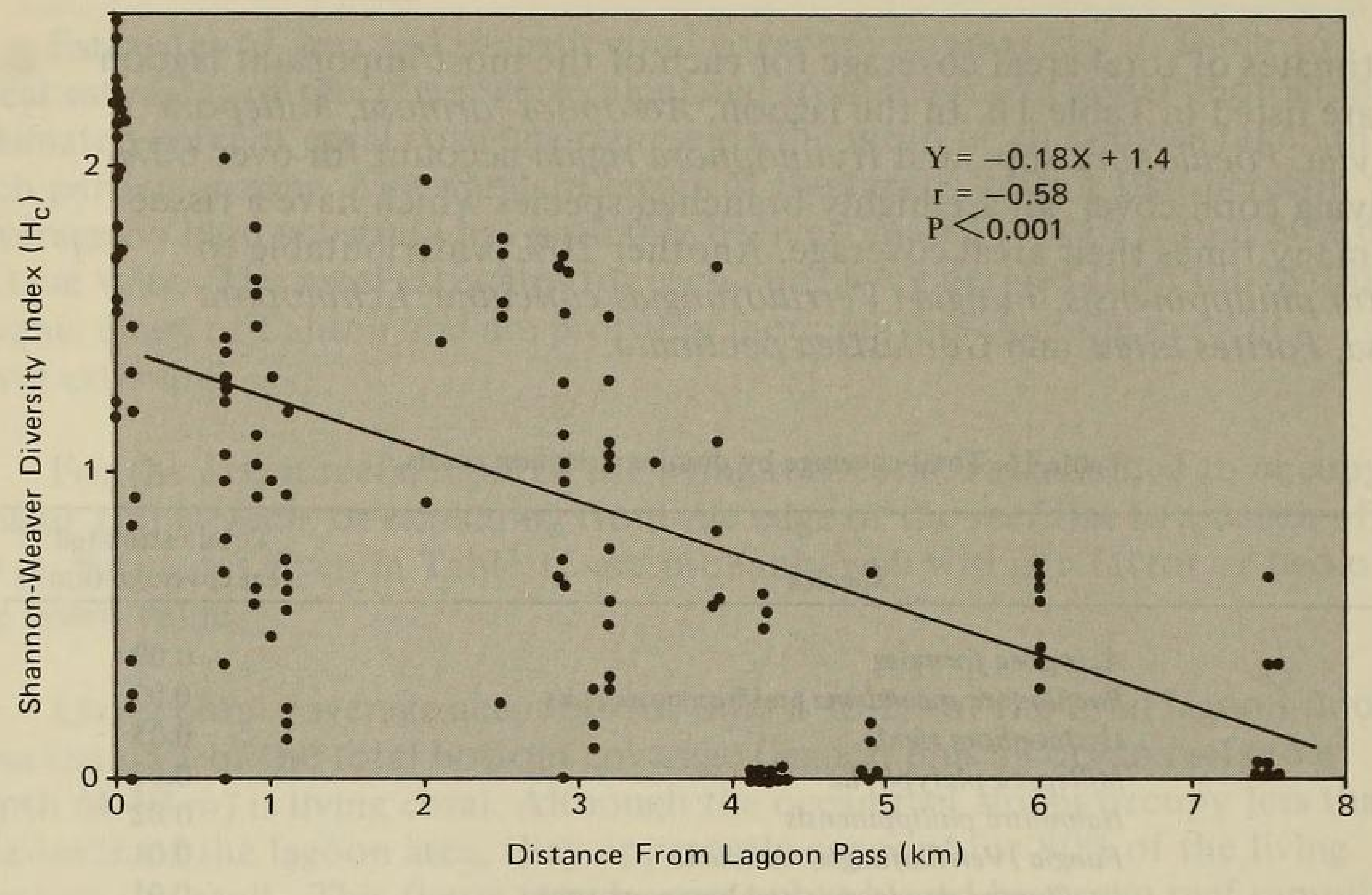


Figure 31. Relationship between Shannon-Weaver diversity index and distance from the pass.

Range Transect

The range transect demonstrates along a single, well-defined axis the general trends observed in the atoll-wide survey. Data on coral coverage, substratum type, and water chemistry are presented in Tables 17 through 19 and Fig. 32. The condition of the coral reefs deteriorates with distance from the lagoon pass. Coral coverage on suitable hard substratum (living coral zone), as well as number of coral genera present, diminishes with distance from the pass (Table 17). This decrease in total coral coverage with distance is even more pronounced than is immediately suggested by Fig. 32, because the amount of available hard substratum suitable for coral growth also diminishes with distance from the pass. All water chemistry parameters undergo obvious changes, and these may indicate increasingly unfavorable conditions for coral growth (Table 19). Inorganic plant nutrients (especially nitrate and phosphate) and specific alkalinity decrease, while salinity increases.

Sediments become progressively finer with both distance from the pass and water depth (Fig. 32 and Table 18). Two mechanisms of sediment dispersal control this pattern: tidal currents and wind-induced waves. Sediment suspension and removal is effected by tidal currents that are greatest near the pass and diminish with increasing distance from this region. Wind-induced waves exert their maximum influence at the sea surface, sweeping fine sediments from the shallow areas into deeper water.

Analysis of the chemical composition of the sediments (Tables 18 and 19) demonstrates that 80–90% of the sedimentary material is aragonite; most of this probably derived from coral skeletons, because other common aragonitic organisms (for example, mollusks and green algae) did not appear sufficiently common to account for a significant amount of this material.

Table 17. Coral and substrata along range transect.

Station	Distance from Lagoon Pass (km)	Number of coral genera encountered	% Coverage living coral on hard substrata	Maximum depth (m)	Lower limit of living coral (m)	*Acropora*	*Cyphastrea*	*Echinopora*	*Echinophyllia*	*Favia*	*Fungia*	*Goniastrea*	*Halomitra*	*Herpolitha*	*Hydnophora*	*Leptastrea*	*Leptoseris*	*Lobophyllia*	*Millepora*	*Montipora*	*Pavona*	*Platygyra*	*Pocillopora*	*Porites*
1	4.7	0	0	5	0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	4.3	3	1	5	1	–	X	–	–	X	–	–	–	–	–	–	–	–	–	–	–	–	X	–
3	3.8	8	23.0	5	1.5	X	–	X	–	X	X	X	–	–	–	–	–	–	X	–	–	–	X	X
4	3.6	12	29.6	5	2	X	X	X	–	X	X	X	X	–	–	–	–	–	X	X	–	X	X	X
5	3.3	9	29.7	5	2	X	X	X	–	X	X	X	–	–	–	–	–	–	–	X	–	–	X	X
6	2.9	12	43.2	5	2.5	X	X	X	–	X	X	X	X	–	–	–	–	–	X	X	–	X	X	X
7	2.2	13	34.6	10	10	X	X	X	–	X	X	X	X	–	X	–	–	–	–	X	X	X	X	X
8	1.5	19	48.6	10	10	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X	X

Table 18. Sediment composition along range transect.

Station	Distance from Lagoon Pass (km)	Sediment median grain size (mm)			% Aragonite			% Mg substitution for Ca in calcite fraction		
		depth (m)								
		1	3–5	10	1	3–5	10	1	3–5	10
1	4.7	0.111	0.037	–	72	70	–	13	12	–
2	4.3	0.146	0.070	–	88	76	–	13	13	–
3	3.8	0.152	0.137	–	88	89	–	16	16	–
4	3.4	*	0.162	–	*	84	–	*	15	–
5	3.3	*	0.164	–	*	83	–	*	13	–
6	2.9	*	0.283	–	*	93	–	*	16	–
7	2.2	*	0.278	0.322	*	85	61	*	13	9
8	1.5	*	*	*	*	76	77	*	13	11

*Hard substrata (rubble and cemented reef rock).

Table 19. Water quality along range transect. (From smoothed water quality distribution maps in Smith and Jokiel, this report)

Station	Distance from Lagoon Pass (km)	Salinity (°/oo)	Specific Alkalinity	NO_3-N (μg at/liter)	NH_3-N (μg at/liter)	PO_4-P (μg at/liter)
1	4.7	37.7	0.116	0.6	0.72	0.12
2	4.3	37.7	0.116	0.7	0.60	0.13
3	3.8	37.7	0.118	0.8	0.48	0.14
4	3.4	37.2	0.119	0.9	0.36	0.15
5	3.3	37.0	0.120	1.0	0.36	0.15
6	2.9	37.0	0.120	1.1	0.34	0.23
7	2.2	36.5	0.123	1.3	0.40	0.35
8	1.5	36.0	0.124	2.0	0.50	0.48

DISCUSSION

Similarity Analysis and Dendrograph

The dendrograph produced from Sørensen Similarity Indices (Fig. 28) has four clusters which correspond to the zones identified during the qualitative survey (Frontispiece). Cluster I consists mainly of samples from the Line Reef Zone, along with a few samples from shallow locations in other zones. Samples in this cluster are characterized by high coverage of *Millepora* and represent physically harsh environments with high water motion and extreme levels of solar radiation. Many of the samples are from areas exposed during low tide and subjected to altered salinity or elevated temperature or both. Cluster I may be subdivided into two subclusters: the smaller subcluster represents a mixed *Millepora–Porites* association found in the Line Reef Zone, near the back lagoon; the larger cluster consists of samples dominated by *Millepora* alone. Most of the shallow samples (depth less than 6 m) from the Leeward Ocean Reef Zone are in Cluster I.

Cluster II consists almost entirely of samples from the Altered Zone. These samples are characterized by low coverage with various species of sediment-resistant corals, none of which is clearly dominant.

Cluster III consists almost entirely of samples from the Leeward Ocean Reef Zone, but the cluster also includes a few of the richest Pass Zone samples from Coral Gardens. All samples in this group are characterized by high coverage and high diversity.

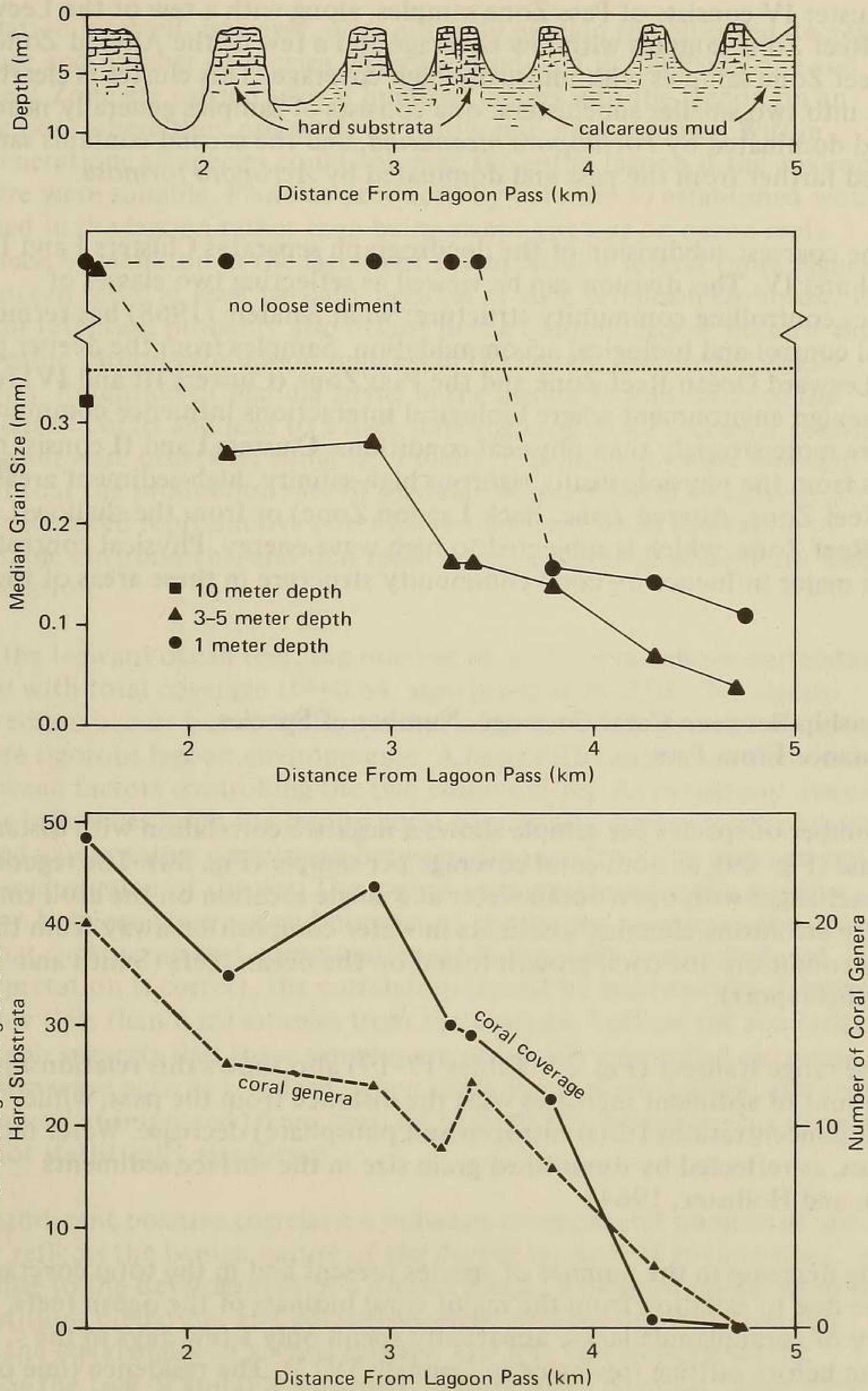


Figure 32. Relationship between various parameters along range transect.

Cluster IV consists of Pass Zone samples, along with a few of the Leeward Ocean Reef Zone samples with low coverage and a few of the Altered Zone and Line Reef Zone samples with unusually high coverage. This cluster is clearly divided into two smaller subclusters: one consists of samples generally near the pass and dominated by *Pocillopora meandrina*, and the second contains samples collected farther from the pass and dominated by *Acropora formosa*.

The coarsest subdivision of the dendrograph separates Clusters I and II from III and IV. This division can be viewed as reflecting two classes of processes controlling community structure: what Sanders (1968) has termed physical control and biological accommodation. Samples from the deeper part of the Leeward Ocean Reef Zone and the Pass Zone (Clusters III and IV) represent a benign environment where biological interactions influence community structure more strongly than physical conditions. Clusters I and II consist of samples from the physiologically rigorous high-salinity, high-sediment areas (Line Reef Zone, Altered Zone, Back Lagoon Zone) or from the shallow Leeward Ocean Reef Zone, which is subjected to high wave energy. Physical control exerts a major influence on coral community structure in these areas of the atoll.

Relationship Between Coral Coverage, Number of Species, and Distance From Pass

Number of species per sample shows a negative correlation with distance from pass (Fig. 29), as does coral coverage per sample (Fig. 30). The lagoon water exchanges with open ocean water at a single location on the atoll rim, and there are strong chemical gradients in water composition away from the optimal conditions for coral growth found on the ocean reefs (Smith and Jokiel, this report).

The range transect (Fig. 32, Tables 17–19) also shows this relationship. The amount of sediment increases with the distance from the pass, while nutrient concentrations (total nitrogen and phosphate) decrease. Water motion decreases, as reflected by diminished grain size in the surface sediments (Heezen and Hollister, 1964).

The decrease in the number of species present and in the total coverage could be due to isolation from the major coral biomass of the ocean reefs. The majority of coral planula larvae apparently spend only a few days in the plankton before settling (reviewed in Connell, 1973). The residence time of water in the back lagoon is nearly 100 days (Smith and Jokiel, this report). Therefore, planulae produced in the rich ocean reefs probably are not able to colonize the back lagoon directly.

Isolation by itself, however, does not fully explain the observed decrease in coverage and number of species. Planulae produced in the Pass Zone and Ocean Reef Zone are carried several hundred meters into the lagoon on an incoming tide, where they can settle and grow into new colonies. Within several generations all species could colonize the entire lagoon if the environment there were suitable. Planulae produced by colonies so established would be retained in the lagoon rather than being swept away as on ocean reefs. The biomass of plankton in the lagoon of Bikini Atoll is several times higher than on ocean reefs, at least partially because of such retention (Johnson, 1954). Significant retention probably also occurs in the Canton lagoon, because much of the organic carbon production remains in the lagoon (Smith and Jokiel, this report). Retention of planula larvae in the lagoon should enhance the recruitment of corals and lead to a high standing crop of all species if conditions in the lagoon were otherwise suitable. Finally, it is implicit in the isolation argument that the production rate of planulae decreases with distance from the pass. Reduced reproductive potential would itself be an indication of an unsuitable environment, and that reduction is a factor in addition to simple simple isolation.

On the leeward ocean reef, the number of species per sample correlates positively with total coverage ($r=+0.64$, significant at $P<0.01$). No significant correction occurs between the number of species and coverage for samples from more rigorous lagoon environments. A basic difference must therefore exist between factors controlling the two communities. As previously discussed, the major influences upon the lagoon coral community appear to be physical, manifested as a negative correlation between distance from the pass and both coverage and number of species. The logical interpretation for the positive correlation between coverage and number of species per sample on the ocean reefs is that such ocean reef communities are biologically accommodated. If this interpretation is correct, the correlation should be improved by deleting the shallow (less than 6 m) samples from the analysis, because the similarity dendrograph suggests that these samples are physically controlled (scouring by intensive wave activity). Indeed, when these samples are deleted, the correlation is somewhat improved (from $r=+0.64$ to $r=+0.82$); however, this improvement is not statistically significant.

A significant positive correlation between coverage and number of species probably reflects the benign nature of the deeper ocean reef environment, in turn leading to the development of a diverse fauna. Biological interactions such as competition, predation, and parasitism shape community structure and promote the coexistence of several species. The ultimate limiting factor probably is the lack of suitable substrata. The primary physical factor controlling substrata (and hence coverage and species diversity) appears to be the breaking of large waves, especially the infrequent storm waves, against the reef. Local residents informed us that such storms generally approach the atoll from the west. Large dikes have been built along the western shoreline to prevent wave damage to the western (populated) portion of the atoll. Large storm waves can remove living corals and redistribute unconsolidated material on the reef, thereby producing the observed community structure. Maragos (1974a,b) reached similar conclusions about wave control of coral communities at Fanning Atoll.

Outcrops of well-lithified reef rock are more stable with respect to wave activity than is loose debris. These outcrops thus develop a high-diversity, high-coverage "climax" community. Generally, areas of reef rock outcrops have a much steeper slope than adjacent rubble areas. Unconsolidated rubble is unable to hold an angle of repose steeper than about 30 degrees in calm water and probably a much lower angle under storm conditions. Undoubtedly material. shifts downslope during periods of high waves. Although nearly all substrata on the ocean reef appear suitable for coral colonization, the materials differ widely in degree of stability and frequency of disruption.

The dendrograph further suggests that the Leeward Ocean Reef Zone and Pass Zone could be combined on the basis of the major factor controlling community structure (that is, biological accommodation), while the Line Reef Zone and Altered Zone could be combined on the basis of physical control. Combining all samples from the Leeward Ocean Reef Zone with all samples taken in the Pass Zone produces a positive correlation ($r = +0.65$, $P<0.001$) between the number of species present per sample and the distance from the pass. These correlations suggest that both biological and physical controls on the community are operating in the Leeward Ocean Reef and Pass Zones. By contrast, combining all stations from the Line Reef Zone with those from the Altered Zone produces no significant correlation between coverage and number of species present per sample, but does produce a negative correlation ($r=-0.48$, $P<0.001$) between coverage and distance from pass. This pattern of correlations probably indicates physical control of the coral communities in these provinces. Species unsuited to the increasingly harsh conditions are eliminated.

Coral Coverage, Shannon–Weaver Diversity Index, and Distance From Pass

The Shannon–Weaver diversity index for all ocean stations correlates positively with total coverage ($r = +0.46$, significant at $P<0.05$), as does diversity of the 14 deep (greater than 6 m) ocean stations ($r = +0.50$, $P<0.05$). Lagoon stations show no correlation between diversity and coverage ($r = +0.05$, P not significant), but show a negative correlation ($r = -0.43$, significant at $P<0.001$) between diversity and distance from the pass. As mentioned previously, the dendrograph of similarity indices suggests that Leeward Ocean Reef Zone stations and Pass Zone stations cluster together (biological accommodation) and that Altered Zone and Line Reef Zone stations from a second cluster (physical control). Diversity for all Leeward Ocean Reef Zone stations combined with all Pass Zone stations correlates positively with total coverage ($r = +0.35$, significant at $P<0.001$). This relationship does not hold for the remaining Line Reef and Altered Zone stations ($r = +0.14$, P not significant). For these stations, diversity correlates negatively with distance from pass ($r = -0.41$, $P<0.001$) and probably reflects physical control with increasingly harsh environmental conditions.

Origin of the Lagoon Fauna

The windward ocean reefs were not sampled, but the data in Table 10 are representative of at least the leeward reefs. The most important lagoon species (Table 16) also are among the most important leeward ocean reef corals; the differences apparently result from the decrease in the number of species with the increased distance from the pass. The faunal similarity between ocean and lagoon presents a striking contrast to the Marshall and Line Islands, where dominant lagoon species differ from the dominant ocean reef species; some species are even considered to be exclusive lagoon types (Wells, 1954; Maragos, 1974b). Possibly this difference occurs because several atolls of these island groups have relatively large, open lagoons which favor the recruitment and development of distinctive lagoon coral populations. Atolls in the Phoenix Island group generally lack lagoons or have restricted exchange with the open ocean. Consequently, the Canton lagoon coral fauna probably has been derived almost entirely from the available ocean reef species.

CONCLUSIONS

The various biogeochemical gradients and processes controlling community function and structure at Canton are described by Smith and Jokiel (this report). It is apparent that poor circulation results in an increasingly isolated and physically harsh environment in the lagoon with increasing distance from the pass. As pointed out by Wells (1954), local coral distribution has long been known to be controlled primarily by light and water motion. On the ocean reefs breaking waves limit coral development in the shallows. At intermediate depths, good light penetration and vigor of circulation due to wave action result in a diverse, high-coverage coral reef community. The maximum depth to which good coral reefs can exist along the ocean margin is ultimately limited by the penetration of light and by the depth to which wave action produces sufficient water circulation.

In the shallow lagoon at Canton, light probably does not severely limit the maximum depth of coral development. The strongest environmental gradients (salinity, nutrients, tidal current, sediment) exist in the horizontal plane, and result in differences in biotic composition between the pass and back lagoon. Wind chop produces a strong vertical water motion gradient which enhances the growth of corals in the shallows. Throughout most of the lagoon (Line Reef Zone, Altered Zone, Back Lagoon Zone) living coral is rare below a depth of 2 m, even though water chemistry is uniform with depth.

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