FANNING ISLAND EXPEDITION, JULY AND AUGUST, 1972

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JULY 1973

Prepared for
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HAWAII INSTITUTE OF GEOPHYSICS
UNIVERSITY OF HAWAII
Frontispiece. Fanning Island.
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Nineteen researchers comprising the Second Fanning Island Expedition left Honolulu in mid-July 1972, for a proposed eight-week study of the atoll. The objective of the expedition was, as in 1970, to focus on studies of the physical and chemical oceanography of the lagoon, and to learn something of the dynamics of various biota. The expedition members came from a variety of disciplines from four institutions: the University of Hawaii; the Bernice P. Bishop Museum, Honolulu; the University of Guam; and the Smithsonian Institution, Washington, D. C. As in 1970, we found that such a diverse group "could work together, talk together, and learn together from the environment and from each other."

Transportation for the initial phase of the journey, from Honolulu to Christmas Island, was provided by the United States Air Force. From Christmas Island we were ferried in groups of four or five to Fanning Island by Dr. Martin Vitousek. Our return to Honolulu in late August was complicated by a hurricane which affected Johnston Island and forced several members of the party to remain on Christmas Island for two weeks, from whence they were eventually ferried to Honolulu by the United States Coast Guard. Other members of the party flew directly from Fanning to Honolulu with Dr. Vitousek.

To acknowledge all the hospitality, support, and help we received in mounting the expedition and accomplishing our goals is an almost impossible task. We especially acknowledge the hospitality of John Briden of Christmas Island and that of John Fleetwood and Philip Palmer of Fanning Island. Ray Jeffcott provided us with untold technical assistance on Fanning. Philip Helfrich and Mike Aurnig supplied us with boats. Ed Houlton of the Hawaii Institute of Geophysics kept track of us by radiophone and kept our families informed of our activities. W. R. Coops of the Research Corporation of the University of Hawaii cut through much red tape, as he had done in 1970, and smoothed our path in a myriad of ways. We gratefully acknowledge the editorial assistance of Mrs. Ethel McAfee in the preparation and publication of this report, and the typing assistance of Mrs. Barbara Hoshida.

The Second Fanning Island Expedition was supported by National Science Foundation Grant GA 313111.

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E. Alison Kay

31 January 1974
Atolls are unique features on the surface of the earth because they are essentially the products of living organisms and their activities; indeed, they have been called biological oases in the aquatic deserts of tropical and subtropical oceans. Despite their biological origin, however, physical and chemical factors such as winds, waves, water chemistry, and light combine to mould them and to sustain them. It is the continuing interaction of these processes, as well as their history, that has stimulated study of Fanning Island by two expeditions from the University of Hawaii, the first in January 1970, the second in July and August, 1972. Some of the results of the first expedition were published in Pacific Science in April 1971; several reports from the 1972 expedition will appear in the April 1974 issue of Pacific Science.

Fanning Island (3°55'N, 159°23'W) is a small (125 km\(^2\)), roughly oval atoll lying midway in the string of shoals and atolls extending from 8°N Latitude to 12°S Latitude in the Line Islands. The major islands in the group are about 1000 miles south, southeast, and northeast of Hawaii, Johnston Island, and the Phoenix Islands, respectively; 1200 miles northwest of Tahiti, and 1500 miles northwest of the Tuamotu Islands. The relatively small size of Fanning, its nearly complete encirclement by land, and its relatively undisturbed state contribute to its usefulness for study as a single system. Its geographic location, on the southerly and easterly fringe of the Central Pacific faunal region of Ekman (1955), make it of special interest in biogeographical studies.

The biota of Fanning Island is principally of Indo-West Pacific derivation, resembling that of the Central Pacific rather than Hawaii. Peculiarities of species composition were suggested by Gosline (1971) and Kay (1971) as due to ecological conditions of islands rather than open water distances between them. Maragos (p. 97, this report) indicates that the coral fauna is far richer than might have been expected in the area, and Townsley and Townsley (p. 173, this report) report densities of the echinoderm fauna as greater than those reported elsewhere.

The ocean water surrounding Fanning Island is of nearly constant composition, with salinities of about 35 o/oo, suspended calcium carbonate load of less than 0.03 mg/l (Smith et al., 1971), and concentrations of total and particulate carbon of about 1.2 mg/l and 32 μg/l, respectively (Gordon, 1971). During much of the year, Fanning lies in the path of the southeasterly tradewinds, which blow across the lagoon at mean speeds of 10 knots from 135°. The tradewinds and surf from the southeast have moulded the windward reefs into rather narrow structures margined only occasionally by a spur-and-groove system. Fields of broken coral and rubble and the absence of reef corals on the upper slopes, suggest that wave action is a significant factor in the development of the windward reefs.
(Maragos, cited above). The leeward ocean reef slopes in contrast are wider, more fully developed, and harbor the greatest diversity and abundance of corals on the atoll (Maragos, cited above). Corals dominate the reef slopes to depths of 36 m, and both corals and fish show pronounced vertical zonation (Maragos, p. 187 this report; Chave and Eckert, p. 135, this report).

The reefs and islets comprising the atoll almost completely encircle the lagoon. The reefs are breached only in one place by a deep pass (ca 8 m) on the west (English Harbor), through which 90 per cent of the water exchange between lagoon and ocean occurs. Two shallow passes (or interisland reef flats), North Pass and Rapa Pass, the latter on the southeast, separate the islets.

Inside the lagoon, conditions are quite different from those of the seaward aspect of the atoll: lagoon water varies widely in composition, salinity, alkalinity, and pH (Gordon and Schiesser, 1970; Smith and Pesret, p. 21, this report); calcium carbonate concentrations vary from 1 mg CaCO$_3$/L in clearwater sectors to 4 mg CaCO$_3$/L in turbid water areas (Smith et al., 1971); concentrations of organic carbon are higher in the lagoon than outside it; and the composition of the biota is distinct from that of the seaward reef flats and slopes.

The most unusual features of the Fanning lagoon are its turbidity and high productivity, the latter estimated in 1970 as perhaps an order of magnitude greater than that reported for other atolls (Gordon, 1971). Smith and Pesret (cited above), using CO$_2$ as a tracer, find net organic carbon transfer in the lagoon is near zero, and suggest a close balance between production and consumption. Biological calcification accounts for most or all of the CaCO$_3$ precipitated in the lagoon; but calcification rates of about 1 kg CaCO$_3$ m$^{-2}$ year$^{-1}$, are lower than those estimated from standing crop and growth rate of corals (Smith and Pesret, cited above).

The high calcium carbonate load of lagoon waters and its consequent turbidity affect both topography and the distribution of organisms within the lagoon. In turbid water sectors, ribbon-like reefs form networks across the sandy floor, enclosing a series of ponds or basins (Roy and Smith, 1971). The dominant corals of these reefs are ramose Acropora and Stylophora (Maragos, p. 97, this report). In the clearwater sectors massive corals such as Porites predominate. The distribution of fishes, mollusks, echinoderms, and algae is clearly associated with variations in turbidity and salinity and the type of reefs (Chave and Eckert, cited above; Townsley and Townsley, cited above; Russell, p. 75, this report; Tsuda, p. 69, this report).

The characteristics of the lagoon are determined no only by the amount and rate of water exchange between the ocean and lagoon and between rainfall and evaporation, but also by the landmass of the atoll from which nutrients and groundwater leach into the lagoon. Three islets surround the lagoon,
vegetated by coconut trees which provide raw materials for the copra industry employing approximately 600 Gilbertese natives. *Pisonia* forest occurs where phosphate rock forms the substratum. *Pandanus*, including two species described by St. John (p. 301 this report), is a dominant plant on the atoll, as are *Messerschmidia* and *Scaevola*. Among the terrestrial animals, crustaceans replace fossorial insects, annelids, and vertebrates of continents and volcanic islands as soil mixers; the land crab, *Cardisoma*, alone may turn over as much as $9.53 \text{ m}^3/\text{ha} \cdot \text{yr}$ of soil (Fellows, p. 251, this report).

The landward portions of the atoll are also important in determining lagoon characteristics because of brackishwater flats or ponds which dissect the islands of the atoll. Along the lagoon shore, inlets increase the area of the island margin and focus fresh or brackish discharges at specific points along the lagoon margin (Guinther, 1971; p. 263, report). Not only are the inlets the regions where terrestrial and marine environments meet, but also, they are significant in providing, in an otherwise homogeneous environment, regions where there are extreme fluctuations in salinity and temperature and hence habitats for euryhaline biota (Guinther, cited above).

The structure of the atoll, distribution of land around the rim, the patterns of distribution of the line and patch reefs in the lagoon, the extensive development of brackishwater ponds, and the occurrence of phosphate rock all suggest a complicated history of atoll formation and development. To explain some of the observations of the 1970 expedition, it was suggested that the atoll is tilting toward the west, and that a post-Pleistocene shift in the meteorological equator and in the equatorial current system had occurred (Roy and Smith, 1971). Events and observations during the 1972 expedition suggest that in addition to long-range processes, abrupt and perhaps even catastrophic events are also significant in atoll development. The rubble fields and structure of the seaward reefs, as well as shingle berms of seaward sections of the islets, indicate a significant role of severe wave action in forming the atoll (Maragos, cited above; Gallagher, 1970). Accumulations of dead mollusk shells may have been caused by abrupt changes in salinity and/or turbidity (Kay and Switzer, cited above). That extreme changes in salinity do occur was given ample evidence during the eight-week visit of the second expedition when a mean rainfall of 1.5 cm/day was recorded in July and August. This extensive rainfall, associated with instability of the Intertropical Convergence Zone in 1972, effectively raised the Ghyben-Herzberg lens of the landward parts of the atoll, flooding low ground (Guinther, cited above), and shifted lagoon salinities from near seawater salinities recorded in 1970 to less than 32 o/oo in 1972 (Smith and Pesret, cited above).

References


ABSTRACT

The flood-tide jet entering Fanning Atoll lagoon is described, and is shown to be effective in promoting exchange between lagoon and ocean water. The residence time of lagoon water must thus be substantially less than the maximum of eleven months suggested by earlier studies. The bathymetry of the lagoon area subject to the jet is described.

INTRODUCTION

The first Fanning Island Expedition (1970) determined that the significant exchange of water between ocean and lagoon occurred through the deep pass at English Harbor (Fig. 1). The shallow North and Rapa passes contributed minor amounts to this exchange (Gallagher et al., 1971).

One of the major questions raised by the work of the first expedition concerned the mean residence time of the water in the lagoon. An estimate of maximum residence time, assuming no significant mixing between incoming ocean water and lagoon water, was eleven months (Gallagher et al., 1971). Unfortunately, insufficient precautionary comments were appended to this figure, and it has since been to some extent misunderstood. It should be re-emphasized here that this was an extreme estimate, based on the following conditions, which were known to be unrealistic: except for a small amount of flow-through driven by input at North and Rapa passes, all ocean water entering during a flood tide leaves the lagoon, without mixing, on the following ebb. Clearly, mixing does occur, and the true residence time must be less, and probably much less, than this maximum figure.

The unusually heavy and constant rainfall before and during the second (1972) expedition allowed an independent estimate of residence time, yielding a figure which seems much more reasonable (see Smith and Pesret, p. 21, this report).

A second finding of the 1970 expedition also involved the degree of mixing between the incoming ocean water and the lagoon water: this was the surprising indication that there was a net influx of suspended calcium carbonate to the lagoon during the tidal cycle, even though the water...
entering during the flood is visibly very much less turbid than that leaving during the ebb (Smith et al., 1971).

In response to the results of the first expedition, the primary effort of the physical oceanography group during the second Fanning Island Expedition (1972) was to develop a description of the jet of clear ocean water entering through English Harbor Pass on the flood, and to learn what happens to this water during the following ebb. The jet was tracked with an in situ transmissometer, since the most striking difference between lagoon and ocean waters is in turbidity, and by following drogues launched in and near the channel. A preliminary bathymetric survey was needed because of the inadequacy of available charts.

Secondary tasks of the physical oceanography group included assistance in monitoring the flow in English Harbor Pass over a tidal cycle, and the monitoring of lagoon tides during the period of the expedition.

**BATHYMETRY**

The proposed bathymetric, transmissometer, and drogue studies of the area of mixing between the incoming clear-water jet and the turbid lagoon water required a means of position-finding within the central region of the lagoon, inward from English Harbor Pass. The nearly continuous stands of coconut trees along the encircling islets offer almost no unambiguously identifiable reference points, so that our first task was to erect and fix the positions of a network of day-beacons. Pairs of horizontal angles taken on any three of the beacons from the survey boat with a sextant then fixed the boat's position. The locations of the beacons are shown in Figure 2.

The beacons consisted of paired 3-foot x 5-foot day-glo colored cloth flags flown from 25-foot (approximately) bamboo poles which were guyed into position on the shallow reef flats. Flag colors were varied for identification of the individual beacons.

The number of beacons proved barely sufficient for the job; under certain conditions of visibility, distant beacons became very difficult to locate. If a similar array were erected in the future, we would advise at least one additional beacon on or near the prominent point south of English Harbor. For surveys toward the northern or southern ends of the lagoon, the extension of the beacon array with adequate precision would be far too time-consuming. We would recommend a short-range, small-boat radionavigation system for accuracy and speed.

A measured baseline was laid out along Cartwright Point, as shown in Figure 2. From this, the positions of all beacons were determined by triangulation. The position of the monument on the spit protecting Mr. Palmer's boat slip, at the south side of English Harbor Pass, was also determined; the distance from Cartwright Point to the monument, across the inner mouth of the pass, was shown to be 294 meters.
Fig. 1. Fanning Island. Heavy line approximately indicates the lagoon area near English Harbor covered by Figs. 2, 4, and 6-9. The general area of sounding lines in the large south pond, discussed in the text, is shown by the letter "S".
Fig. 2. English Harbor and vicinity. Short-dash line is approximate edge of shallow reef areas, drawn from aerial photographs and surveyed points. 8-, 12-, and 16-m contours shown; 4-m contour generally coincides closely with reef edge. Circled crosses are navigational reference beacons; baseline for survey extends along Cartwright Point from point "B" to the tip.
With the beacons in and fixed, a program of echo-sounding observations was undertaken to develop a general picture of the bathymetry of the central lagoon area. The instrument used was a Raytheon Model DE-719 portable, battery-powered depth recorder; soundings were calibrated in the field by direct measurements to a reflecting bar suspended at known depths beneath the boat. Approximately 32 km of sounding lines were run, but the complex topography of a coral-reef area such as this would require a very much higher density of observations to develop a complete bathymetric description. This would have needed far more time than we had available, as well as a higher degree of precision in navigation. Our results, presented in Figure 2, should be considered in the nature of a reasonably accurate sketch of the area. Prominent points along the reefs were fixed during the survey, with aerial photographs used to help draw-in the shapes of the reefs themselves. Note that, because of the limitations mentioned, we did not correct the soundings for the small range in lagoon tide (mean range 35 cm; see Tide discussion).

Results

The primary features of the bathymetry may be described as follows:

English Harbor Pass. This narrow channel is deepest toward its southern side. Figure 3 shows a section across the inner mouth, from Cartwright Point to the monument; the greatest depth is 10 meters. The bottom is hard, with both dead and living coral; the very strong tidal currents permit little sediment accumulation. Movement of loose material can be heard underwater in the channel during the strong flow.

Sediment fan. Inward from the Pass the living coral gradually thins out and disappears, with sediment cover increasing. The sediment is coarse initially, becoming finer with distance from the high-velocity region close to the Pass. A broad, nearly level fan of sediment extends into the lagoon, ending abruptly about 0.7 miles (1.1 km) from the inner mouth of the pass. Depths over the sediment fan are 4-6 meters.

English Harbor Main Basin. The main basin, inside the sediment fan, is essentially free of obstructions over an area approximately 1.6 miles (2.6 km) N-S by 0.6 miles (1.0 km) E-W. The echo-sounder records indicate a generally smooth bottom with little development of living coral. Depths in the central part of the basin are about 12 to 16 meters.

Inner Reef Line. The inner border of the main basin is marked by a nearly continuous curved line of shallow patch reefs, connected by slightly deeper saddles. Except for the wide, sandy flat on the large patch reef at the northern end of the line, these reefs support dense communities of living corals. A maze of small patch reefs extends between the southern end of the inner reef line and the fringing reef along the lagoon shore; no attempt was made to survey this complicated area.

Inner Deeps. Between the inner reef line and the elaborate complex of reefs and ponds which fill the remainder of Fanning lagoon is an irregular
series of small basins which contain the greatest depths recorded in the lagoon. The greatest individual recorded depth was 19 meters, in the northern end of the line of inner deeps. The echo-sounding records suggest that the bottom in these basins consists largely of living coral, with a relief of 1 to 2 meters.

The relatively great depths in these basins may result from the fact that, because of their proximity to English Harbor, they receive water with considerably lower average suspended sediment load than the basins farther from the Pass, while at the same time they are protected by the inner reef line from the direct transport of coarser sediments.

Large South Pond. Several sounding lines were run in the large pond, which extends across most of the width of the lagoon, about half-way between English Harbor and Rapa Pass at the southeast end of the atoll (Fig. 1). Only subsequently was it discovered that our attempts to extend our triangulation net to this area, using shoreline features, were accumulating significant errors. We therefore do not present a chart of this area. Observed depths in the pond were mostly near 8 meters with fluctuations between 4 meters and 12 meters. Most of the bottom was characterized by small-scale irregularity, indicating a substantial cover of live coral, with a relief of 2 to 3 meters.

TRANSMISSIVITY OBSERVATIONS

Methods

The development and mixing of the incoming, clear-water tidal "jet" was observed using a portable transmissometer (Hydro Products Model 612, 1-meter path-length). Measured transmissivities ranged from about 12% in Suez Pond (near the middle of the northern part of the lagoon) to almost 65% in the incoming ocean water.

During an initial familiarization period, a random pattern of observations was made in the English Harbor area at times near high- and low-water slack. Many of these data have been rejected because of instrument-calibration problems.

For future reference, it was learned that, in this climate, calibration could be obtained only with the entire underwater unit totally dry. With water drops falling on the interior surfaces of the transmission tube, transient wisps of condensation formed and evaporated on the windows of the light source and the photocell. Calibration could thus be checked before and after a day's work, but not in the field. These checks showed adequate instrument stability.

After satisfactory instrumental performance had been demonstrated, a pattern of lines (Fig. 4) was set up along and across the path of the incoming jet. These lines were marked by a series of anchored buoys and natural features. (Note that the later drogue studies confirmed our choice of our longitudinal track, Line C.) The lines were run at constant speed,
Fig. 3. Left: Smoothed section across inner mouth of English Harbor Pass. Right: Location of section. "C" is Cartwright Point; "M" is monument at tip of southern point.
Fig. 4. Location of transmissivity lines, English Harbor area. Location references correspond to those in Fig. 5.
with readings from the towed transmissometer taken at fixed time-intervals. The time at which the boat passed the buoys or other marks was also recorded, so that the positions of the instrument readings could be interpolated along the lines. All readings were made with the instrument towed at a depth of 1 to 2 meters, since the initial trials had shown little variation of transmissivity with depth in the areas studied.

Readings were taken at 30-sec intervals (approximately 75 meters) along lines A, B, and C. Along line E, across the inner mouth of English Harbor Pass, the readings were taken at 15-sec intervals (approximately 40 meters), and the position of the boat along the line was monitored by radio signals from a sighting station on shore.

Lines E and A were run at approximately 2-hour intervals during a complete flood-ebb cycle, extending from dawn to dusk on 17 August. Additional buoys were positioned and fixed on 18 August, and lines A, B, and C were run three times during flood tide on 19 August. (See Fig. 10 for the lagoon tide for these dates.)

Transmissivity was also determined during drogue studies which followed the tidal-jet observations; these data will be discussed in conjunction with the drogue results.

Results

The data from the individual transmissivity runs are presented in Figure 5. These distributions were used to develop the overall patterns of transmissivity described below, and the individual lines are discussed in conjunction with these patterns.

In developing the overall patterns, adjustments had to be made to correct for the time interval between lines. All available subsidiary information was used in making these adjustments, but, because of the large and rapid changes which occur at the turn of the tide, and because of the natural variability of this turbulent regime, subjective judgement played a significant role. The patterns should be regarded as interpretive summaries of the observations.

**Low Water.** (Fig. 6) This figure is based primarily on data from lines A and B, 19 August, run 0.5 and 0.8 hours after low-water slack respectively, plus data from the initial random observation pattern.

Turbid water is found extending along the lagoon shores and into the English Harbor Pass (see the last few transects on line E, Fig. 5). A pool of relatively clear water remains back in the main basin, with variable transmissivity generally in the range of 40 to 50%. This water is seen toward the right (inner) end of line C, first transect on 19 August. (Note that this transect was not otherwise used in Figure 6, since the flood had already started; ocean water is evident in the high transmissivities at the left (oceanward) end of the line.)
Flood Tide. (Fig. 7) The penetration of ocean water into the lagoon is shown for approximately 1.5 hours and 3.5 hours after low-water slack. The distribution at 1.5 hours is based on line C, 19 August, 1.2 hours; and line A, 17 August, 1.6 hours after slack. The 3.5 hours distribution is based on lines A, B, and C, 19 August, at 3.4, 3.7, and 4.1 hours after slack respectively. Line E data, and visual observations, were used to extend the distributions to the vicinity of English Harbor Pass.

The incoming flow develops rapidly and advances across the relatively shallow sediment fan at high speed. Sharp fronts can initially develop between the ocean water and the turbid water remaining near the pass from the previous ebb (see line C, first run, and the drogue results below). Such fronts were observed repeatedly near the inner edge of the sediment fan, where the sudden depth increase leads to a sharp drop in the velocity of the inflow.

As it leaves the pass, the inflow takes the form of a distinct jet of clear water, separated from the relatively still water on either side by violent, narrow shear zones which broaden, and become less energetic, with distance inward. Turbid lagoon water is entrained in these turbulent shear zones on both sides of the neck of the jet, so that a compensating flow of this turbid water develops, moving relatively slowly along the lagoon shores toward the pass from the north and south.

As the flood tide continues, the incoming water extends across the fan and the main basin. The vigorous lateral turbulence at the sides of the jet continues to entrain turbid water and to mix it into the inflow. By the time the water has crossed the main basin, its transmissivity has been decreased to approximately 50%; see line C at 4.1 hours. Unmixed ocean water (over 60% transmissivity) can be identified on this line to a position slightly beyond the crossing with line B, about 3/4 of the way from English Harbor Pass to the inner reef line.

The extent of the unmixed water represents a balance between the rate of inflow and the rate of mixing with lagoon water. During the latter part of the flood period the rate of inflow is decreasing, while the mixing is still vigorous; as shown by the distributions of transmissivity (Fig. 5, especially line A), the extent of unmixed water is decreasing during this period. It seems likely that the 3.5 hours distribution shown in Figure 7 represents close to an average maximum extent for the unmixed water, although some probably occasionally gets as far as the inner reef line.

Time did not permit studies of the inflow after it passed beyond the main basin, but the few measurements available, plus visual observations, suggest that the lagoon line reefs act as very effective turbulence-inducing baffles, causing the water which accelerates as it crosses them to mix rapidly with the water in the pond on the far side. Visual observations of foam lines, indicating sharp convergences, lying along the inner edge of line reefs were made on several occasions during flood tide. The result of this mixing is a seemingly tendency for transmissivity to change discontinuously from pond to pond (see discussion of drogue run B, below). More observations are needed to confirm this feature.
Fig. 5a. Transmissivity data, 17 August 1972. Location references correspond to map in Fig. 4. Each run identified at its right end by hours and minutes since Low Water (0600 local time). Transmissivity given by ticks separated by 10%; reference value given alongside each line. Left: line A. Right: line E. Note difference in horizontal scale.
Fig. 5b. Transmissivity data, 19 August 1972. Low Water was 0840 local time. Top: line A. Middle: line B. Bottom: line C.
Fig. 6. Smoothed Low Water transmissivity pattern, English Harbor area.
Fig. 7. Smoothed flood tide transmissivity patterns, English Harbor area. Dashed lines, approximately 1 h after Low Water; solid lines, approximately 3.5 h after Low Water.
High Water. (Fig. 8) This figure is based primarily on data from lines A, B, and C, 19 August, run 6.2, 6.5, and 7.1 hours after low-water slack respectively. Ebb flow began in the middle of the run and was well developed by the completion of line C. The transmissivities of over 60% on line A were ignored, since the last of the flood was still flowing across this line at the time it was run.

The main basin is filled with ocean water which has been mixed with a relatively small component of lagoon water entrained in the jet; transmissivities in the basin are 50 to 60%. As described above, entrainment into the jet during flood tide has maintained high-turbidity water along the lagoon shore immediately to either side of the pass. At high-water slack, this turbid water mixes rapidly across the former path of the jet, sharply decreasing the transmissivity just within the lagoon from the pass, and separating the moderately clear water now filling the main basin from the ocean water outside.

Ebb Tide. The ebb period was followed only on lines E and A (Fig. 5). Within the Pass (line E), as the ebb begins it immediately draws on the very turbid water to the north and south, along the lagoon shore, as well as on the less turbid mixed water directly inward from the pass. As the water approaches the Pass, the lateral convergence and longitudinal acceleration greatly intensifies the lateral turbidity gradients. The resultant distribution, with turbid water flowing out along either side of the pass and clearer water in the middle, is visually striking; this can also be seen in the line E curves at 8.7 and 10.8 hours, although the actual gradients were sharper than indicated by these 15-sec observations. Later during the ebb the water approaching the Pass is older, in terms of lagoon residence, and such sharp gradients in turbidity have been eliminated by mixing. The general level of turbidity also increases during the ebb, as water from farther within the lagoon reaches the Pass.

Similar, but much broader, patterns can be seen along line A (Fig. 5), which lies across the ebb flow approaching the Pass. Mixed water from the main basin (transmissivity 40 to 50%) can be seen near the center of the line; toward either end one sees turbid water approaching the pass from the north and south. The turbidity increases during the ebb, as water from farther within the lagoon crosses line A.

DROGUE OBSERVATIONS

Methods

Drogues were used to follow the water entering the lagoon during flood tide. The drogues were in the form of crossed muslin panels, 6 feet square, extended top and bottom by crossed bamboo poles. The drogues were weighted at the bottom and buoyed at the top, with the combination adjusted to be slightly heavy in the water. The entire assembly was then suspended by a light 6-foot line from a single 1-gallon plastic "bleach bottle" at the surface. At this depth the drogues were roughly centered in the water column over the shallow part of the sediment fan.
Six drogue-runs were completed during the period 15 to 20 August. All drogues were launched in or near the English Harbor Pass, during flood tide. The drogue tracks are shown in Figure 9. Fixes are identified by number along each track. Table 1 gives time to each fix, mean speed since the previous fix, transmissivity measured at each fix, and remarks on each drogue run.

Results

All drogues launched in the Pass moved rapidly inward with the flood. The launching was in the center of the channel, estimated by eye; it was impossible to anchor or to control position exactly in the very strong current.

Two of these releases (Tracks B and E, Fig. 9; note that Track B represents two drogues launched close together) produced tracks extending straight across the main basin. These drogues essentially followed the track which we had earlier established as transmissometer line C; drogue E actually passed through the gap in the inner reef line which we had used for line C.

One of the mid-Pass releases (Track A, Fig. 9) was late during the flood period; this drogue slowed rapidly, and at high-water slack had only reached the edge of the main basin, where it turned northward.

The final mid-Pass release (Track C, Fig. 9) was made in conjunction with a release just outside the jet (see description of Track D, following). Drogue C travelled slightly south of the direct inward line until it reached the main basin, where it slowed and turned sharply south, leaving the main jet.

Drogue D (Fig. 9) was launched in the turbid water just south of the Pass. This drogue moved toward the Pass and entered the violent shear zone at the edge of the jet only some 15 meters from the end of the point off the English Harbor monument. The drogue was pulled under, surfacing about 1 minute later approximately 100 meters downstream. (Drogue C was launched in mid-Pass at approximately the time that D entered the edge of the jet.) Drogue D moved to the south, apparently at one point being caught in an eddy for half an hour. D lagged and stayed to the right of the track of C. Both drogues passed between the two patch reefs south of the Pass.

Note that a second drogue was launched in the turbid water south of the jet; this also moved to the jet and entered the shear zone, but it was pulled down, snagged on the bottom, and destroyed. No drogues were released in the turbid water north of the jet because of insufficient water depth.

Transmissivity Along Drogue Tracks

All mid-Pass drogue launches were in unmixed incoming ocean water, with transmissivity near 64%. Drogues A, B (a close pair), and C encountered
Fig. 8. Smoothed High Water transmissivity pattern, English Harbor area. Contours within the Pass estimated; conditions here change rapidly with turn of tide.
Fig. 9. Drogue tracks, flood tide, English Harbor area. Drogue runs indicated by letters; selected fixes identified by numbers along each track. Data on individual runs given in Table 1.
visible fronts between ocean water and more turbid water; in each case these fronts were first observed near the point at which the drogue left the sediment fan and moved over the greater depth of the main basin. Transmissivity dropped from 5% to 20% across the fronts. The encounter with a front coincided with the sharp northward turn of drogue A and the similar southward turn of C. In the case of B, the front was observed to be moving away from the Pass, ahead of the incoming water. Lateral mixing was increasing the turbidity of the moving water, however, so that when drogue B had crossed the main basin and reached the inner reef line most of the water in the basin behind them had transmissivity reduced to near 55%. (This was approaching the time of high-water slack.)

Drogue E, launched late during the flood period, did not encounter a visible front; transmissivity decreased gradually to 57% on the far side of the inner reef line, at a time within one hour of high-water slack. Note that during drogue run B, relatively earlier in the flood period, a visible turbidity change was observed across the inner reef line, with transmissivity dropping from 58% to 45 to 48% across the reefs. During run E, late in the flood, the transmissivities had increased and no sharp change was observed across the reef line.

The fronts are obviously transient, rapidly changing phenomena; no clear idea of their pattern can be gained from the limited viewpoint of a single boat. The tendency for the fronts to appear first at the edge of the main basin is probably associated with the sudden slowing of the inflow because of the sharp increase in depth, as mentioned earlier. The most intense front observed was that encountered by drogue C. Transmissivity decreased from 63% to 44% across this front, which was observed underwater; the ocean water was slightly under-running the turbid water, with the frontal surface sloping steeply down (approximately 45°) toward the lagoon. The drogue crossed the surface line of the front then remained near it; within an hour all evidence of the front dissipated and then transmissivity near the drogue was 55%. Transmissivity near drogue C decreased rapidly after the drogue passed south between the patch reefs, reaching a value of 45% at the time the drogue was retrieved.

Drogue D was launched just south of the jet in water with transmissivity of 43%. Immediately after becoming caught in the shear zone the transmissivity at the drogue was 58%, indicative of the rapid mixing at the sides of the jet. Transmissivity remained 58-60% until the drogue paused (in an eddy?), where transmissivity dropped to 50%. Transmissivity remained in the range 50-55% as the drogue moved southward. No visible front was observed along this track.

SUMMARY - THE TIDAL JET

Tidal flow through English Harbor Pass is effective in bringing about exchange between ocean and lagoon. This exchange involves two processes:
**TABLE 1**

Drogue-track data. Time is local, speed is average since previous fix, transmissivity is measured at
fix. See Figure 9.

<table>
<thead>
<tr>
<th>Fix</th>
<th>Time</th>
<th>Speed (cm/sec)</th>
<th>Xmiss (%)</th>
<th>Remarks</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>1045</td>
<td>-</td>
<td>64</td>
<td>launched mid-Pass near end of flood</td>
</tr>
<tr>
<td>2</td>
<td>1103</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>1118</td>
<td>42</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>1122</td>
<td>42</td>
<td></td>
<td>at visible front</td>
</tr>
<tr>
<td>5</td>
<td>1208</td>
<td>10</td>
<td></td>
<td>ebb beginning (HW 1125)</td>
</tr>
<tr>
<td>6</td>
<td>1229</td>
<td>neglig.</td>
<td></td>
<td>end</td>
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**Dropues B, 16 August**

<table>
<thead>
<tr>
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<th>Speed (cm/sec)</th>
<th>Xmiss (%)</th>
<th>Remarks</th>
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<tr>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>0845</td>
<td>-</td>
<td>64</td>
<td>launched mid-Pass, approx. 3 h after L W</td>
</tr>
<tr>
<td>2</td>
<td>0905</td>
<td>120</td>
<td>65</td>
<td>visible front observed at edge of main basin</td>
</tr>
<tr>
<td>3</td>
<td>0951</td>
<td>32</td>
<td>64</td>
<td>at front with transmissivity dropping to 60%</td>
</tr>
<tr>
<td>4</td>
<td>1040</td>
<td>16</td>
<td>60</td>
<td>end at sides of gap in inner reef line (HW 1220)</td>
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</table>

**Dropue C, 20 August**

<table>
<thead>
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<th>Speed (cm/sec)</th>
<th>Xmiss (%)</th>
<th>Remarks</th>
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<td></td>
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<td></td>
</tr>
<tr>
<td>1</td>
<td>1112</td>
<td>-</td>
<td>62</td>
<td>launched mid-Pass, approx. 1 h after L W</td>
</tr>
<tr>
<td>2</td>
<td>1128</td>
<td>91</td>
<td>63</td>
<td>approaching front with xmissivity dropping to 44%</td>
</tr>
<tr>
<td>3</td>
<td>1140</td>
<td>32</td>
<td>63</td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>1146</td>
<td>-</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>1210</td>
<td>8</td>
<td>53</td>
<td>still near front, turning to south</td>
</tr>
<tr>
<td>6</td>
<td>1230</td>
<td>20</td>
<td>55</td>
<td>visible front dissipated</td>
</tr>
<tr>
<td>7</td>
<td>1242</td>
<td>27</td>
<td>56</td>
<td>passed between</td>
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<td></td>
</tr>
<tr>
<td>10</td>
<td>1325</td>
<td>11</td>
<td>45</td>
<td>end (HW 1640)</td>
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**Drogue D, 20 August**

<table>
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<th>Longitude</th>
<th>Value</th>
<th>Notes</th>
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<tr>
<td>1055</td>
<td>-</td>
<td>43</td>
<td></td>
<td>launched in turbid water south of Pass, approx. 1 h after L W</td>
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<tr>
<td>1110</td>
<td>14</td>
<td>-</td>
<td></td>
<td>caught in turbulent shear zone at edge of jet, briefly submerged; Drogue C launched</td>
</tr>
<tr>
<td>1116</td>
<td>58</td>
<td>58</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1125</td>
<td>45</td>
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</tr>
<tr>
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<td>50</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1214</td>
<td>7</td>
<td>50</td>
<td></td>
<td>eddy?</td>
</tr>
<tr>
<td>1225</td>
<td>20</td>
<td>51</td>
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<td></td>
</tr>
<tr>
<td>1236</td>
<td>18</td>
<td>53</td>
<td></td>
<td></td>
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<tr>
<td>1247</td>
<td>17</td>
<td>55</td>
<td></td>
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</tr>
<tr>
<td>1300</td>
<td>11</td>
<td>53</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1332</td>
<td>13</td>
<td>53</td>
<td></td>
<td>end (HW 1640)</td>
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**Drogue E, 20 August**

<table>
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<th>Time</th>
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<th>Longitude</th>
<th>Value</th>
<th>Notes</th>
</tr>
</thead>
<tbody>
<tr>
<td>1350</td>
<td>-</td>
<td>64</td>
<td></td>
<td>launched mid-Pass, approx. 4 h after L W</td>
</tr>
<tr>
<td>1426</td>
<td>71</td>
<td>62</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1445</td>
<td>29</td>
<td>60</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1512</td>
<td>11</td>
<td>59</td>
<td></td>
<td>approaching gap in inner reef line</td>
</tr>
<tr>
<td>1555</td>
<td>17</td>
<td>57</td>
<td></td>
<td>end on far side of inner reef line (HW 1640)</td>
</tr>
</tbody>
</table>
One is associated with vigorous lateral mixing generated along each side of the incoming jet. Even as the ebb begins, there is no unmixed ocean water from the preceding flood found within the lagoon.

The other involves the patterns of flow water near the Pass. During the flood, the inflowing narrow jet injects clear ocean water well back into the lagoon. At the same time, turbid lagoon water is drawn along the lagoon shore toward the Pass, from both sides, by the entrainment occurring along the edges of the jet. During the ebb, the outflow draws water broadly from the area surrounding the inner mouth of the Pass. The outflow thus comprises a sizeable component of turbid lagoon water, as well as some of the (already partially mixed) ocean water from the preceding flood. At the end of the ebb, some of the water from the preceding flood still remains in the main basin, directly inward from the Pass. This water is pushed still farther into the lagoon by the following flood, with mixing enhanced by the complex, interconnected pattern of shallow line-reefs.

Quantitative estimates of proportions of lagoon and ocean water passing out during the ebb (that is, of the rate of exchange associated with tidal flushing) await further attempts to quantify the values of transmissivity in terms of suspended particulate load (an attempt to do this during the second expedition proved to be unsuccessful). With the present information, we can only emphasize that the expected exchange does occur, and that the residence time of the water in the lagoon is thus significantly less than the maximum of eleven months given in the report of the first expedition.

LAGOON TIDE OBSERVATIONS

Methods and Results

A recording tide station was maintained at the Cable Station lagoon pier, approximately 3.5 miles north of English Harbor Pass, from 20 July until 21 August. These observations were made primarily for the convenience of the various expedition members who were working in the lagoon. The smoothed tide record is presented in Figure 10. The mean observed tide range was 34 centimeters. The maximum range over a single tide was 40 centimeters, and the minimum was 12 centimeters.

A tide record was also made at the north side of the end of Cartwright Point, only a few tens of meters from the inner end of English Harbor Pass, from 24 July until 9 August. Since no significant difference was observed between the records at the two locations, the Cartwright Point records are not reproduced here. There was some indication that low water at the Cable Station lagged that at Cartwright Point by about 11 minutes, but this may well be fictitious, since the time-resolution of the records is no better than 8 minutes. There was no indication of a lag in high water.

No adequate site was available for mounting a tide gauge to record sea level outside the lagoon. The brief records obtained by Gallagher et al. (1971) showed the severe distortion of the lagoon tide caused by the
Fig. 10. Smoothed record of Fanning Island lagoon tide recorded at the Cable Station (Fig. 1).
Fig. 11. Fanning Island lagoon tide at the Cable Station (Fig. 1), from midnight to noon 6 August 1972, showing effect of squalls.
restricted communication with the sea: the interior tide has about half the range of the ocean tide, and it lags the ocean tide by variable periods up to approximately 3 hours.

Wind Effects

During the month of tidal observations many squalls passed over the lagoon, with winds approximately from the southeast. These squalls caused a rise in water level along the leeward lagoon shore. The measured rise at the Cable Station was larger than that at Cartwright Point, as would be expected by the location of Cartwright Point next to English Harbor Pass, as well as by the fact that the Cable Station was farther downwind for most of the squalls. Figure 11 shows the tide record at the Cable Station lagoon pier for the morning of 6 August, during which four squalls occurred. Note that the water level responds with a single peak and no oscillations, suggesting a large frictional dissipation in the reef-choked lagoon. The largest observed rise in water level associated with a squall during the month of observations was approximately 6 centimeters.

ACKNOWLEDGMENTS

The authors particularly thank Mr. Peter W. de Witt, the third member of the physical oceanography group, for his invaluable assistance during the expedition. We also gratefully acknowledge the cheerful cooperation and ready support of all other expedition members. Without them we would soon have succumbed to the inexorable operation of Murphy's Law.

REFERENCES


PROCESSES OF CARBON DIOXIDE FLUX IN THE FANNING ISLAND LAGOON

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ABSTRACT

Carbon dioxide follows a variety of transfer pathways through marine systems, and a budget of CO₂ can be used to enumerate those pathways. In a coral reef system, the biogeochemical pathways of organic carbon production-consumption and calcification are likely to be prominent. We measured the temperature, salinity, pH, and total alkalinity of about 400 water samples to describe the CO₂ budget of the lagoon at Fanning Island, Line Islands, during July and August 1972.

Mean lagoon salinity was about 31.5 o/oo, or 3.3 o/oo below the open ocean salinity there, as a result of heavy rainfall and groundwater seepage. This salinity depression, together with data on rainfall and tides, was used to calculate a mean lagoon water residence time of about one month.

The CO₂ budget of the lagoon water can be described in terms of processes altering the ocean-water composition. Gas exchange accounted for a net CO₂ evasion of less than 1.4 moles m⁻² month⁻¹. Freshwater dilution lowered the CO₂ content by about 0.5 moles m⁻² month⁻¹. Calcification lowered CO₂ by 0.9 moles m⁻² month⁻¹; and CO₂ changes attributable to organic carbon transfer lay between -0.1 and +1.3 moles m⁻² month⁻¹.

Net organic carbon transfer in the lagoon is near zero, suggesting a close balance between organic carbon production and consumption. Calcification is about 1 kg CaCO₃ m⁻² yr⁻¹, much lower than the rate which can be estimated from the standing crop and expected growth rate of corals there. It seems possible that the CO₂ system of the Fanning lagoon, and perhaps of other coral reefs as well, may be potentially limiting to biological activity.

INTRODUCTION

Carbon dioxide is involved in a variety of processes affecting coral atolls. The high rate of gross organic carbon productivity and the
skeletal calcium carbonate precipitation attest to the biogeochemical importance of CO$_2$ in such a system. Physical processes such as evaporation, rainfall, and freshwater seepage can also alter the CO$_2$ content of atoll water. All of these processes change the CO$_2$ concentration, and thereby alter the CO$_2$ partial pressure from that of the neighboring oceanic waters. Such alterations affect the transfer rate of CO$_2$ across the air-sea interface.

The present investigation was designed to describe the CO$_2$ budget for the lagoon of a coral atoll. Thus, CO$_2$ serves as a tracer which clarifies the behavior of processes within the lagoon system. Moreover, some of the interdependencies which emerge suggest possible mechanisms which merit more detailed future investigation.

Fanning Island (4°N, 159°W, in the Line Islands) is the site for the present investigation. Unlike most atoll lagoons, the Fanning lagoon is almost entirely surrounded by islands rather than by reefs. Despite being nearly landlocked, the lagoon supports abundant and diverse reef biota, apparently similar to that of less restricted lagoons. Therefore, the physiographic peculiarities which make the lagoon convenient to study do not detract from the likelihood that we can use our results to draw conclusions about atoll lagoons in general.

Experimental Design and the CO$_2$ System

The CO$_2$ content of lagoon water results from a variety of processes. Each process imparts distinctive characteristics upon the lagoon water, so we can at least partially isolate the various processes. Both the concentration and the state of CO$_2$ in the water, along with the salinity of that water, are used in calculating this budget.

Mixing several water types results in water with an intermediate composition. Three water masses enter into such mixtures at Fanning: ocean water, rainwater and groundwater.

Internal chemical reaction alter both the total CO$_2$ content and the partitioning of CO$_2$ species in the water. The primary internal reactions affecting CO$_2$ in sea water are CaCO$_3$ precipitation-solution (here termed "net calcification") and organic carbon production-respiration ("net production"). Both processes lower the total CO$_2$ content of sea water by one mole for each mole of carbon produced. Calcification lowers the total alkalinity of sea water by two equivalents for each mole of CaCO$_3$ precipitated, while net organic carbon production does not alter the total alkalinity (see Park, 1969; Smith, 1973).

The partial pressure of CO$_2$ in sea water is sensitive to any process which alters the amount and partitioning of dissolved CO$_2$ constituents in the water. Moreover, net CO$_2$ flux across the air-sea interface is driven by any differential CO$_2$ partial pressure across the interface (Kanwisher, 1963; Sugiura et al., 1963). Hence, the preceding processes alter the CO$_2$ exchange rate in the lagoon from that of the adjacent open ocean.
The Fanning lagoon is a partially isolated body of water which exchanges its water with oceanic water through the flushing action of tidal currents which reverse their flow semidiurnally. The \( \text{CO}_2 \) alteration processes mentioned above act to prevent the lagoon water from reaching the composition of the ocean-water source. Let us consider the lagoon to be a well-mixed, constant-volume system, continually flushed by water from an infinite reservoir of constant composition. A random sample of this lagoon water will have a composition reflecting the rate at which the processes within the lagoon act relative to rate of replenishment with ocean water (residence time). It is convenient to express the relationship among the rates of internal alterations \((A)\) by some process, the composition difference between the ocean and lagoon \((\Delta X)\), and the lagoon water residence time \((\tau)\) by means of a simple equation:

\[
A = \frac{\Delta X}{\tau}
\]  

\(A\) is in the unit: rate of change per unit volume of lagoon water. Multiplying \(A\) by the mean water depth of the lagoon will yield the unit: rate of change per unit area of lagoon floor. The above model assumes a time-series steady state and spatial homogeneity. We will discuss and defend the steady-state assumption; substituting average values from a lagoonwide array of data for one random sample overcomes the obvious inhomogeneity of lagoon waters.

METHODS

Field Techniques

Over 400 water samples were collected from more than 100 localities at Fanning Island. Samples were collected at the localities shown in Figure 1. Surface water was scooped directly into one-gallon plastic bottles. Samples 2 meters below the surface and within 1 meter of the lagoon bottom were pumped into the bottles with the immersion pump described by Schiesser (1970). Water temperature was measured by placing a thermometer in the sample bottles as the samples were collected.

Except for specific tide-cycle, or diurnal-cycle sampling, most samples were collected before midday to minimize the effect of any diurnal cyclicity which might bias wide-area sampling. Samples sat on the open deck of our skiff (but were usually within about \(2^\circ\text{C}\) of their \(29^\circ\text{C}\) average collection temperature) for a few minutes up to a maximum of about 5 hours before they were returned to the laboratory for analysis. Most samples were returned to the lab within 2 hours of their collection time. Up to 15 sample stations were occupied during a single day.

Besides the wide-area sampling, three levels of time-series samples are reported here. Water was collected near noon each day for about 10 days at Suez Pond. Suez Pond was also sampled approximately every 2 hours over one 26-hour period. Repeated sampling at five locations across the mouth of English Harbor was done over one 13-hour period. These named sample localities are identified on Figure 1.
Laboratory Analysis

Our laboratory at the Cable Station (Fig. 1) was an air-conditioned room maintained near 25°C. Samples were returned to that room as quickly as possible after collection, left for an hour or more to approach room temperature, and then analyzed.

Salinity was measured with a Bissett-Berman model #6230 conductivity salinometer. Alkalinity and pH were measured with an Orion model #801 pH meter and Beckman electrodes (#1617 pH; #1615 reference).

We soaked the electrodes in slightly acidified tap water overnight between analysis periods and calibrated the meter with commercial buffers (pH 7.00 and 4.01) before the day's analyses. We then soaked the electrodes for at least one hour in acidified sea water previous to alkalinity measurements and ran an initial dummy alkalinity measurement to stabilize the electrodes before analyzing a batch of alkalinity samples; we did not rinse the electrodes between analyses. We then soaked the electrodes in unacidified sea water until pH readings stabilized before measuring a batch of sea water pH values. pH measurements were made on unfiltered water samples.

Alkalinity measurements were made according to the procedure of Culberson et al. (1970), using water filtered with a Millipore® 0.8μ pore-size filter, plastic in-line filter holder, and plastic syringe. Titrisol®, commercially available pre-standardized HCl, was diluted to 0.010 N and used for the analyses. Analytical precision was not a limiting consideration, so only single analyses were run on most samples.

As outlined in the appendix, calculations of the various parameters in the CO₂ system follow from the temperature, salinity, pH, and total alkalinity data.

RESULTS

Water Composition at Fanning Atoll

The waters of Fanning Atoll can be divided into four categories, each with its distinctive composition: oceanic water, lagoon water, groundwater, and rainwater. Table 1 summarizes mean salinity and CO₂ characteristics for these water types.

About 20 samples of inflowing water at English Harbor provided the primary record of ocean water composition. This material had a constant composition. Salinity (S) was 34.8 o/oo; total alkalinity (T.A.) was 2.35 meq/liter; and pH was 8.25. These values yield a total CO₂ content (∑CO₂) of 2.0 mmoles/liter and a specific alkalinity (S.A. = T.A./Cl) of 0.122.

Lagoon water varied widely in composition, as is evident from maps of salinity (Fig. 2); but a large amount of data was available for calculating mean composition of the lagoon. Planimetry of the area between contour...
Fig. 1. Index map of Fanning Atoll stations locations. Locations discussed by name are shown on the map, and the sites of the Suez Pond 1-day survey and the English Harbor tide-cycle survey are circled.
### Table 1. Composition of Major Water Masses at Fanning Atoll.

<table>
<thead>
<tr>
<th>Water Mass</th>
<th>Salinity (o/oo)</th>
<th>pH</th>
<th>Total Alkalinity (meq/liter)</th>
<th>$\sum CO_2$ (mmoles/liter)</th>
<th>Specific Alkalinity (T.A./chlorinity)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Open Ocean</td>
<td>34.8</td>
<td>8.25</td>
<td>2.35</td>
<td>2.0</td>
<td>0.122</td>
</tr>
<tr>
<td>Lagoon</td>
<td>31.5</td>
<td>8.1</td>
<td>1.9</td>
<td>1.7</td>
<td>0.108</td>
</tr>
<tr>
<td>Rainwater</td>
<td>0.0</td>
<td>6.4</td>
<td>0.0</td>
<td>0.0</td>
<td>-----</td>
</tr>
<tr>
<td>Groundwater</td>
<td>0.0</td>
<td>7.7</td>
<td>3 to 5*</td>
<td>3 to 5*</td>
<td>-----</td>
</tr>
</tbody>
</table>

* These are subjective estimates based on the most frequent values encountered rather than being mean values.
lines on maps of salinity, specific alkalinity, and pH yields mean lagoon values of 31.5 °/oo, 0.108, and 8.1, respectively. From these values, a mean total alkalinity of 1.9 meq/liter and a mean total CO₂ content of 1.7 mmoles/liter can be calculated.

A limited number of samples (10) and extreme variability of these samples made groundwater composition difficult to characterize. All samples had a salinity near 0 °/oo, and a pH between 7.6 and 7.9. Total alkalinity ranged from 1.5 to 6.8 meq/liter. It will become evident that our interpretation of the effects of various processes on CO₂ composition of Fanning waters is not particularly sensitive to our estimate of the exact groundwater composition. We initially judge "typical" groundwater total alkalinity to have been about 3 meq/liter, but we then consider in our calculations the possibility that a typical groundwater alkalinity value might have been as high as 5 meq/liter. To a first approximation, the total CO₂ content of the groundwater equals alkalinity at the pH of these waters.

Rainwater was a significant water type during our stay. If rainwater pH (measured to be about 6.4) is considered to result from the solution of CO₂ in distilled water, then rainwater contained about 10⁻³ mmoles/liter total CO₂. Rainwater salinity was not measurably different from 0 °/oo.

**Fanning Lagoon Water Budget**

Some volume of ocean water (V₀) enters the lagoon each day. Rainwater (V₉) is a second major source of water entering the lagoon. Some of the ocean water and rainwater entering the lagoon each day stays there, and some is exchanged for lagoon water which departs (Vₑ). In order that the lagoon volume remain constant (after adjustment is made for tidal variations), Vₑ must equal the sum of V₀ plus V₉; or, by rearrangement:

\[ V₀ = Vₑ - V₉ \]  

Actually, two other terms also enter into this equation, but they are small and approximately offset one another. Data given by Wyrtki (1966) demonstrate that evaporation in the vicinity of Fanning Island ordinarily amounts to about 0.3 cm/day during the months of July and August. That value is about 20% of the 1.5 cm/day mean rainfall which was measured at two rain gauges during those months in 1972; the weather conditions associated with the high rainfall during that period probably lowered evaporation well below this usual rate.

Groundwater seepage adds water to the lagoon. Zipser and Taylor (1968) list the land area of the atoll to be one-fifth as large as the lagoon area. Data by Guinther (see p. 263 this report) suggest that the freshwater lens of Fanning was filled to capacity during the summer of 1972 and that rainwater falling on the islands quickly seeped into the ocean and lagoon. If half this seepage entered the lagoon, and if lagoon and island rainfall per unit area equaled one another, then groundwater provided about one-tenth as much water to the lagoon as did direct rainfall.
Fig. 2. Maps of surface (A) and near-bottom (B) lagoon salinity at Fanning Atoll.
Combined evaporation and groundwater apparently lower the total fresh water contribution to the lagoon less than 10% below the rainfall contribution; equation (2) is therefore an adequate representation of the water budget.

Residence Time of Water in Fanning Lagoon

Gallagher et al. (1971) presented an approach to estimating one extreme limit of water residence time in the lagoon, and a second extreme can be extracted from their discussion. Residence time (\(T\), in days) is the water volume of the lagoon (\(V_L\)) divided by the daily net volume of lagoon water exchanged for ocean water and rainwater (\(V_E\), equation 2):

\[ T = \frac{V_L}{V_E} \] (3)

Exchange of ocean and lagoon water occurs almost entirely at the three passes between the ocean and the lagoon and is accomplished almost entirely by tidal flow. Gallagher et al. (1971) found that over a 24-hour period, about 95% of the total water inflow and outflow occurred at English Harbor. That pass had a slight net outflow of water on a tide cycle, while both of the smaller passes had a net inflow.

By assuming the only net exchange over 24 hours to be accomplished through the excess of water inflow over outflow at the two eastern passes, Gallagher et al. (1971) arrived at a "lower" (longer) limit of lagoon water residence time. They took the lagoon volume to be \(4.1 \times 10^8 \text{ m}^3\) and the net input at the two eastern passes to be \(1.2 \times 10^6 \text{ m}^3 \text{ day}^{-1}\). These values yield a residence time estimate of 340 days, according to equation (3).

An "upper" (shorter) limit on residence time can also be derived from the study by Gallagher et al. (1971). Those authors point out that the semidiurnal tidal exchange is equivalent to about 5% of the lagoon volume. If all incoming ocean water were to displace lagoon water without mixing, then 20 periods of inflow (about ten days) would be needed to replace all the lagoon water. The correct residence time cannot be shorter than this value.

The best estimate of residence time obviously lies somewhere between these broad extremes, and an ocean-to-lagoon salinity differential set by the heavy rainfall preceding and during our 1972 expedition provided a basis for arriving at this best estimate. Two different approaches presented here yield comparable results. Water was sampled eight times at each of four localities across the English Harbor pass during a tide cycle. Incoming water had a near-constant salinity of 34.8 \(^\circ\text{o/o}\) (Table 1). Outgoing water was more variable in composition but averaged 33.8 \(^\circ\text{o/o}\). The mean lagoon salinity was approximately 31.5 \(^\circ\text{o/o}\) (Table 1). If \(X\) is the proportion of lagoon water existing English Harbor, then:
As discussed above, about 10% of the lagoon volume takes part in daily tidal exchange. If 30% of the total daily outflow through the passes on ebb tides is lagoon water, then according to this calculation 3% of the lagoon water is removed daily, and the mean residence time is 33 days.

A second method of estimating lagoon residence time from the salinity differential makes use of available rainfall data. Because high and relatively constant rainfall had occurred for well over a month preceding our lagoon salinity survey, it was assumed that lagoon salinity had reached a steady state value. Rain gages at the Cable Station and at English Harbor showed considerable day-to-day differences from one to the other, but recorded essentially identical rainfall over periods of a week or more both before and during our expedition. The records from these two gauges were assumed to represent the atoll rainfall as a whole.

The following equations refer to mean ocean and lagoon salinity as \( S_0 \) and \( S_L \), respectively, and the mean daily rain volume as \( V_R \). \( V_E \) is the exchange volume as defined in equation (3). Only water flowing in or out of the passes exchanges salt between the ocean and the lagoon; rainfall does not. Yet rain does contribute to total water input; for the lagoon volume to stay constant, outflow must equal the sum of ocean water inflow plus rain input (equation 2). The salt budget can be represented by the following three equations:

\[
\begin{align*}
\text{Daily salt output} &= V_E S_L \\
\text{Daily salt input} &= (V_E - V_R) S_0
\end{align*}
\]

Since lagoon salinity is assumed to have reached a steady-state (constant) value, salt input equals salt output:

\[
V_E S_L = (V_E - V_R) S_0
\]  

(7)

Combining equations (3) and (7) yields:

\[
\tau = \frac{V_L}{V_R} \left[ \frac{S_0 - S_L}{S_0} \right]
\]

(8)

The ratio of lagoon volume to daily rainfall volume is equivalent to the ratio of lagoon depth (\( Z \approx 5 \text{m} \), according to Roy and Smith, 1971) to daily rainfall height (\( h \), in meters). Equation (8) can be modified accordingly:

\[
\tau = \frac{Z}{h} \left[ \frac{S_0 - S_L}{S_0} \right]
\]

(8a)
Most of our lagoon salinity measurements were made between 23 July and 1 August, 1972. Mean rainfall from June through July was 1.5 cm/day (Taylor, 1973, plus additional unpublished data gathered at the Cable Station). That value in equation (8a), 34.8 o/oo for \( S_0 \), and 31.5 o/oo for \( S_1 \) (Table 1) give a mean residence time of 32 days. Thus, the two estimates of \( T \) based on equations (4) and (8a) are each about one month, the value used in our subsequent calculations.

It is worth speculating briefly about the lack of a significant ocean-to-lagoon salinity differential during January 1970 (Gordon and Schieser, 1970). Data in Taylor (1973) show that rainfall during and immediately preceding the 1970 expedition was near normal, and data in Wyrtki (1966) and Taylor (1973) show that rainfall approximately equals evaporation during December and January. That situation should not generate an ocean-to-lagoon salinity differential. On the other hand, 1969 total rainfall was about 35% above normal; and mean rainfall ordinarily exceeds evaporation by about 1 meter in the vicinity of Fanning. Were the 340-day maximum residence time estimate of Gallagher et al. (1971) a close estimate of the true residence time, then the lagoon salinity would have been depressed to well below 30 o/oo in January 1970.

The assumptions of steady-state salinity, spatially constant rainfall, and low groundwater input apply to the lagoon as a whole and do not rigorously describe the age of individual water parcels. For example, the low salinity "rim" about the periphery of the lagoon (Fig. 2) surely represent an "edge" effect from groundwater seepage. Nevertheless, the salinity maps (particularly those in Fig. 4, crudely corrected according to the procedure to be described on p. 31 for groundwater effects) are likely to represent a general pattern of relative water age. That is, "pockets" of water, probably up to two months old, occur near the central portion of the north and south basins of the lagoon, while water near the passes has resided in the lagoon no more than a few tide cycles.

Responses of Lagoon Water Composition to Controlling Processes

A procedure of stepwise data analysis can be employed to estimate the contribution of various processes to the \( \text{CO}_2 \) content of lagoon waters. The first of these processes to be considered is gas exchange. Carbon dioxide partial pressure in lagoon waters (\( P_{\text{CO}_2} \)) can be calculated from pH and total alkalinity (Appendix). During our survey, virtually the entire lagoon had surface-water \( P_{\text{CO}_2} \) values well above the atmospheric mean of about 320 \( \mu \text{atm} \). Values near the lagoon margin were below 400 \( \mu \text{atm} \), while lagoon-center values were greater than that value.

Values were too variable to allow the \( P_{\text{CO}_2} \) to be contoured satisfactorily. This variability probably represents, in part, the relatively large errors inherent in calculating \( P_{\text{CO}_2} \) from water chemistry data (Keeling, 1968). Nevertheless, our mean values are based on a sufficient number of data points to be reliable. Ocean water entering English Harbor averaged 370 \( \mu \text{atm} \); for comparison, Keeling et al. (1965) reported Central Pacific surface waters between 340 and 380 \( \mu \text{atm} \). The
mean lagoon surface water value was 400 μatm, so various processes had apparently raised the lagoon water P\textsubscript{CO}_2 by about 30 μatm, to about 80 μatm above the atmospheric value.

Any gas transfer between lagoon waters and the atmosphere should represent net evasion in order that lagoon P\textsubscript{CO}_2 values be lowered towards the atmospheric level. Both the experimental work of Sugiura et al. (1963) and the theoretical calculations of Keeling (1965) suggest that an appropriate CO\textsubscript{2} evasion coefficient is probably something less than 0.018 moles m\textsuperscript{-2} month\textsuperscript{-1} μatm\textsuperscript{-1}. With a mean air-to-sea differential of about 80 μatm, this maximum evasion coefficient yields a gas evasion rate of about 1.4 moles m\textsuperscript{-2} month\textsuperscript{-1}. There is no reason to believe that this process is subject to gross variation, although variations in wind speed and lagoon-water P\textsubscript{CO}_2 will affect the rate somewhat. Our estimate is probably an upper limit unless the lagoon water P\textsubscript{CO}_2 which we measured was particularly below usual values. A lower limit on gas evasion from the lagoon waters is zero; unless the air-to-sea P\textsubscript{CO}_2 gradient sometimes reverses direction, there should be no net CO\textsubscript{2} invasion. The oceanic water feeding the lagoon has a P\textsubscript{CO}_2 value about 50 μatm above the atmospheric value, and we consider it unlikely that processes in the lagoon ever alter the CO\textsubscript{2} content sufficiently to reverse the direction of the observed gradient. Limited data gathered in 1970 (Gordon and Schiesser, 1970) and in 1973 (Dyrrsen, 1973) also suggest lagoon P\textsubscript{CO}_2 values significantly above atmospheric.

Figure 3, a plot of salinity versus total alkalinity, can be used to calculate the effects of freshwater dilution and calcification. The dense cluster of points at salinities higher than about 30 °/oo represents the bulk of the lagoon water. Point A represents mean ocean water. Salinities downward to near 0 °/oo come from the periphery of the lagoon, including the tidal inlets described by Guinther (1971; p. 263 this report). Values at 0 °/oo include samples from water wells and other sites directly accessible to the freshwater lens of the atoll.

Rainwater dilution of ocean water, free of other influences, would alter the composition of that water along line AB, from pure ocean water (A) towards pure rainwater (B). Groundwater dilution alone would move ocean water along line AD if 3 meq/liter is an appropriate groundwater alkalinity (Table 1). If 5 meq/liter is a more appropriate groundwater alkalinity, then point D and line AD would be adjusted accordingly. CaCO\textsubscript{3} precipitation alone would lower total alkalinity with negligible effect on salinity (line AA'C). Water is altered by a combination of these processes, so the alteration pathways are more complex than has been described so far. The following assumption allows us to sort out these combined processes.

Line A'E of Figure 3 has been drawn along an obvious boundary of data points above a salinity of 31 °/oo. Below that salinity, the lower boundary of the points deviates markedly from the line. No samples have undergone a sufficient alkalinity change relative to salinity depression to fall significantly below that line. We interpret the line to represent the alteration path of samples subjected to the net effect of calcification and rainfall dilution without a significant contribution from groundwater dilution. Over most of the salinity range encompassed by lagoon water, line A'E is an acceptable representation of the boundary.
Fig. 3. Total alkalinity versus salinity at Fanning Atoll. The various letters and lines are explained in the text.
Most samples are subjected to groundwater dilution as well as to rainwater dilution and calcification. Such groundwater dilution moves samples from the position they would occupy somewhere along line A'E in the absence of groundwater, towards point D. Some hypothetical sample at point F would have had the composition found by projection from point D through point F to point I on line A'E in the absence of a groundwater component. Such a "groundwater-corrected" composition can be determined either graphically or algebraically for each sample point. From the geometry of the diagram and the location of most of the sample points, it can be seen that the groundwater-corrected composition for most points is not particularly sensitive to the alkalinity at point D.

For hypothetical sample point F projected back to line A'E, the distances IC and IH partition freshwater dilution (CH) between rainwater and groundwater. Moreover, the distance IG is the alkalinity depletion attributable to calcification. Equivalent constructions can be made for each sample point on the diagram.

Projecting points back to a groundwater-corrected salinity also allows the construction of salinity maps from which the groundwater component has been crudely removed (Fig. 4). Planimetry of the areas between contour lines on those maps yields a mean groundwater-corrected lagoon salinity of 32.7 °/oo if D is 3 meq/liter. This salinity, together with the mean ocean and lagoon salinities given in Table 1, suggest the mean ratio of ocean water:rainwater:groundwater in the lagoon to have been 91:6:3 during the summer of 1972. If D is 5 meq/liter, then the groundwater-corrected salinity averaged 32.1 °/oo; and this ratio was 91:8:1 at the time of our survey.

The ratio of lagoon area to land area (about 5:1) suggests that most freshwater in the lagoon was probably derived directly from rainwater; hence, the second ratio and a mean groundwater alkalinity near 5 meq/liter are likely to be most nearly correct. However, either combination of freshwater dilution processes would have lowered the CO$_2$ content of the lagoon by closely comparable amounts. The values in Table 1 can be used to calculate the expected CO$_2$ content of a mixture of ocean water, rainwater, and groundwater in either of the above ratios:

\[ \Sigma \text{CO}_2 = 0.91 (2.0) + 0.06 (0.0) + 0.03 (3.0) = 1.91 \text{ moles/m}^3 \quad (9) \]
\[ \Sigma \text{CO}_2 = 0.91 (2.0) + 0.08 (0.0) + 0.01 (5.0) = 1.87 \text{ moles/m}^3 \quad (10) \]

This mixture has been estimated to result from water with a mean residence time of one month, so that freshwater dilution of ocean water to the mean lagoon salinity apparently lowers \( \Sigma \text{CO}_2 \) by about 0.1 moles m$^{-3}$ month$^{-1}$ or, over the 5-meter mean lagoon depth, 0.5 moles m$^{-2}$ month$^{-1}$. The effect of freshwater dilution is undoubtedly highly variable in response to variations in rainfall. For example, Gordon and Schiesser (1970) reported no difference between ocean and lagoon salinity during January 1970; suggesting no net freshwater component to the CO$_2$ budget at that time. Samples gathered in March 1973 by Dyrrsen (1973) suggest some salinity depression in the lagoon, but these data are insufficient to estimate the
amount of depression. Rainfall records since 1907 (Taylor, 1973) reveal few sustained periods with greater rainfall than that we observed, hence the CO$_2$ depression we observed in response to freshwater dilution was larger than usual.

The divergence of lines AB and A'E (Fig. 3) from one another can be used to estimate the calcification rate in the lagoon. Line AB, which demarks the pathway which would be taken by sea water only altered by dilution with rainwater, has a slope of about 0.07 meq liter$^{-1}$ o/oo$^{-1}$. Line A'E, interpreted to represent the net effect of calcification and rainfall dilution in the absence of groundwater dilution, slopes about 0.20 meq liter$^{-1}$ o/oo$^{-1}$. The difference between the slopes of these two lines, that is the slope attributable to calcification alone, is 0.13 meq liter$^{-1}$ o/oo$^{-1}$.

The discussion on p. 31 has suggested that rainfall lowered salinity of water in the lagoon by about 2.7 o/oo month$^{-1}$. Multiplying this dilution rate by the calcification-induced alkalinity/salinity slope yields a rate estimate: 0.35 meq liter$^{-1}$ month$^{-1}$. $\Sigma$CO$_2$ is lowered by 0.5 moles for each equivalent of total alkalinity depression during calcification, so calcification lowered the $\Sigma$CO$_2$ by 0.175 moles m$^{-3}$ month$^{-1}$ (or about 0.9 moles m$^{-2}$ month$^{-1}$ through the 5-meter water column).

Some evidence for consistent deviations from this mean rate can be inferred from Figure 3. The offset of point A' from point A may represent initial rapid calcification from ocean water before the salinity of that water was significantly lowered by dilution. Dyrrsen (1973) estimated the calcification rate suggested by a single water sample, which he gathered in March 1973, 1,000 meters southeast of English Harbor, to be 0.0063 moles m$^{-3}$ hour$^{-1}$. It is difficult to relate quantitatively an estimate based on a single sample with our more extensive data, but this value is qualitatively consistent with rapid alkalinity depletion of water immediately upon its entrance into the lagoon. At low salinities, the deviation of points from line A'E may result from eventual decrease in calcification rate with no increase in dilution rate. Over the majority of the salinity range encountered in the lagoon, the straight-line approximation fits the data well. Further attention will be given in the Discussion to the possible significance of such variations in the calcification rate.

Organic carbon production can be estimated as the difference between the total rate of CO$_2$ changes in the lagoon and the sum of those terms previously estimated. Table 2 summarizes those terms. Within the uncertainty limits attached to the estimate of gas exchange, net organic carbon production in the lagoon did not differ significantly from 0 during our survey. The possible range of organic carbon flux consistent with our data is -0.1 moles m$^{-2}$ month$^{-1}$ (net production) to +1.3 moles m$^{-2}$ month$^{-1}$ (net consumption). Interpretation of these results will be deferred to the Discussion.
Fig. 4. Surface (A) and near-bottom (B) salinity maps from which the ground-water effect has been removed according to the procedure discussed in the text.
Table 2. CO$_2$ Budget for the Fanning Lagoon. The calculations are based on an estimated mean lagoon water residence time of one month and a mean lagoon depth of 5 meters.

<table>
<thead>
<tr>
<th>PROCESS</th>
<th>MEAN MONTHLY CHANGE</th>
<th>COMMENTS</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>moles/m$^3$</td>
<td>moles/m$^2$</td>
</tr>
<tr>
<td>Gas Evasion</td>
<td>0.00 to -0.28</td>
<td>0.0 to -1.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Based on minimum to maximum gas evasion rate constants.</td>
</tr>
<tr>
<td>Freshwater dilution</td>
<td>-0.10</td>
<td>-0.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>From equations (9) and (10).</td>
</tr>
<tr>
<td>Calcification</td>
<td>-0.18</td>
<td>-0.9</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Difference in slopes between lines AB and A'E of Figure 3.</td>
</tr>
<tr>
<td>Organic carbon production</td>
<td>-0.02 to +0.26</td>
<td>-0.1 to +1.3</td>
</tr>
<tr>
<td>or consumption (+)</td>
<td></td>
<td>Difference between net CO$_2$ change (below) and the sum of the terms given above.</td>
</tr>
<tr>
<td>Net</td>
<td>-0.30</td>
<td>-1.5</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sum of the above terms. Also follows from Table 1.</td>
</tr>
</tbody>
</table>
Temporal Variation in Lagoon Composition

Schmalz and Swanson (1969) criticized earlier analyses of CO₂ data from reef systems because those analyses ignored diurnal cycles in the concentration and partitioning of CO₂ in sea water. To minimize this source of potential variability, we gathered most samples for our lagoon-wide sampling survey between middle and late morning. We also conducted a day-long sampling series at Suez Pond (Fig. 1) to determine the likely magnitude of diurnal cyclicity to the Fanning lagoon CO₂ system. That location was chosen to be out of direct influence from both ocean water exchange and groundwater seepage but sufficiently close to our laboratory to be reached by skiff at night.

Salinity effects on total alkalinity have been "normalized" out of these diurnal cycle data by the calculation of specific alkalinity (total alkalinity/chlorinity). Actually, the salinity effect is small, because salinity varied by only about 0.6 ‰ at a given depth during the 1-day sampling period.

Figure 5 qualitatively confirms the pH trends observed by Schmalz and Swanson (1969), but shows no strong trend in specific alkalinity. Diurnally-varying pH and a constant total alkalinity will yield a diurnal variation in carbonate alkalinity and other CO₂ parameters. Nonetheless, the diurnal variation in CO₂ parameter was only a small fraction of the geographic variation encountered during this study. Thus, while we concur with the general expectation of a diurnal CO₂ cycle discussed by Schmalz and Swanson, we do not find such a cycle to be quantitatively significant in the lagoon. Diurnal periodicity there superimposes only a small oscillation upon the much greater effects of a month-long history of water "incubation."

Certainly there is longer term variation in the composition of lagoon waters. In particular, we evaluated our assumption that the lagoon salinity had reached a steady state composition by the time of our sampling.

Water samples were gathered in Suez Pond about noon on most days of our survey. Additional data are available for each of the days spanned by our 1-day survey (August 10 and 11) and for August 4. Figure 6 shows evidence for an increase in mean salinity from about 29.3 ‰ to about 30.6 ‰ over several days.

Increasing salinity is not obviously consistent with a gradual adjustment of the lagoon salinity to the heavy rainfall regime which prevailed during our stay. Nor is such a changing salinity indicative of an entirely steady state system. We suggest that superimposed on a generally steady state pattern there may have been minor oscillations of lagoon salinity in response to lunar cycles in the tide range and flushing characteristics of the lagoon. Moreover, the general agreement between one residence time calculation, dependent on the assumption of steady-state salinity, and a second calculation, independent of that assumption (pp. 27 to 28), suggests that any departure of lagoon composition from steady state was relatively small.
Fig. 5. Variation of tide height, salinity, specific alkalinity, and pH over a 1-day cycle at Suez Pond.
Fig. 6. Mean salinity and specific alkalinity at Suez Pond from 22 July to 11 August, 1972. Open circles represent sampling stations other than the standard, repeated station.
A final aspect of temporal variability comes from comparing our data from Suez Pond with other available data. We found the average salinity of that pond to be 30 o/oo, while four values in January 1970 (Gordon et al., 1971) averaged 35 o/oo. A drought which began in April 1973 was sufficient to raise the salinity of Suez Pond to 37 o/oo by November 1973 (two samples collected by M. Vitousek and R. Taylor).

Specific alkalinity values reported by Gordon et al. (1971) for Suez Pond averaged 0.109, compared with 0.101 for our 1972 data. Considering slight differences in analytical technique between the two studies, as well as the range of alkalinity values which we found in Suez Pond (Fig. 6), we doubt that this difference in specific alkalinity is significant. Both our values and the earlier ones are distinctly different from constant offshore values of 0.122. The various data cited above suggest that the temporal variability in specific alkalinity is considerably less than the temporal salinity variations in the lagoon.

Vertical and Horizontal Variations in Lagoon Composition

Maps of both salinity and specific alkalinity (Figs. 2 and 7) show considerable variation in the lagoon composition. Characteristically, values near the passes are similar in composition to oceanic values. This pattern reflects the relatively recent oceanic derivation of such water. Near the land, lagoon water has high specific alkalinity and low salinity due to the contribution of groundwater. The low salinity rim is absent when the water composition is corrected for the groundwater contribution (Fig. 4). Water in both the north and the south basins, away from the lagoon margins, has low alkalinity and intermediate salinity due to the small groundwater contribution, large rainfall component, and relatively long history of calcification. Samples of this water tend to fall near line A'E of Figure 3.

Vertical variations in lagoon composition are considerably less prominent than the horizontal gradients. Generally there is a slight increase in salinity with depth. Only in the vicinity of the passes does this increase express itself as well-defined stratification. There the tidal influence of incoming high-salinity ocean water to a great extent offsets the effective vertical mixing which prevails through much of the lagoon (Stroup and Meyers, p. 7, this report).

Percent CaCO₃ Saturation of Lagoon Waters

Percent CaCO₃ saturation is commonly defined (e.g., by Berner, 1971) to be 100 times the ratio of seawater CaCO₃ ion activity product (IAP) to the solubility product constant (Ksp) of the mineral of interest. Discrepancies between investigators in estimating the saturation state of seawater can be attributed to different estimates of the calcium and carbonate activity coefficients (γ⁰Ca and γ⁰CO₃) and of the appropriate Ksp. Following Berner (1971), we have used 0.20 and 0.02 for γ⁰Ca and γ⁰CO₃,
respectively. Figure 9 summarizes the $K_{sp}$ values we have used. Details of our calculations are reported in the appendix.

Using these values, we have found that oceanic water is approximately 200% saturated with respect to the $K_{sp}$ of aragonite (Fig. 9). This value is in substantial agreement with Lyakhin (1968) whose map shows ocean surface waters near Fanning to be approximately 300% saturated with respect to aragonite.

By contrast, lagoon waters show greatly depressed IAP values. Figure 8 shows maps of IAP values, and Figure 9c is a histogram of IAP as a function of percent lagoon volume. There is a slight discrepancy between our calculated values and measured saturation states; three samples calculated to be 95 to 100% saturated with respect to calcite tested (by the saturometry technique of Weyl, 1961) to be slightly supersaturated with respect to reagent-grade CaCO$_3$ (calcite).

Even with allowances for some uncertainty in absolute saturation states, it is evident that lagoon waters are approximately saturated with respect to aragonite and that the average lagoon saturation state is less than half that of the adjacent open-ocean water. This depressed saturation state is similar to that observed by Broecker and Takahashi (1966) across the Bahama Banks and can be ascribed to the interacting biological, chemical, and physical processes which have so drastically altered the CO$_2$ composition of lagoon water.

DISCUSSION

Our budget has demonstrated the significance of various pathways of CO$_2$ flux in the lagoon of a coral atoll. Of particular interest are the metabolically important processes of organic carbon production and calcification.

Data for the windward reef flat of Eniwetok Atoll (Smith, 1973; Smith and Marsh, in press) suggest that instantaneous rates of CO$_2$ flux associated with organic carbon production exceed the instantaneous flux associated with calcification there. Water remains on the reef flat of Eniwetok only a few minutes, so any impact of CO$_2$ changes in the water on that system must be in response to such instantaneous flux patterns.

By contrast, water in the Fanning lagoon undergoes a month-long history of CO$_2$ alteration; the reef system is exposed to the results of the integrated, rather than of the instantaneous, record of these processes. The absolute effect of organic carbon production on the CO$_2$ system in that lagoon is certainly not much larger than the calcification effect and is probably smaller (Table 2).

Coral knolls and reefs cover over 40% of the lagoon floor at Fanning, and live corals themselves occupy over 30% of the lagoon area (Roy and Smith, 1971). While we recognize that the corals themselves are probably not the major metabolic component of reefs (discussed, e.g., by Smith and
Fig. 7. Surface (A) and near-bottom (B) maps of (specific alkalinity x1000) in Fanning lagoon.
Fig. 8. Surface (A) and near-bottom (B) maps of \((-\log IAP)\) in Fanning lagoon.
Fig. 9. Diagram comparing \((-\log k_{sp})\) of (a) various Mg-calcites from data in Winland (1969), and of (b) aragonite from Winland (1969), Smith (1941), and Cloud (1962), and a summary of values in Broecker and Takahashi (1966), with (c) the frequency distribution of \((-\log \text{IAP})\) in Fanning lagoon. The arrow and vertical bar on (c) represent the lagoon mean and the range of IAP values encountered in the lagoon and adjacent ocean waters, respectively.
Marsh, in press), we suggest that their presence is probably a reliable indicator of the high metabolic activity which most investigators attribute to coral reef communities. For example, previously-described reef flat communities (summarized in Helfrich and Townsley, 1963; Stoddart, 1969; Smith and Marsh, in press) have gross production rates exceeding 3 g C m$^{-2}$ day$^{-1}$. The organic carbon flux of the community in Fanning lagoon, inclusive of benthos, nekton, and plankton, lies between a net production rate of 0.04 g C m$^{-2}$ day$^{-1}$ and a net consumption rate of 0.5 g C m$^{-2}$ day$^{-1}$ (as calculated from Table 2). Thus, even if the Fanning lagoon has the high daytime metabolic activity which characterizes other reef communities, there is no significant net carbon production. Any daytime excesses are apparently consumed at night. In fact, the data suggest that there may need to be some net carbon input to support the lagoon reef ecosystem.

Gordon et al. (1971) report on the $^{14}$C productivity of the Fanning lagoon and suggest that plankton productivity there is high compared to that of other lagoons. Unfortunately, more recent and more extensive $^{14}$C measurements by Krasnick (see p. 51, this report) suggest that $^{14}$C measurements by conventional techniques in the turbid waters of that lagoon are probably unreliable, largely because of $^{14}$C exchange between the suspended CaCO$_3$ particles and the incubation medium. However, even if the net productivity of the Fanning lagoon is as low as that of other lagoons listed by Gordon et al. (0.025 to 0.1 g C m$^{-2}$ day$^{-1}$ through the 5-meter water column), then the lagoon reef benthos plus nekton are almost certainly slight net heterotrophs.

Our survey was conducted during a period of generally heavy cloud cover. We suggest that this consideration might shift the carbon flux to be expected under more usual conditions of greater light intensity slightly backward toward the direction of net carbon production, but any such shift seems likely to be small. Thus, our estimate representing a record of carbon flux integrated over a timespan of a month and an area of 100 km$^2$ is indistinguishable from zero.

Two additional observations further support the likelihood that net organic carbon production is near zero. Schiesser (in Gordon, 1971) found that Fanning sediments have only about 0.1% organic carbon, in general agreement with the low organic carbon content reported for the sediment of other coral atolls (Emery et al., 1954). Moreover, Gordon (1971) suggests that suspended plus dissolved organic carbon flux to and from the Fanning lagoon via the passes amounts to only about 0.01 moles C m$^{-2}$ month$^{-1}$, a negligible fraction of the CO$_2$ budget (Table 2). Thus, the lagoon does not appear to be a significant source or a sink for organic carbon. It seems likely therefore that the community of Fanning lagoon, and perhaps the communities of other atoll lagoons as well, produce almost exactly as much organic carbon as they consume.

By contrast, CaCO$_3$ precipitation does result in net carbon flux. The data of Smith et al. (1971) suggest that there is little or no net transport of this CaCO$_3$ from the lagoon, although there is apparently some exchange of CaCO$_3$ precipitated in the lagoon for CaCO$_3$ originating on the ocean reef outside the lagoon.
Biological calcification accounts for most or all of the CaCO₃ precipitation in the lagoon. Scanning electron microscopy of lagoon muds reveals the grains to be predominantly blocky fragments, including composite grains of lath-like bundles resembling the pelecypod and coral debris illustrated by Hay et al. (1970). Much of the material has a maximum diameter of less than 5 microns, precluding unequivocal resolution of phyletic origins. However, abundant corals living in the lagoon are probably the major CaCO₃ producers. The coral skeletons are broken down, probably in large part by boring sponges, which are found on the line reefs throughout the lagoon, and also by boring bivalves. Some silt-sized grains in the mud look much like the chips of material resulting from sponge boring (Cobb, 1969; Rützler and Rieger, 1973). The observations by Neumann (1966), Cobb (1969), and Rützler and Rieger (1973) suggest that boring sponges dissolve less than 10% of the material which they erode, so such bioerosion should not lower net calcification estimated from alkalinity depletion significantly below gross calcification.

Our data (Table 2) indicate a net calcification rate of about 1 kg CaCO₃ m⁻² yr⁻¹. Based on the abundance of live corals in the lagoon (> 30% cover, according to Roy and Smith, 1971) and the known CaCO₃ production rates of common reef corals (> 10 kg CaCO₃ m⁻² yr⁻¹ per square meter of cover, according to Chave et al., 1972), we would have expected the CaCO₃ production rate to have been at least three times as high as the observed rate. That estimate, while subject to considerable uncertainty, is likely to err by being too low; it is based on the lower estimates of coral cover and production rate, and the estimate does not include CaCO₃ production by organisms other than corals in the lagoon. The large discrepancy between estimates of CaCO₃ production based on water chemistry and on expectations based on coral standing crop-growth data, and the observation that the CaCO₃ ion activity product of water in the Fanning lagoon is near the solubility product constant of aragonite (Figs. 8 and 9) provide a basis for speculating about factors which might affect the calcification rate of marine organisms.

Two alternative explanations could link these observations. Total gross calcification may proceed at a rate well in excess of 1 kg CaCO₃ m⁻² yr⁻¹, but re-solution of CaCO₃ may increase the alkalinity and offset much of this gross calcification. The resultant net calcification rate would represent the balance between CaCO₃ precipitation and solution but would be largely attributable to solution. Such a model ascribes the low net calcification rate and the CaCO₃ ion activity product of lagoon waters to relatively rapid and thermodynamically controlled solution, in accord with the view of Schmalz (1967) and Schmalz and Swanson (1969) that sea water is usually in thermodynamic equilibrium with the most soluble CaCO₃ mineral with which that water is in contact.

There appear to be several problems with such an interpretation. Most of the lagoon water is approximately saturated with respect to aragonite; some of the water is apparently even saturated with respect to low-Mg calcite, which is far less soluble than aragonite (Figs. 8 and 9). Yet in addition to abundant aragonite, 15 mole-percent Mg calcite (roughly twice as soluble as aragonite, according to Fig. 8) is present both in the
sediments and among the suspended materials (Smith et al., 1971; plus additional unpublished X-ray diffraction data by Smith and K. Roy). Moreover, scanning electron microscopy of the lagoon muds provides no evidence for grain etching, which should accompany extensive solution of calcareous materials.

The following alternative mechanism to explain this situation seems more plausible. The CaCO₃ ion activity product of seawater or something closely related to that product may limit the calcification of some marine organisms. Certain calcifying organisms (such as corals) may be able to calcify only when the aqueous medium surrounding them exceeds some minimum CaCO₃ ion activity product. The effect of IAP may be similar to that of other limiting constituents. That is, organisms may slow their calcification rate as the surrounding medium approaches some limiting IAP.

Such a model does not take issue with the various models (e.g., Goreau, 1959; Simkiss, 1964; Pearse and Muscatine, 1971) which have been advanced to explain coral calcification; rather, we suggest that some process may affect the supply of ions from sea water to the calcification sites of corals and some other calcifiers before any of the internal controls can exert themselves. Recent experiments (Smith, unpublished) demonstrate that direct manipulations of the CO₂ system in aquaria by additions of acid or base can alter the calcification rate of corals in the aquaria. Recognized correspondence between photosynthetic activity and calcification rate (Goreau, 1959; Pearse and Muscatine, 1971) can also be attributed to alterations of the CO₂ system external to the organism, rather than (or in addition to) the internal effects postulated by those authors.

If such a model of external IAP control of biological calcification is at least partially correct, then the effect of Ca⁺⁺ on the calcification rate of marine organisms would tend to be less than the CO₃⁻⁻ effect. The concentration of Ca⁺⁺ is large and essentially invariant in ocean water, while CO₃⁻⁻ is present in low and variable quantities. Hence the latter ion is the more important ion to the product of the two.

The proposed model is by no means universal. For example, Chave (personal communication) has observed abundant barnacles living along the shore of the Gulf of Alaska in waters undersaturated with respect to the low-Mg calcite which those organisms precipitate. We suspect that many mollusks and echinoderms may exhibit similar hardy ability to calcify in low-IAP waters. However, sediments rich in reef components such as hermatypic corals and calcareous green algae are much more restricted in latitudinal distribution (Hayes, 1967; Lees and Buller, 1972) and are not described from waters undersaturated with respect to their mineral phase (aragonite).

Rodgers (1957) and others have suggested that a general restriction of calcareous sediments to the tropics might be largely attributable to the presence there of waters highly supersaturated with respect to CaCO₃. Chave (1967) pointed out two misconceptions associated with that statement. In the first place, virtually all surface open-ocean water, even at high latitudes, is supersaturated with respect to calcite. Secondly, as has
already been mentioned, calcareous sediments are produced at high latitudes. Yet, despite erroneous bases for associating CaCO$_3$ deposition with supersaturation, our data suggest that the saturation-state mechanism for limiting CaCO$_3$ production may work in some situations.

Broecker and Takahashi (1966) used the proportional relationship between CaCO$_3$ precipitation rate and the degree of CaCO$_3$ supersaturation on the Bahama Banks as an argument that precipitation of aragonite muds there was probably largely inorganic. However, such proportional relationships generally describe the response of metabolism to any limiting factor. Moreover, Neumann and Land (1969) and Stockman et al. (1967) have offered convincing evidence that biological processes probably account for most or all of the aragonite mud precipitation on the Bahama Banks and other similar environments. The CaCO$_3$ muds in the Fanning lagoon are obviously biogenic (p. 38), and our data hint of a change in calcification rate similar to that documented by Broecker and Takahashi (1966). In both areas cited as possible examples of an IAP limitation to biological calcification (Fanning and the Bahamas), aragonite is the overwhelming mineral phase precipitated—as is generally true for areas of tropical neritic carbonate sedimentation. The high latitude sediments described as exceptions to such a model are dominantly calcite. Hence, the suggestion that IAP might limit the CaCO$_3$ production rate of marine ecosystems so far finds support only in calcifying systems dominated by aragonite precipitation.

Several other candidates besides CaCO$_3$ IAP to limit calcification in the Fanning lagoon also merit attention. Temperature has been suggested as a possible control of coral calcification. However, the 29°C mean water temperature in the Fanning lagoon during our survey lies near the optimum temperature for coral growth in Hawaii and Eniwetok (Clausen, 1971, 1972; Coles, 1973). Hence, temperature can be dismissed from further consideration as a likely factor suppressing calcification in the Fanning lagoon during our survey.

Salinity was depressed during the 1972 expedition below the 34 to 36 o/oo range which Wells (1957) considered to be optimum for coral growth. That optimum range is open to some question, however. For example, Yamazato (1970) found the calcification rate of a common Hawaiian coral to be relatively unaffected by salinities as low as 27 o/oo. Moreover, the limited earlier data for the Fanning lagoon do not suggest that higher salinities are accompanied by lower specific alkalinity (Gordon et al., 1971).

Light and/or turbidity is a complex factor or set of factors which may limit lagoon calcification. Much of the Fanning lagoon is very turbid from large concentrations of CaCO$_3$ suspended in the water column (Smith et al., 1971; Stroup and Meyers, p. 7, this report). Roy and Smith (1971) pointed out that neither light attenuation nor sedimentation prevents survival of common reef biota in the lagoon. However, neither those authors nor we have sufficient information to evaluate the possible sublethal effects of turbid water on the energetics of the reef biota. If some aspect of water clarity does limit the calcification rate in the Fanning lagoon, then that
influence is likely to be continual; lagoon water there apparently remains turbid most of the time.

In fact, there is a possible relationship between the \( \text{CaCO}_3 \) ion activity product and the turbidity. Increased turbidity could, by lowering available light, also lower photosynthesis—hence \( \text{pH} \), \( \text{CO}_3^- \) concentration, and the \( \text{CaCO}_3 \) ion activity product of the water.

**CONCLUSIONS**

Emery (1962), Schmalz and Swanson (1969), Kinsey (1972), and Smith (1973) have reported on coral reef systems showing marked diurnal oscillation in the \( \text{CO}_2 \) composition of their waters; the present study and that of Broeckner and Takahashi (1966) describe reef systems which alter \( \text{CO}_2 \) biogeochemistry in a long-term, integrated fashion.

The high organic carbon metabolic activity of reef communities may, in many instances, result in diurnally imposed oscillations in the \( \text{CO}_2 \) content of associated waters. However, because coral reef communities apparently produce about as much organic carbon as they consume, such metabolic activity seems unlikely to impose long-term changes on the \( \text{CO}_2 \) content of those waters. That role on coral reefs is apparently reserved for \( \text{CaCO}_3 \) reactions, plus the physical processes of gas exchange, mixing of ocean water with freshwater, and evaporation.

While coral reefs are bathed by waters which are initially far supersaturated with respect to common \( \text{CaCO}_3 \) minerals (see, e.g., Lyakhin, 1968), the combined physical configuration and biogeochemical characteristics of reef systems may make these systems unique in their ability to alter the \( \text{CO}_2 \) composition of the water impinging upon them. If that observation is correct, then coral reef communities are perhaps the most likely of all present-day marine communities to be affected by the availability and speciation of \( \text{CO}_2 \).

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APPENDIX

The calculations summarized below, as well as an algebraic solution of the procedure outlined on p. 30 for the interpretation of Figure 3, were carried out on the University of Hawaii IBM 360 computer.

The procedure of analyzing CO₂ data combines theoretical and empirical relationships either given in or derived from Park (1969), Skirrow (1965), and Berner (1971). A brief glossary of the symbols used in this appendix follows:

\[ a_{H^+}, a_{OH^-} \] Activity of hydrogen and hydroxide: \( 10^{-pH} \) and \( 10^{-pOH} \), respectively; assumed equivalent to concentrations, in moles/liter.

B.A. Borate alkalinity, in eq/liter: \( (\text{H}_2\text{B}_03^- + 2(\text{B}_03^-) \).

C.A. Carbonate alkalinity, in eq/liter: \( (\text{HCO}_3^- + 2(\text{CO}_3^2-) \).

\((\text{Ca}), (\text{CO}_3), \text{etc.}\) Concentration of \( \text{Ca}^{++}, \text{CO}_3^{=} \), etc., in moles/liter.

\( \text{Cl} \) Chlorinity, in g/kg.

\( \text{IAP} \) \((\text{Ca}) (\text{CO}_3) \) ion activity product.

\( K_1^c, K_2^c, K_1^b, K_2^b \) First and second apparent dissociation constants for carbonic acid and boric acid in seawater.

\( P_{\text{CO}_2} \) Partial pressure of \( \text{CO}_2 \) in seawater, in atm.

\( S \) Salinity, in g/kg.

\( t \) Temperature, in °C.

T.A. Total alkalinity, in eq/liter: \( (\text{HCO}_3^- + 2(\text{CO}_3^2-) + (\text{H}_2\text{B}_03^-) + 2(\text{B}_03^-) + (\text{OH}^- - (\text{H})^+ \).

\( \Sigma B, \Sigma \text{CO}_2 \) Concentrations of the sum of carbonic acid and boric acid species in seawater, in moles/liter.

\( \infty \) Henry's Law coefficient for \( \text{CO}_2 \) in seawater.

\( \gamma_{\text{Ca}}, \gamma_{\text{CO}_3} \) Activity coefficients for \( \text{Ca}^{++} \) and \( \text{CO}_3^= \).

The \( \text{CO}_2 \)-related parameters calculated for this investigation include \( \Sigma B, P_{\text{CO}_2}, \) and IAP. The first of these is calculated for the water sample at laboratory temperature (25°C), while the other two are calculated at the appropriate field temperature (27 - 30°C). Let us
consider each in turn. The direct sample measurements on which these
calculations are made include temperature, total alkalinity, pH, and
salinity.

\[ \Sigma \text{CO}_2 \text{ is calculable from } C.A., a_H, \text{ and the dissociation constants for carbonic acid. } C.A., \text{ is calculated from } T.A. \text{ and } B., \text{ which, in turn, is a function of } a_H, Cl, \text{ and the boric acid dissociation constants:} \]

\[ Cl = \frac{S - 0.03}{1.805} \quad (a1) \]

\[ \Sigma B = 2.06 \times 10^{-5} Cl \quad (a2) \]

\[ B.A. = \Sigma B \left[ \frac{a_H K_{1b} + 2K_{1b} K_{2b}}{a_H^2 + a_H K_{1b} + K_{1b} K_{2b}} \right] \quad (a3) \]

\[ a_{OH} = 10^{-14}/a_H \quad (a4) \]

\[ C.A. = T.A. - B.A. - a_{OH} + a_H \quad (a5) \]

\[ \Sigma \text{CO}_2 = C.A. \left[ \frac{K_{1c a_H}^{'2} + K_{1c} K_{2c}^{'2} + a_H^2}{K_{1c a_H} + 2K_{1c} K_{2c}^{'}} \right] \quad (a6) \]

\[ P_{\text{CO}_2} \text{ can be calculated from } a_H, C.A., \text{ and } C:\]

\[ P_{\text{CO}_2} = \frac{C.A. a_H^2}{K_{1c} \alpha C \frac{a_H}{a_H + 2K_{2c}^{'}}} \quad (a7) \]

Both the Henry's Law coefficient for CO$_2$ and the apparent dissociation constants for carbonic and boric acids are temperature and chlorinity-dependent. Over the temperature and chlorinity range encountered throughout most of the Fanning lagoon, the following linear approximation to Lyman's data (as given in the appendix of Riley and Skirrow, 1965) are satisfactory:

\[ K_{1c}^' = 10^{-6} \left[ 0.55 + 0.024 \frac{Cl}{C1} \right] \quad (a8) \]

\[ K_{2c}^' = 10^{-10} \left[ 0.52 + 0.4 \frac{Cl}{C1} + 0.014 \frac{t}{t} \right] \quad (a9) \]

\[ K_{1b}^' = 10^{-9} \left[ 0.5 + 0.08 \frac{Cl}{C1} \right] \quad (a10) \]

\[ K_{2b}^' = 10^{-11} \left[ -0.3 + 0.69 \frac{Cl}{C1} \right] \quad (a11) \]

\[ \alpha = 0.051 - 0.0002Cl^{-} - 0.0007 t \quad (a12) \]
For freshwater samples, the appropriate constants were taken directly from the values reported in Riley and Skirrow rather than being derived from such empirical calculations.

IAP can be calculated from Berner's (1971) estimates of $\gamma_{Ca}$ and $\gamma_{CO_3}$ at the ionic strength of seawater (0.2 and 0.02, respectively), the relation of (Ca) to Cl, and the calculation of (CO$_3$):

\[ (Ca) = \frac{Cl}{1900} \quad (a13) \]

\[ (CO_3) = \frac{C.A. K_{2c}'}{a_H + 2K_{2c}} \quad (a14) \]

\[ IAP = \gamma_{Ca} (Ca) \gamma_{CO_3} (CO_3) \quad (a15) \]

The constant relationship between (Ca) and Cl (equation a13) does not strictly apply when some process other than evaporation or dilution by ion-free water alters the composition of seawater. The calculation of (Ca) according to that equation is subject to two small errors which tend to offset one another at Fanning. Text equations (9) and (10) have demonstrated that groundwater contributes an average of less than 0.1 mmoles/liter $\sum$CO$_2$ - and probably (Ca) - to the lagoon water. According to the discussion on p. 32, calcification has lowered $\sum$CO$_2$, and also (Ca), by about 0.2 mmoles/liter. These two effects suggest a net overestimate of (Ca) by equation (a13) of less than 0.2 mmoles/liter, or less than about 2%.

The above situation causes a small error in calculating IAP, but a far more serious potential error comes from the estimates of $\gamma_{Ca}$ and $\gamma_{CO_3}$. The activity coefficient product which we have used is 0.0040, while the product of the $\gamma_{Ca}$ and $\gamma_{CO_3}$ coefficients reported by Garrels and Thompson (1962) is 0.0048. The resultant discrepancy between IAP value derived from each of these two products is 20%. Such a discrepancy makes it particularly difficult to compare results between investigators but should not affect the internal consistency within any given study.
LITERATURE CITED


INTRODUCTION

An essential part of any synoptic ecological survey is an investigation of the dynamics of the first trophic level, the primary producers. A reasonable, if only qualitative understanding of the base of the food chain is necessary to understand the dynamics of higher trophic levels. Fanning Atoll encloses a relatively shallow, yet extremely turbid lagoon. In terms of net productivity it can be expected that planktonic algae contribute a significant amount of energy to herbivore populations. The present study was designed to describe, potentially quantitatively, but at least qualitatively, the dynamics of the phytoplankton community in Fanning Lagoon.

Light was assumed sufficient for maximal growth at least in the near-surface waters, although data from the previous expedition (Gordon, et al., 1971) indicate the possibility of light limitation below about 5 meters in turbid lagoon waters. As a first approximation, the most likely potential growth-limitants were thought to be either phosphorus or a form of fixed-nitrogen. Measurements were made of ambient concentrations of reactive phosphate and nitrate (+nitrite) as well as ammonium ion in the lagoon. The latter metabolite is the preferred source of nitrogen to phytoplankton, and its presence actively suppresses nitrate uptake (Grant et al., 1967).

Relative population size throughout the lagoon was determined by measuring plant pigment concentrations in the water column. C-14 uptake experiments were run to quantify productivity rates. The intent was to analyse the intra-lagoonal and ocean-lagoon differences on the basis of the productivity index (Cushing et al., 1958), a measure of the growth rate per unit population. The C-14 experiments were unsuccessful, and the difficulties will be discussed below. The above measurements were designed to yield information essential for future modeling attempts. However, failure of the rate measurements made this goal unattainable. Nevertheless the descriptive data on nutrient and plant pigment concentrations can be presented.

The field survey consisted of sampling two depths at each of 13 locations within the lagoon, and three depths at an ocean station approximately one-half mile offshore (Fig. 1). The parameters noted above were also measured on a six-station transect of Napa Nalaroa estuary, and nutrient determinations were made on water from a three-station transect of the estuary north of Cable Station. The nutrient content of the ground waters was ascertained by sampling 12 wells located at various locations on the island.
For comparative purposes, the lagoon was divided into three sectors. Sector 1 includes the northwestern portion of the lagoon, and the southeastern portion is termed sector 3. These two areas are nearly bisected by the deeper, clearer waters of the English Harbor area, sector 2.

METHODS

Sampling was standardized with respect to time of day (1030-1130) to reduce the variability of C-14 determinations (Doty and Oguri, 1957). Incubations were from 1200 to 1400. Near the channel at English Harbor tidal exchange is significant, and some stations were sampled at more than one tidal state as circumstances allowed. Sampling was done with a 2 liter Van Doren bottle from a small motor boat. Usually three stations of two depths each (1 and 5 m) were done on each sampling day. At each station temperature and salinity (refractometer) were noted. Sufficient water was collected from each depth to fill one 250 ml polyethylene bottle for nutrient analyses, three standard (300 ml) BOD bottles (2 light, 1 dark) for C-14 determinations, and a 3.5 liter plastic bottle which supplied 2 liters of water for pigment analyses as well as water for total carbonate alkalinity determinations. Only after all bottles had been filled, and the nutrient samples stored in an ice chest, were C-14 inoculations begun. This always took place at the last station sampled, but the stations were grouped and sampled roughly on the basis of water clarity. Thus the light regime during incubation was not thought to be significantly different from where the sample was taken. Each sample was inoculated with 5.0 \( \mu \)Ci of NaH\(^{14}\)C\(_2\) in 1.0 ml of sterile water at pH 9.5 (source: New England Nuclear Corp., Boston, Massachusetts). Incubation was at the depth from which the samples were taken. Three polypropylene lines were rigged with floats, weights, and bottle holders. The bottle holders were triangular plates of plexiglass with a semicircular notch at each corner large enough to receive the neck of a BOD bottle. Holes were drilled on either side of the notch, and a doubled piece of surgical tubing attached for securing each bottle. The line was fed through a central hole in the plates, and movable cable clamps attached to the line to keep the plates at the appropriate depths. Incubation was terminated at 1400 hours by retrieval of the bottles, and injection of 2 ml of 40\% formaldehyde solution. Upon returning to the Cable Station the nutrient samples were immediately placed in a freezer, and the C-14 and pigment samples filtered according to the method of Strickland and Parsons (1968). C-14 samples were filtered through 0.45\( \mu \) Millipore\(^R\) filters, rinsed, fumed with HCl, glued to copper planchette, and stored in a dessicator. Upon returning to Hawaii the filters were counted in a gas-flow Geiger counter ( Nuclear Chicago Model 1042 with a micromil end window and scaler). Calibrations were by the liquid scintillation method of Wolfe and Schelsky (1967).

Pigment analyses were done according to the method outlined in Strickland and Parsons (1968) with one modification. The water samples were initially filtered through Millipore\(^R\) AA filters, and extracted over night in several ml of 90\% acetone. The following day the extracted samples were refiltered through Whatman glass fiber filters, and made to a volume of 10 ml before extinction readings were taken. The Parsons and Strickland equations were used to calculate concentrations.
FIGURE 1. STATION LOCATIONS AND SECTOR BOUNDARIES IN FANNING LAGOON
<table>
<thead>
<tr>
<th>Station</th>
<th>z (m)</th>
<th>S (°/oo)</th>
<th>NO₃</th>
<th>PO₄</th>
<th>NH₄</th>
<th>Chlorophylls</th>
<th>Carot-</th>
<th>Phaeo-</th>
</tr>
</thead>
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<td></td>
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<td></td>
<td></td>
<td>a</td>
<td>b</td>
<td>c</td>
</tr>
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<td>0.13</td>
</tr>
<tr>
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<td>0.00</td>
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<tr>
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<td>0.15</td>
<td>0.22</td>
<td>0.00</td>
</tr>
<tr>
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<tr>
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</tr>
<tr>
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<td>0.92</td>
<td>0.20</td>
<td>0.57</td>
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<td>0.32</td>
<td>0.28</td>
</tr>
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<td>1.05</td>
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<td>0.06</td>
<td>0.63</td>
<td>0.64</td>
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</tr>
<tr>
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<td>0.56</td>
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<td>0.34</td>
<td>0.30</td>
</tr>
<tr>
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<td>0.30</td>
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<tr>
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<td>0.32</td>
<td>0.25</td>
<td>0.32</td>
<td>0.58</td>
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<td>0.94</td>
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<tr>
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<td>0.68</td>
</tr>
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<td>2.45</td>
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<td>0.86</td>
<td>0.31</td>
<td>0.30</td>
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</tr>
<tr>
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<td>1</td>
<td>34.5</td>
<td>1.08</td>
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<td>0.86</td>
<td>0.14</td>
<td>0.19</td>
<td>0.09</td>
</tr>
<tr>
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<td>0.46</td>
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<td>0.36</td>
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</table>
TABLE 2
SECTOR MEANS

<table>
<thead>
<tr>
<th>Sector</th>
<th>z (m)</th>
<th>Chlorophyll a (µg/l)</th>
<th>Nutrients (µg-at/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>NH₄</td>
</tr>
<tr>
<td>1</td>
<td>1</td>
<td>0.62</td>
<td>0.37</td>
</tr>
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<td>5</td>
<td>0.34</td>
<td>0.58</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>0.38</td>
<td>0.52</td>
</tr>
<tr>
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<td>5</td>
<td>0.34</td>
<td>0.24</td>
</tr>
<tr>
<td>3</td>
<td>1</td>
<td>0.23</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>0.33</td>
<td>0.48</td>
</tr>
</tbody>
</table>
To avoid wasting time and reagents the nutrient determinations were made after a sufficient number of samples had accumulated in the freezer (3 or 4 days). Reactive nitrate+nitrite nitrogen, and reactive phosphate phosphorus were determined by the methods of Strickland and Parsons (1968). Ammonia was determined by the phenolhypochlorite method of Solorzano (1969).

All extinction readings were taken using 1-cm path length cuvettes since the Beckman Model DU spectrophotometer could not accommodate larger path length cells.

RESULTS

The nutrient and pigment data for the lagoon and ocean stations were summarized in Table 1. Phosphate concentrations were low and relatively uniform throughout the lagoon and at the ocean station (taken on a strong rising tide). The mean concentration at 1 m was 0.21 μg-at/l, and at 5 m, 0.26 μg-at/l. The mean of the three samples taken at the ocean station was 0.25 μg-at/l. Although phosphate concentrations were generally low, phosphate was always detectable, and thus apparently non-limiting (Fuhs, 1969) at all stations sampled. The lowest concentrations encountered were in surface waters of the northwest portion of sector 1. This was, conversely, the area of highest pigment concentrations in the lagoon. The highest phosphate concentration in the surface waters was found in station 5 near North Pass. Generally there was rather insignificant variation in phosphate concentration with depth, however where circulation of deeper water was restricted by line reefs, for example in Suez Pond (station 22), there were slightly higher concentrations at depth. Sector 1 had generally higher phosphate concentrations than did the remainder of the lagoon (Table 2).

Nitrate concentrations were much higher and more variable than phosphate concentrations. The means at 1 and 5 m respectively were 1.23 and 1.61 μg-at/l. The ocean station mean was 1.17 μg-at/l. The ranges for the 1 and 5 m samples respectively were 0.05 to 2.86, and 0.92 to 2.45 μg-at/l. As with phosphate concentrations, the lowest surface nitrate concentrations are found in the northwestern corner of the lagoon (Sector 1), and the highest surface concentrations in the southeastern portion (Sector 3). There appears, however, to be abundant nitrate available for growth at all stations. Nitrate accumulation in older, deeper water is more pronounced than that of phosphate; for instance at station 22 the concentration at 1 m was 0.20 μg-at/l, while at 5 m it was 2.45 μg-at/l. Concentrations generally increased southward toward Rapa Pass.

Ammonia is the preferred source of nitrogen to phytoplankton. Ammonia determinations were made to augment nitrate data in the event that fixed-nitrogen limitation was suspected. The nitrate concentrations observed make this unlikely, and it appears that nitrate is abundant in all areas of the lagoon. Since ammonia is taken up very rapidly by phytoplankton, and excreted by many organisms, its distribution in space and time over a short survey period would be expected to yield less information than a nutrient with a longer turnover time. Ammonia concentrations observed in Fanning
Lagoon were variable, but the means of the 1- and 5-m samples were identical at 0.41 μg-at/l.

Chlorophyll a concentrations in the lagoon were significantly higher than those measured at the ocean station. The 1- and 5-m means were 0.39 and 0.34 mg/m³ respectively. Concentrations were generally higher in sector 1 than in the remainder of the lagoon. In sector 1 concentrations were higher at 1 m than at 5 m, but the reverse occurred in sector 3. Accessory chlorophylls and carotenoids were generally higher in the surface waters of areas with more restricted circulation. Large quantities of phaeopigments were found at stations 20 and 21 (Fig. 1). Growth rates in this area of the lagoon are presumably slow, but the relative isolation of this water permits a large population to accumulate, and the water is visually discolored.

The estuary samples were characterized by very low nitrate concentrations, but phosphate and ammonia were abundant (Table 3). The estuaries may thus be a significant supplementary source of phosphate to the lagoon.

Well samples, taken to assess the nutrient load in ground waters of the atoll, showed nutrient characteristics that were quite different from those of the estuaries (Table 4). Evidence of sewage contamination was unmistakable in wells near occupied villages. Nitrate concentrations exceeding 100 μg-at/l were found in four wells in the English Harbor village. Isolated wells had nutrient concentrations more like those found in lagoon waters. Phosphate concentrations in these wells were nearly identical with lagoon waters, but nitrate concentrations were higher. If these data reflect the nature of the ground waters, and are not artifacts due to the wells themselves, these waters could represent a supplementary nitrate input to the lagoon. Ammonia concentrations were also relatively high in the isolated wells.

The C-14 experiments, as mentioned, were unsuccessful. Dark counts varied from several hundred per minute to over 16,000 per minute. Light bottles showed nearly the same range of variation, and were frequently lower than the respective dark-bottle count. Even so this should have allowed relative comparisons to be made from the light counts alone, but the two light bottles from each depth rarely replicated well. The author has never encountered this problem working in Hawaiian waters, but one series of experiments conducted on Christmas Island resulted in dark counts which exceeded light counts. The procedure usually followed was modified for this expedition in two ways: Fanning Lagoon was known to have large quantities of suspended carbonate in the water, and the acid treatment recommended by Strickland and Parsons (1968) was employed. Acid treatment may well have been ineffectual in this extreme environment. The other modification was the addition of formaldehyde to terminate incubation. When working on board ship or close to a lab this can be avoided, but in this survey logistics dictated that filtration of the samples be delayed for about two hours after incubation was completed. Although all apparatus was thoroughly acid-washed after each set of experiments, there may have been a residual toxic effect of some kind. The erratic replication of the light bottles suggest a third possible source of error. Morris et al. (1971) in experiments with ampoules
<table>
<thead>
<tr>
<th>Station</th>
<th>z (m)</th>
<th>S (°/oo)</th>
<th>Nutrients (µg-at/l)</th>
<th>Pigments (µg/l)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>NO₃  PO₄  NH₄</td>
<td>Chlorophylls a</td>
</tr>
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<td>1.86  1.50  1.28</td>
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<tr>
<td>N2</td>
<td>0</td>
<td>4.66</td>
<td>0.30  2.63  1.46</td>
<td>0.75  1.10  0.00</td>
</tr>
<tr>
<td>N3</td>
<td>0</td>
<td>4.85</td>
<td>0.00  1.93  1.23</td>
<td>0.58  0.81  0.37</td>
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<tr>
<td>N4</td>
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<td>20.99</td>
<td>0.00  0.64  0.69</td>
<td>0.49  0.94  1.43</td>
</tr>
<tr>
<td>N5</td>
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<td>25.60</td>
<td>0.00  0.79  0.92</td>
<td>1.01  1.28  2.48</td>
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<tr>
<td>N6</td>
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<td>0.73  0.71  1.45</td>
</tr>
<tr>
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<td></td>
<td>0.23  1.19  1.69</td>
<td></td>
</tr>
<tr>
<td>E2</td>
<td>0</td>
<td></td>
<td>0.25  0.99  1.08</td>
<td></td>
</tr>
<tr>
<td>E3</td>
<td>0</td>
<td></td>
<td>0.20  0.69  0.92</td>
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</tr>
<tr>
<td>Location of Well</td>
<td>Approx. Depth to Bottom (m)</td>
<td>Nutrients (µg-at/l)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>------------------------------------------------------</td>
<td>----------------------------</td>
<td>--------------------</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Near Copra shed, English Harbor</td>
<td>1</td>
<td>PO₄ 64.88 NO₃ 1.20 NH₄ 0.13</td>
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<td></td>
</tr>
<tr>
<td>North end, English Harbor</td>
<td>2</td>
<td>PO₄ 118.92 NO₃ 2.35 NH₄ 0.94</td>
<td></td>
<td></td>
</tr>
<tr>
<td>West of drying shed, English Harbor</td>
<td>2</td>
<td>PO₄ 117.14 NO₃ 0.90 NH₄ 0.63</td>
<td></td>
<td></td>
</tr>
<tr>
<td>South of Protestant Church, English Harbor</td>
<td>2</td>
<td>PO₄ 117.14 NO₃ 5.10 NH₄ 1.07</td>
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<td></td>
</tr>
<tr>
<td>Near Post Office, English Harbor</td>
<td>2</td>
<td>PO₄ 130.48 NO₃ 0.60 NH₄ 0.31</td>
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<td></td>
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<tr>
<td>Three miles south of village (near bridge)</td>
<td>3</td>
<td>PO₄ 3.22 NO₃ 0.10 NH₄ 0.88</td>
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<td></td>
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<tr>
<td>Village near North Pass</td>
<td>1</td>
<td>PO₄ 7.94 NO₃ 0.25 NH₄ 4.84</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Village between Cable Station and dock</td>
<td>2</td>
<td>PO₄ 25.85 NO₃ 0.45 NH₄ 2.78</td>
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<td></td>
</tr>
<tr>
<td>Next to cistern at Cable Station</td>
<td>3</td>
<td>PO₄ 4.02 NO₃ 0.79 NH₄ 2.94</td>
<td></td>
<td></td>
</tr>
<tr>
<td>(being pumped for toilets)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Front of Kam Chou's house, Cable Station</td>
<td>3</td>
<td>PO₄ 3.50 NO₃ 0.74 NH₄ 0.95</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Galley tap, Cable Station</td>
<td>-</td>
<td>PO₄ 6.73 NO₃ 0.05 NH₄ 0.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Manager's house tap, Cable Station</td>
<td>-</td>
<td>PO₄ 6.00 NO₃ 0.05 NH₄ 0.00</td>
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<td></td>
</tr>
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</table>
purchased from the same source reported significant amounts of labeled organics in their solutions. They instituted zero-time blanks, and found errors as large as 1500 cts/min. Similar experiments have since been run in our laboratory using ampoules from the same shipment used in this survey, and zero-time blanks as large as 5787 cts/min were found (P. Lambertson, personal communication). Future expeditions would be well advised to include among the apparatus a portable geiger counter to monitor results in the field, and permit the necessary modifications in methods to be made.

DISCUSSION

The lack of rate measurements makes a discussion of the dynamics of the phytoplankton in the lagoon impossible. Comparisons based on standing crop determinations are not likely to be valid because of variations in growth rates in different areas. The conclusions of the present study are thus entirely descriptive.

The highest concentrations of Chlorophyll a were found in the surface waters of sector 1. These were also the waters with the highest phosphate concentrations, and the lowest nitrate concentrations. This sector seems to receive substantial amounts of phosphate from the estuaries which drain into it. The phosphate does not accumulate, but is rapidly utilized with the simultaneous reduction of the residual nitrate in the water column. High concentrations of ammonia are typically found in the deeper waters in this sector, perhaps indicating high biological activity. Offshore areas of this sector are more akin to waters of the other two sectors.

Sector 2 opens directly to the ocean through English Harbor, but the effect of tidal exchange is not as marked as one would expect. Values for all parameters are similar to those in the other two sectors. Chlorophyll a concentrations are slightly higher at 1 m than at 5 m, while nitrate and phosphate concentrations are slightly lower. Ammonia is relatively high at the surface, but reaches the lowest recorded values at 5 m.

Sector 3 has the most sluggish water circulation, and the longest residence times of the three sectors. Chlorophyll a is higher at 5 m than at 1 m, perhaps because of the high light intensities near the surface. Nutrient concentrations are essentially constant with depth, but there is a trend of increasing nitrate concentrations from north to south in this sector.

From the available data several conclusions may be drawn. Plant pigment concentrations within the lagoon are much higher than in the surrounding ocean. Nutrient concentrations, however, are not radically different in the two environments. Fixed-nitrogen is abundant, and may be accumulating in older waters. Ground waters may be an important source of this essential element. The primary supplementary source of phosphate on the other hand, seems to be estuarine waters.
LITERATURE CITED


The 29 species of algae reported by DeWreede and Doty (1970), collected during the first University of Hawaii expedition to Fanning Atoll (January 4-16, 1970), represents the only algal listing for the atoll. During the second expedition (July 20-August 19, 1972) to this atoll, 69 additional species were found by Mr. Russell and the senior author in collections obtained from 79 stations located throughout the lagoon and on the seaward reefs (Fig. 1). Four species were found only in the guts of herbivorous fishes.

The purpose of this paper is to provide a checklist of all the algal species thus far known from Fanning Atoll. The listing consists of 98 species in four Divisions representing: Cyanophyta (10), Chlorophyta (39), Phaeophyta (7), and Rhodophyta (42).

Analysis of species composition indicates that the Fanning Atoll flora is by no means unique but rather conforms to a general phytogeographic pattern in which the number of species becomes reduced or simplified as one moves eastward across the tropical Pacific Ocean. We feel that our collections represent approximately 70 to 80 percent of the total number of species present on this atoll.

The immature condition of some algal specimens and/or the lack of adequate monographs prevent us from attaching a specific epithet to some of the entities, especially algae in the Division Rhodophyta. Workers interested in the descriptive aspects of the latter should consult the keys, descriptions, and illustrations of Taylor (1950), Dawson (1954, 1956, 1957), and Trono (1968, 1969). Voucher specimens cited are deposited in the University of Guam Herbarium. Species reported by DeWreede and Doty (1970) are preceded by an asterisk.
DIVISION CYANOPHYTA
(blue-green algae)

Order Chroococcales

*Agmenellum thermale* (Kütz.) Dr. & Daily - Found in gut of *Acanthurus triostegus* (Linnaeus).

*Anacystis dimidiata* Dr. & Daily - RT 4508b.

*Entophysalis conferta* (Kütz.) Dr. & Daily - RT 4603.

*Entophysalis deusta* Dr. & Daily - RT 4536d.

Order Oscillatoriales

*Calothrix confervicola* (Roth) Ag. - RT 4536.

*Calothrix pilosa* B. & Fl. - Found in gut of *Ctenochaetus strigosus* Bennett.

*Hormothamnion solutum* B. & Fl. - Found in gut of *Abudefduf sordidus* (Forsskal).

*Microcoleus lyngbyaceus* (Kütz.) Crouan - RT 4539, RT 4602, RT 4615.

*Schizothrix calcicola* (Ag.) Gomont - RT 4516c, RT 4595.

*Schizothrix mexicana* Gomont - RT 4521f.

DIVISION CHLOROPHYTA
(green algae)

Order Ulotrichales

*Enteromorpha lingulata* J. Ag. - RT 4516d, RT 4569.

*Ulva fasciata* Delile - RT 4612.

Order Cladophorales

*Chaetomorpha indica* Kütz. - RT 4623b.

*Cladophora socialis* Kütz. - RT 4538, RT 4568, RT 4616e.

*Cladophora* sp. 1 - RT 4517.

*Cladophora* sp. 2 - RT 4594.
Fig. 1. Map of Fanning Atoll, showing collecting stations during July-August, 1972.
Cladophora sp. 3 - RT 4622.

Cladophora sp. 4 - RT 4623a.

Chaetophoraceae - RT 4583 (unidentified boring alga).

Order Siphonales

* Avrainvillea lacerata J. Ag. - RT 4495, RT 4646b.

* Bryopsis pennata Lamx. - RT 4560.

Bryopsis hypnoides Lamx. - RT 4643.

Caulerpa ambiguа Okamura - RT 4644.

Caulerpa fastigiata Montagne - RT 4651.

* Caulerpa racemosa (Forssk.) W. v. Bosse = C. peltata Lamx. - RT 4497, RT 4613.

* Caulerpa urvilleiana Montagne - RT 4531.

Caulerpa webbiana Montagne - RT 4591, RT 4617.

* Codium edule Silva - Reported by DeWreede and Doty (1970).

Derbesia attenuata Dawson - RT 4634.

Halimeda bikinensis Taylor - RT 4597, RT 4637.

Halimeda discoidea Decaisne - RT 4609, RT 4624.

* Halimeda fragilis Taylor - RT 4608, RT 4641.

Halimeda gracilis Harvey - RT 4540.

Halimeda incrassata (Ellis) Lamx. - RT 4515.


Halimeda sp. - RT 4616, RT 4640 (possibly a new species).

Ostreobium reineckei Bornet - RT 4506.

Rhipidiphyllon reticulatum Askenasy - RT 4618.

Order Siphonocladales

* Boodlea composita (Harvey) Brand - Reported by DeWreede and Doty (1970).
Boodlea vanbosseae Reinbold - RT 4579.
Cladophoropsis gracillima Dawson - RT 4599.
Cladophoropsis luxurians Gilbert - RT 4632.
Cladophoropsis sundanensis Reinbold - RT 4558, RT 4590.
* Dictyosphaeria cavernosa (Forsskal) Boerg. - RT 4494, RT 4637.
* Dictyosphaeria versluysii W. v. Bosse - RT 4530.
Valonia aegagropila C. Ag. - RT 4542.

Order Dasycladales

Acetabularia clavata Yamada - RT 4566.
Acetabularia moebii Solms-Laubach - RT 4555.
Neomeris vanbosseae Howe - RT 4598.

DIVISION PHAEOPHYTA
(brown algae)

Order Ectocarpales

Ectocarpus breviarticulatus J. Ag. - RT 4566.
* Feldmannia indica (Sonder) Womersley & Bailey - RT 4525b.

Order Sphacelariales

Sphacelaria carolinensis Trono - Found in gut of Arothon hispidus (Lacepede).

Sphacelaria tribuloides Meneghini - RT 4565.

Order Dictyotales

* Dictyota friabilis Setchell - RT 4548.
* Lobophora variegata (Lamx.) Womersley - RT 4496.

Order Fucales

* Turbinaria ornata (Turn.) J. Ag. - RT 4525a.
DIVISION RHODOPHYTA (red algae)

Order Goniotrichales

Goniotrichum elegans (Chauvin) Zanardini - RT 4545i.

Order Bangiales

Bangia fuscopurpurea (Dillw.) Lyngb. - RT 4545e.

Order Nemalionales

Acrochaetium sp. - RT 4614.

Order Gelidiales

Gelidiella myriocladia (Boerg.) Feldmann - RT 4575.
Gelidiella tenuissima Feldmann & Hamel - RT 4616d, RT 4636.
Gelidium pulchellum (Turn.) Kütz. - RT 4533, RT 4572.

* Gelidium pusillum (Stackhouse) Le Jolis - Reported by DeWreede and Doty (1970).

Wurdemannia sp. - RT 4541.

Order Cryptonemiales

Fosliella farinosa (Lamx.) Howe - RT 4514.

* Jania capillacea Harvey - RT 4501, RT 4616h, RT 4636.

* Jania natalensis Harvey - RT 4573, RT 4616f.

* Peysonnelia rubra (Grev.) J. Ag. - RT 4626.

* Porolithon gardineri (Foslie) Foslie - RT 4534, RT 4579c, RT 4616h.

Porolithon onkodes (Heydrich) Foslie - RT 4505.

Order Gigartinales

Gelidiopsis intricata (Ag.) Vickers - RT 4582.
Gracilaria cf. lichenoides (L.) Harvey - RT 4616g.

* Gracilaria sp. - Reported by DeWreede and Doty (1970).

Hypnea cervicornis J. Ag. - RT 4506, RT 4524h, RT 4563.

Hypnea japonica Tanaka - RT 4515b.

Hypnea nidulans Setchell - RT 4562.

Hypnea cf. pannosa J. Ag. - RT 4600, RT 4611.

* Hypnea sp. - Reported by DeWreede and Doty (1970).

Order Rhodymeniales

Rhodymenia sp. - RT 4620.

Order Ceramiales

Callithamnion sp. 1 - RT 4598, RT 4625.

Callithamnion sp. 2 - RT 4628.

Centroceras apiculatum Yamada - RT 4630.

Centroceras clavulatum (C. Ag.) Montagne - RT 4570, RT 4635.

Ceramiella huysmansii Boerg. - RT 4645.

Ceramium gracillimum Griffiths & Harvey - RT 4605.

Ceramium mazatlanense Dawson - RT 4580, RT 4581a, RT 4582b.

Chondria repens Boerg. - RT 4616a, RT 4629.

Chondria sp. - RT 4588.

Griffithsia ovalis Harvey - RT 4565.

Griffithsia tenuis C. Ag. - RT 4638c.

* Laurencia surculigera Tseng - RT 4610.

Herposiphonia parca Setchell - RT 4616c.

Polysiphonia howei Hollenberg - RT 4503, RT 4596, RT 4633.

* Polysiphonia scopulorum Harvey - RT 4512.
Polysiphonia sphaerocarpa Boerg. - RT 4516b.

* Polysiphonia sp. - Reported by DeWreede and Doty (1970).

Wrangelia argus (Mont.) Montagne - RT 4638d.

LITERATURE CITED


FUNCTIONAL GROUP ANALYSIS OF THE MARINE BENTHIC ALGAE

IN FANNING LAGOON, LINE ISLANDS

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Past investigations on marine benthic algae of Pacific atolls have mainly focused on floristic aspects of their distribution (Tsuda, 1966). Few studies include descriptions of algal communities associated with atolls. Doty and Morrison (1954) provide a general description of algal communities on shallow reef flats of Rarotia Atoll. Ecological observations reported by Gilmartin (1960) in Eniwetok Lagoon provide information on algal communities of the lower subtidal zone. DeWreede and Doty (1970) describe algal communities observed at 12 collecting stations on Fanning Atoll.

Another method of describing the marine floral community of an atoll is functional group analysis (IDOE-CITRE proposal, 1972) where floristic elements are compartmentalized with respect to their secondary roles in the ecosystem. Primary production is assumed to be the primary role of all photosynthetic organisms; secondary roles define functional groups. Eight functional groups of algae (Table 1) are recognized in Fanning Lagoon based on the species observed in the lagoon during July and August, 1972 (Tsuda, p. 69, this report). An alga can belong to more than one functional group, e.g., Calothrix as a potential nitrogen fixer and also as a food organism in the turf.

The purpose of this paper is to describe the marine algae of Fanning Lagoon, as functional groups in the lagoon ecosystem. This method of characterizing the benthic flora is still very much descriptive, but provides an additional means of assessing the uniqueness and importance of certain floral components in the lagoon.

FLESHY MACROALGAE -- The primary reason for reports (Bakus, 1964; DeWreede and Doty, 1970) of the depauperate nature of the marine flora on Fanning is the relative absence of fleshy benthic algae which predominate on reef flats of high islands and, especially, in temperate regions. Only six genera of algae appear large enough to provide adequate shelter for reef macro-organisms.

Turbinaria ornata (Turn.) J. Ag. is by far the largest (up to a meter high) and most dominant alga in the lagoon. Its distribution and factors associated with its distribution are described by Russell (see p. 75, this report). As suggested by Russell, the most important factors which seem to restrict the growth of this alga are the availability of substrata and the absence of rapid water movement in the northern and southwestern sides of
Table 1. Characteristics of functional groups recognized in Fanning Lagoon.

<table>
<thead>
<tr>
<th>FUNCTIONAL GROUPS</th>
<th>ALGAL GENERA</th>
<th>CHARACTERISTICS</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. Fleshy Macroalgae</td>
<td>Turbinaria, Avrainvillea, Caulerpa, Dictyosphaeria, Valonia, Codium</td>
<td>Fleshy erect algae, usually over 5 cm high, which provide shelter or substratum for other reef organisms.</td>
</tr>
<tr>
<td>2. Turf Algae</td>
<td>Polysiphonia, Gelidiella, Hypnea, Cladophora, Enteromorpha, Laurencia, Sphacelaria, Schizothrix, Microcoleus, etc.</td>
<td>Erect or prostrate algae less than 5 cm high which serve as food source for the majority of herbivores.</td>
</tr>
<tr>
<td>3. Crustose Coralline Algae</td>
<td>Porolithon, Peysonnelia</td>
<td>Calcareous algae important in forming and cementing reef framework through their CaCO₃ production.</td>
</tr>
<tr>
<td>4. Carbonate-Producing Algae</td>
<td>Halimeda, Jania, Porolithon, Peysonnelia, Fosliella, Neomeris</td>
<td>Articulate and crustose coralline algae which contribute to carbonate sediments.</td>
</tr>
<tr>
<td>5. Boring Algae</td>
<td>Ostreobium, unidentified Chaetophoraceae</td>
<td>Filamentous and siphonaceous Chlorophyta which inhabit the carbonate matrix of the reef and contribute to reef degradation.</td>
</tr>
<tr>
<td>7. Nitrogen-Fixing Algae</td>
<td>Calothrix, Hormothamnion</td>
<td>Heterocystous Cyanophyta which are hypothetically important in nutrient cycling.</td>
</tr>
<tr>
<td>8. Microalgae</td>
<td>Agmenellum, Anacystis, Entophysalis</td>
<td>Unicellular forms (usually blue-green, diatoms and flagellates) found in sediment and surface film used as food source for herbivores.</td>
</tr>
</tbody>
</table>
the lagoon. There seems to be no seasonality in this species since thalli at all stages of growth are present.

Avrainvillea lacerata J. Ag. shows a spotty distribution in that this alga is most common in the shallow pass areas of North Pass and Rapa Pass.

The remaining four genera, Dictyosphaeria, Caulerpa, Codium, and Valonia, are rather scarce in the lagoon. Stands of Dictyosphaeria cavernosa (Forsskal) Boerg. and Caulerpa urvilliana Montagne are abundant, however, at isolated sites on the seaward reef flat and reef slope.

In addition to the role of providing shelter, fleshy macroalgae also provide a substrate on which epiphytes occur. Approximately 25 species of benthic algae were found epiphytic on these larger macroalgae in Fanning lagoon.

TURF ALGAE -- Although 40 of the 56 algal genera now known from Fanning Lagoon can be considered as belonging to this category, most of the genera are rare and in most cases occur as epiphytes. The sandy substratum, which makes up about 40 percent of the lagoon area (based on values obtained using the point method within a 25x25 cm quadrat), possesses two distinct types of turf communities: a Schizothrix calcicola (Ag.) Gomont - Microcoleus lyngbyaceus (Kütz.) Crouan community along the shore, away from the passes, where water movement is minimal; and a Polysiphonia spp. - Enteromorpha lingulata J. Ag. - Hypnea spp. community near the passes where some water movement is present. Isolated stands of Cladophora are also present near shore.

Dead coral and coral rubble substrata make up about 30 percent of the lagoon area and afford habitats for several of the turf-like algae. The Polysiphonia spp. - Gelidiella spp. community is by far the most dominant on the patch reefs, regardless of depth. Another distinct association is the Acetabularia clavata Yamada - Sphacelaria tribuloides Meneghini community restricted to the murky waters along the shore near English Harbor.

CRUSTOSE CORALLINE ALGAE -- This group of algae attains its greatest growth on the windward (northeast) seaward reef of the atoll. Therefore, it is not surprising to find representatives of this group near North Pass and Rapa Pass. Parolithon onkodes (Heydrich) Foslie is commonly found encrusting coral rubble in these areas. A luxuriant coralline algal patch reef is present near North Pass. It is difficult to assess the importance of this group of algae in a lagoon environment because the major growth of these algae is in the pass areas which are transition zones between the oceanic environment and the lagoon proper.

CARBONATE-PRODUCING ALGAE -- The relative lack of Halimeda, as noted by Roy and Smith (1971), contrasts this atoll with atolls in the Micronesian region where this alga is abundant and constitutes a major component of the carbonate sediments. Only one stand of Halimeda incrassata (Ellis) Lamx. was found in the lagoon, growing on a patch reef in sandy substratum off the Cable Station. Visual examination of sand particles from various
locations in the lagoon seems to confirm the relative absence of this genus in the lagoon. *Jania natalensis* Harvey is the only articulate carbonate producer which can be considered common in the lagoon. However, its occurrence is restricted in the pass areas, especially at Rapa.

Crustose coralline algae probably contribute more to calcium carbonate sediments in Fanning Lagoon than do articulate coralline algae. However, the overall role of the Fanning algae as contributors to sediments is minimal.

**BORING ALGAE** -- This little known group of algae apparently plays an insignificant role in the degradation of reef structure in the Fanning Lagoon. The only boring algae observed at Fanning were *Ostreobium reinekei* Bornet and an unidentified member of the Chaetophoraceae. Both were restricted to the seaward reef slope.

**SAND-BINDING ALGAE** -- *Microcoleus lyngbyaceus* (Kütz.) Crouan and *Schizothrix calcicola* (Ag.) Gomont are two algae which can function in binding sand grains together. The importance of this group in the marine environment would appear to be minimal because they occur in areas of little current action where the calcium carbonate sediments are already in a compact state. These two species show their maximum functional importance in low-lying wet areas, near estuaries, where they consolidate the substratum; thus, these areas have been used as landing strips for light planes.

**NITROGEN-FIXING ALGAE** -- Whereas heterocystous blue-green algae are plentiful on certain reefs in Micronesia, this group is almost absent in the lagoon of Fanning Atoll and on the seaward reefs. A single collection of *Calothrix confervicola* (Roth) Ag. was made during the month-long study on the atoll and it consisted merely of a few epiphytic filaments. About two filaments of *Hormothamnion solutum* B. & Fl. were found in the gut of *Abudefduf sordidus* (Forsskal). If the hypothesis of Johannes *et al.* (1972) on the role of heterocystous blue-greens as important nitrogen fixers on reefs is correct, their role at Fanning is unimportant simply because of the relative absence of this group.

**MICROALGAE** -- Observations on microalgae were not made during my stay on Fanning. It is probable, however, that this group represents an important food source for selective fishes and micro-organisms.

**CONCLUSIONS**

When one considers species diversity in the context of functional groups, the roles of the algae in Fanning Lagoon can be understood. Obviously, the dominant functional group of algae in the lagoon is the turf community which serves as the primary food source for herbivores. This community also provides habitats for micro-organisms. Macroalgae as shelters for larger reef animals, e.g., fishes and invertebrates, play a major role but only in restricted areas of the lagoon. Crustose and articulate coralline algae seem to play a minor role in the lagoon, either
as reef builders or as calcium carbonate producers. The role of algae in reef degradation, nitrogen fixation and sand binding appears negligible in Fanning Lagoon.

This method of compartmentalizing the marine flora into functional groups is only the first step toward understanding their role in the lagoon ecosystem. The next step, and by far the most difficult, is to characterize and quantify the external driving forces and their respective flow rates for each group.

LITERATURE CITED


THE DISTRIBUTION OF TURBINARIA ORNATA (TURN.) J. AG.

IN FANNING ATOLL LAGOON

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A variety of algae grow within the Fanning Atoll lagoon (Tsuda et al., see p. 61, this report) but only one large brown alga, Turbinaria ornata (Turn.) Ag. is found there. Although Turbinaria occurs on many Pacific atolls (Taylor, 1963, 1966), its distribution within an atoll lagoon has seldom been investigated. Rhyne (1971) noted the most abundant growth of Turbinaria conoides was near the southeastern lagoon shore of Diego Garcia, Chagos Archipelago, in the western Indian Ocean, but in other portions of the lagoon the thalli were stunted, dwarfed, or absent. Similar observations of Turbinaria ornata in the northwestern portion of Fanning Atoll were made by Bakus (1964), and DeWreede and Doty (1970) suggested causative factors for greater Turbinaria growth on the windward margin of one patch reef within the lagoon.

A study of Turbinaria ornata in the lagoon of Fanning Atoll was made with three objectives in mind: (1) to attempt to detect patterns of Turbinaria distribution within the lagoon; (2) to detect areas of "good" and "poor" growth; and (3) to detect environmental factors which may be associated with the observed distribution.

METHODS

Aerial inspection of the atoll was conducted, using a Piper Aztec flown by Dr. M. Vitousek, to observe patterns of substratum distribution. Close inspection of each reef passed by boat was made to interpret the aerial observations and to determine the presence or absence of Turbinaria. A search pattern radiating from the cable station was also conducted by boat and the distribution of the alga toward the center of the lagoon traced and recorded. Special effort was made to investigate the more remote portions of the lagoon.

Selected samples of Turbinaria were picked in the northern portion of the lagoon where Turbinaria grew well and in other areas where it was abundant but not so large. Samples were obtained by picking all thalli

*Support from U. S. Department of Commerce, NOAA Office of Sea Grant, grant no. 2-35243 and NSF grant GA 313111, is gratefully acknowledged.
within a 46-cm diameter stainless steel ring placed around the largest
individual Turbinaria thalli on the reef. Thalli were measured, sun dried,
and weighed. Voucher specimens are deposited in the herbarium of the
author (University of Hawaii, Honolulu, Hawaii).

Four sites were selected for a detailed study of the environmental
factors that might enhance or limit the growth of Turbinaria. Each site
remained submerged at lower low water and was located in the northwestern
portion of the lagoon. All contained sufficient solid calcium carbonate
substrata suitable for Turbinaria attachment, but differed in how well
Turbinaria grew, distance from the shore, and water clarity.

Measurement of water movement was made using calcium sulfate clod cards
(Doty, 1971) attached to wooden stakes or pieces of roofing tile. The
dissolution of calcium sulfate and consequent field weight loss was compared
to weight loss in still water and converted into a diffusion factor (DF)
representing the degree to which diffusion or dissolution was enhanced by
water movement during a 24-hour period.

Intervenient sites were provided by fir stakes 110 X 7.5 X 1.3 cm
driven into the bottom, with a 75 X 7.5 X 1.3 cm movable cross member
attached horizontally to them. The cross member was held securely in place
by a "C" clamp. Four plastic clod cards were stapled upon the cross member
and a maximum-minimum thermometer (see Doty and Russell, p. 85, this
report) suspended below it by rubber bands. The cross members were adjusted
to about 1.0 to 2.0 cm below lower low water level. The stakes were placed
at various intervals at sites A and C while only one stake was used at
North Pass. The values obtained from the clods on stakes were compared
with the values obtained from clods placed on the bottom. The latter were
taped to pieces of roofing tile for anchorage. No stakes were used at Site
B. Depth measurements were recorded at each clod location using a premarked
stake. The depths were later corrected to lower low water values.

Site A was an area containing large Turbinaria thalli, located 2
kilometers northeast of the Cable Station, about 400 meters south of the
northern copra camp and about 200 meters east of "Q" marker (the northern-
most channel marker in the lagoon used by the copra workers) (Fig. 2).
Turbinaria was growing in patches on the solid calcium carbonate bottom and
on mounds of calcium carbonate surrounded by silt-free sand in clear water.
Three stakes were placed 7.0 meters from each other in a line perpendicular
(southeast) to the shore and another stake placed 7.0 meters southwest of
the center stake. Tiles with clods attached were placed on rocks adjacent
to each clod stake. Thalli were removed from the rocks to prevent
obstruction of water movement and/or abrasion by the algae. Maximum-
minimum thermometers were attached to the innermost and outermost cold
stakes. No storms passed during the period of observation.

Site B was an area containing small Turbinaria thalli, formerly studied
by DeWreede and Doty (1970). It was located 1.25 kilometers southeast of
the cable station adjacent to "Suez Canal", a man-made boat passage
traversing the northwestern line reef of Suez Pond (Figs. 1 and 2). Here,
Turbinaria was growing on solid calcium carbonate substrata along the margin
of the 20-meter-wide reef in murky water. No stakes or thermometers were
FIG. 1. Fanning Atoll lagoon. Arrows indicate the darker edges of coarse material along the line reefs. Sites B and C within Suez Pond are indicated and English Harbor (EH) is in the background. The large dark irregular shadow in the lower right corner was caused by a cloud.
Fig. 2. Distribution of *Turbinaria ornata* within Fanning Atoll lagoon.
placed at this site. Tiles with clods attached were placed at 3.0-meter intervals in an "I" formation similar to the one used by DeWreede and Doty (1970). Three pairs of clods were also placed in the boat channel and one pair on the southwestern bank. Storms prevailed during the period of this investigation.

Site C was an area with no Turbinaria located within the northern portion of Suez Pond 0.5 kilometers northeast of "Suez Pond" (Figs. 1 and 2). Several large calcium carbonate mounds were present on this sandy patch reef and much Acropora rubble and large dead Porites heads lay along the southeastern edge in murky water. Five stakes were placed along an east-west line extending the length of the patch reef. Two were placed near the center, one at each end of the reef and one in the sand about 5.0 meters beyond the eastern edge. A sixth stake was placed about 10 meters north of the center stake. Tiles with clods attached were placed at 5.0-meter intervals perpendicular to the east-west line of clod stakes until a grid of twenty locations had been covered. Maximum-minimum thermometers were attached to the two easternmost stakes. Current direction and rate were detected by observing the movements of seven submerged plastic gallon bottles as they passed over the reef. Investigations at Sites B and C were conducted during the same 24-hour period.

A fourth site was located at North Pass in mid-channel at the second stake used in a separate investigation (See p. 85, this report). Turbinaria was growing on large calcium carbonate stones and mounds in clear water. One maximum-minimum thermometer was attached to the stake.

RESULTS

Turbinaria ornata is not distributed evenly throughout the lagoon. It is most abundant in the northwestern sector of the lagoon (Fig. 2), but is absent from the central portion of the lagoon and only infrequently encountered along the shoreline south and east of English Harbor. It occurs in a large area near Teharoa Iti, but few thalli were encountered at Rapa Pass.

The largest dry-weight values of Turbinaria (1983 gms/m²) were encountered at Site A southwest of North Pass (Table 1). Similar large dry-weight values were obtained at North Pass (up to 1313 gms/m²) and in one small area on the northeastern edge of the entrance to Rapa Pass (811 gms/m²). This latter area is adjacent to high concentrations of alcyonarian corals that covered most of the solid calcium carbonate rock bottom. Only 15 mm tall Turbinaria thalli were growing on the few large rocks exposed amidst the soft corals.

Patches of Turbinaria in densities of 379 gms/m² were growing near Fenua Urn on solid calcium carbonate pavement in murky water, but were absent from similar seemingly suitable substrata away from shore. Similar distribution patterns were seen at Taru Fefe, Vai Tepu and Puta Tutae. All were in murky water.
Table 1
Weights and Sizes of *Turbinaria ornata* within the Lagoon of Fanning Atoll

<table>
<thead>
<tr>
<th>Location</th>
<th>Dry Weight (gms/m²)</th>
<th>Maximum Thallus Height (mm)</th>
<th>Water Clarity</th>
<th>Lower Low Water mm Above Bottom</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site A</td>
<td>1983</td>
<td>320</td>
<td>clear</td>
<td>300</td>
</tr>
<tr>
<td>Site B</td>
<td>191*</td>
<td>---</td>
<td>murky</td>
<td>---</td>
</tr>
<tr>
<td>North Pass (moat)</td>
<td>1313</td>
<td>300</td>
<td>clear</td>
<td>500</td>
</tr>
<tr>
<td>North Pass</td>
<td>828</td>
<td>350</td>
<td>clear</td>
<td>1000</td>
</tr>
<tr>
<td>North of Mataua Pt.</td>
<td>607</td>
<td>150</td>
<td>clear</td>
<td>300</td>
</tr>
<tr>
<td>Rapa Pass</td>
<td>811</td>
<td>220</td>
<td>clear</td>
<td>400</td>
</tr>
<tr>
<td>Fena Urn</td>
<td>379</td>
<td>170</td>
<td>murky</td>
<td>200</td>
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*This is 14% of the largest wet weight value given by DeWreede and Doty (1970) for this location. The percentage is based on weight retained upon drying of *Sargassum* and is most likely the same for *Turbinaria*.

Table 2
Maximum-Minimum Water Temperatures (°C)

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The area between Teharoa Iti and Rapa Iti consists of large calcium carbonate mounds with *Turbinaria* growing on them, however a similar area north of Pono Tai was devoid of *Turbinaria*. Both areas were in murky water.

The English Harbor area does not have any *Turbinaria* growing in the clear, deep water there, although suitable substrata are available. This area was not as thoroughly searched as desired because of the depth and uncertain currents encountered. Nevertheless, *Turbinaria* thalli were not present in the areas of English Harbor examined.

A pattern of substratum distribution is easily seen from the air. Patch and line reefs are darker on the eastern to northeastern (windward) edges except where they are influenced by currents flowing through the passes (Fig. 1). The darker edges of the reefs consist of coarse material; lighter areas are sand.

Diffusion enhancement by water movement values (see Appendix) are given in relation to reef topography in Figures 3 to 5. Diffusion values (DF) were generally higher on the windward side of each reef studied. The DF value at North Pass (30.5) was probably lower than the correct value because the clods were washed off the stake and fell to the slower moving waters on the bottom during part of the exposure time.

All maximum-minimum water temperature readings during the investigation were between 32.0-26.0°C (Table 2).

**DISCUSSION**

*Turbinaria ornata* is unevenly distributed throughout Fanning Atoll lagoon, and its distribution appears to be associated more closely with factors derived from land runoff than with water movement, substratum availability, water clarity, temperature, or depth.

*Turbinaria* is most abundant and grows larger (as measured in gms/m²) near the large land mass along the northwestern rim of the atoll than in the southern and eastern portions of the lagoon. The land/lagoon ratio and therefore the runoff/lagoon ratio is higher in the northwestern sector of the lagoon than in the latter sectors, and salinities are lower (see p. 85, this report).

Water movement may also affect the growth pattern of *Turbinaria*. Although *Turbinaria* was found to be abundant on the windward side of a reef at Suez Pond (DeWreede and Doty, 1970), its occurrence there may be due to the availability of coral rubble caused by greater water movement on that side of the reef. Aerial inspection of the atoll and inspection of lagoon reefs by boat confirmed that the coarser material upon which *Turbinaria* usually grows is more abundant on the windward side of reefs.

DF values were quite different at North Pass and Site A where standing crops of *Turbinaria* were highest. High values (30.5) at North Pass and moderate values (14.5) at Site A accompanied the greatest growth of
Turbinaria found in the lagoon. DF values between these (about 20.0) were measured by both DeWreede and Doty (1970) and the author at Site B, a place of low Turbinaria growth. These observations would indicate some factor other than water movement limits Turbinaria growth in that portion of the lagoon.

The availability of solid calcium carbonate substratum is not the complete explanation of the uneven distribution of Turbinaria. Coral rock was available at all four sites investigated, but Turbinaria was absent from one of the sites, and at English Harbor, an area with much coral rock and clear water.

Water clarity is apparently also important in the distribution of Turbinaria. The greatest dry weights of Turbinaria were found not only near shore, but also in clear water. All of the murky water areas sampled yielded less dry weight per square meter than the clear water areas.

Water temperature varied between 26.0-32.0, a range easily tolerated by Turbinaria. Depth may also play a minor role at the sites studied and may have prevented the growth of Turbinaria in the large shallow sandflat areas adjacent to the passes.

BIBLIOGRAPHY


Fig. 3. Site A bottom contours (given in meters). DF values on stakes are underlined, those on tiles are not.
Fig. 4. Bottom contours at Site B at "Suez Canal" (in meters). DF values on stakes are underlined, those on tiles are not.
Fig. 5. Bottom contours at Site C in Suez Pond (in meters). DF values on stakes are underlined, those on tiles are not.
APPENDIX

Site A: these data represent the clods on the stakes shown in Figure 3 and are given in order from West to East as they are drawn.

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SOME ENVIRONMENTAL FACTORS IN THE NORTH
AND RAPA PASS AREAS OF FANNING ATOLL

Maxwell S. Doty
Botany Department, University of Hawaii, Honolulu, Hawaii 96822

Dennis J. Russell
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Continuing the work of the previous expedition (DeWreede and Doty, 1970) Dr. Roy T. Tsuda and the second author visited Fanning Atoll (Fig. 1) during July and August, 1972, as members of a second field party. The purpose of this work is to move toward an understanding of the relationships between variations in environmental factors and algal communities. Our ultimate goal is the best intelligent usage of environmental resources through their thoughtful conservation and their reasoned economic exploitation.

To this end, it is essential that an inventory of the algae at Fanning be completed and their values and natural roles be understood. The algal inventory has been extended by Tsuda et al. (see p. 61, this report) beyond that recorded by DeWreede and Doty (1970).

Our present goal is to determine the possible usefulness of the Fanning Atoll lagoon as a farm site for certain tropical seaweeds for which there is an industrial demand. The Fanning algal flora neither is extensive nor does it include algae known to be economically desirable or extensive beds of any other larger fleshy algae. Because seaweeds for which there is economic demand do not now grow there and because additional farm space for them is becoming critical, special attention was paid to studying what might be the most ecologically variable sites in the lagoon and those most likely to be useful for marine agronomy. During this second period of study, the shallow areas (Fig. 1) near two of the three passes were especially studied.

High-standing seaweed crops or successful farms for them appear to require relatively high amounts of light, fertilizer concentrations, and water motion. Water motion and temperature are major desiderata for the successful farming of Eucheuma striatum on southeast Asia reefs (Doty, 1973). Light dosage and fertilizer in the habitats are important but no rational way of measuring them could be included in this study, and the actual requirements of the algae of interest are not known.

Working under the assumption that the organisms are the best integrators of environmental factors as a function of time as well as the best actual indicators of the levels of intensity of the different factors,
the field party was equipped to record the distributions of the variations of some of the factors. The results (Tables 1 to 3) were mapped (Figs. 2 and 3) from aerial photographs taken for the purpose by Dr. Martin Vitousek and the second author. The areas distinguished were labeled from samples collected in each area and from field examinations.

The environmental measurements made were of maximum and minimum water temperatures (Tables 1, 2 and 3) depth below the contemporary low tides, bottom character, dominant algal or other cover, and water motion. Using "6-type" maximum-minimum thermometers, obtained from A. Gallenkamp & Co., Ltd., Box 290, London EC2, model no. TJ-934c, temperature measurements were made. The authors have found these thermometers satisfactory, although they must be calibrated within the temperature range in which they are to be used if accuracies within 1 degree Celsius are to be obtained. They are advantageous for they are inexpensive and have no parts that would corrode in salt water. The values reported here (Tables 1 and 2) are for the near 24-hour periods of thermometer exposure.

Water motion was obtained with clodcards used in pairs and exposed for 24-hour periods. The resultant values (Figs. 2 and 3) are averages of two or four clods (Tables 1 and 2) except when one was lost or declared "wild" and discarded, in which case the value given is that of the remainder. These values are believed (Doty, 1971) to represent the degree to which water movement at the site increased diffusion from and onto surfaces over what it would have been had the water been motionless.

Depth was recorded (Tables 1 and 2) by averaging the height of the water on a meter stick and correcting this for tide height. Neither salinities nor specific alkalinites were measured, but the frequent and almost always inward motion of the water seemed insurance against these factors being outside the range thought essential to the well-being of benthic algae. Salinity and alkalinity measurements were made by Smith and Pesret (see p. 21, this report), and show values of 34.0/00 and 115.0/00 respectively, on the bottoms. Both are practically open-ocean-water values. Additional evidence of the non-limiting nature of these factors was the occurrence of benthic algae, such as *Turbinaria ornata* (Turner) J. Agardh, well within the lagoon and other benthic algae (Figs. 1 and 2) in the pass regions where the measurements were made.

Our results are systematically recorded in Tables 1, 2 and 3 for the different factors by station. As extended by interpolation and extrapolation from the aerial photographs, Figures 2 and 3 give tentative distributions of the biota and substrate types in the pass areas as well as some, e.g., in the case of water motion, of the mean values obtained from measurement of the environmental factors.

DISCUSSION

The pass areas in respect to several factors seem to have been correctly chosen as sites where the larger benthic algae might be grown best at Fanning Atoll. The depths (Tables 1 and 2) are those which are
Table 1. Environmental qualities measured near the North Pass into Fanning Atoll. The station locations are shown on Figure 3 by dots near the respective data. The following abbreviations appear in reference to the bottom characters: "Clad" = Cladophoropsis spp.; "Hyp" = Hypnea spp.; "Poly" = Polysiphonia spp.; and "Turb" = Turbinaria ornata.

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Table 2. Environmental qualities measured near Rapa Pass into Fanning Atoll. The station locations are shown on Figure 3 by dots near the respective data. The following abbreviations appear in reference to the bottom characters: "Clad" = Cladophoropsis spp.; "Hyp" = Hypnea spp.; "Poly" = Polysiphonia spp.; and "Turb" = Turbinaria ornata.

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Table 3. Bottom cover of Rapa Pass. The values given for the different types of material or organism are in terms of the percentage of the surface they were estimated on 29-VII-72 to cover. These data were contributed by Dr. Roy T. Tsuda.

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productive of, e.g., *Eucheuma* species in southeast Asia waters. Depths are not contoured as there is not a great deal of variation over the areas most intensively studied. At the lagoonward margins of the passes, the large areas shown are rather sharply defined and 3 or more meters deep.

Water motion drops from the seaward high DIF levels of 31 in the narrows of near 1-meter depth where most of the water entry into North Pass can be expected. The DIF values then drop to about half that in the shallower but much broader inner-island inner pass areas before dropping still further as the water deepens in the large areas bordering the lagoonward pass margins. The same phenomena can be seen, though less clearly, in the Rapa area. While we did not measure it during this trip, water movement as turbulence appears higher at the edges of the lagoonward deep areas.

Temperature variation increases as the passes are entered; the most seaward measurements exhibiting 3 to 5 degrees C variations during the 24-hour sample periods. Variations further into the lagoon increase to 4 to 11 degrees C. It is suspected, but not experimentally substantiated, that more than 5 degrees variation per day is not a desirable habitat quality for most large benthic algal species. However, in the case of algae such as *Eucheuma striatum*, *Gracilaria eucheumoides*, and some *Hypnea* species, similar variations have been frequently recorded where these species are abundant in their natural southeast Asia habitats.

Both passes are flanked to the north or northwest by large sandy areas where depth of water was less than 0.1 meter during low tides. Incoming tidal waters partially flushed these areas, momentarily forcing sun-heated water downward as it entered the lagoon, thus possibly accounting for some of the larger unexpected temperature variations in these areas.

It is interesting that in Rapa Pass and North Pass there are occasional patches of *Echinometra*-like sea urchins. Similar aggregations but of *Diadema* or *Echinothrix* are found downstream (e.g., at Calatagan on the island of Luzon, Philippines) from the most productive *Eucheuma striatum* areas (Doty, 1973). At Fanning Atoll, *Diadema* and *Echinothrix* are found only near English Harbor (Townsley, personal communication). The presence and abundance of *Hypnea*, mixed as it was here with *Gelidium* and polysiphonaceous red algae in mat-like communities, is usually interpreted as indicating fertile water, but a water perhaps too calm for the best growth of coarser seaweeds.

One might ask how we are to account for the fact that, if the habitat is favorable, none of the larger fleshy seaweeds other than *Turbinaria* are present at Fanning Atoll. Two major kinds of explanation are likely. One is that the habitat is not suitable for them. The well-known high-island phenomenon in respect to *Ulva* and *Sargassum* is recalled at this point (Doty and Oguri, 1956). However, there are several seaweeds of economic importance that do not seem to grow around high islands and, indeed some, like *Eucheuma spinosum*, seem to thrive on reefs far from any igneous matter. At least for these latter, one has to consider the alternative hypothesis that they just never got to the site. This alternative hypothesis would seem to be tested by the blossoming of such species as...
Fig. 1. The area locations at Fanning Atoll for the 1972 algal studies. Figures 2 and 3 provide details plotted on larger scales.
Fig. 2. Environmental conditions in North Pass of Fanning Atoll. The areas above high tide line, as interpreted from the black intertidal zone showing on the aerial photographs, are cross hatched. The station positions are shown by the larger dots. The symbols used for water motion value, as DIF, are placed above the dots indicating station position with the water depth at low tide in meters being shown below. The maximum and minimum temperatures for the nearest station position are in boxes. The dashed lines with arrows indicate the paths followed by nearly submerged plastic bottles during inflowing tidal movements. The following abbreviations are used to indicate the dominance on the bottom areas set off by a line surrounding them: A=Acropora rubble; B=beach rock; C=coralline algal modules or rubble; Cl=Cladophoropsis; H=Hypnea mat; P=Porites; Pa=Polysiphonia; Pv=coralline algal pavement; R=rubble usually of dead coral or coralline algae and a loose mixture of sand and gravel sized particles; S=sand; Sc=soft coral; Sh=shingle beach of coral fragments; and T=Turbinaria ornata; U=sea urchins. Short horizontal lines indicate no measurement available.
Fig. 3. Environmental conditions in the Rapa Pass of Fanning Atoll. The capital letters to the right of the dots designate the stations referred to in Table 3.
Acanthophora spicifera, following its accidental introduction into the Hawaiian Islands (Doty, 1961).

The possibilities of seaweed farming at such an atoll as Fanning are positive. Such reef species as Eucheuma spinosum or E. arnoldii might do very well physiologically. If they could be imported and planted without bringing in their natural biological destructors, the grazers, significantly profitable farms might very well be developed. However, the isolation of Fanning Atoll and the paucity of information on both this site and Eucheuma would hardly justify a pilot run without a further, more detailed and much longer measurement period. A small pilot introduction of several of the economically desirable species should be made with initiation of the longer basic site study considered essential before the planning of farming trials would be justified.

In any case no introductions of any sort should be made if there are any indications at all that significant damage to the local communities was a possibility.

Enroute to Honolulu from Fanning Atoll in August 1973, several days were spent on Christmas Atoll. Observations there, near Cook Island, of Turbinaria ornata growths in 7.0 meters of water indicate there are, possibly, favorable sites for farming Eucheuma lagoonward of this island. A more detailed study of this area in addition to or in conjunction with further studies at Fanning Atoll could be worthwhile.

Conversations with Mr. John Fleetwood, Manager of the Fanning Atoll copra operations, and Mr. John Bryden, Manager of the Christmas Atoll copra operations, indicate the demand for copra is steadily decreasing, and that efforts are underway on Christmas Atoll to find additional crops. The production and export of farmed dried algae might be a profitable supplement to the economy of these two atolls as the demand for copra declines.

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BIBLIOGRAPHY


REEF CORALS OF FANNING ISLAND

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ABSTRACT

Recent surveys indicate the diversity of reef corals at Fanning Island is greater than previously estimated. Most of the approximately 70 species belonging to 32 genera and subgenera are typically found in one of three environments. A turbid lagoon fauna has high abundance but lower diversity of predominantly branching forms. The clear lagoon coral fauna has both high abundance and diversity of predominantly massive and encrusting corals. The greatest number of species and forms of corals are found on the leeward ocean reefs. The abundance and diversity of corals along windward reef slopes are controlled by wave action. Although Fanning and others of the Line islands presently contain the greatest generic diversity of corals of any island group in the central and eastern Pacific, diversity is considerably less than reported for island groups in the western Pacific. Geographic isolation appears to be the most plausible factor accounting for this reduced coral diversity. The reef coral fauna is more nearly comparable to the fauna of island groups south and west than to those of the north (Hawaii).

INTRODUCTION

Previous studies of reef-building corals at Fanning Island (3°N, 159°W, Line Islands) have been confined to collections and surveys of specific areas within the lagoon. A tentative report on the species list of corals collected from Fanning lagoon (Maragos, et al., 1970) suggested that Fanning Island, and perhaps the Line Islands as a group, include a greater variety of reef corals than previously thought (Wells, 1954). Other studies indicated that flourishing coral communities existed within the lagoon (Roy and Smith, 1971). A second expedition to Fanning in July and August, 1972 provides the basis for a description of the distribution and abundance of reef corals from a broad spectrum of both lagoon and ocean reefs. Information gathered during the assemblage of a large coral collection from the atoll is used to compare the relationships of the Fanning fauna with that of coral faunas of other Pacific islands.
METHODS

Fifty reef sites were visited by a team of scientists working from a small skiff; locations of these sites are found in Figure 1 of Chave and Eckert (see p. 135 this report). At each site, divers gathered information on various reef organisms, including the corals. Notes on circulation, depth, substrate composition, relief, and other physical properties were also recorded. A reference collection of reef corals was assembled. Skeletons were cleaned in dilute hypochlorite (chlorox), and shipped to Hawaii for analysis. The corals were identified using reference collections of the author, the Bernice P. Bishop Museum, Honolulu, Hawaii, and the Hawaii Institute of Marine Biology, University of Hawaii, Honolulu, Hawaii. John W. Wells of Cornell University generously identified some of the corals. Useful references consulted included those of Vaughan (1918), Vaughan and Wells (1943), Crossland (1952), Wells (1954, 1956), and Wijsman-Best (1972). A species list of the corals including their relative abundance at Fanning is given in Table 1.

RESULTS

The Lagoon

Fanning lagoon is a shallow, oval-shaped basin of approximately 116.6 km², with a single deep pass at English Harbor on the west through which 95 per cent of lagoon/ocean water exchange occurs (Gallagher, et al., 1971; Stroup and Meyers, see p. 7, this report). Two shallow passes, Rapa on the southeast, and North Pass on the north, are shallow flats less than a meter in depth. Because of the restricted movement of water into and out of the lagoon, the physical and chemical character of the lagoon water is noticeably different from that of the oceanic waters (Smith and Pesret, see p. 21, this report). The lagoon basin is divisible into two areas on the basis of water clarity; a clear water sector in the vicinity of the deep pass (English Harbor) and turbid water sectors where the water clarity is reduced by the presence of suspended calcium carbonate (Smith and Pesret, cited above) in the north and south basins of the lagoon.

The turbid lagoon is characterized by long, narrow, ribbon-like reefs which form networks across the sandy bottom and enclose a number of basins or ponds (Roy and Smith, 1971; Gordon and Schiesser, 1970). The tops of the line reefs are within one meter of the sea surface. The walls have gentle to steep slopes. Coral cover is relatively high considering the amount of sediment cover and sediment in suspension, and average coral cover in one northern pond was estimated to be over 30 per cent (Roy and Smith, 1971). Lagoon ponds adjacent to North Pass showed higher average coral cover; areas away from the passes showed lower overall cover. Corals grow profusely on the tops and sides of most of the line reefs. Where sand is common, especially on the leeward side of the wider reefs, coral abundance is locally reduced. Corals also grow abundantly on numerous patches and pinnacles on the floor of the ponds. The turbid lagoon in the vicinity of Rapa Pass is shallow and essentially a large sandy reef flat. Numerous microatoll formations of Porites lutea occur on this flat.
<p>| SPECIES LIST OF STONY CORALS FROM FANNING ATOLL |
|-------------------------------|----------|----------------|--------|-----------|
| DISTRIBUTION                  | FREQUENCY|
| Clear Ocean                   | Turbid Lagoon | Rare | Average | Abundant |
| Acropora sp. cf. A. abrotanoides (Lam.) | x | x | x | x |
| Acropora corymbosa (Lam.) 2/ | | x | x |
| Acropora cymbicyathus (Brook) | x | | x |
| Acropora sp. cf. A. delicatula (Brook) | x | x | x |
| Acropora formosa (Dana) | | | | x |
| Acropora humilis (Dana) | | x | x |
| Acropora nasuta (Dana) | | x | x | x |
| Acropora polymorpha (Brook) | x | | x |
| Acropora reticulata (Brook) | x | x | x |
| Acropora syringodes (Brook) | x | x | x |
| Acropora vaughani Wells | | | | x |
| Agariciella ponderosa (Gardiner) | | | | x |
| Alveopora verrilliana Dana | | | | x |
| Astreopora sp. cf. A. gracilis Bernard | | x | x |
| Astreopora listeri Bernard | x | x | x |
| Astreopora myriophthalma (Lam.) | x | x | x |
| Astreopora ocellata Bernard | x | x | x |
| Coscinaraea ostreaformis Van der Horst | x | | x |
| Culicia stellata 3/ | | x |
| Distichopora violacea (Pallas) 3/5/ | | x | x |
| Echinophyllia aspera (Ellis &amp; Solander) | x | | x |
| Favia pallida (Dana) | | | x | x |
| Favia speciosa (Dana) | x | x | x | x |
| Favia stelligera (Dana) | x | x | x | x |
| Favites abdita (Ell. &amp; Sol.) | x | x | x |
| Favites halicora (Ehr.) 2/ | x | | x |
| Fungia fungites Dana | x | x | | x |
| Fungia (Pleurotis) scutaria Lamarck | x | x | x | x |
| Fungia (Verrillofungia) concinna Verrill | x | | x |
| Herpolitha limax (Esper) | x | | x |
| Hydnophora microconos (Lam.) | x | x | | x |</p>
<table>
<thead>
<tr>
<th>Species</th>
<th>DISTRIBUTION</th>
<th>FREQUENCY</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hydnophora rigida (Dana)</td>
<td>x</td>
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</tr>
<tr>
<td>Leptastrea purpurea Dana</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Leptastrea transversa Klz.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Leptoria phrygia (Ell. &amp; Sol.)</td>
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<td>x</td>
</tr>
<tr>
<td>Leptoseris mycetosoides Wells</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Lobophyllia costata (Dana)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Merulina ampliata (Ell. &amp; Sol.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Millepora platyphylla Hemp. &amp; Ehr.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora elschneri Vaughan</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora hoffmeisteri Wells</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora petula Verrill</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora socialis Bernard</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora tuberculosa (Lam.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora verrilli Vaughan</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Montipora verrucosa (Lam.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pachyseris speciosa (Dana)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Parahalomitra robusta (Quelch)</td>
<td>x</td>
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</tr>
<tr>
<td>Pavona clavus (Dana)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pavona divaricata Lam.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pavona gigantea Verrill</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pavona variana Verrill</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pavona (Pseudocolumnastrea) pollicata Wells</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Platygyra lamellina (Ehr.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Platygyra sinensis (Lam.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Plesiastrea sp. cf. P. curta (Dana)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Plesiastrea versipora (Lam.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pocillopora damicornis (Linnaeus)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pocillopora eydouxi M. Ed. &amp; H.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pocillopora meandrina var. nobilis Dana</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pocillopora molokensis Vaughan</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Pocillopora paucistellata Quelch</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td></td>
<td>DISTRIBUTION</td>
<td>FREQUENCY</td>
</tr>
<tr>
<td>----------------</td>
<td>-------------------------------------------</td>
<td>-----------</td>
</tr>
<tr>
<td></td>
<td>Clear Lagoon</td>
<td>Turbid Lagoon</td>
</tr>
<tr>
<td>Pocillopora verrucosa (Ell. &amp; Sol.)</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Porites lobata Dana</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Porites lutea M. Ed. &amp; H.</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Porites pukoensis Vaughan</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Porites (Synaraea) vaughani Crossland</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Psammocora contigua (Esper.)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Psammocora verrilli Vaughan</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Psammocora (Plesioseris) profundacella Gardiner</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Stylaster elegans Verrill 3/1/</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Stylophora mordax (Dana)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Stylophora pistillata (Esper)</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Tubastrea coccinea Lesson 3/</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Turbinaria veluta Bernard 1/</td>
<td>x</td>
<td></td>
</tr>
</tbody>
</table>

| Total Number | 48 | 46 | 27 |
| Number of unique forms | 21 | 9  | 5  |

1/ Christmas Atoll only
2/ Vaughan (1918) only
3/ ahermatypes
4/ hydrozoan corals
Where the line reefs and pinnacles reach the sea surface, the reefs are dominated by the branching corals *Stylophora mordax* and *Acropora delicatula*. *Pocillopora damicorns*, *Acropora formosa*, *Platgyrra lamellina*, and *Montipora verrucosa* are also common. On the sides of the reefs and pinnacles several varieties of *Acropora* usually occur, and *Astreopora*, *Platgyrra*, and *Favita* are common. *Merulina*, *Favita*, *Pavona*, and *Psammocora* are less frequently seen growing under ledges. The unattached solitary coral *Fungia* (P.) *scutaria* was also seen on some shallow sand flats in the turbid lagoon. Most of the corals are attached to hard substrate. Except under coral ledges, average colony size was large.

A preponderance of branching forms occur in the turbid lagoon compared with other lagoon environments at Fanning (Roy and Smith, 1971). The prevalence of branching forms may imply that these forms better resist sedimentation (Roy and Smith, 1971) or that they can outcompete other forms for suitable substrates.

Despite the relatively high coral cover, the number of corals characterizing the turbid lagoon environment is few relative to other environments at Fanning (Table 1). Only 5 species of 71 were restricted to the turbid lagoon. The same common species were repeatedly seen at most all of the sites surveyed within the turbid lagoon. Environments for reef building corals in the turbid lagoon appear to be favorable for only a small number of corals which may compete among one another for the limited amount of hard substrate available for coral settlement.

The middle of the lagoon adjacent to the pass at English Harbor comprises the clear lagoon (Chave and Eckert, Fig. 1, cited above); it is characterized by greater depths than occur in the turbid sectors of the lagoon, clearer water and swifter currents. The line reef network of the turbid lagoon is replaced by concentrations of coral pinnacles of variable size. The larger of these formations are widely spaced and do not restrict exchange of water. Rippled sand dominates the substrates between the patches. These observations indicate that both circulation and exchange of lagoon water occurs more readily in the clear lagoon than in the turbid lagoon. The reef coral fauna is more diverse and more abundant than that of the turbid lagoon. Coral coverage was approximately 60% in one area of the clear lagoon and massive and encrusting types of corals predominated (Roy and Smith, 1971). The average size of individual colonies appears to be smaller than in the turbid lagoon. Several species of encrusting *Montipora* usually dominate the hard substrate and *Platgyrra*, *Favita*, *Porites lobata*, *Pocillopora meandrina*, *Hydnophora*, *Leptastrea*, *Pavona*, *Astreopora*, *Lobophyllia*, and *Plesiastrea* were also common. Vertical zonation of corals was not apparent. Most of the species of the clear lagoon were also recorded within either the turbid lagoon or oceanic reef environments. These observations also suggest clear lagoon habitats for corals are intermediate between oceanic and turbid lagoon environments.
**Seaward Reefs**

Tradewinds and surf are predominately from the southeast at Fanning, and the character of the windward ocean reefs is grossly different from that of the leeward ocean reefs. Rubble or shingle ramparts are found both offshore on reef flats and onshore along much of the seaward coastline of Fanning. These beaches may have been formed during times when wave action and storm activity were severe (Gallagher, 1970). Some of the offshore ramparts enclose old reef flat, forming shallow moats characterized by moderate sediment and currents; water in these moats is oceanic. Coral composition within these moats is not unlike that of the clear lagoon. Although the fauna varies from location to location, *Acropora*, *Pocillopora*, *Psammocora*, *Hydnophora*, and *Favia* are consistently present. Solitary corals of the genus *Fungia* are occasionally found. The abundance and average colony size is usually small, although coral development in the large moat near English Harbor (Danger Point Tidepool of Chave and Eckert, cited above) is locally flourishing.

On reef flats lacking offshore ramparts, coral development is usually poor. Calcareous or fleshy benthic algae apparently outcompete corals on these flats. Coral cover is also low where moving sand is common, especially along some leeward shores. Wide and shallow reef flats occur at Greig Point (Chave and Eckert, Fig. 1, cited above) and other localities along the leeward coast. Elsewhere the reef flats are poorly developed and are deeper. Along much of the windward coast (east and southeast) the reef flats are almost non-existent. Because of the absence of an outer reef edge, waves break near shore. Except for a few hardy forms of *Leptastrea*, *Hydnophora*, and *Pocillopora*, reef corals are nearly absent in these environments. It has been suggested that Fanning atoll is tilting so that the windward (eastern) islands are becoming submerged relative to land areas along the wester rim (Roy and Smith, 1971). This hypothesis may also explain, at least in part, the poor reef flat development along windward coasts.

The deep windward reef slopes were not surveyed in great detail because of logistical problems. The upper slopes appear to be dominated by calcareous red algae (*Porolithon*), and loose shingle is also common within the upper few meters. The groove and spur system is well developed at some locations, but apparently absent or destroyed in others, such as offshore from North Pass. Reef corals are absent from the upper several meters of the windward slopes. Beginning at a depth of 6 meters, a broad shelf extends seaward for several hundred meters. Sediment is absent and reef corals are common, especially encrusting *Millepora*, tabulate *Acropora*, and branching *Pocillopora*. At depths of about 15 meters, coral coverage may be 50 per cent or greater. The most common corals included *Acropora reticulata*, *Millepora platyphylla*, *Stylophora mordax*, *Hydnophora microconos*, *Pocillopora meandrina*, and *Favia speciosa*. Between the coral patches are large fields of broken coral fragments and rubble. Reef slope environments may be periodically devastated by large waves and moving rubble. Coral coverage is poor above depths of 10 meters and the fauna is not so diverse as off leeward ocean reefs. None of the corals appeared to be unique to windward reefs. These observations suggest that the character of shallow windward reef slopes is strongly controlled by wave action and associated factors.
In contrast to the windward reef slopes, the leeward ocean-reef slopes harbor greater abundance and diversity of reef corals. Shingle and calcareous red algae are common within the upper few meters as on the windward reef slopes, but below these depths coral dominates all substrates to depths of 35 meters or more. Average coral abundance for the reef slope north of English Harbor Passage was about 70 per cent. Corals (Maragos, see p. 187 this report) and reef fish (Chave and Eckert, see p. 135 this report) were found to be strongly zoned with respect to depth. The most common corals along leeward ocean reefs from shallow to progressively greater depths include *Millepora platyphylla*, *Acropora reticulata*, *Pocillopora meandrina*, *Stylophora mordax*, *Pavonia varia*, *Lobophyllia costata*, *Sarcophyton sp.* (a soft coral), *Echinophyllia aspera*, and *Leptastrea purpurea*. Several varieties of solitary unattached fungiid corals were also noted at moderate depths. The bottom of the coral reef slope community terminates at a sand talus which appears to extend to great depths. The great number of coral species, and the many unique species found along leeward ocean reefs suggest that habitat diversity is greatest in this area and that environmental conditions are favorable.

**DISCUSSION**

The coral fauna at Fanning atoll can be conveniently classified into turbid lagoon, clear lagoon, and ocean components (Table 1). The degree of circulation, wave action, depth, and sediment cover appear to determine which forms predominate in each of these environments.

The Fanning atoll reef coral fauna is much more diverse than previously reported (Wells, 1954; Stehli and Wells, 1971). Recent investigations (including Maragos et al., 1970) have nearly tripled both the number of species and genera reported from an earlier study at Fanning (Vaughan, 1918). Intensive and more efficient collection by SCUBA probably accounts for most of the discrepancy, as does sampling in the lagoon which had not been previously sampled (Vaughan, 1918). The species list of 71 hermatypes should be considered conservative especially for corals belonging to the genera *Montipora* and *Acropora*. Growth form variation noted among individual species of especially these two genera during this study has led to some revision of the earlier list (Maragos et al., 1970) that had been compiled without the advantage of reef observations.

Because of the problems associated with growth form variation in corals, systematic treatment at the species level is less reliable than at higher taxonomic levels. For this reason, recent studies of the zoogeography of reef corals are based on the distribution of the subgenera and genera (Wells, 1954; Stehli and Wells, 1971; Woodhead and Weber, 1969; and Weber, 1973a, 1973b, in press).

The new records from Fanning atoll increase the number of genera and subgenera of reef corals in the Line Islands from 23 to 35 (Table 2). These results reemphasize the importance of Wells' (1954) discussion of the problems of comparing areas where coral sampling effort is available. The Line Islands were thought to be an area well sampled for reef corals (Stehli
Table 2. **LIST OF SUBGENERA (in parentheses) AND GENERA OF REEF BUILDING CORALS REPORTED IN THE LINE ISLANDS**

<table>
<thead>
<tr>
<th>Existing Records</th>
<th>New Records</th>
</tr>
</thead>
<tbody>
<tr>
<td>Acropora</td>
<td>Parahalometra</td>
</tr>
<tr>
<td>Astreopora</td>
<td>Pavona</td>
</tr>
<tr>
<td>Cyphastrea *</td>
<td>Platygyra</td>
</tr>
<tr>
<td>Favia</td>
<td>Plesiastrea</td>
</tr>
<tr>
<td>Favites</td>
<td>(Plesioseris)</td>
</tr>
<tr>
<td>Goniatetrea *</td>
<td>(Pleuractis)</td>
</tr>
<tr>
<td>Herpolitha</td>
<td>Pocillopora</td>
</tr>
<tr>
<td>Hydnophora</td>
<td>Porites</td>
</tr>
<tr>
<td>Leptastrea</td>
<td>Psammocora</td>
</tr>
<tr>
<td>Lobophyllia</td>
<td>Stylophora</td>
</tr>
<tr>
<td>Merulina</td>
<td>Turbinaria *</td>
</tr>
<tr>
<td>Montipora</td>
<td></td>
</tr>
</tbody>
</table>

* Not reported at Fanning Island

After Wells (unpublished); Wells, 1954; Maragos, et al., 1970; and present study.
and Wells, 1971) even before the recent expeditions to Fanning. No doubt future intensified collection by SCUBA may thus alter the generic coral diversities of any Pacific Island group.

The 35 subgenera and genera of reef corals in the Line Islands are the highest number presently reported for any island group to the east of Samoa. However, comprehensive collections have not been assembled from the Phoenix Islands or other Central Pacific islands, and future collections may well alter the present pattern. Nevertheless, coral diversity in the Line Islands is not so great as that reported for Samoa, the Marshall Islands, or other island groups of the western Pacific (Wells, 1954; Stehli and Wells, 1971). The absence of *Heliopora*, *Seriatopora*, *Symphyllia*, and many other common western Pacific corals support this argument. Stehli and Wells (1971) suggest that the evolution of reef coral genera is occurring more rapidly on the western sides of the Pacific; these areas also show the greatest generic diversity.

Mean annual seawater temperatures are noticeably higher on the western edge than in the central or eastern Pacific (Stehli and Wells, 1971). Greatest coral diversities occur where annual seawater temperatures are greater than 80°F (Stehli and Wells, 1971). Because the Line Islands are located on the Equator and are well within the 80°F isotherm, temperature *per se* does not appear to explain the lower diversity of corals, at least under present climatological conditions.

The greater number of island groups in the western Pacific may have promoted greater diversification of corals there because of greater habitat space and types (Stehli and Wells, 1971). The closer proximity of island groups to one another in this area of the Pacific may tend to reduce geographic isolation and promote homogeneity, and therefore, greater diversity of corals at each island group. The main Line Islands (Washington, Palmyra, Fanning, and Christmas) are about 1600 km south, southeast, and northeast of Hawaii, Johnston Island, and the Phoenix Islands, respectively. The Society Islands, the Marquesas, and the Tuamotus lie 1800 to 2300 km south and southeast of the Line Islands. The Cook Islands lie 1600 km to the southwest. Lack of sufficient island habitat space in the vicinity of the Line Islands could thus be one factor in limiting coral diversity.

Geographic isolation appears to be an important factor in explaining the relatively poor coral diversity of the central Pacific. Although no one island area in the central Pacific is characterized by more than 35 genera or subgenera of corals (Table 3), collectively nearly 50 genera and subgenera are reported from the whole of the central Pacific. Assuming fairly complete collection from these areas, the figures suggest some isolation between individual island groups.

The Hawaiian Islands are well sampled and form the island chain closest to the Line Islands. However, a markedly different coral fauna is found in Hawaii and generic diversity is low (14). The taxa (*Stephanaria*) and *Cycloseris* are apparently absent in the Line Islands although common in Hawaii. Even more striking is the absence of *Porites compressa* or any
Table 3. SUBGENERA (in parentheses) AND GENERA OF REEF CORALS IN CENTRAL AND EASTERN PACIFIC

<table>
<thead>
<tr>
<th>SUBGENERA</th>
<th>GENERA</th>
</tr>
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<tr>
<td>Acanthastrea (2,3,5)</td>
<td>Halomitra (3,5,9)</td>
</tr>
<tr>
<td>Acropora (2,3,5,6,9)</td>
<td>Herpolitha (2,3,5,6,9)</td>
</tr>
<tr>
<td>Agariciella (3,6)</td>
<td>Hydnophora (2,6,9)</td>
</tr>
<tr>
<td>Alveopora (1,5,6)</td>
<td>Leptastrea (1,2,3,5,6,9)</td>
</tr>
<tr>
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<td>Leptoseris (1,3,5,6,7)</td>
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<tr>
<td>(Danafungia) (3,9)</td>
<td>Millepora (2,3,5,6,7,9)</td>
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<tr>
<td>Echinopora (2,9)</td>
<td>Montipora (1,2,3,4,5,6,9)</td>
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<td>Parahalomitra (3,6)</td>
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<td>Pavona (1,2,3,5,6,7,8,9)</td>
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<tr>
<td>Goniastrea (2,9)</td>
<td>Platygyra (2,3,5,6,9)</td>
</tr>
</tbody>
</table>

1 - Hawaiian Is.       Data from Wells (1954, unpubl.), Stoddart and Pillai (1972), and results of this study.
2 - Cook Is.
3 - Society Is.
4 - Marquesas Is.
5 - Tuamotu Is.
6 - Line Is.
7 - Panama
8 - Galapagos Is.
9 - Phoenix Is.
branching equivalent of Porites at Fanning; branching Porites is perhaps the most common Hawaiian form (Maragos, 1972). An analogous branching form, Stylophora mordax dominates habitats in Fanning lagoon which might otherwise be quite favorable for branching Porites. Isolation may also explain discrepancies in occurrence of genera among the individual atolls of the Line Islands. Although Cyphastrea, Turbinaria, and Goniatrea have been reported from Christmas or other atolls, they were not found by the author at Fanning, after an extensive search.

The islands of the central and eastern Pacific collectively do not show generic coral diversity as high as individual island groups in the central Pacific to the west of Samoa. Thus, not only is isolation between archipelagoes of the central Pacific possible, but isolation of the whole area from the western Pacific is probable.

It has been suggested (Vaughan, 1907; and others) that the planula larval stage of corals does not survive long enough to facilitate coral dispersal between island groups separated by wide distances. Although Harrigan (1972) has shown that Pocillopora larvae can remain viable and settle after several months, other studies (Maragos, 1972) suggest that Pocillopora may be adapted for high dispersal associated with better survival in certain reef habitats. Other corals may not produce nearly as many larvae or produce planulae which will survive as long as those of Pocillopora.

Central Pacific island groups are isolated from the western Pacific in other ways. Prevailing winds and currents tend to move east to west. Since coral planulae probably cannot swim against currents, corals in the central Pacific are essentially "upstream" from the western Pacific, which is the center of evolution of reef corals in the Pacific (Stehli and Wells, 1971). Thus, a combination of distance and current patterns may account for isolation resulting in lower coral diversity of areas in the central and eastern Pacific. The greater similarity of the Line Islands coral fauna to that of the Marshall Islands suggest that the former fauna was derived recently from areas to the west.

The dissimilarity and low diversity of the Hawaiian coral fauna suggest the island group is more isolated from the western Pacific than are the Line Islands. Kay (1971) came to similar conclusions regarding the shallow water molluscan fauna of Fanning. Dora Banner and Albert Banner (personal comm.) have also noted a lower number of species of alpheid shrimps occurring in Hawaii compared to that of island groups to the west of Hawaii. This pattern may characterize the distribution of other reef organisms as well.

ACKNOWLEDGMENTS

I would like to thank Edith Chave and Dave Eckert for their assistance and cooperation during the diving surveys. I would also like to thank Keith Chave and Alison Kay for their support and interest. John Wells identified many of the corals. The Hawaii Institute of Marine Biology
typing assistance. This study was supported by NSF Grant F331-0-260-3230 and NSF Sea Grant 04-3-158-29. This is CORMAR Contribution No. 3.

BIBLIOGRAPHY


ABSTRACT

Lagoon molluscan assemblages at Fanning Island are described in terms of three topographical areas: the lagoon reef flat, the patch reefs, and the lagoon floor. Among the large mollusks, Clypeomorus breve, Rhinoclavis asper, Pupa sulcata, Pyramidella sp., and two bivalves, Fragum fragum and Tellina robusta, are the principal components of the fauna of the reef flat; Cypraea moneta and Trochus histrio are the dominant epifaunal mollusks of rubble on patch reefs; and sessile bivalves, Cardita variegata, Electroma sp., Ostrea sandwicensis, and Tridacna maxima are associated with coral. The micromolluscan assemblages of the lagoon reef flat are dominated by Tricola variabilis, and patch reef and lagoon floor assemblages by Diala flammea. Obtortio sulcifera is the second most abundant mollusk on the patch reefs and O. pupoides the second most abundant mollusk on the lagoon floor. The patch reef and lagoon floor assemblages are distinguishable into assemblages associated with turbid water and clear water areas of the lagoon. Standing crops of micromollusks are greatest on the windward or southeastern periphery of the lagoon reef flat.

The lagoon mollusks are distinguished from the seaward reef mollusks in terms of species composition, modes of life, and feeding habits. The lagoon assemblages are predominantly herbivores and suspension feeders among the macrofauna, and are epifaunal herbivores among the microfauna. The seaward reef macrofauna is dominated by carnivores and herbivores, and the microfauna by faunal grazers. Standing crops of seaward reef micromollusks are less than those in the lagoon and the species diversity index is higher.

INTRODUCTION

A survey of the littoral marine mollusks of Fanning Island in 1970 reported a faunal list of 305 species and showed a clear distinction between the species composition of the seaward reefs and that of the lagoon (Kay, 1971). Distribution patterns for the mollusks of the seaward reefs indicated discrete assemblages associated with various features of topography. It was suggested that species composition and distribution of
the lagoon mollusks would also reflect topographical structure of the lagoon. A second expedition to Fanning Island in July and August, 1972, gave opportunity to make a detailed survey of the distribution of the lagoon mollusks. In this paper we explore the relationships between molluscan assemblages and lagoon parameters such as topography, sediment distribution, salinity, and algal distribution, and compare aspects of the species composition and modes of life of lagoon and seaward-reef mollusks.

METHODS

During July and August, 1972, the 42-km perimeter of the Fanning lagoon reef flat was surveyed on foot and observations and collections of mollusks and sediments made at 98 stations. Twenty-three patch reefs were sampled by snorkel diving and estimates were attained of distribution and abundance of the mollusks by throwing a 0.25 m² quadrat on the surface of the reefs, counting all large mollusks visible in the quadrat, and recording substrate types. Fifteen stations on the lagoon floor were sampled by SCUBA diving and clam shell dredge. The general distribution of the stations sampled is shown in Figure 1.

Sediments from all stations were put into plastic bags upon collection and returned to the laboratory where they were placed in open containers and air-dried. Sediment samples were processed in the laboratory for micromollusks, that is, for shells less than about 10 mm in greatest dimension. Shells were sorted under a binocular dissecting microscope from standard 25 cm³ volumes. This volume produced standing crops as great as 77 shells per cm³, and an average of 10 shells per cm³. The samples were deemed sufficient for subsequent analysis, as larger samples would have been difficult to deal with in a routine manner. Although live/dead shell ratios were not determined, it is assumed, because living specimens of most species were found, that the dead biofacies patterns reflect the general occurrence of living populations.

A list of mollusks recorded from Fanning Island is presented in Appendix A, and the most commonly encountered micromollusks of the lagoon and seaward reefs illustrated in Figure 4. Species counts are based on all mollusks except for triphorids and some small rissoids which were lumped together in each of the categories respectively because of difficulties in identification.

Several techniques were utilized to gain a quantitative insight into the distribution of individual species. Relative abundance values, or percentage composition of the assemblages; frequency, the number of occurrences of a species in a habitat type; and standing crop, the number of shells per cm³ of sediment, were computed. Trophic structure was determined by counting the number of individuals associated with a particular feeding habit and dividing by the total number of individuals in the sample. Species diversity was calculated using the function \[ H = -\sum p_i \log p_i \], where \( p_i \) equals the fraction of the total number of individuals represented by each species (Pielou, 1969).
Fig. 1. General distributions of the stations sampled at Fanning Island.
Samples from 29 stations were utilized in sediment analysis. A representative portion of each sample was sorted through a series of sieves, each 20 cm in diameter. Table 1 shows the phi (φ) and mesh sizes of the sieves used. Each fraction obtained was weighed and its percentage of the sample calculated. Cumulative dry-weight percentages were plotted on probability paper. The graphic mean, \( M_z \), was plotted, the mean defined as \( M_z = \frac{\phi_{16} + \phi_{50} + \phi_{84}}{3} \) (Folk, 1968). The formula \( \sigma = \frac{\phi_{84} - \phi_{16}}{2} \) was used to determine graphic standard deviation.

LAGOON TOPOGRAPHY

The lagoon molluscan assemblages are conveniently described in terms of three general topographical areas: the lagoon reef flat, the patch reefs of the lagoon basin, and the lagoon floor. Details of topography, salinity, nutrient concentrations, etc. are found in Stroup and Meyer, Smith and Pesret, and Maragos (see p. 7, 21, and 187, this report).

The lagoon reef flat is a predominantly sandy flat extending from 50 to 300 m in width around the lagoon shore. Most of the reef flat is exposed at zero tides. Patches of turf-forming algae such as Hypnea, Polysiphonia, and Schizothrix occur on the flat, as do occasional patches of rubble and exposed sections of fossil reef studded with Tridacna valves in situ. The lagoonward edge is marked by the occasional occurrence of colonies of Acropora and/or Porites and clumps of the brown alga Turbinaria. Two types of discontinuity interrupt the otherwise continuous reef flat: (1) passes between the islands of the atoll, and (2) brackish water inlets. Three passes dissect the lagoon reef flat, a single deep pass (ca 10 m in depth) at English Harbor and two shallow passes (ca 1 m in depth) at North Pass and Rapa Pass. The reef flat in the shallow passes is paved with coralline algae and mats of Hypnea and Polysiphonia (Doty and Russell, see p. 85, this report). The lagoon shore is dissected by inlets which effect changes in salinity in the surrounding lagoon (Guinther, 1971; see p. 263, this report). The lagoon reef flat north of English Harbor is distinguished by a short stretch of rubble and shingle shoreline.

The lagoon basin is divisible into a clear-water sector in the vicinity of English Harbor (Fig. 1) where visibility is from 10 to 15 m, and turbid water sectors in the north and south basins where visibility is less than 2 m (Roy and Smith, 1971). In the turbid lagoon, patch reefs are predominantly fringed by ramose Acropora (Roy and Smith, 1971; Maragos, cited above). The lagoon floor, 10 to 15 m deep in the clear water area and 4 to 8 m deep in the turbid lagoon, is comprised of living corals and carbonate mud sediments. Live corals cover 62 per cent of the clear water area and 31 per cent of the turbid lagoon floor (Roy and Smith, 1971).
<table>
<thead>
<tr>
<th>Phi Scale</th>
<th>Mesh Opening (mm)</th>
<th>Size Class</th>
</tr>
</thead>
<tbody>
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<td>-2.0</td>
<td>4.00</td>
<td>Granule</td>
</tr>
<tr>
<td>-1.0</td>
<td>2.00</td>
<td>Very coarse sand</td>
</tr>
<tr>
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<td>1.00</td>
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</tr>
<tr>
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<td>0.50</td>
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</tr>
<tr>
<td>2.0</td>
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<td>3.0</td>
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<tr>
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<td>Silt</td>
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RESULTS

Lagoon Reef Flat Assemblages. Approximately 100 species were recorded from the lagoon reef flat, of which 33 were large mollusks and 65 micro-mollusks. Of the large mollusks, 16 were recorded alive and the remaining 17 consisted of juveniles and/or fragments in the sediments. The most frequently occurring of the living mollusks were two cerithids, *Rhinoclavis asper* and *Clypeomorus brevis*; two opisthobranchs, *Pupa sulcata* and *Pyramidella* sp.; and two bivalves, *Fragum fragum* and *Tellina robusta*. All are sand-dwellers and, except for *Clypeomorus* which occurs on the surface of the substrate, were found buried or partially buried in sand. The distribution of *Rhinoclavis*, *Clypeomorus*, and *Pupa* is shown in Figure 2. *Pupa* is the most frequently occurring of these mollusks, recorded from 47 per cent of the stations. It is most frequent (f = 33 per cent) on the northeast near Vai Tepu. *Fragum* and *Tellina* occurred at 25 per cent of the stations, with *Fragum* most frequent (f = 30 per cent) on the northeast and *Tellina* most frequent (f = 37 per cent) on the southwestern perimeter. *Pyramidella* is most frequent (f = 40 per cent) on the reef flat of the northeastern perimeter. *Rhinoclavis* is most frequent (f = 37 per cent) on the eastern shore near Vai Tepu, noticeable on the south shore, and relatively infrequent on the western shore (f = 3 per cent). *Clypeomorus* is restricted to the southern, southwestern, and eastern lagoon reef flat.

In addition to the dominant macromollusks of the reef flat, six localized assemblages were recorded: a complex *Cypraea moneta/C. annulus* assemblage on the rubble shoreline near English Harbor (Kay, 1971); three colonies of *Cypraea moneta* in the infrequent rubble patches along the shore, two north of the Cable Station and one at Vai Tepu; three colonies of *Macoma dispar*, one near the Cable Station and two on the southern perimeter; two colonies of *Conus pulicarius*, one near English Harbor and the other near Rapa Pass; a single assemblage of *Strombus gibberulus* and *Natica gualteriana* off the village north of the Cable Station; and occasional specimens of *Gafrarium pectinatum* near brackish water inlets at Vai Tepu and Napu Naiaaroa.

The distribution of the most frequently occurring of the sand-dwelling mollusks is, at least in part, associated with sediment grain size and salinity. Table 2 lists several stations (shown in Fig. 1) according to mean grain size, the standard deviations, and presence or absence of the six most commonly occurring large mollusks. Mean grain size ranges from -0.52 to +1.58 (0.76 mm to 0.35 mm). *Pupa* inhabited the widest range of grain size habitats. *Clypeomorus* was restricted to a smaller range of larger grain size (0.07 to 0.43). Subjective observations that *Rhinoclavis* was usually located in areas of fine sand were substantiated in the analysis with the species found in samples of mean grain size of +0.13 to +1.50.

The distribution of *Clypeomorus* is also associated with salinity: this gastropod was exclusively confined to areas where brackish water inlets open to the reef flat on the southern, southwestern, and eastern perimeter of the lagoon (Fig. 2). No specimens were encountered in our sampling on the northwestern lagoon reef flat where similar conditions were present,
TABLE 2

Stations (shown in Figure 1) according to mean grain size, standard deviations, are presence or absence of the six most commonly encountered large mollusks in Fanning lagoon.

<table>
<thead>
<tr>
<th>STATION</th>
<th>Mz (φ)</th>
<th>g (φ)</th>
<th>Clypeomorus</th>
<th>Pugum</th>
<th>Pyramidalis</th>
<th>Rhinoclavis</th>
<th>Tellina</th>
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<td>1.15</td>
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Fig. 2. Distribution of Clypeomorus, Pupa, and Rhinoclavis in Fanning lagoon.
although occasional shells were found there in 1970 (Guinther, 1971). *Clypeomorus* withstands salinities as great as 55 o/oo, but becomes inactive at salinities less than 27 o/oo, and its occurrence on the lagoon shore may be associated with a migration from the brackishwater inlets of the interior of the islands (Guinther, personal communication).

We did not attempt to estimate standing crops of large mollusks in terms of biomass, and, because of variations in the sizes of these mollusks (*Rhinoclavis* averages 32 mm in length, *Tellina* and *Pupa* 14 mm and 18 mm, respectively), estimates of standing crop would be meaningless without further analysis. Estimates of density, however, suggest that *Clypeomorus* occurs in the greatest numbers per unit area of substrate, with densities of more than 70 per m². Greatest densities were recorded on the southern perimeter of the lagoon where *Clypeomorus* predominated, and on the eastern (windward) shore where *Rhinoclavis* was dominant.

Trophic structure of the large mollusks is a mixture of grazing herbivores, suspension feeders, and infaunal carnivores, with the grazing herbivores (or detritus feeders) *Rhinoclavis* and *Clypeomorus* predominant.

The micromolluscan assemblages of the lagoon reef flat are marked by the inordinate abundance of the small (ca 1 mm in length) phasianellid, *Tricola variabilis*, which comprises 46 to 77 percent of the assemblages (Fig. 3 and Table 3). *Tricola* is most abundant on the reef flat of the northwestern and southwestern perimeters (Fig. 3). Other small mollusks which form dominant components of the assemblage are three diastomids, *Diala flavanea*, *Obtortio pupoides*, and *O. sulcifera*; a rissoid, *Merelina* sp. A; a turbinid, *Leptothyra* sp. cf. *wellsii*; and the opisthobranch *Acteocina* sp. cf. *sandwicensis* (Fig. 3, Table 3). Shells illustrating these species are shown in Figure 4. The skeneid *Parviturbo minutissimus* and two minute "vitrinellids" were found in lesser abundance (Table 3).

The occurrence of the dominant forms was remarkably consistent at all stations except in the passes where *Tricola* was relatively more abundant and *Diala* and the two species of *Obtortio* less abundant or absent (Table 3). *Diala* was the only species which was more abundant than *Tricola* at any of the stations; on the two sections of the reef flat where it dominated (Fig. 3), grain sizes approximate those of the patch reefs. All the micromolluscan species encountered are epifaunal except for *Acteocina* which is infaunal. Although time did not permit detailed studies of the habitats of micromollusks, we noted living *Tricola* and *Diala* in mats of the red algae *Hypnea* and *Polysiphonia* in the passes, and we found *Diala* on the brown alga *Turbinaria* floating in the lagoon, on *Hypnea* associated with rubble on the lagoon reef flat, and on *Polysiphonia* on the patch reefs.

Standing crops of micromollusks were greatest on the eastern periphery of the reef flat from Vai Tepu south and at Rapa Pass (Fig. 5). Trophic structure of the micromolluscan assemblages is predominantly grazing herbivore (Table 3). Species diversity values are highest north of the Cable Station (CS, Fig. 1), one of the few areas where there was rubble on the reef flat; lowest values were recorded in the passes and in the northeastern sector of the lagoon.
TABLE 3

Standing crop, species diversity, relative abundance and trophic structure of the most common micro­mollusks in the lagoon. Species composition and trophic structure are given as percent composition. + signifies less than 1% of the assemblage.

<table>
<thead>
<tr>
<th></th>
<th><strong>Lagoon Reef Flat</strong></th>
<th><strong>Patch Reefs</strong></th>
<th><strong>Lagoon Floor</strong></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>CS²</td>
<td>P²</td>
<td>V²</td>
</tr>
<tr>
<td><strong>Ave. No./cm³</strong></td>
<td>4.5</td>
<td>8.4</td>
<td>17.5</td>
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<tr>
<td><strong>Species diversity (H')</strong></td>
<td>3.0</td>
<td>2.4</td>
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<tr>
<td><strong>Species composition</strong></td>
<td></td>
<td></td>
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</tr>
<tr>
<td><strong>Leptothyra</strong></td>
<td>7</td>
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<td>4</td>
</tr>
<tr>
<td><strong>Tricola</strong></td>
<td>46</td>
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<td>57</td>
</tr>
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<td>3</td>
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<td>&quot;Vitrinellids&quot; (2 spp.)</td>
<td>2</td>
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<tr>
<td><strong>Merelina sp. A.</strong></td>
<td>4</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td><strong>Diala</strong></td>
<td>10</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td><strong>Obtortio pupoides</strong></td>
<td>2</td>
<td>4</td>
<td>2</td>
</tr>
<tr>
<td><strong>O. sulcifera</strong></td>
<td>5</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><strong>Triphoridae (6 spp.)</strong></td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td><strong>Acetocina</strong></td>
<td>6</td>
<td>6</td>
<td>4</td>
</tr>
<tr>
<td><strong>Pyramidellids (5 spp.)</strong></td>
<td>4</td>
<td>2</td>
<td>+</td>
</tr>
</tbody>
</table>

**Trophic Structure**²

<table>
<thead>
<tr>
<th></th>
<th>Herbivores</th>
<th>Suspension/deposit feeders</th>
<th>Faunal grazers</th>
<th>Predators/scavengers</th>
<th>Parasitic</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lagoon Reef Flat</strong></td>
<td>87</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>4</td>
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<tr>
<td><strong>Patch Reefs</strong></td>
<td>91</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>2</td>
</tr>
<tr>
<td><strong>Lagoon Floor</strong></td>
<td>92</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>6</td>
</tr>
</tbody>
</table>

1. Reef flat stations refer to those in Figure 1.
2. CS, P and V refer to the inlets of the atoll shown in Figure 1.
3. Herbivores include archaeogastropods (Tricola and Leptothyra), rissoids, cerithids, diastomids, etc.; suspension or deposit feeders are represented by bivalves; faunal grazers include triphorids, cerithiopsids, and marginellids which feed on sponges, etc.; predators/scavengers are columbellids, turrids and others of the neogastropods and some opisthobranchs; the pyramidellids are considered parasitic.
Fig. 3. Molluscan species composition in terms of relative abundance in Fanning lagoon.
FIG. 4. Micromollusks common in the lagoon and on the seaward reefs at Fanning Island. A. *Tricola variabilis*, length 1 mm; B. *Leptothyras* sp. cf. *wellsii*, height, 1 mm; C. *Parviturbo minutissimus*, height 0.5 mm; D. *Merelina* sp. A, length, 0.75 mm; E-F. *Diata flammea*, two color variations, 3 mm; G. *Obertio pupoides*, length, 4 mm; H. *O. sulci/era*, length, 4 mm; I. *Odostomia* sp. cr. oodes, length, 0.75 mm; J. *Turbonilla* sp. A, length 2.5 mm; K. *Acteocina sandwicensis*, length, 3 mm; L. *Euchelus angulatus*, height, 3 mm; M. *Merelina* sp. B., length 1.5 mm; N. *Triphora* sp. cf. *minuta*, length, 2 mm; O. *T*. sp. cf. *tessellata*, length, 2.5 mm; P. *T*. sp. cf. *decorata*, length, 2.5 mm.
Fig. 5. Distribution of the standing crop of micromollusks in Fanning lagoon.
Patch Reefs. Thirty-two species of large mollusks and 44 species of micromollusks were recorded from the patch reefs. Of the macrofauna, 15 species occurred with frequencies of more than 10 percent. The habits of the macromollusks are divisible into three categories, epifaunal species associated with rubble and coral, sessile bivalves attached to coral, and those which are infaunal in sand.

Cypraea moneta is the most ubiquitous of the epifaunal mollusks, found at 52 percent of the stations. Trochus histrio (f = 30 percent) and Cymatium pyrum (f = 26 percent) were found on both living coral and rubble, but were more frequent on the former than the latter. Three bivalves were associated with living coral and two with living and dead coral. Electroma sp. was found most frequently on Acropora; Ostrea sandwicensis occurred more frequently on Stylophora than on Acropora; and Barbatia decussata was found only in massive heads of Porites. Tridacna maxima and Cardita variegata were found in Porites and Acropora but were not limited to living coral. Large numbers of small vermetids were also associated with corals, especially those encrusted with coralline algae. The sand dwellers Rhinoclavis and Cerithium sculptum were found more frequently in sand under living coral than in sand under rubble, but the bivalves Gafrarium, Pitar, and Trapezium were found more frequently in sand under rubble than under living coral.

The distribution of the large mollusks reflects the division of the lagoon into clear- and turbid-water sectors: Tridacna and Barbatia were limited in their distribution to the massive corals of the clear lagoon (Fig. 6). Gafrarium, Pitar, and Trapezium occur in greater numbers on the rubble-covered reefs of the southern turbid lagoon than in other sectors, and we noted that the boring mytilid, Lithophaga, is more common in corals of the turbid lagoon than in the clear lagoon. Electroma and Ostrea are distributed throughout the lagoon, but densities of Electroma appeared greater in the turbid lagoon than in the clear lagoon. Other mollusks reported as characteristic of the lagoon such as Cymatium and Nassarius (Kay, 1971) were found to be restricted almost entirely to the patch reefs of the clear lagoon.

The mollusks associated with living coral and the infaunal forms of the patch reefs are predominantly suspension feeders because of the preponderance of bivalves and vermetids. The rubble-associated mollusks are largely grazing herbivores.

The dominant component of the micromolluscan assemblages of the patch reefs is Diala flammea (Fig. 3; Table 3). Obtortio sulcifera and Tricolia were found in lesser abundance, and Merelina, Leptothyra, and Acteocina are least abundant (Table 3). There is some indication of a distinction between the micromolluscan assemblages of the clear lagoon and those of the turbid lagoon, although it is not so striking as with the large mollusks. Diala and O. sulcifera are more abundant in the clear lagoon than in the turbid lagoon, and Tricolia, Leptothyra and pyramidellids are more abundant in the turbid lagoon than in the clear lagoon (Table 3). The clear lagoon sediments are also characterized by a greater proportion of small tellinids
(comprising 64 percent of the bivalves (suspension feeders, Table 3) ) than occurs in the turbid lagoon (29 percent of the bivalves).

Lagoon Floor. Relatively few large mollusks were recorded from the lagoon floor. In the clear lagoon, *Terebra maculata*, *Atrina vexillum*, and two or three species each of *Mitra* and *Conus* were recorded, while only *Gerithium sculptum* and *Codakia divergens* were recorded from the calcareous mud sediments of the turbid lagoon.

Fifty-three species of micromollusks were recorded from the sediments of the lagoon floor, with 31 species found only in the clear lagoon and 8 species recorded only in the turbid lagoon. *Diala* is the dominant species in both the clear and turbid sectors, comprising more than 50 percent of the assemblages (Table 3). *Obtortio pupoides* is second in abundance and is clearly predominant in the turbid lagoon (Table 3). *Leptothyra* and *Merelina* were not recorded from the sediments of either the clear or the turbid lagoon, nor were *Tricolia*, *Parviturbo*, or the "vitrinellids" found in the turbid lagoon sediments. Pyramidellids comprise about 10 percent of the gastropod assemblages in both areas (Table 3), with *Odostomia* sp. cf. *odes* forming 53 percent of the pyramidellids of the turbid lagoon and *Turbonilla* sp. A, making up 81 percent of the pyramidellids in the clear lagoon versus 36 percent in the sediments of the turbid lagoon. The clear lagoon is also distinguished from the turbid lagoon by a higher proportion of bivalves (suspension feeders, Table 3), and small tellinids comprise 71 percent of the bivalves in the clear sector.

Dead Shells and Fossils. The occurrence of several accumulations of dead shells shoreward of the lagoon reef flat and on the patch reefs, and mounds and flats of fossil shells, is also noteworthy. We found accumulations of large shells of *Fragum* and *Gafrarium* both on the lagoon reef flat and on the patch reefs; fossil *Tridacna* valves in situ on sand free areas of the reef flat were noted above. In addition we recorded several species as fossils in mounds on Cable Station Island and at Vai Tepu; these included specimens of *Strombus lentiginosus*, *Philippia*, and *Terebra* which have not been recorded alive at Fanning.

Seaward Reefs. The molluscan assemblages of the seaward reefs have been described (Kay, 1971). The dominant mollusks of the seaward reef flats are the herbivores *Turbo*, *Astrea*, *Patella*, and *Cypraea moneta*, and the carnivorous thaisids, fasciolarids, *Vasum*, cones, and miters. Of the 20 macromollusks which can be considered common on the seaward reef flats, only *Cypraea moneta* was also dominant and widespread in the lagoon. *Vasum*, *Maculotriton*, and *Cymatium pyrum* were also recorded in the lagoon but were found only in the clear-water sectors or near English Harbor.

For purposes of comparison of the microfauna of the seaward reefs and the lagoon, samples from the leeward seaward reef flat, moats near English Harbor, and from depths of 10, 21 and 36 m off the reef slope were analyzed. Sixty-six species of micromollusks were recorded in these samples. Only the *Triphoridae* and *Merelina* sp. A, the latter also common in the lagoon, are consistently present at all the stations. Each of the three shallow stations shows a different species dominant: on the reef
Fig. 6. Distribution of Barbatia, Electroma, Ostrea, and Tridacna in Fanning lagoon.
flat, *Euplica varians*; in the moats, *Mitrella vorida*; and at the 10 m station, *Merelina* sp. A. The two deep stations resemble each other in the high proportion of triphorids present. Trophic structure is predominantly faunal grazer at all of the stations; standing crops are less than those recorded in the lagoon and the species diversity index is higher (Table 4).

DISCUSSION AND CONCLUSIONS

Approximately 350 species of mollusks have now been recorded from Fanning Island. In this paper we describe the distribution of the lagoon mollusks, attempt to relate distribution patterns to various parameters within the lagoon, and compare species composition, abundance, and diversity with that of the seaward reefs. Three characteristics of the assemblages exhibit empirical patterns: mode of life, species composition, and species diversity. In addition, we find a striking contrast between the community structure of the macrofauna and that of the microfauna on the same grounds.

The three habitat types initially distinguished, lagoon reef flat, patch reef, and lagoon floor subsume three major types of substrates, sand, rubble, and living coral. These substrate types at once serve to define some of the distributional patterns observed for the large mollusks. Sand-dwelling mollusks are found in all three habitat types, that is, on the lagoon reef flat, on patch reefs, and on the lagoon floor. Coral-associated forms are restricted to the occurrence of living corals, most of which are found on the patch reefs and particular types of which are associated with the turbid and clear water areas of the lagoon respectively. Rubble-associated mollusks occur where there is rubble, primarily on the patch reefs and to a lesser extent on the reef flat.

The dominant sand-dwelling mollusks are cerithids, opisthobranchs, and the bivalves *Fragum*, *Gafrarium*, *Pitar*, *Tellina*, and *Trapezium*. The coral-associated mollusks are predominantly sessile bivalves, *Barbatia*, *Cardita*, *Electroma*, and *Tridacna*; and the epifaunal mollusks are comprised primarily of *Cypraea moneta* on rubble and *Trochua* on coral.

Within each of the major substrate types there are subsidiary distribution patterns which we associate with salinity, turbidity, and sediment grain size. *Clypeomorus* appears to be associated with the brackish water inlets which dissect the lagoon shore; *Barbatia* and *Tridacna* are found only in clear-water areas of the lagoon; and the distribution of *Rhinoclavis*, *Pupa*, *Pyramidella*, and *Tellina* is associated with sediment grain size. The sand-dwellers also appear to be influenced by the presence or absence of rubble: three species (*Pupa*, *Pyramidella*, and *Tellina*) occur almost exclusively on the reef flat where there is little rubble; *Rhinoclavis* is more frequent on the lagoon reef flat than on the rubble-covered patch reefs; and *Cerithium sculptum*, *Gafrarium*, *Trapezium*, and *Pitar* are almost entirely confined to rubble-covered sand on the patch reefs.

The habitat types of the macrofauna parallel those reported by Salvat (1972) for the lagoon mollusks at Reao, Tuamotu Islands. Salvat reports
TABLE 4

Standing crop, species diversity, relative abundance and trophic structure of the most common micromollusks of the leeward seaward reefs. Species composition and trophic structure are given as percent composition. + signifies less than 1% of the assemblages.

<table>
<thead>
<tr>
<th>Reef Flat</th>
<th>Moat 2</th>
<th>10 m²</th>
<th>21 m²</th>
<th>36 m²</th>
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<tr>
<td>Ave. No./cm³</td>
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<td>4.5</td>
<td>3.9</td>
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<tr>
<td>Species diversity (H')</td>
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<td>4.5</td>
<td>3.9</td>
<td>3.6</td>
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Species composition

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<tr>
<td>Paryiturbos</td>
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<td>Vitrinellid (1 sp.)</td>
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<td>Merelina sp. B</td>
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<td>---</td>
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<td>8</td>
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</tr>
<tr>
<td>Bittium zebrum</td>
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<td>6</td>
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<td>---</td>
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<td>4</td>
<td>+</td>
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</tr>
<tr>
<td>Obtortio pupoides</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>---</td>
<td>+</td>
</tr>
<tr>
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<td>39</td>
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<tr>
<td>Acetocina</td>
<td>26</td>
<td>3</td>
<td>4</td>
<td>---</td>
<td>+</td>
</tr>
<tr>
<td>Pyramidellids (3 spp.)</td>
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</table>

Trophic Structure

<table>
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<tbody>
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<td>3</td>
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</tr>
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</tr>
<tr>
<td>Predators/scavengers</td>
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<td>8</td>
<td>7</td>
</tr>
<tr>
<td>Parasitic</td>
<td>---</td>
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<td>6</td>
<td>---</td>
<td>2</td>
</tr>
</tbody>
</table>

1. Data from coral/algal washings in 1970.
2. Shallow tidepools described by Chave and Eckert (p. 135, this report) and stations on the seaward reef transect described by Maragos (cited above.)
3. From one station on the reef slope off the Cable Station.
4. Categories as described in Table 3.
only 28 species of mollusks in the lagoon of Reao, and species composition is somewhat different from that at Fanning, a fact consistent both with Salvat's (1967) suggestion that it is species composition of lagoons which distinguishes the biota of atolls in the Pacific, and the location of Fanning at the eastern periphery of the Central Pacific faunal region. Of the infaunal species reported for Reao (Salvat, 1972), only Tellina robusta is also dominant in Fanning lagoon. Macoma dispar and Codakia divergens are present but not in the apparent numbers reported for Reao. Three of the Reao species are represented by ecological equivalents at Fanning: Cerithium fasciatum appears to be replaced at Fanning by Rhinoclavis; Solidula solidula is replaced by Pupa; and Cerithium salebrosum, which occurs in the fine sediments of the Reao lagoon, may be replaced by Cerithium sculptum at Fanning. Of the species of the Reao coral assemblage (Acropora facies of Salvat, 1972), Tridacna and Cypraea moneta are also dominant at Fanning, but Pinctada maxima and Astralium petrosum appear to be replaced by Electroma and Trochus, respectively. Both dominant species of the massive corals at Reao, Arca ventricosa and Chama imbricata, are present in Fanning lagoon, but the dominant species of massive corals at Fanning is a third species, Barbatia decussata, which was not recorded from Reao.

In contrast to the obvious division of the macrofauna into groups associated with substrate types and differences in trophic structure among the major habitats, the micromollusks exhibit somewhat different patterns. The micromollusks are predominantly epifaunal and grazing herbivore throughout the lagoon, but each habitat type is distinguished in terms of species composition. Although we know little of the specific habits of the micromollusks encountered, it is tempting to relate differences in species composition to patterns of algal distribution reported by Tsuda (see p. 69, this report), who notes that "functional groups" of algae are distributed in recognizable patterns throughout the lagoon, with a Schizothrix-Microcoleus community along the shore where water movement is minimal, a Polysiphonia-Enteromorpha-Hypnea community near the passes where there is considerable water movement, and a Polysiphonia-Gelidiella community on the patch reefs. The distribution of micromollusks may also be associated with water clarity: tellinids predominate among the bivalves in the clear-water areas of the lagoon, both on the patch reefs and on the lagoon floor, and different species of the diastomid genus Obtortio and pyramidellids characterize clear and turbid water areas, respectively. It is of perhaps some interest that we have also recorded Obtortio pupoides (or a closely related species) in areas similar to those on the lagoon floor at Fanning, that is, where there is little water movement and where sediments are fine silt or sand (Kay, unpublished). Standing crops are, in general, greater on the reef flat, where there is relatively little topographical diversity, than on the patch reefs or lagoon floor, and species diversity is in general higher in the clear-water areas of the lagoon. Whatever the factors responsible for the distribution of micromollusks, it is clear from the patterns reported there is little sediment transport among lagoon reef flat, patch reef, and lagoon floor at Fanning. If, in future studies, we are able to more clearly define the factors affecting the distribution of micromollusks, they will serve as useful indicator organisms in reconstructing the history of lagoons.
The lagoon mollusks are distinguished from the seaward reef assemblages in both species composition and feeding types. On the seaward reefs the macrofauna is predominantly epifaunal, and carnivorous, or herbivorous; in the lagoon there is a high proportion of sessile bivalves and, hence, suspension feeders. The microfauna of the seaward reefs is predominantly faunal grazer, that of the lagoon is grazing herbivore. These differences reflect major differences in substrate and water chemistry between lagoon and seaward reefs. On the seaward reefs water clarity, wave action, and a predominantly solid substrate prevail; in the lagoon sand and rubble predominate, water movement is minimal, and the waters of the lagoon have both higher nutrient concentrations and variable salinity (Gordon, 1971; Smith and Pesret, cited above). Standing crops of micromollusks on the seaward reefs are noticeably less than in the lagoon, and species diversity noticeably higher.

Several features of the lagoon mollusks suggest both contemporaneous fluctuations in molluscan populations and changes which have occurred in the past. The accumulations of dead shells we noted are similar to those reported by Salvat (1972) at Reao, which were attributed to a local "epidemic". We suggest the accumulations of dead shells at Fanning were caused by local fluctuations in salinity and/or turbidity in the lagoon. The occurrence of fossil Tridacna in situ on various sectors of the lagoon reef flat where no living Tridacna now occur, and the presence of Strombus lentiginosus, Philippia, Terebra, etc. in fossil beds on the lagoon shore, indicate past changes in the lagoon. These changes may be associated with the closure of former passes into the lagoon and consequent changes in water clarity, coral growth, etc., and/or with changes in sea level.

ACKNOWLEDGMENTS

All members of the expedition to Fanning Island in 1972 contributed immeasurably to our report by assiduously noting and collecting mollusks for us. We are grateful to each one. We also thank Dr. Harry Ladd and Dr. Harald Rehder of the Smithsonian Institution, U.S. National Museum, Washington, D.C. for their criticisms and review of the manuscript.

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LITERATURE CITED


APPENDIX A

List of mollusks recorded from Fanning Island

AMPHINEURA
Chitonidae
Ischnochiton sp.

GASTROPODA
Scissurellidae
Scissurella coronata Watson, 1886
Scissurella sp.
Fissurellidae
Diodora granifera (Pease, 1861)
Emarginula bicancellata Montrouzier, 1860
E. diletta A. Adams, 1851
Hemitoma sp.
Patellidae
Patella flexuosa Quoy and Gaimard, 1834
Trochidae
Euchelus angulatus Pease, 1867
Monilea nucleus (Philippi, 1849)
Monilea sp.
Trochus histrio Reeve, 1848
Stomatellidae
Stomatella rosacea (Pease, 1867)
Synaptococheila concinna (Gould, 1845)
Turbinidae
Astrea calcar (Linn., 1758)
Leptothyra sp. cf. wellsi Ladd, 1966
Turbo argyrostromus Linn., 1758
Phasianellidae
Tricola variabilis (Pease, 1860)
Neritopsidae
Neritopsis radula (Linn., 1758)
Neritidae
Nerita albicilla Linn., 1758
N. plicata Linn., 1758
N. polita Linn., 1758
Puperita bensoni (Recluz, 1850)

1Rehder (personal communication) indicates an additional 14 species probably should be added to the list, the specimens collected by Dr. Charles Staseck in 1963 and now in the California Academy of Science.
2As Emarginula peasei Thiele, 1918 (Kay, 1971).
3As Patella stellaformis Reeve, 1842 (Kay, 1971).
4As Astrea helicina (Gmelin, 1791) (Kay, 1971). Rehder (personal communication suggests that A. confragosa plicatospinosa Pilbsry may be a more appropriate name.
5As Nerita bensoni (Kay, 1971).
Phenaco1epadidae
Phenaco1epas sp.
Littorinidae
Littorina coccinea (Gmelin, 1791)
L. scabra (Linn., 1758)
L. undulata Gray, 1839
Rissoidae
Alvania sp. cf. kenneyi Ladd, 1966
Alvania sp.
Merelina (2 spp.)
Pyramidelloidea sp. cf. miranda (A. Adams, 1861)
Parashiela beetsi Ladd, 1966
Rissoina ambigua Gould, 1851
R. exasperata Souverbie, 1866
R. sp. cf. incisa (Laseron, 1956)
R. miltozona Tomlin, 1915
R. plicata A. Adams, 1851
R. tenuistriata Pease, 1867
R. turricula Pease, 1860
Zebina semipliicata (Pease, 1863)
Z. tridentata (Michaud, 1830)
Assimineiidae
Assiminea nitida Pease, 1864
Vitrinellidae
Teinostoma (2 spp.)
Vitrinellids (2 spp.)
Skeneidae
Parviturbo minutissimus (Pilsbry, 1921)
Rissoellidae
Risoe1la sp.
Truncatellidae
Truncatella sp.
Omalogyridae
Omalogyra japonica (Habe, 1972)
Architectonicidae
Heliacus sp.
Philippia sp.
Vermetidae
Serpulorbis ali Hadfield and Kay, 1972
Dendropoma (2 or 3 spp.)
Caecidae
Meioceras sp. cf. sandwichensis de Folin, 1879
Elephantenellum sp.
Planaxidae
Planaxis lineatus (Da Costa, 1776)

---

6As a vitrinellid, Lophocochlias (Kay, 1971).
7This is the first record of this minute shell described as Ammonicera outside of Japan.
8Rehder (personal communication) suggests the Indo-Pacific species is separable as P. zonatus A. Adams, 1853.
Diastomidae

*Diata flamma* (Pease, 1867)

*Obertio diplax* (Watson, 1886)

*Q. pupoides* (A. Adams, 1860)

*Q. sulcifera* (A. Adams, 1862)

*Obertio* sp.

*Alaba goniochila* (A. Adams, 1860)

Cerithiidae

*Bittium impendens* (Hedley, 1899)

*E. zebrum* Kiener, 1841

*Bittium* (2 spp.)

*Cerithium atromarginatum* Dautzenberg and Bouge, 1933

*C. articulatum* Adams and Reeve, 1850

*C. bavayi* Vignal, 1902

*C. columna* Sowerby, 1855

*C. echinatum* (Lamarck, 1822)

*C. nesioticum* Pilsbry and Vanatta, 1906

*C. scultptum* Pease, 1869

*Clypeomorus brevis* (Quoy and Gaimard, 1834)

*Plesiotorochus* sp.

*Rhinoclavis asper* (Linn., 1758)

*R. procera* (Kiener, 1851)

*R. sinensis* (Gmelin, 1791)

*Seila* sp.

Cerithiopsidae

*Cerithiopsis* (5 spp.)

*Cerithiopsis turrita* (Laseron, 1956)

Triphoridae

*Triphora cancellata* Hinds, 1843

*T. cingulifera* Pease, 1861

*T. sp. cf. decorata* (Laseron, 1958)

*T. incisa* Pease, 1861

*T. sp. cf. minuta* (Laseron, 1958)

*T. regalia* Jousseaume, 1884

*T. rubra* Hinds, 1843

*T. sp. cf. tesselata* (Kosuge, 1963)

*T. triticea* Pease, 1861

*T. violacea* Quoy and Gaimard, 1833

*Triphora* (4 spp.)

Epitonidae

*Epitonium* sp. cf. *symmetrica* Pease, 1867

*Epitonium* (4 spp.)

Eulimidae

*Balcis* (4 spp.)

*Leiostraca* sp.

Stiliferidae

*Stilifer* sp.

---

9 As *Obertio pyrrhacme* (Melvill and Standen, 1896) (Kay, 1971).

10 As *Triphora dolicha* Watson, 1886 (Kay, 1971).
Strombidae

Strombus gibberulus gibbosus (Roeding, 1798)
S. lentiginosus Linn., 1758
S. luhuanus Linn., 1758
S. maculatus Sowerby, 1842
Lambis chiragra chiragra Linn., 1758
L. truncata sebae (Kiener, 1843)

Hipponicidae

Capulus tricarinata (Linn., 1758)
Hipponix conicus (Schumacher, 1817)

Fossaridae

Fossarum cumingii (A. Adams, 1853)
Fossarus sp.

Vanikoridae

Vanikoro gueriniana (Recluz, 1843)

Calyptraeidae

Cheilea equestris (Linn., 1758)

Cypraeidae

Cypraea annulus Linn., 1758
C. arabica Linn., 1758
C. argus Linn., 1758
C. asellus Linn., 1758
C. caputserpentis Linn., 1758
C. carneola Linn., 1758
C. childreni (Gray, 1825)
C. clandestina Linn., 1767
C. cribraria Linn., 1758
C. depressa Gray, 1824
C. erosa Linn., 1758
C. fimbriata Gmelin, 1791
C. goodalli Sowerby, 1832
C. helvola Linn., 1758
C. isabella Linn., 1758
C. lynx Linn., 1758
C. maculifera Schilder, 1932
C. mauritiana Linn., 1758
C. moneta Linn., 1758
C. nucleus Linn., 1758
C. poraria Linn., 1758
C. scurra Gmelin, 1791
C. schilderorum Iredale, 1939
C. talpa Linn., 1758
C. teres Gmelin, 1791
C. testudinaria Linn., 1758
C. tigris Linn., 1758
C. vitellus Linn., 1758

Ovulidae

Ovula ovum (Linn., 1758)

Eratoidae

Pedicularia pacifica Pease, 1865
Proterato sulcifera schmelziiana (Crosse, 1867)
Trivirostra pellucidula (Gaskoin, 1846)
Trivia sp.
Naticidae

Natica gua1teriana Recluz, 1814
Natica robillardi Sowerby, 1893
Polinices melanostomus (Gmelin, 1791)
P. tumidus (Swainson, 1840)

Cassidae

Cassaria ponderosa ponderosa (Gmelin, 1791)

Cymatiidae

Charonia tritonis (Linn., 1758)
Cymatium gemmatum (Reeve, 1844)
C. muricinum (Röding, 1798)
C. nicobaricum (Röding, 1798)
C. pileare (Linn, 1758)

Bursidae

Bursa bufonia (Gmelin, 1791)
B. granularis (Röding, 1798)

Tonnidae

Tonna perdix (Linn., 1758)
Malea pomum (Linn., 1758)

Muricidae

Chicoreus sp.
Murex sp.
Thaisidae

Drupella elata (Blainville, 1832)
Drupa morum Röding, 1798
D. ricina (Linn., 1758)

Drupina grossularia (Röding, 1798)

Maculotriton digitalis (Reeve, 1844)

Morula anaxeres (Kiener, 1835)
M. margaritica (Broderip, 1832)
M. uva (Röding, 1798)

Nassa serta (Bruguiere, 1799)

Thais acu1eata (Deshayes in Milne-Edwards, 1844)
T. armigera (Link, 1807)
T. intermedia (Kiener, 1836)

Corallophilidae

Corallophila violacea (Kiener, 1836)

Corallophila (2 spp.)

Magilus fimbriatus (A. Adams, 1852)

Quoyula madreporarum (Sowerby, 1834)

Columbellidae

Euplica palumbina (Gould, 1845)
E. variana (Sowerby, 1832)

Mitrella rorida (Reeve, 1859)
Seminella varia (Pease, 1861)

Anarithma metula (Hinds, 1843)

11As Natica marochiensis (Kay, 1971).
12As Polinices mamilla (Kay, 1971).
13As Bursa cruentata (Sowerby, 1835) (Kay, 1971).
14As Drupella cornus (Röding, 1798) (Kay, 1971).
Buccinidae

Cantharus undosus (Linn., 1758)
Engina maculata (Pease, 1869)
E. mendicaria (Linn., 1758)
E. tuberculosa Pease, 1863
Pisania truncata (Hinds, 1844)\textsuperscript{15}
P. ignea (Gmelin, 1791)

Nassariidae

Nassarius gaudiosus (Hinds, 1844)
N. graniferus (Kiener, 1834)
N. ravidus (A. Adams, 1851)

Fasciolariidae

Latirus amplustris Dillwyn, 1817
L. iris Lightfoot, 1786
Peristernia gemmata Reeve, 1847
P. nassatula (Lamarck, 1822)

Vasidae

Vasum armatum (Broderip, 1833)

Harpidae

Harpa amouretta Roding, 1798

Marginellidae

Hyalina elliptical (Redfield, 1870)
Granula sandwicensis (Pease, 1860)

Marginellida (4 spp.)

Mitridae

Imbricaria conovula (Quoy and Gaimard, 1833)
I. punctata (Swainson, 1821)
M. acuminatus Swainson, 1824
M. coffea Schubert and Wagner, 1829
M. cucumerina Lamarck, 1811
M. ferruginea Lamarck, 1811
M. litterata Lamarck, 1811
M. mitra (Linn., 1758)
M. paupercula (Linn., 1758)
M. saltata Pease, 1865
M. stictica Link, 1807

Pterygia crenulata (Gmelin, 1791)

Vexillum lautum (Reeve, 1845)
V. rubrum (Broderip, 1836)

Conidae

Conus catus Hwass in Brug., 1792
C. chaldaeus (Röding, 1798)
C. ebraeus Linn., 1758
C. flavidus Lamarck, 1810
C. lividus Hwass in Brug., 1792
C. miles Linn., 1758
C. miliaris Hwass in Brug., 1792
C. pulicarius Hwass in Brug., 1792
C. rattus Hwass in Brug., 1792

\textsuperscript{15}As Caducifer truncatus (Hinds, 1844) (Kay, 1971).
Elysidae

Elysia ornata (Pease, 1860)
E. rufescens (Pease, 1870)

Oxynoidae

Lobiger sp.

Aplysiidae

Dolabrifera dolabrifera (Rang, 1828)
Stylocheilus longicauda (Quoy and Gaimard, 1824)

Dorididae

Dendrodoris nigra (Stimpson, 1856)
Jorunna tomentosa (Cuvier, 1804)

BIVALVIA

Limopsidae

Cosa sp.

Arcidae

Aca r plicata (Dillwyn, 1877)
Arca ventricosa Lamarck, 1819
Barbatia decussata (Sowerby, 1833)
B. parva (Sowerby, 1833)

Mytilidae

Modiolus metcalfi Reeve, 1858
Lithophaga nasuta (Philippi, 1846)
Septifer (2 spp.)

Isognomonidae

Isognomon isognomon (Linn., 1758)
I. perna (Linn., 1767)

Pteriidae

Electroma sp.

Pinctada margaritifera (Linn., 1758)

Pinnidae

Atrina vexillum (Born, 1778)
Pin na muricata Linn., 1758

Pectinidae

Chlamys sp.

Gloripallium pallium (Linn., 1758)
Spondylidae

Spondylus ducalis Röding, 1798
Spondylus (2 spp.)

Limidae

Lima fragilis (Gmelin, 1791)
Ostreidae

Ostrea hanleyana Sowerby, 1871
O. sandvicensis Sowerby, 1871

Chamidae

Chama imbricata Broderip, 1834

Lucinidae

Codakia bella (Conrad, 1837)
C. punctata (Linn., 1758)

Wallucina sp. cf. gordon (E. A. Smith, 1886)
"Lucina" edentula (Linn., 1758)
C. retifer Menke, 1829
C. sponsalis Hwass in Brug., 1792
C. tulipa Linn., 1758
C. virgo Linn., 1758

Terebridae

Terebra affinis Gray, 1824
T. argus Hinds, 1844
T. crenulata (Linn., 1758)
T. dimidiata (Linn., 1758)
T. flavofasciata Pilsbry, 1921
T. maculata (Linn., 1758)
T. subulata (Linn., 1767)

Hastula penicillata (Hinds, 1844)

Turridae

Carinapex minutissima (Garrett, 1873)
Daphnella interrupta Pease, 1860
Etrema sp. cf. scalarina (Deshayes, 1863)
Eucithara angiostoma (Pease, 1868)
Kermia pumila (Mighels, 1845)
Macteola sp. cf. thiasotes (Melvill and Standen, 1897)

Microdaphne sp.

Tritonoturris sp.

Iredaelea (2 spp.)

Turrids (7 spp.)

Pyramidellidae

Chemnitzia (2 spp.)

Herviera giliriella (Melvill and Standen, 1896)

Odostomia sp. cf. oodes Watson, 1886
Q. sp. cf. scopulorum Watson, 1886

O. sp. (3 spp.)

Otopleura mitralis (A. Adams, 1855)

Pyramidella sp.

Turbonilla sp. A.

Turbonilla (2 spp.)

Aceteonidae

Pupa sulcata (Gmelin, 1791)

Pupa sp.

Hydatinidae

Haminea sp.

Scaphandridae

Acteocina sp. cf. sandwicensis (Pease, 1860)

Agaliidae

Chelidonura sp.

Eolidoids

Eoloids (2 spp.)

Atyidae

Atys cylindrica (Helbling, 1779)

Diniatys dentifer (A. Adams, 1850)

Cylichna pusilla (Pease, 1860)

Ellobiidae

Melampus sp.

Melampus flavus (Gmelin, 1791)
Erycinidae
Ke1lia sp.
Neobornia sp.
Carditidae
Cardita variegata (Bruguier, 1792)
Cardidae
Cardium sp.
Fragum fragum (Linn., 1758)
Mesodesmatidae
Rochefortina sandwichensis Smith, 1885
Tridacnidae
Tridacna maxima (Röding, 1798)
Trapeziidae
Trapezium oblongum (Linn., 1758)
Tellinidae
Arcopagia scobinata (Linn., 1758)
Quidnipeagus palatam Iredale, 1929
Macoma dispar (Conrad, 1837)
Tellina tongana (Quoy and Gaimard, 1833)
T. robusta (Hanley, 1844)
T. virgata Linn., 1758
Tellinids (4 spp.)
Semelidae
Semelangulus crebrimaculatus Sowerby, 1835
Veneridae
Gafarrarium pectinatum (Linn., 1758)16
Periglypta reticulata (Linn., 1758)
Periglypta sp.
Pitar prora (Conrad, 1837)
Sportellidae
Anisodonta sp. cf. lutea Dall, Bartsch, and Rehder, 1933
Dipondontidae
Diplodonta sp.

16 As Asaphis violascens (Kay, 1971).
DISTRIBUTIONS OF FISHES AT FANNING ISLAND

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Department of Zoology, University of Hawaii

D. E. Eckert
Department of Zoology, University of Hawaii

INTRODUCTION

The fishes of Fanning Atoll are mainly Indo-Pacific in origin and appear to represent an eastern extension of the Marshallese fauna (Gosline, 1971). Fanning and others of the Line islands are unusual in that the reef fishes are not exploited, nor has their habitat been disturbed by man.

There are few observations and relatively few fishes reported from Fanning in the literature. Fowler (1928) recorded some species from Fanning but no locality records were cited. Bakus (1964) observed some of the effects of fish grazing on algae and invertebrates in the Fanning lagoon and the Danger Point tidepool, but identified most of the fishes only to genus. Gosline (1971) reported on two collections from the tidepools at Danger Point and North Pass, the collections forming the basis for a checklist of Fanning Atoll inshore fishes (Gosline, 1970) and used as evidence in support of the hypothesis that ecological conditions around atolls rather than open-water distances between them are associated with differences in composition of fish faunas (Gosline, 1970, 1971).

The present study was undertaken to sample the Fanning Atoll fish fauna more thoroughly, to provide a baseline for comparison with other areas, and to investigate the composition of communities. Substrate and food preferences of some of the fish species are discussed. Measures of abundance are given and indices of diversity presented. Analysis of these data indicate specific problems in ecological relationships which require further study.

METHODS

Field Methods. Observations were made by SCUBA and free diving, and photography, narcotics, poison, and spears and nets were used to obtain fishes for identification. Fishes were identified in the field from descriptions of Gosline (1970), Schultz et al. (1953-1966), and Randall (1955). Other identifications were made by Dr. John E. Randall of the Bernice P. Bishop Museum, Honolulu, Hawaii.
Eight transect lines were traversed during July and August, 1972, and six in April 1973 (Figs. 1, 2, and 3). Polypropylene lines with numbered lead weights at 1-m intervals were placed perpendicularly to patch reef and outer reef slopes. Tabulations were made in 5-m increments by two divers, one on either side of the line, and the fishes counted when they occurred within 1.5 m on either side of the line and within 3 m above the substrate. The area of each sampled station was, therefore, 15 m². Qualitative observation were made at sites also shown in Figures 1 and 2.

Table 1 lists the fishes observed by us. Family names follow those of Greenwood et al. (1966). We made no special efforts to obtain fishes with secretive habits. We are uncertain of our field identifications of young carangids; the group is thus omitted from further consideration in this paper.

The average lengths (cm S.L.) of the most common fishes were estimated from specimens in the Bernice P. Bishop Museum, Honolulu, Hawaii, and at the University of Hawaii.

Statistical Methods. The distributions of most fishes, other organisms, and substrates are indisputably non-normal. Nevertheless, we use the Pearson product-moment correlation as a measure of association between species. Comparisons of techniques dealing with large correlation matrices suggest that the Pearson r is as robust as existing non-parametric correlation statistics, even where the data are not normally distributed (S. V. Smith, personal communication). A "non-parametric r", however, is merely a mathematical index, not a sample statistic which estimates population parameters (Sokal and Rohlf, 1969), and valid confidence limits are therefore not available.

Of the fishes we recorded, some were considered to occur in numbers too low for useful analysis. Two criteria were employed to select "reliable" variables: (1) fish, coral, and algal species and other substrate categories were required to occur in at least 6.67 per cent of the stations; and (2) mean cover for each coral species and algal and other substrate category per segment of transect was required to exceed 0.3 per cent and the mean density of each fish species was required to exceed 0.25 individuals per station. Data from the three 100-m transects were combined. Only positive correlations between 0.5 and 1.0 (indicating at least 75 per cent positive overlap) are discussed.

Because it was not possible to expend the same amount of sampling effort in every habitat area, and because some species observed within the habitats were absent from transects made there, we restricted further analysis to semiquantitative abundance ranks (Table 1). Each rank was arbitrarily assigned a quantitative coding corresponding to its minimum abundance, that is, fishes classed as "abundant" were assigned a code abundance of 20, those classed as "common" a code abundance of 5, and those classed as "occasional" an abundance code of 2. Diversities in bits per individual were calculated from the Shannon-Weaver equation. The amount of association between each pair of habitat-characteristic faunas was measured with the simple matching coefficient (Sokal and Sneath, 1963), which
Fig. 1. Location of study sites at Fanning Island. The numbers represent observation sites and the Ts, transect lines. The dashed line shows the margins of clear-lagoon waters.
Fig. 2. Location of the study sites in or near English Harbor Channel. The numbers represent observation sites and the Ts, transect lines. Site 31, represented by a row of dots, is a series of continuous observations in the middle of the channel.
Fig. 3. Danger Point tidepool. (a) A diagrammatic sketch of the tidepool illustrating substrate distribution—the dark line shows the position of the 60-meter Tₜ transect line. (b) The bottom profile along the transect line—stipple marks indicate sand; cross-hatched area, dead reef; coral heads, rubble, and shingle are also shown.
### TABLE 1 FISHES OBSERVED AT FANNING ISLAND IN 1972-1973

<table>
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<tr>
<th>Family</th>
<th>LS</th>
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<tbody>
<tr>
<td><strong>Family Albulidae</strong></td>
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<td>Albula vulpes (Linnaeus)</td>
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<td>Gymnothorax flavimarginatus (Ruppell)</td>
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<td>G. javanicus (Bleeker)</td>
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<td>G. margaritophorus Bleeker</td>
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<td>G. pictus (Ahl)</td>
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<td>G. undulatus (Lacepede)</td>
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<td>Chanos chanos (Forsskal)</td>
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<td>Belone platyura Bennett</td>
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<td>Adioryx caudimaculatus (Ruppell)</td>
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<td>A. lacteoguttatus (Cuvier)</td>
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<td>A. microstomus (Gunther)</td>
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<td>A. spinifer (Forsskal)</td>
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<td>A. tieroides (Bleeker)</td>
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<td>Flammee samara (Forsskal)</td>
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<td>Myripristis aeneus Castelnau</td>
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<td><strong>Family Fistulariidae</strong></td>
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<td>Fistularia petimba Lacepede</td>
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<td>Doryrhamphus melanopleura (Bleeker)</td>
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<td>Scorpaena albobrunnea Gunther</td>
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### Family Pomacentridae

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<td>Velichthys niger (Bloch)</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>Rhinecanthus aculeatus (Linnaeus)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>R. rectangulus (Bloch &amp; Schneider)</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
<tr>
<td>monacanthid species</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Family Tetraodontidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arothron hispidus (Linnaeus)</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
<td>O</td>
</tr>
<tr>
<td>A. meleagris (Lacepede)</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
</tr>
</tbody>
</table>

2 specimen at B.P. Bishop Museum, Honolulu, Hawaii
3 C. fallalca = C. ulitensis (W.C. Burgess, pers. comm. 1972)
4 photography of specimen available
6 Randall, H. (MS)
7 Randall, J.E. (MS)
8 S. axillaris and S. linearis are two forms of S. bandensis Bleeker
9 Randall, Pacific Sci., in press
10 S. brevifillis is the female form of S. chlorodon, Choat & Randall, ms.
11 S. frenatus is the male form of S. sexvittatus (Randall, J.E. 1963. Copeia)
12 Losey (ms); Smith-Vaniz & Randall (ms)
13 R.R. Rosenblatt (pers. comm.)
14 specimen like P. microlepis and with a tail marked as in Upeneus arge (Mullidae)
utilizes only presence/absence information. The simple matching coefficient of association is also equal to unity less the relative distance measure advocated by Blackith and Reyment (1971). Another association measure, Morisita's index of overlap, as modified by Horn (1966) for sampling with replacement, was also calculated. This measure utilizes the quantitative information contained in the abundance codes. Inasmuch as these statistics are presented for use in the generation of hypotheses rather than for testing, they are not to be considered population parameters and confidence limits are not appropriate (Pielou, 1972).

All transect data acquired from Fanning Atoll in 1972 are stored with the Hawaii Coastal Zone Data Bank at the Hawaii Institute of Geophysics, University of Hawaii, Honolulu, Hawaii.

Descriptive Methods. Fishes are described in the text and in Table 1 as "abundant", "common", "occasional", and "rare". Definitions for these terms are given above. Rare fish species (one individual per site or transect line) are included only in Table 1. Additional species poisoned in the Fanning tidepools by Gosline (1970), but not observed by us, are listed in Table 2. Food habits of the common and abundant species, where known, are recorded in Table 3. A list of occasional fishes and their locations within the habitats is presented in Table 4. Fishes restricted to a single habitat area, or seen only once outside of a single habitat, are listed in Table 5. Figures 4 to 9, depicting the abundance and average length of the common and abundant species are cited once and follow our listings of the abundant fishes in each habitat. The average lengths of the abundant and common fishes not listed in Figures 4 to 9 are cited in the text.

HABITAT CATEGORIES

The habitat areas used were subjectively selected and defined. Their limits are based primarily on our perceptions of discontinuities of physiography, water depth, and water clarity.

The lagoon shoreline habitat includes the entire rim of the lagoon. Most parts are sand or sandy-mud flats, with varying algal cover and microfauna (Kay and Switzer, p. 111, this report). The area adjacent to Cartwright Point (Fig. 1) was studied most intensively; it includes an atypically large quantity of natural and man-made cover. The only cover along most of the lagoon shoreline is provided by fallen coconut palms and rare limestone outcroppings. This habitat showed the greatest range of salinities: 34.8 °/oo in 1970 (Roy and Smith, 1971) and 29.0 °/oo in 1972 (Smith and Pesret, p. 21, this report). Except in the immediate vicinity of the passes, the lagoon shoreline is characterized by extremely turbid waters. Diver vision was limited to about 60 cm vertically and 20 cm horizontally, even at Cartwright Point. Occasional brief squalls provided only slight wave action and currents were not noticeable. The lagoon shoreline habitat was observed for 2½ hours.
Table 2 Additional Species Taken at Fanning Island in 1970

The following species are listed by Gosline (1970) from poison stations in tidepool areas at Fanning Island. They are mostly secretive species and were not seen by us in 1972.

<table>
<thead>
<tr>
<th>Family Moringuidae</th>
<th>Moringua (ferruginea?)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Family Muraenidae</td>
<td>Anarchias leucurus</td>
</tr>
<tr>
<td></td>
<td>Echidna nebulosa</td>
</tr>
<tr>
<td></td>
<td>E. unicolor</td>
</tr>
<tr>
<td></td>
<td>Gymnothorax bayeri</td>
</tr>
<tr>
<td></td>
<td>G. buricensis</td>
</tr>
<tr>
<td></td>
<td>G. gracilicaudus</td>
</tr>
<tr>
<td></td>
<td>G. margaritophorus</td>
</tr>
<tr>
<td></td>
<td>G. monostigma</td>
</tr>
<tr>
<td></td>
<td>G. petelli</td>
</tr>
<tr>
<td></td>
<td>Muraena pardalis</td>
</tr>
<tr>
<td></td>
<td>Uropterygius polypilus</td>
</tr>
<tr>
<td></td>
<td>U. tigrinus</td>
</tr>
<tr>
<td></td>
<td>U. xanthopterus</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Family Opichthidae</th>
<th>Leiuranus semicinctus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Muraenichthys gymnotus</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Family Antennariidae</th>
<th>Antennarius altipinnis</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Family Brotulidae</th>
<th>Dinematicichthys (sp.?)</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Family Scorpaenidae</th>
<th>Pterois antennata</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Scorpaenodes guamensis</td>
</tr>
<tr>
<td></td>
<td>Scorpaenopsis gibbosa</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Family Serranidae</th>
<th>Cepholopholis leopadus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Epinephelus elongatus</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Family Apogonidae</th>
<th>Apogon marmoratus</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Gymnapogon urospilotus</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Family Blenniidae</th>
<th>Rhabdoblennius (sp?)</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Family Tripterygidae</th>
<th>Tripterygion hemimelas</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Family Callionymidae</th>
<th>Synchiropus laddi</th>
</tr>
</thead>
</table>

<table>
<thead>
<tr>
<th>Family Gobiidae</th>
<th>Ctenogobius?</th>
<th>tongarevae</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Drombus tutilae</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Eviota epiphanes</td>
<td></td>
</tr>
<tr>
<td></td>
<td>E. prasites</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Gobiodon quinque-lineatus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>G. rivulatus</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Paragobiodon kerri</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Valenciennes hasselti</td>
<td></td>
</tr>
<tr>
<td></td>
<td>V. sclateri</td>
<td></td>
</tr>
</tbody>
</table>
The turbid-lagoon patch reef habitat includes most of the lagoon and ranges from variably sized, isolated coral heads to extensive reticular reef formations, rising from a flat, calcareous mud bottom. The tops of the patch reefs are rimmed by dense growths of *Acropora delicatula* and other branching corals to depths of 3 to 5 meters. The reef surfaces are often within 15 cm of low water (Roy and Smith, 1971) and include sand flats ringed with rubble. Salinities ranged from 35.7 °/oo in 1970 (Roy and Smith, 1971) to 31.5 °/oo in 1972 (Smith, cited above). Water circulation is very slow inside some of the ponds formed by reef networks (Smith, cited above). The most striking feature of this habitat is the turbidity of the water. At Suez Pond (T7 in Fig. 1) the extinction coefficient was 0.13 m⁻¹ as opposed to 0.28 m⁻¹ for clear water areas in 1970 (Roy and Smith, 1971); a 1-m path-length transmissometer gave readings of about 12% for the turbid lagoon in 1972 (Stroup and Meyers, see p. 7, this report). Wave action is negligible except during brief squalls. Currents in the turbid lagoon were clocked at 0.1 to 0.2 knots in 1970 (Gallagher et al., 1971). Nearly 14 hours were spent observing fishes on the turbid lagoon patch reefs; one 100-m transect (T2) and one 20-m transect (T7) were traversed (Fig. 1).

The clear lagoon patch reefs are similar to those in the turbid lagoon but lie within the English Harbor region of the lagoon (Fig. 1) and are subject to alternating clear (ocean-water) and turbid (lagoon-water) tidal flows. The substrate is sandy and flat; water depths range between 2 and 14 meters. Frequent limestone outcroppings vary in size and form from rounded massive structures to linear reefs with central sandy plateaus. The surfaces of the outcroppings range from depths of 1 to 13 meters. The number of coral species is greater here than on turbid lagoon patch reefs, but the amount of live coral cover is lower: in the turbid lagoon living coral covered 23% of the transect (T7); in the clear lagoon, 8% (T1) (Maragos, pers. comm.). *Porites lutea* and *Leptastrea purpurea* make up about 43% of the living coral in the clear lagoon. Salinities ranged from 34.8 °/oo in 1970 (Roy and Smith, 1971) to 33.0 °/oo in 1972 (Smith, cited above). Diver visibility varied between 2 and 15 m according to the tide and distance from the channel. Transmissometer readings from this habitat ranged from 15% to 40% (Stroup and Meyers, cited above). Wave action was strong only during squalls, and currents were much weaker than in the channel habitat. Ten and one-half hours were spent observing fishes on the clear lagoon patch reefs. One 100-m transect (T1) and three 20-m transects (T4-6) were traversed (Fig. 1).

The three passes differ from one another but all are characterized by rapid, nearly continuous water movement, with alternating cycles of clear and turbid water separated by brief periods of slack tide. The current velocity in English Harbor pass often exceeded 5 knots. The bottoms of the passes were scoured limestone overlain with rubble, "boulders" with or without encrusting hard corals, soft corals, and some loose sand. The sides of the English Harbor pass were of loose shingle; those at Rapa and North Pass were coarse sand. Depths in the channels were 2 to 8 m (Gallagher et al., 1971). Salinities were similar to those of the open ocean: 35 °/oo in 1970 (Roy and Smith, 1971) and 34 °/oo in 1972 (Smith, cited above). Diver visibility was often more than 20 m on incoming tides;
the outgoing water was usually turbid, with visibility less than 4 meters. Transmissometer readings ranged from 20% to 64% (Stroup and Meyers, cited above). A little more than 2 hours in 1972, and 14 hours in 1973, were spent observing the fishes, mostly in the English Harbor channel. Four 20-m transects were made in 1973 (Fig. 2).

The tidepool habitat at Fanning Island typically possesses a flat, sandy bottom with considerable relief from living hard and soft corals, limestone outcroppings, shingle, and dead coral rubble. The edges of the pools are variously sand, cobble, rubble, shingle, and limestone. There is constant water exchange with the open ocean, across the outer reef, or with one of the channels. Depths range from 0 to 2 meters. The only tidepool habitat intensively studied was at Danger Point (Fig. 2). Other areas included in this habitat category are the extensive shallow flats inside the fringing reef at North Pass, and pools in a similar but smaller and less well-defined moat at Rapa Pass. The Danger Point tidepool had ranges of salinity and turbidity similar to those in the adjacent pass. Visibilities in the pools were from 2 to 15 meters. The pools were studied for 7 hours (6 at the Danger Point tidepool). One 60-m transect (T8) was traversed at Danger Point (Fig. 3).

The outer reef flats are platforms from 5 to 30 m wide, backed by shingle berms. The flats are comprised of living hard corals, dead coral, rubble, shingle, and varying algal cover. The reef flats are generally submerged in 0.5 to 2 m of water, but may become partially exposed by very low tides. The seaward portions and surge channels, which run perpendicular to the shore, are always submerged. The most impressive features of the outer reef-flat habitat are strong surge and wave conditions. Visibility ranged from 2 to 20 m but was often reduced by the bubbles formed by breaking waves. Two 20-m transects (T10 and T12, Fig. 1) were traversed during 6.5 hours of observation of the outer reef flats.

The outer reef-slope habitat was intensively studied only in the English Harbor pass area, particularly at the transect site (T3, Fig. 1). An attempt to study the slope outside North Pass was abandoned because of the persistent attention of numerous grey reef sharks (Carcharhinus amblyrhinchos). The substrate of the Danger Point reef slope is typically live corals (forming about 53 per cent cover; Maragos, p. 187 this report) and rubble, providing much topographical relief. Throughout the hard substrate are scattered occasional small pockets of sand. Depths on the T3 transect were from 7 to 36 m, with a slope of 10° to a depth of 15 m and of 19° to 36 m. The coral and rubble are replaced by a sandy slope at about 36 m depth. Salinities over the slope are typical of oceanic conditions: 35.1 °/oo (Roy and Smith, 1971) to 34.8 °/oo (Smith, cited above). Visibility varied from 8 to 20 m, the lesser visibilities associated with the turbid, ebb-tidal plume from the English Harbor pass which often extended over the study area. The outer reef slopes included the greatest amount and greatest diversity of corals encountered at Fanning (Maragos, cited above), as well as the greatest depth range. Nearly seven hours of observations were made on the reef slope habitat and 100 m of transect traversed. 
TABLE 3 Food habits of the abundant, common, or unrestricted fishes at Fanning Island (for which information is available)

<table>
<thead>
<tr>
<th>Species</th>
<th>Food Habits</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chanos chanos</td>
<td>filamentous microalgae on sand</td>
<td>1</td>
</tr>
<tr>
<td>Hyporhamphus acutus</td>
<td>epibenthic fishes &amp; invertebrates</td>
<td>1</td>
</tr>
<tr>
<td>Belone platyura</td>
<td>pelagic fishes &amp; crustaceans</td>
<td>1</td>
</tr>
<tr>
<td>Hypoptychus kuntee</td>
<td>(nocturnal) crustaceans</td>
<td>1,13</td>
</tr>
<tr>
<td>L. murdjan</td>
<td>fishes, crustaceans, worms</td>
<td>1,2</td>
</tr>
<tr>
<td>Cephalopholis argus</td>
<td>fishes, benthic crustaceans, mollusks</td>
<td>1,3,8</td>
</tr>
<tr>
<td>Epinephelus merra</td>
<td>plankton</td>
<td>6</td>
</tr>
<tr>
<td>Mirolabrichthys sp.</td>
<td>plankton</td>
<td>1</td>
</tr>
<tr>
<td>Pseudanthias sp. nov.</td>
<td>plankton</td>
<td>1</td>
</tr>
<tr>
<td>Cheilodipterus quinguelleata</td>
<td>plankton</td>
<td>1</td>
</tr>
<tr>
<td>Caesio xanthonotus</td>
<td>fishes</td>
<td>1</td>
</tr>
<tr>
<td>Lutjanus bohar</td>
<td>(nocturnal) crustaceans &amp; fishes</td>
<td>2,3</td>
</tr>
<tr>
<td>L. fulvus</td>
<td>fishes</td>
<td>1</td>
</tr>
<tr>
<td>L. monostigma</td>
<td>(nocturnal) benthic sand invertebrates</td>
<td>2</td>
</tr>
<tr>
<td>Bulleidichthys flavolineata</td>
<td>(nocturnal) benthic fishes &amp; sand invertebrates</td>
<td>1,2</td>
</tr>
<tr>
<td>M. samoensis</td>
<td>benthic fishes &amp; sand invertebrates</td>
<td>6</td>
</tr>
<tr>
<td>P. barberinus</td>
<td>algal fronds &amp; sponges</td>
<td>1,14</td>
</tr>
<tr>
<td>Centropyge flavissimus</td>
<td>benthic epifauna, coral polyps &amp; algae</td>
<td>1</td>
</tr>
<tr>
<td>C. auriga</td>
<td>coral tips &amp; algae</td>
<td>1</td>
</tr>
<tr>
<td>C. lupula</td>
<td>benthic epifauna</td>
<td>6</td>
</tr>
<tr>
<td>C. ornatissimus</td>
<td>coral polyps</td>
<td>2</td>
</tr>
<tr>
<td>Abudedefduf dicki</td>
<td>algae (browser)</td>
<td>1</td>
</tr>
<tr>
<td>A. glaucus</td>
<td>filamentous algae &amp; its epifauna, epifauna of its corals (grazer)</td>
<td>1</td>
</tr>
<tr>
<td>A. imparipennis</td>
<td>filamentous algae &amp; epifauna (browser)</td>
<td>1</td>
</tr>
<tr>
<td>A. sordidus</td>
<td>plankton</td>
<td>6</td>
</tr>
<tr>
<td>Chromis acares</td>
<td>zooplankton, fish eggs</td>
<td>1,12</td>
</tr>
<tr>
<td>G. atripectoralis</td>
<td>zooplankton</td>
<td>6</td>
</tr>
<tr>
<td>C. marraciner</td>
<td>&quot;</td>
<td>2</td>
</tr>
<tr>
<td>G. vandobelli</td>
<td>zooplankton, algae &amp; epibenthic crustacea filamentous algae (grazer) &amp; fish eggs</td>
<td>1</td>
</tr>
<tr>
<td>Dascyllus aruanus</td>
<td>plankton</td>
<td>2</td>
</tr>
<tr>
<td>Pomacentrus albofasciatus</td>
<td>filamentous algae on sand (grazer), substrates</td>
<td>1,2</td>
</tr>
<tr>
<td>E. coelestis</td>
<td>crustaceans &amp; fishes</td>
<td>2</td>
</tr>
<tr>
<td>P. nigricans</td>
<td>small fishes &amp; crustaceans</td>
<td>2</td>
</tr>
<tr>
<td>Citrinichthys ocycephalus</td>
<td>microalgae</td>
<td>1</td>
</tr>
<tr>
<td>Paracirrhites forsteri</td>
<td>&quot;</td>
<td>1</td>
</tr>
<tr>
<td>Chelon vaigiensis</td>
<td>juveniles clean crustaceans from interstices of coral</td>
<td>6</td>
</tr>
<tr>
<td>Crenimugil crenilabis</td>
<td>benthic &amp; fossorial, hard-bodied gastropods &amp; crustaceans</td>
<td>1,2</td>
</tr>
<tr>
<td>Bodianus loxozonus</td>
<td>benthic fauna</td>
<td>1</td>
</tr>
<tr>
<td>Compsoheter variegatus</td>
<td>epifauna invertebrates especially hermit crabs</td>
<td>1</td>
</tr>
<tr>
<td>Halichoeres centriquadrus</td>
<td>fish parasites, plankton &amp; benthic invertebrates</td>
<td>1,2</td>
</tr>
<tr>
<td>H. marraritaceus</td>
<td>plankton</td>
<td>1</td>
</tr>
<tr>
<td>H. trimaculatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Labroides dimidiatus</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Note:** The table lists species associated with their respective food habits and references.
<table>
<thead>
<tr>
<th>Species</th>
<th>Food Habits</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>S. rubrolabiliatus</td>
<td>fish parasites, plankton</td>
<td>6</td>
</tr>
<tr>
<td>Pseudochelinus hexataenia</td>
<td>benthic invertebrates</td>
<td>1</td>
</tr>
<tr>
<td>Stethoalula axillaris</td>
<td>(non-selective carnivore)</td>
<td></td>
</tr>
<tr>
<td></td>
<td>mostly benthic polychaetes, crustacea, foraminifera</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>benthic epifauna</td>
<td>6</td>
</tr>
<tr>
<td>Thalassoma ambycephalus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. lunare</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. quinquennitata</td>
<td></td>
<td></td>
</tr>
<tr>
<td>T. purpureum</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>small fishes, benthic invertebrates</td>
<td>1</td>
</tr>
<tr>
<td>Chlorurus gibbus</td>
<td>nips or breaks off dead coral</td>
<td>6</td>
</tr>
<tr>
<td>Scarus hardi</td>
<td>nips at dead coral</td>
<td>6</td>
</tr>
<tr>
<td>S. jonesi</td>
<td>grazer, coral &amp; algae</td>
<td>6</td>
</tr>
<tr>
<td>S. eporeidus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cirrippectes variologus</td>
<td>filamental algae &amp; its epifauna</td>
<td>1, 6</td>
</tr>
<tr>
<td>Istiblennius edentulus</td>
<td>filamental algae &amp; its epifauna, detritus (grazer)</td>
<td>1</td>
</tr>
<tr>
<td>J. paulus</td>
<td>filamental algae &amp; its epifauna, detritus (grazer)</td>
<td>1</td>
</tr>
<tr>
<td>Amblyoplobus albimaculatus</td>
<td>(omnivore) detritus, invertebrates</td>
<td>1</td>
</tr>
<tr>
<td>Gnatholipis anjerensis</td>
<td>sifits sand</td>
<td>6</td>
</tr>
<tr>
<td>Paragobiodon echinocephalus</td>
<td>fish eggs, worms from the interstices of coral</td>
<td>1</td>
</tr>
<tr>
<td>Acanthurus gahnm</td>
<td>filamental algae, (grazer on sand)</td>
<td>1, 2, 5</td>
</tr>
<tr>
<td>A. glaucopeariae</td>
<td>algae (browser)</td>
<td>1</td>
</tr>
<tr>
<td>A. lineatus</td>
<td>red algae (browser)</td>
<td>1</td>
</tr>
<tr>
<td>A. olivaceus</td>
<td>scrapes algae from hard substrate &amp; from compacted sand</td>
<td>1, 2</td>
</tr>
<tr>
<td>A. triostegus</td>
<td>algae epifauna (browser)</td>
<td>5, 9, 10, 11</td>
</tr>
<tr>
<td>A. xanthopterus</td>
<td>filamentous algae (grazer)</td>
<td>1, 5</td>
</tr>
<tr>
<td>Ctenochaetus cyanoguttatus</td>
<td>plankton</td>
<td>6</td>
</tr>
<tr>
<td></td>
<td>algae sponges</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>algae grazer</td>
<td>7</td>
</tr>
<tr>
<td>C. striatus</td>
<td>sponges, foraminifera, epifauna crustaceans</td>
<td>7</td>
</tr>
<tr>
<td></td>
<td>(grazer)</td>
<td></td>
</tr>
<tr>
<td>Rhinecanthus aculeatus</td>
<td>(indiscriminate omnivore)</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>algae, Acropora tips, gastropods</td>
<td></td>
</tr>
<tr>
<td>B. rectangulus</td>
<td>(omnivore) algae, crustaceans</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>(opportunistic carnivore)</td>
<td></td>
</tr>
<tr>
<td>Arctothron hispidus</td>
<td>land crabs</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The following references are listed in full in the bibliography.

8. Bengheyfield (1971)
RESULTS

Widely Distributed Species

The fishes discussed in this section were found in most or all of the areas studied. Many seemed to be limited to specific habitat sites by general substrate characteristics rather than water conditions. *Chlorurus gibbus* was an apparent exception: it was seen in small groups in the lagoon and tidepools, often in large schools in the English Harbor pass and over the outer reef slope, over every substrate type, and at depths of from 0 to 25 m. This species was observed feeding on dead coral in the tidepools and over the outer slope.

**Sand Patches Near Limestone Outcroppings.** *Halichoeres trimaculatus* and *Acanthurus xanthopterus* are characteristic of areas dominated by sand flats with occasional outcroppings of rubble or live coral. *Halichoeres trimaculatus* is one of the most widely distributed species at Fanning (Table 1); abundant in the lagoon, tidepools, and passes, and absent only where there are unbroken stretches of either coral or sand. Elsewhere this species is characteristic of sandy lagoons (Randall, 1955). *Acanthurus xanthopterus* was present over sandy areas in the turbid lagoon channels and over reef flats, and common in the clear lagoon and on the outer reef slope.

**Coral and Limestone Outcroppings.** *Chaetodon auriga*, *C. lunula*, *Gomphosus varius*, *Labroides dimidiatus*, *Thalassoma amblycephalus*, and *Ctenochaetus striatus*, are present wherever there is substrate relief provided by dead or living coral.

*Chaetodon auriga* generally wander in pairs over live coral and coralline rubble. *C. lunula* is most often seen in pairs or small groups near the sand at bases of coral outcroppings. *C. auriga* was more common (0.4 per station) on all calm water reefs of the lagoon and outer reef slopes than *C. lunula* (0.2 per station). Tidepool and pass transects included more *C. lunula* than *C. auriga* (0.4 *C. auriga*, and 1.1 *C. lunula* per station).

*Gomphosus varius* occurs in greatest numbers along the outer reef slope, with females and juveniles occurring more frequently in the lagoon and tidepools than adult males. *Labroides dimidiatus* had established cleaning stations singly or in small groups in areas where large numbers of fishes were observed. These are more common in the pass than elsewhere (except at the marginal T6 transect (see below). Yellow and green colored morphs of this wrasse are common only on the outer reef slope. *Thalassoma amblycephalus* are abundant in the pass, clear lagoon, and tidepools. The young often formed schools over clear water patch reefs (3.5 and 3.8 indiv. per station on the upper halves of T1 and T6), while adults were encountered in smaller numbers. The species is common on the outer reef flats.

*Ctenochaetus striatus* was found in smaller numbers in the lagoon than elsewhere (0.1 per station in the lagoon; 10.0 on the outer reef flats; 7.2 on the upper half of the reef slope transect; 2.3 in the pass and on the
lower half of the reef slope transect). It is common in the tidepools along the shingle ramparts (Fig. 3).

** Depths of 0-15 m. ** The following fishes are widely distributed in the shallow waters in areas of moderate to high relief.

** Epinephelus merra ** is found in semiprotected crevices, bases of coral heads, and so forth. It is the most common grouper in the tidepools and on clear lagoon patch reefs. Two specimens were seen on the outer slope transect, not deeper than 13 meters. ** E. merra ** was found in a wide variety of habitats at Eniwetok, particularly "in areas of dead coral rubble and fairly calm water" (Bengeyfield, 1971) and Randall and Brock (1960) found this species at depths above 27 m in the Society Islands, although not on outer reef slopes.

** Pomacentrus albofasciatus ** is abundant to common in all shallow water regions except along the sandy lagoon shore and outer reef flats (6.1 indiv. per station; T1, T2, T4-8). A zone of abundant ** P. albofasciatus ** occurred in the rubble and shingle along the shoreline of English Harbor pass (18.0 per station; T9) but they were only occasionally seen elsewhere in the channel (T11, 13-14). These fish dig burrows under rocks and defend territories around them.

** Thalassoma purpureum ** and its young, "** T. umbrostigma " ** (Kato, 1972), ** are seen occasionally in all areas of the lagoon and tidepools, and are abundant on the pass and outer reef flat transects.

** Scarus harid ** is the mostly widely distributed shallow water parrotfish at Fanning Island. Schools of adult males are seen most often on the reef flats; females are more frequently found in the tidepool areas and both sexes are in the passes.

** Acanthurus triostegus ** is often seen in large numbers on the outer reef flat, channel, and tidepools. It is common in the clear lagoon, and present in lesser numbers in turbid lagoon waters and along the shoreline.

** FISHES FOUND IN SPECIFIC AREAS OR HABITATS **

** Lagoon Shoreline Fishes **

** Chanos chanos, Chelon vaigiensis, ** and ** Crenimugil crenilabis, ** typically schooling species, are common in this habitat. ** Chanos chanos is also common in the clear lagoon, Chelon vaigiensis in the Danger Point tidepool, ** and ** Crenimugil crenilabis ** on the outer reef flat; the last is abundant in the tidepools. ** Lutjanus fulvus ** is common primarily near Cartwright Point in areas with considerable cover (rubble, fallen coconut trees, etc.), and also in the turbid lagoon and tidepools.

** Occasional shoreline fishes are listed in Table 4 (A).**
<table>
<thead>
<tr>
<th>Table 4</th>
<th>Occasional fishes observed at Fanning Island</th>
</tr>
</thead>
<tbody>
<tr>
<td>A. Lagoon Shore</td>
<td>C. Clear Lagoon</td>
</tr>
<tr>
<td>1. Sandy areas</td>
<td>1. Sandy areas</td>
</tr>
<tr>
<td>Albula vulpes</td>
<td>Malacanthus latovittatus</td>
</tr>
<tr>
<td>Mullolldichthys flavolineata</td>
<td>Parupeneus barberinus</td>
</tr>
<tr>
<td>Parupeneus barbatus</td>
<td>Ambyizzois albo fasciatus</td>
</tr>
<tr>
<td>Acanthurus triostegus</td>
<td>Asteropertervx semipunctatus</td>
</tr>
<tr>
<td>A. xanthopterus</td>
<td>Electrides xricha</td>
</tr>
<tr>
<td>Sararicus triocellatus</td>
<td>Pterolepis miroplexis</td>
</tr>
<tr>
<td>Arothron hispidus</td>
<td>2. Coral and rubble areas</td>
</tr>
<tr>
<td></td>
<td>Centropyge flavissima</td>
</tr>
<tr>
<td>2. Near rocks</td>
<td>Abudefuf dieki</td>
</tr>
<tr>
<td>Lutjanus monostigma</td>
<td>Chromis atripectoralis</td>
</tr>
<tr>
<td>Abudefuf glaucus</td>
<td>C. marmorifer</td>
</tr>
<tr>
<td>A. sorcius</td>
<td>Dascyllus sp. nov.</td>
</tr>
<tr>
<td>Pomacentrus albofasciatus</td>
<td>Citholineus termi</td>
</tr>
<tr>
<td>Thalassoma purpueum</td>
<td>Pseudocheilinus hexataenia</td>
</tr>
<tr>
<td>juvenile scarids</td>
<td>Cirrhiproccus sp. nov.</td>
</tr>
<tr>
<td>Rhinecanthus aculeatus</td>
<td>Pygopontus neophyton</td>
</tr>
<tr>
<td></td>
<td>Quinquelus naraharae</td>
</tr>
<tr>
<td></td>
<td>Ctenochaetus striatus</td>
</tr>
<tr>
<td>B. Turbid Lagoon</td>
<td>3. Holes and caves</td>
</tr>
<tr>
<td>1. Sandy areas</td>
<td>Adiorxy lacteoguttatus</td>
</tr>
<tr>
<td>Parupeneus barberinus</td>
<td>Kyphophis amamens</td>
</tr>
<tr>
<td>Chlorurus gibbus</td>
<td>C. pullus</td>
</tr>
<tr>
<td>Scarus harris</td>
<td>Cephalopholis argus</td>
</tr>
<tr>
<td>Acanthurus triostegus</td>
<td>C. urodolus</td>
</tr>
<tr>
<td>A. xanthopterus</td>
<td>Epinephelus fascioguttatus</td>
</tr>
<tr>
<td>Rhinecanthus aculeatus</td>
<td>Apogon frena</td>
</tr>
<tr>
<td>2. Patch reef tops</td>
<td>A. robustus</td>
</tr>
<tr>
<td>Monotaxis grandoculis</td>
<td>Chelidodentrus quinque lineata</td>
</tr>
<tr>
<td>Chaetodon auriga</td>
<td>4. Errant</td>
</tr>
<tr>
<td>C. lunula</td>
<td>Lutjanus fulvus</td>
</tr>
<tr>
<td>C. trifasciatus</td>
<td>Gnathodentrus aureolineatus</td>
</tr>
<tr>
<td>C. vagabundis</td>
<td>Monotaxis grandoculis</td>
</tr>
<tr>
<td>Dascyllus sp. nov.</td>
<td>Parupeneus barberinus</td>
</tr>
<tr>
<td>Pomacentrus nigricans</td>
<td>L. multifasciatus</td>
</tr>
<tr>
<td>Labroides dimidiatus</td>
<td>Chaetodon auriga</td>
</tr>
<tr>
<td>Thalassoma amblycephalus</td>
<td>C. packati</td>
</tr>
<tr>
<td>T. quinquevittata</td>
<td>C. ellipsoideum</td>
</tr>
<tr>
<td>T. purpureum</td>
<td>C. lunula</td>
</tr>
<tr>
<td>Scarus oviceps</td>
<td>C. ornatusisimius</td>
</tr>
<tr>
<td>S. pectoralis</td>
<td>C. semeion</td>
</tr>
<tr>
<td>Zebrasoma veliferum</td>
<td>C. trifasciatus</td>
</tr>
<tr>
<td></td>
<td>C. uiletensis</td>
</tr>
<tr>
<td></td>
<td>Megaprotodon strigangulus</td>
</tr>
<tr>
<td>3. Patch reef sides</td>
<td>Pomacentrus pavo</td>
</tr>
<tr>
<td>Epinephelus mero</td>
<td>Crenimuridqu crenilabis</td>
</tr>
<tr>
<td>Epiptera distigma</td>
<td>Chelinus undulatus</td>
</tr>
<tr>
<td>Fusciobius neophyton</td>
<td>Epibulus insidiosus</td>
</tr>
<tr>
<td>Gnatholepis anjerensis</td>
<td>Gomphogobius varius</td>
</tr>
<tr>
<td>Ctenochaetus striatus</td>
<td>Thalassoma quinquevittata</td>
</tr>
<tr>
<td></td>
<td>T. purpureum</td>
</tr>
<tr>
<td></td>
<td>Chlorurus gibbus</td>
</tr>
<tr>
<td>Arothron hispidus</td>
<td>Scarus ghobban</td>
</tr>
<tr>
<td>3. Sandy areas</td>
<td>S. globiceps</td>
</tr>
<tr>
<td>Malacanthus latovittatus</td>
<td>S. harid</td>
</tr>
<tr>
<td>Parupeneus barberinus</td>
<td>S. longis</td>
</tr>
<tr>
<td>Ambyizzois albo fasciatus</td>
<td>S. oviceps</td>
</tr>
<tr>
<td>Asteropertervx semipunctatus</td>
<td>A. sorcius</td>
</tr>
<tr>
<td>Electrides xricha</td>
<td>juvenile scarids</td>
</tr>
<tr>
<td>Pterolepis miroplexis</td>
<td>Zebrasoma veliferum</td>
</tr>
<tr>
<td>Quinquelus naraharae</td>
<td>Rhinecanthus aculeatus</td>
</tr>
</tbody>
</table>
D. Channels

1. Sandy areas
   Malacanthus latovittatus
   Parupeneus multifasciatus
   P. pleurostigma
   Hemipteronotus leolaeus
   Parapercis cephalophiactatus
   Labroides striatus
   Fusigobius neophytus
   Ptereleotris microlepis
   Balistoides viridescens
   Rhinecanthus aculeatus
   Arothron hispidus

2. On or within rocks or coral heads
   Cephalopholis argus
   E. merri
   Epinephelus fuscoguttatus
   E. spilotoiceps
   Cirrhitichthys oxycephalus
   Paracirrhites forsteri
   Pseudochelinus hexataenia

3. Near rocks or coral heads
   Monotaxis grandoculis
   Chaetodon auriga
   C. ephippium
   C. quadrimaculatus
   Holocanthus sp. nov.
   Abuderdaf clausus
   A. imparipennis
   Chromis lepidolepis
   C. vanderbilti
   Pomacentrus lividus
   P. hexagonatus
   Cirrhilabrus temmincki
   C. sp. nov.
   Coris avula
   C. galardi
   Gomphosus varius
   Halichoeres marginatus
   Hemigymnus fasciatus
   Hemipteronotus taeniourus
   Stethocephalus lineatus
   Cirrhiprion sebae
   Istiblennius paulus
   Plagiotremus sp.
   Helcogramma sp. nov.
   Trinervion minutus
   Trinara sp.
   Gomphosus sp.
   Zanclus canescens
   Zebrasoma veliferum
   Balistapus undulatus

4. Errant
   Lethrinus xanthoncheilus
   Lutjanus bohar
   L. gibbus
   L. monostigma
   Chelinus undulatus
   Scarus brevifilis
   S. frenatus
   S. ephippium
   S. pectoralis
   S. sexvittatus
   S. sordidus
   juvenile scarids
   Acanthurus achilles
   A. lineatus
   A. xanthonceilus
   Paracanthus hepatus

E. Tidepools

1. Along the rubble rampart
   Adioryx microstomus
   Flammeo salmara
   Apogon erythrinus
   A. savageonii
   Monotaxis grandoculis
   Gomphosus varius
   Halichoeres centriquadrus
   Labroides dimidiatus
   Thalassoma hardwickei
   T. quinquevittata
   Cirriformes sp.
   C. variolus
   juvenile scarids
   Acanthurus lineatus
   Ctenochaetus sp.

2. In the central portion
   Adioryx spinifera
   Scorpaena albobrunnea
   Caranx sexfasciatus
   Cephalopholis argus
   Epinephelus fuscoguttatus
   E. hexagonatus
   E. spilotoiceps
   Parupeneus barberinus
   E. multifasciatus
   Chaetodon auriga
   C. ephippium
   C. luniula
   Abuderdaf dicki
   Chromis marginata
   Pomacentrus coelestis
   Cirrhitichthys oxycephalus
   Chelinus undulatus
   Coris avula
   Halichoeres marginatus
   Pseudochelinus hexataenia
   Stethocephalus axillaris
   Thalassoma lunare
   T. purpureum
   Chlorurus gibbus
   Scarus frenatus
   S. chobban
   S. loricatus
   S. ovatus
   S. sexvittatus
   Plagiotremus sp.
   Bathygobius fuscus
   Epinephelus strigatus
   Fusigobius neophytus
   Acanthurus glaucopterus
   Zebrasoma veliferum
   Balistapus undulatus
   Rhinecanthus aculeatus
   Arothron melaenops

3. Along the sandy shore
   and dead reef
   Lutjanus monostigma
   Abuderdaf epistilactatus
   A. sordidus
   Entomacrodus striatus
   Istiblennius lineatus
F. Reef Flat

1. From 0 to 0.5 m depth
   Gymnothorax pictus
   Caranx maculatus
   Epinephelus merra
   L. spilotoceps
   Apogon septemfasciatus
   Abudefduf sordidus
   Pomacentrus albifasciatus
   P. vaillii
   Cirrhithichthys oxycephalus
   Gomphus varius
   Halichoeres centriquadrus
   H. trimaculatus
   Thalassoma hardwickei
   T. jupiter
   Entomacrodus striatus
   Istiblennius afillnuchalis
   L. lineatus

2. From 0.5 to 1 m depth
   Albula vulpes
   Chanos chanos
   Kuhlia marginata
   Letirinthus xanthochelius
   Kyphosus cinareascens
   Centropyge flavissimus
   Chaetodon auriga
   Cheiron valenciensis
   Cheilinus undulatus
   Labroides dimidiatus
   Pseudochelinus hexataenia
   S. linearis
   Chlorurus gibbus
   Scarus brevifilis
   S. trenatus
   S. ghobban
   S. ovicaps
   S. pectoralis
   Acanthurus achilles
   A. guttatus
   A. xanthopterus
   Ctenochaetus cyanoguttatus
   Zebrasoma rostratum
   Melichthys niger

G. Outer Reef Slope

1. Sandy areas
   Chanos chanos
   Halichoeres trimaculatus
   Pomacentrus coelestis

2. On or within coral heads
   Adioryx spinnifer
   Caranx maculatus
   Cephalopholis urodelus
   Epinephelus fuscoguttatus
   Paracirrhites forsteri
   C. hexagonus
   E. spilotoceps
   Cirrhithichthys oxycephalus
   Paracirrhites arcatus
   P. hemistictus
   Epibulus insidiator
   Cirrhipectes variolosus

3. Near rocks or coral heads
   Centropyge loriculus
   Chaetodon bennetti
   C. ephippium
   C. lineolatus
   C. linula
   C. meyeri
   C. punctatofasciatus
   C. trifasciatus
   C. ulietensis
   Megaprotodon atrigangulus
   Pomacentrus imperator
   Abudefduf imparipinnis
   Chromis lepidolepis
   Pomacentrus vaili
   Bodianus axillaris
   E. diana
   Hemigymnus fasciatus
   Labroides bicolor
   Thalassoma amblycephalus
   T. lutescens
   Aspidontus taeniatus
   Balistapus undulatus
   Melichthys niger

4. Errant
   Gracila albimarginata
   Variola louti
   Letirinthus xanthochelius
   Lutjanus gibbus
   L. monostigma
   Monotaxis grandoculis
   Sphyraena forsteri
   Pomacentrus pavo
   Cheilinus undulatus
   Scarus brevifilis
   S. chlorodon
   S. forsteri
   S. ghobban
   S. globiceps
   S. harid
   S. journi
   S. ovicaps
   Acanthurus gahhm
   A. lineatus
   Ctenochaetus sp.
   Zanclus canescens
   Zebrasoma rostratum
   Z. velliferum
   Arothron meleagris
Fig. 4. Abundant and common fishes in the turbid lagoon transects (T₁ and T₇). The histogram - the number of individuals of each species per station; the solid bars, the average length of each species.
Turbid Lagoon Patch Reef Fishes

*Chromis atripectoralis*, *Pomacentrus lividus*, *Halichoeres trimaculatus*, and *Scarus sordidus* are the most abundant fishes on the patch reefs of the turbid lagoon (Fig. 4). *Chromis atripectoralis* is invariably found in aggregations above ramose "thickets" of *Stylophora* and *Acropora*, as is true at Eniwetok (Swerdloff, 1970). These corals are found elsewhere only in small numbers on the edges of the clear lagoon waters, and a few *Chromis atripectoralis* may be found in them. *Pomacentrus lividus* is also associated with these corals, living among the bases of the branches and defending territories there. It is distributed similarly to *Chromis atripectoralis* except that it was abundant along the T6 transect in the clear lagoon (see below) and occasionally encountered in the shingle along the sides of English Harbor pass centrally to the *P. albofasciatus* zone (see above). In addition it is abundant along the shingle side of Danger Point tidepool. *Scarus sordidus* is abundant only in the turbid lagoon. Just two of the 42 recorded were found on T2, the rest occurring in very shallow water on the reef top at Suez (T7). *Halichoeres trimaculatus* has been discussed above.

*Cheilodipterus quinque-lineata* is common under overhangs and at the margins of ramose coral heads; a few were also observed on the clear lagoon patch reefs. This small species was not as secretive as the other Fanning apogonids. *Dascyllus aruanus* and *Pomacentrus albofasciatus* also live among the corals. *Dascyllus aruanus*, found in small bush-like coral heads which do not harbor *Pomacentrus lividus*, occasionally co-occurred with *Chromis atripectoralis* in a single coral head. *Dascyllus aruanus* is abundant on the clear-water patch reefs and in the tidepools. *Gomphosus varius* is another common resident of the turbid patch reefs. Its distribution is discussed above. *Thalassoma lunare* is also common here. It is abundant on clear lagoon patch reefs and common in English Harbor pass. Small groups of *Lutjanus fulvus* were observed under overhangs. Juvenile scarids are common in the turbid lagoon but do not occur in large numbers elsewhere. Two species of gobies are common in the turbid areas of the lagoon. *Amblygobius albimaculatus* and *Asterropteryx semipunctatus* (qualitative observations), found at coral/sand and coral/rubble interfaces. The former burrows in the sand under hard substrates, the latter is found in rubble at the bases of coral heads. Both species are found occasionally in the clear lagoon.

Occasional fishes are listed in Table 4 (B).

Along transect T7, 25 species of fishes were present. Ten of these were represented by one to three individuals. Of the remainder, 75-100% of the individuals of eight species are coincident with *Acropora delicatula* and *A. formosa* on the slope of the patch reef. These fishes are *Cheilodipterus quinque-lineata*, *Chaetodon vagabundus*, *Chromis atripectoralis*, *Dascyllus aruanus*, *Pomacentrus lividus*, *Scarus oviceps*, unidentified juvenile scarids, and *Ctenochaetus striatus*. We believe these organisms represent a distinct community. Part of this community was also found along the T2 transect. Significant correlations ($P<0.05$) indicate association of *Chromis atripectoralis* and *Pomacentrus lividus* with *Acropora delicatula* and *A. formosa*. 
Two additional species, *Pomacentrus albofasciatus* and *Halichoeres trimaculatus* are present in large numbers on the T7 reef top, which is a mixture of sand, algae, rubble, and dead reef. Neither of these fishes are found in association with *Acropora delicatula* on T7. *Pomacentrus albofasciatus* is found at the bases of *A. delicatula* colonies on T2, perhaps, because there was little dead reef and rubble along this transect.

Clear Lagoon Patch Reef Fishes

The most abundant fishes in the clear lagoon are *Dascyllus aruanus*, *Pomacentrus albofasciatus*, *P. coelestis*, *P. nigricans*, *Halichoeres trimaculatus*, *Thalassoma amblycephalus*, and *T. lunare* (Fig. 5). *Pomacentrus coelestis* is abundant in the clear-water lagoon at depths below 5 m (7.4 per station below 5 m; 1.7 above 5 m; T1). They are also abundant in English Harbor pass in sand patches toward the center of the pass (3.4 per station; T11 and T14). These fish dig holes in the sand under available solid cover. They often hover above relief features and may form small aggregations there, but descend and defend the substrate area around their burrows (field observations). *P. coelestis* are found in areas providing less cover than those in which the other blue pomacentrid, *Abudefduf glaucus*, occurs. *Pomacentrus nigricans* is found most abundantly at the coral-rubble interfaces of clear lagoon patch reefs and in the tidepools. The other species have been discussed above.

Fishes commonly encountered are small wandering schools of *Chanos chanos*, *Hyporhamphus acutus*, *Acanthurus gahhm*, *A. triostegus*, and *A. xanithopterus*. *Hyporhamphus acutus* is common at the surface everywhere except in turbid lagoon waters. *Acanthurus gahhm* is abundant in the passes, common in the clearwater lagoon and in the tidepools. A few were observed on the deeper outer slope. The other common species have been discussed above.

*Epinephelus merra*, *Eviota distigma*, and *Gnatholepis anjerensis* are found individually on the bottom in crevices on the sand or among the rubble at the bases of coral heads. *Eviota distigma* and *Gnatholepis anjerensis* are common on the clear-water patch reefs, in English Harbor pass, and in tidepools. *Cirrhitichthys oxycephalus* was seen on small coral heads or on rubble.

Small aggregations of *Chromis lepidolepis* and *C. margaritifer* occurred in waters deeper than 5 m (1.0 and 0.8 per station; T1). These two species are associated with individual coral or limestone outcroppings, into which they duck when approached. *C. lepidolepis* was found by Randall (1955) in clear lagoon areas in the Gilberts; we also found small groups in English Harbor pass and on the outer slope at Fanning Island. *Chromis margaritifer*, although listed as occasional in the clear lagoon, is described here because it may be very common in the deeper lagoon waters. It is the most abundant fish throughout the outer reef slope transect (36.8 per station). It occurs in small numbers in the tidepool, commonly in the pass, and is evenly distributed within almost all of the areas mentioned.
Fig. 5. Abundant and common fishes of the clear-lagoon patch reef transects (T1 and T4–6). The histogram - the number of individuals of each species per station; the solid bars, the average length of each species.
Occasional species from this habitat are given in Table 4 (C).

Analyses of data from $T_1$ and $T_{4-5}$ yielded similar assemblages of fishes. These do not, however, appear to be associated with any particular substrate or coral. The abundant Dascyllus aruanus, Pomacentrus coelestis, Halichoeres trimaculatus, and Thalassoma lunare appear to be intercorrelated and are representative of all three clear lagoon transects. Due to the complex and heterogenous topography of the clearwater patch reefs, smaller quadrat sizes will probably be necessary to yield more specific information about this community.

Transect $T_6$ was traversed over a Porites lutea microatoll on the edge of the clearwater zone. At the time of our single visit the visibility was less than 1 meter. Of the 27 species observed here, nineteen are elements of both turbid and clearwater lagoon faunas. Chromis strioptera, abundant only in the turbid lagoon, occurred here. Pomacentrus lividus present on the microatoll at a density of 10.0 per station, is abundant in the turbid lagoon. Four species present on the microatoll occur commonly in the clear lagoon, but only rarely if at all in the turbid lagoon. Cephalopholis argus, Centropyge flavissimus, and Pomacentrus coelestis, and Labroides dimidiatus. The densities of both Labroides dimidiatus and Pomacentrus lividus (3.5 and 10.0 per station) were considerably higher here than elsewhere at Fanning Island and are perhaps artifacts of our choice of transect site.

Fishes of the Passes

The most abundant species in English Harbor pass are Pomacentrus albofasciatu, P. coelestis, Halichoeres trimaculatus, Thalassoma amblycephalus, T. purpureum, T. quinquevittata, Acanthurus gahnm, A. olivaceus, A. triostegus, and Ctenochaetus striatus (Fig. 6). All have been discussed above except for Thalassoma quinquevittata, which also occurred occasionally in the lagoon and tidepools, and Acanthurus olivaceus. This latter species was seen by us in English Harbor and North Pass, where it was in most parts occasional to rare although it was abundant at the ocean ends of the passes (7.8 indiv. per station; $T_3$).

A number of fishes seem to utilize topological relief features as shelter from the current. Abudefduf sordidus and Gnatholepis anjerensis are common in areas of shingle and dense rubble along the sides of English Harbor pass (qualitative observations). A. sordidus is also seen occasionally along the lagoon shoreline at Cartwright Point, in the tidepools, and on the outer flats. Commonly sheltering near larger blocks of rubble, variously encrusted with reef corals, typically Millepora, or the soft coral Sarcophyton, are Centropyge flavissimus, Abudefduf dicki, Pomacentrus aureus, and Eviota distigma. Centropyge flavissimus is also common on the upper regions of the outer reef slope (1.4 per station above 21 m depth). This species typically associates with living coral (Hiatt and Strasburg, 1960) on outer reef slopes (Randall, 1955). Individuals are widely spaced, remaining in close proximity to the substrate, and retreating into crevices when approached by divers. Abudefduf dicki is also common on
the outer reef flats and abundant on the slope. *A. dicki* is found on the slope from 23 m to 8 m depth, growing more numerous as the depth decreased (3.4 per station from 23 to 15 m depth and 11.0 per station between 15 m and 8 m depth). These damselfish occur as individuals or in pairs and are closely associated with vasiform *Acropora reticulata* on the outer slope; vasiform corals were not found in the channels. *Pomacentrus aureus* was seen at Fanning Island only in English Harbor pass and on the outer reef flat, where it was also common. This species is often seen hiding in soft coral in the channel. *Eviota distigma* has been discussed above.

The behavior of many species did not appear altered by the tidal currents. The pomacentrid and labrid species, *Chromis margaritifer*, *Labroides dimidiatus*, and *Thalassoma lunare* commonly swim above the bottom, maintaining constant position with respect to the substrate despite the current. Other errant species swim freely about the bottom, remaining close to the substrate and taking shelter only when the current is strongest. These include *Parupeneus barberinus* and *P. bifasciatus*, the former occasional throughout the lagoon and tidepools, the latter essentially restricted to the channel, *Chaetodon lunula*, discussed above, and the labrids, *Halichoeres centriguadrus* and *Stethojulis axillaris*, both of which are occasional on the outer reef flats and in the tidepool.

The common species of the larger, typically vagile families--scarids and acanthurids--similarly seemed unaffected by the currents in the passes. Occasional sightings of large schools and solitary individuals of *Chlorurus gibbus* are combined to give the species an abundance rating of "common", although only one fish happened to pass over the four pass transects. Schools of *C. gibbus* are not infrequently accompanied by an irregular compliment of other scarids and acanthurids. These families also form irregular, fluid, multispecific aggregations. The common scarids in the channel are *Scarus ghobban*, *S. harid*, and *S. jonesi*. *S. ghobban* is occasional everywhere else at Fanning Island except in the turbid waters of the lagoon. *S. harid* has been discussed above; *S. jonesi* was not seen on the pass transects but substantial numbers were observed especially at low tide, feeding in the shallow shingle and rubble near the passage between the Danger Point tidepool and English Harbor pass. *S. jonesi* is also common on the outer reef flats and tidepools. The common, errant acanthurids in English Harbor pass are *Acanthurus glaukoparierus* and *Ctenochaetus cyanoguttatus*. *Acanthurus glaukoparierus* is generally seen as solitary individuals, or in pairs or small groups. This species is occasionally found in tidepools, common on the outer reef flats (2.0 per station on T10 but absent from T12), and abundant on the outer slope. The species is characteristic of shallow lagoon and outer reef coral areas (Randall, 1955), particularly where water movement is strong (Schultz et al., 1953-1966). It was not seen by us in the lagoon at Fanning Island. *Ctenochaetus cyanoguttatus* is also common on the upper reef slope (1.3 per station between 77 m and 11 m depth) and occasionally seen on the outer reef flats.

Species which were seen only occasionally in the channels are listed in Table 4 (D).
Fig. 6. Abundant and common fishes of the channel transects (T9, T11, T13-14). The histogram = the number of individuals of each species per station; the solid bars, the average length of each species.
Tidepool Fishes

Abundant tidepool fishes are *Abudefduf glaucus*, *Dascyllus aruanus*, *Pomacentrus albofasciatus*, *P. lividus*, *P. nigricans*, *Halichoeres trimaculatus*, *Thalassoma amblycephalus*, and large schools of *Mullloidichthys flavolineata*, *Crenimugil crenilabris*, and *Acanthurus triostegus* (Fig. 7, qualitative observations).

*Abudefduf glaucus* was observed excavating holes in the sand under rocks and defending territories around them. In the nearshore rubble and dead reef (Fig. 3) 26.1 per station were found, whereas in other parts of the tidepool densities approached 0.7 per station. This species is abundant on the outer reef flat (1.8 per station) and a few were also found in the shoreline rubble at Cartwright Point and with *Pomacentrus albofasciatus* in English Harbor pass. *Dascyllus aruanus* was found in *Pocillopora* heads in the middle of the tidepool and *Pomacentrus albofasciatus* is abundant throughout. *P. lividus* and *P. nigricans* were found in areas containing more than 10% live coral, or of extensive rubble. In such regions were found 6.0 *P. lividus* and 3.8 *P. nigricans* per station. In the shingle rampart, densities of *P. lividus* reached 28 per station. *P. nigricans* attained a mean density of 13.0 per station in the shingle.

*Halichoeres trimaculatus* was spread along the tidepool transect line except for the shingle rampart area. *Thalassoma amblycephalus* was most numerous in the nearshore dead reef area of the transect. This latter wrasse forms wandering aggregations, however, and more evidence is needed before suggesting that the species prefers dead reef.

*Mullloidichthys flavolineata* was observed in large schools in the Danger Point tidepool during the day. A few may also be found along the lagoon shore at Cartwright Point. The remaining abundant species, *Crenimugil crenilabris* and *Acanthurus triostegus*, have been discussed above.

Smaller schools or aggregations of *Hyporhamphus acutus*, *Belone platyura*, *Lutjanus fulvus*, *Mullloidichthys samoensis*, *Chelon vaigiensis*, *Scarus harid*, *S. jonesi*, and *Acanthurus gahhm* are common, frequently with admixtures of other species (Table 4). *Belone platyura* was observed only over the outer reef and in the tidepools. *Mullloidichthys samoensis* is found in the Danger Point tidepool near the shingle rampart, behaving in much the same manner as *M. flavolineata*. The other species have been discussed above.

*Epinephelus merra*, *Eviota distigma*, and *Gnatholepis anjerensis* are common at the bases of coral heads and in crevices of the dead reef, shingle, and rubble. *Ctenochaetus striatus* is common near the rampart (qualitative observations). *Paragobiodon echinocephalus* is common in *Pocillopora* heads wherever they occurred in the tidepools and outer reef flats. *Iattiblenius edentulus* (no transect data) and *I. paulus* are found on or adjacent to nearshore dead coral ledges and shingle. Both occur only in tidepools in the Marshall Islands (Schultz et al., 1953-1966), but *I. paulus* was seen on the outer flats and occasionally in English Harbor pass at Fanning Island.
Fishes seen occasionally in the tidepools are listed in Table 4 (E).

**Outer Reef Flat Fishes**

One of the most abundant species on the shallow outer reef is *Acanthurus triostegus* (Fig. 8). Individuals move about singly or in groups or schools of varying size, often remaining in the deeper tidepools. *A. lineatus* and *Ctenochaetus striatus* are also abundant but in deeper water (from 1 to 3 m on T10) at low tide. *Acanthurus lineatus* was most commonly found in a similar habitat in the Gilbert Islands (Randall, 1955).

Smaller fishes in abundance on the reef flats are *Abudefduf glaucus, Halichoeres margaritaceus*, and *Thalassoma purpureum*. *Halichoeres margaritaceus* remained close to the substrate and retreated into holes when approached. It was seen only occasionally in other areas (Table 1). The other species have been discussed above.

Fishes commonly observed on the shallower parts of the reef flat (between 0 and 1 m, T12) are *Abudefduf imparipennis*, *Thalassoma amblycephalus*, and *Istiblennius paulus*. The habits of *Abudefduf imparipennis* are similar to *A. glaucus*, however the former species is found in dead reef or cemented rubble areas. Those species commonly found in deeper water (1 to 3 m, T10) are *Abudefduf dicki, Pomacentrus aureus, Scarus harid, Cirripectes variolosus, Paragobiodon echinocephalus, Acanthurus glaucoparius*, and *Ctenochaetus cyanoguttatus*. All have been discussed except for *Cirripectes variolosus* which seem to prefer depth zones from 2 to 10 m (0.5 per station from 7 to 10 m, T3 and 2 to 3 m, T10; 0.3 per station from 10 to 37 m, T3 and 1 to 2 m, T10, and 0 to 1 m, T12). These blennies were usually found perched on top of living coral heads.

We have only qualitative observations on some of the schooling species; those forming large schools and seen in the area more than once were classified common: *Hyporhamphus acutus, Belone platyura, Crenimugil crenilabris*, and *S. jonesi*.

*Rhinecanthus rectangulus*, of a density bordering between common and occasional, is seen on the shallow reef flat (T12) in much larger numbers than elsewhere.

Occasional species of the reef flat habitat are given in Table 4 (F).

**Outer Reef Slope Fishes**

*Mvipristis kuntee* and *M. murdian* were abundant along the T3 transect (Fig. 9). *M. kuntee* often hovers above the substrate in large groups of widely spaced individuals during the day (4.0 per station on the upper half of the transect). *M. murdian*, apparently a more secretive species, was observed in small groups under coral heads, especially under vasiform *Acropora* (4.8 per station on the upper half of the transect). *M. murdian*
Fig. 7. Abundant and common fishes on the tidepool transect (T₁₈). The histogram = the number of individuals of each species per station; the solid bars, the average length of each species.
Fig. 8. Abundant and common fishes along the outer reef flat transects (T10 and T12). The histogram = the number of individuals of each species per station; the solid bars, the average length of each species.
Fig. 9. Abundant and common fishes of the outer reef slope transect (T3).
The histogram = the number of individuals of each species per station; the solid bars, the average length of each species.
occurs only on the outer slope at Fanning Island; *M. kuntee* was occasionally seen near clear lagoon patch reefs.

Individual *Cephalopholis argus* were abundant throughout the transect except in large patches with reduced relief. This fish is the dominant outer slope grouper in the Society Islands, where it moreover is "abundant throughout lagoons and bays, wherever there is coral and rock shelter" (Randall and Brock, 1960). At Fanning Island, *C. argus* is rarely found in the turbid lagoon and only in small numbers on the fringes of the lagoon, passes, and tidepools.

*Mirolabrichthys* sp., *Pseudanthias* sp. nov., *Chromis acares*, and *C. vanderbilti* form large clouds—dense, feeding aggregations and schools swimming against the surge currents to maintain a specific position above the substrate. When approached by a diver the entire cloud takes cover within the interstices of the coral head above which it normally hangs. Individual clouds are of variable species composition. *Mirolabrichthys* sp. and *Pseudanthias* sp. nov. are in different aggregations along the transect; *Mirolabrichthys* from 29 to 23 m in clouds of about 90 per station; *Pseudanthias* from 22 to 8 m at a density of 45.4 per station. However they were occasionally seen in mixed clouds elsewhere over the slope. *Chromis vanderbilti* and *C. acares* were similarly separated from each other along the transect. *C. acares* occurred at a density of 6.9 per station in clouds with *Mirolabrichthys* sp. from 29 to 23 m depth; *Chromis vanderbilti* at a density of 20.1 per station in clouds with *Pseudanthias* sp., from 21 to 8 m. The distributions of the two *Chromis* species were not found to overlap elsewhere. *Abudefduf dicki* and *Chromis margaritifer* are very abundant on the slope. Their distributions have been discussed above.

The "cleaner" wrasses, *Labroides dimidiatus* and *L. rubrolabiatus*, occur individually, in monospecific pairs, or in mixed-species groups. *Pseudocheilinus hexataenia* and *P. sp.* are secretive, hiding individually or in pairs in the interstices of coral heads or in holes in rubble. *P. hexataenia* is abundant on the outer slope (4.9 per station from 23 to 8 m); individuals were found occasionally on lagoon patch reefs, in tidepools, in English Harbor pass, and on the outer reef flat, usually in rubble areas. Schultz et al. (1953-1966) found *P. hexataenia* at a depth of 13 m; at Fanning Island it occurs at 23 m depth. *P. sp.* was found only on the outer slope, ranging below and overlapping *P. hexataenia*; one individual was seen in English Harbor pass.

*Caesio xanthonotus*, *Chlorurus gibbus*, and sometimes *Acanthurus glaucopariegus* are seen in large schools. One school of over 100 *Caesio xanthonotus* (each fish about 20 cm in length) crossed the transect line once; schools when present ranged from the surface to the bottom, moving over the substrate. *C. xanthonotus* was not seen elsewhere at Fanning Island. The species is noted to occur on outer reef slopes (Randall, 1955).

*Acanthurus glaucopariegus* generally occurs alone, in pairs, or in small groups near the surface of the substrate. It's density along the transect line was fairly uniform. Large schools were seen less often. *Ctenochaetus*
strombus is abundant around and within heads of living coral on the slope. The distributions of these surgeon fishes have been discussed above.

The fishes mentioned next are common on the slope transect but in lesser densities than the above.

_Hyporhamphus acutus_ and _Belone platyura_ were seen schooling on the surface.

_Lutjanus bohar_ wander in large groups or alone in the deeper parts of English Harbor pass and over the outer reef slope. Eight of these snappers were counted along the outer slope transect, but many more were present well off the substrate.

The most common angelfish and butterflyfishes on the slope were _Centropyge flavissimus_, _Chaetodon auriga_, and _C. ornatissimus_. The latter species was found on the outer reef slopes in areas of rich coral growth in areas of rich coral growth in the Gilbert Islands by Randall (1955).

_Plectroglyphidodon johnstonianus_ has habits similar to those of _Abudefduf dicki_ but is closely associated with low coral heads such as _Favia stelligera_ instead of large vasiform corals. It is seen only alone, not in pairs (1.2 per station from 23 to 9 m). _Paracirrhites forsteri_ was common in transect, sitting on the surfaces of coral heads. Schultz et al. (1953-1966) found it on deep reefs; Randall (1955) in regions of dense coral in lagoons and outer reefs. At Fanning Island it is seen occasionally on coral heads in English Harbor pass, and rarely in the tidepools and on clear lagoon patch reefs.

_Bodianus loxozonus_ and _Gomphosus varius_ commonly wander individually over the coral heads (_Bodianus_ 1.1 per station below 14 m, and _Gomphosus_ 1.8 per station above 23 m). _Bodianus loxozonus_ were observed cleaning other fishes; the adults followed the divers about, and the true density is probably much lower than our data suggest. Green male _Gomphosus varius_ are more common than females and juveniles on the slope, and _vice versa_ in the shallow water. This species is discussed above.

_Acanthurus xanthopterus_, common in midwater above the slope, has also been discussed above. _Ctenochaetus cyanoguttatus_ is not as abundant as _C. strriatus_ on the slope (1.3 indiv. per station between 27 and 11 m).

The fishes seen only occasionally are presented, with observations of their habits, in Table 4 (G).

Pearson product moment correlations suggest the presence along T3 of a community of corals, algae, and fishes, all of which are negatively correlated with sand. The common and abundant benthic fishes associated with each other (r>0.5) are _Myripristis kuntee_, _M. murdjan_, _Cephalopholis argus_, _Pseudanthias sp._, _Centropyge flavissimus_, _Chaetodon ornatissimus_, _Abudefduf dicki_, _Chromis margaritifer_, _C. vanderbilti_, _Plectroglyphidodon johnstonianus_, _Bodianus loxozonus_, _Gomphosus varius_, _Labroides dimidiatus_, _L. rubrolabiatus_, _Pseudocheilinus sp._, _Acanthurus glaucoparleus_, _
TABLE 5 Occasional to abundant fishes with distributions restricted to one habitat under the present study

<table>
<thead>
<tr>
<th>A. Lagoon Shore</th>
<th>B. Turbid Lagoon</th>
<th>C. Clear Lagoon</th>
<th>D. Channels</th>
<th>E. Tidepools</th>
<th>F. Reef Flat</th>
<th>G. Reef Slope</th>
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<tr>
<td>Samarsiscus triocellatus</td>
<td>Chaetodon vagabundus</td>
<td>Apogon frenatus</td>
<td>Adioryx lacteoguttatus</td>
<td>Adioryx microstomus</td>
<td>Gymnothorax pictus</td>
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<td>Gnathodentex aureolineatus</td>
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<td></td>
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Ctenochaetus cyanoguttatus, and C. striatus. These are associated with Dictyota friabilis, Lobophora variegata, coralline algae, Acropora reticulata, A. sp., Favia stelligera, Lobophyllia costata, Millepora platyphylla, and Porites meandrina. Replications of the T3 transect should reveal if this community is static or variable.

Mirolabrichthys sp. and Chromis acares are similarly associated with each other, with a soft coral (Sarcophyton sp.) and Leptastrea purpurea, and with depth (Pearson r > 0.5). Both of these corals had deeper distributions than the others seen along the transect.

DISCUSSION

The marine environment of Fanning Island has been divided into a series of habitat types and the characteristic fish fauna of each has been described. Analysis has been restricted to qualitative rankings (Table 1), with the exception of a factor analysis of the data from three 100-m transects. The carangids have been eliminated from all but passing mention (Table 1) because of uncertain identification, as are those species of which only one individual was observed in the present study ("rare" in Table 1).

The following discussion assumes that the distributional patterns of the fishes at Fanning Island reflect variations in ecological parameters, i.e., faunal differences are due to ecological differences (Lambert and Dale, 1964). A corollary assumption is that species restricted to one or a few habitats are more sensitive to environmental variations than are widely ranging species.

Fourteen species of fishes range widely throughout most of the habitats. Chlorurus gibbus is absent only from the lagoon shore. Halichoeres trimaculatus and Acanthurus xanthopterus are found on the edges of sand patches near coral or dead reef outcroppings in all habitats. The other unrestricted fishes are associated with particular substrate types and are rare on or absent from either the lagoon shore or the outer reef slope. Epinephelus merra, Pomacentrus albofasciatus, Thalassoma purpureum, Scarus harid, and Acanthurus triostegus are characteristic of shallow water areas of high relief; Chaetodon auriga, C. lunula, Gomphosus varius, Labroides dimidiatus, Thalassoma amblycephalus, and Ctenochaetus striatus are found near limestone surfaces covered by live coral.

The lagoon shoreline habitat supports 19 species of occasional to abundant fishes, 6 of which are among the widely ranging, apparently unrestricted, species discussed above. The lagoon shoreline fauna is the smallest, and thus the least diverse (4.12 bits/individual; Table 6), of any encountered at Fanning Island. Inasmuch as this diversity is higher than the number of species might suggest, the individuals must be relatively evenly dispersed among the component species. The simple matching coefficients of association (Table 7 (a) ) suggest that the lagoon shoreline fauna is most closely related to the fauna of the turbid lagoon patch reefs. Morisita's indices of overlap (Table 7 (b) ), using Horn's
TABLE 6: FAUNAL CHARACTERISTICS OF THE PANNING ISLAND HABITAT AREAS
Abbreviations as in Table 1.

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(1966) modification for sampling with replacement, suggest a greater similarity between the lagoon shoreline and outer reef flat faunas. Because Morisita's index is the probability of selecting two successive individuals of the same species from the combined sample, relative to the probability of selecting two successive individuals of the same species from either population alone (Horn, 1966), Table 7 implies that the species common to both the lagoon shoreline and outer reef flat faunas are relatively abundant in both habitats. Each habitat may be considered severe, although for different reasons: salinity, temperature, and probably oxygen fluctuations along the turbid lagoon shoreline, and extreme turbulence from wave action along the outer reef flat. Of the nineteen lagoon shore forms, ten errant species were observed; these may move into other areas such as the tidepools when conditions become adverse. Two pomacentrids found along the lagoon shore (Abudefduf glaucus and A. sordidus) were present only at Cartwright Point. Both were found in a shallow-water band along the lagoon shore in this region and along the sides of English Harbor pass and tidepools. The low levels of similarity (low mean association and low mean overlap) between the lagoon shoreline fauna, and the faunas of other Fanning Island habitats, and the low absolute numbers of shoreline fishes, demand extra caution against reliance upon a strictly quantitative assessment of the faunistic affinities of the lagoon shoreline.

Of the 38 species regularly observed in the turbid lagoon patch reef habitat, 14 are considered unrestricted and 24 restricted. The turbid-lagoon patch reef fauna is the second smallest, and the second-least diverse (4.59 bits/individual). Its highest affinities are with the faunas of the other calm, shallow water habitats; it is ecologically most similar to the adjacent clear-lagoon patch reef habitat. The turbid lagoon patch reef fauna has low coefficients of association with the outer reef flat and outer reef slope faunas; the former, as noted above is relatively barren, while the latter has a high complement of species unique to it (see below). Discrepancies between simple matching coefficients and modified Morisita indices, presumably due to the effect of quantitative information, are most notable with regard to the tidepool fauna (Table 7). The proportion of overlapping species is substantial (Table 7 (a)), but their numbers are low (Table 7 (b)). This may be due to the preponderance of rubble over live coral in the tidepool habitat, or perhaps a filtering effect exerted by the strong currents in the passes on fishes which would otherwise pass between tidepool and turbid-lagoon patch reef. Although ten out of twelve errant species from the turbid lagoon were also found in the tidepool, most of the less vagile turbid-lagoon species were restricted to the hard substrate of patch reefs. Interchange between the tidepool and turbid lagoon may be thus minimized due to distance.

The clear-lagoon patch reef habitat contains 76 species, of which 62, or approximately four-fifths, are restricted. The diversity here is higher than in either of the previous faunas (5.53 bits/individual), in keeping with the higher sample size. The greatest species-similarity of the clear-lagoon patch reef fauna is to the turbid-lagoon patch reef fauna, followed closely by similarities to the clear, shallow-water pass and tidepool faunas (Table 7 (a)). When abundance data are included, Morisita's indices show greater affinities with the adjacent turbid-lagoon patch reef
TABLE 7: SIMILARITIES BETWEEN HABITAT-CHARACTERISTIC FAUNAS;
   a) SIMPLE MATCHING COEFFICIENT OF ASSOCIATION;
   b) MORISITA'S INDICES OF OVERLAP. See text for details.
   Abbreviations as in Table 1.

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and pass faunas (Table 7 (b)); the index of overlap between clear-lagoon patch reef and tidepool faunas is much less than the coefficient of association, indicating that the species which are numerous in one are not so in the other. Possible reasons for this discrepancy include a preponderance of rubble in the tidepool and the strong pass currents separating tidepool and clear lagoon. The latter interpretation receives some support from the fact that the fauna of the outer reef flat, similarly separated from the clear-lagoon patch reefs but normally experiencing strong wave surge and perhaps more capable of withstanding the pass currents, has a slightly higher index of overlap with the clear-lagoon fauna than does the tidepool fauna. The overlap index between the clear-lagoon patch reef fauna and outer reef slope fauna is much lower than the species-limited coefficient of association: although some species occur in both habitats they are not numerous in both, perhaps because of the difference in depth ranges.

The fauna of English Harbor pass is the largest sampled at Fanning Island, both in species number (99) and diversity (5.96 bits/individual). A large proportion of the pass species also occur in other habitats, particularly in the tidepools and on the clear-lagoon patch reefs (Table 7 (a)). Although the association coefficient between pass and outer reef flat faunas is lower, the corresponding index of overlap is relatively high. Apparently individuals of the species which occur in both of these shallow, turbulent, clear-water habitats are numerous. The close affinities of the pass fauna to those of the calmer clear-lagoon patch reefs and tidepools probably reflect the large complement of pass species which take advantage of protected microhabitats, as discussed above. The pass fauna least resembles those of the lagoon shoreline, discussed above, and the outer reef slope. Despite proximity of the pass and slope habitats, depth, and perhaps currents, seem to restrict many of the outer slope species.

The tidepool fauna is less speciose (83 species) and therefore less diverse (5.66 bits/individual) than the pass fauna, with which it had the greatest species-similarity (Table 7 (a)). Tidepool species occurred consistently in most of the other habitats, giving them the highest mean coefficient of association. This might suggest that the tidepool fauna is most typical of the entire marine environment at Fanning Island. The indices of overlap (Table 7 (b)), however, are less consistent. They indicate that the open-ocean species which also occurred in the tidepool habitat are quite numerous. Elements of the pass fauna also occur in substantial numbers in the tidepool habitat; somewhat surprisingly, the clear-lagoon patch reef species apparently do not. One factor which may be significant is that the amount of algal-encrusted rubble is much greater in the tidepool, outer reef flat, and outer reef slope habitats than on the clear-lagoon patch reefs, which are cemented limestone structures variously covered with living coral. Another factor which may be relevant is unequal accessibility: the tidepool habitat is continuous with the open ocean at high tide, whereas the passage between the tidepool and English Harbor pass is narrow and shallow. Thus many lagoon residents, even in an ebbing current, would probably be carried to the open ocean and miss the tidepool entirely. The extensive tidepool habitat areas near North Pass and Rapa Pass, are further separated from the nearest clear-lagoon patch reefs by long stretches of turbid lagoon and numerous linear reefs (Fig. 1).
The fauna of the outer reef flat includes the fewest species (64) and has the lowest diversity (5.35 bits/individual) of any from a clear-water Fanning Island habitat. This observation may reflect the relatively low sampling effort to which the outer reef flats were subjected, but it may also be indicative of the effects of tidal fluctuation and wave action. The outer reef flat habitat is continually moving back and forth with the tides, in many areas contracting and expanding; it is likely that protected microhabitats are few since most of the corals are the encrusting type and the direction of the strong surge currents constantly changes. The outer reef flat fauna is in greatest accord with that of the tidepool habitat. As discussed above, these habitats to some extent intergrade and there is probably considerable movement of individuals from one into the other. The outer reef flat fauna also resembles that in English Harbor pass, the other shallow, clear-water habitat typically with strong water movement. Although the association coefficient between outer reef slope faunas is not high (Table 7A), the index of overlap indicates that numerous individuals of overlapping species are in each habitat (Table 7B). Any demarcation separating these habitats is arbitrary; species and individuals of the fauna of the upper reef slope undoubtedly mix with the outer reef flat faunas.

The outer reef slope fauna comprises 91 species, only 10 of which can be considered unrestricted, the lowest proportion (11%) of any Fanning Island fauna sampled. In contrast, 19 of the 91 species (21%) were not found in other habitats (Table 5), the highest proportion of "habitat-unique" species encountered. These data support the subjective impression that the outer reef slope habitat includes unique ecological features, the most obvious of which is depth. Other features which may have similar importance are the constancy of physical conditions characteristic of the open ocean, and a diverse substrate consisting of a deep layer of small rubble pieces with numerous crevices, variably sized rubble blocks, a great variety of living hard and soft corals (see Maragos, cited above), and small, scattered sand patches. As might be expected, there is almost no resemblance between the faunas of the lagoon shoreline and the outer slope. The species of the outer reef slope fauna most closely resemble those of the adjacent English Harbor pass fauna, and then successively the clear-lagoon, tidepool, and outer reef flat faunas (Table 7 (a) ). Inclusion of numerical data alters these relationships somewhat (Table 7 (b) ). The greatest overlap of the outer slope fauna is now with the tidepool fauna; as noted above it must be relatively easy for fishes to swim or be swept by waves from the upper slopes, across the reef flat, and into tidepools. Somewhat surprisingly, the overlap between reef flat and reef slope faunas is far lower than that between tidepool and reef slope faunas. This again may be in part a function of low sampling effort, but also suggests that at least some of the species common to tidepool and outer reef slope may be adversely affected by wave action in reef flat areas.
SUMMARY

The nearshore marine environment of Fanning Island has been partitioned into seven habitat types, which, with their characteristic faunas, are described from qualitative and quantitative observations. Within-habitat distributions of the most numerous fishes are discussed in the text; distributional patterns of the other fish species, and food habits where known, are presented in tables. Conclusions about the habitats were reached on the basis of semi-quantitative comparisons of their fish faunas.

1. The lagoon shoreline habitat has the most depauperate and the least diverse fish fauna of the habitat types at Fanning Island. This habitat is the most vulnerable to fluctuations of temperature, salinity and dissolved oxygen, and typically includes little substrate relief.

2. The turbid-lagoon patch reef habitat, also relatively barren and homogeneous in its fish fauna, is probably subject to greater fluctuation of physical conditions than are the clear-water habitats at Fanning.

3. The clear-lagoon patch reef habitat apparently shares many important ecological relationships with adjacent habitats, particularly with the clear-water English Harbor pass area as reflected by the fish fauna.

4. The (English Harbor) pass habitat, while subject to strong tidal currents, provides considerable sheltered microhabitat; it is centrally located, has the richest and most diverse fish fauna, and shows the greatest overall within-and-between species structure (i.e., mean overlap) of any Fanning Island habitat.

5. The tidepool habitat, with a moderately diverse fish fauna, also is most similar to adjacent habitats judging from their fish faunas; it particularly resembles the outer reef flat with respect to community structure, and least resembles the more distant turbid-water habitats of the lagoon.

6. The outer reef flat habitat, subject to strong wave action, and tidal fluctuation, has the smallest and least diverse fish fauna of any clear-water habitat at Fanning; the overall distributions of individuals and species most closely approach those of the tidepool habitat.

7. The outer reef slope habitat, with a large and diverse fish fauna, contains the greatest number of unique species among habitats sampled and is the most distinct among the clear-water habitats, due to its depth range and probably physical constancy and substrate variety; it shared the largest number of species with the pass habitat, but the overall community structure most clearly resembled the calmer tidepool habitat.
ACKNOWLEDGMENTS

We wish to thank James E. Maragos, University of Hawaii, and Roy Tsuda, University of Guam, for their diving support and allowing inclusion of their coral, algae, and substrate data into our report, and Aki Sinodo for diving and assistance with fish collecting.

We are grateful to Dennis T. O. Kam of the Hawaii Coastal Zone Data Bank for preparing the computer programs used in data analysis and Roberta Choy for her amazing patience as a typist.

We acknowledge a tremendous debt of gratitude to John E. Randall of the Bernice P. Bishop Museum, for identifications of fishes and especially for sharing his invaluable knowledge of the nomenclature of tropical Pacific fishes. Our thanks to John S. Stimson, University of Hawaii, for helpful comments concerning statistical analyses.

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LITERATURE CITED


A Preliminary Investigation of the Biology and Ecology of the Holothurians at Fanning Island

Sidney J. Townsley

Department of Zoology, University of Hawaii

Margaret P. Townsley

Assistant to the Expedition

INTRODUCTION

Among the most conspicuous, and perhaps most important, animals inhabiting the shallow littoral regions of coral reefs are the echinoderm Class Holothuroidea. Their activities in establishing and maintaining equilibrium conditions on reefs have been reported and discussed for over a century (Darwin, 1897; Guppy, 1889; Wood-Jones, 1910; Mayor, 1918; Gardiner, 1931; Crozier, 1915, 1918; Baker, 1925; Yonge, 1931; Bertram, 1936; Yamanouchi, 1929, 1939; Clark, 1946; Fish, 1967). All report the filtering capacity or ingestion of substrate by sea cucumbers and the ecological importance of the animals in the trophic structure of the reefs. There are also detailed studies of the morphology and histology of the gut of holothurians (Hamman, 1883; Cuvier, 1948; Stott, 1957; Tanaka, 1958; Trefz, 1958; Choe, 1962; Fish, 1967a). The quantity of information available, notwithstanding, the process of digestion and utilization of materials by sea cucumbers is still not fully understood.

The lack of knowledge about holothurians is partially explained by the still unsatisfactory knowledge of the classification of the Class. It is for this reason that faunal composition and abundance in many areas is imperfectly known. Most authors recognize that, among the echinoderms, the holothurians are the only class of echinoderms which have direct economic value despite the few echinoids whose gonads are used for food in several widely separated areas.

The present paper is a summary of a series of investigations concerning the fauna and biology of the holothurians at Fanning Island made during the period from July to August, 1972. The principal aim of the study was to establish a record of the composition of the sea cucumbers, their distribution on the atoll, and the dominant and conspicuous species. Population density and the biology of the dominant species were investigated insofar as facilities and time permitted.
METHODS

For the estimation of the populations of the dominant holothurian species several procedures were adopted, depending upon the individual species and the physical or topographical conditions prevailing. The larger species were censused by combining transects and quadrats. A plotless method used in forest and plant ecology (nearest neighbor) was adapted for some conditions (Smith, 1966). In some instances more than one technique was employed to establish reliable measurements of the density.

Collections and observations were made at nine locations, four in the seaward passes or reefs and five within the lagoon. The seaward stations were at Danger Point, Cable Station, North Pass, and Rapa Pass (see Fig. 1, p. 7, this report). The lagoon locations were Cartwright Point, Napu Naiaroa, Camp at North Pass, Vai Tepu, and the lagoon adjacent to Rapa Pass.

At all sampling stations collection of substrate immediately in front of recorded specimens and fecal pellet samples (when available) were made. Length and breadth of animals were recorded, and representative specimens collected for study of gut composition.

Analysis of grain size from substrate, gut contents, and fecal pellets was made by washing 50 grams (wet weight) of the collected material through geological sieves (4, 2, 1, 0.5, 0.25, and 0.1 mm mesh). The sieved material was dried in an oven to constant weight. Percentage composition of each sample was calculated on the basis of total dry weight of each aliquot.

The dermal ossicles and the sex of animals (or reproductive state) were recorded when ingested sand was removed from collected specimens. Animals appearing to be fissioning transversely were collected, and gross morphological examination of the body wall and internal organs made. Specimens believed to have fissioned were also collected and morphological examination of the internal organs studied.

The pH of the lumen of the fore-, mid-, and hindgut and the coelomic fluid was measured in freshly collected animals, starved animals, and animals fed after one week of starvation. Measurements were made using a combination glass electrode and a Beckman Expandomatic pH Meter. The mean of three measurements to the nearest hundredth of a pH unit was recorded.

Samples (10 grams) of ingested sand, material from the three portions of the digestive tract, and feces were extracted in 100 ml acetone. This extract was sealed in vials, wrapped in foil, and kept at -50°C until return to Honolulu. The acetone extracts were concentrated in N₂ atmosphere and the residue suspended in petroleum ether. Absorption curves for both acetone and petroleum ether extracts were made using a Beckman Model DBG recording spectrophotometer in 1 cm² cells and the solvent as reference. Thin-layer silica-gel chromatograms of the acetone and petroleum ether extracts were also made to determine the components present.
RESULTS

Five genera representing thirteen species were collected (Table 1). The nine collecting sites presented in this table represent generalized environmental conditions at Fanning as available echinoderm habitats. The stations are arranged so that the fauna of the four seaward reefs or passes may be compared with one another or contrasted with the fauna occurring in the lagoon and patch reefs. As shown in this table, the field observations clearly indicated that some species were more abundant within the lagoon than in the passes. It was not immediately recognized what factor(s) was most important for the apparent species distribution. Six of the 9 (2/3) of the localities possessed holothurian faunas composed of more than 50% of the recorded species: Danger Point, North Pass, Rapa Pass, Napu Naiaroa, Vai Tepu, and the south lagoon. The data also demonstrate that six species are present at five or more of the localities. No species was found at all stations; however, *Holothuria leucospilota* and *H. monocaria* occurred at eight localities. *Holothuria atra*, *H. argus*, and *Stichopus chloronotus* were recorded at six of the stations, while *Polypectana keffersteini* was present at five of the locations. The remaining species were recorded only from one to four of the localities. Only three species of sea cucumbers were found at the one station on the seaward reef (Cable Station) and one in the lagoon (Napu Naiaroa). One of these species (*H. leucospilota*) was noticeable in both passes and the lagoon.

The echinoids were the only other dominant echinoderms, with seven species recorded (Table 1). All seven species occur on the seaward reefs or in the passes; only two species were recorded within the lagoon, *Echinometra mathaei* and *Tripneustes gratilla*.

Other echinoderms were infrequently observed. Among these were the starfishes *Acanthaster planci*, *Linckia laevigata*, *Linckia multifora*, and *Mithrodia* sp. Ophiuroids were not actively sought and hence are not represented in our records. No comatulid crinoids were found either in the lagoon or in the passes.

The population density of *Holothuria atra*, *H. leucospilota*, *H. monocaria*, and *Stichopus chloronotus* was measured at several stations (Table 2). *S. chloronotus* is the most abundant species on the reefs at Fanning Island, and the next most abundant are *H. leucospilota* and *H. monocaria*. The population size of these species and other species are presented for comparison with the information collected at these locations. The calculated estimate of the quantity of substrate processed by the species at various locations is also presented to illustrate the importance of these animals in the distribution of material on reefs. The density of *H. atra* and *H. leucospilota* at Kabira, Ishigaki Island in the Ryukyus, approximates those at Fanning (Townsley, unpublished).

Transverse fissioning was observed in specimens of *H. leucospilota*. Large numbers of small individuals of this species were found on the lagoon reefs of the village near North Pass and at Vai Tepu. Relative frequency of fissioning in two random samplings from these locations was 0.3 and 0.2, respectively. Fissioning animals were recorded at other locations, but the
Table 1. Holothuroid and echinoid fauna occurring on the seaward reefs or in passes and in the lagoon at Fanning Island.

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<td></td>
</tr>
<tr>
<td>Stichopus sp.?</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Polypelectana</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>kessleriandi</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Chiridota rigida</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>7</td>
<td>3</td>
</tr>
<tr>
<td>Echinoidea</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Echinometra</td>
<td></td>
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<tr>
<td>mathaei</td>
<td></td>
<td></td>
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<tr>
<td>Echinosthenia</td>
<td></td>
<td></td>
</tr>
<tr>
<td>dianemus</td>
<td>x</td>
<td></td>
</tr>
<tr>
<td>Tripneustes</td>
<td></td>
<td></td>
</tr>
<tr>
<td>grattlia</td>
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<td></td>
</tr>
<tr>
<td>Heterocentrotus</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>mamillatus</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lytechinus sp.?</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Toxopneustes sp.?</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Euclidaris sp.?</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Kehinostrophus sp.</td>
<td>x</td>
<td>x</td>
</tr>
<tr>
<td>Total</td>
<td>5</td>
<td>7</td>
</tr>
<tr>
<td>Location</td>
<td>Species</td>
<td>Density (^1) (No./m(^2))</td>
</tr>
<tr>
<td>-------------------------------</td>
<td>------------------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>Bermuda</td>
<td>Stichopus mobili</td>
<td></td>
</tr>
<tr>
<td>Rongalap Atoll, Marshall Islands</td>
<td>Holothuria leucospilota</td>
<td>0.37 }</td>
</tr>
<tr>
<td>Kaneoa Bay, Hawaii</td>
<td>H. atra</td>
<td>0.7 }</td>
</tr>
<tr>
<td>Palau Islands, Western</td>
<td>H. leucospilota</td>
<td>0.1 }</td>
</tr>
<tr>
<td></td>
<td>H. atra</td>
<td>0.9 }</td>
</tr>
<tr>
<td>Kabira, Ishigaki I.,</td>
<td>H. leucospilota</td>
<td>0.072</td>
</tr>
<tr>
<td>Ryukyu Islands</td>
<td>H. atra</td>
<td>0.44</td>
</tr>
<tr>
<td>Fanning Island</td>
<td></td>
<td></td>
</tr>
<tr>
<td>North Pass</td>
<td>H. leucospilota</td>
<td>0.6 (\pm) 0.1 (79)</td>
</tr>
<tr>
<td></td>
<td>S. monocaria</td>
<td>0.1 (\pm) 0.03 (41)</td>
</tr>
<tr>
<td></td>
<td>S. chloronotus</td>
<td>7.0 (\pm) 2.3 (30)</td>
</tr>
<tr>
<td>Rapa Pass</td>
<td>H. leucospilota</td>
<td>0.05 (\pm) 0.01 (13)</td>
</tr>
<tr>
<td></td>
<td>H. monocaria</td>
<td>4.1 (\pm) 1.6 (771)</td>
</tr>
<tr>
<td></td>
<td>H. atra</td>
<td>0.05 (\pm) 0.01 (11)</td>
</tr>
<tr>
<td></td>
<td>S. chloronotus</td>
<td>5.0 (\pm) 1.21 (371)</td>
</tr>
<tr>
<td>Pink Reefs</td>
<td>H. leucospilota</td>
<td>0.24 (\pm) 0.1 (29)</td>
</tr>
<tr>
<td></td>
<td>S. chloronotus</td>
<td>0.36 (\pm) 0.1 (41)</td>
</tr>
</tbody>
</table>

\(^1\) Mean values plus or minus one standard error. Numbers in parentheses represent numbers of individuals sampled.

\(^2\) Nearest neighbor method of censusing populations. Plotless method beginning at the first specimen closest to the shore and continuing in a direction perpendicular from shore. Closest neighbor distances used for determining relative abundance.

\(^3\) Transects beginning at the entrance of the pass into the lagoon and continuing 400-600 meters into the lagoon. Two parallel transects, 50 meters apart for each set of population measurements. Three random 1-m\(^2\) quadrats were sampled along each transect at 20-meter intervals. Each group of measurements represent from 120 to 180 quadrats.
highest frequency occurred on these reefs. The smaller size of the specimens at these locations was the principal reason for investigating fissioning as a normal process of reproduction. Because these reefs are exposed during the day at low tides, it was believed that high temperatures could stimulate the process. Investigation of specimens collected from the reefs showed many individuals that contained only the anterior organs, calcareous ring, Polian vesicles and the buccal cavity. No other part of the digestive tract or the respiratory system was present. Posterior fragments appeared with about equal frequency, but somewhat less than expected. In these, there was no digestive tract present, but the cloaca, as a blind sac, and portions of the respiratory trees were recognizable. In none of these was there any indication of regeneration of the anterior portion of the body.

A number (13) of specimens of H. leucospilota were collected with a constriction in the anterior one-third of the body. All of these animals were found on reefs exposed to desiccation, high light intensity, and high temperature. These animals were believed to be in the process of fissioning, and were placed in tanks to observe the process. None of the animals survived the laboratory conditions. It was hoped that these observations would demonstrate the possession of a natural site for fissioning, but the question remains unresolved.

No facilities were available for studying rate of ingestion and turnover of sand by the sea cucumbers; consequently, no data are available for comparing the quantity of sand moved on these reefs with those estimated elsewhere.

Moderate success was obtained in an experiment designed to determine the change in the pH of the gut lumen with starvation. Other studies (Yamanouchi, 1941, 1942; Tanaka, 1958) have indicated that the pH of the gastric cavity may be an indication of the optimum for metabolic enzyme activity or that it is associated with the chemical dissolution of sand within the gut. The percent composition of substrate, gut contents, and fecal pellet samples from H. leucospilota and S. chloronotus as a function of grain diameter (mm) is shown in Figures 1 and 2. These figures show that the major components of the gut contents of S. chloronotus are also the major components of the substrate and fecal pellets of this species. It also demonstrates that the larger fragments of the substrate are rarely ingested by these animals, and hence either are selectively rejected, removed, or dissolved within the lumen. The same conditions are also recognized in the analyses made of ingested and excreted material from H. leucospilota. This species also ingests larger particles more frequently than does S. chloronotus, and hence the two species may be limited in their distribution on the basis of available substrate for ingestion. Analysis of sand from the foregut, midgut, and hindgut of these animals indicated that percentage composition changes as material is passed through it. In both species percentage composition of the foregut was similar to that of the substrate, but the midgut and hindgut consistently showed higher frequency of smaller particles. These observations suggest that the difference can be accounted for by (1) oral
Fig. 1. The percentage composition of the substrate, gut contents, and fecal pellets associated with *Stichopus chloronotus* as a function of grain size (mm). △ = substrate, ○ = gut contents, □ = fecal pellets.
Fig. 2. The percentage composition of the substrate, gut contents, and fecal pellets associated with Holothuria leucospilota as a function of grain size (mm). △ = substrate, ○ = gut contents, □ = fecal pellets.
egestion of the larger particles, (2) physical grinding of large particles, or (3) dissolving of particles by chemical means.

The possibility that chemical activity could dissolve the particles was investigated by placing specimens of *S. chloronotus* and *H. leucospilota* in pens constructed of wire mesh (0.5 in²). The pens, 5 meters in diameter and 1.5 meters high, were placed in the lagoon so that the animals were covered with water at all times, but the pens were never completely submerged. One pen was placed directly on the lagoon substrate; the other was lined with heavy weight plastic. Thus the animals in each condition were provided with substrate for ingestion or allowed only to collect fine silt deposited by the water. Fifteen specimens of each species were placed in each of the pens for a period of 1 week. At the end of the period the pH of the foregut and hindgut of six specimens of *H. leucospilota* and three *S. chloronotus* from each pen was measured by inserting a combination electrode directly into the mouth and rectum (3 cm). A lateral incision (1 cm) was made in each of these animals and the pH of the coelomic fluid measured. The animals were then opened and the connection between the foregut and the stomach slit open. The electrode was inserted 3 cm into the lumen of the midgut. The remaining animals in each pen were placed in the opposite pen for 24 hours. At that time they were treated in a similar manner, and the pH of the various regions measured. The data from these measurements are presented in Table 3. No difference from sea water was found in the foregut or hindgut, and both species were found to have lower pH in the midgut when placed on sand than if starved. Similar low pH was also observed in those individuals that were starved and then placed on sand for 24 hours. An increase in midgut pH was also observed in individuals transferred from sand to plastic for 24 hours (starved).

The foregut (stomach, Fish, 1967a) of many specimens of *S. chloronotus* and *H. leucospilota* was pale orange or rosy pink, and the gonads were also well developed. Most highly colored specimens were mature females. Acetone extractions of the foregut and the contents, in either acetone or petroleum ether, showed three absorption peaks: one at 450 mµ (4500 nm), another at 475 mµ, and a less distinct peak at about 425 mµ. These peaks appear to be due to absorption of β-carotene, although, the possibility of this being another compound has not been discounted. For equal aliquots and w/v extractions of the tissue and the ingested material, the mean percent transmission at 450 mµ was found to be 4.6 ± 1.0% and 19.1 ± 3.2%, respectively. It would appear from these measurements that the material is being concentrated within the gut tissue. The measurements of the tissue at the midgut and the hindgut were 43 ± 1.6% and 41 ± 2.3%, respectively.

DISCUSSION

Throughout these investigations it became evident that the holothurian fauna at Fanning Island resembles that of other tropical and semitropical faunas of the Indo-Pacific. The ubiquitous species of *Holothuria, H. atra, H. leucospilota, H. monocaria, H. argus,* and *H. bivittata* emphasize this relationship. However, the presence of *Actinopyga mauritiana, Stichopus chloronotus,* and *Polypelectana keffersteini* also indicates that this fauna
Table 3. Measurements of pH of midgut lumen of *Holothuria leucospilota* and *Stichopus chloronotus* which were provided with substrate for ingestion or prevented from ingestion of substrate. (See text for methods)

<table>
<thead>
<tr>
<th>Species</th>
<th>Sand (1 week)</th>
<th>Plastic</th>
<th>Plastic/Sand (24 hours)</th>
<th>Sand/Plastic</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>H. leucospilota</em></td>
<td>6.73 ± 0.05</td>
<td>7.15 ± 0.04</td>
<td>6.70 ± 0.08</td>
<td>7.18 ± 0.091</td>
</tr>
<tr>
<td></td>
<td>(6)</td>
<td>(6)</td>
<td>(5)</td>
<td>(5)</td>
</tr>
<tr>
<td><em>S. chloronotus</em></td>
<td>6.68 ± 0.01</td>
<td>7.03 ± 0.02</td>
<td>6.78 ± 0.07</td>
<td>7.20 ± 0.032</td>
</tr>
<tr>
<td></td>
<td>(3)</td>
<td>(3)</td>
<td>(3)</td>
<td>(3)</td>
</tr>
</tbody>
</table>

See Water pH 7.8  
Coelomic Fluid pH 7.6

1 Control left on sand, pH 6.8  
2 Control left on sand, pH 6.7
is little different from that found on other atolls or islands of the Pacific (Edmondson, 1946; Fisher, 1907; Yamanouchi, 1939; and Clark, 1946). Except for *S. chloronotus* and the *Toxopneustes* found at Fanning Island, the species are identical with those of the Hawaiian Archipelago.

The sea cucumber fauna at Fanning Island is markedly represented by specimens either limited to the lagoon or the passes and the seaward reefs. The lagoon forms are the apodus species *Polyplectana keffersteini* and *Chiridota rigida*. The seaward reef species are *Actinopyga mauritiana* and *A. nobilis*. The other species are more generally distributed either in the lagoon or in the passes, and their distribution seems best accounted for by suitable substrate, available food material, or water movement. Both *H. leucospilota* and *S. chloronotus* seem to overlap in their distribution, and the initial observations suggest that the former is the most abundant species on the reefs. The population census made at three areas in (Table 2) indicates that *S. chloronotus* is the most abundant species. The extremely high values obtained seemed somewhat questionable when compared with other species and data collected from other areas. However, these data can be explained by the very high densities of this species which occur in pools at the entrance to the lagoon. In these areas we found large beds of the brown alga *Turbinaria*. The presence of this alga was associated with great clumps of small individuals of this cucumber. The animals in these locations were wound about the algal stipe and passing their tentacles over the surface. These are believed to be either areas of unusually rich food resources or as nurseries for young individuals.

The major sand components of the gut of *S. chloronotus* and *H. leucospilota* are shown in Figures 1 and 2. The major component of the former is 0.25 mm or smaller; in the latter it is as great as 0.5 mm. The availability of suitable food resource or the presence of fine sand therefore seems to be of major importance in the distribution and abundance of these two species. For confirmation of this hypothesis studies were made at the lagoon reef adjacent to the Camp near N. Pass and at Cartwright Point. The reef near the Camp was composed of coarser sand particles than at North Pass, and the dominant species was *H. leucospilota*. This reef was also found to have a very sparse and patchy cover of *Turbinaria*. In the patches of the alga were the occasional specimens of *Stichopus*. The observations at Cartwright Point are similar, although there is very little *Turbinaria* in the pass (see Russell, p. 75, this report). Many specimens of *S. chloronotus* were found in the crevices of the beach rock at the margin of the pass. In these crevices there were accumulations of very fine sediment associated with this species. At Cartwright Point where the lagoon is partially enclosed on the North, the substrate is composed of coarse sand particles and the dominant sea cucumber species is *H. leucospilota*. Near the tip of the point the two species seem to occur in equal abundance; the *S. chloronotus* on patches of fine sand, *H. leucospilota* on coarser sediments.

The high density of *H. monocaria* was universally associated with rubble. This species is therefore limited in its distribution to areas near the passes where either blocks of coral or *Porolithon onkoides* comprise the major substratum. *Holothuria argus* and *H. bivitatta* were also limited to the passes and the entrance into the lagoon. They seem to be limited in
their distribution at Fanning Island to regions in which the water is continuously flowing or where the temperature does not increase markedly with tidal flow.

Very defined limits for the distribution of the apodus Chiridota rigida were also recognized. Throughout its geographic range this small, apodus sea cucumber lies just beneath the surface of fine sand. It is also present in areas in which fresh water may be mixing in littoral environments. It was most abundant adjacent to all fresh-water runoff areas, such as those occurring at Napu Naiaroa, the Camp at North Pass, and Val Tepu. Chiridota has the same pattern of distribution in the Hawaiian Islands and in the Ryukyu Islands.

The abundance of the dominant sea cucumbers on these reefs is higher than those reported for other tropical areas (Crozier, 1918; Yamanouchi, 1939, 1954; and Bonham and Held, 1963). The explanation for these differences can be ascribed to the methods employed and the aggregations already described. The aggregations may have led to estimates higher than one would expect for the entire island. It is equally remarkable that few other echinoderms were encountered, and the absence of comatulid crinoids is especially noticeable. The echinoids were the only other group regularly observed, and they were restricted to the seaward reefs. The only exception was the accumulation of Tripneustes gratilla at North Pass with S. chloronotus in the beds of Turbinaria or Echinometra mathaei at Rapa Pass among Porolithon onkoides. It seems that both food sources and available substrate are important in the distribution of these sea urchins on the Fanning reefs. A census of E. mathaei in the coralline algae of the pink reefs in the northern lagoon established a density of 0.08 per square meter. This is lower than Kelso (1970) found for this species on Oahu or that encountered on Okinawa (Townsley, unpublished data).

If the values we report here for the density of the sea cucumbers are reliable, we must assume that the rate of turnover of the substrate in the lagoon is higher than that measured elsewhere. There is a need for more measurements and seasonal observations before more can be said. Because these animals represent a very substantial population and high protein content it seems important to examine the efficiency of conversion.

The high frequency of regenerating individuals also indicates an effective mechanism for conversion or absorption of nutrients to protein within these animals. We recorded relative frequencies of 0.2 and 0.3 in two populations of H. leucospilota to fissioning or regenerating. Crozier (1915) encountered 10% regenerating H. surinamensis. Others (Frizell and Exline, 1955; Bonham and Held, 1963) have remarked on fissioning as a mechanism for reproduction. However, the problem has been given very little attention (Smith, 1971a, b). Our measurements of possible carotenoid pigments within the sand and the stomach of these animals suggest that there are specializations of the integument or gut that may be effective concentrating agents (Darwin, 1949a, b; Matsuno et al., 1969).

The amount of sand ingested by holothurians has received much attention (Crozier, 1918; Mayor, 1918; Yamanouchi, 1939; Bonham and Held, 1963). The
discussions have centered on sand as a suitable food resource and the physical dissolution of the reef. Whether holothurians are selective in the material ingested has been questioned (Fish, 1967a). The frequency of particle ingestion by H. leucospilota and S. chloronotus we encountered is consistent with that found for Cucumaria elongata (Fish, 1967a) indicating that some selection does occur. The percentage composition of the gut contents and fecal pellets from these animals compared with the substrate composition suggests that either selection of size or physical or chemical dissolution occurs. Starvation experiments (Table 3) indicate that feeding animals maintain lower pH of the midgut than do starved animals. These findings contrast with those of Tanaka (1958) who reported lower pH in starved animals than in those fed. The difference may be related to the time intervals used for starvation. Tanaka starved his animals for 12 hours, whereas our animals were starved for 1 week and for 24 hours, respectively. Differences in the method of measuring pH may also be responsible for the values obtained, but these seems unlikely. We believe the mechanism is available to dissolve the carbonate by chemical means, but the actual evidence is yet to be demonstrated.

There were no opportunities to make extensive investigations of the fecundity of the two dominant species. The records obtained showed very few reproductively active animals. We do not know whether reproduction is seasonal or continuous. No plankton tows were made to examine for larvae. Many small individuals were found (S. chloronotus) at the entrance to the lagoon at North Pass. We have already mentioned the significance of these individuals, but the information gathered was insufficient to establish size or age classes of this species. There are relatively few predators of sea cucumbers (the mollusks Tonna and Charonia), but neither was found in these environments. The local inhabitants apparently do not use sea cucumbers for food, and hence the population is probably close to equilibrium at most times, except for extreme environmental stress. The natural areas and the conditions obtaining at Fanning Island make this a suitable area for further investigations of species composition and population structure and control.

SUMMARY

1. Five genera and thirteen species of sea cucumbers were recorded at Fanning Atoll: Holothuria leucospilota, H. monocaria, and Stichopus chloronotus were the dominant species. All three species occurred within the passes or in the lagoon.

2. The apodus species Chiridota rigida occurred within the lagoon in sand adjacent to fresh water runoff.

3. Actinopyga mauritiana and A. nobilis were found only on the seaward reefs or at the entrance to the passes.

4. Species composition and distribution is similar to that found on other Indo-Pacific Islands.
5. Eight species of echinoids were found, predominantly in the passes where food or clear water were most available.

6. The presence of algae or substrate difference is considered to be important in distribution and abundance of the dominant species of holothurians.

7. The nutrition and role of the holothurians in transport of materials was examined. Comparison of the substrate composition with the ingested and excreted material indicates selectively or dissolution of material by physical and chemical processes. The possibility that material may be chemically dissolved within the gut was investigated. The pH of the gut of feeding animals was found to be lower than starving animals, suggesting that some chemical action acts on the ingested carbonate.

REFERENCES


ABSTRACT

The coral community on a 1 x 100 meter-long vertical section of the leeward ocean reef slope at Fanning Island was quantitatively investigated using SCUBA and a quadrat transect technique. Forty-seven species of corals were noted, and coral cover averaged over 60 per cent on the transect. Common coral species were restricted to certain depth regimes, resulting in pronounced vertical zonation. The community as a whole could be objectively divided into three assemblages with respect to depth. The deepest assemblage (30 to 35 m) was characterized by low coral cover, small average colony size, and high species diversity. Some of the species were specialized types not found elsewhere on the transect. Environmental conditions appeared stable with respect to wave action, but suboptimal with respect to light and sediment cover. At intermediate depths (20 to 25 m) the coral assemblage showed higher cover, larger average colony size, but lower diversity values due to dominance by a few species. Environmental conditions appeared to be both optimal and stable, with biological interactions determining the nature of the assemblage. At shallow depths (8 to 15 m) the assemblage showed slightly lower cover, moderately higher diversity, and moderately smaller average colony size. Wave action may periodicaly disrupt the environment which is otherwise optimal for coral development. In the shallowest environments near-shore reef substrates are dominated by coralline algae, and corals are rare. Environmental conditions are probably both suboptimal and unstable, resulting in the inhibition of coral development. The structure and probable factors controlling the structure of the Fanning coral community are similar to those of other reef slope communities recently studied, particularly in the Red Sea.

INTRODUCTION

The evolution of a reef follows a sequence in which reef slopes must first form and grow before the reef flats can develop. Environmental conditions on reef flats are quite different from those on the deeper slopes and it is not surprising that community composition and structures are correspondingly different. Nevertheless, most generalizations regarding the ecology of reef communities have been derived from the study of reef flats. Because of the inaccessibility and risk involved, the study of ocean reef slopes has been largely neglected.
The purpose of this investigation was to gain a better understanding of the forces which control the community structure of corals on an ocean reef slope at Fanning Island (3°N, 159°W). Corals are the dominant benthic organisms on many of the leeward ocean reefs of the atoll. Recently, coral communities on reef slopes have been quantitatively assessed by Porter (1972 a, b, c) in Panama and by Loya (1972) in the Red Sea. The Fanning Island site is subjected to more wave activity than the other two regions. Other common reef organisms, including fish, algae, and echinoderms were also investigated on the Fanning site (Chave and Eckert, p.135, this report; Tsuda, p. 69, this report; Maragos, p. 97, this report; and Townsley and Townsley, p. 173, this report).

METHODS

The study reef was located 400 m north of English Harbor Pass (transect 3, Fig. 1, p. 135 this report). A transect was established perpendicular to the depth contours of the reef slope. The coral community was measured using a contiguous quadrat technique. From these data estimates of abundance, size, diversity, pattern, evenness, zonation, distribution, and ordination of the corals were extracted. An attempt is made to correlate patterns of community structure with physical and biological factors.

The reef tract surveyed was 100 meters long and 1 meter wide with the upper end (quadrat no. 100) located at a depth of 8 m and the deeper end (quadrat no. 1) located at 36 m. All investigations were carried out using SCUBA during a series of dives conducted from anchored skiffs. A 100-meter-long polypropylene rope of 1/4-inch diameter with small lead markers at 1-meter intervals was paid out along the transect and tied to the reef with strands of wire. Numbers stamped on each of the markers corresponded to quadrat numbers. It was originally planned to run a parallel transect some distance down the reef, but weather and logistics prevented this. Identification of most of the corals was made on sight. Unidentified species were assigned code names, and samples of these corals were later identified in Hawaii. A reference collection of all corals from Fanning is described in Maragos (p. 97, this report). The entire transect was also photographed using color slide film and a Nikonos II underwater camera mounted on a rigid frame. Each photograph covered a constant area of the transect. The photographs were used as checks against data acquired by the quadrat method and also provided a baseline for future planned studies.

The quadrat consisted of a frame 1 meter on a side subdivided by wires into a grid of 100 squares of equal area. Beginning at one end of the transect, the quadrat was centered over the line between the lead reference markers. Quadrat number and depth were read and recorded on underwater writing slates. The abundance of coral was estimated by counting the number of squares occupied by each coral colony. Similar estimates of sediment cover were also recorded on site. The quadrat was then placed over the second meter interval and the above procedures repeated until the entire transect of 100 quadrats was surveyed.

The contiguous quadrat method was chosen because the author has used it in the past (Maragos, 1972) and has found it to be an efficient means of
acquiring data when time in the field is limited. Quadrat sampling can acquire the same kind and amount of data compared to line intercept methods but over a smaller dimension of the reef. Because a major consideration in this study was to examine data variations along both large and small intervals of the reef, it was necessary to choose a method which could conveniently provide information on both. The quadrats were all contiguous and allowed their grouping (pooling) in order to facilitate investigation of data at a variety of sampling dimensions. Unfortunately this study was carried out before the recent studies of Porter (1972 a, b, c) and Loya (1972) were available for review. These authors employed similar line intercept methods. More consideration will be given to using comparable methods in the future since one of the basic problems in the comparative investigations of reefs has been the lack of standardization of sampling procedures (Stoddart, 1969 a, b).

The quadrat data were used to compute a variety of descriptive parameters. Topography and steepness of slope were computed from the depth information. Coral abundance data were expressed as percent cover. The distribution of each coral species was plotted with respect to quadrat number (i.e., depth) and provided the basis for the zonation studies. A size index of the corals was computed from the ratio of total cover to the number of colonies for each quadrat. Because many colonies were not entirely within the boundaries of the frame, this measure is only an approximation of true colony size (area). The quadrat abundance data for each of the common species were also subjected to pattern analysis using the index of dispersion (Greig-Smith, 1964) which is simply the ratio of the variance to the mean abundance for a group of $n$ samples of equal size. This index can be statistically tested to determine whether distributions are significantly random, even, or aggregated. For each species the index was computed within a range of gradients where the species was commonly found. The quadrat data also provided the estimates of species richness, that is, the number of species per unit area and a measure of diversity. The Shannon-Weaver (1949) index $H'_c$ was computed using: $H'_c = \sum p_i \ln p_i$, where $p_i$ is the proportion (percent cover) of the "ith" species in a sample and $\ln$ refers to the natural logarithm. This index is also a measure of diversity, but differs from species richness in that it also considers the relative proportion of each species as well as the number of species. When the abundance of all species in a sample is the same, $H'_c$ is at a maximum. The ratio of the observed $H'_c$ to the maximum value of $H'_c$ is called the evenness index (Pielou, 1966). Presumably this index is a good measure of dominance. When one or a few species in a sample are much more abundant than the rest, the evenness index is low.

The coral abundance data for individual quadrats were subjected to dendrograph analysis (McCammon and Wenninger, 1970). The analysis graphically determines the relative similarities among groups of variables. A dendrograph was computed on the individual quadrats to determine whether the transect could be objectively divided into discrete zones. This examination also provided a basis for determining the maximum number of quadrats which could be pooled at regular intervals along the transect.

Analysis of the relative differences in the above properties along the transect was the major consideration of this study. Since many of these
expressions are dependent on sample size, comparisons were made only between groups of quadrats or transects intervals of equal size. The criterion for the determination of the minimum sampling interval corresponding to maximum diversity values (see Loya, 1972) was not considered because it was not important to determine the absolute values of some of the parameters.

RESULTS

Bathymetry of the transects is indicated in Figure 1. The slope of the reef is gradual and consistent. At small intervals (±1 meter) substrate relief is irregular. The lack of large-scale relief is in part due to the poor development of a spur and groove system on this reef, a feature more common along windward slopes. The upper end of the transect terminates on the outer edge of a broad shelf (in 8 meters of water) which gradually shoals towards the shoreline located in 200 m landward. Although the outer edge of this deep reef "flat" is not distinct, long-period swells generate noticeably stronger surge currents here before passing overhead and breaking onshore. Surge currents inhibited sampling in shallow water and were a primary reason for abandoning a shoreward extension of the transect. Qualitative surveys showed that coral cover and colony size diminished while coralline algae abundance increases towards shore and shallow water. In the surf zone, the pink coralline alga Porolithon dominates substrate cover. Large, overturned colonies of Acropora reticulata and abundant, old, eroded shingle formed from the skeletons of these corals indicate that at times wave action must be severe along this coast (Gallagher, 1970; Gallagher, et al., 1971).

The deep end of the transect was located at the bottom of the reef slope at a depth of 36 m near the upper edge of a sand talus which appears to extend to great depths. In the marginal zone between reef and sand are isolated rubble fragments to which corals are frequently attached. Sand is rare above depths of 30 m (quadrat no. 15). Hard substrate and live coral covered 99 per cent of the transect above this point. Normally the deep reef environment is not subjected to much wave surge. Water is extremely transparent at all areas of the transect, and both vertical and horizontal visibility usually approached 50 m or more.

A species list of the transect corals and a summary of their abundance, distribution, and pattern are presented in Appendix A. The reef tract was judged to be the most diverse and flourishing with respect to corals of any area at Fanning. At least 47 species were present within the boundaries of the transect. These included 40 scleractinian hermatypes, one milliporinid hermatype, three alcyonaceans, two stylasterinids, and one antipatharian. About 60 percent of the hermatypic coral species of Fanning (see p. 97, this report) were present.

Live coral cover on the reef was high (Figs. 1 and 2) averaging over 60 percent. Excluding the sand zone at the bottom, coral cover approached 75 percent along the reef slope. Corals are locally rare on the deep slope, presumably because of the lack of suitable substrates for larval attachment. Harrigan (1972) has shown that coral larvae (planulae) do not settle on sediment particles the size of sand or smaller. Elsewhere on the transect
Fig. 1. Bathymetry of reef slope and coral abundance. Per cent cover plotted for each of 100 quadrats. No vertical exaggeration.
Fig. 2. Coral abundance and the Shannon-Weaver diversity index plotted as a function of transect location (depth). (A) values based on pooling of contiguous pairs of quadrats; (B) values based upon pooling of contiguous groups of 5 quadrats.
Fig. 3. The Shannon-Weaver diversity index plotted as a function of transect location (depth) for individual quadrats, groups of 5 quadrats, and groups of 10 quadrats.
coral abundance was both high and variable (Fig. 1). Pooling the quadrats into larger groups tended to reduce variability between groups (Figs. 1 and 2).

Pattern analysis on coral abundance data showed trends of patchiness for most of the species (Appendix A). Only for two corals, *Porites (S.) vaughani* and *Pavona clavus*, was there an indication of random or even distributions. Both of these corals are small encrusting forms which occupy crevices and local dead patches between larger colonies. This habitat type is fairly common along the reef and may be randomly distributed. By maintaining small dimensions, both *Porites* and *Pavona* may be occupying habitat space which is limited in space but commonly distributed throughout the reef even in areas where larger corals predominated.

The Shannon-Weaver diversity index computed for the individual quadrats showed wide fluctuations, but tended to become smoothed out when progressively larger groups of quadrats were compared (Figs. 2 and 3). It has been suggested (Porter, 1972 b, c; Kinzie, 1970) that local variations in substrate relief can affect diversity values. Data were sufficient to test this hypothesis. Diversity values for each of the 50 quadrat pairs were pooled into one of three classes, depending on steepness of slope within each interval and then subjected to analysis of variance (Table 1). Species richness, diversity indices, and evenness indices were significantly or nearly significantly higher on steep reef slopes compared to values obtained from moderate or flat slopes. These findings may indicate corals preferentially settle on steep reef slopes but dominance is correspondingly reduced in such environments. However, it is also important to note that depth and slope showed partial but significant correlation along the transect (Table 1). Hence the significantly greater diversities on steep slopes may in part be due to the effect of depth.

In general, data from Figure 2 show no visual or consistent correlation of diversity with coral abundance, implying each parameter is controlled by different sets of factors. Pooling the quadrats into larger groups tended to smooth out small-scale variations, but large-scale variations in diversity and abundance persisted even when large groups of quadrats were analyzed (Fig. 3). One area of the transect between quadrats 30 to 40 showed significantly lower diversity values than adjacent regions (Table 2). This suggests that dominance of the substrate is probable because coral cover is high. The situation is different for the bottom 20 quadrats of the transects which as a group also showed significantly lower diversity indices (Table 2). However, pooling the quadrats into successively larger groups resulted in a greater increase of diversity at the deep end of the reef relative to other regions (Fig. 3). The increase was so great that the diversity values at the deep end were higher than elsewhere when contiguous groups of ten quadrats are compared. This zone also coincides with that of high sediment cover and low coral abundance. Diversity may be low in small sample sizes because the number of corals encountered are few. Combining quadrats substantially raised the apparent diversity because there is a larger proportion of new species added, none of which dominates the others. Thus, over large sampling areas (that is, groups of ten quadrats) coral populations at the deep end of the transect are characterized by high diversity and greater heterogeneity compared to other areas of the transect.
A. A list of the slopes for each gradient on the transect. Numbers refer to quadrat number. A = slope less than 15° (flat); B = slope 20-30° (moderate); C = slope greater than 45° (steep). Correlation between slope and depth = 0.57 and was significant at p = 0.01.

| 1-2 | B | 27-28 - C | 53-54 - A | 79-80 - B |
| 3-4 | B | 20-30 - C | 55-56 - C | 81-82 - B |
| 5-6 | C | 31-32 - B | 57-58 - B | 83-84 - B |
| 7-8 | C | 33-34 - B | 59-60 - A | 85-86 - A |
| 9-10 | C | 35-36 - A | 61-62 - C | 87-88 - A |
| 11-12 | B | 37-38 - B | 63-64 - B | 89-90 - A |
| 15-16 | C | 41-42 - A | 67-68 - C | 93-94 - A |
| 17-18 | C | 43-44 - B | 69-70 - B | 95-96 - A |
| 19-20 | C | 45-46 - A | 71-72 - B | 97-98 - A |
| 21-22 | C | 47-48 - B | 73-74 - B | 99-100 - A |
| 23-24 | C | 49-50 - A | 75-76 - B | 99-100 - A |
| 25-26 | C | 51-52 - A | 77-78 - B | 99-100 - A |

B. Analysis of variance results: slope comparisons

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Type of Comparisons</th>
<th>Probability</th>
</tr>
</thead>
<tbody>
<tr>
<td>Species richness</td>
<td>Steep, moderate slopes</td>
<td>.018</td>
</tr>
<tr>
<td></td>
<td>Steep, flat slopes</td>
<td>.019</td>
</tr>
<tr>
<td>Shannon Weaver diversity index</td>
<td>Steep, moderate slopes</td>
<td>.009</td>
</tr>
<tr>
<td></td>
<td>Steep, flat slopes</td>
<td>.032</td>
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<tr>
<td>Evenness index</td>
<td>Steep, moderate slopes</td>
<td>.055</td>
</tr>
<tr>
<td></td>
<td>Steep, flat slopes</td>
<td>.087</td>
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</tbody>
</table>

Summary of probabilities of occurrence based upon analyses of variance to determine whether coral diversity values at 2-meter intervals on steeper reef slopes are significantly different from those of moderate or flat slopes. Steep is defined here as greater than 45° slope, moderate is 20-30°, and flat is 15° or less. The parameters tested measure various aspects of coral diversity and included species richness, Shannon-Weaver index, and the Pielou evenness index.
### TABLE 2

**ANALYSIS OF VARIANCE RESULTS: DEPTH COMPARISONS**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Transect intervals upon which comparisons are based (Quadrat no.)</th>
<th>Probability</th>
</tr>
</thead>
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<tr>
<td>Species richness</td>
<td>0-10, 10-20</td>
<td>&lt;.001</td>
</tr>
<tr>
<td></td>
<td>10-20, 20-30</td>
<td>.121</td>
</tr>
<tr>
<td></td>
<td>20-30, 30-40</td>
<td>.004</td>
</tr>
<tr>
<td></td>
<td>30-40, 40-50</td>
<td>.004</td>
</tr>
<tr>
<td>% coral cover</td>
<td>0-10, 10-20</td>
<td>&lt;.001</td>
</tr>
<tr>
<td></td>
<td>10-20, 20-30</td>
<td>&lt;.001</td>
</tr>
<tr>
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<td>.044</td>
</tr>
<tr>
<td></td>
<td>10-20, 20-30</td>
<td>.039</td>
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<tr>
<td></td>
<td>20-30, 30-40</td>
<td>.004</td>
</tr>
<tr>
<td>Evenness index</td>
<td>0-10, 10-20</td>
<td>.068</td>
</tr>
<tr>
<td></td>
<td>10-20, 20-30</td>
<td>.887</td>
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<tr>
<td></td>
<td>20-30, 30-40</td>
<td>.011</td>
</tr>
<tr>
<td>Shannon-Weaver diversity index</td>
<td>0-10, 10-20</td>
<td>.012</td>
</tr>
<tr>
<td></td>
<td>10-20, 20-30</td>
<td>.140</td>
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<tr>
<td></td>
<td>20-30, 30-40</td>
<td>.002</td>
</tr>
<tr>
<td></td>
<td>30-40, 40-50</td>
<td>.012</td>
</tr>
</tbody>
</table>

Summary of probabilities of occurrence based upon analyses of variance to determine whether coral diversity, size, and abundance values within selected intervals of the transect differ significantly from those of adjacent zones. The three measures of diversity used here include species richness, evenness index, and the Shannon-Weaver diversity index. Each interval comprises a group of 10 contiguous quadrats.
Loya (1972) noted higher coral diversities at the bottom of reef slopes and Porter (1972b, c) noted lower values at the bottom of his study reef where coral cover ends.

Essentially the same trends were noted for the species richness comparisons (Fig. 4). Greater variability is evident for smaller sampling increments. Again the transect region between quadrats 30 to 40 show a consistent "low" at all size comparisons. At the deep end, species richness also shows greater increases than those for other regions of the transect when comparisons involved progressively larger numbers of pooled quadrats. These observations suggest the same factors control both species richness and the Shannon-Weaver function. Porter (1972c) also postulated that both these expressions are simultaneous properties of the coral community.

Regional variations in evenness (H'/H max) are plotted for selected size increments in Figure 5. Again, the transects region between quadrats 30 to 40 showed lower values (that is, higher dominance), although evenness estimates were also low in other areas of the transect. The fact that dominance in most areas of the transect did not result in a reduction of diversity or species richness, suggests dominance by corals within the 30-to 40-quadrat range was more severe, resulting in the exclusion as well as reduced abundances of other species. At opposite ends of the transect, evenness indices were higher and indicate a lack of relative dominance. Both abundant sediment, and reduced sunlight could account for the greater evenness values at the deep end, while it is tentatively suggested that wave and, possibly, storm activity prevent dominance at the shallow end of the transect. Grigg and Maragos (1974) present a similar hypothesis to explain the relatively high community diversity of reef corals along exposed coasts in Hawaii.

The abundance of common colonial and solitary corals are plotted as a function of transect location (depth) in Figures 6 and 7. These diagrams show pronounced overlapping vertical zonation among the corals. Dives to either side of the transect line indicated the zonation pattern persisted for considerable distances along the reef face.

Lobophyllia costata and Sarcophyton sp. are the dominant corals of the region between quadrats 30 to 40, a zone previously showing significantly reduced values of species richness, diversity indices and evenness indices. Individual colonies of both species are spread out over large areas of the reef. Hence, these colonies can effectively exclude other corals and reduce diversity. Lobophyllia is a mussid coral with large polyps; according to Lang (1970) and Connell (in press) such forms are more likely to rank high among the competition-predation hierarchy of corals inhabiting a reef. The possibility exists that predation by Lobophyllia may aid the coral in achieving dominance, an idea which will be investigated in future studies. Sarcophyton on the other hand, is a soft coral characterized by a continuous spongy "corallum" which seemingly smothers other corals by growing over them. The alcyonacean may be capable of rapid growth which may help in achieving local dominance.

Several varieties of unattached, solitary corals were found principally in depressions between larger corals, frequently stacked upon
Fig. 4. Species richness plotted as a function of transect location (depth) for individual quadrats, groups of 5 quadrats, and groups of 10 quadrats.
Fig. 5. Evenness index ($H'/H_{max}$) plotted as a function of transect location (depth) for individual gradients, groups of 2, groups of 5, and groups of 10 quadrats.
Fig. 6. The abundance of the common colonial corals plotted as a function of transect location (depth.)
Fig. 7. The abundance of the common solitary hermatypic corals plotted as a function of transect location.
each other. Although these corals were not so common as some of the colonial forms, their capacity to move and live unattached to the substrate may enable solitary forms to be less affected by competition for space by other common and sessile colonial corals.

A correlation matrix based upon the data of each quadrat was generated and formed the basis for the dendrograph in Figure 8. The analysis shows the transect quadrat may be objectively subdivided into a series of discrete clusters each of which characterizes a certain depth regime. Loya (1972) used a similar approach to describe coral community zonation in the Red Sea. In this study, each association roughly encompassed groups of 10 quadrats or greater. There are seven smaller clusters (Fig. 8) which appear to be portions of the three major regions of the transect. One major zone encompasses quadrats mostly on the upper half of the transect (quadrats 50 to 100). Another major zone appears to be located at the bottom of the transect between quadrats 0 to 20. The final major zone includes quadrats 20 to 50 located at moderate depths along the transect.

The quadrat data and dives in shallow water indicated only 7 species were confined to shallow regions of the reef, while 17 of the total of 47 species recorded were confined to the deep areas of the transect (below 18 meters). The greatest number of species (23) was found both above and below a depth of 18 meters (Appendix A). The greater number of both total and unique forms in deeper water suggest that the environment there is more favorable for the coexistence of corals than in shallower water.

Analysis of the index of average size (Fig. 9) indicates the smallest colonies existed at the deep end of the reef where presumably sediment and light conditions are suboptimal. The largest colonies predominated within the 30-to 40-quadrat range and support the hypothesis that the larger colonies of both Lobophyllia and Sarcophyton may physically exclude other corals. Colonies along the remainder (shallower portion) of the transect were generally of moderate size.

DISCUSSION

Results of this study indicate that at small intervals (1 to 2 meters) along the reef there is marked variation in coral abundance, distribution, diversity, evenness, and colony size. Much of this variability may be attributed to variations in slope or substrate relief (Table 1). Accumulation of sediment in reef depressions may also promote greater heterogeneity and reduced abundance. For coral communities (Figs. 1 to 3), large size and dominance by some corals may inhibit the development of other forms and lead to small-scale patchiness of abundance for individual species. Predation, and competition (for space) may periodically disrupt continued development of some corals, resulting in a community more patchy in abundance. Non-uniform larval settlement (both in space and time) and natural coral mortality are other factors which may account for small-scale patchiness; Connell (in press) has attempted to investigate some of the factors responsible for this phenomenon.
The pronounced zonation and diversity of the Fanning reef coral community suggests that a variety of strategies have evolved among corals which enable them to persist on reefs. Solitary, unattached fungiid corals may "avoid" the effects of competition for space by having the ability to move and live apart from the substrate. Lobophyllia and Sarcophyton grow to large size which results in dominance and the exclusion of other forms. Large colony size is achieved in habitats not subjected to catastrophic events such as storms, which enables continuous growth. Some corals persist by inhibiting the growth of other corals by predatory activity. Elsewhere in tropical oceans, staghorn Acropora (Shinn, 1972; Manton and Stephenson, 1935; Crossland, 1938) form extensive thickets excluding other corals by reducing light or circulation. A similar strategy applies to branching Porites platforms in Hawaii (Maragos, 1972) and for the alcyonacean Sclerophyllum in Samoa (Cary, 1931). Other corals may exist on reefs only at small dimensions. Nevertheless Porites (S.) vaughani and Pavona clavus achieve a common and even distribution on Fanning reef by living in the small spaces between larger colonies or upon the local dead portions of larger colonies. Elsewhere Porolithus (Maragos, 1972) and Stylophora (Loya, 1972) appear to remain on reefs as fugitive species (Hutchinson, 1951).

The reef coral community at Fanning may be subjectively divided into a number of vertical "zones" based upon the dendrograph and other analyses. At greatest depths on the transect physical factors such as sediment and low light intensity may limit both the growth and dominance of corals. However, the environment is too deep to be periodically disrupted by storm waves and therefore may allow a greater coexistence of specialized and different forms. At intermediate depths (quadrats 30 to 50) the environment may be both stable with respect to storm waves and optimal with respect to light conditions. A stable and favorable environment may allow biological interactions to determine the nature of the community. For example, a few forms may find conditions optimal and dominate reef substrates as does Lobophyllia and Sarcophyton. At shallower depths, the environment becomes periodically disrupted by wave action but light conditions are optimal for development of a variety of small forms. In the shallowest environments above the transect, breaking waves, scour, and diurnal variations in temperature, salinity, light, and exposure result in unpredictable and suboptimal conditions (see Loya, 1972). The diversity and development of corals is lower there than elsewhere. The coral community is replaced by other organisms such as coralline algae.

Loya (1972) came to similar, although not the same, conclusions regarding community structure of reef corals of Eilat, Red Sea. One discrepancy was that he speculated that light is limiting to coral growth and development at moderate depths, rather than at deeper ones. He based this conclusion on a strong direct correlation of illumination intensity and average coral size for a variety of depths. His Figure 13 shows that illumination underwent the greatest attenuation between depths of 2 and 10 meters. However, according to Jerlov (1968) and Holmes (1957), the greatest attenuation of solar energy occurs within the upper meter of the surface due to the preferential absorption of red and other long-wavelength light by water. It is obvious then that the vertical distribution of light energy and light illumination are not the same. It seems likely that
Fig. 8. Dendrograph showing associations among the individual quadrats of the transect. Numbers refer to quadrats which were enumerated chronologically beginning at the deep end of the transect. To avoid crowding, the numbers were placed in two columns. Distance is a spatial measure of the dissimilarity between individual or groups of quadrats. The arc cosine transformation was used to convert the correlation coefficients to a distance measure. A maximum distance of \( \pi/2 \) (or 1.57) corresponds to a minimum correlation of zero.
Fig. 9. The size index (an estimate of average colony area) plotted as a function of transect location (depth).
available light energy is functionally related to the biological processes of calcification and photosynthesis, and that Loya's (1972) presumed correlation of "coral growth" to illumination may be either coincidental, or that his measure of colony size is not a good indicator of coral growth. Nevertheless, it seems likely that at deep depths light limits the development of corals at both the Red Sea and Fanning transect sites.

Loya (1972) concluded that the deeper coral communities at Eilat existed in a stable environment, facilitating more rapid evolution of new and more specialized corals. He also noted that most of the corals existing in the environment were not found in shallow water, a fact which also applies to corals on the Fanning reef slope. Specialized corals such as the solitary fungiids, Cirripathes, Echinophyllia, Pachyseris, and Leptoseris were confined to deeper waters. At shallower environments at Eilat the greater unpredictability of the environment was due to extremes in tides, salinity, and temperature, as well as waves. At Fanning, the upper end of the transect was not shallow enough to be affected by these factors; it seems more likely that storms and wave action take on greater significance in inhibiting the development of coral communities at shallow depths at Fanning.

Slobodkin and Sanders (1969) have postulated that environments which are both unpredictable and suboptimal show lower species diversity and evolution than environments which are either optimal or predictable. Species immigration is more likely to occur from unpredictable to optimal environments than the reverse. In this study the deepest environment showed the greatest diversity. Hence it may be postulated that environments which are predictable and suboptimal are more diverse than those environments which are both predictable and optimal because dominance is less likely to occur in the deeper suboptimal environment which allows greater coexistence, and, perhaps, more rapid evolution of new species.

CONCLUSIONS

1. Substrates with steep relief appear to enhance diversity and inhibit dominance by corals. Such environments may be characterized by greater habitat diversification.

2. Sediment cover appears to limit corals by restricting the amount of available substrate suitable for attachment. This has the tendency to reduce abundance and diversity of corals at small reef dimensions.

3. Growth and perhaps maximum size of corals along the deeper portions of the transect may be limited by reduced light intensities at depths greater than 30 meters.

4. A combination of suboptimal light and substrate conditions at depth coupled with a predictable (wave-free) environment may have enabled a greater number of corals to coexist.
5. The structure of the coral community may be determined by biological interactions at intermediate depths. Optimal and predictable physical conditions enable some species to achieve dominance at the expense of other corals resulting in reduced diversity.

6. At moderately shallow depths, environmental conditions are more unstable due possibly to periodic wave damage. This has the tendency to reduce both dominance and the number of coral types.

7. Qualitative observations in shallow water indicate the environment is both unpredictable and suboptimal. Scour and mechanical stress from waves and a host of other factors may limit both the number of kinds and the abundance of corals. Coralline algae appear to find these environments more favorable than do the corals.

8. Species distribution and dendrograph analyses have indicated that coral communities of the seaward leeward reef slope at Fanning are strongly zoned and are probably very complex and mature assemblages.

9. Corals have adopted a variety of strategies enabling them to persist and dominate on reefs.

10. The phenomenon of small-scale patchiness prevails in practically all of the quantitative expressions used to describe the coral community. Potentially numerous factors control the local development of corals, and point to the need for future studies of the phenomenon.

11. Contiguous quadrat sampling offered some unique approaches in the investigation of the ecology of reef corals. Nevertheless, studies which have employed other techniques have reached similar conclusions regarding community structure.

ACKNOWLEDGMENTS

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REFERENCES CITED

Cary, L. R. (1931) Studies on the coral reef of Tutuila, Amer. Samoa, with
special reference to the Alcyonaria. Publs. Carn. Inst. Wash. 413:
53-98.

Coral Reefs. A. Jones and Ebdese (Ed.) Academic Press, in press.


Geophys. 70-23: 191-192.

191-205.

Ltd. 256 pp.

on submerged lava flows in Hawaii. Ecology, in press.

Lunar periodicity of swarming and substratum selection behavior. Ph.D.

Holmes, R. W. (1957) Solar Radiation, Submarine Daylight, and photo-
synthesis. In: Treatise on Marine Ecology and Paleoecology, Hedgpeth

32(3): 571-577.

N. Y. 194 pp.

of Discovery Bay, Jamaica, Ph.D. Thesis, Yale University, New Haven.

Lang, J. C. (1970) Inter-specific aggression within the scleractinina

Loya, Y. (1972) Community structure and species diversity of hermatypic


## APPENDIX A

<table>
<thead>
<tr>
<th>Name</th>
<th>Abundance (% cover)</th>
<th>(Number of quadrats)</th>
<th>Index of dispersion</th>
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<tr>
<td>All corals</td>
<td>62.38</td>
<td>100</td>
<td>5.93</td>
</tr>
<tr>
<td>Echinophyllia aspera (Ell. &amp; Sol.)</td>
<td>0.51</td>
<td>22</td>
<td>D 1.97</td>
</tr>
<tr>
<td>Acropora abrotanoides (Lam.)</td>
<td>0.01</td>
<td>1</td>
<td>S</td>
</tr>
<tr>
<td>Acropora humilia (Dana)</td>
<td>1.03</td>
<td>9</td>
<td>*</td>
</tr>
<tr>
<td>Acropora nasuta (Dana)</td>
<td>0.17</td>
<td>3</td>
<td>D</td>
</tr>
<tr>
<td>Acropora reticulata (Brook)</td>
<td>6.97</td>
<td>52</td>
<td>16.29</td>
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<tr>
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<td>5</td>
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<tr>
<td>Astreopora listeri Bernard</td>
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<td>2</td>
<td>D</td>
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<tr>
<td>Ciriopathes spp. ++</td>
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<tr>
<td>Distichopora violacea (Pallas) ++</td>
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<td>1</td>
<td>S</td>
</tr>
<tr>
<td>Favia speciosa (Dana)</td>
<td>0.28</td>
<td>8</td>
<td>*</td>
</tr>
<tr>
<td>Favia speciosa c.f. F.s. puteolina (Dana)</td>
<td>0.44</td>
<td>23</td>
<td>*</td>
</tr>
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<td>Favia stelligera (Dana)</td>
<td>9.35</td>
<td>75</td>
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<td>6</td>
<td>*</td>
</tr>
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<tr>
<td>Hydnophora microconos (Lami)</td>
<td>0.28</td>
<td>8</td>
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<tr>
<td>Lobophyllia costata (Dana)</td>
<td>5.99</td>
<td>38</td>
<td>18.41</td>
</tr>
<tr>
<td>Merulina ampliata (Ell. &amp; Sol.)</td>
<td>0.09</td>
<td>5</td>
<td>D</td>
</tr>
<tr>
<td>Millepora platyphylla H. &amp; E.</td>
<td>3.95</td>
<td>34</td>
<td>15.34</td>
</tr>
</tbody>
</table>
APPENDIX A (cont'd.)

<table>
<thead>
<tr>
<th>Name</th>
<th>Abundance (% cover)</th>
<th>(Number of quadrats)</th>
<th>Index of dispersion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Montipora hoffmeisteri Wells</td>
<td>0.08</td>
<td>3</td>
<td>*</td>
</tr>
<tr>
<td>Montipora patula Verrill</td>
<td>0.01</td>
<td>1 D</td>
<td>*</td>
</tr>
<tr>
<td>Montipora socialis Bernard</td>
<td>0.32</td>
<td>4 S</td>
<td>*</td>
</tr>
<tr>
<td>Montipora verrilli Vaughan</td>
<td>0.75</td>
<td>27</td>
<td>*</td>
</tr>
<tr>
<td>Pachyseris speciosa (Dana)</td>
<td>0.08</td>
<td>5</td>
<td>*</td>
</tr>
<tr>
<td>Parahalomitra robusta (Quelch)</td>
<td>0.03</td>
<td>1 D</td>
<td>*</td>
</tr>
<tr>
<td>Pavona clavus (Dana)</td>
<td>0.49</td>
<td>29</td>
<td>1.72 **</td>
</tr>
<tr>
<td>Pavona gigantea Verrill</td>
<td>0.23</td>
<td>12 D</td>
<td>*</td>
</tr>
<tr>
<td>Pavona varians Verrill</td>
<td>3.32</td>
<td>66</td>
<td>7.92</td>
</tr>
<tr>
<td>Pavona (Pseudocolumnastrea) pollicata</td>
<td>0.54</td>
<td>11 D</td>
<td>*</td>
</tr>
<tr>
<td>Platygryra lamellina (Ebr.)</td>
<td>0.31</td>
<td>18</td>
<td>*</td>
</tr>
<tr>
<td>Platygryra sinensis (Lam.)</td>
<td>0.07</td>
<td>5 D</td>
<td>*</td>
</tr>
<tr>
<td>Plesiastrea versipora (Lam.)</td>
<td>0.19</td>
<td>10 S</td>
<td>*</td>
</tr>
<tr>
<td>Pocillopora eydouxi M. Ed. &amp; H.</td>
<td>1.01</td>
<td>13</td>
<td>*</td>
</tr>
<tr>
<td>Pocillopora meandrina Dana</td>
<td>5.80</td>
<td>72</td>
<td>6.36</td>
</tr>
<tr>
<td>Pocillopora molokensis Vaughan</td>
<td>0.06</td>
<td>1 D</td>
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</tr>
<tr>
<td>Porites lobata Dana</td>
<td>0.16</td>
<td>4 D</td>
<td>*</td>
</tr>
<tr>
<td>Porites (Syntaraea) vaughani Crossland</td>
<td>0.36</td>
<td>32</td>
<td>0.57 **</td>
</tr>
<tr>
<td>Psammocora verrilli Vaughan</td>
<td>0.12</td>
<td>7</td>
<td>*</td>
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<tr>
<td>Sarcophyton sp +</td>
<td>7.47</td>
<td>25 D</td>
<td>30.64</td>
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<tr>
<td>Stylaster elegans Verrill ++</td>
<td>0.02</td>
<td>2 S</td>
<td>*</td>
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<tr>
<td>Stylophora mordax (Dana)</td>
<td>6.34</td>
<td>61</td>
<td>8.58</td>
</tr>
<tr>
<td>Unidentified alcyonarian (#1) +</td>
<td>1.19</td>
<td>7 D</td>
<td>*</td>
</tr>
<tr>
<td>Unidentified alcyonarian (#2) +</td>
<td>0.76</td>
<td>17</td>
<td>22.50</td>
</tr>
</tbody>
</table>

+ ahermatypic corals.
++ soft corals.
* data insufficient for calculation.
** pattern not significantly clumped at \( p = 0.05 \) level.

S = confined to depths less than 18 meters.
D = confined to depths of 18 meters or more.
Blank = found in both zones.
THE ORDINATION OF COMMON REEF ORGANISMS AT

FANNING ATOLL

J. E. Maragos

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E. H. Chave

Department of Zoology

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ABSTRACT

Information on the abundance of 113 common taxa reef organisms were gathered at 60 stations at Fanning Atoll. Results of ordination analysis show that the turbid lagoon, clear lagoon, and oceanic reef slope each support a different biota. The oceanic reef slope may be further subdivided into three distinct assemblages, each characterizing a different depth regime. Environmental conditions appear to control or determine the distribution of each assemblage. Associations among corals and fish correspond to those described in other studies (see p. 135 this report). Although each of the two ordination techniques was based on different mathematical approaches, the results obtained were comparable.

INTRODUCTION

Ecological communities comprise an assortment of different organisms living in proximity to one another. Associations among these organisms presumably reflect interaction or control by similar parameters. The study of patterns of community composition may, therefore, reveal species specific associations and mechanisms of environmental regulation.
Classification and ordination are two common approaches to the study of communities (Greig-Smith, 1964). Both techniques attempt to simplify or order complex arrays of organism distribution data into smaller sets of associations. Classification involves the arrangement of organisms into groups each having in common a number of characters which set that group apart from other groups. The process by which organisms are classified into categories depends upon the characters selected. Hence, the choice of characters determining the nature of each group is often a subjective process. Ordination on the other hand stems from the concept of a community as a continuum. An attempt is made to place each organism group in relation to one or more reference positions in such a way that a statement of its position relative to the reference position conveys the maximum information about its composition. The reference positions themselves are usually determined by mathematical means.

Reef communities are often regarded as among the most diverse of those reported in marine environments (Wells, 1957). However, there has been only one previous ordination study of a reef community (Smith, 1973). Such studies are limited by the numbers of specialists available to simultaneously investigate designated reef habitats because reefs are usually located in areas without research facilities.

During July and August, 1972, specialists on reef echinoderms, corals, algae, and fish engaged in a number of field studies at Fanning Atoll. Through mutual cooperation, a considerable amount of data on the abundance of over 150 macroscopic reef organisms was gathered at the same 60 stations. Uniformity in sampling methods yielded data adequate for ordination analysis. One hundred thirteen species, included 7 benthic algae, 43 corals, 3 holothurians, and 60 fish are considered in the analyses. Organisms not found at four or more of the stations were omitted from the analysis.

Two types of ordination techniques are employed. One technique is that of principal component factor analysis with varimax (orthogonal) rotation (Rummel, 1970); the other technique is a type of cluster analysis in which the results are presented as a dendrograph (McCammon and Wenninger, 1970). For brevity, the latter method will be referred to as dendrograph analysis. Results obtained from both methods are compared and possible environmental and behavioral parameters explaining the observed patterns are discussed. Results of the Fanning reef ordination are compared with a similar study carried out in Hawaii (Smith, 1973).

METHODS

The sampling stations were located along three transects, each 100 m long, in the clear lagoon, turbid lagoon, and ocean reef slope, respectively (see Fig. 1 in Chave and Eckert, p. 135 this report). Each transect was subdivided into twenty 5-meter intervals yielding a total of 60 stations. The distribution of the stations was highly non-random within each region, since time prevented the study of a large number of widely distributed sites. The length and location of the transect lines were set to yield the maximum
amount of information within representative environments. Methods used to estimate the abundance of fish, corals, and algae are detailed in Chave and Eckert (p. 135 this report), and Maragos (p. 187 this report). Data from 1-meter-square quadrats laid along the transect line at 1-meter intervals provided data on abundance of corals and echinoderms. Quadrats were similarly placed at 1-meter intervals during algal surveys, but, the area of each quadrat was 0.1 m² (see Tsuda, p. 69, this report). Different quadrat sizes were used for corals and algae because they were distributed differently along the transects. Within each station, abundance data from the five quadrats were summarized and expressed as percent cover of algae, corals, and echinoderms. Fish abundance was estimated using a visual method adopted from Brock (1954) and expressed as absolute density.

Ordination was accomplished using two different techniques so that the results could be compared. In general there is a lack of standardization of ordination methods (see Greig-Smith, 1964; Gauch and Whittaker, 1972). Both techniques used in this study are based on the analysis of the correlation matrix between species as computed from raw data on abundance.

Factor analysis has recently been used for a number of environmental and ordination studies (see Smith, 1973, for a review) and provides a variety of different types of information. As applied here, the analysis first delineates a number of independent associations. At an intermediate step, the investigator then chooses the number of factors to be further analysed. The last stage includes orthogonal rotation of factor matrix and computation of the factor scores. Choice of factor number is largely subjective and is usually based on the purpose of the analysis. The criterion of including only those factors which will explain a sufficient proportion of the total data is useful for uncovering major associations. With this goal the number of factors usually chosen varies between two and six. Under other circumstances, however, the investigator may wish to include a greater number of factors. In this study only the major associations were investigated using factor analysis.

The strength of each factor on a variable is indicated by the magnitude of the factor loadings which vary in value from plus one to minus one. Loadings are simply correlation coefficients between the variable and the generated factors (see Table 1). Squaring the factor loading (analogous to the coefficient of determination) gives an estimate of the amount of variation explained by the factor. The communality is the sum of the squares of the loadings for a given variable and provides an estimate of the proportion of the total variation in the data which is explained by the analysis. The sum of the squares of the loadings for a given factor provides an estimate of the total variation in the data explained by the factor. These expressions denote the relative success of the analysis and determine which organisms (variables) are strongly associated with the factors. Another type of information provided is the factor scores. The magnitude of the scores, either positive or negative, represent the strength of a particular factor at a particular station. Hence, factor analysis provides information about the nature, size, and spatial distribution of associations.
The second ordination technique, referred to here as dendrograph analysis, is considerably easier to understand and explain. Where most of the results of factor analysis are presented in numerical form, the final results of dendrograph analysis are usually presented in graphical form. The method computes distance between individual variables and groups of variables based on their respective degree of correlation. The distances are usually plotted in a two-dimensional plane, the dendrograph (McCammon and Wenninger, 1970). Distance is a general term synonymous with the geometrical concept of distance. The greater the correlation, the less distance separates two variables or groups. The correlation coefficients of the correlation matrix were converted to a measure of distance using the arc-cosine transformation. Using this transformation, a correlation of zero corresponds to a maximum distance of 1/2 or 1.57, while a maximum absolute correlation of 1.0 corresponds to a minimum distance of zero.

RESULTS

Different physical environments characterized each of the transect sites. The clear lagoon site (transect 1) was characterized by greater seawater transparency, relatively strong currents, moderate relief including numerous coral-covered boulders, and abundant sandy sediment. Depth along the transect varied from 5 to 15 meters. The turbid lagoon site (transect 2) was characterized by large amounts of mud, high water-turbidity, moderate to high substrate relief where coral pinnacles occurred, and relatively low water exchange and circulation. Depth along this transect was fairly shallow (ca 1 to 7 meters) and light intensities were presumably moderate to high (see Roy and Smith, 1971). The ocean reef site (transect 3) was low in sediment, contained little substrate relief, and showed wide variation in depth, light intensity, and water motion. Seawater was transparent and well mixed compared to lagoon sites. More information about the environmental conditions at each of these regions can be found in Stroup and Meyers (p. 7, this report).

Because of these differences in the physical environment, it was not surprising to find strong regional differences in community composition and structure. Results of the factor analysis are presented in Table 1 and Figure 1. The rotated factor matrix shows that five major associations (factors) among 113 reef organisms could account for 45 percent of the total variation in the data. Each of these factors included some combination of fish, corals, and usually algae. Factor one indicates high association among 1 alga, 12 corals, and 15 fish. Most of these species appear to be common at moderate depths on the ocean-reef slope. Factor two shows a high association among 2 algae, 8 corals, and 7 fish, and most of these are confined to the deeper portions of the ocean reef slope. Factor three indicates a high association among 1 alga, 4 corals, 1 echinoderm, and 11 fish. Most of these organisms appear to be common in clear lagoon habitats. Factor four shows a high association among 1 alga, 8 corals, and 7 fish. These organisms are confined to shallow depths, principally at the ocean-reef site. Factor five shows a high association of 4 corals and 6 fish which are found most commonly within the turbid lagoon. The high loadings of particular fishes and corals with individual factors support the conclusions of Chave and Eckert (p. 135 this report) which indicate that
Table 1. Rotated Factor Matrix

<table>
<thead>
<tr>
<th>Factor Number</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
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<tbody>
<tr>
<td>Percent of Total Variance</td>
<td>11.3</td>
<td>8.7</td>
<td>8.5</td>
<td>10.5</td>
<td>4.9</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Variable Name</th>
<th>Communality 5 Factors</th>
</tr>
</thead>
<tbody>
<tr>
<td>ALGAE</td>
<td></td>
</tr>
<tr>
<td>F. CHAETO</td>
<td></td>
</tr>
<tr>
<td>Family Chaetophoracea</td>
<td>0.12</td>
</tr>
<tr>
<td>L. VARLEG</td>
<td></td>
</tr>
<tr>
<td>Lobophora variegata</td>
<td>0.34 -0.56</td>
</tr>
<tr>
<td>D. FRIABI</td>
<td></td>
</tr>
<tr>
<td>Dictyota frabilis</td>
<td>0.48 -0.58</td>
</tr>
<tr>
<td>POLYSIPH</td>
<td></td>
</tr>
<tr>
<td>Polysiphonia sp.</td>
<td>0.25</td>
</tr>
<tr>
<td>CRUS. COR</td>
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<tr>
<td>Crustose coralline</td>
<td>0.33 0.45</td>
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<tr>
<td>G. INTRIC</td>
<td></td>
</tr>
<tr>
<td>Gelidiopsis intricata</td>
<td>0.36 0.54</td>
</tr>
<tr>
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<td></td>
</tr>
<tr>
<td>Gelidiella sp.</td>
<td>0.46 0.67</td>
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<tr>
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</tr>
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<td>A. ABROTA</td>
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<tr>
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<tr>
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<tr>
<td>MERULINA</td>
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<td>Merulina ampliata</td>
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Table 1. (Continued)

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<th>Factor Number</th>
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<th>4</th>
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<td>Percent of Total Variance</td>
<td>11.3</td>
<td>8.7</td>
<td>8.5</td>
<td>10.5</td>
<td>4.9</td>
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<table>
<thead>
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<td><strong>CORALS</strong></td>
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<td></td>
</tr>
<tr>
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</tr>
<tr>
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<tr>
<td>Favites abdita</td>
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<tr>
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<tr>
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<tr>
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<tr>
<td>Favia speciosa puteolina</td>
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Table 1. (Continued)

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<tr>
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<td>11.3</td>
<td>8.7</td>
<td>8.5</td>
<td>10.5</td>
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<td>0.72</td>
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>80% sediment
>20% hard substrate

Fig. 1. Graph showing bathymetry profiles, substrate composition, and the factor scores for each of the three transects. Bathymetry plotted with 2X vertical exaggeration. Only the scores having absolute values greater than 1.0 are shown. There are 20 stations per transect. The transects are located in the turbid lagoon, clear lagoon, and ocean reef slope.
certain species of reef fish live within or near certain species of reef corals. For example, *Pomacentrus lividus* and *Chromis stripectoraria* show statistical correlation with *Acropora delicatula* and *A. formosa*, two varieties of branching corals. Similar associations were noted between the fishes *Mirolabrichthys* sp. and *Chromis acares* and the corals *Sarcophyton* sp. and *Leptastrea purpurea*. Diving observations indicated these species of fish used the specified corals for refuge.

The distribution of factor scores (Fig. 1) supports the contention that each of the factors is regionally distributed. Factor three characterizes the shallow, clear lagoon, typically in areas of hard substrate and high relief; factor five characterizes hard substrate stations in the turbid lagoon; and factors one, two, and four were confined to the ocean reef. The low factor scores at lagoon stations dominated by loose sediment can be attributed to the low abundance of most common reef organisms except near areas of high relief and hard substrate. Nor do the echinoderms which were found predominately on the sand during daylight hours show much association with any of the factors. The greatest scores of factors one, two, and four provide an objective vertical zonation of the ocean reef community.

Results of the dendrograph analysis (Fig. 2) confirm the results of the factor analysis. The species of each cluster of the dendrograph were the same as those sharing mutual association in the rotated factor matrix. It is difficult to decide the exact number of clusters presented in the dendrograph and our estimates vary from five to seven. Each of the clusters is numbered and appears to characterize the following environments: (1) moderate depths in the clear lagoon and ocean reef slope; (2) shallow ocean reef slope; (3) moderate depths only on the ocean reef slope; (4) deep ocean reef slope; (5) turbid lagoon; (6) shallow lagoon (turbid and clear); and, (7) clear lagoon. An association corresponding to the small cluster of two echinoderms and two corals (cluster no. 6) was not delineated in the factor analysis, perhaps because the association involved relatively few species. The factor analysis tended to define only the larger clusters.

One main difference in the results of the two analyses is the possible addition of two wide-ranging associations (1 and 6) in the dendrograph analysis. These may be intermediate associations between some of the other clusters. Although individual clusters were fairly distinct from one another, the great distances among organisms within each cluster indicates a lack of strong correlation. Small-scale variation in the distribution of individual species may account for the lack of stronger correlation.

Station-by-station comparisons could not be carried out using the dendrograph technique because the abundance of the organisms involved were expressed in two different units, fish abundance in absolute density, and benthic biota abundance in percent cover. It is difficult to convert absolute density and percent cover into a uniform expression of abundance and consequently station-to-station comparisons are rendered uncertain.
DISCUSSION

Although each ordination technique employed separate mathematical approaches and computations, the results are comparable. The kinds of questions asked from an ordination analysis should be the main criteria for the choice of an appropriate method. For example, factor analysis delineates a variety of different properties about inherent associations, and some of these may be more useful than others depending upon needs. Factor analysis also provides numerical estimates of the proportion of data explained by each factor, for each variable, and by the analysis as a whole. The scores show spatial or geographical patterns in the factors. Results of factor analysis may be further manipulated. Some workers maintain that the differences between factors can be subjected to significant testing (see Rummel, 1970). Most of the results of the analysis are usually presented in numerical form.

When the main objective of an ordination is to merely define patterns in abundance for a group of organisms, cluster analysis may be both sufficient and preferred. Presentation of the results in a dendrograph may enable readers unfamiliar with ordination techniques to grasp and assimilate the nature of associations to a greater extent than if data are presented numerically. If the data are all expressed in the same units, than there is greater justification for a geographical comparison between stations. For example, Maragos (p. 187 this report) successfully determined associations between quadrats along the ocean transect based upon the abundance of corals.

In both techniques, the interpretation of the number of associations appeared to be the most subjective portion of the analyses. In factor analysis, the choice of factor number is made at an intermediate step while in dendrograph analysis, the decision can be made after the final results are plotted. From this standpoint readers may find it easier to review the conclusions of the author by merely re-examining the dendrograph. In order to review the decision regarding the number of factors in factor analysis, the original correlation matrix or unrotated factor matrix must be presented in order to recompute new rotated factor matrices. Such a review would be difficult and tedious. If space is a major criterion on deciding ordination method, considerably more space is probably needed to describe the methods and results for a factor analysis.

Results of both techniques show that the Fanning reef biota can be objectively divided into regional components: turbid lagoon, clear lagoon, and ocean reef slope. Water transparency, circulation, light intensity, depth, substrate composition, and biotic interactions may all be important in explaining regional variations in the reef biota at Fanning Atoll. The oceanic assemblage can be further subdivided into three vertical (depth) components. Chave and Eckert (p. 135 this report) and Maragos (p. 187 this report) independently concluded the same ocean reef transect could be objectively divided into three zones based on the distribution of fish and corals, respectively. The boundaries of the three zones show greater similarity between the "fish" zonation and the factor analysis than between the "coral" zonation and the factor analysis. This may in part be due to
Each cluster is numbered and described in the text.

Formed on correlation coefficients, arrows point to boundaries between adjacent clusters. Distances are based upon the arc-cosine trans.

Fig. 2. Dendrogram showing abundance associations between individual and groups of reef organisms.
the preponderance of fish species (60) in the analysis compared to the number of coral species (43). In any case, variations in physical conditions along the transect may account for the distinct vertical zonation of the reef slope. It is possible that vertical gradients in light, sediment, and water circulation may control the vertical distribution of many coral species and, in turn, the distribution of the corals may partially control the vertical distribution of fish.

Only one other study (Smith, 1973) has applied similar ordination techniques to describe reef community associations. Factor analysis was applied to the presence/absence data of common reef biota in Kaneohe Bay, Oahu, Hawaii. Smith found that combinations of corals, fish and other benthic animals and plants characterized each of four factors. Although the species of reef organisms in Kaneohe Bay were considerably different from those at Fanning, most of the physical parameters thought to explain the associations (substrate texture, relief, water quality, and circulation) were the same. Although the regional distribution of the factors were not as distinct in Kaneohe Bay as at Fanning, this may in part be due to the more random distribution of sampling stations and the greater heterogeneity within Kaneohe lagoon environments.

It should be emphasized that investigations such as these are largely at an experimental stage. There is yet no standardization of methods nor widely accepted statistical methods to evaluate the significance of the results of either of the techniques utilized in this study. Furthermore, there is a lack of unanimity in the value of using such approaches as principal component factor analysis (Gauch and Whittaker, 1972). Nevertheless some techniques as factor analysis are capable of answering a greater number of questions than other methods. In any case ordination techniques may provide useful information on the nature and distribution of marine communities and help outline future research goals.

SUMMARY AND CONCLUSIONS

The common reef biota of Fanning Atoll can be objectively divided into several distinct assemblages. Environmental conditions appear to explain the distribution of each assemblage. Associations between individual species may also affect the nature of each of these assemblages. In general, the results of this study support the findings of Chave and Eckert (p.135 this report) and Maragos (p.187, this report). Results of the Fanning study are similar to those of another study conducted in Hawaii (Smith, 1973).

Comparison of the two ordination methods show that factor analysis yields a variety of information principally in numerical form. If the main purpose of a study is to define associations between organisms, a combination of cluster analysis results presented in dendrograph form may be intuitively easier to describe, to understand, and to review. Both methods yielded similar results on the nature of the major reef organism associations at Fanning Atoll.
ACKNOWLEDGMENTS

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BIBLIOGRAPHY


Behavioral Ecology of the Ghost Crabs
Ocypode ceratophthalmus and Ocypode cordimana
at Fanning Atoll, Line Islands

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ABSTRACT

Burrows and zonation patterns in O. cordimana (semiterrestrial) and O. ceratophthalmus (intertidal) were studied in two different habitats at Fanning Island. Gross interspecific zonation correlates closely with the fresh water tolerances of the two species but appears unrelated to salt water tolerance. O. cordimana displays an intraspecific zonation pattern based on age and sex. No such pattern was found for O. ceratophthalmus except that reproductive burrows occupied by mature males are almost invariably placed below the preceding high tide mark. In both species burrow structure varies according to inhabitant sex and age. A comparison of O. ceratophthalmus behavior throughout the Indo-Pacific suggests that intraspecific differences in behavior depend largely upon genetic rather than environmental factors.

INTRODUCTION

Crabs of the nocturnal genus Ocypode occur in large numbers on sandy beaches in tropical and subtropical regions. Of the 19 Indo-Pacific species of Ocypode, O. ceratophthalmus (Pallas) is perhaps the most extensively distributed. It is, in fact, one of the most widespread of all Indo-Pacific crabs (Forest and Guinot, 1962).

Because of its ready availability, O. ceratophthalmus has been the subject of several ecological and behavioral investigations. These include the work of Hayasaki (1935) and Takahasi (1932, 1935) in Taiwan, Barrass (1963), Cott (1929), and Hughes (1966) in Mocambique, Jones (1972) in Kenya, Tweedie (1948, 1950) in Malaya, George and Knott (1965) in Western Australia, and Fellows (1966) in Hawaii. With few exceptions, these reports are characterized by three features: (1) they are almost exclusively restricted to western populations of the species; (2) there is a very noticeable lack of agreement among the various authors; and (3) few contain sufficient quantified data suitable for the reconciliation of these differences.
The 1972 Fanning Expedition provided an excellent opportunity to compare certain aspects of the ecology and behavior of an isolated, relatively undisturbed central Pacific population of *O. ceratophthalmus* to the Hawaiian and western populations of this species and additionally offered a chance to observe a single population under radically varying environmental conditions. When, upon arrival at Fanning, a population of *O. cordimana* Desmarest was discovered, an investigation of this previously unstudied species was also undertaken.

THE EXPERIMENTAL ANIMALS

General Habits

*O. ceratophthalmus* is an intertidal species restricted to the sandy beach habitat. The few references to *O. cordimana* demonstrate a more terrestrial niche for this species. Rao (1968), for example, reported *O. cordimana* burrowing as much as 200 yards inland on the east coast of India, and presented evidence that it possesses physiological and anatomical adaptations not found in intertidal *Ocypode*. Even so, *O. cordimana* is apparently restricted to areas having a sandy shoreline and often inhabits the uppermost portion of the beach proper (Takahasi, 1935; Farrow, 1971). At Fanning both inland and beach populations of *O. cordimana* were found, but the beach populations were sparse compared to those of *O. ceratophthalmus*.

Despite approximate equality in size (maximum carapace width of both species is about 45 mm), the two species differ decidedly in their aggressiveness. *O. ceratophthalmus* is a fast-moving, highly active, and aggressive species which frequently preys on smaller *Ocypode* of its own and other species (Takahasi, 1935; Hughes, 1966; Fellows, 1966). In contrast, *O. cordimana* is relatively slow-moving and docile, though when sufficiently threatened the massive chelae are used defensively. This difference may reflect conditions in the respective habitats of the two species: vegetation in the supratidal zone offers concealment but impedes locomotion, whereas the converse is true in the *O. ceratophthalmus* habitat. In this respect it is worth noting that the semiterrestrial *O. laevis* found in Hawaii is similarly quite unaggressive, and that both it and *O. cordimana* have significantly shorter legs than does *O. ceratophthalmus* (Fellows, unpublished data), a feature which may increase maneuverability in grass at the expense of speed in the open.

In Hawaii and elsewhere, adult *O. ceratophthalmus* are generally nocturnal. Although Barrass (1963) reported that nocturnal activity is further moderated by tidal cycling, Jones (1972) demonstrated an endogenous nocturnal activity rhythm devoid of any tidal component, suggesting that response to tidal fluctuation may depend upon continuous sensory input. In contrast, a high incidence of diurnal juvenile activity has been recorded from certain localities. Hughes (1966) investigated juvenile behavior on several beaches in Mocambique and reported that activity was inversely proportional to human beach usage. On the most isolated beaches, juveniles were more active during the daylight hours than at night, and Hughes
suggested that this reversal might serve to reduce adult predation on the young. Although activity was greatest after dark at Fanning, large numbers of adults and juveniles alike were observed diurnally, especially at low tide on overcast days, but little aggressive interaction between age classes was noted. No activity records have been found for *O. cordimana*, but at Fanning the species appears to be almost entirely nocturnal.

Excepting cannibalism by *O. ceratophthalmus*, relatively few predators on *Ocypode* have been reported. At Fanning, these include the moray eel *Gymnothorax pictus*, which frequently leaves the water in pursuit of Crustacea inhabiting the waterline (Chave and Randall, 1971), and the puffer *Arothron hispidus*, which feeds along the beachline either singly or in small schools. The former is more common in rocky intertidal areas and consequently represents a more serious threat on the ocean beach than on the lagoon beach. The puffer appears to be quite common in the lagoon, and small schools often followed my activities on the beach, preying upon *Ocypode* driven into the water. The full extent of *Arothron* predation on *Ocypode* is unknown; gut analysis of 19 specimens (range 64 to 302 mm total length, average 136 mm) captured along the lagoon beaches disclosed no *Ocypode* remains, although two had been feeding on *Grapsus grapsus*, one on *Cardisoma carnifex*, and three others on assorted portunids. Moreover, the puffer is potentially a more serious threat to *Ocypode ceratophthalmus* than to *O. cordimana* because when disturbed the former commonly retreats into the water whereas the latter turns inland. Inland populations of *O. cordimana*, of course, are spared from predation by these and by *O. ceratophthalmus*; as autopredation was not observed among *O. cordimana* even when dissimilar-sized individuals were confined together, it seems likely that their only potential predator may consist of the atoll's large and fairly common rats.

**Indices of Maturation**

Among Hawaiian *Ocypode*, zonation and burrow design correlated so closely with sex and maturity level that this approach was extended to the present study. Behavioral and gross anatomical criteria used in the earlier study (Fellows, 1966) suggested that males enter puberty at about 26 to 28 mm* and become fully mature at about 35 mm. Females also were judged to enter puberty at about 28 mm, but no evidence of an intervening adolescent stage prior to the onset of full maturity was found. These findings were confirmed by a much more detailed study in which Haley (in press) showed that sperm production begins at 28 mm in the male, but that spermatophore production is delayed until about 33 mm. Among females, copulation and vitellogenesis may be found at a minimum of 26 mm but do not become common until 28 to 30 mm. Because the onset of puberty corresponds

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*All measurements of crab size in this paper indicate the greatest width of the carapace.*
closely with the first appearance of the styliform eye process in both sexes, the possession of the styliform process was used in this study to signify maturity.

In keeping with the relatively small size of the *Q. cordimana* population at Fanning, a limited sample of 18 females between 21- and 45-mm carapace width were sacrificed for examination. All crabs smaller than 30.5 mm retained the abdominal-thoracic hook and had short, sparse pleopod hair. The abdomen : carapace width ratio increased steadily in crabs up to 32 mm then stabilized around an average of 0.572, marking a change from allometric to isometric growth at this point. Swollen, well-developed spermathecae, indicative of copulation, were first found at 32 mm, and functional ovaries were found in all specimens 33.5 mm and over. These data suggest that females of this species mature at approximately 30 to 32-mm carapace width.

Size at maturation is less certain in the case of males. A series of 23 males in the 14 to 41-mm size range was examined. The abdominal-thoracic hook, which is lost at maturity by *Q. ceratophthalmus*, is retained by *Q. cordimana*, as is the usual case in Brachyura. The gonopods extend anterior to the suture between the fourth and fifth thoracic segments and assume isometric growth only in crabs larger than 27 mm, though the sternal depression in which the gonopod tips rest does not develop the characteristic hair patch until the carapace is at least 29 mm wide. Testes first become apparent in 27 mm individuals but remain small and relatively inconspicuous until 32 mm. It thus appears that male maturation develops over at least two molt intervals, with puberty beginning at 27 mm and the attainment of full maturity at approximately 32 to 33 mm. As this species lacks the styliform eye process, *Q. cordimana* of both sexes were assumed for the sake of consistency to be mature at 30-mm carapace width.

Relative to maturation, it should be added that *Q. cordimana*, unlike *Q. ceratophthalmus*, appears to breed seasonally. Although Haley (in press) finds histological evidence that the latter species has a peak breeding period during the spring and summer months in Hawaii, the year-round presence of large numbers of megalopa and first post-megalopa suggests continuous reproductive activity in *Q. ceratophthalmus*. Opposed to this, the smallest *Q. cordimana* found at Fanning was 10-mm carapace width, and none of the mature females dissected showed signs of vitellogenesis.

**STUDY AREAS**

The ocean beach habitat at Fanning Atoll is composed of a series of discontinuous wave beaches separated by wide stretches of coral shingle. Of these, only the well-developed beach fronting the cable station grounds was investigated, both because of its accessibility and because of its general resemblance to certain of the beaches I have studied in Hawaii. During this study, the beach was 500 to 600 m long, up to 15 m wide at low tide, and had an estimated maximum elevation of 3 to 3.5 meters. Profile varied laterally: some portions of the beach face sloped at a continuous 12 to 15° from vegetation to waterline, whereas in other areas a flat 6- to
7-m-wide berm terminated abruptly in a 30 to 35° scarp. On the average, the beach was approximately 8 m wide at high tide, and even during spring tides and storm surf the uppermost 2 to 3 m remained dry. The sand was relatively fine though poorly sorted and angular. Directly fronting the cable station grounds, the beach terminated in a wide beach-morning-glory (Ipomoea sp.) zone; elsewhere along the beach front, vegetation consisted of an almost impenetrable Scaevola-Messerschmedia thicket.

In contrast, the lagoon beach is a generally low, narrow strand nearly continuous around the lagoon. In the area studied, maximum elevation was generally under 0.35 m, width at low tide was 2 to 3 m, and wave coverage was frequently complete at high tide. In a few areas the beach widened to as much as 8 m at low tide due to the development of a low front berm, but even here there was little dry beach at high tide because the fresh water lens rose into the depression behind the berm (Fig. 1). This same figure also shows the large amount of debris characteristic of the lagoon beach and the moderately dense coconut-Messerschmedia vegetation bordering the beach.

ZONATION

Methods

Zonation data were obtained on the ocean beach from 32 transects 1 m wide, extending from vegetation to waterline. Although a variety of profiles was surveyed, little variation was evident, and all data were combined for analysis. The restricted width of the lagoon beaches precluded transect studies, and complete sampling of randomly chosen 25-to-50-m beach sectors was substituted. Both wide and narrow beaches were included in this survey. A 55-to-75-m-wide transect through the cable station grounds from ocean beach to lagoon beach was examined in detail, and all Ocypode burrows encountered were dug up to determine the sex and size of the inhabitant.

Results

O. ceratophthalmus: In Hawaii this species exhibits a clearcut zonation pattern common to all beaches yet studied, provided the beach is wide enough for zonation to develop. Large mature males inhabiting spiral burrows (see below) and juveniles of both sexes inhabit a shifting "daily intertidal zone," the upper limit of which is delineated by the highest wave penetration during the preceding tidal cycle. Mature females and adolescent males (28 to 35 mm) are almost exclusively restricted to the dry beach zone above the daily intertidal (Fellows, 1966).

Results obtained on the ocean beach transects at Fanning differed from this in several respects. The transects were sampled early in the morning at low tide. As shown in Table 1, approximately 88% of the juveniles and only 68% of the combined mature female-adolescent male population occurred above the level of the preceding nocturnal high. If plotted relative to
Table 1. Distribution of *Q. ceratophthalmus* on the ocean beach relative to tidal height.

<table>
<thead>
<tr>
<th>Relative to</th>
<th>Position</th>
<th>Juveniles</th>
<th>Mature Females</th>
<th>Adolescent Males</th>
<th>Large Males</th>
</tr>
</thead>
<tbody>
<tr>
<td>Preceding nocturnal high tide line</td>
<td>above</td>
<td>50</td>
<td>17</td>
<td>19</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>below</td>
<td>7</td>
<td>9</td>
<td>8</td>
<td>13</td>
</tr>
<tr>
<td>Maximum preceding 24-hour high tide line</td>
<td>above</td>
<td>24</td>
<td>8</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>below</td>
<td>33</td>
<td>18</td>
<td>18</td>
<td>14</td>
</tr>
</tbody>
</table>
FIG. 1. Lagoon beach at high tide. The pool behind the berm is fresh water; note coconut rubble characteristic of lagoon beaches.
the preceding 24-hour maximum high, the juvenile zonation somewhat more nearly resembles that in Hawaii, but the adolescent male-mature female population zonation is now completely reversed. Thus, of the four age-sex categories, only large mature males maintain the restricted intertidal position occupied in Hawaii.

On the lagoon side, the generally restricted elevation and width of the beaches prevented the development of any noticeable zonation patterns, except that large mature males were again entirely intertidal and generally tended to burrow 0.5 to 1 m lower on the beach than did any of the other age-sex groups. On steeper-sloped but relatively narrow beach sectors, *Q. ceratophthalmus* shared whatever dry beach existed with *Q. cordimana* and extended into the uppermost intertidal. If no dry beach was available, all age-sex classes were normally present in the upper intertidal. However, the low population densities observed in such areas suggest that conditions there are sub-optimal for this species. On wider beaches with a brackish or fresh-water pool inland of the berm, *Q. ceratophthalmus* tends to congregate on the top and upper lagoon side of the berm, very few being found inland of the pool. In these areas the low beach elevation and the proximity of ground water produce a uniformly damp berm and, as noted above in the case of intertidal populations, densities were low.

*Q. cordimana*: Locality data for all crabs captured are illustrated in Figure 2. The three-population treatment used here was employed for ease of handling only. The ocean beach and cable station crabs undoubtedly form a single continuous seaward population. Whether interaction also occurs between the seaward and lagoon populations is unknown, though it seems certain that larval recruitment would prevent genetic isolation of the two populations even if postlarval migration between the two areas is lacking. The same is equally true, of course, for *Q. ceratophthalmus*.

These data suggest that *Q. cordimana* is vertically zoned according to sex and size, with juveniles and mature females inhabiting inland areas and large mature males predominating on the beaches. This is especially evident in the seaward population (ocean beach and cable station grounds) but was also observed on the lagoon beaches where adult males inhabit the beach proper and juveniles are found almost exclusively at the beach-vegetation interface.

The inland zonation of females is further suggested by the observation that approximately 90% of all female *Q. cordimana* taken on the lagoon beach were regenerating at least one appendage. Because (1) few injured males were found in any population, and (2) the incidence of injured females in the cable station population was negligible, it is tempting to consider females as transient visitors to the lagoon, either migrating there following injury elsewhere or perhaps remaining there only if injured while on the beach. In this context it should be noted that molting is stimulated by limb loss in *Gecarcinus lateralis* (Skinner and Graham, 1970) and that the process of molting in *Q. cordimana* varies according to the salinity of water available to the crab during proecdysis (Rao, 1968). Alternatively, because the incidence of females was about the same on all lagoon beaches regardless of proximity to known inland populations, it may
be that females reside on the lagoon beach for life but somehow are more exposed to injury or predation, perhaps while mating or releasing larvae.

Within-habitat zonation patterns are poorly defined. On the ocean beach, *Q. cordimana* males occur in greatest frequency on the dry beach, particularly in the uppermost few meters adjacent to the vegetation line. Intertidal burrows were found, however, and these were occupied on successive nights despite repeated tidal coverage. On the lagoon beaches, as previously noted, juveniles were commonest at the vegetation interface and, in a few instances where ground cover permitted and soil was well drained, they extended inland a few meters, though moderate were extensive inland populations found fronting the lagoon. On wide, low beaches with a fresh-water pool, mature *Q. cordimana* inhabited a narrow strip on the crest and landward side of the berm and were frequently observed burrowing at low tide within the basin of the pool itself. On narrower beaches, mature specimens were restricted to the upper portions of the beach and were seldom found in areas lacking a dry beach zone.

A rather interesting pattern emerged on the cable station grounds. To the best of my knowledge, every *Q. cordimana* inhabiting the survey area exclusive of zone I is depicted in Figure 3. Although the survey extended the width of the island, only the portion inhabited by *Q. cordimana* is shown here. The figure suggests that the seaward portion of the cable station grounds is inhabited almost exclusively by juveniles. These become scarcer with increasing distance from the ocean beach and terminate in zone II. Moreover, size data indicate that small juveniles are restricted to the near-beach zone; the average size of zone I juveniles was 16.3 mm, versus a minimum size of 19 mm and an average of 23.6 mm for zone II juveniles.

Figure 3 also illustrates a nonrandom placement of burrows in zones II and III. The only discernible feature common to the various colonies was the proximity of a road or footpath providing access to the ocean beach. Other factors such as substrate composition, ground cover, exposure to rain or sun, etc., varied greatly from colony to colony. Clustering of burrows along paths was reported from the Maldives (Borradaile, 1903), and a statement to this effect also appears in the unpublished field notes of the Marine Biological Laboratory at Eniwetok, Marshall Islands. However, because large tracts of ground adjacent to roads were not colonized, it seems quite possible that the crabs may respond to social or additional environmental factors that I failed to consider. The partial sampling of zone I disclosed a random rather than clumped distribution. Because physical conditions in zone I are relatively uniform, it might be argued that colonies elsewhere are a response to specific physical parameters. The "access" hypothesis is also supported here, however, because of the ease with which the juveniles can maneuver among the beach morning glory predominating in this zone.

Finally, the deepest inland penetration observed was approximately 200 m from the edge of the beach. This is in close agreement with Rao's (1968) reported 200-yard maximum in India. What determines this limit is unknown; although most of zone IV was low swampy ground heavily colonized
FIG. 2. Population composition of *O. cordimana* in three habitats. Stippling indicates individuals not associated with a burrow.
Fig. 3. Distribution of *O. cordimana* on Cable Station grounds.
by Cardisoma, the first 50 to 75 m adjacent to zone IV appeared perfectly suitable for Q. cordimana and its absence there is puzzling.

SALINITY TOLERANCES

The heavy and prolonged rains experienced at Fanning and the distribution of the two species reported above suggest that the species might differ in their salinity tolerances. The following preliminary work was undertaken to test this hypothesis and to determine its significance as a determinant of zonation.

Methods

Five each juveniles, mature females, and mature males of each species were tested for tolerance to fresh and salt water. Aluminum 12-oz soft drink cans with perforated sides and aluminum hardware-cloth covers served as individual test chambers. These were submerged in groups of six in plastic buckets containing 8 liters of either rain water or normal sea water; O₂ saturation was maintained with aerators; and the water was changed every 12 hours to minimize waste product concentration. Water temperature during the test period ranged from 26 to 28.5°C. As results warranted, the crabs were examined at intervals of 1 to 3 hours for loss of coordination (inability to right the body) or death (total lack of response to appendage manipulation).

Results

As might be expected, Q. cordimana had a greater tolerance to fresh water than did Q. ceratophthalmus. On the average, Q. ceratophthalmus showed total loss of coordination within 8.5 hours, and death occurred after 10.7 hours of submergence. In comparison, average time to death for Q. cordimana was 29.8 hours, and, of the 15 specimens, only two showed loss of coordination prior to death. The species' difference in death times was highly significant (t = 16.225, df = 28, P << 0.001). In both species the juveniles displayed the least, and the mature females the greatest, average tolerance to fresh water, but in neither species were there significant differences between age-sex categories.

Under natural conditions prolonged submergence would probably be accompanied by O₂ stress, and the tolerances would no doubt be proportionately reduced. However, it seems clear that the difference in tolerances displayed by the two species is ecologically significant. Gross (1964) demonstrated that Q. ceratophthalmus can maintain its blood concentration within narrow limits while submerged in 50 to 170% sea water (17.25 to 58.6°/oo) for periods up to 24 hours. Ground water in the Q. ceratophthalmus zone on the lagoon beach at Fanning varied between 2 to 50°/oo and 3 to 10°/oo on two days with heavy rainfall, but during these same two days lagoon water within 0.5 m of shore ranged respectively from 14 to 25°/oo and 15 to 26°/oo (see Guinther, p. 263, this report) and thus
provided a sufficiently saline refuge for *Q. ceratophthalmus*. In contrast, *Q. cordimana* burrows were covered with fresh water for hours during and after heavy rains, and although this species apparently prefers well-drained areas, its high tolerance to fresh water undoubtedly enhances survival when drainage proves insufficient.

The sea water test gave less definitive results. When the experiment was terminated after 83 hours, none of the *Q. ceratophthalmus* showed any signs of stress, but among the *Q. cordimana* three mature males and two mature females (i.e., 50% of the adults tested) lost coordination within 10 to 17 hours and all of these died after an average of 34.8 hours (range 20 to 57 hours). The remaining *Q. cordimana* survived the entire test period without visible effect and several began to burrow in normal fashion immediately upon release.

The tolerance shown by *Q. ceratophthalmus* was expected, since prior work (Fellows, 1966) had established that this species can survive at least a month of continued immersion in sea water. In contrast, the individual variation displayed by *Q. cordimana* was surprising, especially because the mature males seemed most susceptible in spite of their beach habitat. However, it should be noted that none of the individuals tested were harmed by submersion for such periods as might be encountered on any part of the beach during normal tidal cycles. The apparently greater tolerance displayed by *Q. ceratophthalmus* might thus have relatively little ecological significance.

**BURROW STRUCTURE**

**Methods**

Burrows were either traced by hand or were cast using very liquid Plaster of Paris. In the latter technique an effort was made to catch the inhabitant outside of the burrow prior to casting to assure that all chambers of the burrow were open. Sex and size of the inhabitant, as well as the external features of the burrow, were recorded for comparison with Hawaiian data.

**Results**

*Q. ceratophthalmus*: Typical burrows constructed by this species in Hawaii are shown in Figure 4. Four types of burrows are recognized, each of which is constructed by a different age-sex group.

Juveniles of both sexes construct either of two types of burrows. Those larger than 12 mm dig a "Y" burrow, the construction sequence of which is illustrated in Figure 4 a-g. From the sequence it is evident that the crab first digs a "U" burrow and then excavates the lower chamber. The ascending arm of the "Y" generally terminates 3 to 4 cm below the surface and apparently serves as an escape route (Borradaile, 1903; Cowles, 1908). Burrow diameter corresponds closely to the size of the inhabitant. Mean
FIG. 4. *Ocypode ceratophthalmus* burrows from Hawaii. a-g: stages in construction of “Y” burrows; h-j: “I” burrows; k and l: modified “I” burrows dug by captive crabs; m-o: adult female burrows; p: adolescent male burrow; q: burrow dug by maturing male; r: spiral burrow of maturing male.
depth is about 35 cm, although burrows up to 70 cm deep have been found. Excavated sand is generally broadcast around the burrow but may be dumped in a loose, low mound adjacent to the entrance. The burrow is plugged flush with the surface in the manner described for *O. arenaria* by Cowles (1908).

Smaller juveniles dig a simple, straight shaft with a mean depth of 12 cm (Fig. 4 h-j). Although occasionally constructed by captives, branched burrows of this type have not been encountered in the field. Moreover, the placement of the upper arm in such burrows suggests a sequence of construction different from that used by larger juveniles (Fig. 4 k-l). Sand disposal and plugs are as described above.

Mature females and adolescent males dig an almost straight, unbranched shaft penetrating at an angle of 25-45° (relative to the vertical) to a depth of 30 to 40 cm. At terminal depth the burrows frequently run horizontally for another 10 to 20 cm. In most cases only the initial portion of the burrow is cleared of sand, this being disposed of as described for juvenile burrows. As burrowing proceeds further, loosened sand is shoved toward the entrance, forming a thick subsurface plug. A surface plug identical in mode of construction to those found in juvenile burrows is, however, frequently encountered.

Although fully mature males may dig a straight, simple shaft, they generally construct a radically different burrow. This is characterized externally by a wide, oval entrance (up to 75 x 165 mm) and a well-defined and sometimes carefully packed sand pile 30 to 50 cm from the entrance. Internally the burrow describes a wide, shallow spiral descending approximately 20 to 25 cm per turn. The burrow usually makes two complete loops then levels and extends horizontally for 20 to 30 cm. Only the first three-fourths or so of the initial loop is cleared of sand; the remainder is plugged in the manner of the female burrow. Only one burrow intermediate between the spiral and female styles of burrows has been found in Hawaii (Fig. 4 q). This burrow was inhabited by a 35-mm male and may represent a true transitional stage in the ontogeny of behavior.

These same four burrow types, each occupied by the same age-sex class as in Hawaii, were found on the ocean beach at Fanning. As far as could be determined, juvenile and spiral burrows are identical internally and externally to those described above.

A consistent deviation from Hawaii occurred in the mature female-adolescent male class. Whereas these burrows normally form a single vertical plane in Hawaii, about 50% of the Fanning burrows have a moderate to strong lateral curvature similar to Figure 4 q. Within the size category, there appeared to be no correlation between the degree of curvature and the sex or size of the inhabitant. In addition, both males and females in this category were occasionally found occupying "U" shaped burrows, some of which were open at both ends. Though reported common elsewhere (Takahasi, 1932; Farrow, 1971) such burrows have not been found in Hawaii.
On the lagoon beaches, the proximity of ground water exerts a strong modifying effect on burrow structure. "Y" burrows dug by juveniles, for example, seldom have more than a rudimentary lower chamber and in most cases are simply shallow "U" tubes with a maximum depth of 10 to 12 cm. Female style burrows are also shallow, generally attaining a maximum depth of 15 cm before leveling off or turning upward. Only the spiral burrows are relatively consistent with those found in Hawaii, perhaps owing to their distinctly intertidal placement, but even these tend to be shallower than normal and frequently terminate after completing 1 to 1-1/2 turns.

Takahasi (1932) and Hayasaki (1935) report that in Taiwan *O. ceratophthalmus* burrows invariably extend to ground water. The above observations suggest that this is true only where beach elevation is less than the mean depth of burrows dug on higher beaches. Lagoon burrows were deepest and best developed during spring lows when the water table was lower than usual, but on higher beaches I have been unable to find any relationship between ground water level and burrow depth. It seems safe to conclude that ground water merely limits the normal digging behavior of this species.

Q. cordimana: On the ocean beach and cable station grounds where ground water levels were well below the surface, four types of burrows were encountered.

Both sexes up to about 26 to 28 mm construct "Y" burrows resembling those of *O. ceratophthalmus* (Fig. 5 a-h) but differing from them in two respects: (1) the upper "U" portion is normally 6 to 8 cm deep, compared to 15 to 22 cm deep for *O. ceratophthalmus* burrows; (2) the ascending chamber characteristically breaks the surface, whereas that of *O. ceratophthalmus* burrows terminates 3 to 4 cm below the surface. Both features adapt the burrow to inland conditions where buried obstructions and compacted substrate might otherwise prevent use of the escape arm during or after construction. Burrow irregularity is at least partially due to contact with buried obstacles, but even when constructed in a homogeneous substrate the burrows are less regular than those of *O. ceratophthalmus*. Externally, excavated sand is widely broadcast, and plugs, though seldom encountered, are exclusively of the deep subsurface variety.

Larger males and females on the cable station grounds dig simple, straight shafts (Fig. 5 i-l) similar to those of mature female *O. ceratophthalmus*. Variation in depth (10 to 40 cm) and inclination is greater than that encountered in comparable *O. ceratophthalmus* burrows, however, and in most cases appears independent of substrate conditions. Excavated sand is broadcast around the entrance, and a subsurface plug is standard.

The same type of burrow is occupied by the few mature females and many of the mature males inhabiting the ocean beach. In addition, two other burrow patterns are utilized there by mature males. The "meander" (Fig. 5 o) is a long, wandering shaft paralleling the surface at a depth of 8 to 12 cm, frequently with short side chambers and an entrance at each end.
FIG. 5. *Ocypode cordimana* burrows. a-h: "Y" burrows dug by juveniles; i and j: mature female burrows from cable station grounds; k and l: mature male burrows from cable station grounds; m and n: mature male burrows from ocean beach; o: top view of short meander burrow from ocean beach.
Mean length is perhaps 1.25 to 1.5 m, but one burrow in excess of 3 m was discovered. The "plunge" burrow begins as a meander, but after running 50 to 75 cm suddenly descends almost vertically to a depth of at least 1 meter. Unfortunately, none of these were cast nor were any successfully followed to the end, and thus total depth and terminal configuration remain unknown.

Externally the only feature distinguishing any of these from *O. ceratophthalmus* burrows was afforded by the plug, which is frequently elevated somewhat above the surrounding surface. Though more common in the plunge and meander burrows than in the straight-shafted type, this feature is a reliable species indicator whenever it occurs.

The relationship between the three burrow types is unknown. The meander does not appear to be a simple extension of a straight-shafted inland type burrow; burrows m and n (Fig. 5) were cast after three days' occupancy, whereas burrow o was initiated approximately three hours prior to casting. The plunge burrow may be a modified meander, but this seems unlikely as no evidence of a second entrance was encountered in any of the burrows observed. Nor, finally, was there any evident correlation between crab size and burrow type or between burrow type and location on the beach. This may in part be due to the small sample size available, but all data so far suggest a completely random pattern in these respects.

On the lagoon beach, burrow depth and configuration are limited by the water table. During extreme low tides all burrow types exclusive of the plunge burrow are constructed by the appropriate age-sex classes, but during most of the monthly cycle no set patterns are evident. Juveniles are found in short meanders, shallow "Y" and "U" burrows, and horizontal "Y" burrows with an entrance at the end of all three chambers. Adults of both sexes were found in both meanders and "U" burrows, generally with a maximum depth of but a few centimeters.

The several burrow styles inhabited by mature males and the confusion of burrow types on the lagoon beaches suggest some degree of behavioral plasticity in *O. cordimana*. This is supported by studies of burrows elsewhere (Farrow, 1971; Borradaile, 1903; Takahasi, 1935) in which little agreement with the present work is evident. Unfortunately, all of these studies are very superficial and provide little basis for meaningful comparison. Moreover, as demonstrated below, the burrows of *O. ceratophthalmus* and *O. saratan* play a central role in reproductive behavior. *O. ceratophthalmus* breeds throughout the year, with the result that all burrow types are present regardless of season. *O. saratan*, in contrast, is a seasonal breeder (Linsenmair, 1967) and constructs the specialized reproductive burrow only during the reproductive season. In view of the apparent non-breeding condition of the *O. cordimana* population at the time of my visit to Fanning, it seems likely that a valid analysis of this species' burrowing behavior may require a long-term study in each of several localities.
DURATION OF BURROW OCCUPANCY

Takahasi (1932), Barrass (1963), and Hughes (1966) all report that *Q. ceratophthalmus* burrows may be reoccupied on successive nights. However, whereas Takahasi and Barrass hold this to be true only of supratidal individuals, Hughes claims that over 90% of intertidal burrows are also reoccupied. In Hawaii, human activity has precluded any attempt to study the duration of occupancy, but Fanning offered an opportunity for preliminary investigation of the question.

Methods

Fifty intertidal burrows each on the lagoon and ocean beaches were staked at night during low tide. To minimize disturbance, the stake was placed 75 cm seaward of the entrance. External burrow characteristics were recorded, and each burrow site was revisited the following night about two hours after maximum low tide. Burrows that had not been submerged by intervening tides were judged reoccupied if the burrow showed evidence of repair or bore a fresh plug. Intertidal burrows, which have to be totally reconstructed after the occupant emerges, were judged reoccupied if a burrow of similar size and type was found within a 15-cm radius of the original entrance. The experiment was conducted at a time when nocturnal highs occurred early in the evening (2000 hrs) in hope that the ensuing long activity period would provide maximum opportunity for the crabs to emerge, forage, and return to their burrows.

Results

Table 2 shows the rate of reoccupancy relative to the extent of tidal coverage during the test period. Four burrows were lost when wave action on the ocean beach washed out the marker, and two other burrows were invaded early in the morning by adult *Cardisoma*. In all, of 84 *Q. ceratophthalmus* burrows on the two beaches, only nine were reoccupied, and of these, only two (2.7% of the total) were within the daily intertidal. These results thus support the conclusions drawn by Takahasi and Barrass that intertidal burrows are seldom reoccupied, at least by the same individual.

Special attention was paid to the possible use of "emergence holes" (Barrass, 1963) which are left by *Ocypode* leaving burrows that have collapsed under wave action. These are near-vertical shafts filled with sand to within a few centimeters of the surface and lack a sand pile beside the entrance. It was to these that Hughes attributed a high reoccupancy rate, though he did not specify whether by the same individual. In all, only 22 emergence holes (of which 16 were on the lagoon beach) were found at *Q. ceratophthalmus* sites, suggesting that crabs occupying burrows low in the intertidal may have left or had been washed out of their burrows prior to tidal recession.
Table 2. Reoccupancy of intertidal burrows on the lagoon and ocean beaches on two successive nights.

Values represent no. reoccupied/total no. of burrows marked.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Times Burrow Covered by Tide</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>0</td>
</tr>
<tr>
<td>O. ceratophthalmus</td>
<td>Lagoon</td>
<td>0/1</td>
</tr>
<tr>
<td>mature males</td>
<td>Ocean</td>
<td>0/0</td>
</tr>
<tr>
<td>O. ceratophthalmus</td>
<td>Lagoon</td>
<td>7/14</td>
</tr>
<tr>
<td>all others</td>
<td>Ocean</td>
<td>0/0</td>
</tr>
<tr>
<td>O. cordimana</td>
<td>Lagoon</td>
<td>1/3</td>
</tr>
<tr>
<td></td>
<td>Ocean</td>
<td>3/3</td>
</tr>
</tbody>
</table>
Regardless of emergence hole frequency, however, there was no indication that other Ocypode utilized these as starting points in burrow construction. Only two burrow sites were occupied by new individuals, and in neither case was there evidence that the new burrow had been constructed atop an emergence hole left by the previous tenant. Moreover, a recheck of marked and unmarked emergence holes just before tidal inundation showed that none of them had been enlarged into a burrow.

In view of Hughes' (1966) findings, the nonreoccupation of burrows at Fanning by O. ceratophthalmus is especially interesting. Hughes attributed the disagreement between himself and Barrass (1963) to differences in beach profile in their respective study areas. Yet at Fanning, where the lagoon and ocean beaches offer radical extremes, reoccupancy was nil in both habitats; casual observation on numerous beach types in Hawaii suggests that the same is true there. This indicates that reoccupancy either occurs only under very limited conditions of beach profile and tidal cycle or else that it depends upon intrinsic factors peculiar to some populations but not to others.

In contrast, O. cordimana does appear to occupy permanent or semi-permanent burrows at Fanning. All but 2 of the 10 intertidal burrows included in the survey (Table 2) were reoccupied on the second night despite the predominantly supratidal nature of this species. All 10 burrows, however, were located in the uppermost fringes of the wave wash zone and as such received minimal coverage. Additionally, a number of burrows on the dry beach were observed to be occupied over a period of several days, while inland burrows were occupied continuously for at least two weeks. In the absence of continuous daily destruction, of course, the energy expenditure involved in burrow construction (especially in compacted terrestrial deposits) undoubtedly favors continuous inhabitation by this species.

DISCUSSION

Wherever appropriate, I have discussed my results in the preceding text. In view of the scant literature of O. cordimana, it is felt that nothing more can be added here on that species. Instead, I want to concentrate on two aspects of the biology of O. ceratophthalmus which have received wide study in the western Indo-Pacific, frequently with contradictory results. These aspects are zonation and burrow structure.

Zonation

Zonation data reported here for O. ceratophthalmus are not readily comparable to other localities. The majority of workers have examined their populations as a whole, relative to a fixed point such as HWST. These studies are in fair agreement with each other and with the present study so far as they generally place O. ceratophthalmus somewhere within the zone between HWNT and HWST. In addition, several reports (Barrass, 1963; Hughes, 1966; Jones, 1972) indicate that the population migrates
vertically as the tidal cycle progresses from neaps to springs and back again. Where more detailed work has been done, however, there is relatively little agreement. Takahasi (1932) reported adults in Taiwan living higher on the beach than juveniles, whereas Hughes (1966) reported the reverse from Mocambique. Takahasi's (1932) failure to find evidence of sexual zonation in Taiwan also contrasts strongly with the present study.

The significance of the reported differences is questionable. Hughes (1966) and Jones (1972) attribute variation to differences in beach profile. To a certain extent this seems plausible in view of the different zonations observed on the lagoon and ocean beaches at Fanning. Additional inconsistencies may stem from the use of different techniques; for example, the lack of zonation by sex in Taiwan may have resulted from Takahasi's failure to distinguish between different age groups, and reports of predominantly supratidal populations (Cott, 1929; Tweedie, 1950) may stem from short-term, daylight investigations.

Yet a third possibility is suggested by a comparison of Hawaiian wave beaches with the ocean beach at Fanning. Physically, the ocean beach differs little from many Hawaiian beaches that I have studied using the same methods, yet only the large mature male zonation is consistent in the two localities.

Feeding habits of the two populations may be of importance in this case. In Hawaii, mature females and adolescent males feed heavily on the much smaller species O. laevis. The latter are dug out of their burrows and consumed, after which the burrow may be enlarged and utilized by the successful O. ceratophthalmus. The restriction of O. laevis to the dry beach zone (Fellows, 1966) may thus be responsible for the supratidal distribution of mature females and adolescent males in Hawaii. Also, because (1) O. laevis burrows are almost identical to juvenile O. ceratophthalmus burrows (Fellows, 1966), and (2) juvenile O. ceratophthalmus are also eaten by larger conspecifics, an advantage might accrue to juvenile O. ceratophthalmus inhabiting the intertidal where the more compact substrate might be expected to hinder a pursuing adult.

At Fanning similar adult behavior was noted (many adult burrows were built on top of smaller juvenile burrows), but as the only suitable prey (at least on the ocean beach) would be juvenile conspecifics, a rather different pattern might be expected, such that adult distribution would parallel the distribution of juveniles. Such a pattern is evident in Table 1.

Finally, it is possible that certain aspects of this species' zonation may reflect prey relationships in other areas. Hughes (1966) lists several species of crabs, some of them fossorial, hunted by O. ceratophthalmus in Mocambique, and Takahasi (1932) reports the takeover of Ilyoplax burrows in Taiwan. If this is the case, then zonation details might be expected to vary among populations according to available prey species.
Burrow Structure

Table 3 summarizes burrow types inhabited by *O. ceratophthalmus* in various areas of the western Indo-Pacific. It is evident that there is little agreement from locale to locale among these reports and further that none of the reports match the data presented in this paper.

Hughes (1966) and Barrass (1963) suggest that the behavioral plasticity displayed by different populations of *O. ceratophthalmus* reflects variation in the physical environment. The present study suggests as an alternate hypothesis that intraspecific differences, at least in burrow structure, stem from genetically determined innate differences among populations. Intuitively at least, it would seem difficult to hypothesize any combination of prevailing conditions within the sandy intertidal that would cause the extreme differences among the populations in Table 3; in particular, the sometimes presence of sex-specific burrow structures is difficult to reconcile with the environmental model.

Three additional lines of evidence support this conclusion: (1) Age-sex specific burrow structure is constant over the entire range of beach profiles available for study in Hawaii (Fellows, 1966). Likewise, the same basic burrow types, though modified, are found on both the ocean and lagoon beaches at Fanning, despite the environmental extremes prevailing in these habitats. (2) The ocean beach at Fanning closely resembles some beaches on the north shore of Oahu in Hawaii, yet the mature female-adolescent male class behaves differently in the two localities. Moreover, if the observed differences within this age-sex group are indeed caused by physical variables, then these variables should also be reflected by other classes within the population. (3) Minor differences notwithstanding, all researchers working along a contiguous 3500-km stretch of East African coast are in reasonably close agreement on burrow structure, yet their descriptions are strongly contradicted by Farrow's (1971) report from Aldabra, which in spite of its proximity to the African study area, is isolated from it by approximately 650 km of open ocean.

The role of the burrow is also pertinent in this respect. The prime function is undoubtedly protection from lethal environmental extremes (Bliss, 1968), but the additional influence of predation pressure is indicated by such features of the juvenile burrow as shape, wide dispersal of sand, and the flush surface plug.

The burrow also provides special protection during particularly vulnerable periods in the life cycle; the shallow burrows on the lagoon beach yielded several molting *Ocypode* of both species and a large number of ovigerous *O. ceratophthalmus*. This is the first direct evidence that *Ocypode* molt in the burrow (see Bliss, 1968) and also explains the almost complete absence of ovigerous female *O. ceratophthalmus* in my records. Because each molting or ovigerous specimen was in a long, solidly plugged burrow, it is assumed that such individuals dig an especially deep burrow, seal it completely, and remain there until ecdysis is complete or the eggs are ready to hatch.
<table>
<thead>
<tr>
<th>Locality</th>
<th>Author</th>
<th>Burrow structure</th>
</tr>
</thead>
<tbody>
<tr>
<td>West African Coast</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mocambique</td>
<td>Cott 1929</td>
<td>Juveniles: Simple unbranched straight shafts.</td>
</tr>
<tr>
<td></td>
<td>Barrass 1963</td>
<td>Adults: Both sexes construct spiral burrows completely cleared of sand. Initial 20-30 cm a slightly inclined, perpendicular straight shaft. Oval entrance, sand usually in heap beside or removed from entrance.</td>
</tr>
<tr>
<td></td>
<td>Hughes 1966</td>
<td></td>
</tr>
<tr>
<td>Kenya</td>
<td>Jones 1972</td>
<td>Same as Mocambique except that males make sand pile and females scatter excavated sand around entrance.</td>
</tr>
<tr>
<td>Aldabra Island</td>
<td>Farrow 1971</td>
<td>Females in multibranched U burrows, males in spirals with adjacent sand pile. No Y burrows in study area.</td>
</tr>
<tr>
<td>Formosa</td>
<td>Hayasaki 1935</td>
<td>Juveniles: Smallest specimens dig straight simple shafts, larger ones construct U or Y burrows.</td>
</tr>
<tr>
<td></td>
<td>Takahasi 1932,</td>
<td>Adults: Both sexes construct complexly branched U and Y burrows. Occasional spiral burrow high on sand dunes. Sand scattered or heaped.</td>
</tr>
<tr>
<td></td>
<td>1935</td>
<td></td>
</tr>
<tr>
<td>Western Australia</td>
<td>George and Knott 1965</td>
<td>Only straight simple shafts reported. Sand dispersed around burrow entrance.</td>
</tr>
<tr>
<td>Maldives</td>
<td>Borradaile 1903</td>
<td>Juveniles: J or U burrows. Adults: Both sexes in spiral burrows.</td>
</tr>
</tbody>
</table>
In addition to the protective role, Linsenmair (1967) has firmly established that the spiral burrows constructed by male O. saratan function in reproduction. The sand pyramid adjacent to the entrance serves as a static display, attracting the female to the immediate vicinity of the burrow entrance. The waiting male then uses stridulatory signals to lure her into the burrow, where copulation occurs. The direction of burrow spiral and the placement of the pyramid relative to the entrance indicate the "handedness" of the inhabitant (males with the major chela on the right dig clockwise burrows); this is apparently evaluated by the female, as both members of a copulating pair are always of the same handedness.

Spiral burrows at Fanning and in Hawaii also appear to have a signal function. The intertidal placement of such burrows, together with their enlarged entrance and consolidated sand pile, are in striking contrast to the inconspicuousness of burrows belonging to other age-sex classes. The construction of such burrows, moreover, coincides closely with the attainment of full sexual maturity in the male (Haley, in press).

Unlike O. saratan, male O. ceratophthalmus clear only the initial portion of the burrow of sand and, as the occupant is seldom found in the cleared portion, it is doubted that active courtship at the burrow entrance occurs in this species. To date, only four copulating pairs have been found in the several hundred spiral burrows examined. In each case the female had begun to dig toward the entrance to the male burrow from a position about half way between the sand pile and the entrance of the male burrow and had intercepted the latter somewhere in the lower loop of the spiral. Haley (pers. comm.) has also observed this behavior in Hawaiian O. ceratophthalmus.

Assuming these few cases to be representative of normal reproductive behavior, the features of the spiral burrow take on even greater significance in O. ceratophthalmus than in O. saratan. The sand pile and enlarged entrance serve both to attract the female and orient her digging, whereas the spiral enhances the probability of interception and may also provide information on handedness. A significant change in any of these features would require a concomitant change in overall mating behavior, and though it is relatively easy to visualize a slow evolution of different patterns in isolated populations, an abrupt change from, for example, the Hawaiian to the Taiwan pattern as an immediate response to environmental change appears highly unlikely. Other age-sex classes would not be as subject to selection, of course, except that convergence of such burrows toward the male pattern would be deleterious to the mating habit described above.

Acceptance of this hypothesis raises two questions. First, what is the taxonomic status of O. ceratophthalmus: do the various populations form a single, potentially interbreeding, species, or are they in fact reproductively isolated from each other by behavioral barriers? Secondly, is the behavioral similarity of the Hawaiian and Fanning populations evidence of close genetic relationship between these populations? Answers to either question would be premature at this point. The first question hinges upon direct observation of mating behavior both in Hawaii and in other areas where the burrowing behavior is decidedly different. As to the
second, Gosline (1955, 1971) presents evidence that the Line Islands serve as a "communications center" for the dispersal of inshore fishes between the Hawaiian and Central Pacific regions. Hawaiian molluscs (Kay, 1967, 1971) and ophiuroids (Clark, 1949), on the other hand, exhibit a strong Indo-West Pacific affinity, suggestive of a more direct migration by way of the Caroline and Marshall islands. In this respect an examination of Ocypode behavior in the Marshalls might be especially rewarding, not only in terms of better understanding of the behavior of O. ceratophthalmus, but also as a clue to migration routes in the Central Pacific.

ACKNOWLEDGMENTS

The field assistance provided by Frederick J. Lighter at Fanning proved invaluable to this work and is greatly acknowledged. The many suggestions provided by Hubert W. Frings and the late Albert J. Bernatowicz contributed greatly to my M. S. thesis on Hawaiian ghost crabs, parts of which are summarized here. Finally, to my wife Danielle I also owe a debt of gratitude: it is rare and understanding wife who is willing to stay home with the kids while her husband prowls Polynesian beaches under a full moon.

LITERATURE CITED


SIGN STIMULI AND THREAT DISPLAY OF THE FIDDLER CRAB

UCA TETRAGONON: A PRELIMINARY INVESTIGATION

Frederick J. Lighter

Department of Zoology

INTRODUCTION

A sign stimulus is defined by Verplanck (1957) as "a specified part, or change in a part, of the environment correlated in an orderly manner with the occurrence of a species-specific response that is not a reflex response." When such a stimulus is presented by either the behavior or physical structure of another animal, it is termed a releaser (Lorenz, 1970). Thus, in highly social animals, a particular behavior or a particular structure, or a combination of both, may serve to release a species-typical behavior pattern in a conspecific.

It is the purpose of this study to investigate, in a preliminary manner, the stimuli involved in the threat display of the fiddler crab Uca tetrogonon. A conspecific may be viewed as a configurational stimulus (Tinbergen, 1969), that is, an assemblage of stimuli in the form of a "gestalt." In order to investigate which stimuli are actually involved in the release of a given behavior pattern, models may be used. Previous work (reviewed by Marler and Hamilton, 1966) has shown that often one or two parameters of the entire stimulus situation are responsible for eliciting a particular behavior. This study attempts to delineate which stimulus characteristics present in a model serve the releasing function.

MATERIALS AND METHODS

A dense aggregation of two species of fiddler crabs, one of which is Uca tetrogonon, occurs in the estuarine mudflats of Napu Naiaora, Fanning Island. These animals are diurnally active during low tides. To the casual observer, a great deal of social interaction can be seen, and waving displays are common.

Eighteen adult male U. tetrogonon were used as test subjects. A series of five models was presented, each model on a different day. Each male occupied a burrow, and burrows were marked for identification. It is assumed that the same male occupied the same burrow throughout the test period, although males may have been displaced by others without my knowledge.
At the start of the testing program, the simplest model (Model I) was used. Each following model was made more complex by the addition of another stimulus parameter. All models were placed directly on the substratum 10 centimeters from the burrow entrance of a test crab. Animals were observed through binoculars, and times of responses were recorded with the aid of a stop watch.

The models are described as follows:

Model I: a solid wooden block, 4.1 cm wide, 2.0 cm high, and 2.6 cm thick, painted black. These dimensions were selected to represent the overall dimensions of a *U. tetragonon* male (carapace plus walking legs in resting position) whose major cheliped was used in Models III and IV.

Model II: same as Model I, except that the front surface and the front edges of both end surfaces were painted red. This color pattern was selected to represent the general coloration of a male *U. tetragonon*, which has a black dorsal surface, red front and ventral surfaces, and red on the walking legs.

Model III: same as Model II, except that a normally colored major cheliped was attached in the usual resting position. The cheliped was held in such a way that it rested across the front surface, and the fingers of the claw were closed. In this species, the manus is red, while the tips of the pollex and dactyl are pinkish-white.

Model IV: same as Model III, except that the cheliped had been painted completely white.

Model V: an adult male *U. tetragonon* approximately the same size as the wooden model. The animal was frozen with the walking legs and chelae in the resting position. The colors of the specimen were as usual. The eyestalks were lowered rather than erect and a difference between a live individual and the model thus existed due to the position of the eyestalks.

Categories of behavioral responses for all test individuals are as follows:

1. Latency: the time in seconds between the crab's appearance at the burrow entrance and its next behavioral response. As a crab came to the surface, it oriented toward the model for varying lengths of time before showing further responses.

2. Approach: the crab moved toward the model.
3. Withdraw: the crab moved away from the model.

4. Wave: the major cheliped was raised away from the crab at approximately 45°, and then suddenly lowered with one sharp movement back to the resting position.

5. Threat: the major chela was brought forward and slightly flexed, the fingers of the claw opened.

6. Feed: the crab picked up bits of mud from the substratum with the minor chela and transferred these to the mouth.

7. Plug burrow: the crab entered its burrow, pulled a ball of mud into the burrow with its walking legs, and placed this as a plug slightly below the surface of the burrow entrance.

8. Clean burrow: the crab removed loose particles of sand and mud from around the burrow entrance.

Responses 2 through 8 represent the behavioral acts following Latency. If no Latency was present, categories 2 through 8 represent the behavioral acts of the crab upon emergence from the burrow. Each animal was timed one minute after emergence; thus, one animal could show more than one response (for example, Approach and Feed) for each trial.

RESULTS

Results are summarized in Table 1. Although a full wave display was elicited only once (Model III), threat displays occurred in three test situations (Models III, IV, and V). It would appear that the presence of the major cheliped is necessary for the release of this aspect of agonistic behavior. Interestingly, the same models were responsible for burrow plugging in a small number of animals. If burrow plugging is considered escape or retreat, the major chela is necessary for this second aspect of agonistic interactions.

Model IV produced a longer average latency of response and a higher frequency of approach than Models III or V. Although I can find no literature references to color vision in fiddler crabs, it may be that the white claw of Model IV, because of its contrast with the rest of the model, provides an effective stimulus for the release of agonistic behavior. A lengthy hesitancy of response, and a high frequency of approach and threat, also found with this model, are consistent with this hypothesis. If we consider the trials in terms of percentage of animals responding, we see that more animals show a hesitancy of response to Model V than to any other. Because Model V is the most "realistic"--in terms of carapace shape, color, presence of walking legs, etc.--it probably most closely approximates the
<table>
<thead>
<tr>
<th>Stimulus Presented</th>
<th>Average Latency (in seconds)</th>
<th>Approach</th>
<th>Withdraw</th>
<th>Wave</th>
<th>Threat</th>
<th>Feed</th>
<th>Plug Burrow</th>
<th>Clean Burrow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Model I</td>
<td>7.6 (55.6)</td>
<td>8 (44.4)</td>
<td>10 (55.6)</td>
<td>0</td>
<td>0</td>
<td>18 (100)</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Model II</td>
<td>4.4 (55.6)</td>
<td>9 (50.0)</td>
<td>9 (50.0)</td>
<td>0</td>
<td>0</td>
<td>18 (100)</td>
<td>0</td>
<td>1 (5.6)</td>
</tr>
<tr>
<td>Model III</td>
<td>3.1 (33.3)</td>
<td>7 (38.9)</td>
<td>9 (50.0)</td>
<td>1 (5.6)</td>
<td>2 (11.1)</td>
<td>15 (83.3)</td>
<td>2 (11.1)</td>
<td>0</td>
</tr>
<tr>
<td>Model IV</td>
<td>5.8 (55.6)</td>
<td>10 (55.6)</td>
<td>6 (33.3)</td>
<td>0</td>
<td>4 (22.2)</td>
<td>15 (83.3)</td>
<td>2 (11.1)</td>
<td>0</td>
</tr>
<tr>
<td>Model V</td>
<td>4.4 (72.2)</td>
<td>7 (38.9)</td>
<td>10 (55.6)</td>
<td>0</td>
<td>4 (22.2)</td>
<td>15 (83.3)</td>
<td>1 (5.6)</td>
<td>0</td>
</tr>
</tbody>
</table>

Table 1: Summary of Data

Responses (N = 18 for each trial. Numbers in parentheses represent the percentage of animals showing the response).
normal condition. A male *U. tetragonon* hesitates upon emergence from its burrow when it perceives a male conspecific nearby. The size and behavior of the intruder may play a role in determining the resident's agonistic response. A period of latency would be required by the resident in order to determine the situation before responding.

**DISCUSSION**

The waving display of fiddler crabs has been extensively recorded (Crane 1941, 1943, 1957, 1958, 1966, 1967), but investigations of the stimuli involved in waving and threat are limited (Salmon and Stout 1962; Aspey 1971). The former workers conclude that the large cheliped is the dominant visual cue in sexual discrimination. Aspey (1971) suggests that the ratio of cheliped size/body size may be important as a visual signal. Both studies serve to show the importance of visual stimuli in the social behavior of *Uca*. Schone (1961) states that the appearance of the beckoning claw and its special movement pattern are specialized, functioning as a social releaser.

No critical ethological analysis of fiddler display has been made although Crane (1957) reports the basic repertoire of behaviors. Salmon (1965) has recorded movements and temporal patterns of display for three species, and Salmon (1967) and Salmon and Atsides (1968) investigated both visual and acoustical signals. Crane (1957, 1967) discusses *U. tetragonon* only briefly.

The present study is preliminary in nature, designed to gain some insight into the sign stimuli involved in agonistic behavior. Unfortunately, the numbers are too small for rigorous statistical analysis, and, no moving models were utilized. From the works of Aspey (1971) and Salmon and Stout (1962), it appears that movement is an important parameter in the total stimulus. A few tentative conclusions may be made, however: (1) It appears that the major cheliped is necessary to elicit agonistic behavior in adult male *U. tetragonon*. (2) Color or contrast may also be important in behavior; a chela which contrasts with the background elicits greater average latency and a higher frequency of approach than less contrasting models. (3) Finally, the frequency of latency of response may serve as an indicator of the animal's aggressive motivation. In a highly realistic (Model V) situation, more time may be required for the animal to "analyze" the situation before fully emerging from a burrow.

It is hoped that a more complete study can be made in the future. These tentative conclusions should be better understood by using a greater number of animals and by utilizing more refined models. Moving models could be designed by attaching a rotor arm and motor to chelipeds of different colors to investigate the interaction of color and movement. Live animals could be painted and then released into an undisturbed population. A thorough ethological investigation should be made of the waving and threat displays of both species of fiddler crabs found at Fanning Island. Finally, an attempt should be made to determine the sign stimuli involved in both species, in an effort to understand the behavioral isolating mechanisms involved between these two species which live so closely together.
SUMMARY

A preliminary study of the sign stimuli responsible for the release of the threat display in adult male Uca tetragonon was made at Napu Naiaroa, Fanning Island. Models were used in an attempt to determine which stimulus parameters are involved. Tentative conclusions indicate that the presence of the major cheliped is necessary for the release of threat behavior. Second, the contrast between chela and carapace may serve as an important visual cue. A program for further study is briefly outlined.

LITERATURE CITED


INTRODUCTION

Terrestrial Crustacea are ubiquitous on vegetated coral atolls and undoubtedly constitute the most conspicuous element in the land fauna of many island groups (Wiens, 1962; Niering, 1956). Of the several species present at Fanning Atoll (Guinther, 1970) the giant land crab Cardisoma carnifex (Herbst) appears, because of its large size and numbers, to be of greatest significance, although it may be surpassed in sheer numbers by hermit crabs of the genus Coenobita.

Despite its wide distribution throughout the Indopacific (Edmondson, 1923) and its obvious importance in local biotas, little is known about the biology of C. carnifex. The genus is, in fact, known almost entirely as the result of intensive studies on the Caribbean species C. guanhumi (see Bliss, 1968, for review).

This paper presents the results of incidental observations and a preliminary population survey undertaken at Fanning Atoll in July and August, 1972. Though preliminary in nature and scope, it is hoped that the following data will: (1) serve to stimulate work on the several species of Indopacific Cardisoma; (2) provide a base for further studies on C. carnifex at Fanning Atoll; and (3) yield comparative information to further the study of C. guanhumi and other members of this pantropic genus.

GENERAL OBSERVATIONS

Edmondson (1923) reported both C. carnifex and C. rotundum at Fanning Atoll, but no C. rotundum were observed during the present study, nor were any found by the 1970 University of Hawaii expedition (Guinther, 1970). Because Edmondson considered C. rotundum synonymous with C. hirtipes, a species generally described as an inland fresh water form (Silas and Sankarankutty, 1960; Shokita, 1971), the lack of suitable habitat (though
sufficient fresh water exists, "inland" area is absent) at Fanning makes its occurrence there somewhat problematical. The present work was, however, restricted to the Cable Station Island, and it is possible that other islands in the atoll may house a second species.

Though more numerous at night, C. carnifex at Fanning Atoll carry out considerable daytime activity, especially in shady areas. The Andaman Islands population, in contrast, is reportedly entirely nocturnal, with burrows being sealed during daylight hours (Silas and Sankarankutty, 1960). Diurnal activity at Fanning appears largely confined to the immediate vicinity of the burrow, but it was not uncommon to find individuals many meters distant from the nearest hole. This may in part reflect the relative absence of predators at Fanning; although the puffer fish Arothron hispidus successfully preys upon Cardisoma of all sizes in the lagoon and estuaries, the large size of the adult crabs (maximum measured carapace widths for males and females respectively were 94 mm and 87 mm) would seem to preclude attack from any terrestrial organism other than man, dogs, and a few semi-wild pigs. Small juveniles from 5-25 mm*, which might be preyed upon by Ocypode ceratophthalmus on the beach proper, or by rats farther inland, were less commonly seen during the day.

In general, C. carnifex appears to be an opportunistic scavenger on both plant and animal material. Herreid (1963) reported C. guanhumi feeding on 77 genera belonging to 35 families of plants at the U.S.D.A. Plant Introduction Station near Miami, Florida, and on the basis of casual observation, C. carnifex appears equally catholic in its food habits. This, coupled with the wide distribution, large population size, and general mobility of C. carnifex at Fanning, suggests that this species might constitute an important mechanism for transporting organic matter between lagoon and ocean and from the terrestrial to the marine ecosystem. It should be noted that although dead crabs were consumed by their conspecifics, no evidence of autopredation was found. Indeed, little antagonistic behavior was apparent within the sometimes crowded colonies, in spite of the fact that mature males almost invariably bear deep scars, presumably inflicted by other males, on the meropodite of the major cheliped.

REPRODUCTION

Examination of the reproductive morphology of 18 females and 10 males suggests a maturation size of approximately 65 mm for females and somewhat larger for males. Among females, heavy pleopod hair characterized all individuals above 57 mm, and all individuals above 67 mm were either ovigerous or possessed well developed ovaries and swollen spermathecae. Copulation (as evidenced by full spermathecae) occurs as early as 62 mm, although the smallest ovigerous specimen captured was 67 mm. In males the testes, vas deferens, and androgenic organs first become evident at 65 mm, but well-developed reproductive systems were found only in specimens 72 mm and larger. Minimal size of males at copulation is unknown; the smallest observed while mating was 82 mm.

*All measurements refer to maximum carapace width.
Six copulating pairs were observed, four at night and two in the early morning (0720 and 0930). Both sexes mate when hard. Positions observed included male dorsal, male ventral, and both sexes upright (see Bliss, 1968). In one instance copulation occurred just within the entrance to the male's burrow; the remaining five pairs were not associated with burrows. One copulating male was missing the major cheliped, suggesting that the sexually dimorphic enlarged chela is not essential to normal mating behavior. What, if any, hormonal stimuli are active in determining female receptivity is unknown; of two females examined immediately after copulation one appeared ready to ovulate, whereas the other possessed almost rudimentary ovaries.

One pair was observed copulating in daylight for 30 minutes before spontaneous separation occurred. During this period no movements were noted, nor did the crabs react to slow movements by the observer some 4 meters distant. Both individuals held an upright position with abdomens opposed and weight supported on the posterior three pairs of walking legs. The female's chelae were flexed and held at the leading edge of the carapace, whereas the male extended both chelipeds anteroventrally to loosely embrace the female. After separation the male remained motionless for approximately 3 minutes while the female wandered off with a "mechanical" jerky gait which gradually diminished and gave way to normal smooth locomotory motion.

Gifford (1962) and Shokita (1971) have respectively shown that C. guanhumi and C. hirtipes spawn in sharp peaks during the 3- to 4-day full moon period when large numbers of females migrate to the beaches and release their larvae. This appears true also of C. carnifex; during the full moon period of 26 to 29 July, large numbers (50 to 75, estimated) of ovigerous females were observed on the station grounds and among the equipment scattered on the storeroom patio. None were seen from that time until 19 August when three ovigerous females were dug out of their burrows. Unfortunately, the party left Fanning before the full moon of 24 August, thus barring the collection of quantitative data. Whether copulatory behavior is similarly tied to the lunar cycle is unknown. The only copulating pair seen in July was observed 6 days before the full moon, whereas in August copulation was noted only on the 3 days following new moon.

BURROWS

In general, the C. carnifex burrows observed at Fanning conform to the pattern described for C. guanhumi in Florida by Herreid and Gifford (1963). Though multiple entrance burrows were encountered, the burrows are generally simple shafts having a single entrance flush with the surface. Slope is variable, ranging from almost vertical to nearly horizontal. Most terminate in an enlarged chamber just at or below the water table, and the appearance of fresh mud at the entrance to many burrows during a comparatively dry period suggests that burrows are deepened as the water table falls. C. carnifex burrows described from the Andaman Islands (Silas and Sankarankutty, 1960) open atop steep-sided 50- to 75-cm high mounds.
Although such "castles" were not observed at Fanning, low (25- to 35-cm high) rounded mounds inhabited by several crabs were encountered in the tidal flats of Napu Naiaroa Estuary, thus supporting the idea that the Andaman structures are a response to high tidal fluctuation. Unlike the Andaman burrows which are reportedly invariably plugged during the daytime (Silas and Sankarankutty, 1960), very few of the Fanning burrows were found to be plugged at any time.

Burrow diameter only loosely correlates with the size of the inhabitant, the fit being somewhat closer for small individuals than for full adults (Table 1). Moreover, because the burrow is commonly entered sideways, the burrows could be approximately 25% narrower than the inhabitant's carapace width, and the disparity of fit is thus greater than indicated in Table 1.

At least a part of the disparity is undoubtedly due to wear on the burrow entrance during long periods of inhabitation, but is also appears evident that vacant burrows are commonly reoccupied. On several occasions disturbed crabs took refuge in the nearest burrow, and multiple inhabitation of undisturbed burrows was not uncommon. Large Cardisoma of both sexes were also observed taking over and enlarging burrows belonging to mature male Ocypode ceratophthalmus on the lagoon and ocean beaches.

Though no in-depth studies were conducted, there do not appear to be any differences between burrows occupied by the different age or sex classes. Moreover, because the burrow seems to play no role in sexual behavior, differences would not be expected.

**DISTRIBUTION AND DENSITY**

A preliminary study was undertaken on a 2-m-wide transect extending the width of the Cable Station Island a few hundred meters west of the inlet to Napu Naiaroa Estuary. Starting at the lagoon beach, the survey passed through three distinct habitats as follows (Fig. 1):

**Zone 1:** Open coconut grove with open canopy and little understory except for isolated Messerschmidia argentea; moderate to heavy ground cover of coconut husks and bunchgrass (*Lepturus repens*); soil dry and fine with a few rocks.

**Zone 2:** Upper tidal flats and cyanophyte basin of Napu Naiaroa Estuary; no tree cover, sparse ground cover of Sesuvium portulacastrum and *Lepturus*; depressions lined with a thin mat of mixed blue-green algae; substrate fine silt overlying coral and shell rubble; submerged at high tide. (See Guinther, 1971, for detailed description.)

**Zone 3:** Dense mixed thicket of coconut, Scaevola sp. and Messerschmidia, with closed canopy and thick ground cover of coconut husk and leaf litter. Substrate mixed coral shingle and soil near estuary, becoming 100% shingle near ocean beach.
Fig. 1. Distribution of Cardisoma burrows on island-wide transect through Napu Naiaroa Estuary. Elevations shown in transect profile are relative to height of lagoon beach. "m" indicates extent of Messerchmidia cover in Zone 1. Graph A: burrows up to 50 mm diameter; Graph B: burrows over 50 mm diameter.
Table 1. Relationship between maximum entrance diameter of burrow and carapace width of resident *Cardisoma carnifex*.

<table>
<thead>
<tr>
<th>Burrow Size Class (mm)</th>
<th>N</th>
<th>Ave. Burrow Diameter (A)</th>
<th>Ave. Carapace width (B)</th>
<th>Average % difference ( \frac{(A-B)}{B} \times 100 )</th>
<th>Range of % differences (individual)</th>
</tr>
</thead>
<tbody>
<tr>
<td>25 and less</td>
<td>3</td>
<td>21.0 mm</td>
<td>17.0 mm</td>
<td>23.5 %</td>
<td>-5.6 to +42.8 %</td>
</tr>
<tr>
<td>26-50</td>
<td>13</td>
<td>42.9 mm</td>
<td>38.4 mm</td>
<td>11.7 %</td>
<td>-15.5 to +40.0 %</td>
</tr>
<tr>
<td>51-75</td>
<td>11</td>
<td>62.6 mm</td>
<td>59.6 mm</td>
<td>5.4 %</td>
<td>-17.4 to +37.8 %</td>
</tr>
<tr>
<td>76-100</td>
<td>17</td>
<td>86.0 mm</td>
<td>70.8 mm</td>
<td>21.4 %</td>
<td>-2.6 to +78.8 %</td>
</tr>
<tr>
<td>over 100</td>
<td>15</td>
<td>114.9 mm</td>
<td>83.0 mm</td>
<td>38.4 %</td>
<td>+7.5 to +53.9 %</td>
</tr>
</tbody>
</table>
All burrows falling within 1 m of either side of the transect line were measured and included in the survey; no attempt was made to distinguish between inhabited and uninhabited burrows, though every effort was made to count only burrow entrances. Burrows were recorded in five size categories: 0 to 25 mm; 26 to 50 mm; 51 to 75 mm; 76 to 100 mm; and over 100 mm.

Figure 1 compares the distribution of burrows with the relative elevational profile of the transect. Size classes were combined only for ease of presentation. Each point on the density curves represents the total number of burrows per 5 linear meters of transect (10 m²). It is evident that small burrows predominate over large burrows in all portions of the transect with the possible exception of Zone 2. On the tidal flats, counts were rendered difficult because small Cardisoma burrows could not readily be distinguished from those of Uca and Metapographe and thus were counted only if positive identification could be made. The decision to exclude doubtful burrows was made at the 300-m mark, and the data for the initial portion of the tidal flats are thus questionable. Actual totals for each size class are shown in Table 2.

It is apparent from Figure 1 that the relative abundance of large crabs parallels the distribution of small crabs. This suggests that habitat preferences remain constant throughout life. A possible exception to this may exist among the smallest crabs, however. Table 2 shows a generally inverse relationship between burrow size and frequency. This is expected in view of attrition with increasing age. Burrows in the 0- to 25-mm size range do not conform to this general pattern, indicating that the smallest specimens may be concentrated in other habitats. Alternatively, this pattern may reflect the existence of a seasonal spawning period with subsequent sporadic recruitment of small juveniles. Seasonal breeding patterns have been demonstrated for C. guanhumi in Florida (Gifford, 1962) C. hirtipes in Okinawa (Shokita, 1971) and is also mentioned in conjunction with an unidentified species from Ifalik Atoll in the Central Carolines (Bates and Abbott, 1958).

Variables which might influence distribution tend to co-vary and are difficult to evaluate on the basis of a single transect. Consistently high densities were encountered at relative elevations of 0.5 to 1 m and dropped off sharply as elevation increased or decreased. This relationship is seen throughout Zone 1 and also in the initial and terminal portions of Zone 3, and suggests that the proximity of ground water may influence the distribution of burrows. The initial 20 to 25 m of Zone 3, however, in addition to being of moderate elevation, also resemble Zone 1 in vegetation, and the peak distribution at the ocean beach terminus of Zone 3 coincides with a restricted pocket of rock-free soil. Also, in Zone 1 it was noted that some peak densities appeared to be associated with scattered Messerschmidia growth (Fig. 1). Because C. carnifex feeds readily on leaves and twigs of this tree it seems reasonable to assume that burrows might be located close to an abundant food supply, as is the case with C. guanhumi (Herreid, 1963). A more detailed study will undoubtedly show whether or not this association is real.
Table 2. Total number of burrows by size class in each zone of transect.

<table>
<thead>
<tr>
<th>Zone</th>
<th>0-25</th>
<th>26-50</th>
<th>51-75</th>
<th>76-100</th>
<th>over 100</th>
<th>total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>276</td>
<td>555</td>
<td>180</td>
<td>49</td>
<td>31</td>
<td>1091</td>
</tr>
<tr>
<td>2</td>
<td>8</td>
<td>29</td>
<td>5</td>
<td>8</td>
<td>3</td>
<td>53</td>
</tr>
<tr>
<td>3</td>
<td>33</td>
<td>43</td>
<td>31</td>
<td>14</td>
<td>22</td>
<td>143</td>
</tr>
<tr>
<td>Total</td>
<td>317</td>
<td>627</td>
<td>216</td>
<td>71</td>
<td>56</td>
<td>1287</td>
</tr>
</tbody>
</table>
Finally, it should be noted that the abundance of burrows is only a partial indicator of habitat preference. Although few burrows were found in the central portion of Zone 3, a large but undetermined number of *Cardisoma* were found sheltered in the coconut litter there. Niering (1956) reported that the greatest concentrations of "land crabs" (*C. rotundum* and *Gecarcoides lalandei* combined) at Kapingamarangi Atoll occurred in areas of compacted coconut rubble where few burrows were found. It seems possible that abundant ground cover may provide shelter in preference to a burrow, but at least in the case of Zone 3 the heavy coral shingle content of the substrate generally seemed to preclude successful burrowing there.

Transect data can be used to obtain an estimate of population densities in each habitat. Burrow occupancy rates in the three zones are unknown but can be estimated with reasonable accuracy. Based on reports by Niering (1956) and Bates and Abbott (1958) plus personal experience with a limited number of burrows, it is assumed that approximately 50% of the burrows in Zone 1 were inhabited. On the estuarine flats, 100% occupancy is assumed on the basis that unoccupied burrows would be obliterated by tidal action. Occupancy of 100% is also assumed for Zone 3 (50% of burrows occupied plus an equal number of free-living crabs in coconut rubble). Density estimates based upon these assumptions are presented in Table 3. These densities are generally greater than those calculated from Niering's (1956) combined data on *Cardisoma* and *Gecarcoides* at Kapingamarangi (500/ha average, 3400/ha maximum) but are within reason considering the 11,880 *Cardisoma* sp./ha estimate derived from Bates and Abbott's (1958) data from Ifalik.

**BIOMASS**

If it is further assumed that the average carapace widths of crabs inhabiting each burrow class (Table 1) is reasonably representative, it is possible to approximate the average total wet weight of the *Cardisoma* population in the survey area. Figure 2, comparing wet weight against carapace width, is based on frozen crabs obtained at Fanning and weighed several months later, and the weights are probably somewhat below live field weight. From Table 1 and Figure 2, it is estimated that the average weight per crab in each burrow size class is successively 2, 24, 85, 162, and 245 grams. These estimates, combined with the density estimates in Table 3, yield the estimated wet weights appearing in Table 4. These figures may be compared with Gifford's (1962) estimated 1-2 metric tons/ha attained by *C. guanhumi* in Florida. Gifford's estimate was unaccompanied by any supportive data, however, and in view of the disparity between his data and the present estimate, it is suggested that the range of values in Florida may be unrealistically high.

**SOIL TURNOVER**

The environmental impact of *C. carnifex* at Fanning Atoll in terms of resource utilization, deposition of organic wastes and salts in burrow water, and so forth, cannot be estimated without a great deal more information. It is, however, possible to estimate, as one parameter of ecological impact,
Fig. 2. Cardisoma carnifex: wet weight versus carapace width.
Table 3. Estimated *Cardisoma* density in 3 habitats by burrow size class. See text for further explanation.

<table>
<thead>
<tr>
<th>Zone</th>
<th>Area Surveyed</th>
<th>Density (Crabs/ha)</th>
<th>0-25</th>
<th>26-50</th>
<th>51-75</th>
<th>76-100</th>
<th>over 100</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>496 m²</td>
<td></td>
<td>2783</td>
<td>5590</td>
<td>1812</td>
<td>495</td>
<td>313</td>
<td>10993</td>
</tr>
<tr>
<td>2</td>
<td>660 m²</td>
<td></td>
<td>121</td>
<td>440</td>
<td>76</td>
<td>121</td>
<td>50</td>
<td>808</td>
</tr>
<tr>
<td>3</td>
<td>306 m²</td>
<td></td>
<td>1079</td>
<td>1405</td>
<td>1012</td>
<td>457</td>
<td>720</td>
<td>4673</td>
</tr>
<tr>
<td>Transect Average</td>
<td></td>
<td></td>
<td>1328</td>
<td>2478</td>
<td>967</td>
<td>358</td>
<td>361</td>
<td>5491</td>
</tr>
</tbody>
</table>
Table 4. Estimated wet weight of *Cardisoma* in 3 habitats by burrow size class. See text for further explanation.

<table>
<thead>
<tr>
<th>Zone</th>
<th>0-25</th>
<th>26-50</th>
<th>51-75</th>
<th>76-100</th>
<th>over 100</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>5.6</td>
<td>124.2</td>
<td>154.0</td>
<td>42.1</td>
<td>76.7</td>
<td>402.6</td>
</tr>
<tr>
<td>2</td>
<td>0.2</td>
<td>10.6</td>
<td>6.5</td>
<td>19.6</td>
<td>12.3</td>
<td>48.9</td>
</tr>
<tr>
<td>3</td>
<td>2.2</td>
<td>33.8</td>
<td>86.0</td>
<td>74.1</td>
<td>176.4</td>
<td>372.5</td>
</tr>
<tr>
<td>Transect Average</td>
<td>2.7</td>
<td>56.2</td>
<td>82.2</td>
<td>45.3</td>
<td>88.5</td>
<td>274.9</td>
</tr>
</tbody>
</table>
the amount of substrate turnover represented by burrows in the transect area. For this purpose it is assumed that the average burrow, regardless of diameter, is 50 cm long and that the average burrow diameters in Table 1 are representative of each size class. Based on these assumptions, the average volume of soil removed from each burrow-size class (from smallest to largest) is respectively: 173, 726, 1560, 2950, and 5195 cm$^3$. These combined with the counts in Table 2 give total volumes of soil removed as follows: Zone 1: 20.97 m$^3$/ha; Zone 2: 0.75 m$^3$/ha; and Zone 3: 7.84 m$^3$/ha.

These values suggest that existing burrows represent a relatively modest turnover of soil compared to the approximately 5000 m$^3$/ha within reach of the crabs in the upper half-meter or so of soil. However, it must be remembered that we are dealing with "standing crop" rather than turnover rates, and total impact may be far greater or far less depending upon the rate at which burrows are constructed and obliterated. Again, the fauna of Fanning Atoll no doubt lacks many fossorial insects, annelids, and vertebrates of importance elsewhere, and the relative value of Cardisoma as a soil mixer is therefore increased; for example, assuming 1.25 tons/yd$^3$ of topsoil, Darwin's (1881) estimates of soil turnover by earthworms in England range from 11.61-27.86 m$^3$/ha/yr. Finally, soil turnover may be greatly increased over the average in localized spots; in the peak density area from 150 to 155 m inland of the lagoon (Fig. 1) calculations suggest that about 1.1% of the upper one-half meter of soil had been excavated during burrow construction.

SUMMARY

Preliminary observations on the natural history of Cardisoma carnifex at Fanning Atoll show that these crabs exhibit a considerable amount of diurnal activity, are active burrowers and opportunistic scavengers, and appear to have a spawning peak correlated with the period of the full moon. It is suggested that these animals play an important role in the transport of organic matter within the atoll ecosystem.

It appears that, with the possible exception of the very young, habitat preferences remain constant throughout life. The data suggest that elevation, depth of ground water, vegetation, soil composition, and the amount of ground cover may all be important variables determining the distribution of C. carnifex.

An average density of 5,491 crabs/ha and an average biomass of 275 kg/ha are estimated from the data for one transect. It is further suggested that Cardisoma plays an important role in substrate turnover; an average of 9.85 m$^3$/ha of soil had been moved in the sampling area.
Bibliography


GROUNDWATER AND NEARSHORE HYPOSALINE CONDITIONS AT FANNING ATOLL DURING A PERIOD OF HIGHER THAN NORMAL RAINFALL

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ABSTRACT

Exceptionally high rainfall levels accompanying instability of the Intertropical Convergence Zone in 1972 greatly expanded the freshwater realm on Fanning Atoll. Changes in the head of the groundwater body (a Ghyben-Herzberg aquifer), as measured at frequent intervals in 11 wells, revealed variations in sediment permeabilities, but proved an unsuccessful technique for determining amounts of freshwater discharge into inlets along the lagoon shore. The aquifer was found to store freshwater and then maintain reduced salinities in the inlets long after an initial salinity depression during a period of precipitation. The spatial and temporal distribution of salinities in the inlets closely resembled those of an estuary. However, the factors contributing to salinity fluctuations in each inlet are sufficiently complex and show both regular and irregular patterns of temporal variation, so that the inlets constitute highly unpredictable environments. The biological implications of this unpredictability are deemed interesting because of the close proximity to the predictable and reasonably stable environments of the shallow-water lagoon reefs.

The major atolls of the Line Islands are located in the Central Pacific between 2° and 6° North Latitude. Mean annual rainfall in this region of the Pacific increases northward from the equator reaching a maximum at the Intertropical Convergence (ITC), which at this longitude normally lies between 5° and 8° N (Seelye, 1950). The position and extent of the ITC varies seasonally; it is generally farthest north during the months of September through November and farthest south from April through June. These periods thus correspond to the dry and wet seasons of the Line Islands. Differences in mean annual rainfall among the atolls of Christmas, Fanning, and Washington are nearly as great as the seasonal differences in rainfall received by any one of the atolls (New Zealand Meteorological Service, 1956).

The normal seasonal pattern of rainfall is interrupted irregularly by an interval of abnormally high rainfall producing maximum monthly rains in December through March (Doberitz et al., 1967). These periods of exceptionally high rainfall correspond with El Nino of the eastern Central Pacific and are imposed upon the annual cycle so that the normal wet season
may also show above normal rainfall (R. Taylor, personal communication). Beginning in May 1972, rainfall in the Line Islands was measured at near- and above-record levels. Christmas Atoll, normally the driest of the four major atolls, experienced the greatest above-normal deviations in rainfall of the Line Island atolls over the succeeding 9 months.

In an earlier paper (Guinther, 1971) the occurrence of estuarine conditions in shallow arms of the Fanning Atoll lagoon was described as observed in January 1970. The present paper extends those observations to cover the period of heavy rains in July and August, 1972 during the second Fanning Island Expedition.

A PROBLEM OF DEFINITIONS

Seawater dilution along a shoreline can occur in a wide variety of situations not readily encompassed in a definition designating a particular type of environment (Day, 1951; Caspers, 1967; Pritchard, 1967). Consequently, despite similarities in one aspect or another, few generalizations can be made concerning the ecology of brackish waters. At one end of the spectrum are those physiographic features widely accepted as befitting the term estuaries: the mouths of rivers entering a tidal sea. At the other extreme are freshwater springs which discharge directly into offshore marine waters as described by Kohout and Kolipinski (1967) in Florida. A central problem in "estuarine ecology" is that of deciding where in the spectrum of brackish waters the term "estuary" should be used.

The origin of all freshwater eventually producing a salinity depression in the marine environment (or combining with saline water to produce a brackish water environment) is ultimately some form of condensation from the atmosphere. The importance of the hydrologic cycle notwithstanding, it is the focus at a specific point along the coastline of water precipitated over some wider area which is of primary interest to the aquatic biologist. The precipitated water may reside for some period of time in a groundwater body before being discharged into a stream of directly into the marine environment. The absence of above-ground flow in many instances is a consequence of land soils with a high porosity relative to the amount of rainfall received. Above-ground flow may be absent even though the amount of rainfall precipitated on the drainage basin is considerable.

The absence of a freshwater surface flow constitutes the primary objection to the use of the descriptive term estuary for brackish bodies of water on atolls. However, this objection must apply along any coast where significant stream flow into the ocean is intermittent. The statement of Caspers (1967) that "estuaries are limited to river mouths..." is unnecessarily restrictive if one accepts the usual definition of a river as a "stream of water larger than a brook or creek" (Webster's New Collegiate Dictionary). A broader definition of an estuary is given by Pritchard (1967):
"An estuary is a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted with fresh water derived from land drainage."

This definition might also encompass the central lagoon at Fanning. Although a differentiation between estuaries and lagoons is provided by Caspers (1967): "Estuaries, in contrast to lagoons, are characterized by poikilohalinity and the instability of environmental factors" precise definitions of "poikilohalinity" and "instability" must still be agreed upon to clarify the distinction.

A practical reason for excluding inlets and coastal ponds on atolls from inclusion within the term lagoon is the confusion arising from the presence of a perfectly respectable lagoon as a dominant feature on most atolls. Environments on Diego Garcia Atoll (Indian Ocean), similar in many respects to the inlets described on Fanning (Guinther, 1971), are referred to as "barachois" by Stoddart and Taylor (1971).

With the exception that rivers are absent on low coral islands (although short, intermittently flowing streams may be present), most definitions of estuaries can apply to the inlets at Fanning Island for durations of days to perhaps months. However, these bodies of water rapidly become hypersaline or "inverse estuaries" (Pritchard, 1952) when evaporation exceeds precipitation.

Because the tendency in the literature is to restrict the term estuary as has Caspers (1967), I define the brackish-water bodies of water on Fanning Island as "inlets", if a free connection with the lagoon or ocean is present (see Fig. 12), and "ponds", if no free connection exists. My use of the term inlet is thus comparable with "barachois" of Stoddart and Taylor (1971). The terms inlet or pond refer to geomorphological features and imply nothing about either the hydrology or chemistry, which may differ from atoll to atoll. I demonstrate in this paper that the inlets at Fanning Atoll behave as estuaries under conditions when precipitation exceeds evaporation.

THE GHYBEN-HERZBERG LENS

The low-salinity, groundwater body of porous islands is of the Ghyben-Herzberg type. The relationships between precipitation, island size, permeability, and porosity of soils, and the formation and maintenance of a basal groundwater-body are discussed by Cox (1951) in reference to coral islands, and by Wentworth (1947) in reference to high volcanic islands.

The formation of a body of freshwater within the porous structure of an island is the result of the downward percolation of water derived from precipitation and the relative inhibition of mixing processes (such as diffusion and turbulent water movement) by the island sediments. The lower density of freshwater as compared with the density of seawater causes freshwater to float on, or displace, seawater within the island sediments.
The difference in density between fresh and normal seawater is such that for every unit of freshwater floating above sea level, there must be a corresponding 40 units of freshwater displacing seawater below sea level. For brackish water, the expected depth of the lens below sea level would decrease as the difference in salt content between the brackish and sea water decreased. A sharp boundary between fresh and sea water is seldom maintained in the groundwater body, the lens being progressively saltier with depth; precise determination of the depth of the body is thus non-simple on theoretical grounds.

For the purpose of discussion, I assume an island without a fresh groundwater body and with sediments of equal porosity throughout. An evenly distributed addition of freshwater by precipitation over this island will result initially in the formation of a downward percolating body of freshwater. This freshwater body will encounter seawater at sea level, and, while density adjustments (vertical adjustments) occur, some freshwater near the shoreline will be lost by outward (lateral) flow. The remaining freshwater, or at least that excess not removed from the groundwater by plants or by evaporation, can only be lost by lateral flow toward the shoreline. Because all of the water lost from the groundwater body by lateral flow must flow through the island margins, while only that water falling on the center of the island must flow through the inland portions of the island, an even flow can be maintained only if the hydraulic gradients determining the rate of flow are steeper near the shoreline (Cox, 1951). The hydraulic gradient is the change in head (elevation of the freshwater level above sea level) per unit distance measured in the direction of flow. The resultant shape of the head is thus convex upward in cross section, highest at the center of the island, and curving steeply downward at the margins. Although some of the freshwater remains above sea level, the greater part of it (40 units of depth for every unit of head) will reside below sea level. The base of the groundwater body, that portion below sea level, will be convex downward, so that the overall form is lenticular in cross section.

An adjusted Ghyben-Herzberg lens can constitute a vast storage reservoir of freshwater on low, coral islands, because the great bulk of the groundwater is found below sea level. The actual size of the aquifer and the salinity of the water within it will vary with time in response to the long- and short-term inputs of rainwater. In addition, the depth of the lens and its salinity at any given point will bear a relationship to the island size and shape, the porosity and permeability of the sediments, and the tidal range. Tidal fluctuations are transmitted through the lens and contribute to the mixing of fresh with salt water as the interface between them moves up and down through the sediments. Damping of these fluctuations and hence reduction of tidal mixing increases with decreased sediment permeability and distance inland from the shore. Small islands of high permeability may not maintain a freshwater lens long after a period of precipitation.

An island with a freshwater aquifer will discharge fresh or brackish water along its margins as long as the lens maintains a head above sea level. Without additional input the lens will become progressively more
brackish, decrease in size, and eventually disappear altogether. Were this to occur, the groundwater would be as saline as the ocean water.

The inlets of the lagoon increase the linear extent of the island margin and also serve to focus fresh or brackish water discharge from the aquifer at specific points along the lagoon margin. Salinities in the inlets are reduced immediately during precipitation on their surface waters, but salinity reduction can continue for some period thereafter by discharge of water from the aquifer. Relative to the volume of the receiving water, the inlets are surrounded by a greater length of aquifer margin than is the lagoon proper.

METHODS

Salinity reduction in the inlets is not entirely a direct one resulting from precipitation falling on the inlet waters, but is also related to various properties of the island aquifer. For this reason a study of the extent of and changes in the aquifer at Fanning Atoll was undertaken during the 1972 Fanning Atoll Expedition. Shallow wells were constructed in the vicinities of the Cable Station Inlet and the Napu Naiaroa Inlet (Figs. 1, 2, and 3) and water levels in the wells followed intermittently during July and August, 1972. All wells were dug by hand to a decimeter or more below the water table and the hole encased with asbestos pipe (Transite). A cover was placed over the pipe opening to reduce evaporation. The elevation of a mark on the upper lip of each casing was determined in relation to a U.S.C.G.S. Bench Mark at the Cable Station and an arbitrary fixed point at Napu Naiaroa using a Path Automatic Level. Water levels in the wells were recorded as the distance from the casing lip to the water surface measured by a meter rule. Later, these data were transformed by adjustments to the common fixed point at each locality. The results of three, nearly continuous surveys of water levels, each spanning a complete tidal cycle, are presented in Figures 4, 5 and 6.

Elevations of the casing lip, ground elevations around the well, and lower end of the casing (the depth from which water in the well was drawn) are given in Table 1.

Rainfall amounts were recorded daily at the Cable Station and these data are given in Table 2 for the period covering the Expedition's visit. The rain gage was read each morning and these measurements are arranged with the 24-hour total given for the day and following night of the listed date. Individual rain squalls during the continuous survey periods are indicated by the letter "P" at the top of Figures 4 and 5. No precipitation occurred during the 26-hour survey at Napu Naiaroa. A temporary rain gage was installed at Napu Naiaroa for 11 days in August.

Tidal changes in the lagoon were measured continuously by two float-type gages, one located at the end of the lagoon pier near Cable Station Estuary and the other located on the bridge over Napu Naiaroa Estuary. The letter gage was in place for only six days. The tide records were related to the fixed points at each locale, although this determination was less
Table 1: Elevations of Wells and Fixed Points on Fanning Atoll

<table>
<thead>
<tr>
<th>Napu Naiaroa 1</th>
<th>Elevation (meters)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Casing Top</td>
</tr>
<tr>
<td>Bridge Abutment (NE)</td>
<td>1.000</td>
</tr>
<tr>
<td>Well #1</td>
<td>0.819</td>
</tr>
<tr>
<td>Well #2</td>
<td>0.716</td>
</tr>
<tr>
<td>Well #3</td>
<td>0.834</td>
</tr>
<tr>
<td>Well #4</td>
<td>1.055</td>
</tr>
<tr>
<td>Well #5</td>
<td>0.766</td>
</tr>
<tr>
<td>Well #6</td>
<td>0.454</td>
</tr>
<tr>
<td>Well #7</td>
<td>0.426</td>
</tr>
<tr>
<td>Cable Station 2</td>
<td></td>
</tr>
<tr>
<td>Bench Mark #1</td>
<td>2.606</td>
</tr>
<tr>
<td>Bench Mark #3</td>
<td>0.979</td>
</tr>
<tr>
<td>Well #11</td>
<td>0.851</td>
</tr>
<tr>
<td>Well #12</td>
<td>0.876</td>
</tr>
<tr>
<td>Well #13</td>
<td>1.238</td>
</tr>
<tr>
<td>Well #14</td>
<td>1.141</td>
</tr>
<tr>
<td>Station 5 (Mark on bridge curb)</td>
<td>1.038</td>
</tr>
<tr>
<td>Station 10 (Mark on bridge curb)</td>
<td>1.001</td>
</tr>
</tbody>
</table>

1 Elevations at Napu Naiaroa relative to an arbitrary elevation of 1.000 on bridge abutment.
2 Elevations at Cable Station relative to U.S.C.G. Bench Mark #1, reported elevation 8.55 ft. rel. MLLW lagoon (taken as 2.606 meters here) and 8.36 ft. rel. MLLW ocean.
3 U.S.C.G. Bench Mark #3 reported at 3.23 ft. MLLW lagoon and 3.04 ft. MLLW ocean. Elevation given above is based on our survey and is relative to MLLW lagoon as determined from BM #1.
4 Elevation of inlet bottom.
Fig. 1. Fanning Atoll showing the location of the two inlets studied.
Fig. 2. The inlet at Cable Station and the Cable Station grounds showing sampling sites and well locations. Sampling stations on the inlet are indicated by numbers; those on the lagoon shore by letters. Map based on ground survey and aerial photographs. Dotted lines in the sectional drawing beside map are the upper and lower elevations of the water table observed during the study.
Fig. 3. The inlet at Napu Naiaroa showing sampling sites and well locations. Sampling stations indicated by numbers or letters. Map based on ground survey and aerial photographs.
Table 2: 24-Hour Rainfall\(^1\) Totals Measured before 0800 on the Cable Station Grounds

<table>
<thead>
<tr>
<th></th>
<th>July</th>
<th>August</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>9</td>
<td>10</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>0.28</td>
<td>1.17</td>
<td>0.56</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>12</td>
<td>13</td>
</tr>
<tr>
<td></td>
<td>0.33</td>
<td>0.91</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>15</td>
<td>16</td>
</tr>
<tr>
<td></td>
<td>0.00</td>
<td>0.00</td>
<td>0.51</td>
</tr>
<tr>
<td></td>
<td>17</td>
<td>18</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>0.96</td>
<td>2.92</td>
<td>0.00</td>
</tr>
<tr>
<td></td>
<td>20</td>
<td>21</td>
<td>22</td>
</tr>
<tr>
<td></td>
<td>0.91</td>
<td>0.18</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>24</td>
<td>25</td>
</tr>
<tr>
<td></td>
<td>0.86</td>
<td>0.23</td>
<td>0.48</td>
</tr>
<tr>
<td></td>
<td>26</td>
<td>27</td>
<td>28</td>
</tr>
<tr>
<td></td>
<td>0.00</td>
<td>2.67</td>
<td>2.90</td>
</tr>
<tr>
<td></td>
<td>29</td>
<td>29</td>
<td>30</td>
</tr>
<tr>
<td></td>
<td>1.12</td>
<td>2.90</td>
<td>6.73</td>
</tr>
<tr>
<td></td>
<td>31</td>
<td>31</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>0.91</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\(^1\)Rainfall given in centimeters; 24-hour total is the amount of rain recorded between 0800 on the date given and 0800 the next day; values given in parentheses () were recorded near the tide gauge at Napu Naiaroa.
accurate than that giving the well elevations. The tide records in Figures 4, 5 and 6 are shown as wide bands reflecting this uncertainty. Matching the tidal curve to the fixed point required measuring the water level while concomitantly marking the tide trace on the recorder. The position of the tide record in Figures 4 and 5 is based on two estimates which differed from each other by 0.006 meter. The tide curve is drawn as the shaded area between these two estimates. Five estimates relating the tide curve to the fixed point at Napu Naiaroa were made. One of these was made on August 10 and is shown in Figure 6 (labeled TM). Relative to this estimate, the other four estimates have the following deviations:

<table>
<thead>
<tr>
<th>Estimate</th>
<th>Deviation</th>
</tr>
</thead>
<tbody>
<tr>
<td>2</td>
<td>-0.025</td>
</tr>
<tr>
<td>3</td>
<td>+0.009</td>
</tr>
<tr>
<td>4</td>
<td>-0.024</td>
</tr>
<tr>
<td>5</td>
<td>+0.066</td>
</tr>
</tbody>
</table>

The shaded tidal curve in Figure 6 is drawn with the upper edge at estimate 1, judged as the best estimate because of its close correspondence with the water level at Station 6 at the following high tide (deviation of the Station 6 reading from estimate 1 at 2100, Aug. 10 = -0.001 meter). The lower edge of the tidal curve represents the median between estimates 1 and 2 and encompasses the mean of the estimates after discarding estimate 5. Water levels in the inlets were measured with either a meter rule from a mark on a span above the station (Stations 5 and 10 at Cable Station) or by a meter rule affixed to a stake (Station 6 at Napu Naiaroa).

Elevations at Cable Station Inlet were adjusted to MLLW in the lagoon from the reported elevation of Bench Mark No. 1 at 8.55 feet (2.606 meters). Bench Mark No. 2 could not be located but repeated surveys relating BM No. 1 to BM No. 3 revealed the latter (mounted on an iron pipe) to be 6 mm lower than the reported elevation of 3.23 feet (0.985 meter). The reported datum (MLLW) is approximately 36 cm below the lowest low water recorded on the lagoon tide gauge at Cable Station during the period of our stay.

The difference between MLLW in March 1967, when the elevations of the U.S.C.G.S. bench marks were established relative to the lagoon and LLW in the summer of 1972 is probably due to a real difference in sea level. Fanning Atoll is located just south of the equatorial countercurrent and sea level fluctuates seasonally. Exceptional positive deviations occur when transport by the countercurrent is strong, as would be indicated by the occurrence of El Nino in the Eastern Equatorial Pacific during the latter half of 1972 (Wyrtki, 1973). A decrease in the mean water level of the lagoon of over 30 cm was noted between December 1972 and April 1973 by James Jones (personal communication).

I have attempted to relate the elevations at Napu Naiaroa to those at Cable Station by comparing the tide records made simultaneously at these locations. The tide at Napu Naiaroa has an amplitude which is approximately 80% that of the lagoon tide at Cable Station. In addition, the Napu Naiaroa tide lagged behind the Cable Station tide by some 20 to 60 minutes. The shallow reef flat fronting Napu Naiaroa and the narrow entrance into the enclosed shore of Napu Naiaroa Inlet may be responsible for these
Fig. 4. Water level changes in wells and in the inlet at Cable Station on July 31 and August 1, 1972. Tidal curve shown as a stippled line. The occurrence of rain squalls is indicated by the letter P along the upper margin.
differences. Separate regressions of the nine high tides and the ten low tides recorded simultaneously at Napu Naiaroa and the Cable Station between 10 August and 14 August were made. The linear regression of the nine high tide levels at Napu Naiaroa upon the same tidal points at Cable Station gave the best fit (correlation coefficient = 0.986, as compared with 0.847 for the low water points) as might be expected, because high water would be least affected by restrictions on water flow at Napu Naiaroa. Surprisingly, however, the linear regression of all 19 (high and low water) tidal points at Napu Naiaroa on the same tidal points at Cable Station gave an even better fit (correlation coefficient = 0.997) and the regression equation:

\[
\text{sea level at Napu Naiaroa} = 0.80 \times (\text{sea level at Cable Station}) - 0.194 \text{ meters.}
\]

The absence of a one-to-one unit correspondence between water levels at these two locations in an expression of the tidal damping observed at Napu Naiaroa, but creates problems in attempting to relate elevations at Napu Naiaroa to the Bench Marks at Cable Station. It seems unjustified to add 0.194 meters to the arbitrary fixed point at Napu Naiaroa (and hence to all elevations at Napu Naiaroa) since it can never be true that:

\[
\text{elevations at Napu Naiaroa} = 0.80 \times (\text{elevations at Cable Station}).
\]

In terms of groundwater levels, an absolute correspondence at MSL would be more meaningful than a correspondence at MLLW (which is \(x = 0, y = 0\) in the regression equations above).

GROUNDWATER OBSERVATIONS

The description of a Ghyben-Herzberg lens presented earlier was greatly simplified to facilitate understanding of the general principles involved. In particular, island sediments were assumed to be homogeneous. Although it is likely that the island on which both the Cable Station and Napu Naiaroa are located (Fig. 1) holds one large aquifer, this aquifer shows variation in response to vertical tidal fluctuations and horizontal flow from place to place. Such variation indicates heterogeneities in the permeabilities of the island sediments. Three types of wells can be differentiated on the basis of tidal damping.

**TYPE 1** - Characterized by Well No. 1, the lens shows only slight tidal damping with a time lag on the order of 30 minutes. The small tidal damping indicates sediment of relatively high permeability.

**TYPE 2** - Characterized by moderate tidal damping expressed particularly by a reluctance to follow the tidal lows. Time lag is greater for tidal lows than for highs. Wells located on the lagoon beach (Well No. 11) or on the inlet flat (Well Nos. 6 and 7) illustrate this pattern. Essentially the same pattern is shown by the open inlet stations (Stations 5 and 10 at Cable Station and Station 6 at Napu Naiaroa). The aquifer is apparently shallow at these well sites and salinity fluctuations may be great.
TYPE 3 - Wells in which the tidal amplitude is highly damped. Tidal lag increases with distance from the shoreline. Well No. 2 is particularly interesting. A type 1 or 2 response might be expected because this well is located within 1 meter of the inlet shore. The small tidal amplitude shown by this well is a function of low-permeability sediments, particularly in the deeper regions through which tidal fluctuations are transmitted. Note that the tidal effect on the level of water in Well No. 12 is very noticeable on August 6-7 when the tidal range in the lagoon was great, and not so noticeable on July 31-August 1 when the lagoon tidal range was smaller.

The wells show a progressive increase in head with increasing distance from the shore, in accordance with Ghyben-Herzberg Theory. A cross section of the island (A-A') and aquifer at the Cable Station grounds is included in Figure 2. The ground surface is the upper solid line (and the dashed line at Well No. 14 to the north of the transect). The two dotted lines represent the upper and lower limits reached by the groundwater during the course of this study as measured at each of the wells. Well No. 14 appears to be near the region of maximum head. Well No. 15 was excavated to a depth of more than 1 meter below the ground surface without penetrating the aquifer. Well No. 16 is the old freshwater well for the Cable Station and the distance from its lip to the water surface (more than 2 meters) made monitoring of level changes difficult.

The aquifer is close to the surface in the lagoonward portion of the transect, and is periodically exposed in depressions over the lower ground to the north of the transect. The Gilbertese natives on Fanning take advantage of the close proximity of the aquifer to the surface in such areas to construct taro patches and freshwater fish-ponds. The low ground between these features at the Cable Station was flooded throughout the period of this study. The presence of flooded ground does not necessarily indicate a low permeability of the soils. Rather, the lens itself "breaks the surface" in these areas and is contained by the surrounding higher ground. A slow but constant flow drains the flat into the estuary through a narrow stream (Station 10). Thus the configuration of the ground at Cable Station allows the inlet to intercept a large portion of the aquifer head adjacent to it and the inlet maintains a low salinity. The narrow entrance connecting the Cable Station Inlet to the lagoon and the overall shallow depth of this inlet further contribute to the low salinity by restricting tidal exchange.

Rain squalls approached the study sites from the southwest, passing first over the lagoon. Each squall was accompanied by a seiche which was recorded on the tide record. A rain squall usually produced an immediate rise in the level of water in every well; the magnitude of this rise involves consideration of the amount of rain falling, the duration of the rainfall, and the carrying capacity (porosity) of the upper sediments. The amount of precipitation in individual squalls was not recorded, and cannot be related to the increase in head without some estimate of the actual volume of water represented by a particular increase. Very rough estimates of the water volumes involved may be gleaned from the data obtained at the Napu Naiaaroa Village well and Well Nos. 12 and 13 at Cable Station Inlet. The level in the Village well rose approximately 15 cm on August 19.
Fig. 5. Water level changes in wells and in the inlet at Cable Station on August 6 and 7, 1972.
following a rainy period when precipitated 3.7 cm of water. These numbers indicate that the porosity of the upper soils is about 25%. This estimate is probably high, since the input was spread over most of the day and some loss in head was occurring by lateral and particularly by vertical flow. On August 7, the rainfall over a 2-hour period measured at the Cable Station was 0.7 cm. The rise in water levels at Well Nos. 12 and 13, taking into account the loss rate that was occurring prior to the input period, amounts to about 5 cm. These values give an estimate of the porosity of 14%.

If we compare the increase in water level of each well following a particular squall we see that the increase is greatest near the lagoon margin and decreases inland. (Note: Well No. 11 responds additionally to the seiches). Whether this decrease in response inland is the result of changing porosities (capacities of the soil to hold water) or shoreward flow of the rainfall excess is not clear. Those wells closest to the shoreline also lost water more rapidly after the rain ceased.

The course of water level changes in the wells at Napu Naiaroa during a 26-hour survey on August 10-11 (Fig. 6) was uncomplicated by pulses of freshwater input (rain squalls). For each well at Napu Naiaroa, the mean water level between 0900 on August 10 and 1000 of August 11 was calculated by reading the respective curves at 63 consecutive points (every 12 minutes). These data are given in Table 3.

Note that the mean water level at Well No. 1 is below that at Well No. 2, although the latter is closer to the shoreline. Well No. 1 is located on a spit of land probably built up from sediments derived from the lagoon reef (mostly sand). The narrowness of the spit also imposes limits on the size and depth of the aquifer. Well No. 2, on the other hand, is located in a region where at least the upper sediments are derived from the inlet and adjacent coconut grove. Mention has already been made of the differences in tidal responses between these two wells.

Well No. 6 and Well No. 7 are both located at the same elevation on the lower flat of Napu Naiaroa Inlet. Although Well No. 7 is located nearly 200 meters farther up the Inlet and its tidal curve correspondingly lags behind that of Well No. 6, the mean water level in these two wells was identical during the 25-hour period. This result may be partly coincidental since water in Well No. 7 does not reach as low a level as that in Well No. 6 (see Fig. 6), but the close correspondence of the water in these two wells over a tidal cycle may indicate a homogeneous geomorphology of the lower flat. Salinities in Well No. 7 were lower than those at Well No. 6 during the survey period.

The recording tide gage was moved from Napu Naiaroa Inlet (Station 5) to the drinking-water well at the nearby village for the period from August 14 to August 21. The continuous trace obtained shows a progressive decrease in the head of the freshwater aquifer until August 9 when rainfall again raised the aquifer head. (The village, occupied on a temporary basis, was not in use at this time). The rates of head change for four consecutive 24-hour periods beginning at midnight on August 14-15 were:
Table 3: Mean Water Levels in the Wells at Napu Naiaroa between 0900 on August 10 and 1000 on August 11

<table>
<thead>
<tr>
<th>Site</th>
<th>Mean Water Level&lt;sup&gt;1&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Inlet (Sta. 5)&lt;sup&gt;2&lt;/sup&gt;</td>
<td>0.253</td>
</tr>
<tr>
<td>Well No. 1</td>
<td>0.257</td>
</tr>
<tr>
<td>Well No. 2</td>
<td>0.272</td>
</tr>
<tr>
<td>Well No. 4</td>
<td>0.611</td>
</tr>
<tr>
<td>Well No. 5</td>
<td>0.406</td>
</tr>
<tr>
<td>Well No. 6</td>
<td>0.312</td>
</tr>
<tr>
<td>Well No. 7</td>
<td>0.312</td>
</tr>
</tbody>
</table>

<sup>1</sup>in meters, based on arbitrary base point elevation

<sup>2</sup>based on Estimate 1 (TM); see text
Fig. 6. Water level changes in wells and in the inlet at Napu Naiaroa on August 10 and 11, 1972. Base point of elevation scale is arbitrary and not the same as that used for Figures 4 and 5 (see text).
-0.027, -0.034, -0.040, and -0.024 meters/24 hours. The apparent decrease in loss rate during the fourth 24-hour period is in part the result of recharge (0.9 cm precipitation measured at Napu Naiaroa) on the afternoon of the 18th. Using the estimate of porosity calculated above for this location, the rainfall input could have increased the head by 0.036 meter, giving a corrected change in head of -0.060 meters/24 hours.

The discharge of freshwater to the shore involved in the head changes calculated above could be determined only if the porosity of the sediments, the contribution of increasing displacements of saltwater by freshwater (vertical flow), and the loss of groundwater by transpiration were known. Porosity is likely to vary from place to place, so that the pattern of water loss per unit area per unit time could be quite different from the pattern of head change per unit time as indicated by any particular series of wells. A more accurate estimate of freshwater discharge into the inlets could be obtained from water volume transports through the narrow entrances to the inlets, if measured over several tidal cycles. A limited number of such measurements were made at both Napu Naiaroa and Cable Station inlets and will be reported on in a later paper.

Water in the inland wells remained fresh (refractive index = 1.3330) during the course of this study. On the other hand, salinities varied in wells close to shore. For example, at Napu Naiaroa on August 10 and 11 the following ranges were recorded:

<table>
<thead>
<tr>
<th>Well No.</th>
<th>Refractive Index</th>
<th>Salinity (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1.3330 - 1.3332</td>
<td>0 - 1</td>
</tr>
<tr>
<td>2</td>
<td>1.3330 - 1.3333</td>
<td>0 - 2</td>
</tr>
<tr>
<td>6</td>
<td>1.3359 - 1.3364</td>
<td>16 - 18</td>
</tr>
<tr>
<td>7</td>
<td>1.3336 - 1.3337</td>
<td>3 - 4</td>
</tr>
<tr>
<td>8</td>
<td>1.3359 - 1.3373</td>
<td>16 - 23</td>
</tr>
</tbody>
</table>

No consistent pattern related to the tide curve emerges from the time course of these variations. Salinities were not always higher on the 11th compared with those on the 10th. Salinities in these wells were within the ranges given when subsequent measurements were made on 13, 18, 19 and 20 August. Well No. 1 may be an exception; although the salinity was not measured following approximately one week of very little rain, the water in this well was brackish enough on August 17 to be undrinkable.

At the Cable Station refractive indices exceeded 1.3330 only in Well No. 11 (1.3330 - 1.3332; 0 - 1%0 salinity) and Well No. 10 (1.3334 - 1.3349; 2 - 10%). Well No. 10 was dug into the beach slope in front of Well No. 11 to sample groundwater salinities at the shoreline. Lagoon salinities just offshore of Well No. 10 varied between 16 and 26%0 (R.I. = 1.3359 to 1.3380) during this period. These three sampling sites illustrate the steep salinity gradient which existed over a few meters of lagoon beach in August 1972.
OBSERVATIONS ON THE INLETS

Water levels and salinities at selected open-water stations were measured during the course of the three extended surveys at Napu Naiaroa and Cable Station inlets. Water levels were measured at three stations (two at Cable Station and one at Napu Naiaroa) in addition to the records provided by the tide gages. These data appear in Figures 4, 5, and 6. The locations of all sampling stations on the inlets and lagoon shore are indicated on Figures 2 and 3. Water-level changes at the three stations studied were similar to those described for the Type 2 wells. High tides lagged behind those of the lagoon and the lag time increased upstream. Low water was higher than low water in the lagoon and appeared independent of the lagoon tide. Station 6 at Napu Naiaroa was a pond separated from the inlet by a sill at approximately 0.35 meter (relative to the arbitrary fixed point). The independent (lower) level reached by the water in this pond may have been close to that of the surrounding water table. Salinities in the pond on August 10 were between 5 and 6‰ (R.I. = 1.3339 - 1.3340) until 1900 hours when water flooded the pond on the rising tide and raised the salinity to 18‰. The LHW on August 10 did not introduce inlet water into the pond, nor would have the high tides on August 9. The LHW on August 11, while adding some water to the pond did not change the salinity from 18‰. Salinities at Station 6 fluctuate in response to direct precipitation and tidal additions, but the water level in the pond could be maintained against the hydraulic gradient at low tide only if relatively impermeable sediments surrounded and lay beneath this site. The absence of tidal fluctuations in nearby Well No. 2 further suggests that this area is underlain by sediments of low permeability, and these sediments must extend well into the region of the Ghyben-Herzberg lens. Sediments near the inlet shore are fine, almost clay-like and contain considerable organic matter derived from the nearby coconut grove.

The water at Station 5 and Station 10 (Cable Station Inlet) is not separated from the lagoon by a sill, although the hydraulic gradient between these stations and the lagoon is small when the distances involved are considered. Water flowed out of the estuary during the entire time the level of water at these stations was at the low plateau, and the restriction of this flow at low tide maintained the head. In fact, outflow at Station 5 continued for two hours after the water level began to rise with the tide. At Station 10 on July 31 flow was always outward, and inward flow on August 1 persisted for less than 2 hours (Fig. 7). During periods of heavy input to the aquifer, Station 10 is functionally a stream that feeds water intercepted by the low ground to the north of Station 10 into Cable Station Inlet. Salinities given in Figures 7 and 8 show that the water in Cable Station Inlet was mostly derived from land drainage. Lagoon water appears briefly at Station 5 with each flooding tide.

Another feature at Cable Station Inlet serves to focus freshwater lost from the lens through the Inlet. On the lagoon beach, between the beach berm and the vegetation line, there is a shallow depression which slopes to the south. Well No. 11 was located in this depression. As the groundwater body within the beach rises with the tide, the aquifer head "surfaces" in
Fig. 7. Salinity changes along the lagoon shore (Station C) and two inlet locations (Stations 5 and 10) on Cable Station Inlet on July 31 and August 1, 1972. Direction of water flow at the two inlet stations is indicated by the small arrows.
Fig. 8. Salinity changes on August 6 and 7 at Cable Station Inlet.
Fig. 9. Salinity changes along the lagoon shore (Station D) and at three inlet locations (Stations 5, 12, and 35) in Napu Naiaroa Inlet on August 10 and 11, 1972. At Station 5, two samples were taken, one at the surface (S) and one approximately a meter deeper (B).
the depression and freshwater flows into the channel of Cable Station Inlet just below Station 5 (Fig. 10).

ECOLOGICAL SIGNIFICANCE OF SALINITY CHANGES: CONCLUSIONS

The primary determinant of salinities in any given body of water at Fanning Island is the relationship between precipitation and evaporation that exists and has existed earlier over some period of time. The balance between these two factors is more or less the same over the entire atoll at any one time, and three additional factors contribute to salinity variations that are seen from place to place: (1) the degree of restriction of seawater flow into the body of water; (2) the area of the drainage basin and tidal flats relative to the volume of the pond or inlet; and (3) the relationships between aquifer, permeability of sediments, and the configuration of the body of water. Isolated ponds may be exposed extensions of the groundwater body and reflect the salinity of the groundwater in their vicinity.

The 1972 visit of the University of Hawaii Expedition to Fanning Atoll coincided with the early months of an exceptionally high rainfall period lasting through the first quarter of 1973. During the period of observations, the extent of freshwater in the groundwater body must have been near maximum. Mean salinities in open bodies of water, including the lagoon (see Smith and Pesret, p. 21, this report), were greatly reduced from the values observed in January, 1970 (see Gordon and Schiesser, 1970). Flooding of low ground was common in 1972, promoted both by the high rainfall and the high sea level which accompanies the rainfall anomaly (Wyrtki, 1973). The observations reported herein thus represent conditions near the low-salinity extreme for Fanning Atoll.

Napu Naiaroa Inlet is typical of the larger inlets scattered about the Atoll in the size and depth of the inlet itself and in the extent of its associated tidal and supratidal flats. Daily salinity variations at Napu Naiaroa are the result of several factors including precipitation, evaporation, and tidal currents. However, precise measurements of these factors over several days, combined with an understanding of the hydrodynamics of the inlet would not permit a prediction of salinity changes without knowledge of the conditions over some indefinite period prior to the observations. A brief, heavy rainfall, isolated in time, will drastically affect salinities in the inlet for only a few days at most. Several tidal flushings return salinities to those of the lagoon, but the extremes in salinity which occur between the high and low tides during the period of readjustment depend on the conditions of the aquifer and the salinity of the lagoon fronting the inlet (in addition to the amount of freshwater precipitated). The condition of the aquifer is dependent upon the amount and distribution in time of rainfall over a period of several weeks, while the salinity of the lagoon reflects the balance between precipitation and evaporation over many months. Fluctuations in mean sea level change the dynamics of both the aquifer and the tidal exchange between the inlet and the lagoon. Salinities in the inlet thus result from complex interactions between factors with daily, monthly, seasonal, and even longer patterns of
variation. The physical characterization of each inlet must be based on
collection of these island-wide factors in addition to the three
categories of local features listed above.

The result of climatic changes having seasonal or longer periodicities
is to shift the dominance of salinity regimes in the inlets and ponds; that
is, freshwater may predominate for some period of time and then, as a result
of a change in climatic factors, hypersalinity may predominate. These
shifts are accompanied by changes in conditions in the groundwater and the
lagoon, so that the terrestrial and marine environments are also affected
to some degree. At Fanning, the enclosed and semi-enclosed, shallow-water
environments undergo regular, although somewhat unpredictable changes in
physiography. The far reaches of the inlets in January 1970 were inhabited
almost solely by mats of blue-green algae (Guinther, 1971). These mats
were present in August 1972, but were modified in color and form, reflecting
a shift in the dominant species (or perhaps the physiology of the same
species) of cyanophytes (Fig. 11). Typically freshwater invertebrates
(larvae of Odonata and Chironomidae) were present, in addition to the
ubiquitous land crabs (Cardisoma carnifex) and euryhaline fishes (Chanos
chanos and Tilapia mossambica).

Fanning Atoll is a moderately "wet" island with a mean annual rainfall
of 206 cm (New Zealand Meteorological Service, 1956). Salinities in the
ponds and inlets seldom reach upper extremes which might exclude life.
However, the fluctuations in salinity that occur are unpredictable in a
biological sense (see Slobodkin and Sanders, 1969). In this respect the
inlets differ from many "true" estuaries having relatively constant sources
of fresh and salt water (i.e., a river and the open ocean). In these
estuaries the range and duration of salinity fluctuations at any given
place are reasonably predictable from time to time. Even if the amplitude
of the fluctuation varies, its periodicity is closely linked to the tidal
cycle, and organisms inhabiting these regions have behavioral or physiolo-
gical mechanisms which enable them to survive in the fluctuating environment.
Successful colonization in an unpredictable environment can occur only if
the species is eurytopic or if colonizers are available when conditions to
which the species is adapted appear (Fig. 12). The duration of each
salinity regime relative to the life cycles of potential stenotopic
colonizers becomes an important aspect of the problem of colonization.
Thus, the lack of predictability of salinity fluctuations may contribute as
much to species distributions in the inlets at Fanning as the range of
these fluctuations.

The wide variety of hydrologic features at Fanning provide refuges for
stenohaline species regardless of the conditions predominating at any one
time. In January 1970, bodies of water could be found which were nearly
fresh (6‰ salinity) while other locations experienced hypersalinity (up to
42‰). In August 1972, hypersaline environments could not be found, but
the various bodies of water displayed salinities from essentially freshwater
to normal seawater.

The occurrence of highly unpredictable environments adjacent to
relatively benign and predictable environments (the tropical, shallow-marine
environments of the lagoon and ocean reef flat) is of experimental interest regarding questions on the relationship between species diversity and environmental stability (see Sanders, 1968; Slobodkin and Sanders, 1969). The experimental value of the inlets is further enhanced by the fact that shifts in salinity regimes occur on a time scale which allows colonization by stenotopic organisms.

**SUMMARY**

1. Instability in the Intertropical Convergence Zone during the latter half of 1972 resulted in above normal amounts of precipitation at Fanning Atoll (Line Islands).

2. The high level of rainfall received by the Atoll produced extreme conditions of hyposalinity in inlets and ponds. The groundwater body (a Ghyben-Herzberg aquifer) was expanded and may have reached maximum capacity by July 1972.

3. The response of the groundwater body to recharge and the effect of tides on the aquifer were studied in wells by frequent measurements of the groundwater head. These studies revealed differences in sediment permeabilities and pointed out the difficulty of determining aquifer discharge to the shore from changes in the elevation of the water table.

4. The inlets, shallow arms of the lagoon, became brackish or fresh water environments during periods of heavy precipitation. Discharge from the aquifer maintained lowered salinities in the inlets long after precipitation had ceased. The spatial and temporal distribution of salinities in the inlets closely resembled those of an estuary.

5. Although precipitation, predominating over evaporation during the study period, tended to lower salinities in the lagoon as a unit, the inlets "focused" loss of freshwater from the aquifer at specific points along the shoreline.

6. Salinity variation in the inlets was deemed highly unpredictable as such variation is dependent upon the long- and short-term balance between precipitation and evaporation, tidal parameters, and the mean level of the sea. These parameters show both regular and irregular patterns of variation at Fanning.

7. The degree of response to any combination of the above parameters varied from inlet to inlet, owing to differences in tidal exchange between inlet and lagoon and differences in the configuration of each inlet relative to the aquifer.

8. It was hypothesized that the unpredictability of the inlet environments with reference to salinity contributes to the distribution, in space and time, of organisms inhabiting these bodies of water and the shallow reef flats of the lagoon shore.
ACKNOWLEDGMENTS

The 1972 Expedition to Fanning Atoll was supported by National Science Foundation Grant GA313111. I am indebted to S. Townsley and Fred Lighter for helping to collect the data at Napu Naiaroa during the early hours of the morning. Fred Lighter additionally served as rod man on the numerous elevation surveys. Figures 2 and 3 are based on aerial photographs kindly provided by M. J. Vitousek. I wish also to thank E. A. Kay, D. C. Cox, and S. V. Smith for reading and commenting on the manuscript.

REFERENCES


FANNING ISLAND: Preliminary Archaeological Investigations of Sites Near the Cable Station

Under the auspices of the:
Bernice Pauahi Bishop Museum, Department of Anthropology

Akihiko Sinoto
Honors Program, University of Hawaii

PREFACE

Previous to this study, undertaken during July and August, 1972, no formal archaeological research had been done on Fanning Atoll except for several unfortunate cases of vandalism and looting of sites following western discovery of Fanning Island in 1789, and for two brief in-transit stops on the island in 1924 and 1934 by Kenneth P. Emory of the Bernice Pauahi Bishop Museum, Honolulu, Hawaii. During his visits, Emory conducted surface surveys and mapping of sites in the vicinity of the Cable Station (Emory, 1934, 1939). My primary concern was to conduct test excavations on these sites in addition to locating new sites.

This paper presents the results of a three-week field study of eight prehistoric Polynesian sites. Several difficulties encountered during the course of the field work prevented a more detailed study. Foremost was the limitation imposed by the number of days spent in actual field work: a few days of heavy rain, lack of experienced personnel, and the dense vegetation cover which had to be manually cleared substantially limited the number of days available for excavation.

INTRODUCTION

Until recently, atolls have been largely neglected in archaeology, as evidenced by the mountainous volume of works dealing with high or large islands that overshadow the materials dealing with atolls. Some of the traditional views and reasons behind this neglect are brought to light by Davidson (1967), whose work on Nukuoro, a Micronesian atoll, in 1965, represents one of the first intensive archaeological studies undertaken on an atoll. In Polynesia, the Tuamotu Archipelago has been sporadically studied, but other Pacific Equatorial Islands have been ignored after superficial surveys. Because of their size and location, atolls have long been regarded as temporary transit stops for prehistoric seafarers:
"The low coral islands within six degrees of the Equator in Polynesia, though uninhabited when discovered by Europeans are supposed to have served as resting places for the Polynesian voyagers in their journeys between the high archipelagos." (Emory, 1934.)

While, some atolls may have served as resting places, the question of more permanent types of settlements has recently been raised.

In the traditional view, atolls existed only as links among high-island archipelagos. But with the present focus of archaeological studies shifting to an environmental perspective, the atoll ecosystem is emerging as a significant and challenging aspect of Pacific archaeology:

"...a small atoll affords unique archaeological opportunities not encountered on larger islands. On a larger land mass any archaeological survey must of necessity be merely a sample, whereas on Nukuoro or a similar atoll it is possible for one person to carry out a total survey in a short time and quickly acquaint himself with those areas on which archaeological evidence, whether structural or in the form of midden deposits has accumulated ...The limited and concentrated nature of the archaeological evidence on an atoll, however, means that a greater understanding of the prehistory of the culture concerned can be gained in a relatively short time than would be the case in a large or diversified island or group." (Davidson, 1967.)

BRIEF EARLY HISTORY

Fanning atoll (Fig. 1) was discovered by Captain Edmund Fanning of the ship "Betsy," on June 11, 1789 and subsequently named after him. Fanning wrote in his journal that the island was uninhabited, and that he could find no signs of habitation or that the island had ever been inhabited previous to his arrival. However, he continues:

"...Capt. Donald MacKay...a few years (later) being at anchor some weeks at Fanning Island...on one of his walks (inland) had come across some heaps of stones, which, to all appearance, from their order and regularity, were thus placed by the hands of men, although from the coat of crust of weather with which they are covered, it must have been at some remote date. Being prompted by curiosity and desire for further information upon this subject, he caused one of these piles to be removed and found it to contain, a foot or two under the surface of the ground, a stone case filled with ashes, fragments of human bones, stone, shell, and bone tools, various ornaments, spear and arrow heads of bone and stone, etc." (Fanning, 1924.)
Fig. 1. Location of Fanning Island (indicated by arrow).
MacKay was not the last to disturb the sites; many people after him looted these sites, and unfortunately many of the artifacts they recovered have since been lost. In addition, many of the structures have suffered extensive damage, such that if certain characteristics or features had been present they are now beyond recognition.

SITE DESCRIPTIONS AND EXCAVATIONS*

FAN1-1: Probable ceremonial structure judging from size and elaborate construction.

Emory describes this site in detail (1934, pp. 12-14; 1939, pp. 180-182), thus only the major points will be briefly treated here. However, it should be noted that additional disturbance has occurred subsequent to Emory's visits, perhaps during World War II when allied military forces were stationed on the island.

This is the largest of the sites recorded from Fanning. Its construction utilizes dressed slabs forming a rectangular enclosure, measuring about 22 m by 20 m: the longer sides align roughly in an east-west orientation. Located at the southwest and southeast corners are dressed, L-shaped corner-stones. The northwest and northeast corners are disturbed and poorly defined, although a depression at the northeast corner may indicate the removal of a corner-stone. The area of greatest disturbance is at the northwest corner where most of the slabs are missing from the northern alignment. However, at the approximate location of the corner stands a small coral upright measuring 25 cm by 20 cm by 5 cm (h/l/w). The southern alignment is well preserved and almost wholly intact. Centered within this enclosure is a smaller rectangle measuring 18 cm by 16 m. This smaller rectangle, defined by small, upright, coral slabs, is raised about 5 to 20 cm above present ground level and its interior floor appears to have been partially paved with coral shingles. More paving was exposed by running a test trench across the feature. The space between the outer, dressed-curb border and the inner raised feature is filled with a thin superficial layer 2 to 3 cm in thickness comprised mainly of coral pebbles of roughly uniform size. The inner feature appears to have been raised by bringing in sand and coral stones as fill from some nearby place.

The large dressed boundary curbs were identified as conglomerate reef rock, composed primarily of Pocillopora, Porites, Acropora, and several kinds of mollusks. Other corals utilized at this site include Leptastrea, Favia, Stelligera, Lobophyllia, and some Acropora covered with coralline algae. Some of the mollusks in the conglomerate were identified as Turbo argyrostromus, Trochus histrio, Cypraea caputserpentis, Astrea calcara, Ostrea sp., Littorina sp., and vermetid tubes.

*These follow the standardized Bishop Museum site designation system, the number immediately following FAN represents the islet and the number assigned to the site follows the hyphen. See map (Fig. 2).
Emory (1934) noted that "shelves" had been artificially cut into the sides of the dressed slabs. However, upon close inspection and with an understanding of the process of reef conglomerate formation, it would appear that not all of these "shelves" can be attributed to artificial creation. Layers or strata of conglomerate material may be laminated to form thick slabs such as those utilized for the site. Individual layers can split off resulting in a shelf-like, natural formation at the zone of truncation. Examples of this type of formation can be seen in areas of phosphatized reef conglomerate deposits. One such deposit occurs near the Cable Station (Map, Fig. 2). Of conglomerate deposits on Fanning, Roy (1970) says:

"Man has exploited the phosphate rocks of Fanning Island for some time. A 16th Century temple on Fanning is in part made of phosphate rock. Distinct planar bedding allowed the stone to be easily worked. At least 19,500 metric tons of phosphate rock were shipped off Fanning during the period from 1877 to 1887. Both the mining for the temple and the commercial mining were done about one-half mile south of the site of the old cable station."

It is possible that the curbs found at the site were "quarried" from this deposit. More relevant and accurate information may be obtained through careful comparative analysis of the constituent materials in this deposit and those found in the bordering curbs of the site.

Excavations. Test pits were located in five areas within this site.

An initial test pit, (TP-1), 0.5 m by 1 m, was placed parallel to the eastern alignment on the interior of the structure. This was later extended 0.5 m in both north and south directions. At a depth of 5 cm, a thin layer of coral pebbles was exposed, and at -15 cm, small bone fragments and shells were recovered (Table 1). The base of the boundary slabs was located at a depth of 30 to 35 cm below ground surface. The bottom 5 cm of the curbstones intruded into a white, sterile layer. Fresh water percolated into the pit at a depth of 40 cm. The stratigraphy indicated (1) 3 to 5 cm of overburden; (2) a 2-to 3-cm superficial fill of coral pebbles; (3) light-brown, sandy soil with fragments of coral about 22 to 25 cm in thickness, with the top 7 cm of this layer containing some midden material, perhaps indicating a shallow fill during the construction phase of the structure; and (4) a sterile white, hard pan at a depth of about 30 cm from ground surface. These layers were roughly in accordance in color and composition with horizons I-III of the soils of an atoll (Naval Intelligence Division, 1939-1945).

A 1 m-square pit on the southern alignment, (TP-2), was excavated transecting a large curbstone. This pit yielded stratigraphy similar to TP-1 and no differences were noted between the interior and the exterior of the structure. Turbo fragments and a porpoise tooth were recovered.

The presence of a possible pavement prompted the third test pit, TP-3. It was centrally located on the interior, raised feature. A pavement of
Fig. 2. Sites and surrounding features in the Cable Station area, Fanning Island, August 1972.
<table>
<thead>
<tr>
<th>MATERIAL</th>
<th>FAN1-1</th>
<th>-2</th>
<th>-5</th>
<th>-6</th>
<th>-7</th>
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<tr>
<td>porpoise tooth</td>
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<td>x</td>
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<td><em>Trochus</em> sp.</td>
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**TABLE 1.** List of the presence or absence of the midden materials from the excavated sites on Fanning Island.
coral shingle was exposed at depths of 20 to 25 cm below the surface, however the paving seemed to concentrate only at this spot. Subsequent northward extension of this pit revealed that the pavement never reached the upright, inner, bordering slabs, and expansion in other directions also showed the pavement to be limited to the immediate area of the initial test pit. A bonito-hook point and a cut pearl-shell fragment were recovered at depths of 5 and 15 cm, respectively. A possible adze-blank fragment of fossilized *Tridacna* was also found, at a depth of 10 cm.

The exposed pavement, buckled and disturbed, showed no apparent relationship to either the exterior curbstone enclosure or to the interior feature. The pavement may be the remnant of a structure that preceded the present one, which may explain the sporadic presence of midden materials in the test pits without any well-defined cultural component appearing in the stratigraphy. Except for the marked absence of the thin pebble layer, the stratigraphy follows that of TP-1 and TP-2. Sterile, hard pan appears below the exposed pavement.

A trench measuring 2 m by 0.5 m was located parallel to three large slabs of the northern outer alignment and forms TP-4. It yielded similar data to TP-1 and TP-2. Two cut pearl-shell fragments and a pearl-shell hook blank were recovered from a depth of 20 cm.

A pit 1 m square was placed near the southwest corner of the interior enclosure (TP-5) to determine if a pavement was present in that direction. Two unassociated slabs were exposed 5 cm from the surface but no indication of a pavement was present.

The bonito hook point recovered from TP-3 shows so-called Western Polynesian Type traits, with two holes at the extension on the proximal end of the base for attachment to the lure shank (Fig. 3). In Samoa and Tonga, this type of hook is known only from ethnological collections. However, identical forms are reported from the early Marquesan phase I assemblage, excavated from Hane, Uahuka (Sinoto, 1970, p. 106). The Fanning point compares even more favorably because of the similarity in size and material as well as their known prehistoric provenience (Fig. 4). Although the Tongan and Samoan points of this type are morphologically similar, the Tongan forms generally are much larger, and they were often manufactured from raw materials other than pearl-shell.

Interpretations. Fanning Island stoneworking techniques and utilization can be compared with examples reported from Tonga (McKern, 1929), Marquesas (Suggs, 1961), Easter Island (Metraux, 1940), and Hawaii (Bennett, 1931). However, when the characteristics of the whole structure are taken into account, the closest affinities appear to be with Tonga, and Emory (1934; 1939) compares this structure in detail with the Tongan "langi" reported by McKern.

The preceding data provide grounds on which to base the following sequence of events involving FAN1-1. The area was first occupied by a smaller site(s), perhaps a house. Subsequent to abandonment or the destruction of this site, the larger structure was built directly on the
remnants of the former. During the construction process, midden material was scattered about and churned into and mixed with the fill material. The hook and other artifacts, therefore, associate not with this second structure, but probably with the previous one(s).

**FANl-2: Probable tomb (Fig. 5).**

This site was found to be in nearly the same condition as reported by Emory (1939), although three small areas of additional disturbance were noted. Only modifications to Emory's assessment of the site are included here. Although, at first glance this structure in its present state appears as "a shapeless mass" of coral rubble, certain tentative reconstructions can be inferred from the remnants. At the time of original completion, it was most likely a square enclosure measuring about 10 m on each side. The sides display scant hints of double-walled construction with a width of 1.5 to 2 m and a maximum height of 1.5 meters. From the descriptions given, this appears to be the same structure that MacKay had "caused to be opened" (Fanning, 1924).

**Excavations.** TP-1 was a pit located near the southeast corner of the enclosed interior floor. It measured 1 m by 1.5 m. At a depth of 15 cm, what appeared to be the disturbed remnant of a crypt or cist, consisting of three small upright coral slabs, similar to that described by MacKay, was exposed. The cist theory was later confirmed when at depths of 25-30 cm, nine porpoise-tooth pendants were recovered. Three to 5 cm below this appeared sterile sand and coral fragments.

A second pit, TP-2, was excavated in an unsuccessful attempt to locate the interior basal slabs of the southern wall. The extent of disturbance in this area was too great to permit its location, however, and the slabs were most probably removed and broken.

A third pit, TP-3, was placed in the interior floor of the structure. From this very shallow pit, sterile sand and coral fragments appeared at a depth of 15 cm.

**Interpretations.** The porpoise-tooth pendants recovered from TP-1 (Fig. 6) resemble those from the Marquesas (Fig. 7) again from the phase I assemblage (Bishop Museum Collection) of Hane, Uahuka (Sinoto, 1970), and are probably of the same type as those reported by Emory (1934). The use of porpoise-tooth ornaments was rare in Polynesian groups other than the Marquesas (Emory, 1934). Three such necklaces are reported from Hawaii, but their origins are questionable (Buck, 1957).

**FANl-2** as described in the reconstruction bears some stylistic resemblances to structures from the Tuamotu Archipelago and the Society Islands, especially to those small, enclosed "maae" with cists from Tetiaroa (Sinoto, personal communication). If, however, the morphology of this structure is not an enclosure, but a platform with vaults or cists as Emory (1939) assumes, again a Tongan affinity is indicated (Emory, 1934). In any case, due to the badly disturbed condition of this site, conclusive comparisons are extremely difficult to draw. Structural styles can be the
consequences of various external influences, for example, to what extent would the locally available construction materials dictate the style of a structure? Thus in many cases, stylistic similarities alone are not adequate bases for tracing the origins of the builders.

FAN1-3, -4, and -5,

FAN1-5 (Fig. 8) is definitely structure 3c described by Emory (1939), but whether -3 and -4 are the two other sites reported is debatable. Their condition at present indicates much subsequent (since 1934) deterioration, from both natural causes and military activities during World War II. These sites were apparently bulldozed for access to several machine gun emplacements constructed in the vicinity. Thus, structure 3b (Emory, 1939) may have been totally destroyed. No sites resembling the description given were found in the area. No excavations were undertaken at FAN1-3 or -4.

Three test pits were placed in FAN1-5. No artifacts were recovered from these test pits; however, the stratigraphy showed a single cultural component 20 to 25 cm in thickness containing bone fragments, shells, and porpoise teeth (Table 1). Sterile white sand appeared at depths of 25 to 30 cm.

Many artifacts, exposed by erosion, were recovered from the surface. These will be collectively discussed in a latter portion of this paper.

FAN1-6 through FAN1-8. Newly recorded sites.

FAN1-6: (Fig. 9).

This site is located about 30 cm west of FAN1-5, and its condition is poor. A bulldozer-cut, about 10 m wide running through the central portion of the site area, has caused both banks of this cut to erode badly and consequently the scanty remnants of the site were also affected. This area may actually represent the remains of more than one site, judging from the large area defined by the rubble; however, in its present condition, any such distinctions are impossible to render. The only recognizable features are comprised of a few upright coral slabs along the eroded bank on the northern extremity of the site area. A concrete machine gun emplacement is located at the eastern end of this bank.

Two test pits were excavated, yielding a few sample materials, but no artifacts. However, TP-2 (Fig. 9) contained a charcoal/ash lens at depths of 15 to 20 cm from the surface (Fig. 10.) Charcoal samples were collected from this lens and the results of the radiocarbon analysis conducted by Gakushuin University, Tokyo on sample 2 (GaK-4557) was 880±85 (B. P. 1950). Applying this value to the most current radiocarbon corrections (Ralph et al., 1973) the date of A. D. 1080 is obtained and the parameter for the occupational period of this site can then be roughly defined by the date range A. D. 1020-1190. The exposed conditions of the site and the shallowness of the deposit provoke some question regarding the purity of the sample material.
Fig. 8. Diagram of site FAN1-5, August 1972.

Fig. 9. Diagram of site FAN1-6, August 1972.
The surface artifacts were collected from the surrounding area, concentrated mostly in and around the bulldozer-cut.

FANI-7: (Fig. 11)

This site is located about 25 m west of FANI-6 at the end of the bulldozed area. It is bounded on the west by an old tennis court and a graded cricket field. These disturbances from both east and west have contributed to the rapid erosion of this site, and the remaining surface features are very scanty.

The surface recovery of a single-piece, pearl-shell fishhook fragment with a head form displaying salient Marquesan characteristics prompted test pitting at this site. The test pit was arbitrarily placed at a central spot (Fig. 11), well away from the disturbed or eroded areas. This pit revealed a solitary cultural layer 25 cm in thickness, and a sterile, white layer at 30 cm. A sample was obtained from a charcoal/ash lens at a depth of 20 cm. The analysis of this sample (GaK-455B) yielded an age of 1560±85 (B. P. 1950), or A. D. 410, applying radiocarbon correction. This places the occupational period of this site somewhere in the range A. D. 350-530. Although the conditions at this site are better than those at FANI-6, the possibility of contamination cannot be overlooked.

The single-piece, pearl-shell fishhook fragment (Fig. 12) displays early Marquesan traits. The reduction of the shank near the head and opposite the knob is one diagnostic feature characteristic of hooks from phases I and II of Sinoto's Marquesan cultural sequence (Sinoto, 1970). A comparison of this hook with one from the Hane, Uahuka phase I assemblage illustrates their similarity (Fig. 13).

Three artifacts were recovered from the excavation: a Terebra-shell chisel blank from 25 cm; a pearl-shell hook blank; and a fragment of a Cassis-shell chisel, from a depth of 5 cm (Fig. 14). These also appear similar to some Marquesan material.

FANI-8

Located on the ocean-side at the northern extremity of the Cable Station is a rectangular burial cist set into the ground. Its sides and floor are lined with coral slabs. No evidence of morticing or dressing these slabs can be seen. Larger slabs used as cap stones close off the top; thus, once closed, the cist is almost impossible to locate amidst the other coral shingles on the ground. Its dimensions are 50 cm by 1.5 m by 50 cm (w/l/d), and indicate use as a secondary burial or flexed burial containment. According to one local informant's description, a secondary burial is inferred. This site was reportedly vandalized during the 1920's or 1930's by Cable Station personnel and the bones taken to England. No records are available regarding this incident or the recovered contents of the cist.

Similar forms of burial cists are reported from the Tuamotu and Society islands, and from Tongareva, Tonga, and the Marquesas.
No excavation was done at this site and no artifacts were recovered.

Discussion

In light of the present excavations and new data, earlier interpretation of some of these sites as burials (Emory, 1939) perhaps requires some modification. The presence of cultural deposits (midden, charcoal, etc.) and surface artifacts strongly suggests that these sites were primarily utilized as habitation sites. Elsewhere in Polynesia are examples of dwelling sites subsequently modified and utilized as burials, for example in Ha'atuatua, Marquesas (Suggs, 1961).

Although the general settlement patterns of atolls are not clearly established, Davidson (1967) suggests for Nukuoro, "a long tradition of a nucleated settlement on the principal islet," and few or no remains on the other islets. A similar pattern is seen for Fanning Island from the available evidence. Information from long-time residents indicate that other sites or settlements have never been found on the other islets. Fanning Islet I possesses many favorable attributes: large size, elevation, and dry land; and appears to have been the prominent islet for the prehistoric inhabitants. Settlements also often occur in the vicinity of deep-water passes (Davidson, 1967). Geophysical studies reveal traces of a pass that once existed at the Cable Station area:

"The Cable Station was built on an infilled pass. The two peninsulas on the lagoon side of the island near the Cable Station are spits (see Fig. 2) that were built along the sides of the old pass" (Roy, 1970).

Additional evidence regarding the location of this pass is the presence of beach berms on the north and south sides of the Cable Station area. Their axes align with the location of the two spits. Unfortunately, no dates are available regarding the closing of this pass.

The east-west alignment of sites FAN1-3 through -7 parallel to the pass, may be an indication that the pass existed at the time of occupation of the sites. Thus, from the presently available data, the south side of the pass may be regarded as the nucleus settlement, comprised of habitation sites (further excavations are needed to firmly establish the exact nature of these sites; a key factor would be determining the relationship, intrusive or contemporaneous, between the sites and any burials found within) and larger ceremonial or religious structures (FAN1-1 and -2). These types of prominent structures would tend to be near the habitation areas as Emory (1970) points out for the Tuamotu Islands:

"Every lineage had its 'marae' which stood upon land where its members lived."

Isolated or hidden burials occur in many Polynesian groups and the presence of FAN1-8 on the north side of the pass may imply such a practice. This
Fig. 10. Stratigraphic profile, site FAN1-6, TP-2, August 1972.

Fig. 11. Diagram of site FAN1-7, August 1972.
side of the former pass would not have been favored for habitation due to the different environment created in part by the phosphate deposits.

ARTIFACTS: SURFACE COLLECTION

The following artifacts, with a few exceptions, were all recovered in the immediate vicinity of sites FAN1-3 through -7, along the zone of disturbance and erosion caused by the bulldozer-cut.

Except for one worked basalt of unknown function, shell and coral were the materials used for the manufacture of artifacts. Although it was unfortunate that these artifacts were not found from known proveniences within the sites, they still play an important role in comparative analysis with artifact assemblages from other Polynesian groups (Fig. 16).

A bonito lure fragment was found by M. J. Vitousek in 1958 in the same area (Fig. 15). The slender shoulder and pointed head end characterize a Marquesan lure type (Fig. 17) which occurs in phases II and III of the cultural sequence (Sinoto, 1967). The earlier form occurring in the phase I and II periods possesses sharp snood shoulders and flattened or blunt head ends (Sinoto, 1967). The two hooks acquired on this occasion, in addition to the two collected by Emory in 1924, show the occurrence of both forms at Fanning (Fig. 18). The size of bonito hooks varies; in the Marquesas larger or massive forms were more prevalent in the earlier periods, but with both heads forms being represented (Sinoto, from unpublished tables).

Cassis-shell chisels seem to be uniquely Marquesan, and a chronological sequence based upon their typology has been established from the Hane, Uahuka excavations (Sinoto, 1970). Four chisels were recovered on Fanning Island, including one with a double edge; however, the forms of the other three could not be determined due to their fragmentary state. Double-edged chisels in the Marquesas occur only in phase II (Fig. 19).

Terebra shell chisels commonly occur from the Society Islands and the Marquesas, and have also been reported from Tonga (Poulsen, 1968). However some of the Marquesan and Fanning types appear with the head (opposite the tip) or aperture of the shell chipped off (Fig. 20).

According to Sinoto (1967), well-ground hook blanks and tabs are characteristic of Marquesan fishhook manufacture. The hook blank recovered from FAN1-7 (Fig. 14), as well as the two blanks collected from the surface (Fig. 21), display this trait. The "filing and notching method" of fishhook manufacture is evident on the larger blank. This method was used for the manufacture of jabbing hooks (Sinoto, 1967).

From another area approximately 40 m south of FAN1-7, a small one-piece jabbing hook and a fragmented hook bend were found (Fig. 22). This form of fishhook occurs commonly in phase III from the Hane, Uahuka excavation (Sinoto, 1970), but may overlap into the earlier phase II as well.
A flat, water-worn, basalt rock with a drilled hole was found by George J. Krasnick at the ocean-side beach of the Cable Station. The notch that appears on the right edge of the rock (Fig. 23) was probably another hole. The origin and function of this object are unknown; however, the holes appear to have been drilled with a modern bit, indicating recent historic origin.

Much archaeological data has become available since 1939, thus Emory's statements regarding the basalt adzes from Fanning Island requires updating. All four of the adzes described (Emory, 1939) possess proto-Polynesian forms, but they are now known to occur from areas other than Samoa and Tonga. They are widely distributed, and similar forms appear from the Society Islands, Hawaii, Marquesas, Easter Island, Cook Islands, and New Zealand. However, the highest percentage of occurrence so far is yielded from the early assemblages of Hane, Uahuka in the Marquesas (Emory, 1968). Petrographic analysis may prove useful in determining the origin of the basalt.

SAMPLES COLLECTED FROM EXCAVATIONS

Table 1 shows only the presence or absence of the 32 midden materials listed, from each of the sites excavated. The nature of the excavations and the lack of time did not allow for quantitative controls to be imposed on any of the test pits. Identification is tentative for some of the materials.

SUMMARY AND CONCLUSIONS

At this preliminary stage of investigation, with limited sampling of both sites and artifactual material, and with many questions still left unanswered, only tentative conclusions can be drawn.

Several statements concerning the prehistory of Fanning Island may now be made with some certainty. The occupation of Fanning probably lasted longer than formerly assumed. Presumably, the building of sites such as FAN1-1 and -2 require time, not only for the physical effort, but for stable social conditions needed to initiate such projects. Furthermore, the identification of the Cassis shell, utilized for the chisels, as Cassis rufa, of Indo-Pacific origin and distributed only as far east as the Tuamotu Archipelago, but not to the Marquesas, infers their manufacture on Fanning Island utilized locally available shell. In addition, the possible Tridacna adze blank found at FAN1-1 may indicate the exploitation of substitute materials after the depletion of imported basalt tools. The use of local resources requires time to become familiarized with the ecosystem, and therefore long-term occupation is implied.

It is curious that no inhabitants were present at the time of Western contact. Why was Fanning abandoned? Or, did some factor lead to the extinction of the population? The closing of the pass may have significant implications here. Catastrophic closing of the pass, as suggested by
Gallagher (1970, p. 192) would have had severe effects on the lagoon ecosystem, which in turn would have affected man, dependent on these resources for food, materials for tools, etc. Such events are known to occur on atolls elsewhere, as in the Ellice Islands recently (Maragos, 1972).

Determining the prehistoric relationship of Fanning Island with other island groups, leads to the problem of establishing the origin of its inhabitants. The artifactual evidence points toward the Marquesas, while the prominent structural style points toward Tonga. Here one of the major difficulties that faces all Pacific archaeologists arises: that of the melange of discontinuous archaeological and ethnographic data, often with only one of these two types of data available for (a) specific area(s).

"Although archaeology is fortunate in sharing the field with ethnography in Oceania, a fruitful cooperation between the two disciplines will depend on a critical appraisal of their respective natures. Seen from the archaeological point of view, ethnographic data perhaps cannot always be accepted at face value" (Poulsen, 1970).

The matter of limited sampling may constitute the problem in attempting to associate Fanning with either Tonga or the Marquesas. Although the artifactual evidence displays salient, early Marquesan characteristics, so far, prehistoric Tongan artifactual data from archaeological context is markedly lacking. At the same time, presently available data on early Marquesan structures may not be an adequate representation of the whole range of structural forms that once existed; some may well have become assimilated as time passed. The same situation may apply to Tonga.

"As with any other artifact, morphological parallels between 'marae' types may not accurately reflect historical relationship" (Bellewood, 1970).

There also exists the additional variable of the materials used for construction. Coral and limestone were readily available and often used for construction in Tonga, whereas in the Marquesas, the use of volcanic stone predominated. More information regarding the proto-Polynesian element would undoubtedly aid in determining the exact nature of Fanning Island prehistory. Meanwhile, the archaeologist must work with the material evidence at hand.

It should be noted, however, that the prevailing winds at Fanning are from the southeast. This would tend to favor the Marquesas over Tonga in terms of embarkation points for drift voyages arriving at Fanning Island.

The Fanning Island artifact assemblage, including those recovered during this field work and those reported previously, exhibits salient Marquesan characteristics. The chisels, one-piece fishhooks, porpoise-tooth pendants, and the bonito lures and point especially show close affinities with Marquesan assemblages of the phase I and II periods from Sinoto's Hane, Uahuka excavations.
Unfortunately, the same cannot be stated regarding the structural remains. No one cultural affinity is predominant. FAN1-1 is stylistically close to Tongan "langi" forms, although data on early Marquesan ceremonial structural forms is markedly lacking. Some of the other sites, FAN1-2 and -8 especially, exhibit strong similarities with Tuamotu and Society Islands remains. The other sites are too badly disturbed, or more sub-surface features, if present, must be exposed before stylistic comparisons can be attempted.

Since only one cultural component was evidenced from all of the test pits, it seems reasonable to assume an occupation by one cultural group and to associate the surface artifacts to the sites. Also at this point of investigation, no evidence regarding the appearance of a secondary intrusive culture is indicated.

The two radiocarbon dates obtained pose a slight problem. Although both fit into the Marquesan chronological sequence quite well, phases I and II = A. D. 300-1300, a discontinuity of 600 years seems implausible, even assuming long-term occupation, for the situation presented at FAN1-6 and -7. Perhaps sample contamination is the answer here. Contamination as the cause of sample anomalies, in the Pacific, is discussed in some detail by Shutler (1971). Recent atomic testing in the Pacific can certainly be a cause of contamination to carbon samples.

Finally, the following reconstruction is suggested for the origin of prehistoric Fanning Island inhabitants:

An ancestral group with proto-Polynesian affinities (adzes, structural forms) settled somewhere in the Marquesas. Later, the descendants of this group, now possessing tool kits with salient Marquesan characteristics, but still retaining earlier proto-Polynesian cultural attributes, set off on a migratory voyage, sometime between A. D. 400-1100, but most likely after A. D. 600 according to the phase II artifactual chronology, and arrived at Fanning Island where they settled till abandonment or extinction took place. Phase II period was the period where migrations from the Marquesas to marginal Polynesian Islands took place (Sinoto, 1968).

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BIBLIOGRAPHY


Buck, Peter H. 1927. The Material Culture of the Cook Islands, Thomas Avery & Sons, New Zealand.


Fanning, Capt. Edmund. 1924. Voyages and Discoveries in the South Seas, Salem.


The Vascular Flora of Fanning Island,
Line Islands, Pacific Ocean

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The flora of Fanning Island has been reported upon before. When the island was discovered in 1798 by Capt. E. Fanning, it was noted that a grove of old coconut trees was present, which was an indication of previous visitation and settlement (Fanning, 1833).

In the Report on the Botany of the Challenger Expedition, Hemsley (1885, 1(4): 116) printed a list of 15 species that had been collected on Fanning by J. T. Arundel, 2 of them cultivated, 4 of them adventive, and 9 indigenous plants.

The basic report on the botany of Fanning is that by Erling Christophersen (1927, 37-44), with the botanical results of the Whippoorwill Expedition. He gives a good account of the geography, climate, soils, vegetation, and the higher flora. He lists a total of 46 vascular plants. This total includes 7 ornamentals, 6 food plants, 14 adventives, and 19 indigenous species.

C. R. Long, botanist of the Pacific Ocean Biological Survey Program, visited Fanning in July 1965 and made a good collection of plants.

A new summary of the flora is desirable due to these collections and the ones made in July 1972 by Dennis J. Russell and Roy T. Tsuda. Their collections have added to the floristic list 3 indigenous species, 15 adventives, and numerous cultivated ornamentals.

Also the collections made in 1934 by H. St. John and F. R. Fosberg have not previously been reported upon.

In the present summary of the flora of Fanning, there are listed 39 ornamentals, 13 food plants, 28 adventives, 20 indigenous plants, and 2 endemics, making a total flora of 102 species and varieties.
The names of the indigenous and the endemic plants are marked for bold face type.

**PSILOTACEAE**


**POLYPODIACEAE**

*Phymatodes Scolopendrium* (Burm. f.) Ching. Ball 6; Christophersen 19; C. R. Long 3, 523; 3, 549; Russell & Tsuda 38.

**PANDANACEAE**
Pandanus fanningensis sp. nov. (sect. Pandanus).

Figs. 1, 2, and 3.

Diagnosis Holotypi: Arbor fere 6 m. alta cum ramulis multis in coronam ellipsodeam est, radicibus fere 1 m. longis, trunco laevi, ramulis inter cicatrices brunneis lucidi et in apice fere 5.5 cm. diametro, foliis 1.5 m. longis proxima basem 7.5 cm. latis in medio 5.6 cm. latis coriaceis supra viridibus lucidis infra pallide viridibus et glaucis in sectione mediali cum 56 nervis parallelis secundaris in dimidio quoque sed nervis tertiiis non evidentis lamina gladiata ex basi in apice trigono gracile subulato deminuienti (apice interito) basi inermi pallida, ex 9-10 cm. marginibus cum aculeis 2.2-2.5 mm. longis 7-15 mm. separatis subulatis compressis adpresse adscendentibus stramineis, ex 34 cm. midnervo infra cum aculeis 2-2.5 mm. longis 18-24 mm. separatis subulatis adpresse adscendentibus stramineis cum apicibus rubris, in sectione mediali marginibus cum aculeis 1.8-2 mm. longis 3-7 mm. separatis subulatis adpresse adscendentibus stramineis, proxima apicem marginibus et midnervo infra cum aculeis 0.3 mm. longis 3-7 mm. separatis arcuatis subulatis adscendentibus stramineis, plicis inermibus, infructescentia cum syncarpio solitario, pendunculo 17 cm. longo 15 mm. diametro trilaterato foliosi-bracteato, syncarpio 21 cm. longo 14.5 cm. diametro ellipsodeo trilaterato, phalangibus 5.7-6.3 cm. longis 3.5-5.2 cm. latis (6.1-6.5 cm. latis in geminibus cum 12-13 carpehis) 3-4.2 cm. crassis cuneatis obovoideis vel late obovoideis 5-6-angulosis lateribus inferis planis parte 1/3 supera libera cum lateribus laevibus carpellarum marginalium cum 0-2 angulis secundaris et cum planis sursum curvatis, carpelis 5-8 radiatis, apicibus marginalibus oblate pyramidalis-hemisphaericis et rare 1-2 cum areola concava distali 2-3 mm. lata, stigmatibus 3-4 mm. latis suborbicularibus vel reniformibus prostratis horizontalibus vel subelevatis, sinibus proximalibus fissura ½-2/3 ad fondam extensis, endocarpio minime supramediali 3 cm. longo osseoso subbrunneo late ellipsodeo cum humeriis mediialibus late curvatis adscendentibus apice obtuso, seminibus 15-18 mm. longis anguste ellipsodeis, mesocarpio in apice carpelae cuisque cavernam 10-22 mm. longam cum aerenchyma fibris longitudinalibus forbis et membranis pallidis, mesocarpio basali 18-20 mm. longo fibroso et carnoso.

Diagnosis of Holotype: Tree about 6 m. tall, many branched into a compact ellipsoid crown; prop roots about 1 m. long, numerous brown; trunk smooth; branches brown and shiny between the pale annular leaf scars; branchlets at apex 5.5 cm. in diameter; leaves 1.5 m. long, 7.5 cm. wide near the base, 5.6 cm. wide at the middle, coriaceous, above shiny green, below paler green and glaucous, at midssection with 56 parallel secondary veins in each half, but no visible tertiary veins, the blades sword-shaped, tapering from base to the trigonous slender subulate apex, (the tip lost), the base unarmed, pale; beginning at 9-10 cm. the margins with prickles 2-2.5 mm. long, 3-7 mm. apart, nearly straight subulate, ascending, stramineous; beginning at 34 cm. the midrib below with prickles 2-2.5 mm. long, 18-24 mm. apart, subulate, appressed ascending, stramineous with red tips; at midssection the margins with prickles 1.8-2 mm. long, 3-7 mm. apart, subulate, appressed ascending, stramineous; the nearby midrib below with prickles 2.2-2.5 mm. long, 7-15 mm. apart, subulate, compressed, appressed
ascending, stramineous; near the apex the margins and midrib below with prickles 0.3 mm. long, 3-7 mm. apart, arcuate subulate, ascending, stramineous; infructescence of a solitary syncarp; peduncle 17 cm. long, 15 mm. in diameter, 3-sided, leafy bracted; syncarp 21 cm. long, 14.5 cm. in diameter, ellipsoid, 3-sided; phalanges 5.7-6.3 cm. long, 3.5-5.2 cm. wide, (6.1-6.5 cm. wide in doubles with 12-13 carpels), 3-4.2 cm. thick, cuneate obovoid or broadly so, 5-6-angled, the lower sides flat, the upper 1/3 free, its sides smooth, shining, the lateral carpel sides with 0-2 secondary angles and the intervening planes gently upcurved; carpels 5-8, radial, the marginal apices oblate pyramidal hemispheric and rarely 1-2 with a concave distal platform 2-3 mm. wide; stigmas 3-4 mm. wide, suborbicular to reniform, flush and horizontal, or partly elevated; proximal sinuses a crack running ½-2/3 way to valley bottom; endocarp slightly supramedian, 3 cm. long, bony, brownish, broadly ellipsoid, with median shoulders, widely curved ascending, the apex obtuse; seeds 15-18 mm. long, narrowly ellipsoid; mesocarp forming in the apex of each carpel a cavern 10-22 mm. long, with aerenchyma of strong longitudinal fibers and pale membranes; basal mesocarp 18-20 mm. long, fibrous and fleshy.

Staminate Plant (Russell & Tsuda 31): Tree about 5 m. tall, freely branched into a dense, hemispheric crown; staminate inflorescence about 80 cm. long, cernuous; floral bracts foliaceous but white, the lower one 68 cm. long, 5 cm. wide, the upper ones 18 cm. long; staminate spikes several, 6-13.5 cm. long, 3.5-4.5 cm. in diameter; staminate fascicles with about 37 stamens; column 11 mm. long, stout; free filament tips 0.5-1.7 mm. long; anthers 2.4-4 mm. long, narrowly lanceoloid, the 2 basal lobes rounded, the apex bearing a subulate prolongation of the connective 0.35-1.5 mm. long.


Specimens Examined: Line Islands, Fanning Island, near Cable Station, staminate, July 1972, Russell & Tsuda 31 (BISH).

Discussion: P. fanningensis is a member of the section Pandanus, as its nearest relative, P. pukapukaensis St. John, of the Danger Islands, Pukapuka Island, a species with the phalange 6.8 cm. long; endocarp apex ovoid, the shoulders inframedian and long ascending; basal mesocarp 22-26 mm. long; stigmas 2-2.7 mm. long, suborbicular (or broadly elliptic); staminate spikes 2-2.5 cm. in diameter; staminal column 5 mm. long, the fascicles of about 16 stamens; anthers 1.7-2.7 mm. long. P. fanningensis has the phalanges 5.7-6.3 cm. long; endocarp apex low convex, the shoulders median, shortly ascending; basal mesocarp 18-20 mm. long; stigmas 3-4 mm. wide, suborbicular to reniform; staminate spikes 3.5-4.5 cm. in diameter; staminal column 11 mm. long, the fascicles with about 37 stamens; anthers 2.4-4 mm. long.

The new epithet is formed from the name of the type locality, Fanning; and -ensis, the Latin adjectival geographic suffix.
Fig. 1. Pandanus fanningensis St. John, from holotype. a, phalange, lateral view, X 1; b, profile of phalange apex; c, phalange, longitudinal median section, X 1; d, phalange, apical view, X 1; e, carpel apex and stigma, X 4; f, half of leaf base, lower side, X 1; g, half of leaf middle, lower side, X 1; h, leaf apex, lower side, X 1.
Fig. 2. *Pandanus fanningensis* St. John, from Russell & Tsuda 31.  
a, staminate inflorescence, X 1/4; b, staminate spike, X 1;  
c, leaf base, lower side, X 1; d, half of leaf middle, lower side, X 1.
Fig. 3. *Pandanus fanningensis* St. John, from Russel & Tsuda 31. Staminate fascicle, X 10.

Figs. 4 and 5.

Original Diagnosis: "Phalanges druparum magnae, ambitu subglobosae, compressae, supra plano-convexiusculae, 6 cm. spissae, 4.5 cm. crassae, et 9 cm. latae, in tertiam inferiorem partem fibrosae, rotundatae, vix attenuatae, ima basi latae; drupis vel loculis numerosissimis (circiter 17), transverse triseriatis, subprofunde et latiuscule separatis, rotundato-pyramidatis, pentagonis, a sulco longitudinali percursis, loculis exterioribus satis majoribus, lateraliter acute prominentibus, pentagonis, faciebus latis, subplanis et secus suturas druparum sulco longitudinali profundo excavatis; stigma hippocrepiforme planum ad verticem loculorum situm, in loculis exterioribus latissimum (5 mm.), crassum; endocarpium osseum, plus quam tertiam inferiorem partem et totam latitudinem phalangis occupans, fere 3.5 cm. spissum, superne rimosum, ambitu convexiusculum, inferne truncatum, rimalosum; mesocarpium superum fere 2 cm. spissum, fibroso-medullosum, cavernis exterioribus amplis, ovatis, inferum brevissimis fibrosum."

Expanded Diagnosis of Holotype (a single phalange, half of it in Berkeley, half in Firenze): Phalange 6-6.2 cm. long, 10 cm. wide, 4.5 cm. thick, transversely ellipsoid, 6-8-angled, the apex convex, lower sides not seen, the lateral sinuses deep, V-shaped valleys running far down, the upper 2.5-3 cm. free, the surface rather smooth, shining; carpels 17, each lateral one with its outer side rounded, elevated, running far down as a projection, and their apices semiorbicular, but the tip laterally turned and salient; the inner carpel apices slightly olate hemispheric, with several low angles, the platform lacking on all; stigmas 4-5 mm. long, broadly elliptic to cordate, flush, brown, papillose; proximal sinuses narrow but deep, extending half to all the way to the valley bottom; central apical sinuses 4-6 mm. deep, curving, V-shaped; endocarp 13-20 mm. distant from the apex, 35-37 mm. long, bony, dark reddish brown, transversely ellipsoid, the apex convex, but with a few short lanceoloid projections, the margins with prominent wing-like curved ascending shoulders, lateral walls 4-8 mm. thick, within smooth, shining; seeds 15-18 mm. long, ellipsoid; mesocarp forming in the apex of each carpel a cavern 15-27 mm. long, with aerenchyma of longitudinal fibers and pale membranes, the part of the basal mesocarp which remains is 2-7 mm. long.

Supplementary Description: Upright tree 5 m. tall; bark gray, rough; leaves 1.85-2 m. long, 8.6 cm. wide near the base, 6.2 cm. wide at the middle, coriaceous, U-sulcate, 2-pleated, shiny olive green above, pale green and apparently glaucous below, at midsection with 58 parallel secondary veins in each half, the tertiary veins obscure, the blade sword-shaped, tapering from base to the trigonous slender subulate apex, this at the point 10 cm. down 1.5 mm. wide, the base unarmed, pale; beginning at 12 cm. the margins with prickles 2-3 mm. long, 3-8 mm. apart, arcuate subulate, compressed, geniculate near the base, ascending, stramineous with dark brown tips; the midrib below unarmed for 24 cm.; at midsection the margins with prickles 1.2-1.8 mm. long, 6-11 mm. apart, arcuate stout
subulate, compressed, strongly ascending, dark maroon; the nearby midrib below with prickles 1-1.4 mm. long, 12-22 mm. apart, subarcuate subulate, compressed, appressed ascending, dark maroon; on the subulate apex the margins and midrib below with prickles 0.2-0.3 mm. long, 2-7 mm. apart, thick subulate ascending, maroon; infructescence with a solitary syncarp; phalanges 7.3-7.8 cm. long, 5.3-7.4 cm. wide, 3.8-4.3 cm. thick, broadly cuneiform, widest near the top, 5-6-angled, the apex rather low convex, lower sides flat, lateral sinuses narrow but extending down to beyond the middle, the upper 1/3 free, its sides smooth, shining, each lateral carpel with 1-3 angles and gently curving plane surfaces; carpels 6-11, radial, the marginal ones with apices hemispheric or oblately so, angled, and many of those on the phalange sides with a nearly vertical outer plane side rising to the stigma, and all with a concave platform 2-3 mm. wide, distal of the stigma and more or less level; inner carpel apices from 1/2 as large to as large as the outer ones; stigmas 2.5-4 mm. long, obdeltoid, elevated, oblique, running down the steep inner carpel face; proximal sinuses a deep crack running 3/4 way to valley bottom; central apical sinuses 4-6 mm. deep, wide V-shaped, straight; endocarp in the upper 3/7 and 25-26 mm. long, bony, dark brown mahogany colored, the central body ellipsoid, the apex with short lanceoloid projections over the seeds, the shoulders inframedian, wide sweeping upcurving and winglike, the upper surface with a semicircular profile, lateral walls above the shoulders 2-3 mm. thick, within smooth, shining, dark red mahogany colored; seeds 12-13 mm. long, ellipsoid, mesocarp forming in the apex of each carpel a cavern 15-28 mm. long, with aerenchyma of strong longitudinal fibers and pale membranes; basal mesocarp 30-35 mm. long, fibrous and fleshy.

Holotype: Eastern Polynesia, Fanning Island, on beach, Aug. 1924, W. B. Herms (FI). Type examined. Isotype (UC).

Specimens Examined: Pacific Equatorial Islands, Fanning Island, coral sand islet, 1 m. alt., April 21, 1934, H. St. John & F. R. Fosberg 14, 106 (BISH).

Discussion: Martelli did not state the location of the type and there is no implication in his publication to help one decide the question. Only a single phalange was collected. Later, this phalange was cut in two, and one half rests in Firenze, the other in Berkeley.

Martelli (p. 145) speculated on the origin of this drift fruit, saying, "It is highly probable that this characteristic Pandanus is not a native of Fanning Island, or of any of the neighboring small islands, and that the single drupe picked up on the beach originated on some larger island, and reached Fanning Island through the medium of ocean currents."

In an article on Australian Pandanus, Martelli (1933: 23) later evidently mentioned P. Hermesianus, inadvertently calling it P. fanningensis Martelli. He stated that he considered the species a waif, drifted to Fanning; that it belonged in the group of P. spiralis R. Br. of Australia. On rapid reading, it would seem that Martelli was reducing his own species to synonymy, but on careful reading it is clear that he said
Fig. 4. Pandanus Hermsianus Martelli, from holotype and isotype.

a, phalange, lateral view, X 1; b, phalange, half of longitudinal median section, X 1; c, phalange, half of apical view, X 1;
d, profile of phalange apex.
Fig. 5. Pandanus Hermsianus Martelli, from St. John & Fosberg 14,106.

a, phalange, lateral view, X 1; b, profile of phalange apex; c, phalange, longitudinal median section, X 1; d, phalange, apical view, X 1; e, carpel apex and stigma, X 4; f, half of leaf base, lower side, X 1; g, half of leaf middle, lower side, X 1; h, leaf apex, lower side, X 1.
that he considered the Fanning Island plant not native there, and to be of the same group of species as \textit{P. spiralis}.

\textit{P. spiralis} is known only by the type collection from Allen Island, of the Wellesley Group, Gulf of Carpentaria, northern Australia. Drift from there to Fanning Island in a direct line would be some 1,120 miles, and in a more probable circular route would be perhaps 2,000 miles. Such a voyage for a bit of flotsam would take years, and the prolonged soaking by sea water and the battering by stormy waves would cause much erosion on such a fruit as a \textit{Pandanus} phalange. Logs of \textit{Pseudotsuga} that drift the 2,000 miles from the Straits of Juan da Fuca, northwest America to \textit{Hawaii} take \(4\frac{3}{4}\) years for the voyage with a direct sea current, and arrive cleaned of the 15-30 cm. of bark and with the wood of the trunk washed and polished till it looks and feels like satin.

Having been found only on the beach of Fanning Island, this single known phalange of \textit{P. Hermsianus} may have arrived there by sea drift after a short or a long voyage. No such species is known on any of the adjacent Line Islands. If by a long voyage, it should be evidenced by an extreme degree of weathering. On the contrary, the free upper part of the phalange of the holotype (except where damaged or destroyed by clumsy sawing), is clean, fresh-looking, and not weathered. The stigmas are well preserved, only the brown papillose surface being mostly gone. The surface of the carpel apices is waxy and shiny, and unweathered, not at all eroded. This part could not have been in sea water for several years. The basal mesocarp is represented only by the bases of its fibers, the fleshy and the rest of the fibers having completely vanished. When ripe this tissue between the fibers is soft and juicy. In a few days in the water it would all float away. If undisturbed on the land surface, it would soon dry and largely fall away. However, the phalange has not been undisturbed. The fibers of the basal mesocarp which once attached it to the syncarp core, were of equal length, and the phalange base was originally truncate, now the fibers have been trimmed to a length of 2-7 mm., close to the base of the bony endocarp and conforming exactly to its rounded basal profile. Weathering or erosion would not trim off the fibers in this manner. The writer's long field experience and that with hundreds of species of the section \textit{Pandanus}, has taught him that the basal fibers are long enduring, and that under nearly all circumstances all (or most of them) are of equal length and persist, and show the position of the flat base and the original length of the phalange.

On the coral atolls, if ripe phalanges fall to the ground and escape man, they are quickly eaten by animals. On the Line Islands, such as Fanning, this is usually done by the swarms of hermit crabs. Less commonly they could be eaten by rats, or coconut crabs, or other crabs, or birds, or ants, etc. Such animals bite or chew the flesh from the base, but do not leave the basal fibers in a spiral twist, as do humans. It is clear that this phalange grew on Fanning Island, ripened, fell to the ground, where its soft flesh and the fiber tips were eaten or chewed off by some animal.

Fanning Island was uninhabited when discovered in 1798, but there are archaeological stone structures indicating occupation for some period by
early Pacific native voyagers, and coconuts had been introduced and established. Its present status is different. In the 19th Century it was settled and developed as a large copra plantation. Laborers are brought in under short term contract from the Gilbert Islands, and they live in a permanent Gilbertese village. That the Gilbert Islanders have brought some of their crop plants with them and successfully cultivated them, is evidenced by the growth by their village of Cyrtosperma Chamissonis, and one, large fruited, edible cultivar of Pandanus, called "kaina."

It is known that the Gilbert Islands is one of the two areas with a large number of edible cultivars of Pandanus. The many scores of such cultivars in the adjacent Marshall Islands are now quite well known, due to the investigations of Kanehira, St. John, and especially by B. C. Stone. The knowledge of the cultivars in the Gilbert Islands is still rudimentary, resting mostly upon the recording by anthropologists of the vernacular names of the varieties. The estimates of the total of varieties varies from 160 to 194. All of the varietal names are different from those in use by the Marshallese. Of all these, only one has been described, (as a species by Martelli). There are but few collections available even yet. The writer (in 1966) knew only nine of these cultivars. One of them, the cultivar "kaina" was collected in the Gilbertese village on Fanning and from the islets with copra plantations. Cable Islet, however, had a natural stand of brush and trees. The Pandanus here formed a small, dense grove, close to the lagoon beach, and was in undisturbed natural growth. The phalanges that the writer gathered there in 1934 were not quite ripe, as the apex was green, but the contiguous lower sides were yellow and soft. Drawings and measurements were made of this fresh material. The phalanges were from 7-7.8 cm. long, 5-7.4 cm. wide, 3.8-4.4 cm. thick. The one here illustrated is one of average size. It differs from the type of P. Hermsianus in being longer and narrower, 7 x 6.3 cm., but the apex has the same big, rounded carpel apices, wide valleys 4-6 mm. deep. The basal mesocarp is longer, being complete and undamaged. There are two larger phalanges in this collection, 7.1 and 7.3 cm. wide, and they even more closely resemble the single phalange of P. Hermsianus which was 10 cm. wide, and of 17 carpels. So close is the resemblance that the author sees no reason to keep them apart. He now gives a supplementary description, based upon adequate material, and establishes P. Hermsianus in the status of a well known, valid species, evidently endemic to Fanning Island.

A later discussion of this species by B. C. Stone appeared in (1968 (=1969): 92), under a heading, "Disposition of Pandanus Hermsianus Martelli." He deprecates the publication of a species based upon a single damaged phalange; agrees with Martelli that it resembles Australian broader-than-long phalanges; and suggests that the basal mesocarp may have been chewed off by animals, or cut off by man. He concludes "In other words, it seems to me that this could well be a drift phalange from the Marshall or Gilbert Islands. I suggest it is probably one of the large cultivars of Pandanus fischerianus Martelli, such as CV. 'edwaan-en-an-Nelu' of the Marshall Islands. I very much doubt that it represents a distinct species. In any case it is an example of unnecessary and unwise description and nomenclature." To this it can be agreed that the type specimen was too meager, but Stone does not report examining the holotype.
in Berkeley or the clastotype in Firenze. There is nothing wrong with the nomenclature of the species. The cultivar 'edwan-en-an-Nelu' has phalanges 10-12 cm. long, and the endocarp usually in the upper third of the phalange, the leaves 2 m. long and 8 cm. wide. In these and other characters it differs from *P. Hermsianus*.

As the writer has demonstrated, the holotype of *P. Hermsianus* has the stigmas and the apex of the phalange fresh and unharmed, so that it cannot have drifted in the ocean the thousands of miles from Australia or the Gilbert or the Marshall islands.

Now there is new evidence on the problem, due to the collection of adequate material of a native *Pandanus*, St. John & Fosberg 14,106, from Fanning Island. It was gathered on Cable Islet, a different and distant islet from Napia, the one with the Gilbertese village.

From these data it is deduced that *P. Hermsianus* is a wild species, endemic to Fanning Island.
Pandanus tectorius Warb., var. novi-caledonicus Martelli, cv. 'KAINA',
cultivar nov.

Figs. 6 and 7.

Nom. Vern.: "kaina" (Gilbertese).

Diagnosis of Holotype: Tree 3.2 m. tall, branched; leaves 1.62
(+0.27?) m. long, 7 cm. wide (at perhaps 12 cm. from the base), 6.8 cm.
wide near the middle, thickish coriaceous, above shining green, below pale
green and apparently glaucous, U-sulcate, 2-pleated, at midsection with 50
parallel secondary veins in each half, the tertiary cross veins faintly
visible on the upper side towards the base, forming short oblong meshes,
the blade sword-shaped, tapering from the base to the slender apex (the tip
lost), the base not preserved; near the base the margins with prickles
2.8-3.6 mm. long, 5-14 mm. apart, arcuate subulate, ascending, stramineous,
with very slight red tips; the midrib below unarmed for about 32 cm., then
with prickles 3 mm. long, 25-35 mm. apart, arcuate subulate, similar, but
the first one strongly reflexed, and the following ones appressed
ascending; at midsection the margins with prickles 2-3 mm. long, 5-12 mm.
aper, subarcuate subulate, strongly ascending, stramineous below but red-
tipped; the nearby midrib below with prickles 2-2.2 mm. long, 12-22 mm.
apart, arcuate subulate, compressed, almost appressed ascending,
stramineous with red tips; syncarp not preserved; phalanges 12-13 cm. long,
7-8 cm. wide, 5.9-6.7 cm. thick, broadly pyriform, with 4 major angles and
1-2 secondary ones on each marginal carpel, the lower 2/3 fleshy enlarged,
deep orange red, when dry with a slight rounded shoulder, upper 1/3 free,
the sides smooth, shining, the apex high convex; carpels 10-13, the
marginal ones with their apices obliquely convex, sloping in conformity
with the convexity of the phalange apex, each with a shallow concave
platform 4-12 mm. wide, distal of the stigma, the interior apices 1/4-2/3
as large as the marginal, low convex, symmetrical; stigmas 3.5-5 mm. long
or wide, apical, elevated and oblique, oval to reniform or even truncate,
brown, papillose; proximal sinuses running 1/3-1/4 way to valley bottom;
central apical sinuses 1-3 mm. deep, nearly straight, very wide; endocarp
at upper 2/5 and 3 cm. long, bony, mostly stramineous, saucer-shaped, with
a central hemispheric mound, the lateral walls 17-22 mm. thick, and only
around the seed cavity brown, within shining, spirally ridged; seed
cavities 25-27 mm. long, narrowly cylindric, with many fibers, apparently
without seeds and sterile; mesocarp forming in the apex of each carpel a
cavern 16-25 mm. long, filled with aerenchyma of a few fibers and a few
longitudinal white membranes; basal mesocarp 7.5-8 cm. long, fibrous and
with much edible flesh.

Pacific Ocean, Line Islands, Fanning Island, Teuru Mangaro Islet,
planted at village, n. e. end of island, July 2, 1965, C. R. Long 3, 524
(BISH).

Discussion: The syncarp as seen in a photograph is elliptic-subglobose
and about 31.5 cm. in diameter. The photographs were taken by Prof. W. B.
Herms in Aug. 1924 in the Gilbertese village. This cultivated variety,
Fig. 6. Pandanus tectorius Warb., var. novi-caledonicus Martelli, cv 'KAINA', from holotype. a, phalange, lateral view, X 1; b, phalange, longitudinal median section, X 1; c, profile of phalange apex.
Fig. 7. Pandanus tectorius Warb., var. Novi-caledonicus Martelli, cv 'KAINA', from holotype. a, phalange, apex, X 1; b, half of leaf base, lower side, X 1; c, leaf middle, lower side, X 1; d, leaf apex, lower side, X 1.
seen in 1924, is obviously the same as that collected by Long in the same village in 1965.

No vernacular name for this variety was recorded by the collector, but it was a tree cultivated in the village by the Gilbertese laborers. It is obvious that the tree was introduced from their home land, one of the atolls of the Gilbert Islands. There the Pandanus is an important, staple food. Numerous cultivated varieties have been developed, and for them the native use nearly 200 vernacular names. Not knowing the true cultivar name for this one, it cannot be used, hence the one announced here is arbitrarily chosen. "Te kaina" means the Pandanus tree, in Gilbertese speech. So, "kaina", the general name for the whole group, is here used as the new cultivar name. The cultivar is here attached to a somewhat similar wild plant, described as P. tectorius Warb., var. novi-caledonicus Martelli, a native of New Caledonia.

This plant really belongs in our list of cultivated plants.
GRAMINEAE


Cenchrus echinatus L. A weed, *St. John & Fosberg* 14, 117; *Russell & Tsuda*.

Cynodon Dactylon (L.) Pers. In the settlement lawn, fide *Christophersen*.


Eragrostis tenella (L.) Beauv. ex R. & S. Weed at the settlement, *Long* 3, 560; *Russell & Tsuda* 36. This is *E. amabilis* of Christophersen's report.

Lepturus repens (Forst. f.) R. Br. Arundel; Ball 7; Christophersen 18; *Long* 3, 506; 3, 538; 3, 571; 3, 553; *Huber & Sibley* 3, 510; *Russell & Tsuda* 13; 14.


CYPERACEAE

Cyperus rotundus L. Weed. *Russell & Tsuda*.

Fimbristyliis atollensis St. John. *Ball* 8; *Christophersen* 17; *Long* 3, 512; 3, 514; 3, 552; *Russell & Tsuda* 49.

PALMAE

Cocos nucifera L. Cultivated, abundant.

URTICACEAE

Laportea ruderalis (Forst. f.) Chew. Weed. *Ball* 10; *Christophersen* 20; *St. John & Fosberg* 14, 107; 14, 112; *Russell & Tsuda* 2.

AMARANTHACEAE

NYCTAGINACEAE

Boerhavia diffusa L., var. tetrandra (Forst. f.) Heimerl. Ball 5; 16.

AIZOACEAE

Sesuvium Portulacastrum (L.) L. Long 3, 533; 3, 591; Huber & Sibley 3, 578; Russell & Tsuda 7.

PORTULACACEAE

Portulaca lutea Soland. Christophersen 22.
P. oleracea L. Weed. Russell & Tsuda 12.

LAURACEAE

Cassytha filiformis L. Long 3, 534; 3, 575; Russell & Tsuda 39.

CRUCIFERAE

Lepidium bidentatum Montin. Arundel; Christophersen 16; St. John & Fosberg 14, 108; Long 3, 554; Russell & Tsuda. Formerly determined as L. piscidium, and L. owaihiense.

CRASSULACEAE


LEGUMINOSAE

Cassia occidentalis L. Weed, fide Christophersen.
Crotalaria retusa L. Weed. Long 3, 516.
Desmodium triflorum (L.) DC. Weed, fide Christophersen.
SIMAROUBACEAE

Suriana maritima L. Reported by Streets, fide Christophersen.

EUPHORBIACEAE


E. hirata L. Weed. Ball 17; Long 3, 542. As E. pilulifera 1, fide Arundel.

E. prostrata Ait. Weed. fide Christophersen.

Phyllanthus amarus Schum. Weed. Ball 2; Long 3, 544; Russell & Tsuda 9. Formerly as P. niruri.

TILIACEAE

Triumfetta procumbens Forst. f. Arundel; Ball 13; Russell & Tsuda.

MALVACEAE

Malvastrum coromandelianum (L.) Garcke. Weed. fide Christophersen.

Sida fallax Walp. Arundel; Ball 15; Russell & Tsuda 8; 33.

ASCLEPIADACEAE

Asclepias curassavica L. Weed. Arundel, fide Hemsley, 1885.

CONVOLVULACEAE

Ipomoea brasiliensis (L.) Sweet. Russell & Tsuda 51.

I. tuba (Schlecht.) Don. Arundel; Long 3, 540; Russell & Tsuda 11. Previously called I. glaberrima, and I. grandiflora.
BORAGINACEAE

*Cordia subcordata* Lam.  *Ball* 12; *Russell & Tsuda* 52.


*Messerschmidia argentea* (L.) Johnst. *Ball* 1; *Long* 3, 520. Formerly called *Tournefortia argentea*.

VERBENACEAE

*Stachytarpheta urticaefolia* (Salisb.) *Sims*. Weed. *Russell & Tsuda* 68.

Rubiaceae


GOODENIACEAE

*Scaevola Taccada* (Gaertn.) Roxb. *Ball* 3; *St. John & Fosberg* 14, 116. Formerly called *Scaevola frutescens*.

COMPOSITAE


*Erigeron bonariensis* L. Weed. *fide Christophersen*. Formerly called *E. albidus*.


*Sonchus oleraceus* L. Weed. *fide Christophersen*.

*Synedrella nodiflora* (L.) Gaertn. Weed. *Ball* 9; *Russell & Tsuda* 44.

ORNAMENTALS AND FOOD PLANTS IN CULTIVATION

ARAUCARIACEAE

Araucaria sp.  Russell & Tsuda 57.

ARACEAE


PALMAE

Phoenix dactylifera L.  Observed by Russell & Tsuda.

BROMELIACEAE


COMMELINACEAE

Rhoeo spathacea (Sw.) Stearn.  Russell & Tsuda 28.

LILIACEAE

Crinum asiaticum L.  Russell & Tsuda 24.

Gloriosa superba L.  Russell & Tsuda 70.

TACCACEAE


MUSACEAE

Musa paradisiaca L.  Observed by Russell & Tsuda.

CASUARINACEAE

Casuarina equisetifolia Stickm.  Russell & Tsuda 22.
MORACEAE

Ficus sp. Arundel, fide Hemsley (1885: 116); Christophersen (1927: 43).

POLYGONACEAE
Antigonon leptopus H. & A. Russell & Tsuda 73.

NYCTAGINACEAE
Bougainvillea sp. Russell & Tsuda 67.
Mirabilis Jalapa L. Russell & Tsuda 71.

CRASSULACEAE
Kalanchoe pinnata (Lam.) Pers. Russell & Tsuda 72. Also naturalized.

LEGUMINOSAE
Bauhinia monandra Kurz. C. R. Long 35B.
Caesalpinia pulcherrima (L.) Sw. Russell & Tsuda.
Leucaena leucocephala (Lam.) de Wit. Russell & Tsuda 47.

RUTACEAE
Citrus aurantifolia (Christm.) Swingle. Observed by Russell & Tsuda.

EUPHORBIACEAE
Acalypha Wilkesiana Muell.-Arg. in A.DC. Russell & Tsuda.
Codiaeum variegatum (L.) Bl., var. pictum (Lodd.) Muell.-Arg. Russell & Tsuda 65.
Manihot esculenta Crantz. Russell & Tsuda 64.

ANACARDIACEAE
Mangifera indica L. Observed by Russell & Tsuda.
MALVACEAE

Hibiscus rosa-sinensis L. Long 3, 584.

GUTTIFERAE

Calophyllum Inophyllum L. Long 3, 583.

CARICACEAE


PASSIFLORACEAE

Passiflora foetida L., var. hispida (DC.) Killip. Long 3, 497; Russell & Tsuda 29.

COMBRETACEAE

Terminalia Catappa L. Observed by Russell & Tsuda.

MYRTACEAE

Psidium Guajava L. Christophersen (1927: 43).

ARALIACEAE


Polyscias Scutellaria (Burm. f.) Fosb. Russell & Tsuda 25.

OLEACEAE

Ligustrum sp. Russell & Tsuda 78.

APOCYSACEAE

Nerium Oleander L. Russell & Tsuda 85.

Plumeria rubra L., forma. Russell & Tsuda 43.
VERBENACEAE


Lantana Camara L. Russell & Tsuda 79.

LABIATAE

Ocimum Basilicum L. St. John 14, 113.

SOLANACEAE

Capsicum annuum L. Observed by Russell & Tsuda.

Nicotiana Tabaccum L. Arundel, fide Hemsley (1885: 116).

SCROPHULARIACEAE

Russelia equisetiformis L. Russell & Tsuda 76.

BIGNONIACEAE


Spathodea campanulata Beauv. Observed by Russell & Tsuda.

RUBIACEAE

Guettarda speciosa L. St. John & Fosberg, in 1943, a single cultivated tree at the settlement; Russell & Tsuda 26.

Morinda citrifolia L. Christophersen (1927: 43).

CUCURBITACEAE

Cucurbita Pepo L. Observed by Russell & Tsuda.

COMPOSITAE

Gaillardia pulchella Foug., var. picta (Sweet) Gray. Russell & Tsuda.

Zinnia sp. Observed by Russell & Tsuda.
LITERATURE CITED


