Paul L. Jokiel

HIG-70-23

FANNING ISLAND EXPEDITION, JANUARY 1970

K. E. CHAVE
Principal Investigator

in collaboration with the following

University of Hawaii
Department of Oceanography

BRENT S. GALLAGHER
F. I. GONZALEZ, JR.
DONALD C. GORDON, JR.
GEORGE J. KRASNICK
J. E. MARAGOS
KENNETH J. ROY
HAROLD G. SCHIESSER
GLENN L. SHEPHERD
K. M. SHIMADA
STEPHEN V. SMITH
E. D. STROUP

Department of Botany

ROBERT DeWREEDE
MAXWELL S. DOTY
ROBERT O. FOURNIER

Department of Zoology

E. H. (NEIL) CHAVE
ERIC B. GUINTHER
WILLIAM A. GOSLINE
RICHARD C. WASS

Department of General Science

E. ALISON KAY

Hawaii Institute of Marine Biology

DORA M. BANNER
and
Bernice P. Bishop Museum, Honolulu, Hawaii
HELEN A. RANDALL

FINAL REPORT

NOVEMBER 1970

Prepared for
NATIONAL SCIENCE FOUNDATION
UNDER GRANTS GA-10890 AND GB-15581

HAWAII INSTITUTE OF GEOPHYSICS
UNIVERSITY OF HAWAII

1907

Frontispiece. View of Fanning Island, looking north, with English Harbor in the middle distance. (Photograph by E. H. (Neil) Chave.)

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K. M. Shimada
Stephen V. Smith
E. D. Stroup

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Approved by Director
George P. Woollard

Date: 30 November 1970

CONTENTS

FOREWORD

INTRODUCTION

It is an exciting experience to lead 26 faculty and students, from 5 separate departments, on a expedition into an essentially unknown area. We found we could work together, talk together, and learn together from the environment and from each other. The following reports attest to the success of our efforts.

The expedition sailed for Fanning Island aboard the R/V MAHI on 28 December 1969, arriving 2 January 1970. Three members joined us by plane on 12 January, and four left us on 13 January the same way. We sailed for home on 25 January, arriving in Honolulu on the 31st.

The work of the expedition was divided into two phases: a sea phase and an island phase. The sea phase (NSF Grant GA-10890), conducted by E. D. Stroup and S. V. Smith, involved measurements in the South Equatorial Current and Undercurrent, and measurement of the contribution of detritus from Fanning Island to the open sea.

The island phase (NSF Grant GB-15581), involving most of the personnel, was largely aimed at the physical oceanography of the lagoon, biogeographical problems, and productivity studies.

Valuable support for all work was supplied by Ray Jeffcott, fixer of everything; Deetsie Chave and Gene Gilley, cooks; and Mike Aurnig, radioman. Phillip Palmer and John Fleetwood, managers of the Burns-Philp copra plantation provided invaluable assistance. Martin Vitousek supplied the plane. Phillip Helfrich, of the Hawaii Institute of Marine Biology, lent us boats and equipment. The crew of the R/V MAHI provided excellent support. Finally. W. R. Coops of the Research Corporation of the University of Hawaii cut through much red tape and got us supplied in the last few hectic weeks, when Hawaii was in the midst of a lengthy shipping strike, and it was Christmas time.

Fanning Island

Fanning Island is a beautiful atoll in the Line Islands chain at $3^{o}55'$N, $159^{o}23'$W. The island was discovered in 1798 by the American whaler BETSY, under captain Edmund Fanning, at which time the island was uninhabited. Emory (1934, 1939) however reports inhabitation in the 16th century. Copra and guano were produced on the island on and off between 1848 and 1935 when it was purchased by Burns-Philp, Ltd. Since then the plantation has exported between 600 and 1000 tons of dried copra per year.

British Cable and Wireless established a cable station on Fanning in 1902 as a link between British Columbia and Suva. The greatest excitement ever at Fanning was the attack by a German warship (under the French flag) in September 1914, during which the cables were cut and the batteries destroyed. The cable station was abandoned in 1963. In 1966 the University of Hawaii leased the station land and its fifteen buildings the Gilbert and Ellice Islands Colony. The University has since added a 2500-foot airstrip on the Island.

Fanning Atoll is composed of three islands enclosing a shallow lagoon. It is about 12 miles long and 6 miles wide (See footnote below). Although the island is inhabited by some 600 Gilbertese copra workers, there is very little influence of man on the waters of the island. There is no effluent from the copra operations, and relatively little fishing due to a constant threat of ciguatera poisoning. Because of the unspoiled nature of the environment, it is an ideal area for many types of studies.

Fanning Island and the other islands of the Line Island chain--Palmyra, Washington, and Christmas--are of great importance biogeographically, being the easternmost equatorial islands in the Pacific.

All in all, Fanning is an ideal place for many types of studies. It is beautiful, isolated, yet easily accessible by air, and the Cable station buildings are in good condition, with electricity and fresh water available, as well as cooking and sleeping facilities.

Acknowledgment

The Expedition was supported by funds from the National Science Foundation, under Grants GA-10890 and GB-15581.

Members of the Expedition

F. M. Aurnig. Marine Technician, Hawaii Institute of Geophysics.
C. J. Berg. Graduate Student, Department of Zoology.
K. E. Chave. Professor of Oceanography.
Edith H. Chave. Graduate Student, Department of Zoology.
R. E. De Wreede. Graduate Student, Department of Botany.
B. S. Gallagher. Assistant Professor of Oceanography.
E. G. Gilley. Marine Technician, Hawaii Institute of Geophysics.
F. I. Gonzalez, Jr. Graduate Student, Department of Oceanography.
D. C. Gordon, Jr. Assistant Professor of Oceanography.
W. A. Gosline. Professor of Zoology.
E. B. Guinther. Graduate Student, Department of Zoology.
R. A. Jeffcott. Marine Technician, Hawaii Institute of Geophysics.
E. Alison Kay. Professor of General Science.

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[1] See Fig. 1 facing p. 20 this report.

G. S. Key. Graduate Student, Department of Zoology.
G. J. Krasnick. Graduate Student, Department of Oceanography.
G. L. Petersen. Graduate Student, Department of Zoology.
K. J. Roy. Assistant Professor of Oceanography.
H. G. Schiesser. Graduate Student, Department of Oceanography.
G. L. Shepherd. Graduate Student, Department of Geosciences.
K. M. Shimada. Graduate Student, Department of Oceanography.
S. V. Smith. Graduate Student, Department of Oceanography.
E. D. Stroup. Associate Professor of Oceanography.
J. P. Villagomez. Student, Department of Botany.
M. J. Vitousek. Associate Geophysicist, Hawaii Institute of Geophysics.
P. M. Volk. Graduate Student, Department of Oceanography.
R. C. Wass. Graduate Student, Department of Zoology.

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Emory, Kenneth P. 1934. Archaeology of the Pacific Equatorial Islands. B. P. Bishop Museum 123, 43 p.

_______________. 1939. Additional notes on the Archaeology of Fanning Island. B. P. Museum Occ. Pap. 15, 179-189.

The editorial assistance provided by Mrs. Ethel McAfee in the preparation of this report for publication is greatfully acknowledged.

K. E. Chave

30 November 1970

TIDES AND CURRENTS IN FANNING ATOLL LAGOON

B. S. Gallagher, K. M. Shimada,
F. I. Gonzalez, Jr., and E. D. Stroup

Department of Oceanography and Hawaii Institute of Geophysics

As part of the Fanning Island Expedition 1970, selected physical studies were conducted in the atoll lagoon. The major effort was the measurement of volume, salt, and heat transports through the three main atoll openings over a 24-hour period. In addition, lagoon and ocean tides were recorded, and a cursory survey was made of circulation in a small, reef-enclosed pond within the lagoon.

TRANSPORT STUDY

Fanning Island is a roughly oval atoll whose lagoon, although almost entirely enclosed, does exchange water with the surrounding ocean. Tidal flow in and out of the lagoon occurs at four locations and amounts to roughly 5 percent of the lagoon volume over a semidiurnal cycle. About 90 percent of this exchange takes place at English Harbor, through a channel with a maximum depth of approximately 8.5 m and a minimum width of 290 m. Opposite English Harbor, on the east side of the atoll, is a shoal opening (Rapa Pass) which handles about 2 percent of the total exchange. A similar channel to the north (North Pass) accounts for roughly 5 percent. Air photos show one additional, meandering route which may or may not lead from the lagoon to the sea. This possible fourth opening about 5 km along the south shore from Rapa Pass, was ignored in our study.

Exchange between ocean and lagoon was monitored for 24 hours, starting at local noon on 7 January 1970. Current velocity, temperature, and salinity were recorded at each of the three passes.

Both North and Rapa passes were treated in simple fashion. In each case, a straight section was established by stringing a cross-channel line, along which bottom topography was measured. (At North Pass, there is, in addition to a main channel, an expanse of shoals which uncover at low water. This was ignored--with an estimated maximum, resulting local volume transport error of 13 percent.) A single station was chosen at a point along the section that appeared to be in the main flow (see Figs. 1 and 2). At this location, current velocity, temperature, and salinity were sampled each hour, within 0.5 m of the surface. Water level was read hourly from a tide staff mounted in a sheltered spot near shore. Figures 1 to 3 show the measurements. The various transports through these passes were computed by assuming the measured parameters to be constant over the channel cross sections.

Flow through English Harbor channel was sampled in far greater detail because it was expected to be overwhelmingly important in the total-exchange picture. H. O. Publication 80 reports that currents in the channel exceed 5 knots. Taking measurements from a skiff would be very difficult at best in such a flow. Consequently, transports were monitored along a semicircular section enclosing the lagoon end of the channel and through which a more moderate flow could be expected. Figure 4 shows the section and a smoothed fathometer trace along it. Anchored buoys were emplaced at stations 1 to 6. The section was traversed continuously by a skiff which was made fast to each buoy in turn. Seventeen cycles of measurements were completed during the 24-hour study. At each buoy, current velocity, temperature, and salinity were measured at the depths shown in Figure 4. These data were integrated over the cross section to obtain transport figures.[1] Averages of all the temperature and salinity measurements at buoys 2, 3, and 4 for each measurement cycle are presented in Figure 5, along with the volume transport through the entire channel.

A recording current meter was later placed near the surface at buoy 3, the site of strongest flow. The resulting record is shown in Figure 6.

RESULTS OF THE TRANSPORT STUDY

Volume

Currents through the channel at English Harbor display an interesting pattern. During each period of inward flow, a jet develops and extends into the lagoon from the channel itself. The jet appears at buoys 2, 3, and 4, where speeds exceeding 3 knots can be found. On either side of the base of the jet, eddying motion, which can be observed visually, appears in the measurements of volume transport at stations 1, 5, and 6. During the ebb, however, there is outward flow at all locations across our section, funnelling into the channel. Figure 7 illustrates these patterns in the volume transports at each buoy. The same jet-like flow also develops on the seaward side of the channel during ebb and can often be seen from shore. Another noteworthy feature of the current is its rapid reversal, with relatively short periods of weak flow between strong ebb and strong flood. This indicates that the lagoon has a nonlinear response to tidal excitation. The presence of non-tidal overtones is seen in the current and lagoon tide records displayed together in Figure 6. As one would expect, the current shows strong relation to the tide's

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[1] Details of all calculations, lists of instruments used, and a description of the buoy-anchoring method are given in the appendix at the end of this paper.

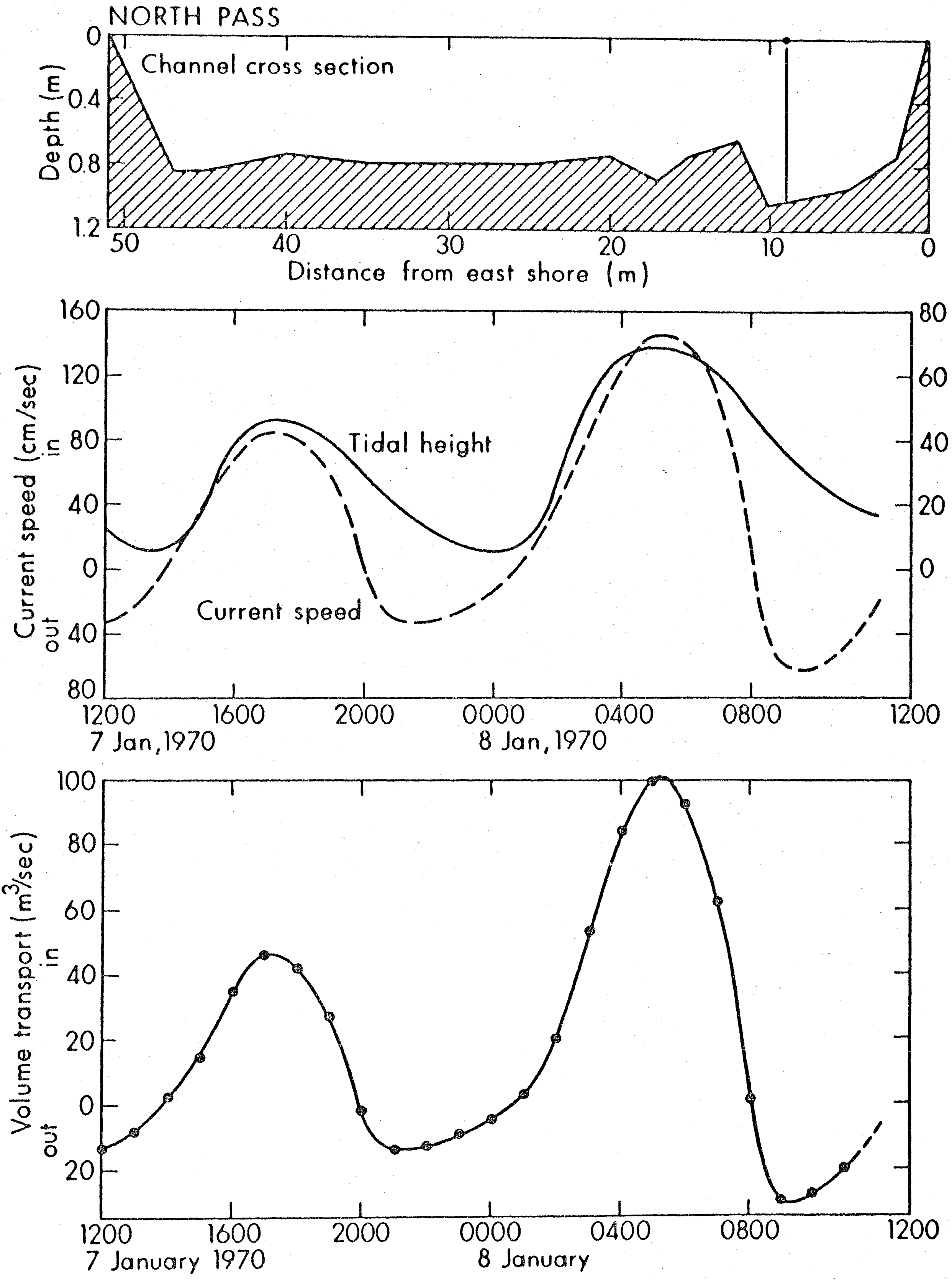

Fig. 1. Channel cross section showing station position (solid dot and vertical line), tidal height and current speed, and volume transport for North Pass during the 24-hour transport study. Dense patches of the algae *Turbinaria* that nearly reach the surface at low tide are located between 20 m and 40 m from the east shore. Cross-sectional depths are relative to a tidal height of; 13 cm. Absolute sea level is arbitrary.

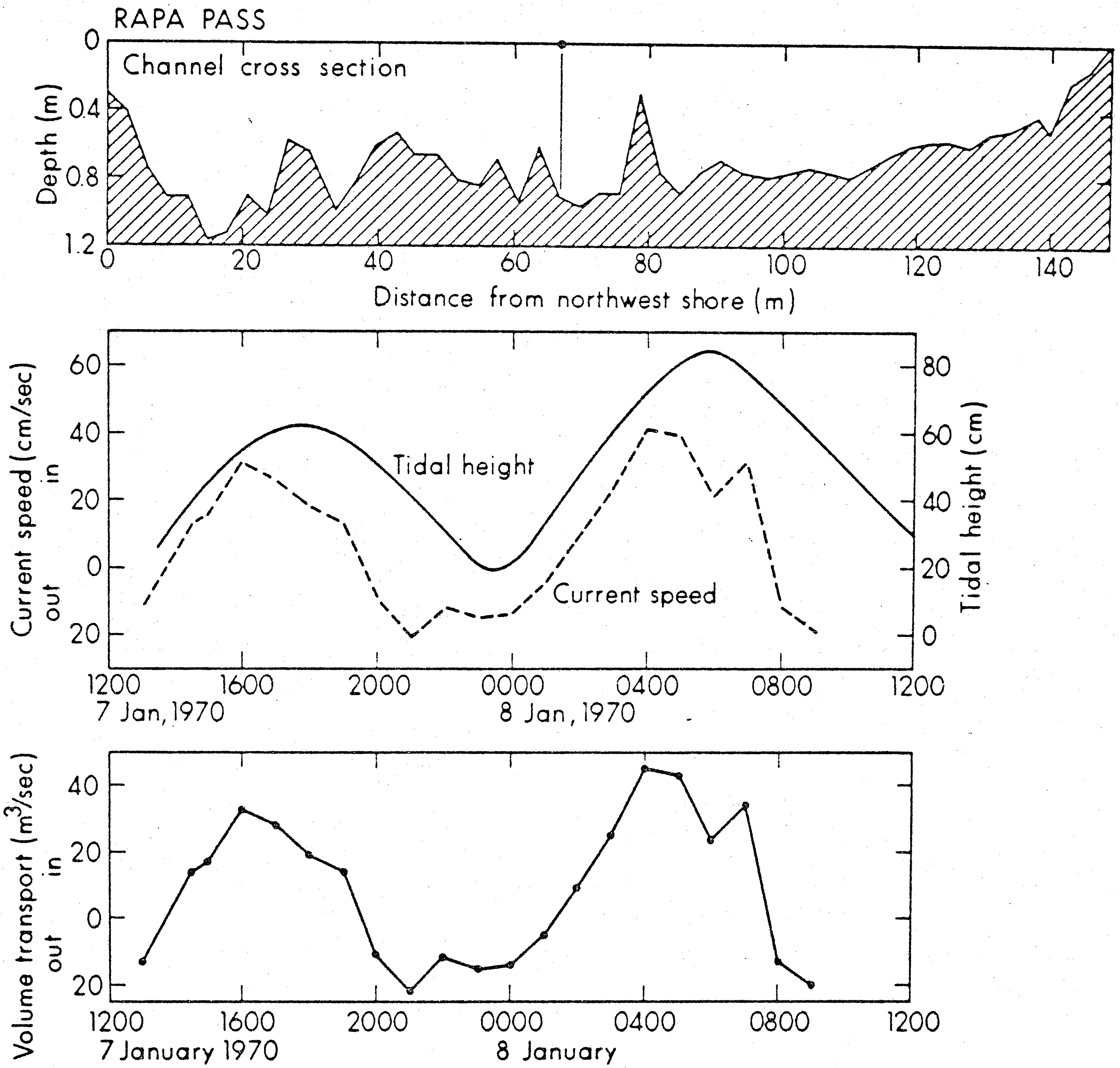

Fig. 2. Channel cross section with station position (solid dot and vertical line), tidal height and current speed, and volume transport for Rapa Pass during the 24-hour transport study. Cross-sectional depths are relative to a tidal height of 38 cm. Absolute sea level is arbitrary.

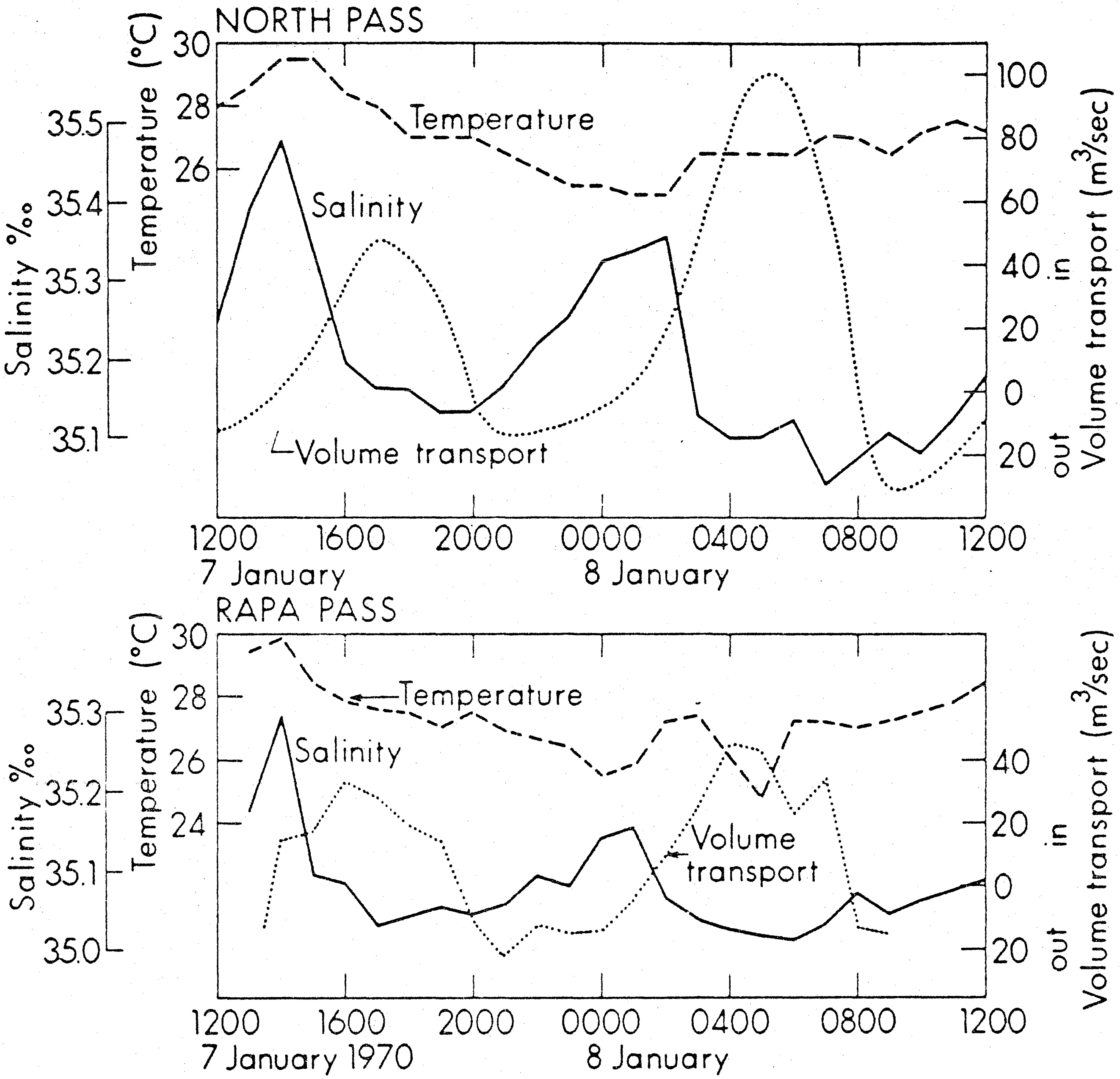

Fig. 3. Salinity, temperature, and volume transport for North and Rapa passes during the 24-hour transport study.

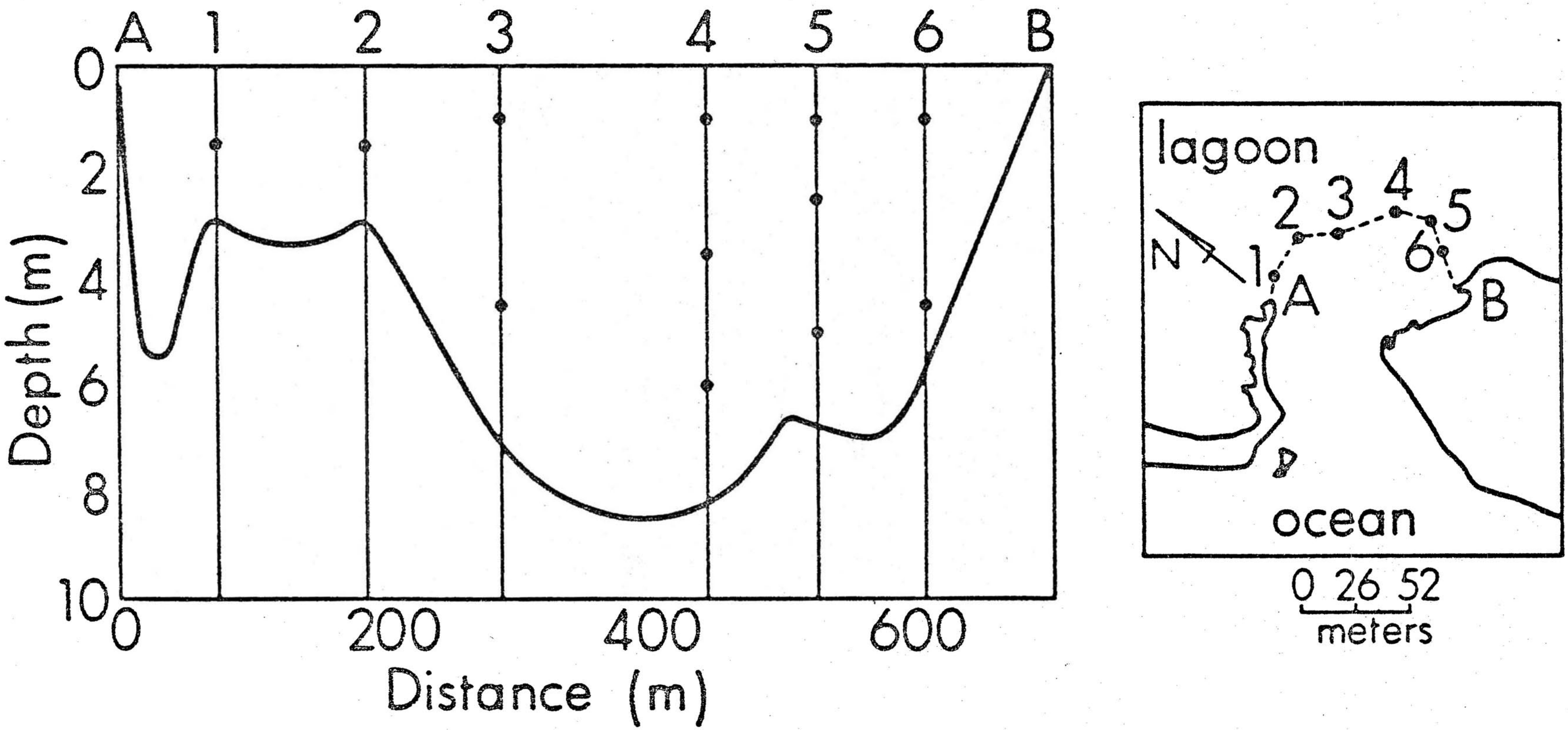

Fig. 4. Smoothed channel cross section (left) and buoy locations (right) for English Harbor channel. Depths (in meters) at which measurements were most often taken during the 24-hour transport study are indicated for each buoy.

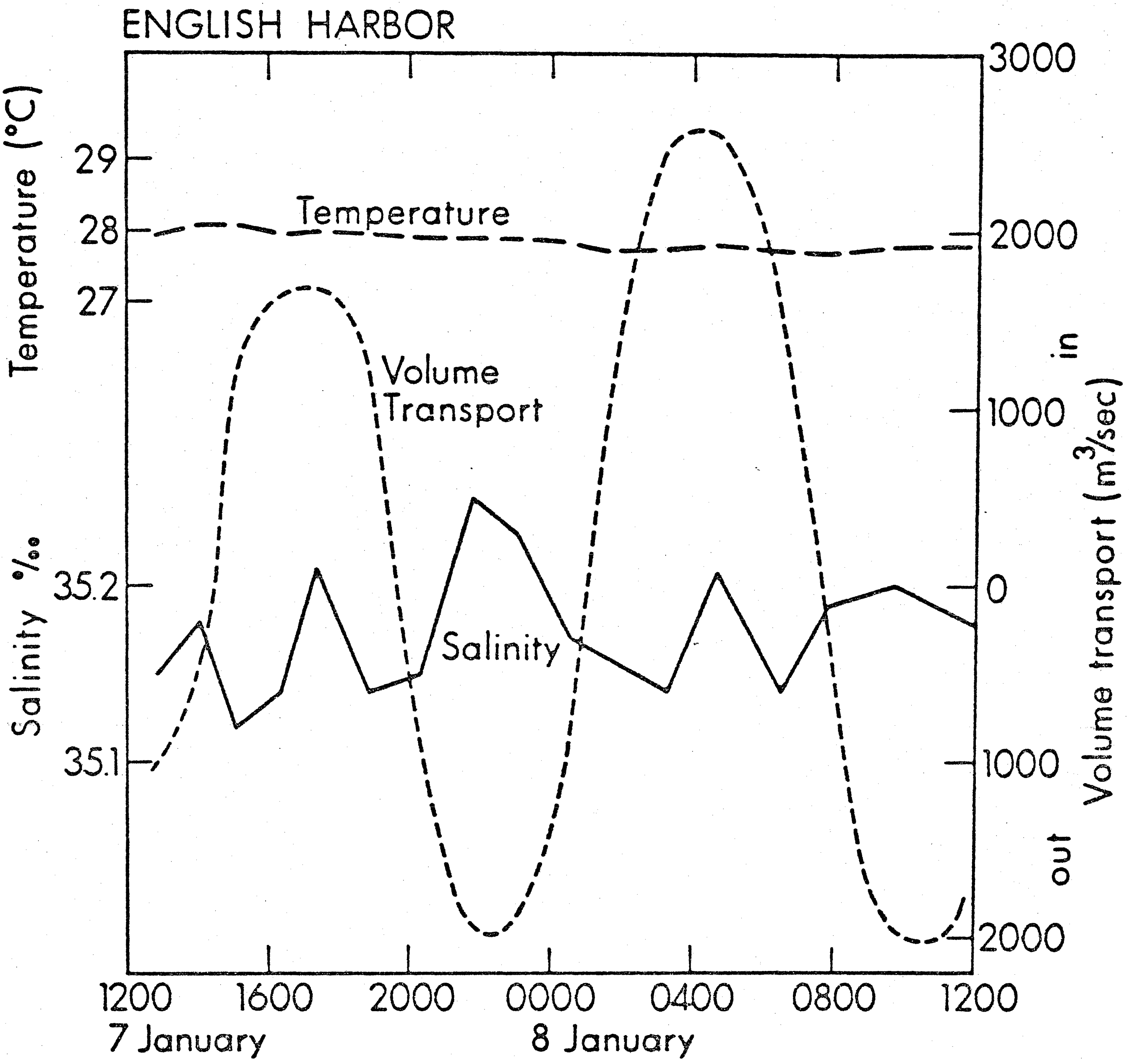

Fig. 5. Averages of the salinity and temperature measured at buoys 2, 3, and 4, English Harbor channel, and volume transport across the entire channel, during the 24-hour transport study.

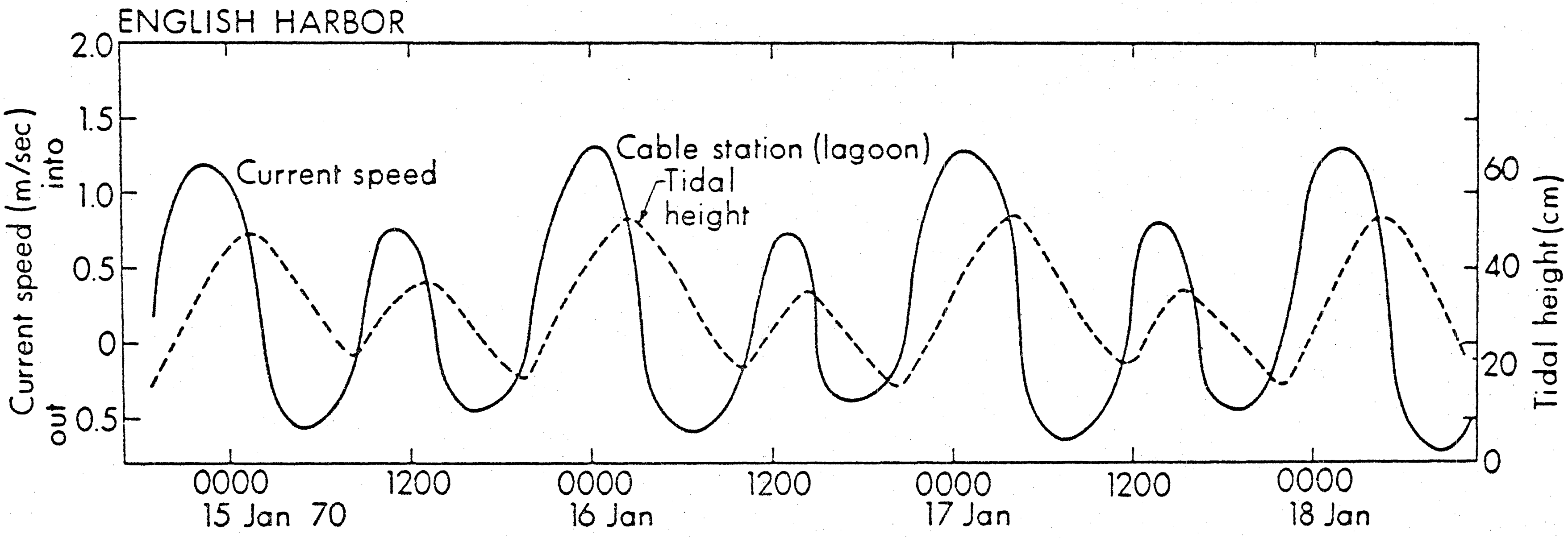

Fig. 6. Aanderaa current meter record at buoy 3, English Harbor channel, and lagoon tide. Absolute sea level is arbitrary.

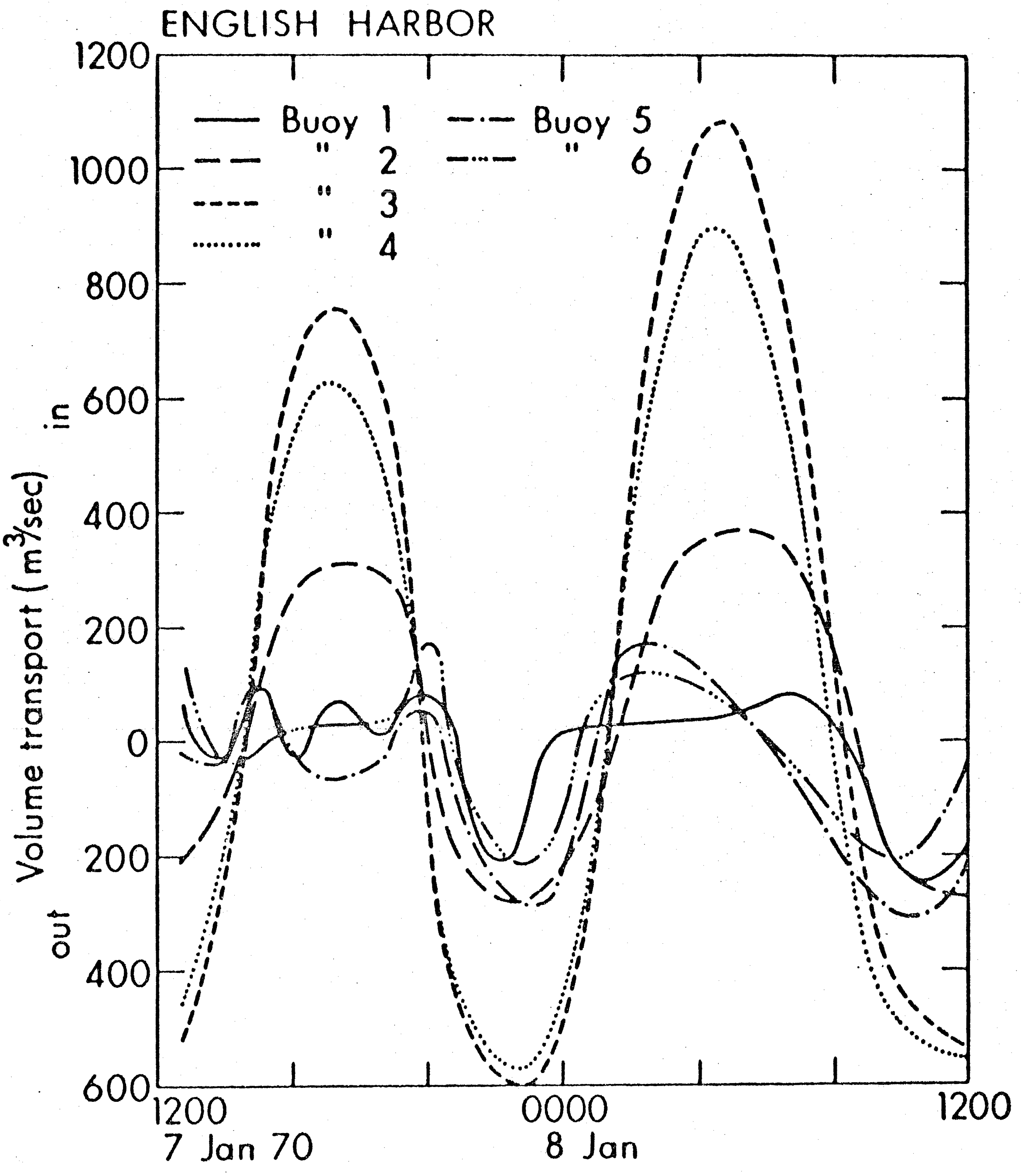

Fig. 7. Volume transports assigned to each buoy at English Harbor channel during the 24-hour transport study.

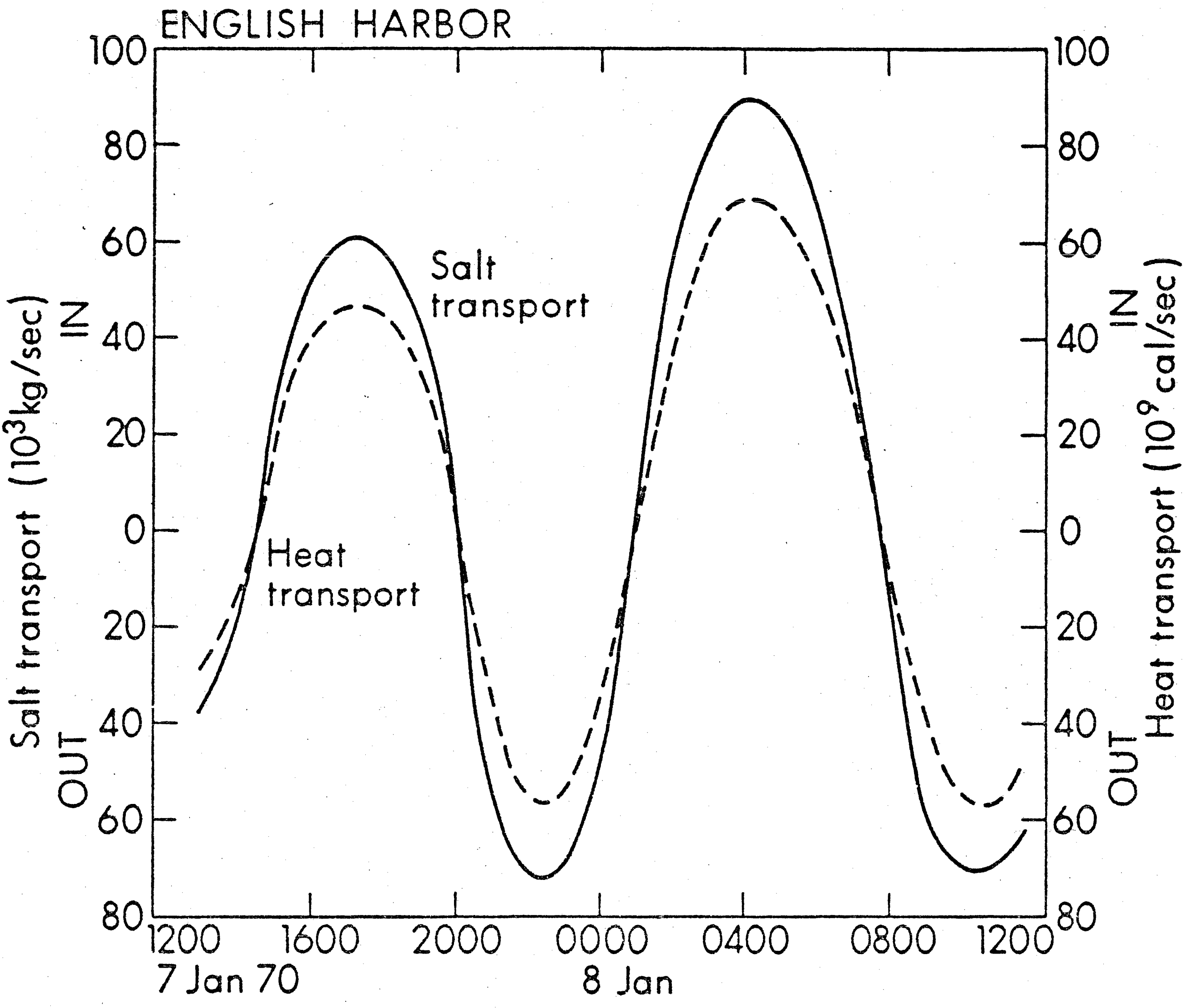

Fig. 8. Salt and heat transports at English Harbor channel during the 24-hour transport study.

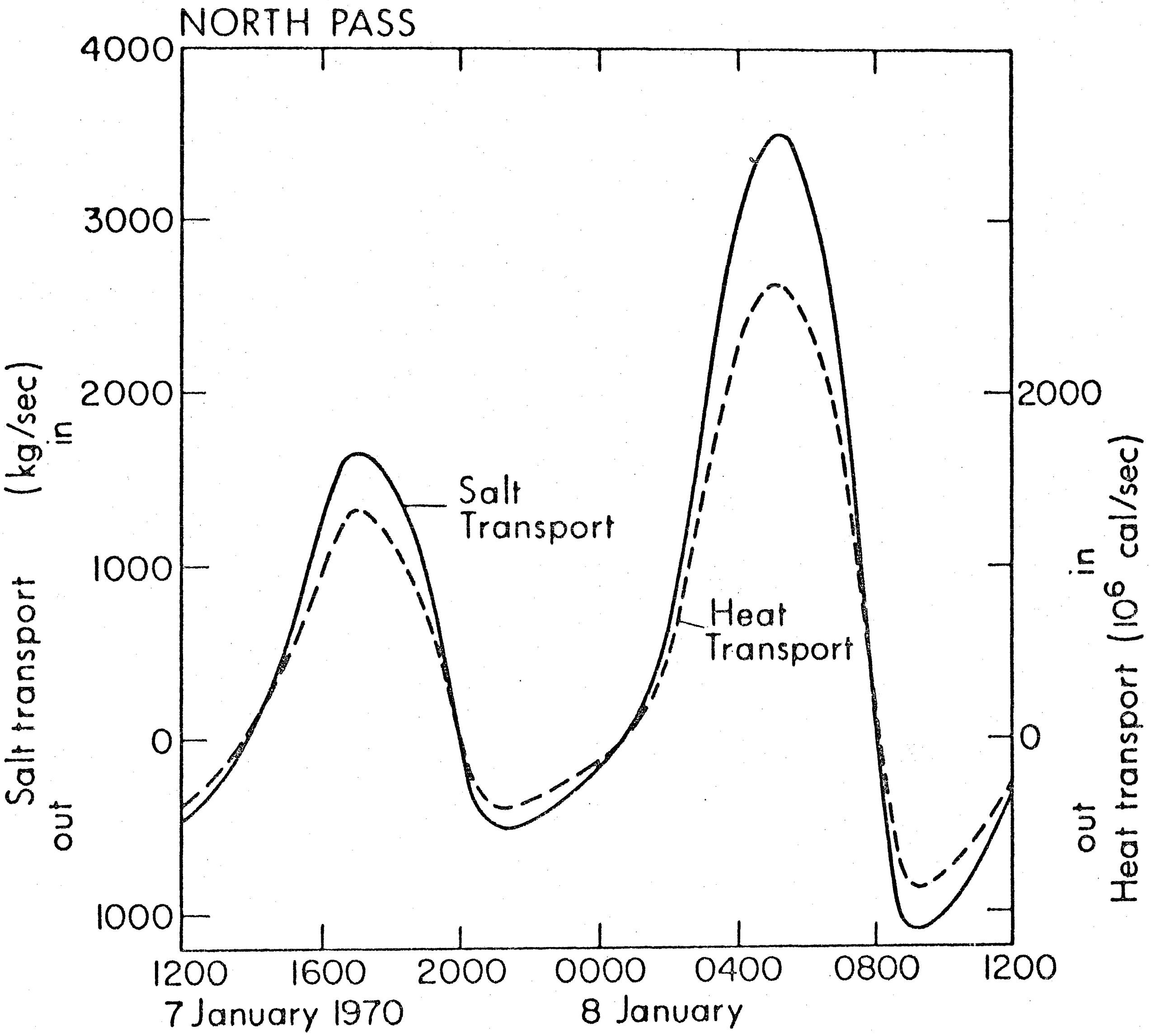

Fig. 9. Salt and heat transports at North Pass during the 24-hour transport study.

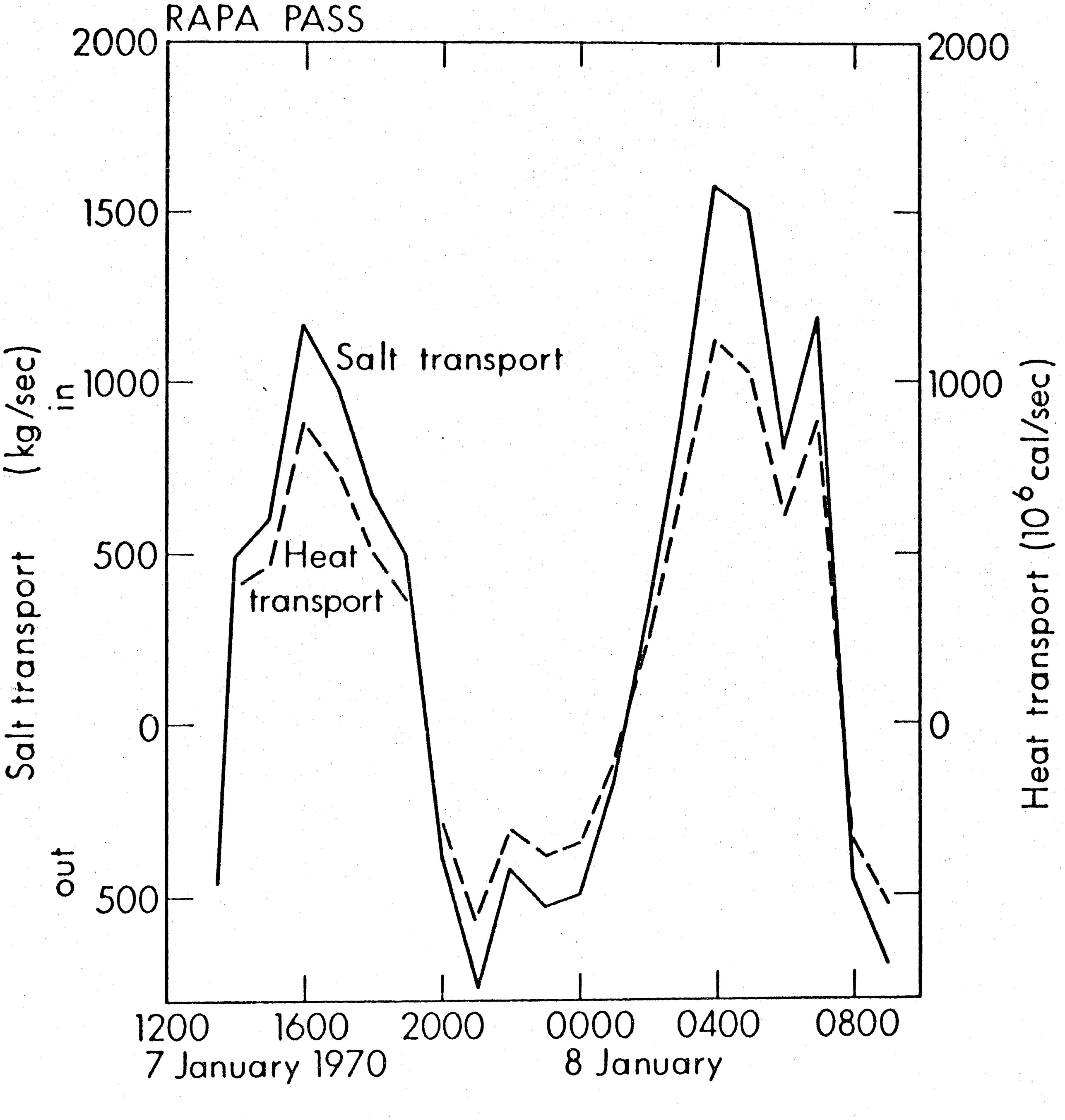

Fig. 10. Salt and heat transports at Rapa Pass during the 24-hour transport study.

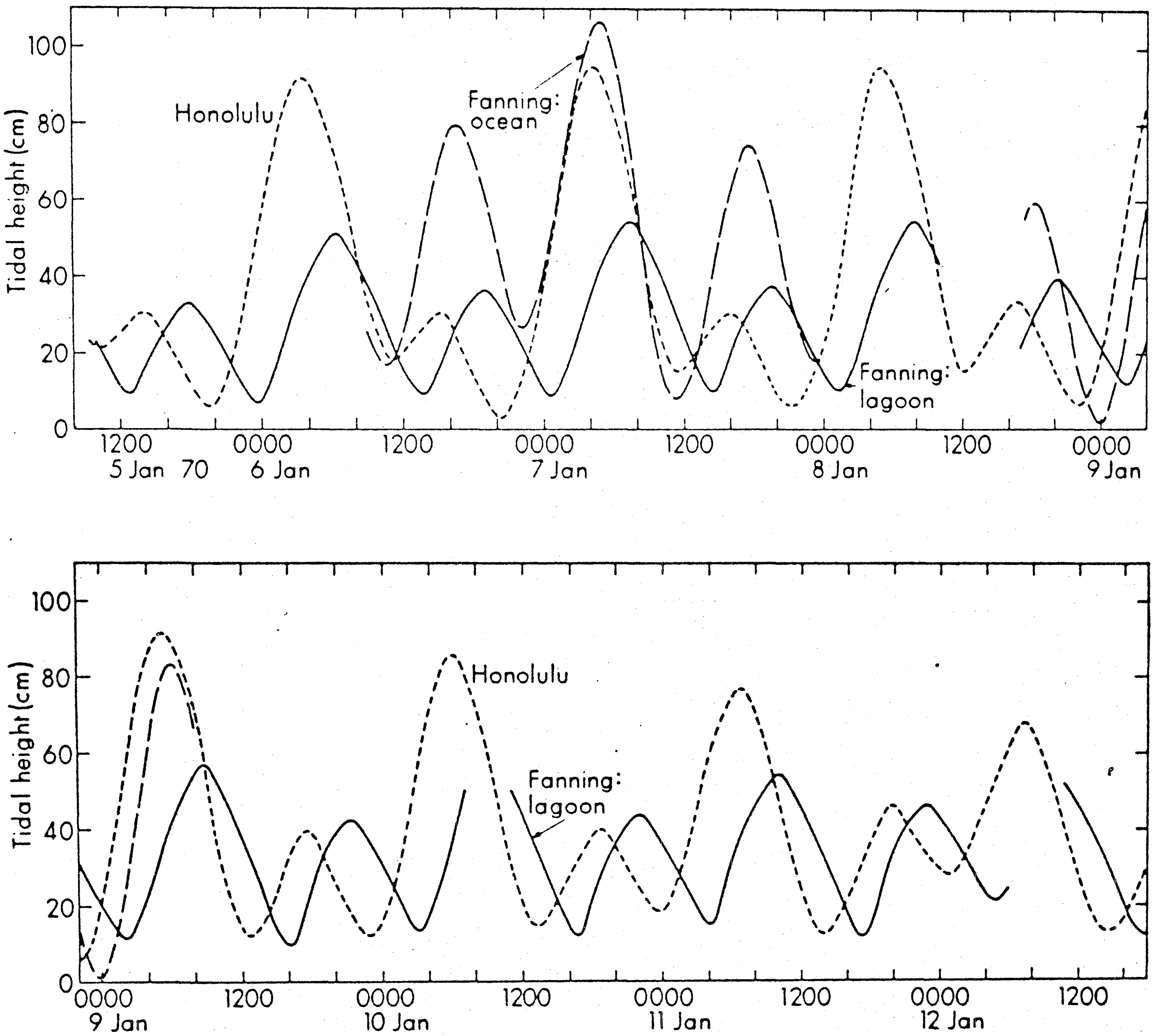

Fig. 11. Tidal height measured in the lagoon and the ocean near the Cable Station, Fanning Island, compared with tide at Honolulu (CGS record). Absolute sea level is arbitrary in the Fanning records.

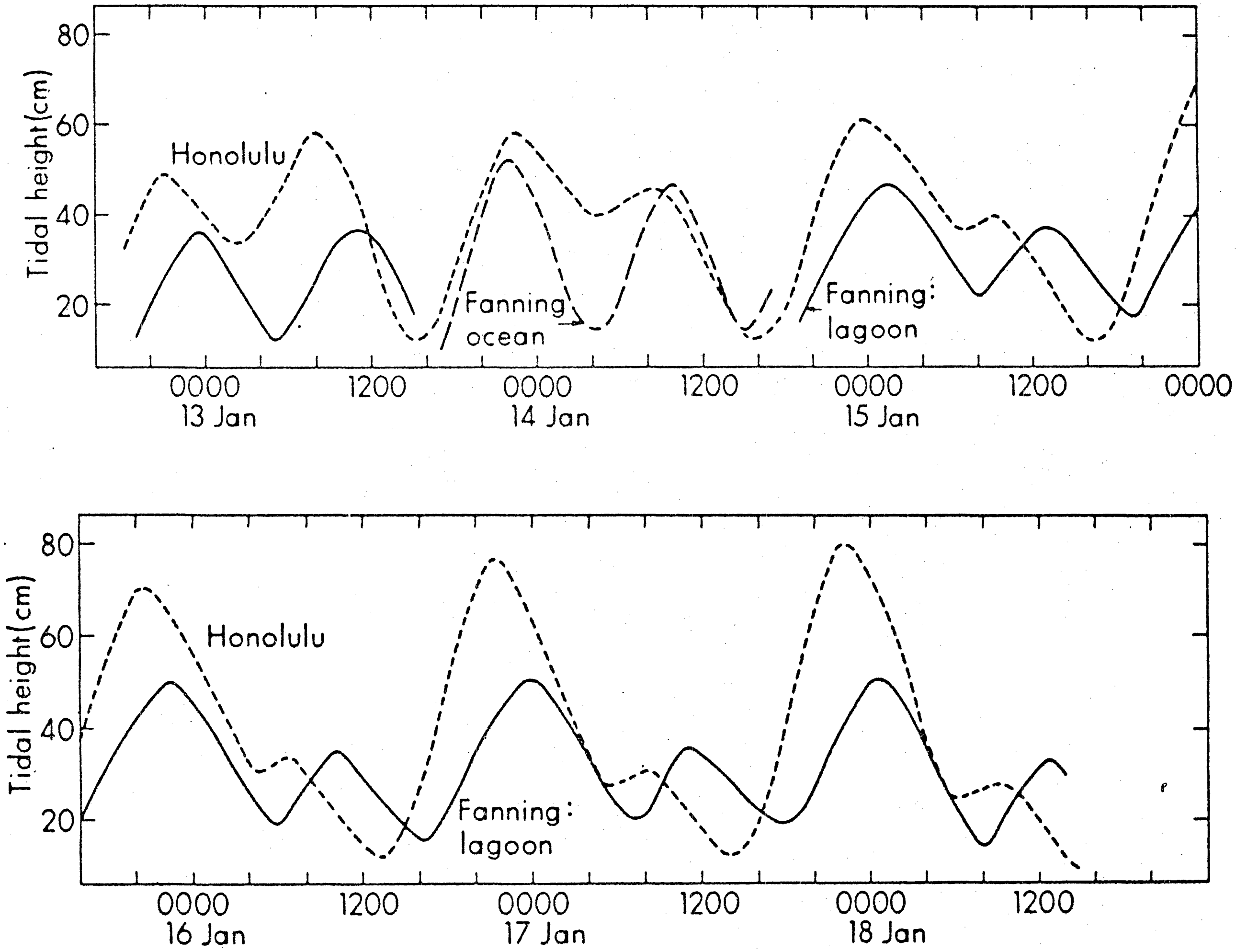

Fig. 11. (Continued.)

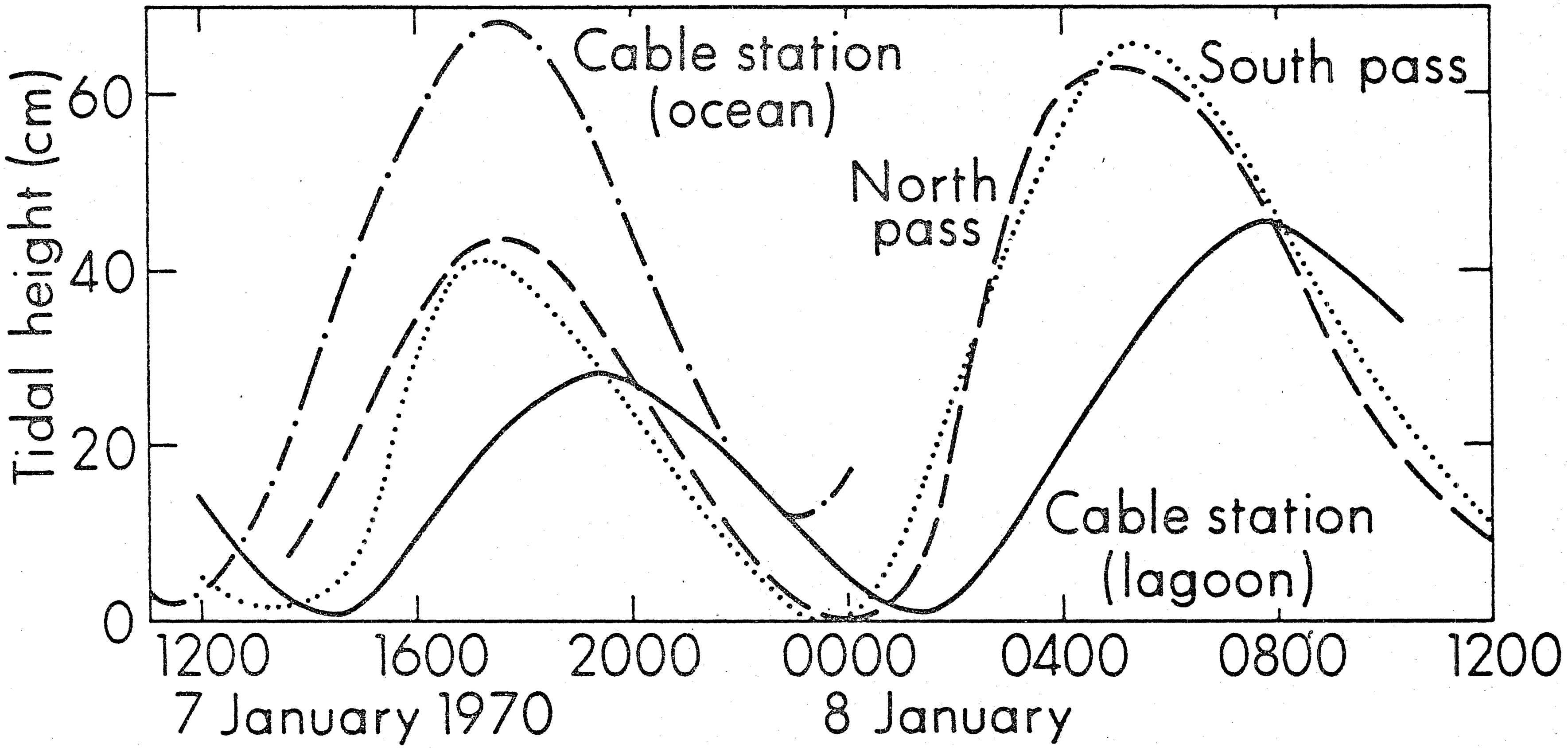

Fig. 12. Tidal heights at North and Rapa passes, and in the lagoon and the ocean near the Cable Station, during the 24-hour transport study. Absolute sea level is arbitrary.

rate of change, but both processes clearly reflect nonlinear distortion.[2] The lagoon's response to the ocean tide would be an intriguing subject for further study.

The first, semidiurnal cycle of transport studied coincided with a typical tidal excursion. During this period (1440 to 0120 hrs.) 0.025 km^3 of water was computed to have entered the lagoon through the three passes. The computed outflow was 0.026 km^3. The agreement between these numbers is gratifying, because the tidal records show no net change in lagoon water level over this particular period. Moreover, the measured exchange, 6 percent of the mean lagoon volume, agrees with the value estimated using tidal range and mean depth in the lagoon. In spite of these consistency checks, however, the transport figures calculated from our measurements should not be regarded as exact. Inaccuracies in current speeds, directions, and areas of channel cross sections lead to a volume transport uncertainty of ±15 percent.

There was a net inflow of water through North and Rapa Passes during the first, semidiurnal tidal cycle monitored. The amount was 0.56×10^{-3} km^3, or 0.1 percent of the lagoon volume. Thus there is an overall flow across the lagoon which must exit at English Harbor; most probably this flow is driven by wind and wave transport over the windward and northern reefs.

Salt

During the first transport cycle, the computed total salt transport into the lagoon (90×10^7 kg) matched (within our limits of accuracy) the total salt transport out of the lagoon (91×10^7 kg).

At English Harbor channel, outflow (90×10^7 kg) also matched inflow (86×10^7 kg) within our limits of accuracy (see Fig. 8). Salinity followed no discernible pattern (see Fig. 5).

At North and Rapa Passes, (Figs. 9 and 10), inflow exceeded outflow by 2.0×10^7 kg of salt. Salinity in these passes decreased during flow into the lagoon and increased during outflow. Because these passes are shallow, solar heating may cause the levels of evaporation in the lagoon to exceed open-ocean levels, at least locally near the mouths of the passes. The higher salinity outflow could be partly caused by the mixing of incoming sea water with more saline lagoon water. However, this cannot be proven. If the ocean water merely flowed in and out of the lagoon, with no mixing, estimates show that local evaporation in the lagoon is sufficient to account for the observed salinity increase.

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[2] There is also very probably some error in the relative phases of the curves in Figure 6; the current should not lag the lagoon tide derivative. We cannot find a timing mistake in either record and can only point out this discrepancy.

Heat

In the first transport cycle, during which net volume transport was zero, net heat transport (see Figs. 8 to 10) was also zero to within the accuracy of our measurements. Total inflow (68 x 10^{13} calories) was closely matched by outflow (66 x 10^{13} calories). There was a net inflow of heat at the small passes (1.6 x 10^{13} calories), but this reflects the particular phasing of the diurnal temperature curves with the semidiurnal current variations, and may have no particular significance. It does seem strange, however, that the temperature variations are diurnal and do not show the effects of the tidal flows which appear in the salinity curves. The disagreement in the periodicities of the temperature and salinity occurs at both passes. It seems likely that this illustrates the rapid response of temperature in this shallow-water environment to the large diurnal variation in the flux of radiant energy. The diurnal variation in evaporation is proportionately very much smaller, so that no diurnal salinity fluctuation is obvious in the record. At English Harbor, there is no significant temperature variation. This agrees with other observations which indicate that the water which enters and leaves through the channel is essentially open-ocean water. Changes incurred by mixing with lagoon water were too small to be detected.

Mixing

Replacement of water in the lagoon appears to be a slow process. A major reason for this is the fact that the lagoon is divided into numerous, small ponds by interconnecting line reefs, many of which are almost uncovered at low water. Flow is thus restricted to a shoal surface layer and to meandering passes through the reefs. An exception is the area receiving flow through the channel at English Harbor. Lagoonward from the channel, the bottom is scattered with large coral formations, but these are isolated and do not seriously baffle the flow. The water here is relatively deep, and quite clear. The clear water contrasts markedly with the extremely turbid water found throughout the rest of the lagoon, and the boundary between clear and turbid water appears vertical and often only a few meters wide. This boundary was sometimes observed moving in response to tidal inflow and outflow through the channel. These facts, together with the temperature and salinity records from the transport study, indicate that very little mixing occurs between lagoon water and the water that participates in the predominant tidal exchange. Mixing is likely to be relatively more important very locally near North and Rapa Passes where no topographic or turbidity boundaries are apparent and the water is shoal. Such mixing would not greatly reduce lagoon-wide residence times, because of the line reefs and because the volume exchange through these passes is relatively very small.

One possible lower limit on residence time can be calculated by using the observed volume of net inflow through the two small passes. If this inflowing water is assumed to mix completely throughout the lagoon before exiting at English Harbor, then we have

$$\text{residence time} = \frac{\text{Lagoon volume}}{\text{Rate of net exchange}}$$

$$= \frac{.41\ \text{km}^3}{.56 \times 10^{-3}\ \text{km}^3/11\text{hr}} \cong 11\ \text{months}.$$

Tides

The main tidal records were kept near the Cable Station, on the northwest side of the island, in the lagoon, and in the ocean. The ocean gauge was fastened to an outhouse piling a few meters seaward from the water's edge, while the lagoon record was obtained at the end of a small pier. The measurements were used to make daily predictions for biologists on the expedition who were involved in nearshore collecting. The tide curves, shown in Figure 11, are useful for examining ranges and phases. However, the records are not related to any common reference level. Moreover, the curves contain several interruptions occasioned by instrument malfunctions, and no attempt was made to maintain a constant zero-level between fragments of a given record.

The observed tidal range in the lagoon is typically 40 cm. This provides an immediate estimate of the volume of tidal flow: Half the tidal range is 5 percent of the mean lagoon depth estimated by the geologists, implying that 5 percent of the lagoon volume takes part in tidal exchange. Direct measurement of the volume transport through the passes confirms this value. The range in the lagoon is roughly half that in the ocean outside.

The lagoon tide lags that of the surrounding ocean by a typical period of 1 hr, 40 minutes as shown in Figure 12. The figure also shows tides measured in North and Rapa Passes during the transport survey, and the tide outside the Cable Station. Although the measurements in the passes were taken roughly halfway between lagoon and sea, the curves appear about the same in phase and in range as the ocean tide measured at the Cable Station.

There is a temptation for practical reasons to see whether the ocean tide at Fanning Island is related in some simple way to Honolulu tides. The Honolulu tide is therefore shown in Figure 11. No relation that could be used to give rough Fanning predictions based on Honolulu records is apparent. Semidiurnal phase lags, based on very scanty records, vary from 16 minutes to 1 hr 42 minutes for high water, and from -48 minutes to 2 hr for low water. The amplitudes are also seen to be quite different.

Suez Pond

A large part of Fanning Island lagoon is subdivided into small ponds by interconnecting line reefs that reach nearly to the surface. A typical example, called Suez Pond[3] in this paper, was chosen for intensive geological and chemical study; we attempted to provide some supporting information about water circulation.

Water movements in the pond proved to be extremely complex and usually too weak to measure quantitatively with standard current meters. Winds, tides, and thermohaline forces all appear to be important in the circulation. Furthermore, processes on the bordering reefs and in adjacent ponds seem to have an influence as well. Our time and instrumentation were almost totally inadequate for the task of describing the circulation, and we are able to make only qualitative comments.

During much of the year Fanning Island lies in the southeasterly tradewinds, which blow across the lagoon at mean speeds of 10 knots from 135°. There are diurnal speed variations with afternoon winds being 10 to 20 percent stronger than morning winds. (This information is published in "Line Islands, Meteorological Notes 11-B, September, 1956" prepared by the New Zealand Meteorological Service, Wellington). Short, choppy waves up to 0.3 m high are generated within the lagoon itself. With exceptions to be noted later, surface flow across the pond and adjacent reefs is in the direction of the wind. Within the pond, the directly wind-driven layer is less than 1 m deep with speeds on the order of 0.1 knot. We found no simple pattern of return flow at depth; currents at 3 m were variable in direction with speeds too low to measure (<.05 knot). Sand from the tops of the adjacent reefs is found deposited almost exclusively along the windward boundary of the pond, indicating the directional consistency of the wind-generated waves and currents over the reefs, and supporting the finding that currents at depth are weak.

Tidal effects are superposed and sometimes masked by the wind-driven flow. Currents were measured at several locations on the shoal reefs bounding the pond both during rising and during falling tides. At Suez, a channel roughly 1 m deep and 5 m wide dredged through the leeward reef, an ebb flow moved against the wind at 0.1-0.2 knots. Tidal reversals were not detected at any other location. Tidal currents almost surely cross the reefs at other places, and future measurements should include a study under conditions of no wind. To the north and west (and not communicating with the pond) is a meandering pass which can be followed through the reefs from the Cable Station to English Harbor. It is possible that this serves as a channel for overall southward flow in the area; the ebbing tide and the necessary return of wind-driven surface transport may be minimal in Suez Pond itself.

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[3] See "Sedimentation and Coral Reef Development in Turbid Water: Fanning Lagoon" by K. Roy and S. Smith, p. 61 of this report, for a further description of the pond itself.

Tracing subsurface flow with dye was attempted, but was of limited value because of the high turbidity in the pond. On one occasion however, we were able to detect subsurface movement against the wind. Dye introduced in a vertical streak near the windward edge of the pond broke into two patches. A surface patch moved with the 9-knot wind at a maximum estimated speed of 0.4 knot, and became too diffuse to see after about 40 minutes. A second patch, extending downward from about 0.5 m, moved up against the windward reef at an estimated speed of 0.06 knot and could not be seen coming to the surface. The dye may have moved downward, or it may have ascended very slowly and became too diffuse to detect in the surface flow. Dye injected as a point source in the same location at 3 m depth was never detected throughout 2 hours of observation.

Distributions of properties show a complicated pattern of inhomogeneities. Salinity was sampled with depth at five stations during a 3-hour period. At four locations salinity increased by .01 to .03°/oo from the surface to the bottom, and one station showed a decrease of .01°/oo. Variations of .04°/oo over distances of a few hundred meters occur at all depths. One of the stations was repeated after 24 hours, and salinity had increased almost 0.3°/oo at all depths. There appears to have been no water of this higher salinity in the pond on the previous day, so the rapid replacement of the 8-m water column at this station does indicate vertical movement. The salinity data indicate thermohaline circulation which is very irregular in space and in time. Probably patches of high salinity water originate over the wide, shoal, boundary reefs, are advected into the pond, and perhaps with night-time cooling, give rise to vertical circulations which can have horizontal dimensions small compared to the pond. The pattern of such circulation would be further complicated below about 3 m by the very irregular topography.

The distribution of extinction coefficients in the water column is shown in Figure 12, in "Sedimentation and Coral Reef Development in Turbid Water: Fanning Lagoon" by K. Roy and S. Smith.[4] Several factors appear. A patch of high turbidity, covering about one-third of the pond's area, is apparent at the surface and extends down to about 2 m. Within the patch suspended load decreases with depth, indicating that the patch is quite recently formed. The horizontal distribution strongly implies that this highly turbid water has been entering the pond through Suez canal during the falling tide, and flowing out over the surface. Shallow tidal flow against the wind also appears to be bringing turbid water from the leeward reef into the pond to the east of Suez. At depths between 2 m and 4 m additional horizontal patches of suspended load can be seen. They are less intense and have no apparent connection with those at the surface; they may be remnants of surface patches in the process of settling. (Particulate matter of this size has a settling rate on the order of 1 m/day.) Below 4 m the turbidity becomes almost uniform horizontally, with an intensity that appears to be close to an average value for the overlying water.

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[4] Facing page 68 of this report.

The salinity and suspended load data weakly suggest some general conclusions about mixing in the pond. The uniformity of turbidity at depth, along with the settling rate of the particles, makes it seem likely that the pond has a mixing time of less than about five days. Salinity indicates that the mixing time certainly exceeds a few hours, and that at least part of the mixing may be associated with diurnal, thermohaline processes. One might suspect that deeper portions of the pond are filled by relatively dense water that is renewed only infrequently by unusual events. However, there are no indications of stagnation; oxygen concentrations are close to saturation at all depths. Thus there must be a fairly regular downward transport of buoyancy, indicating an external source of mixing energy. The most probable agent is the wind-driven flow, but we have insufficient measurements for proposing a circulation model which could explain the mixing and the observed distributions of properties.

Should a future expedition wish to obtain a comprehensive picture of physical processes in the pond, they would face a difficult task. A first step would be to employ very sensitive current meters (responsive to 1 cm/sec or less) to see whether any average, overall patterns of movement can be discerned. Great effort would be required to ensure no motion of the meters themselves; they cannot simply be lowered from a singly-anchored skiff. Hourly vertical profiles should be obtained at as many stations as possible (at least four on a line roughly parallel with the wind and through the center of the pond). We advocate this direct approach because the patchy and transient nature of property distributions would limit their value for inferring motion unless they were based on very dense sampling. If a general circulation pattern was found, then temperature, salinity, and turbidity measurements could be planned to complement and take advantage of it. Such a plan should be designed to maximize the density of readings in both time and space; variations that occur rapidly and over short distances are to be expected. On-the-spot instrument readout would be extremely valuable.

ACKNOWLEDGMENTS

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Appendix

Explanation of Transport Computations

Volume transport. Volume transports were calculated by approximating the integral:

$$\text{Transport} = \int_{s=0}^{L} \int_{z=0}^{D(s)} u(s,z)\, ds\, dz$$

where s = the coordinate along the cross-channel section, and z = the depth coordinate.

For Rapa Pass, a straight section across the channel was used. We assumed that the current velocity measured at our station in mid-channel was constant throughout the channel. Also, the current direction was assumed to be normal to the channel cross section. Thus the transport integral simplifies to the product of one current speed and one cross-sectional area for every observation hour. Errors were caused by uncertainties in the channel width, channel depth, and current velocity data. We had measured the channel width along a 1/2-inch polypropylene line strung across the channel, but this line was not taut. If taut, it would have been about 6 m shorter. Uncertainties of 4% in channel width, 4% in channel depth, and 5% in current velocity led to an error of 13% in the volume transport numbers for Rapa Pass.

For North Pass, we used assumptions similar to those for Rapa Pass--a straight section, and normal currents constant throughout the channel. Most of the volume transport was assumed to have occurred through the west side of the channel. Gross calculations show that the neglected flow over the rest of the channel could have been at most 13% of the measured flow in the main channel. With a 5% uncertainty in the channel width, depth, and current speed for the west side of the channel, a total error of 18% was possible in the volume transports.

For English Harbor, the transport integral involved cross-sectional area data from seven sections and current velocity data from six stations. The seven sections were chosen along straight lines between the buoys and straight lines between the end buoys and the shore. The bottom contour was known along the straight lines between the buoys, while the bottom contour between buoy 1 and the shore and buoy 6 and the shore was estimated from visual observations in the field. With these data and with tidal heights to the nearest tenth of a meter, we calculated the cross-sectional areas.

The current velocity data from the six stations had to be corrected because the zero calibration of the Hydro Products 451 A Current Speed Readout and the 452 A Current Direction Readout drifted during the 24-hour measurement period. The Aanderaa current meter data taken later at buoy 3 were used for this correction. To correct the current speed, we assumed that the slope of the tidal curve recorded in the lagoon near the Cable Station was related to the current speed. We calculated the ratio between the average slopes of the tidal curves recorded during the 24-hour transport study and the average slopes of the tidal curves recorded during the time the Aanderaa meter was being used. This ratio gave a factor by which the Aanderaa record should be increased to reflect a tidal curve that existed during the time of the 24-hour study. The adjusted Aanderaa data were assumed to be correct. Then the maximum corrected Aanderaa current speed was compared with the maximum current speed recorded with the Hydro Products current meter. A correction ratio of 1.32 was calculated and used to correct all the Hydro Products current speed data.

To correct the current direction, the Aanderaa record was again used. This showed a flow into the lagoon at about 40° (magnetic) and a flow out of the lagoon at about 216° (magnetic). For each observation run, we first corrected the current direction that had been measured at buoy 3 at 1 m. These directions were corrected to either 216° or 40° depending on whether the sea-level record showed an inflow or outflow. Using this same angular increment, we then changed the current directions at the other buoys--on the assumption that the meter used during the survey, although drifting, was self-consistent over an hour's time. If there were current directions that remained inconsistent with those at the other buoys, we used an average inflow or outflow direction for that particular buoy from other observation runs.

The corrected velocity data were used to evaluate the transport integral. The currents observed at each depth at each buoy were resolved into components normal to the two sections adjoining the buoy. Then a depth-averaged, normal velocity was found at each end of each section. For this process, we assumed a weighted average,

$$\text{average} = \frac{1}{D}\int_{o}^{D} u(z)\, dz$$

$$= \frac{u_1\Delta z_1 + u_2\Delta z_2 + \ldots}{D}$$

where u = current velocity

z = depth over which u is assumed constant

D = total depth or $z_1 + z_2 + \dots$

Finally, an overall, normal velocity through each section was taken as the mean of the depth-averaged values at either end. This involves the assumption that $u_{\text{normal}}(s,z) = f(s) \times g(z)$, with the physical implication that the local topography between stations does not distort the flow. This overall current velocity and the cross-sectional area of the section were used in approximating the transport integral.

To assign a transport to each station, we took the sum of one-half the transports through the sections on either side of a buoy. The transport at the end stations included the transport through the entire section between the end buoys and the shore.

Errors were caused by uncertainties in the buoy positions, the time, and height of the tidal changes, and current speed readings. Uncertainties in locating the buoy positions led to an error of about 1% in determining the width of the sections between buoys. The tide data taken in the lagoon near the Cable Station was applied at English Harbor channel. A phase lag between the tides at these two positions might have led to a maximum error of 10%, and a more probable error of 3%, in determining channel depth. In the calculation of a correction factor for the Hydro Products current speed data, a 4% error was involved in determining the slope of the tidal curves. Uncertainties in reading the Hydro Products current meter might have led to a 10% error in the current speed. The total uncertainty in the volume transports for English Harbor channel may have been about 18%.

Salt Transport. Salt transports were calculated by approximating the integral:

$$\int_{s=0}^{L} \int_{z=0}^{D(s)} u(s,z)\ S(s,z)\ \rho(s,z)\ ds dz,$$

where S is salinity, and ρ is density.

At North Pass and Rapa Pass the salinity and the density were assumed constant throughout the channel. At English Harbor channel we averaged the salinity at buoys 2, 3, and 4 where most of the volume transport occurred and assumed this average to be constant throughout the channel. We took $\rho = 1$. Therefore the integral reduced to

$$\text{Salt transport} = S \int_{s=0}^{L} \int_{z=0}^{D(s)} u(s,z)\, dsdz$$

$$= S \times \text{volume transport.}$$

Heat transport. Heat transport calculations were similar to those for salt transport and the integral

$$\int_{s=0}^{L} \int_{z=0}^{D(s)} u(s,z)\, T(s,z)\, \rho(s,z)\, c_p(s,z)\, dsdz$$

reduced to

Heat transport = .962 x Temperature x volume transport

where

$.962 = c_p$ for water of $35^{o}/oo$ and 27.5°C.

Anchoring System at English Harbor

Each buoy was held in place by two 15-lb Danforth anchors. The anchors, about 20 m apart, were set so one would hold against an incoming current and the other against an outgoing current. Two meters of chain and twenty meters of double 1/4-inch Manila line connected each anchor to the buoy. During a measurement cycle, a 16-foot skiff (Boston Whaler) was moored to the buoy and a current meter lowered. The anchoring system was able to hold the buoy in position despite the skiff, current meter, and 3-knot currents.

Instruments Used

TRANSPORT STUDY (7 to 8 January)

North Pass

Aanderaa current meter
Bucket thermometer
Hytech Model 6210 Laboratory Salinometer

Rapa Pass

Hydro Products Model 460A Current Speed Sensor
Bucket thermometer
Hytech Model 6210 Laboratory Salinometer

English Harbor

Hydro Products Modular Current Meter System combining the Model 460A Current Speed Sensor and the Model 465A Current Direction Sensor

Hydro Products Hydrotemp Model 403 Sensing Unit (for temperature measurements)

Beckman RS5-3 Portable Salinometer

Raytheon Model DE-719 Fathometer

Aanderaa Current Meter (used 15 to 18 January)

TIDES

Belfort Instrument Company's Liquid Level Recorders

SUEZ POND

Hydro Products Modular Current Meter System

Sims Electronic Anemometer Model BT

TEMPERATURE, SALINITY AND OXYGEN OBSERVATIONS AT FANNING ISLAND

Donald C. Gordon, Jr. and Harold G. Schiesser

Department of Oceanography and Hawaii Institute of Geophsics

INTRODUCTION

A survey was run to determine the distribution of temperature, salinity and oxygen within the lagoon. In addition, salinity was determined in each of the three channels (English Harbor, North Pass, and Rapa Pass) during the 24-hour study.

METHODS

Water for analysis was either dipped from the surface or collected with an *in situ* pumping apparatus. Temperature was determined with a laboratory thermometer. Salinity samples were collected in 250-ml glass bottles having tight-fitting screw caps. Salinity was determined within 48 hours of collection using a Hytech Model 6210 Laboratory Salinometer which was standardized daily with Copenhagen water. Dissolved oxygen was determined by the Winkler method. Samples were collected in BOD bottles, pickled immediately, and titrated in the laboratory within a few hours.

RESULTS

Lagoon Survey

The values of temperature, salinity and oxygen are summarized in Table 1. Station locations are shown in Figure 1.

The lagoon was nearly isothermal. The average temperature was slightly below 28 C and fluctuations were only of a few tenths of a degree. There was no observed gradient with depth.

Salinity within the lagoon was quite variable, ranging from a low of 34.562‰ (Sta A) to a high of 35.281‰ (Station 172). There was a very slight tendency for salinity to increase with depth (about 0.020‰ per 7m). Salinity within Suez Pond at a given time was fairly uniform but during the eleven days of observation it increased continuously from 34.809‰ to 35.281‰. All lagoon salinities determined prior to 9 January were lower than those at English Harbor, while all but one determined afterwards were higher. Thus, it appears that the salinity of the entire lagoon was gradually increasing during the course of these observations.

The saturation concentration of dissolved oxygen in lagoon water is calculated to be 4.69 ml/l. Therefore, except at the surface at Stas 175-177, the lagoon water was undersaturated with oxygen, averaging about 90%

saturation. The three super-saturated samples were collected during and just after a rain squall when surface samples should be highly oxygenated. Oxygen tended to increase about 0.1 ml/l in the upper 3 m, presumably due to an increase of photosynthesis with depth in this layer. All oxygen samples were taken during daylight hours (0900-1200) when oxygen concentrations should be the highest. Unfortunately, no diurnal data were obtained.

24-Hour Study

The salinity values during the 24-hour study at all three channels are plotted in Figure 2. There were no significant fluctuations at the English Harbor station (Buoy 4). Salinity remained very constant at about 35.010‰, which is characteristic of oceanic water surrounding Fanning Island. However, pronounced variations were observed at North and Rapa passes; salinity decreased during the flood and increased during the ebb. All values at these two passes were higher than those at English Harbor and generally higher than those in the lagoon (Table 1). These high salinities were presumably due to excessive evaporation in the shallow regions of the lagoon just inside from North and Rapa passes.

DISCUSSION

These results give some insight into the circulation of the lagoon. The absence of pronounced vertical gradients indicates that the water column is well mixed. Although values are fairly uniform in different parts of the lagoon, minor differences, especially in salinity, suggest that horizontal mixing is somewhat restricted due to the numerous line reefs which criss-cross the lagoon.

These data also suggest that the lagoon has a very low flushing rate. The fact that lagoon water was fresher than English Harbor water and then gradually increased in salinity indicates that the salinity of the lagoon is controlled more by precipitation and evaporation than by exchange with the surrounding ocean water. Also, the constant salinity of about 35.010‰ during the 24-hour study at English Harbor, where practically all exchange occurs, suggests that although there is much exchange of water there is little mixing.

ACKNOWLEDGMENTS

The authors wish to thank Glenn Shepherd for his assistance in the field operations.

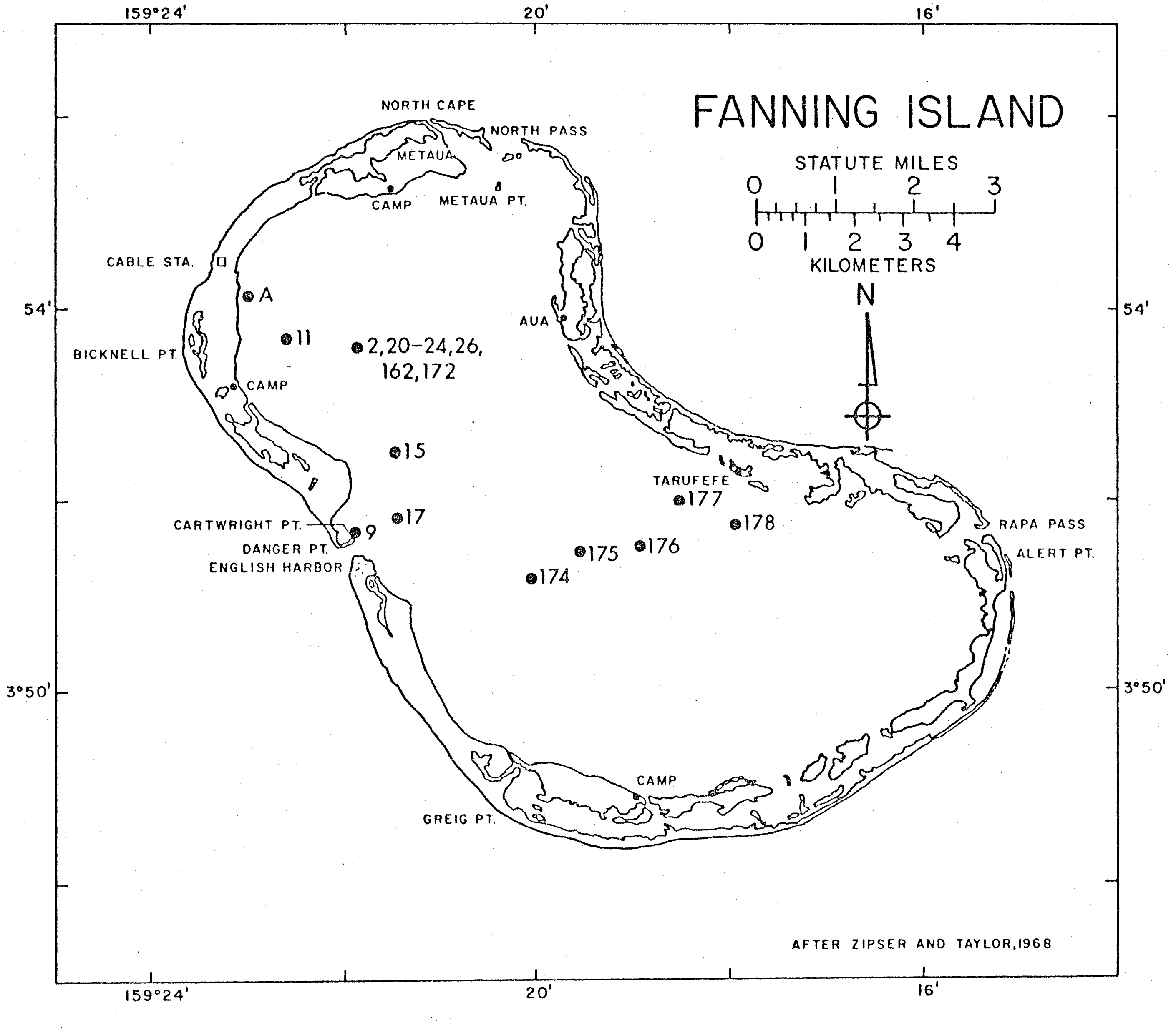

Fig. 1. Station locations at Fanning Island.

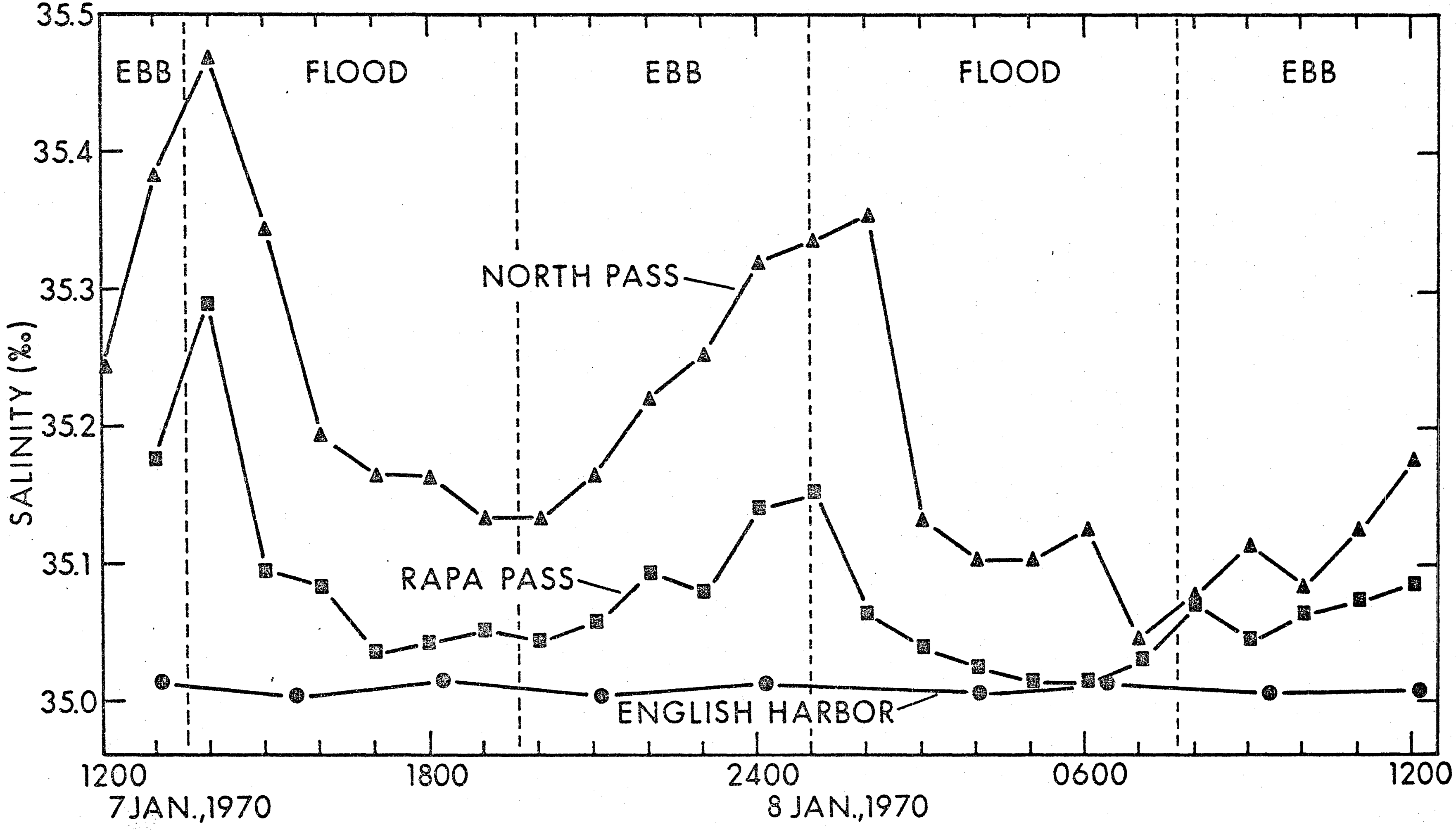

Fig. 2. Salinity values from 24-hour study. Station locations are shown in Figure 1. Values at English Harbor station were taken at Buoy 4; samples from 0, 3, and 6 m are averaged together. Surface values at North and Rapa passes. Dashed vertical lines indicate approximate times of current reversal.

Table 1. Summary of temperature, salinity and oxygen values in Fanning Lagoon

Date	Station	Z (m)	Temp (°C)	Salinity (‰)	Oxygen (ml/l)
4 Jan	2	0	28.5	34.809	4.18
	9	0	28.0	35.041	4.18
	A	0		34.562	
5 Jan	11	0	27.6	34.826	3.96
		2	27.6	34.826	4.27
		4	27.6	34.828	3.96
	15	0	28.0	34.733	4.14
		3	28.0	34.726	4.05
		5	28.0	34.726	4.10
	17	0	27.7	34.989	4.27
		3	27.5	34.965	4.05
		6	27.5	34.980	4.18
		9	27.5	34.989	4.07
		14	27.5	35.006	
6 Jan	20	0	27.8	34.916	4.12
		2	27.8	34.931	4.24
		5	27.6	34.947	4.34
	21	0	27.8	34.914	4.14
		2	27.8	34.913	4.17
		5	27.8	34.906	4.32
	22	0	28.0	34.886	4.29
		3	27.8	34.886	4.43
		6	27.8	34.891	4.34
	23	0	27.8	34.913	4.13
		2	27.8	34.918	4.24
		5	27.8	34.924	4.30
	24	0	28.0	34.916	4.23
		3	28.0	34.916	4.36
		8	28.0	34.943	4.34
9 Jan	26	0		35.147	4.06
		2		35.153	4.09
		4		35.165	4.06
		7		35.175	4.24
14 Jan	162	0		35.183	
15 Jan	172	0		35.281	
16 Jan	174	0		35.006	4.47
	175	0		34.924	5.11
	176	0		34.979	4.78
	177	0		34.995	4.69
	178	0		35.140	4.54

ORGANIC CARBON BUDGET OF FANNING ISLAND LAGOON

Donald C. Gordon, Jr.

Department of Oceanography and Hawaii Institute of Geophysics

ABSTRACT

The concentrations of total and particulate organic carbon in the waters of Fanning Island Lagoon are high and fairly uniform throughout, averaging 1.68 mg/l and 80 μg/l, respectively. Phytoplankton and reefs in the lagoon produce 7.8×10^4 kg of organic carbon daily, giving a turnover time of only 11 days for organic carbon. Only 0.4% of the daily production is lost from the lagoon by tidal exchange, the remainder is respired by organisms in the lagoon. Fanning Lagoon is a rich and unique environment which because of its low flushing rate of about 230 days has little effect on the surrounding ocean.

INTRODUCTION

Atolls are often referred to as biological oases in the aquatic desert of the tropical and subtropical ocean. The high productivity of coral reef communities has been well illustrated by the classic studies of Sargent and Austin (1949) and Odum and Odum (1955). However, atolls by definition consist of a lagoon as well as encircling reefs and islands. Therefore, an understanding of processes in lagoons is also necessary for comparing atolls with and describing their effect on the surrounding ocean.

The few measurements made (Sargent and Austin, 1949; Doty and Capurro, 1961) indicate that phytoplankton productivity in lagoons is generally low. With the exception of a few determinations by Odum and Odum (1955) and Johannes (1967) at Eniwetok, the concentrations of organic carbon in lagoons are unknown. In addition, nothing is known as to how much organic carbon a lagoon loses by water exchange.

The Fanning Island Expedition offered an excellent opportunity to construct an organic carbon budget for a Pacific atoll lagoon. The small size and enclosed nature of Fanning Lagoon (Fig. 1) made it easy to study the distribution of organic carbon within the lagoon and to monitor its exchange with the ocean.

METHODS

Both total and particulate organic carbon were measured at various locations and depths within the lagoon and at three-hour intervals at each of the three passes during a 24-hour sampling program. Seawater for analysis was either dipped from the surface or collected with an _in situ_ pump

(Schiesser, 1970) suspended from a Boston Whaler. Station locations are shown in Figure 1. During the 24-hour study, samples at English Harbor were collected at Buoy 4 from surface, 3 m, and 7 m (just off the bottom). At North and Rapa passes, which are only a few feet deep, only surface samples were collected.

Total organic carbon was determined by treating unfiltered water with the dissolved organic carbon method of Menzel and Vaccaro (1964), as modified by Strickland and Parsons (1968). Collected water was placed in 250-ml glass bottles and processed and autoclaved in the laboratory as soon as possible, usually within a few hours. The analyses were completed a month later back in Hawaii.

Water for particulate organic carbon analysis was collected in 4-l plastic bottles. Upon return to the laboratory, 1 l was filtered through a precombusted 25-mm Gelman Type A glass fiber filter (the remaining water was used for other analyses). After a rinse of 5 ml of distilled water, filters were placed in numbered plastic petri dishes and frozen until return to Hawaii. Then, each filter was placed in a 10-ml glass ampoule containing 5 ml of low-carbon distilled water (prepared by saturating glass-distilled water with potassium persulfate and autoclaving for 1 hr) and treated like total organic carbon samples. The only differences in handling were that twice as much potassium persulfate and phosphoric acid were added to each ampoule and a lower gain was used on the infrared carbon dioxide analyzer.

RESULTS

Lagoon Survey

The concentrations of both total and particulate organic carbon observed within the lagoon are plotted in Figure 2. Dissolved organic carbon concentrations can be obtained by subtracting the particulate from the total. As expected, the distributions of each were similar. Differences within the lagoon were evident, particularly between Stations 11, 15, and 17. Concentrations dropped as English Harbor was approached. At each station, concentrations were fairly uniform with depth. Temperature, salinity, and oxygen had a similar vertical distribution (Gordon and Schiesser, 1970), indicating that the water column is well mixed. In a few instances, sediment was stirred up when near-bottom samples were being collected. The particulate organic carbon concentrations of these samples (not recorded in Fig. 2) were several times greater because of organic carbon associated with the sediment.

Within the lagoon, the average total and particulate organic carbon concentrations were 1.68 mg/l and 80 μg/l, respectively. These mean values are much higher than those reported in the lagoon at Eniwetok. Odum and Odum (1955) reported an average total organic matter concentration of 1 mg/l which is equivalent to a total organic carbon concentration of about 0.5 mg/l, and Johannes (1967) observed an average particulate organic carbon concentration of 33.6 μg/l just leeward of the Japtan inter-island reef.

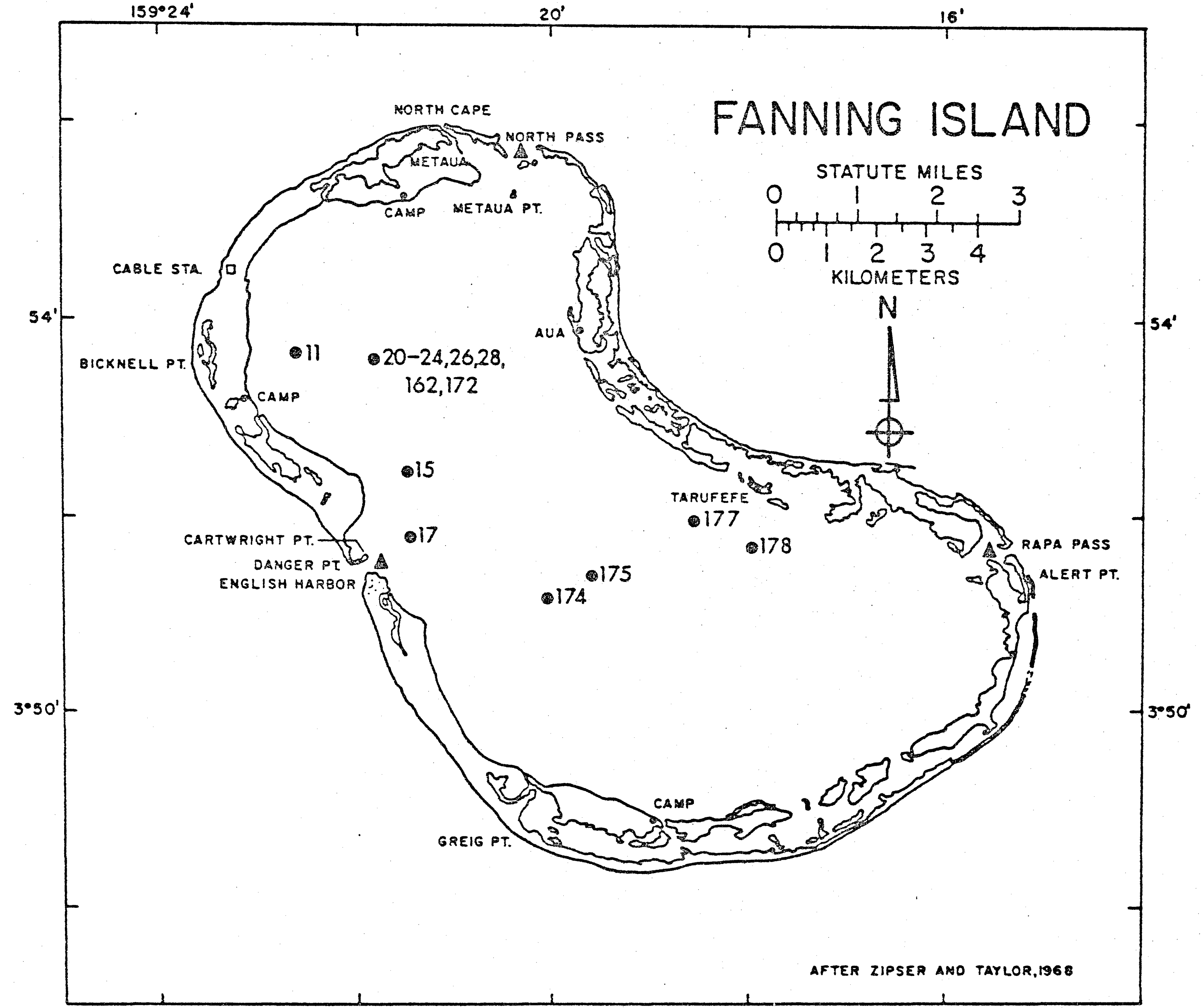

Fig. 1. Station locations at Fanning Atoll. The three triangles represent the stations during the 24-hour study.

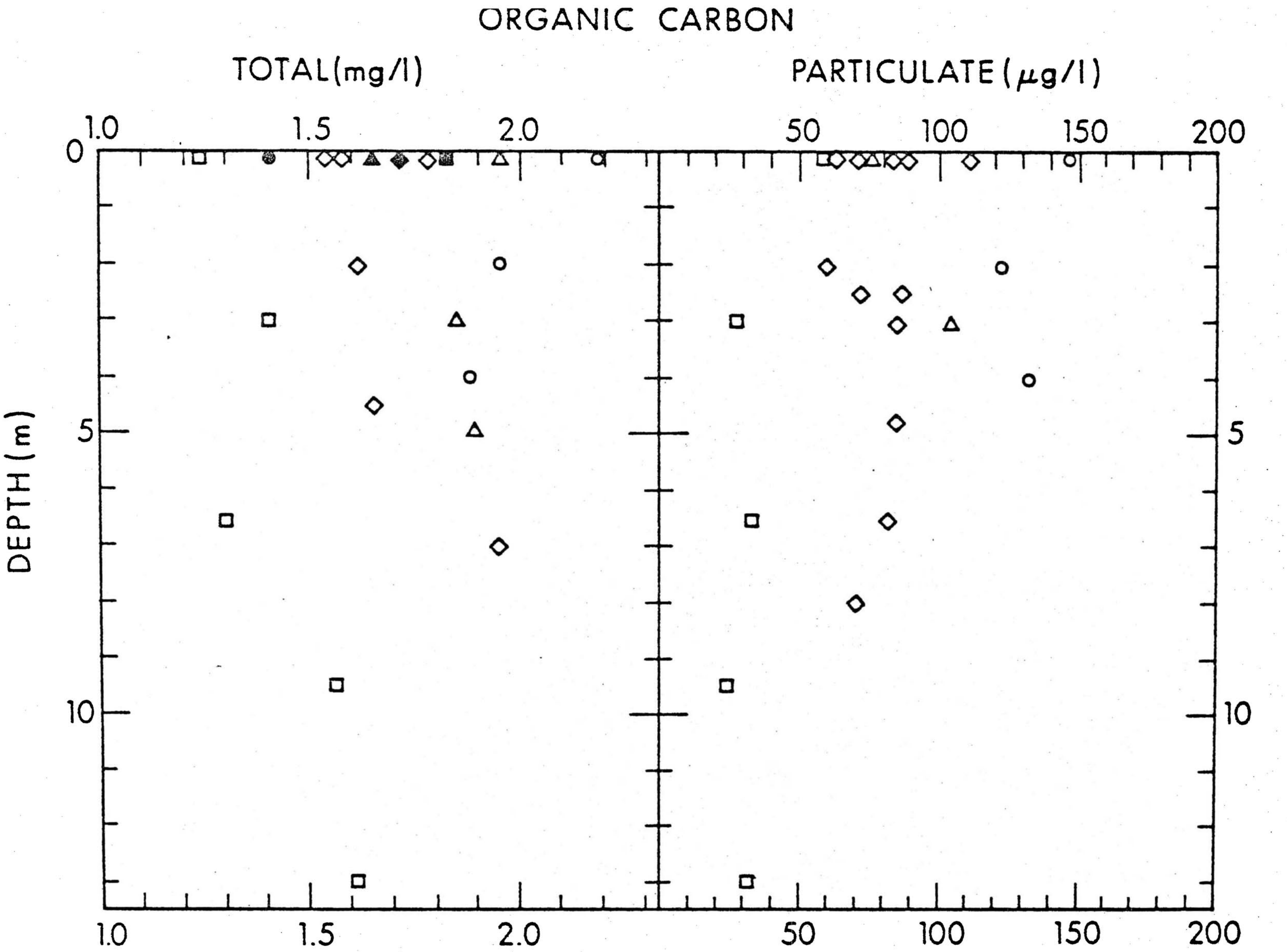

Fig. 2. Concentrations of total and particulate organic carbon in Fanning Lagoon. See Figure 1 for station locations. Stations 20-24, 26, 162, and 172 are in Suez Pond. Symbols: open circle, station 11; open triangle, station 15; open square, station 17; open diamond, stations 20-24, 26, 162, and 172; solid circle, station 174; solid triangle, station 175; solid square, station 177; solid diamond, station 178.

Thus, it is readily apparent that Fanning Lagoon is a much richer environment than Eniwetok Lagoon. The concentrations in Fanning Lagoon are in fact in the range of those reported by Klim (1969) just leeward of the main reef in Kaneohe Bay, Hawaii, a partially polluted embayment on the windward coast of Oahu.

Organic carbon concentrations in surface water changed near the line reefs which divide the lagoon into numerous ponds. Concentrations of both total and particulate organic carbon decreased steadily along a transect extending downwind from the line reef on the windward side of Suez Pond (Fig. 3), except for one anomalous particulate value. These gradients suggest that line reefs are contributing a significant amount of organic carbon to lagoon water.

24-hour Study

As expected, since the water column is well mixed, there were no significant changes of either total or particulate organic carbon with depth at the English Harbor Station. Therefore, the three values at each sampling time were averaged. These averaged values are presented in Figure 4 along with the data from North and Rapa passes. The concentrations of both total and particulate organic carbon were much lower in the passes than in the lagoon which indicates that the concentrations in the lagoon are higher than in the surrounding ocean.

Looking closely at the data (Fig. 4), a trend of higher ebb tide and lower flood tide concentrations becomes visible, particularly during the second half of the observations (8 Jan.). When the ebb and flood concentrations of both total and particulate organic carbon at each channel are averaged, the mean ebb concentrations are in fact greater than the mean flood concentrations in all cases. However, these means were not significantly different when tested with a t-test. The data were then tested on the hypothesis that the differences between successive observations in different tidal stages were significantly different from zero. This test demonstrated that the particulate organic carbon differences were significant ($p = 0.05$), while those of total organic carbon were not. Thus, the lagoon is losing some particulate organic carbon through tidal exchange.

DISCUSSION

A crude budget for organic carbon in the waters of Fanning Lagoon can be constructed from the available data. Assuming that the processes affecting organic carbon in the lagoon are in equilibrium, production and import must be exactly balanced by export and respiration. This appears to be a reasonable assumption since atolls are generally considered to be ecological climax systems which by definition are quite stable.

Photosynthetic production by phytoplankton in the lagoon was measured by Gordon *et al.* (1971) using the radiocarbon method. The average rate typical of the entire lagoon equaled 49 $mgC/m^2/hr$. This rate is approximately an order of magnitude greater than those previously reported from other Pacific atoll lagoons. Since the radiocarbon method is thought to measure principally net production, this figure is a meaningful estimate of the rate at which organic carbon is formed in the lagoon by phytoplankton activity. Assuming 12 hr of production daily and a lagoon area of 103 km^2, approximately 6.1 x 10^4 kg of organic carbon are produced each day by this process in the entire lagoon.

Some organic carbon in the lagoon water undoubtedly originates from the numerous line and patch reef communities which cover approximately 35% of the lagoon floor. This production is illustrated by the gradients of organic carbon in the vicinity of line reefs (Fig. 3). According to Johannes (1967), this exported material is principally mucus, and he calculated that it is produced at a rate of 0.02 $g/m^2/hr$ on Japtan Reef at Eniwetok. Applying this rate to the Fanning Lagoon reefs, approximately 1.7 x 10^4 kg of organic carbon should be released into the lagoon from reefs each day. This figure is certainly not accurate because of major differences between Japtan Reef and the reefs in Fanning Lagoon. It is however a first approximation which if anything is probably too high.

It is significant to note that the phytoplankton in the lagoon are producing three times the amount of organic carbon exported by the reefs. Thus, the high concentrations of organic carbon in the lagoon are due principally to the high production rate of phytoplankton. The combined figures yield a daily total production of 7.8 x 10^4 kg of organic carbon for the entire lagoon.

Preformed organic carbon can be imported into the lagoon by two mechanisms: runoff and tidal exchange. Unfortunately, there are no data for the former. It could be of some importance however, since, except for the three narrow passes (Fig. 1), the lagoon is completely surrounded by vegetated land and the atoll does receive 81 inches of rain annually (Wiens, 1962). The quantity of organic carbon added by tidal exchange is calculated in Table 1. At both North and Rapa passes, there is a net inflow of water since they are on the windward side of the atoll. Despite higher concentrations during ebb tides, there is also a net import of organic carbon amounting to 47 kg/day.

Export of organic carbon from the lagoon by tidal exchange is also calculated in Table 1. At English Harbor, where most of the water exchange occurs, 413 kg of organic carbon are lost daily. Subtracting the import of organic carbon at North and Rapa passes, there is a net export of 366 kg from the lagoon each day, all in the particulate form.

It should be noted that there is probably some water exchange through the atoll rim in the southeastern sector. This exchange is probably less than at Rapa Pass and should have little effect on the organic carbon budget of the entire lagoon.

Some organic carbon must also be lost to the sediments on the lagoon floor, but, as in the case of runoff, there is not sufficient data to calculate the rate of loss. It is assumed that this loss would be more or less

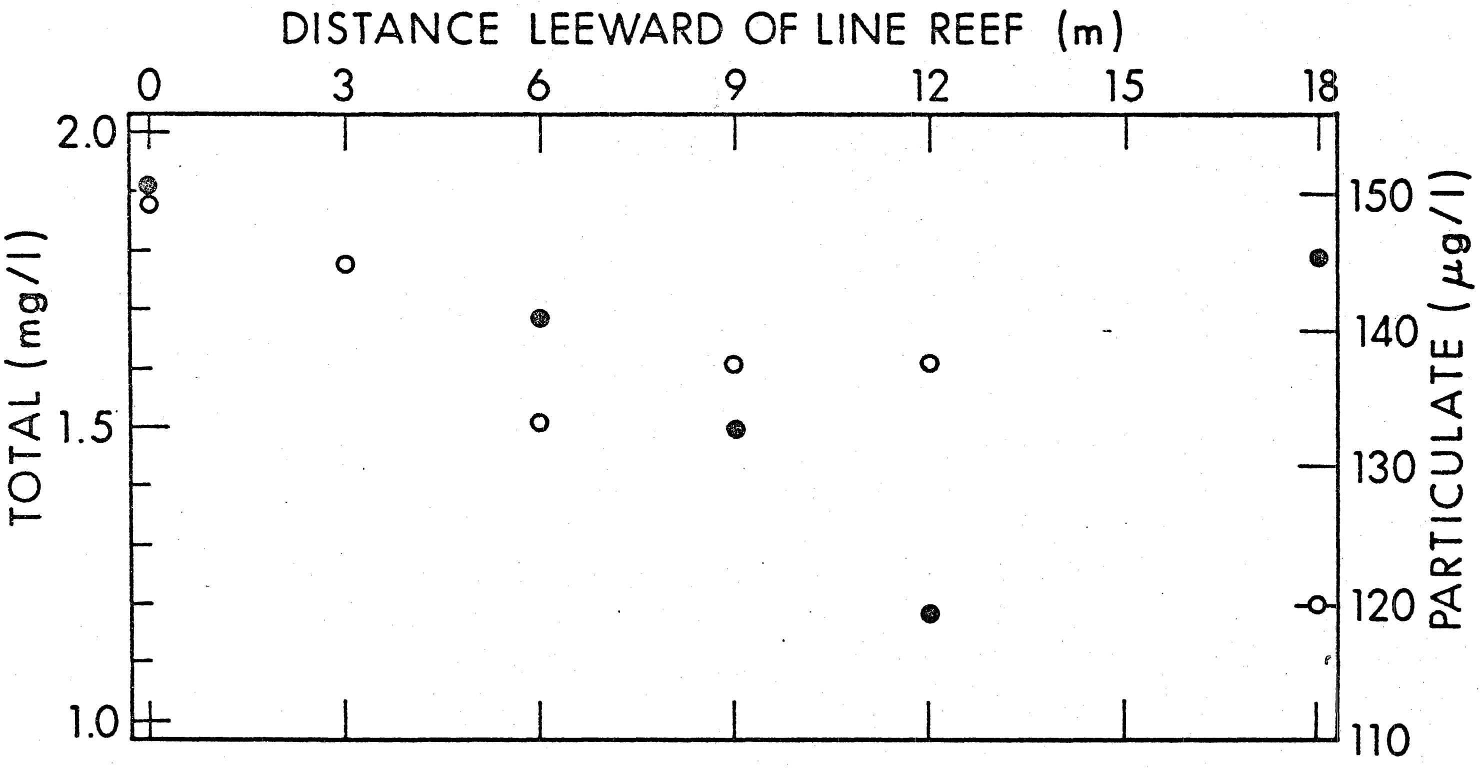

Fig. 3. Organic carbon concentrations at the surface along a transect downwind from a line reef in Suez Pond. Open and closed symbols denote total and particulate organic carbon, respectively.

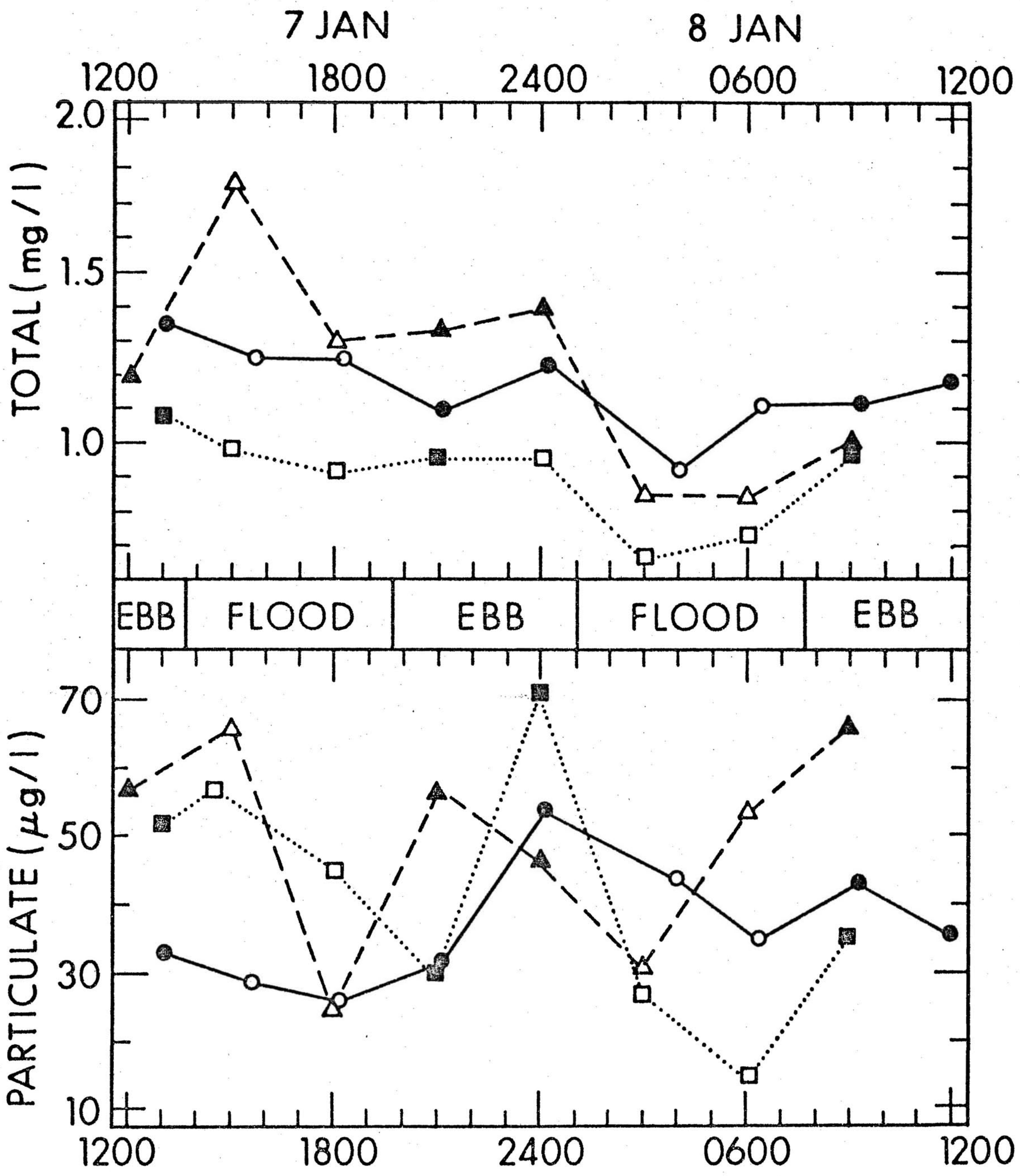

Fig. 4. Total and particulate organic carbon concentrations observed during the 24-hour study. Open and closed symbols denote flooding and ebbing tides, respectively. English Harbor: ○———●. North Pass: △———▲. Rapa Pass: □———■.

Table 1. Calculation of net organic carbon flux during the 24-hr study. Daily water flux from Gallagher et al. (1971). Daily organic carbon flux determined by multiplying the mean particulate organic carbon concentrations (POC) for each tidal stage (Fig. 4) by the water flux.

			Daily Flux		
Location	Tide Stage	Mean POC (µg/l)	Water (m^3)	Organic Carbon (kg)	Δ Organic Carbon (kg)
English Harbor	Flood	34	488×10^5	1659	
	Ebb	40	518×10^5	2072	
					413 Export
North Pass	Flood	44	15.1×10^5	67	
	Ebb	59	3.7×10^5	22	
					45 Import
Rapa Pass	Flood	36	7.5×10^5	27	
	Ebb	47	5.3×10^5	25	
					2 Import
					366 Net Export

balanced by the runoff input, so both items are omitted in the remainder of the discussion. The few analyses run (Schiesser, unpublished data) indicate the organic carbon concentration in Fanning Lagoon sediments is about 0.1%. Organic carbon could also be removed by fish coming into the lagoon to feed. This is logical to expect because of the much higher productivity in the lagoon than outside, but there are no data available to indicate whether this does or does not occur.

Balancing the above figures for production, import, and export, it is apparent that only 0.4% of the daily production of organic carbon is lost from the lagoon by tidal exchange. The remaining 99.6% must be respired by planktonic organisms in the lagoon. This respiration rate is equivalent to 31 $mgC/m^2/hr$.

Possible errors in estimating import and export have little effect on the conclusion that organic carbon cycling within Fanning Lagoon operates as a more or less closed system with only a slight loss to the surrounding ocean water. The rate of cycling is rapid as the turnover time (total amount/production rate) of organic carbon is only about 11 days.

The principal reason for the small export of organic carbon from the lagoon is the apparently low flushing rate of the lagoon. The salinity data of Gordon and Schiesser (1970) and the organic carbon data herein indicate that inflowing oceanic water at English Harbor, where most of the tidal exchange occurs, does not mix appreciably with lagoon water before flowing out. However, from the tidal volume transport data of Gallagher *et al.* (1971) it is apparent that each day there is a net inflow at North and Rapa passes and a net outflow at English Harbor of approximately 22×10^5 m^3. Dividing this amount into the total lagoon volume gives a flushing rate of about 230 days. In contrast, Von Arx (1954) calculated a flushing rate of 35 days for Bikini Lagoon.

In conclusion, it is apparent that the biological processes in the lagoon play an important part in the total ecology of Fanning Atoll. A low flushing rate and a high rate of phytoplankton production have worked together to form a rich and unique environment.

ACKNOWLEDGMENTS

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A NOTE ON THE PLANKTONIC PRIMARY PRODUCTION IN FANNING ISLAND LAGOON

Donald C. Gordon, Jr.

Department of Oceanography and Hawaii Institute of Geophysics

Robert O. Fournier

Department of Botany

George J. Krasnick

Department of Oceanography

ABSTRACT

A single series of representative observations indicate that both the productivity and standing crop of phytoplankton in Fanning Lagoon are much greater than reported in the lagoons of other Pacific atolls. Productivity, as measured by the radiocarbon method, averaged 9.29 $mgC/m^3/hr$, while chlorophyll a averaged 0.548 µg/l. Phytoplankton, principally dinoflagellates with some diatoms and coccoid blue-greens, averaged 12.6 x 10^4 cells/l. The relative richness of this lagoon compared to others appears to be due to the greater availability of nutrients which in turn is caused by the unique geographic features of the atoll.

INTRODUCTION

Various investigations, notably those of Sargent and Austin (1949) and Odum and Odum (1955) on Rongelap and Eniwetok atolls in the Marshall Islands, have demonstrated the remarkably high productivity of reef communities. In contrast, the few measurements made in the lagoons associated with these and other atolls indicate that both phytoplankton production and standing crop are quite low, in fact often not significantly higher than in the surrounding open sea (Sargent and Austin, 1949). As a result of these observations, there has emerged the concept that a "typical" tropical Pacific atoll consists of highly productive reefs encircling a relatively unproductive lagoon.

As part of a larger University of Hawaii program, planned as a multidisciplinary synoptic study of Fanning Atoll, an attempt was made to assess the applicability of the above-stated concept to this particular atoll.

METHODS

Observations were restricted to a single station in the northwestern part of Fanning Lagoon (Fig. 1) on 9 January 1970. This station (No. 26) was located in Suez Pond in 8m of water, about 200m from the closest line reef. Water samples for productivity measurements, chlorophyll analyses, phytoplankton enumeration, and enrichment for cultivation were collected at four depths (0.5, 2.5, 4.5, and 7.0 m) using an in situ pump (Schiesser, 1970). Productivity was determined using the radiocarbon method as outlined by Strickland and Parsons (1968). Two light and two dark bottles from each sampling depth were innoculated with radiocarbon bicarbonate solution (1.49 x 10^7 dpm/2ml). These were than attached to a weighted line and suspended from a buoy at their depths of collection. Light bottles were covered during the preliminary handling with aluminum foil to prevent excessive sun exposure. Following a 3-hr incubation period (1122 to 1430 hours), the contents of each bottle was filtered through a 25-mm, 1.2-μ Millipore® filter which was subsequently rinsed with filtered seawater, placed on a copper planchette, and stored in a desiccator. The filters were counted one month later in a Nuclear Chicago Model 1042 Geiger Counter. Both the efficiency of the geiger counter and the absolute activity of the radiocarbon solution were determined by liquid scintillation counting, according to the method of Wolfe and Schelske (1967).

Chlorophyll a was determined using the procedure of Strickland and Parsons (1968). Phytoplankton enumeration was carried out solely on Millipore® filters. This was accomplished by filtering 100ml of seawater through a 25-mm, 1.2-μ filter, followed by a distilled water rinse, desiccation, and eventual clearing and mounting on a slide with Permount®. Cultivation was attempted by adding variable amounts of seawater to previously prepared screw-top tubes containing three different sterile media: "AM" medium (Antia and Kalmakoff, 1965), "B" medium (Antia and Strickland, unpublished), and Ed Schreiber medium. Enriched samples were stored in an air-conditioned room out of direct sunlight until they could be placed in a proper incubator upon return to Hawaii several weeks later.

RESULTS

The data collected is summarized in Table 1, along with some relevant physical and chemical observations from the same station reported by Gordon (1971), Gordon and Schiesser (1970), and Smith et al. (1971). These observations indicate that the water at the station is well mixed.

With regard to the productivity observations, the mean for the four samples was 9.29 mgC/m^3/hr, while the range was from 7.30 to 11.58 mgC/m^3/hr. The maximum rate of photosynthesis occurred at 2.5 m where the light intensity was measured to be 25% of that at the surface. Integrating these data over the 8m water column, the production at this station equals 67 mgC/m^2/hr.

The chlorophyll a values were relatively constant: 0.515-0.567 μg/l. Expressing photosynthesis as a function of chlorophyll a concentration yielded a mean of 16.9 mgC/m^3/hr/mg chl a, while the range varied from 13.4 to 20.6. The maximum value was at 2.5m, presumably related to the high productivity measured at this depth. These ratios are high and have undoubtly been affected by the necessity of freezing the filters and conducting extractions a month later in Hawaii. Unfortunately the magnitude of this error is unknown.

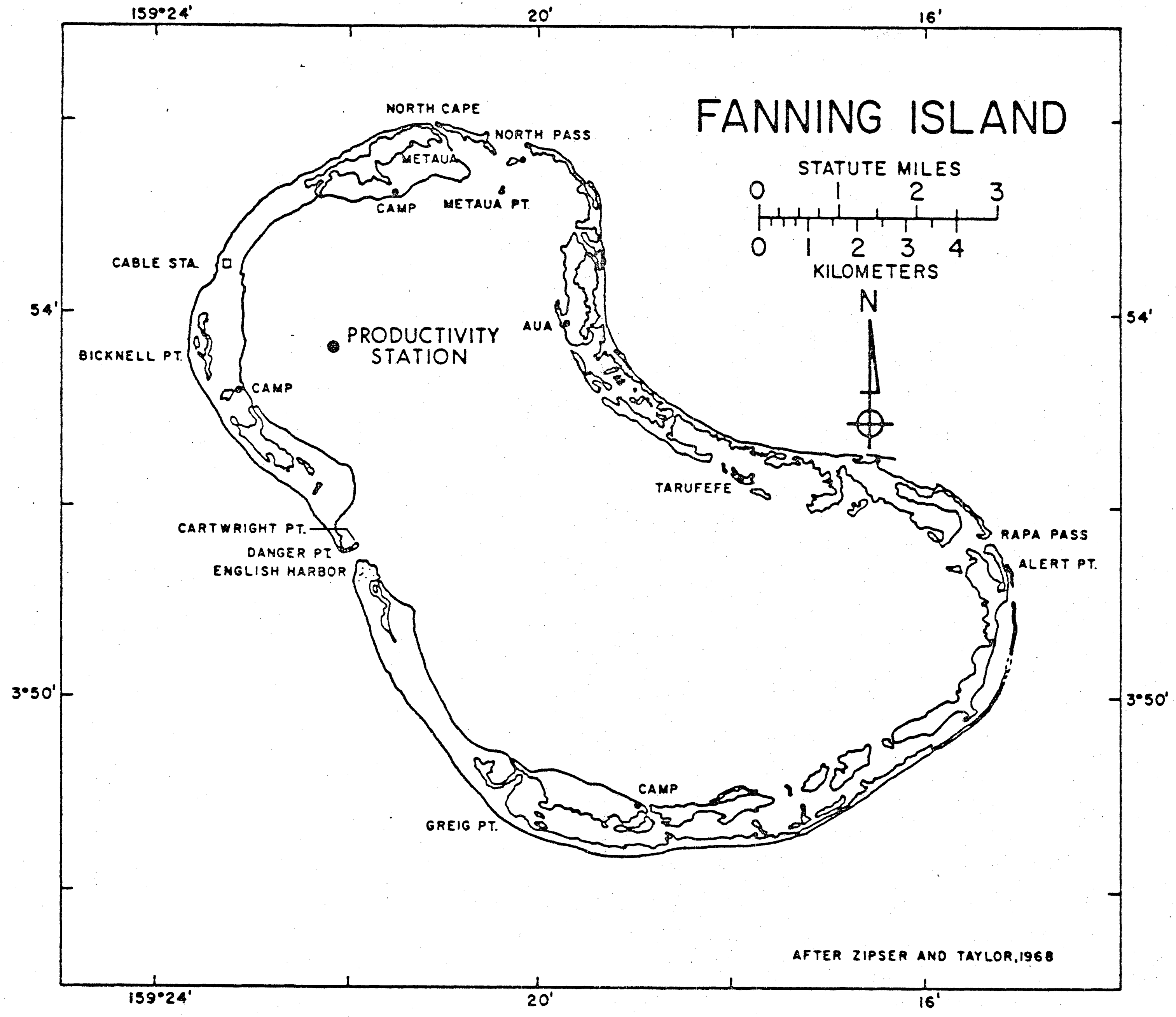

Fig. 1. Location of productivity station (No. 26), Fanning Lagoon.

Table 1. Summary of observations made at the productivity station in Fanning Lagoon; 9 January, 1970

	Depth (m)			
	0.5	2.5	4.5	7.0
Mean absolute CPM, Light	16,625	22,760	18,953	14,309
Mean absolute CPM, Dark	297	434	284	223
Photosynthesis (mgC/m^3/hr)	8.63	11.58	9.68	7.30
Chlorophyll *a* (μg/l)	0.515	0.562	0.567	0.546
Photosynthesis/Chlorophyll *a*	16.7	20.6	17.1	13.4
Cells per liter (x 10^4)	19.2	13.1	5.7	--
Total organic carbon (mg/l)	1.78	1.61	1.64	1.95
Carbonate alkalinity (meg/l)	2.09	2.05	2.05	2.05
pH	8.06	8.08	8.09	8.09
Salinity (°/oo)	35.147	35.153	35.165	35.175
Oxygen (ml/l)	4.06	4.09	4.06	4.24
Relative light intensity (%)	50	25	14	9

Since filters permit observation of only those organisms capable of withstanding the rigors of the procedure, the resultant cell counts must be considered as minimal estimates. Such is the case with the cell numbers presented in Table 1, yet despite this limitation it is obvious that quite a sizable phytoplankton standing crop was present at the time the radiocarbon observations were conducted. They ranged from a high of 19.2 x 10^4 cells/l at the surface to a low of 5.7 x 10^4 cells/l at 4.5 m, which was the deepest depth from which a sample was obtained. The mean of these three observations was 12.6 x 10^4 cells/l.

The standing crop, as seen on the filters, was composed of diatoms, coccoid blue-greens, and dinoflagellates, with the latter group dominant. In fact, the dinoflagellates were so abundant that they were the overwhelming majority of the cells enumerated. The single most prominent dinoflagellate was a gymnodinioid organism which possessed a cell wall of sufficient strength to resist disruption on the filters. These same organisms were also observed in the cultures although there the diatoms and blue-green predominated, due apparently to their greater adaptability to culture conditions. Nothing can be said about the phytoflagellate contribution to this standing crop since if they were present they were undoubtedly destroyed by the filtration process.

DISCUSSION

A single series of four observations made at one station does not constitute a comprehensive survey. However, several factors suggest that, although the absolute values of productivity may vary somewhat, the level of these values is representative of most of the lagoon. The physical and chemical observations of Gordon (1971), Gordon and Schiesser (1970), and Smith, *et al*. (1971) reveal that the conditions at the site of the productivity station are, with the sole exception of depth, quite representative of the lagoon as a whole. In addition, the well-known absence of seasonality (or conversely, the high degree of stability) in tropical phytoplankton cycles suggests that the level of these observations would vary only slightly with time.

Assuming that the station is representative of the entire lagoon and that the level of both productivity and standing crop measurements are relatively accurate, then it becomes immediately obvious (Table 2) that in terms of these parameters Fanning Lagoon is unique among those lagoons which have been studied to date. It contains a large standing crop of phytoplankton which is capable of fixing approximately ten times more carbon per unit volume than has been observed in both Eniwetok and Rongelap Lagoons (Sargent and Sustin, 1949; Doty and Capurro, 1961) and six to seven times more carbon per unit area than in the lagoon at Palau (Motoda, 1969). In fact, the productivity in Fanning Lagoon is so high that it compares favorably with measurements made in Kaneohe Bay (Doty and Capurro, 1961), a partially polluted embayment on the windward coast of Oahu, Hawaii.

Table 2. Summary of production and chlorophyll *a* data from Pacific Lagoons

		Production		Chlorophyll *a*	
Location	Method	mgC/m^3/hr	mgC/m^2/hr	µg/l	Reference
Marshall Islands:					
Eniwetok Lagoon	Oxygen	1.67	--	0.331	Sargent and Austin (1949)
"	Radiocarbon	0.75	--		Doty and Capurro (1961)
Rongelap Lagoon	Oxygen	0.42	--	0.174	Sargent and Austin (1949)
"	Radiocarbon	0.44	--		Doty and Capurro (1961)
Palau:					
Iwayama Bay	Ryther and Yentsch (1957)	--	7	--	Motoda (1969)
Anchorage		--	8	--	
Hawaii:					
Kaneohe Bay	Radiocarbon	5.39	70*	0.925	Doty and Capurro (1961)
Line Islands:					
Fanning Lagoon	Radiocarbon	9.29	49†	0.548	

* Assuming average depth of 13 m.

† Assuming average depth of 5 m.

The relatively high productivity and standing crop in Fanning Lagoon are due to very favorable growth conditions which are not found in the other lagoons studied. These are principally the availability of nutrients and to a lesser degree the turbidity of the water.

The level of nutrients in Fanning Lagoon is closely linked with four interrelated factors: (1) lagoon area, (2) nature of the surrounding land and precipitation, (3) lagoon depth, and (4) the residence time of water within the lagoon.

With an area of 103 km^2 (Fig. 1) Fanning Lagoon is considerably smaller than those in the Marshall Islands. Bikini and Rongelap lagoons are about 700 and 800 km^2, respectively. In addition to influencing the volume of the lagoon, this smaller area means that no point within the lagoon is ever far from a rich supply of nutrients in the form of a highly productive reef, the shoreline, or the islands themselves.

Fanning Atoll is one of only six atolls in the entire Pacific having dry land around virtually the entire rim. The only breaks in the land are the three narrow passes (Fig. 1). This land is completely vegetated, principally by coconut palms which support a copra industry employing the approximately 600 Gilbertese inhabitants of the atoll. Phosphate rock, presumably originating from guano deposits, is widespread (K. Roy, personal communication). The land therefore constitutes an important source of nutrients which would be carried into the lagoon by runoff. Fanning Atoll does in fact receive a moderate amount of rainfall; 81 inches/yr compared to 53 inches/yr at Eniwetok (Wiens, 1962). The presence of considerable runoff from the islands into Fanning Lagoon is indicated by the low salinities reported by Gordon and Schiesser (1970). The maximum rainfall generally occurs during April-May, so nutrient levels and therefore productivity at and just after that time might even be greater than reported herein for January.

The mean depth of Fanning Lagoon is approximately 5 m which makes it quite shallow compared to the 49 m average for the lagoons of the northern Marshall Islands (Sargent and Austin, 1949). These shallow conditions allow the wind to mix the entire water column, thereby aiding the circulation of nutrients and generally helping the entire regenerative process to operate at a high rate of efficiency.

The final factor which influences nutrient availability is the flushing time of the lagoon, or in other words the residence time of the nutrients already in the system. The shorter the flushing time, the lower the productivity since nutrient-rich water would continually be replaced by nearby, nutrient-poor ocean water. Using the current data of Gallagher, et al. (1971), Gordon (1971) calculates a flushing time of approximately 230 days. This is about seven times slower than the 35 days estimated for Bikini Lagoon (Von Arx, 1954), which is quite similar to the lagoons at Eniwetok and Rongelap. This long flushing or residence time is probably the single most important factor governing the size of the standing crop since it would allow a larger number of organisms to recycle the available material.

Due to the high suspended load, principally calcium carbonate particles, the waters of Fanning Lagoon are extremely turbid, except for a clear water area just inside English Harbor (Smith, et al., 1971). As a result, half of the incident radiation is absorbed in the first half-meter (Table 1). Therefore, most of the water column has relatively low light intensities which are the most favorable for photosynthesis. In contrast, the water in Rongelap Lagoon has a very small suspended load and an average Secchi disc reading of 18 m (Sargent and Austin, 1949). In such cases, light intensities in the upper part of the water column are probably high enough to inhibit photosynthesis considerably.

In conclusion then, it appears that both the phytoplankton production and standing crop in Fanning Lagoon are much higher than has been previously measured in the lagoons of other atolls, principally those of the Marshall Islands. These higher measurements are believed to be due principally to the greater input and retention of nutrients in the lagoon which in turn is due to the geographic features of the atoll.

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NOTE ON COCCOLITHOPHORIDS IN THE SURFACE WATERS AROUND FANNING ATOLL

R. O. Fournier

Department of Botany

A study of suspended calcium carbonate in the surface waters around Fanning Atoll was made by Smith, et al. (1971). In this study, water samples were taken at various locations around the atoll, and at English Harbor where falling tides eject a plume of lagoon water. The water samples were filtered through 0.8 μ millipore® filters. The filters were then washed with fresh water and air-dried. Some were mounted on glass slides for microscopic examination. Three of the slides were examined for coccolithophorids: sample 8, taken in the plume; sample 26, taken outside the plume on the western side of the atoll (the leeward side); and sample 21, taken on the eastern side of the atoll (Fig. 1). The three water samples were drawn from a depth of 5 m, and 2.5 liters of water were filtered to make the slides.

Two transects were run across each slide. In order of decreasing abundance, the species of coccolithophorids observed were: 1. *Coccolithus huxleyi*, 2. *Cyclococcolithus fragilis*, 3. *Gephyrocapsa oceanica*, 4. *Thoracosphaera heimii*, 5. *Rhabdosphaera stylifer*, and 6. *Coccolithus pelagicus*.

The species composition in all three samples was almost identical with regard to the coccolithophorids (Table 1). In samples 26 and 21 there was little difference in species composition or in number of individuals present, but in sample 8 (the plume water) there was a marked decrease in the abundance of coccolithophorids relative to the other samples. This is in keeping with the observations of Gordon, et al. (1971) on the phytoplankton of Fanning lagoon, which showed that the most abundant phytoplankters in the lagoon are dinoflagellates and not coccolithophorids.

The low number of species, but high cell numbers found in all three samples, is contrary to what is expected in the tropics. In this case, the presence and influence of the atoll is most likely the cause of the anomaly.

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Table 1. Coccolithophorids observed in three samples from the surface waters around Fanning Atoll. All samples were taken from the 5 m depth.

Location	Species Observed	Notes
Sample 8 (in the plume)	Coccolithus huxleyi Cyclococcolithus fragilis Gephyrocapsa oceanica Thoracosphaera heimii	Coccolithophorids appear less abundant than in Sample 26. Phytoplankton dominated by diatoms.
Sample 26 (outside plume on leeward side)	Coccolithus huxleyi Cyclococcolithus fragilis Rhabdosphaera stylifer	Coccolithophorids are extremely abundant, they are the dominant phytoplankton.
Sample 21 (outside plume on windward side)	Coccolithus huxleyi Cyclococcolithus fragilis Coccolithus pelagicus	Sample 21 is much like sample 26.

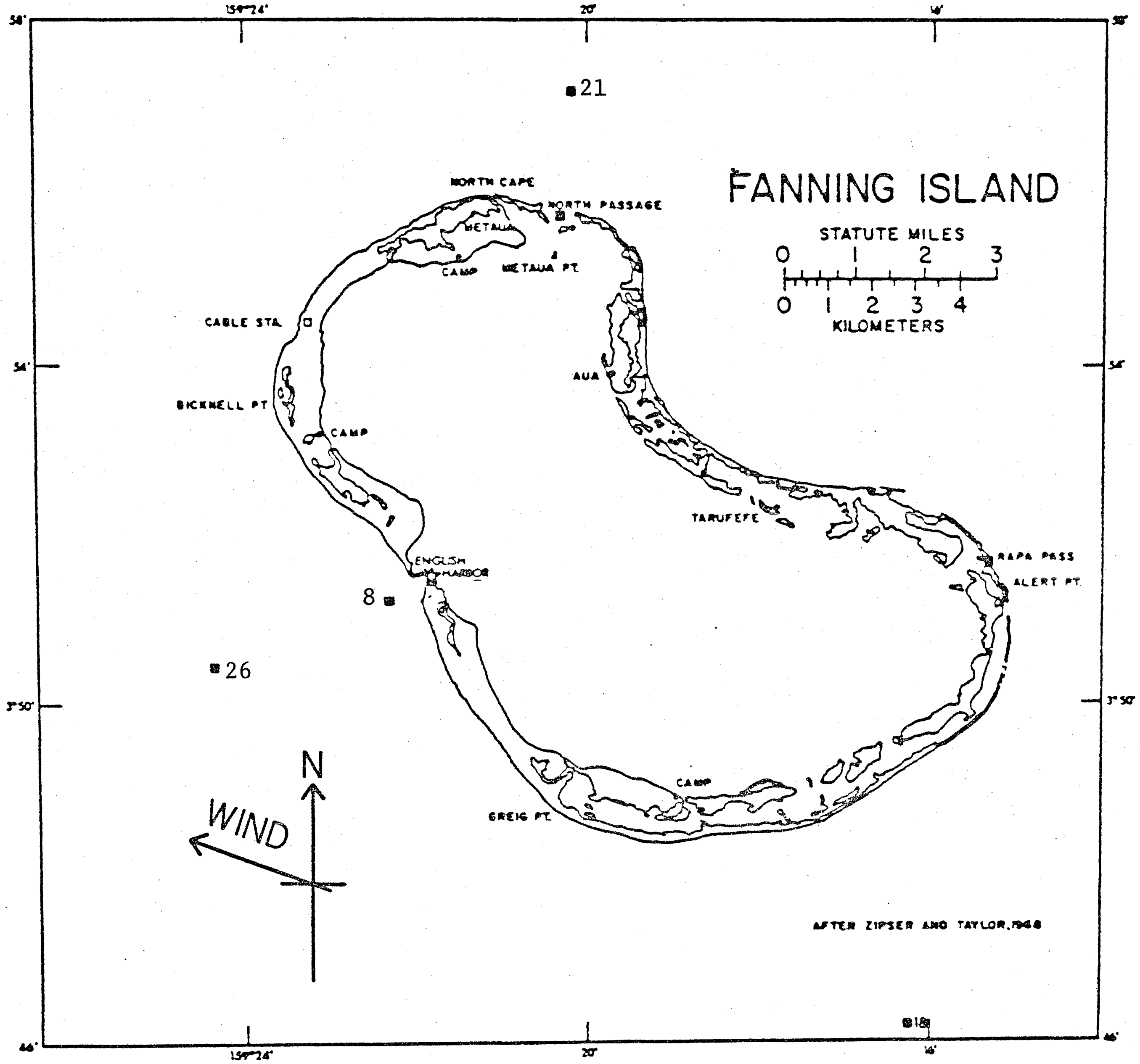

Fig. 1. Location of stations 8, 21, and 26.

FLUX OF SUSPENDED CALCIUM CARBONATE ($CaCO_3$), FANNING ISLAND LAGOON

S. V. Smith, K. J. Roy, H. G. Schiesser,
G. L. Shepherd, and K. E. Chave
Department of Oceanography and Hawaii Institute of Geophysics

ABSTRACT

A plume of turbid, $CaCO_3$-laden water (0.24 mg/l) is expelled from English Harbor, Fanning Atoll, on outgoing tides. On incoming tides, the concentration is 0.36 mg $CaCO_3$/l. At the two other passes of the atoll, incoming $CaCO_3$ concentrations also are higher than outgoing concentrations. Lagoon waters contain 1 mg $CaCO_3$/l in the clear central portion of the lagoon and 4 mg $CaCO_3$/l elsewhere. Offshore concentrations out of the plume area are 0.03 mg $CaCO_3$/l. The lagoon and plume $CaCO_3$ material is reef-derived detritus (aragonite and high-Mg calcite). Offshore $CaCO_3$ particles are primarily coccoliths (low-Mg calcite).

During a 24-hour survey 10 tons of suspended $CaCO_3$ were transported into the lagoon. It is likely that the English Harbor plume represents little or no sediment loss from the lagoon.

The plume debris is interpreted to be material produced on the outside fringing reefs, sucked into the lagoon on incoming tides, and subsequently expelled. Production of $CaCO_3$ in the lagoon may be filling the lagoon faster than sea level is rising.

INTRODUCTION

A plume of turbid water flows out of English Harbor, the major pass through Fanning Atoll, on each falling tide (Fig. 1). Because the turbidity results primarily from suspended calcium carbonate ($CaCO_3$) (Backus, 1968), the flux of suspended load is crucial in the analysis of lagoon sedimentation. Chave (unpublished data) has demonstrated the feasibility of tracing both the quantity and the mineralogy of reef-derived material moving westward from Jamaica. That investigation inspired us to measure the amount of calcareous material in Fanning Island lagoon, to monitor the amount of this material leaving the lagoon, and to trace the path of the material outside the lagoon.

Materials and Methods

Samples were gathered for quantitative analysis of suspended $CaCO_3$ content, for mineralogy, and for microscopic analyses of $CaCO_3$ grain size and morphology. A generalized outline of procedure from sample collection through sample analysis will be presented in this section.

Offshore samples were collected aboard the R/V MAHI, using 30-l Niskin bottles. Water depths reported are uncorrected for wire-angle, which was generally low at the surface. Surface, midwater, and bottom samples were collected in English Harbor using a skiff and a small immersion pump. The water was pumped directly into clean 4-l plastic ("bleach-type") bottles.

At North Pass, samples were scooped into the 4-l bottles by a wader. At Rapa Pass and at various lagoon localities a skiff was used and the water was scooped or collected with the immersion pump.

Most samples were filtered through 0.8 μ Millipore® filters. Some English Harbor samples were filtered through Gelman type A glass fiber filters. The offshore samples were filtered within a few minutes of collection. Samples from all the passes sat for a few hours up to about two days before filtration.

Approximately 5- to 10-l samples were filtered for the offshore samples. Generally the pass sample volumes were 1 l or less. The volume of water filtered was recorded. For many stations a second sample, approximately the same volume as the first, was filtered for x-ray diffraction analysis, and a third sample--about 250 ml--was filtered for microscopic analysis. In the case of the offshore samples, this third sample proved to have too little material, and part of the x-ray filter served for microscopic examination. All filters were rinsed two times with distilled water after filtration in order to remove any remaining seawater.

Quantitative analysis of $CaCO_3$ content was carried out either by EDTA analysis of total divalent cation (Land, 1966) using .01 or .001 molar EDTA or by infrared analysis of CO_2 (Smith, 1970).

Permount® (index of refraction--1.54) was used to clear the filters for microscopic analysis.

For x-ray diffraction analysis, filters were dissolved in acetone and the residue after centrifugation was placed on a slide. No mineral discrimination beyond "high-Mg calcite", "low-Mg calcite", and aragonite was attempted.

Analysis of variance has been used in order to pool quantitative data and in order to recognize patterns in those data. The notation employed follows that of Snedecor (1956).

Fig. 1. Aerial photograph of the plume of turbid water flowing out of English Harbor on an outgoing tide. Photograph by R. DeWreede.

Results

Suspended Load Analysis

Suspended load concentrations of $CaCO_3$ are reported in Tables 1 through 4. Before differences among stations are presented, some consideration must be given to the within-sample variability. Sample localities 40 through 49, reported in Table 1, provide data from which this variability has been assessed. At each of these lagoon stations a pair of samples was collected off the bow of the skiff and a third sample was collected off the stern. For pairs of bow samples the mean coefficient of variation ($100 \times s/X = V$) is 15 percent. The mean coefficient of variation is 14 percent for samples from each of the three sample bottles at a station, and for replications within bottle, the coefficient of variation is 12 percent. Thus, there appears to be no more variability from one sample to the next at a station than there is within a sample; also, no evidence exists for small-scale suspended load "patchiness".

Provided that the distilled water rinse has removed all dissolved sea salts from the filter, that the volume of water filtered is recorded relatively accurately, and that a satisfactory titration endpoint is reached, the titration error should be small relative to the variability seen. Therefore, the variability can probably be attributed primarily to sample inhomogeneity introduced by materials sticking to the sample-bottle wall and from the presence of occasional large grains. Some large grains were seen on filters; the presence of others was occasionally suggested by extremely large titration volumes. Such samples were refiltered and re-titrated if sufficient water was available. Some filters saved for other uses were later used for extra quantitative analyses.

Because offshore sample volumes were larger than lagoon and pass samples, and because the samples were filtered before the grains had much time to stick to container walls or to settle, there probably was a smaller error resulting within the sampling bottles. Nonetheless, 15 percent is taken to be the analytical error for all samples.

Figure 2 illustrates the suspended load localities within the lagoon, and Figure 3 shows one area of more intensive sampling ("Suez Pond" in Roy and Smith (1971). The data of Table 1 are summarized in Table 7 and generalized in Figure 4. Several characteristics need pointing out.

Observation of the lagoon reveals a distinctive interface between clear water in the vicinity of English Harbor and turbid water elsewhere. The approximate boundary between the two water masses is illustrated in Figure 4; the exact position of the boundary--particularly the eastern boundary--fluctuates with tide and weather conditions. The clear water area has a mean suspended load content of about 1 mg $CaCO_3$/1 (Table 7).

Table 1. Suspended CaCO$_3$ concentrations in Fanning Lagoon. All values were obtained by EDTA titration. Sample localities are shown on Figures 2 and 3.

Station Number	Sample Depth (m)	mg CaCO$_3$/l
28	0	4.15
	2	4.43
	4	22. *
29	0	6.94
	3	5.86
	6	12. *
30	0	5.08
	2	4.36
	5	14. *
32	0	4.22
	2	3.39
	4	3.65
	6	4.02
33	0	1.98
34A	0	4.52
B	0	4.30
C	0	3.70
D	0	3.85
E	0	6.42
F	0	5.05
35	0	3.48, 2.80
36	0	3.33
37	0	3.07
38	0	2.75
39	0	3.40
40 stern	0	3.32
bow	0	4.68
bow	0	3.40, 3.94
41 stern	0	3.27
bow	0	3.12
bow	0	3.84
42 stern	0	3.63
bow	0	2.88
bow	0	3.30
43 stern	0	4.75
bow	0	4.28
bow	0	4.27, 5.41
44 stern	0	3.52
bow	0	4.46
bow	0	3.52
45 stern	0	4.24, 3.62
bow	0	3.18
bow	0	2.50
46 stern	0	2.94
bow	0	4.35
bow	0	3.12
47 stern	0	3.02
bow	0	3.82
bow	0	2.94, 3.58
48 stern	0	3.42
bow	0	3.80
bow	0	3.26, 3.57
49 stern	0	3.40
bow	0	2.65
bow	0	3.74
50	0	5.47
	2	6.32
	4	6.89
51	0	6.31
	3	6.38
	5	83. *
52	0	1.31
	3	2.70
	6	1.15
	9	1.30
	12	2.40
53	0	0.95
54	0	2.20, 2.80
55	0	1.00
56	0	0.65
57	0	1.98
58	0	2.64
59	0	2.78
60	0	3.08
61	0	0.65, 1.00
62	0	3.18
63	0	3.30

* Pump apparently hit bottom and stirred sediment up. These values not used in calculations.

Table 2. Suspended $CaCO_3$ concentrations (mg/liter) at various depths at English Harbor for the 6 sampling locations during the 24-hour survey from 7 January to 8 January 1970. Values in parentheses were obtained by infrared analysis. Other values were determined by EDTA titration. Sample localities are shown on Figure 5.

Buoy #	1	2	3			4			5			6		Direction of flow*
Time	0m	0m	0m	10m	18m	0m	10m	20m	0m	10m	18m	0m	10m	
1240	(0.74)	(0.50)	(0.34)	(0.40)	(0.45)	(0.29)	(0.32)	(0.23)	(0.22)	(0.21)	(0.22)	(0.34)	(0.36)	out
1505	1.48	0.20	(0.04)	0.28	0.11	(0.15)	0.29	(0.16)	(0.18)	0.34	(0.17)	(1.07)	1.97	in
1800	1.23	0.10	(0.14)	0.10	0.06	(0.18)	0.40	(0.30)	(0.33)	0.38	(0.07)	(0.37)	0.40	in
2055	0.32	0.18	0.35	0.20	0.20	0.19	0.22	0.15	0.15	0.20	0.11	0.16	0.16	out
2400	0.48	0.49	--	0.41	--	(0.04)	(0.03)	(0.01)	--	0.12	--	--	0.22	out
0340	0.21	0.02	--	0.18	--	0.29	0.30	0.50	--	0.22	--	--	0.13	in
0640	0.71	0.20	--	0.13	--	0.40	0.29	0.51	--	0.19	--	--	0.35	in
0903	0.25	0.14	--	0.18	--	0.12	0.36	0.36	--	0.35	--	--	0.19	out
1154	0.22	0.22	--	0.25	--	0.10	0.13	0.10	--	0.18	--	--	0.06	out

* Relative to lagoon

Table 3. Suspended $CaCO_3$ concentration (mg/liter) at North Pass and Rapa Pass during the 24-hour survey from 7 January to 8 January 1970. All samples were analyzed by EDTA titration. Sample localities are shown on Figure 2.

Time	North Pass mg $CaCO_3$/l	Direction of flow*	Rapa Pass mg $CaCO_3$/l	Direction of flow*
1200	0.82	in		
1300			1.15	out
1500	0.71	out	3.60	in
1800	0.60	in	0.90	in
2100	0.37	in	0.66	out
2400	0.73	out	0.99	out
0300	0.82	in	0.60	in
0600	2.8	in	0.96	in
0900	0.34	out	1.00	out

* Relative to lagoon

Table 4. Concentration of suspended $CaCO_3$ in offshore samples (mg/liter). All values were obtained by EDTA titration. Sample localities are shown on Figure 2.

Station*	Station Depth (m)	Sample Depth (m)	$CaCO_3$ mg/liter
1(c)	20	0	0.04
		10	0.04
2(a)	90	0	0.16
		10	0.16
		25	0.03
3(c)	360	0	0.11
		25	0.13
4(b)	no record	0	0.02
		50	0.03
		100	0.02
		200	0.01
		300	0.01
		400	0.01
5(d)	90	0	0.03
		10	0.04
		25	0.05
6(a)	90	5	0.33
7(a)	500	5	0.07
		25	0.06
8(c)	660	5	0.04
		25	0.03
9(b)	400	5	0.01
		25	0.06
10(b)	280	0	0.09
		5	0.02
		25	0.03
		50	0.02
		100	0.02
11(b)	720	0	0.03
		25	0.03
		50	0.05
		100	0.04
		200	0.02
12(b)	1200	0	0.02
		25	0.02
		50	0.04
		100	0.05
		200	0.02
13(d)	90	5	0.02
		25	0.03
14(a)	90	5	0.21
15(c)	860	10	0.04
		50	0.03
		200	0.07
16(c)	no record	5	0.07
		25	0.03
17(f)	620	5	0.03
		25	0.03
		100	0.04
		200	0.02
18(f)	1040	5	0.03
		25	0.04
		100	0.03
		200	0.02
19(f)	1040	5	0.03
		25	0.03
		100	0.03
		200	0.02
20(f)	1000	10	0.02
		100	0.04
		200	0.05
21(f)	1060	5	0.04
		25	0.03
		100	0.02
		200	0.01
22(f)	660	5	0.03
		25	0.05
		100	0.02
		200	0.01
23(e)	1800	5	0.03
		25	0.04
		100	0.02
		200	0.01
24(f)	440	5	0.04
		25	0.03
		100	0.07
		200	0.03
25(c)	870	5	0.05
		25	0.03
		100	0.10
		200	0.02
26(f)	no record	5	0.03
		25	0.03
		100	0.03
		200	0.02

*The stations can be separated into objective classes useful to text discussions: (a) in obvious plume, (b) in drogue path out of plume, (c) in vicinity of English Harbor out of plume, (d) at plume locality at slack tide immediately before ebb tide, (e) in extrapolated trajectory of drogue path, and (f) around the perimeter of the island.

Eastward from the clear water area the turbidity apparently increases gradually to about 3 mg $CaCO_3$/l (Fig. 4) while northward, the turbidity increases more abruptly to 6 mg $CaCO_3$/l. Presumably the turbidity south of the clear water area is similar to that of the northern part of the lagoon.

The intensely sampled Suez Pond area has a mean suspended load of about 4 mg $CaCO_3$/l (Fig. 4). No significant areal variability could be detected there.

The mean $CaCO_3$ content of the turbid water area is about 4 mg $CaCO_3$/l (Table 7).

English Harbor data are reported in Table 2. From 1240 hours, 7 January 1970, until 1154 hours the following day, samples were collected at approximately 3-hour intervals at the six buoy locations shown in Figure 5. Samples were collected at one to three different depths at each station.

As indicated in Table 2, the $CaCO_3$ content of some samples was determined by EDTA titration at Fanning Island. Other samples were dried and returned to the University of Hawaii for infrared analysis of $CaCO_3$. Analysis of variance (case 1 in Table 5) indicates that no statistically significant difference exists between the results of the two analytical methods. Therefore, data were pooled for all subsequent statistical considerations.

Sample collection at each buoy was not done consistently for all depths during each sampling period. If the variability among depths at a time was significantly less than the overall variability, it would be convenient to pool data at all depths for each buoy at a time in order to arrive at a simpler data array and a complete buoy-time data matrix. Case 2 in Table 5 justifies this pooling procedure, and such a matrix was used for subsequent calculations.

Case 3 in Table 5 is a further analysis of the suspended load variability at the English Harbor buoys. Variability among the buoys (case 3a) is greater than error variability by only a small amount (significance level = 0.1); variability from one time to another at a buoy is much greater than error variability (significance level = 0.025).

Snedecor (1956) presents and modifies a technique by Tukey by which the members of the sample population can be separated and ranked according to their contribution to the sample variance (Table 6). By this technique buoys 1 and 6 (the end buoys) differ from one another in their suspended load concentration (0.63 versus 0.37 mg $CaCO_3$/l) and from the four central buoys (with an average of 0.23 mg $CaCO_3$/l). The pattern of significant differences among the times is more complex. Six times of significantly different suspended loads can be differentiated. If the times are related to direction of tidal current flow, the following pattern emerges. Incoming water tends to be more turbid than outgoing water. One instance of relatively clear incoming water and one instance of relatively turbid outgoing water break the pattern. Suspended load concentrations of incoming and outgoing water are summarized in Table 7.

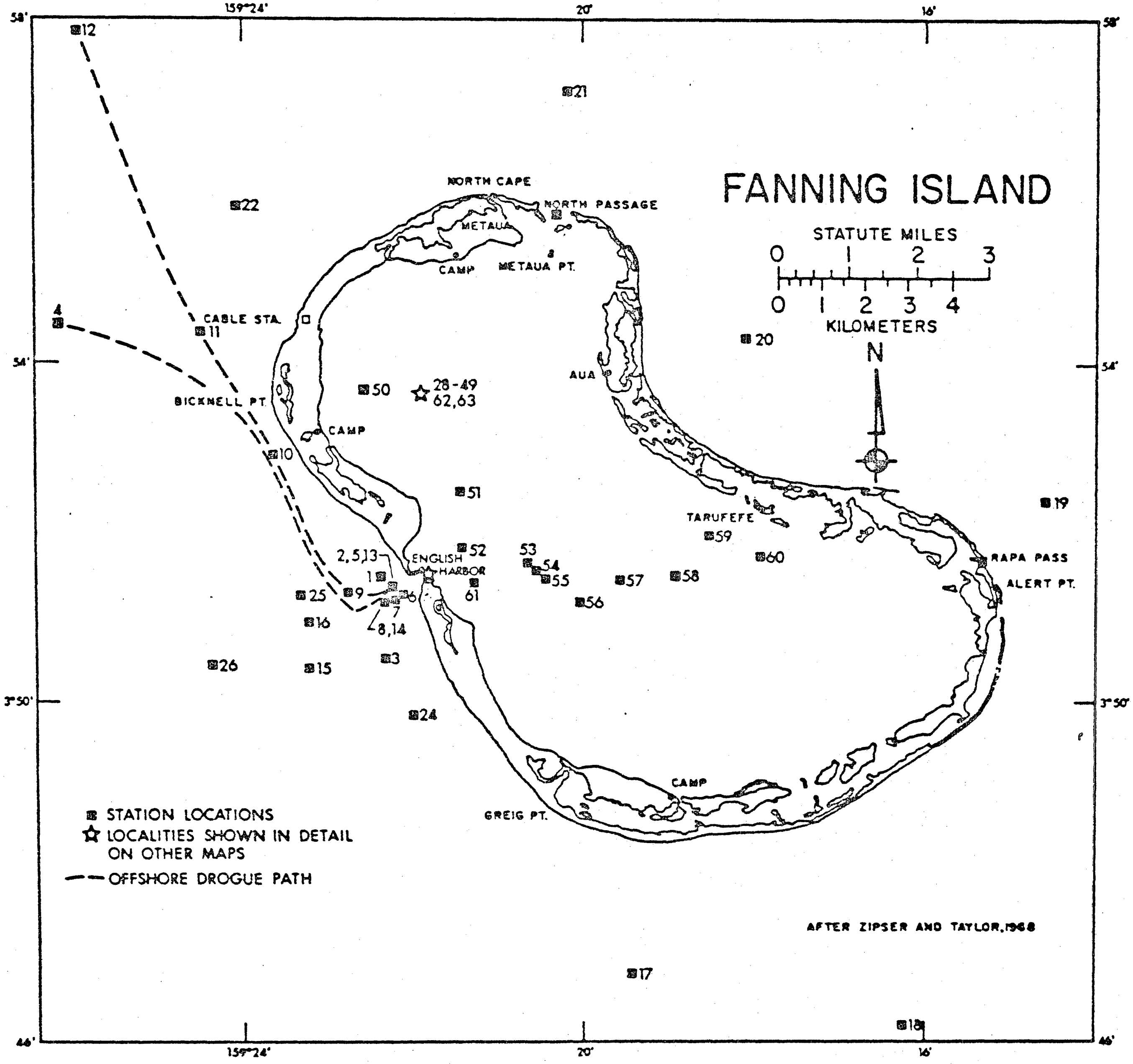

Fig. 2. Map of Fanning Island, showing suspended load sampling localities. The areas marked by stars are shown on Figures 3 and 5. Also shown on this figure are the 12-hour trajectories of drogues released in the English Harbor plume on outgoing tides.

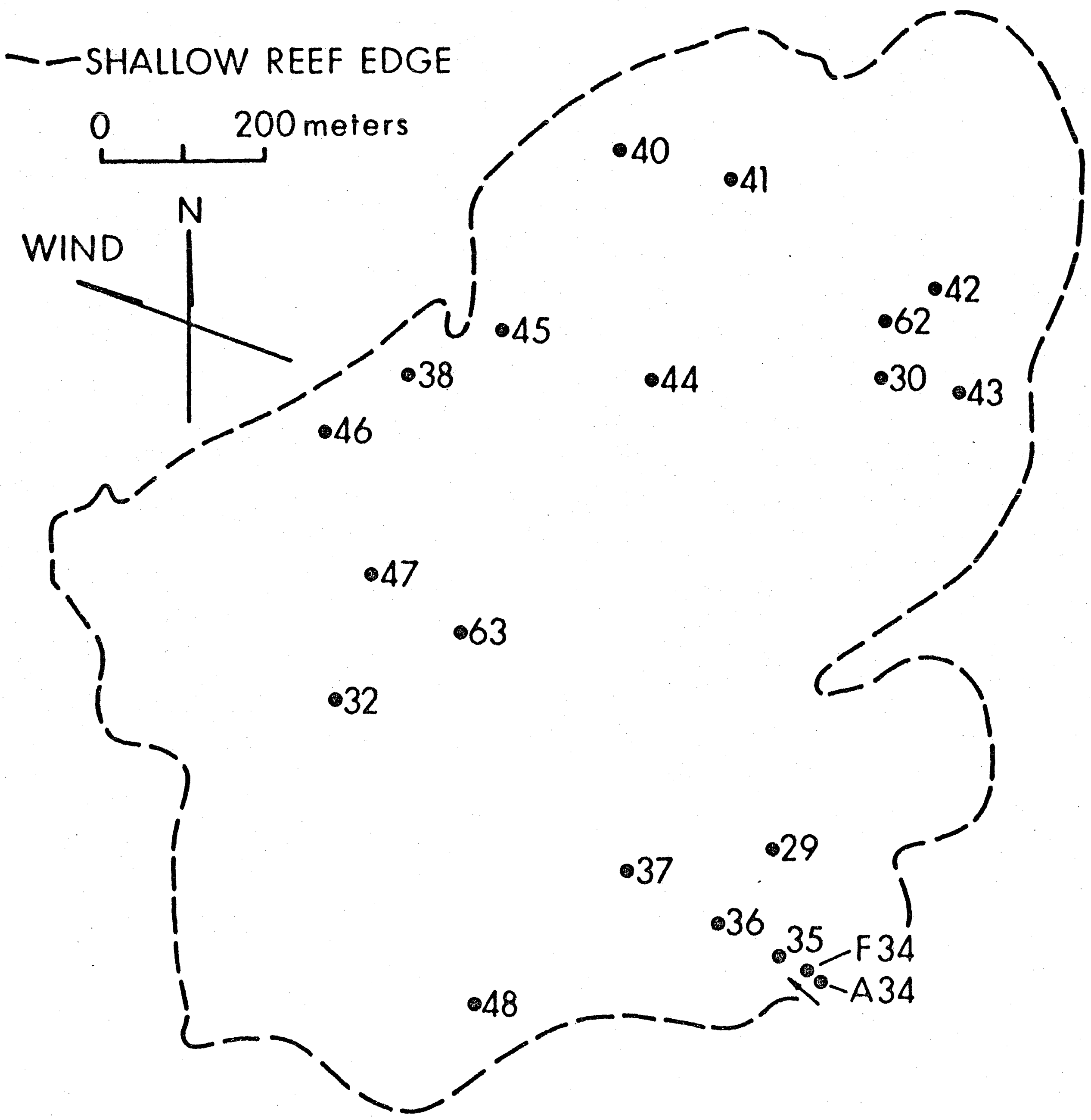

Fig. 3. Suspended load sampling localities in Suez Pond (marked by a star in Fig. 2).

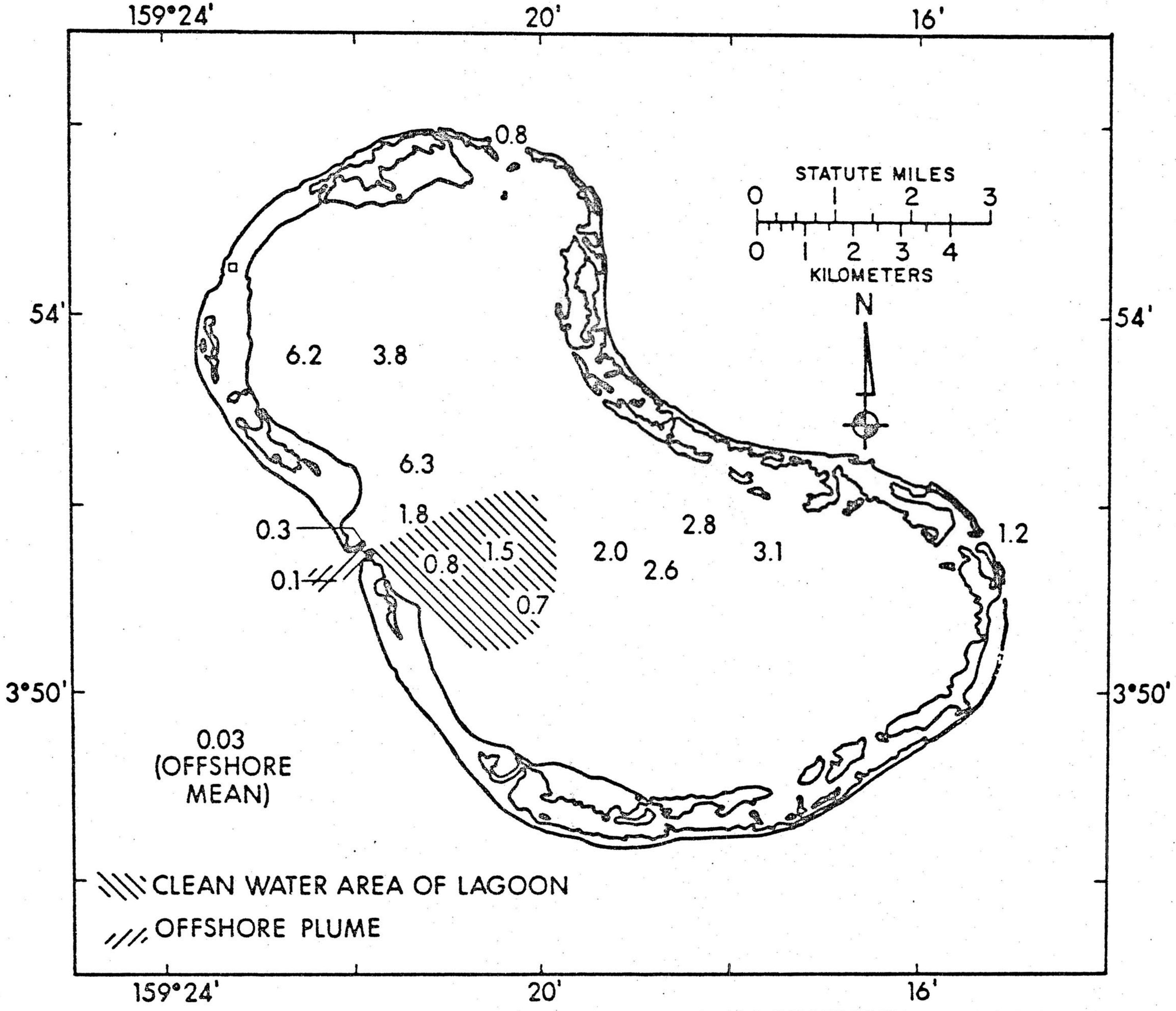

Fig. 4. Generalized map of suspended load $CaCO_3$ concentrations in mg/l at Fanning Island. The approximate locations of the clear water central portion of Fanning lagoon and of the offshore plume are also shown.

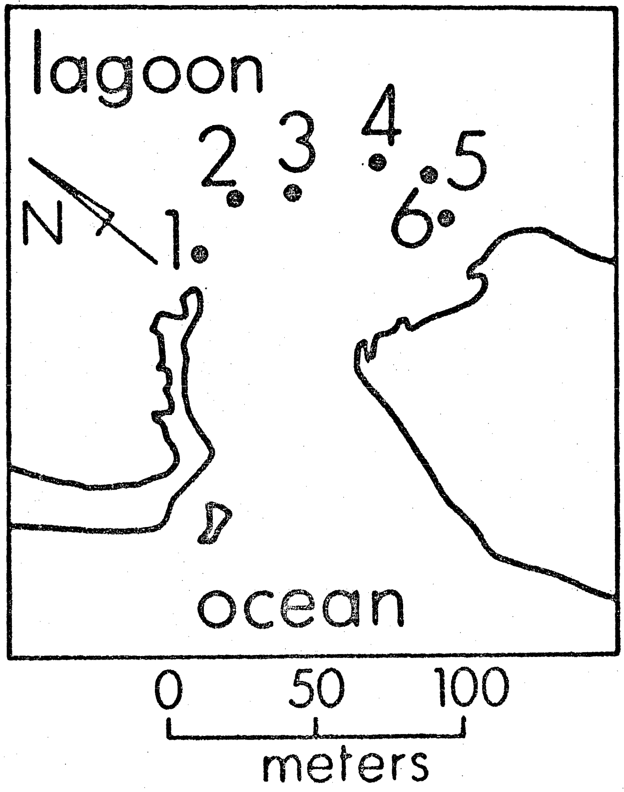

Fig. 5. English Harbor buoy locations, 24-hour survey (marked by a star in Fig. 2).

Table 5. Analyses of variance, suspended load data. A significance level of 0.1 (90% confidence) has been taken as the arbitrary level for accepting or rejecting the null hypothesis. If the significance level is higher than 0.1 (<90% confidence of a difference between the two populations in question, the null hypothesis is accepted)

	Null Hypothesis:	F Ratio	Degrees of Freedom	Significance Level for rejecting Null Hypothesis
1.	The variability between analytical methods is no greater than the variability within the methods. For English Harbor 24-hour data, (accept).	0.5	1, 90	0.5
2.	The overall English Harbor variability is no greater than the variability at each buoy (reject).	10.7	20, 38	<0.0001
3a.	At a time at English Harbor variability from one buoy to another is no greater than error variability (reject).	3.5	5, 40	0.025
3b.	At a buoy at English Harbor variability from time to time is no greater than error variability (reject, barely).	1.9	8, 40	0.1
4.	Variability between English Harbor offshore data and English Harbor 24-hour data is no greater than variability within the two data sets (accept).	2.2	1, 96	0.75

Table 6. Snedecor (1956, p. 251; 301) presents a method modified from Tukey for deciding which members of a population are contributing significantly to the variance and which are not. The difference between each pair of population means is examined to decide if those two differ from one another. The upper part of this table considers differences between buoys; the lower part considers differences between times. Means are reported in mg $CaCO_3$/liter; significant differences (at p = 0.05) are underlined.

(a) Differences between buoys; differences greater than 0.05 mg/liter are significant.

Buoy #	$\bar{X}$	$\bar{X}_i-\bar{X}_5$	$\bar{X}_i-\bar{X}_3$	$\bar{X}_i-\bar{X}_2$	$\bar{X}_i-\bar{X}_4$	$\bar{X}_i-\bar{X}_6$
1	0.63	$\underline{0.42}$	$\underline{0.40}$	$\underline{0.40}$	$\underline{0.39}$	$\underline{0.26}$
6	0.37	$\underline{0.16}$	$\underline{0.14}$	$\underline{0.14}$	$\underline{0.13}$	
4	0.24	0.03	0.03	0.03		
2	0.23	0.02	0.00			
3	0.23	0.02				
5	0.21					

(b) Differences between times; Differences greater than 0.07 mg/liter are significant.

Time	Flow*	$\bar{X}$	$\bar{X}_i-\bar{X}_{1154}$	$\bar{X}_i-\bar{X}_{0340}$	$\bar{X}_i-\bar{X}_{2055}$	$\bar{X}_i-\bar{X}_{0903}$	$\bar{X}_i-\bar{X}_{2400}$	$\bar{X}_i-\bar{X}_{0640}$	$\bar{X}_i-\bar{X}_{1800}$	$\bar{X}_i-\bar{X}_{1240}$
1505	in	0.56	$\underline{0.39}$	$\underline{0.37}$	$\underline{0.35}$	$\underline{0.33}$	$\underline{0.27}$	$\underline{0.23}$	$\underline{0.16}$	$\underline{0.14}$
1240	out	0.42	$\underline{0.25}$	$\underline{0.23}$	$\underline{0.21}$	$\underline{0.19}$	$\underline{0.13}$	$\underline{0.09}$	0.02	
1800	in	0.40	$\underline{0.23}$	$\underline{0.21}$	$\underline{0.19}$	$\underline{0.17}$	$\underline{0.11}$	0.07		
0640	in	0.33	$\underline{0.16}$	$\underline{0.14}$	$\underline{0.12}$	$\underline{0.10}$	0.04			
2400	out	0.29	$\underline{0.12}$	$\underline{0.10}$	$\underline{0.08}$	0.06				
0903	out	0.23	0.06	0.04	0.02					
2055	out	0.21	0.04	0.02						
0340	in	0.19	0.02							
1154	out	0.17								

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* relative to lagoon.

Table 7. Summarized Characteristics of Suspended $CaCO_3$ Concentration, Fanning Island

Population	Number of samples	Mean mg/liter	Standard Deviation (mg/liter)	Coeff. of variation (%)
Lagoon				
a. turbid	68	3.771	1.252	33
b. clear	5	1.186	0.747	63
English Harbor				
a. outgoing	50	0.244	0.141	58
b. incoming	42	0.360	0.395	110
North Pass				
a. outgoing	3	0.593	0.220	37
b. incoming	5	1.082	0.978	90
Rapa Pass				
a. outgoing	4	0.950	0.207	22
b. incoming	4	1.515	1.399	92
Outside				
a. obvious plume	7	0.143	0.114	80
b. drogue path, out of plume	23	0.029	0.019	66
c. vicinity of English Harbor plume, out of plume	15	0.057	0.034	60
d. plume locality, slack tide	5	0.034	0.011	32
e. extrapolated trajectory, drogue path	4	0.025	0.013	52
f. around perimeter of island	31	0.031	0.013	42

The North Pass and Rapa Pass (Fig. 2) data arrays (Table 3) are considerably simpler than the English Harbor data. At North Pass suspended $CaCO_3$ concentrations range from 0.34 to 2.8 mg $CaCO_3$/l and average 0.90 mg $CaCO_3$/l. At Rapa Pass the range is 0.60 to 3.6 mg $CaCO_3$/l and the average is 1.2 mg $CaCO_3$/l. At both passes the highest suspended load concentration occurs on an incoming current, and the lowest concentration is on an outgoing current. Table 7 lists the characteristic of ebb and flood-tide suspended loads.

The initial attempt of offshore sampling was to trace the path of the turbid water plume leaving English Harbor. The procedure consisted of bringing the R/V MAHI as close to the mouth of English Harbor as was prudent near the beginning of the outgoing current. A drogue (consisting of a 1-m diameter nylon parachute with enough weight to sink it, a 10-m line to a surface float, and a 3-m line from the surface float to a spar buoy containing an orange flag and radio transmitter) was dumped into the plume at this point and suspended load samples were taken. The spar buoy was repeatedly approached, and samples were taken. Such a procedure was undertaken twice with similar results. After moving southwestward about 1 km to the edge of the obvious plume visible in Figure 1, the drogue was entrained in a northwesterly current and moved on that bearing at approximately 25 cm/sec until retrieved (Fig. 2).

In addition to the samples collected along the drogue path, numerous other samples were taken in the vicinity of English Harbor and around the perimeter of Fanning Island. The sample localities, illustrated in Figure 2, can be divided into six objective categories: (a) in the obvious plume, (b) in the drogue path but out of the obvious plume, (c) in the vicinity of English Harbor plume but out of the obvious plume, (d) at the plume locality but at slack tide when the plume is not present, (e) in the extrapolated trajectory of the drogue path northwest of the island, and (f) around the perimeter of the island. The sample categories are noted in Table 4, and the population characteristics of the categories are noted in Table 7.

Stations taken in the obvious plume offshore do not differ significantly in suspended load from English Harbor stations (case 4, Table 5). Station 2 (Table 4) is interesting in that the 25-m sample apparently penetrated the plume.

Inspection of the data is sufficient to demonstrate that while samples near English Harbor out of the plume are somewhat high in suspended load concentration, all other non-plume samples--including those in the drogue path--contain about 0.03 mg $CaCO_3$/l. This value is close to the suspended $CaCO_3$ concentration reported by Wangersky (1969) in the North Atlantic Ocean. Station 3, listed as "in the vicinity of English Harbor", was taken at night and may have actually been in the plume.

Microscopic Analysis

Microscope slides were prepared to ascertain the nature of the suspended $CaCO_3$. These data are presented in a qualitative fashion. The suspended carbonate of the plume samples is primarily < 1 to 5 μ equant or elongate

Table 8. Suspended Load Flux Calculation Based on $CaCO_3$ Concentration and Approximate Water Volume Transport

Category	Volume Transport* (m^3/day)	Suspended $CaCO_3$ (g/m^3)	$CaCO_3$ Flux g/day	$CaCO_3$ Flux Metric t/day
English Harbor				
in	$+5 \times 10^7$	0.36	$+1.8 \times 10^7$	
out	-5×10^7	0.24	-1.2×10^7	
net $CaCO_3$ flux			$+0.6 \times 10^7$	+6
North Pass				
in	$+20 \times 10^5$	1.08	$+21.6 \times 10^5$	
out	-5×10^5	0.59	-3.0×10^5	
net $CaCO_3$ flux			$+18.6 \times 10^5$	+2
Rapa Pass				
in	$+10 \times 10^5$	1.52	$+15.2 \times 10^5$	
out	-5×10^5	0.95	-4.8×10^5	
net $CaCO_3$ flux			$+10.4 \times 10^5$	+1
Net $CaCO_3$ Flux for Total Lagoon				+9

* Data from Gallagher, et al. (1970). Into lagoon is +; and out of lagoon is -.

grains of nondescript material. Occasional grains are of obvious skeletal origin. The majority of the grains cannot be ascribed to particular organisms from microscopic characteristics, but their irregular habit seems to preclude an inorganic precipitation origin. Much of the material is loosely bound together, probably by an organic matrix (Chave, 1965).

Non-plume material is distinguished from plume debris by microscopic character as well as quantity. A few nondescript grains are present, but 1- to 10-μ coccoliths are the predominant grains. Planktonic foraminifera are present on some slides. Organically bound aggregates are present but are not so prominent as in the plume samples.

Mineralogic Analysis

X-ray diffraction analysis also distinguishes plume samples from offshore material. Plume carbonates are a mixture of aragonite, high-Mg calcite, and low-Mg calcite. Aragonite makes up 50 to 75 percent of the plume and lagoon suspended materials, and high-Mg calcite makes up most of the remainder. The "low-Mg" calcite apparently has near 0 percent Mg substitution of Ca, while the "high-Mg" calcite apparently has its mode near 13 percent Mg. This mixed mineral content, of carbonate minerals characteristic of corals and coralline algae, further demonstrates that the fine-grained carbonates of the plume are skeletal in origin.

Offshore samples contain low-Mg calcite, characteristic of both planktonic foraminifera and coccoliths, as the only distinguishable carbonate material.

DISCUSSION

Sediment Flux Calculations

In association with our 24-hour sampling of the three passes, Gallagher et al. (1970) gather data for calculating volume transport. Their data can be used to estimate the transportation of suspended $CaCO_3$ to or from the lagoon: Suspended Flux = Volume transport · suspended concentration.

$$(g/m^3) = (m^3/sec) \cdot (g/m^3)$$

For an initial approximation, the calculations can be made using only the mean suspended load concentration on incoming and outgoing tidal currents and the volume transport in and out. The results of these calculations are presented in Table 8. All three passes show a net input of $CaCO_3$, with English Harbor having about twice that of the total of the other passes. According to this calculation, 9 metric tons of $CaCO_3$ were added to the lagoon during our survey.

Another approach is to calculate the instantaneous flux ($g \cdot m^{-2} \cdot sec^{-1}$) at each sampling period and to integrate the results. Figure 6 is a graphical approximation to the instantaneous flux integration. The results are similar to those of the previous calculation, i.e., about 12 metric tons were added to the lagoon during the survey.

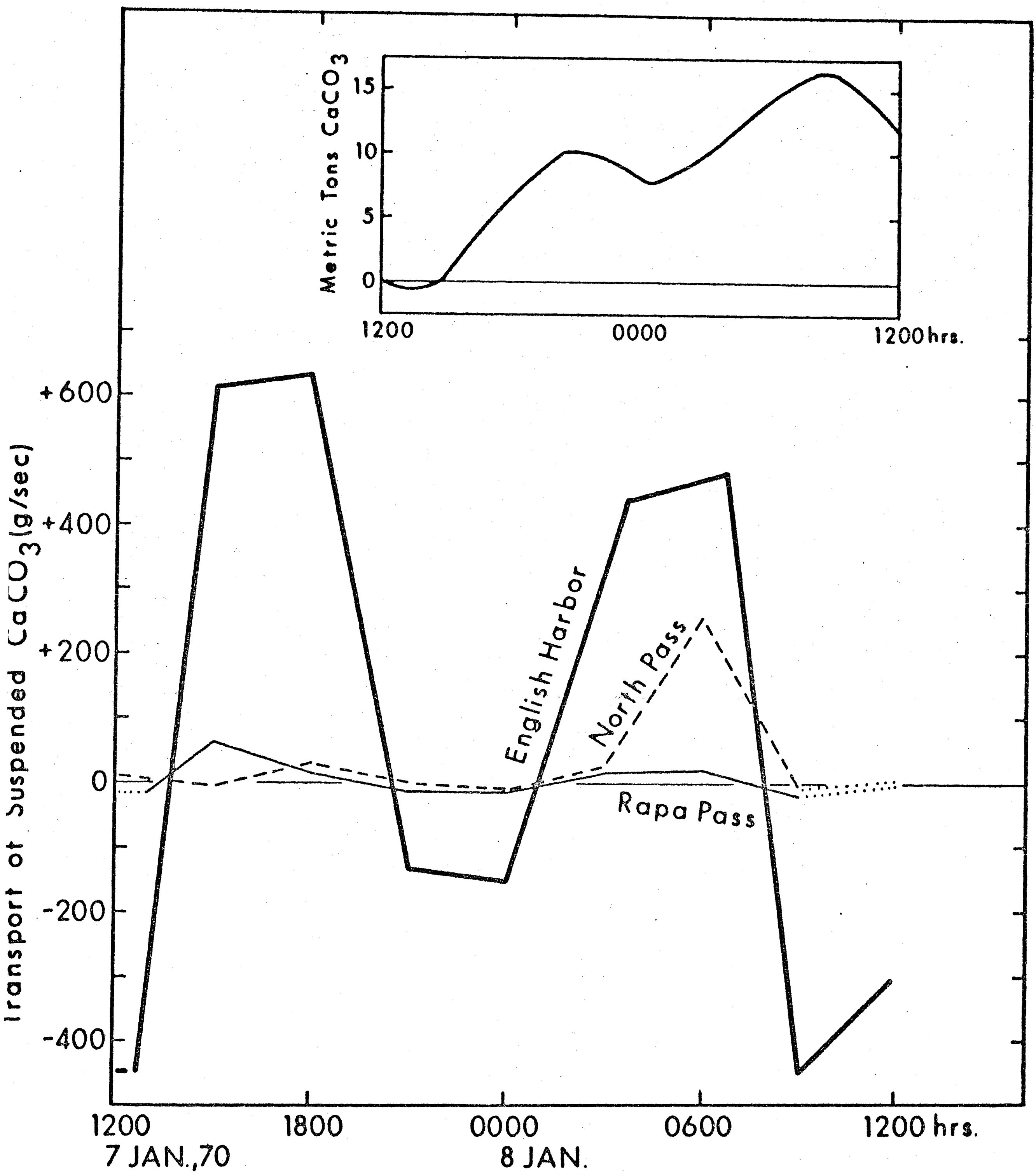

Fig. 6. Suspended $CaCO_3$ flux at Fanning Island during the 24-hour survey. The large diagram shows the instantaneous flux at each pass; the inset diagram shows the integrated flux.

Although a plume was seen coming out of English Harbor during the 24-hour survey, approximately 10 metric tons of material were brought into the lagoon over that period. If these results typify what occurs over a year, then perhaps 4 x 10^3 metric tons of material are supplied to the lagoon annually. Even if our survey period does not typify year-around conditions it seems likely that little, if any, suspended $CaCO_3$ is lost from the lagoon over the year.

Table 8 shows that about 2 x $10^6 m^3$ of excess water entered North and Rapa passes over the sampling period. If this water displaces very turbid (~4 g/m^3) water out English Harbor, then 8 x 10^6g (8 metric tons) of material might be expected to be lost from the lagoon at English Harbor. This value is somewhat smaller than the estimate of suspended load input calculated by the other procedures, again suggesting that little, if any, suspended $CaCO_3$ is lost from Fanning Lagoon.

The total lagoon floor area is about 5 x $10^8 m^2$, so 4 x 10^9 g/yr input or output represents only about 10 (g/m^2)/yr gain or loss of $CaCO_3$.

This discussion provides the basis for considering two other questions. What is the explanation for the plume of turbid water at English Harbor? Can any implications be drawn about Fanning Island carbonate sedimentation from these calculations of suspended load flux?

English Harbor Plume

Figure 1 aptly demonstrates that a distinguishable plume of water does pour out of English Harbor on an outgoing tide. Yet Table 7 suggests that the water returning through English Harbor on an incoming tide has much the same properties as the outgoing water. One possible explanation, of course, is that the turbid water simply sits outside the harbor and awaits the next incoming tide. Several lines of evidence refute this argument. First, the plume water is distinctly greener and more turbid than surrounding oceanic water. The green color is absent from the water at the mouth of English Harbor on a slack tide. Second, the suspended load content of that slack tide water outside English Harbor more mearly resembles non-plume water than plume water (Table 7). The behavior of the drogue (Fig. 2) suggests that plume water is entrained in an offshore current. It is likely that the plume characteristics are lost by mixing the relatively small volume of plume water with the much larger volume of oceanic water. Perhaps the initial mixing results in the intermediate composition of the English Harbor non-plume water (Table 7).

An alternative explanation for incoming concentration of suspended $CaCO_3$ is that much plume sediment is deposited at the mouth of English Harbor on an outgoing tide and re-suspended on the next incoming tide. The very large discrepancies between short-term and long-term deposition rates observed by Backus (1968) certainly indicate that such a mechanism may be a partial answer. However, the following consideration demonstrates that this explanation is only minor. As far into the plume as the MAHI could proceed, non-plume water could be demonstrated to be present under the plume (Station 2, Table 4). That station was in 90 meters of water, so much of the suspended load moves over areas of relatively deep water before there is opportunity to settle. The sediment settling rate is undoubtedly insufficient for it to settle to the sea floor before the tidal current reverses, so the sediment along with the water must be entrained in the offshore current. This conclusion once again suggests that material is removed from the vicinity of English Harbor by mixing processes. Any material which does settle to the sea floor in the mouth of English Harbor can be only a relatively small part of the total material transported outward.

We suggest the following source for the inward supply of suspended $CaCO_3$. On an incoming tide, water only a few centimeters to a few meters deep over the fringing reefs outside English Harbor flows laterally over the reefs and into English Harbor. The suspended load picked up and carried into the lagoon, then, is material produced on the fringing reefs outside the lagoon. The outgoing tide spits this material free of English Harbor, and the next incoming tide sucks in new material. This mechanism is transporting reef-produced debris from Fanning Island, but the transported material is primarily produced on the fringing reefs rather than in the lagoon.

Some qualitative evidence can be offered to support this model. As aforementioned, much high-Mg calcite is present in the suspended load of the plume water, as well as in the incoming water. Coralline algae, probably a reef's most prolific producer of high-Mg calcite, are abundant on the algal ridge of the fringing reefs but are not particularly abundant inside the lagoon (Roy and Smith, 1970). The aragonite of the plume suspended load could have originated from corals either inside or outside the lagoon.

Some flow was noted from the fringing reefs into the English Harbor channel during incoming tides. The importance of this flow was not appreciated at the time of our investigation, so no attempt was made to monitor this flow during our survey. Another study of suspended load flux at Fanning Island would certainly help to verify this model.

If the model is correct for English Harbor, it probably also operates on a smaller scale at the other two passes.

The plume debris can be recognized no farther than the visible plume. The plume exits English Harbor as a southwesterly current and is entrained in a northwesterly current (Fig. 3). Over the 12 hours of outgoing tide, the volume transport out English Harbor is approximately $10^3 m^3/sec$ (from Table 7).

The volume of water mixing with the plume water can be assumed to extend to the thermocline (~150 m), to be approximately 1 km wide, and to be flowing at approximately 25 cm/sec. Then the volume transport of this offshore current is about $4 \times 10^3 m^3/sec$. Thus, mixing 1 part plume water (0.14 g $CaCO_3/m^3$) with 4 parts offshore water (0.03 g $CaCO_3/m^3$) should produce water with about 0.05 g $CaCO_3/m^3$. This value is about 1 standard deviation unit higher than the observed concentrations in the drogue path (0.03 ± 0.02 g $CaCO_3/m^3$). In view of the crudeness of approximating the volume transport of the offshore current, this agreement seems satisfactory.

This situation can be contrasted with Chave's unpublished observations of the $CaCO_3$ plume west of (and downcurrent from) Jamaica. There the plume results from transportation of the debris off fringing reefs (Goreau, 1959) along both the north and south coasts of Jamaica. Both the suspended $CaCO_3$ concentration and the carbonate mineralogy distinguish this material for a distance of 200 km.

Calcium Carbonate Sedimentation of the Lagoon

Material deposited in the lagoon must represent the difference between the inputs of sediment and the outputs of sediment. A priori, the general inputs are biological production, chemical precipitation, mechanical transfer. The general outputs are mechanical transfer and solution. This model follows that of Smith (1970).

It seems likely that bottom—load transfer of material to or from the lagoon is small. We have demonstrated that suspended load transfer appears negligible (about 10 $(g/m^2)/yr$). Inorganic solution is unlikely to occur in the supersaturated waters of a coral reef environment except, perhaps, for local environments such as shallow tide pools where diurnal fluctuation of P_{CO_2} may effect solution (Schmalz and Swanson, 1969).

Deposition rate of the lagoon, then, is apparently the difference between biological production rate of $CaCO_3$ and biological solution rate. If it is assumed that biological solution is minor compared to carbonate production, then the deposition rate of Fanning Island lagoon approximately equals the carbonate production rate in that lagoon.

Part of the material produced remains in place. The reefs attest to this fact, as do infauna which are not subsequently displaced.

Smith (1970) and Chave, et al. (1970) have summarized coral reef $CaCO_3$ production rates. These rates range from about 1500 $(g/m^2)/yr$ to 30,000 $(g/m^2)/yr$. The lower rate, summed over the entire lagoon would amount to a deposition rate of about 1 mm/yr (assuming 50% sediment porosity). This rate is probably only slightly more rapid than the present rate of sea level rise (Shepard and Curray, 1967), so it would be approximately sufficient to maintain the reefs at sea level and the lagoon floor at its present depth. The higher production rate would be equivalent to a deposition rate of about 2 cm/yr. If the mean depth of the lagoon is 5 m, then this latter rate would be sufficient to fill the Fanning Island lagoon in 250 years. Of course, before that happened, suspended load transport would undoubtedly become much more efficient at carrying excess debris away from the lagoon. Presently the baffling effect of the line reefs in the lagoon (Roy and Smith, 1970) is probably quite effective in retaining sediments produced in the lagoon.

The present amount of suspended material (4 g $CaCO_3/m^3$) and an average lagoon depth of 5 m is equivalent to a suspended load of 20 g/m^2. If the $CaCO_3$ production rate is 1500 $(g/m^2)/yr$ and none of the material is lost, then the rate of suspended $CaCO_3$ renewal in the water column must be 75 times per year, or about once per 5 days. Since perhaps half of the $CaCO_3$

produced remains in place, the renewal rate may be half that figure. With essentially no flushing of the suspended $CaCO_3$, production rates of $CaCO_3$ much more rapid than 1500 $(g/m^2)/yr$ would seem to demand unreasonably rapid renewal (and unreasonably rapid deposition) of suspended $CaCO_3$.

The optimum deposition rate for lagoon survival is obviously that necessary to match sea level rise. Those lagoons whose infilling rate lags behind the rate of sea level rise must eventually become too deep to support reef production. The "overproducing" lagoons would eventually fill. Perhaps the large percentage of Fanning Lagoon floor which supports corals (Roy and Smith, 1970) as well as the relatively shallow depths of the lagoon suggests that this lagoon is producing somewhat "too much" material.

ACKNOWLEDGMENTS

This investigation was supported by National Science Foundation Grants number GB-15581 and number GA-10890. We wish to thank all the other members of the Fanning Island Expedition for their cooperation. Particular thanks go to G. Krasnick, who aided in the offshore sampling, and K. Shimada who supplied volume transport calculations. The crew of the R/V MAHI provided excellent cooperation during offshore sampling.

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SEDIMENTATION AND CORAL REEF DEVELOPMENT IN TURBID WATER: FANNING LAGOON

Kenneth J. Roy and S. V. Smith
Department of Oceanography and Hawaii Institute of Geophysics

ABSTRACT

Lack of light and excessive sediment deposition rates are factors limiting coral reef development. The presence of very turbid water and muddy bottom does not mean, however, that coral growth is prohibted. Fanning lagoon has a turbid-water area (visibility, 2 m) and a clear-water area (visibility, 10 to 15 m). Both areas have a muddy bottom. Because of the shallow depth and the light-scattering effect of the suspended $CaCO_3$, relative light intensity at the bottom is greater than 5 percent. The cleaning mechanism of the corals is sufficient to handle the deposition of sediment. Live corals cover 62 percent of the clear-water area and 31 percent of the turbid. Reefs in the turbid water are ecologically different from the ones in clear water, but they are still living reefs. Ramose corals make up 55 percent of the individuals in the turbid water and only 10 percent of those in the clear water. This difference is reflected in the structure of the reefs; those in clear water are massive and steep-sided, while those in the turbid water have gentler slopes and are more open with sediment infill. Fanning lagoon is an example of penecontemporaneous formation of reef and intervening muddy sediment with bathymetric relief never more than 8 m.

INTRODUCTION

The statement that coral reefs develop in clear, warm seas is commonly made when dealing with studies of reef growth and development. By induction, reefs therefore do not develop in turbid, warm seas. Stratigraphic analyses of ancient reef complexes are often done using modern coral reef analogues. The idea of clear, warm water is carried into the interpretation as a result of logic. Because of the association between turbid water and deposition of fine-grained sediments, this approach leads to a vision of reefs with tens of meters of relief standing in clear epicontinental seas. Later introduction of fine-grained sediment stunts and kills the reefs and deposits the fine-grained rocks commonly found in the inter-reef areas.

Biological and marine geological literature contains a number of references to survival and growth of corals and coral reefs in turbid water (Crossland, 1928; Kuenen, 1950; Motoda, 1939; Shepard, 1963; Wells, 1957; Yonge, 1930). However, there also are documented cases of reef-kill by floods of turbid water associated with periods of extreme fresh-water runoff. Decrease in salinity may be the major cause of death of the coral (Banner, 1968; Goreau, 1964). The range of salinity tolerance of corals is from about 27 to 40 parts per thousand (Wells, 1957). As long as the salinity remains within these limits, fresh-water flooding will not seriously affect the coral population as a whole.

The suspended load has two effects. One is blockage of light. When the light intensity falls below some limiting value, many reef building organism die, but only after a period of time. Corals, for example, can live in the dark for some days (Edmondson, 1928). Goreau (1964, p. 384) reports that "...14 weeks after the floods, many of the bleached colonies bleached due to loss of zooxanthellae were still much paler than normal although they appeared to be healthy in other respects." Temporary lack of light is not a serious problem.

The second effect of the suspended load is the smothering of organisms by deposits of sediment. Some corals have quite effective cleaning mechanisms (Wells, 1957; Yonge, 1930). Complete coverage can kill the coral, but Edmondson (1928) and Mayer (1918) demonstrated that many species can live for more than a day when completely covered by some centimeters of sediment.

Marshall and Orr (1931) describe experiments in which Favia, Fungia, Psammocora, and Porites showed little or no ill effects from being introduced into water with 800 mg/liter of suspended mud. They quote Mayer's (1924) observation that under natural conditions 3700 mg/l of suspended mud kills some corals, but suggest that the observed kill may have been related to decrease in salinity. Marshall and Orr (1931, p. 131) conclude that some species are more susceptible than others to deposition of sediment but that "... Pocillopora, Galaxea, Symphyllia, Fungia, and Acropora were all able to deal with large quantities of sediment under natural conditions, and it is difficult to believe that they can be killed by sediment falling from above." They of course dealt with growing colonies which may be able to withstand greater sediment deposition than could coral larvae trying to settle. The need for suitable substrate to settle on is a problem to coral larvae in turbid, muddy environments.

Extensive coral reefs intimately associated with muddy sediments are present in Fanning Lagoon both in clear and in turbid waters. An area in the turbid water was compared to one in the clear water in order to evaluate the effect of water turbidity on reef development.

PHYSICAL SETTING

Fanning Island ($3^{o}55'$ N, $159^{o}23'$ W) is in the central Pacific Ocean about 1500 km south of Hawaii. Rainfall is about 200 cm per year, and there is a prevailing 10-knot east to southeast wind (Zipser and Taylor, 1968). The lagoon is ovate in shape, about 13 km by 6.5 km. It is land-locked except for three passes, two that are shallow, about 2 m, and one, English Harbor, which is up to 8.5 m deep. During the study period there was a net tidal influx of water into the lagoon through the two shallow passes and a net outflow through English Harbor (Gallagher, et al., 1971). Although large volumes of water move in and out of English Harbor with the tides, there does not appear to be much mixing with the resident lagoon waters. Residence time of water in the lagoon is apparently about 11 months (Gallagher, et al., 1971).

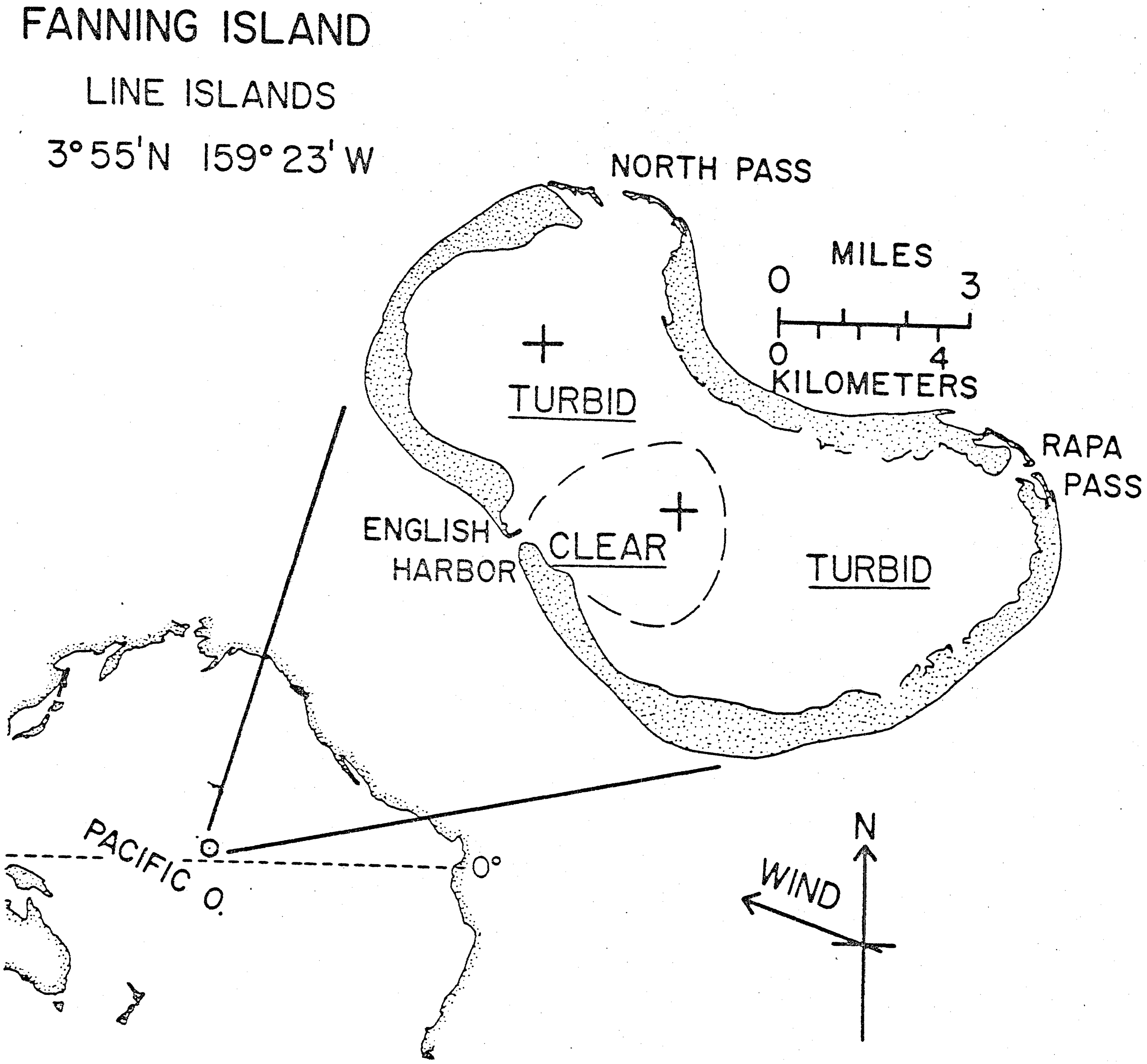

Fig. 1. Location of Fanning Island (3°55'N, 159°23'W). Crosses mark location of the benthic surveys in the clear- and turbid-water areas.

A clear water body is maintained in the lagoon in the vicinity of English Harbor (Fig. 1) and, at least on the north side, the contact between the clear water and the turbid, resident lagoon water is visibly sharp and distinct. Visibility in the clear water is about 10 to 15 m while in the turbid water it is 2 m or less. The temperature and salinity of all of the lagoon water was about 28°C and 35 parts per thousand. This is about the same as the surface waters of the open ocean around Fanning Island.

A maximum lagoon depth of 18 m was encountered in the clear water. Depths are commonly 10 to 15 m in the clear water and 4 to 5 m in the turbid water. The maximum depth measured in the turbid water was 8.5 m.

Line reefs and narrow linear reefs, up to 200 m wide, cross the lagoon and cut it up into a number of ponds approximately 1000 m wide (Fig. 2). The tops of the line reefs are 0.5 to 2 m deep below the water surface. The azimuths were measured on sections of line reef 300 m long. There is a primary mode of azimuths perpendicular to the prevailing wind direction and a secondary mode parallel to the prevailing wind. Line reefs wider than about 20 m have a medial sand strip. The wider the line reef, the wider is the medial sand strip and the less abundant is the coral on the leeward edge. On reefs wider than about 100 m there is little or no coral on the leeward side. Sand drifting off the reefs builds sand wedges into the pond on the leeward side of the line reefs. This causes the profile of the reefs to be asymmetric--steep slopes on the windward side and gentle slopes on the leeward side (see Fig. 13).

The origin of the line reefs is not known. Although there are growth features that appear to be related to present day wind and current patterns, the basic pattern may be related to karst topography formed during subaerial exposure of the island.

WORK DONE AND METHODS USED

In order to compare reef development in the clear and turbid waters, suspended load, light intensity, and bottom cover were measured in the two areas located approximately by the crosses shown on Figure 1. The area sampled in the turbid water is a pond in the central part of the northern half of the lagoon. None of the passes into the pond are deeper than 1 to 2 m (Fig. 8). A channel (locally called Suez), 6 m wide and 2 m deep has been dug across the line reef on the north side of the pond (Figs. 3 and 8). This particular pond was chosen as representative of the turbid water area of the lagoon. A few dives were made in other parts of the turbid area. These dives, together with numerous grab samples and the character of the bottom as shown on the fathometer traces taken in other areas, indicate that the pond is typical of the lagoon except for that part of the lagoon near shore. Shallow sand flats up to 400 or 500 m wide are common around the edge of the lagoon.

The clear-water sampling area was chosen to duplicate the physiography of the turbid water pond as closely as possible. The area is also a pond of sorts, but the reef perimeter is less well defined than in the turbid

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Legends for Figures 2 through 7 on facing page.

Fig. 2. Line reefs in Fanning Lagoon. The view was taken above North Pass looking toward English Harbor.

Fig. 3. Suez channel across the line reef on the north edge of the turbid-water sampling area. The sampling area is in the foreground.

Fig. 4. A massive coral knoll in the turbid water. The knoll is 2 m wide.

Fig. 5. A massive coral knoll in the clear water. The shark prod is 2 m long.

Fig. 6. Acropora and calcium carbonate mud on a coral knoll in the turbid water. The view covers about 1 m.

Fig. 7. A diver doing a benthic survey along the edge of a clear water knoll.

Fig. 2.

Fig. 3.

Fig. 4.

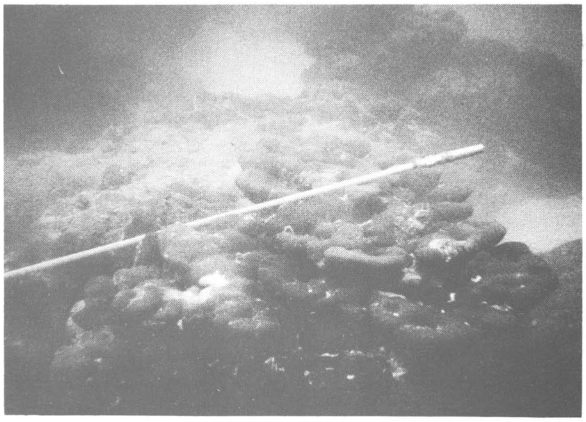

Fig. 5.

Fig. 6.

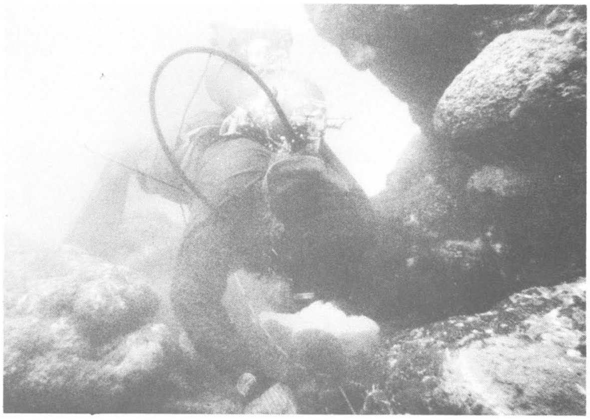

Fig. 7.

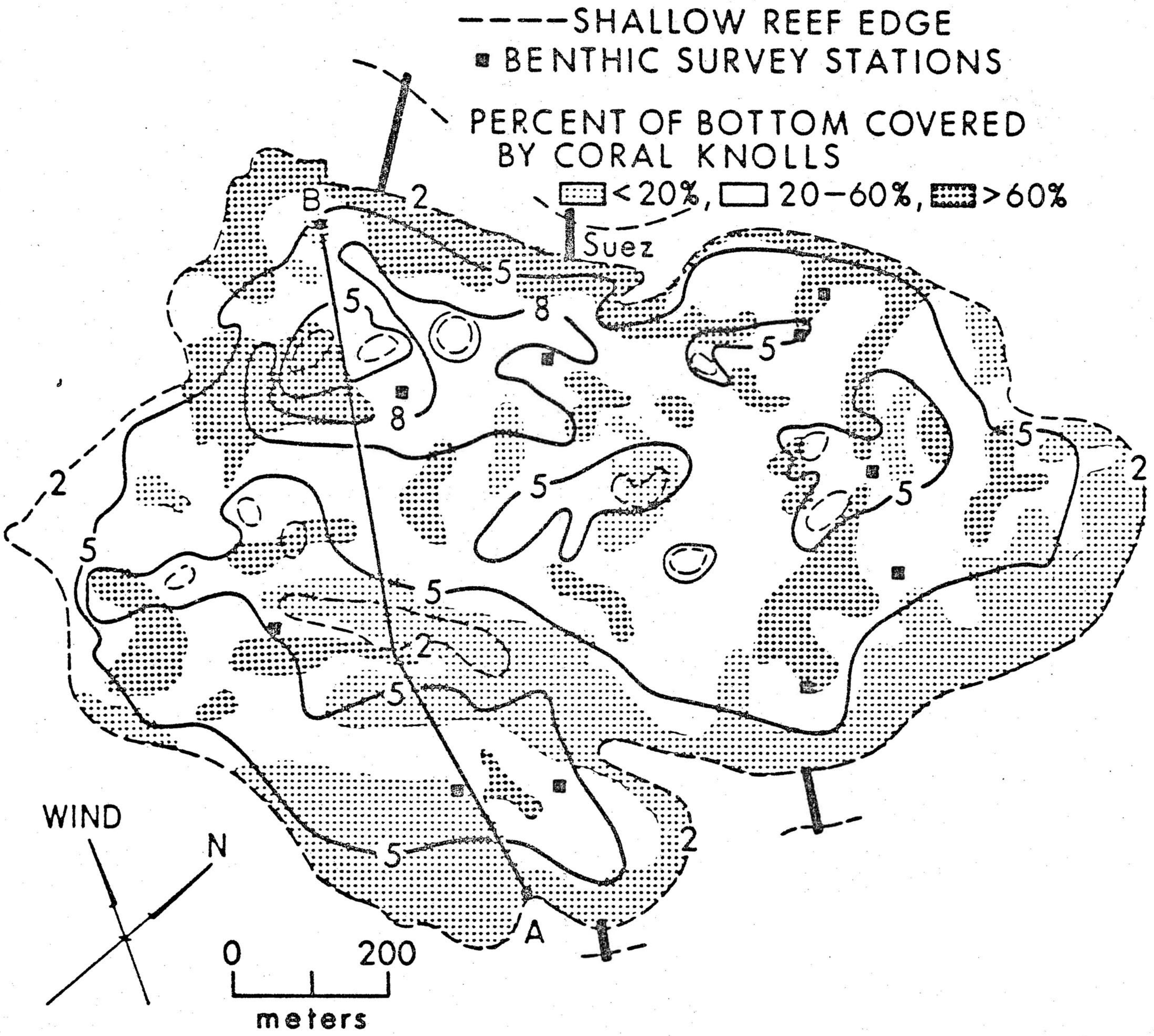

Fig. 8. Bathymetry and coral knoll abundance in the turbid-water pond. The line A-B is the profile shown in Figure 13. Contour interval is 3 m.

pond. The sampling area is on the periphery of the main clear-water area. Visibility in the water decreases markedly on the turbid-water side of the line reef that marks the southeast side of the clear-water sampling area. The reef on the English Harbor side of the pond is 3 to 4 m deep. Passes into the central part of the clear-water area are up to 6 m deep.

Sediment samples were taken from the lagoon bottom with a van Veen-type sampler. Water samples were taken at the surface and at various depths using an *in situ* pumping apparatus (Schiesser, 1970). Chemical analyses were done on 163 samples to determine the calcium carbonate suspended load (Smith, *et al.*, 1971). Visible light intensity was measured with a Wesson submersible photometer. No filters were used. Twenty-two lowerings were done and readings were taken at 1-m intervals. Relative light intensities were calculated using synchronous deck and submerged cell readings. Vertical extinction coefficients (α) were calculated for 1-m depth intervals using the formula $[\alpha = -\ln (I_z/I_z-1)]$

Divers using SCUBA equipment determined the bottom cover at 0.25-m intervals on a 10-m-long sampling line. The benthic survey was done at 22 localities in the turbid water and at 11 in the clear water. In all, 450 m of bottom in the turbid water and 200 m of bottom in the clear water were surveyed. A major problem encountered in the benthic survey was stirring up of the sediment into the water. Any agitation of the water near the bottom stirred clouds of muddy sediment into the water and reduced visibility to zero. The only workable way to sample was to lay the line down and swim along it--sampling ahead where visibility was adequate. This was the reason for using this 'one-line' sampling method rather than grids.

Bathymetric surveying was done with a small boat and a Raytheon model DE-719 portable fathometer. Detailed surveys were made of both the clear and turbid water ponds. Bathymetric lines were also run in various other parts of the lagoon to determine the general nature of the bathymetry. Sample locations and survey track positions were determined by sextant fixes on objects on shore that could be located on the map of the island. For the detailed surveys and sampling locations in the ponds, local markers were set up, surveyed in, and used as reference points. In all, 9.5 km of continuous fathometer track were run in the turbid-water pond and 4.7 km in the clear-water pond.

The bottom of the ponds is very irregular due to the presence of coral knolls. To arrive at bathymetric data which could be contoured, the depths were determined with reference to a generalized bottom trend arrived at by extrapolating the general bottom through all knolls. Coral knolls were arbitrarily defined as steep-sided areas greater than 2 m deep and rising higher than 0.3 m above the general bottom profile. Knolls that rise to within 1 or 2 m of the surface are considered to be patch reefs. All dimensions associated with the coral knolls were measured with reference to the smoothed generalized bottom profile.

Widths of coral knoll crossings, heights of coral knoll crossings, and interknoll distances were determined from fathometer traces from the turbid- and clear-water sampling areas. Lines of about equal length, one parallel and the other perpendicular to the direction of the prevailing wind, were used to obtain the knoll statistics. The data are summarized in Figure 9. Eight-hundred and forty meters of track and 45 knoll crossings were used from the clear-water area, and 1490 m of track and 73 knoll crossings from the turbid-water area. All the traces from the turbid-water pond were divided into 30-m intervals and the percentage of coral knoll in each interval was determined. These data were plotted and contoured (Fig. 8).

WATER TURBIDITY

Suspended load

The calcium carbonate ($CaCO_3$) suspended load is about 3.5 mg/l in the turbid water, about 1.0 mg/l in the clear water, about 0.3 mg/l in the water of the outside fringing reef (interpreted from the values in the inflowing water of English Harbor), and about 0.03 mg/l in the open-ocean waters surrounding Fanning Island (Smith, et al., 1971). The outside fringing reef is very well developed, and the suspended load of 0.3 mg/l might be a representative number to expect for water associated with reefs of this type.

The suspended load $CaCO_3$ in the lagoon is about 65 percent aragonite and 35 percent calcite (x-ray diffraction analysis). The calcite fraction is a mixture of magnesian calcites. There are modes at 0 and 13 mole percent $MgCO_3$. The 13 percent mode is the major one. This distribution of aragonite, calcite, and magnesian calcites is very similar to that in the clay-sized fraction of the pond bottom sediments (Fig. 10). Most of the material in suspension is less than 6μ in diameter. The modal size is 3 to 4μ (petrographic microscope analysis). Large particles appear to be cleavage fragments.

The suspended $CaCO_3$ appears to be the product of biological and mechanical abrasion of skeletal materials on the reefs. Inorganic precipitation seems unlikely in view of the composition and appearance of the suspended material. The presence of extensive sand wedges in the lee of the line reefs is evidence of sand transport and indirectly, of mechanical abrasion. Most coral skeletons in the lagoon show evidence of extensive boring by sponges. Boring pelecypods are common. Much of the hard substrate shows evidence of fish grazing. In Fanning lagoon, as in many other areas, bioerosion is very extensive (Bardach, 1961; Gardiner, 1931; Neumann, 1966).

Light

At any given depth the relative light intensity is 10-20 percent higher in the clear water than it is in the turbid water (Fig. 11). In the turbid water, concentration of suspended $CaCO_3$ is high and the standing crop of plankton is large (Gordon, et al., 1971). Yet the minimum relative light intensity on the pond bottom is about 5 percent. There are two reasons for this. The depths are not great, so even with large absorption coefficients, much light penetrates to the bottom. Second, the fine-grained suspended material scatters light without greatly affecting the measured vertical

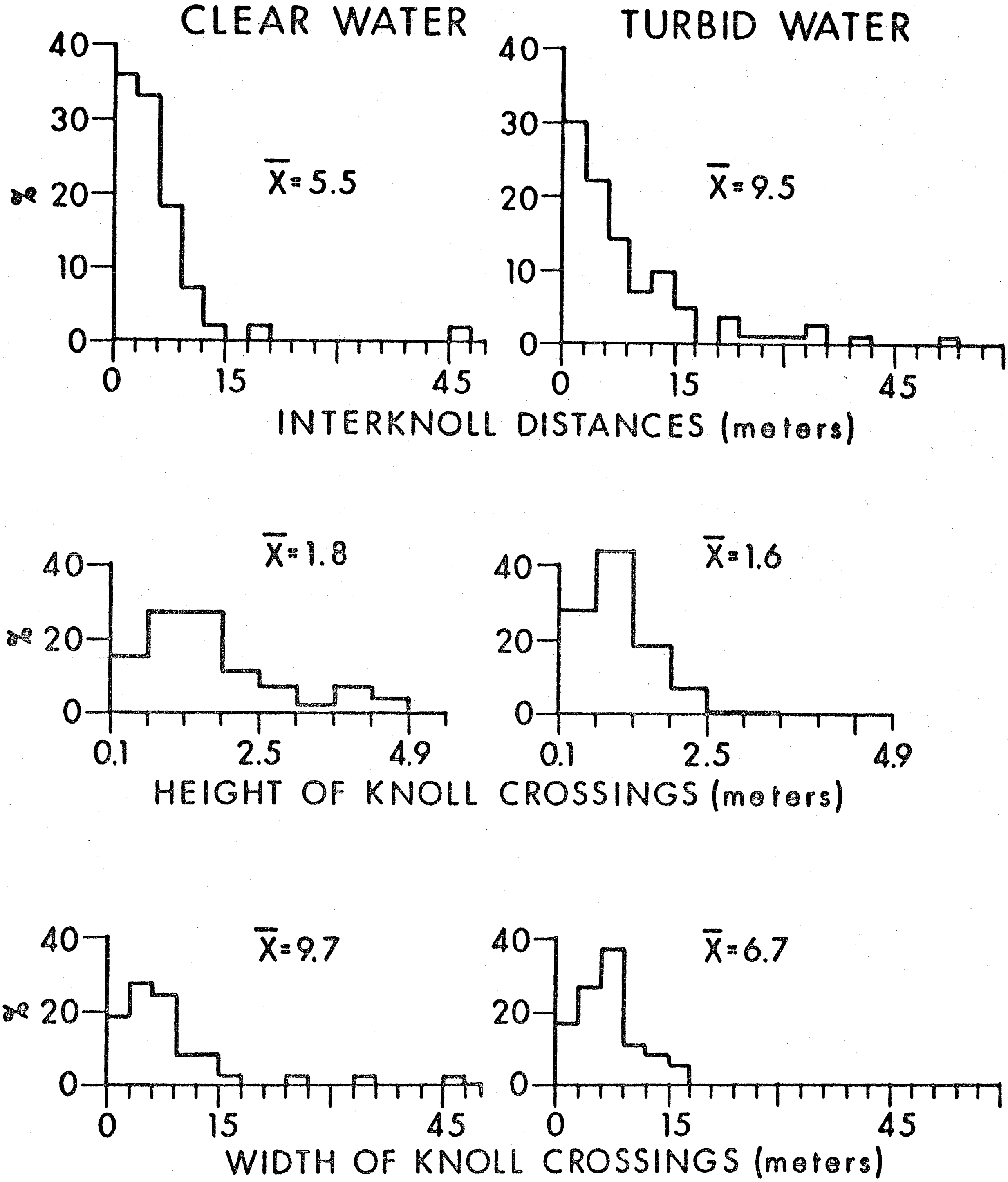

Fig. 9. Comparison of interknoll distance, height of knoll crossings, and width of knoll crossings in the clear- and turbid-water sampling areas.

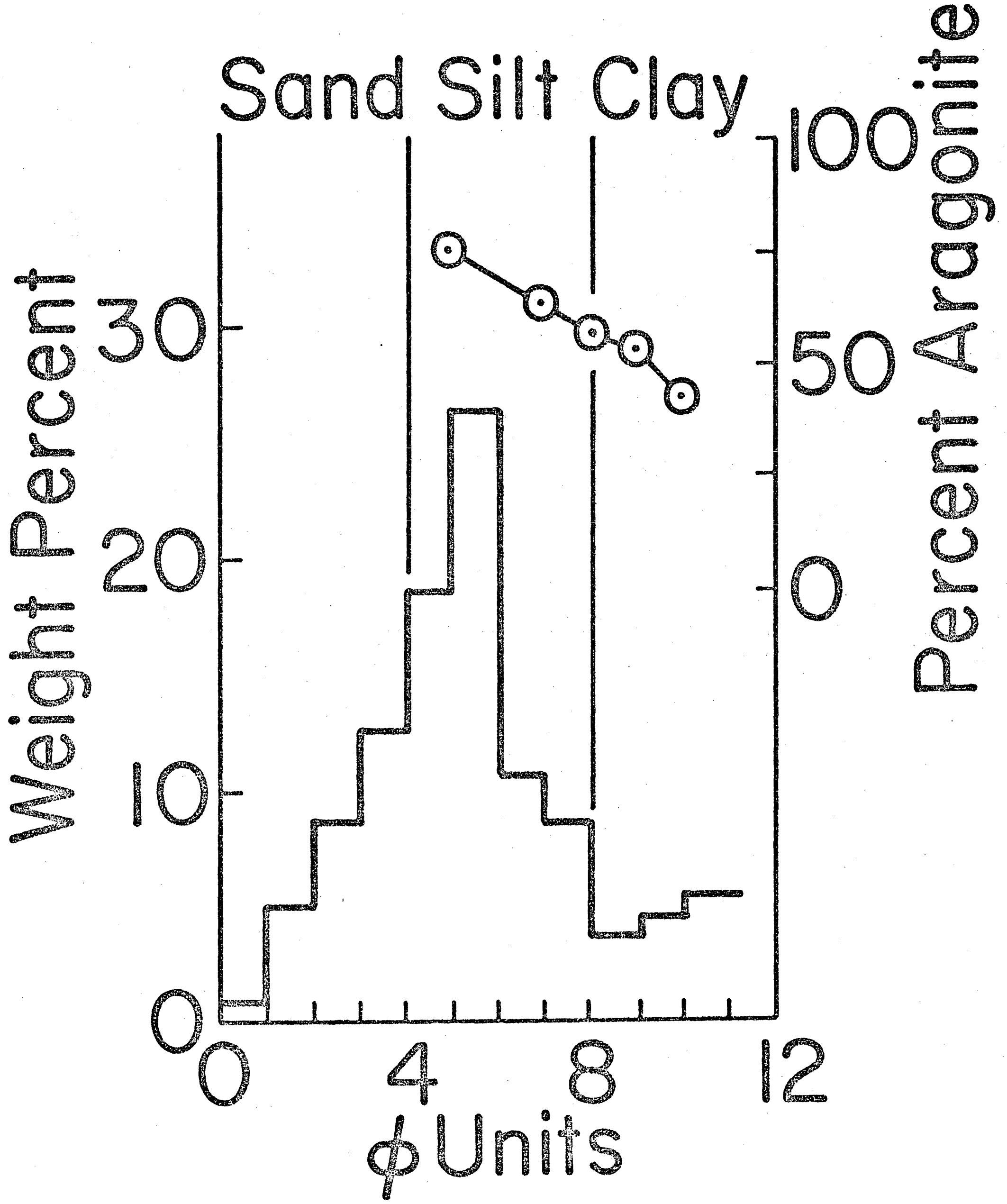

Fig. 10. Size and mineralogic composition of a representative mud sample from the bottom of the turbid pond.

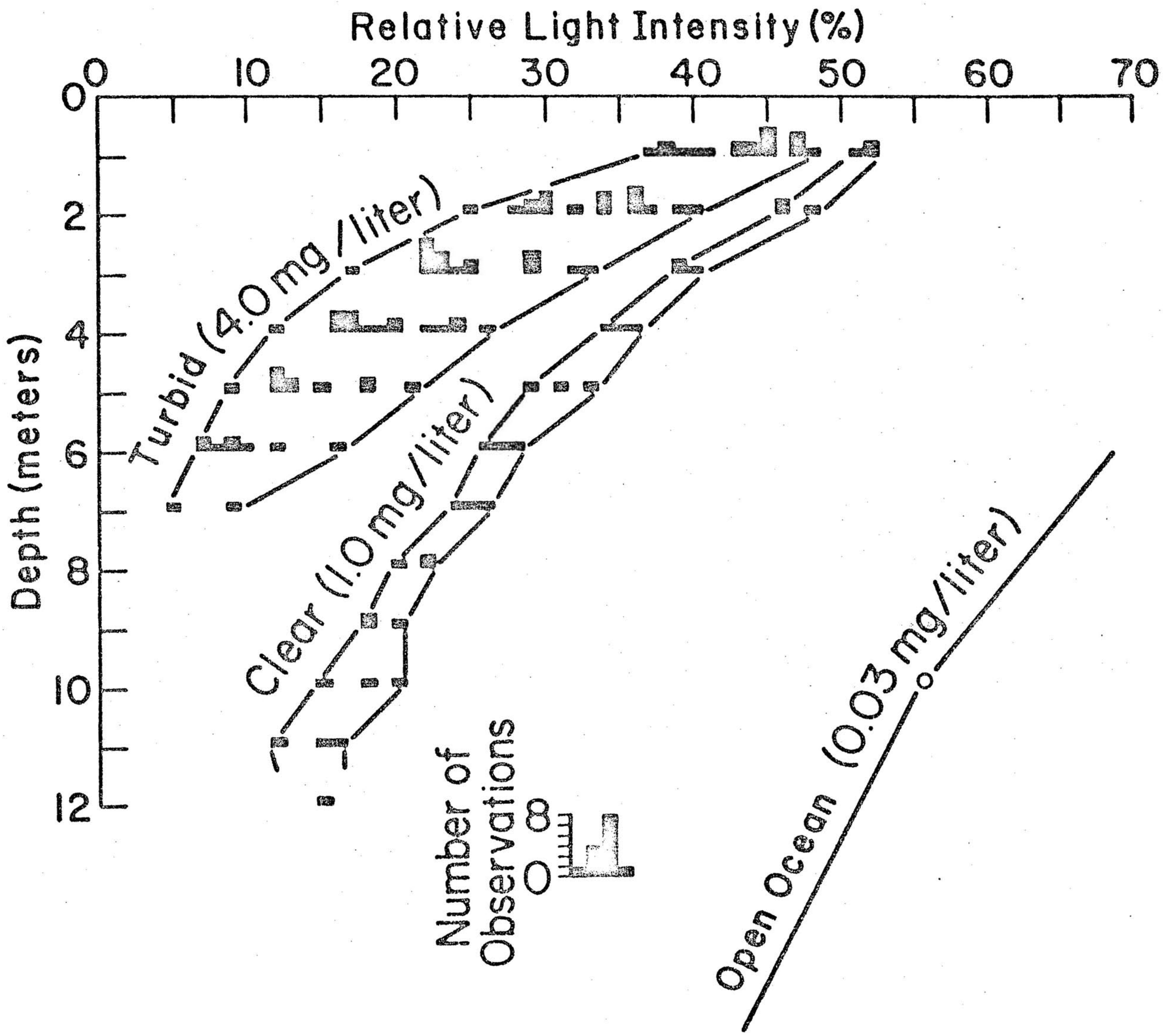

Fig. 11. Relative light intensity versus depth in the clear-water area, the turbid-water area, and the open ocean. The suspended load (e.g., 4.0 mg/l) is the average weight of suspended $CaCO_3$ in each of the three areas. The relative light intensity in the open ocean is for an area off Hawaii.

extinction (Holmes, 1957). The mean extinction coefficient in the clear water area is 0.13/m and 0.28/m in the turbid water. These values are about the same as extinction coefficients for green light in average oceanic and average coastal water (Sverdrup, et al., 1942).

According to Wells (1954) most coral reef growth occurs in depths of 30 m or less, although growth does continue down to about 100 m and at Bikini Atoll to about 160 m. Relative light intensity at 30 m in average oceanic waters is less than 1 percent (Sverdrup, et al., 1942). About the same amount of solar radiation reaches the sea surface at Fanning and Bikini atolls (Neumann and Pierson, 1966), so at 5 percent, the relative light intensity at the bottom of the turbid pond is well above the minimum light requirements for reef growth. Light is not a limiting factor in reef development in the turbid water of Fanning lagoon.

The distributions of extinction coefficients at various depths in the turbid pond show definite areal patterns of variability (Fig. 12). In general the extinction coefficients in the surface water are large except in the downwind part of the pond. At intermediate depths there are minumum values while below 4 m the extinction coefficients are essentially constant at values somewhat higher than the minimum.

Circulation in the pond is complex. The observations were taken on a falling tide. This may explain the relatively high values in the surface water and around Suez. Fine material taken into suspension over the leeward reef is moved out into the sampled pond by the tide. Suez channel may be a region of maximum volume transport of water across the reef during the tidal cycle. This could explain the tongue of turbid water upwind from Suez.

The extinction coefficient profile across the turbid pond (Fig. 13) suggests the following simplified circulation model. The wind drives surface water over the windward reef and sediment is put into suspension. The water moves across the pond; the suspended material settles, leaving the surface water of the downwind side of the pond less turbid. Then the surface waters reach the leeward reef, some of the water goes over the reef into the next pond and some sinks and flows upwind at depth to replace the water upwelling on the upwind side of the pond. Dye experiments indicate upwind water movements at depth (Gallagher, et al., 1971). The return flow appears to be at about 3 m depth. Below 3 m the flow is restricted by coral knolls (Fig. 13). Coral thickets act as baffles. Mud between Acropora branches on the knolls is finer than the mud of the interknoll areas.

BOTTOM TYPES

The sampled areas can be divided into three categories: pond bottoms, reef slopes, and reef flats. These areas have distinct boundaries and, in most cases, distinct bottom characteristics with respect to nature and type of coral cover, and sediment type and distribution (Table 1).

Table 1. The nature of the bottom-cover as determined by benthic surveys in the clear- and turbid-water sampling areas.

							LIVE CORAL		
		live coral (%)	dead coral and coral rubble (%)	encrusting coral-line algae (%)	sand (%)	mud (%)	*Montipora*[2] (%)	*Acropora* (%)	ramose corals (%)
TURBID WATER	pond bottom[1]	35	10	1	0	54	21	41	46
	reef slope	28	35	2	35	0	0	78	96
	reef flat	21	29	9	41	0	1	51	71
	coral knolls	78	--22---						
CLEAR WATER	pond bottom	59	13	0	0	28	57	0	1
	reef slope	73	7	11	1	8	75	2	5
	reef flat	46	15	15	24	0	48	21	38
	coral knolls	83	--17---						
AVERAGES[3]	turbid water	31	21	3	73	27	13	55	55
	clear water	62	12	7	4	17	52	5	10

[1] The pond bottom includes coral knolls as well as areas of sediment. The division coral knolls is a subdivision of the pond bottom.

[2] The percent of the live coral that is *Montipora*.

[3] The values are weighted averages, using 50 percent pond bottom, 32 percent reef slope, and 18 percent reef flat as the relative percentages of the various lagoon areas. The percentages were obtained from analysis of the bathymetric map of the turbid pond. The same weighting was used for the clear and the turbid water areas.

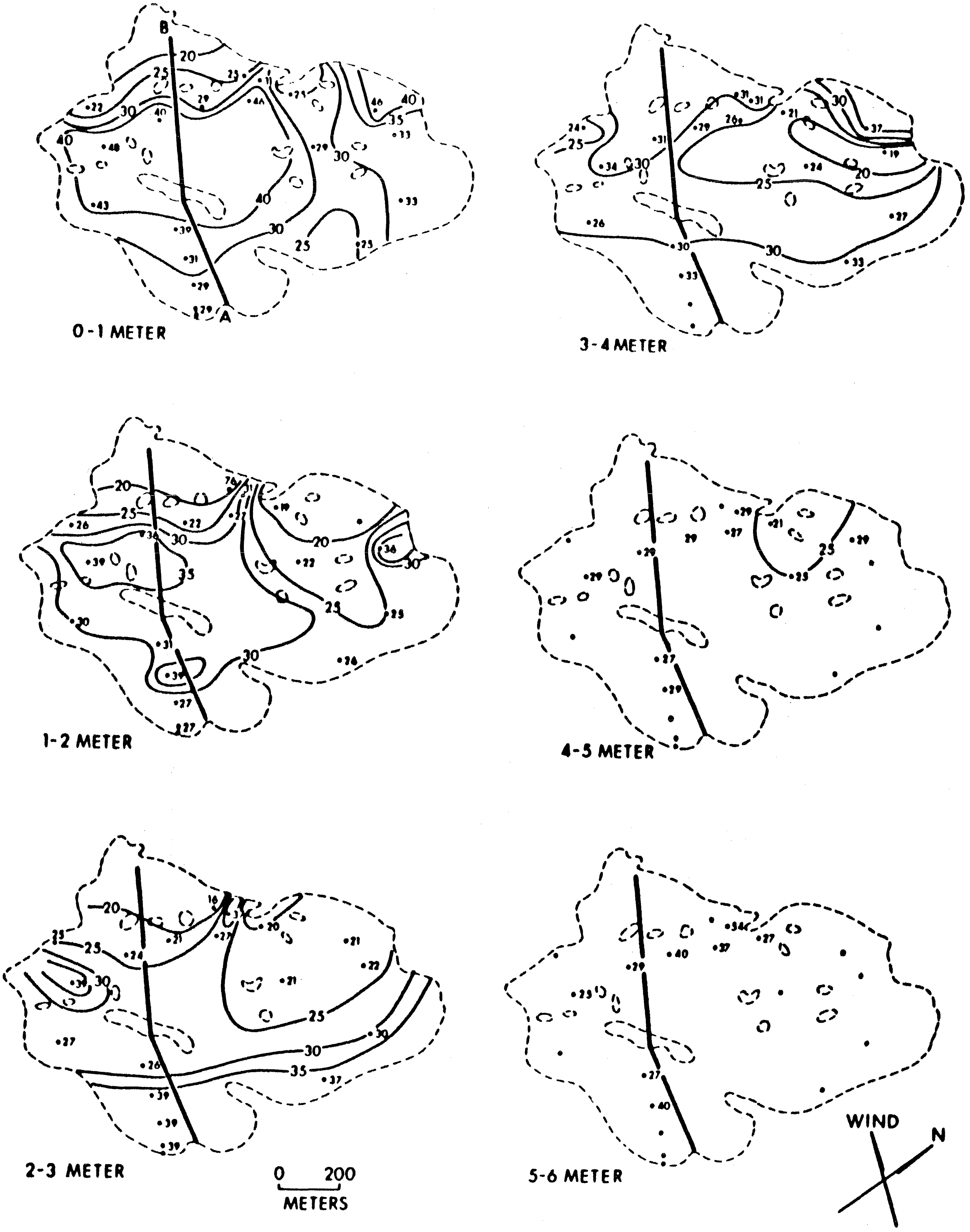

Fig. 12. Horizontal distribution of vertical extinction coefficients at various depths in the turbid-water pond. The line A-B is the profile shown in Figure 13. The extinction coefficients are in units of x 10^2 per meter.

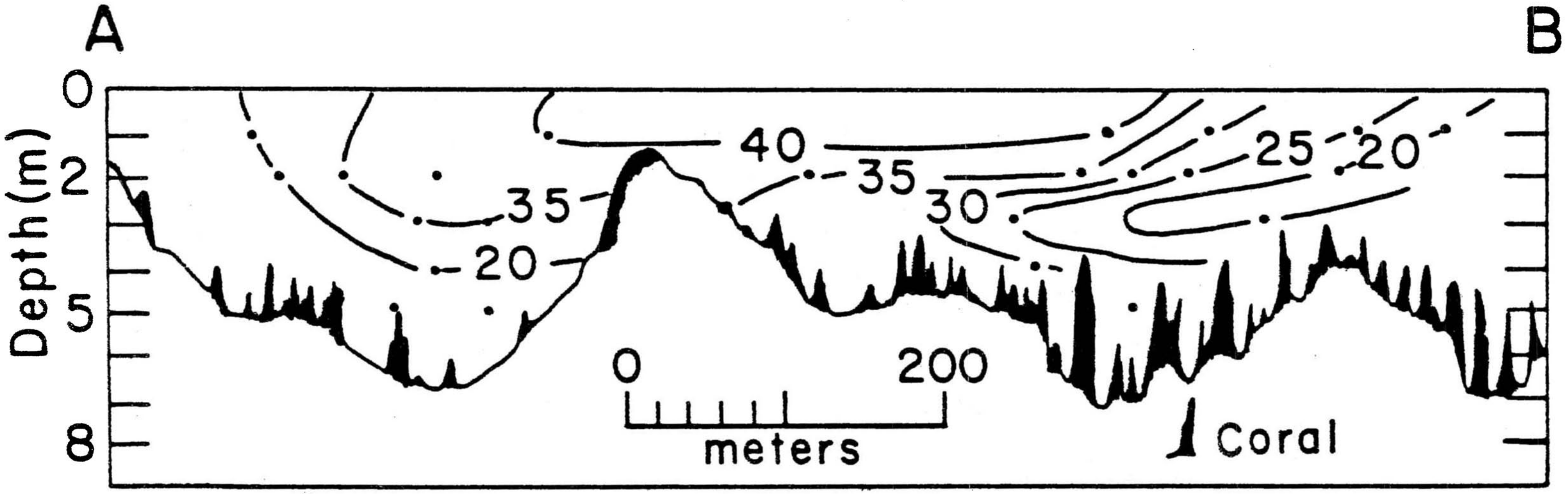

Fig. 13. A bathymetric and vertical extinction coefficient profile across the turbid-water pond. The line of section is shown on Figures 8 and 12. The extinction coefficients are in units of x 10^2 per meter.

Sediments

The sand on the reef flats of both areas is coarse- to medium-grained. Because the reef tops are shallower in the turbid water than in the clear water the sand on the turbid-water reefs tends to be finer and better sorted. On the lee side of the reefs there are distinct wedges of muddy sand that extend out about 60 m into the pond before grading into the mud of the pond bottom. The pond bottom muds have a silt-sized mode (Fig. 10). Sand wedges were not found in the clear water area examined although the mud at the base of the reefs is sandier than in the central part of the clear-water pond. Apparently little sand is produced on the clear-water reef flats. This may be a function of their deepness.

The micro-mullusk fauna in the pond muds is distinct from that on the reef flats (Kay, 1971). Foraminifera are present in the lagoon muds, and their abundance appears to be a function of nearness to coral knolls. There is an average of 310 foraminifera tests per gram of sediment. There are few species, and, of these, *Ammonia beccarii tepida* is most abundant (J. Resig, personal communication). Both the number of species and the number of individuals is low compared to other atolls (Emery, *et al.*, 1954).

Another organism that is common on other atolls but rare in Fanning lagoon is *Halimeda*. Live *Halimeda* plants are seldom seen in the lagoon. Emery, *et al.*, (1954) give 36 percent *Halimeda* and 5 percent foraminifera tests as the composition of the average sediment from four lagoons in the Marshall Islands. In Fanning lagoon both *Halimeda* and foraminifera make up less than 1 percent of the volume of the sediment. The reason for the low abundance is not known.

Alcyonarians are present in small numbers in both the clear and the turbid waters of the lagoon and red alcyonarian spicules are noticeable in many turbid-water-area mud samples. On the average there are 350 spicules per gram of mud. The alcyonarians live on the coral knolls. Alcyonarian spicules and foraminifera tests make up comparable proportions of the sediment.

Coral

Bottom-cover by coral in the clear- and turbid-water areas differs in amount and in type (Table 1). Live coral covers about 60 percent of the bottom in the clear water and about 30 percent in the turbid water. Figure 9 shows the distribution of live coral cover with depth as determined by the benthic surveys. Although the coverage is almost constant with depth in the clear water, there are large changes with depth in the turbid water.

The low abundance of coral at shallow depths is due to lack of coral on the reef flats. Reef flats sampled in the clear water were all greater than 1 m deep thus explaining the relatively high values for coral cover relative to the 0.5 m deep reef flats in the turbid water.

Coral knolls in the turbid water have about 80 percent live coral cover according to the benthic surveys (Table 1). The knolls cover 37 percent of the area of the pond bottom (Fig. 8). These figures yield an average coral cover of 30 percent--the same as the estimate derived from the benthic survey data (Table 1). Thus, mapping the distribution of coral knolls using the bathymetric data gives a more detailed picture of the distribution of coral in the turbid water than is possible from the relatively few benthic survey stations occupied. The coral knolls have a distinct, though irregular, distribution pattern: low abundance in the upwind part of the pond, and increasing abundance downwind.

The general pattern can be explained using the previously discussed model of sedimentation in the pond. The coral is killed by deposition of sediment in the upwind portion of the pond. The deleterious effect decreases downwind, and maximum knoll development occurs along the downwind edge of the pond. In general the distribution of coral knolls appears to result from progressive decrease in the amount of deposition of material away from the upwind edge of the pond and by encroachment of the sand wedge into the pond.

The apparent discrepancy between Figure 14 which shows less than 10 percent live coral cover in the turbid water deeper than 6 or 7 m, and Figure 8 which shows the area deeper than 8 m to be 20 to 60 percent coral knoll, has two explanations. The area below 8 m depth shown on Figure 8 is actually between 20 and 30 percent coral knolls, with much of it closer to 20 percent. Also, it is possible that the three deeper, low coral cover stations could have missed coral knolls by random chance. It seems that there are two effects operating to restrict knoll development in the pond. One is the encroachment of the sand wedge into the pond, and the other is the uniform settling of fine material out of suspension. This last mechanism is not very effective except in the deeper areas of the pond where the bottom physiography causes water movements to be restricted.

BOTTOM PHYSIOGRAPHY

The trend of the line reefs perpendicular to the prevailing wind is reflected in the bathymetry of the turbid-pond bottom even in ridges that do not reach within a meter of the surface. Over most of the turbid pond the coral knolls with up to 3 m relief cover about 37 percent of the bottom. The average knoll crossing in the turbid water is 1.6 m high and 6.7 m wide and the average interknoll distance is 9.5 m (Fig. 9). In the clear water the same statistics are 1.8 m, 9.7 m, and 5.5 m. There is little difference in the size of knolls in the clear and in the turbid water, although the mean crossing width in the clear water is larger due to the presence of a few very large knolls. In each case the dimensions parallel and perpendicular to the prevailing wind are very similar so the knolls appear to be more or less equidimensional in plan view. The average interknoll distance in the clear water is about one-half that in the turbid water, perhaps reflecting the less favorable environment in the turbid water.

What the average crossing dimensions mean in terms of the actual average knoll dimensions is a problem. If the knolls are approximated by hemispheres the average crossing dimensions are 0.85 the actual average dimensions. The

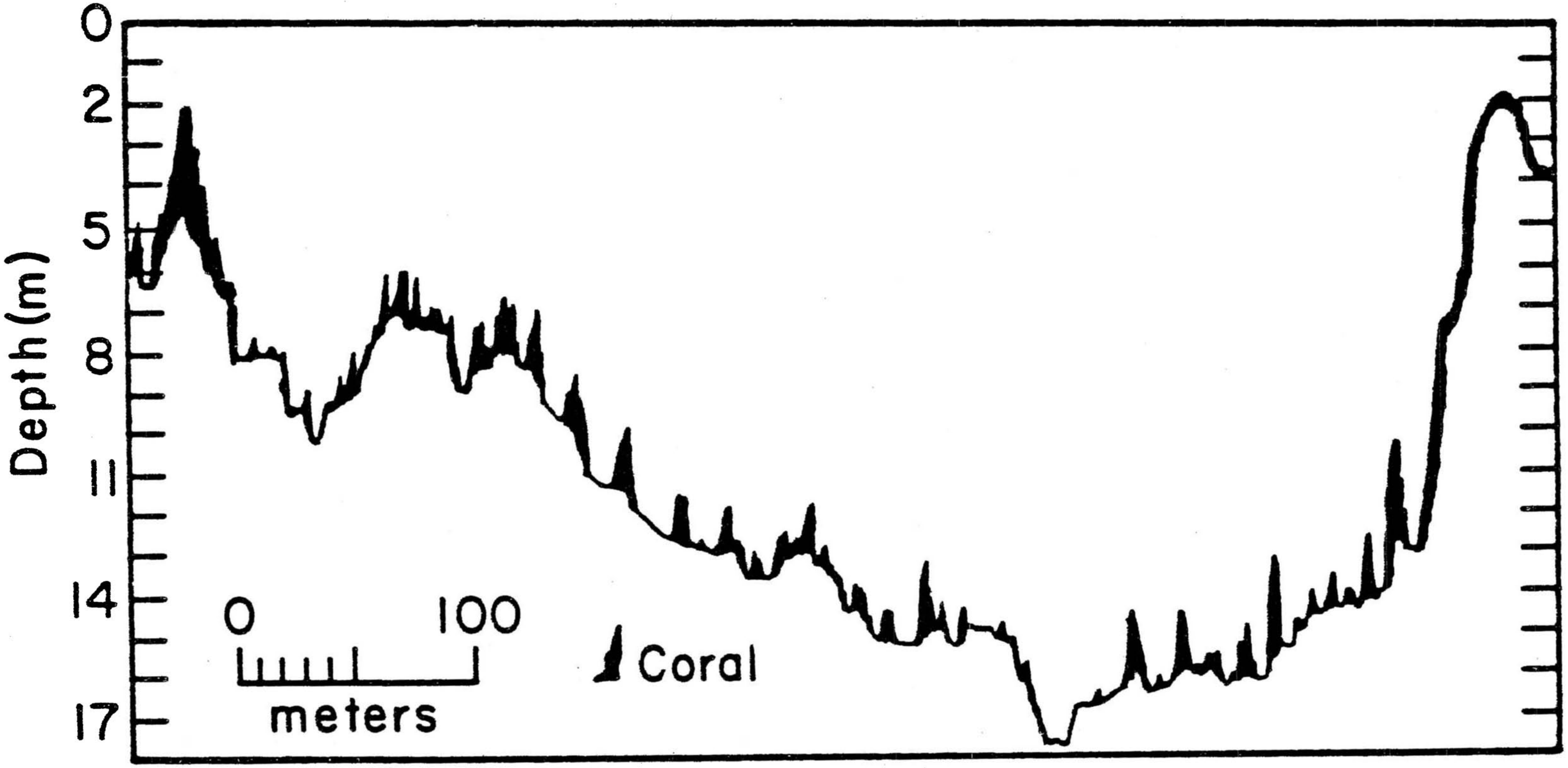

Fig. 14. A bathymetric profile in the clear-water sampling area.

knolls are more closely modeled by rectangular prisms so that the average crossing dimensions may be somewhat conservative but should be within 5 or 10 percent of the actual average dimensions.

SPECULATION ON AGE OF TURBID ENVIRONMENT

The interpretation of the turbid-water coral reef development is tempered by uncertainty about the age of the environment. Are the reefs actually developing in the turbid water or are they merely a degenerate skin on a relict topography? The environment is at least 150 years old, as no mention of major change is made in the recorded history. Beyond that, there are no definitive data. There are however, observations that allow speculation.

The distribution of land around the rim of Fanning Atoll is peculiar. Much of the windward area is swampy intertidal or shallow subtidal (Guinther, 1971). Nearly all of the leeward area is land. The windward fringing reef is about the same width as the leeward reef. Both the reef widths and the land distribution are the reverse of what is generally found on atolls (Wiens, 1962, p. 41). Rapa Pass appears to have been formed by the breaching of a conglomeratic beachrock ridge. Erosional remnants of the beachrock occur for some distance out onto the reef flat in the vicinity of Rapa Pass. These observations suggest that the atoll is tilting upward to the west. This tilting, of course, would change the configuration of passes around the lagoon and circulation within the lagoon.

Tilting could explain the infilled pass at the site of the Cable Station. The two spits on the lagoon side at the Cable Station are cemented shingle with well-developed imbricate structure. The imbricate structure of the two spits has opposing dips and strikes into the lagoon. The unconsolidated sediment filling the old pass is interpreted to be younger than the phosphatized conglomerates making up this part of the atoll rim.

Another feature that appears to be of fairly recent origin is the complex of apparent relict tidal deltas that occur at the lagoon edge about 5 km west of Rapa Pass (See Fig.1, Guinther, 1971). At present there is a free flow of water through this area but the path is rather tortuous. It seems unlikely that the features could form under the present regime. The short distance from the open sea to the deltaic features is blocked by a long, narrow, boulder ridge. If both the southern pass and the Cable Station pass were open, circulation in the lagoon would be different and perhaps the water would be less turbid. The Cable Station pass appears to have been similar to the present English Harbor pass, so conditions in the lagoon by the Cable Station pass may have been similar to those now found in the vicinity of English Harbor.

Along the lagoon shore about 500 m south of the Cable Station pass is a temple reported to have been built in the 16th century (Emory, 1939). On the shingle ridge on the south side of the pass there are graves that appear to also be 16th century. It is not clear whether the pass was open at the time the temple was built. At present canoes can land from the open sea in the vicinity of the Cable Station. This, plus the availability of building stone in the area, may explain the location of the temple without requiring that the pass be open. The graves however are on the shingle ridge so the pass existed at least 400 years ago.

This period is not long geologically, but is long enough to have allowed the turbid water community to stabilize. This community has produced at least a meter of apparently continous reef growth on the line reefs. If this growth has occurred over 400 years, then the net production is comparable to other coral reef areas (Smith, 1970; Chave et al., 1970). This does not say that the present coral reef configuration in the turbid-water area is not undergoing progressive degeneration. Although the corals themselves generate new substrate suitable for larval settlement, it seems that the general trend, however slow, is to decrease the favorable area through encroachment of sediment on the hard substrate. In a closed area, through time, reefs will bury themselves in their own debris unless the rate of sea level rise is sufficient to accommodate skeletal production.

CONCLUSIONS

While coral reefs will not develop in environments with less than some minimum light intensity and more than some maximum sediment deposition rate, these requirements are less stringent than is generally realized. Extreme water turbidity and muddy bottoms do not necessarily mean that the limiting values are exceeded.

Reef development in the turbid water of Fanning lagoon is of the same magnitude as it is in the clear water. Coral knolls have about the same dimensions in both areas although they are less abundant in the turbid- than in the clear-water area. In both areas the knolls are surrounded by calcium carbonate mud.

Only four of the coral species that were found in the clear water were not found in the turbid water, (Maragos and Roy, 1970). The major difference in the coral fauna is in the relative abundance of individuals of a species and in growth forms present. In the turbid water ramose growth forms make up 50 percent of the individuals while in the clear water they make up only 10 percent.

While the reefs of the two environments differ from one another ecologically, stratigraphically they are similar in form and in distribution. Because of the difference in faunal composition, the reefs in the turbid water tend to be structurally different from those in the clear water. Clear-water reefs are made up primarily of encrusting and massive corals. The reefs tend to have vertical walls and overhangs and are massive (Fig. 7). The turbid-water reefs, because of the abundance of ramose growth forms, tend to be more open, to have gentler slopes, and to be infilled by fine sediment as a result of the baffling effect of the corals on the knolls.

In conclusion, Fanning lagoon is an area where visibility in the water is about 2 m; where suspended load is about 100 times that of the open ocean;

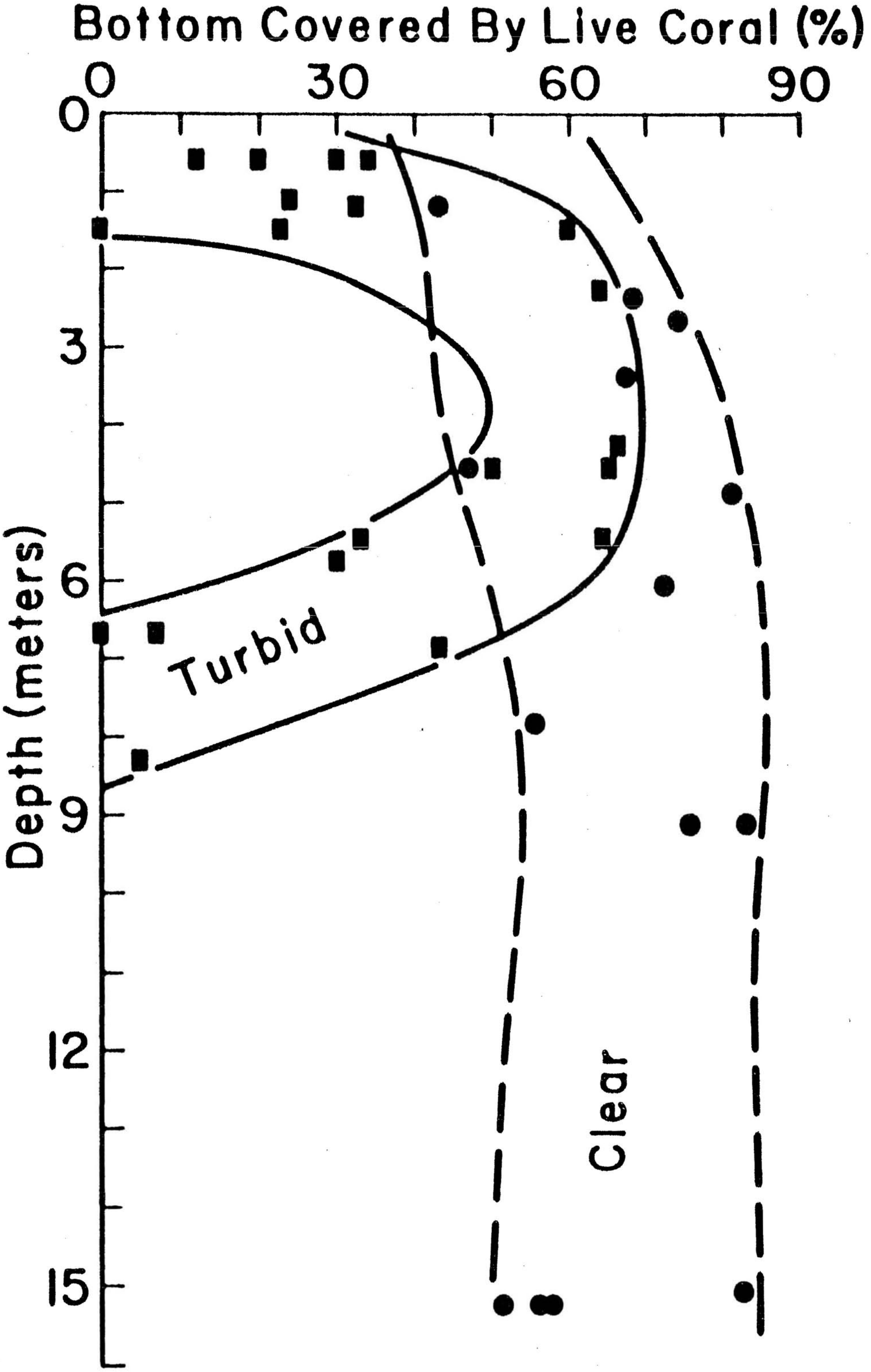

Fig. 15. Coral cover at various depths in the clear- and turbid-water areas (benthic survey data).

where the bottom is covered with calcium carbonate mud; where depositional rates appear to exceed 1 mm/year; and where about 30 percent of the bottom is covered with live coral. While there is a decrease in abundance of coral knolls from the clear to the turbid water, both areas have lush reef development. If the lagoon were to fill, it would produce a limestone body composed of areas of coral biolithite surrounded and in part infilled by micrite and calcilutite. The fine-grained rocks would be penecontemporaneous with the biolithite and never would the bathymetric relief exceed 8 m.

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CORALS COLLECTED AT FANNING ATOLL, 1968-1970

J.E. Maragos, K.J. Roy, and S.V. Smith
Department of Oceanography and Hawaii Institute of Geophysics

INTRODUCTION

Corals are abundant in both clear and turbid water in the lagoon of Fanning Atoll. Visibility in the turbid water is about 2 m, and the suspended load of $CaCO_3$ is about 4 mg/liter (Smith, *et al.*, 1971). The visibility in clear water is about 8 m, and the suspended load is about 1 mg/liter. Nowhere in the lagoon does the relative light intensity at the bottom fall below about 5 percent (Roy and Smith, 1971). Calcium carbonate mud covers much of the lagoon floor. Corals cover about 60 percent of the bottom in the clear water, and about 30 percent in the turbid. About 11 percent of the water area in the lagoon is clear (Roy and Smith, 1971).

During visits to Fanning Atoll in the Line Islands (February 1968, and January 1970, NSF Grants GP-949 and GB-15581), Roy and Smith collected corals in conjunction with sedimentation studies, from both the clear and turbid water areas in the lagoon. E. H. (Neil) Chave also provided some specimens that she collected during the 1970 trip. All corals were collected by diving. J.E. Maragos identified the specimens collected.

In 1970, SCUBA equipment was used to do benthic surveys at 33 locations in the lagoon (Roy and Smith, 1971). The bottom cover was determined at intervals of 0.25 m along transect lines 10 m long. In all, 650 m of bottom were examined in this manner. Field identification of corals was done rapidly, under poor conditions. The genera *Acropora*, *Tubastrea*, *Fungia*, *Hydnophora*, *Merulina*, *Montipora*, *Lobophyllia*, *Pocillopora*, *Porites*, and *Stylophora* are distinctive enough so that the field identifications are reliable, but corals identified as *Astreopora*, *Favia*, or *Platygyra* may likely belong to a number of different genera (Table 1).

CORALS PRESENT

Identification of coral specimens was done by comparison with specimens available in the collection of the Hawaii Institute of Marine Biology and using the following references: Crossland, 1952; Vaughan, 1907, 1918; Vaughan and Wells, 1943; Wells, 1954. There is some doubt as to the identification of some of the specimens at the species level; however identification at the generic level is reliable.

Forty-two species of coral were identified in the lagoon. Of the 42, 28 of the identifications were of specimens collected in the turbid water (Table 1). Only five species (*Tubastrea aurea*, *Fungia scutaris*, *Lobophyllia costata*, *Pavona varians*, and *Pocillopora verucosa*) were definitely not

Table 1. List of coral species collected or seen in the lagoon of Fanning Atoll. Location of collection site (clear or turbid water) is given, as well as field observations.

Species of Coral	Collected		Seen		Field Observations
	clear	turbid	clear	turbid	
Family Pociolloporidae					
Stylophora mordax Dana		X	X	X	*S. mordax* and *S. pistillata* not differentiated; common along windward edge of line reefs in turbid water, rare in clear water; *S.* species seen only in clear water. The specimens as collected at 10 m.
Stylophora pistillata (Esper)					
Stylophora sp.					
Pocillopora damicornis (Pallus)		X	X	X	Common in clear and turbid water; seen only on the LCM boat; one specimen seen at 5 m depth in turbid water; Common on reefs in clear water, not seen in turbid water.
* *Pocillopora ligulata* Dana		X	?	X	
* *Pocillopora* sp.		X		X	
* *Pocillopora verrucosa*	X			X	
Family Acroporidae					
* *Acropora formosa* (Dana)	X	X	X	X	Except for the growth form of *A. surculosa*, the species of *Acropora* were not differentiated; In the turbid water *Acropora* occurs at all depths; In the clear water is is near the top of the reefs and on the reef flats. *Acropora* makes up most of the coral on the windward reef slopes in the turbid water. *A.* species is common at depth in the turbid water. In clear water *A. surculosa* has a solid, smooth trunk up to 10 cm in diameter; above the trunk is an arborescent fan of branches.
* *Acropora nasuta* (Dana)	X		X	?	
* *Acropora pharaonis* (Milne-Edwards)	?		?		
* *Acropora pulchia* (Brook)		X	?	X	
* *Acropora* sp.		X	?	X	
* *Acropora squarrosa* (Ehrenberg)		X	?	X	
* *Acropora surculosa* (Dana)	X	X	X	X	
* *Acropora syringodes* (Brook)	X	X	X	X	

* *Astreopora gracilis* Bernard		X	?	X	Species of *Astreopora* were not differentiated.
Astreopora myriophthalma Lamarck		X	?	X	
* *Astreopora ocellata* Bernard		X	?	X	
* *Astreopora* sp.	?		?	?	
* *Montipora hoffmeister* Wells		X	?	X	Species of *Montipora* were not differentiated; *Montipora* is common in both the turbid and clear water.
Montipora informis Bernard	?		?	?	
* *Montipora spumosa* Lamarck	X		X	?	
* *Montipora venosa* Ehrenberg		X	?	X	
Montipora verrilli Vaughan		X	?	X	A specimen was collected at 5 m in the turbid water.
Montipora verrucosa Lamarck		X	?	X	
Family Agariciidae					
Pavona varians Lamarck	X		X		The only specimen seen was in the clear water.
Family Fungiidae					
Fungia scutaria Lamarck	X		X		*Fungia* is common on the reef flats in the clear water.
Family Poritidae					
* *Porites australiensis* Vaughan		X	?	X	Species of *Porites* were not differentiated. *Porites* is common in all environments. *P. solida* found in clear water at 10 m grows as large inverted pyramids^{a}.
* *Porites solida* Forsh	X	X	X	X	
#* *Alveopora verrilliana* Dana	?		?	?	Only one specimen was seen.
Family Favidae					
Favia speciosa Dana		X	?	X	Species of *Favia* and *Plesiastrea* were not differentiated.
Favia stelligera Dana		X	?	X	

* *Plesiastrea versipora* (Lamarck)			?	?	
Platygyra rustica Dana	X	X	X	X	Species of *Platygyra* and *Leptoria* were not differentiated.
* *Platygyra lamellina* (Ehrenberg)	X		X	?	
* *Platygyra* sp.		X	X	X	
#* *Leptoria phrygia* (Ellis & Solander)	X	X	X	X	
Hydnophora ridgida (Dana)		X	X	X	
* *Merulina ampliata* (Ellis & Solander)		X	X	X	Common in all environments. Seen in both clear and turbid water below 2 m.
Family Mussidae					
#* *Acanthastrea echinata* (Dana)		X	X	X	Specimen collected at 5 m in the turbid water. One specimen seen.
#* *Lobophyllia costata* (Dana)	X		X		Common in the clear water; also occurs on the reef outside the atoll.
Family Dendrophylliidae					
Tubastrea aurea Quoy & Giamard	X		X		Specimen collected by Edith H. Chave on reef in clear water. Not seen by other collectors.

Genera not listed in Vaughan (1918) or in Wells (1954)

* Species not listed in Vaughan (1918).

[a] A head of *Porites solida* of this type is shown in Fig. 5 of Roy and Smith (facing page 64 of this report).

collected nor seen in the turbid water. Only one species, Pocillopora sp. (Table 2) was definitely seen only in the turbid water.

DISCUSSION

The 1968-1970 collection has 17 genera of hermatypic scleractinian corals in it. Vaughan (1918) lists 12 genera from Fanning Atoll. Wells (1954) lists 19 genera from the Line Islands. Of the 19, 13 are in our 1968-1970 collection from Fanning Island. Four genera are new reports for the Line Islands (Table 1). Of the four, only Lobophyllia is common in the lagoon, and it is found only in the clear water. Vaughan (1918) lists 24 species of hermatypic scleractinian corals from Fanning Atoll. Of these, 14 are in the 1968-1970 collections. Twenty-seven species in the 1968-1970 collections are not on Vaughan's list; eight of these are species of Acropora.

An explanation for the difference in the collections is that the 1968-1970 collections were taken entirely from the lagoon, and in large part from the turbid water. Also, collecting in 1970 was done during three weeks of benthic surveying using SCUBA equipment. This sampling was no doubt more intensive than previous samplings.

The new reports increase the number of genera in the Line Islands to 23. While this increase does not seriously alter the pattern of isopangeneric lines that Wells has drawn (Wells, 1954, plate 186), it does reemphasize Wells' discussion of the problems of comparing areas in which the completeness of sampling is variable. No descriptions are available for corals obtained by diving on the outside reefs. Thus it is likely that more than 23 genera occur in the Line Islands.

The most abundant coral in the turbid water of the lagoon is Acropora, while in the clear water Montipora is the most abundant (Table 3). However, because the area of clear water is small relative to that of turbid water, Acropora covers about twice as much of the lagoon floor as does Montipora. Although there are about as many genera of coral in the turbid water as there are in the clear, the abundance of the various genera is variable (Table 3). The growth forms also differ. About 55 percent of the corals in the turbid water are ramose, while only 10 percent of those in clear water are (Roy and Smith, 1971). There is no lack of either individuals or of species of coral in the very turbid water of Fanning lagoon.

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Table 2. Corals in the 1968-1970 collection that were identified only to the generic level.

Coral Genera	Notes
Acropora sp.	This is a delicately branching specimen with an overall form similar to A. syringodes.
Platygyra sp.	A massive coral that is very similar to P. rustica, but the wall separating the calices are more massive in Platygyra sp.
Pocillopora sp.	The branches are thin and are similar to those of the delicate forms of P. damicornis but are much more elongate and have fewer divisions.
Stylophora sp.	The specimen is similar to S. pistillata except that the branches of Stylophora sp. are much larger and more massive, and the calices are farther apart.

Table 3. The distribution of coral genera in various environments in the lagoon. Data collected during benthic surveys. Coral genera not listed are either very rare or were not distinguished from the genera listed.

		Acropora	*Montipora*	*Favia*	*Merulina*	*Stylophora*	*Porites*	*Pocillopora*	*Astreopora*	*Platygyra*	*Hydrophora*	*Fungia*	% live coral	% of area	% of lagoon
Turbid Water															89
% of live individual	pond bottom	41	21	12	17	4	0	0	2	1	1	0	35	50	
	reef slope	79	0	1	0	15	1	3	0	1	0	0	28	18	
	reef flat	51	1	3	0	19	23	1	0	2	0	0	21	32	
% of turbid water area covered		14[a]	4	2	3	3	2	<0.5	<0.5	<0.5	<0.5	0			
Clear Water															11
% of live individuals	pond bottom	0	57	19	4	1	17	0	0	1	1	0	59	50	
	reef slope	2	74	6	1	3	11	1	0	2	0	0	73	18	
	reef flat	20	47	5	0	6	5	12	2	1	0	2	46	32	
% or clear water area covered		3	33	7	1	2	7	2	<0.5	1	<0.5	<0.5			
% of lagoon covered		13[b]	7	3	3	3	2	0.5	<0.5	<0.5	<0.5	<0.5			

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[a] The sum of (% *Acropora* X (% live coral/100) X (% of area/100)) for the three environments, pond bottom, reef slope, and reef flat.

[b] The sum of (% of turbid water area covered X (% of lagoon/100) + (% of clear water area covered X (% of lagoon/100)).

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PHYCOLOGICAL INTRODUCTION TO FANNING ATOLL

Robert DeWreede and Maxwell S. Doty

Department of Botany

ABSTRACT

During January 4-16, 1970, the different major algal ecological situations in the atoll (03° 54' N. Lat. and 159° 24' W. Long.) were surveyed. Fourteen of the more conspicuous and dominant community members of the Chlorophyta, four Phaeophyta, nine Rhodophyta, and three Cyanophyta are enumerated here. A comparison with the algal floras of Howland, Baker, Palmyra, Johnston, and Mururoa atolls and the high island of Tahiti is made. Floristically, Fanning conforms to the general biogeographic pattern which becomes simplified as one moves eastward in the Central Pacific. Transect studies were made, and in one case algal growth is correlated with the results of the diffusion enhancement studies carried out. Water movement, hence diffusion, is related to algal growth qualitatively and quantitatively, with diffusion being enhanced by water movement most at mid-tide levels. A key for the identification of the algae is given.

INTRODUCTION

With the abandonment of the recently renovated Fanning cable station of the Cable and Wireless Company, Ltd., London, and the need for an atoll research site in the eastern part of the Central Pacific, it has become desirable that the algal aspects of Fanning be known. Only Bakus (1964), discussing fish grazing, has reported algae from Fanning. Bakus mentions four species in the genera *Caulerpa*, *Lobophora* (as *Pocockiella*), *Enteromorpha*, and *Turbinaria*.

Very few publications (Dawson, *et al.*, 1955; Dawson, 1959a; Howe and Lyon, 1916; Doty, 1954) have touched on the algae of any of the Line Islands, of which Fanning (Fig. 1) at 03° 54' N. Lat. and 159° 24' W. Long., is one. Tsuda and Buggeln (1969) list the algae of Johnston Atoll, Tsuda and Trono (1968) those of Howland and Baker atolls, and Dawson (1959b) enumerates the algae from Canton Atoll, all in the Central Pacific. Doty postulated absence of *Sargassum* and, reciprocally, of *Rhipilia* from atolls in Fanning's geographic location, i.e., between 16° N. and 16° S. Lat. and 141° W. and 165° E. Long. While the genus *Ulva* is apparently absent (Tsuda, 1968) from the majority of the Micronesian islands and atolls (0° to 16° N. Lat. and 135° to 173° E. Long.), it is rather common on the surrounding Pacific islands. For example, in the Line Islands, *U. fasciata* has been reported (Tsuda, 1968) from Jarvis and Christmas atolls as well as (Tsuda and Trono, 1968) from nearby Howland and Baker atolls. *Turbinaria* reflects another distributional pattern, being present west of 147° W. Long. and absent or at least not yet found in the Tuamotu Islands (Doty, 1954) or at Mururoa (Chevalier *et al.*,

1968) both of which are farther east. These remote atolls are of great interest in reference to such real and hypothetical biogeographical situations.

Thus, the opportunity of obtaining information on the algal ecology and floristics of this atoll at 03° 54' N. Lat. and 159° 24' W. Long., as provided by an expedition organized by Dr. Keith Chave of the University of Hawaii, was seized upon. The main botanical interests of the expedition centered around two objectives: (1) determining which algae are present, where they grow, and the variations in their biomass; and (2) the physical factors dominating the lagoon and reef, and what might be relevant to future algal experimental work especially as might lead to marine agronomic use of Central Pacific atolls.

To achieve our ends, floristics and such water characteristics as temperature, dissolved organic matter, salinity, and motion were recorded along with algal distributions with respect to bottom character. The field work was carried out by the senior author with the assistance of several others, most notably Mr. Joaquin Villagomez. Aerial support for transportation and aerial photography were provided by Dr. Martin Vitousek, and this enabled us to obtain almost complete vertical photography for an eventual mapping of the vegetations. Drs. Kenneth Roy and Keith Chave have provided arrangements of the photography and many other details, as has Dr. Donald Gordon, in respect to water chemistry. The work was done during the period of January 4-16, 1970; for which period the present paper provides a preliminary report.

Methods

Investigations were made throughout the atoll (Fig. 1), though all observations were not possible at all stations. Collections for taxonomic and distributional studies were prepared as exsiccati or wet preserved specimens. Some biomass data were obtained, but with extreme difficulty due to the low turf-like habit of the majority of the algae. In places these algal materials were scraped off the substratum and the weights with contained sand measured. Turbinaria ornata was picked and weighed wet. All such sampling was done within the area of an objectively placed stainless steel ring 46 cm in diameter and calculated to square meter values. Voucher specimens for the algae are deposited in the herbarium of the junior author.

The degree to which water movement enhanced diffusion (=DIF) was measured with clod-cards (Doty, in press), a method involving the measurement of weight loss from ice-cube-size $CaSO_4$ blocks attached to upright stakes or chunks of coral for 24 hours, i.e., one tidal cycle. DIF is obtained by dividing the rate of dissolution in still water for the particular lot of clod-cards into the rate of weight loss in the field.

In addition to the algal collections and diffusion studies discussed in this paper, samples for or measurement of dissolved organic matter, temperature, and salinity were taken at the different collection and observation sites. In addition, dissolved organic and Ca^{++} samples were obtained at every degree enroute to and near the island, along with NO_3---N and PO_4---P samples for comparative purposes. These data are not reported upon at this time.

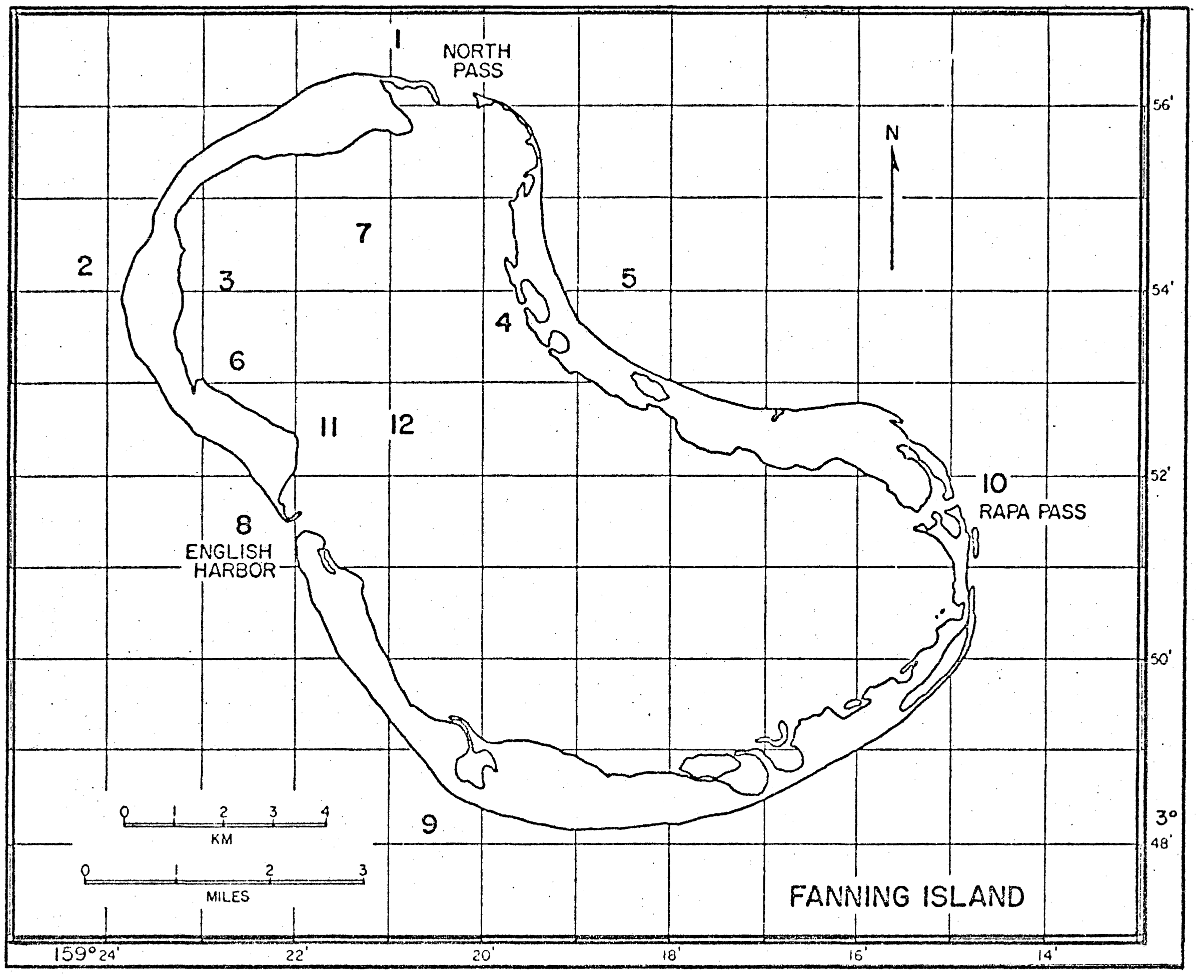

Fig. 1. Map of Fanning Atoll showing North Latitude, West Longitude, and the approximate locations of the work stations: i.e., Station 1, North Pass; Station 2, Cable Station (ocean reef); Station 3, Cable Station (lagoon); Station 4, Copra Village (lagoon); Station 5, Copra Village (ocean); Station 6, Napu Naiaroa Pond; Station 7, a lagoon pond; Station 8, English Harbor; Station 9, Southwestern Point; Station 10, Rapa Pass; Station 11, Dead Tree Reef; and Station 12, a lagoon reef.

Results and Discussion

The algal collections, while meager, turned up 14 members of the Chlorophyta, four entities among the Phaeophyta, nine Rhodophyta, and at least three Cyanophyta. Many of the algae were only collected once and commonly showed strong evidence of grazing by herbivorous fishes and possibly by the sea urchins, Tripneustes and Heterocentrotus, and a long-spined, black sea urchin (Diadema?), making algal identification quite difficult or impossible. This is especially true of the reef-flat Rhodophyta. A list (Table I) of the species and genera forming the most conspicuous elements in the principal communities is provided here. To provide a comparison, Table I also indicates the occurrence of the same species as shown from Mururoa (20° 51' S., 138° 55' W.), Howland (0° 48' N., 173° 38' W.), Baker (0° 15' N., 176° 27' W.), Johnston (16° 45' N., 169° 31' W.) and Palmyra (5° 52' n., 162° 06' W.) atolls and from the high island, Tahiti (17° 30'S., 149° 30' W.), where more intensive studies have been made.

Algae collected at Fanning Atoll by S. A. Wainwright in July 1963, were studied during the present investigation insofar as they represent the same genera as in the present collections. These former include two unidentified species of Halimeda (20090[a] and 20117), Jania natalensis (20099), one Hypnea (20114), Caulerpa urvilliana (20101) and Avrainvillea lacerata (20698 and 20699). All are of forms very similar to those obtained during the present expedition with the exception of Halimeda. Wainwright's Halimeda collections are of unique varieties of the two species of Table I at best, if not different species entirely.

Avrainvillea lacerata appears to be rather common at Fanning in view of there being six collections at hand. We have illustrated (Fig. 2) specimen #11882 from Raroia in the Tuamotu Islands which is very similar to #1217 from Fanning. Setchell (1926) reports this same species from Tahiti and, while we have not seen Setchell's specimen, we have seen a collection by Dr. Jan Newhouse (his #3134a) which seems to be A. erecta (Berkeley) Weber-van Bosse, a quite different and stupose species.

In a 50-meter transect taken about one kilometer north of the Cable Station (Fig. 1, #2) on the seaward reef, low, prostrate, seldom-fertile Turbinaria was present in every one of the ring samples spaced two meters apart. The thalli were "normally dense" forms. Other transect studies (Fig. 3) verified the observation that Turbinaria ornata appeared more commonly on the windward side of reef patches (e.g., at Station 7) than elsewhere in the lagoon. The result of the diffusion study (Fig. 4) showed greater rates of diffusion, DIF, related to water movement there; though the values for DIF are only some 7 percent higher for the windward edges of the reef patches. However small, this would seem to be the known factor most closely relatable to the higher crops (Fig. 3) of Turbinaria being there. It must be kept in

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[a] Such five-place numbers and those preceded by "RDW" identify the voucher specimens in the junior author's herbarium. The numbers preceded by "RDW" designate collections of the senior author.

TABLE I. Algae recognized in the collections at hand from Fanning and a listing of their distribution on other atolls in the Central Pacific. The four-place numbers are the collection numbers of R. E. DeWreede. The initials have the following place-author meanings: BT, Baker Island and Tsuda; HT, Howland Island and Tsuda; JT, Johnston Atoll and Tsuda; MC, Mururoa Atoll and Chevalier; PD and PH, Palmyra Atoll and respectively Dawson and Howe; and TS, Tahiti and Stechell. An asterisk is used to indicate that the genus alone was reported, or that a different species of the same genus was reported.

Species	Collection number	Nearby records
CHLOROPHYTA		
Avrainvillea lacerata J. Ag.	1217, 1237, 1255	TS
Boodlea composita (Harvey) Brand	1250	PD, JT
Bryopsis pennata Lamouroux	1235	PD, MC, TS*, JT
Caulerpa peltata Lamouroux	1215	HT*, TS, MC*, JT*
Caulerpa racemosa (Forsk.) Weber van Bosse	1239, 1240	MC, HT*, TS, JT
Caulerpa urvilliana Montagne	1213, 1222	MC, HT*, PD, TS*, JT
Codium edule Silva *in* Egerod	1243a	MC*, TS*, JT*
Dictyosphaeria cavernosa (Forskal) Borgesen	1226	BT, HT, MC*, PD[1/], TS*
Dictyosphaeria versluysii Weber van Bosse	1224	BT, MC*, TS*, JT
Enteromorpha lingulata J. Ag.	1220	PD*, MC*, BT*, TS, JT*
Halimeda fragilis Taylor	1223	PD*[2/], MC*, TS*, JT*
Halimeda lacunalis Taylor	1242, 1249, 1254	PD*[2/], MC*, TS*, JT*
Neomeris vanbossea Howe	1243	MC, TS
Ulva fasciata Delile	1234	HT, BT, TS*
PHAEOPHYTA		
Dictyota friabilis Setchell	1202, 1212	HT, TS, JT*
Ectocarpus indicus Sonder	1211	BT, TS, JT
Lobophora variegata (Lam.) Wormersley	1216, 1236, 1253	MC, TS, JT
Turbinaria ornata (Turner) J. Ag.	1214, 1219, 1241	PD*, BT, TS

(TABLE I, continued)

Species	Collection number	Nearby records
RHODOPHYTA		
Gelidium pusillum (Stackhouse) LeJolis	1228, 1247	TS*, JT
Gracilaria sp.	1225	
Hypnea sp.	1238	BT*, TS*, JT*
Janis natalensis Harvey	1227	MC*, BT*, HT*, PD*, TS*, JT*
Laurencia surculigera Tseng	1218	MC*, TS*, JT*
Peyssonnelia rubra (Greville) J.Ag.	1230a	TS
Polysiphonia scopulorum Harvey	1301	TS*, JT*
Polysiphonia sp.	1256	TS*, JT*
Porolithon gardineri (Foslie) Foslie[3]	1229, 1230	PD, MC*, TS*
CYANOPHYTA		
Entophysalis conferta Dr. & Daily	1252	MC*, TS*, JT*
Schizothrix calcicola (C. Ag.) Gom.	1252	BT, JT
Schizothrix mexicana Gomont[4]	1221, 1251	PH

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[1] Identified as *D. favulosa* (Ag.) Decaisne by Howe and Lyon.

[2] Ten specimens of *Halimeda* were collected from Baker and Howland Islands, but not further identified.

[3] Identified as *Lithophyllum kaiserii* Heyd. by Howe and Lyon.

[4] Identified as *Lyngbya gracilis* (Menegh.) Rabenh. by Howe and Lyon.

mind that during other weather or tidal conditions very different results might well prevail. From studying Figure 3, one gets the impression that neither elevation nor substratum are the factors and that substratum and water movements such as observed are not well correlated.

Measurements of the effect of water movement on diffusion as a function of elevation in the tidal system were made (Fig. 5) in the lagoon at (Fig. 1) Stations 7, 11, and 12. At Station 7, the western (leeward) measurement was (Fig. 5, "stake 1") 15 clod-cards, the bottom clod-card being 18 cm from the sea bottom, with 10 cm between the bottom four and top four and 5 cm between the other clod-cards. The eastern (windward) measurement was (Fig. 5, "stake 2") 25 clod-cards, the bottom clod-card being 18 cm from the bottom, with 10 cm between the bottom four and top four clod-cards and 5 cm between the others. At Station 12, the devices were lost. Station 11 had one measurement (Fig. 5, "stake 3"), 21 clod-cards, the bottom clod-card being 18 cm from the bottom, the bottom six and top four being 10 cm apart and the others 5 cm apart.

The results show the greatest DIF values near mean sea level. All of the vertical measurement devices were so placed as to span the mean tide range of 0.37 m (spring range 0.49 m), and Figure 5 is arranged to emphasize this. There was no way to determine the elevation of the stakes precisely, and the tidal range and other features were accepted as projected from Honolulu, thus MSL on Figure 5 is entirely arbitrary. However, results obtained elsewhere lead us to accept the level where the DIF is greatest to be essentially mean sea level.

Floristically, Fanning appears to be (Table I) quite similar to other atolls nearby in the Central Pacific. In this respect it has *Turbinaria ornata* and *Ulva fasciata*. The former is seemingly absent on atolls east of 147° W. Longitude and the latter, as Tsuda suggests, absent on Western Pacific atolls. *Avrainvillea lacerata* may be a special case worthy of further study, but the taxonomy of this genus and confusions of it with *Rhipilia*, to which the junior author may have contributed the idea but with faulty taxonomy (1954), make it a case requiring monographic efforts as a preliminary.

The present effort was primarily ecological, and taxonomic work was confined to the conspicuous algae. Many of these are taxonomically most difficult and sterile, and as in the cases of the *Hypnea* sp., *Gracilaria* sp. and *Polysiphonia* sp. of Table I, often impossible to identify. The cures are monographic studies and watching the populations for fertile material over a period of a few months or a year. For example *Bryopsis pennata*, as shown in Table I, is reported from Fanning, and both Doty (1954) and Dawson (1959a) report it from Palmyra, but all on the basis of sterile material.

Many other algae reported from nearby places by Doty, Dawson, and others are in the present collections and in time will enable a more detailed report. Some such as *Asterocytis* (Doty, 1954) from Palmyra are almost ubiquitous and of little value in biogeographic or other ecological studies. Sometimes they are small or microscopic and so of limited value for ecological work as in the case of *Polysiphonia scopulorum*. A simple dichotomous

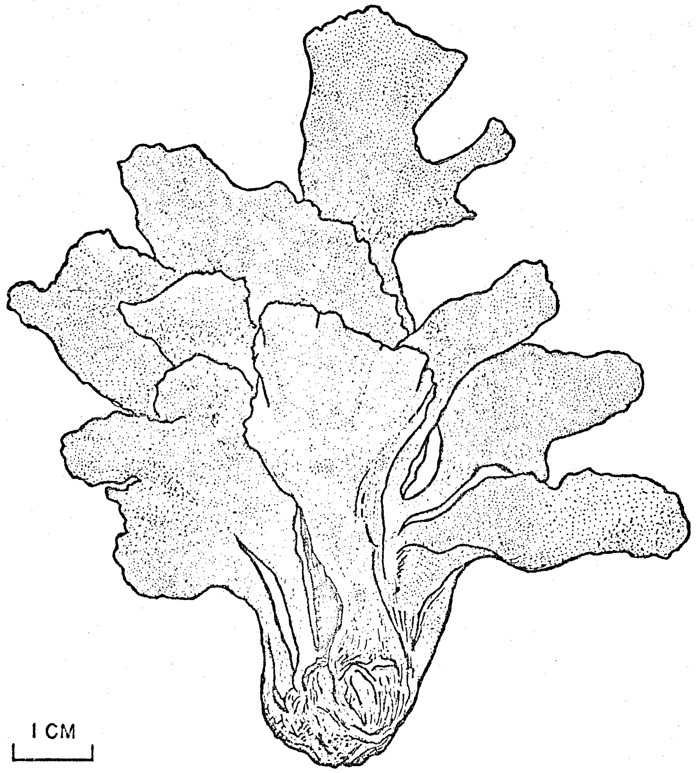

Fig. 2. *Avrainvillea lacerata* (MSD 11882) from the atoll of Raroia. This alga is a soft felted mass of fibers.

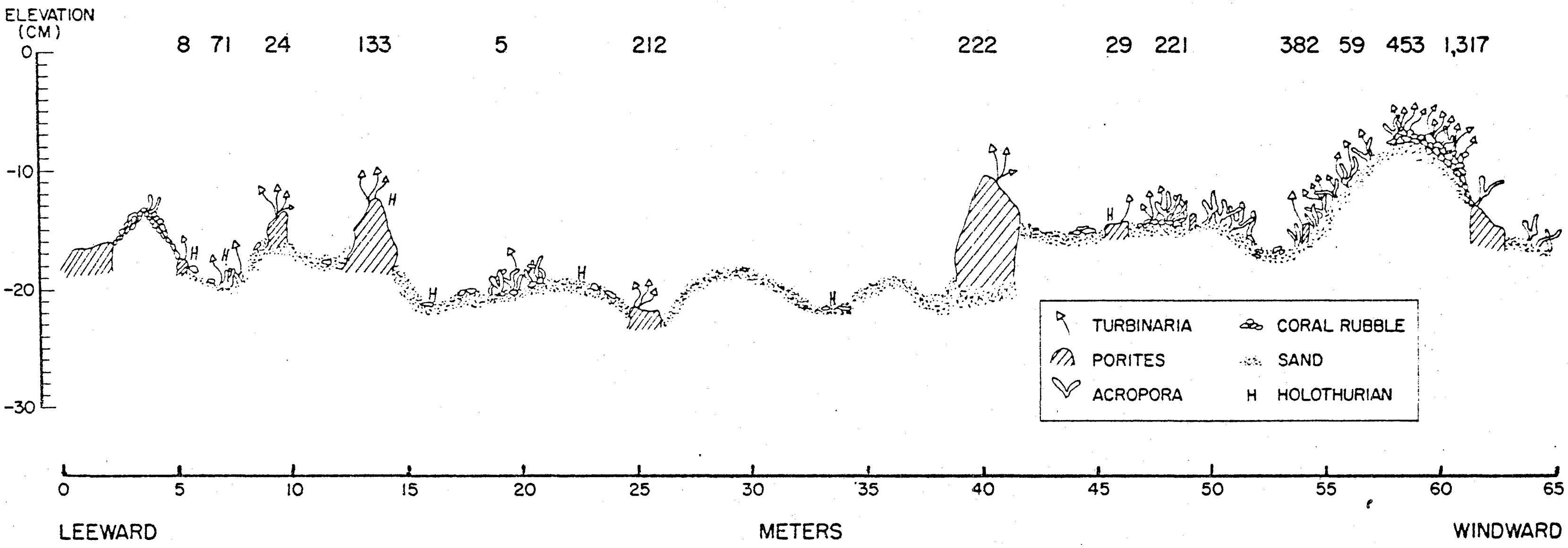

Fig. 3. Transect at Station 7 reef near entrance to lagoon pond. Acruss the top of the figure, wet weight of <u>Turbinaria</u> is given in grams per square meter above the area where measured. Due to inadequate tidal records, no relationship to mean sea level is given. However, the elevations given are near those of Figure 5, but must be considered relative and for comparison between these two figures only.

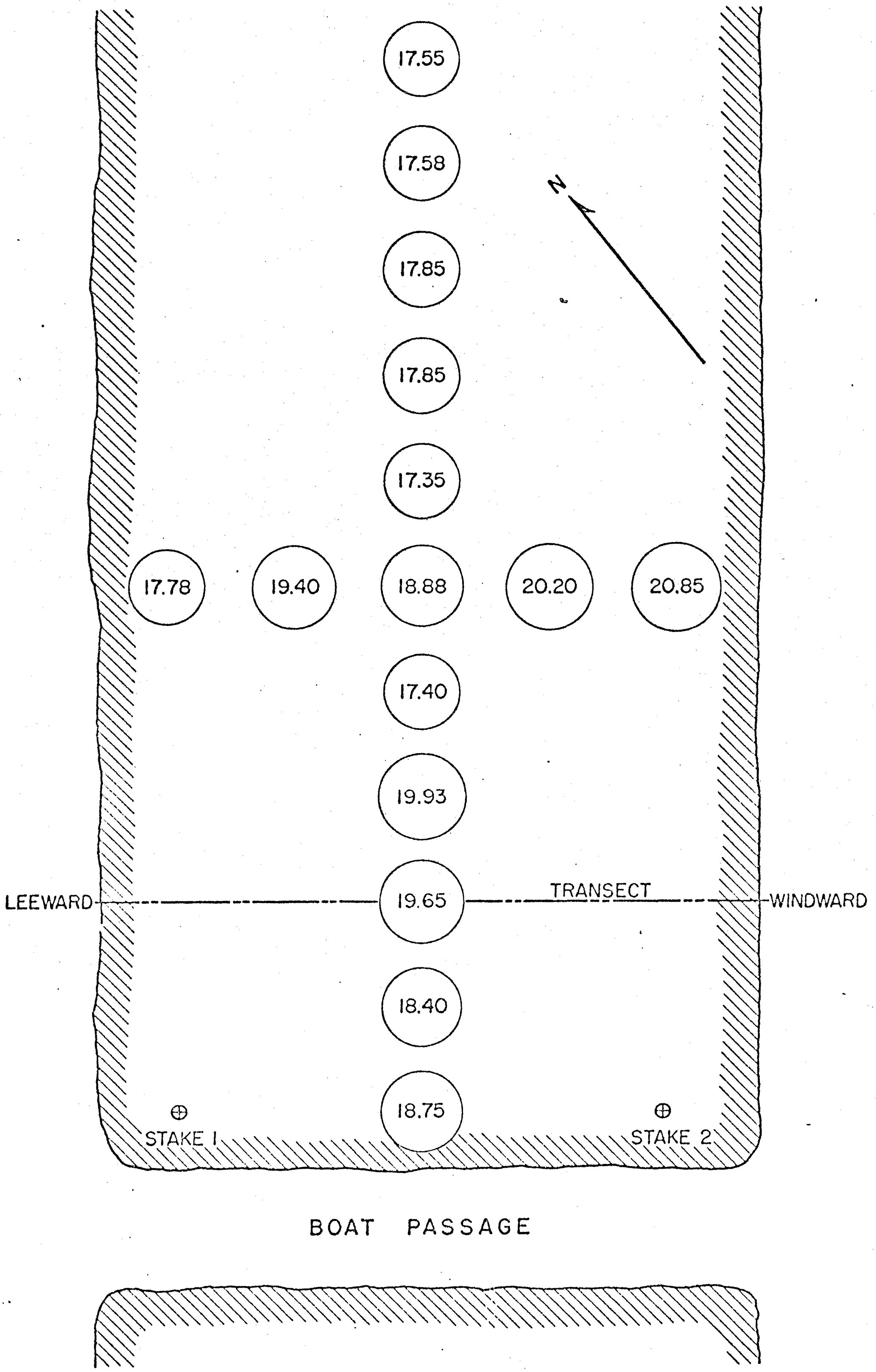

Fig. 4. The distribution of DIF measurements across the reef at Station 7. Numbers denote DIF value, with each number being the average from two measurements. The distance between sites where the measurements were made is 2 meters. Stakes 1 and 2 (see Fig. 5) were the sites for measurement of DIF as a function of height. The transect location is that of Figure 4.

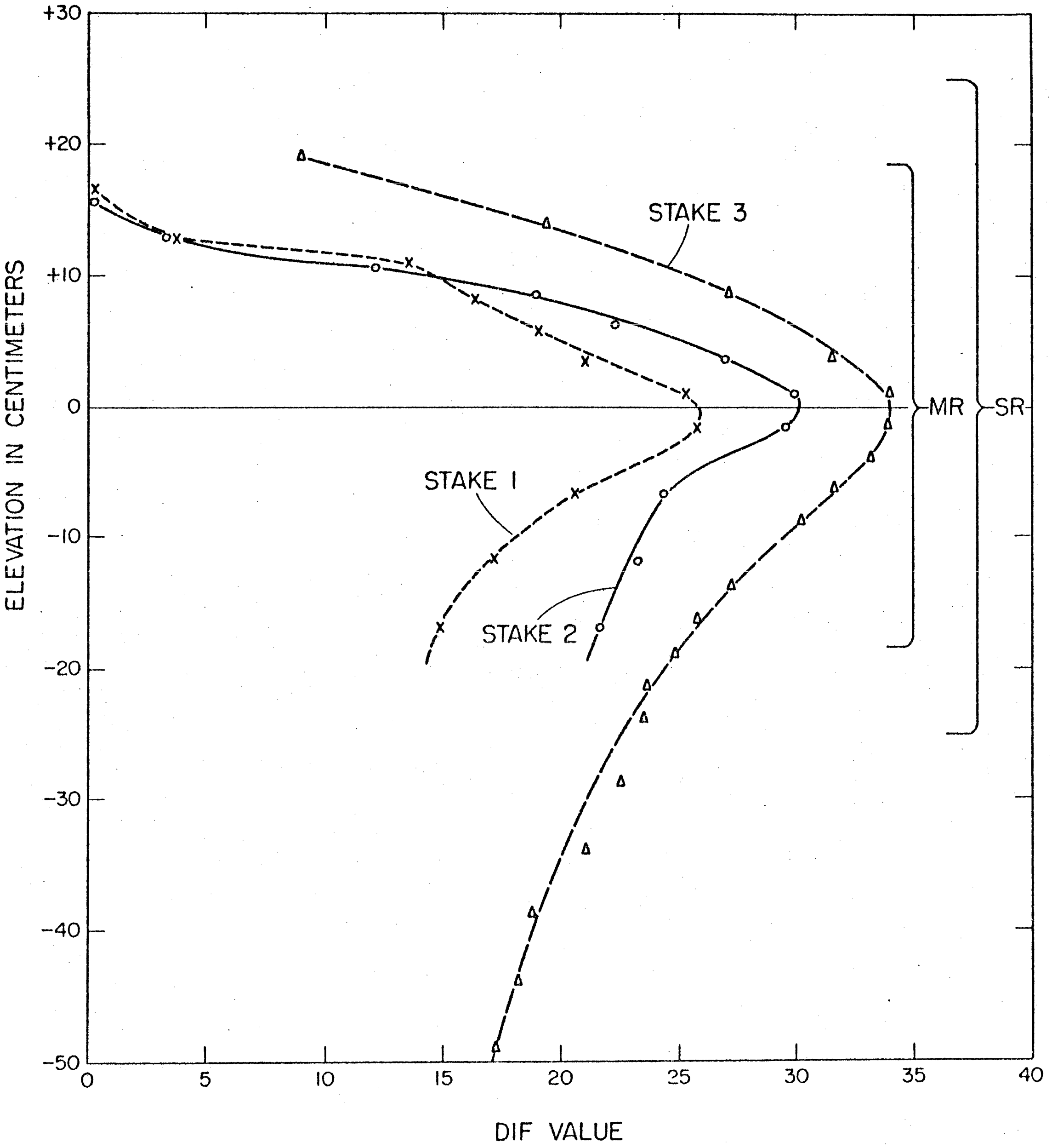

Fig. 5. Graph of DIF value as a function of height above the bottom as measured on stakes 1 and 2 at Station 7 and stake 3 at Station 12. Stake 1 was near stake 2, but on a more windward reef edge. MR and SR are the mean and spring tide ranges, respectively.

"key" to the genera of seaweeds found at Fanning or expected, since they have been found nearby, is included as an Appendix A to aid others concerned with the work being done at this atoll.

In terms of algal habitats, Fanning Atoll waters can be divided into at least three initial types, i.e., sea reef, lagoons, and ponds*. The lagoon flora is sparse, with the most noticeable component being also the largest in size, Turbinaria ornata (RDW 1214^a, 1219 and 1241). East-facing beaches in the lagoon commonly had windrows of Turbinaria, the windrows of lax T. ornata var. ornata f. ecoronata Taylor being noticeably lacking in other algal components. The same lax forms have been observed in the lagoon of Canton Atoll by the junior author. The same species, T. ornata var. ornata, from the sea reefs is much more compact and shows occasional intra-marginal spines.

Scattered patches of Halimeda lacunalis (RDW 1242, 1249 and 1254) were also found in the lagoon growing both on dead coral patches and on lagoon pavement lightly covered with sand. Its depth of occurrence varied from one meter to seven meters. The species is known from Christmas Island and the Marshalls from as deep as 55 meters. In terms of biomass, hence contribution to carbonate sediments, it would seem to be insignificant.

In the ponds found within the land mass of the island and often connecting at high tide with the ocean, a different sort of flora is found. The most common vascular plant, Sesuvium portulacastrum, is found on mounds of compact soil within areas generally covered by one to five centimeters of standing water. The surrounding substratum is generally a fine silt, in which an average person might sink well above the ankles. Such non-consolidated bottoms are poor habitats for benthic algae, and the few found are generally epiphytic or attached to small coral chunks. Exceptions are the clumps or layers of blue-greens found covering the bottom sediments and the nearly horizontal beach areas. Both soft bottoms and lack of large algae we would say are results of the low DIF values, i.e., related to lack of turbulence.

Quite common in "pond" areas are clumps of Entophysalis conferta (RDW 1252) and Schizothrix calcicola (RDW 1252) growing on such flat bottom sands as found in Napu Naiaroa Pond. Similar clumps binding sand and suggested by Taylor (1950) as part of an ongoing process of beach-rock formation were found on an extensive Sesuvium flat near Vae Tepu (Fig. 1, no. 4) on the most northeastern island of the atoll. This type of blue-green algal crust is (Newhouse, 1954) called "kopara" at Raroia Atoll.

An alga found commonly in the ponds on coral pebbles and Turbinaria in moving waters near the lagoon is Ectocarpus indicus (RDW 1211), where it forms fairly dense streaming hair-like clumps which are light brown in color. However, the blue-green algae are predominant if the entire pond area is considered.

On the seaward reef the algal population varies greatly with reef form and exposure. A quite different group of algae is found, though again none is very common and no large forms were noted at all. Even the Turbinaria found here was generally a small compact form and relatively inconspicuous.

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*The term "ponds" as used here is not the same as the lagoon ponds, such as Suez pond mentioned in other papers in this report.

At the southwest tip of the atoll the algal reef is deeply dissected with channels one to two meters wide and with occasional upward boulders or knees which are submerged at high tide. The predominant alga here in terms of biomass is Jania natalensis (RDW 1227), an articulated coralline. It forms dense sand-holding mats over the intertidal boulders, the biomass of which is from 344 to 440 grams per square meter. Additionally, a square meter of such a mat was measured to hold an estimated 594 additional grams of calcareous sand.

In subtidal regions at the southwestern point of the atoll (Fig. 1, no. 9) on the vertical faces of the boulders, mats of Halimeda fragilis (RDW 1223) can be found. This species has been reported previously from the Gilbert and the Marshall islands and from the Indian Ocean. If the identification is correct, this represents an eastward extension of its range. As seems so often to be the case with the Pacific algae, the presently postulated range is probably more that of collecting rather than a likely description of actual algal distribution. One-third-square-meter patches of Caulerpa urvilleana (RDW 1222) adorned the wave-washed rocks along with small thalli of Dictyosphaeria versluysii (RDW 1224) which were also common.

On the east-facing seaward beach of the northeast island (Fig. 1, no. 5) the reef is a more extensive flat area with but few protruding boulders. Inshore the surface is covered by flat thin "shingles" of dead coral which form a vertically packed layer. On the seaward-facing lower portions of these shingles 2- to 4- centimeter tufts of Ulva fasciata (RDW 1234) were noted. This is the only place where this alga was found. However, Tsuda (1968) reports Ulva fasciata from both Jarvis and Christmas islands nearby. On the seaward faces of the few scattered protruding boulders, minute growths of sterile Jania natalensis and some Neomeris vanbossea (RDW 1243) were seen, whereas on the surf-protected beach faces of these same rocks a sterile Hypnea (RDW 1238) grows thickly. In addition, patches of the crustose brown alga, Lobophora variegata (RDW 1236) and one thallus of Avrainvillea lacerata (RDW 1237) were found on dead-coral blocks. This latter genus has not previously been found (Tsuda, 1970) east of the 180th meridian except that Dawson et al. (1955) has recorded it from Palmyra in the gut contents of fishes.

Near this same site is found a canal situated between two shingle dikes. At first sight and without further study it appears as though the atoll is moving seaward in this area since the landward dike is thickly covered with Messerschmidea argentea, whereas the seaward dike is barren except for an occasional low-growing bush of the same species. However, other factors such as salt spray, occasional wave wash and consequent substratum movement, as well as the lack of an accessible fresh-water layer, surely all contribute to this apparent barrenness.

The reef immediately west of North Pass (Fig. 1, no. 1) is a nearly smooth coral pavement near the sandy beach. Farther out a raised rough-topped conglomerate area is exposed to the air at mid-tide levels. Seaward, this surface drops one and one-half meters to an area of fine sand interrupted with live coral heads. A rubble ridge, some 175 to 200 meters from the shore, rises and then drops off steeply into the deep water. This ridge protrudes between waves at high tide but is constantly in the air at low tide when the sea is calm. The only conspicuous algae are patches of Caulerpa urvilliana (RDW 1213), Turbinaria ornata (RDW 1214), and some Avrainvillea lacerata. Walking along the beach, the only beach drift noted was a rare Turbinaria or Halimeda.

The English Harbor seaward reef (Fig. 1, no. 8) and the seaward Cable Station Reef (Fig. 1, no. 2) are quite similar except that the latter seems to receive generally heavier surf. The algal populations of these reefs consist largely of Laurencia surculigera (RDW 1218) and patches of Caulerpa peltata (RDW 1215) growing over a coral rubble or shingle and small boulder substratum. Immediately adjacent but northwest of the pass is a pool protected from normal wave action by a shingle wall, though it connects with the pass via an opening on its northeast side and with the ocean at high tide. The depth ranged, when examined, from 0.3 to 1.5 meters during a rising tide. The pool measures an estimated 200 meters by 125 meters and abounds with fish, live coral, and even a Tridacne. Perhaps due to the abundance of herbivorous fish, algal growths are kept cropped to a low turf of minute species. The water is relatively clear, except at high tide, when the turbulence of moving water limits vision.

Noticeable at the Cable Station Reef (Fig. 1, no. 2) was the horizontal algal zonation on the cement jetty carrying the sewage line. Enteromorpha lingulata (RDW 1220) grows from the sand to the general level of the incoming waves on the wall. Above this, Schizothrix mexicana (RDW 1221) is found. The Enteromorpha was also seen on a table of dead coral boulders along this same beach. The growth of the Enteromorpha may indicate the presence of occasional or even regular fresh-water outflow and perhaps to a lesser extent higher fertilizer content of the water related to the sewer outfall.

It is often noted in the tropics that the algal population increases upwards toward mean sea level to where desiccation and sun-burning reduce it. Our feeling is that the DIF values, being highest at mean sea level, as well as these other two factors permit this upward extension, these specialized conditions compensating for the adverse factors such as insolation, disiccation, and rain. Since measurements of such factors could not be suitably made, the degree of responsibility of each factor cannot be estimated at present.

CONCLUSION

The apparent paucity of macroscopic algae is striking. Two factors must be kept in mind here, however, and that is the short time spent on the atoll in relation to any possible algal seasonality and the fact that not all areas were explored. On the other hand, one could argue that most areas of the eastern part of the atoll have been looked at and that previous workers in the Line Islands have also found but few algae. One gets the impression that the atoll flora is continually depauperated by grazing organisms.

The second objective, that of obtaining physical measurements of atoll waters, was accomplished variously. Turbinaria does not appear to grow very well anywhere on the atoll and the increased water movement on the windward sides of lagoon reef patches may well be the reason for its greatest abundance there. Likewise, it would seem to be near the eastward limits of its range in the Central Pacific.

From what is known thus far, factors favoring utilization of Fanning Atoll as a Biological Station are--from the standpoint of algal growth--its distance from any volcanic high island mass, areas of strong and weak currents, unpolluted waters, general lack of strong winds, excellent housing, and facilities such as electricity and water. On the negative side would have to be listed the high turbidity of most of the lagoon waters, the large populations of browsing fish, and difficult transportation problems related to its distance from frequented travel routes. It would seem a good choice for controlled aquaculture.

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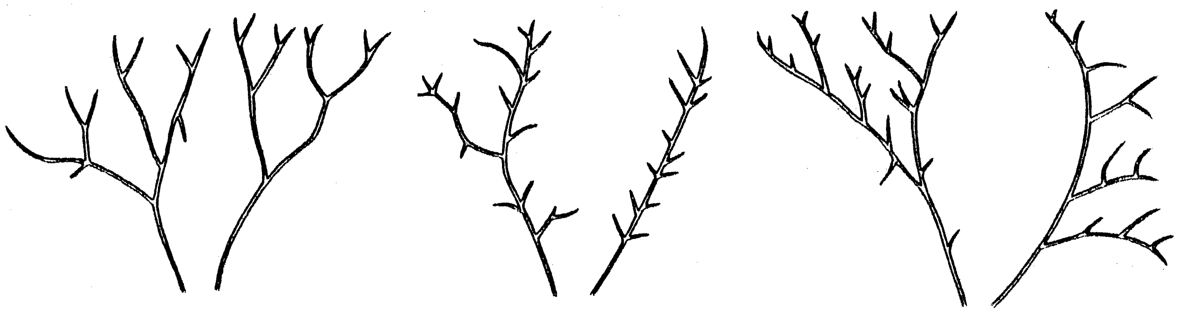
Appendix A

KEY TO THE FREQUENTLY FOUND GENERA
of larger
Central Pacific Seaweeds

The following is what biologists call a "key." It is so constructed that one is presented with a series of alternate choices or pathways. If one makes only "right" choices, with regard to one of the conspicuous seaweeds, *i.e.*, benthic algae, commonly found in the Central Pacific, the pathways will always lead to the same end, a generic name for that seaweed.

The whole individual alga is referred to as a *thallus* (plural: thalli). There are pairs of diagrams illustrating unilateral, dichotomous and pinnate branching, below. The word *blade* is used for any flat form attached by one edge or end like the blade of a leaf of grass, castor bean, kiawe, etc. A *crust* is a thin piece of matter attached to something larger by one flat side; like a drop of paint spilled and dried on the floor. *Stony* means inorganic and usually of carbonate or limy material hard like concrete. *Filaments* are cylindrical objects not unlike hairs in proportion or size. *Prostrate* means lying down. *Reproductory lumps*, *i.e.*, conceptacles or cystocarps, are swellings or spots on the surface in which the reproductory structures are born.

This key is the result of usage by people having little or no algal training. Thus, non-algologists often are more successful in the use of this key than are the more professionally qualified. As an aid to measurement in the field, a dime is 18 by 1, a penny 19 by 1.5 and a nickel 21 by 2 millimeters.



DICHOTOMOUS PINNATE UNILATERAL

Types of branching.

1- Thallus an erect pliable frond, lump or mass of filaments (hairs) *or* microscopic in size.........................13

1- Thallus a crust or consisting of smooth inflexible branches or knobs and macroscopic in size......................... 2

2(1)- Thallus not stoney though it may be hard; red to black, green or brown in color.................. 9

2(1)- Thallus stoney; pink to white in color................. 3

3(2)- Thallus a crust or a series of small horizontal shelves........... 5

3(2)- Thallus of erect rigid knobs or branches......................... 4

4(3)- Terete branches over 3.0 mm in diameter or flattened just below their gently rounded apexes; without zones on the non-lustrous surface; from wave washed reef marginal areas..................: *Porolithon*.

4(3)- Terete branches less than 2.5 mm in diameter just below their truncate apexes and with zones on the smooth or glazed surface; from reef channel or deep water areas..................: *Goniolithon*.

5(3)- Forming thick (over 2 mm), often extensive (often several decimeters) pavements covering coelenterates or other calcareous organisms; growing just above or near low tide line..........................: *Porolithon onkodes*.

5(3)- Forming thin (less than 2 mm) crusts or flakes which are in some cases attached by their edges; growing below low tide line....................... 6

6(5)- Thalli about 1 mm thick or over, and growing on rock or calcareous materials....... 8

6(5)- Thalli far less than 1 mm thick, or growing on non-calcareous algae... 7

7(6)- Some reproductory lumps (conceptacles), having many pores in their upper surface; thalli about 0.1 mm thick; on other algae, glass and different substrata..................: *Melobesia*.

7(6)- All reproductory lumps having but one pore in their upper surface; thalli up to 1 mm thick; on non-calcareous algae.................: *Fosliella*.

8(6)- Some reproductory lumps (conceptacles) having many pores in their upper surface..............................: *Lithothamnion*.

8(6)- All reproductory lumps having but one pore in their upper surface...........: *Lithophyllum*.

9(2)- Thallus colored other than brownish...............................11

9(2)- Thallus brown to blackish-brown....................................10

10(9)- Thallus with radial markings; margin usually free from substratum..........: *Lobophora*.

10(9)- Thallus without radial markings; margins adhering to the substratum....: *Ralfsia*.

11(9)- Thallus green and soft, not striated............: *Codium*.

11(9)- Thallus red or radially striated..................................12

12(11)- Thallus with radial markings..........: *Cruoriella*.

12(11)- Thallus without radial markings.......: *Peysonnelia*.

13(1)- Thalli neither jointed nor conspicuously segmented..19

13(1)- Thalli with regularly or irregularly spaced joints; often conspicuously segmented by rings of hairs or the joints themselves..........................14

14(13)- Thalli green to white with flat segments.............................: *Halimeda*.

14(13)- Thalli red to white, cylindrical if segmented..15

15(14)- Thallus with a hole in apex of each branch if branches over 1 mm in diameter and cylindrical; without segments if flat...........: *Galaxaura*.

15(14)- Thallus without holes in branch apices; branches much smaller if cylindrical; segmented if flat..16

16(15)- With rings of hairs at intervals; no regular joints.......................: *Actinotrichia*.

16(15)- Surfaces smooth; with many joints.....................17

17(16)- Branching dichotomous and reproductory lumps (conceptacles) terminal..................: *Jania*.

17(16)- Branching pinnate or reproductory lumps lateral...18

18(17)- Branching pinnate; conceptacles terminal...............................: *Corallina*.

18(17)- Branching dichotomous; conceptacles lateral...............................: *Amphiroa*.

19(13)- Thallus with colors other than a tint or shade of grass-green; plastids may be absent..............................52

19(13)- Thallus some tint or shade of grass-green someplace; chloroplasts present..................................20

20(19)- Thallus essentially felt-like; irregular patches, lumps, blades or solid dichotomous branches; consisting of densely interwoven microscopic filaments...................................49

20(19)- Thallus not a dense felt-like, interweaving of filaments; if consisting of many filaments then filaments free from one another or grown together (thallus microscopic in some cases) or thallus parenchymatous...............21

21(20)- Fronds arising from a prostrate runner (rhizome)..: *Caulerpa*.

21(20)- Fronds not arising from a rhizome....................................22

22(21)- Thallus essentially a filament, tube or blade; not of radially branched filaments..30

22(21)- Thallus of radially branched filaments or essentially a lump or ball of one or more cells...23

23(22)- Thallus with radial organization; surface consisting of cells too small to be seen at arm's length with the unaided eye................................28

23(22)- Thallus without radial organization; surface consisting of cells visible to the unaided eye at arm's length..24

24(23)- Thallus presenting a uniform surface of laterally joined largely uniform cells..............................: *Dictyosphaeria*.

24(23)- Thallus consisting of large solitary cells or irregularly connected cells..................25

25(24)- Thallus consisting of large cells not regularly connected..27

25(24)- Thallus of cells connected in clusters or filaments...26

26(25)- Thallus soft of pyriform cells over 5 mm in diameter connected together at their bases.......................: *Boergesenia*.

26(25)- Thallus rigid, of tubular cells in branches of irregularly cylindrical cells less than 1 mm in diameter (if larger see *Valonia*)..............: *Cladophoropsis*.

27(25)- Cells attached to surface of substratum.........: *Valonia*.

27(25)- Cells with one major rhizoidal portion penetrating the substratum.....................: *Halicystis*.

28(23)- Thallus with a stalk and cap, like a minute umbrella or stool..: *Acetabularia*.

28(23)- Thallus a ball or cylinder 29

29(28)- Thallus cylindrical...........................: *Neomeris*.

29(28)- Thallus spherical.............................: *Bornetella*.

30(22)- Thallus essentially filamentous or a network of filaments.................................34

30(22)- Thallus essentially parenchymatous and a perforated or non-perforated blade or tube..31

31(30)- Thallus tubular, branched or unbranched.........: *Enteromorpha*.

31(30)- Thallus a branched, unbranched or perforated blade..32

32(31)- Thallus essentially a monostromatic wedge of laterally joined filaments on a filamentous stem................: [See *Tydemania* (42) and *Udotea* (50)]

32(31)- Thallus a parenchymatous blade without a stem..33

33(32)- Thallus one cell thick..........................: *Monostroma*.

33(32)- Thallus two cell layers thick...................: *Ulva*.

34(30)- Thallus of branched filaments or networks..36

34(30)- Thallus an unbranched filament.........................35

35(34)- Attached by a specialized basal cell............: *Chaetomorpha*.

35(34)- Free-floating or attached by rhizoids...........: *Rhizoclonium*.

36(34)- Thallus with branch tips free from one another..39

36(34)- Thallus with branch tips adhering and forming an irregular crisp mass, blade or cup..37

37(36)- Thallus an irregular mass or other system of branches....................................: *Boodlea*.

37(36)- Thallus a cup-shaped or blade-like network.....................38

38(37)- Thallus merely a network of branches..: *Microdictyon*.

38(37)- Thallus with a central axis and stem below...........................: *Struvea*.

39(38)- Microscopic, embedded in other materials........: *Ostreobium*.

39(38)- Macroscopic, standing free in the water or prostrate on surfaces..................................40

40(39)- Thallus of cellular filaments.......... 47

40(39)- Thallus of non-cellular filaments, *i.e.*, coenocytic or siphonaceous.........................41

41(40)- Thallus prostrate, dichotomously or irregularly branching and lacking a central axis......................44

41(40)- Thallus erect with short lateral branches from relatively long central axes...............................42

42(41)- Thallus with a frequently-constricted axis or stem and blades or divaricately dichotomous "heads" of filaments........: *Tydemania*.

42(41)- Thallus with a central non-constricted axis and ultimate orders of similar branches...43

43(42)- Branches radially arranged and reproductory structures assymetric lateral growths on the branches....................................: *Trichosolen*.

43(42)- Branches pinnate or unilateral and reproductory structures symmetrical undifferentiated branches..: *Bryopsis*.

44(41)- Branch filaments with constrictions at their bases...46

44(41)- Branch filaments lacking constrictions at their bases...45

45(44)- Thallus of erect little or non-branched filaments less than 1 cm tall, arising from a horizontally muchly ramified basal system embedded in coral.............................: *Pseudochlorodesmis*.

45(44)- Thallus of erect filaments often over 1 cm tall and branched several times, arising from a horizontal system of filaments on the surface of the substratum but with penetrating rhizoids (=*Derbesia* stage)...........: *Halicystis*.

46(44)- Apical portions of erect parallel filaments consisting of long segments with few or no constrictions above their bases.............................: *Chlorodesmis*.

46(44)- Apical portions of divaricating filaments consisting of short or frequently constricted segments....................: *Boodleopsis*.

47(40)- Branches straight; coarse main axes bearing short bristle-like coarse side branches..........: *Siphonocladus*.

47(40)- Branches curved; no distinction of main axis from side branches or frond lax.................................48

48(47)- Principal branches erect ambient axes with pliable secondary branches....: *Cladophora*.

48(47)- Principal branches repent, rigid and thalli without an axis.............: *Cladophoropsis*.

49(20)- Thallus not ultimately terminating in flat blades..........: *Codium*.

49(20)- Thallus terminating in flat blades..........50

50(49)- Blades covered with a specialized layer of cells, *i.e.*, utricles..........: *Udotea*.

50(49)- Blades lacking a specialized surface layer..........51

51(50)- Marginally directed filaments of the blade with lateral branchlets that attach to adjacent filaments..........: *Rhipilia*.

51(50)- Marginally directed filaments of the blade not connected..........: *Avrainvillea*.

52(19)- Thallus not olive brown, or (if brownish) then with pink tinges in some places; not turning green in 240 seconds in water at 65 degrees Celsius..........68

52(19)- Thallus clearly brown, sometimes with an olive greenish or yellowish cast but without a pink tinge; turning green in 120 seconds when dipped in water at 65 degrees Celsius..........53

53(52)- Thallus parts over 1 mm broad; not of fine hair-like parts..........56

53(52)- Thallus parts less than 1 mm broad; entirely of fine hair-like parts..........54

54(53)- Tufts broadest toward base and consisting of unbranched and often of coiled filaments..........: *Microcoleus*.

54(53)- Tufts narrowing to base and consisting of branched non-coiled filaments..........55

55(54)- Dark brown, branches straight and many of same length, cells in transverse tiers..........: *Sphacelaria*.

55(54)- Light brown, branches lax and of various lengths, one cell broad..........: *Ectocarpus*.

56(53)- Thallus erect, branched or unbranched..........58

56(53)- Thallus essentially a brown hollow lump..........57

57(56)- Thallus with conspicuous holes through the surface..: *Hydroclathrus*.

57(56)- Thallus without holes through the surface.........: *Colpomenia*.

58(56)- Thallus with many leaves, short branches, or outgrowths from main branches or stems......................................65

58(56)- Thallus not organized into stem-like and branch-like parts...................................59

59(58)- Thallus dichotomously branched.................................61

59(58)- Thallus fan- or wedge-shaped, or of rounded blades...............60

60(59)- Thallus with margin inrolled (like a hem)...........................: *Padina*.

60(59)- Thallus with margin not inrolled........: *Stypopodium*.

61(59)- Thallus parts hollow..............................: *Rosenvingea*.

61(59)- Thallus parts not hollow...62

62(61)- Thallus parts cylindrical, about 1 mm thick, often beset with tufts of very short hairs; commonly growing intertidally....: *Chnoospora*.

62(61)- Thallus parts flat, strap-shaped; growing subtidally.................................63

63(62)- Flat parts with a midrib, which may resemble a stem in older portions.........................: *Dictyopteris*.

63(62)- Flat parts with no midrib present, no stem-like part below........64

64(63)- Flat parts up to 3 mm broad.............: *Dictyota*.

64(63)- Flat parts 5 mm to 1 cm broad; margins often toothed..................: *Spatoglossum*.

65(58)- Thallus straw-colored to greenish-black; main branches beset with small thorn-like growths...: *Acanthophora*.

65(58)- Thallus with leaves or coarse outgrowths..........................66

66(65)- Thallus with harsh, conical or shield-shaped "branches"; cylindrical or lax depending on closeness of the rigid peltate leaves...: *Turbinaria*.

66(65)- Thallus with relatively flat, thin leaves; bushy and lax.................................67

67(66)- Leaves branching; leaf midribs persisting as stems in old parts; berry-like floats never present..: Dictyopteris.

67(66)- Leaves mostly unbranched; leaves growing from the stems; berry-like floats often present........: Sargassum.

68(52)- Thallus neither slimy nor whitened by limy deposits near the base..........................70

68(52)- Thallus lubricous or slimy at least at the tips of the branches and whitened by limy deposits near the base..........................69

69(68)- Thallus decidedly slimy or gooy throughout even if white below..............................: Trichogloea.

69(68)- Thallus usually slimy only near the tips and near the base even if white not slimy.............: Liagora.

70(68)- Thallus with all parts essentially solid, and cylindrical or only slightly flattened, sometimes less than 1 mm broad...82

70(68)- Thallus with some parts hollow, or flat and at least a millimeter broad....................71

71(70)- Thallus flat or round but not with berry- or leaf-like structures arising from a round axis...................74

71(70)- Thallus with parts like berries, or leaves arising from a round axis..................................72

72(71)- With berry-like parts..................: Botryocladia.

72(71)- With leaf-like parts................................73

73(72)- Leaves over 5 mm long, whorled and crowded toward the apex of the axis bearing them on a stony substrata............................: Amansia.

73(72)- Leaves less than 2 mm long; alternately arranged along the axis bearing them; epiphytic.......................................: Leveillea.

74(71)- Fronds without a network or lace-like outer edge; not iridescent..............................77

74(71)- Fronds network-like or with a lace-like outer edge; some genera iridescent yellow, blue or pink.....................................75

75(74)- Base membranous, margin a network of multicellular bands, iridescent..................: *Hemitrema.*

75(74)- Whole thallus a network of filaments...........................76

76(75)- Thallus of flat blades.................: *Haloplegma.*

76(75)- Thallus quadrate in cross section.......: *Dictyurus.*

77(74)- Thallus a broad blade, palmately or a pinnately branched.............................: *Halymenia.*

77(74)- Thallus cylindrical or a flat pinnate or dichotomous frond with narrow branches...................................78

78(77)- Cylindrical, hollow, often iridescent blue under water.......................: *Champia.*

78(77)- Flat or hollow, not iridescent.........................79

79(78)- Thallus dark colored; with few branches and neither uniform nor regular in appearance; and successive branch orders increasingly narrower toward thallus apex...................: *Grateloupia.*

79(78)- Thallus light colored; with many branches uniform and regular in appearance, and the branches as broad or broader than the central axis..80

80(79)- Fronds round or merely compressed, often unilaterally branched or brownish in part, over 1 cm tall..................: *Gelidiella.*

80(79)- Fronds flat above the cylindrical base, often pinnate if taller than 1 cm or, when smaller, cylindrical..............................81

81(80)- Branches usually bent upwards and not constricted or smaller near point of origin; cylindrical below, fertile fronds becoming flat; female fruiting bodies bilateral.........................: *Gelidium.*

81(80)- Branches constricted or smallest near their origin and not bent upwards; all branches tending to be thin and flat; female fruiting bodies unilateral...............................: *Pterocladia.*

82(70)- Thallus with at least the base much larger in diameter than a hair or flattened.......................................90

82(70)- Thallus as fine as a hair throughout (filamentous)...................................83

83(82)- Dichotomous or composed of transverse tiers of cells..86

83(82)- Unbranched or pinnate and but one cell broad....................84

84(83)- Filaments unbranched, purple or black, entangled on coarser algae; cells shorter than their diameter............: *Microcoleus*.

84(83)- Filaments growing attached to larger algal species; cells longer than their diameter..............85

85(84)- Cells visible to the unaided eye.................: *Griffithsia*.

85(84)- Cells invisible to the unaided eye...............: *Acrochaetium*.

86(83)- Branching predominantly unilateral......: *Herposiphonia*.

86(83)- Branching dichotomous or spiraled.......................87

87(86)- Branching dichotomous; cells of axis not all in transverse tiers; every axial cell corticated at least in part..............89

87(86)- Branching spiraled, profuse, lax; cells of axis corticated by transverse tiers of cells of their same length...............88

88(87)- Thallus a soft cushion of furry branches with many short determinate branchlets; trichoblasts unbranched.....: *Tolypiocladia*.

88(87)- Thallus of freely erect smooth intermediate branches; trichoblasts usually branched........................: *Polysiphonia*.

89(87)- Axis completely covered by cells in longitudinal rows..............................: *Centroceras*.

89(87)- Axis not completely covered by cells.............: *Ceramium*.

90(82)- Thallus without fine hair-like terminal branches...................................94

90(82)- Thallus with terminal branches fine and fur-like...................................91

91(90)- Branches mostly in one plane.....................: *Wrangelia*.

91(90)- Branches appearing in more than one plane.........................92

92(91)- Upper branches not sharply different from the multiseriate terminal branches; base not iridescent..........: *Asparagopsis*.

92(91)- Upper coarse branches sharply different from the fur-like coating of uniseriate ultimate branches..93

93(92)- Upper parts densely furry, deep rose-red; base iridescent...: *Dasya*.

93(92)- Upper parts sparsely furry, yellowish to brownish, not iridescent.........................: *Spyridia*.

94(93)- Branch tips tapered or pointed, without an apical pit or tuft of hairs.................96

94(93)- Branch tips blunt, with a pit, groove or tuft of hairs...95

95(94)- Branch tips with a tuft of microscopic hairs......: *Chondria*.

95(94)- Branch tips without a tuft of hairs..............: *Laurencia*.

96(94)- Thallus with cylindrical lateral branches of no regular length; or only one or two thalli growing in a place; subtidal if dichotomous.....................100

96(94)- Thallus with some lateral branches flattened and many about the same length, often forming dense turfs; intertidal if dichotomous.............................97

97(96)- Branches largely cylindrical and dichotomous......: *Ahnfeltia*.

97(96)- Branches flattened and pinnate...98

98(97)- Branchlets smallest at their bases and thalli pinnate.......................: [See *Gelidium* and and *Pterocladia* (81)]

98(97)- Branchlets largest at their bases and either incurved at their tips or thalli somewhat unilaterally branched..........................99

99(98)- On main branches a "spine" subtends each smaller branch system; ultimate branchlets straight-tipped; branching somewhat unilateral; with no odor...: *Plocamium*.

99(98)- No regular alternation of spines with branch systems; ultimate branchlets sometimes laterally incurved at their tips; branching pinnate throughout; with a drug-like odor................: *Chondrococcus*.

100(96)- Main branches with many warty lateral branches covered with spiny points........................: *Acanthophora*.

100(96)- Main branches having lateral branches each with merely a tapered tip....................101

101(100)- Thalli with few if any short branches arising between successive longer branches...............: *Gracilaria*.

101(100)- Thalli with many short unbranched branches between the longer rebranched branches of the same axis...102

102(101)- Thalli uniaxial; limber; less than 3 mm in diameter..................: *Hypnea*.

102(101)- Thalli multiaxial; rigid; reaching over 3 mm in diameter someplace....: *Eucheuma*.

THE LITTORAL MARINE MOLLUSKS OF FANNING ISLAND

E. Alison Kay

Department of General Science

Whereas there is a wealth of taxonomic literature on the marine mollusks of the Indo-West-Pacific and a surfeit of speculation on the characteristics and relationships of insular faunas in the region, the ecological aspect of the zoogeography has been largely neglected. An expedition to Fanning Island in the Line Islands in January 1970 gave an opportunity for determining the commonly occurring reef and lagoon mollusks of this Pacific atoll, and also for preliminary surveys on their general ecology, especially of the dominants, and their local distribution. Information so obtained is used to describe the composition of the Fanning Island marine molluscan fauna and its relationships with those of other Pacific islands. A list of species from the Line Islands (Table 2) compiled from collections in the Bernice P. Bishop Museum, Honolulu, Hawaii, made during the Whippoorwill Expedition in 1924, is included for comparative purposes.

Fanning Island lies midway in the string of shoals and atolls extending from 8°N Latitude to 12°S Latitude which comprise the Line Islands. Above the Equator these islands form the most southerly and easterly fringe of the faunal area termed by Ekman (1953) the "Central Pacific". The major islands in the group (Washington, Palmyra, Fanning, Christmas) are about 1000 miles south, southeast, and northeast of Hawaii, Johnston Island, and the Phoenix Islands, respectively. They are 1200 miles northwest of Tahiti and 1500 miles northwest of the Tuamotu Islands. An outlier, Jarvis Island, is 400 miles southwest of Fanning; other outliers such as Malden, Starbuck, and Flint are below the Equator.

METHODS

A variety of sampling methods was used in the study, adapted to tides, wave action, topography, and available time. Four seaward reef stations were sampled by transect, with quadrat counts from a 30 cm ring or timed counts made at meter intervals from the shore toward the seaward edge of the reef. The lagoon mollusks were surveyed by sampling patch reefs and analyzing sediments and beachdrift. Additional records were obtained from various collections made by divers engaged primarily in studies of fish populations.

SUPRATIDAL AND HIGH TIDAL MOLLUSKS

The supratidal and high tidal regions (littorinid zone of Stephenson and Stephenson, 1949; littoral fringe and upper eulittoral of Morton and Challis, 1969) of seaward and lagoon shores are characterized at Fanning as everywhere else by littorines and nerites. Three species of _Littorina_ occur, although only _L. coccinea_ is abundant. This species is found on shingle landward of the seaward reef flat, on beachrock and raised limestone along lagoon shores, and on trees overhanging the water. L. scabra is much less common; specimens were found on the branches of Messerschmidia (Tournefortia) along the lagoon shore and on rocks at Napu Naiaroa (Fig. 1). Fewer than six specimens of L. undulata were recorded, from two areas only, along a channel between the berm and the island at Vai Tepu (Fig. 1, S-D) and on shingle at Cartwright Point (Fig. 1, L-A).

Two marine pulmonates and two prosobranchs are also found in the littorinid zone, Melampus ater and M. luteus, Truncatella guernii, and Assiminea nitida. These gastropods occur under loose rubble and deep in shingle along both seaward and lagoon shores. Assiminea was also found in the estuarine flat at Napu Naiaroa (Guinther, 1971).

Nerita plicata, the widespread nerite characteristic of most tropical shorelines from east Africa to the east Pacific barrier (Ekman, 1953), is the single dominant nerite seaward of the littorines. It is found in great abundance wherever there is shingle or other hard substrate, some animals ranging as high as the littorines, but the major portion of the population being at MLW with the snails moving landward and seaward with the tides. Most of the nerites are found along the seaward shoreline; they are perhaps less common along lagoon shores because of the absence of suitable substrate.

MOLLUSKS OF THE SEAWARD REEFS

Reef Topography

The seaward reef platform is a narrow (ca 30 m) flat backed by a shingle berm which encircles the atoll, broken only at the three passes (Fig. 1).

At Danger Point and North Pass (Fig. 1, S-A, S-C), the two pass-areas sampled, three types of habitat are conveniently distinguished; moat, shingle, and beachrock. Relatively large moats or pools are separated from the seaward reef flat in both areas by an offshore ridge of shingle which rises to a height of about 2 m (Fig. 2). The moats (ca 125 m by 225 m and larger) vary in depth from a few cm to more than an m depending on tide and wave action. Temperatures were on the order of 27.5°C in January (De Wreede, personal communication); Bakus (1964) reports 31.5°C at Danger Point in August. Salinities were approximately 35 ‰ (De Wreede, personal communication). The moats contain a variety of habitats; a rich assemblage of corals such as Porites and Pocillopora, dead coral heads and rubble, patches of sand, and some reef limestone with varying algal cover. Seaward of the moats the offshore ridge slopes as shingle over the reef flat for more than 20 m. The shingle is smooth, and slippery with Centroceros and other red algae. At Danger Point the shingle is replaced at the north end of the moats by a relatively smooth substrate of beachrock, and emergent patches of beachrock are scattered along the shoreward edge of the moats. The latter patches are somewhat protected from wave action by the offshore wall; they are covered thinly by algae and sand. At North Pass similar islands of beachrock are scattered throughout the shallow, sandy pass-area, some of the patches are more pitted and rubble-strewn than others. Both shingle and beachrock are alternately exposed and inundated by the tides.

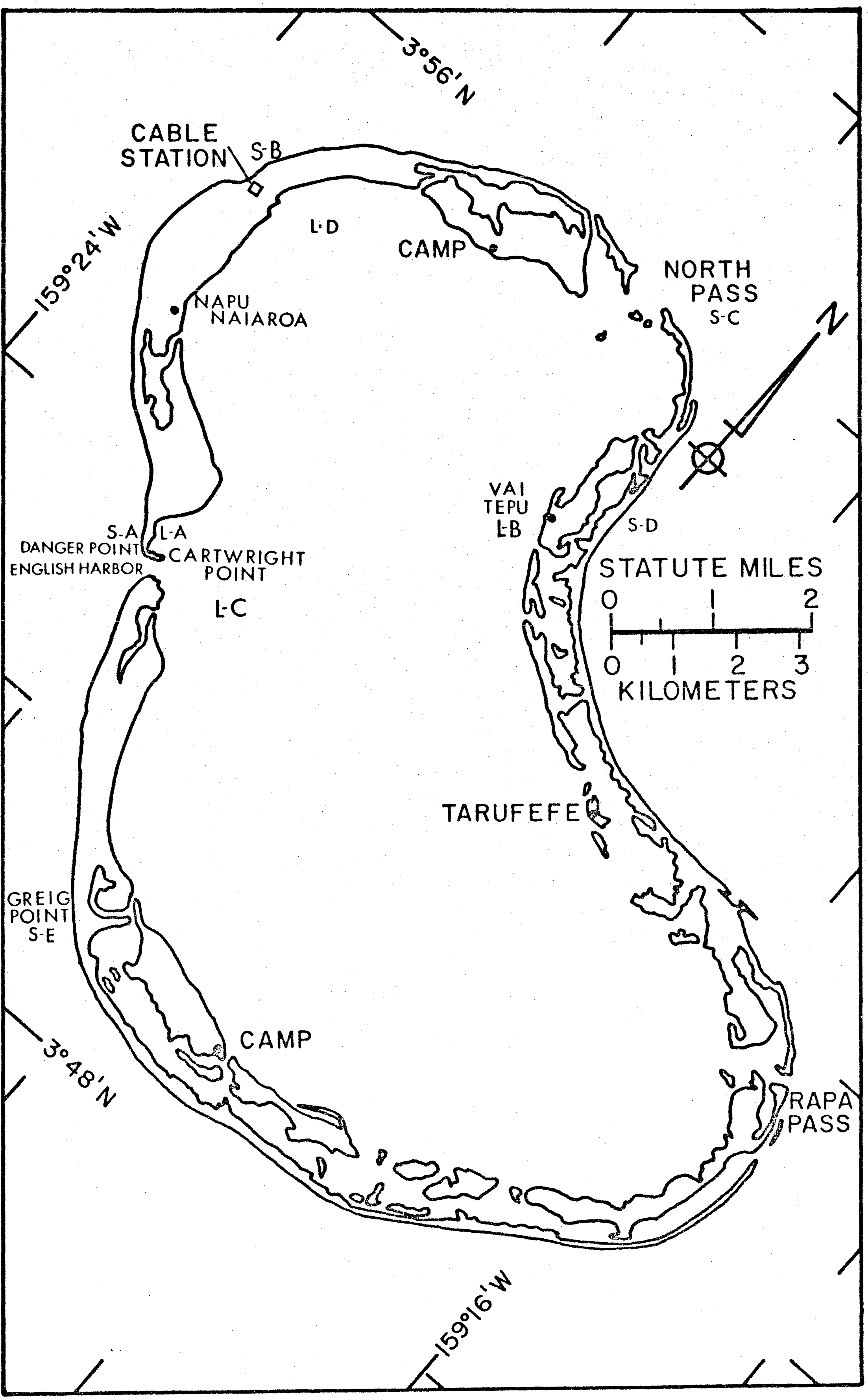


Fig. 1. Map of Fanning Island, showing the areas collected in January, 1970.

Fig. 2. Moats at Danger Point with shingle and beachrock backshore and the offshore ridge.

The reef flats are narrow, backed at the shoreward extremity by beachrock and/or shingle and broken 20 to 30 m seaward by emergent coral boulders separated by deep, wide surge channels (Fig. 3). Physically similar, yet the reefs differ in appearance at each of the stations sampled. At Greig Point (Fig.1, S-E) the reef flat is covered by a thick mat of the red coralline alga Jania which forms tufts up to 3 cm in height in the shoreward portions of the flat. The alga binds considerable amounts of sand among its fronds and the mat is estimated as consisting of from 50 to 60 percent sand. At Vai Tepu (Fig. 1, S-D) the reef flat is littered by shingle festooned with green algae such as Caulerpa and Ulva. At Teuru Mangaru (Fig. 1, S-B) the reef flat is surfaced with an algal-sand mat tufted with Turbinaria and Padina and pitted by depressions, some of which contain small heads of Porites. All three reefs are generally submerged except at extreme low tides and all are subject to strong surf and surge.

Molluscan Fauna

The macromolluscan fauna of the seaward reefs consists of large percentages of the thaisids Drupa, Morula, and Maculotriton, and lesser numbers of Vasum, Patella, Cypraea, and Conus.

The moats in the pass areas support the most diverse molluscan fauna. The most abundant species at Danger Point, Morula uva, Drupina grossularia, Cypraea moneta, Turbo argyrostomus, Conus sponsalis, Euplicata turturina, and Latirus amplustris, make up more than 60 percent of the samples (Fig. 4). The moat-dwelling gastropods reflect the variety of habitats available in the pools. The dominants are principally found on beachrock and large pieces of rubble, and among the less abundant ones, some are associated with living coral (Coralliophila and Quoyula) and others are sand-dwellers (Imbricaria spp. and Terebra spp.). The gastropod:bivalve ratio (based on species) is 97:3. In terms of food habits, 34 percent of the prosobranch species are algal feeders, 51 percent active predators, 8 percent scavengers, and 7 percent faunal grazers.[1] Two of the bivalves are suspension feeders, byssally attached or cemented to the subtratum (Modiolus metcalfei and Tridacna maxima); the third is an erycinid, which moved freely in the rubble.

In addition to the 44 macromolluscan species in the Danger Point moats, 65 species of micromollusks (those less than 1 cm in length) were recorded from samples of beach drift at the edge of the moats. Although this fauna may have been partially of waifs, one or two specimens of most of the species were collected alive in the pools, and it is felt that the assemblage gives some indication of the great variety associated with the microhabitats in the moats. The dominant species are shown in Figure 5. The faunal composition of the assemblage is somewhat different from that recorded for the larger species: there is a greater percentage of bivalves in the gastropod: bivalve ratio (86:14), and among prosobranch species, 42 percent are algal feeders, 39 percent faunal grazers, and 19 percent active predators.

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[1] Calculations for feeding habits based on numbers rather than species do not appreciably change the figures.

Shingle supports a lesser number of species than do the moats; 14 species were recorded from Danger Point and 19 from North Pass. The assemblage is dominated by *Maculotriton digitalis*, *Euplica varians*, *Engina tuberculosa*, and *Drupa ricina* (Fig. 6); their local distribution at North Pass is shown in Figure 7. The only bivalve found among the gastropods is *Ostrea hanleyana*, which is occasionally cemented to the undersurfaces of the shingle. At Danger Point, 28 percent of the prosobranch species are algal feeders, 58 percent active predators, 7 percent scavengers, and 7 percent faunal grazers. At North Pass, 37 percent are algal feeders, 52 percent active predators, and 10 percent scavengers. Most of the mollusks of the shingle are cryptofaunal at least during the day and are found on the undersurfaces.

Beachrock also supports fewer species than do the moats: at Danger Point eight species were recorded on the wave-washed seaward reef flat and five on the protected flats shoreward of the moats (Fig. 8). *Drupa ricina* and *Morula granulata* are dominant on the seaward-facing beachrock, and *Drupina grossularia* and *Vasum armatum* on the protected shoreward beachrock. At North Pass, where the beachrock is more physically varied and protected from the main force of the waves, 21 species were recorded; *Vasum* is again dominant, and *Cypraea moneta* and *Morula uva* are also present. A few specimens of *Thais aculeata* were noted on backshore beachrock at North Pass but they do not appear in the samples. Of the prosobranch species, 27 percent are algal feeders, 66 percent active predators, and 7 percent scavengers.

In faunal composition the two reef flats sampled by transects differ from the habitats of the passes. Seventeen species were recorded from a 20 m transect at Teuru Mangaru (Fig. 1, S-B) and 30 from the *Jania*-sand mat transect at Greig Point (Fig. 1, S-E). The dominant species at Teuru Mangaru are *Morula uva* and *Drupina grossularia* which form 56 percent of the samples (Fig. 9); the vermetid gastropod *Serpulorbis* is also conspicuous on the reef flat but densities were not estimated because of surge. At Greig Point, *Drupa ricina*, *D. morum*, and *Patella stellaeformis* form 62 percent of the samples (Fig. 9). The local distribution of the dominants is shown in Figure 10. No bivalves were recorded in the transects at Greig Point although occasional specimens of *Tridacna maxima* and *Modiolus metcalfei* were found in the area. In terms of food habits, 24 percent of the prosobranch species are algal feeders, 76 percent active predators, and 7 percent and 3 percent, respectively, faunal grazers and scavengers at Greig Point, and 24 percent algal feeders, 76 percent active predators at Teuru Mangaru.

The reef flat at Vai Tepu (Fig.1, S-D) was not sampled by transect because of surge, but mollusks collected randomly on the reef were similar in species composition to those at Teuru Mangaru and Greig Point, with the exception of a greater number of specimens of *Thais armigera* in the surge channels at this station.

Micromollusks are found in the algal-sand mat of the reef flats. Thirty-four species are recorded from Teuru Mangaru, 10 from Greig Point, and 6 from Vai Tepu. *Euplica varians* is the most abundant species at Teuru Mangaru and Vai Tepu, but was second in abundance at Greig Point where minute specimens of the trochid *Monilea* are dominant (Fig. 11). At Teuru Mangaru algal feeders comprised 60 percent of the prosobranch species, active predators 21

Fig. 3. The reef flat at Greig Point. (Photograph by E. D. Stroup.)

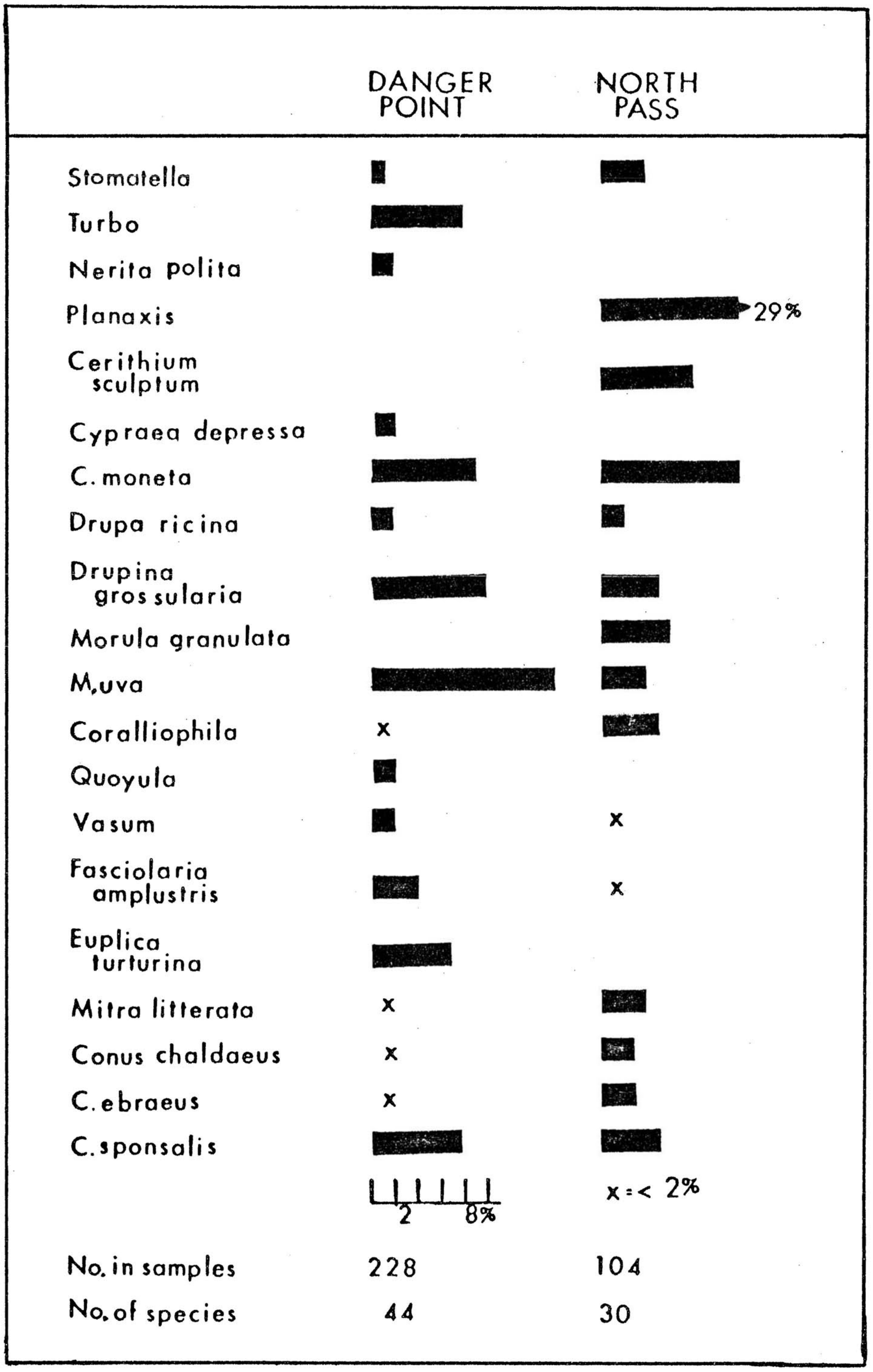

Fig. 4. Assemblages of macromollusks at Danger Point and North Pass moats. Percentages show relative abundance in total assemblage in this and succeeding figures. Species occurring in monotypic genera at Fanning are cited by genus only.

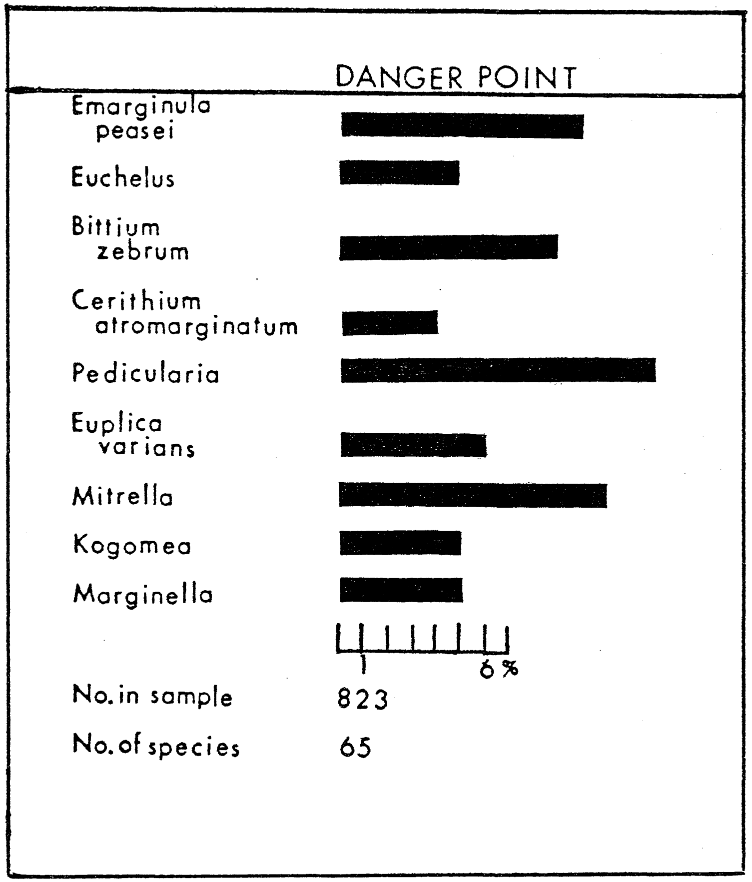

Fig. 5. The assemblage of micromollusks collected from beachdrift in the Danger Point moats.

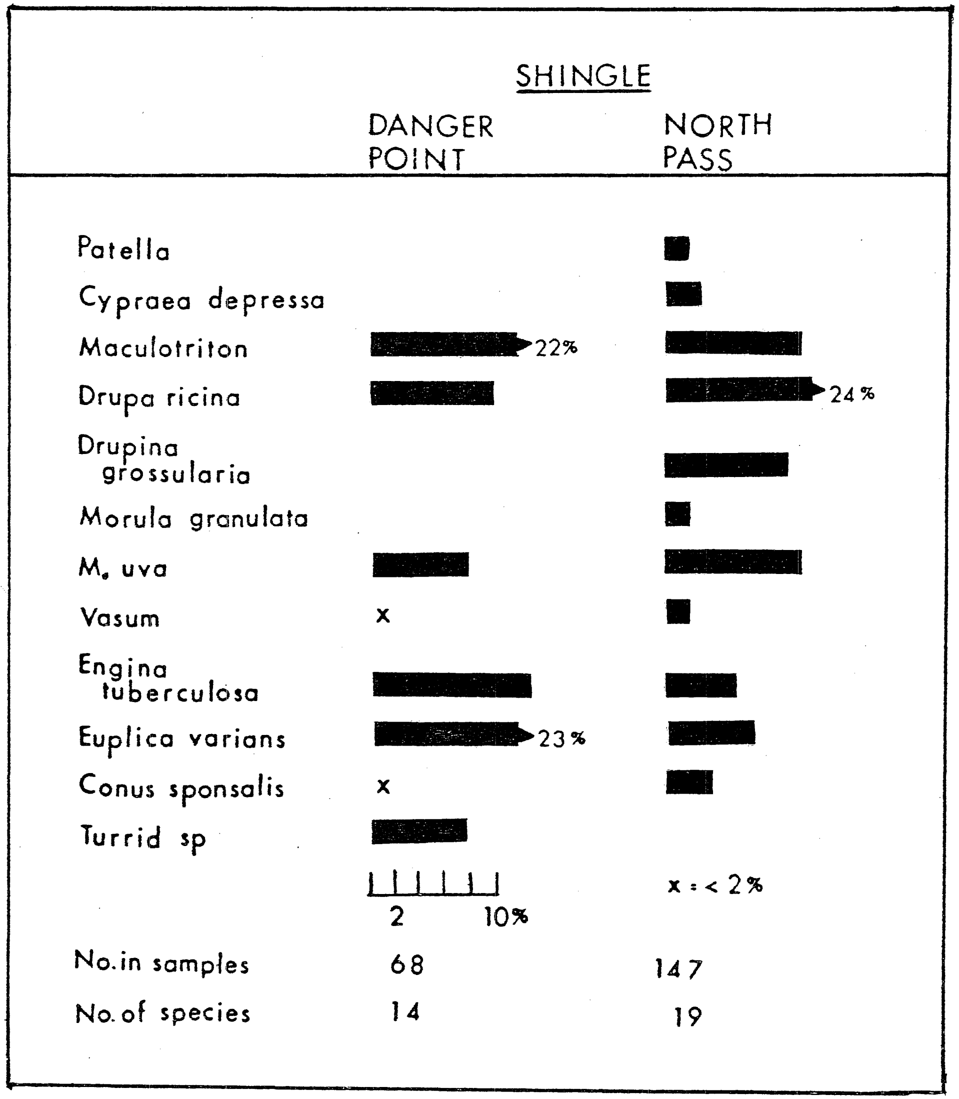

Fig. 6. Assemblages of macromollusks from shingle at Danger Point and at North Pass.

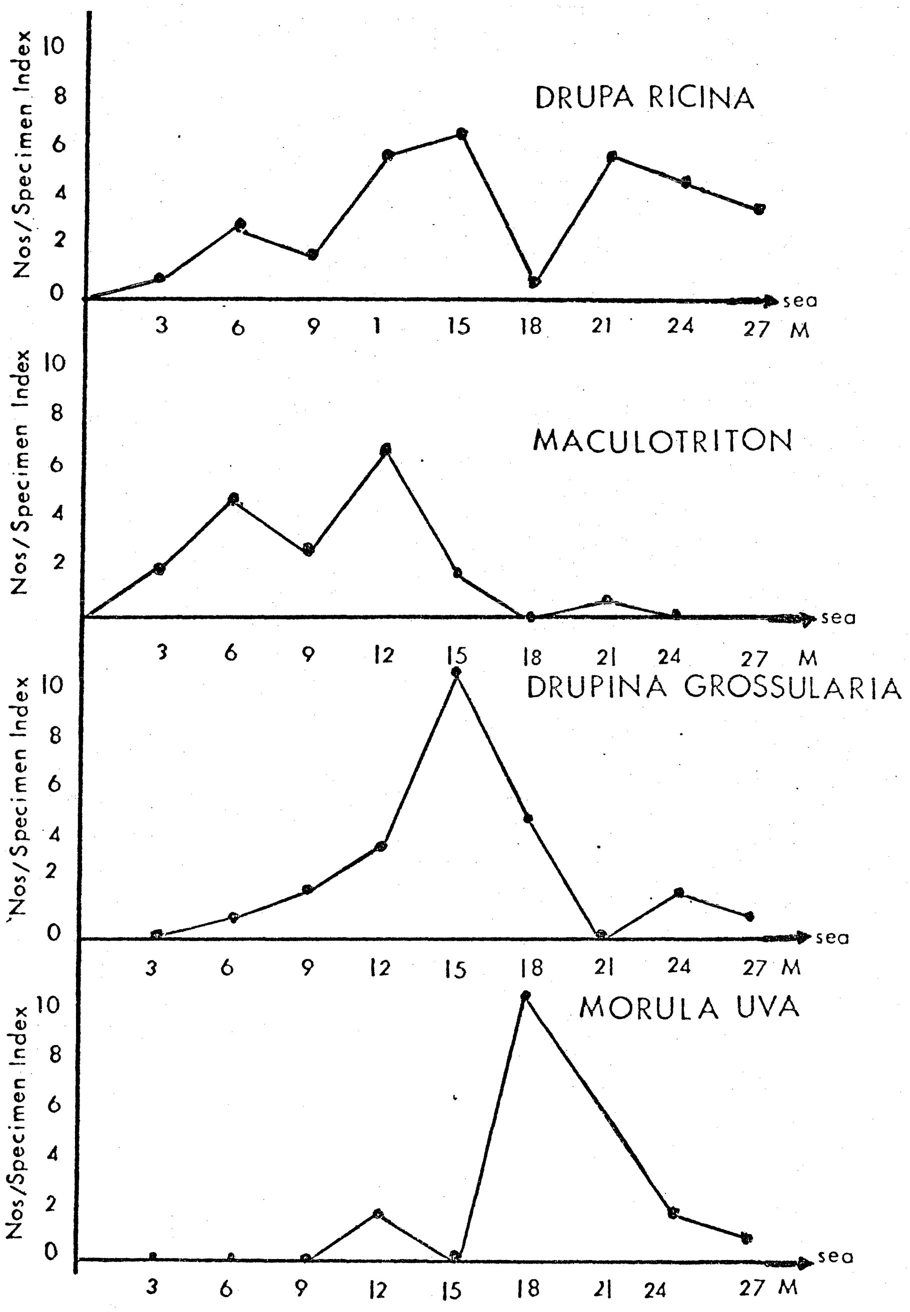

Fig. 7. The distribution of the most abundant species on shingle at North Pass. The specimen index represents three 20-second counts at each meter interval.

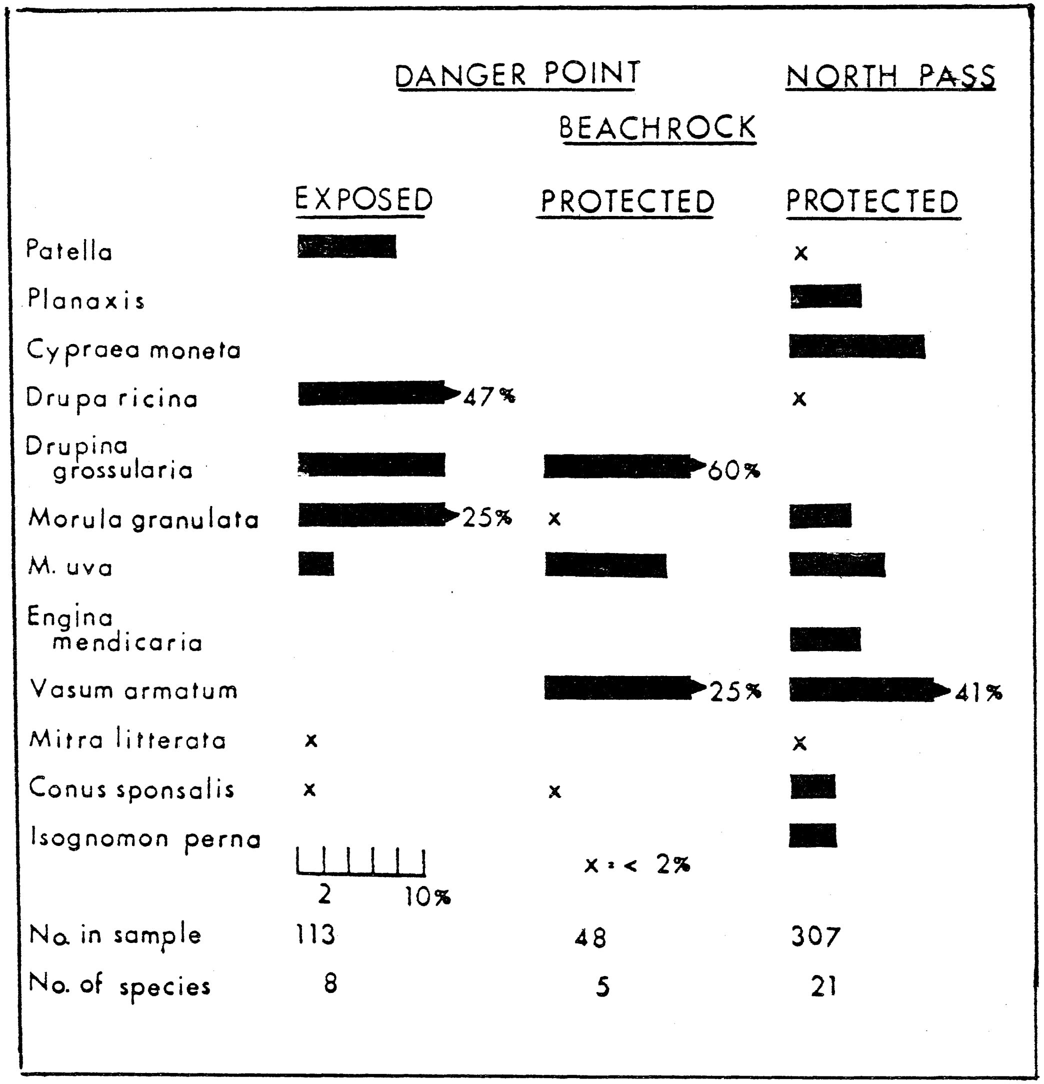

Fig. 8. Assemblages of macromollusks from beachrock at Danger Point and at North Pass.

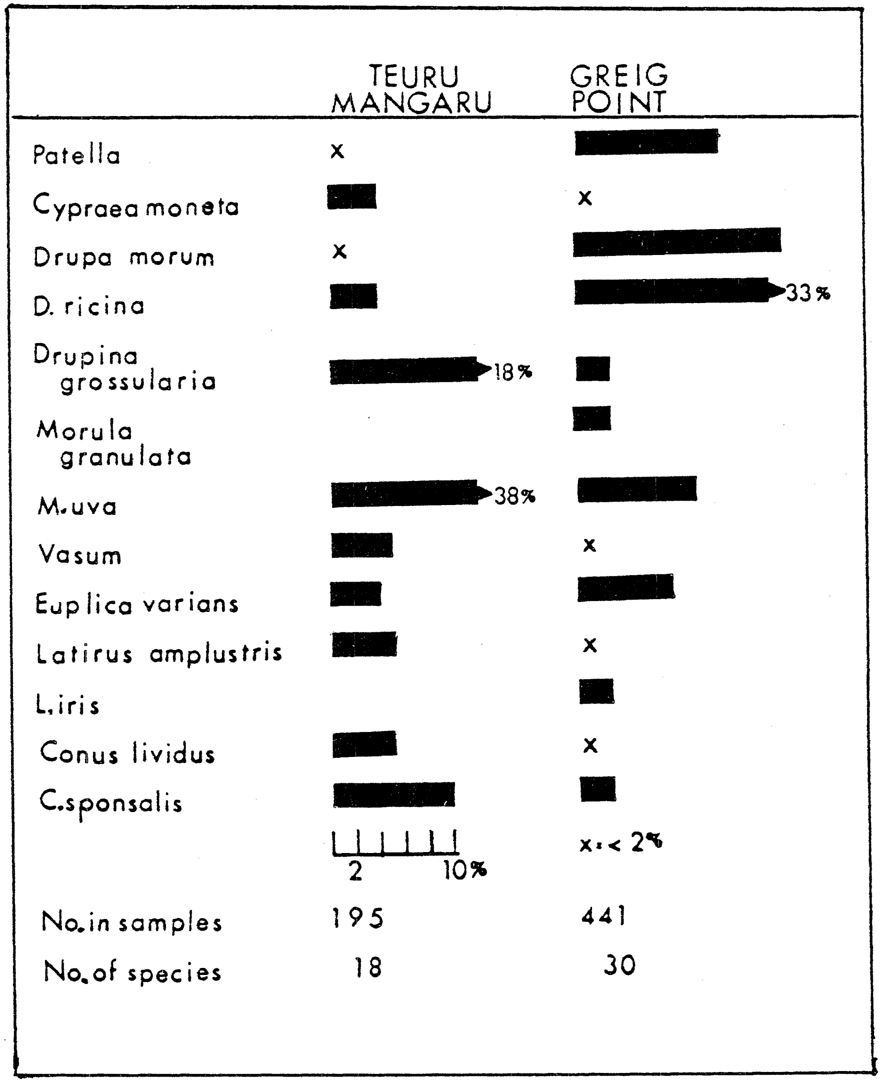

Fig. 9. Assemblages of macromollusks on the reef flats at Teuru Mangaru and at Greig Point.

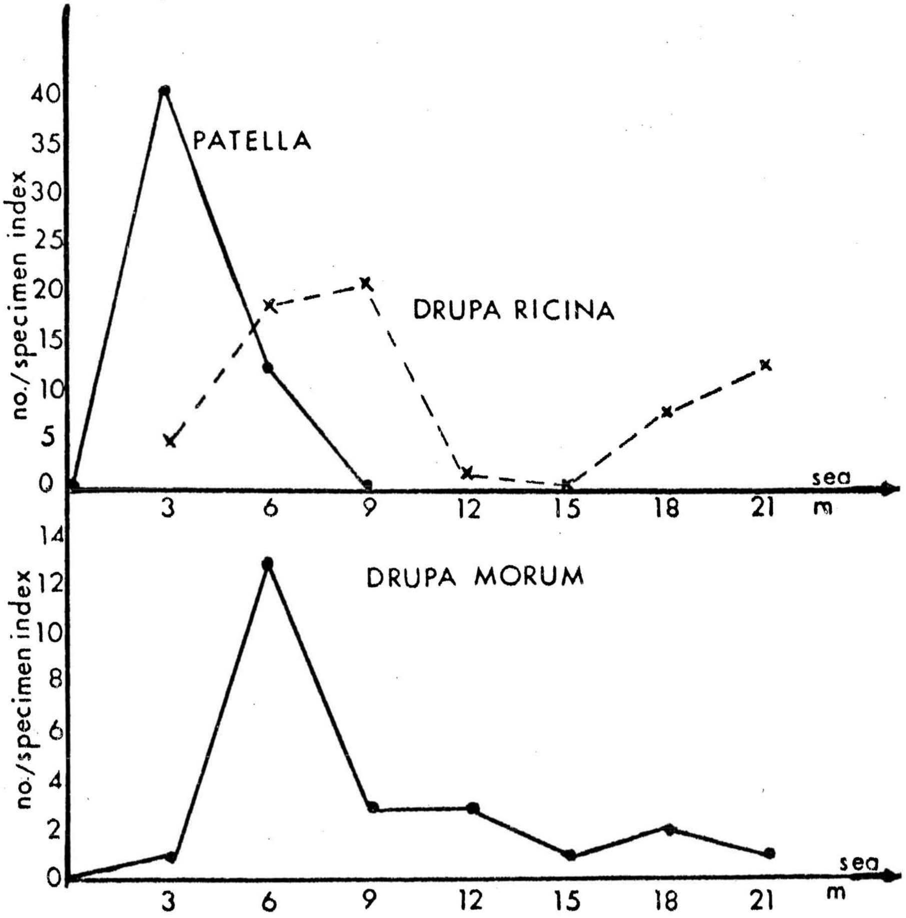

Fig. 10. The distribution of the most abundant species of macromollusks on the reef flat at Greig Point. The specimen index represents four 20-second counts at each meter interval.

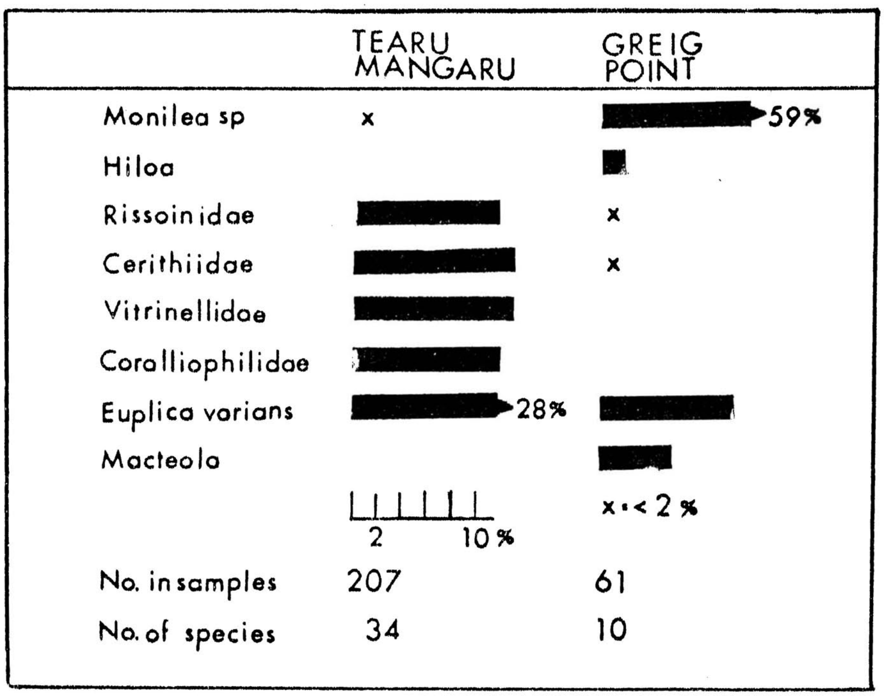

Fig. 11. Assemblages of micromollusks from the algal-sand mat of the reef flats at Teuru Mangaru and Greig Point.

percent, and faunal grazers 18 percent. At Greig Point algal feeders formed 70 percent of the prosobranchs, active predators 10 percent, and faunal grazers 20 percent.

Discussion

Perhaps the most conspicuous feature of the molluscan populations of the seaward reefs is the faunal homogeneity. Of the 20 most abundant species of macromollusks, 78 percent occur in more than half the sampling areas. Gastropods are far more numerous than bivalves at all stations. Among food habits of the prosobranchs, active predators are dominant among the macromollusks at all stations whereas algal feeders and faunal grazers predominate among the micromollusks (Fig. 12).

Drupa ricina and Morula uva are the most regularly found gastropods in the samples, Drupa being somewhat more generally distributed across the reef flats than Morula (Fig. 10). Drupa is a food generalist, feeding on mollusks, barnacles, and worms; Morula is more a food specialist, eating principally on sessile gastropods of the family Vermetidae (Miller, personal communication). Drupina grossularia is also a dominant at most of the stations, but it shows a more irregular distribution across the reef flats than do the former two species.

The faunal homogeneity is not perfect, of course, since a number of local distribution patterns exist. These are principally associated with substrates which are alternately exposed and immersed by tidal and wave action, the shingle and beachrock of the pass-areas, and the reef flats. Drupa morum is found only on algal-sand mat (on the reef flats rather than on shingle or beachrock), a habit no doubt consistent with its diet of worms and siphunculids (Bernstein, personal communication). Morula granulata and Vasum occupy principally smooth substrates; the former is a food generalist feeding on other mollusks and tube worms and is found in more exposed situations than the latter. Maculotriton, Engina tuberculosa, and Euplica varians in concert are characteristic of shingle, although E. varians is also abundant in the algal-sand mat of the reef flats. Engina mendicaria and Thais aculeata live on beachrock in protected backshore areas but do not overlap in their distribution and are restricted to small areas. Thais armigera, which was not recorded in the transects, is found at the outer edge of the reef flats near or in surge channels. Latirus amplustris and L. iris are at most stations, with the former usually submersed and the latter exposed on shoreward areas of the reef flat.

The diverse fauna of the moats includes not only species which forage over shingle, beach rock, and the reef flats (42 percent of the macromollusks) but forms which are characteristically subtidal, such as Coralliophila, Columbella tuturina, Terebra, and Imbricaria. The physical structure of the moats forms, in part at least, an essentially subtidal habitat similar to that of subtidal coral reef platforms.

LAGOON MOLLUSKS

The Fanning lagoon is a shallow basin of approximately 116.55 km^2, with a deep pass at English Harbor. The most active area of coral growth is in the western lagoon near the English Harbor pass, where the reefs are at depths of 10 m. The passes in the southeast (Rapa) and north (North Pass) are not well defined; they are shallow sand flats covered by less than a meter of water. The northern and southern portions of the lagoon are shallow and laced with line and patch reefs. Water temperatures in January were about 27.5°C throughout the lagoon with little vertical change; salinities fluctuated around 35‰ (Gordon and Schiesser, 1971). At least five major molluscan assemblages can be recognized in the lagoon, with little overlap in species among the assemblages.

The lagoon reef flat, with the exception of a small area at Cartwright Point, is almost entirely of sand. At Vai Tepu (Fig. 1, L-A) the dominant macromollusk is the cerithid Rhinoclavis asper; in addition specimens of Cerithium breve occur, but this species is principally estuarine (Guinther, 1971). Thirty-five species of micromollusks were also listed from sediment samples from this station; most of the shells were dead and the habits of these animals, with the exceptions of Acteocina, which is a sand-dweller, and Hiloa which is on algae, are not known. Diala flammea, Obtortio pyrrhacme, and Hiloa variabilis comprised 82 percent of the assemblage (Fig. 13). The gastropod:bivalve ratio is 85:15; and prosobranch:opisthobranch ratio (based on species) is 86:14.

Collections of dead shells from the shoreline of the reef flat in other areas suggest additional assemblages occur at various places around the lagoon. These collections included shells of Pupa, Pyramidella, Ctena divergens, and various tellinids.

A unique lagoon reef-flat habitat occurs at Cartwright Point near English Harbor where a spit on the lagoon reef parallels the pass (Fig. 1, L-A). The shoreline is of coral slabs which extend from 3 to 6 m into the lagoon but which are never more than 0.5 to 1 m in depth.

The living fauna is a mixture of species associated with the seaward reefs, patch reefs of the lagoon, and species which were found nowhere else at Fanning. Cypraea moneta, Euplica varians, Neritina bensoni, Planaxis lineata, and Maculotriton digitalis formed approximately 70 percent of the assemblage (Fig. 14). Of these, only Planaxis is locally distributed, occurring in the shoreward two meters of the transects. The gastropod:bivalve ratio is 78:22, and among the prosobranchs 44 percent are algal feeders, 56 percent active predators. Mollusks occurring here which were not found elsewhere include the prosobranchs Cypraea annulus, Nerita albicilla, Morula margariticola, and the opisthobranch Jorunna tomemtosa.

Micromollusks found in drift in sandy patches among the coral slabs are a mixture of lagoon and seaward species; none was found alive and their occurrence is attributed to transport from both the seaward reefs and the patch reefs in the lagoon.

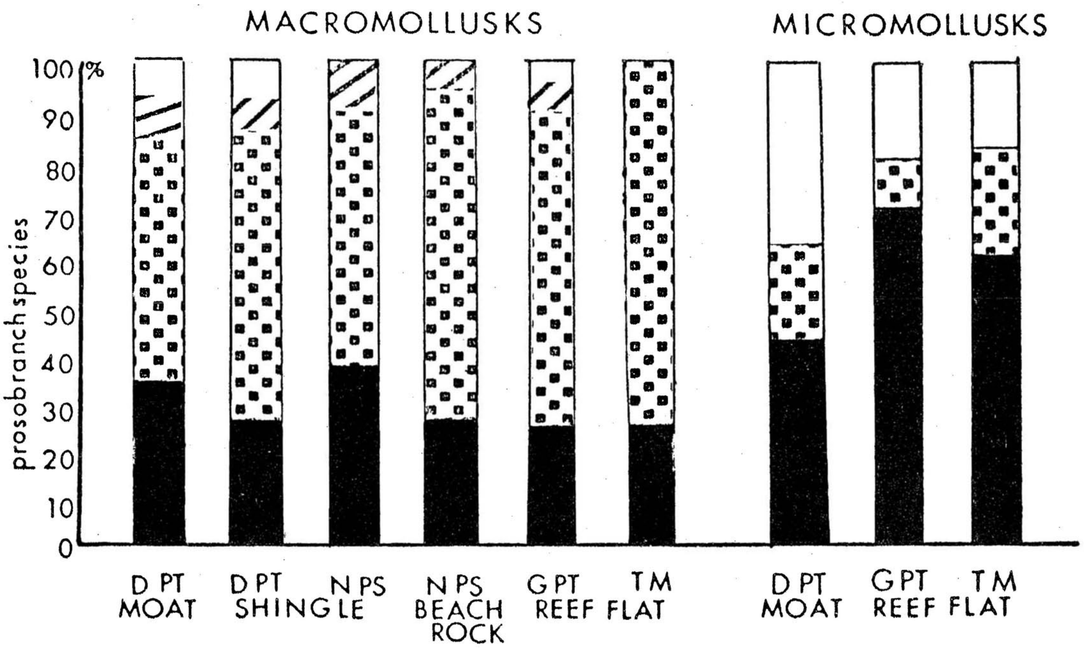

Fig. 12. Summary of the feeding habits of macro- and micromollusks on the seaward reefs. Solid black represents algal feeders; dots, active predators; diagonals, scavengers; and clear, faunal grazers. D. Pt. = Danger Point; N. Ps. = North Pass; G. Pt. = Greig Point; T. M. = Tearu Mangaru.

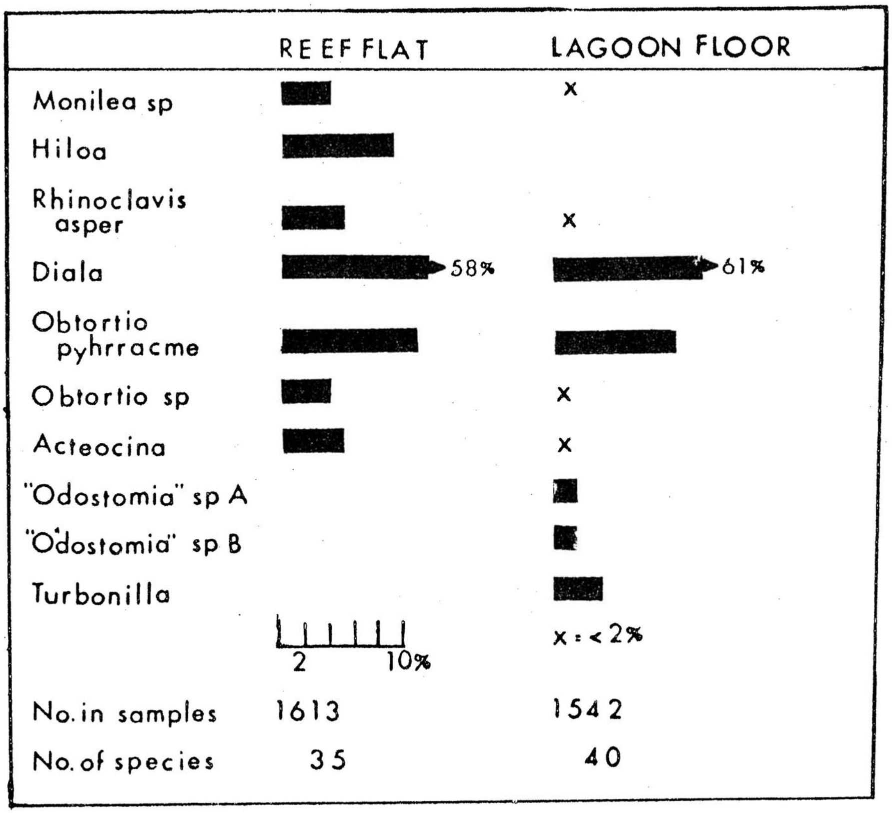

Fig. 13. Assemblages of micromollusks from the lagoon reef flat (Station L-A) and the lagoon floor (Station L-D).

Shallow, subtidal patch reefs cover about 35 percent of the lagoon floor. Attached to much of the coral (*Porites* and *Acropora*) are *Turbinaria*, *Halimeda*, and filamentous green algae. *Cypraea moneta*, *Conus lividus*, and *Cymatium muricinum* are the most conspicuous epifaunal gastropods (Fig. 15), but the micromollusks *Diala flammea* is also an important constituent of the fauna, forming up to 90 percent of the species composition of coral washings. The numbers of bivalves were not counted, but four were obviously abundant; *Electroma* sp. is the dominant byssally attached form on *Acropora* and *Porites*, with *Ostrea sandwichensis* in lesser numbers; *Cardita variegata* and *Barbatia decussata* are the most abundant attached species on the undersurfaces of coral blocks. The gastropod:bivalve ratio is 81:19, and of the prosobranch species, 30 percent are algal feeders, 65 percent active predators, and 5 percent faunal grazers. The infauna around the coral includes *Nassarius arcularis*, *Trapezium oblongum*, and *Periglypta reticulata*.

Sediment samples from the lagoon floor (Fig. 1, L-D) are characterized by the micromollusks *Diala flammea* and *Obtortio pyrrhacme* which are also abundant on the sandy reef flat, another species of *Obtortio* and two species of the pyramidellid *Turbonilla* (Fig. 13). None was found alive. The gastropod:bivalve ratio in this assemblage is 89:11, and prosobranch:opisthobranch ratio 69:31.

The deep, clear water of the western lagoon (Fig. 1, L-C) supports a more diverse molluscan fauna than do either the reef flat or the patch reefs. No attempt was made to analyze this assemblage during the study, but the massive coral growth at depths of 8 to 10 m harbors such species as *Pinctada margaritifera*, *Terebra maculata*, *Atrina vexillum*, *Spondylus ducalis*, and *Tridacna maxima*.

COMPARISON OF SEAWARD REEF AND LAGOON MOLLUSKS

Two features of the molluscan species composition of the seaward reefs and lagoon are salient: the seaward reef fauna is more homogeneous than that of the lagoon, and few species occur both on the seaward reef and in the lagoon. Among the macromollusks, 17 percent are at home both on the seaward reef and in the lagoon, whereas this is true for only 14 percent of the micromollusks. The figures may be somewhat generous, however, and if those species which occur only very rarely in either area (for example 140 shells of *Hiloa* in the lagoon versus 8 on the seaward reefs) are omitted, the overlap for both macro- and micromollusks is about 9 percent.

Most of the overlap is among the mollusks of the patch reefs. Species in apparently equal abundance on the seaward reefs and on the patch reefs are *Morula anaxeres*, *Conus pulicarius*, *Conus lividus*, and *Coralliophila neretoides*. *Drupa ricina* is far more abundant on the seaward reefs than on the patch reefs; *Cypraea moneta* is more numerous on patch reefs. *Cymatium muricinum* and *C. nicobaricum* appear to be more often associated with the patch reefs than the seaward reefs, but *Bursa* spp. are more often on the seaward reefs.

More species were recorded from the seaward reefs than from the lagoon, but individual numbers were low compared with the abundance of some lagoon species. The seaward reef mollusks are predominantly gastropod and epifaunal. The lagoon mollusks include both epifaunal and infaunal forms, and there is a corresponding increase in the number of bivalves in proportion to gastropods, and of opisthobranchs in proportion to prosobranchs.

FAUNAL COMPOSITION

The Fanning Island molluscan faunal list consists of approximately 265 species of littoral marine forms; although the list cannot be considered complete, the collections were extensive (more than 6000 specimens were analyzed for this study), and, with the exception of the rather cursory observations of the deep reefs near English Harbor Pass and of the windward reefs, the present record is considered fairly representative of the fauna. If the species recorded from the Line Islands during the Wippoorwill Expedition (B. P. Bishop Museum collections) are added to my list, the Line Islands molluscan fauna is composed of about 305 species (Table 2). This figure may be compared with those reported for other atolls: 504 for the Cocos Keeling Islands, Indian Ocean (Maes, 1967); 420 for Funafuti, Ellice Islands (Hedley, 1899a); and an estimated 500 to 600 for the Tuamotu Islands (Morrison, 1954; Salvat, 1967).

Although distance has traditionally been cited as a primary cause of attenuation (Hedley, 1899b; Salvat, 1967; Cernohorsky, 1970), it is difficult to reconcile this explanation with the occurrence of *Cassis* and *Siphonaria* at as far-flung an Indo-West-Pacific outpost as Hawaii, and with the records of *Oliva*, *Harpa*, *Planaxis sulcatus*, and *Asaphis violascens* which are apparently also absent at Fanning, from other islands in the Line group. Nor does the distance-effect account for distributional anomalies: the patchy occurrence of *Thais aculeata* and *Engina mendicaria* on seaward reef flats, and the very rare occurrence of *Littorina undulata* and *Strombus* spp. (four specimens only, all dead shells, were recorded during this expedition). That nutrients may be a factor in the occurrence of marine mollusks has been suggested by Maes (1967); however, the high concentrations of total and particulate organic carbon in the water at Fanning and the extraordinary magnitude of photosynthetic production reported for the atoll (Gordon, 1971) may possibly preclude this factor as a determinant of faunal composition. Lack of topographical diversity was proposed by Morrison (1954) to account for the short faunal lists of atolls, and Kohn (1967) has stated that habitat diversity is a more important factor in determining species diversity in *Conus* than are longitudinal gradients.

Two features of the Fanning Island molluscan faunal lists are consistent with those reported for other insular faunas. The gastropod:bivalve ratio of 81:19 is similar to that reported for the Hawaiian Islands (Kay, 1967), the Cocos Keeling Islands (Maes, 1967), and Niue Island (Cernohorsky, 1970), and is on the order of that which has been proposed as a general characteristic of insular faunas (Kay, 1967). The virtual absence of scaphopods, cephalopods, and amphineurans is also consistent with the small numbers of these groups mentioned in the faunal lists of other islands (Kay, 1967; Maes, 1967;

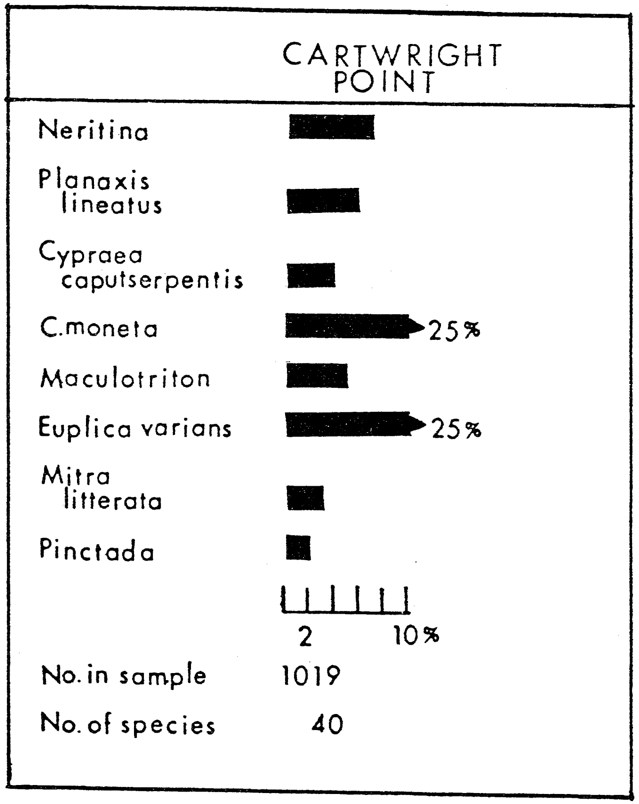

Fig. 14. The assemblage of macromollusks from Cartwright Point.

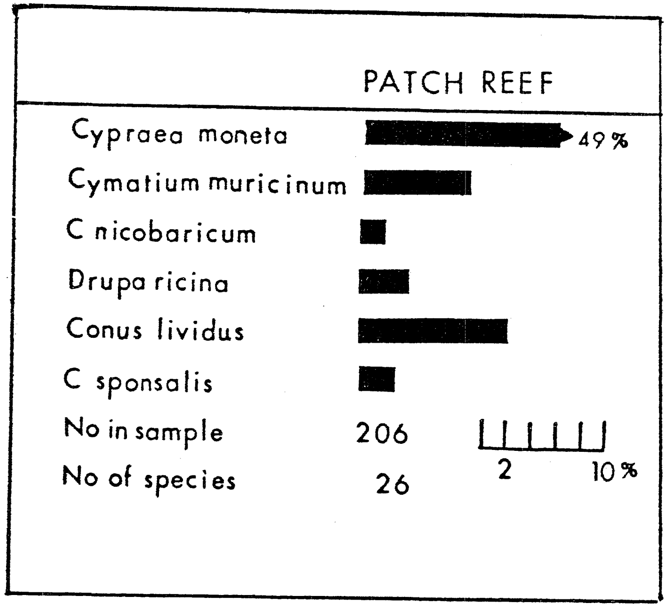

Fig. 15. The assemblage of macromollusks from patch reefs in the lagoon.

Table 2. List of Mollusks from the Line Islands

Class, Family and Species	Fanning		King.	Palm.	Wash.	Xmas	Jar.
	Sea	Lag.					
AMPHINEURA							
Chitonidae							
Chiton sp.	+					+	
GASTROPODA							
Scissurellidae							
Scissurella coronata Watson, 1886	+						
Scissurella sp.	+						
Fissurellidae							
Diodora granifera (Pease, 1861)	+						
Emarginula bicancellata Montr. 1860	+						
Emarginula peasei Thiele, 1918	+						
Hemitoma sp.	+						
Patellidae							
Patella stellaeformis Reeve, 1842	+						
Trochidae							
Euchelus angulatus Pease, 1867	+						
Monilea nucleus (Philippi, 1849)		+					
Monilea sp.	+	+					
Trochus histrio Reeve, 1848	+		+	+		+	
Stomatiidae							
Stomatella rosacea (Pease, 1867)	+						
Turbinidae							
Astrea helicina (Gmelin, 1791)	+		+	+	+	+	
Turbo argyrostomus Linn., 1758	+		+	+	+	+	
Phasianellidae							
Hiloa variabilis (Pease, 1860)	+	+					
Neritidae							
Nerita albicilla Linn., 1758		+		+			
Nerita plicata Linn., 1758	+	+	+	+	+	+	+
Nerita polita Linn., 1758	+			+		+	
Nerita reticulata Karsten, 1789				+			
Neritina bensoni (Recluz, 1850)		+					
Littorinidae							
Littorina coccinea Gmelin, 1791	+	+		+	+		
Littorina scabra Linn., 1758		+		+			
Littorina undulata Gray, 1839		+					

Class, Family and Species	Fanning Sea	Fanning Lag.	King.	Palm.	Wash.	Xmas	Jar.
Vitrinellidae							
Lophocochlias minutissimus (Pilsb. 1921)	+						
Vitrinellids (3 sp.)	+						
Truncatellidae							
Truncatella	+						
Rissoinidae							
Alvania spp. (2 sp.)	+	+					
Rissoina ambigua Gould, 1851	+					+	
Rissoina exasperata Souverbie, 1866	+						
Rissoina miltozona Tomlin, 1915	+						
Rissoina plicata A. Adams, 1851	+						
Rissoina semiplicata Pease, 1863						+	
Rissoina tenuistriata Pease, 1867	+						
Rissoina turricula Pease, 1860	+						
Assimineidae							
Assiminea nitida Pease,		+					
Architectonidae							
Heliacus sp.		+					
Vermetidae							
Serpulorbis sp.	+					+	
Dendropoma maximum (Sowerby, 1825)							
Vermetids spp.	+						+
Planaxidae							
Planaxis lineatus (Da Costa, 1776)	+	+				+	
Planaxis sulcatus Born, 1778				+			
Diastomidae							
Obtortio pyrrhacme (Melve. & St. 1896)		+					
Obtortio sp.		+					
Diala flammea (Pease, 1867)		+					
Cerithiidae							
Bittium zebrum Kiener, 1841	+						
Cerithium atromarginatum Dautz & Bouge, 1833	+						
Cerithium breve Quoy and Gaimard, 1833		+		+	+	+	
Cerithium columna Sowb. 1855	+			+	+	+	
Cerithium echinatum Lamarck, 1822	+				+		
Cerithium nesioticum Pilsb. & Vanatta, 1909	+						
Cerithium sculptum Pease, 1869	+						
Rhinoclavis asper (Linn., 1758)		+		+		+	
Rhinoclavis procera (Kiener, 1841)		+				+	
Rhinoclavis sinensis (Gmelin, 1791)		+		+	+	+	
Seila sp.	+	+					

Class, Family and Species	Fanning Sea	Lag.	King.	Palm.	Wash.	Xmas	Jar.
Cerithiopsidae							
Cerithiopsis (2 sp.)	+						
Triphoridae							
Triphora dolicha Watson,	+						
Triphora regalis Jouss., 1884	+						
Triphora violacea Quoy & Gaimard, 1833	+						
Triphora (5 sp.)	+	+					
Viriola cancellata (Hinds,	+						
Epitoniidae							
Epitonium (2 sp.)	+						
Eulimidae							
Balcis (3 sp.)		+					
Leiostraca sp.	+						
Stiliferidae							
Stilifer sp.	+*						
Hipponicidae							
Hipponix conicus (Schumacher, 1817)	+						
Calyptraeidae							
Cheilea equestris (Linn., 1758)						+	
Fossaridae							
Fossarus cumingii (A. Adams, 1853)	+						
Fossarus sp.	+						
Strombidae							
Strombus gibberulus gibbosus (Röding, 1798		$+^1$		+			
Strombus luhuanus Linn., 1758		$+^1$		+			
Strombus maculatus Sowerby, 1842		$+^1$		+	+		
Lambis chiragra chiragra Linn., 1758	$+^1$					+	
Lambis truncata sebae (Kiener, 1843)	$+^1$					+	
Ovulidae							
Calpurnus verrucosus (Linn., 1758)						+	
Ovula ovum (Linn., 1758)	+				+	+	
Triviidae							
Pedicularia pacifica Pease, 1865	+						
Proterato sulcifera schmeltziana (Crosse, 1867)	+						
Trivirostra pellucidala (Gaskoin, 1846)	+						
Trivia sp.	+						

Class, Family and Species	Fanning Sea	Fanning Lag.	King.	Palm.	Wash.	Xmas	Jar.
Cypraeidae[1]							
Cypraea annulus Linn., 1758		+		+			
Cypraea arabica Linn., 1758		+	+	+	+	+	
Cypraea asellus, Linn., 1758		+					
Cypraea bistrinotata Schild. & Schild., 1937						+	
Cypraea caputserpentis Linn., 1758	+		+	+	+	+	+
Cypraea carneola Linn., 1758	+			+	+	+	
Cypraea childreni Gray, 1825	+					+	
Cypraea chinensis Gmelin, 1791					+	+	
Cypraea cicercula Linn., 1758				+		+	
Cypraea clandestina Linn., 1767		+		+			
Cypraea cribraria Linn., 1758				+			
Cypraea depressa Gray, 1824	+		+	+	+	+	
Cypraea erosa, Linn., 1758	+			+		+	
Cypraea fimbriata Gmelin, 1791				+		+	
Cypraea goodalli Sowerby, 1832						+	
Cypraea helvola Linn., 1758	+*			+	+	+	
Cypraea irrorata Gray, 1828						+	
Cypraea isabella Linn., 1758	+		+	+	+	+	
Cypraea lynx, Linn., 1758		+		+	+	+	
Cypraea maculifera Schilder, 1932				+			
Cypraea mauritiana, Linn., 1758	+*			+			
Cypraea moneta, Linn., 1758	+	+	+	+	+	+	+
Cypraea nucleus, Linn., 1758	+				+	+	
Cypraea poraria Linn., 1758	+		+	+	+	+	
Cypraea scurra Gmelin, 1791	+			+	+	+	
Cypraea schilderorum Iredale, 1939	+			+	+	+	
Cypraea stolida Linn., 1758						+	
Cypraea talpa Linn., 1758	+			+	+	+	
Cypraea teres Gmelin, 1791					+	+	
Cypraea testudinaria Linn., 1758					+		
Cypraea tigris, Linn., 1758	+	+					
Cypraea ventriculus Lamarck, 1811					+		
Cypraea vitellus Linn., 1758		+*				+	
Cassidae							
Casmaria erinaceus kalosmodix (Melv., 1883)				+		+	
Casmaria ponderosa ponderosa (Gmelin, 1791)	+*					+	
Cypraecassis rufa (Linn., 1758)					+		

Class, Family and Species	Fanning Sea	 Lag.	King.	Palm.	Wash.	Xmas	Jar.
Tonnidae							
Tonna perdix (Linn., 1758)				+	+	+	+
Malea pomum (Linn., 1758)				+	+	+	+
Naticidae							
Natica marochiensis Gmelin, 1791		+		+			
Natica robillardi Sowerby, 1893		+					
Polinices mammilla (Linn., 1758)		+		+			
Polinices melanostoma (Gmelin, 1791)		+		+		+	
Cymatiidae							
Charonia tritonis (Linn., 1758)	+			+		+	+
Cymatium gemmatum (Reeve, 1844)		+	+	+	+		
Cymatium muricinum(Röding, 1798)		+		+			
Cymatium nicobaricum (Röding, 1798)		+		+	+	+	
Cymatium pileare (Linn., 1758)		+		+		+	
Bursidae							
Bursa Bubo (Linn., 1758)					+		
Bursa bufonia (Gmelin, 1791)	+			+	+	+	+
Bursa cruentata (Sowerby, 1835)						+	
Bursa granularis (Röding, 1798)	+			+	+	+	+
Muricidae							
Chicoreus torrefactus (Sowerby, 1841)						+	
Chicoreus sp.	+						
Thaisidae							
Drupa morum Röding, 1798	+		+	+	+	+	+
Drupa ricina (Linn., 1758)	+		+	+	+	+	+
Drupella cornus (Röding, 1798)				+		+	
Drupina grossularia (Röding, 1798)	+		+	+	+	+	+
Drupina rubusidaeus (Röding, 1798)	+						
Maculotriton digitalis (Reeve, 1844)	+	+	+	+	+	+	+
Morula anaxeres (Kiener, 1835)	+	+					
Morula cariosa (Wood, 1828)		+		+		+	
Morula sp. cf. *chaidea* (Duclos, 1832)				+			
Morula crossei Lienard, 1874				+			
Morula granulata (Duclos, 1832)	+	+	+	+	+	+	+
Morula margariticola (Broderip, 1832)		+		+		+	
Morula ochrostoma (Blainville, 1832)				+		+	
Morula uva (Röding, 1798)	+		+	+	+	+	+
Nassa serta (Bruguiere, 1799)		+		+	+	+	
Thais aculeata (Deshayes in Milne-Edwards, 1844)	+			+	+		
Thais armigera (Link, 1807)	+			+	+	+	
Thais intermedia (Kiener, 1836)	+						
Vexilla vexillum (Gmelin, 1791)					+	+	

Class, Family and Species	Fanning		King.	Palm.	Wash.	Xmas	Jar.
	Sea	Lag.					
Coralliophilidae							
Coralliophila violacea (Kiener, 1836)	+	+					
Coralliophila (2 sp.)	+	+					
Magilus fimbriatus (A. Adams, 1852)	+						
Magilus sp.					+	+	+
Quoyula madreporarum (Sowerby, 1834)	+	+		+		+	
Vasidae							
Vasum armatum (Broderip, 1833)	+				+		
Colubrariidae							
Colubraria sp.						+	
Buccinidae							
Caducifer truncatus (Hinds, 1844)	+						
Cantharus farinosus (Gould, 1849)						+	
Cantharus undosus (Linn., 1758)		+			+	+	+
Engina maculata Pease, 1869	+						
Engina medicaria (Linn., 1758)	++			+	+	+	
Engina tuberculosa Pease, 1863	++						
Pisania billeheusti (Petit, 1853)						+	
Pisania tritonoides (Reeve, 1846)	+		+	+			
Nassariidae							
Nassarius gaudiosus (Hinds, 1844)	+						
Nassarius ravidus (A. Adams, 1851)						+	
Nassarius graniferus (Kiener, 1834)	+						
Columbellidae							
Euplica turturina (Lam., 1822)	+	+				+	
Euplica varians (Sowerby, 1832)	+	+		+		+	
Mitrella rorida (Reeve, 1859)	+	+					
Seminella varia (Pease, 1861)	+						
Fasciolariidae							
Latirus amplustris Dillwyn, 1817	+			+	+	+	+
Latirus iris Lightfoot, 1786	+			+	+	+	+
Peristernia gemmata Reeve, 1847	+					+	
Peristernia nassatula (Lamarck, 1822)	+						
Fasciolaria filamentosus (Röding, 1798)							+
Harpidae							
Harpa amouretta Röding, 1798						+	
Olividae							
Oliva sp.						+	
Marginellidae							
Cysticus sp.	+						
Marginellids (3 sp.)	+	+					
Kogomea sandwichensis (Pease, 1861)	+	+					

Class, Family, and Species	Fanning		King.	Palm.	Wash.	Xmas	Jar.
	Sea	Lag.					
Mitridae							
Imbricaria conovula (Q. and G., 1833)	+						
Imbricaria punctata (Swainson, 1821)	+						
Mitra auriculoides Reeve, 1845	+	+					
Mitra cucumerina Lamarck, 1811	+		+	+			
Mitra litterata (Lamarck, 1811)	+	+		+	+	+	+
Mitra mitra (Linn., 1758)	+						
Mitra ferruginea Lamarck, 1811	+						
Mitra stictica (Link, 1807)	+			+	+	+	+
Pterygia nucea (Gmelin, 1791)				+			
Pusia consanguinea (Reeve, 1845)						+	
Strigatella acuminata (Swainson, 1824)		+	+			+	+
Strigatella paupercula (Linn., 1758)		+		+			
Strigatella oleacea (Reeve, 1844)			+			+	
Conidae							
Conus catus Hwass in Brug., 1792	+			+	+	+	+
Conus chaldaeus (Röding, 1798)	+			+	+	+	
Conus ebraeus Linn., 1758	+			+	+	+	+
Conus eburneus Hwass in Brug., 1792						+	
Conus flavidus Lamarck, 1810	+						
Conus lividus Hwass in Brug., 1792	+	+		+	+	+	
Conus miles Linn., 1758						+	
Conus miliaris Hwass in Brug.	+			+			
Conus nussatella Linn., 1758						+	
Conus pulicarius Hwass in Brug., 1792	+	+		+		+	
Conus rattus Hwass in Brug., 1792	+			+	+		+
Conus retifer Menke, 1829	+					+	+
Conus sponsalis Hwass in Brug., 1792	+		+	+	+	+	+
Conus tulipa Linn., 1758	+		+	+	+	+	+
Conus virgo Linn., 1758		+					
Terebridae							
Terebra affinis Gray, 1834	+			+		+	
Terebra argus Hinds, 1844		+		+			
Terebra cerithina Lamarck, 1822				+		+	
Terebra chlorata Lamarck, 1822						+	
Terebra crenulata (Linn., 1758)		+		+		+	
Terebra dimidiata (Linn., 1758)				+		+	
Terebra maculata (Linn., 1758)		+		+		+	
Terebra subulata (Linn., 1767)		+		+		+	
Turridae							
Anarithma metula (Hinds, 1843)	+						
Anacithara angiostoma Pease, 1868	+						
Carinapex minutissima (Garrett, 1873)	+						
Daphnella interrupta Pease, 1860	+						
Etreme sp. cf. *scalarina* (Desh., 1863)	+						
Kermia pumila (Mighels, 1845)	+						
Macteola sp. cf. *thiasotes* Melv. & Standen, 1897)	+						
Tritonoturris sp.	+						
Turrids (7 sp.)	+						

	Fanning						
Family, Class and Species	Sea	Lag.	King.	Palm.	Wash.	Xmas	Jar.
Pyramidellidae							
Odostomia (2 sp.)		+					
Pyramidella sp.	+	+					
Turbonilla (2 sp.)		+					
Aplysidae							
Dolabrifera dolabrifera (Rang, 1828)	+	+					
Atyidae							
Atys cylindrica (Helbling, 1779)		+				+	
Cylichna pusilla (Pease, 1860)		+					
Scaphandridae							
Acteocina sandwicensis (Pease, 1860)	+	+					
Acteonidae							
Pupa sp. cf. solidula (Linn., 1758)		+					
Retusidae							
Retusa sp.		+					
Hydatinidae							
Haminea sp.		+					
Dorididae							
Dendrodoris nigra (Stimpson, 1856)		+					
Jorunna tomentosa (Cuvier, 1804)		+					
Aeolididae							
Aeolids (2 sp.)	++	+					
Oyxnoidae							
Lobiger sp.							
Ellobiidae							
Melampus ater Gmelin, 1791	+	+					
Melampus luteus Quoy and Gaimard, 1833	+	+					
Truncatellidae							
Truncatella sp. cf. guernii A. & J. Villa, 1841		+					
BIVALVIA							
Limopsidae							
Cosa sp.		+					
Arcidae							
Acar plicata (Dillwyn, 1817)	+	+					
Barbatia decussata (Sowerby, 1833)		+					
Barbatia parva (Sowerby, 1833)	+	+					
Mytilidae							
Modiolus metcalfei Reeve, 1858	+				+	+	
Lithophag nasuta (Philippi, 1846)	+						
Lithophaga sp.	+						

	Fanning						
Class, Family, and Species	Sea	Lag.	King.	Palm.	Wash.	Xmas	Jar.
Isognomonidae							
Isognomon isognomon (Linn., 1758)		+					
Isognomon perna (Linn., 1767)	+	+		+	+	+	
Pteriidae							
Electroma sp.		+					
Pinctada margaritifera (Linn., 1758)		+			+	+	+
Pinnidae							
Atrina vexillum (Born, 1778)		+		+		+	
Pinna muricata Linn., 1758		+				+	
Pectinidae							
Chlamys cookei Dall, Bartsch & Rehder, 1938						+	
Chlamys sp.	+						
Gloripallium pallium (Linn., 1758)						+	
Spondylidae							
Spondylus ducalis Röding, 1798		+				+	
Spondylus sp.	+						
Spondylus sp.						+	
Limidae							
Lima fragilis (Gmelin, 1791)		+					
Ostreidae							
Ostrea hanleyana Sowerby, 1871	+						
Ostrea sandvicensis Sowerby, 1871		+		+	+	+	
Chamidae							
Chama inbricata Broderip, 1834		+		+			+
Lucinidae							
Codakia divergens (Philippi, 1850)		+				+	
Codakia punctata (Linn., 1758)		+					
Wallucina sp. cf. *gordoni* (E.A. Smith, 1886)		+					
"Lucina" edentula (Linn., 1758)		+					
Erycinidae							
Kellia sp.	+						
Erycinid sp.		+					
Carditidae							
Cardita variegata (Brug., 1792)		+					
Cardiidae							
Cardium sp.		+					
Fragum fragum (Linn., 1758)		+		+		+	
Mesodesmatidae							
Rochefortina sandwichensis Smith, 1885	+						
Tridacnidae							
Tridacna maxima (Röding, 1798)	+	+		+	+	+	+

Class, Family, and Species	Fanning Sea	Fanning Lag.	King.	Palm.	Wash.	Xmas	Jar.
Trapeziidae							
Trapezium oblongum (Linn., 1758)		+		+	+	+	
Sanguinolariidae							
Asaphis violascens (Forskal, 1775)				+		+	
Tellinidae							
Arcopagia scobinata (Linn., 1758)						+	
Quidnipagus palatam Iredale, 1929		+					
Pharaonella tongana (Quoy and Gaimard, 1833)		+					
Pinguitellina pinguis (Hanley, 1845)		+					
Scissulina dispar (Conrad, 1837)		+		+		+	
Semelangusus sp.		+					
Tellinids (4 sp.)		+					
Veneridae							
Lioconcha hebraea (Lamarck, 1818)				+		+	
Periglypta reticulata		+			+	+	
Pitar prora (Conrad, 1837)		+		+		+	
Diplodontidae							
Diplondonta sp.		+					

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[1] Other species of Cypraea reported from various islands in the Line group include *C. argus* Linn., 1758; *Cypraea dillwyni* Schilder, 1922; *C. globulus* Linn., 1758; *C. mappa* Linn., 1758; *C. mariae* Schilder and Schilder, 1927; and *C. serrulifera* Schilder and Schilder, 1938 (Jweell, 1962).

Cernohorsky, 1970). Faunal lists are, however, singularly uninformative with respect to the distribution and abundance of species. The following discussion is, therefore, directed toward ascertaining the sources of attenuation at Fanning.

The mollusks of the littorine zone form a well-known ecological assemblage throughout the world, and include not only littorines but nerites, archaeogastropod limpets, pulmonate limpets, and Planaxis sulcatus. As many as three littorines, three nerites, two archaeogastropod limpets, and two pulmonate limpets have been reported in the assemblage in various parts of the Indo-West-Pacific (see Kalk, 1958; Purchon and Enoch, 1954; Taylor, 1968). Among some islands of the Pacific, however, the assemblage appears to be fairly simple. In the Tuamotus, Littorina coccinea, Tectarius grandinatus, and Nerita plicata are found in the zone above the seaward reefs (Morrison, 1954; Salvat, 1967). At Kwajalein and Majuro in the Marshall Islands, Littorina coccinea, L. undulata, and Nerita plicata occur along seaward shorelines and Siphonaria, Peasiella, and Planaxis sulcatus occur in patches along the lagoon and in the passes (Kay, unpublished). At Fanning where a single littorine and nerite are found on seaward shorelines and where only occasional clusters of Littorina scabra and very rarely specimens of L. undulata are found, in addition, along lagoon shores, the composition of the littorine zone appears to be one of the simplest recorded.

The mollusks of seaward reef flats may be similarly examined. Salvat (1967), in an analysis of the marine mollusks of the Tuamotu Islands, noted that seaward reefs exhibit a topographical and faunal homogeneity but did not list the mollusks. A standard set of species can be proposed for seaward reef flats in the Pacific, the list of 22 species (Table 1) which appear rather consistently in the faunal lists for the Tuamotu Islands (Morrison, 1954; Chevalier et al., 1968); at Onotoa, Gilbert Islands (Banner, 1952); at Kwajalein and Majuro, Marshall Islands (Kay, unpublished); and at Fanning. Of these, 17 species are abundant on the reefs at Fanning, two (Thais aculeata and Cypraea annulus) occur but are much restricted in their occurrence, and two (Cerithium spp. and Dendropoma maximum) do not appear to occur at Fanning. Based on this analysis, the molluscan assemblages of the Fanning seaward reefs appear to show little attenuation.

The fauna of the lagoon is more difficult to discuss, for as Salvat (1967) has pointed out for the Tuamotu Islands, no two atolls have identical lagoon faunas, and he suggests that it is the lagoon fauna which characterizes each atoll. Comparison of the Fanning lagoon with those of the Tuamotu Islands and that of Funafuti demonstrates the dissimilarites: of the 34 species listed for Raroia (Morrison, 1954), only 15 occur in the Fanning lagoon; of the 13 common species mentioned for Mururoa (Chevalier, et al., 1968), only 6 occur at Fanning; and of the 51 species cited as common or abundant at Funafuti (Hedley, 1899a), only 23 occur at Fanning.

The distinction between open and closed lagoons has been drawn for the atolls of the Tuamotu Islands; in open lagoons there is a greater variety of molluscan species, but the species occur in lesser numbers than in closed lagoons (Salvat, 1967). Lagoon topography is, however, more complex than is indicated by the terms "open" and "closed". Some lagoon reefs resemble sea-

Table 1. Seaward Reef Gastropods in the Pacific

Patella stellaeformis Reeve, 1842

Turbo argyrostomus Linn., 1758 (and/or *Turbo setosus* Gmelin, 1791)

Cerithium spp. (for example, *Cerithium alveolus* Hombron and Jacquinot, 1841 or *C. sejunctum* Iredale, 1929)

Dendropoma maximum (Sowerby, 1825)

Cypraea caputserpentis Linn., 1758

Cypraea depressa Gray, 1824

Cypraea annulus Linn., 1758

Cypraea moneta Linn., 1758

Maculotriton digitalis (Reeve, 1844)

Drupa morum Röding, 1798

Drupa ricina (Linn., 1758)

Drupina grossularia (Röding, 1798)

Morula granulata (Duclos, 1832)

Morula uva (Roding, 1798)

Vasum spp. (*V. armatum* is Polynesian; two other species elsewhere)

Engina mendicaria (Linn., 1758)

Euplica varians (Sowerby, 1832)

Conus ebraeus Linn., 1758

Conus sponsalis Hwass in Brug. 1792

Mitra litterata (Lamarck, 1811)

Thais aculeata (Deshayes in Milne-Edwards, 1844) ward reefs, on others there are beds of *Thalassia*, *Cymodocea*, or *Halophila*, or mangrove swamps encroach on the reef; and lagoon slopes are covered by talus or thick coral growth (Wells, 1957). If each of these features also harbors one or more mulluscan assemblages, then the rather short list of mollusks reported from Fanning may reflect the somewhat simplified topography of the lagoon.

The hypothesis serves both to explain features of the Fanning Island faunal list, and to predict features for other atolls. The apparent absence of *Asaphis* and *Planaxis sulcatus* and the rare occurrence of *Strombus* and *Lambis* may be associated with the absence of the topographical features which determine the occurrence of these mollusks. The small amount of overlap between seaward reef and lagoon mollusks may be attributed to the lack of appropriate lagoon reef at Fanning. And one may predict that in those lagoons which have extensive seaward-type lagoon reefs, there will be a greater degree of overlap between seaward reef and lagoon faunas than occurs on atolls which do not have such reefs.

It should also be practical to extend the hypothesis to include physical features of the seaward reefs. Refined sampling techniques will undoubtedly delimit molluscan assemblages on the seaward reefs which are not recognized in this rather general survey. With smaller assemblages, the restricted distribution of certain species and the rare occurrence of others may also be explicable in terms of topographical features.

Topographical diversity is not considered a panacea to account for faunal composition among Pacific islands. The history of the occurrence of the organism (that is, time of arrival), the history of the atoll itself, community structure, competition, and other biotic factors are essential parts of the picture. The hypothesis does have the advantages, however, of being testable, and of directing attention to more specific aspects of molluscan distribution than have heretofore been recognized.

FAUNAL RELATIONSHIPS

The faunal relationships of the Line Islands mollusks are most conveniently discussed in terms of three groups of species: those which are distributed apparently with equal abandon throughout the Indo-West-Pacific; those which are endemic to the Pacific basin; and those which are endemic to Polynesia. Polynesia is here recognized as including the Cooke, Society, and Tuamotu islands and extending to Easter Island (Schilder and Schilder, 1939). Indo-West-Pacific species form 86 percent, Pacific endemics 12 percent, and Polynesian endemics 2 percent of the fauna. The figures cited are based only on those species for which the distribution is known.

One Polynesian endemic and two which are questionably referred to Polynesia in concert distinguish the Line Islands fauna from that of the Tuamotu, Phoenix, Gilbert, Marshall, and Hawaiian islands: the common occurrence of *Vasum armatum*, *Latirus amplustris*, and *L. iris* on the seaward reefs. *Vasum armatum* is endemic to the Tuamotu, Phoenix, and Line islands (Abbott, 1959). The distribution of the two species of Latirus is not known, *L. amplustris* was described from Anaa (Tuamotu Islands) and L. iris from Tahiti; neither appear in collections I have seen from the Tuamotu Islands, and, indeed, Morrison (1954) records L. nodatus, the Pacific basin fasciolarid, in the lagoon at Raroia. L. amplustris and L. iris are common at Baker and Howland ouliers of the Gilbert Islands, but not at Canton in the Phoenix Islands (Kay, unpublished). The Baker and Howland fauna differs from that of the Line Islands, however, in that Vasum turbinellus (Linn., 1758) is the common vasid, and, in addition, Cantharus undosus, which is rare in the Line Islands is a prominent component of the reef fauna.

In most respects the Line Island fauna appears more closely related to that of the Central Pacific (Gilbert, Phoenix, and Marshall islands) than to that of either Polynesia or Hawaii. It lacks, for example, several Polynesian cowries (Cypraea obvelata), and none of the Hawaiian endemic mollusks is recorded from these islands.

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PHYSICAL AND BIOLOGICAL DATA COLLECTED IN ESTUARINE ENVIRONMENTS AT FANNING ATOLL

Eric B. Guinther
Department of Zoology

INTRODUCTION

Standing or flowing bodies of fresh water are rare on atolls because of the high permeability of the soil. The basal ground-water body of porous island structures is of the Ghyben-Herzberg type (Cox, 1951; Arnow, 1954) and, excepting regular but damped tidal oscillations, daily and seasonal fluctuations in precipitation account for gross changes in the head or level of the ground-water above sea level. Fresh or brackish water pools that form, do so in depressions extending below the water table. Although the factors that determine the degree of mixing of sea water and fresh water in the Ghyben-Herzberg lens are complex (see Cox, 1951), all water added to the lens through rainfall and not subsequently withdrawn and transpired by plants eventually emerges along the shoreline as brackish water. Brackish water outflow along the seaward shore is probably inconsequential in the ecology of the shoreline since the mixing of the brackish water with sea water before it emerges is promoted by two factors, substantial wave action and coarse sediments. Along the lagoon shore, however, where sediments tend to be fine and wave action is reduced, estuarine conditions may result with the outflow of brackish water from the aquifer. The distribution of these low salinity environments is dependent on local topographic and geologic features and the magnitude and duration of the rainfall recharging the aquifer. In addition, lagoon organisms may also be subjected to increases in salinity resulting from evaporation in shallow shoreline water. The data necessary to assess both the extent to which wide variations in salinity along lagoon shores occur and the importance of such variations in the ecology of the lagoon have not been reported.

In January 1970, as part of a team surveying the biota of Fanning Atoll (Line Islands), I made a series of physical and biological observations in lagoon areas exposed to incursion by brackish water. Many of these environments also regularly become hypersaline relative to ocean water. The short period of time over which the data were collected and the non-quantitative nature of the biological observations allow only a characterization of the estuarine environments.

Certain properties of Fanning Atoll tend to enhance variations in the salinity of the water along the lagoon shores. The islands of the atoll nearly enclose the lagoon and hence lagoon water mixes only slowly with open ocean water (Gallagher, _et al._, 1971). The lagoon is, for the most part, shallow, and relative to land area, tidal flats are extensive (see Fig. 1). The total area of Fanning Atoll is 134.39 km^2, with the lagoon comprising 116.55 km^2. Almost half of the remaining 17.84 km^2 are "salt flats"

(Zipser and Taylor, 1968). The mean annual rainfall at Fanning is 206 cm (based on 41 years of data provided by the New Zealand Meteorological Service, 1956). The rainfall is spread over much of the year, although the months of September through October constitute a dry season (when the monthly mean is about 7.4 cm). Droughts occur occasionally. The islands of the atoll are large, and this fact combined with the generally ample rainfall indicates that well-developed Ghyben-Herzberg lenses may be expected.

Although all shallow water along the lagoon shore may decrease in salinity during rainy periods and increase in salinity during conditions that enhance evaporation, variations in salinity (and temperature as well) are accentuated in the tidal and subtidal inlets and channels dissecting the islands of the atoll. These "extra-lagoonal" bodies of water may be termed estuarine in a broad sense. That is, they are regions of often steep and variable gradients in salinity, temperature, and tidal currents. Three conditions seem important in producing and maintaining estuarine conditions in the inlets: (1) a generally restricted flow of water between the estuary and the lagoon, (2) the association of extensive tidal flats with the estuaries, and (3) intimate contact with the Ghyben-Herzberg lens of the surrounding island structure. The relative degree to which each of these features exists along any part of the shore determines the magnitude of the response of the particular body of water to variable rates in precipitation and evaporation.

Figure 1 depicts shoreline and estuarine-associated features at Fanning as interpreted from aerial photographs and ground surveys. The dotted line, which marks the outer margin of the seaward and lagoon reefs is based on the lagoon slope in the lagoon and the line of breakers on the outside of the island ring.

ESTUARY AT NAPU NAIAROA

The estuary at Napu Naiaroa was selected for detailed sampling because its proximity to my residence at the Cable Station allowed regular monitoring of physical conditions, and because it appears to typify over a well-delimited area those features of the salt flats and estuaries observed on other parts of the atoll. Figure 2 shows the Napu Naiaroa estuary and the station locations.

Several physically distinct regions of the estuary may be distinguished. The main body of the estuary is an inlet trending roughly NNW-SSE, with its mouth narrower than its head. Sand bars partially block the mouth of the estuary enclosing a portion of the lagoon reef flat (a sand shoal along the lagoon shore) against the island shore (Stations 1 to 4) and I term this region the "enclosed shore." The shoreline of the inlet above the bridge (Stations 5 to 12) is a tidal flat of variable width dissected by tidal channels. At the head of the inlet a branching main channel (Stations 20 to 40, Fig. 7) drains numerous smaller channels covering a more extensive tidal flat ("lower flat"). The latter tidal flat is covered with hard-packed sand, although sediments on the channel bottoms are fine silt. Sediments of the inlet bottom and inlet tidal shore are less consolidated than

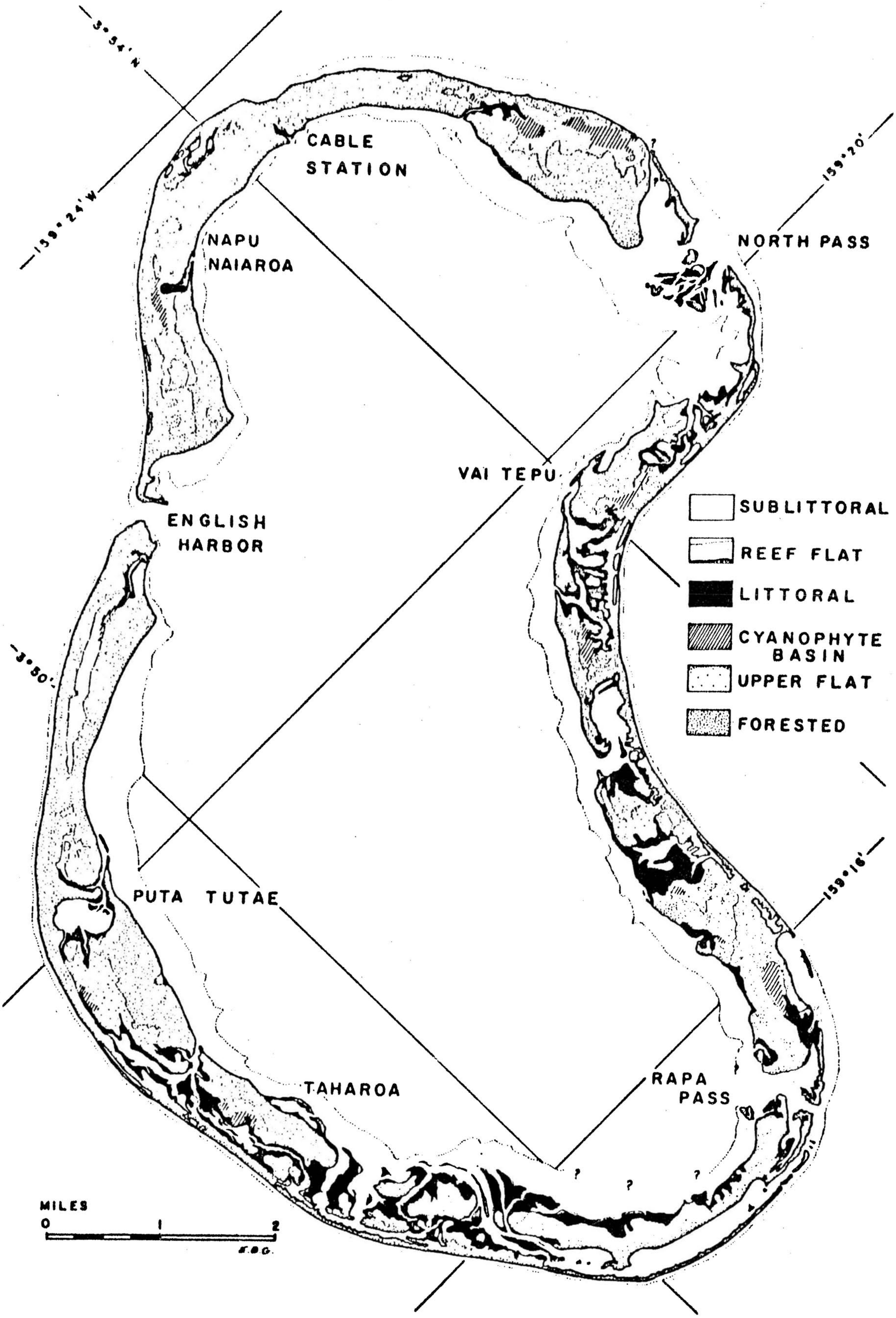

Fig. 1. Environments associated with estuarine conditons on Fanning Atoll.

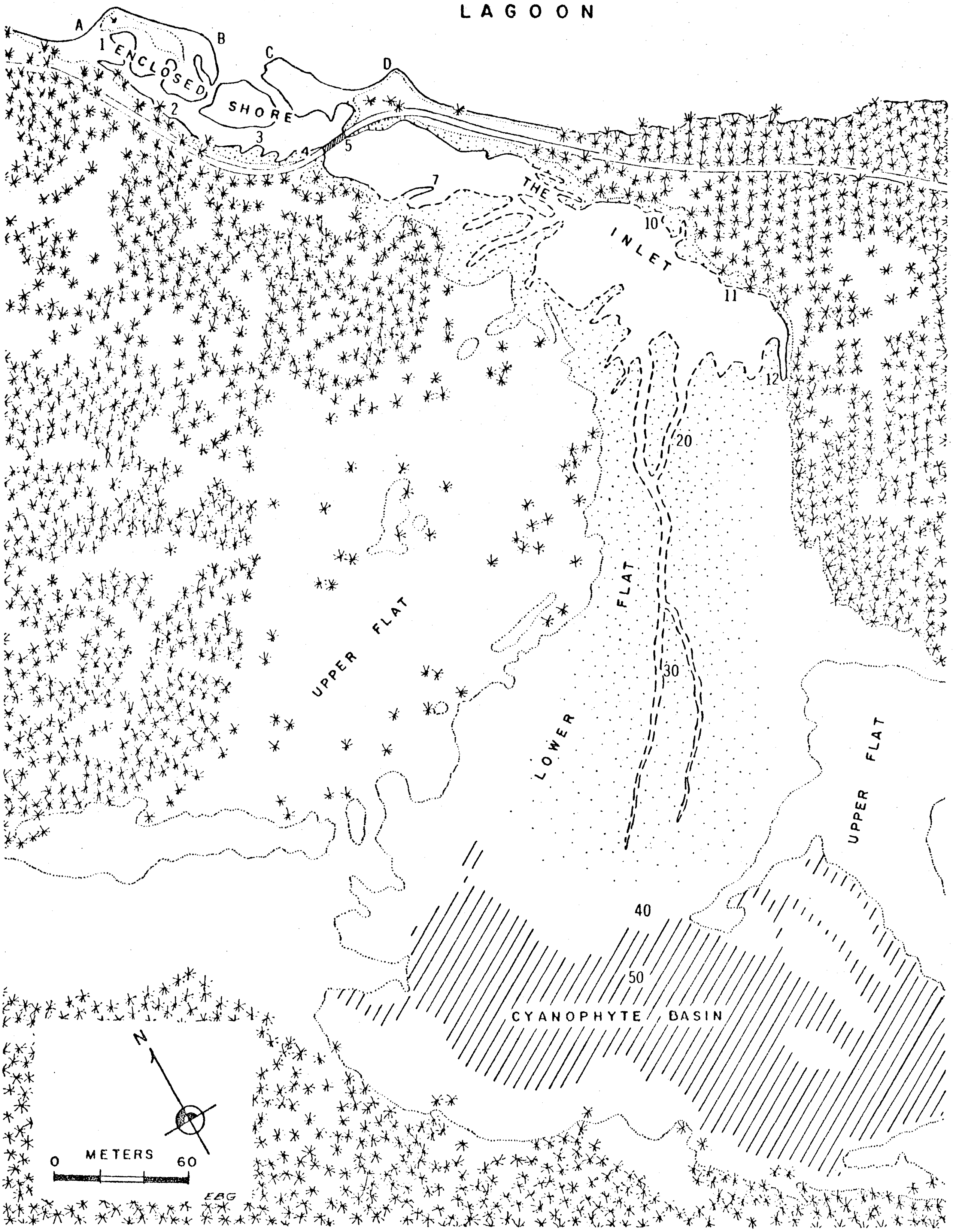

Fig. 2. Map of Napu Naiaroa study area, based on ground survey and aerial photographs. Scale is approximate. Broken line of shoreline indicates extensive channel development and hence approximate shoreline; stippling indicates distribution of Uca; diagonal lines delimit cyanophyte basin; dotted line shows margin of grass cover. Letters designate lagoon shore sampling stations; numbers designate estuary sampling stations.

on the tidal flat Southwest of Station 20, and walking is difficult along the inlet shore.

The tidal channels are unusual in a number of respects. Their pattern (Fig. 3) is vaguely dendritic and individual channel courses are only slightly sinuous. Often many channels run roughly parallel to each other in a herring-bone pattern. Close to the main channel or the inlet the channel pattern is anastomotic. The width of the flat between each channel is approximately the same as the width of the channels (ca. 1 to 2 meters), although the inter-channel distance increases as the channels narrow toward the upper end of the flat. The main channel and much of the course of the smaller channels are subtidal; the inter-channel flat is intertidal. Isolated pools of water remain in the upper reaches of some of the channels as the tide recedes.

The "upper flat" consists of a high intertidal basin, the "cyanophyte basin" (named for the mats of blue-green algae that predominate here), and an extensive supralittoral flat on which a sparse growth of grass occurs. Channels are absent on the "upper flat", although there is some indication of them in aerial photographs of the cyanophyte basin. Coarse gravel forms a reticulate pattern in low ridges on the dry flat. Christophersen (1927) mentions these "polygon fields" in the Line Islands and includes an excellent photograph from Christmas Island (Christophersen, 1927, Plate I-A). The phenomenon producing the reticulate pattern is not limited to dry flats, the polygons occur also intertidally in sheltered areas. The cyanophyte basin is a shallow depression in which water collects and evaporates, at times producing a highly saline environment.

Physical data

Salinity and temperature measurements were made at most Napu Naiaroa stations once or twice daily from January 13 to January 18. Salinity was measured in the field with an AO refractometer, but on one occasion water samples were collected and salinity determined in the lab with an inductive salinometer. The salinities determined by the latter method are presented in Table 1. A comparison of the salinities obtained by the two methods (on the assumption that the inductive salinometer value is closest to the "true" salinity) revealed a deviation of the refractive index values from the manufacturer's curve relating refractive index to salinity. The manufacturer's curve and the corrected curve for the refractometer used in this study are presented as Figure 4. Temperatures and salinites obtained at Napu Naiaroa stations between January 13 and 18 are given in Table 2. Salinity ranges based on the data collected at Napu Naiaroa during six sampling periods are illustrated in Figure 5. The tide record is included to indicate the relative height and condition of the tide prior to and at the time of sampling, although mean datum was not established.

The amount of rainfall occurring in the vicinity of the estuary is an important factor in determining the salinity of the estuary water. Accurate rainfall records were not kept for the period of study at Napu Naiaroa, but days on which rainfall occurred were noted. A few days prior to our arrival

Table 1. Salinity values at various Napu Naiaroa Stations on January 17, 1970 determined from conductivity ratios (inductive salinometer)

Station	Salinity (‰)
A	32.38
1	21.84
1 (near road)	18.11
1 (toward Station 2)	19.33
2	27.74
3	29.60
4	31.52
D	32.45
5	31.65
10	31.17
11	25.67
12	21.39
20	11.58
30	7.75
50	11.90

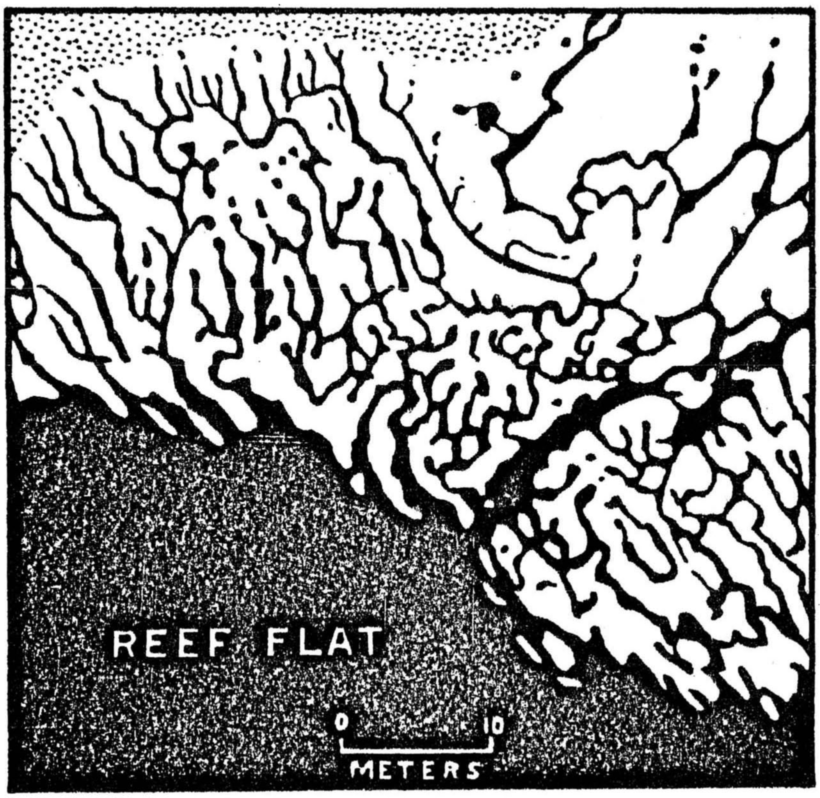

Fig. 3. Diagram of tidal channels, based on low-level aerial photographs. Scale is approximate.

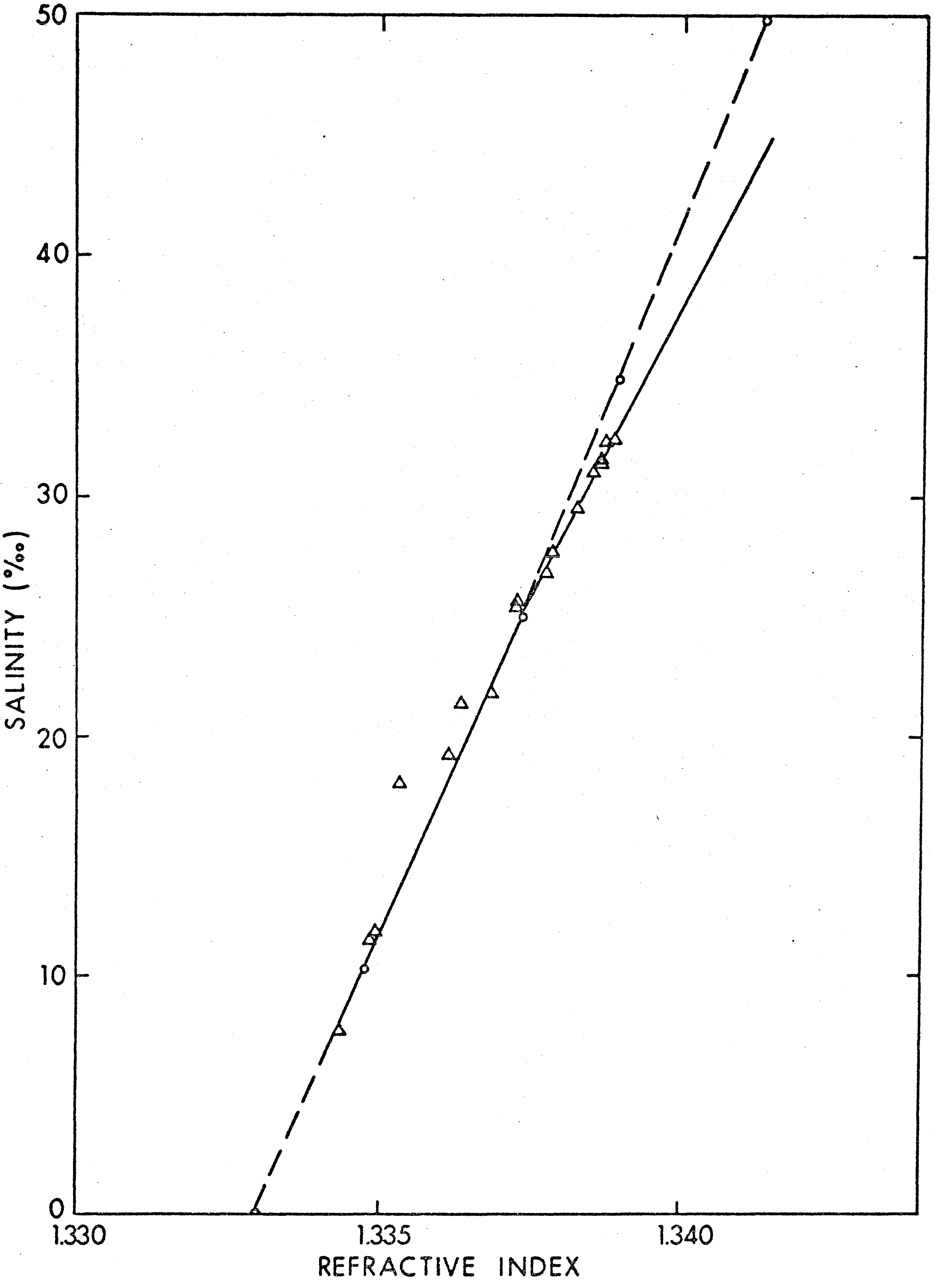

Fig. 4. Curve relating refractive index to salinity (in parts per thousand) for the refractometer used in this study.

on Fanning (Jan. 3) heavy rainfall occurred on the atoll, but very little precipitation occurred between January 3 and January 15. Some rain fell for a brief period on January 13, the evening of the 15th, and most of the morning of the 17th.

A general increase in the salinity of the water in the channels and in the cyanophyte basin was observed in the estuary from January 14 to January 16. The increase followed a dilution of the water resulting from the rainfall of the 13th. Despite rain on the 15th, salinities were high on the 16th, possibly reflecting the addition of salt from the cyanophyte basin as the high early morning tide flooded the basin. The long period of rainfall on the 17th resulted in low salinities over all of the estuary and out onto the lagoon reef flat fronting the estuary.

Exceptionally low salinities were recorded at Stations 1 and 12 on the 17th as well as during most sampling periods earlier in the week. It is apparent that these two stations are located near regions where underground brackish water enters the estuary, probably as runoff from the Ghyben-Herzberg lens. On the 16th, 20 refractometer readings were made in the enclosed shore and a low salinity (12.7 ‰) seepage area no more than 1 or 2 meters across was detected along the shore between Stations 1 and 2 (Fig. 6). The salinity values obtained along the lagoon shore at Station A were generally lower than those obtained at Stations C or D.

Air temperatures, measured during the day at Station 1 varied from 27.2 to 30.0 °C over the period from January 14 to January 17. Water temperatures were a few degrees to nearly ten degrees higher than ambient air temperature. The air temperature around 2100 hours on January 18 was 27.8 °C, and the water temperatures taken at that time (Table 2) indicate a slow cooling rate after dark.

In addition to the temperatures taken concurrently with the refractometer readings, a maximum-minimum thermometer was set out (at Stations 5, 20, and 30) for three 24-hour periods and the temperature ranges recorded are given in Table 3. The low of 26.1 °C recorded at Station 5 was the water temperature at 1500 hours on the 17th when the thermometer was retrieved. In additon to a steady rain on the morning of the 17th, skies were overcast most of the afternoon and water temperatures were, as a result, relatively low over all of the estuary.

Samples for determining dissolved oxygen by the Winkler method were collected during the morning of the 15th at three stations and the afternoon of the 16th at three stations. The calculated oxygen concentrations are presented in Table 4. All of the values obtained indicate supersaturated solutions. No samples were taken at night, but a distinct odor of hydrogen sulfide was most noticeable on the flats after dark. Digging in the sediments of the estuary revealed that, during the day as well, hydrogen sulfide was being produced just below the surface.

Table 2. Temperature, refractive index, and salinity of the water at various Napu Naiaroa Stations from January 13 to January 18, 1970.

Station	Water Temperature (°C)	Refractive Index	Salinity[a] (‰)
January 13 (ca 1300)[b]			
2	32.5	1.3392	34.2
9	35.0		
January 14 (ca 0900)			
A	26.5	1.3397	36.6
1	27.1	1.3387	31.7
2	27.7	1.3394	35.2
4	27.1	1.3399	37.6
10	27.4	1.3396	36.2
11	28.5	1.3397	36.6
12	28.8	1.3391	33.5
20	28.8	1.3395	35.7
30	28.3	1.3394	35.2
40	31.8	1.3386	31.2
40		1.3393	34.7
50	32.9	1.3393	34.7
January 14 (1345)			
A	32.7	1.3396	36.2
1	35.0	1.3396	36.2
2	34.5	1.3396	36.2
4	30.4	1.3397	36.6
D	30.4	1.3397	36.6
10 (inlet)	33.5	1.3395	35.7
10 (channel)	38.5		
11	36.0	1.3395	35.7
12	37.3	1.3392	34.2
20	36.2	1.3394	35.2
25	38.1	1.3393	34.7
30	36.8	1.3393	34.7
40	35.8	1.3395	35.7
50	36.6	1.3399	37.6
January 15 (0830)			
A	26.6	1.3396	36.2
1	27.0	1.3373	24.7
2	26.4	1.3386	31.2
4	26.2	1.3396	36.2
C	27.0	1.3396	36.2
D	26.1	1.3395	35.7
5	27.3	1.3397	36.6
10 (inlet)	28.4	1.3397	36.6
10 (channel)	27.7	1.3397	36.6
11	28.5	1.3396	36.2
12	28.8	1.3367	21.2
20	28.2	1.3395	35.7
30	28.0	1.3398	37.1
40	28.2	1.3387	31.7
50	(no water standing in depressions)		
January 15 (1215)			
D	29.7	1.3397	36.6
5	30.1	1.3396	36.2
January 16 (0830)			
A	27.3	1.3396	36.2
1	28.2	1.3391	33.5

1 (near road)	29.7	1.3352	12.7
2	27.0	1.3393	34.7
2	27.7	1.3390	33.2
3		1.3394	35.2
4	27.0	1.3394	35.2
C	27.0	1.3396	36.2
D	27.1	1.3396	36.2
5	27.4	1.3396	36.2
10	27.2	1.3398	37.1
11	29.1	1.3398	37.1
12	29.5	1.3372	24.7
20	29.1	1.3398	37.1
30	30.2	1.3399	37.6
40	31.2	1.3402	39.0
50	32.2	1.3409	42.3
60	33.0	1.3409	42.3
January 16 (1500)			
A	32.3	1.3396	36.2
1	33.1	1.3392	34.2
1 (near road)		1.3389	32.7
2	33.3	1.3393	34.7
3	33.7	1.3394	35.2
4	34.2	1.3395	35.7
C	33.4	1.3397	36.6
D	31.2	1.3395	35.7
5	34.5	1.3394	35.2
10 (inlet)	35.2	1.3394	35.2
10 (channel)	39.7		
11	39.0	1.3393	34.7
12	37.6	1.3391	33.5
20	36.6	1.3397	35.6
30	35.4	1.3396	36.2
40	33.6	1.3397	36.6
50	33.7	1.3409	42.3
January 17 (1430)			
A	27.1	1.3388	32.2
1	27.0	1.3369	22.4
1 (near road)	26.2	1.3354	13.9
1 (toward 2)	26.1	1.3362	18.4
2	26.9	1.3379	27.9
3	26.8	1.3383	29.8
4	26.4	1.3387	31.7
C		1.3389	32.7
D	26.9	1.3389	32.7
5	27.1	1.3387	31.7
10 (inlet)	27.5	1.3386	31.2
10 (channel)	27.2	1.3380	28.3
11	27.4	1.3373	24.7
12	27.3	1.3364	19.5
20	27.0	1.3349	11.0
30	26.1	1.3344	8.3
40	25.6	1.3343	7.8
50	25.1	1.3350	11.6
January 18 (2100)			
A	27.4		
1	28.0		
C	29.3		
11	30.1		
20	30.3	1.3358	16.1
30	26.5		
50	25.8	1.3349	10.9

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[a] Value based on refractive index as interpreted from Fig. 4.

[b] Time of day at which first station (Station A) water was sampled. Stations were then sampled in approximately the order given in the table for each sampling period. Determining temperature and refractive index at 15 or more stations required between 1 and 2 hours.

Table 3. Maximum-minimum thermometer values

Station	Date set out	Minimum and maximum Temperatures recorded
30	Jan. 14 - Jan. 15	28.6 - 36.1 °C
20	Jan. 15 - Jan. 16	28.3 - 33.9 °C
5	Jan. 16 - Jan. 17	26.1 - 33.9 °C

Table 4. Dissolved Oxygen Determinations

Station	Time	Date	O_2 Concentration ($ml\ O_2$/liter)
5	0900	Jan. 15	4.42
5	1220	Jan. 15	6.41
20	1010	Jan. 15	5.90
30	1020	Jan. 15	5.81
5	1500	Jan. 16	5.89
11	1545	Jan. 16	5.79
30	1600	Jan. 16	6.64

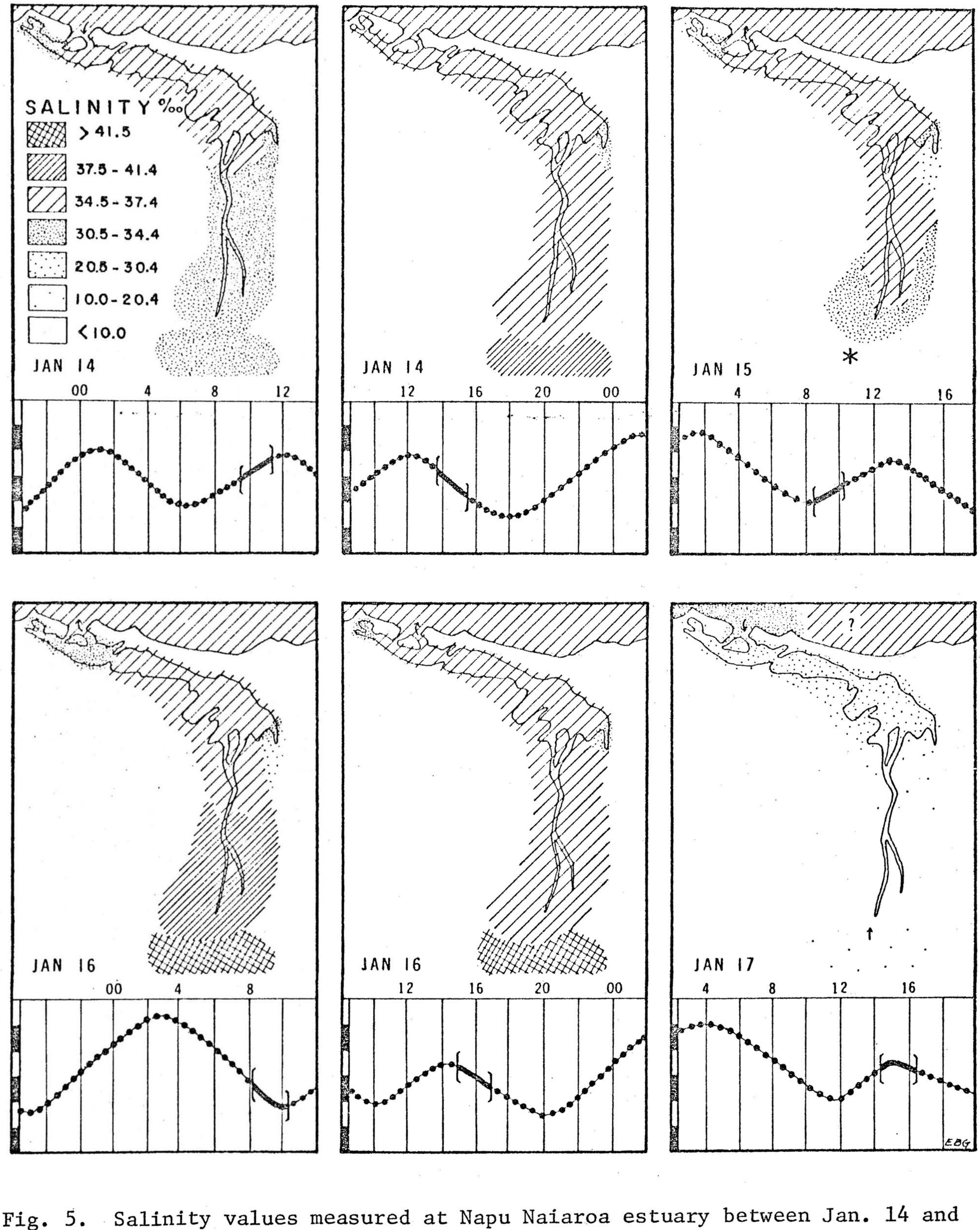

Fig. 5. Salinity values measured at Napu Naiaroa estuary between Jan. 14 and Jan. 17, 1970. Time of day of sampling period is indicated by brackets along the tide record. The tide record is from a gauge located at the Cable Station (lagoon) and adapted from Gallagher *et al*. (1970). Vertical scale on tide curve marked in 10-cm intervals; time of day indicated across the top of horizontal axis. Asterisk indicates no standing water present. Arrows indicate observed direction of water flow.

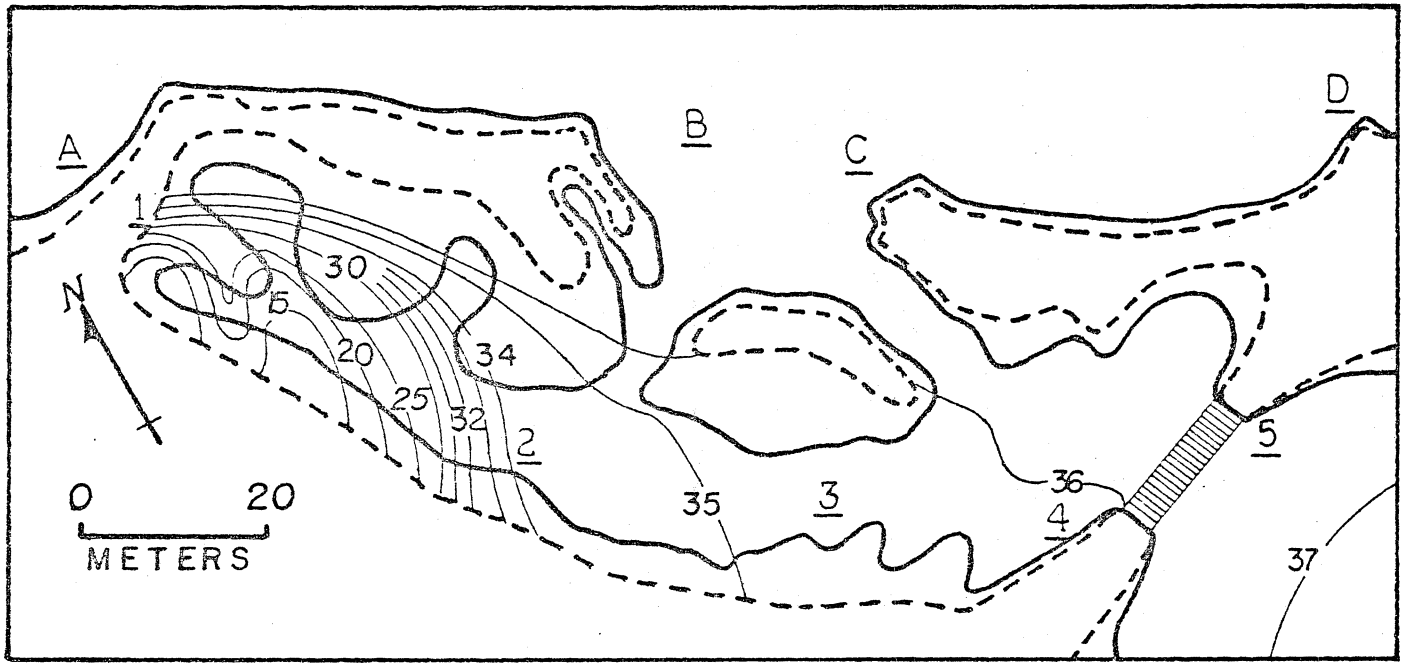

Fig. 6. Salinities (in $^{o}/oo$) in the enclosed shore of Napu Naiaroa estuary on the morning of Jan. 16, 1970. Dashed line indicates high-tide shoreline.

Faunal and floral distributions

The lagoon reef-flat fronting Napu Naiaroa extends for a considerable distance out into the lagoon as a gradually sloping, sublittoral shelf. The bottom sediments are a fine white sand with occasional chunks of larger carbonate material. A sparse growth of the alga, Ectocarpus sp., occurs on these chunks. Schools of mullet (Mugil spp.) range offshore and occasionally enter the estuary. On the lagoon-face of the sand bars, as along the lagoon beaches, the ghost crab, Ocypode ceratophthalmus (Pallus), makes its burrow. Between Stations A and B, on top of the sand bar, several young plants, including Cocos nucifera Linn., Messerschmidia (Tournefortia) argentea (Linn.) and Sesuvium portulacastrum Linn., have become established.

The enclosed shore (behind the sand bars) is shallow and much of the bottom is exposed at low tide. Schools of young Tilapia mossambica (Peters) and young mullet of at least two species (one is Mugil engeli Bleeker) are common in the enclosed shore. At high tide some of the more typically lagoon fishes (Lutjanidae, Diodontidae) may be seen under the road bridge (Stations 4 and 5). Small (12 to 18 inches) reef black-tip sharks (Carcharhinus melanopterus Quoy and Gaimard) are common visitors to the estuary from the lagoon reef flat. Near Station 1, living on the silty bottom, are a goby (Oxyurichthys sp.) and a palaemonid shrimp. The fishes of the estuary inlet and main channels include large Tilapia mossambica, several species of mullet, and the milk-fish, Chanos chanos Jordan and Evermann.

A few specimens of the snail, Cerithium breve Quoy and Gaimard, were found near Station 4 on sand. The small nerited snail, Neritina bensoni (Recluz), occurs on the lower rocks of the roadway fill at Station 4, and some individuals of the supratidal species, Nerita plicata Linn., are found wherever emergent solid substrate occurs (Stations 3, 4, 5, and 7). The latter species grows to a large size in the quiet waters of the estuary at Napu Naiaroa. One other supratidal snail, Littorina scabra Linn., is rare but has a distribution similar to that of N. plicata.

The most striking inhabitant of the estuary shore is the black and red fiddler crab, Uca tetragonon (Herbst). These crabs live in densely populated colonies, particularly concentrated on the inter-channel flats. Their overall distribution at Napu Naiaroa is shown in Figure 2, but the crabs are most abundant from Station 5 to beyond Station 20. The grapsid crab, Metopograpsus thukuhar (Owen), is a high intertidal form which may burrow into mud, but is most abundant in rocky areas. This crab seem to be limited to the enclosed shore and inlet shores, and, in general, lives slightly higher up the shore than does Uca. If chased, however, Metopograpsus may seek refuge in occupied Uca burrows.

The most evident terrestrial animal at Fanning Atoll is Cardisoma carnifex (Herbst), the land crab. This crab is most numerous at Napu Naiaroa within the shaded coconut groves, some individuals burrowing close to the shore where shade is available. At night these crabs become active (although many are "out" during the day) and range over much of the estuary shore. Sluggish, moribund individuals found in shallow burrows in the middle of the flats may have been caught in the open at sunrise far from protective shade.

At night two species of terrestrial hermit crab (*Coenobita*) also become active and may be seen foraging along the estuary shore and upper flat (*C. brevimanus* Dana), and on the lagoon beaches and enclosed shore beaches (*C. perlatus* M. Edw.). Although the shore crab, *Metopograpsus*, is active at night, *Uca* is conspicuously absent above ground after dark.

A very diverse fauna occurs at Station 7, a low rocky spit (man-made?) extending out into the inlet. Animals found here include *Metopograpsus thukuhar*, *Nerita plicata*, and *Littorina scabra*. Under the rocks an isopod (Trichoniscidae ?), a collumbolid, and an oligochaete are common.

The only vascular plant growing on the lower flat is *Sesuvium portulacastrum* Linn., a fleshy, bright green herb found most extensively along the main channel from Station 20 to beyond Station 30. A tiny beetle (Carabidae) and a gammarid amphipod (Talitridae) are common on the lower flat between the channels, but the distribution of both extends onto the upper flat. In the channels a palaemonid shrimp is particularly abundant, as are young *Tilapia*. Nest sites of the *Tilapia* are made occasionally in these channels, although most of the nests are found along the inlet shore. Considerable transport of sand from the channel wall occurs as the bowl-shaped nests are constructed, and it would appear that in this manner these fish contribute to the shaping of the channels. Both *Tilapia* and *Gambusia* sp. are introduced species at Fanning, but at Napu Naiaroa *Gambusia* (mosquito fish) were found only in an enclosed pond (Station 11) that is inundated at higher high tides. The pond contains, in addition to *Gambusia*, several brooding *Tilapia*, numerous palaemonid shrimp, and, on occasion, land crabs. The bottom sediment of the pond is a yellow-brown color, differing markedly from the white to grey sediment of the nearby channels, and possibly reflecting the exclusion from the pond of bottom-feeding mullet.

The transition between the lower and upper flat is gradual. The degree of relief between the channels and the inter-channel ground decreases until the channels are no longer discernible. The tufted grass growing over much of the upper flat may be the same species as the bunch-grass, *Lepturus repens* (Forster) Brown, which covers the ground under the *Cocos* trees, although the growth habit of the grass is different in the two areas. On the flat the plants are shorter, less leafy, and far apart. On the slightly higher ground of the coconut groves the grass is larger and closer together. The grass around the *Cocos*, in January at least, has greener leaves and fewer dry portions than does the grass on the open flat.

In the zone of transition between upper and lower flats the small mesogastropod, *Assiminea nitida* Pease, is particularly abundant, but active only at night. A terrestrial isopod (*Tylos latreilli* Audouin and Savigny) occurs here. Each grass plant of the upper flat harbors a small spider which constructs a simple "web" of only two or three threads.

The cyanophyte basin differs markedly from both the grass-covered upper flat and the channeled lower flat. The basin is actually a series of shallow depressions which retain water that comes onto the flat at higher high tides. The sediment in the basin is vertically layered with color bands of yellow, pink, and green. The depressions in the basin are coated with a red to purple, cartilaginous material. Both the convoluted cartilaginous layer and the sediments beneath it contain a mixture of species of blue-green algae, including Schizothrix spp. and Anacystis dimidiata (Kuetzing). A similar algal mat has been described at Raroia Atoll (Newhouse, 1954). No animals were collected from the cyanophyte basin.

Several species of shore birds frequent the upper and lower flats. A list of the birds sighted on Fanning during the expedition is given by Gordon (1970, see p. 189-190 this report).

OTHER ESTUARIES ON FANNING ATOLL (See Figs. 7 and 8)

The division of Napu Naiaroa estuary into regions is based on physical features and the regions are easily recognized in the field. Tidal and supratidal flats, inlets, and tidal "lakes" are common features on Fanning Atoll (Fig. 1), and each estuary is structured much as that described for Napu Naiaroa, although the relative extent of the regions (e.g., enclosed shore, inlet, upper and lower flat) varies. It seems reasonable to assume that differences between the regions are the result of tide-related phenomena and differences in substrate elevation. For example, the size and location relative to the estuary proper of the enclosed shore may be determined by both longshore and estuarine tidal currents. The extent of the lower flat and the form of its channels are the result of the interaction between ground slope and tidal transport of currents. The transition between the lower and upper flat occurs, and is probably determined by, the level of higher high water.

Although the distribution of physical regions is largely determined by tidal factors, biological distributions over the estuary are determined, in addition, by factors such as temperature and salinity. The biota of each physical region at different estuaries will vary because the relative degree of the three conditions responsible for enhancing variations in salinity and temperature (p. 136) differs from estuary to estuary. The following biological distributions may thus be explained in terms of the above hypothesis.

Cerithium breve shows a very scattered distribution at Fanning. It is rare at Napu Naiaroa, present on rocks in the enclosed shore at Vai Tepu, and abundant on both sides of the sand bars of the enclosed shore at Teharoa. The snails were found at several locations in the upper channels of the Vai Tepu estuary on January 6, but on January 15 they were absent at this location except for one group on some rocks in the middle of a main channel nearby.

Living specimens of Rhinoclavis asper Linn. were not found at Napu Naiaroa, although shells of this cerithiid gastropod occur there. The snail is common in the enclosed shore and on the reef flat fronting the estuary at Vai Tepu. A few individuals were also seen in the inlet of this estuary. No living Rhinoclavis were found in the expanded inlet at Puta Tutae, but empty shells do occur in the fine bottom sediments.

Table 5. Miscellaneous salinity and temperature data collected in estuaries at Fanning Atoll

Estuary	Physical Region and Date	Water Temperature (°C)	Refractive Index	Salinity[a] (‰)
Vai Tepu	Channels near center of island east of camp Aua; Jan. 6.	33.1	1.3400 to 1.3415	38.0 to 45.1
Vai Tepu	Same; Jan. 15.	34.5	1.3401 1.3402	38.5 39.0
Vai Tepu	Enclosed shore fronting camp Aua; Jan. 6.	28.8	1.3395	35.7
(Vai Tepu)	Pond separated from ocean by shingle beach and high berm; Jan. 6.	28.2	1.3394	35.2
(Vai Tepu)	Ocean water on reef flat opposite pond (entry above); Jan. 6.	27.8	1.3394	35.2
Puta Tutae	West shore of "lake"; Jan. 5	34.0	1.3340	6.5
Cable Station	Inlet; Jan. 10	27.6	1.3392	34.2

[a] Based on refractive index as interpreted using Fig. 4.

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Legends for Figures 7 and 8 on facing page.

Fig. 7. Tidal channels at Napu Naiaroa at a high tide. This view from Station 20 looking toward Station 30 shows the main channel (center, right) and the herb, Sesuvium portulacastrum, growing on the emergent inter-channel flat.

Fig. 8. The inlet of the estuary northeast of the Cable Station is a tidal creek. Forest in the background consists of Cocos nucifera, Messerschmidia argentea, and Scaevola (probably frutescens). The grass under the coconut trees (center, right) is the open-flat form of Lepturus repens.

Fig. 7.

Fig. 8.

(See facing page for legends to figures.)

Uca has a wide distribution at Napu Naiaroa, but is less abundant or rare along channels in some parts of the estuaries examined elsewhere on Fanning. Sesuvium portulacastrum shows a variable distribution, but most often occurs close to the channels or inlets. At Napu Naiaroa it is also found with Cocos and Messerschmidia on the sand bar at the estuary mouth and at Vai Tepu it occurs intermixed with the open-flat form of Lepturus repens.

The predatory gastropod, Natica robillardi Sowerby, appears to be common in the inlet and enclosed shore of the Vai Tepu estuary, but it was not collected elsewhere. A small, unidentified anemone (these are rare in the lagoon at Fanning) occurs in the expanded part of this estuary as does a swimming crab, Thalamita integra Dana.

In each estuary the daily and seasonal ranges over which physical parameters (e.g., temperature, salinity) may vary are probably not parallel. The few salinity and temperature measurements taken in estuaries on Fanning excluding Napu Naiaroa are given in Table 5. Conditions in some estuaries at Fanning may reach extremes for sufficiently long periods to exclude for a time many of the residents of the body of water. The expanded inlet or "lake" at Puta Tutae contains an enormous number of empty shells of Cerithium breve in the muddy bottom sediment. In addition, shells of Rhinoclavis, Pupa sp., Nassa serta (Bruguiére), and two species of tellinid clams are present. Many of these species are more typical of the sandy lagoon reef-flat, but transport of the empty shells to the inlet seems improbable. The salinity of the Puta Tutae inlet on January 5 was 6.5 ‰. Tilapia and a few Cardisoma were then the only inhabitants in the lake. Shells of C. breve in particular are common on Fanning in channel sediments and as drift on the flats. Local "fresh water" kills may therefore occur regularly, affecting the populations of this snail and perhaps the populations of other low salt tolerant species as well.

DISCUSSION AND CONCLUSIONS

Many of the organisms living under estuarine conditions at Fanning are widespread in the Indo-West-Pacific. Although their occurrence on atolls has often been noted (Banner and Randall, 1952; Morrison, 1954; Morton and Challis, 1969; and others), salinity values taken concomitant with the collections are seldom given in the literature and presumably are not made. Often the author may describe an area as "brackish", if there appears reason to suspect fresh-water influx. Doty and Morrison (1954) describe a series of inter-island channels on Raroia Atoll, some closed by sediments at the seaward end only, and others closed at both ends. In one of the completely closed ponds were recorded the cyanophyte mats described by Newhouse (1954), while in others occurred Cerithium breve, Neritina bensoni, a palaemonid shrimp (Palaemon debilis Dana), and mullet. The closed inlets at Raroia must be ecologically similar to the estuaries at Fanning, whereas the fauna in the Raroia inlets open at least to the lagoon resembles those at the Fanning lagoon channels at North and English Harbor passes. Lagoon-oriented inlets at Fanning tend to be estuarine, whereas, pools isolated from the ocean-side only by the coarse, shingle berm, are marine. In one such pond, separated from the ocean by a 4-meter-high shingle berm and inhabited only by Littorina coccinea Gmelin, L. undulata Gray, Nerita plicata, Assiminea nitida, Truncatella sp., and Melampus spp., the salinity was 35.2 ‰.

Brackish water influence on the distribution of lagoon organisms is probably not uncommon on most atolls with extensive island development. On many atolls the presence of "mangroves" (see Macnae, 1968; Morton and Challis, 1969) indicates regions corresponding to the estuaries at Fanning. Plant species having a mangrove life-form, however, have not been reported from Fanning Atoll.

The lagoon shore, complicated by inlets, channels, and sand spits, is a region where fresh water influx may be localized sufficiently to produce estuarine conditions. The inhabitants of areas subject to regular depressions in salinity on atolls must be euryhaline species par excellence. It is suggested that the intermittancy in the occurrence of hyposaline water (relative to the lagoon) will preclude species adapted only to brackish or fresh water (stenohaline organisms of low salinity environments). Salinities over most of the Napu Naiaroa estuary varied from hypersaline to nearly fresh water during the short period of observations. I would conclude, as does Morrison (1954, p. 5) that "Such [environments] offer a habitat in which only a few low salt tolerant species...flourish." Most of the estuary inhabitants at Fanning are either migratory forms (most of the larger fish excluding Tilapia) or high intertidal forms. The latter group of organisms is subject to fresh water inundation by rainfall on any shore. Those high intertidal and supratidal species adapted to quiet water situations, typical of lagoon shores, constitute the best candidates available for populating the estuaries on atolls.

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This work has been supported by the National Science Foundation grant, GB-15581. I would like to thank Dr. Alison Kay for identification of molluscs and for reviewing the manuscript, Dr. William A. Gosline for identification of fish, Dr. Ernie Reese for identification of terrestrial hermit crabs, and Robert DeWreede and Joaquin Villa-Gomez for identification of algae and for providing some physical data on estuaries at Fanning other than Napu Naiaroa. Dr. Don Gordon and Harold Schiesser aided in salinity and oxygen determinations and to them I am grateful. I would also like to thank Dr. Ken Roy for helpful discussion concerning the figures and physical descriptions of the estuary in the text, and for reviewing the manuscript. Text figures 1, 2, and 3 are based, in part, on aerial photographs kindly provided by K. Roy, M. Vitousek, A. Malahoff, Bob Kendall, and E. H. (Neil) Chave. Without the support and thoughtful guidance of the expedition leader, Dr. Keith Chave, this study would not have been possible, and to him I am particularly grateful.

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CRUSTACEA COLLECTED DURING THE FANNING ATOLL EXPEDITION, 1970

Eric B. Guinther
Hawaii Institute of Geophysics

WITH A LIST OF ALPHEID SHRIMP COLLECTED IN THE LINE ISLANDS

Dora M. Banner
Hawaii Institute of Marine Biology

Records of Crustacea from the Line Islands have been the subject of papers by Streets (1877), Edmondson (1923), Banner (1959), and Banner and Banner (1964). Edmondson lists the decapod and stomatopod crustacea collected during three expeditions to the Line Islands (Cooke and Rock to Palmyra in 1913; Thurston and Thaanum to Palmyra in 1922; and Edmondson and Ball to Fanning in 1922), as well as those species reported previously by Streets. Crustacea collected by the Whippoorwill Expedition to the Line Islands in 1924 were not reported in a single paper, but new records appeared in several later papers by Edmondson (1933, 1935, 1951, 1952). Several other collections made since 1923 on Palmyra, Washington, Fanning and Christmas atolls have been examined recently by Dr. John S. Garth and an updating of Edmondson's 1923 paper is forthcoming (personal communication with Dr. Garth, Allan Hancock Foundation, University of Southern California). Most of the Crustacea listed below were collected during the University of Hawaii, Fanning Atoll Expedition made in January, 1970. A few specimens were provided by Dora M. Banner from an earlier visit to the Line Islands. The species list of Alpheidae is based on specimens collected by her at Palmyra, Fanning and Washington in November 1968 and on specimens collected by E. H. (Neil) Chave at Fanning in 1970.

The 1970 collecting areas at Fanning Atoll are shown in Figure 1, and briefly described below:

Area 1 - A well-protected moat on the seaward reef. Water circulation is good and coral growth luxuriant. Maximum depth is about 1-½ meters.

Area 2 - Protected lagoon area behind the spit (Cartwright Point) just north of English Harbor. The bottom here is mostly sand with occasional pieces of dead coral. Area 2a is the lower intertidal portion of the coral shingle beach at the tip of Cartwright Point.

Area 3 - An area of living and dead coral at a depth of 1 to 2 meters along the lagoon reef north of English Harbor.

Area 4 - A lagoon reef, termed locally "Beacon 1", with luxuriant coral growth. Depth varies from 1 to 10 meters.

Area 5 - A shallow inlet off the lagoon at "Napu Naiaroa". Area described in Guinther (1970) (see pp. 135 this report).

Area 6 - The sand beach along the lagoon shore near the Cable Station pier.

Area 7 - Reef flat seaward of the Cable Station and (7a) shingle and cobble beach at the shoreline. The reef flat is covered with about 0.5 meter of water at low tide.

Area 8 - A shallow pass into the lagoon. Specimens were collected from a channel (up to 2 meters deep) and under stones intertidally. Area 8a is the lagoon side of the pass.

Area 9 - An inlet off the lagoon at "Vai Tepu" similar to area 5.

Area 10 - A portion of the seaward reef flat along the eastern coast of the atoll. Most specimens were collected near shore or from off emergent consolidated reef rock toward the outer edge of the reef flat.

Area 11 - Crabs collected at this mid-lagoon station were taken from living and dead coral material brought back to the laboratory.

Area 12 - A portion of the seaward reef flat along the western coast of the atoll (at "Greig Point") similar to area 10. Calm seas allowed collecting from under rubble in the grooves of the reef front at a depth of from 2 to 5 meters.

Area 13 - Sand beach in the vicinity of "Rapa Pass".

In the list that follows (Table 1), previous records of species from the Line Islands are given in parentheses below each species name, listing author, synonymy, and location (atoll) of the previous record. Unless otherwise indicated, references to Edmondson are to his 1923 paper. The collection data in Table 1 are presented as number of each sex collected, collection area (from Fig. 1), and maximum carapace width of specimens in centimeters. Ovigerous females are indicated by the symbol (e) following their carapace measurement.

The format of the list of "Alpheid shrimp from the Line Islands" by Dora M. Banner is similar, but size and sex of the specimens are not indicated.

Most of the material reported herein has been deposited at the Bernice P. Bishop Museum in Honolulu, and catalogue numbers (e.g., S7950) are given for such material. This work was supported by grant GB-15581 from the National Science Foundation. I would like to acknowledge E. H. (Neil) Chave, Alison Kay, Carl Berg, and Glenn Shepherd, all expedition members, who helped by providing specimens. Appreciation is also given to Dr. Dennis Devany who, as curator, provided access to the invertebrate collection of the Bernice P. Bishop Museum. I thank Dr. Ernie Reese for aid in identification of the hermit crabs.

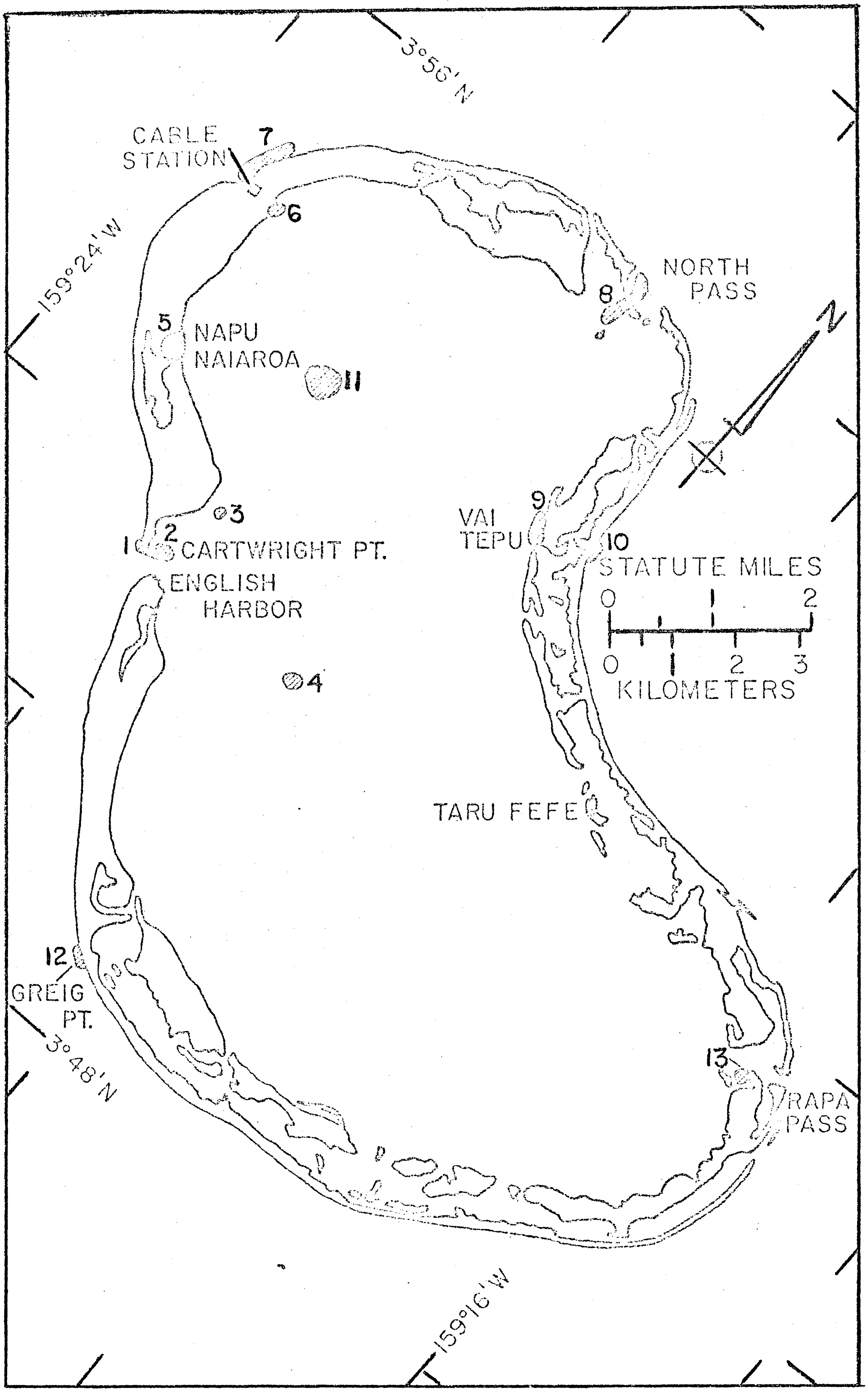

Fig. 1. 1970 collection sites at Fanning Island. Numbers refer to area descriptions in text.

Table 1. List of Crustacea collected by the University of Hawaii - Fanning Atoll Expedition, 1970[1]

FAMILY ACANTHONYCHIDAE			
Manaethius monoceros (Latr.)			
1 female	Washington Atoll at 15 meters (11/68)		S7936
FAMILY CALAPPIDAE			
Calappa hepatica spinosissima M. Edw. (Edmondson, as *C. spinosissima* from Palmyra)			
1 female	Area 2	7.78	S7890
FAMILY PORTUNIDAE			
Thalamita admete (Herbst)[2]			
3 males	Area 7	1.32, 1.28, 1.10	S7891
5 females	Area 7	1.23(e), 1.10(e), 0.92(e), 0.86(e), 0.81	S7891
1 female	Area 3	1.23(e)	S7892
Thalamita integra Dana			
1 female	Area 9	1.30	S7893
Thalamita picta Stimpson			
2 females	Area 7	1.50, 1.39(e)	S7894
FAMILY XANTHIDAE			
Carpilius convexus (Forskal)(Edmondson, from Fanning)			
1 male	Area 10	6.15	S7895
Carpilius maculatus (Linn.)(Edmondson, from Fanning)			
1 male	Area 10	7.07	S7896
Zosimus aeneus (Linn.)			
1 male	Area 1	6.56	S7897
Platypodia granulosa (Rüpp)[3]			
1 male	Area 11	1.73	S7898
Leptodius sanguineus (M. Edw)(Edmondson, from Fanning)			
1 male	Area 8	3.18	S7900
1 female	Area 1	2.47	S7899
Xanthias lamarckii (M.Edw.) M. Edw. (Edmondson, from Fanning)			
1 male	Area 7	1.62	S7901
1 female	Area 11	1.51(e)	S7901
1 male	Area 8	1.42	S7901
1 female	Area 1	1.31(e)	S7901

Paraxanthias notatus (Dana)

1 female	Area 10	1.07	S7902

Etisus electra (Herbst) Alcock (Edmondson, as *Etisodes electra* from Palmyra)

1 female	Area 11	1.47(e)	S7903
1 female	Area 3	1.06(e)	S7903
1 male	Area 11	0.82	S7903
1 male	Area 2	0.81	S7903

Etisus laevimanus Randall

1 male	Area 11	1.98	S7904

Chlorodopsis venusta Rathbun (Edmondson, as *C. scabriculus* from Fanning and Palmyra

4 males	Area 3	0.93, 0.56, 0.45, 0.26	S7905
1 male	Area 1	0.89	S7906
1 male	no data	0.87	S7907
1 male	Area 11	0.51	S7906

Chlorodopsis sp.[4]

1 male	Area 8	1.33	S7977

Chlorodiella niger (Forskal)(Edmondson, from Fanning and Palmyra)

1 female	Area 11	1.29(e)	S7908
2 females	no data	0.91, 0.68(e)	S7909
2 males	no data	1.15, 0.71	S7909

Actaea nodulosa White[5]

1 female	Washington Atoll at 15 meters (11/68)		S7975

Cymo andreossyi (Audouin) De Haan[6] (Edmondson, from Palmyra)

1 female	Area 11	1.09	S7910
2 males	Area 8	1.06, 0.80	S7910

Cymo melanodactylus De Haan (Edmondson, from Fanning and Palmyra)

2 females	Area 11	1.09(e), 0.98(e)	S7911
1 male	Area 11	1.03	S7911

Pseudozius caystrus (Adams and White) Dana (Edmondson, from Fanning and Palmyra)

1 female	Area 8	1.84	S7912
1 male	Area 2a	1.58	S7913
2 males	Area 8	0.83, 0.66	S7912

Eriphia laevimana Latreille (Edmondson, as *E. sebana* from Fanning and Palmyra)

1 female	Area 7	7.04(e)	S7914
1 female	Area 8a	3.85	S7915

Eriphia scabricula Dana (Edmondson, from Fanning and Palmyra)

1 male	Area 7	1.91	S7917
2 females	Area 10	1.38(e), 1.35(e)	S7916
1 male	Area 10	1.32	S7916

Domecia hispida Eydoux and Souleyet (Edmondson, from Palmyra)

3 females	no data	0.91, 0.81, 0.73(e)	S7918
4 males	no data	0.90, 0.80, 0.66, 0.66	S7918
1 male	Area 3	0.66	S7919

Daira perlata (Herbst) Alcock (Edmondson, from Fanning and Palmyra)

1 male	Area 12	1.91	S7920

Lybia tesselata (Latreille) (Edmondson, from Fanning and Palmyra)

1 female	Area 7	1.00(e)	S7921
1 male	Area 7	0.77	S7921
1 female	near English Harbor (10/68)	0.77	S7922

Trapezia cymodoce (Herbst) Alcock (Edmondson, from Palmyra)

1 female	near English Harbor at 20 meters (10/68)	1.33(e)	S7923
3 females	no data	0.98(e), 0.90, 0.81	S7924

Trapezia cymodoce ferruginae (Latreille)(Edmondson, from Palmyra)

2 females	Washington Atoll at 15 meters (11/68)	1.81(e), 1.26(e)	S7925
2 males	same as above	1.57, 1.44	S7925
1 male	Washington Atoll (11/68)	1.01	S7976
4 males	no data	0.91, 0.90, 0.65, 0.60	S7926
3 females	no data	0.73, 0.65(e), 0.60	S7926

Trapezia digitalis (Latreille)(Edmondson, from Palmyra)

2 females	no data	0.71, 0.59(e)	S7927
1 male	no data	0.65	S7927

Tetralia glaberrima (Herbst)(Edmondson, from Palmyra)

1 no data	near English Harbor entrance (10/68)	1.15	S7928
4 females	Areas 4 & 11	no data	S7929
6 males	Areas 4 & 11	no data	S7929

FAMILY OCYPODIAE

Ocypode ceratophthalmus (Pallas)(Edmondson, as *O. ceratophthalma* from Fanning and Palmyra)

1 male	Area 13	4.19	S7931
1 male	Area 5	3.93	S7930
2 males	Area 6	3.67, 2.07	S7932
1 male	Area 2	2.93	S7933
1 male	Area 7a	0.63	S7934

Uca tetragonon (Herbst)(Edmondson, from Palmyra)

6 males	Area 5	3.67, 3.52, 3.47, 2.62, 1.44, 1.32	S7935
1 male	mudflat 2 mi. NE of Cable Sta. (1/70)	2.91	

FAMILY GRAPSIDAE

Geograpsus grayi (M. Edw.)[7]

1 male	no data	1.60	S7937

Geograpsus stormi De Man

1 male	Area 1	2.56	S7938
1 male	Area 7a	1.72	S7939

Metopograpsus thukuhar (Owen)[8](Edmondson, as *M. messor* from Fanning)

4 males	Area 5	3.46, 1.68, 0.72, 0.58	S7940

Pachygrapsus minutus M. Edw. (Edmondson, from Fanning and Palmyra)

4 males	Area 1	1.01, 0.95, 0.84, 0.74	S7941
2 females	Area 1	0.82(e), 0.80(e)	S7941
1 male	Area 8	0.57	S7942

Cyclograpsus audouinii (M. Edw.)(Edmondson, from Fanning and Palmyra)

2 females	Area 2a	0.79, 0.74(e)	S7943

Plagusia depressa tuberculata Lam.

1 male	Area 10	2.11	S7944

Percnon abbreviatum (Dana)[9] (Edmondson, from Fanning)

1 male	Washington Atoll at 15 meters (11/68)	1.67	S7945

Percnon planissimum (Herbst) Alcock (Edmondson, from Fanning and Palmyra)

1 male	Area 7a	1.03	S7946

FAMILY GECARCINIDAE

Cardisoma carnifex (Herbst)(Edmondson, from Fanning and Palmyra)

1 female	on land at Cartwright Point (1/70)	8.25	S7948

1 female	Cable Sta. grounds (1/70)	7.48	
1 male	Cable Sta. grounds (1/70)	5.52	S7947

FAMILY PORCELLANIDAE

Petrolisthes coccineus (Owen)

1 female	Area 12	0.60(e)	S7949

Petrolisthes lamarckii (Leach)(Edmondson, as *P. speciosa* from Fanning and Palmyra)

2 males	Area 8	1.06, 0.46	S7950
5 males	Areas 1 and 2a	1.00, 0.88, 0.73 0.70, 0.56	S7950
4 females	Areas 1 and 2a	0.93(e), 0.90, 0.76(e) 0.58	S7950
1 female	Area 3	0.51(e)	S7950
1 male	Area 7	0.31	S7950

FAMILY COENOBITIDAE

Coenobita brevimanus Dana (Edmondson, from Fanning and Palmyra)

3 males	Cable Station grounds (1/70)	2.00, 1.69, 1.04	
1 female	same as above	1.28	

Coenobita perlatus M. Edw. (Edmondson, as *C. rugosa* from Fanning and Palmyra)

5 males	near Cable Sta. (1/70)	1.74, 0.59, 0.42, 0.39, 0.35	
6 females	same as above	1.55, 1.50(e), 1.38, 1.26, 0.91, 0.76	
1 no data	same as above	no data	

FAMILY PAGURIDAE

Calcinus elegans (M. Edw.) (Edmondson, from Fanning and Palmyra)

1 male	Area 1	0.79	S7951

Calcinus laevimanus (Randall) (Edmondson, as *C. herbstii* from Fanning)

2 males	Area 1	0.68, 0.51	S7952
1 female	Area 8	0.31(e)	S7953
1 male	Area 3 on *Acropora*	0.25	S7954

Calcinus latens (Randall) (Edmondson, as *C. terrae-reginae* and *C. latens* from Palmyra)

1 male	Area 8	0.33	S7955
2 females	Area 11	0.27, 0.25	S7956

Diogenes gardineri Alcock			
2 males	Area 9	0.29, 0.26	S7957
3 females	Area 11	0.24(e), 0.21, 0.21	S7958
1 male	Area 11	0.22	S7958
Dardanus deformis (M. Edw.)			
1 female	Area 7	0.44	S7959
Dardanus guttatus (Olivier)[10]			
1 female	Area 8a	0.85	S7961
Dardanus megistros (Herbst)(Edmondson, as *Pagurus punctulatus* from Palmyra)			
1 male	Area 8a	1.02	S7960

FAMILY GNATHOPHYLLIDAE

Gnathophyllum fasciolatum Stimpson (Edmondson, from Palmyra)			
1 no data	Area 8	no data	S7962

FAMILY PALAEMONIDAE

Periclimenes depressus Stimpson (Edmondson, as *Harpilius depressus* from Palmyra)			
2 no data	Washington Atoll at 15 meters (11/68)		S7963
Coralliocaris sp.			
1 no data	Area 3	no data	S7964
Conchodytes tridacnae Peters			
12 no data	Area 4 in living *Pinctada margaritifera*		S7965

FAMILY SQUILLIDAE

Gonodactylus demanii Henderson			
1 no data	Area 7	total length = 2.15 cm	S7966
Gonodactylus guerinii White			
1 no data	Area 7	no data	S7967

FOOTNOTES TO TABLE 1.

[1] Unless otherwise indicated, all specimens listed were collected at Fanning Atoll in January, 1970.

[2] Edmondson (1923) records both *Thalamita edwardsi* and *T. auauensis* from Palmyra. The specimens I am calling *T. admete* are small and not easily distinguished from *T. edwardsi* or *T. auauensis*. My specimens differ from *T. edwardsi* in having well-defined ridges on the outside of the palm of the cheliped, they differ from *T. auauensis* in lacking definite granules on the base and inside of the palm.

[3] Edmondson (1923) records *P. eydouxi* (M. Edw.) from Palmyra. His specimen differs from mine only in having the lobes of the carapace less well-defined.

[4] The antenna is not excluded from the orbit in my specimen, although the flagellum tends to lie in the notch between the front and the supra-orbital border and the basal segment of the antenna extends into the orbital hiatus. The carapace of this specimen is smooth, but microscopically granular; the regions are defined by shallow grooves and the dorsal surface is nearly glabrous except for a few scattered, plumose hairs.

[5] The B.P. Bishop Museum collection includes several specimens (B.P.B.M. S6893) identical to my *Actaea* sp. collected by L.G. Eldredge off Waikiki, Oahu at 60-80 fathoms which are labled "*Actaea* sp."

[6] Alcock (1898 - p. 174) lists several characteristics differentiating *Cymo melanodactylus* from *C. andreossyi*, the most obvious being the black fingers of *C. m.* I have used only this character in separating my *Cymo* specimens. In Edmondson's Line Islands material, as well as my Fanning specimens, the other characteristics listed by Alcock (lumpier carapace and more distinct indications of lobules on the antero-lateral border of *C. m.*) are not apparent. One of my *C. a.* specimens (area 11) has grey (instead of white) fingers.

[7] Material from Washington Atoll collected by the Whippoorwill Expedition (1924) and identified by Edmondson as *G. crinipes* (B.P.B.M. S1976) is actually *G. grayi*. Edmondson's record of *G. crinipes* from Fanning and Palmyra, however, is still valid.

[8] According to the differences stated in Edmondson (1959) distinguishing *M. messor* and *M. thukuhar*, most of Edmondson's Fanning Atoll specimens (B.P. B.M. S795) could easily be *M. thukuhar*.

[9] The depth at which this specimen is recorded as having come from seems doubtful.

[10] Specimen was living in a *Conus* shell and has a very depressed carapace.

ALPHEID SHRIMP FROM THE LINE ISLANDS

Dora M. Banner

Automate gardineri Coutière

2 Fanning, 10/27/68, near shore under rocks (area 2)

Athanas djiboutensis Coutière

2 Fanning, 10/30/68, from coral at 3 meters near English Harbor

Alpheopsis diabolus Banner

1 Fanning, 10/68, seaward reef at 7 meters near English Harbor

Synalpheus anceps Banner

1 Washington, 11/5/68, from growth on old anchor at 15 meters (coll: Heywood and Fredholm)

Synalpheus charon (Heller)

1 Fanning, 10/68, seaward reef at 7 meters near English Harbor
2 Fanning, 1/14/70, seaward moat (area 1) (coll: E. Chave) S7968

Synalpheus laticeps Coutière

2 Fanning, 10/30/68, symbiotic with sponge

Synalpheus paraneomeris Coutière

(Edmondson, from Palmyra)
(Banner, from Jarvis)
(Banner & Banner, from Christmas)
2 Fanning, 10/68, seaward reef at 7 meters near English Harbor

Synalpheus tumidomanus (Paulson)

3 Fanning, 10/30/68, from coral at 3 meters near English Harbor

Alpheus amirantei sizou Banner & Banner

4 Fanning, 10/25/68, from coral brought up from 20 meters

Alpheus clypeatus Coutière

1 Washington, 11/5/68, from growth on old anchor at 15 meters (coll: Heywood and Fredholm)

Alpheus collumianus inermis Banner

1 Palmyra, 11/13/68, from coral at 1-2 meters (coll: J. Randall and D. Banner)

Alpheus collumianus medius Banner

(Edmondson, as *Crangon collumianus* from Palmyra)
(Banner, from Jarvis)
(Banner & Banner, from Christmas)

1 Fanning, 10/68, seaward reef at 7 meters near English Harbor.
2 Fanning, 10/30/68, from coral at 3 meters near English Harbor.
2 Washington, 11/5/68, from growth on old anchor at 15 meters; (coll: Heywood and Fredholm).

Alpheus crassimanus Heller

2 Fanning, 1/70, seaward reef near Cable Station (area 7); (coll: E. Chave). S7969

7 Palmyra, 11/13/68, under rocks at low tide.

Alpheus crockeri Armstrong

1 Fanning, 10/29/68, from coral at 11 meters; (coll: J. Randall)

Alpheus funafutensis Borradaile

2 Fanning, 1/70, seaward moat (area 1) near English Harbor; (coll: E. Chave). S7970

Alpheus gracilipes Stimpson

1 Palmyra, 11/13/68, from coral at 1-2 meters; (coll: J. Randall and D. Banner).

Alpheus gracilis Heller

(Banner and Banner, from Christmas)
1 Fanning, 10/68, seaward reef at 7 meters near English Harbor.

Alpheus leviusculus Dana

4 Fanning, 1/70, seaward moat (area 1) near English Harbor; (coll: E. Chave). S7971

Alpheus lottini Guérin

(Edmondson, as *Crangon ventrosus* from Palmyra)
1 Fanning, 10/26/68, from coral at 20 meters near English Harbor.
2 Fanning, 10/68, from coral at 7 meters outside English Harbor.
2 Fanning, 10/30/68, from coral at 3 meters near English Harbor.
4 Fanning, 1/14/70, seaward moat (area 1) near English Harbor; (coll: E. Chave). S7972
8 Washington, 11/5/68, from growth on old anchor at 15 meters; (coll: Heywood and Fredholm).

Alpheus macrochirus Richters

(Edmondson, as *Crangon macrochirus* from Palmyra)
(Banner, from Washington)
(Banner & Banner, from Christmas)
2 Fanning, 10/30/68, from coral at 3 meters near English Harbor.

Alpheus obesomanus Dana
(Edmondson, as *Crangon obesomanus* from Palmyra)

7 Washington, 11/5/68, from growth on old anchor at 15 meters; (coll: Heywood and Fredholm)
5 Palmyra, 11/13/68, from coral at 1-2 meters: (coll: J. Randall and D. Banner)

Alpheus pacificus Dana

(Banner & Banner, from Christmas)

1 Fanning, 1/70, seaward moat (area 1) near English Harbor; (coll. E. Chave). S7973

3 Fanning, 1/70, seaward reef flat (area 7) near Cable Station; (coll. E. Chave). S7974

Alpheus paracrinitus Miers

(Edmondson, as *Crangon paracrinitus* from Palmyra)
(Banner & Banner, from Christmas)

2 Washington, 11/5/68, from growth on old anchor at 15 meters; (coll: Heywood and Fredholm).

1 Palmyra, 11/13/68, from coral at 1-2 meters; (coll: J. Randall and D. Banner).

Alpheus paragracilis Coutière

2 Fanning, 10/68, from coral at 7 meters outside English Harbor.

1 Fanning, 10,30/68, at 7 meters near English Harbor.

2 Fanning, 10/30/68, from coral at 3 meters near English Harbor.

Alpheus superciliaris Coutière

4 Palmyra, 11/13/68, from coral at 1-2 meters; (coll: J. Randall and D. Banner).

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FANNING ISLAND INSHORE FISHES

William A. Gosline
Department of Zoology

The objective of the fish collecting done at Fanning Island in January 1970 was strictly zoogeographic. To simplify regional comparison, fishes were taken by only one method: rotenone poisoning, and in only one zone: the seaward side of the atoll in 0 to 2 meters of water. The fishes taken from this zone indicate that the Fanning Island forms are of predominantly Marshallese type, although a number of fishes, in the Marshall Islands, some of them ubiquitous, apparently do not occur at Fanning. On the other hand a few species (*Parapercis* sp., *Dascyllus* sp., and *Pomacentrus aureus*) taken at Fanning have yet to be recorded in the Marshall Islands; they suggest a small Central Pacific element that has either become restricted to the area east of the Marshall Islands, or alternatively, has had an eastern Central Pacific origin and has not reached as far west as that island group.

On the basis of fishes from Fanning and other Central Pacific islands the hypothesis has been developed (Gosline, 1971) that the ecological condition around atolls rather than the open-water distances between them is responsible for such differences as occur in the fish faunas of islands within the Central Pacific.

The following species were taken at Fanning and are now in the University of Hawaii fish collections. The names used are those of Schultz, *et al*. (1953-1966) except for those of the moringuid (Castle, 1968), cirrhitids (Randall, 1963), acanthurids (Randall, 1955, 1956), gobies and eleotrids (identified tentatively from various sources), and of the single species of *Entomacrodus* (Springer, 1967) among the blennies.

Family Ophichthidae
    Muraenichtys gymnotus
    Leiuranus semicinctus

Family Moringuidae
    Moringua (*ferruginea*?)

Family Muraenidae
    Muraena pardalis
    Echidna nebulosa
    E. unicolor
    Gymnothorax buroensis
    G. pictus
    G. bayeri
    G. monostigmus
    G. flavimarginatus
    G. petelli
    G. gracilicaudus
    G. margaritophorus
    G. undulatus
    Anarchias leucurus
    Uropterygius tigrinus
    U. polyspilus
    U. xanthopterus

Family Belonidae
    Belone platyura

Family Hemiramphidae
    Hyporhamphus acutus

Family Syngnathidae
    Choeroichthys sculptus

Family Holocentridae
Holocentrus spinifer
H. tieroides
H. lacteoguttatus
H. microstomus
H. sammara
Myripristis adustus
M. argyromus

Family Mugilidae
Crenimugil crenilabrus

Family Kuhliidae
Kuhlia marginata

Family Apogonidae
Apogon erythrinus
A. snyderi
A. nubilus
A. robustus
A. marmoratus
Gymnapogon urospilotus

Family Serranidae
Epinephelus fasciatus
E. horridus
E. elongatus
E. spilotoceps
E. melanostigma
E. hexagonatus
E. merra
E. macrospilos
Cephalopholis argus
C. urodelus
C. leopardus

Family Grammistidae
Pseudogramma polyacantha

Family Lutjanidae
Lutjanus bohar
L. gibbus
L. monostigma
L. vaigiensis

Family Sparidae
Monotaxis grandoculis
Gnathodentex aureolineatus

Family Mullidae
Mulloidichthys samoensis
M. auriflamma
Parupeneus barberinus

Family Cirrhitidae
Paracirrhites forsteri
P. arcatus
Cirrhitichthys oxycephalus

Family Parapercidae
Parapercis (sp.?)

Family Carangidae
Trachinotus bailloni

Family Pomacentridae
Dascyllus (sp.?)
D. aruanus
Abudefduf sordidus
A. glaucus
A. dicki
A. imparipennis
Pomacentrus nigricans
P. aureus
P. coelestis

Family Labridae
Cirrhilabrus temmincki
Xyrichthys taeniourus
Cheilinus undulatus
Pseudocheilinus hexataenia
Labroides dimidiatus
Coris gaimardi
C. aygula
Thalassoma hardwickei
T. lunare
T. umbrostigma
T. amblycephalus
T. quinquevittata
Gomphosus varius
Stethojulis linearis
Halichoeres hortulanus
H. trimaculatus
H. margaritaceus

Family Scaridae
Scarus (spp.?)

Family Chaetodontidae
Centropyge flavissimus
Megaprotodon strigangulus
Chaetodon trifasciatus
C. lunula
C. ephippium
C. auriga

Family Acanthuridae
- *Ctenochaetus striatus*
- *Acanthurus triostegus*
- *A. gahhm*
- *A. lineatus*
- *A. xanthopterus*
- *A. glaucopareius*
- *Zebrasoma veliferum*

Family Eleotridae
- *Valenciennesia strigata*
- *Trimma* (near *eviotops*)
- *Eviota* (sp.?)
- *E. distogma*
- *E. prasites*
- *E. epiphanes*

Family Gobiidae
- *Gobiodon rivulatus*
- *G. quinquelineatus*
- *Paragobiodon echinocephalus*
- *P. kerri*
- *Bathygobius fuscus*
- *Fusigobius neophytus*
- *(Ctenogobius?) tongarevae*
- *Drombus tutilae*
- *Valenciennea hasselti*
- *V. sclateri*

Family Blenniidae
- *Cirripectes variolosus*
- *C. sebae*
- *Entomacrodus striatus*
- *Rhabdoblennius* (sp.?)
- *Istiblennius afilinuchalis*
- *I. lineatus*
- *I. edentulus*
- *I. paulus*

Family Tripterygiidae
- *Tripterygion hemimelas*
- *T. minutus*

Family Brotulidae
- *Dinematichthys* (sp.?)

Family Callionymidae
- *Synchiropus laddi*

Family Scorpaenidae
- *Pterois antennata*
- *Sebastapistes albobrunnea*
- *Scorpaenodes guamensis*
- *Scorpaenopsis gibbosa*

Family Caracanthidae
- *Caracanthus maculatus*

Family Balistidae
- *Rhinecanthus aculeatus*
- *R. rectangulus*
- *Balistapus undulatus*

Family Tetraodontidae
- *Arothron meleagris*

Family Antennariidae
- *Antennarius altipinnis*

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THE SHARK FAUNA AT FANNING ISLAND

Richard C. Wass

Department of Zoology

INTRODUCTION

The objectives of my study were to identify the inshore sharks commonly occurring at Fanning Island and to determine their relative abundance. A further objective was to collect data on *Carcharhinus menisorrah* for my Ph.D. dissertation.

A brief literature survey revealed no published records on inshore sharks of the Line Islands.

METHODS

Most of the sharks were captured on a setline consisting of a mainline of 3/8-inch polypropylene which was buoyed and anchored at both ends. Fifteen droppers, consisting of a short length of polyporpylene line, a swivel, a length of galvanized steel leader, and a 14/0 or 4/0 hook, were attached at 10-fm intervals along the mainline. This line was set in the late afternoon and hauled the following morning. The hooks were baited with fish.

Handlines were also used for catching sharks. In conjunction with handlining, fish were chopped very finely and scattered around the boat and down the current to attract sharks.

The following data were taken for each specimen captured: Species, total length, pre-caudal length (distance from tip of snout to the pre-caudal pit at the origin of the caudal fin,) weight, stomach contents, sex, clasper length and whether or not they were calcified--if the individual was a male--or uterus breadth--if the individual was a female--and sizes and number of young, if the individual was a pregnant female.

In addition to sharks actually captured, records were kept of all sharks observed while diving or wading.

RESULTS AND DISCUSSION

Eight *Carcharhinus melanopterus*, five *Carcharhinus menisorrah*, and one *Negaprion acutidens* were captured. The data from these specimens appear in Table 1.

Carcharhinus melanopterus, the reef blacktip, was the most common inshore shark at Fanning. It occurs throughout the shallow waters of the lagoon and on the seaward side of the island to a depth of at least 30 m. It appears to be most abundant on the seaward reef flat, often occurring at depths of less than 0.5 m.

Carcharhinus menisorrah, the gray reef shark, was the most common shark in the deeper water (greater than 10 m) outside the lagoon. No individuals of this species were captured or observed inside the lagoon or in English Harbor Channel where depths are generally less than 10 m.

One *Negaprion acutidens* was captured inside the lagoon at a depth of 12 m about 1 km from English Harbor Channel. In addition, two of these sharks were observed while diving outside the lagoon at a depth of 6-16 m.

Also observed while diving outside the lagoon at depths of 6-16 m were two hammerhead sharks (*Sphyrna*), approximately 180 cm total length, and one "Gray" shark (*Carcharhinus*), about 200 cm long.

With one exception, the shark fauna of Fanning Island appears to be similar to that observed at Eniwetok, Marshall Islands, which is the "typical" fauna of the oceanic islands in the west-central, tropical Pacific. However, *Triaenodon obesus*, the reef whitetip, was not seen. Quite likely, it is present at Fanning, but in low numbers. Certainly, *T. obesus* is less common at Fanning than in the Marshall Islands or at Johnston Island.

Table 1. Sharks caught at Fanning Island from Jan. 12 - Jan. 17, 1970.

Specimen Number	Species	Total length (cm)	Pre-caudal length (cm)	Weight (kg)	Sex	Clasper length (mm)	Clasper calcified/not	Uterus breadth (mm)	Total length (mm) and sex of embryos
01	<u>Carcharhinus</u> <u>melanopterus</u>	93	71	5.0	M	37	not		
02	<u>Carcharhinus</u> <u>melanopterus</u>	80	62	3.2	M	27	not		
03	<u>Carcharhinus</u> <u>melanopterus</u>	?	89	11.3	F			14	
04	<u>Carcharhinus</u> <u>melanopterus</u>	*							
05	<u>Carcharhinus</u> <u>melanopterus</u>	111	84	9.1	M	127	Calcified		
06	<u>Negaprion</u> <u>acutidens</u>	220	172	?	F				590 M, 593 M, 599 F, 602 M, 606 F, 601 M, 620 F, 626 M, 610 F
07	<u>Carcharhinus</u> <u>melanopterus</u>	146	115	29.5	F				482 M, 474 F, 472 M, 474 M
08	<u>Carcharhinus</u> <u>melanopterus</u>	*							
09	<u>Carcharhinus</u> <u>menisorrah</u>	100	76	5.9	F			02	
10	<u>Carcharhinus</u> <u>menisorrah</u>	77	59	2.7	F			02	
11	<u>Carcharhinus</u> <u>menisorrah</u>	*							
12	<u>Carcharhinus</u> <u>menisorrah</u>	93	69	5.0	F			02	
13	<u>Carcharhinus</u> <u>menisorrah</u>	107	80	8.6	F			03	
14	<u>Carcharhinus</u> <u>melanopterus</u>	140	110	21.3	F				471 F, 491 M, 481 F, 479 M

* Only the head was on the hook, sharks had eaten the rest of the body.

FEEDING BEHAVIOR OF THE MORAY EEL, *Gymnothorax pictus*

E. H. (Neil) Chave
Department of Zoology
Helen A. Randall
Bernice P. Bishop Museum, Honolulu, Hawaii

Moray eels of the genus *Gymnothorax* have been described as being nocturnal (Hiatt and Strasburg, 1960; Starck and Davis, 1966; and others). However, as least one shallow-water Indo-Pacific species, *Gymnothorax pictus*, habitually swims in exposed locations on the reef flat searching for food during the day. Hobson (1968) reports that *G. castaneus*, an Eastern Pacific form, also makes frequent diurnal forays away from cover. During the day, other *Gymnothorax* species often stick their heads out of holes, but little else is seen of them unless dead animals are in the water.

Only a few species are known to come out of their holes in search of living, apparently healthy, food items. *G. castaneus* not only swims over open-bottom some distance from cover, but in one exceptional incident was observed in midwater snapping at a school of larval fish (Hobson, 1968). Hobson and Chave (pers. obs.) have repeatedly seen *G. petelli* in the open at night. On three occasions this species was seen chasing small portunid crabs across underwater sand patches. *G. pictus*, however, not only leaves cover but was observed jumping out of the water after grapsid crabs and leaving the water to capture prey on the beach.

Gymnothorax pictus is widely distributed in the Indo-Pacific region from East Africa to the archipelagoes of eastern Oceania (Harry, 1953; Randall, 1955; Schultz, *et al*. 1953; Weber and de Beaufort, 1916; and Smith, 1949). It is known to inhabit very shallow water. In the Marshall and Mariana Islands, Schultz *et al*. (1953) stated, "It is the one most frequently encountered at low tide cruising around on the reef out of water or nearly so, along the margin of water at high tide, and in pools left at low tide." In the Gilbert Islands it frequently occurs under exposed rocks on the outer reef flat, and the Gilbertese natives take advantage of this fact in hunting it for food (Randall, 1955). Harry (1953) and Hiatt and Strasburg (1960) give similar reports.

Our observations on this moray eel were made at Fanning and Palmyra in the Line Islands where the species is abundant on the seaward reef flats. It occurs under ledges in tidepools or under coral boulders in potholes on the landward sections of reefs exposed at low tide. At night, and on days when there are very low tides, inactive morays occur in these holes singly or in groups. The eels in six tidepools on the seaward reef close to the beach near the Cable Station at Fanning Island were observed for a total of eight hours. Four of these pools contained more than one individual. As the tide rose, the eels often left the pool in groups and swam across the reef flat, most frequently toward the shore. Usually they circumnavigated the dry spots of the reef; however, when they were chasing something or were being chased, they often wriggled over the dry places. About 50 m was the farthest that we saw an eel away from one of the six pools from which it had emerged. When this particular eel was chased it swam rapidly to the pool and hid beneath a ledge. A minute later it extended its head into view, but on seeing its pursuer it opened its mouth and withdrew slightly. It left the pool ten minutes later and again began swimming about the reef flat.

We chased other eels that were in the shallows away from their pools, and most returned to these pools. Table 1 summarizes the observations of G. pictus in the six tidepools. We do not know whether all of the eels return to particular pools on successive days, but we did observe one eel with distinctive markings leaving and entering the same 10.9 m^2 tidepool each day for five days. We also noted that the eels returned directly to their pools when chased, even though this often meant excursions from the water. Distinctive topographical features on the reef may serve as cues for the location of the pools. Perhaps the sun is also used.

Hiatt and Strasburg (1960) examined the stomach contents of six specimens, 400 to 725 mm long from Arno and Eniwetok. Of the four which contained food, three had eaten fishes and two contained the fragments of small crabs. Backus (1964) briefly mentioned intense predation by moray eels pursuing grapsoid crabs over exposed reefs at Fanning Island. Undoubtly the species he saw was G. pictus. In a popular article, drawing in part on our data, J. Randall (1969) wrote that G. pictus feeds primarily on crabs and comes at least partly out of water in quest of grapsids.

We examined the stomach and gut contents of 33 specimens of G. pictus from the Line Islands and other islands of Oceania. Those in the latter catagory were obtained from the fish collections of the Bishop Museum and the University of Hawaii. Freshly ingested fishes removed from the stomachs of morays collected with rotenone were not included. Table 2 presents the alimentary tract contents of the 16 eels which contained food. Crabs constitute the most important item of diet.

Gymnothorax pictus is readily distinguished from other muraenids by its dentition (Schultz, 1943, 1953; Weber and de Beaufort, 1916). Its teeth are relatively short for the genus, and there are no long depressible fangs on the intermaxillary plate. The relatively short canine teeth of G. pictus compared to other species of Gymnothorax would seem better adapted for feeding on crabs. As pointed out by Randall (1967), an eel with long needle-like teeth would have difficulty rending a large crustacean into ingestible pieces.

G. pictus obtains food in three distinct ways. We estimate that about 90% of the eel's hunting time is spent beneath the surface searching under rocks and ledges on the reef flat. The common occurrence of wholly aquatic xanthid crabs in the stomach and gut contents confirms the preponderance of submerged feeding. We saw G. pictus searching for food along the beach at high tide. When waves receded, they were often completely exposed (Fig. 1). We observed eels feeding on a dead fish, two unidentified hermit

Table 1. Observations on movements of *Gymnothorax pictus* to and from tidepools at Fanning Island

Pool Bottom area (m^2)	Number of individuals first observed	Number seen leaving in a group	Number returning when chased	Number seen in pool on succeeding days
10.9	5	2-3	3	2-5
11.7	3	2-3	2	3
3.8	2	1-2	0	0
4.0	2	2	2	2
1.5	1	1	0	2
3.2	1	1	0	0

Table 2. Analysis of the Stomach and Gut Contents of Sixteen Specimens of _Gymnothorax_ _pictus_ from Islands of Oceania

Island	Specimen Length (mm)	Stomach and Gut Contents
Fanning	521	Grapsid crab chelae and carapace (11 mm)
Palmyra	552*	Crab remains
Palmyra	510	Crab remains
Palmyra	431*	Crab remains
Palmyra	418	Crustacean remains
Palmyra	400	Calappid crab remains, xanthid crab chelae, and unidentified small crab (8 mm)
Palmyra	352	Crab remains
Palmyra	200	Two crab legs
Penrhyn	457	Late postlarval _Chaetodon_ sp. (16 mm SL)
Penrhyn	271	Two crab chelae and one crab leg
Makatea	560	Two partially digested fishes; one 55 mm SL, the other a prejuvenile of _Adioryx_ sp. (52 mm SL)
Makatea	417*	Xanthid crab chelae, hermit crab thorax and chelae, and fish bones
Makatea	390	Two xanthid crabs (9 and 10 mm carapace)
Makatea	365	Well-digested fish and crab remains
Wake	354	Terminal end of third maxilliped of spiny lobster (_Panulirus_ sp.) (8 mm)
Marcus	830	Fish vertebrae and eye lens

* Gravid females; those from Palmyra were collected in November and those from Makatea in March. In addition two (405 and 423 mm) more eels from Makatea were gravid among those with empty stomachs.

Fig. 1. Gymnothorax pictus searching for food at high tide at Fanning Island.

crabs, and one ghost crab (Ocypode) on the beach at Fanning. The third and most dramatic, of the three feeding behaviors involves leaping from the water to capture grapsid crabs. The crabs run up and down exposed rocks as the waves wash in and out. When the grapsids move, the eels head toward the rocks and circle them. They leap at the crabs with jaws snapping and fall back into the water, with or without their prey. One was seen in a vertical jump with its entire body out of water. Seven eels were observed at Fanning and one at Palmyra attempting to capture grapsids in this fashion. Three of the Fanning eels were successful after an average of six leaps. After eight to 13 jumps without catching crabs, the four unsuccessful eels swam away.

The importance of olfaction in feeding by morays has been stressed by Bardach et al. (1959) who demonstrated that blinded eels readily found a food source in an experimental tank. However, vision clearly plays a major role in feeding by G. pictus, because the eels are first attracted by movement of the crabs on exposed reef. A stick that was moved back and forth on a rock out of water was approached by two out of six eels in the vicinity. The two eels circled the rock once and departed. A comparison was made of the eye of G. pictus to that of seven other species of Gymnothorax which are not believed to normally leave the water. No differences could be noted in the shape of the cornea or lens. Species of Gymnothorax have a slightly flattened lens compared to that of Conger, Myrichthys, and Anguilla.

Olfaction is also important in feeding by Gymnothorax pictus. A stick moved quickly in the water in the vicinity of six eels resulted in an approach by four of them, but no contact was made. When the stick was soaked in the extract of either a fish or a crab, however, it was seized and carried beneath an overhang in a tidepool.

More than one individual of G. pictus may feed on a single large item of food. A land crab (Cardisoma carnifex) introduced into a tidepool was grabbed by one of a pair of eels in the pool and dragged under a ledge. The second eel followed and both tore the crab apart. An eel which caught a grapsid crab at the edge of a tidepool and dragged it around a rock to a crevice was joined in consuming the crab by another G. pictus which emerged from the crevice.

G. pictus is not the only muraenid known to leave the water during the day in search of food. Hiatt and Strasburg (1960) observed an unidentified moray (but probably not pictus) come out of a pool in Hawaii, slither up a rock edge, catch a lined shore crab (Grapsus grapsus tenuicrustatus), and fall back into the water. Randall (1967) reported the remains of the ghost crab (Ocypode albicans) from the intestine of a 900-mm green moray (Gymnothorax funebris) taken in the West Indies near the shore in early morning hours. The largely terrestrial habits of this crab may have required the eel to leave the water in making the capture.

On dark nights G. pictus is not active. It is clearly a diurnal animal. In fact, our observations, and those of Hobson (pers. comm.) suggest that a number of other morays will be found to be primarily diurnal.

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NOTE ON GROWTH OF *Pocillopora ligulata*

K.J. Roy and S.V. Smith

Department of Oceanography and Hawaii Institute of Geophysics

INTRODUCTION

Estimates of coral growth rates under natural conditions are necessary to calculate rates of $CaCO_3$ production by reefs. One way of determining a minimum growth rate is to measure growth on a surface with a known history. This method was used at Fanning Island where there was an LCM boat that had been in the lagoon for 2.5 years.

The history of the LCM hull is complex. The boat was towed from Hawaii to Fanning in June 1967. The boat had been in dry dock before leaving Hawaii, and the hull was clean of coral when it arrived at Fanning. After arrival, the boat was beached in the cove behind Cartwright Point. The bow was on the beach while the stern was in about 2.5 m of water (the boat has a draught of about 1.5 m). In January 1969 an anchorage was established for the boat about 150 m from shore, in 4 m of water, in the center of the cove. The water near the beach and at the anchoring site is similar to the average turbid lagoon waters discussed in Smith, *et al*. (1971).

In the two weeks prior to sampling, the boat was used to unload the R/V MAHI. Five round-trips were made to the open sea outside English Harbor. Some coral may have been dislodged during these operations. However no scars or dead corals were noticed on the hull when the sampling was done about 10 days after the last trip.

METHOD

All the coral was scraped from a 6-square-meter area on the hull (forward from the stern 6 meters, and down from the water line 1 meter). Sixty-one specimens of coral were collected from the 6-square-meter area. In addition, 48 specimens were collected from elsewhere on the hull. The only coral species present was *Pocillopora ligulata* (identification by J.E. Maragos). Other calcareous organisms present on the hull were oysters, pelecypods, and vermiform gastropods. About 5 percent of the hull was covered by encrusting calcareous organisms.

The material collected from the 6-square-meter area was weighed. Measurements were made of the height, weight, length, and width of individual corals. (Length was taken to be the maximum diameter; width, the longest dimension perpendicular to the maximum diameter. The colonies vary from circular to elliptical in plan view.) Measurements were made only on specimens that were unbroken, or had what appeared to be not more than 10 percent of the specimen missing. Twenty-nine specimens, selected to cover the size range of all specimens, were soaked in fresh water for two days, after this time the wet weight of individuals and the volume of water displaced by their skeletons were determined.

$CaCO_3$ production

The relation between height and length is shown in Figure 1, and that between height and weight in Figure 2. The frequency distribution of length of coral colonies (Fig. 3) includes only the corals from the 6-square -meter area. The frequency distribution is unimodal with a strong mode at about 3.5 cm.

If it is assumed that the largest colony started when the boat was brought to the lagoon, then that colony is 2.5 years old (started June 1967). Assuming that January 1970 is represented by zero size, and that length increase is linear with time, Time Scale 1 on Figure 1 can be devised. Time Scale 2 (Fig. 3) assumes that weight increase is linear with time. Neither assumption is likely to be true, but over the short period of time that is being considered, the assumptions are probably not far wrong. In both cases, the modal-sized coral apparently settled sometime after January 1969 (the time at which the boat was moved off the beach). It is also possible that corals had settled earlier, but had not grown very much. It seems more likely however, that there was no significant settlement or any significant survival of corals on the hull before the boat was moved. The nearshore environment all around the lagoon appears to be unfavorable for coral growth. Coral abundance is generally very low near the shore, probably due to sand movement, increased water temperature, or extreme turbidity.

Because of the low coral coverage (Table 1), the production rate of $CaCO_3$ per unit area sampled is low. Therefore, to get a more useful number, the area actually covered by coral was used.

One of the problems in the production calculations is the uncertainty of how long the corals have been growing; whether 2.5 years (from the time the boat was beached) or 1 year (from the time the boat was anchored in lagoon). Using a 2.5-year period, the production rate of the corals per unit area of coral cover is computed as 4,500 $(gCaCO_3/m^2)/yr$ (Table 1). Using the heaviest coral, the rate is 7,600 $(gCaCO_3/m^2)/yr$. Using 2.5 years and the projected area of the specimen, the rate is 5,700 $(gCaCO_3/m^2)/yr$ for the longest coral. Using 1 year as the growth period, and the weight of corals that are less than 49 mm long (about modal size (Fig. 3)), the rate is 8,300 $(gCaCO_3/m^2)/yr$.

These production estimates are conservative, since about 25 percent of the coral on the hull was not collected, and since the area used in the calculations was the area of the hull covered by the corals collected. Because the area would increase as the corals grew, a more representative number for calculation of production per unit area might be one-half the area covered by coral. These considerations suggest that a reasonable rate for production of $CaCO_3$ by *P. ligulata* is 1.6×10^4 $(g/m^2)/yr$. A production rate of 2×10^4 $(gCaCO_3/m^2)/yr$ is at the low end of the range of production values given for *Pocillopora* by Chave, *et al.* (1970).

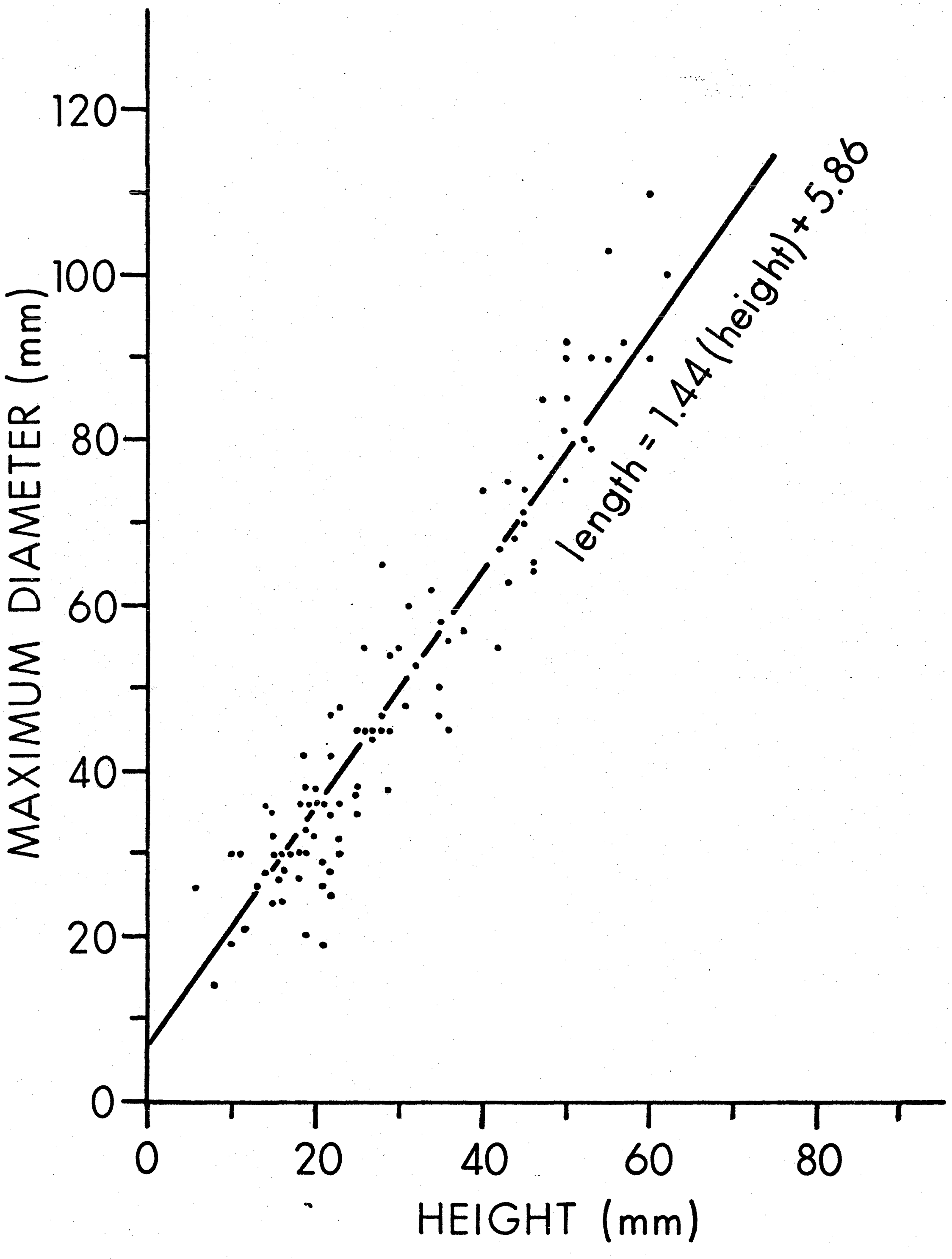

Fig. 1. The relation between colony length and colony height. Measurements from 88 specimens were used. The line is the least-squares regression of length on height.

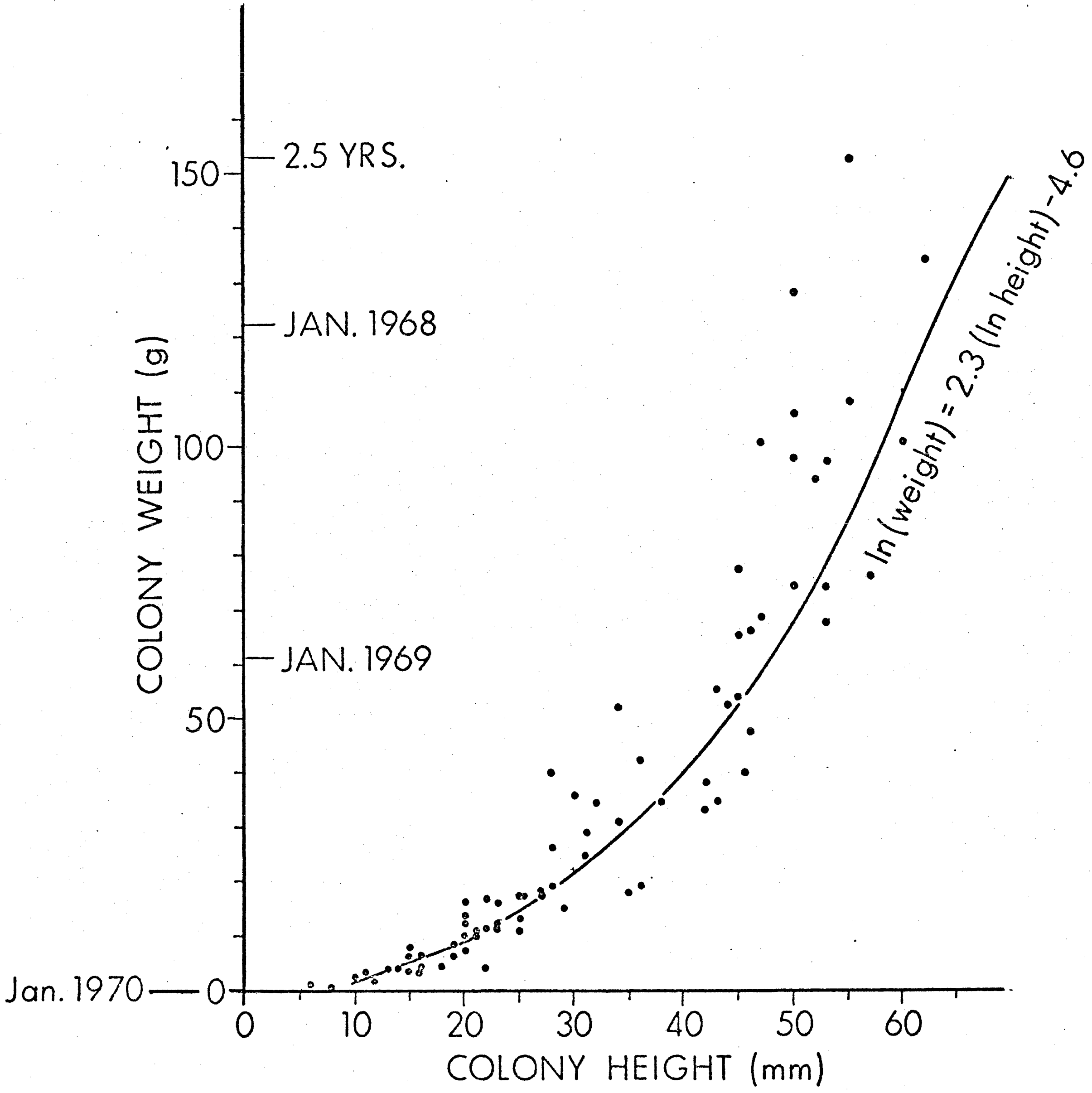

Fig. 2. The relationship between colony weight and colony height. Measurements from 88 specimens were used. The line is a least-squares regression of ln (weight) on ln (height).

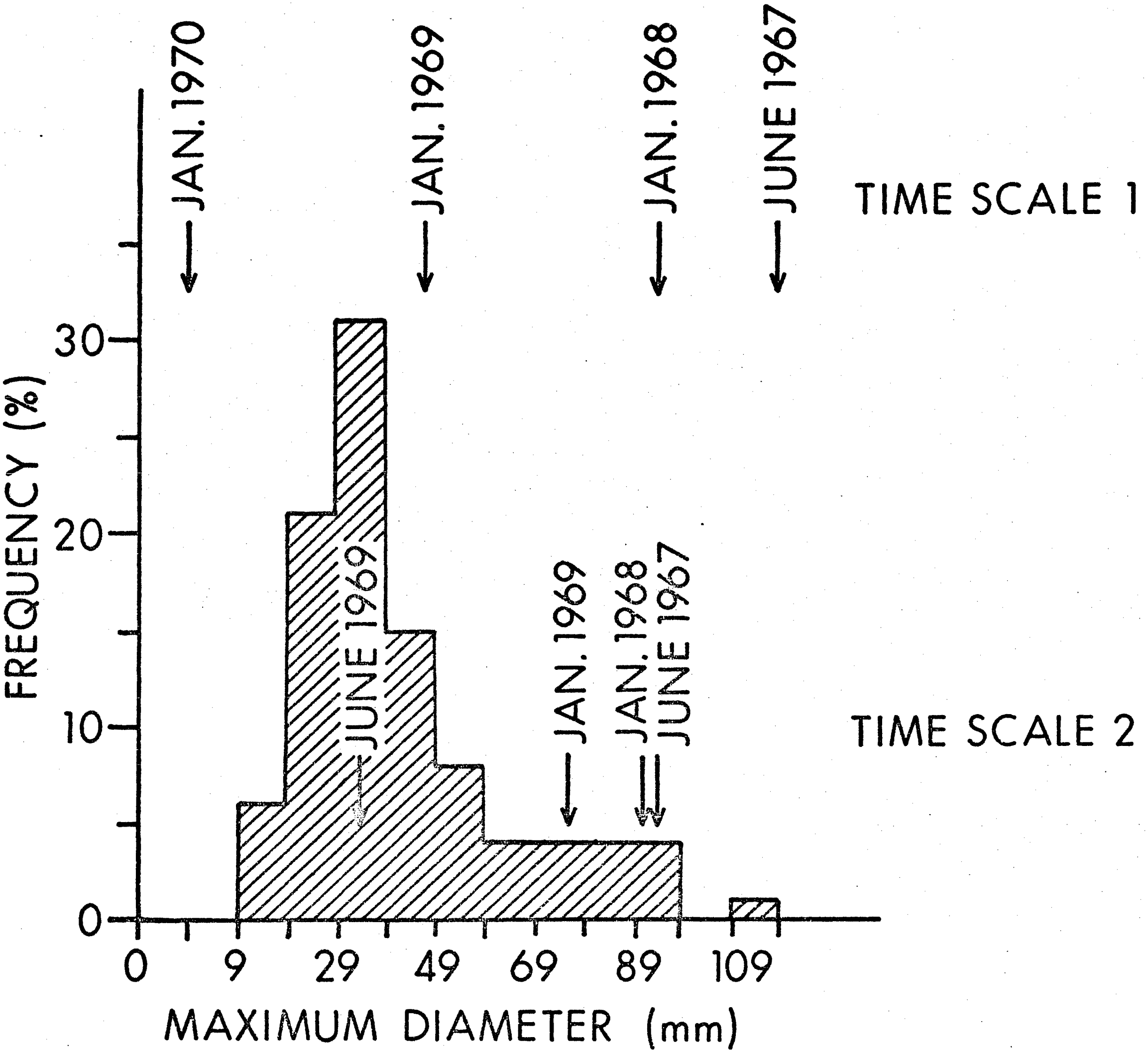

Fig. 3. The frequency distribution of the length measurements from specimens. The time scales refer to age of various-sized specimens. Time scale 1 assumes linear length increase with time. Time scale 2 assumes linear weight increase with time.

Table 1. Calculations of $CaCO_3$ production rates

	Total Collection	Total Collection	Heaviest Coral	Longest Coral	Corals in Collection less than 49 mm long
weight (g)	1267.3	1267.3	153.2	118.2	277.6
area covered (m^2)	6[a]	0.11[b]	0.0081[b]	0.011[b]	0.033[b]
time (yr)	2.5	2.5	2.5	2.5	1[c]
production [(g/m^2)/yr]	120	4500	7600	5700	8300

[a] Total area sampled.

[b] Area covered by coral.

[c] Assuming that the corals in the modal size have grown for less than one year.

Table 2. (a) Data on 29 water-soaked specimens of P. ligulata.
1. - dry weight; 2. - wet weight; 3. - volume; 4. - height; 5. - length; 6. - width; 7. - wet weight-dry weight; 8. - length x height x width. (See text for explanation of length and width.) These same parameters are listed in (a) through (d) of Table 2.

(a)

	1.	2.	3.	4.	5.	6.	7.	8.
1	72.900	83.200	52.000	5.100	8.200	7.000	10.300	292.740
2	133.200	153.200	99.000	6.000	10.700	10.000	20.000	642.000
3	95.700	107.600	68.000	5.000	9.500	7.500	11.900	356.250
4	89.400	102.100	68.000	5.000	8.200	7.800	12.700	319.800
5	102.700	120.200	84.000	5.300	9.000	8.000	17.500	381.600
6	125.300	139.800	85.000	4.500	9.600	8.800	14.500	380.160
7	97.900	109.400	82.000	5.400	9.000	8.200	11.500	398.520
8	54.700	64.300	53.000	4.400	7.500	7.500	9.600	247.500
9	64.300	77.100	56.000	5.700	7.000	6.000	12.800	239.400
10	75.200	87.200	63.000	4.500	7.000	6.500	12.000	204.750
11	63.500	72.000	45.000	4.500	7.500	5.800	8.500	195.750
12	51.300	59.000	35.000	3.100	6.500	6.000	7.700	120.900
13	51.100	60.400	51.000	4.900	6.900	6.900	9.300	233.289
14	34.600	41.500	26.000	3.800	5.700	5.600	6.900	121.296
15	34.500	41.700	46.000	4.400	6.400	5.400	7.200	152.064
16	41.400	47.300	32.000	3.700	5.200	4.700	5.900	90.428
17	35.500	43.400	34.000	3.300	5.900	5.000	7.900	97.350
18	34.100	40.100	34.000	3.200	5.300	4.100	6.000	69.536
19	16.700	20.600	21.000	2.400	4.600	4.000	3.900	44.160
20	25.800	30.700	31.000	3.000	4.500	3.700	4.900	49.950
21	18.400	22.700	30.000	2.700	4.300	3.700	4.300	42.957
22	17.500	21.200	32.000	3.200	4.700	3.500	3.700	52.640
23	19.200	23.600	30.000	3.300	4.000	3.400	4.400	44.880
24	11.800	14.800	28.000	2.100	3.200	2.700	3.000	18.144
25	16.200	19.400	28.000	2.300	3.700	3.700	3.200	31.487
26	12.800	15.400	23.000	2.500	3.600	2.700	2.600	24.300
27	11.600	14.500	21.000	2.200	3.300	3.000	2.900	21.780
28	10.800	13.100	20.000	2.000	3.500	3.000	2.300	21.000
29	12.000	14.700	22.000	2.200	3.700	3.300	2.700	26.862

Table 2. (Continued.)

(b)

Mean and standard deviation of parameters 1 to 8

	MEAN	ST. DEV.
1.	49.314	36.359
2.	57.248	40.890
3.	44.793	22.451
4.	3.783	1.224
5.	6.145	2.186
6.	5.431	2.069
7.	7.934	4.707
8.	169.705	156.251

(c)

Simple linear correlation coefficient matrix

	1.	2.	3.	4.	5.	6.	7.	8.
1.	1.000							
2.	0.999	1.000						
3.	0.968	0.970	1.000					
4.	0.868	0.876	0.877	1.000				
5.	0.968	0.969	0.936	0.915	1.000			
6.	0.956	0.958	0.932	0.897	0.977	1.000		
7.	0.958	0.967	0.953	0.906	0.943	0.944	1.000	
8.	0.962	0.965	0.964	0.894	0.958	0.958	0.951	1.000

Table 2. (Continued.)

(d)

Slope and intercept values for simple linear regression equations relating all combinations of parameters

INDEPENDENT	DEPENDENT	SLOPE	Y INTERCEPT
1	1	1.000	0.0
1	2	1.124	1.819
1	3	0.598	15.317
1	4	0.029	2.342
1	5	0.058	3.276
1	6	0.054	2.749
1	7	0.124	1.819
1	8	4.134	-34.148
2	1	0.889	-1.563
2	2	1.000	0.0
2	3	0.533	14.289
2	4	0.026	2.282
2	5	0.052	3.179
2	6	0.048	2.655
2	7	0.111	1.563
2	8	3.687	-41.360
3	1	1.568	-20.911
3	2	1.768	-21.926
3	3	1.000	0.0
3	4	0.048	1.642
3	5	0.091	2.061
3	6	0.086	1.584

Table 2. (Continued.)

(d) (Continued.)

3	7	0.200	-1.015
3	8	6.706	-130.678
4	1	25.778	-48.197
4	2	29.264	-53.451
4	3	16.079	-16.031
4	4	1.000	0.0
4	5	1.634	-0.038
4	6	1.517	-0.306
4	7	3.486	-5.253
4	8	114.078	-261.823
5	1	16.092	-49.570
5	2	18.124	-54.119
5	3	9.613	-14.278
5	4	0.512	0.635
5	5	1.000	0.0
5	6	0.925	-0.251
5	7	2.031	-4.548
5	8	68.435	-250.814
6	1	16.788	-41.865
6	2	18.936	-45.593
6	3	10.110	-10.113
6	4	0.530	0.902
6	5	1.032	0.539
6	6	1.000	0.0
6	7	2.147	-3.728

Table 2. (Continued.)

(d) (Continued.)

6	8	72.305	-222.986
7	1	7.398	-9.386
7	2	8.398	-9.386
7	3	4.545	8.734
7	4	0.236	1.913
7	5	0.438	2.668
7	6	0.415	2.139
7	7	1.000	0.0
7	8	31.573	-80.808
8	1	0.224	11.327
8	2	0.252	14.399
8	3	0.138	21.298
8	4	0.007	2.595
8	5	0.013	3.871
8	6	0.013	3.279
8	7	0.029	3.071

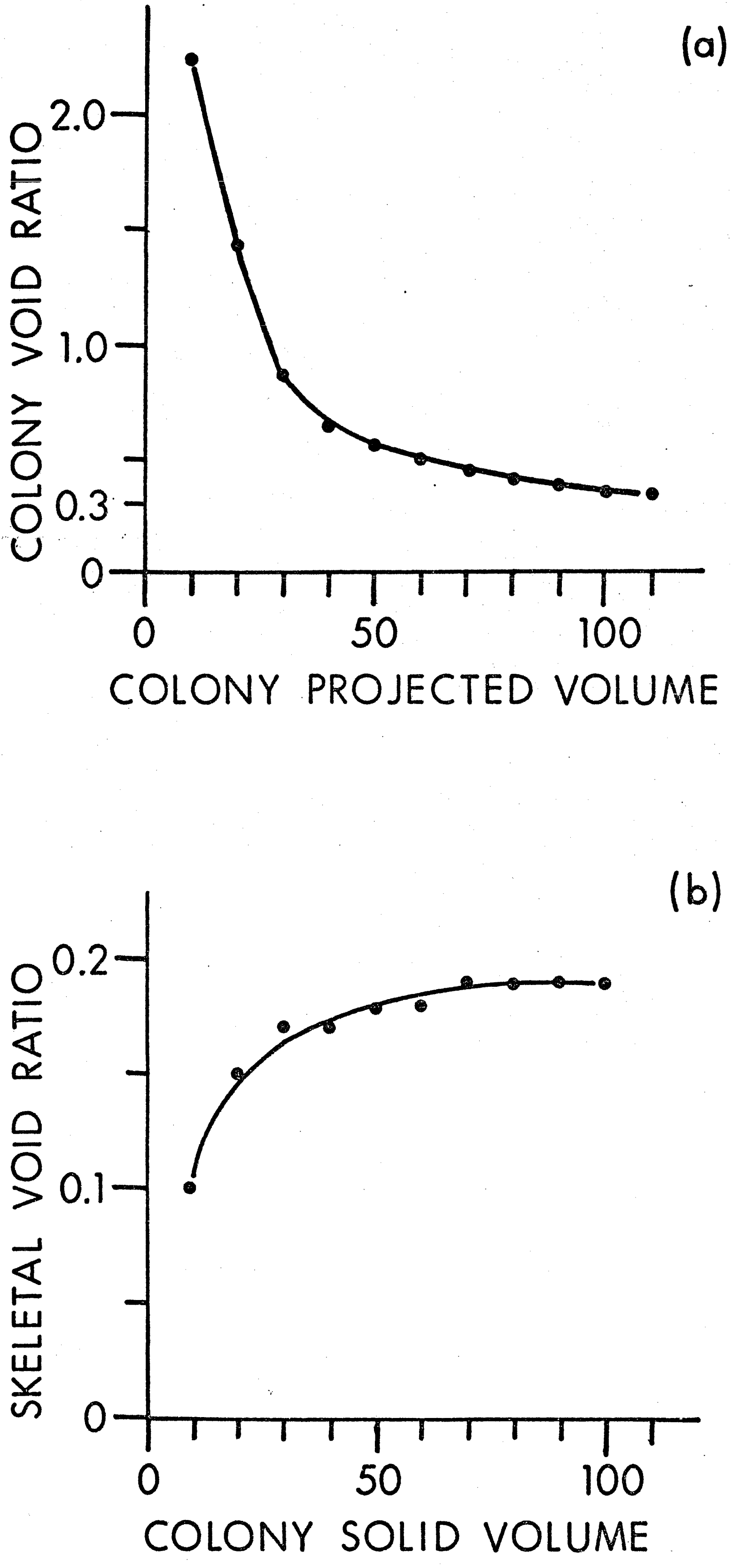

Fig. 4. (a) Relationship between the colony void ratio and total colony volume (length x width x height). (b) Relationship between void ratio in the skeleton and volume of the skeleton.

Dimensional relations of P. ligulata

Twenty-nine specimens were selected to cover the entire range of size and weight of corals in the collection. Dry weight, length, height, and width of the specimens were measured. Then the specimens were soaked in fresh water for two days and the wet weight and the volume displaced by the colony were measured (Table 2a). Simple linear correlation and regression coefficients were calculated for all pairs of parameters (Table 2b, 2c).

For P. ligulata, 83 percent or more ($100r^2$) of the variance of all parameters is accounted for by using the length as a predictor (Table 2c). The regression coefficients with length as the independent variable are starred in Table 2d.

The density of the coral skeletons, as obtained from the regression equations relating weight and volume, is 1.6 g/cm^3. The density of aragonite, the skeletal material of the coral, is 2.95 g/cm^3. Thus the porosity of the skeleton is about 45 percent.

The effective skeletal porosity (Pse), that porosity which is permeated by water during a 2-day soaking period, can be calculated from:

$$Pse = (P7/P3) \times \rho_{H_2O} = 0.2 - (1.02/P3).$$

P3 is the volume displaced and P7 is the difference between the wet and dry weight of the colony. The equation is related to the regression equation ($P7 = (-1.02 \times P3) + 0.2$) given in Table 2d. The relation of Pse to the colony volume is shown in Figure 4b. The porosity increases to a maximum of about 20 percent as the colony volume increases. A porosity of 20 percent corresponds to a density of 2.4 g/cm^3. Therefore, with the methods used, 25 percent of the skeletal porosity is not effective, i.e., blind holes.

If it is assumed that length times width times height represents the projected volume of the coral colony, the colony porosity (Pc) can be calculated from:

$$Pc = (1 - P3/P8) = 1 - 0.14 - (21.3 \times P8).$$

This equation is related to the regression equation ($P3 = (0.14 \times P8) + 21.3$). The relation between Pc and the colony projected volume is shown in Figure 4a. Pc decreases to a minimum of about 30 percent as the colony volume increases. Thus about 30 percent of solid reef rock composed of P. ligulata must be infilling material from an external source.

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BIRDS OBSERVED AT FANNING ISLAND, JANUARY 1970

Donald C. Gordon, Jr.

Department of Oceanography and Hawaii Institute of Geophysics

The following is a list of the bird species observed at Fanning Island during January 1970. Most of the observations were made in the vicinity of North Pass, the Cable Station, Cartwright Point, and the airport.

A. Landbirds

1. Parrakeet (*Vinis kühlii*) (only 2 seen)

B. Seabirds

1. White-tailed Tropicbird (*Phaethon lepturus*)
2. Brown Booby (*Sula leucogaster*)
3. Red-footed Booby (*Sula sula*)
4. Great Frigatebird (*Fregata minor*)
5. Sooty Tern (*Sterna fuscata*)
6. Brown Noddy (*Anous stolidus*)
7. White-capped or Hawaiian Noddy (*Anous minustus*)
8. Fairy Tern (*Gygis alba*)

C. Migratory Species

1. Pacific Golden Plover (*Pluvialis dominica*)
2. Wandering Tattler (*Heteroscelus incanum*)
3. Ruddy Turnstone (*Arenaria interpres*)
4. Bristle-thighed Curlew (*Numenius tahitiensis*)

D. Accidentals

1. Snowy egret (*Leucophoyx thula*) (1 seen)

Previous observations of birds on Fanning Island were reported by Tristram (1883), Streets (1877), Wetmore (1925), and Kirby (1925). Those of Tristram (1883) appear to be somewhat incomplete for he listed only eight species, of which none were boobies. He did, however, comment upon the abundance of the parrakeet and of a warbler (*Conopoderas pistor*, Tristram).

Kirby (1925) reported these two landbirds (the parrakeet and the warbler) plus nine species of seabirds and three migrants. He observed that the number of birds on Fanning Island was decreasing markedly due to the clearing of vegetation by the copra plantation which destroyed nesting sites.

It is obvious from these 1970 observations that the abundance of the warbler and parrakeet has continued to decrease. Only two parrakeets and no warblers were observed. Since the warblers are hard to observe (Kirby, 1925) some may still be present, but their numbers are certainly extremely low. These two landbirds are also found on Washington and Christmas islands.

The only notable change in seabird populations was a minor one. No blue-faced boobies (Sula dactylatra) were seen. Kirby (1925) reported them, but noted that they were very scarce.

There were only two species of birds observed that had not been previously reported: the ruddy turnstone and the snowy egret. The turnstones were very abundant, particularly in the North Pass area, and it is surprising that they were not recorded by Kirby (1925) for they are a common migrant in this part of the Pacific. The egret, seen at the Cable Station, appears to be a true accidental.

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A NOTE ON SURF AT FANNING ISLAND

B. S. Gallagher

Department of Oceanography and Hawaii Institute of Geophysics

While conducting physical studies reported elsewhere in this volume, the author had occasion to observe surf conditions at Fanning Island. Between 2 and 10 January 1970, two separate swells arrived from the North, each lasting three to four days. The first swell produced 2.5 m (8 ft) breakers; 3.7 m (12 ft) surf occurred during the second. For several days between there was relative calm, with about 1 m surf. Because of its location, the island probably has a surf "climate" quite similar to Hawaii's.

At Fanning Island, waves break on the outer edges of the reefs, 50 to 200 meters offshore. The breakers are very long-crested, indicating that the outer contour of the reef is fairly unbroken and regular. The surfline is continuous even across North Pass. Except at English Harbor and at the Cable Station, there seem to be no deep channels having low wave-action, or places where wave energy is concentrated over isolated shoals--as there are on the coasts of the Hawaiian Islands. These observations apply to the north swell exposure (roughly from the Cable Station to North Pass, and between North and Rapa passes), but one would expect similar conditions to obtain around the rest of the atoll as well.

Surf probably breaks extremely rarely across the entrance to the deep tidal channel which enters the lagoon at English Harbor. At the Cable Station, there is a channel, about 5 m wide, through the fringing reef. When the surf exceeds roughly 2.5 m (8 ft), waves do break across this channel. During less severe surf, the breaker-line terminates at either edge of the channel, and a strong rip current is present. The breaking waves advancing over the reefs bordering the channel are very well formed for board surfing. However, numerous, isolated coral heads punctuate the reef flats, often coming almost to the water's surface; surfing here is definitely dangerous and produced one injury during our expedition.

The east side of the island receives trade wind swell, choppy and irregular in form; north swell can also impinge directly on much of the eastern shore because of its orientation. Several wide, steep berms of large, coral shingle extend inland from the water's edge--indicating occasional periods of very large surf. Similar berms show that strong swells have broken up parts of the reef on the west shore as well. These waves probably arrived from the South and West during summer seasons. The berms themselves present an interesting question. They extend above and behind the present water line, yet the large surf that we observed was breaking on the outer edges of the reefs--100 to 200 m seaward. It is possible that uncommon circumstances might occasionally have produced a temporary rise in water level over the reefs, allowing large waves to break at the shore itself and thus build the berms. Such events might be imagined as similar to the period of destructive surf that hit north Oahu shores in December 1969. However, the berms are built of well-worn coral, which would not have acquired this condition in just a few days of unusual surf. Perhaps the rounded shingle is produced on the outer reefs by ordinary surf, accumulates on the reef flat over long periods, and is swept up into a shoreline berm during unusual events. If so, one might be able to study the rate of occurrence of "catastrophically" big surf by dating the sequence of berms.

NOTE ON PHOSPHATE ROCK AT FANNING ISLAND

K. J. Roy

Department of Oceanography and Hawaii Institute of Geophysics

INTRODUCTION

Phosphate rocks on atolls result from the replacement and cementation of calcium carbonate sediments by carbonate-apatite minerals. The cement and the replacement material are precipitated from phosphatic solutions formed during leaching of guano deposits (Frondel, 1943). Phosphate rocks have been or are being mined on many Pacific atolls, and can be very important to local economies(Hutchinson, 1950).

Man has exploited the phosphate rocks of Fanning Island for some time. A 16th Century temple on Fanning (Emory, 1939) 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 (Hutchinson, 1950). 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 (Fig. 1). The mined area is now covered with dense thickets of Scaevola, Messerschmidia, and Pandanus.

North of the Cable Station, the land elevation rises to about 2 meters on a phosphate rock platform. An extensive Pisonia forest is developed on this platform. Some of the trees are larger than 3 meters in diameter. Although at one time the bird rookeries on Fanning were extensive (Hutchinson, 1950), the bird colonies now present are small.

Phosphate rock is found on Palmyra, Washington, and Fanning islands, but not on Christmas Island. Hutchinson (1950) believed that the distribution of phosphate rock in the Line Islands reflects a shift in the intertropical convergence and that the phosphate rocks in the Line Islands are not contemporary.

The gross chemical composition of phosphate rocks is quite well known (Frondel, 1943; Hutchinson, 1950), but the petrography of the rocks has not had much attention. This note compares the petrography of the phosphate cements of Fanning Island with those of Remire Island in the Indian Ocean (Braithwaite, 1968), and discusses the implications of the similarities in terms of temporal changes in the phosphatizing solution.

STRATIGRAPHY

The Cable Station (Fig. 1) was built on an infilled pass. The two peninsulas on the lagoon side of the island near the cable station are spits that were built along the sides of the old pass. When the pass was open the configuration of the shoreline was probably similar to that presently seen at English Harbor. The rocks of the peninsulas have imbricate structure that resulted from positioning of tabular pieces of coral by the waves breaking on the shore. Imbricate structure is common in the modern boulder ramparts around the atoll.

The rocks of the spits are calcirudites. About one quarter of the rock is coral boulder, about half is pebble, again mostly coral, and the remaining quarter is medium-to-coarse calcarenite. The rock is slightly cemented by $CaCO_3$ but does not seem to be phosphatized.

The phosphate rocks in the vicinity of the Cable Station are coarse calcarenites grading to calcirudites. Generally, beds are about 5 to 10 cm thick, but vary in thickness from about 30 cm to 1 cm. Dips are shallow, generally less than 5°. The measured strikes are variable and unreliable because the dips are so small. Along the lagoon shoreline in the northern area the phosphate rock crops out in about a 1-meter-high wave-cut cliff. The bedding is planar, and strikes toward the lagoon. The phosphate rocks do not crop out on the ocean side of the island. South of the cable station the dips are very small, and the strike of the beds is parallel to the present shoreline. No cross-bedding was seen in the phosphate rocks.

Fragments of coralline red algae; corals, including Acropora and Favia, Turbo shells, and Tridacna and other pelecypod shells are common in the phosphate rocks of the northern area. Tree molds are also common. In the southern area the rock is well sorted pebble calcirudite, and large coral fragments or shells were not seen.

The phosphate rocks are very similar in fragment composition and in texture to the sands and gravels that occur over a few thousand square meters of area lagoonward of the boulder ramparts near English Harbor. The sands and gravels are composed of fringing reef-flat material that was washed over the beach ridges during periods of extreme storm.

MINERALOGY OF THE PHOSPHATE ROCKS

The wash-over gravels associated with the infilled pass at the site of the cable station were cemented by phosphate minerals to produce the phosphate rocks. No calcium carbonate cement was found in these rocks, and the clasts have not been changed from their original mineralogy. Although the larger clasts look chalky, calcite, magnesian calcite, and aragonite are still present. Recrystallization and obliteration of microstructure has not occurred. Many of the gastropod shells are still nacerous. Some solution of the calcium carbonate has taken place since the deposition of the phosphates as there are bridges of cement in some voids. Also, on some surfaces, the cement stands up in a box-work pattern as a result of selective solution of the calcium carbonate grains. No clasts were observed to be phosphatized.

Phosphate mineralogy is complex. Deer et al. (1962) describe an isomorphous series with four end members; fluor-apatite ($Ca_5(PO_4)_3F$), chlorapatite ($Ca_5(PO_4)_3Cl$), hydroxyapatite ($Ca_5(PO_4)_3OH$), and carbonate-apatite ($Ca_5(PO_4)CO_3,OH)_3(F,OH)$. The names of the individual mineral species are largely based on the ratio of CO_2:OH:F:Cl in a chemical analysis (Frondel,

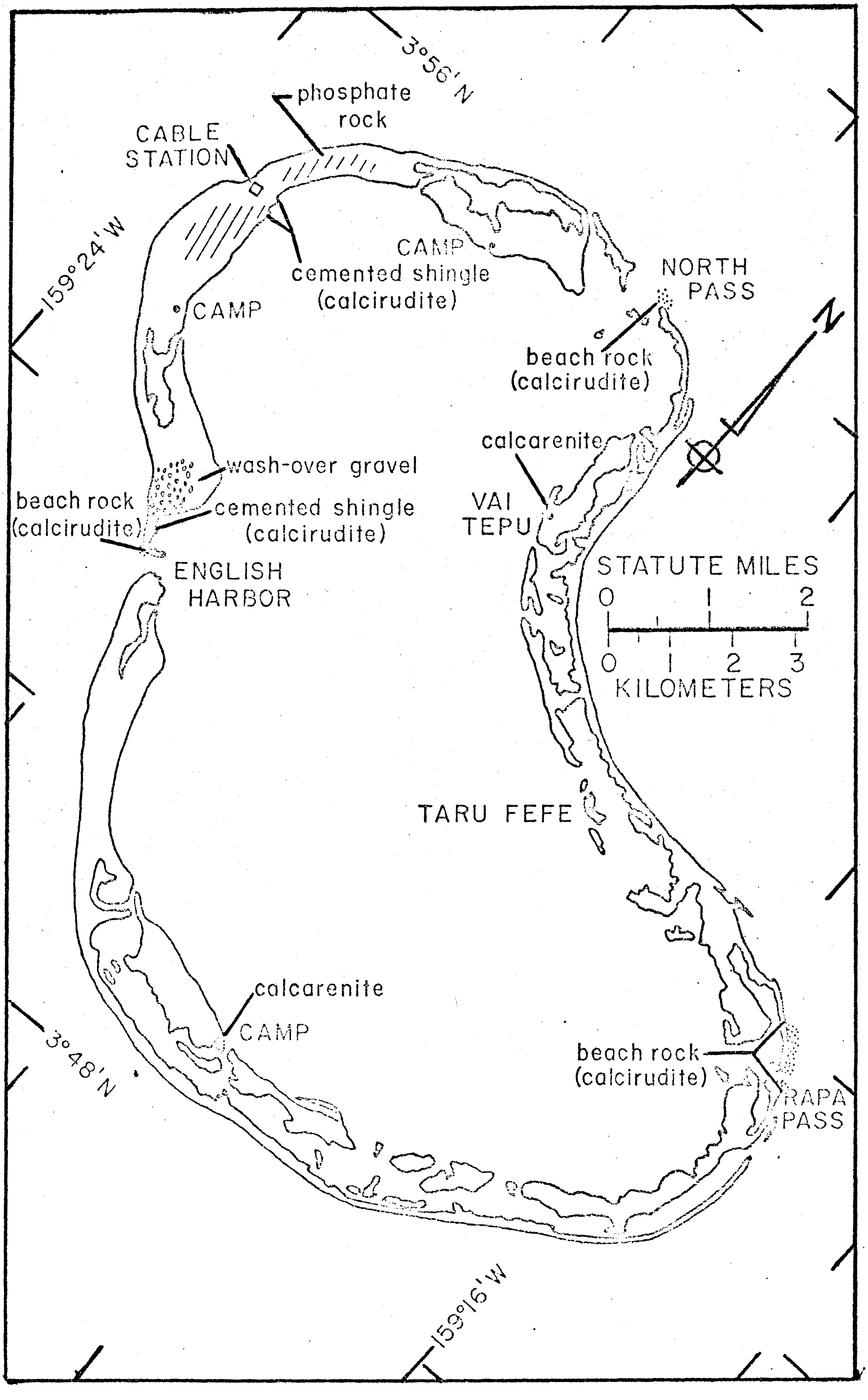

Fig. 1. Mineral locations on Fanning Island.

1943). In the carbonate-apatite series, there are two end-members, francolite (appreciable CO_2 and more than 1 percent F) and dahllite (appreciable CO_2 and less than 1 percent F) (Deer et al., 1962).

Most of the phosphate minerals in island deposits are in the francolite-dahllite series (Frondel, 1943). No hydroxyapatites have been reported from insular deposits. Phosphate minerals reported with rare occurrence are brushite ($CaHPO_4 \cdot 2H_2O$), monetite ($CaHPO_4$), and whitlockite ($Ca_3(PO_4)_2$).

Hutchinson (1950) gives a chemical analysis of phosphate rock from Fanning. The material has slightly over 1 percent F, suggesting that francolite is present. An X-ray diffractogram (CuKα, Ni filter) of the phosphate cement from Fanning is shown in Figure 2. Peak positions and relative intensities are given in Table 1. The major peaks of francolite (Milton and Bennison, 1968) as well as those of whitlockite occur on the diffractogram (Table 1). The four main peaks that Braithwaite (1968) reports form the phosphate rocks on Remire are duplicated in the analyses of the Fanning samples. The phosphate cements of Fanning are a mixture of carbonate-apatites (francolite-dahllite) and whitlockite and callophane.

Although, in terms of phosphate mineralogy and textures of the cement, the phosphate rocks of Fanning Island appear to be remarkably similar to those of Remire. One feature not seen in the Fanning rocks was phosphatized skeletal debris. There may be two reasons for this: the Fanning phosphate rocks are not well developed, and were not sampled extensively.

Table 2 shows a typical sequence of cements. The light yellow cement is cryptocrystalline to microfibrous. Generally, the farther away from the clast, the more fibrous the yellow cement. The contact with the clast is irregular, but the clasts have not been replaced by the cement. The clear cement is cryptocrystalline, and, under crossed polarizing prisms, shows laminar to colliform textures. The translucent brown cement occurs in the central part of the cement sequence and contains laminae of clear and of yellow cement. Laminae of clear and yellow cement commonly make up as much as one third of the zone. The yellow laminae are more common than are the clear. Generally the laminae have a varve-like relation with the brown cement. The contact between the brown and the inner clear or yellow laminae is often irregular and gradational. The contact between the brown cement and the outer clear or yellow laminae is generally sharp. There are many alternations of cement types from the clast surface to the void. The major thickness of clear cement occurs near the clasts, and the ratio of yellow to clear laminae appears to increase away from the clasts.

The sequence of cements shown in Table 2 is oversimplified and indicates only the major trends. The outermost fibrous yellow cement is not always present, although the yellow laminae in the translucent brown zone tend to be fibrous.

The fibrous crystals are the only crystals seen in the cement (400 x magnification). The crystals are elongate perpendicular to the surface of the cement, although often they form fans with their apices near the contact with the brown cement. In places the fibrous crystals form microdrusy linings of voids. Some of the smaller voids have been completely infilled by fibrous

Table 1. Comparison of d-spacings and relative intensities of peaks shown on the diffractogram of Fanning Island phosphate cements. The intensity and major peak positions for various materials are also given (1. -the major peaks of the Remire phosphates (Braithwaite, 1968); 2. -bladed crystals in voids (Braithwaite, 1968); 3. -whitlockite, three major peaks (Index to powder diffraction file); 4. -francolite (Milton and Bennison, 1968); 5. -dahllite (Ames, 1950, and Index to powder diffraction file). The asterisks indicate presence of peaks.

°20	Å	Relative Intensity	Intensity[a]				
			1	2	3	4	5
55.77	1.648	32					
53.28	1.719	39					
49.55	1.840	32	20				*
46.69	1.945	41					*
34.56	2.595	66		*			*
34.20	2.622	46					
32.88	2.724	70	60		60	57	70
32.18	2.778	100				100 & 55	100
31.81	2.813	89	100	*	100		
31.20	2.667	93					
27.90	3.188	73		*			
25.90	3.440	91	30		30	43	70

[a] materials 1, 2, 3, 4, and 5 have d-spacings different from the ones shown in the table but the peaks are overlapped by peaks on the sample diffractogram.

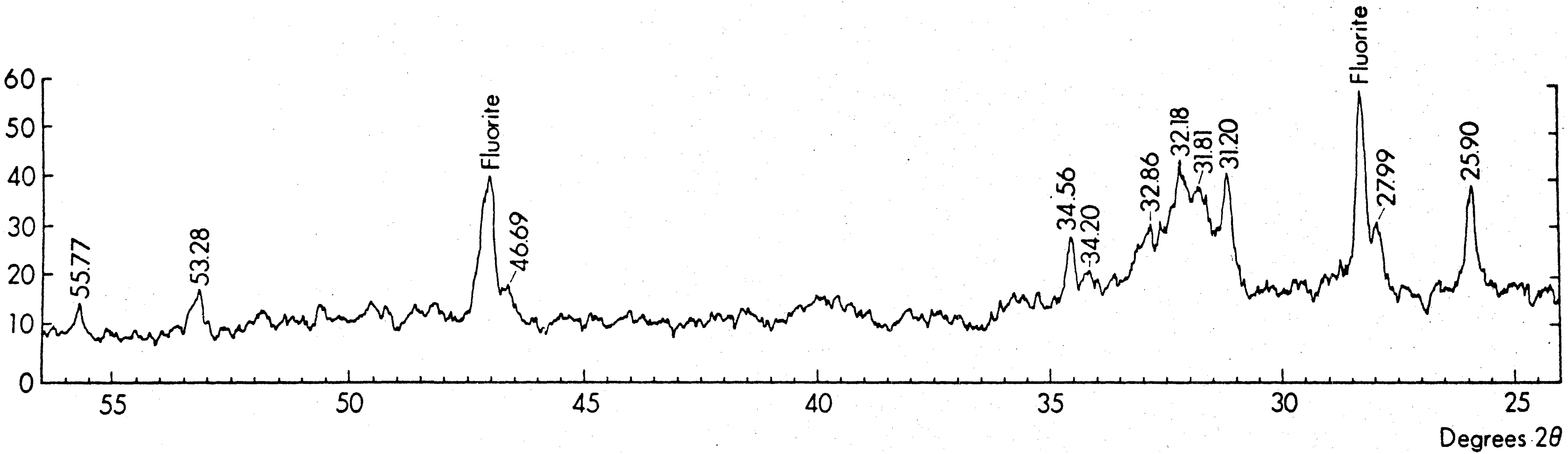

Fig. 2. X-ray diffractogram of phosphatic cement from Fanning Island (CuKα, Ni filter, 35 kv, 20 ma, detector 2-1, 600 v, rate meter - 100, time constant - 4, divergence slit - 1°, receiving slit - 0.006", antiscatter slit - 1°, Norelco type 42273/1).

Table 2. Typical sequence of phosphate cements in the Fanning Island phosphate rocks.

	Zone		Thickness (μ)	Index of refraction[a]	Birefringence
Void					
Cement	6	light yellow, fibrous	0-10		
	5	light yellow, structureless	2		
	4	translucent brown, laminated	4		≈.004[c]
	3	light yellow, structureless	4	$\eta_2<\eta_3<\eta_4$	≈.004
	2	clear, laminated to colliform	2	~1.54[b]	≈.001
	1	light yellow, structureless	1	less than calcite	
Clast					

[a] White light used.

[b] Slightly larger than canada balsam.

[c] The interference colors are masked by the color of the cement but they appear to be about the same as those of the light yellow cement.

cement. Cement has not entirely filled all the spaces between the clasts. On the walls of the remaining open spaces there often are clusters of bladed tabular crystals that have a rosette growth form.

On top of the outer cement zone in some voids there is a layer of micro- to cryptocrystalline calcium carbonate. The material is poorly sorted and the recognizable grains are angular and irregular in outline. This material may be detritus that had sifted down into the large voids. No geopetal structures were seen, however.

The mineralogy of the cements is not known for certain. The yellow and brown cements are differentiated by slightly different refractive indices and birefringence. The indices of refraction and the birefringence are correct for minerals of the francolite-dahllite series. The fibrous nature of the yellow cement suggests dahllite, and Braithwaite (1968) describes a similar fibrous outer zone of cement which he says is material close to dahllite. A problem is that, although the relative amounts of the cements in the samples are estimated as 10 percent clear, 40 percent brown, and 50 percent yellow, dahllite is quite inconspicuous on the diffraction traces. Generally, the peaks expected from dahllite fall off center of the peaks on the diffractogram of the Fanning Island cement. Dahllite is present only in small amounts if present at all. The same is true of francolite. The high fluoride content shown by the chemical analysis suggests that some of the minerals in the cement are near the francolite end of the series. All that can be said is that the yellow and brown cements contain at least two minerals from the francolite-dahllite series, and at least one carries considerable fluoride. The clear cement appears to be collophane (low refractive indices and very low birefringence).

The bladed crystals in the voids were not examined with the petrographic microscope, the diffractogram indicates whitlockite or something close to it is present. Braithwaite (1968) reports crystals with similar morphology in voids in the Remire rocks and says that they are a mineral close to whitlockite.

SIGNIFICANCE OF THE PHOSPHATE CEMENT

The tripartite cement and the apparent progressive change from one cement type to another suggests a progressive change in the nature of the phosphatizing fluids. The alternation of laminae of the various cements suggests a short-term change in the phosphatizing fluids, perhaps in response to climatic cycles. The general change in the cement from the clast to the void suggests a long-term general change in the fluids.

Perhaps interstitial solutions changed as leaching of the surficial guano progressed. A decrease in the activity of fluoride in the leaching waters could cause a change of cement from francolite to dahllite. The late formation of whitlockite may be due to a late major decrease in the pH of the phosphatizing fluids. The solutions would not be buffered by calcium carbonate once the clasts were sealed off by cement. Another cause of increased pH might be the late formation of a extensive forest on the surficial guano deposit.

It seems unlikely that the complicated patterns of cement mineralogies and textures are by chance so similar on Fanning and Remire islands. A general model of progressive change in phosphatization seems more likely. Just what this model might be is not apparent from the data available.

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AN INEXPENSIVE *IN SITU* PUMP FOR SAMPLING SHALLOW WATERS

Harold G. Schiesser

Department of Oceanography and Hawaii Institute of Geophysics

Field studies of shallow marine and freshwater environments often require the collection of numerous water samples. The use of conventional bottle samplers is inconvenient from the small boats generally used for such sampling. A simple pumping device which brings the water to the surface where it can be collected conveniently is described. The system can be assembled with commercially available components for about $50.

The main component of the system is a submersible bilge pump (MiniKing®, Cromwell Co., Pt. Pleasant, New Jersey) which operates on power supplied by a 12-volt lead-acid storage battery located in the boat. The pump is attached to the end of a 50-foot (15 m) plastic hose, as shown in Figure 1. Power is supplied to the pump by a waterproof electric line, which is taped to the hose. Electrical connections are sealed in silicone cement. Power consumption of the pump is 1.5 amp, allowing many hours of sampling between battery chargings. A thin circular plate of stainless steel, with a diameter somewhat larger than the pump, is bolted to the base to prevent fouling of the impeller blades and to protect the plastic case from damage. A weight is attached to the end of the hose to make it hang vertically in the water.

To operate, the pump is lowered to the desired depth, as indicated by tape markers on the hose, and current is applied to the pump. Approximately 1 minute is required to flush the 50 feet of hose before samples are collected from the surface end of the hose.

The only work the pump must do, aside from overcoming minor frictional resistance, is to lift the sample from the water surface into the boat. The pump described is adequate for boats with up to 1 meter of freeboard. A more powerful model of this (4.9 amp) will be required for larger boats. The only serious limitations on the maximum useful depth of this system are the inconvenience of handling long lengths of hose and the period required to flush the hose.

This pumping system has proven its reliability and convenience in several sampling programs. It has been used to collect samples for dissolved oxygen, dissolved organic carbon, salinity and suspended material.

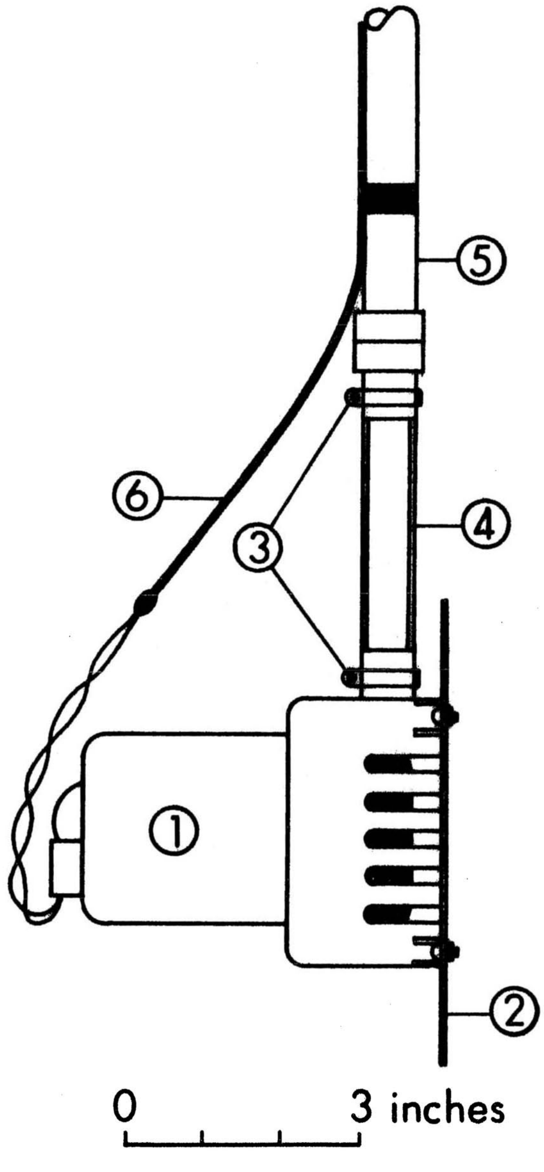

Fig. 1. Pumping system in sampling position: 1, submersible pump; 2, protective plate; 3, hose clamps; 4, Tygon® tubing; 5, plastic hose; 6, waterproof electric cable to provide power from battery at the surface.