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September 1978

ATOLL RESEARCH BULLETIN

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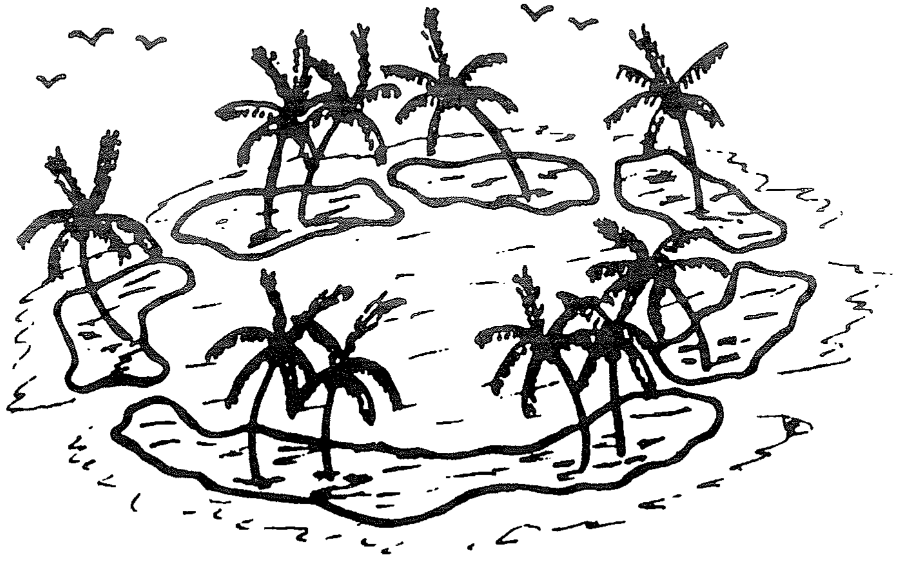
Edited by S. V. Smith and R. S. Henderson



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ACKNOWLEDGMENT

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The Bulletin was founded and the first 117 numbers issued by the Pacific Science Board, National Academy of Sciences, with financial support from the Office of Naval Research. Its pages were largely devoted to reports resulting from the Pacific Science Board's Coral Atoll Program.

This issue, containing ARB no. 221, is the first of several to appear as each is ready, dealing with the Phoenix Islands, prepared under various auspices, the field work for which has been supported logistically by the U.S. Air Force/SAMTEC. The research for this report was performed by personnel of the Marine Management Office (Naval Undersea Center, Hawaii Laboratory) and by members of the University of Hawaii. It was reproduced for internal circulation as report no. NUC TP 395. The research was funded by the Department of the Air Force, MIPR no. FY7616-74-00-202, and by Environmental Protection Agency Grant no. R800906.

CONTENTS

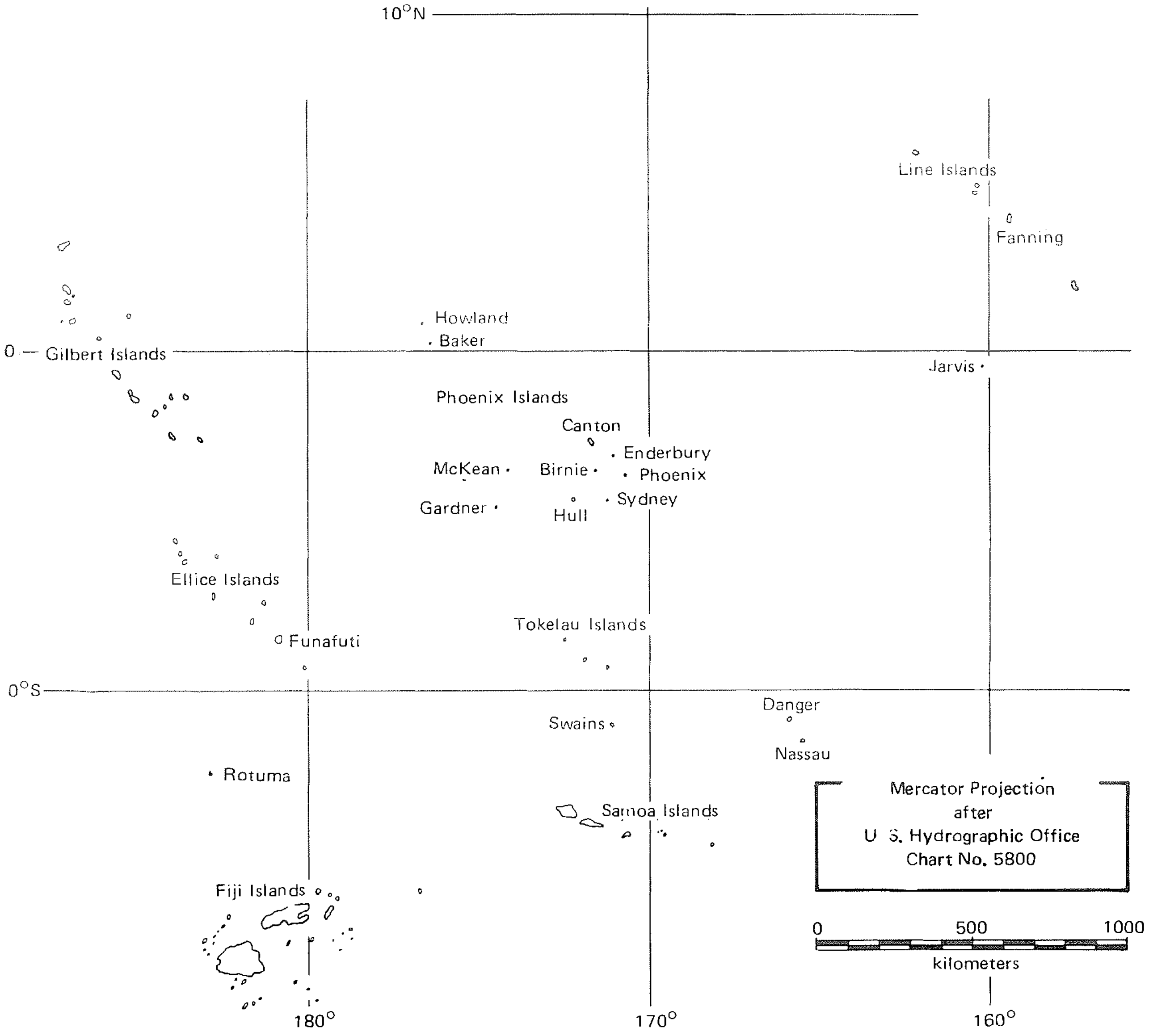
SUMMARY

Canton Atoll has a single passage between the ocean and lagoon and has conspicuous environmental gradients from that passage to the back lagoon. These gradients include the physiography of the lagoon floor, water quality, and the diversity and abundance of corals, fishes, and mollusks. The gradients can apparently be attributed either directly or indirectly to circulation and water motion within the lagoon. Those oceanographic characteristics can, in turn, be attributed to the geological history of the atoll, including some human modification of the pass configuration.

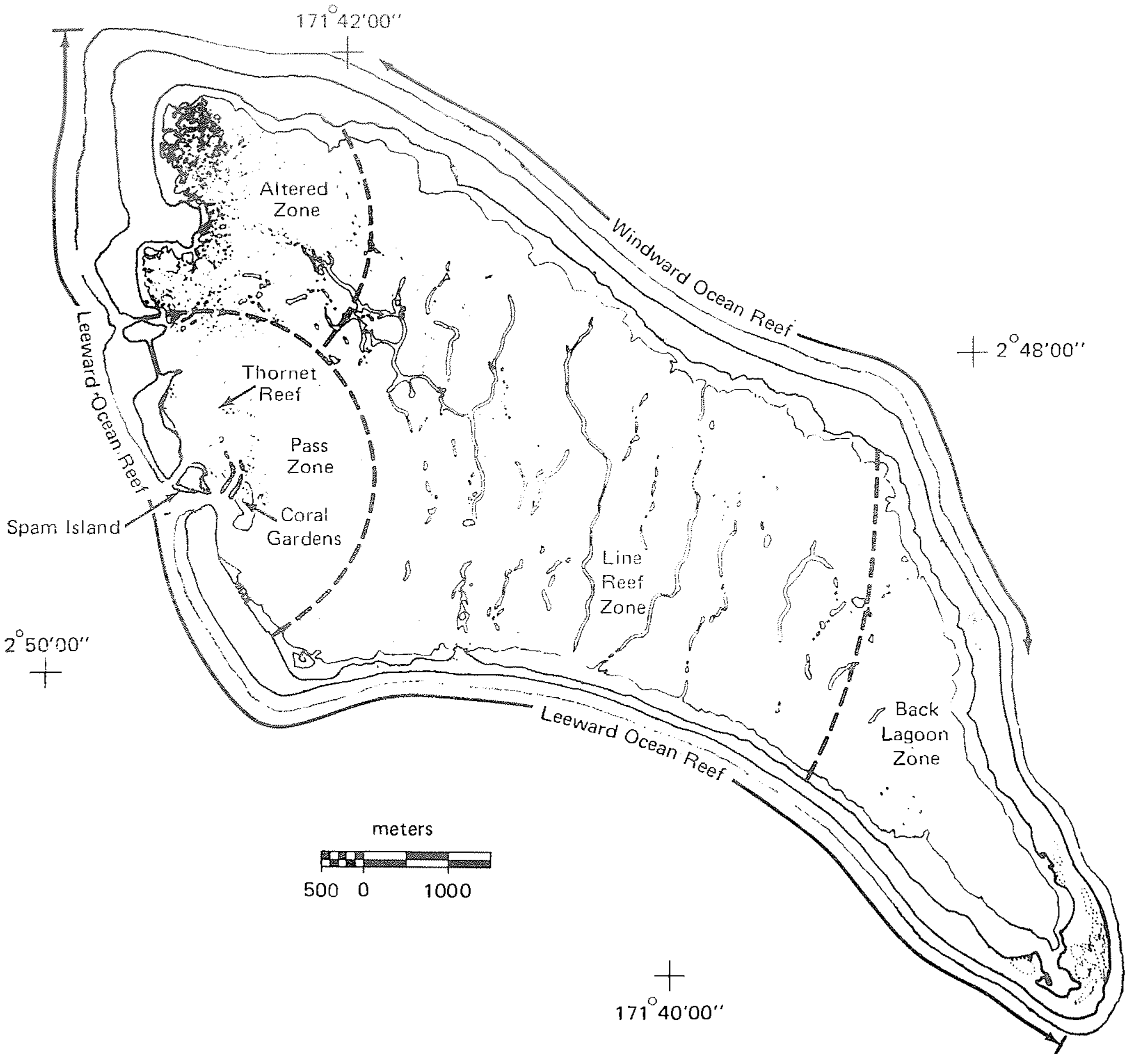
In addition to the studies of the atoll lagoon, the characteristics of the groundwater system are noted. Evidence from isolated standing water bodies on the atoll demonstrates that these features show considerable variability, which may be attributed to a combination of the immediately previous history of these bodies as well as to the physiography of the atoll

ACKNOWLEDGMENTS

Thanks are due to the many individuals who contributed to various stages of this study. In particular, thanks are due to the personnel of Canton Atoll for their hospitality and assistance. Mr. Ed Bryan, and Drs. John Wells and Tom Dana provided unpublished data. Technical assistance was provided by Dr. Don Schell, Dr. Jack Randall, Mr. Chuck Peterson, Mr. Dennis Kam, Capt. Richard Callahan, Sgt. James Cameron, Ms. Karen Klein, Ms. Joann Sinai, and Ms. Lorraine Krau.



Phoenix Islands and adjacent island groups.



Canton Atoll.

SYNOPSIS

Canton Atoll* is the largest of eight islands in the Phoenix Islands of the South Pacific Ocean (Frontispiece). The atoll has been the subject of several surveys, most of which have dealt with aspects of the terrestrial biota. The present report is, for the most part, based on a marine environmental survey conducted by the Marine Environmental Management Office (Naval Undersea Center, Hawaii Laboratory) between 27 November and 11 December 1973, at the request of the USAF Environmental Health Laboratory (Kelly Air Force Base, Texas). Scientists participating in the expedition included E. C. Evans III, J. G. Grovhoug, and R. S. Henderson (MEMO); P. L. Jokiel and E. B. Guinther (Hawaii Institute of Marine Biology, University of Hawaii); and S. V. Smith (HIMB/MEMO). Also present was C. T. Peterson (NUC), who not only provided photographic documentation but also assisted in the various scientific tasks. Additional survey information incorporated into this report includes coral observations by J. E. Maragos (HIMB) in September 1973 and both hydrographic information and coral observations by P. L. Jokiel and R. H. Callahan (USAF) in June 1972. In addition, E. A. Kay (Department of General Science, UH) has analyzed and reported on the micromollusks in sediment samples from Canton lagoon.

The primary justification for MEMO and HIMB participating in this expedition was the opportunity to collect a broad variety of biological and physiochemical data for comparing Canton Atoll with other marine environments, the ultimate goal being the development of an environmental range for the objective intercomparison of geographically separated marine environments. In keeping with such a justification, the Canton data have been stored in the Hawaii Coastal Zone Data Bank of the University of Hawaii.

This survey of the Canton Atoll lagoon was undertaken to determine the distribution of abiotic environmental variables and biotic responses to these variables. In particular, there has been an attempt to find what effects, if any, human influence has had on the atoll. As is true for most surveys of remote sites, the available data are largely restricted to a single instant in time. In view of the tremendous meteorological variations, this limited time frame of data is unfortunate. However, the relatively simple physical configuration of the lagoon, some ancillary data which were gathered before and after the major survey, and

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*The term "Canton Atoll" is officially sanctioned by the US Board on Geographic Names; the term "Canton Island" will be used throughout in reference to the main island of that atoll.

the interpretation of physiographic features in the lagoon allow far-reaching inferences to be made from this survey.

The Canton lagoon is almost landlocked, with a single pass on the western side of the atoll. Other shallower passes, also along the western side of the atoll and north of the present pass, were artificially closed during causeway construction about 1943. The area of the lagoon is about 50 km^2, and the mean depth of the lagoon is about 6 m.

The lagoon physiography and biota can be described in terms of four zones. The first of these (the Pass Zone) is within 2 km of the pass and has well-developed patch reefs and coral knolls. The second zone (Line Reef Zone) extends from 2 to 8 km from the pass and is characterized by linear reefs with fewer corals. The third zone (Back Lagoon Zone) is in the most distant, southeastern corner of the lagoon, has few reef structures and very few live corals. The fourth zone (Altered Zone) has reef structures which are physiographically similar to the Pass Zone, but has a live coral distribution which looks more like that in the Line Reef Zone. The ocean reefs of the atoll undoubtedly also show zonation (at least into windward and leeward reefs). During the present investigation virtually all examination of the ocean reefs was confined to the leeward (western and southern) portion of the atoll.

Water is exchanged between the ocean and lagoon by tidal flushing at the single pass. Flushing is most efficient near the pass; throughout the rest of the lagoon, flushing is accomplished less rapidly by tidal and wind mixing. During the time of this survey, and apparently under most conditions at Canton, there is an excess of evaporation over rainfall. Hence, salinity in the back lagoon is almost 40 o/oo, or 4 o/oo above oceanic values.

Water enters the lagoon relatively nutrient rich (about 0.6 mmole P/m^3, 3.6 mmoles N/m^3). By the time the water reaches the back lagoon, these nutrients have been depleted to near 0. Based on nutrient and CO_2 budgets, the net organic carbon production was 6 g C m^{-2} day^{-1}, and $CaCO_3$ production was 1.4 g $CaCO_3$ m^{-2} day^{-1}. All metabolic rates were highest near the pass. Most of the $CaCO_3$ produced in the lagoon remains there and contributes to lagoon in-filling. The high gross and low net organic carbon production indicate that organic products are effectively recycled by the system. Most of the net organic carbon production which does occur is lost from the lagoon.

The distribution patterns of three major groups of organisms were examined: corals, fishes, and micromollusks. A total of 82 coral species from 38 genera were found at Canton. Corals on the slope of the leeward ocean reef appear to be controlled largely by interactions among the various species. Both on the reef flats of the ocean reefs and in the lagoon, the coral distribution is apparently controlled by physical conditions. The number of species and the coral cover in the lagoon decrease with increasing distance from the pass. Some aspect of circulation, perhaps water motion, is likely to be the major variable controlling this distribution. The number of coral genera observed at Canton is consistent with the generally held idea that coral diversity decreases from west to east across the Pacific Ocean. Comparison of the Canton corals with the biota of other nearby reef areas demonstrates peculiar, and not entirely understood, discontinuities and patterns of dominance from one area to another.

Data from this survey expand the number of fish species reported from Canton Island to 264 species from 50 families. This number is consistent with similarly conducted surveys elsewhere in the Central Pacific Ocean. The fishes also show a general pattern of decreasing numbers and species with distance into the lagoon and away from the pass. As with the corals, the richest fish populations are on the reef slope outside the lagoon. Availability of suitable substrata, largely in the form of corals, is the major parameter controlling the fish distribution. The distributions of selected fish species reveal several distinctive distribution patterns. Several species may be found at any location having adequate substrata. Other groups show subtle variations but a general preference for areas of good reef development.

The third group of organisms examined during this study was the micromollusks. A total of 90 species was recorded. These could be divided into three assemblages: slope of the seaward reef, outer lagoon, and inner lagoon. The seaward reef sample has a low standing crop and high diversity, while both lagoon assemblages have higher standing crops and lower diversities. Some aspect of water composition, perhaps salinity, is postulated to be a major control in these molluscan distribution patterns. Turbidity of lagoon water and the nature of available substrata may also be major controlling variables.

There are common characteristics to all three groups of organisms. The outer reef slope on the leeward side of the atoll has a high species diversity, and competitive pressures seem likely to be the dominant influence on composition. The lagoon biota become progressively less diverse with distance from the pass. Various physical factors can be called upon to explain this diminishing diversity.

Sampling of water bodies on the atoll reveals that these features are also related to the physiography of the atoll. Standing water occurs in various low spots on the atoll, and major groups of ponded water bodies have salinities ranging from well below to well above oceanic values. These patterns must record, in part, the degree of connection between the ponds and the groundwater system of the atoll. Highest salinity values are found in the largest water bodies, which probably have a relatively slow exchange with the groundwater. Nutrient and chlorophyll levels show no such common patterns from one water body to another. It appears that the composition of each pond is sensitive to its immediately previous environmental history.

Thus, the physiography of the atoll, and therefore in large part the geological history of the atoll, exerts major control on both the biotic and abiotic characteristics of the lagoon. Man's effect on the aquatic aspects of the ecosystem can also be expressed in terms of physiography. Alteration of pass configuration along the western side of the atoll has clearly changed circulation, water composition, and biotic composition. On land, man has altered the topography and therefore the characteristics of water bodies. With local exceptions, these artificial effects have apparently been small in comparison with the natural processes of physiographic change over the past several thousand years.

CANTON ATOLL LAGOON PHYSIOGRAPHY AND GENERAL OCEANOGRAPHIC OBSERVATIONS

by

R. S. Henderson
P. L. Jokiel
S. V. Smith
J. G. Grovhoug

ABSTRACT

The four major physiographic zones of the Canton Atoll lagoon are defined as the Pass Zone, the Line Reef Zone, the Back Lagoon Zone, and the Altered Zone. Each of these zones has a characteristic physiography, biota, and water quality. The Altered Zone is noteworthy, because it appears to have originated from the degradation of other zones brought about by dredge and fill operations. There does not appear to be any other major artificial damage to the lagoon, aside from direct mechanical destruction by dredging.

The predominant aspects of lagoon circulation are wind drift and tidal flow. Although lagoon tides show a pronounced lag with respect to the ocean tides, there is no measurable amplitude attenuation from the ocean to the back lagoon.

GENERAL OBSERVATIONS

The Canton Atoll lagoon may be divided into four major physiographic zones: the Pass Zone, the Line Reef Zone, the Back Lagoon Zone, and the Altered Zone. Approximate boundaries of the zones are shown in the Frontispiece. These lagoon zones, although shown as distinctly bounded, are broadly transitional from one to another.

Within the Pass Zone, extending to approximately 2 km from the passage between the ocean and lagoon, tidal flushing is obviously the dominant factor in maintaining an environment that is rich in biota and that has nearly oceanic water quality. Patch reefs are the most common physiographic features in this zone, especially immediately east and southeast of the pass. Nearly half of the lagoon floor in this zone was dredged during the construction of seaplane runways and a ship-turning basin. Figure 1 is an air photograph showing much of the Pass Zone and part of the Line Reef Zone.

Figure 1. Oblique air photograph showing a portion of the northeastern lagoon fringing intertidal flats (foreground), linear reefs, and the apparently open-water area of the Pass Zone (background).

In the central lagoon, within a 2 to 8 km distance from the pass, line reefs extending in an approximately north–south direction or interconnected into a cellular network (Fig. 2) are the predominant features. Along the intertidal flats fringing the lagoon in the Line Reef Zone, some reef patches protrude through the sand-covered slope. The crests of these structures are kept free of sediment by relatively high-velocity tidal currents.

The Back Lagoon Zone is the zone most distant from the influence of the lagoon pass (Fig. 3). In this zone, line reefs are lacking, patch reefs are sparse, and most of the hard substratum (including much of the live coral) is covered with a thin layer of fine sediment. Tidal currents are barely discernible.

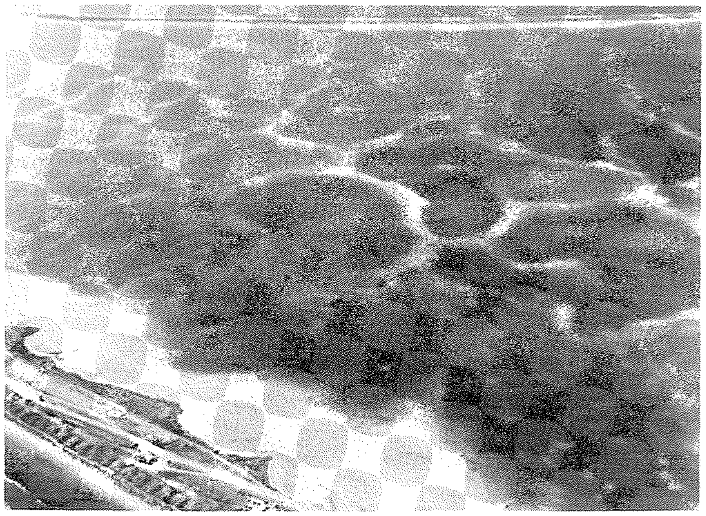

Figure 2. Oblique air photograph from the northeast, across the lagoon in the Line Reef Zone.

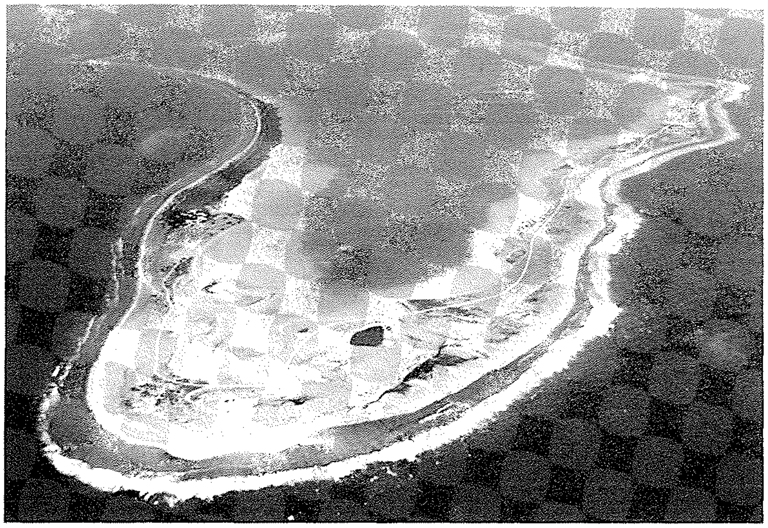

Figure 3. Oblique air photograph from the southeast, showing the Back Lagoon Zone and the edge of the Line Reef Zone.

Some reefs in the Canton Atoll lagoon show definite signs of degradation which have apparently occured recently (within the last 100 years). These changes are most obvious in the Altered Zone, located in the northwestern corner of the lagoon. Patch reefs are common in this zone, and some line reef structures occur in the southeastern portion of the area. Yet live coral is sparse on the reef and is limited to a small number of hardy species; practically all hard and soft substrata are being covered with fine sediment. At present this corner of the lagoon has poor water circulation, relatively high salinity, low nutrients, and very high turbidity. An explanation for the condition of this zone can apparently be found in human modification of the atoll physiography.

A general description of the atoll prior to 1938 has been compiled from a number of sources (field notes of and personal discussion with E. H. Bryan, Jr.; aerial photographs; and a 1938 survey of the atoll by Henslee Towill).

Before human disturbance, the Canton Atoll lagoon was connected to the open ocean by four entrances along the western side of the atoll (Fig. 4, left).

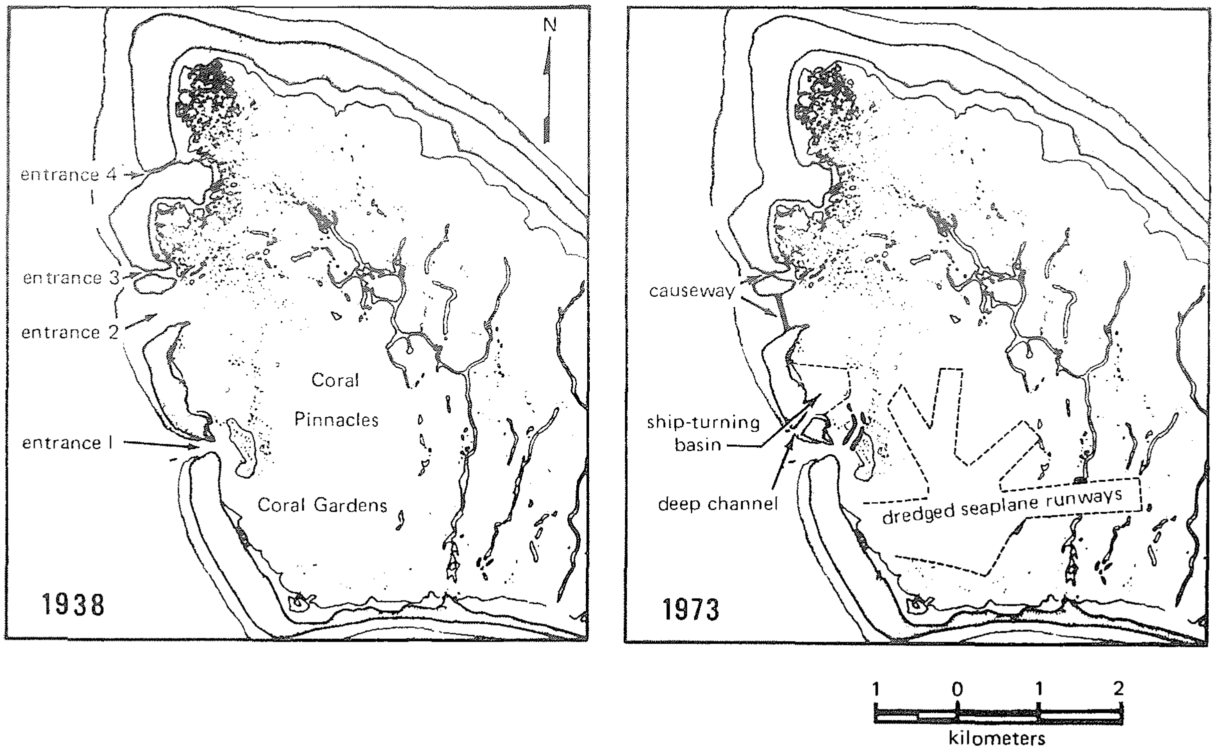

Figure 4. Configuration of the western lagoon and passes in 1938 (left) and 1973 (right).

During the early years of World War II, three of the entrances were closed by causeways, and an additional 8-meter-deep ship channel was cut through the atoll rim, leaving an isolated remnant of land now known as Spam Island, two rows of dredge spoils near the pass, and a small dredged island in mid-lagoon. Entrance 1 still exists; it was deepened in 1943 when the ship channel was dredged (Degener and Gillaspy, 1955). Spam Island, the remaining (double) pass and the dredge spoils can be seen in Fig. 1 and 4 (right).

At the present time, Entrance 1 at its narrowest and shallowest point is approximately 150 m wide and 5 m deep. In his original field notes, E. H. Bryan, Jr. (notes of Whitney South Sea Expedition of the American Museum of Natural History, March 1924; on file at Bishop Museum, Honolulu) described Entrance 1 as "60-150 yards wide, deep, blocked on inside by coral heads." Entrance 2 was "about 200 yards wide, shallow, full of rocks and coral can be easily waded)." He found Entrance 3 to be "15-40 yards wide in places knee deep, but with deeper pools." Entrance 4 was "20-50 yards wide, very long and winding, making two turns, deep in spots (up to 10-12 feet), other places shallow (knee deep)." Water seldom flowed through this pass.

The dredge probably was brought through Entrance 1, cutting the channel through the shallow (exposed at low tide) Coral Garden area. This channel is approximately 5 m deep and 100 m wide. Dredge spoils were deposited along the channels, forming long, narrow, steep-sided islands which rise to a height of over 5 m above sea level. The turning basin was cleared and the deep channel was probably dredged from the lagoon side. Later, the seaplane runways were cleared (Fig. 4, right). In terms of altered water circulation, the most significant result of the runway dredging appears to have been the breaching of the line reefs at the end of the east–west runway.

Prior to dredging, much of the water entering Entrance 1 was deflected south by the Coral Gardens Reef, and water velocity through Entrance 1 probably reached nearly 3 m/s. A smaller portion of the water was deflected north. Lush coral growth typified the entire western portion of the lagoon. The line reefs (called "cross reefs" in Bryan's 1924 notes) were characterized by what Bryan described as "masses of forked, candelabra-like, brown, sharp-tipped coral, which rises out of the water." Undoubtedly he was describing *Millepora.* He also noted the presence of "purple coral." This coral was probably *Montipora tuberculosa*, which is quite eye-catching at Canton and is still to be found on the shallow patch reefs near the pass. Bryan found the back lagoon to be comparatively free of corals, a condition which persists to present times.

Although Entrances 2, 3, and 4 were shallow and probably did not provide as high a volume exchange as Entrance 1, their presence was obviously of great importance to the flushing and circulation of the northwestern lagoon. Without these nearby sources of oceanic water, the patch reefs have ceased normal growth; the general environment of the Altered Zone is more nearly like that of the back lagoon. Closing the northern passes apparently did not reduce the total volume of tidal exchange of the lagoon, as evidenced by the tide-gauge data, which show no attenuation of tidal amplitude from the ocean to the back lagoon (Fig. 5). However, this change did greatly affect the circulation velocities and patterns of the western lagoon. Most of the lagoon environment located beyond the Pass Zone and Altered Zone areas was probably not appreciably affected by the pass modifications. The distance of most of the lagoon to the nearest pass remained unaltered because of the lagoon and pass geometry.

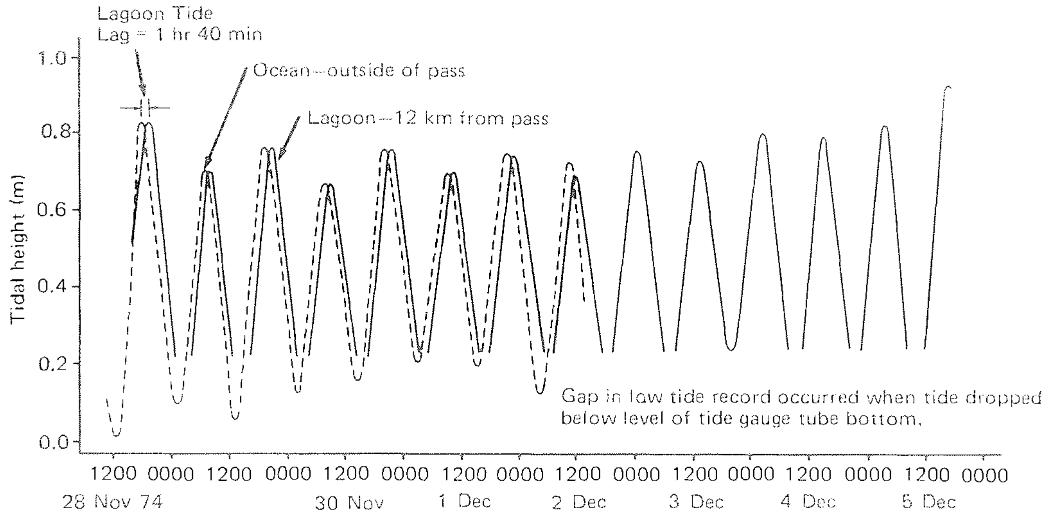

Figure 5. Tide gauge records at ocean station and lagoon station.

Deleterious effects on the marine environment, aside from the purely mechanical demolition of reef structures, are not obvious near the present passes. However, dredging of reef structures within the lagoon has had lasting impact on the circulation and water quality of the inner lagoon zones. For example, in those areas where line reef structures were removed at the eastern portion of the seaplane runway, the edges of the remaining reef are now subjected to only relatively sluggish tidal flow through the deepened channels instead of the strong, shoaling currents that previously crossed these structures. The truncated reef edges exhibit more fine sediment cover, fewer fish, and fewer live corals than undredged portions of line reefs. Thick algal mats and buoyant stringers of algae are common on much of the shallow substrata of these local altered areas.

Aside from the temporary delivery of wind-borne crushed limestone powder (and along with it, possibly ammonia and other terrestrial materials) to the land and lagoon surface of the northern edge of the atoll, no quantitatively significant input of man-made pollutant was noted at the time of this survey.

The intertidal and nearshore areas of the oceanic fringing reef are generally in good health and appear to be unaffected by water exiting the lagoon. Most of the water exiting the lagoon is of approximately oceanic composition because of relatively limited horizontal mixing in the inner lagoon. This plume of water from the lagoon is quickly diluted and dispersed by ocean currents.

Although the intertidal fringing reef flats may appear barren, these areas are important to the atoll biota because of the inconspicuous algal turf that covers most of the surface. Many cryptic organisms (for example, Foraminifera and mollusks) abound in this turf. The turf is grazed by herbivorous organisms and thus provides one of the major food sources in the food web of the reef community. Because of its intertidal location, the turf is vulnerable to pollutants floating on the water surface. Some degree of alteration is presently being imposed upon a small section of the reef flat near the sewage outfall off the northwestern shore of the island.

Two Stevens type F well-level recording devices were installed to compare tide heights and phases at an ocean station immediately outside the pass with a station in the southeastern corner of the lagoon. The locations are labelled TG1 and TG2 on Fig. 6. Figure 5 shows portions of recorder tracings from the two

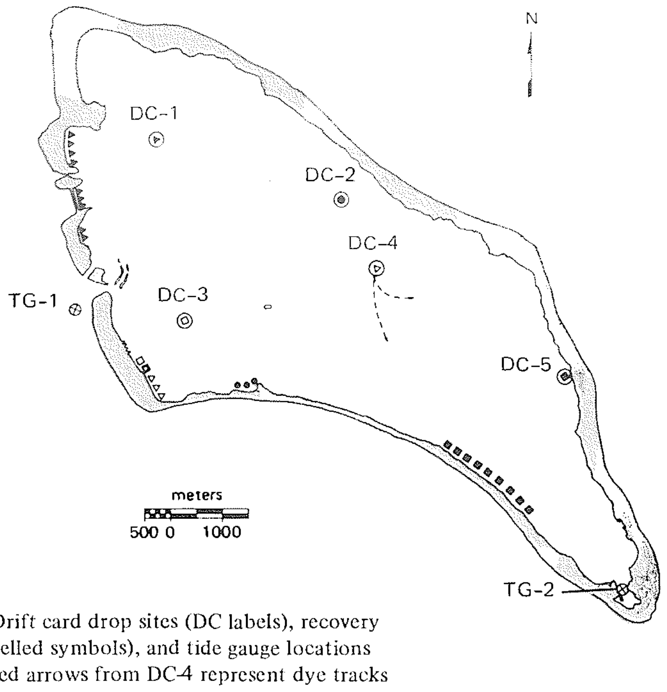

Figure 6. Drift card drop sites (DC labels), recovery sites (unlabelled symbols), and tide gauge locations (TG). Dashed arrows from DC-4 represent dye tracks from bottom-placed dye packet.

stations. There is a 100-minute time lag between the ocean and tidal extremes and those of the lagoon, but no measurable attenuation of tidal amplitude. Some detail may be lost in this tidal record, both because the lagoon gauge became exposed on some low tides and because there was a great deal of high-frequency noise in the ocean record. Nevertheless, the records fail to show the dramatic (about 50%) attenuation which Gallagher *et al.* (1971) observed at Fanning Atoll.

Relatively high-speed tidal currents occur and could be sensed by divers at most locations in the lagoon. Direction of flow is predominantly away from the pass on a rising tide and towards the pass on a falling tide. Along the lagoon shore, the flow is to or from the shoreline (but complicated there by wind drift). Tidal currents are most pronounced as subsurface currents. Dye packets anchored to the bottom or in midwater provided a qualitative impression of flow patterns. The high-speed currents at the pass are tidal, occasionally with an added wind-induced component.

Surface-water wind drift was documented at five lagoon locations by the release of drift cards (flat cardboard milk-carton tops). The release sites are shown in Fig. 6. Such cards indicate how surface, wind-driven pollutants such as oil might disperse; however, the cards reveal little or no information about the wind-driven currents immediately below the water surface. Although the cards tend to move in a general downwind direction, their pattern of movement is not simple. The cards may move some distance off the wind track to one side and then gradually shift their trajectory to another pattern relative to the wind. In some instances, the cards become entrained in small eddies. Part of this behavior undoubtedly can be explained by classical models of wind drift (Ekman currents). The interaction of the tidal currents and the reef obstructions appears to have more important influences on wind-drift patterns. For example, cards released on the upwind side of a reef, but downstream of the reef with respect to tidal flow, were seen to remain "trapped" on the upwind side of the reef even though the top of the reef was submerged by several decimeters. Apparently the tidal currents actually break the surface under these circumstances, with force on the sea surface equal to that of the wind drag.

The net direction of surface drift is ultimately downwind. As shown in Fig. 6, drift cards from all locations except DC-1 were found several days after their release along the lagoon beaches south of the pass. Cards from that single exception (DC-1) were found along the western lagoon shore north of the pass. During the survey period, the wind direction ranged from NE to E.

Incidentally, the drift cards only confirm the pattern suggested by other evidence. Specific recovery sites were sandy beaches heavily littered by flotsam and jetsam. Points or areas clear of recent sand accumulation or debris tended not to collect drift cards.

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WATER COMPOSITION AND BIOGEOCHEMICAL GRADIENTS IN THE CANTON ATOLL LAGOON*

by

S. V. Smith

and

P. L. Jokiel

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*A slightly different version of this paper has also been published in Marine Science Communications, v. 1, pp. 75-100 and 165-207, 1975.

ABSTRACT

Budgets of water, salt, nutrients, carbon dioxide, suspended material, and sediments can be used to establish the dynamics of water exchange, biogeochemical reactions, and sedimentation in the Canton Atoll lagoon.

Maximum water residence time in the lagoon is about 95 days. During that time, net evaporation raises the salinity nearly 4 o/oo above oceanic values. Phosphorus utilization in the lagoon is 0.027 mmole m^{-2} day^{-1}; nitrogen utilization is about 8.5 times this rate. Net excess organic carbon production is assumed to be 100 times the rate of phosphorus utilization (that is, about 3 mmoles m^{-2} day^{-1}, or 36 mg C m^{-2} day^{-1}). Gross production, as inferred from gas exchange between the air and water, is 6 g C m^{-2} day^{-1}. $CaCO_3$ production is 14 mmoles m^{-2} day^{-1}, or 1.4 g $CaCO_3$ m^{-2} day^{-1}. Most of the $CaCO_3$ produced in the lagoon remains there, but a substantial portion of the organic carbon produced is lost from the lagoon.

Water motion is the parameter exerting major influence on the metabolism of the lagoon biotic community. Artificial alteration of water movement patterns has changed part of that community. Neither nitrogen nor phosphorus is likely to limit metabolism of the biota. $CaCO_3$ production in the lagoon has probably been sufficient to fill the lagoon with about 20 m of sediment over the past 8,000 years. It is likely that the present episode of lagoon reef growth has been continuing for that timespan and that the $CaCO_3$ production rate has decreased substantially over that period.

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Our particular thanks to D. Schell, J. Sinai, L. Krau, and K. Klein for sample analyses; D. Kam for computer analyses; E. C. Evans III, K. E. Chave, G. S. Key, and F. R. Fosberg for manuscript review. The work at Canton Atoll could not have been undertaken without the considerable cooperation of the residents of the atoll, and of our colleagues on the expedition.

INTRODUCTION

Coral atolls have long been recognized for their variety, complexity, and fertility in the midst of an oceanic "desert." Most studies of reef systems have primarily considered their composition, with little regard for the dynamic balance of material production, utilization, and removal. Yet the ability of coral reefs to grow and maintain themselves near sea level over millenia is surely their most conspicuous attribute. This growth results from both $CaCO_3$ production and associated organic carbon metabolism by countless organisms inhabiting the coral reefs.

Calcium carbonate production by coral reefs has been estimated by several investigators over the past century (for a recent review, see Chave *et al.*, 1972). The estimates have been made for individual organisms, for portions of reefs, and for entire reef systems. Some recent studies have departed from the traditional approach of estimating $CaCO_3$ production from standing crop and turnover rate, and have turned to alkalinity depletion in the water column as a measure of community $CaCO_3$ production (for a review, see Smith, 1974).

Information about the organic carbon productivity of coral reefs is a more recent development. For the most part, present data are restricted to reef flats. The study by Odum and Odum (1955) at Enewetak Atoll* remains the most comprehensive description of reef-flat productivity. Estimates of organic carbon productivity in reef communities have relied primarily on oxygen changes as a measure of productivity. Kinsey and Domm (1974), Marsh (1974), and Smith (1974) have all reviewed the literature dealing with oxygen-derived estimates of organic carbon metabolism on coral reefs. In addition, Smith discussed the use of carbon dioxide to measure organic carbon metabolism in reef systems.

Other metabolites can also provide information on the organic carbon metabolism of aquatic communities. Studies of oxygen, carbon dioxide, phosphorus, and nitrogen flux across the windward reef flats of Enewetak Atoll demonstrate that there is no simple relationship between oxygen or carbon dioxide flux of coral reef communities and the instantaneous flux of other metabolites through these systems. Pilson and Betzer (1973) found no relationship between instantaneous oxygen metabolic rates and the uptake or release

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*This spelling of the atoll also known as "Eniwetok" has been officially sanctioned by the US Board of Geographic Names.

of phosphate. In fact, those authors could detect little or no instantaneous phosphate uptake or release in the Enewetak communities studied. Webb and his associates (1975) found nitrogen flux of the Enewetak reef-flat community to be even more complicated. The reef flat community exported all forms of dissolved nitrogen and apparently balanced this export with massive fixation of atmospheric nitrogen.

The above studies were undertaken in reef-flat environments where the residence time of water is only a few minutes. Such short-term incubations may not provide the most suitable conditions for quantifying and comparing the net biogeochemical fluxes of various materials. Advective flux may be so great that it masks biogeochemical changes. Moreover, short-term departures of biogeochemical fluxes from a mass balance among the materials in the system may obscure relationships among components even though such imbalances cannot be maintained indefinitely. The long-term net import, export, and storage of organic carbon must be proportional to the net flux and storage of nutrients.

In contrast with rapidly flushed reef flats, atoll lagoons retain water for relatively long timespans (von Arx, 1954). Thus lagoons can provide long-term, integrated records of community biogeochemical activity (Smith and Pesret, 1974). It is the purpose of the present study to consider an atoll lagoon in order to ascertain the net biogeochemical activity of a major, but largely unstudied, portion of coral reefs, and to compare the net rates of uptake or release for various biologically active materials within that lagoon. Circulation of water in an entire lagoon is more complex than water flow across a feef flat, so considerable attention is given in this paper to the manner in which the lagoon system has been analyzed. Budgets of material flux through the lagoon provide quantitative bases for comparing the various materials examined. The spatial distribution of biogeochemical fluxes can be compared with oceanographic, biotic, and physiographic patterns in the lagoon.

DESIGN OF SYSTEM ANALYSIS

Experience at Fanning Atoll, an atoll physiographically similar to Canton, but with certain pronounced differences, has been useful in designing the Canton study and in interpreting the results (see Smith and Pesret, 1974). The lagoons of both atolls are nearly landlocked. Fanning lagoon exchanges water with the open ocean through one large pass and two smaller ones, while Canton lagoon water exchanges at a single large pass with channels to either side of a small, artificial islet. As a result, the lagoon circulation at Canton is simpler than that at Fanning. Fanning has tidal flows at each of three passes, with net advection from east to west across the lagoon (Gallagher *et al.*, 1971). Tidal inflow and outflow at the single pass of Canton necessarily balance one another, except for a slight net inflow to offset evaporative loss.

Smith and Pesret (1974) calculated salt and water budgets for the Fanning lagoon to ascertain the relationship between the residence time (T) of water in the lagoon and salinity:

$$\mathrm{T\ (days)} = \frac{Z}{r}\left[\frac{S_O - S_l}{S_O}\right] \tag{1}$$

where Z is the mean lagoon water depth; r is the mean daily rainfall rate during and immediately preceding the salinity measurements; and S_O and S_l are the mean ocean and lagoon salinities, respectively. Smith and Pesret concluded that during the survey of Fanning lagoon the lagoon-wide effects of evaporation and groundwater seepage were small and approximately compensating processes in the water budget. These processes could be ignored in interpreting the lagoon-wide water budgets at Fanning, although there was a distinct groundwater effect around the lagoon margin.

Canton is ordinarily a dry island (Taylor, 1973). Consequently, details of the Canton water-budget model differ from those of Fanning. The evaporation rate (e) can no longer be ignored, but groundwater apparently can be. There is substantial groundwater at Canton (Guinther, this report), but there is no evidence of significant seepage from the groundwater into the lagoon (samples gathered by E. C. Evans III and E. B. Guinther). In fact, evaporation is a dominant term in the water budget at Canton, as evidenced by the elevated lagoon salinity first reported by van Zwaluwenburg (1941). The appropriate equation to describe lagoon-water residence time in this high-evaporation regime becomes:

$$\mathrm{T\ (days)} = \frac{Z}{(r-e)}\left[\frac{S_O - S_l}{S_O}\right] \tag{2}$$

Note that this general approach to calculating residence time is appropriate only if there is a salinity differential between the ocean and the lagoon. Without such a differential, the equation becomes indeterminant, because the denominator and numerator of the equations are then zero.

In the absence of a groundwater-induced low salinity rim around the lagoon margin, Eq. 2 also describes the relationship between local variations in salinity and the age of water at that locality (if one assumes constant water depth, rainfall, and evaporation throughout the lagoon). In that treatment of Eq. 2, S_l is the salinity at that locality, and T is a local estimate of residence time.

This salinity-residence time equation may be extended to calculate biogeochemical flux of materials within the lagoon. That is, for any constituent of seawater, there is a concentration change which may be called conservative and directly attributed to net evaporation or dilution (that is a "conservative change"); and there may be a residual ("nonconservative") change which results from biogeochemical uptake or release within the lagoon. For any material Y, the biogeochemical change with respect to salinity ($\Delta Y/\Delta S$) may be stated:

$$\frac{\Delta Y}{\Delta S}\ (\text{mole m}^{-3}\ \text{o/oo}^{-1}) = \left[\left(\frac{Y_o}{S_o}\right) S_l - Y_l\right] \Big/ (S_l - S_o) \qquad (3)$$

The subscripts o and l denote ocean and lagoon values, respectively. Both Y_o and Y_l are calculated according to regression equations relating Y to S. A positive value for $\Delta Y/\Delta S$ denotes net uptake from the water; negative is release. It follows from Eq. 2 and 3 that the change in Y with respect to the residence time of the water may also be calculated:

$$\frac{\Delta Y}{\text{T}}\ (\text{mole m}^{-3}\ \text{day}^{-1}) = \frac{(r-e)\,S_o}{Z(S_l - S_o)} \left[\left(\frac{Y_o}{S_o}\right) S_l - Y_l\right] \qquad (4)$$

Multiplying Eq. 4 by the mean water depth expresses the rate of change in Y per unit map area:

$$\frac{\Delta Y}{\text{T}}\ (\text{mole m}^{-2}\ \text{day}^{-1}) = \frac{(r-e)\,S_o}{S_l - S_o} \left[\left(\frac{Y_o}{S_o}\right) S_l - Y_l\right] \qquad (5)$$

Equation 5 and the appropriate regression equation for Y will be used to calculate the rate of change for each of several materials in the lagoon in response to biogeochemical processes for the Canton lagoon.

This record of $\Delta Y/\text{T}$ provides an estimate of the net rate of biogeochemical change in Y as integrated from the pass to the S_l value in question. Equation 5 could be differentiated to yield an estimate of the biogeochemical rate $\Delta Y/\text{T}$ at any location (or salinity). Because the simple polynomial equations impose obviously simplified patterns of change on the data (for example, a constant rate of change in uptake or release if the regression equation used is quadratic), that detailed information has not been extracted. The solution of Eq. 5 along with each appropriate regression equation for the Y_o's at progressively higher salinities provides an estimate of the cumulative history of water incubation between the pass and each salinity (or location) in question.

ANALYTICAL METHODS

Water sampling locations during November–December 1973 are shown in Fig. 7, and the parameters measured are listed in Table 1. In addition to the 1973 measurements, data are available from a preliminary survey conducted by Jokiel during June 1972. The 1972 data will be presented only in comparison with the more extensive 1973 data. Not all of the parameters are

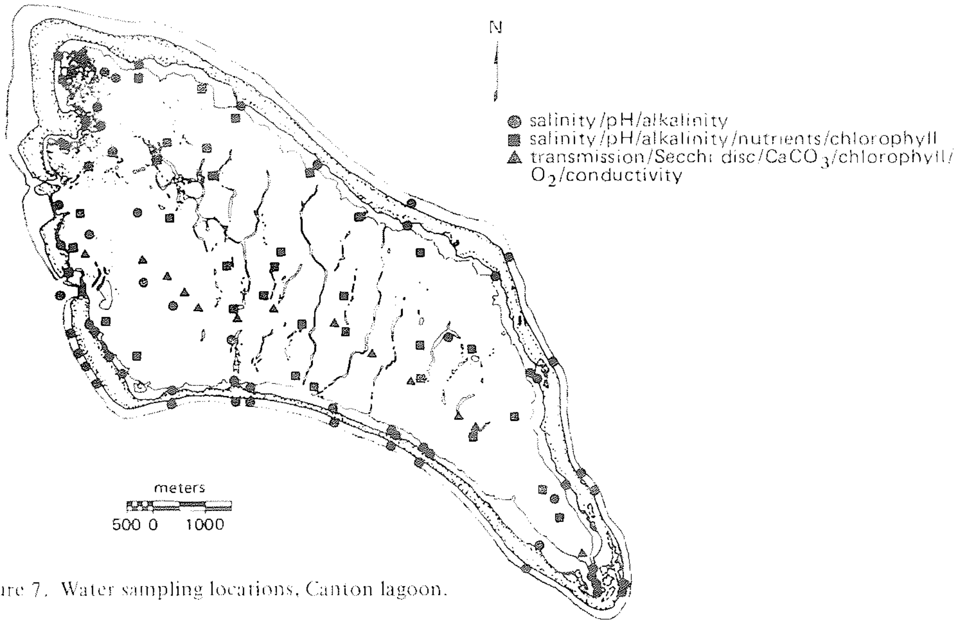

Figure 7. Water sampling locations, Canton lagoon.

Table 1. Water and sediment parameters measured in the Canton lagoon during the 1972 and 1973 surveys.

Parameter	1972	1973
Temperature	X	X
Salinity		X
Nutrients		X
pH		X
Alkalinity		X
O_2	X	X
Conductivity	X	X
Suspended $CaCO_3$		X
Suspended phytopigments		X
Secchi disc	X	X
% light transmission		X
Sediment organic carbon		X
Sediment mineralogy		X
Sediment grain size		X

considered in detail. For example, O_2 measurements made with field polarographic cells yielded values consistently in near equilibrium with the atmosphere. These data warrant no further discussion. The lagoon was nearly isothermal, except for the marked phenomenon of marginal heating in the shallow waters around the lagoon rim. It is of interest to note that in 1972 the lagoon temperature was uniformly about 29°C, and during the 1973 survey the temperature was 27°C. Both values are within the range reported for monthly water temperatures at Canton (U. S. Coast and Geodetic Survey Publication 31-3, revised). Field values of water conductivity are of little value to this study except to confirm the lack of vertical salinity stratification in the lagoon.

Water samples were collected from a small skiff or by wading from shore. Midwater samples were pumped to the surface with a small bilge pump and garden hose. Midwater sampling was abandoned after the first two days because no parameter showed significant vertical variation.

Surface samples were collected directly either into 250-ml polyethylene bottles for salinity, pH, and alkalinity measurements or into a glass flask for on-site filtration of the water through glass fiber filters. The filters were then put into opaque vials containing 90% acetone and retained for phytopigment analyses; filtered water was poured into 250-ml bottles for nutrient analyses. Samples for salinity, pH, and alkalinity were maintained near collection temperature until they could be returned to the laboratory and analyzed. The average time between sample collection and analysis was about 6 hours. Nutrient samples and the vials containing filters for phytopigment analyses were packed in ice until they could be frozen within about 4 hours of collection. These frozen samples were returned to Hawaii for analysis.

At 13 stations, simultaneous measurements were made of Secchi disc readings and percent light transmission, and samples were taken for phytopigments and suspended $CaCO_3$. Secchi disc readings followed conventional field measurement procedures. Percent light transmission was measured with a Hydro-Products model 612 transmissometer equipped with a l-m measurement cell. Samples for phytopigment analyses were collected as described above; samples for $CaCO_3$ analyses were filtered onto 0.8μ pore-size Millipore filters, rinsed with deionized water, and then air-dried.

The laboratory used for salinity analyses was an air-conditioned room maintained near 25°C. A Plessey model 6230N laboratory conductivity salinometer was used for the analyses; it was standardized against a Copenhagen Water primary standard and working substandards. The laboratory used for pH and alkalinity measurements was not air-conditioned but was used because of its ample sink and working space. The room remained near 30°C during most of the measurement periods. A Corning model 101 pH meter and a combination electrode were used for all pH and alkalinity measurements. The analytical procedure closely followed that given by Smith and Pesret (1974). A computer program for calculating CO_2 parameters from pH, alkalinity, salinity, and temperature has been developed by Smith and is on file with the Hawaii Coastal Zone Data Bank (University of Hawaii).

Nutrient samples were returned to Hawaii and analyzed with a Technicon autoanalyzer. Soluble reactive PO_4, NO_3, and Si were measured according to slight modifications of the automated nutrient analysis techniques described by Strickland and Parsons (1968), and NH_3 analyses were modified from the technique described by Head (1971). A Beckman model DBG spectrophotometer was used for phytopigment analyses, after the technique described by Strickland and Parsons (1968). Suspended $CaCO_3$ analyses were performed by dissolving the $CaCO_3$ on the filters in 3N HCl and then measuring Ca and Mg with a Perkin Elmer atomic absorption spectrophotometer.

Sediment organic carbon percentages were determined by weighing a sediment aliquot and then using an F & M model 185 CHN analyzer to measure the amount of CO_2 released at an oxidation temperature of 700°C, according to a slight modification of the technique described by Telek and Marshall (1974).

RESULTS

Salt and Water Budgets

Equation 2 is used to construct the salt and water budgets of the lagoon.

The mean lagoon depth was determined by gridding the Hydrographic Office Chart of the Canton Island Lagoon (No. 83105) into approximately 2,200 squares and estimating the mean depth at each grid intersection. The mean lagoon depth was found to be 6.2 m.

Rainfall records have been maintained at one or both of two weather stations at Canton Atoll since 1940, except for three interruptions (1941–1942, 1945, 1967–1971). Taylor (1973) reports the available data from these two stations through 1972 (except for the period from December 1971 through May 1972; records from that period, plus the period from January 1973 through October 1974, were obtained from U. S. Air Force records). Table 2 summarizes relevant aspects of the rainfall data.

Of particular interest to the present investigation is the period from April 1973 through March 1974. The rainfall averaged about 0.6 mm/day during that period, with only the month of August differing significantly from that average. This average is less than one-third the long-term mean daily rainfall. By contrast, the average rainfall from April 1972 through March 1973 was about 8 mm/day, or four times the long-term mean. Thus over the course of 2 years, Canton experienced the wettest and one of the driest periods in its recorded history.

Evaporation-rate data comparable to these extensive rainfall records are not available, but it is possible to estimate evaporation during and immediately preceding this survey.

Evaporation was measured in plastic containers filled with seawater, then shaded from the sun but exposed to the wind. Measurements were made both in 12-cm-deep pans monitored hourly for periods of up to 9 hours and in a 50-cm-deep container monitored twice daily for 9 days. The parameters measured were initial water depth in the container and salinity at each time increment. Evaporation can be determined more precisely from a change in salinity than from direct depth measurements. Evaporation-pan procedures are generally open to question, largely because of differences between water temperatures in the evaporation pan and the temperature of the water body of interest

Table 2. Canton Atoll rainfall.

Month	1937-1974 mean		1971		1972		1973		1974	
	mm	mm/day	mm	mm/day	mm	mm/day	mm	mm/day	mm	mm/day
January	88.9	(2.9)	–	–	17.8	(0.6)	526.3	(17.0)	0.0	(0.0)
February	45.8	(1.6)	–	–	13.5	(0.5)	286.8	(10.2)	2.3	(0.1)
March	58.5	(1.9)	–	–	16.3	(0.5)	235.2	(7.6)	16.8	(0.5)
April	90.1	(3.0)	–	–	154.2	(5.1)	34.0	(1.1)	69.3	(2.3)
May	76.1	(2.5)	–	–	84.8	(2.7)	33.5	(1.1)	53.6	(1.7)
June	60.4	(2.0)	–	–	21.9	(0.7)	8.6	(0.3)	58.7	(1.9)
July	61.2	(2.0)	–	–	199.6	(6,4)	22.9	(0.7)	100.8	(3.3)
August	56.7	(1.8)	–	–	78.2	(2.5)	82.8	(2.7)	27.9	(0.9)
September	33.0	(1.1)	–	–	134.4	(4.5)	20.1	(0.7)	19.8	(0.7)
October	35.2	(1.1)	–	–	428.5	(13.8)	5.1	(0.2)	5.3	(0.2)
November	51.7	(1.7)	–	–	312.9	(10.4)	0.3	(0.0)	–	–
December	69.3	(2.2)	1.5	(0.1)	427.2	(13.8)	5.1	(0.2)	–	–
Total	726.9	(2.0)	–	–	1889.3	(5.2)	1260.6	(3.5)	–	–

NOTE:

		mm	mm/day
wettest 12-month period:	April 1972–March 1973	2890.0	(7.9)
one of driest 12-month periods:	April 1973–March 1974	231.5	(0.6)
driest 12-month period:	January 1954–December 1954	196.1	(0.5)

(in this case, the lagoon). However, the difference between the pan and lagoon water temperatures never exceeded 1°C, except for elevated temperatures found locally on the shallow intertidal flats fringing the lagoon. Three experiments in the shallow pans and one in the deep container all yielded evaporation rates between 8 and 9 mm/day.

Jacobs (1942) gives a formula for calculating evaporation rate (e) from wind velocity (w) at some height, water vapor pressure at that height (p_h), and the vapor pressure at the sea surface (p_o):

$$e\ (\text{mm/day}) = 0.14\ (p_o - p_h)\ w \qquad (6)$$

The mean wind velocity during the survey, as averaged from U. S. Air Force records, was 6 m/s; mean air temperature and water temperature were both 27°C; mean relative humidity, as calculated from temperature and dew point, was 72%. From Sverdrup *et al.* (1942), the vapor pressure at that temperature and humidity can be calculated to be 25 mbar. At 100% humidity (the assumed sea-surface value) the vapor pressure is about 35 mbar. The calculated evaporation rate is 8 mm/day, the same as the measured values. This lagoon evaporation rate is about twice the long-term mean value reported by Wyrtki (1966) for the open ocean in the vicinity of Canton.

Figure 8 is a map of salinity distribution in the lagoon in December 1973. There was no vertical stratification, so available surface and midwater data have

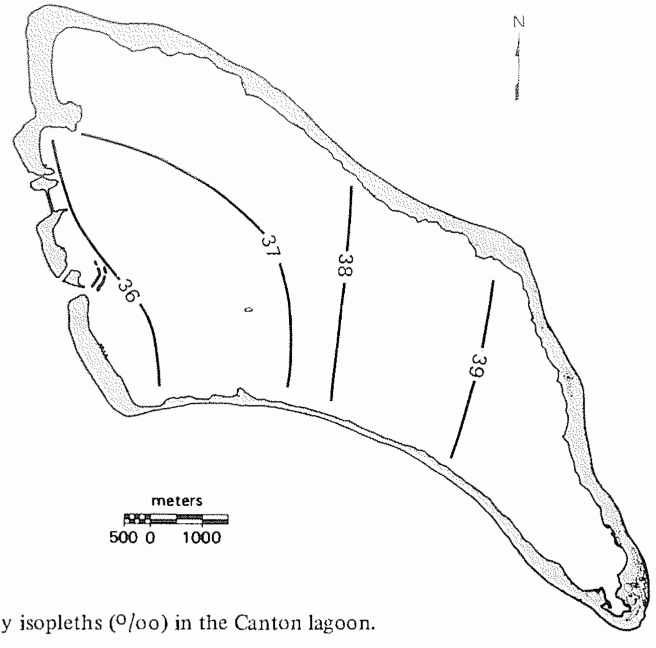

Figure 8. Salinity isopleths (°/oo) in the Canton lagoon.

been combined into this single map. Figure 9 shows salinity as a function of distance from the lagoon pass. At the time of the survey, salinity increased with distance from the pass from an oceanic value of 35.7 o/oo to a back-lagoon value of about 39.5 o/oo. The trend is well approximated (coefficient of determination = 96%) by the following empirical quadratic regression equation:

$$S_l \, (\mathrm{o/oo}) = 35.53 + 0.563X - 0.0202X^2 \qquad (7)$$

S_l is the calculated salinity at any location X km from the pass. Planimetry of the salinity map (Fig. 9) yields a mean lagoon salinity of about 37.7 o/oo.

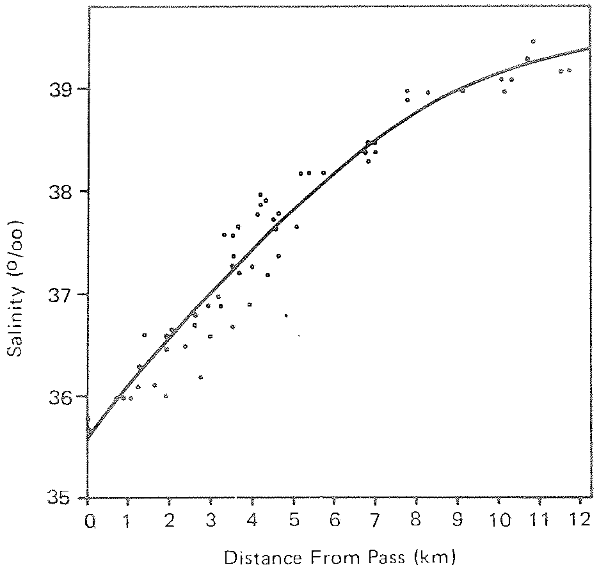

Figure 9. Salinity versus distance from pass, including quadratic regression line.

The various values established above may be substituted into Eq. 2 in order to calculate the residence time of lagoon water. The estimated mean residence time is about 50 days; maximum residence time is about 95 days, and there is about a 25-day residence time for each 1 o/oo salinity increase over the oceanic value of 35.7 o/oo.

The above values are locally inapplicable on the intertidal flats along the lagoon rim. There, the salinity may increase by as much as 1 o/oo over a single tide cycle because the water is temporarily held on these flats and heated during daytime falling tides. On subsequent rising tides, this water is flushed off the flats and mixed with the bulk of the lagoon water. The area of these intertidal flats is sufficiently small so that this local effect has been ignored in constructing lagoon-wide budgets.

Salinity data gathered by Jokiel during a trip to Canton in June 1972 and samples shipped to Hawaii by members of the U. S. Air Force after the 1973 survey establish temporal variations in the patterns described above. The 19 samples gathered by Jokiel have been matched with samples collected from approximately the same locations during the present survey. Data are reported as "salinity excess" above oceanic values, because Jokiel's salinity probe was not adequately calibrated to establish absolute salinities. Figure 10 shows that the 1972 salinity excesses were generally somewhat lower than the 1973 values (which are also expressed here as salinity excesses). This pattern is to be expected, because rainfall during early 1972 was somewhat higher than rainfall during late 1973 (Table 2). Samples collected from the northern corner of the lagoon and shipped to Hawaii from November 1973 until October 1974 also showed a consistent pattern (Table 3). Salinity remained relatively constant

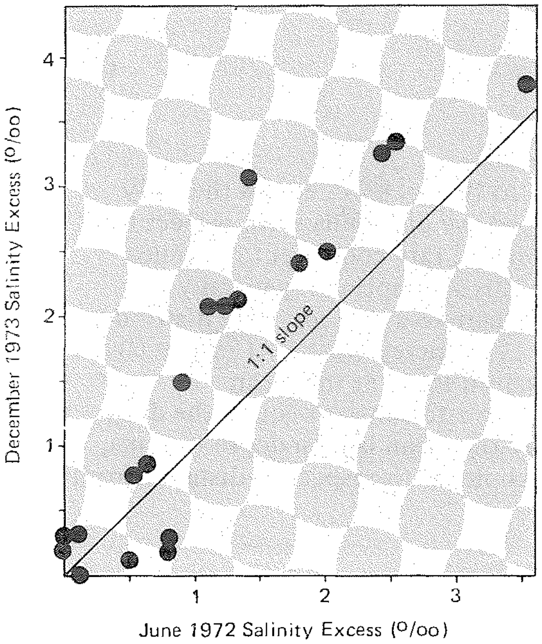

Figure 10. June 1972 versus December 1973 "salinity excess" above oceanic values.

Table 3. Salinity and rainfall, northern portion of the Canton lagoon.

Month	Salinity (o/oo)	Monthly rain (mm)
November 1973	37.8	0
December	37.8	5
January 1974	37.9	0
February	37.5	2
March	38.1	17
April	37.7	69
May	37.0	54
June	36.4	59
July	36.5	101
August	36.5	28
September	37.0	20
October	37.5	5

from November until April 1974 and then decreased by about 1 o/oo. Rainfall from April through July was markedly higher than rainfall over the previous months, so the salinity decrease is to be expected. From August through October, rainfall dropped and salinity rose.

This salinity differential between the ocean and lagoon is obviously maintained by a combination of evaporative water loss, replacement by a net inflow of ocean water, and dispersion of this ocean water through the lagoon. The volume of water entering the lagoon on each rising tide averages about 11% of the total lagoon volume (0.7 m average tidal range divided by 6.2 m average lagoon depth), so apparently only a small fraction of each tidal prism actually remains in the lagoon. Because the exchange of water between the ocean and lagoon is restricted to a single pass, a one-dimensional eddy diffusion model may be assumed to describe salt dispersion through the lagoon (A. Okubo, personal communication):

$$\left(\frac{\partial S}{\partial t}\right)_X \text{ (o/oo day}^{-1}) = \frac{D\partial^2 S}{\partial X^2} + \propto S_l \qquad (8)$$

The local change in salinity with respect to time, $\left(\frac{\partial S}{\partial t}\right)_X$, equals the eddy diffusion coefficient (D) times the second derivative of salinity with respect to distance from the pass (X) plus the net evaporation rate coefficient ($\propto$) times the local salinity (S_l). It can be assumed (and this assumption is generally supported by the data in Tables 2 and 3) that there was a steady-state distribution of salinity before and at the time of the 1973 survey (that is, $\left(\frac{\partial S}{\partial t}\right)_X = 0$). Equation 8 can therefore be rearranged and solved for D at the mean lagoon salinity ($S_l = 37.7$ o/oo). The evaporation rate constant equals the daily net evaporation rate (0.007 m/day) divided by the mean lagoon depth (6.2 m), or 0.00113 day^{-1}. The second derivative of salinity with respect to distance from the pass can be calculated from Eq. 7:

$$\frac{\partial^2 S}{\partial X^2} = 0.0404 \text{ o/oo km}^{-2}$$

Substituting these values into Eq. 8 yields $D = 1.054$ km^2/day, or 1.2×10^5 cm^2/s. This value corresponds closely to the value of 1.0×10^5 cm^2/s calculated from Okubo's (1971) equation relating D to eddy size (using 12 km, the distance from the pass to the back lagoon at Canton, as the appropriate eddy size). It therefore seems probable that the net dispersion of materials through the lagoon at Canton can be accounted for in terms of eddy diffusion.

Nutrient Budgets

Figure 11 is a map of phosphate distribution throughout the lagoon, and Fig. 12 is a plot of that nutrient against salinity. The PO_4 values decreased from a mean of about 0.6 mmole/m^3 near the pass to about 0.1 mmole/m^3 in the back lagoon.* This decrease is empirically well-described (coefficient of determination = 89%) by the following quadratic regression equation:

$$PO_4\ (\text{mmole/m}^3) = 82.567 - 4.289S + 0.0448S^2 \qquad (9)$$

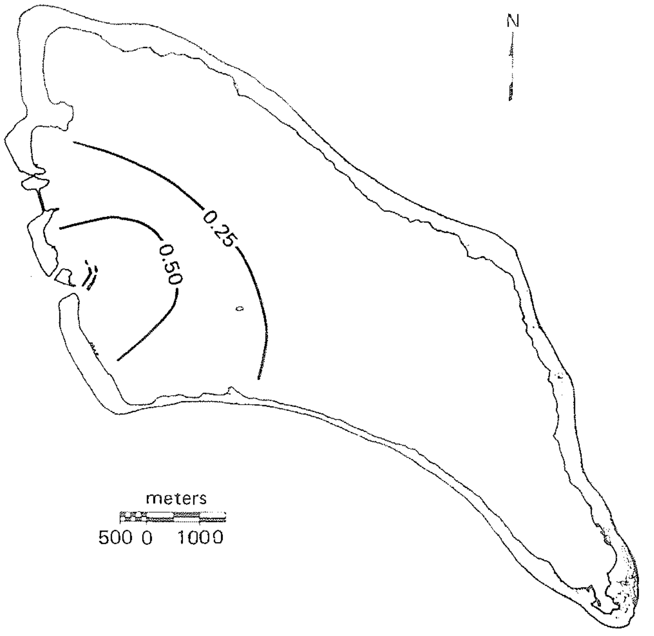

Figure 11. Phosphate isopleths (mmole/m^3) in the Canton lagoon.

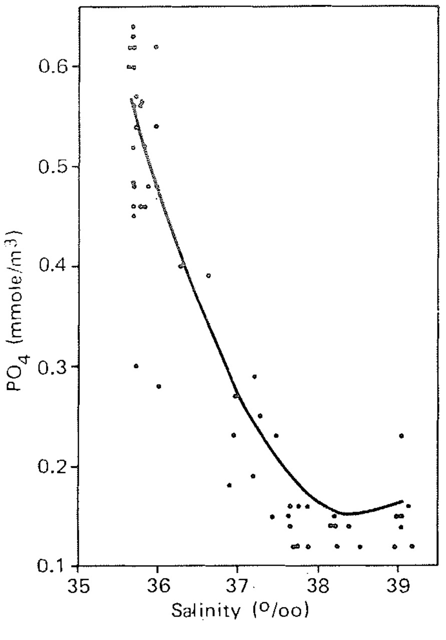

Figure 12. Phosphate versus salinity, including quadratic regression line.

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*For convenience, all notation of nutrient concentrations is given here in terms of mmole/m^3, instead of the more conventional–but equivalent–notation of μg-atom/liter.

Table 4 presents the rates of biogeochemical phosphorus flux as calculated from Eq. 5 and 9. The table presents the data for phosphorus change during the first 0.1 $^o/oo$ salinity increase, as indicative of rates near the pass. The changes are then reported for each unit salinity increase above oceanic (up to 38.7 $^o/oo$) and finally at 39.5 $^o/oo$ (nominally the maximum lagoon salinity). There was net phosphorus uptake throughout the lagoon, and the uptake rate decreased with increasing salinity. Near the pass, the uptake rate was 0.074 mmole m^{-2} day^{-1}; in the back lagoon the uptake rate was 0.027 mmole m^{-2} day^{-1}.

Table 4. Phosphorus utilization in the Canton lagoon, as calculated from Eq. 5 and 9.

Salinity ($^o/oo$)	Residence time, T (days)	Total dissolved phosphorus $\left(\frac{P_o}{S_o}\right)S_l$ (mmole/m^3)	P_l	Phosphorus utilization, $\frac{\Delta P}{T}$ (mmole $m^{-2}day^{-1}$)
35.7	0	0.57	0.57	–
35.8	2.5	0.57	0.54	0.074
36.7	25	0.58	0.32	0.065
37.7	50	0.60	0.18	0.052
38.7	75	0.61	0.15	0.038
39.5	95	0.63	0.21	0.027

It can be assumed that all of this phosphorus uptake went into the production of organic materials. The only other likely phosphorus sink would be inorganic phosphate minerals, but there is no evidence that they are a significant component of reef sediments. Phosphorus taken into the sediments in organic carbon compounds is obviously subject to recycling back into the water as these compounds are oxidized. Such recycling is not of direct concern here, because the budget represents net utilization. One further complication in the phosphorus budget is the possibility of a significant phosphorus source other than dissolved reactive PO_4 input at the lagoon pass. For example, PO_4 derived from phosphatic rocks might seep into the lagoon; the PO_4 versus salinity diagram (Fig. 12) does not suggest such additional complexity.

Two forms of dissolved nitrogen were measured in the lagoon waters: NO_3 and NH_3. Nitrite was not measured, because the level of NO_2 in surface seawater is ordinarily very low. Maps of these parameters are presented as Fig. 13 and 14, and plots of these materials versus salinity are presented as Fig. 15 and 16. The NO_3 distribution (Fig. 13 and 15) was similar to the PO_4 pattern; values decreased from levels of about 2.5 mmoles NO_3/m^3 near the pass to near 0 in the back lagoon. The NH_3 pattern was more complex. Values were about 1.5 mmoles NH_3/m^3 near the pass, followed by an abrupt decrease to about 0.4 mmole/m^3 throughout much of the lagoon. However, there were

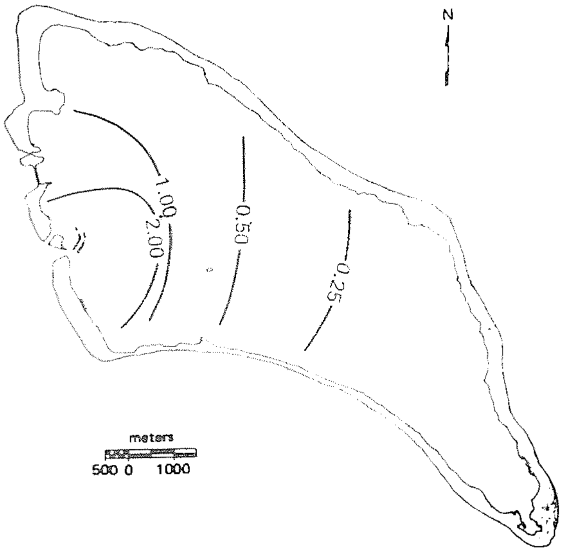


Figure 13. Nitrate isopleths (mmole/m^3) in the Canton lagoon.

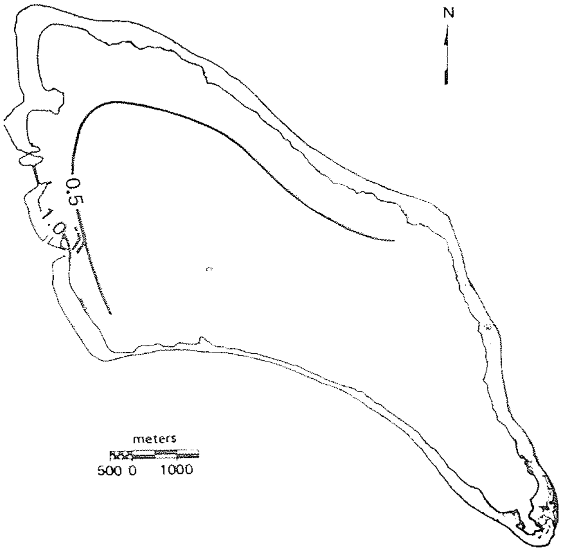


Figure 14. Ammonia isopleths (mmole/m^3) in the Canton lagoon.

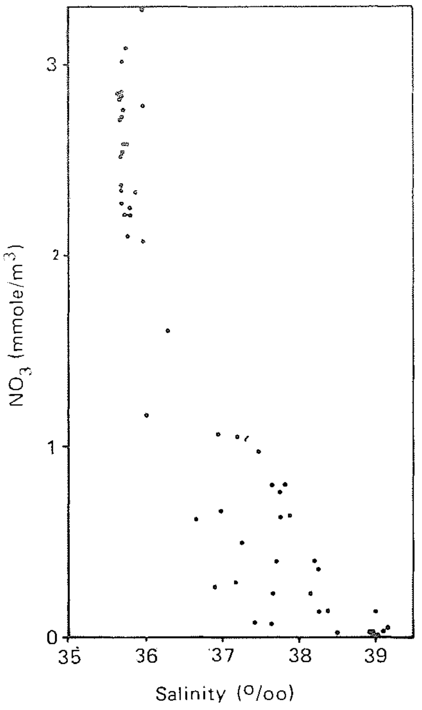


Figure 15. Nitrate versus salinity.

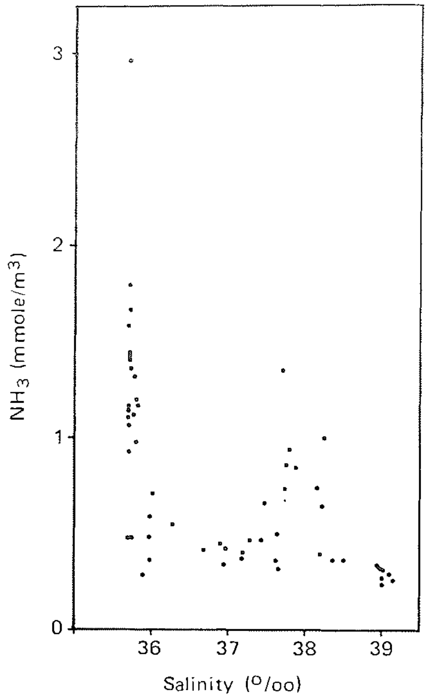


Figure 16. Ammonia versus salinity.

high values (near 1 mmole/m^3) along the northeastern margin of the lagoon. These high NH_3 values can be seen at intermediate salinities on Fig. 16. Figure 17 is a plot of total inorganic nitrogen versus salinity; the regression equation for this relationship is used to establish the dissolved inorganic nitrogen budget for the lagoon. Again, a quadratic equation describes the data well (coefficient of determination = 84%):

$$N\ (\text{mmole/m}^3) = 535.14 - 27.612S + 0.3564S^2 \tag{10}$$

The biogeochemical flux of N as calculated from Eq. 5 and 10 is summarized in Table 5. Nitrogen uptake also decreased with increasing distance from the pass. Near the pass, the uptake rate was 0.55 mmole m^{-2} day^{-1}; the rate decreased to 0.23 mmole m^{-2} day^{-1} in the back lagoon.

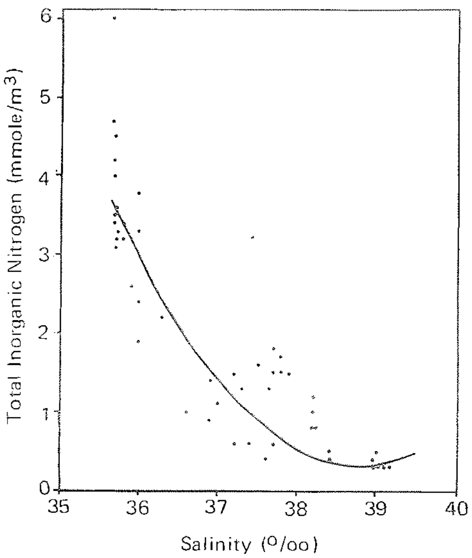


Figure 17. Total inorganic nitrogen versus salinity, including quadratic regression line.

Table 5. Total dissolved inorganic nitrogen utilization in the Canton lagoon, as calculated from Eq. 5 and 10.

Salinity (°/oo)	Residence Time, T (days)	Total dissolved nitrogen (mmole/m^3) $\left(\frac{N_o}{S_o}\right)S_l$	N_l	Nitrogen utilization $\frac{\Delta N}{T}$ (mmole m^{-2}day^{-1})	$\frac{\Delta N}{\Delta P}$
35.7	0	3.62	3.62	–	–
35.8	2.5	3.63	3.41	0.55	7.4
36.7	25	3.72	1.81	0.47	7.2
37.7	50	3.82	0.72	0.38	7.3
38.7	75	3.92	0.33	0.30	7.9
39.5	95	4.01	0.54	0.23	8.5

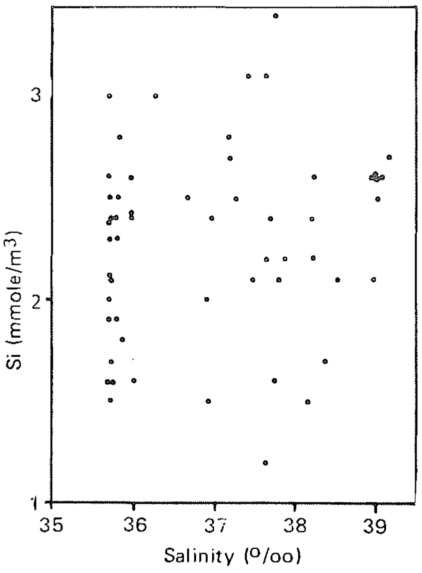
Unlike the phosphorus budget, the nitrogen budget must be regarded as incomplete. There may be at least two additional sources of nitrogen in the lagoon. An input of NH_3 other than that at the lagoon pass is suggested by Fig. 14. The high NH_3 values at intermediate salinities along the northeastern margin of the lagoon probably represent either such additional input or NH_3 regeneration along that portion of the lagoon. Wind may blow NH_3-laden air from bird colonies along the northeastern portion of the island across the water where it can be rapidly dissolved. This mechanism may have been enhanced during the survey by heavy truck traffic; the ammonia may adsorb onto the resultant dust which falls out along the northeastern portion of the island. Some groundwater input of NH_3 from this same island source is also possible, although salinity values do not indicate groundwater influx into the lagoon. Because NH_3 is highly labile, the sampling and storage procedures may have also introduced the high values as a sampling artifact. Nevertheless, the coherent distribution pattern argues against the likelihood of such an artifact.

Webb *et al.* (1975) have demonstrated that blue-green algae on shallow reef flats can fix large amounts of atmospheric nitrogen. Such a mechanism could supply a significant fraction of the total nitrogen utilized by the Canton lagoon community. Drouet (in Degener and Degener, 1959) lists several genera of blue-green algae which are found at Canton and which are known to fix nitrogen.

Because of these possible additional nitrogen sources, the nitrogen utilization rate calculated here and the ratio of N:P uptake (Table 5) are probably lower limits.

Figure 18 is a plot of salinity versus silicon in the lagoon. Unlike nitrogen and phosphorous, silicon shows no functional relationship with salinity. This lack of correlation is actually encouragement for the general interpretation of biogeochemical flux as presented here. Canton, or indeed any coral atoll, has a

Figure 18. Silica versus salinity.



biotic community overwhelmingly dominated by calcification rather than silicification as the major form of net skeletogenesis; hence, any calculation suggesting significant net silicon uptake in a reef environment would be viewed with some surprise.

Carbon Dioxide Budget

Of the various budgets presented here, the carbon dioxide budget is perhaps the most complex. In addition to evaporative change in the CO_2 content of the seawater, there is also change due to organic carbon production or consumption, $CaCO_3$ precipitation or solution, and gas exchange across the air–sea interface.

Figures 19 and 20 are maps of two CO_2 parameters: total CO_2 and total alkalinity. Figures 21 and 22 are plots of these CO_2 parameters versus salinity.

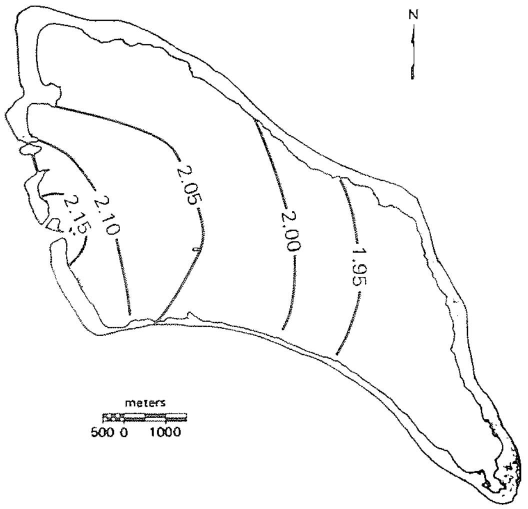


Figure 19. Total CO_2 isopleths (mole/m^3) in the Canton lagoon.

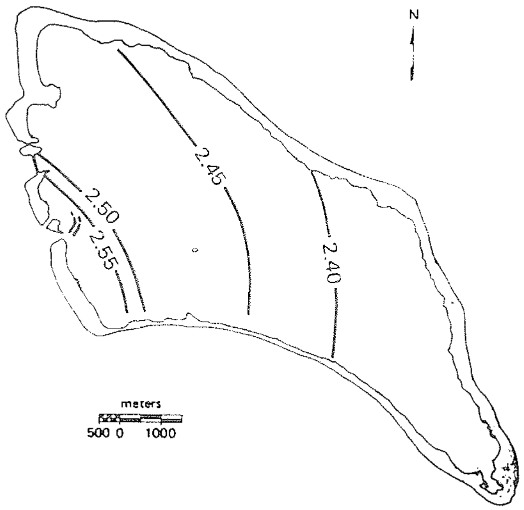


Figure 20. Total alkalinity isopleths (equiv/m^3) in the Canton lagoon.

Total CO_2 decreased regularly from about 2.2 moles/m^3 near the pass to about 1.9 moles/m^3 in the back lagoon. The decrease with respect to salinity is well-approximated (coefficient of determination = 80%) by a linear regression equation:

$$CO_2\ (\text{mole/m}^3) = 4.156 - 0.0568S \qquad (11)$$

Higher-order regression equations do not improve this fit significantly.

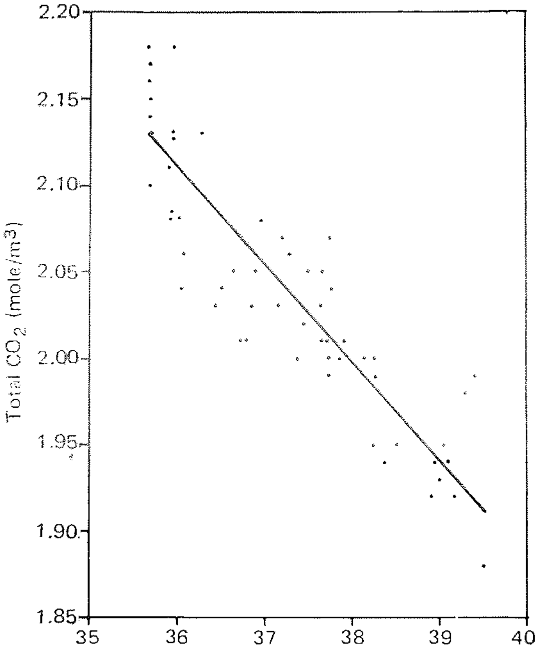


Figure 21. Total CO_2 versus salinity, including linear regression line.

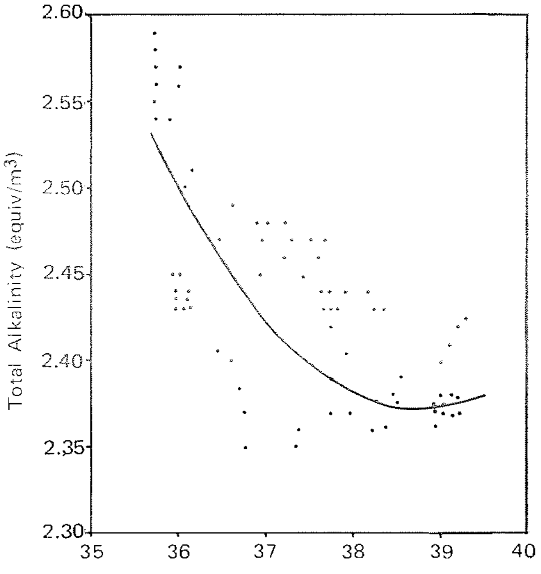


Figure 22. Total alkalinity versus salinity, including quadratic regression line.

Total alkalinity decreased from about 2.55 equiv/m^3 near the pass to about 2.4 equiv/m^3 near the back of the line reef zone. The quadratic regression equation for total alkalinity (TA) versus salinity has a coefficient of determination of 69%:

$$TA\ (\text{equiv/m}^3) \doteq 27.157 - 1.279S + 0.0165S^2 \qquad (12)$$

This descriptive equation is less satisfactory than the nutrient equations presented above, but higher-order polynomials do not improve the fit significantly. The description is least satisfactory near the lagoon pass, where the equation apparently underestimates alkalinity somewhat. The alkalinity decrease indicates that net precipitation of $CaCO_3$ was occurring in the lagoon.

One further CO_2-related parameter considered here but not mapped is CO_2 partial pressure (P_{CO_2}). The P_{CO_2} of water entering the lagoon averaged about 330 μatm, and the mean of the lagoon samples was about 290 μatm. The incoming water was very near the predicted atmospheric equilibrium value for 1973 (about 326 μatm, according to Ekdahl and Keeling, 1973). The mean value for incoming water is in substantial agreement with Keeling's (1968) world map of surface-water P_{CO_2} value in the vicinity of Canton.

Table 6 summarizes the CO_2 budget for the lagoon. Only two of the terms in the budget can be determined directly: the total CO_2 change and that change due to $CaCO_3$ reactions. The remaining terms (organic carbon flux and gas exchange) must be determined by inference from the nutrient budgets and appropriate "bookkeeping."

Table 6. CO_2 utilization in the Canton lagoon.

		Total CO_2		Total alkalinity		CO_2 flux, $\frac{\Delta CO_2}{\tau}$			
Salinity ($^0/oo$)	Residence time, τ (days)	$\left(\frac{Y_o}{S_o}\right)S_l$ (mole/m^3)	Y_l	$\left(\frac{Y_o}{S_o}\right)S_l$ (equiv/m^3)	Y_l	Total	$CaCO_3$ prod (mmole $m^{-2}day^{-1}$)	Organic C flux*	Gas exchange**
35.7	0	2.128	2.128	2.526	2.526	—	—	—	—
35.8	2.5	2.134	2.123	2.533	2.516	29	21	7	1
36.7	25	2.188	2.071	2.597	2.441	29	19	7	3
37.7	50	2.247	2.015	2.667	2.390	29	17	5	7
38.7	75	2.307	1.958	2.738	2.372	29	15	4	10
39.5	95	2.355	1.912	2.795	2.381	29	14	3	12

*The net excess organic carbon production term is 100 times the phosphorus utilization. A positive value for flux indicates net production.

**A positive value for exchange indicates net evasion.

The total CO_2 change averaged 29 mmoles m^{-2} day^{-1} depletion throughout the lagoon, as can be calculated from Eq. 5 and 11. Such a constant depletion rate throughout the lagoon is obviously an oversimplified view of a more complex pattern, but the high (80%) coefficient of determination on Eq. 11 suggests that the simplification does not introduce serious errors. The molar CO_2 change due to the precipitation or solution of $CaCO_3$ equals half the equivalents of alkalinity change (Smith and Key, 1975). Hence, the CO_2 change due to $CaCO_3$ precipitation in the lagoon can be calculated using this relationship along with Eq. 5 and 12. The calculated CO_2 utilization from calcification decreased from 21 mmoles m^{-2} day^{-1} near the pass to 14 mmoles m^{-2} day^{-1} in the back lagoon. Inspection of the regression equation in Fig. 22 suggests that this calcification relationship is a satisfactory description of the high-salinity (integrated record) samples, but that the equation underestimates calcification near the pass.

Organic carbon reactions utilizing or liberating CO_2 cannot be directly calculated from the CO_2 data, but they may be inferred from the nutrient data. Redfield *et al.* (1963) give the ratio of carbon to nitrogen to phosphorus utilization or release by marine organisms to be about 106:16:1. If organic carbon flux at Canton is to be inferred from one of the nutrient budgets, phosphorus is the appropriate nutrient to consider; the nitrogen budget may be too incomplete to be used. Let us assume that CO_2 utilization in the formation of organic carbon compounds is 100 times the phosphorus utilization (that is, about the Redfield ratio). As summarized in Table 6, organic carbon production estimates range from 7 mmoles m^{-2} day^{-1} near the pass to 3 mmoles m^{-2} day^{-1} in the back lagoon. These values represent community net excess production, because such integrated records do not separate out either daytime net production or nighttime respiration.

Unless the lagoon water is greatly enriched with phosphorus, this 100-fold conversion factor is likely to be within a factor or two of the correct value. According to Fuhs (1969), phosphorus deficiency is unlikely to occur in any medium with measurable phosphorus. If the lagoon community stores excess phosphorus, the calculation may overestimate the rate of organic carbon production. The values, however, are remarkably low, making it unlikely that the calculation overestimates net production.

The rate of CO_2 exchange across the air–sea interface may be calculated as the difference between the total CO_2 flux and the sum of calcification plus organic carbon flux. It can be seen from Table 6 that there is apparently net gas evasion (escape) from the water into the atmosphere. This evasion ranges from near 0 at the pass to about 12 mmoles m^{-2} day^{-1} in the back lagoon. This net evasion provides a method for evaluating the magnitude of gross organic carbon production in the lagoon.

Up to this point, the CO_2 budget has been treated in terms of day-to-day net changes, without direct regard for diurnal CO_2 variations from daytime net production and nighttime net respiration. Yet there is undoubtedly a diurnal variation in total CO_2 and P_{CO_2}, in response to the diurnal metabolic cycles (Schmalz and Swanson, 1969; Smith 1973; Smith and Pesret, 1974). Although the daytime P_{CO_2} averages 290 μatm, the gas exchange term of the budget indicates that the 24-hour mean P_{CO_2} must be something above 326 μatm in order to effect net evasion. Smith and Pesret (1974) summarized available data and suggested that the most appropriate CO_2 gas exchange rate coefficient for seawater is about 0.6 mmole m^{-2} day^{-1} for each μatm difference between the air and water. To account for mean evasion rate of 12 mmoles m^{-2} day^{-1}, the above coefficient demands that the 24-hour mean P_{CO_2} be approximately 20 μatm above the equilibrium value, or about 345 μatm. A nighttime mean P_{CO_2} of about 400 μatm, averaged with the daytime mean of 290 μatm yields the appropriate 24-hour average. It can be calculated that this day-to-night P_{CO_2} difference is equivalent to about 0.08 mmole/m^3 total CO_2 difference, or about 0.5 mole/m^2 through a 6.2-m water column. This relatively small diurnal range is comparable to the range observed by Smith and Pesret (1974) during a 24-hour sampling period in the lagoon at Fanning.

This mean day-to-night difference is the difference between daytime net organic carbon production and nighttime respiration. If daytime respiration equals nighttime respiration (the assumption which is almost universally made), then the CO_2 difference between day and night equals gross organic carbon production: 0.5 mole m^{-2} day^{-1}, or 6 gC m^{-2} day^{-1}. Moreover, the near-zero net excess production rate (Table 6) indicates that the 24-hour respiration rate is approximately the same as the gross production rate. That is, the gross production-to-respiration ratio of the lagoon community is near 1.0.

An alternative interpretation of the apparent CO_2 evasion against a P_{CO_2} gradient is that an error in the organic carbon term of the CO_2 budget may have carried over into the gas exchange term. That explanation is unlikely. If no gas evasion occurs, then net excess organic carbon production must be low by a factor of 5 (Table 6). In turn, that error would imply a C:P ratio of over 500:1 for the organic material being produced in the lagoon. Such a ratio would indicate extreme phosphorus limitation to production—far beyond the highest C:P ratios obtained for algal cultures in phosphorus-deficient media (Fuhs, 1969; Ketchum and Redfield, 1949). Yet Fuhs has said that any culture medium with measurable phosphorus is unlikely to be limited by that nutrient. Moreover, the observed N:P ratio (about 8.5; Table 5) does not suggest any such phosphorus limitation.

Budget of Particulate Material Flux

It is also possible to estimate the magnitude of suspended-load transfer between the open ocean and the lagoon. Water in the Canton lagoon is very turbid. This turbidity was documented by Secchi disc readings and by measurements of percent light transmission through a 1-m water column (Fig. 23). It can be seen that the Secchi disc reading decreased by about 1.5 m for each 10% reduction in light transmission. The combined data from 1972 and 1973 yielded a mean Secchi disc reading (Fig. 24) of about 5 m, corresponding to 33% light transmission through a 1-m water column. The maximum turbidity in the lagoon corresponded to 10% light transmission, and the clearest water (near the pass) had 58% light transmission.

In order to determine the major contributors to the turbidity, the suspended $CaCO_3$ content and chlorophyll *a* content of 13 water samples were compared with the light transmission data. Figure 25 shows an apparent negative exponential relationship between $CaCO_3$ and light transmission but no relationship between chlorophyll and transmission. Thus, suspended $CaCO_3$ appears to be the major contributor to the lagoon turbidity. The mean $CaCO_3$ content of the water was about 500 mg/m^3, while the mean chlorophyll *a* content of the water (including a number of samples not illustrated here) was 0.8 mg/m^3. It is assumed to a first approximation that both of these parameters are near 0 in the ocean water.

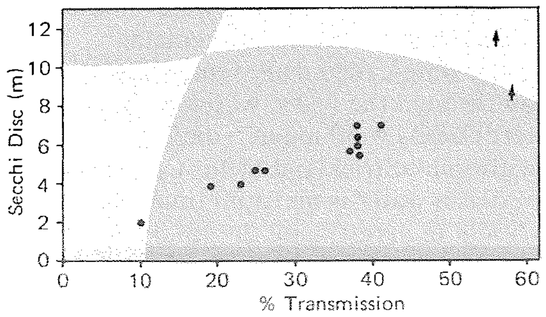
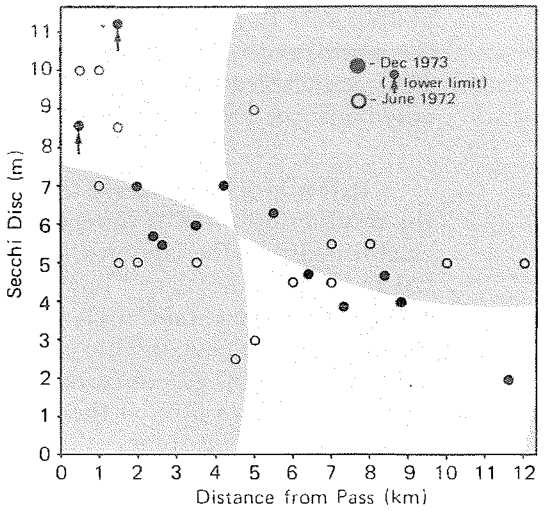


Figure 23. Secchi disc reading versus percent light transmission through a 1-m water column. (For samples indicated by arrows, the Secchi disc was visible on the sea floor.)

Figure 24. Secchi disc reading versus distance from the lagoon pass.



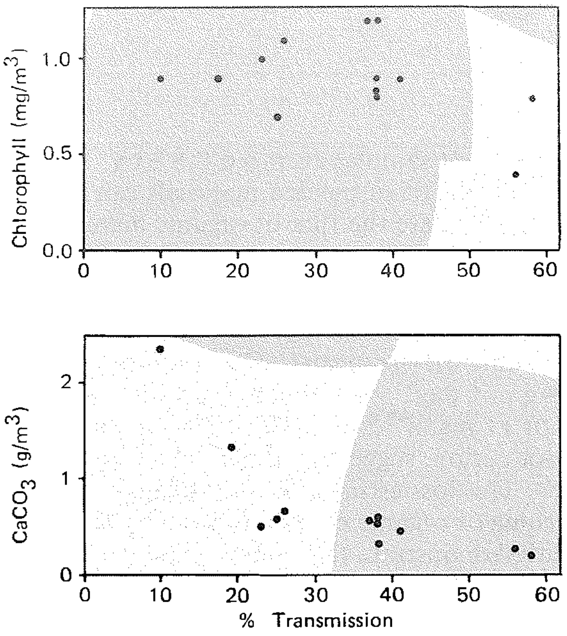


Figure 25. Chlorophyll *a* and suspended $CaCO_3$ versus percent light transmission through a 1-m water column.

Previous calculations have given the mean residence time of water in the lagoon to be about 50 days. If the suspended load concentration remains constant and is flushed proportionally to the water, then daily removal rates of these materials will be their concentration through the 6.2-m water column divided by the residence time of the water: $CaCO_3$ = 60 mg m^{-2} day^{-1}; chlorophyll *a* = 0.1 mg m^{-2} day^{-1}. Data given by Strickland (1965) suggest that the particulate organic carbon content of ocean water is up to 60 times the chlorophyll *a* content. This conversion should underestimate the total particulate organic carbon load, because it does not account for chlorophyll-free detrital material. Comparison of the Fanning lagoon organic carbon and chlorophyll *a* data (Gordon, 1971, and Krasnick, 1973, respectively) suggests that the appropriate conversion factor for lagoon systems may be as high as 200. Thus, something in excess of 6 and perhaps as much as 20 mg organic C/m^2 may be flushed from the lagoon each day.

It is useful to compare these rates of particulate-matter flushing with the production rates of inorganic and organic carbon. The budget in Table 6 established that the lagoon-wide utilization of CO_2 for net precipitation of $CaCO_3$ is 14 mmoles m^{-2} day^{-1} (1.4g $CaCO_3$ m^{-2} day^{-1}). It appears that only about 4% of the total $CaCO_3$ produced in the lagoon escapes as suspended material. Net excess organic carbon production is about 3 mmoles m^{-2} day^{-1}. Multiplication by 12 converts this value to mg organic carbon: 36 mg m^{-2} day^{-1}. Therefore 17% to 56% of the net organic carbon production appears to be flushed from the system.

Organic Material in Lagoon Sediments

The organic carbon content of 16 sediment samples averaged 0.8% by weight (standard deviation = 0.4%). The budgets of suspended materials can be used with these organic carbon analyses to calculate the flux of organic materials into the sediments and from the lagoon.

To a first approximation, no $CaCO_3$ is lost from the lagoon; it is all deposited there. From the CO_2 budget (Table 6), the mean $CaCO_3$ deposition rate in the lagoon is therefore about 1.4 g m^{-2} day^{-1}. The organic carbon deposition is about 0.8% of this figure, or 11 mg $m^{-2}$$day^{-1}$. This figure is about 30% of the net excess organic carbon production, suggesting that 70% of this production must be lost from the lagoon. This loss estimate is only slightly higher than the upper figure for the flushing of organic carbon as given by the suspended-load data. The two values both demonstrate that most of the net excess organic carbon produced in the lagoon does not accumulate there.

DISCUSSION

Organic Carbon Metabolism

With respect to all biogeochemical flux parameters either measured or inferred, the Canton lagoon community shows distinct gradients of decreasing rates with increasing distance from the lagoon pass. These biogeochemical gradients provide a record of the events which occurred in the lagoon during and immediately preceding this survey. The patterns observed are in general accord with both the present distribution of biota in the lagoon and the past distribution as inferred from the distribution of reef structures. A variety of explanations might be offered for the maintenance of these patterns over some period of time. We suspect, however, that the pattern is general confirmation of the notion that water movement favors the growth of coral reefs.

There are clues that water motion is, of all the parameters acting on the system, the major one. Standing crops of fishes and corals are greatest near the pass, where tidally induced water flow is the greatest (Henderson and Grovhoug, this report; Jokiel and Maragos, this report). The richest reefs can be visited safely only during slack tides. By contrast, reefs of the Altered Zone (Frontispiece) are low in both fish and coral standing crops, and experience little water motion. These reefs have obviously been recently damaged, probably by altered circulation. Extensive dredging operations about 1943 closed several small passages along the northwestern side of the lagoon, altered the configuration of the main pass, and cut seaplane runways through patch and line reefs near the main pass (Henderson *et al.*, this report). These operations apparently did not alter the total water flow to and from the lagoon; the present lagoon tidal range is about the same as that of the adjacent ocean. However, the patterns of water flow, and perhaps the net exchange rate between the ocean and the lagoon, have been altered. Almost certainly, the Altered Zone has experienced the greatest change in circulation.

Various aspects of water and sediment composition might be implicated in the limitation of lagoon reef development at Canton. The most conspicuous candidates for limiting reef development are salinity, nutrients, turbidity, light, and deposition of calcareous mud on substrata which might otherwise be available for reef development. All of the above properties progressively deviate from ocean-reef values with increasing distance into the lagoon from the single pass. However, there is evidence that water motion exerts a more direct influence on the reef biota than do any of the above variables. Indeed, decreasing water motion may be viewed as the major cause for the gradients observed in the above parameters.

The lagoon salinity ranges from about 36 to 40 o/oo, outside the 34–36 o/oo range considered by Wells (1957) to be optimal for coral growth. Yet, luxuriant reefs in the Red Sea at salinities up to 42 o/oo have been reported by Loya and Slobodkin (1971).

Both nitrogen and phosphorus are often considered to be materials which may limit metabolic activity of biological systems. The data presented here suggest that the net uptake ratio of dissolved inorganic nitrogen and phosphorus from the lagoon water (8.5:1) is slightly above the relative ratios of those materials in the water entering the lagoon (about 6.4:1); that is, if this uptake rate were maintained, nitrogen would be exhausted slightly before phosphorus. We suspect that neither of these materials alone limits metabolism in the Canton lagoon, nor perhaps in most other coral reef ecosystems.

Turbidity, light, and the deposition of fine sediments represent a complex interaction of factors which have been suggested to limit reef development in other areas. Analogy with the reefs in the lagoon of Fanning Atoll suggests that such limitation is not the case at Canton. Roy and Smith (1971) report that the Fanning lagoon reefs are much richer than those at Canton; yet the water is actually more turbid at Fanning. Calcium carbonate production rates in the two systems (Smith and Pesret, 1974; this paper) suggest that the sediment production rate, and by implication the deposition rate, is perhaps twice as fast at Fanning as at Canton.

Water motion has been suggested by Munk and Sargent (1954), Wells (1954), and many other authors to be an important variable in the development of coral reefs. Riedl (1971) argues that water motion is not an environmental parameter in its own right but is a transportation medium for other materials. A variety of suggestions has been offered to explain the roles of water motion in favoring the growth of coral reefs. Perhaps the most recurrent of these suggested roles have been that the flow of water supplies food, aids in the diffusion of dissolved materials, dissipates heat, transports larvae, removes waste products, and alleviates smothering by sediments. All of these suggestions are undoubtedly valid, and the list could be expanded.

Water motion also provides a substantial subsidy of energy to an ecosystem in addition to that provided by solar radiation. The tidal energy to change the water level in the Canton lagoon may be calculated to be about ten times the caloric input from net organic carbon production,* and energy input into the

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*The input of tidal energy may be approximated by the formula for kinetic energy (K): K equals the mass of water raised or lowered times the acceleration of gravity times the height the water is raised or lowered. The mass of the tidal head per square meter is 700 kg, and the water is raised and lowered twice the mean tidal range (0.7 m) daily. So K is 19×10^4 joules m^{-2} day^{-1}, or about 5 Kcal m^{-2} day^{-1}. The energy associated with a net organic carbon production of 40 mg C m^{-2} day^{-1} is about 10 Kcal per gram of carbon, or 0.4 Kcal m^{-2} day^{-1} (Whittaker and Likens, 1973).

lagoon by wind stirring is not even numerically considered here. Even if only a small percentage of this mechanical energy can be utilized by organisms which would otherwise either move water or move through it in order to serve the roles enumerated above, this subsidy is substantial. In the absence of adequate evidence to demonstrate which aspects of water motion might be the most important, its function may be viewed as that of a generalized transfer coefficient. In any water mass, increased motion will enhance the transfer of materials used or discarded by the biota. This transfer may be considered a subsidy to input of solar radiation. The input of mechanical energy is not evenly distributed throughout the lagoon. Clearly, tidal energy decreases with distance from the pass, and wind energy decreases with water depth. Thus, shallow reefs near the pass are favored by this energy subsidy. Local depressions in the shallow reefs most effectively "channel" the flow of water and support vigorous reef communities. In some portions of the seaward reefs, water motion (energy) may be so great that organisms are excluded or destroyed by mechanical damage. For example, Munk and Sargent (1954) report a mean annual discharge of 8 hp/ft of reef front against the northeast (windward) face of Bikini Atoll. If this power is dissipated over a depth of 20 m on a 30-degree slope (that is, to approximately the 10-fathom terrace), then it is equivalent to an energy input of about 10^4 Kcal m^{-2} day^{-1} against that face—about 2,000 times the mean energy input we postulate for the Canton lagoon. Examination of a windward fore-reef spur at Enewetak Atoll demonstrates these spur and groove structures to be largely the product of erosion (Buddemeier *et al.*, 1975), at least to water depths of about 5 m.

The budget of organic carbon production does not indicate what component of the community is principally responsible for the production. It seems likely that even in the lagoon primary production is dominated by the benthos. In summarizing plankton production rates for reef lagoons, Gordon *et al.* (1971) reported no value higher than about 1 g C m^{-2} day^{-1}. If a gross production-to-respiration ratio of 2 is assumed for plankton communities, then this net production is equivalent to a gross production of about 2 g C m^{-2} day^{-1}. This figure is substantially below the gross production rate calculated for Canton (6 g C m^{-2} day^{-1}). It therefore seems likely that the plankton are not the major producers of that lagoon community.

Canton and indeed several other atolls throughout the equatorial Pacific Ocean are exposed to some of the highest major inorganic nutrient levels to be found in open ocean surface waters (compare the phosphate map of Reid, 1961, with the coral-reef distribution map of Wells, 1957). Under such circumstances it is reasonable to suppose that neither phosphorus nor nitrogen would limit reef metabolism. Alternative micronutrients are demonstrably important to the productivity of phytoplankton in the open ocean (for example, iron; Menzel and Ryther, 1961), and have been suggested to be important in the distribution of some reef algae (for example, *Sargassum*; Doty, 1954; DeWreede, 1973).

These micronutrients might not correlate well with nitrogen and phosphorus, because the micronutrients are largely supplied from local sources, such as the trace metals found in the rocks of high volcanic islands.

Available data suggest that the productivity of atolls is probably similar to that of high-island reefs (compare the data in Marsh, 1974, and Kohn and Helfrich, 1957, with the summary data in Smith and Marsh, 1973). Critical materials may be cycling more rapidly within atoll systems than high-island reefs. Grazing activity (for example, by fishes; Bakus, 1969) is of considerable importance in this recycling—perhaps far beyond the energetic importance of the organisms in question.

The dissolved inorganic nitrogen and phosphorus budgets of the Canton lagoon both show that the community utilizes these materials, hence that the community is autotrophic. The slowness of the net uptake rates in comparison to the high gross production rate demonstrates that the margin of community autotrophy is remarkably slender. In fact, the low net excess production observed for the total lagoon (about 40 mg C m^{-2} day^{-1}) is somewhat below the frequently quoted net production rate for the open ocean (100 mg m^{-2} day^{-1}; Ryther, 1969). Because of the high oceanic nutrient levels near Canton, the net excess production of the ocean planktonic community there may well exceed this value by a considerable margin.

Despite the very low net excess production of the Canton lagoon community, there apparently is net export of organic carbon from the atoll to the open ocean. This conclusion is supported both by the composition of materials suspended in the water column and by the sediment composition. If there were not such export, the sediments should have about 2.5% by weight organic carbon; instead, they average about 0.8%. In constructing a carbon budget for the Bahama Banks, Broecker and Takahashi (1966) noted an apparent discrepancy between the budgetary implications of net organic carbon production and the observed sediment composition. They concluded that their budget was not properly balanced. This does not seem to be the case at Canton, and it may not have been true for the Bahamas budget either. The suspended-load data discussed here suggest that there may be substantial removal of organic material from the lagoon, with relatively little $CaCO_3$ loss. A variety of explanations might be offered for this phenomenon; those given below seem the most reasonable.

In the first place, $CaCO_3$ precipitated by the benthos in the lagoon is less likely than organic carbon to be dislodged from the lagoon floor by either mechanical or biological activity and then to become suspended in the water column. Organic material, once suspended, is less dense than the $CaCO_3$ and will stay in suspension longer. Hence, particulate organic carbon is more susceptible to flushing from the system than is inorganic carbon. Moreover, one major component of the organic carbon inventory in the lagoon has not even been evaluated in these budgets—dissolved organic carbon. This material would also be easily flushed from the system. Indeed, it would be surprising if there were not more organic carbon lost than inorganic carbon.

The suggested export of up to 70% of the excess organic carbon produced in the lagoon makes the narrow autotrophic margin of the lagoon community all the more remarkable. Most of the excess production which does occur does not accumulate but leaks from the system. The gross organic carbon production of the Canton lagoon is almost 10^5 tons/yr. The net excess organic carbon production of the lagoon amounts to approximately 550 metric tons/yr. Of that net production, about 400 tons is lost to the ocean, and the remainder (0.2% of the gross production) accumulates with sediments on the lagoon floor.

Depositional History

The $CaCO_3$ production rate in the lagoon is about 500 g m^{-2} yr^{-1} (Table 6). This rate is about 10 to 15% of the rates which have been reported by the same alkalinity-depletion technique for reef flats (Smith, 1973; Kinsey, 1972), about half the rate found in the Fanning Atoll lagoon (Smith and Pesret, 1974), and the same as the rate reported by Broecker and Takahashi (1966) for the Bahama Banks. If it is assumed that the sedimentary materials being produced have a dry-weight density of about 1.4 g/cm^3 (that is, about 50% porosity), and that none of the material being produced is lost from the lagoon, then this production rate at Canton is equivalent to a mean vertical deposition rate of about 0.3 mm/yr. World-wide mean sea level is presently changing little, if at all (Curray *et al.*, 1970); there is no reason to suspect that large vertical tectonic movements have occurred at Canton.* Therefore, the lagoon floor at Canton is probably not shoaling by more than this small increment. There probably is a balance between "too much" production on the reefs and "too little" production on the lagoon floor. Erosion (largely biological) allows redistribution of materials throughout the lagoon.

Prior to about 8,000 years ago, sea level was rising at a rate approaching 2 cm/yr (Curray *et al.*, 1970). Under such conditions, it is inconceivable that reefs resembling those presently found in the Canton lagoon could have produced sufficient sediment to maintain the lagoon floor at a constant depth

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*There are morphological features which suggest that there may have been as much as a 2-meter high-stand (possibly local) of sea level at Canton within the last several thousand years. This uncertainty is within the range of present debate about eustatic changes and is of no direct concern here.

relative to the rising sea level. In fact, even if such reefs were not being eroded, they probably still could not have maintained themselves at sea level. Yet the reef structures probably do not greatly antedate the present general island morphology. The shape of the reefs appears related to water flow to and from the lagoon.

The entire reef configuration in the lagoon today therefore appears to be less than 8,000 years old, and these reefs have probably grown up from a base approximated by the present maximum depth found in the lagoon (about 25 m). Topographic details of the base cannot be inferred from the present topography. This amounts to a lagoon infilling of about 20 m in 8,000 years, or an average of 2.5 mm/yr.

If this interpretation is substantially correct, then the growth of the reefs in the lagoon has slowed considerably as the lagoon has become clogged with reef structures. One or more passages have existed along the southeast rim of the atoll until relatively recently and have been blocked by the formation of beach ridges or by slight oscillations in relative sea level or by both. The maximum initial rate of reef growth making this model feasible is about 5 mm/yr if the slowdown from that maximum rate has been constant with time. This maximum rate is consistent with the rates which Smith (1973) and Kinsey (1972) have reported for shallow reef environments elsewhere.

Mechanisms governing $CaCO_3$ production rate in the Canton lagoon are probably similar to those which limit organic carbon production. Corals are the most conspicuous calcifying organisms in the lagoon, if not the major ones. The distribution of corals obviously is sensitive to location (Jokiel and Maragos, this report). The growth rates of a few individual coral heads from Canton have been determined by means of x-radiography (R. Buddemeier, personal communication), and these rates do not appear to be directly sensitive to the location from which the coral was collected. Hence, the $CaCO_3$ production rate of the lagoon seems more nearly related to the standing crop of calcifying organisms than to variations in the calcification rates of individual taxa.

The Canton lagoon CO_2 system bears one major contrast with that of Fanning lagoon. Fanning lagoon water was found to be approximately saturated with aragonite, and that saturation state was suggested as a possible factor limiting the $CaCO_3$ production rate there (Smith and Pesret, 1974). At Canton, the calculated saturation state of the water with aragonite remains relatively constant throughout the lagoon, near 200% saturated ($CaCO_3$ ion activity product $\approx 10^{-7.9}$). It thus appears that the rate at which $CaCO_3$ is precipitated in that lagoon approximately matches the increase in $CaCO_3$ ion activity product from evaporation.

SUMMARY AND CONCLUSIONS

Much of the budgetary analysis presented here is highly speculative, and this speculation is offered without apology. The budgets provide a rapid overview of a poorly known environment which constitutes a major portion of coral atolls. Such an overview gives little attention to biological detail; that detail can follow, using the overview as a framework on which to build.

This investigation was undertaken as part of an environmental survey of the Canton lagoon. The budgets provide bases for environmental assessment. The major environmental characteristics suggested by the budget are summarized below.

Evaporation, rainfall, and salinity provide the basis for estimating the residence time of water in the lagoon. Salinity increases from net evaporation as water ages in the lagoon. The mean residence time of water in the lagoon is about 50 days, while the oldest water remains in the lagoon about 95 days.

The productivity of the Canton lagoon community is probably not limited by the major inorganic plant nutrients (nitrogen and phosphorus). Both of these materials are present at high concentrations in water entering the lagoon, and neither is exhausted while the water ages in the lagoon. The net utilization of nutrients demonstrates that the lagoon community is autotrophic, and the slow rate of utilization demonstrates that the margin of autotrophy is narrow. Lagoon-wide phosphorus utilization is about 0.027 mmole m^{-2} day^{-1}, and nitrogen utilization is about 8.5 times this rate.

Net organic carbon production can be inferred from the phosphorus budget to be about 3 mmoles m^{-2} day^{-1}, or about 36 mg C m^{-2} day^{-1}. This rate is probably near the net organic carbon production of the open ocean adjacent to the atoll. Gross organic carbon production is about 6 gC m^{-2} day^{-1}, comparable to rates which have been estimated for coral reef flats elsewhere and over 100 times the net production. Thus, the lagoon maintains a remarkably close balance between the production and consumption of organic compounds. Both the suspended load and the sediments suggest that most of this small excess of organic carbon which is produced is flushed from the lagoon rather than being incorporated into the sediments. Yet the amount of flushed material is a trivial fraction of the gross production.

The rate at which the lagoon community produces calcareous material is much slower than $CaCO_3$ production rates reported for other portions of coral atolls. It appears likely that the lagoon reefs have developed within the last 8,000 years and have filled the lagoon with up to 20 m of sedimentary materials.

The standing crop of organisms in the lagoon is obviously related to local variations in water motion within the lagoon. Net and gross organic carbon production and the production of $CaCO_3$ are also apparently related to this motion. Aside from purely mechanical destruction, the only extensive human damage to the lagoon community appears to be associated with local reduction of water motion within the lagoon. Such artificial damage is minor in comparison with the pervasive geological history of progressive lagoon infilling, enclosure, and restriction of circulation.

Perhaps the most conspicuous attribute of the Canton lagoon material balance is the efficiency with which the system retains materials once formed. In the case of organic materials, this retention is accomplished by virtually complete recycling of materials, with almost no loss of these materials back to the open ocean or to the sediments on the lagoon floor. The small loss which does occur is balanced by the continued uptake of materials from ocean water which flows into the lagoon. Inorganic materials are precipitated and deposited, leading to a gradual infilling of the lagoon with calcareous sediments.

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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.

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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)

(Contd)

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
+☆*Stylaster* sp. cf. *S. elegans* Verrill
☆*Tubastraea coccinea* Lesson
☆*Tubastraea ciphans* (Dana)
Turbinaria sp. cf. *T. irregularis* Bernard – M

☆Ahermatypes
+Hydrozoan corals

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).

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*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 Quelch[1]
Montipora aequi-tuberculata Bernard[2]
M. granulata Bernard[2]
M. informis Bernard
M. venosa (Ehrenberg)
Pavona clivosa Verrill[3]
P. minuta Wells
P. (Polyastra) sp.[4]
Plesiastrea versipora (Lamarck)
Platygyra daedalea (Ellis & Solander)[5]
Pocillopora elegans Dana[6]
P. setchelli Hoffmeister[7]
Porites australiensis Vaughan[8]
P. fragosa Dana[8]
P. solida (Forskaal)[8]
P. (Synaraea) hawaiiensis Vaughan

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

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

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

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

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

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

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

[8] We 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).
+Recorded from Canton only (Wells, unpublished; this report).

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.

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 x 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

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*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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REEF CORALS OF CANTON ATOLL: II. LOCAL DISTRIBUTION

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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.

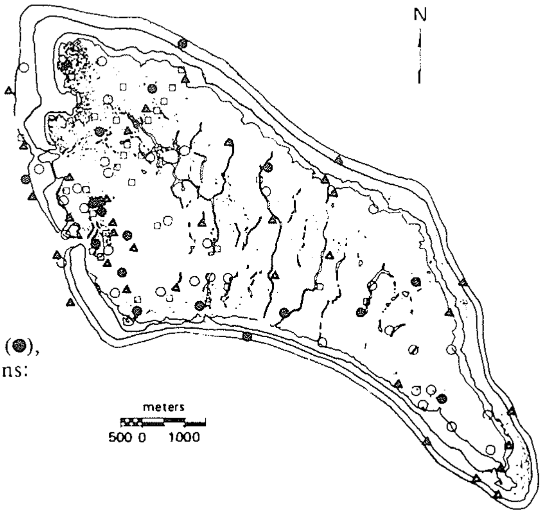


Figure 26. Coral survey stations. Qualitative inventory and specimen collections: June 1972 (●), Sept. 1973 (▲), Dec. 1973 (○). Transect locations: Sept. - Dec. 1973 (□).

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.

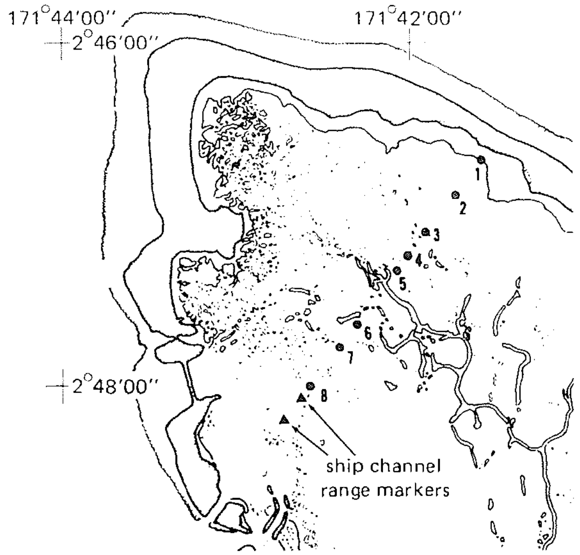


Figure 27. Coral, water chemistry and substratum stations along the range transect.

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

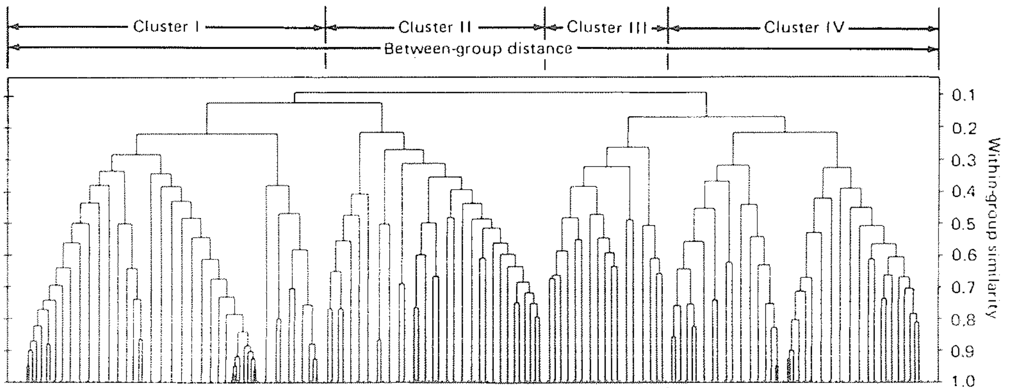
Atoll-Wide Survey

Similarity indices (I) were computed for all sample pairs by using a quantitative modification (Motyka *et al.*, 1950) of the Søensen Similarity Index (Søensen, 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.



Numbers of samples in each cluster from each zone

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)

Interpretation

Line reef	Altered	Ocean reef	Pass	Zone
Millepora → *Millepora* + *Porites*	Few, mixed species, low coverage	Highly diverse, high coverage	*Pocillopora meandrina* / *Acropora formosa*	Dominant species
Physically controlled		Biologically accommodated		Major influence

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.

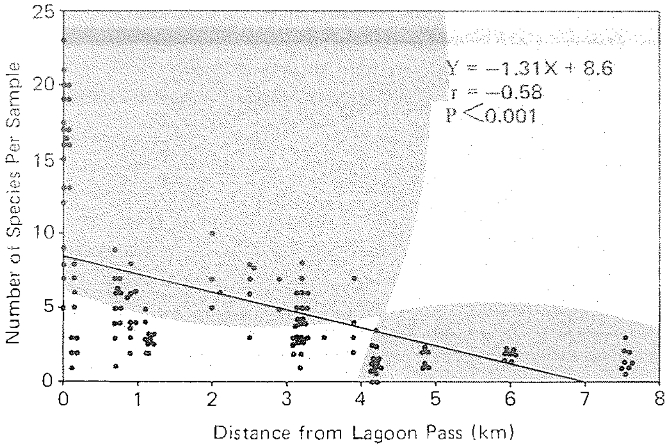


Figure 29. Relationship between number of coral species per sample and distance from pass for all ocean and lagoon samples.

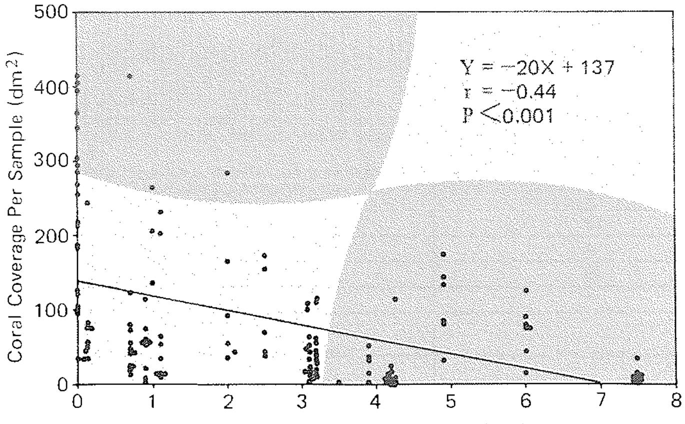


Figure 30. Relationship between coral coverage and distance from pass for all ocean and lagoon samples.

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.

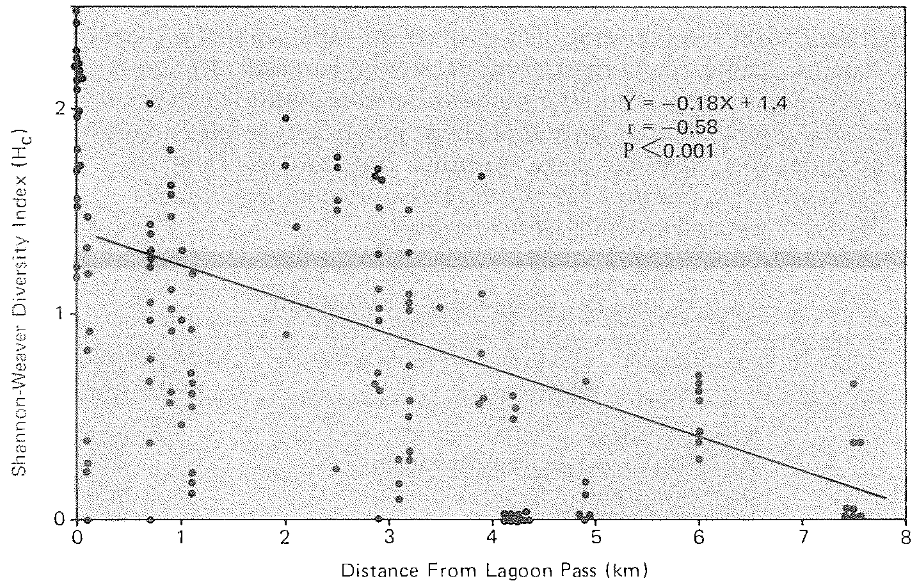


Figure 31. Relationship between Shannon-Weaver diversity index and distance from the pass.

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 ($^{0}/oo$)	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.

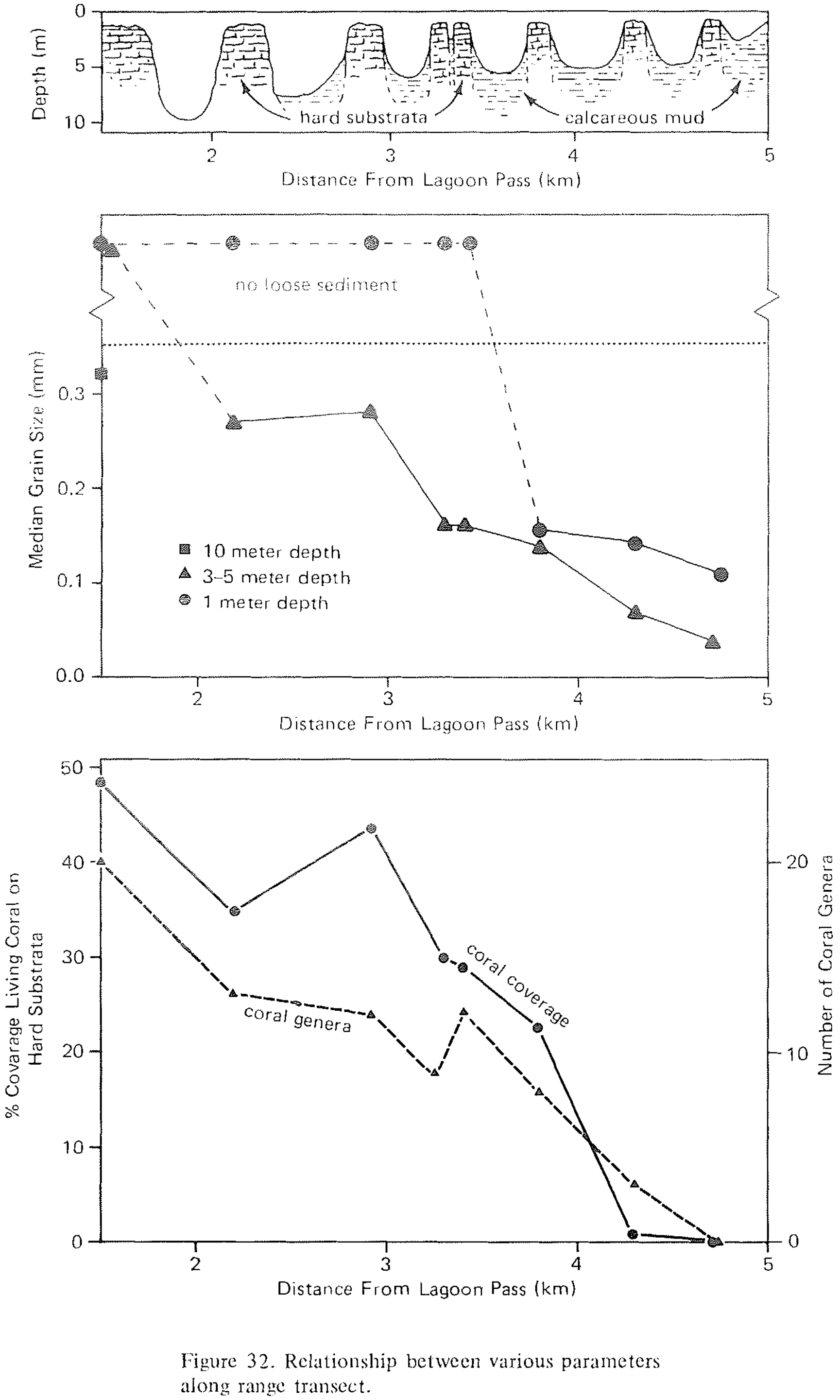


Figure 32. Relationship between various parameters along range transect.

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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DISTRIBUTION OF INSHORE FISHES AT CANTON ATOLL

by

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and
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ABSTRACT

Inshore fishes at Canton were surveyed by visual sampling during a 2-week period in November and December 1973. Data from this survey expand the cumulative checklist for Canton Atoll fish species to 264 species from 50 families. The distribution of inshore fishes was analyzed from transect data, and 20 species were selected for representative distributional display. Several representative patterns of fish distribution emerge. Fish abundance (both individuals and species) is highest immediately outside and in the pass region. In the lagoon, abundance decreases with increasing distance from the pass.

ACKNOWLEDGMENTS

We are grateful for diving locker support from members of the Canton Diving Club and to Ed Bennett, who provided boat maintenance throughout the survey. Special thanks are given to Chuck Peterson, NUC photographer, who freely contributed his time not only to provide complete photographic documentation of the survey, but also to perform a variety of additional supportive tasks. Dr. John E. Randall of the B. P. Bishop Museum, Honolulu, provided assistance in the taxonomic identification of certain fishes. Other members of the general survey team graciously assisted Inshore Fish Survey efforts.

INTRODUCTION

There have been few studies describing the fish fauna of the Phoenix Islands. Schultz (1943) collected 208 species of fishes belonging to 45 families from Canton, Hull, and Enderbury Atolls during the 1939 expedition of the USS Bushnell. Most of that sampling was accomplished by seining and rotenone poisoning; consequently those collections were heavily weighted with species which are members of bottom-dwelling, inconspicuous (cryptic or nocturnal) groups, such as gobies, blennies, and ophichthid eels. Halstead and Bunker (1954) conducted toxicity tests on more than 93 species of fishes (identifications for scarids and labrids were incomplete) from Canton, Enderbury, Hull, and Sydney Atolls from December 1950 through April 1951. Fishes were collected for that study by hook and line, beach seine, spear, throw net, dip net, and rotenone poisoning.

The above studies provide useful general background information; however, these studies do not present quantitative distributional data. Distributional data for other coral atolls have recently been gathered by various visual transect methods. Fishes are often collected for identification and analyzed for specific food preferences when possible. Chave and Eckert (1974) conducted such a study at Fanning Atoll and discuss fish distributions in terms of seven general habitat types. Losey (1973) undertook a similar study at Kwajalein Atoll. Jones and Larson (1972) have conducted transecting studies around Guam and other Micronesian islands.

The purposes of this study are to expand the species list from Canton Atoll and to examine fish distribution within and immediately outside the atoll lagoon. Some explanations for observed distributional patterns are included.

METHODS

During the inshore fish survey, two visual methods of assessing fish species distribution and abundance were used. In areas having high fish diversity and abundance, a weighted 30-m transect line was laid across the bottom; for locations having varied relief and substrata (such as patch reefs or along an outer reef shelf), the transect line was oriented so that it crossed a representative variety of habitats. Biologists with scuba gear swam along either side of the transect line, recorded numbers of individuals, and estimated average lengths (standard lengths, in centimeters) for all observable species. Figure 33 illustrates this transecting procedure. Each biologist counted fishes within an approximately 2-m-wide by 3-m-high corridor adjacent to his side of the line. Counts by the two divers were combined (see the Appendix). The area sampled along each transect was approximately 120 m^2; water volume was about 360 m^3. Use of such a small corridor minimized the effects of reduced visibility, which could invalidate inter-area comparison. The nine stations inventoried in this manner were designated "fish transect stations" and are marked with an "FT" prefix in the Appendix.

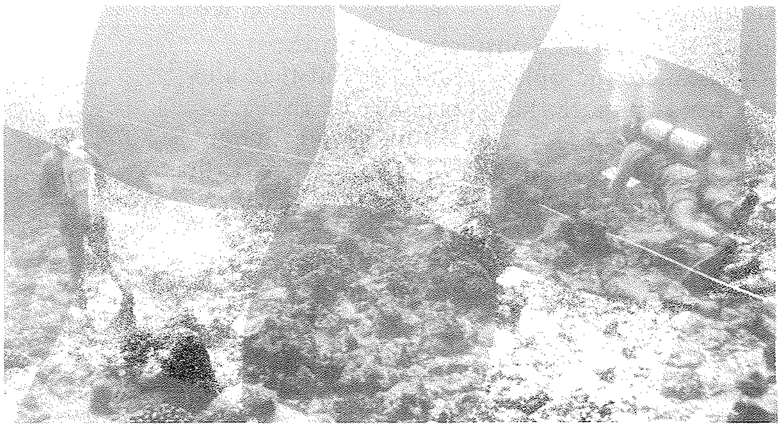


Figure 33. Biologist conducting a fish transect at ocean station.

In areas of low fish abundance (typically intertidal ocean reef shelf and nearshore shallow lagoon sand flats), scuba gear and transect line were not used. Two biologists with snorkeling gear swam along a path of predetermined length and orientation, recording species present (with notes on abundance and length). At three nearshore shallow-water stations, observations were made by wading along the shore. Fifteen such snorkeling and wading stations ("fish observation stations") are labelled "FO" or "FO (w)" in the Appendix. Locations of sampling stations are shown in Fig. 34.

For most transects and observations, a "horizontal identifiable visibility" (HIV) was estimated. The HIV is defined as "the maximum distance through the water (in a horizontal plane) at which a stationary or slow-moving fish (10 cm or longer) can be readily seen and identified by a competent diving biologist, that is, one familiar with the fish fauna of the area under study," Evans (1973). Such HIV values, although subjective, provide data useful for survey intercomparisons and are therefore included in the Appendix. Bottom profiles and composition, dominant coral types and coverage, current characteristics, and other incidental observations are also included in the station descriptions.

Most species encountered could be identified in the field, or described sufficiently well for subsequent identification. Specimens of some species were speared to enable later positive identification. One acanthurid (surgeonfish) could not be identified with existing keys. That specimen was given to Dr. John E. Randall (Bernice P. Bishop Museum, Honolulu). Randall has other specimens of this same species from Washington Island (Line Island Group). He is presently describing these as a new species. The specimen from Canton will be used as a paratype. Two specimens of *Dascyllus trimaculatus* (three-spot damselfish) were also given to Randall. These will probably be described as Phoenix and Line Island color variants of that species.

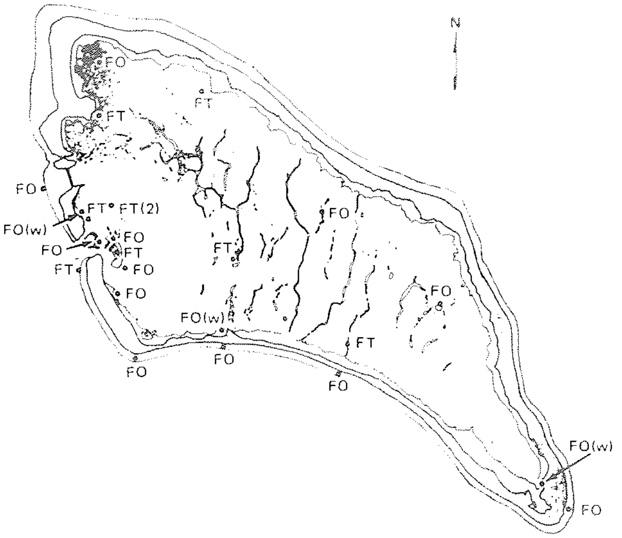


Figure 34. Fish survey stations. FT = fish transect; FO = fish observation (snorkeling); FO (w) = fish observation (wading).

RESULTS

General Distributional Patterns

From the 24 fish transect and fish observation stations, 146 species were observed (see checklist, Table 20); 61 species were new reports for the Phoenix Islands. These records, with the data from Schultz (1943) and Halstead and Bunker (1954), bring the new total to 264 species from 50 families. These numbers are comparable with inshore fish fauna data gathered in other Central Pacific Island groups. The Phoenix Islands are a major component of the Central Pacific faunal "subregion," which includes the Marshall, Gilbert, Line, and Hawaiian Island groups. This subregion is the northeastern component (described by Gosline, 1971) of the extensive Indo-West Pacific faunal region. Strasburg (1953) reported 250 species belonging to 51 families from the southern Marshalls at Arno Island. Randall (1955) recorded 396 species of inshore marine and pelagic fishes from the Gilbert Islands. Gosline (1971) reported 235 species belonging to 40 families from the Line Islands; Chave and Eckert (1974) reported 217 species belonging to 37 families from Fanning Atoll alone. Brock *et al.* (1965) reported 184 species belonging to 46 families from Johnston Island. Gosline and Brock (1960) listed 448 species of inshore or surface-living species from the Hawaiian Islands.

Table 20. Checklist of fishes observed during the 1973 Canton Atoll survey.

Group/Species*	Hawaii Coastal Zone Data Bank No.**
Chlordata/Vertebrata	
Chondrichthyes	
Lamnida	
Carcharinidae	
Carcharhinus melanopterus (Quoy and Gaimard)	8516120501
Hypotremata	
Dasyatidae	8517090000
Mobulidae	
Manta sp.	8517110200
Osteichthyes	
Elopiformes	
Albulidae	
Albula vulpes (Linnaeus)	8521060101
Anguilliformes	
Muraenidae	
Gymnothorax pictus (Ahl)	8522050603
Gymnothorax flavimarginatus (Rüppell)	8522050605
Gymnothorax meleagris (Shaw and Nodder)	8522050606
Salmoniformes	
Synodontidae	8531470000
Gonorynchiformes	
Chanidae	
Chanos chanos (Forsskål)	8533060101
Atheriniformes	
Exocoetidae	
Cypselurus spilonopterus (Bleeker)	8544010603
Hemiramphid sp.	8544015000
Beryiciformes	
Holocentridae	
Adioryx spinifer (Forsskål)	8546180101
Adioryx lacteoguttatus (Cuvier)	8546180103
Adioryx caudimacula (Rüppell)	8546180111
Adioryx violaceous Bleeker	8546180116
Myripristis murdjan (Forsskål)	8546180403
Myripristis amaenus (Castelnau)	8546180404
Myripristis kuntee (Cuvier and Valenciennes)	8546180405
Flammeo sammara (Forsskål)	8546180501
Gasterosteiformes	
Aulostomidae	
Aulostomus chinensis (Linnaeus)	8549060101
Fistulariidae	
Fistularia sp.	8549070100
Syngnathidae	8549120000
Scorpaeniformes	
Scorpaenidae	
Pterois antennata (Bloch)	8552010202

(Contd)

Table 20. (Contd)

Group/Species*	Hawaii Coastal Zone Data Bank No.**
Perciformes	
Serranidae	
Serranid sp.	8554020000
Epinephelus merra Block	8554020306
Epinephelus microdon (Bleeker)	8554020314
Cephalopholis argus Bloch and Schneider	8554020801
Cephalopholis urodelus (Bloch and Schneider)	8554020802
Gracila albomarginatus (Fowler and Bean)	8554021001
Anyperodon leucogrammicus (Valenciennes)	8554022001
Kuhliidae	
Kuhlia sp.	8554140100
Apogonidae	
Cheilodipterus quinquelineata Cuvier and Valenciennes	8554180501
Carangidae	
Scomberoides sancti-petri (Cuvier)	8554290101
Elegatis bipinnulatus (Quoy and Gaimard)	8554290201
Gnathanodon speciosus (Forsskål)	8554290801
Caranx melampygus Cuvier and Valenciennes	8554291204
Caranx sp.	8554291200
Lutjanidae	
Lutjanid sp.	8554380000
Aprion virescens Valenciennes	8554380401
Lutjanus bohar (Forsskål)	8554380701
Lutjanus monostigma (Cuvier and Valenciennes)	8554380703
Lutjanus fulvus (Bloch and Schneider)	8554380704
Lutjanus kasmira (Forsskål)	8554380705
Lethrinus sp.	8554380800
Sparidae	
Monotaxis grandoculis (Forsskål)	8554450101
Gnathodentex aureolineatus (Lacépède)	8554450201
Mullidae	
Mulloidichthys samoensis (Günther)	8554470201
Mulloidichthys auriflamma (Forsskål)	8554470202
Parupeneus bifasciatus (Lacépède)	8554470306
Parupeneus barberinus (Lacépède)	8554470307
Parupeneus trifasciatus (Lacépède)	8554470309
Parupeneus sp.	8554470300
Kyphosidae	
Kyphosus cinerascens (Forsskål)	8554530101
Chaetodontidae	
Forcipiger longirostris (Broussonet)	8554570402
Heniochus acuminatus (Linnaeus)	8554570502
Heniochus permutatus Cuvier	8554570503
Heniochus varius (Cuvier)	8554570504
Chaetodon kleini Bloch	8554570703

(Contd)

Table 20. (Contd)

Group/Species*	Hawaii Coastal Zone Data Bank No.**
Chaetodontidae (continued)	
Chaetodon ephippium Cuvier	8554570705
Chaetodon auriga Forsskål	8554570706
Chaetodon unimaculatus Bloch	8554570707
Chaetodon lunula (Lacépède)	8554570708
Chaetodon trifasciatus Mungo Park	8554570710
Chaetodon ornatissimus Solander	8554570711
Chaetodon quadrimaculatus Gray	8554570712
Chaetodon ulietensis Cuvier and Valenciennes	8554570717
Chaetodon semeion Bleeker	8554570718
Chaetodon meyeri Bloch and Schneider	8554570719
Chaetodon bennetti Cuvier	8554570720
Megaprotodon strigangulus (Gmelin)	8554570801
Centropyge loriculus (Günther)	8554575304
Centropyge flavissimus (Cuvier)	8554575305
Centropyge bicolor (Bloch)	8554575308
Pygoplites diacanthus (Boddaert)	8554575401
Pomacentridae	
Dascyllus aruanus (Linnaeus)	8554640102
Dascyllus trimaculatus (Rüppell)	8554640104
Abudefduf sordidus (Forsskål)	8554640201
Abudefduf imparipennis (Sauvage)	8554640203
Abudefduf phoenixensis Schultz	8554640205
Abudefduf glaucus (Cuvier and Valenciennes)	8554640208
Abudefduf septemfasciatus (Cuvier and Valenciennes)	8554640209
Abudefduf amabilis (De Vis)	8554640210
Plectroglyphidodon dickii (Lienard)	8554640302
Pomacentrus albofasciatus Schlegel and Muller	8554640402
Pomacentrus coelestis Jordan and Starks	8554640403
Pomacentrus nigricans (Lacépède)	8554540405
Pomacentrus sp.	8554640400
Chromis margaritifer Fowler	8554640507
Chromis caeruleus (Cuvier and Valenciennes)	8554640512
Chromis sp.	8554640500
Amphiprion chrysopterus Cuvier	8554640607
Amphiprion sp.	8554640600
Cirrhitidae	
Cirrhitid sp.	8554660000
Paracirrhites arcatus (Cuvier and Valenciennes)	8554660101
Paracirrhites forsteri (Bloch and Schneider)	8554660102
Paracirrhites xanthus Randall	8554660105
Cirrhitichthys aprinus Cuvier and Valenciennes	8554660603
Mugilidae	
Chelon vaigiensis (Quoy and Gaimard)	8555010301
Crenimugil crenilabis (Forsskål)	8555010401

(Contd)

Table 20. (Contd)

Group/Species*	Hawaii Coastal Zone Data Bank No.**
Sphyraenidae	
Sphyraena sp.	8555030100
Labridae	
Labroides bicolor Fowler and Bean	8555070402
Labroides dimidiatus (Cuvier and Valenciennes)	8555070403
Labroides rubrolabiatus Randall	8555070404
Epibulus insidiator (Pallas)	8555070501
Cheilinus undulatus Rüppell	8555070703
Pseudocheilinus hexataenia (Bleeker)	8555070804
Thalassoma lunare (Linnaeus)	8555071403
Thalassoma amblycephalus (Bleeker)	8555071410
Thalassoma hardwickei (Bennett)	8555071411
Gomphosus varius Lacépède	8555071501
Coris gaimardi (Quoy and Gaimard)	8555071604
Stethojulis balteata (Quoy and Gaimard)	8555071801
Anampses caeruleopunctatus Rüppell	8555072103
Halichoeres centriquadrus (Lacépède)	8555072202
Halichoeres trimaculatus (Quoy and Gaimard)	8555072205
Hemigymnus melapterus (Bloch)	8555072302
Scaridae	
Calotomus sp.	8555090100
Scarus sordidus Forsskål	8555090304
Scarus forsteri Cuvier and Valenciennes	8555090305
Scarus frenatus Lacépède	8555090306
Scarus ghobban Forsskål	8555090308
Scarus jonesi (Streets)	8555090311
Scarus pectoralis Cuvier and Valenciennes	8555090313
Scarus sp. (juvenile)	8555090320
Chlorurus gibbus (Rüppell)	8555090601
Gobiidae	
Gobiid sp.	8555600000
Bathygobius fuscus (Rüppell)	8555600802
Amblygobius phalaena (Valenciennes)	8555601802
Acanthuridae	
Acanthurus triostegus (Linnaeus)	8555690101
Acanthurus guttatus Bloch and Schneider	8555690102
Acanthurus achilles Shaw	8555690103
Acanthurus glaucopareius Cuvier	8555690104
Acanthurus olivaceus (Block and Schneider)	8555690109
Acanthurus xanthopterus (Cuvier and Valenciennes)	8555690111
Acanthurus lineatus (Linnaeus)	8555690114
Acanthurus sp.	8555690100
Ctenochaetus strigosus (Bennett)	8555690201
Ctenochaetus striatus (Quoy and Gaimard)	8555690203
Zebrasoma veliferum (Bloch)	8555690302
Zebrasoma scopas (Cuvier)	8555690304

(Contd)

Table 20. (Contd)

Group/Species*	Hawaii Coastal Zone Data Bank No.**
Acanthuridae (continued)	
Naso lituratus (Bloch and Schneider)	8555690401
Naso brevirostris (Cuvier and Valenciennes)	8555690403
Zanclus canescens (Linnaeus)	8555695101
Tetradontiformes	
Balistidae	
Rhinecanthus rectangulus (Bloch and Schneider)	8558020301
Rhinecanthus aculeatus (Linnaeus)	8558020302
Melichthys vidua (Solander)	8558020402
Sufflamen chrysoptera (Bloch and Schneider)	8558020505
Balistapus undulatus (Mungo Park)	8558020601
Balistoides viridescens (Bloch and Schneider)	8558020701
Balistoides flavimarginatus (Rüppell)	8558020703
Tetraodontidae	
Arothron hispidus (Linnaeus)	8558060302
Canthigaster solandri (Richardson)	8558065107

*Group/Species–taxonomic list follows the phylogenetic order proposed by Greenwood *et al.* (1966).

**HZCDB No.–a numerical computer listing maintained by University of Hawaii/Hawaii Institute of Geophysics; all fish data from this report are stored in this bank.

Figure 35 shows the number of species recorded at each station (as dots with areas proportional to the number of species observed). The number of species is plotted against distance from the lagoon pass (Fig. 36). A pronounced decline in the number of species is seen with increasing distance from the pass. These data are consistent with the well-documented preference of most reef species for habitats with substrata of varied relief and generally high live coral coverage (Key, 1973). These habitat types provide protective cover and food for fishes and a large variety of other reef organisms, as seen in the photographs taken adjacent to Spam Island in the pass region (Fig. 37). Regions of abundant and diverse coral coverage are also normally "healthy" areas with good circulation and near-oceanic physicochemical conditions capable of sustaining most reef-associated biota (Smith and Jokiel, this report; Jokiel and Maragos, this report; Kay, this report). Accordingly, the areas with sparse live coral coverage and low relief (see substrata key in Fig. 36) are uniformly low in fish diversity and abundance. In such environments, available habitats appear to overshadow the effects of circulation and overall water quality.

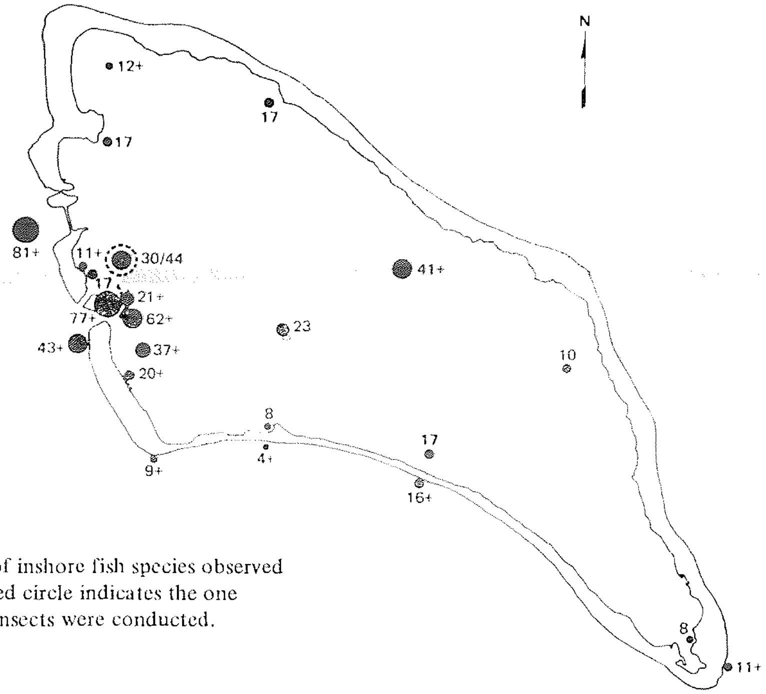


Figure 35. Numbers of inshore fish species observed at 24 locations. Dashed circle indicates the one station where two transects were conducted.

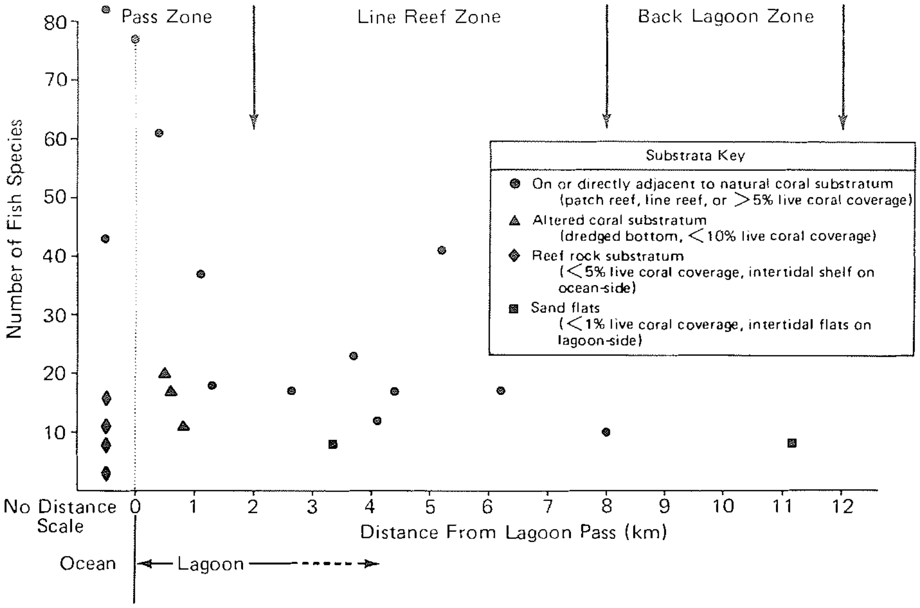
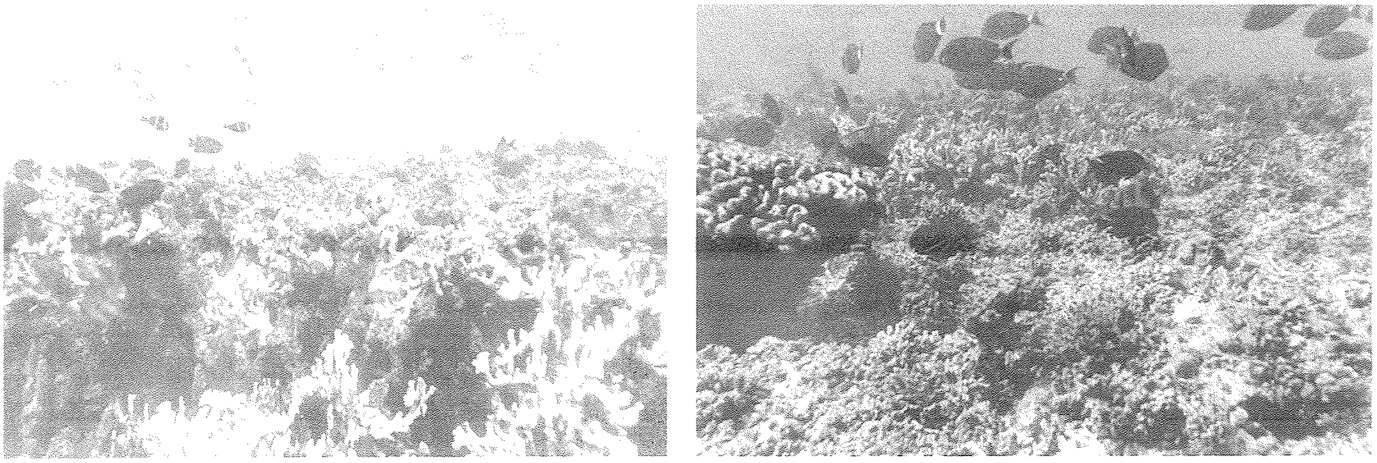
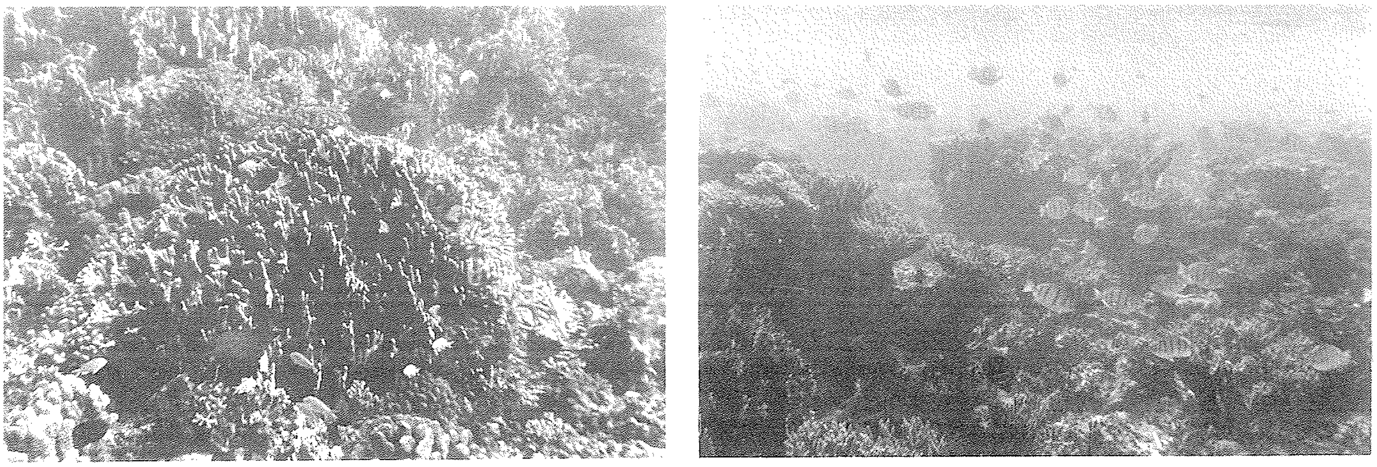


Figure 36. Numbers of fish species versus distance from lagoon pass over four general substrata types at Canton Atoll.



(a) Depth, ½ to 1 m; coral predominantly *Millepora*; obvious fish species seen (top to bottom): *Chromis caeruleus*, *Amphiprion chrysopterus*, and *Pomacentrus nigricans*.

(b) Depth, 1 to 1½ m; coral predominantly *Acropora* and *Pocillopora*; obvious fish species (top to bottom): *Acanthurus xanthopterus*, *Acanthurus* sp., *Scarus ghobban*, *Scarus oviceps*, *Chaetdon ulietensis*, and *Chaetodon bennetti*.



(c) Depth, 1 to 2 m; coral predominantly *Millepora* and *Pocillopora*; obvious fish species shown: *Chromis caeruleus and Cephalopholis urodelis*.

(d) Depth, 1 to 3 m; coral predominantly *Acropora* and *Millepora*; obvious fish species shown (top to bottom): *Chromis* sp., *Acanthurus triostegus*, and *Chaetodon bennetti*.

Figure 37. Shallow reef top environment, lagoonside of Spam Island.

Within the lagoon the number of fish species generally decreases radically beyond a 2-km radius from the pass to about 8–23 species per location for most shoreline and lagoon reef areas. Some mid-lagoon regions along certain line reefs possess luxuriant coral growth (primarily *Acropora* and *Millepora*), with an accompanying diverse and abundant fish fauna. One station (Fig. 38), where over 41 fish species were observed, is typical of such locations. Along the crests and shallower slopes of the line reef structures, tidal currents are increased in speed. This intensified flow appears to enhance biotic diversity.

Figure 38. Line reef crest environment, mid-lagoon station; depth, 1½–2 m; coral predominantly *Acropora*; obvious fish species shown (top to bottom): *Chromis caeruleus*, *Lutjanus fulvus*, *Lutjanus kasmira*, *Acanthurus* sp., and *Gnathodentex aureolineatus*.

Fish diversity is generally high outside the lagoon, with the exception of the shallow wave-swept outer reef flats. Immediately beyond the flats and algal ridge, the groove and spur region of the outer reef supports a fish fauna that becomes increasingly diverse with depth. Observations at two locations along the forereef (water depth, 3–20 m) revealed the presence of an outer reef terrace (shown diagrammatically and by inset photograph in Fig. 39). This terrace supports a diverse coral and fish fauna.

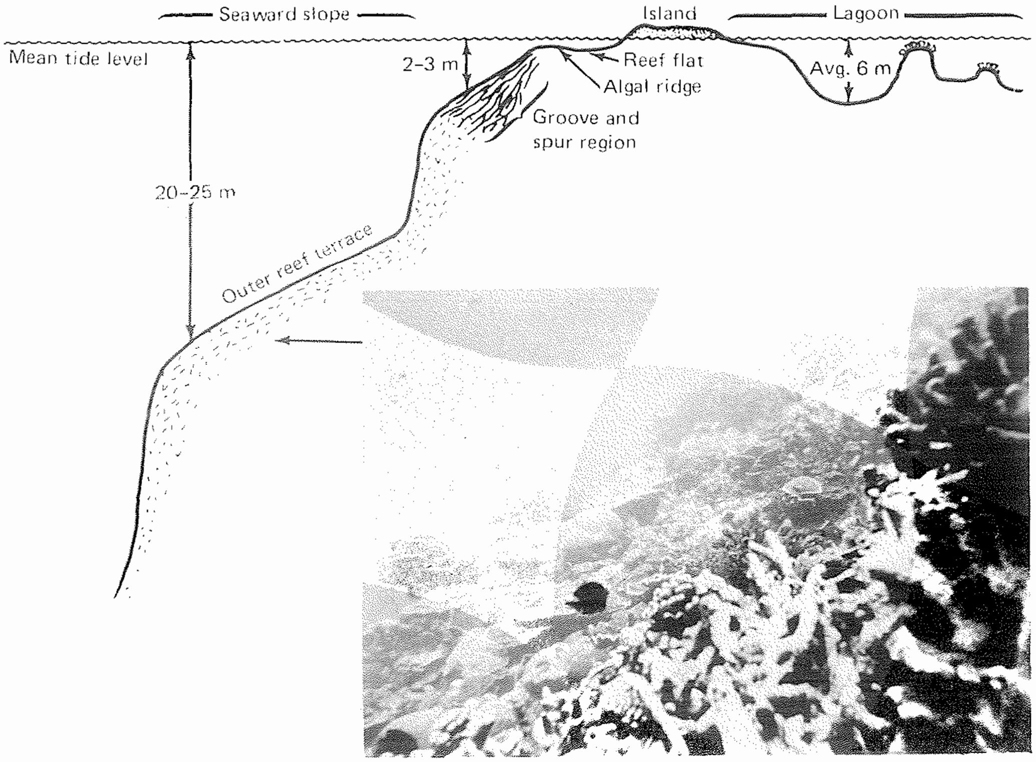


Figure 39. Schematic cross-section of Canton Atoll reef structure (western side). Inset photo was taken at 15 m depth along seaward edge of outer reef terrace.

Distribution of Selected Species

Data on the distribution of fishes were recorded at the 24 transect and observation stations and were also examined for meaningful patterns or trends by taxa. Twenty fish species have been selected (see Table 21) to illustrate the observed patterns in fish distribution at Canton Atoll. Nineteen of these selected species were recorded at 25% or more of the sampling stations. The remaining species, *Arothron hispidus*, was recorded at 20% of the stations; its occurrence is also considered significant to the distributional discussion.

Table 21. Alphabetical listing of selected fish species with remarks on behavior, habitat, and distribution.

Species	Total no. individuals recorded[a]	Behavioral characteristics		General habitat[d]	Possible factors limiting distribution
		Aggregating type[b]	Feeding type[c]		
Acanthurus triostegus	491	schooling	herbivore	P,Rs,Lc	food availability, seasonal movement?
Acanthurus xanthopterus	524	schooling	herbivore	U	algal substrata, vertical relief
Arothron hispidus	54	solitary	carnivore (omni.)	Lt	food availability
Centropyge flavissimus	97	solitary/tr	herbivore	P,O	clean water algal forms
Cephalopholis argus	45	solitary/tr	carnivore	P,O	prey abundance, protective cover
Chaetodon auriga	80	grouping	carnivore (omni.)	U	protective cover
Chaetodon lunula	60	pairing	carnivore (omni.)	O,P,Lc	food availability (proximity to live coral), protective cover
Cheilodipterus quinquelineata	36	grouping	carnivore	U	protective cover, water motion
Chromis margaritifer	525+	schooling	planktivore	O,P	oceanic plankton, protective cover
Dascyllus aruanus	306	schooling	planktivore	P,Lc	abundance of plankton, competition with other pomacentrids
Epinephelus merra	57	solitary/tr	carnivore	U	prey abundance, protective cover with high relief
Gomphosus varius	31	solitary	carnivore	P	prey abundance
Lutjanus fulvus	523	schooling	carnivore	Lt	competition with other carnivores, prey abundance
Monotaxis grandoculis	85	solitary/tr	carnivore	P,Lc	protective cover, competition with lutjanids?
Pomacentrus coelestis	261	schooling	herbivore (omni.)	P,O,Lc	clean water algal forms, protective cover
Pomacentrus nigricans	737	solitary/tr	herbivore (omni.)	U	high relief substratum, territorial competition
Rhinecanthus aculeatus	22	solitary/tr	omnivore	Lc,Lt	protective cover, proximity to sand bottom habitat
Scarus sordidus	231+	schooling	herbivore	U	food availability
Thalassoma amblycephalus	1200+	schooling	planktivore	O,P,Lc	proximity to live coral, abundance of plankton
Zebrasoma scopas	23	solitary/tr	herbivore	O,P	clean water algal forms

[a] These data are conservative because they represent minimum counts of individuals, that is, data recorded greater than (>) were treated as number listed only (see Appendix); + indicates that numbers of individuals were recorded as TNTC (too numerous to count) at some stations.

[b] tr = territorial; grouping = occurring in small aggregations (3-10 individuals); solitary, pairing, and schooling are self-explanatory.

[c] Feeding type information was obtained from Hiatt and Strasburg (1960) and Hobson (1974).

[d] Habitat types: P=pass; Rs=outer reef shelf; Lc=clear lagoon; Lt=turbid lagoon; O=ocean (along outer reef slope); U=ubiquitous.(observed at nearly all habitat types).

Six species show a nearly ubiquitous distribution at Canton Island: *Chaetodon auriga, Pomacentrus nigricans, Acanthurus xanthopterus, Epinephelus merra, Scarus sordidus,* and *Cheilodipterus quinquelineata* (Fig. 40a–40f). These species appear well-adapted to inhabit nearly any available habitat with sufficient bottom relief.

Another group of species is confined to the pass region and at the outside ocean stations. The five species in this group are *Chromis margaritifer, Centropyge flavissimus, Zebrasoma scopas, Cephalopholis argus,* and *Gomphosus varius* (Fig. 40g–40k).

One species, *Dascyllus aruanus*, is restricted to the pass and clear lagoon regions (Fig. 40l). Possible factors which might limit the distribution of this and other selected species are presented in the last column of Table 21.

Three species occur at ocean, pass, and lagoon stations, but are not ubiquitous: *Thalassoma amblycephalus, Pomacentrus coelestis,* and *Chaetodon lunula* (Fig. 40m–40o). The distribution observed for these species suggests a mild preference for clear-water, moderate live-coral-coverage environments. As seen by the distribution for *P. coelestis*, a possible remnant population at a lagoon station north of the present pass is suggested; this station is near ocean passes closed about 30 years before this survey (see Henderson *et al.*, this volume).

Rhinecanthus aculeatus and *Monotaxis grandoculis* occur primarily at lagoon patch reef stations (Fig. 40p and 40q). Both species exhibit solitary behavior patterns (see Table 21).

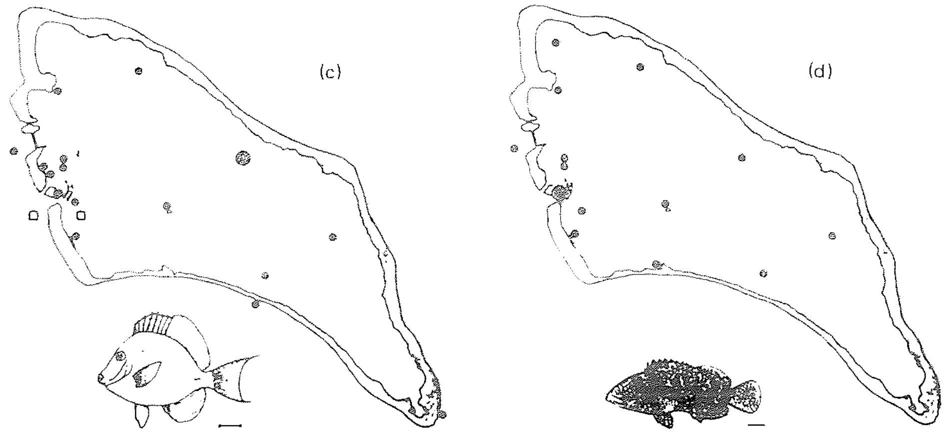
Two other species which have been recorded as abundant in turbid lagoon environments are *Lutjanus fulvus* and *Arothron hispidus* (Fig. 40r and 40s). *A. hispidus* was observed almost exclusively at shallow, turbid-water stations.

One remaining species, *Acanthurus triostegus*, shows a curious distributional pattern at Canton (Fig. 40t). Hiatt and Strasburg (1960) consider the species as being ubiquitous in the Marshall Islands; Chave and Eckert (1974) found a similar distribution at Fanning Atoll. However, at Canton *A. triostegus* was recorded only from the pass, ocean, outside reef shelf, and southern lagoon stations. Possibly some specific food or habitat preference is reflected in the limited lagoon distribution of this species.

Juveniles and young adults of certain selected species were observed predominantly inside the lagoon, while adult forms were seen at outside stations. *Scarus sordidus, Monotaxis grandoculis,* and *Lutjanus fulvus* are representative species which exhibit this pattern.

Threadfin butterflyfish
Chaetodon auriga

Damselfish
Pomacentrus nigricans



Surgeonfish; Pualu
Acanthurus xanthopterus

Honeycomb grouper
Epinephelus merra

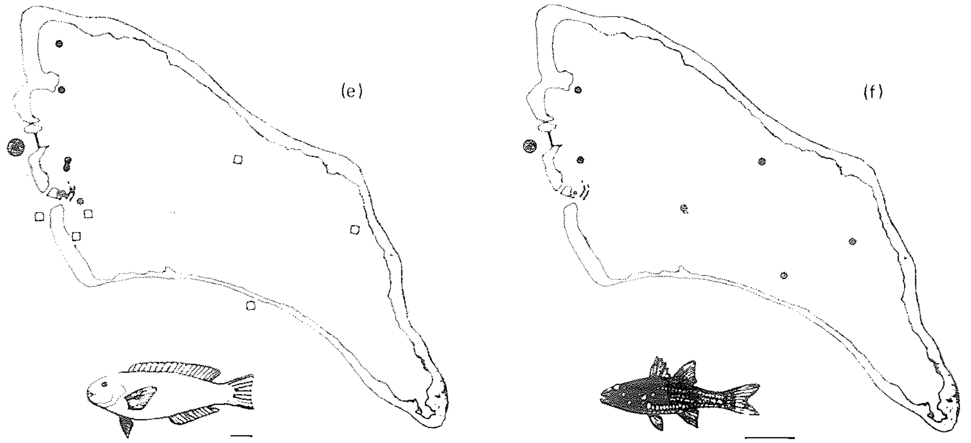
● = 61-80%
● = 41-60%
● = 21-40%
• = 1-20%

size of the "dots" indicates frequency of occurrence of a given species as a percentage of all individuals of that species reported during the survey; excludes individuals of that species too numerous to count (see below)

▨ = individuals too numerous to count or adequately estimate (greater than 1000)

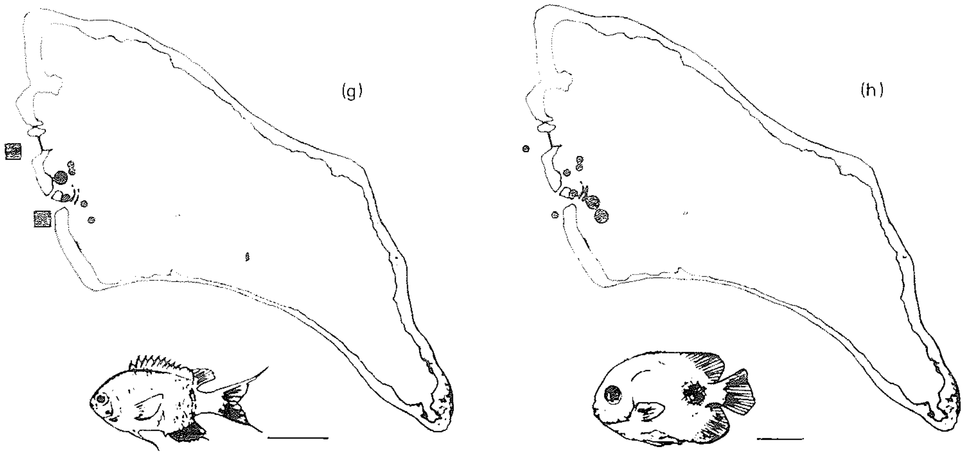
□ = species likely included in data recorded to family level only (based upon subsequent identifications from photos and later taxonomic analysis)

Figure 40. Distribution pattern of 20 representative reef fish species.



Parrotfish; Uhu
Scarus sordidus

Five-lined cardinalfish
Cheilodipterus quinquelineata



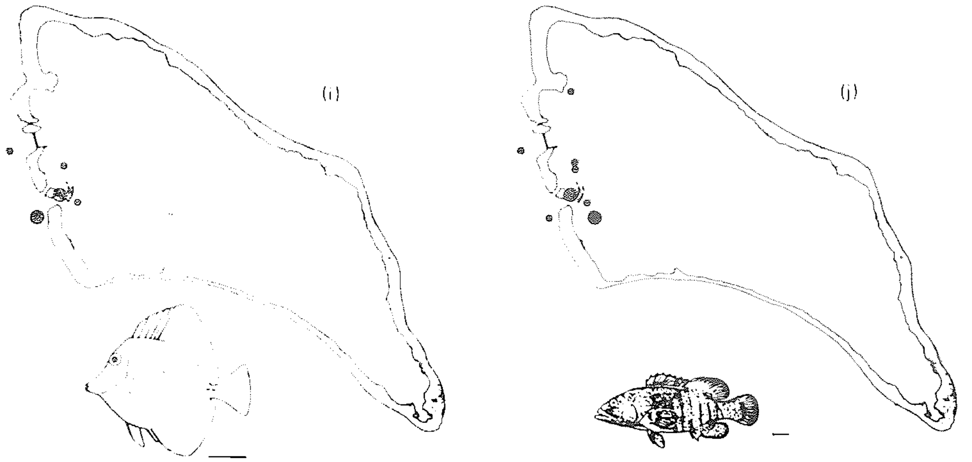
Bicolor chromis
Chromis margaritifer

Lemonpeel; angelfish
Centropyge flavissimus

● = 61-80%
● = 41-60%
● = 21-40%
• = 1-20%

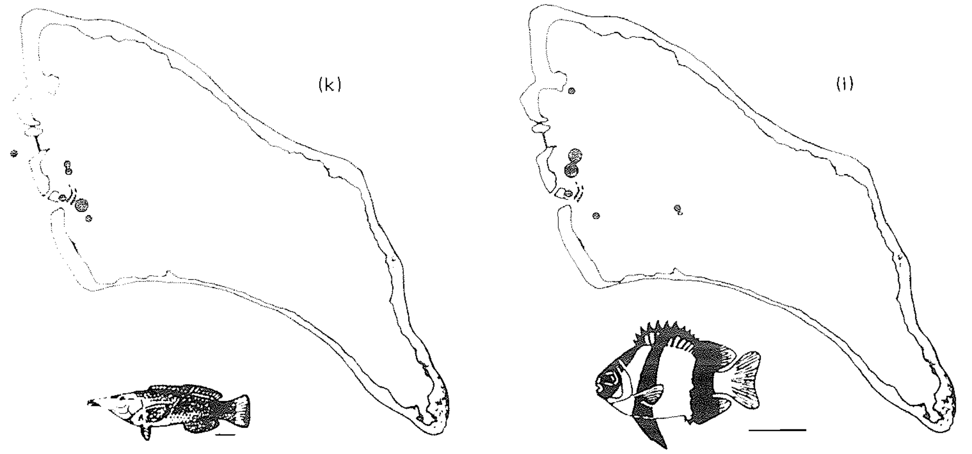
size of the "dots" indicates frequency of occurrence of a given species as a percentage of all individuals of that species reported during the survey; excludes individuals of that species too numerous to count (see below)

Figure 40. (contd)



Surgeonfish; tang
Zebrasoma scopas

Black grouper
Cephalopholus argus



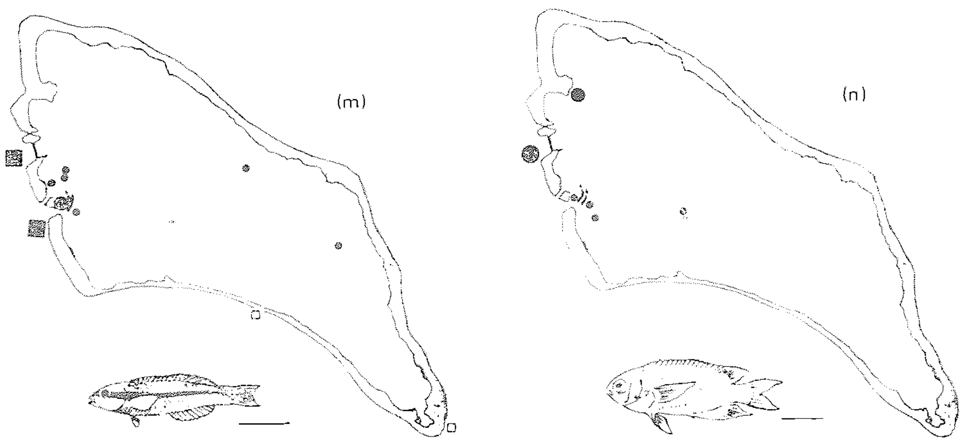
Beaked wrasse
Gomphosus varius

White-tailed damselfish
Dascyllus aruanus

▨ = individuals too numerous to count or adequately estimate (greater than 1000)

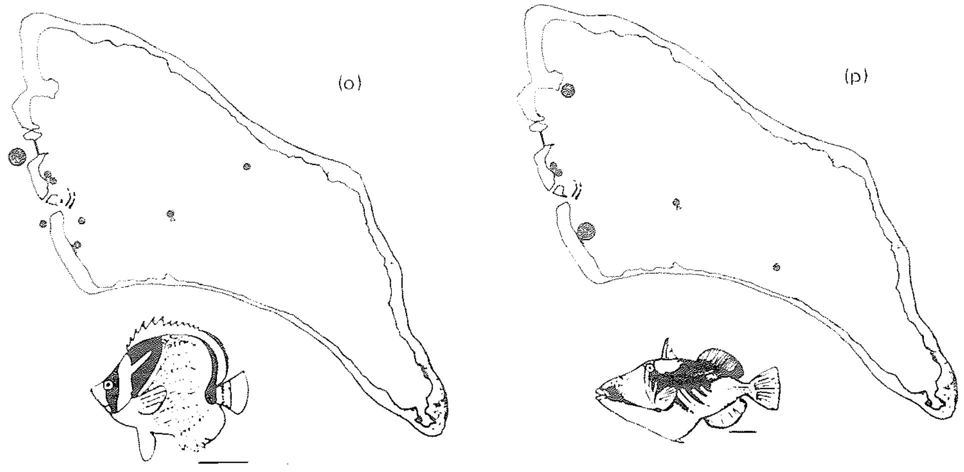
☐ = species likely included in data recorded to family level only (based upon subsequent identifications from photos and later taxonomic analysis)

Figure 40. (contd)



Rainbow wrasse
Thalassoma amblycephalus

Blue damselfish
Pomacentrus coelestis



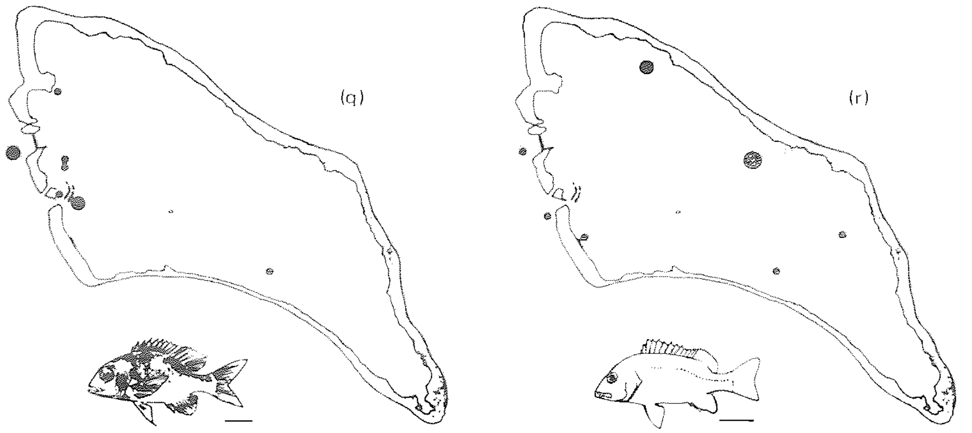
Raccoon butterflyfish
Chaetodon lunula

Triggerfish
Rhinecanthus aculeatus

● = 61-80%
● = 41-60%
● = 21-40%
• = 1-20%

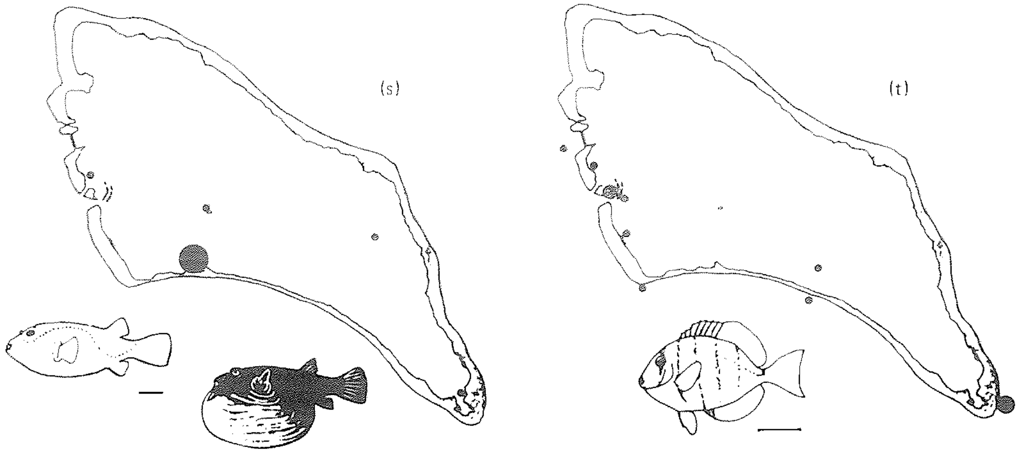
size of the "dots" indicates frequency of occurrence of a given species as a percentage of all individuals of that species reported during the survey; excludes individuals of that species too numerous to count (see below)

Figure 40. (contd)



Big-eye sea bream; Mu
Monotaxis grandoculis

Black-tailed snapper; Toau
Lutjanus fulvus



Soft puffer; Makimaki
Arothron hispidus

Convict tang; Manini
Acanthurus triostegus

▨ = individuals too numerous to count or adequately estimate (greater than 1000)
□ = species likely included in data recorded to family level only (based upon subsequent identifications from photos and later taxonomic analysis)

Figure 40. (contd)

Initially several other species were considered for distribution maps but were subsequently excluded from the presentation for the following reasons: Transect data for the black-tip shark (*Carcharhinus melanopterus*) and the black jack (*Caranx melampygus*), two fast-swimming species, were considered incomplete and therefore unreliable. Recorded distributions for three nocturnally active species—the moray eel (*Gymnothorax pictus*) and two squirrelfishes (*Adioryx spinifer* and *Flammeo sammara*)—were also considered unrepresentative, because all transects and observations during this study were conducted during daylight hours and at slack tides.

For one station (FT 023038, Thornet Reef; see the Appendix) transects were conducted on two different sampling days at similar mid-morning times and tidal conditions. The second transect was aligned perpendicular to the first, and each transect line began on the patch reef and extended into deeper water (4.5-m depth). The data reported were similar in magnitude for both number of species and number of individuals; however, somewhat more species were recorded during the second transect than the first, possibly because observer familiarity with the fishes improved as the survey progressed.

DISCUSSION AND CONCLUSIONS

The most obvious pattern to emerge from the fish distribution data concerns the abundance and diversity of fishes. Both the number of individuals and the number of species decrease with distance away from the pass into the lagoon.

This pattern is undoubtedly a response to a variety of factors, including availability of food and shelter. As with the coral distribution (Jokiel and Maragos, this report) and the distribution of water composition parameters (Smith and Jokiel, this report), water motion obviously plays a major role; the one central lagoon station with abundant and diverse fish fauna is also a site of locally accelerated water flow.

A second and more subtle pattern also emerges from the data when the fish species are examined individually. There is the suggestion that remnant populations of fishes commonly found to inhabit more oceanic conditions may still exist in the lagoon, particularly along the western side of the lagoon north of the present pass. Passes in this area have been closed for about 30 years (Henderson *et al.*, this report), a timespan far beyond the life expectancy of the fishes observed during this survey.

There are several apparent anomalies which appear in the case of particular species. The observed distribution of the convict tang, *Acanthurus triostegus*, was quite unexpected. Possible explanations for this anomaly are food availability and competition with another species. *Lutjanus fulvus*, the black-tailed snapper, was another species for which the recorded distributional pattern indicates competition for food or habitat with other species (probably other lutjanids). The Canton Atoll fish fauna appear to be similar to those recorded from the Line Island group, especially Fanning Atoll (Chave and Eckert, 1974).

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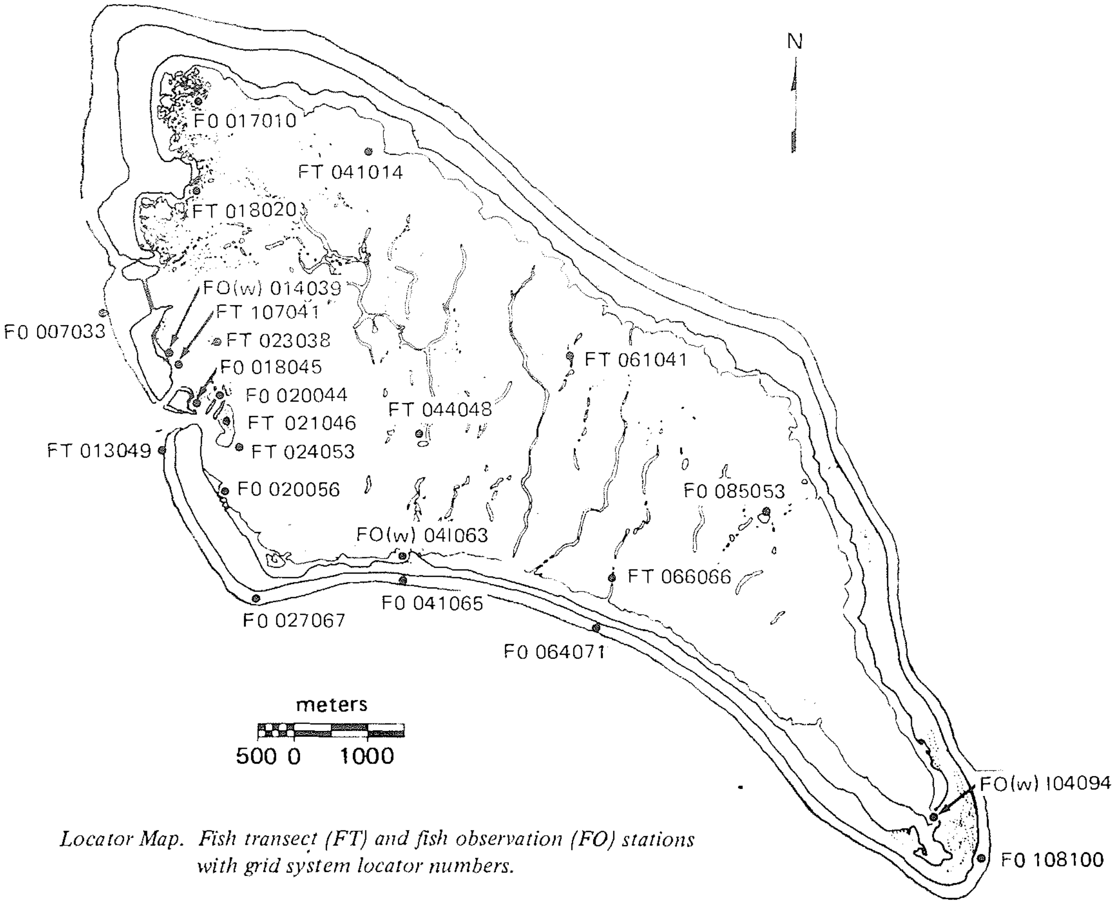
Appendix

FISH TRANSECT AND OBSERVATION DATA

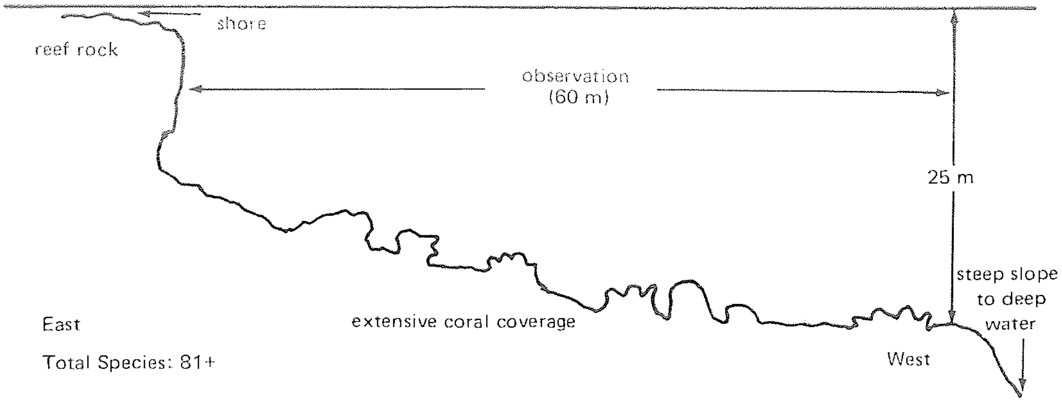


Locator Map. Fish transect (FT) and fish observation (FO) stations with grid system locator numbers.

Fish Observation, **north of pass, ocean**: FO 007033

Surveyed: 9 Dec 73, 1330–1400 hours. Tide: incoming from high-low (15 cm) at 1133 hours. HIV: 21 m. Observation track length: 60 m.

Observation area general description: 1600 m north of lagoon pass, immediately offshore of intertidal reef shelf. Depth 6 to 25 m. Bottom fairly irregular with greater than 50% live coral coverage. Coral types very numerous; most predominant: *Pocillopora, Montipora, Porites, Pavona, Halomitra, Herpolitha.*



Total Species: 81+

Species	Number of individuals	Estimated average length (cm)
Acanthurus achilles	5	25
Acanthurus glaucopareius	4	23
Acanthurus lineatus	10	23
Acanthurus triostegus	> 50	15
Acanthurus spp. (2)	> 300	18
Acanthurus xanthopterus	10	25
Adioryx spinifer	5	25
Anyperodon leucogrammicus	3	30
Aprion virescens	6	36
Aulostomus chinensis	1	46
Balistapus undulatus	8	23
Caranx melampygus	6	76
Carcharinus melanopterus	1	183
Centropyge bicolor	2	10
Centropyge flavissimus	10	10
Centropyge loriculus	10	10
Cephalopholis argus	6	46
Cephalopholis urodelus	4	23
Chaetodon auriga	5	20
Chaetodon bennetti	4	18
Chaetodon ephippium	3	18
Chaetodon kleini	> 20	18

Chaetodon lunula	> 30	20
Chaetodon meyeri	6	20
Chaetodon trifasciatus	> 12	20
Chaetodon ulietensis	10	18
Cheilodipterus quinquelineata	8	8
Cheilinus undulatus	3	76
Chromis caeruleus	> 200	6
Chromis margaritifer	> 2000	5
Chromis sp.	> 3000	9
Ctenochaetus striatus	1	15
Ctenochaetus strigosus	> 50	18
Dascyllus trimaculatus	5	10
Elagatis bipinnulatus	> 30	30
Epinephelus merra	10	25
Epinephelus microdon	5	61
Forcipiger longirostris	3	15
Gomphosus varius	6	15
Gracila albomarginatus	1	25
Gymnothorax flavimarginatus	2	102
Heniochus acuminatus	10	18
Heniochus permutatus	> 12	18
Heniochus varius	3	15
Kyphosus cinerascens	> 20	46
Labridae spp. (3)	> 1000	10
Labroides dimidiatus	3	10
Labroides rubrolabiatus	2	10
Lethrinus sp.	5	36
Lutjanus bohar	> 20	51
Lutjanus fulvus	> 20	46
Lutjanus monostigma	> 20	46
Megaprotodon strigangulus	5	18
Monotaxis grandoculis	> 30	20
Myripristis spp. (3)	> 100	23
Naso brevirostris	> 50	30
Paracirrhites arcatus	10	15
Paracirrhites forsteri	10	15
Parupeneus spp.	> 15	23
Pomacentrus coelestis	> 100	8
Pomacentrus nigricans	20	10
Scarus frenatus	5	41
Scarus ghobban	15	36
Scarus pectoralis	10	41
Scarus sordidus	> 100	20
Scaridae spp. (3)	> 300	41
Scomberoides sancti-petri	4	30
Serranidae spp.	> 15	36
Sphyraenidae sp.	> 30	61
Sufflamen chrysopterus	6	15
Thalassoma amblycephalus	> 1000	8
Thalassoma lunare	12	20
Zanclus canescens	5	18
Zebrasoma scopas	3	15

Fish Observation, **small boat marina, lagoon**: FO(w) 014039

Shoreside observations, in marina (under and around floating docks) on intertidal reef flats nearby.

6 Dec 73, 0900–0905 hours. Tide: slack at low-low (27 cm). HIV: 2.5 m.

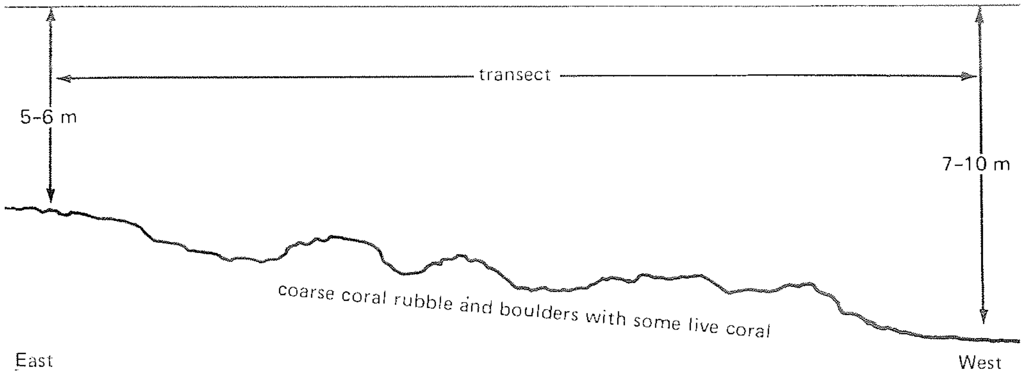
Total Species: 11+

Species	Number of individuals	Estimated average length (cm)
Acanthurus triostegus	1	13
Acanthurus xanthopterus	> 10	23
Balistidae sp.	5	76
Caranx melampygus	> 30	25
Chaetodon auriga	2	15
Chaetodon lunula	1	13
Gymnothorax pictus	> 12	64
Labridae spp. (2)	> 100	6
Mulloidichthys samoensis	8	25
Rhinecanthus aculeatus	1	18

Fish Transect, **south of Taylor wreck, ocean**: FT 013049

Surveyed: 4 Dec 73, 1355–1435 hours. Tide: slack, high-high (1 m) at 1415 hours. HIV: 21 m. Transect length: 30 m.

Transect general description: Approximately 60 m south of President Taylor wreck (at pass). Depth shoreward 5 to 6 m, increasing seaward to 8-9 m. Bottom mostly boulder and irregular formations of dead coral and rubble. Live coral covering approximately 5–10% of bottom; predominant coral types *Pocillopora* and *Porites*.



Total Species: 43+

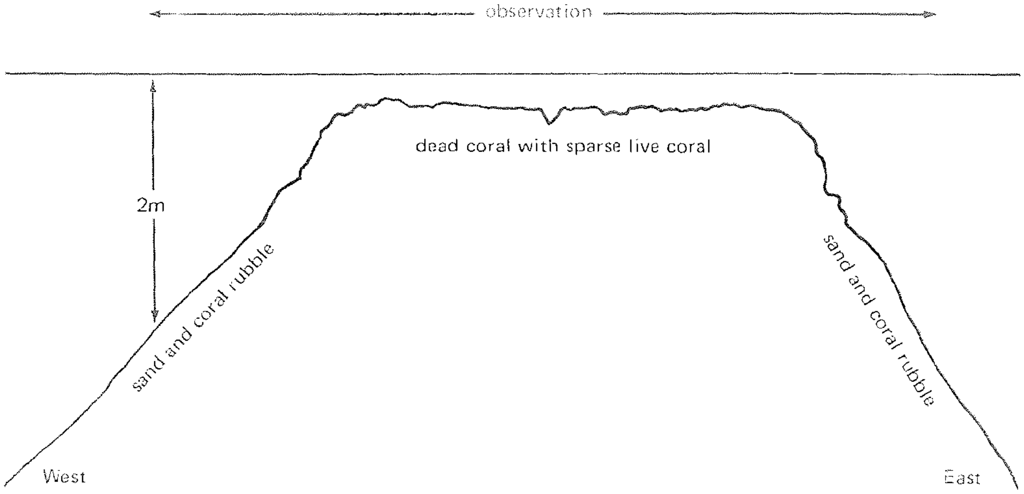
Species	Number of individuals	Estimated average length (cm)
Acanthurus lineatus	> 100	23
Acanthurus olivaceus	2	20
Acanthurus spp. (2)	> 150	18
Carcharinus melanopterus	1	183
Centropyge flavissimus	7	10
Cephalopholis argus	3	25
Cephalopholis urodelis	8	20
Chaetodon auriga	2	13
Chaetodon ephippium	1	20
Chaetodon lunula	1	15
Chaetodon meyeri	2	18
Chaetodon ornatissimus	3	18
Chaetodon quadrimaculatus	5	15
Chaetodon ulietensis	2	18
Chromis caeruleus	46	8
Chromis margaritifer	> 1000	5
Coris gaimardi	2	10
Ctenochaetus strigosus	> 500	18

Species	Number of individuals	Estimated average length (cm)
Epibolus insidiator	3	18
Epinephelus microdon	3	61
Forcipiger longirostris	1	13
Labridae spp. (2)	> 100	10
Lutjanus bohar	13	61
Lutjanus fulvus	20	46
Melichthys vidua	1	15
Paracirrhites xanthus	3	10
Parupeneus barberinus	3	41
Parupeneus trifasciatus	1	25
Plectrogyphidodon dickii	40	8
Pomacentrus sp. (yellow)	> 10	8
Pomacentrus nigricans	> 100	10
Scarus spp. (2)	> 25	23
Thalassoma amblycephalus	> 1000	6
Zanclus canescens	5	18
Zebrasoma scopas	8	15
Species observed off transect:		
Cheilinus undulatus	4	76
Chlorurus gibbus	1	91
Lutjanus monostigma	20	46
Scarus spp. (2)	> 200	36

Fish Observation, **northwest corner, lagoon**: FO 017010

Surveyed: 6 Dec 73, 1015–1035 hours. Tide: incoming from high-low 28 cm at 0907 hours. HIV: 1.2 m. Observation track length: 30 m.

Observation area general description: Patch reef area approximately 600 m off of cantonment area. Patch reef about 10 m in diameter. Gentle-slope sand and coral rubble apron around leeward (southwest) base of reef. Steeper apron around windward side. Reef mostly dead coral, approximately 10% coverage of live coral. Predominant corals: *Acropora*, *Porites*, *Pocillopora*, and *Favia*.



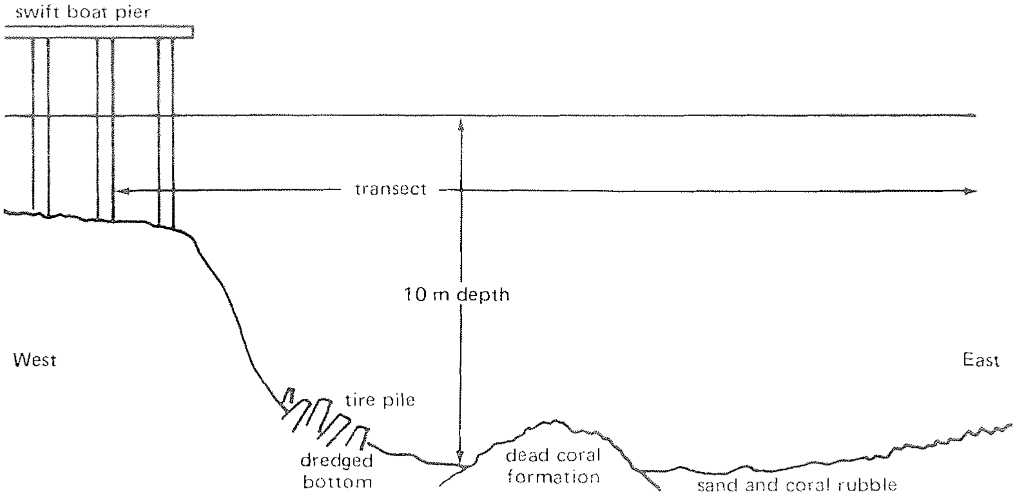
Total Species: 12+

Species	Number of individuals	Estimated average length (cm)
Chaetodon auriga	2	18
Chaetodon trifasciatus	1	13
Chaetodon ulietensis	2	10
Chromis caeruleus	> 30	4
Ctenochaetus striatus	8	13
Epinephelus merra	1	13
Flammeo sammara	10	13
Labridae spp. (2)	> 30	5
Lutjanus kasmira	2	15
Pomacentrus nigricans	> 50	10
Scarus sordidus	4	15

Fish Transect, **main wharf, lagoon**: FT 017041

Surveyed: 1 Dec 73, 1330–1342 hours. Tide: outgoing to high-low (.5 m) at 1720 hours. HIV: 11 m. Transect length: 30 m.

Transect general description: Transect line extended from swift boat pier in offshore (east) direction. Bottom predominantly of sand and coral rubble. Most fish on and around a pile of discarded auto tires and a mound of dead coral. During the transect observation a tidal current of approximately 1 knot was present. No abundant live coral.



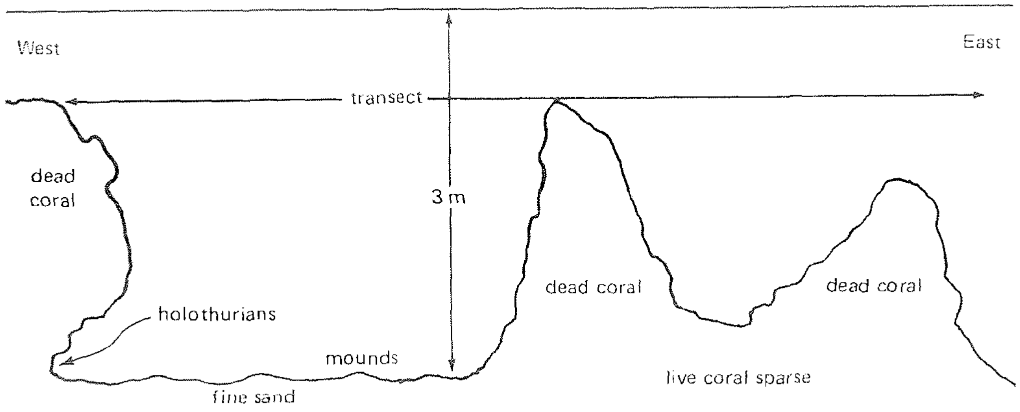
Total Species: 17

Species	Number of individuals	Estimated average length (cm)
Arothron hispidus	1	33
Acanthurus xanthopterus	5	23
Caranx melampygus	4	41
Centropyge flavissimus	1	8
Cephalopholis urodelus	3	20
Chaetodon auriga	7	15
Chaetodon lunula	2	13
Chromis caeruleus	37	8
Chromis margaritifer	> 200	5
Gobiidae sp.	50	4
Heniochus acuminatus	28	13
Labridae sp.	25	6
Rhinecanthus aculeatus	2	9
Rhinecanthus rectangulatus	1	15
Sufflamen chrysopterus	2	13
Thalassoma amblycephalus	30	8
Thalassoma lunare	4	13

Fish Transect, off swimming pool, lagoon: FT 018020

Surveyed: 1 Dec 73, 1155–1220 hours. Tide: outgoing to high–low (.5 m) at 1720 hours. HIV: 2.3 m. Transect length: 30 m.

Transect general description: About 175 m offshore (east of salt water swimming pool site). Many patch reefs, mostly of 10 to 70 m maximum dimension. Coral coverage less than 10% on solid surfaces. Most reef areas showing thin layers of silt. Holothurians at base of reef edge on sand. Dominant coral types: predominantly "lobate," rounded coral forms–*Porites*, *Leptastrea* (?), *Pocillopora*.



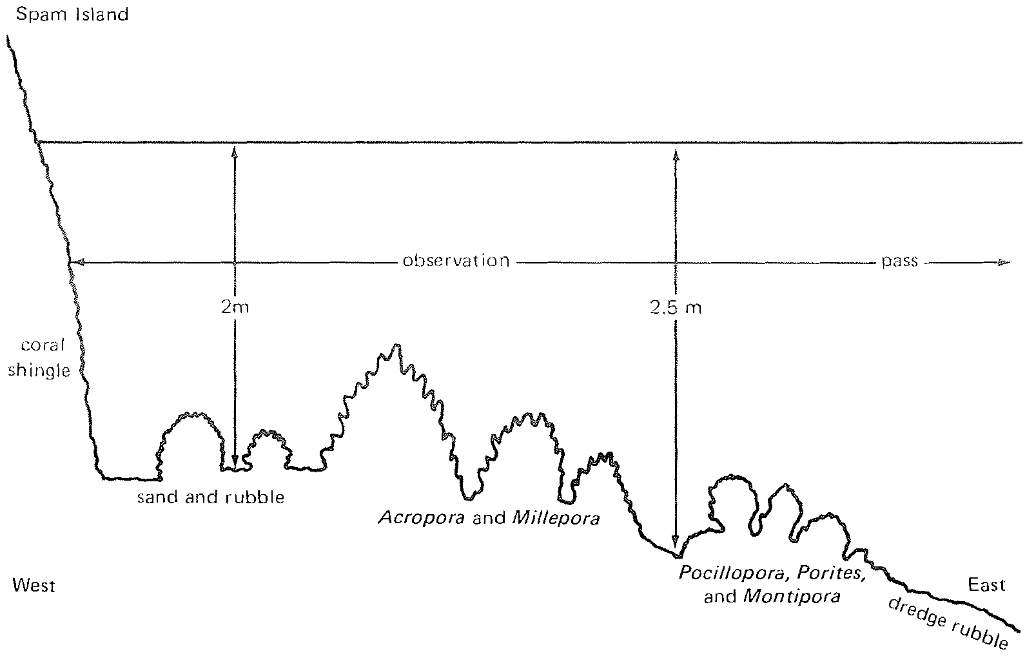
Total Species: 17

Species	Number of individuals	Estimated average length (cm)
Acanthurus xanthopterus	75	25
Cephalopholis argus	6	15
Chaetodon auriga	3	15
Cheilodipterus quinquelineata	5	8
Chromis caeruleus	3	6
Ctenochaetus striatus	40	13
Dascyllus aruanus	16	8
Epinephelus merra	3	20
Gobiidae sp.	> 50	5
Labridae sp.	8	10
Monotaxis grandoculis	2	13
Pomacentrus albofasciatus	25	10
Pomacentrus coelestis	60	8
Pomacentrus nigricans	20	10
Rhinecanthus aculeatus	5	13
Scarus sordidus	5	10
Scarus sp.	10	13

Fish Observation, **Spam Island, lagoon**: FO 018045

Surveyed: 9 Dec 73, 1430–1450 hours. Tide: incoming to high-high (1.3 m) at 1821 hours. HIV: 20 m. Observation track length: 40 m.

Observation area general description: Area immediately to east of lagoon shore of Spam Island. Varied bottom; at shoreline a slope of coral shingle extending down to 25 m depth where bottom is composed of sand, coral rubble, and scattered coral heads. Further north and east, *Acropora* and *Millepora* are very abundant, covering up to 30% of bottom. Further east *Pocillopora, Porites, Montipora,* and *Favia* become dominant although covering less than 10% of bottom. Bottom area without live coral is primarily of medium to large size coral rubble. *Herpolitha, Fungia,* and *Halomitra* are also relatively common on rubble bottom. Area subjected to tidal currents (primarily eddies) of 1 to 3 knots.



Total Species: 77+

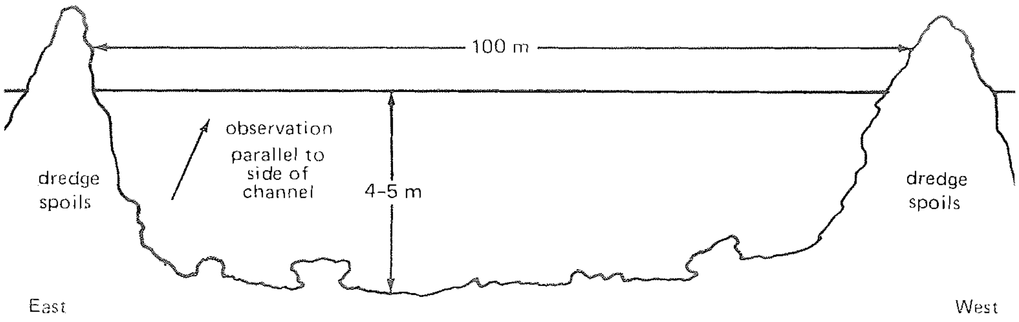
Species	Number of individuals	Estimated average length (cm)
Acanthurus glaucopareius	10	23
Acanthurus lineatus	25	23
Acanthurus triostegus	> 100	15
Acanthurus xanthopterus	> 100	25
Acanthurus spp. (2)	> 200	18
Adioryx spinifer	5	20
Amphiprion chrysopterus	10	10
Anampses caeruleo punctatus	3	10
Anyperodon leucogrammicus	7	28
Aprion virescens	2	25
Balistapus undulatus	6	20
Balistoides flavimarginatus (?)	3	76
Canthigaster solandri	1	8
Caranx melampygus	> 30	36
Carcharinus melanopterus	4	102
Centropyge flavissimus	12	10
Cephalopholis argus	15	30
Cephalopholis urodelus	8	25
Chaetodon auriga	15	20
Chaetodon bennetti	25	18
Chaetodon ephippium	5	18
Chaetodon lunula	10	20
Chaetodon meyeri	4	18
Chaetodon semeion	2	18
Chaetodon trifasciatus	6	18
Chaetodon ulietensis	12	18
Cheilinus undulatus	5	76
Cheilodipterus quinquelineata	6	8
Chromis caeruleus	> 300	6
Chromis margaritifer	> 100	5
Ctenochaetus strigosus	> 100	18
Dascyllus aruanus	> 50	6
Dascyllus trimaculatus	6	10
Epibolus insidiator	10	20
Epinephelus merra	12	25
Epinephelus microdon	8	61
Gnathanodon speciosus	2	64
Gomphosus varius	6	10
Gymnothorax flavimarginatus	3	97
Gymnothorax pictus	2	89
Hemigymnus melapterus	3	18
Hemiramphidae sp.	50	30
Heniochus permutatus	10	18
Heniochus varius	12	15
Labridae spp. (3)	> 75	13
Labroides bicolor	1	9
Labroides dimidiatus	5	10
Labroides rubrolabiatus	2	10

Species	Number of individuals	Estimated average length (cm)
Lethrinus spp. (2)	6	36
Lutjanus bohar	8	41
Lutjanus monostigma	12	36
Megaprotodon strigangulus	8	18
Monotaxis grandoculis	15	23
Naso brevirostris	20	25
Paracirrhites arcatus	10	15
Parupeneus bifasciatus	3	20
Plectroglypidodon dickii	> 25	8
Pomacentrus coelestis	> 30	8
Pomacentrus nigricans	> 100	10
Pterois antennata	8	18
Pygoplites diacanthus	1	20
Scarus ghobban	20	38
Scarus frenatus	15	23
Scarus pectoralis	30	36
Scarus sordidus	> 25	15
Scaridae spp. (2)	> 100	20
Sufflamen chrysopterus	8	13
Thalassoma amblycephalus	> 300	8
Thallassoma hardwickei	10	20
Thalassoma lunare	8	20
Zanclus canescens	12	18
Zebrasoma scopas	6	15

Fish Observation, **dredge channel, lagoon**: FO 020044

Surveyed: 7 Dec 73, 1135–1150 hours. Tide: near slack, high-low (21 cm) at 0955 hours. HIV: 10 m. Observation length: 30 m.

Observation area general description: Dredged channel approximately 100 m wide and 600 m long. Southwestern end 300 m from mouth of main lagoon pass. Subjected to tidal currents in excess of 5 knots. Average depth 5–6 m. Bottom primarily of dead coral rubble (to boulder size) with >10% live coral coverage. Predominant coral types: *Pocillopora, Montipora, Halomitra.* Elongate dredge spoil island along both sides of channel. Observation track parallel with western side of channel.



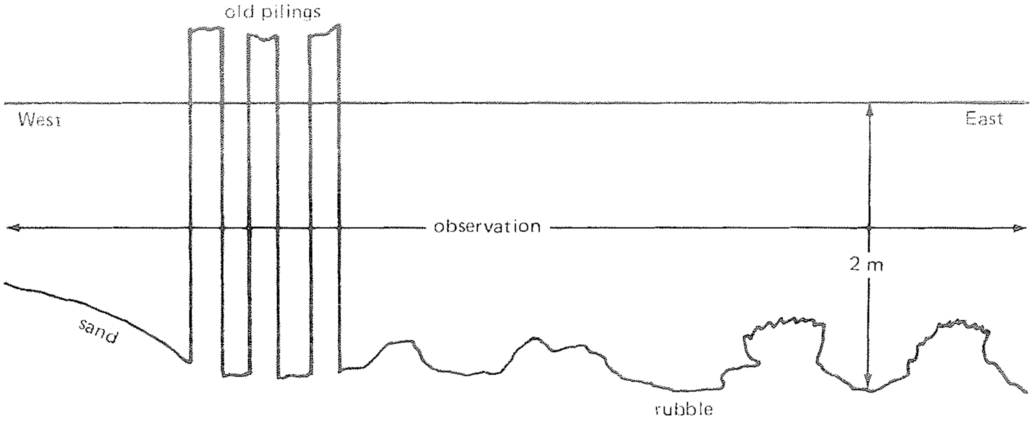
Total Species: 21+

Species	Number of individuals	Estimated average length (cm)
Acanthurus sp.	> 500	15
Adioryx spinifer	2	20
Balistes undulatus	1	20
Centropyge flavissimus	10	9
Chaetodon auriga	2	20
Chaetodon trifasciatis	1	18
Ctenochaetus striatus	> 100	13
Gymnothorax flavimarginatus	1	114
Labridae spp. (3)	> 500	13
Myripristis murdjan	25	18
Pomacentrus nigricans	> 50	10
Scarus frenatus	25	18
Scarus ghobban	30	25
Scarus sordidus	40	13
Scarus spp. (2)	> 200	20
Thalassoma amblycephalus	> 150	8
Zanclus canescens	4	18
Zebrasoma scopas	2	20

Fish Observation, **seaplane moorage, lagoon**: FO 020056

Surveyed: 2 Dec 73, 1405–1415 hours. Tide: outgoing to high-low (0.5 m) at 1819 hours. HIV: 6.5 m. Observation track length: 50 m.

Observation area general description: Dredged bottom immediately offshore between two artificial rock groins (abandoned sea-plane docks). Bottom primarily of coral rubble and concrete block debris. Live coral sparse, predominantly *Pocillopora*.



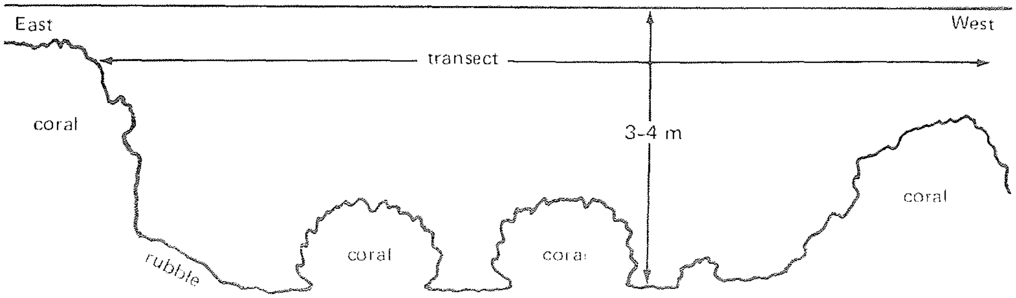
Total Species: 20+

Species	Number of individuals	Estimated average length (cm)
Abudefduf glaucus	10	10
Abudefduf phoenixensis	4	9
Abudefduf sordidus	> 50	13
Acanthurus triostegus	> 40	13
Acanthurus xanthopterus	12	23
Caranx melampygus	3	28
Chaetodon auriga	2	15
Chaetodon lunula	5	13
Chelon vaigiensis	2	23
Epinephelus merra	3	15
Flammeo sammara	1	15
Lutjanus fulvus	5	23
Mulloidichthys samoensis	> 40	25
Pomacentrus albofasciatus	> 50	6
Pomacentrus nigricans	> 30	10
Rhinecanthus aculeatus	10	14
Scarus spp. (3)	> 25	13
Stethojulis balteat	> 30	10

Fish Transect, **Coral Gardens, lagoon**: FT 021046

Surveyed: 30 Nov 73, 1135–1155 hours. Tide: outgoing to high-low (0.5 m) at 1619 hours. HIV: 15 m. Transect length: 30 m.

Transect general description: An area of abundant and large patch reefs approximately 500 m east of the south lagoon pass. From the edge of the patch reef area toward the pass the bottom becomes more uniform in depth (approximately 3–4 m) and coral rubble bottom becomes more prevalent as the pass is approached. The transect line follows the reef edge to coral rubble gradient and is an area subjected to tidal currents of >2 knots. Bottom generally of large dead coral masses covered with approximately 30% live coral and 20% coral rubble. One large anemone. Dominant coral types: *Pocillopora, Millepora, Halomitra, Porites, Herpolitha, Fungia.*



Total Species: 62+, also sighted: 2 turtles (76 cm and 100 cm carapace lengths)

Species	Number of individuals	Estimated average length (cm)
Adioryx caudimaculata	2	20
Adioryx spinifer	2	18
Acanthurus xanthopterus	6	20
Acanthurus sp.	40	15
Amphiprion chrysopterus	6	10
Anyperodon leucogrammicus	3	23
Balistapus undulatus	3	15
Calotomus sp.	9	18
Caranx melampygus	20	36
Centropyge flavissimus	28	9
Cephalopholis argus	2	20
Chaetodon auriga	2	15
Chaetodon bennetti	5	13
Chaetodon trifasciatus	4	15
Chaetodon ulietensis	3	15
Chromis margaritifer	> 100	6
Chromis caeruleus	> 200	6
Ctenochaetus strigosus	> 60	15

Species	Number of individuals	Estimated average length (cm)
Gomphosus varius	8	10
Heniochus acuminatus	1	15
Labridae spp. (>2 juv.)	40	10
Labroides dimidiatus	2	10
Labroides rubrolabiatus	3	9
Lutjanus bohar	2	46
Megaprotodon strigangulus	1	13
Myripristis amaenus	> 10	18
Myripristis murdjan	> 25	18
Myripristis sp.	2	18
Naso brevirostris	12	25
Paracirrhites forsteri	6	13
Paracirrhites xanthus	2	10
Plectroglyphidodon dickii	16	6
Pomacentrus coelestis	> 25	8
Pomacentrus nigricans	36	10
Scarus sordidus	7	15
Scarus sp. (juv.)	> 30	13
Thallasoma amblycephalus	> 120	8
Thallasoma hardwickei	6	18
Thallosoma spp. (2)	> 50	10
Zebrasoma scopas	2	10

Other species sighted in area adjacent to
transect area on 20 Nov 73 observation:

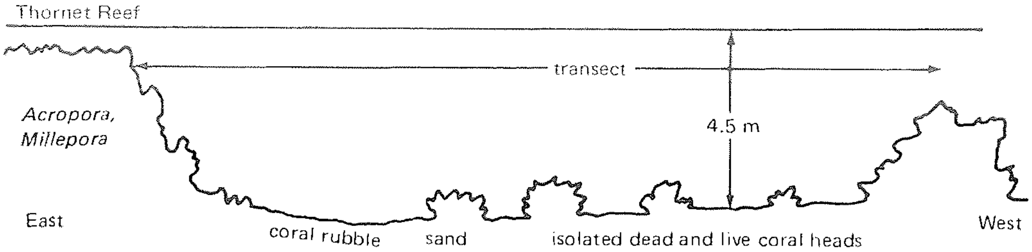
Acanthurus triostegus
Aprion virescens
Balistidae sp. (>50 cm)
Chaetodon ephippium
Chaetodon lunula
Chaetodon meyeri
Chaetodon unimaculatus
Cheilinus undulatus
Epibulus insidiator
Hemiramphidae sp.
Heniochus permutatus
Kyphosus cineracens
Lethrinus sp.
Lutjanus fulvus
Lutjanus monostigma
Monataxis grandolulis
Pygoplites diacanthus
Scarus spp. (adults)
Thalassoma lunare

Also sighted: 2 turtles (76 cm and 100 cm carapace lengths)

Fish Transect, **Thornet Reef, lagoon**: FT 023038

Surveyed: 30 Nov 73, 1012–1050 hours. Tide: incoming to low–high (0.9 m) at 1044 hours. HIV: 15–18 m. Transect length: 30 m.

Transect general description: Patch reef area approximately 800 m east of main wharf area and 300 m from dredged turning basin. Depths in surrounding area 4.5 to 9 m with coral pinnacles and patch reefs of 3 to 15 m diameter rising to within a few feet of the surface. Bottom generally of sand or sand and coral rubble. Dominant coral types: *Acropora*, *Pocillopora*, and *Millepora*. This area was subjected to tidal currents of approximately 1 knot during incoming tides.



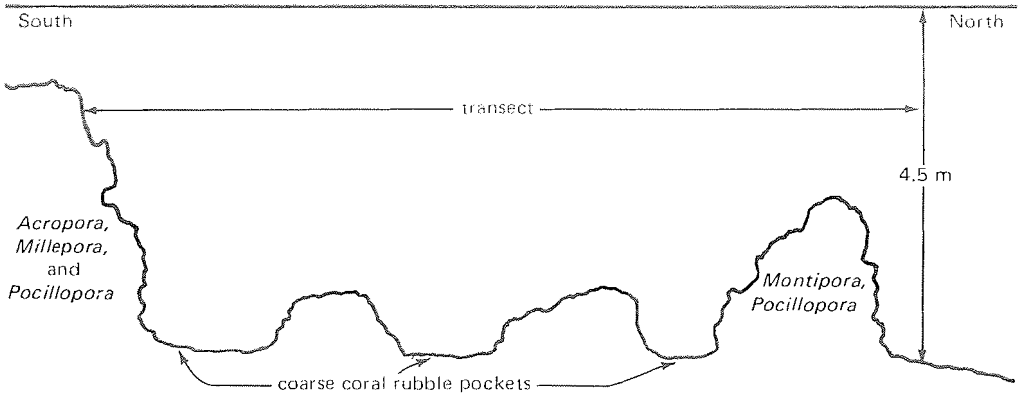
Total Species: 30

Species	Number of individuals	Estimated average length (cm)
Acanthurus lineatus	1	20
Acanthurus sp. (new species Randall)	> 725	18
Acanthurus xanthopterus	10	25
Centropyge bicolor	2	9
Centropyge flavissimus	6	10
Cephalopholis argus	2	20
Cephalopholis urodelus	1	10
Cheilodipterus quinquelineata	5	6
Chromis caeruleus	> 100	5
Chromis margaritifer	> 50	6
Dascyllus aruanus	> 80	5
Epinephelus merra	1	15
Gobiidae spp. (3)	> 100	5
Gomphosus varius	4	9
Labridae spp. (3)	30	10
Megaprotodon strigangulus	1	13
Monotaxis grandoculis	5	13
Paracirrhites forsteri	3	13
Parupeneus barberinus	1	18
Pomacentrus nigricans	45	9
Scarus frenatus	> 40	10
Scarus ghobban	4	25
Scarus sordidus	> 25	13
Scomberoides sancti-petri	5	25
Sufflamen chrysopterus	3	11
Thallasoma amblycephalus	> 100	8

Fish Transect, **Thornet Reef II, lagoon**: FT 023038

Surveyed: 4 Dec 73, 0935-0950 hours. Tide: incoming to high-high (1 m) at 1415 hours. HIV: 10 m. Transect length: 30 m.

Transect general description: Same as 30 Nov 73, FT 023038, except this transect aligned on a north-south orientation. Dominant coral types: *Acropora, Pocillopora, Montipora.*



Total Species: 44

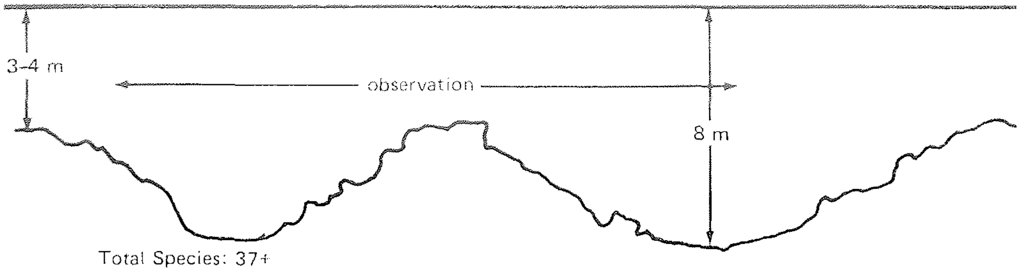
Species	Number of individuals	Estimated average length (cm)
Acanthurus glaucopareius	6	20
Acanthurus xanthopterus	3	20
Amphiprion chrysopterus	12	20
Amphiprion sp.	2	6
Centropyge flavissimus	6	9
Cephalopholis argus	1	20
Cephalopholis urodelus	2	20
Chaetodon bennetti	2	15
Chaetodon kleini	2	13
Chaetodon trifasciatis	3	13
Chaetodon ulietensis	4	13
Cheilinus undulatus	1	76
Chromis caeruleus	50	6
Chromis margaritifer	> 25	8
Chromis sp.	> 50	5
Cirrhitidae sp.	1	10
Ctenochaetus sp.	7	13
Dascyllus aruanus	> 100	5
Dascyllus trimaculatus	2	25

Species	Number of individuals	Estimated average length (cm)
Epinephelus merra	1	15
Gobiidae spp. (2)	> 50	5
Gomphosus varius	2	10
Gymnothorax flavimarginatus	1	122
Labroides dimidiatus	5	11
Labroides rubrolabiatus	2	13
Labridae sp. (juv.)	3	10
Monotaxis grandoculis	2	15
Paracirrhites forsteri	4	14
Parupeneus barberinus	5	18
Plectroglyphidodon dickii	4	9
Pomacentrus coelestis	6	6
Pomacentrus nigricans	> 100	10
Scarus frenatus	> 25	13
Scarus sordidus	> 25	13
Scarus spp. (2)	> 20	20
Stethojulis balteata	2	8
Syngnathidae sp.	1	9
Thalassoma amblycephalus	> 100	8
Thalassoma hardwickei	5	18
Thalassoma lunare	7	15
Zanclus canescens	4	15
Zebrasoma scopas	2	15

Fish Observation, **southwest lagoon**: FO 024053

Surveyed: 6 Dec 73, 1445–1500 hours. Tide: incoming to high-high (1.2 m) at 1641 hours. HIV: 15 m. Observation track length: 30 m.

Observation area general description: 600 m east of shoreline point between old Pan Am hotel and northernmost seaplane ramp. Water 3 to 8 m deep. Bottom with large ravines (3–5 m deep and 25–30 m across) with lengths running east-west. Extensive and diverse coral coverage (estimated >30% of bottom covered). Predominant coral types: *Pocillopora*, *Montipora*, *Porites*, *Pavona*, and *Acropora*.



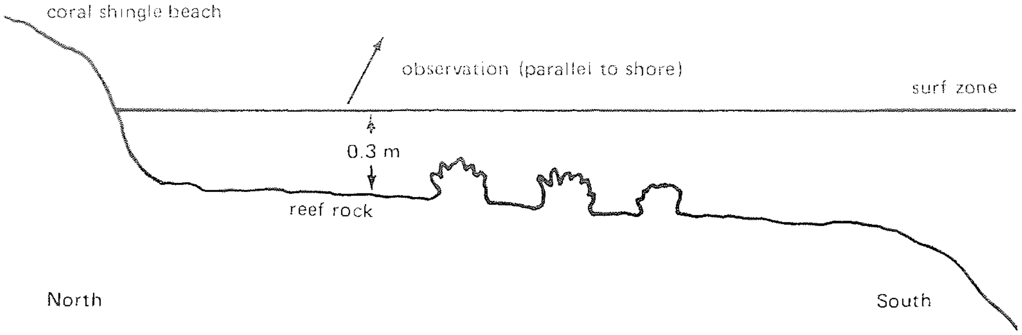
Total Species: 37+

Species	Number of individuals	Estimated average length (cm)
Acanthurus spp. (2)	> 50	15
Centropyge flavissimus	20	10
Cephalopholis argus	10	36
Chaetodon auriga	10	18
Chaetodon kleini	2	15
Chaetodon lunula	3	15
Chaetodon trifasciatus	4	18
Chaetodon ulietensis	12	15
Chanos chanos	> 40	64
Cheilinus undulatus	5	64
Chromis caeruleus	> 300	5
Chromis margaritifer	> 50	5
Ctenochaetus strigosus	> 100	13
Dascyllus aruanus	30	5
Epibolus insidiator	5	25
Epinephelus merra	10	20
Epinephelus microdon	2	64
Gomphosus varius	5	10
Gracila albomarginata	1	18
Gymnothorax flavimarginatus	3	102
Heniochus acuminatus	> 40	18
Labridae spp. (2)	> 100	10
Labroides dimidiatus	5	10
Labroides rubrolabiatus	4	10
Lutjanidae spp. (2)	6	25
Megaprotodon strigangulus	2	18
Myripristis spp. (2)	> 20	18
Plectroglyphidodon dickii	30	8
Pomacentrus nigricans	> 50	10
Scarus spp. (2)	> 50	20
Thalassoma amblycephalus	> 200	8
Zanclus canescens	5	15

Fish Observation, **southwest ocean reef**: FO 027067

Surveyed: 2 Dec 73, 1500–1510 hours. Tide: outgoing to high-low (0.5 m) at 1819 hours. HIV: 9 m. Observation track length: 60 m.

Observation area general description: Ocean reef intertidal shallows, approximately 0.3 m deep. Bottom of shallow gullied reef rock; coral sparse, predominantly small, isolated *Pocillipora* heads. Observation track parallel to shoreline, about 12 m from shore.



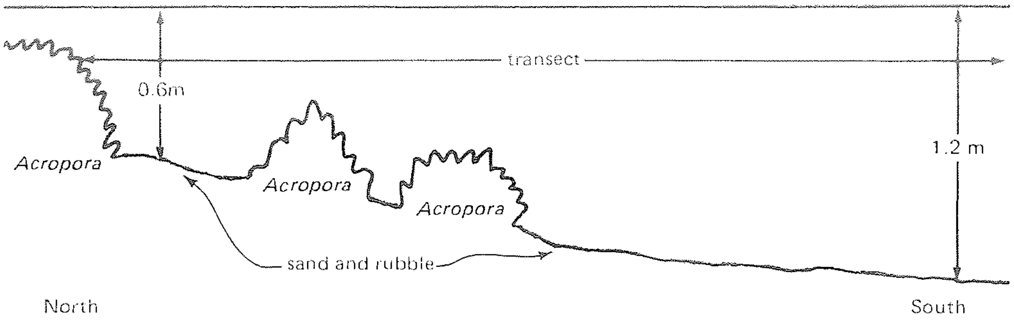
Total Species: 8

Species	Number of individuals	Estimated average length (cm)
Abudefduf glaucus	5	10
Acanthurus triostegus	> 30	13
Carangidae sp.	2	25
Carcharinus melanopterus	4	61
Kuhlia sp.	> 50	18
Lutjanidae sp.	> 100	8
Lutjanus bohar	2	25
Thalassoma hardwickei	3	13

Fish Transect, east runway end, lagoon: FT 041014

Surveyed: 1 Dec 73, 1505–1515 hours. Tide: outgoing to high-low (0.5 m) at 1720 hours. HIV: 2 m. Transect length: 30 m.

Transect general description: On sandy shelf approximately 200 m offshore and 1500 m southeast of east end of main runway. 30 m to the south the bottom begins to drop off steeply to the deeper lagoon water (4.5 m). North end of transect is in a shallow stand of *Acropora formosa* coral; the southern 250 m of the transect is over bottom of sand and shell and coral rubble. All fish except gobies were sighted in the northern 10 m of transect.



Total Species: 17

Species	Number of individuals	Estimated average length (cm)
Acanthurus xanthopterus	20	20
Amblygobius phalaena	1	6
Chaetodon auriga	1	18
Chromis caeruleus	40	5
Ctenochaetus striatus	1	13
Epinephelus merra	1	10
Flammeo sammara	4	11
Gobiidae sp.	2	6
Labridae sp.	5	3
Lutjanus fulvus	> 150	23
Lutjanus kasmira	12	18
Pomacentrus nigricans	3	10

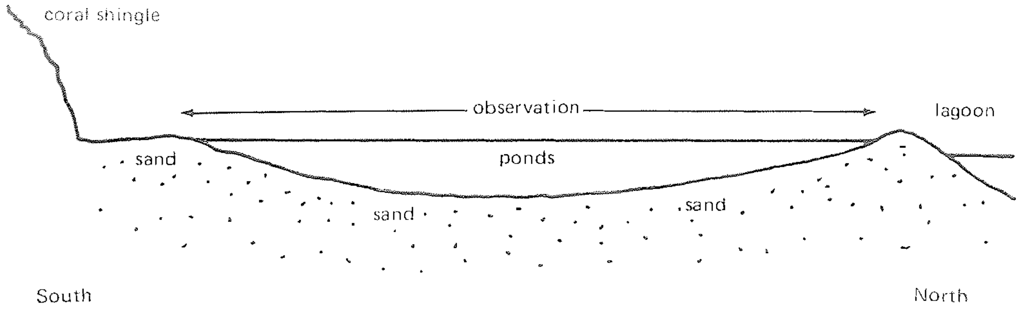
Other species sighted adjacent to area shoreward of transect site on 2 Dec 73 observations:

Albula vulpes
Arothron hispidus
Balistidae sp.
Chelon vaigiensis
Crenimugil crenilabis

Fish Observation, **palm tree row intertidal pond**: FO(w) 041063

Surveyed: 2 Dec 73, 1515–1530 hours. Tide: outgoing to high–low (0.5 m) at 1819 hours. HIV: Not determined. Observation track length: 200 m (waded).

Observation area general description: An intertidal pond complex of approximately 300 m by 400 m. Average depth when surveyed was about 20–25 cm. All bottom of sand with sparse coral rubble; no live coral. Located on southwestern shore of lagoon-side slightly to west of "fisherman's shack." Thin layer of algae covering about 40% of pond bottoms.



Total Species: 8

Species	Number of individuals	Estimated average length (cm)
Abudefduf sordidus	2	13
Arothron hispidus	> 40	15
Carcharinus melanopterus	7	66
Chelon vaigiensis	> 300	18
Crenimugil crenilabis	> 300	20
Epinephelis merra	1	15
Gymnothorax pictus	1	61
Lutjanus fulvus	2	18

Also sighted *Calappa hepatica* (box crabs), about 6 individuals with a mean carapace width of 9 cm.

Fish Observation, **palm tree row, ocean reef**: FO 041065

Surveyed: 2 Dec 73, 1530–1540
All conditions similar to **southwest ocean reef**: FO 027067

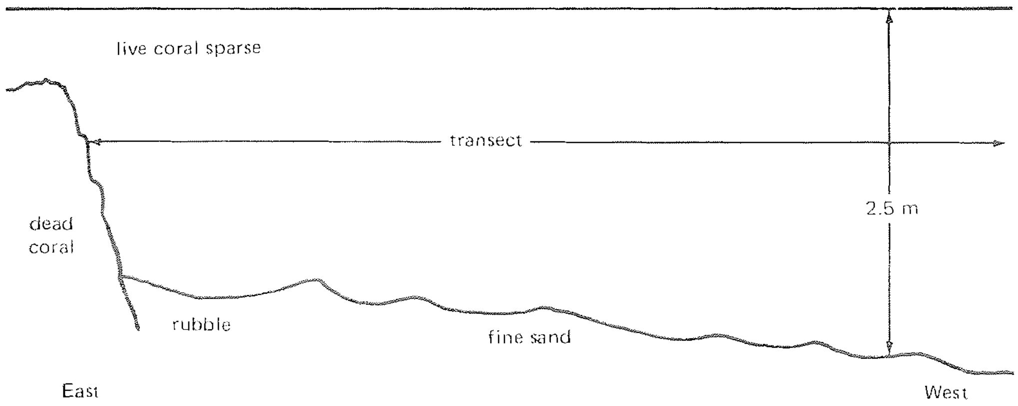
Total species: 4+

Species	Number of individuals	Estimated average length (cm)
Carangidae sp.	4	69
Carcharinus melanopterus	3	25
Labridae spp. (2)	> 50	8

Fish Transect, dredge spoil island, central lagoon: FT 044048

Surveyed: 30 Nov 73, 1530–1600 hours. Tide: outgoing to high-low (0.5 m) at 1619 hours. HIV: 2-4 m. Transect length: 30 m.

Transect general description: Southern tip of a linear reef which terminates at a dredge spoil island about 200 m to the south and extends approximately 3000 m to the north. Live coral is very sparse (covering less than an estimated 5% of hard surface), and a brownish (blue-green?) algae covered substantial areas of the reef flat shallows. A major portion of the reef appeared to be undergoing active siltation. Many holothurians on base of reef slope and on fine-sand bottom. 90% of fish limited to reef and rubble area. Transect on leeward side of reef, and under most conditions this area is upwind of the dredge spoil island (which is heavily populated by birds). No obvious tidal currents. Dominant coral types: *Millepora, Porites, Pocillopora.*



Total Species: 23

Species	Number of individuals	Estimated average length (cm)
Acanthurus xanthopterus	2	15
Balistidae sp.	3	46
Chaetodon ephippium	1	18
Cheilodipterus quinquelineata	4	5
Chromis caeruleus	6	6
Epinephelus merra	6	15
Gobiidae sp.	> 20	5
Rhinecanthurus aculeatus	2	15

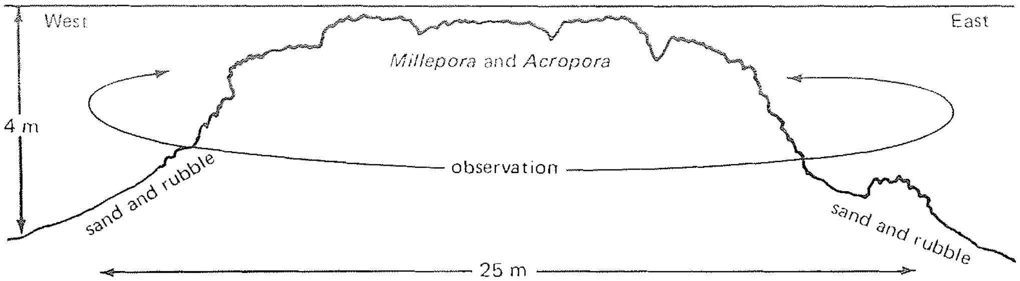
Fish observed off transect on adjacent reef flats (15 species):

Species	Number of individuals	Estimated average length (cm)
Acanthuridae sp.	> 30	20
Amblygobius phalaena	1	8
Arothron hispidus	1	46
Balistoides viridescens (?)	2	20
Caranx melampygus	1	51
Chaetodon auriga	3	18
Chaetodon lunula	2	18
Cheilodipterus quinquelineata	2	5
Chromis caeruleus	> 50	5
Dascyllus aruanus	30	5
Kyphosus cinerascens	2	25
Myripristis sp.	5	15
Pomacentrus coelestis	25	6
Pomacentrus nigricans	> 30	8
Rhinecanthus aculeatus	2	15

Fish Observation, **linear reef, central lagoon**: FO 061041

Surveyed: 6 Dec 73, 1234–1330 hours. Tide: incoming to high-high (1.1 m) at 1553 hours. HIV: 4.5–5.5 m. Observation track length: 30 m.

Observation area general description: Portion of one of the main line reef complexes. Area surveyed approximately 25 m wide by 20 m long. *Millepora* and *Acropora* extremely abundant, covering more than 80% of the bottom. down to approximately 3 m. Sand and coral rubble mound on deeper bottom. Slight current (½ knot) heading east.



Total Species: 41+

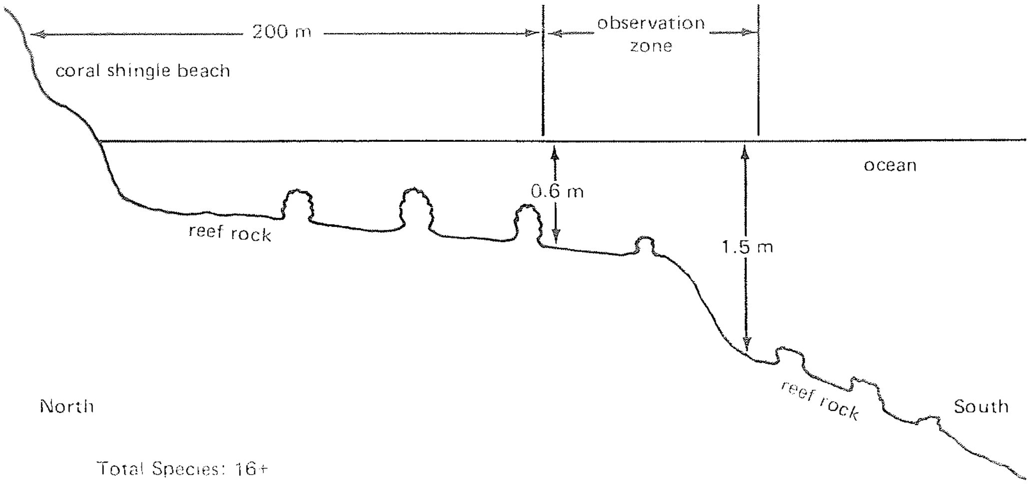
Species	Number of individuals	Estimated average length (cm)
Acanthurus spp. (3)	> 200	18
Acanthurus xanthopterus	> 200	46
Adioryx spinifer	4	41
Balistoides viridescens	4	25
Caranx melampygus	> 12	61
Chaetodon auriga	10	18
Chaetodon ephippium	2	18
Chaetodon lunula	6	15
Chaetodon trifasciatus	4	15
Chaetodon ulietensis	8	15
Cheilinus undulatus	2	41
Cheilodipterus quinquelineata	6	8
Ctenochaetus strigosus	> 150	13
Epibulus insidiator	12	18
Epinephelus merra	5	25
Epinephelus microdon	8	51
Flammeo sammara	25	15
Gnathodentex aureolineatus	> 200	18
Heniochus acuminatus	> 40	18
Heniochus permutatus	> 20	15
Heniochus varius	> 10	15
Lethrinus sp.	12	30
Lutjanus bohar	> 50	36
Lutjanus fulvus	> 300	23

Species	Number of individuals	Estimated average length (cm)
Lutjanus kasmira	> 200	23
Lutjanus monostigma	> 75	23
Megaprotodon strigangulus	6	18
Monotaxis grandoculis	30	18
Mulloidichthys auriflamma	> 200	30
Mulloidichthys samoensis	> 200	30
Myripristis kuntee	> 10	18
Myripristis spp. (2)	> 50	18
Pomacentrus coelestis	15	8
Pomacentrus nigricans	> 100	8
Scarus spp. (2)	> 30	25
Zebrasoma veliferum	6	15
Zanclus canescens	5	18

Fish Observation, **south central ocean reef**: FO 064071

Surveyed: 2 Dec 73, 1630–1645 hours. Tide: outgoing to high–low (0.5 m) at 1819 hours. HIV: 15 m. Observation track length: 15 m.

Observation area general description: Seaward edge of 200-m-wide reef shelf (in surf zone). Depth increasing from intertidal zone (0.6 m) to about 1.5 m. Bottom of gullied beach rock with sparse live coral, mostly small, isolated *Pocillopora* heads. Observation track perpendicular to shoreline. Numerous sea urchins (*Echinometra* sp.) in surf zone.



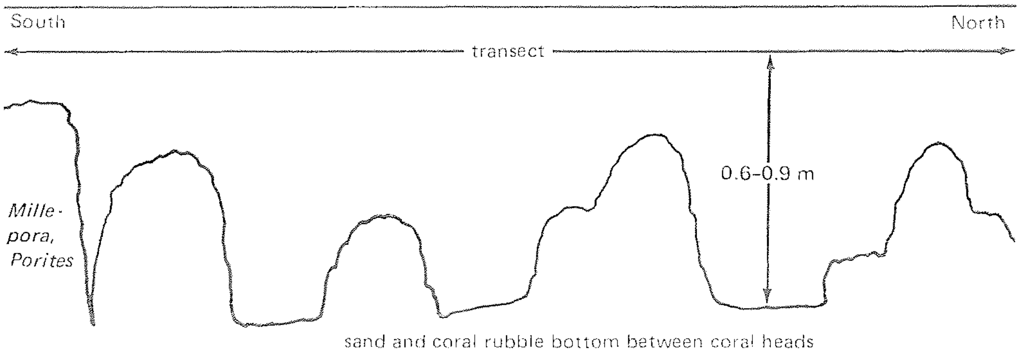
Total Species: 16+

Species	Number of individuals	Estimated average length (cm)
Abudefduf imparipennis	10	5
Abudefduf phoenixensis (?)	1	8
Abudefduf sordidus	> 20	15
Acanthurus achilles	> 40	25
Acanthurus glaucopareius	> 12	23
Acanthurus lineatus	> 20	23
Acanthurus triostegus	> 30	13
Acanthurus xanthopterus	> 20	23
Acanthurus spp. (>2)	> 40	23
Adioryx lacteoguttatus	1	10
Kyphosus cinerascens	15	46
Pomacentrus sp. (yellow)	1	9
Rhinecanthus rectangulatus	10	10
Scarus spp. (2)	> 30	30

Fish Transect, **south fisherman's shack, lagoon**: FT 0660066

Surveyed: 3 Dec 73, 1345–1355 hours. Tide: outgoing from high–high (0.9 m) at 1322 hours. HIV: 3 m. Transect length: 30 m.

Transect general description: Patch of coral (about 30 m in diameter) on shallow sand shelf approximately 300 m offshore. *Millepora* covering estimated 30% of bottom; *Porites* (large rounded heads) covering estimated 10% of bottom. Sand bottom very shelly with some coral rubble. Average depth 0.6–0.9 m. More than 20 *Tridacna* sp. along transect, mostly in *Porites* heads, average size 15–20 cm.



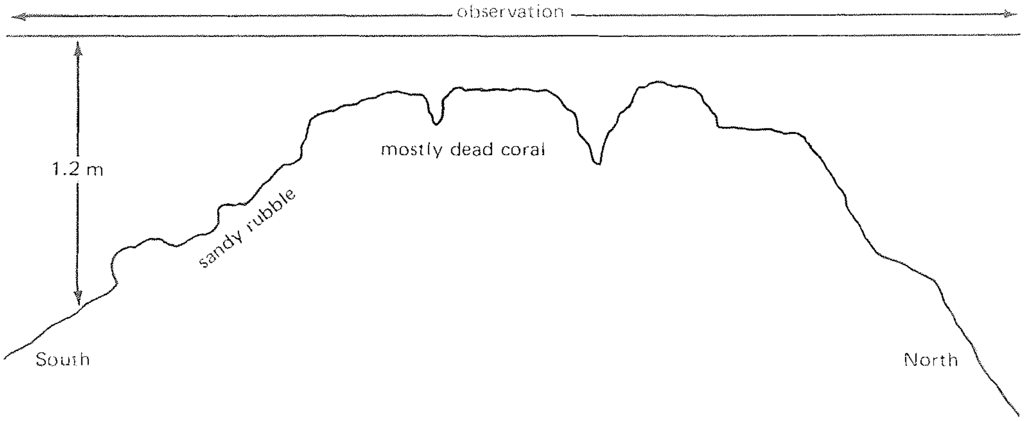
Total Species: 17

Species	Number of individuals	Estimated average length (cm)
Acanthurus triostegus	> 40	10
Acanthurus xanthopterus	> 25	30
Balistoides viridescens	1	25
Chaetodon auriga	> 12	15
Chaetodon ephippium	2	15
Cheilodipterus quinquelineata	3	8
Ctenochaetus striatus	> 30	13
Epinephelus merra	1	15
Flammeo sammara	1	10
Gobiidae sp.	6	8
Labridae sp. (juv.)	20	8
Lutjanus fulvus	> 14	20
Lutjanus kasmira	6	20
Monotaxis grandoculis	1	18
Pomacentrus nigricans	3	10
Pomacentrus sp. (yellow)	1	8
Rhinecanthus aculeatus	2	15

Fish Observation, **east central lagoon**: FO 085053

Surveyed: 6 Dec 73, 1134–1150 hours. Tide: incoming to high-high (1.2 m) at 1553 hours. HIV: 0.9–1.2 m. Observation track length: 30 m.

Observation area general description: 550 m southwest of shoreline point, halfway between north and south poles on southeast shore. Small patch reef (about 15 m in diameter) mostly of dead coral surrounded by sandy rubble. Live coral >5%. Predominant coral types: *Porites* and *Favia*; no *Acropora*. Many large holothurians; more than 20 *Tridacna maxima*.



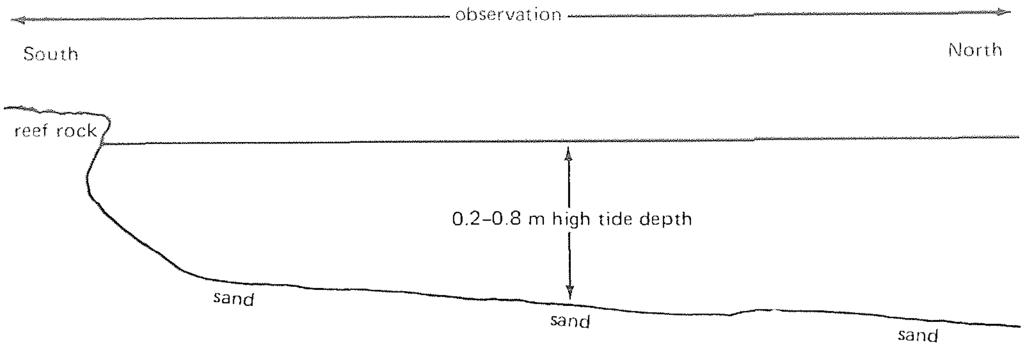
Total Species: 10

Species	Number of individuals	Estimated average length (cm)
Acanthurus xanthopterus	25	20
Arothron hispidus	2	46
Chaetodon auriga	8	13
Chaetodon ephippium	2	18
Chaetodon ulietensis	1	10
Cheilodipterus quinquelineata	1	10
Ctenochaetus strigosus	5	13
Epinephelus merra	2	15
Gobiidae sp.	6	8
Lutjanus fulvus	12	18

Fish Observation, **south tide flats, lagoon**: FO(w) 104094

Surveyed: 5 Dec 73, 1500–1515 hours. Tide: slack at high–high (1.1 m) at 1434 hours. HIV: not estimated. Observation track length: about 30 m.

Observation area general description: Sandy near-shore shallows; dry at low tide. No coral; many *Cerithium* shells (live and dead). Most distant station in site lagoon from main pass.



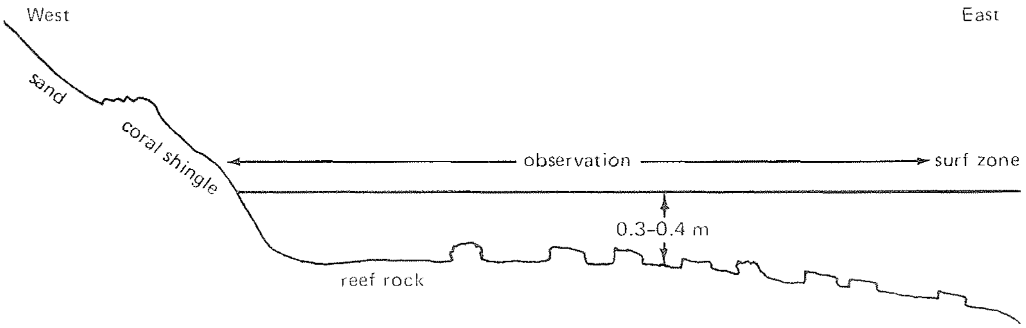
Total Species: 8

Species	Number of individuals	Estimated average length (cm)
Arothron hispidus	10	18
Carcharinus melanopterus	5	61
Chelon vaigiensis	> 20	15
Crenimugil crenilabis	> 15	18
Dasyatidae sp.	1	76
Mullidae spp. (2)	> 25	25
Gobiidae sp.	> 50	5

Fish Observation, **alpha site, ocean tide flats**: FO 108100

Surveyed: 2 Dec 73, 1720–1740 hours. Tide: outgoing to high-low (0.5 m) at 1819 hours. HIV: 15 m +. Observation track length: 100 m.

Observation area general description: A small embayment on the extreme southeastern tip of the island. Bounded to the south by a 100 m+ wide band of dead coral boulders and shingles, bounded to the north only by a slight seaward turn of the coast. Open seaward (east) to the reef shelf edge. Embayment area approximately 100 m by 150 m. Bottom of reef rock with shallow (15–20 cm) ravines. Approximately 10% of bottom covered with loose coral shingle. Coral (small, isolated *Pocillopora* heads) sparse. Average depth 30–40 cm.



Total Species: 11+

Species	Number of individuals	Estimated average length (cm)
Abudefduf amabilis	1	5
Abudefduf imparipennis	12	5
Acanthurus triostegus	> 200	8
Acanthurus xanthopterus	3	41
Carcharinus melanopterus	1	61
Crenimugil crenilabis	> 100	36
Gymnothorax pictus	1	61
Labridae spp. (2)	> 100	6
Rhinecanthus rectangulatus	10	13
Synodontidae sp.	2	10

MOLLUSCAN DISTRIBUTION PATTERNS AT CANTON ATOLL

by

E. Alison Kay

ACKNOWLEDGMENTS

I am grateful to Dr. James Maragos, Dr. Stephen Smith, and Mr. Eric Guinther for providing the sediment samples for the analyses.

ABSTRACT

Micromollusks in sediment samples from Canton Atoll are described in terms of three assemblages: seaward reef; outer, clear water lagoon; and inner, turbid water lagoon. The seaward reef and outer lagoon assemblages are characterized by low standing crops, high species diversity, and a preponderance of microherbivores, in contrast to the inner lagoon, where there are higher standing crops, lower species diversity, and a strong tendency toward suspension feeding. The dominant gastropods in the lagoon are members of the family Diastomidae, including *Diala flammea* and species of *Obtortio* and *Scaliola*. The dominant bivalves are cardiids. The assemblages at Canton resemble those from Fanning Atoll in general aspects, such as standing crops, species diversity, and trophic structure, but differ noticeably in species composition. Differences in species composition are suggested to be associated with differences in water chemistry.

INTRODUCTION

Analysis of molluscan distribution patterns at Fanning Atoll showed a clear distinction in species composition, species diversity, and standing crops between the seaward reefs and the lagoon (Kay, 1971; Kay and Switzer, 1974). Within the lagoon, differences among the mollusks of the lagoon reef flat, patch reefs, and lagoon floor were also detected, associated with substratum types, water chemistry, and turbidity (Kay and Switzer, 1974). Such patterns are of interest because they provide documentation for present and past ecological parameters of atoll reefs and because they are a source of data for both biogeographical and faunistic studies. In this report, patterns of distribution at Canton Atoll are described and are compared with observations from Fanning Atoll.

METHODS

Mollusks from Canton Atoll were obtained from three series of sediment samples. One sample from the slopes of the seaward reef on the lee of the atoll and six samples from the outer lagoon were obtained by hand retrieval from depths between 6 and 35 m by Dr. J. E. Maragos in September 1973 (M stations, Fig. 41). Nine samples from the inner lagoon were collected by Dr. S. V. Smith from dredge hauls at depths of less than 10 m (CL stations, Fig. 41) in December 1973. Two samples from the outer lagoon and one from a "pond" were provided by Mr. E. B. Guinther (G stations, Fig. 41) in December 1973.

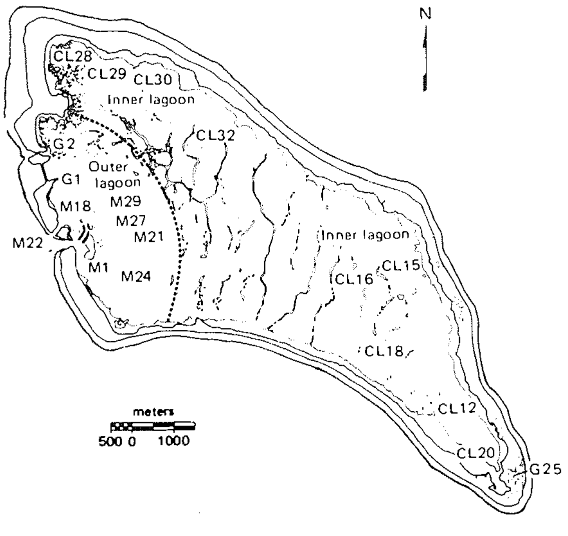


Figure 41. Biotic provinces and micromollusk sample sites.

Mollusks from the sediment samples were obtained by picking shells from standard 25 cm^3 volumes under a binocular dissecting microscope. Most of the mollusks retrieved were small, less than 10 mm in greatest diameter, but cardiid bivalves larger than 10 mm also formed a conspicuous component of the assemblages. Species diversity (H), calculated from the function $H = - \Sigma p_i \log_2 p_i$, and standing crops were obtained for all samples by the methods described in Kay and Switzer (1974). Relative abundance (p_i) values refer to percentage composition of the assemblages.

RESULTS

Ninety species of mollusks were recorded from the samples from Canton Atoll. The samples were divisible into three assemblages, one characteristic of the outer slope of the seaward reef, and two characteristic of the lagoon. One of these was representative of the outer lagoon, the other of the inner lagoon (Fig. 41).

Twenty species were found in the single sample from the slope of the seaward reef at a depth of 35 m. Compared with the samples from the lagoon, this assemblage is characterized by low standing crop and high species diversity (Table 22). Microherbivores predominate, but there is also a high proportion of faunal grazers. Gastropods constitute 93% of the assemblage. The families Cerithiidae, Rissoidae, and Triphoridae are the most abundant, forming 11 to 21% of the assemblage. The bivalves are represented by epifaunal species.

The lagoon is divisible into two sectors on the basis of species composition, standing crop, species diversity, and trophic structure. The outer lagoon stations (M stations and G 1 and 2, Fig. 41) are characterized by lower standing crop, higher species diversity, and a proportionately greater number of faunal grazers than occur in the inner lagoon (Tables 22 and 23). Standing crop averages 9.9 shells per cm^3, and the species diversity index ranges from 1.2 to 3.8. Trophic structure is predominantly microherbivore, with a faunal grazer component comparable to that of the outer reef sample.

Forty-nine species were recorded from the stations in the outer lagoon, of which 24 were restricted to this sector of the lagoon. Gastropods constitute 90% to 99% of the assemblages, and bivalves average about 5% of the assemblages. Species composition and relative abundance of the various groups are shown in Table 22 and Fig. 42 and 43. The dominant gastropods are the Diastomidae, represented by four species and comprising an average of 56% of the gastropods in each sample. *Diala flammea*, the most abundant diastomid, is found in all the samples and averages 93% of the diastomids. *Obtortio*

Table 22. Standing crop, species diversity, and relative abundance of the most common micromollusks at Canton Atoll.

Station	M22	G1	G2	M18	M24	M29	M1	M21	M27	CL28	CL29	CL30	CL32	CL16	CL15	CL18	CL12	CL20	G25
No./cm^3	3.9	23.8	17.6	5.4	14	11.2	5.3	15	8	3.2	4.4	21.6	23.3	26.6	1.4	39	2.2	15.4	8.4
Species diversity	3.8	2.3	1.2	3.8	3.1	2.5	3.7	2.8	2.4	3.0	1.4	2.5	2.7	2.4	2.3	2.1	2.3	2.2	3.1
% Gastropods	93	94	99	93	90	95	99	95	95	63	48	56	59	76	69	41	44	97	75
Tricolia	10	–	–	3	–	–	3	1	+	–	–	–	–	–	–	–	12	+	–
Leptothyra spp.	2	5	2	9	5	4	4	3	2	16	7	6	6	1	–	1	–	–	14
Rissoidae	20	9	7	15	10	10	11	7	5	+	–	+	3	2	–	1	–	–	4
Bittium glareosum	21	–	–	15	8	2	28	7	8	–	–	3	+	+	–	1	8	–	3
Diastomidae	1	72	86	27	44	67	17	66	68	41	70	78	82	69	96	87	50	88	72
*Diala**	+	95	95	94	93	86	100	87	95	38	35	58	36	21	21	28	50	34	63
Obtortio sp.*	–	2	3	3	3	6	–	3	1	14	8	1	13	4	–	18	–	13	24
*Obtortio pupoides**	–	2	3	–	2	2	–	6	2	48	49	39	1	9	12	40	33	39	3
*Obtortio sulcifera**	–	+	1	3	2	7	–	4	1	–	8	1	26	–	12	–	–	2	9
Scaliola spp.*	–	–	–	–	–	–	–	–	–	–	–	+	23	64	54	13	17	12	–
Triphoridae	11	–	–	–	+	+	5	+	+	–	–	–	+	+	–	–	–	–	–
Cerithiopsidae	2	–	–	+	+	–	+	+	+	–	–	–	–	–	–	–	–	–	–
Marginellidae	1	+	–	+	+	+	4	+	1	–	–	–	–	–	–	–	–	–	–
Pyramidellidae	–	6	3	5	3	7	8	3	3	6	7	5	5	2	4	3	8	–	2
Acteocina	–	5	–	11	14	4	2	6	4	27	1	4	–	2	–	5	17	–	+
% Bivalves	7	6	1	7	10	5	1	5	5	37	52	44	41	24	31	59	56	3	25
Fragum†	–	9	17	44	39	60	–	78	36	93	93	95	99	99	99	99	100	100	2
Tellinidae†	–	89	–	28	50	33	25	–	27	–	5	2	–	–	1	–	–	–	8

*As percent of Diastomidae.

† As percent of bivalves

Note: Species composition is given as percentage composition. + signifies less than 1% of the assemblage.

Table 23. Trophic structure representing averages (in percent) from each area.

Trophic structure*	Seaward reef	Outer lagoon	Inner lagoon
Herbivores	65	66	54
Faunal grazers	25	23	+
Predators/scavengers	–	1	3
Parasites	–	+	2
Suspension feeders	10	10	40

Note: + signifies less than 1% of the assemblages.

*Herbivores include archaeogastropods (*Tricolia*, *Leptothyra*), rissoids, cerithids, diastomids, etc.; faunal grazers include triphorids, cerithiopsids, and marginellids that feed on sponges, etc.; predators/scavengers are columbellids, turrids, and others of the neogastropods, and some opisthobranchs; the pyramidellids are considered parasitic; and suspension or deposit feeders are represented by bivalves.

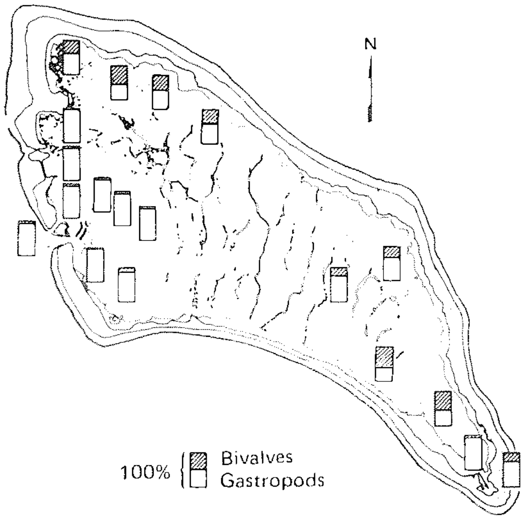


Figure 42. Relative abundance of bivalves and gastropods.

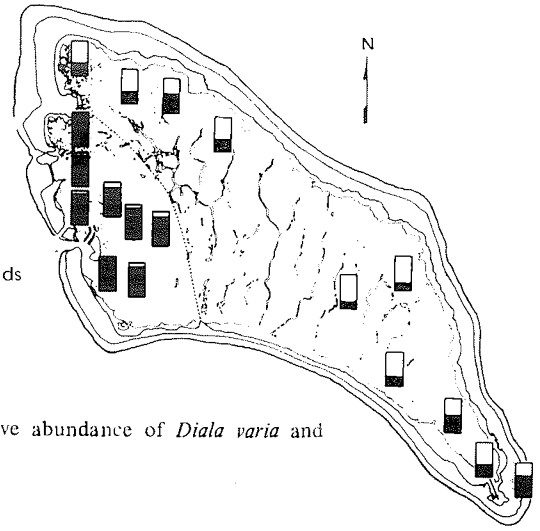


Figure 43. Relative abundance of *Diala varia* and other diastomids.

pupoides, O. sulcifera, and *Obtortio* sp. are less abundant and less frequent, each constituting 2 to 3% of the gastropods in the assemblages. Other prominently represented gastropods are rissoids, represented largely by two species, *Parashiela beetsi* and *Parashiela* sp., and the cerithid *Bittium* cf. *glareosum*. Turbinids of the genus *Leptothyra*, the opisthobranch *Acteocina sandwicensis*, and pyramidellids each constitute about 6% of the gastropod species. *Cerithiopsis* spp. and marginellids (Fig. 44) and triphorids are frequent, occurring in five to seven of the samples; but they are not abundant. The bivalves are represented by cardiids and tellinids, with one species of *Cardium* representing 40% of the bivalves and tellinids 42% of the bivalves.

Two stations are somewhat anomalous: at station M18 near the pass and station M1 on a patch reef, diastomids form a conspicuously lesser proportion of the assemblages than they do elsewhere in the outer lagoon, and *Bittium* a higher proportion. Station M1 also lacked cardiids.

In the inner lagoon, 43 species of mollusks were recorded, of which 26 were also found in the outer lagoon, and 17 were restricted to the area. Standing crop averages 15.2 shells per cm^3, and the species diversity index ranges from 1.4 to 3.0. Trophic structure shows a strong tendency toward suspension feeding (Table 23), although microherbivores are still dominant. The relative abundance of gastropods and bivalves is shown in Table 22, and the distribution of relative abundance of bivalves and diastomids is shown in Fig. 42 and 43.

Gastropods average 63% of the assemblages and bivalves average 37%. Five species of diastomid are present, with *Diala flammea, Obtortio sulcifera,* and *Scaliola* spp. represented by almost equal proportions. Rissoids and cerithids each occurred in five of the nine stations but averaged only 2 and 4% of the gastropods in the samples. *Leptothyra, Acteocina,* and pyramidellids are found in about the same proportions as in the outer lagoon. Cardiids, represented largely by one species of *Cardium*, average 47% of the bivalves in the samples.

Three of the nine stations vary in species composition. At stations CL 28 and CL 12, in the northwestern and southeastern sectors, respectively, the diastomids constitute only 41% and 50% of the gastropods, compared with an average of 81% in the other samples, and there is an apparent concomitant increase in the proportion of *Acteocina*, represented by 27% and 17% of the samples (Table 22). *Scaliola*, which constitutes a significant part of the assemblages at the other stations, was absent at stations CL 28 and CL 29 (Fig. 44). At station CL 20 in the southeasternmost sector, gastropods constitute 97% of the assemblage, a figure similar to that of the assemblages in the outer lagoon. Variations in standing crop do not fall into a pattern and are assumed to depend on the substrata sampled by the dredge.

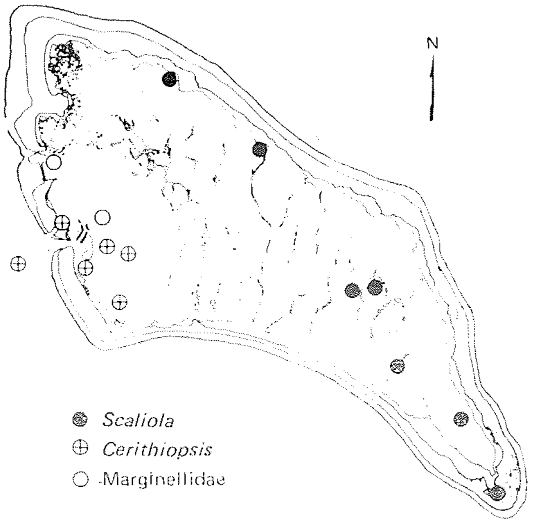


Figure 44. Distribution of *Scaliola, Cerithiopsis,* and marginellids.

DISCUSSION

The occurrence of three distinctive assemblages of mollusks at Canton Atoll parallels that reported for Fanning Atoll (Kay and Switzer, 1974). Canton and Fanning Atolls lie in the same biogeographical region in the Central Pacific and have a rather similar physiography (Henderson *et al.*, this volume). Canton, like Fanning, is a roughly oval atoll with a single deep pass and, like Fanning, the lagoon is subdivided into two sectors by line and patch reefs. At Fanning the equivalent of the outer lagoon of Canton is an area of clear water adjacent to the pass through which currents of more than 5 knots have been recorded. The equivalent of the inner lagoon at Fanning is an area of turbid water (Smith *et al.*, 1971). Much of the inner lagoon at Canton is also turbid (Smith and Jokiel, this report), and this turbidity may be the water quality parameter most closely associated with the similar micromolluscan distribution patterns recorded at Canton and Fanning.

At both Fanning and Canton the seaward reef slope assemblages are characterized by high species diversity, low standing crops, and numerous faunal grazers represented by triphorids, cerithiopsids, and marginellids. At Fanning and Canton the lagoon assemblages are divisible into an outer assemblage and an inner assemblage, the former characterized by lower standing crop, higher species diversity, and a preponderance of epifaunal microherbivores, the latter by higher standing crop, lower species diversity, and a high proportion of suspension-feeding mollusks. In both lagoons a dominant component of the gastropod assemblage consists of the family Diastomidae, with *Diala flammea* predominating in the outer lagoon (clear-water area at Fanning) and species of *Obtortio* characterizing the inner lagoon (turbid-water area at Fanning). Among the bivalves, tellinids predominate in the outer lagoon at Canton, as they do in the clear-water areas of the lagoon at Fanning.

Differences between the molluscan assemblages of Canton and Fanning are as striking as are the similarities, but the differences appear to be primarily in species composition and dominance patterns. It is tempting to suggest that water composition other than turbidity may account for the differences: Fanning is predominantly a low-salinity atoll (Smith and Pesret, 1974), while Canton is dominantly hypersaline (Smith and Jokiel, this report).

The distinguishing features of molluscan species composition in the lagoon at Fanning are the inordinate numbers of the phasianellid *Tricolia variabilis*, which occurs on the reef flats and extends onto the patch reefs of the central lagoon, and the lesser but noticeable numbers of *Merelina* sp. A., *Leptothyra* sp., and *Haplocochlias minutissimus* (Kay and Switzer, 1974). All four species occur at Canton, but are neither abundant nor frequent: a total of 37 specimens of *Tricolia* was recorded at Canton, compared with several thousand at Fanning. All four species are presumably microherbivores, and at Fanning are conspicuously absent or few in numbers on the lagoon floor.

Five species distinguish the species composition at Canton: *Bittium* cf. *glareosum*, *Scaliola* spp., *Parashiela beetsi*, *Parashiela* sp., and a cardiid. *Bittium glareosum*, *Scaliola*, and *Parashiela* sp. were not recorded at Fanning; *Cardium* sp. and *Parashiela beetsi* were present, but not in the numbers recorded at Canton. At Canton, *Bittium* and *Parashiela* sp. are almost entirely restricted to the outer lagoon; *Cardium* sp. occurs in both the inner and outer lagoon, but is relatively more abundant in the inner lagoon; and *Scaliola* was found only in the inner lagoon. Of the five species, the habits of only the cardiid are sufficiently known to suggest a reason for its predominance: cardiids are infaunal suspension feeders, and their occurrence may be associated with peculiarities of the substrata at Canton.

Within the lagoon at Canton anomalies in distribution patterns occur most noticeably in the inner lagoon, where *Scaliola* is conspicuously absent from two stations (CL 28 and CL 29), and where there is a lower proportion of bivalves relative to gastropods at a third station (CL 20). Explanations for the anomalies are not readily apparent. The two stations where *Scaliola* is absent are in a disturbed sector of the lagoon near an old pass. Their presence at stations CL 12 and CL 20, which are also in the regions of old passes, would preclude the explanation for their nonoccurrence at stations CL 28 and CL 29 as being due to oceanic water or outer lagoon conditions. The high proportions of gastropods relative to bivalves at station CL 29 does suggest, however, that oceanic or outer lagoon conditions characterize this area.

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OBSERVATIONS ON TERRESTRIAL SURFACES AND SUBSURFACE WATER AS RELATED TO ISLAND MORPHOLOGY AT CANTON ATOLL

by

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ABSTRACT

Reconnaissance sampling of isolated bodies of water on Canton Island* revealed a pattern in salinities related to the physiography of the channels and flats of the island. Moderate salinities between 13 and 18 ^{o}/oo typified channel-bed ponds, while lower salinities (less than 8 ^{o}/oo) typified potholes and water-filled burrows on the surrounding flats. Highest salinities (greater than 24 ^{o}/oo and up to 152 ^{o}/oo) were encountered in two larger ponds, in lagoon tidal channels, and in a saltern. A wide variation in concentration of nutrients and chlorophyll *a* suggests ecological dissimilarities stemming either from salinity differences where such differences are great or from variations in biological community development owing to vagaries in colonization or previous environmental histories or both.

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*The term "Canton Island" refers to the largest land mass of Canton Atoll.

INTRODUCTION

Because atoll soils are typically highly permeable, standing bodies of water are rare features of the atoll terrestrial environment. Large islets with substantial inputs of freshwater in the form of precipitation will develop groundwater bodies of the Ghyben-Herzberg type (Cox, 1951). The extent of fresh or brackish water in aquifers of this type depends on complex relationships between rainfall, evaporation, islet size, sediment permeability, and tidal range. Atoll islets are low in profile; topographical depressions may expose portions of the water table, resulting in the formation of ponds or, under special circumstances, even streams (Guinther, 1971). The chemical composition of water in such ponds may not always coincide with that of the groundwater in the immediate vicinity, because surface water is subject to different rates from the groundwater in input (rainfall, seepage, tidal inflow), output (evaporation and outflow), and biogeochemical alteration. Nevertheless, exposed bodies of water on atoll islets are ecologically interesting and can also be used to indicate uppermost groundwater conditions. Freshly dug wells serve as the most simple means of sampling groundwater directly.

METHODS

Salinity observations on standing bodies of water at Canton Island were made between 4 and 11 December 1973. In addition, water samples from selected sites were analyzed for NO_3, NH_4, PO_4, Si, and phytopigments. Salinity measurements were of two types. Salinities were determined in the field by measuring the refractive index of small quantities of water with an American Optics hand-held refractometer. At some stations, water samples were collected and the salinity determined in the lab by comparing the sample conductivity with that of a known standard (Smith and Jokiel, this report). This latter method yields more precise (but, at low salinities, not necessarily more accurate) results than does the refractivity method. The results of both types of salinity determinations are presented in Table 24. When both methods were used on the same samples, the values derived by refractivity were about 1.5 $^{o}/oo$ lower than the values derived from conductivity analyses. Although analytically interesting, this difference does not change the basic interpretations of the data.

Table 24. Station descriptions and salinities.

Station	Description	Date	Time	Salinity (^{0}/oo)*	
				A	B
1	Cement-lined sump adjacent to lagoon beach, NASA site (abandoned)	12/5	1630	6.5	
2A	Sump hole at crusher plant (in use)	12/10	pm	26	
2B	Gravel pit behind shingle berm (ocean) at crusher plant	12/10	pm	4.5	
3	Old man-made trench in flat, about 2 km SE of crusher plant	12/10	pm	6	
4	Small ordnance craters on flat	12/8	am	2.5-12.5	
5A	Shallow depression, seaward side of flat	12/8	am	6.5	
		12/11	0900	3	
5B	*Cardisoma* burrow and seepage beneath consolidated shingle rise adjacent to 5A	12/8	am	2	
6	Small ordnance craters on flat	12/8	am	0	
7	Small ordnance craters on flat	12/8	am	4-5	
8	Moderate-sized pond in depression on flat (natural channel)	12/6	1830		17.52
		12/8	0810	12.5-14	14.68
		12/8	1410	14	
		12/8	1630		16.02
		12/11	1000	13	
9	Small ordnance craters	12/8	pm	0-5	
10	Shallow depression, seaward side of flat	12/8	pm	2	
11	Shallow depression on flat (natural channel)	12/8	pm	13	
12	Small ordnance craters	12/8	pm	0.5-2	
13	Small pond in depression on flat (natural channel)	12/8	pm	14	
14	Large ordnance crater on flat	12/8	pm	0.5	2.04
		12/10	1100		2.22
15	Large ordnance crater on flat	12/8	pm	0	
		12/10	1100		2.02
16	Small potholes and *Cardisoma* burrows on flat	12/5	1615	1-2	
17	Shallow pond in depression on flat (natural channel)	12/10	am	15.5	
18A	Moderate-sized pond behind lagoon beach in natural channel leading to flat	12/5	1600	13.5	
18B	*Cardisoma* burrow adjacent to 18A	12/5	1600	8	
19	Shallow hole dug into dry channel	12/5	1615	3	
20	Shallow depression (man-made?) in flat adjacent to Green Pond	12/6	1240	17	18.95
21	Seepage from beneath beachrock rim beside Green Pond	12/5	1015	8-12	
		12/6	pm		10.31
22A	Green Pond; largest "pond" on Canton	12/5	1000	71	
22B	Channels in cyanophyte mat extending outward from shore of Green Pond	12/5	1000	82	
22C	*Cardisoma* burrow in dry channel leading NE from Green Pond basin	12/5	1000	108	
23	Clear Pond; second largest "pond" on Canton	12/5	1125	24	
		12/6	1220		26.84
		12/8	0940		27.92
		12/10	1030		29.27

(Contd)

Table 24. (Contd)

Station	Description	Date	Time	Salinity (^{o}/oo)*	
				A	B
24	Hole dug into center of large salt pan (saltern)	12/5	1530	152	
25	*Cardisoma* burrow on flat just beyond edge of salt pan	12/5	1530	11	
26	Tidal channel on tidal flat	12/5	1130	43	
27	Tidal channel at SE head of tidal flat	12/5	1140	41-43	
		12/5	1500	38.5	
28A	*Cardisoma* burrows at edge of flat	12/5	1515	2	
		12/10	1000	0.5	
28B	Water on low part of flat periodically exposed	12/10	1000	14	
29	Shallow trench (man-made) on flat adjacent to road crossing	12/5	1450	8	
30	Tidal channel in tidal flat (west)	12/6	1045	42	43.42
31	Tidal flat	12/6	1030	43.5	

*Salinity A measured in the field using a refractometer; Salinity B measured in the lab from a bottled sample on a conductivity meter.

OBSERVATIONS

Small, exposed bodies of water on Canton Island are restricted largely to the east and southeast portions of the island. This distribution appears to be a consequence of the factors which initially built the island above the reef base, although construction of fortifications during World War II sufficiently disrupted the ground surface along the northwest and northeast portions of the island so that the original topography there is obscured. The absence of surface water on other parts of the island does not, of course, rule out the occurrence of fresh or brackish groundwater there.

The sampling sites established during this study are shown in Fig. 45 and 46. These stations are described briefly in Table 24. Although an appreciable range of salinities was encountered (from 0 to 152 ^{o}/oo), a pattern in the distribution of surface waters does emerge. This pattern is related to the physiography of the flats on which most surface water occurs. Low ground between the seaward beach berm (normally the highest part of the island) and the lagoon beach occurs in the form of extensive flats (lightly stippled areas in Fig. 46). The detailed origin of these flats is unclear, but they are most

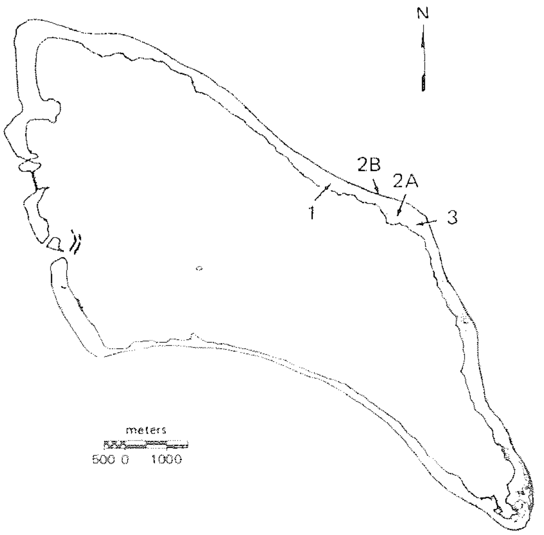

Figure 45. Canton Island, showing water sample sites 1–3.

certainly the work of seawater flowing onto, across, or between ancient islands. The flats are morphologically similar to those described on Fanning Atoll by Guinther (1971) and on Diego Garcia Atoll by Stoddart and Taylor (1971), but the Canton flats differ in not having a regular tidal flow of lagoon water. Evidence for a higher stand of sea level at Canton (either eustatic or tectonic) may be found in the extensive escarpment of detrital limestone surrounding the lagoon and bordering portions of the inland flats. The vertical relief of the limestone exceeds 2 m in some places. A consequence of the subsequent lowering of relative sea level was to strand the intertidally or subtidally formed flats above the present influence of tidal water.

The possibility of present-day seawater incursion onto the flats during the seasonal higher level of the sea at Canton seems unlikely. Our visit coincided with the month of maximum average sea level (December), yet the flats were above any tide level. Nonetheless, particularly large positive deviations in sea level, associated with strong equatorial countercurrent transport (Wyrtki, 1973), might allow occasional tidal flow across the flats. Therefore, formation of these flats at present sea levels cannot be ruled out.

Active tidal flats with well-delimited tidal channels are restricted to one large inlet at the extreme southeast end of the lagoon (stations 26, 27, 30, and 31 in Fig. 46) and to several smaller areas separated from the lagoon by sandbars. The stranded inland flats slope gently toward more or less central dry channels whose courses are eventually lagoonward. These channels apparently connect the inland flats to the lagoon, although the present lagoon beach is not broken where the channels contact the shore. Despite the lack of direct evidence indicating tidal flow, the channel beds of the inland flats are clearly demarcated in most places and appear to be influenced by recent surface flow. Torrential rains during the 1972–1973 period of high rainfall may account for these features.

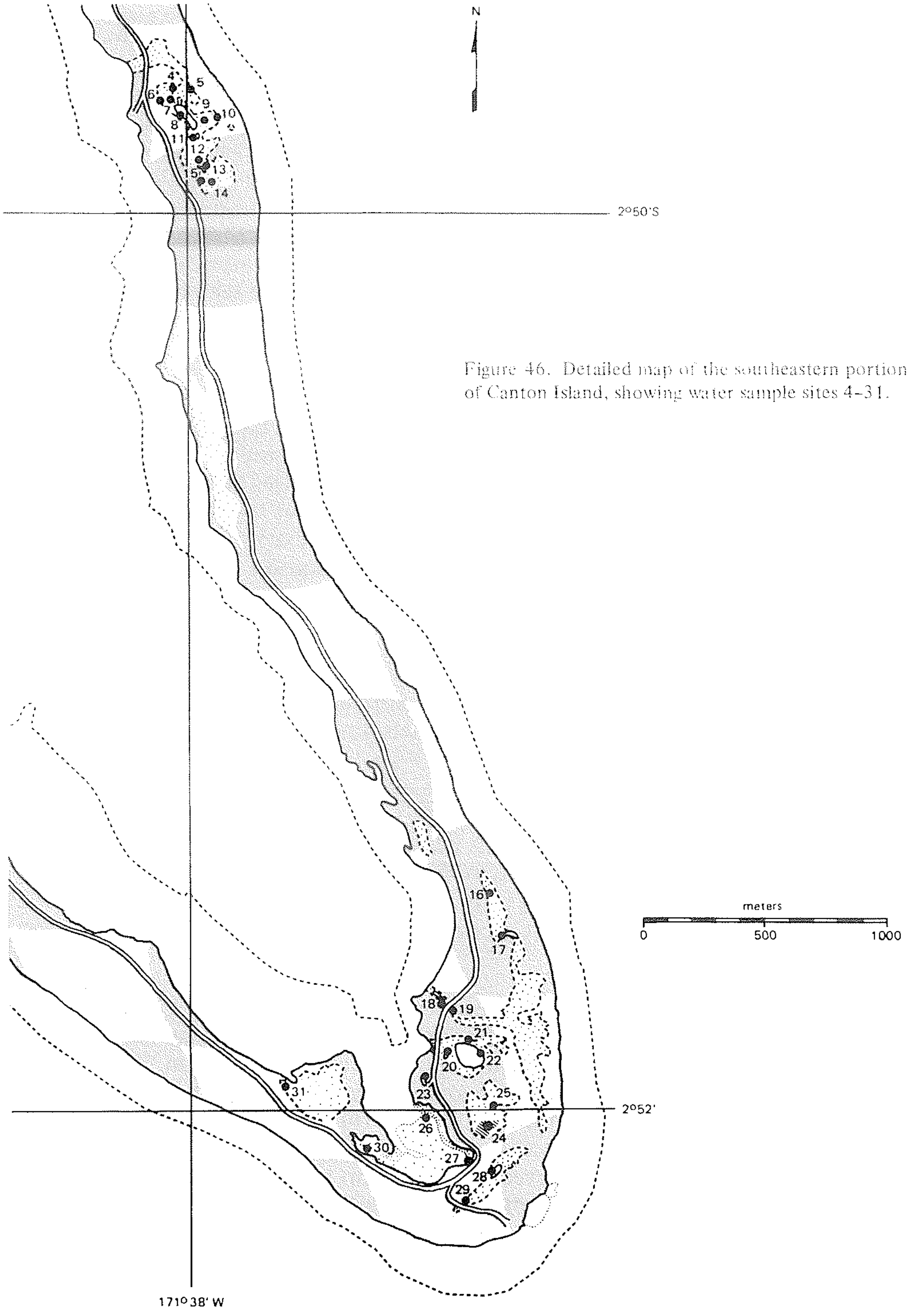

Figure 46. Detailed map of the southeastern portion of Canton Island, showing water sample sites 4–31.

The surface of the inland flats is a continuous sheet of detrital limestone, generally less than 1 cm thick and apparently formed *in situ*. In the channel beds, this hardpan surface is overlain by thin crumbly crusts (dried cyanophytes); terrestrial macroscopic plants are rare. Over the remainder of the flats, excepting areas occupied by standing water, plants are abundant and contrast sharply in their growth and green coloration with the same species occurring on higher ground. The healthier condition of plants on the flats (where the grasses *Lepturus* spp. dominate) indicates the proximity of groundwater to the land surface in these areas. In fact, tidal fluctuations of the groundwater cause it to emerge periodically in some locations; the water table can be seen readily in burrows of the land crab *Cardisoma carnifex* and in shallow depressions on the flats.

Most of the exposed bodies of water associated with the flats fall into one of two groups based on location relative to the channels crossing the flats. Those bodies of water located in the channel beds had salinities between 13 and 18 °/oo. Bodies of water not located in the channels, but found elsewhere on the flats, had salinities ranging from 0 to 8 °/oo. Some exceptions may be found, particularly in areas associated with Green Pond (station 22), Clear Pond (station 23), and the salt pan (station 24).

Differences in salinities between ponds in the channel beds and ponds away from the channels on the flats may be related to surface flow patterns. Perhaps tidal water occasionally enters the channels during exceptionally high tides that are coincidental with anomalously high sea levels. Groundwater flux may also differ in the two types of ponds. Some evidence of low-salinity groundwater entering the pond at station 8 exists in the series of salinity determinations made there. Salinities in this pond appear to fluctuate diurnally, with salinities of about 14 °/oo occurring in the morning and salinities of around 17 °/oo resulting in the evening after a daytime period when evaporation apparently exceeds the influx of groundwater.

During the period of our stay, evaporation exceeded any groundwater influx to Clear Pond (station 23) so that this large pond increased in salinity at a rate of nearly 1 °/oo/day. This rate of increase is probably short-term. Water samples collected from Clear Pond approximately once each month between January and October 1974 revealed that the salinity fluctuated between 25 and 37 °/oo. In general, low salinities coincided with months of high rainfall. At one time the pond basin was observed to contain no surface water, a circumstance probably resulting from an exceptionally low tide rather than from evaporative water loss. During our short stay on Canton, the water level in Clear Pond could be seen to fluctuate daily, although these fluctuations were considerably out of phase with the lagoon tide.

Salinity, nutrient content, and the suspended chlorophyll content of eight selected ponds and one lagoon inlet station are presented in Table 25. The stations have been arranged in order of increasing salinity. The only pattern relative to salinity which emerges is that the silicate concentration decreases slightly with increasing salinity up to approximately normal seawater salinities, and then increases sharply with increasing hypersalinity. The highest levels of nitrate, ammonia, phosphate, and silicate were found at station 24, a shallow well dug down to the water table at the bottom of a natural salt pan. With scattered exceptions, nutrient levels in all the ponds sampled were within the range of concentrations observed in the Canton Atoll lagoon (Smith and Jokiel, this report). Chlorophyll *a* concentrations varied over a range from less than 1 to over 3000 μg/liter. The highest values were in two samples obtained from Green Pond (station 22), and one sample from the crater pond (station 15). Green Pond had a dense, deep green color which obscured visibility beyond a depth of 10 cm.

Table 25. Salinity, nutrients, and chlorophyll *a* levels of selected ponds at Canton.

Station	Salinity (‰)	NO_3 (μg-atom N/liter	NH_4 (μg-atom N/liter)	PO_4 (μg-atom P/liter)	SiO_3 (μg-atom Si/liter)	Chlorophyll *a* (μg/liter)
15	2.02	0.02	0.62	0.30	12.6	239.0
14	2.22	2.41	0.09	0.03	3.2	0.58
21	10.31	5.14	4.70	0.62	2.75	–
8	17.52	0.11	1.33	0.87	2.3	2.89
20	18.95	0.31	1.23	2.21	2.2	4.82
23	29.27	6.65	0.83	0.11	2.1	3.65
30	43.42	0.10	0.51	0.18	2.3	0.98
22	71.0	0.25	0.97	0.45	10.4	3270,2740
24	152.0	2.52	360.0	22.88	23.6	–

Stations 14 and 15 present a particularly curious situation. These two separate bodies of water are located within 5 m of each other on the flat (Fig. 45). Each is a small crater about 1 m across and 0.5 m deep; both were apparently formed by ordnance explosions. Salinity differed only slightly between the ponds in December, but water at station 14 was clear, while that at station 15 was bright green. A comparison of chlorophyll *a* concentrations (Table 25) reveals the magnitude of the difference in phytoplankton abundances. The pond at station 14, with the lowest chlorophyll *a* concentration of all samples taken, showed relatively low levels of ammonia and phosphate, but moderately high concentrations of nitrate. The nutrient concentrations at station 15 were reversed, with moderate levels of both ammonia and phosphate and low levels of nitrate. Silicate concentration was very high at station 15 and consequently did not fit the salinity-to-silicate relationship apparent in the other samples.

The general distribution of chemical nutrients in the aquifer cannot be determined from the data collected. Samples for the analyses reported were taken from open bodies of water in all but one case (station 24), and biological activity in the ponds certainly alters the dissolved nutrient concentrations in the adjacent groundwater as this water enters the ponds. Seepage into Green Pond from the base of a limestone escarpment (station 21) provides some indication of chemical nutrient levels in groundwater having a salinity of 10 $^{0}/_{00}$. Of the dissolved substances measured, only the concentration of silicate is increased by evaporation in the receiving body. However, even in the case of silicate, additional mechanisms must be considered to explain a four-fold increase in silicate with a seven-fold increase in salinity.

The wide variation in nutrient and chlorophyll *a* concentrations from pond to pond suggests that the ponds are ecologically dissimilar. To some extent this dissimilarity would follow from the wide range of salinities encountered. On the other hand, ponds with similar salinities differed appreciably in properties closely tied to biological processes. In at least one comparison (stations 14 and 15) differences in the chemistry of input waters are unlikely, and random introductions of specific phytoplankters or herbivores may serve to explain differences in phytoplankton standing crop as measured by chlorophyll concentration. However, standing bodies of water appearing to be chemically similar at the time of this survey may have recently been dissimilar; random colonizations would then be significant in determining biological community composition. Insufficient time may have elapsed for all potential colonizers to have reached all habitable environments.

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