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Comparative Investigations of Tropical Reef Ecosystems: Background for an integrated coral reef program

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INTRODUCTION

CITRE and IMSWE studies in British Honduras

S. V. Smith

A series of events at the Smithsonian Institution beginning about 1970 and continuing to the present have led to the following group of related papers dealing with various aspects of coral reef ecology, primarily in relation to the reefs of British Honduras (Belize). A brief historical sketch of those events provides useful background information to relate the papers presented here.

During the summer of 1970 researchers from several institutions began considering the possibility of seeking funding for coral reef research from the International Decade of Ocean Exploration (IDOE) office of the National Science Foundation. This consideration, together with draft proposals and informal discussion, led in the spring of 1971 to a grant from IDOE to the Smithsonian Institution for the formulation and coordination of a long-term, multi-disciplinary, multi-institutional investigation of coral reef ecosystems. That project was named "Comparative Investigations of Tropical Reef Ecosystems" (CITRE).

Also in the spring of 1971, the Smithsonian scientists received internal financial support for a more limited effort designed to describe biotic and abiotic characteristics of coral reefs. That project was named "Investigations of Marine Shallow-Water Ecosystems" (IMSWE). Smithsonian scientists involved in the one project were for the most part involved in the other as well, so an effort was made to coordinate the two activities as much as possible.

As soon as CITRE planning funds became available, Smithsonian scientists began gathering available information from which to select sites for establishing facilities on a coral reef. Potential sites were then visited. Dahl, Macintyre, and Antonius reported on these site selection efforts, and their report is presented here in revised form. Glover's Reef, British Honduras, was selected as the initial site for CITRE efforts; a decision on Caribbean secondary sites and on a Pacific primary site was deferred for a later stage in the CITRE project.

During November 1971, a two-week workshop was held at Glover's Reef. The purpose of that workshop was to introduce workshop participants to techniques of quantitative total-ecosystem modeling and to gather material for preparing the formal CITRE proposal. Workshop participants had been selected to be in one or more of nine working groups which had been erected as basic units within the CITRE project. Participants and their primary working groups are given in Table 1. That table does not capture the interaction among the participants; most individuals were involved to some extent in at least one working group besides the primary one in which that table lists them.

The CITRE proposal was submitted to IDOE in January 1972. That proposal was not funded, but the efforts produced valuable results. We are using the Atoll Research Bulletin to make these results generally available rather than losing them because of the fate of the proposal itself. Dahl, Patten, Smith, and Zieman summarize the conceptual model which was developed at Glover's Reef. That model is very preliminary, and parts of it are being or already have been revised for publication elsewhere. Sachet presents the bibliographic section of the CITRE proposal. It should be emphasized that the role of the individuals presenting sections of the proposal has been editorial; all of the workshop participants (Table 1) and many other individuals contributed materially to these papers.

In addition to the papers adapted from the CITRE site selection report and proposal, several related papers have been produced. Largely as a result of efforts during the site survey and workshop, Tsuda and Dawes present a checklist of marine algae at Glover's Reef. Several papers on the geographic and terrestrial aspects of the British Honduran reef area will appear in a subsequent issue of the Atoll Research Bulletin.

We hope that the papers presented in this issue of ARB will continue the considerable interest which has been engendered in the integrated approach to coral-reef ecology as visualized by the CITRE participants. Moreover, we are confident that continued efforts in British Honduras will serve to elucidate the nature of a complex, important, but poorly-known area of Caribbean coral reefs.

Table 1.

Participants at the Glover's Reef Workshop

Stephen V. Smith Smithsonian Institution	Principal Investigator (presently at Hawaii Institute of Marine Biology)
Sir Maurice Yonge Edinburgh, Scotland	External Advisory Committee Member
George D. Grice National Science Foundation	NSF Observer

Ecosystem Analysis Working Group

Bernard C. Patten University of Georgia	Group Leader
Thelma Richardson University of Georgia	
Joseph C. Zieman University of Virginia	

Detritus and Nutrients Working Group

Robert E. Johannes University of Georgia	Group Leader
Donald W. Kinsey Mauri Bros. & Thompson, Sydney, Australia	
Nelson Marshall University of Rhode Island	
Michael E. Q. Pilson University of Rhode Island	
Kenneth L. Webb Virginia Institute of Marine Science	

Benthic Plants Working Group

Arthur L. Dahl Smithsonian Institution	Group Leader

Michael S. Foster
University of California, Santa Barbara (presently at California State University, Hayward)

Roy T. Tsuda
University of Guam

Invertebrate Working Group

Peter W. Glynn — Group Leader
Smithsonian Tropical Research Institute

Arnfried Antonius
Smithsonian Institution (presently Harbor Branch Foundation, Florida)

Judy Lang
Smithsonian Tropical Research Institute (presently University of Texas, Austin)

James Porter
Smithsonian Tropical Research Institute (presently University of Michigan)

Amada Reimer
Smithsonian Tropical Research Institute (presently Pennsylvania State University)

Klaus Ruetzler
Smithsonian Institution

Plankton Working Group

Tom S. English — Group Leader
University of Washington

Arthur Barnett
Scripps Institution of Oceanography

Frank Ferrari
Texas A & N University

Robin Ross
University of Washington

Vertebrates Working Group

Ray S. Birdsong Old Dominion University	Group Leader
James E. Bohlke Philadelphia Academy of Natural Sciences	
Edith H. Chave University of Hawaii	
David W. Greenfield University of Illinois	
C. Lavett Smith American Museum of Natural History, New York	
Frank H. Talbot The Australian Museum	

Geology Working Group

Ian G. Macintyre Smithsonian Institution	Group Leader
Keith E. Chave University of Hawaii	
Clyde Moore Louisiana State University	
Jon N. Weber Pennsylvania State University	

Terrestrial Phenomena Working Group

F. Raymond Fosberg Smithsonian Institution	Group Leader
Marie-Helene Sachet Smithsonian Institution	
Ralph W. Schreiber University of South Florida	
David R. Stoddart Cambridge University	

Oceanography and Meteorology Working Group

Andrew C. Vastano Texas A & M University	Group Leader
Bruce W. McAlister National Science Foundation	

A PRELIMINARY CORAL REEF ECOSYSTEM MODEL

Edited by

A. L. Dahl, B. C. Patten, S. V. Smith, and J. C. Zieman, Jr.

A major goal of the CITRE planning effort was to develop a conceptual framework for a systems model of a coral reef ecosystem suitable for computerization. Both the process of development and the preliminary results may be of some value to future comprehensive studies of complex reef systems.

The preliminary model was conceived not only to outline a possible mathematical model, but also to integrate the proposed research of many specialists into a coherent framework with defined interactions. While the specialists generated the model structure, they also had to modify their research plans to incorporate all major aspects of the system as identified in the model.

No one model can deal with all aspects of an ecosystem. Its properties, however, should ultimately resemble those of the system being modeled and its level of abstraction should suit its intended purpose. Thus no model is static; it must evolve as available knowledge of the ecosystem increases. The preliminary model described here is one fixed point in such an evolving process. It represents an intermediate level of ecological abstraction, which, because of the diversity of the reef system, is nevertheless highly complex. It is based on the great diversity of viewpoints and professional experiences of the investigators involved. Yet, while its details are open to question, it represents a useful benchmark from which to proceed.

The model was developed during a two-week workshop at Glover's Reef, British Honduras, in November 1971. Forty-one participants (see Introduction) representing a wide variety of reef-related disciplines and with experience in many coral reef areas attended this workshop. The principal activity was the development of a conceptual model sufficiently comprehensive that it could be applied to most reef areas. However, the shallow reef flat areas of Glover's Reef served as the prime focus for the initial effort and this may be reflected in some of the details presented here. Overall, the result represents a unique synthesis of current information about the tropical reef ecosystem.

Process of Model Development

CITRE participants were initially chosen to be members of one or more of the nine working groups (Introduction) with responsibility for a major aspect of coral reef ecology. Most working groups met before the workshop for initial discussion of their subject area and an introduction to modeling concepts. The workshop itself included lectures introducing the scientists to some aspects of modeling theory, and presentations by working groups as they fitted their subject matter into the general modeling framework. The working groups proceeded by internal discussions, consultations with the modelers and with other working groups, and field observations to check on the general applicability of the model elements developed. The minor inconveniences of working at a remote site were far outweighed by the freedom from distractions and the ability to "consult the environment."

The model was designed to depict the flow of carbon through the coral reef ecosystem. Each working group first defined the "compartments," or functional units between which the flows were to be measured. An approximate limit of twenty compartments per working group was set to fix the overall model complexity within present computer capabilities. Inter-group discussions resolved problems of overlapping or overlooked functional units. Diagrams were then developed for each compartment relating it to other compartments and flows in the system. The compartments were listed in a matrix, and the interactions between compartments determined jointly by the working groups involved. Some quantification of these interactions was attempted (at least in terms of orders of magnitude), but this was not completed and is omitted here. Revisions and adjustments continued throughout the workshop. The terrestrial section was kept simplified as the primary concern was its interactions with the reef system.

The model developed through a cyclical progression. A statement of the purpose of the model and the definition of compartments was followed by the conceptualization of the initial model and field observations to check the model validity, leading to changes in the conceptualization and (more rarely) in compartment definitions. With each permutation the model became more refined and (hopefully) accurate.

The Model

Compartments

Three basic elements characterize the model: compartments, flows (fluxes) and external driving forces (forcing functions). The compartments are the carbon or carbon-equivalent storage units of the system and may be defined as plant or animal types that act as processing units for the food which they ingest or produce, or as material pools such as detritus or carbon dioxide through which substances pass as they cycle in the system. Compartments in the CITRE model may be considered "functional groups" in that they are abstract condensations of groups of organisms or substances that apparently have the same or similar functions in the ecosystem. In this sense they are "ecological species" as opposed to conventional taxonomic species. For example, Halimeda, Penicillus, Rhipocephalus, Udotea, Jania, and Corallina are distinct genera of algae (even belonging to two phyla); yet in the model they are all considered part of the same compartment--the noncrustose, calcium carbonate-producing macroalgae designated XCBALG* [6] (see Table I). Likewise two compartments are distinguished on whether motile organisms remove solid substratum as they feed ("scrapers": designated XSCRAP [35]), or eat only the overlying organisms ("browsers": XBROWS [36]). All dissolved organic compounds containing nitrogen, and not associated with some other compartment, are similarly grouped (XDON [67]).

Compartment boundaries not only combine dissimilar species on functional grounds, in some cases they even separate parts of organisms with distinct roles or locations. Marine grass blades (XBLADE [9]) were separated from marine grass roots (XROOT [10]) because of the functional differences inherent in the location of these parts above versus below the sediment surface. Transport from one part of the plant to another thus becomes a flow between compartments. When it appeared that the inorganic carbon cycle could be most easily treated as a distinct system, separate compartments were established for the calcium carbonate in the walls of living organisms (XORG [84]) and the remaining (organic) carbon in the organisms. The organisms were therefore defined in the model as controlling the flow of carbon to their skeletons rather than flowing that carbon through the organism compartments. Table I enumerates the preliminary working compartments identified for the CITRE model, with their acronyms and numbers.

Flows

In order that compartments may function within the model, they must be linked or coupled; flows (or fluxes) between them are measured in whatever is the currency of the model--i.e., the material with which exchanges are made. Flows, like compartments, are based on the general objectives of the modeling program. In the case of the CITRE model the following materials were considered significant to the model of a coral reef ecosystem: carbon, inorganic carbon, organic carbon, nitrogen, phosphorus, calcium, biomass, and energy. It was finally agreed to flow carbon through this model because of its mutual importance to the biochemical and geochemical cycles, even though other flows are also important. For example, the nutrients (PO_4, NO_3, etc.) which are important in feed-back loops controlled by photosynthesis, are flowed in the model, but for mathematical consistency, are converted to carbon equivalents.

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*Although there is no standard convention for naming compartments, flows, or other components, certain consistencies make bookkeeping easier and more accurate, such as the use of acronyms. Here X---- stands for compartment, thus XCBALG for CarBonate producing ALGae and XDON for Dissolved Organic Nitrogen. For convenience, all compartments were numbered consecutively as they appeared in the matrix (Fig. 9).

Forcing functions

Forcing functions are driving forces or variables which originate outside the system of reference but which influence the behavior of the system. These variables include light, temperature, inputs of materials, and other influences not under the control of the system.

The diagrams used in this model to illustrate compartments and flows are feedback dynamics or Forrester diagrams (Forrester, 1961). The units of compartments and flows in the CITRE model are grams of carbon per square meter (gC m^{-2}) and grams of carbon per square meter per day (gC m^{-2} day^{-1}) respectively. Figure 1 shows the symbols used in the diagrams and briefly describes meanings attached to these symbols. Although these diagrams may become very complex, they are useful for a graphic representation of the model and as a means to facilitate discussion. The general characteristics of the total CITRE ecosystem model as described by these diagrams is outlined below.

The forcing functions (external driving forces), compartments and flows between compartments, together delineate a preliminary total ecosystem model for a coral reef. Both the large number of compartments (104) and the number of flows between them form a very complex model.

Figure 2 graphically illustrates the couplings and ecological relationships of one compartment, the fleshy algae (XFLALG [5]). CO_2 input from XDISOL (80), a compartment of common interest to the Geology and Nutrients-Detritus groups, is controlled by four integrating functions, three of which (#1 through #3) are abiotic functions that regulate potential photosynthesis. Integrating function #4, coupled with the other three, gives realized photosynthesis. Dashed arrows from the integrating functions to the valves on the flows show that the integrating functions influence flow without contributing material to it, that is they are informational or control couplings rather than material flows or fluxes.

Six feedback loops or cyclical flows, of three basic types, affect this compartment. Two similar loops (diagrammed as one) indicate the cycling of carbon, or carbon equivalents of oxygen, respectively, between the dissolved organic carbon (XDOC [62]) or oxygen (XO2 [70]) compartments and XFLALG (5). These loops are controlled by the amount of the "upstream" or donor compartment present as well as by temperature, salinity, and exposure (integrating function #1). Another type of loop in the diagram shows the cycling of carbon to XTURF (4), XPHPL2 (12), and XPHPL3 (13). Flows to these three compartments from XFLALG (5) are reproduction, and flows back from them are recruitment from settling and growth. The third loop type is that diagramming CO_2 uptake from XDISOL (80) during photosynthesis, and its return during respiration.

Outputs to XDON (67) and XDOP (69) are excretion, as is in part the flow to XDOC (62).

Floating macroalgae, XDTPLT (8) break off from XFLALG (5) and continue living; detritus (XDETR3 [65] and XDETR4 [66]) is similarly derived.

XFLALG (5) also furnishes carbon to XBROWS (36), XGRAZV (48) and XBROWV (49), because these animals eat algae. The dotted arrows on this last set of flows show that these flows are controlled in part by the amount of algal material available, and in part by the biomass of the grazer.

Six more "single compartment" models are also shown in a similar diagram format (Figures 3-8). These diagrams all resemble Figure 2 in their complexity and mode of working. Space does not permit the inclusion of diagrams for all 104 compartments, although these were developed during the two-week workshop.*

Connectivity matrix

While feedback dynamics diagrams are a convenient method for showing individual compartments in detail, they cannot be combined for a model of this scale without becoming unmanageable mazes. An alternative graphical representation that has desirable properties is the connectivity matrix (Figure 9). This matrix is a square binary matrix showing the presence or absence of flows from each compartment to each other one. The size of the matrix is determined by the number of compartments (104 in the case of the CITRE model). Each compartment, from X1 through X104, is listed both across the vertical axis and down the horizontal axis. The direction of flow is from compartments on the horizontal to those on the vertical axis. Flows are indicated by a dot " " located at the intersection square of two components of the matrix. Thus, in Figure 9 for example, the single dot on the bottom line (XORGC 104) indicates a flow from XORGC (104) to XDOC (62) but not the reverse.

The connectivity matrix shows other information of interest. As its name implies, it illustrates the total "connectivity" or percentage of possible interaction. The CITRE matrix with 104 compartments has $(104)^2$ or 10,816 potential interactions. In this coral reef ecosystem model there are about 2,000 interactions or 20% connectivity. Since connectivity is highly dependent on compartment definition and at this level of resolution concerns only material flows, it is not possible to distinguish at this time between properties resulting from the modeling approach, and those inherent in the ecosystem. Complex ecosystems may be characterized by a much higher percentage of information "flows" or non-material interactions. However, these interactions are even more dependent than material flows on the level of model resolution.

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* Copies of the working drafts may be obtained from A. L. Dahl at Department of Botany, Smithsonian Institution, Washington, D. C. 20560. Some working groups are continuing to develop their parts of the model.

There are two disadvantages to the connectivity matrix: it does not show external forcing functions (temperature, currents, etc.) or information processing (which are shown by dashed arrows on the diagrams), and it does not indicate the magnitude of the flows.

A more complex form of matrix, a coefficient matrix, substitutes numerical values for the binary indicators of the connectivity matrix. Turnover rates then appear in the principal diagonal (a_{11}, a_{22}, a_{33},...) of the matrix, and flux or transfer rates appear in the off-diagonal elements. The CITRE matrix of turnovers and transfers is incomplete and is therefore omitted here.

While there is no immediate prospect of continuing to develop the CITRE model in its present form, it should now be possible to begin to piece together the major elements, and to quantify the essential relationships of the coral reef ecosystem. Only in this way will an overall picture of this most fascinating biological community ultimately be assembled.

Literature Cited

Forrester, J. W. 1961. Industrial dynamics. Cambridge, Mass.: MIT Press, 464p.

Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
Benthic Plants (10)			
X1	Nitrogen-fixing algae	XNFIX	Probably important in reef nutrient cycling
X2	Coralline crusts	XCRUST	Important in forming and cementing reef framework through their calcium carbonate production
X3	Benthic microalgae	XBMALG	Primary unicellular forms in sediments and surface films
X4	Turf	XTURF	Composed of species such as *Pterocladia*, *Polysiphonia*, and *Cladophora* less than 2 cm. high
X5	Macro-algae, fleshy	XFLALG	Large fleshy algae over 2 cm. high, such as *Turbinaria*, *Sargassum*, and *Dictyota* that may produce significant macro-habitats
X6	Carbonate-producing macroalgae	XCBALG	Carbonate producing algae other than crusts, such as *Halimeda*, *Rhipocephalus*, *Udotea*, and *Penicillus* that make a significant contribution to carbonate sediments.

X7	Boring algae	XBORE	Includes filamentous and siphonaceous greens such as *Ostreobium*, that occur within the carbonate matrix of the reef and living animals.
X8	Detached plants	XDTPLT	Plants such as *Turbinaria*,*Sargassum*, *Thalassia*, and *Syringodium* that often remain alive for some time as floating aglomerations, as well as *Acanthophora* and *Laurencia*, that sometimes form drift populations on the bottom.
X9	Marine grasses - blades	XBLADE	The emergent portions of *Thalassia*, *Syringodium*, *Diplanthera*, and *Halophyea*
X10	Marine grasses - roots	XROOT	Roots and rhizomes of the seagrasses, as well as the portions of such algae as *Halimeda*, *Udotea*, *Rhipocephalus*, *Penicillus*, and *Avrainvillea* that penetrate into the sediment
Plankton (23)			
X11	Heterotrophic phytoplankton	XPHPL1	Less than 10 u
X12	Autotrophic phytoplankton	XPHPL2	Less than 10 u

Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
<u>Plankton</u> (23)			
X13	Autotrophic phytoplankton	XPHPL3	10-100 u
X14	Autotrophic phytoplankton	XPHPL4	Greater than 100 u
X15	Microholoplanktonic omnivores	XZOOH1	Less than 200 u
X16	Mesoholoplanktonic omnivores	XZOOH2	200-500 u
X17	Macroholoplanktonic omnivores	XZOOH3	Greater than 500 u
X18	Neuston omnivores	XZOON	All sizes
X19	Microepibenthic omnivores	XZOOE1	Less than 200 u
X20	Mesoephibenthic omnivores	XZOOE2	200-500 u
X21	Macroepibenthic omnivores	XZOOE3	Greater than 500 u
X22	Mesoholoplanktonic carnivores	XZOCH2	200-500 u
X23	Macroholoplanktonic carnivores	XZOCH3	Greater than 500 u
X24	Neuston carnivores	XZOCN	All sizes
X25	Mesoepibenthic carnivores	XZOCE2	200-500 u

X26	Macroepibenthic carnivores	XZOCE3	Greater than 500 u
X27	Microholoplanktonic detritus feeders	XZODH1	Less than 200 u
X28	Mesoholoplanktonic detritus feeders	XZODH2	200-500 u
X29	Macroholoplanktonic detritus feeders	XZODH3	Greater than 500 u
X30	Neuston detritus feeders	XZODN	All sizes
X31	Microepibenthic detritus feeders	XZODE1	Less than 200 u
X32	Mesoepibenthic detritus feeders	XZODE2	200-500 u
X33	Macroepibenthic detritus feeders	XZODE3	Greater than 500 u
<u>Invertebrates</u> (14)			
X34	Animal-plant symbionts	XHERM	Sedentary or sessile; derive a portion of their nutrition from symbiotic algae
X35	Invertebrate scrapers	XSCRAP	Motile animals that remove solid substratum along with food
X36	Invertebrate browsers	XBROWS	Motile animals that do not remove solid substratum along with food

Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
X37	Passive suspension feeders	XAHERM	Sedentary or sessile; feed on materials suspended in the water column, passively collecting food brought by ambient water current
X38	Active suspension feeders	XSPONG	Sedentary or sessile; feed on materials suspended in the water column, actively create a water current to bring food through the food gathering apparatus
X39	Microbrowsers (meiofauna)	XMEIO1	Live on or in the sediment or reef framework and feed by passing sediment through their gut (all are less than 2 mm. in smallest diameter)
X40	Macro-deposit feeders	XDEPOS	Feeds by passing sediment through its gut (more than 2 mm in smallest diameter)
X41	Sedentary micropredators	XPRED1	Sessile or sedentary; capture individual prey organisms passing in the water.
X42	Predators on small prey	XPRED2	Motile animals that capture small invertebrates and/or vertebrates

X43	Predators on medium prey	XPRED3	Motile animals that capture medium-sized invertebrates and/or vertebrates
X44	Micropredators (meiofauna)	XMEIO2	Live within the sediment or in the reef interstices and capture small micro-browsers and/or other micropredators.
X45	Parasites/pathogens	XIPARA	Relatively sedentary predator deriving its nourishment from one (or very few) prey individuals
X46	Parasite pickers	XPICKI	Motile animals that remove parasites from other animals
X47	Invertebrate eggs attached to reef	XBEGGI	Attached invertebrate eggs
<u>Vertebrates</u> (11)			
X48	Grazers	XGRAZV	Feed by scraping the substrate and in so doing remove a portion of the substrate
X49	Browsers	XBROWV	Feed by nipping the substrate but do not remove portions of the substrate
X50	Plankton feeders, bottom	XPLNKB	Feed on epibenthic plankton, regardless of their position in the water column

Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
X51	Plankton feeders, midwater	XPLNKM	Feed on holoplankton neuston regardless of their position in the water column
X52	Predators, small	XPREDS	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size less than 50 mm standard length
X53	Predators, medium	XPREDM	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size 51 mm to 250 mm standard length
X54	Predators, large	XPREDL	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size 251 mm to 500 mm standard length
X55	Predators, top	XPREDT	Feed on vertebrates or invertebrates by methods other than browsing or grazing. Size 501 mm and greater
X56	Parasite pickers	XPICKV	Feed on vertebrate ectoparasites
X57	Detritus feeders	XDETV	Feed on detritus

X58	Attached fish eggs	XBEGGV	Vertebrate eggs which are attached to the substratum or superstrate, brooded or guarded (i.e., non-pelagic)

Detritus/Nutrients (21)

X59	NO_3	XNO3	Dissolved nitrate
X60	NO_2	XNO2	Dissolved nitrite
X61	NH_3	XNH3	Dissolved ammonia
X62	Dissolved organic carbon	XDOC	
X63	Suspended detritus	XDETR1	Smaller than 10 u
X64	Suspended detritus	XDETR2	10-100 u
X65	Suspended detritus	XDETR3	Greater than 100 u
X66	Trapped detritus	XDETR4	Detritus that falls to the bottom or moves by saltation along the bottom
X67	Dissolved organic nitrogen	XDON	
X68	Dissolved inorganic PO_4	XPO4	
X69	Dissolved organic P	XDOP	
X70	Dissolved O_2	XO2	
X71	Interstitial dissolved NO_3	XINO3	

Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
X72	Interstitial dissolved NO_2	XINO2	
X73	Interstitial dissolved NH_4	XINH3	
X74	Interstitial dissolved organic C	XIDOC	
X75	Interstitial particulate organic C (dead)	XIDET	
X76	Interstitial dissolved organic N	XIDON	
X77	Interstitial dissolved organic P	XIDOP	
X78	Interstitial dissolved PO_4	XIPO4	
X79	Interstitial dissolved O_2	XIO2	
<u>Geology</u> (9)			
X80	Dissolved inorganic C	XDISOL	Grams carbon, dissolved in the seawater, in the form of CO_2, HCO_3- and CO_3. In motion.

X81	Suspended inorganic C.	XSUSP	Grams carbon, suspended in the seawater, in the form of fine $CaCO_3$. In motion.
X82	Bedload inorganic C	XBED	Grams carbon in the form of coarse $CaCO_3$. In motion, on or near the sea floor.
X83	Frame inorganic C	XFRAME	Grams carbon in the form of $CaCO_3$, representing the rigid framework of the reef
X84	Non-frame/non-sediment inorganic C	XORG	Grams carbon in the form of $CaCO_3$, tied up in living non-frame organisms
X85	Inorganic C in rubble	XRUBBL	Sediment. Grams carbon in the form of $CaCO_3$ in the loose sediment. Greater than 4 mm.
X86	Inorganic C in sand	XSAND	Sediment. Grams carbon in the form of $CaCO_3$ in the loose sediment, 62 u-4 mm
X87	Inorganic C in mud	XMUD	Sediment. Grams carbon in the form of $CaCO_3$ in the loose sediment less than 62 u.
X88	Interstitial dissolved	XH2O	Grams carbon dissolved in the interstitial waters of the sediment in the form of CO_2, HCO_3 and CO_3.

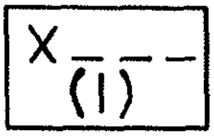
Table 1. List of Model Compartments and Their Characteristics

Compartment Number	Compartment	Mnemonic Name	Characteristics
Terrestrial Phenomena (16)			
X89	Photosynthetic plants	XPPHOT	Agents of primary productivity of carbohydrates
X90	Nitrogen-fixing plants	XNFIXP	Remove N_2 from the atmosphere and add it to the nutrient pool
X91	Nitrogen-transforming plants	XTRAN	Oxidize or reduce nitrogen compounds
X92	Decomposing plants	XPDECM	Convert all other organisms or organic materials into available nutrients, CO_2, and water
X93	Seabirds	XSBIRD	Eat fish from the reef and from the open ocean, and thus transfer nutrients to the cay system from both these sources
X94	Decomposing animals	XADECM	Active in reducing the complex compounds of which plant and animal material is made into soluble, available compounds useful as nutrients for autotrophic plants
X95	Other land animals	XALAND	Herbivores, carnivores, and predators

X96	Nitrogen	XNIT	Dissolved N compounds existing in soil-water and in ground-water
X97	Phosphorus	XPHOS	Exists in calcium carbonate deposits in cay sediments and in soluble forms in soil- and ground water
X98	Calcium	XCAL	Dissolved from sediments and brought in by spray and in bird excrement
X99	Potassium	XPOTAS	In salt spray and in plant and animal detritus and bird excreta
X100	Other mineral nutrients	XMINER	Elements essential in small or trace amounts
X101	Soil water	XSURWT	Interstitial water and films on soil particles
X102	Ground water	XGRDWT	All free liquid freshwater in the system, in the form of a Ghyben-Herzberg lens within the mass of cay sediments
X103	Sediments	XSED	Cays are entirely constructed of sediments that originated on the reef
X104	Organic C	XORGC	Dissolved organic matter leached from or excreted by plant and animal tissues or wastes

Figure 1

Symbols for feedback dynamics diagrams

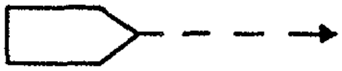


Designates a compartment, or a functional group (gC m-2).

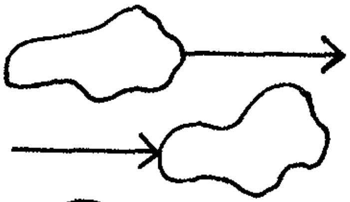
Material flow. This would be fluxed grams carbon or nutrients (gC m^{-2} day^{-1}).

Flows are controlled by "valves".

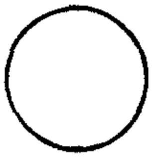
A dashed line is information.



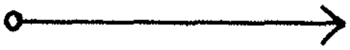
This symbol is a decision function, which serves to integrate information about influences on a flow.



In addition to flows between compartments, material may come from a source, external to the system of definition, or be sequestered in an external sink.



An open circle with a name in it is a variable which comes from outside the system of reference (e.g., sunlight).



This symbol is used in the illustration of small compartment groupings or submodels to show flow from a compartment within the system of definition, but not of interest in the present diagram.

This symbol shows a flow from a compartment to another compartment within the system of definition but not of interest in the present diagram.

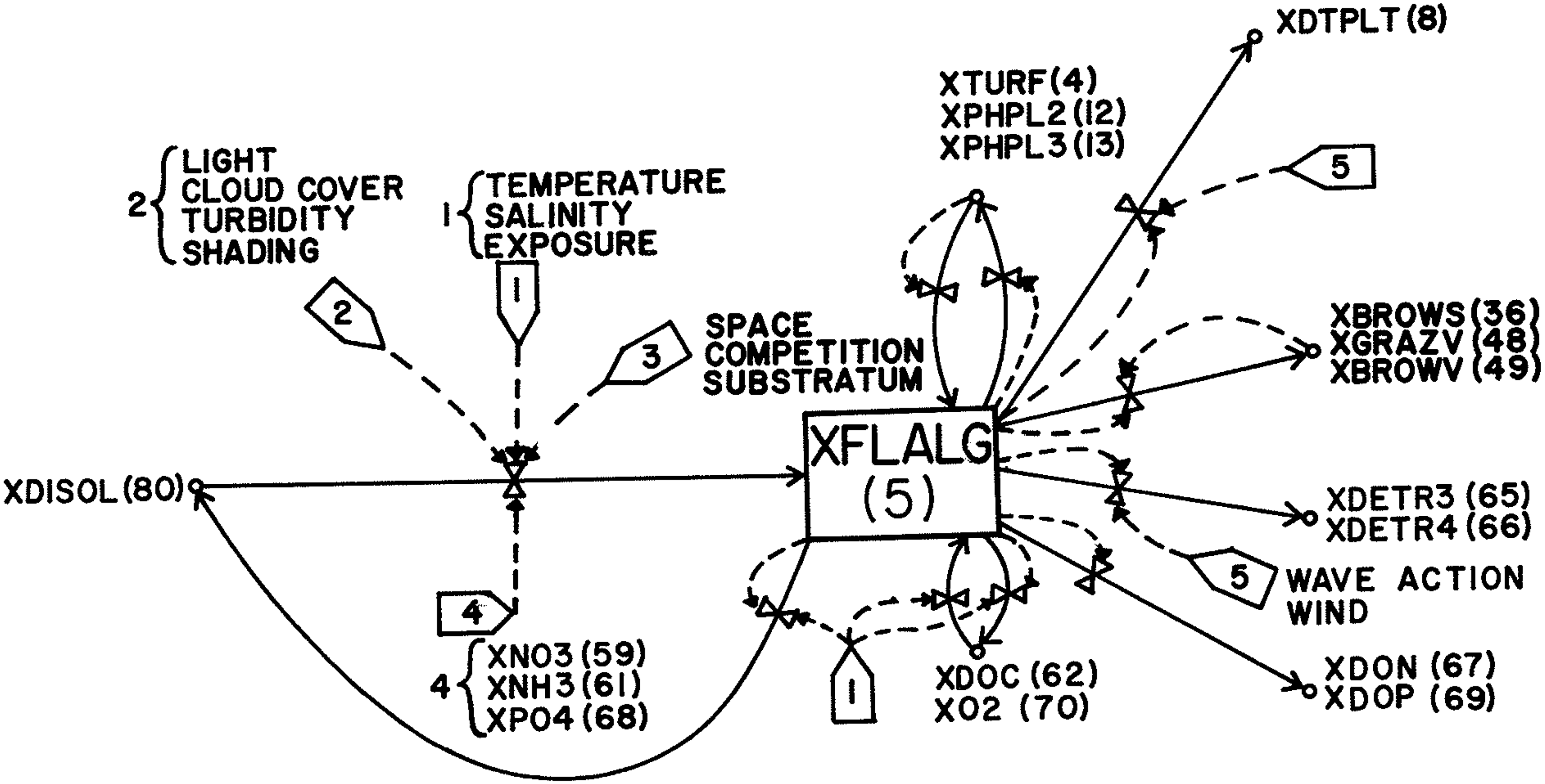


Figure 2. Diagram representing the fleshy macro-algal compartment and its relation to other compartments.

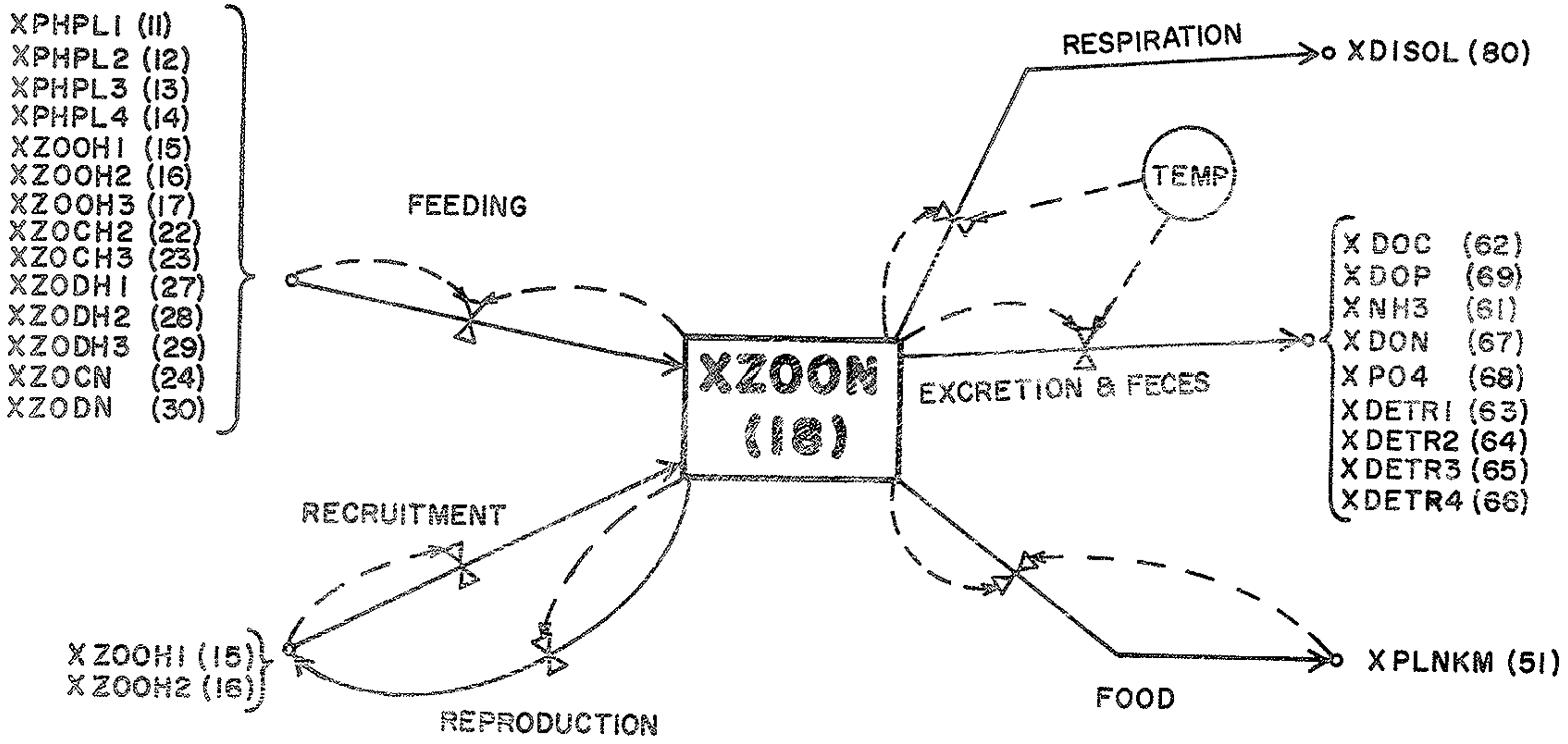


Figure 3. Diagram representing the neuston omnivore compartment and its relation to other compartments.

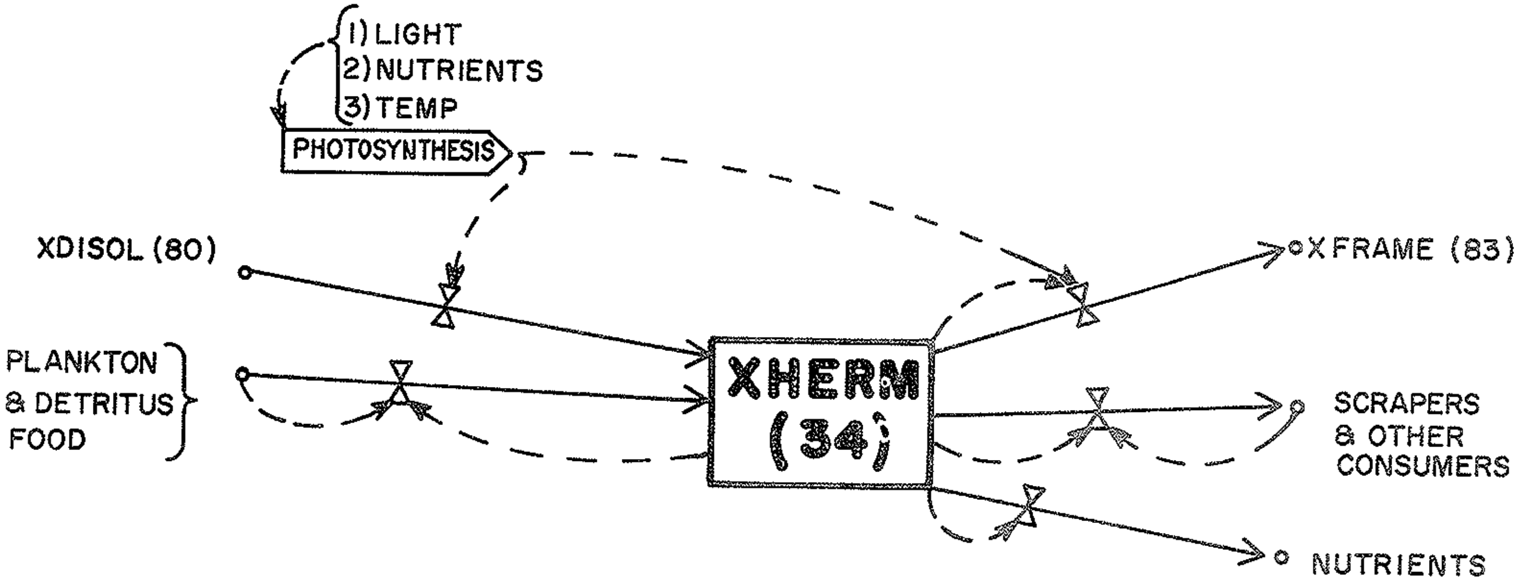


Figure 4. Diagram representing the animal-plant symbiont (hermatypic coral) compartment and its relation to other compartments.

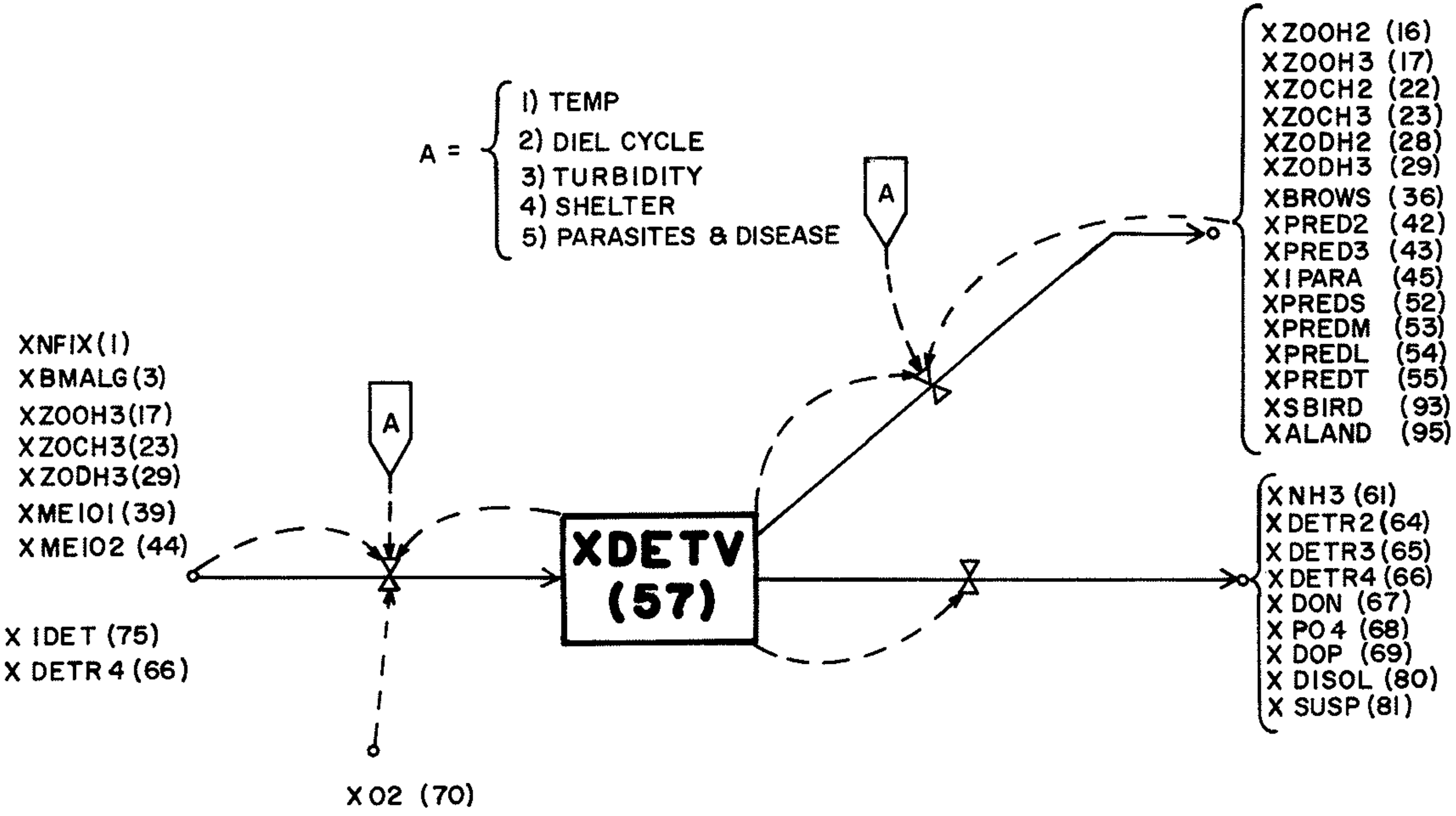


Figure 5. Diagram representing the detritus feeder compartment and its relation to other compartments.

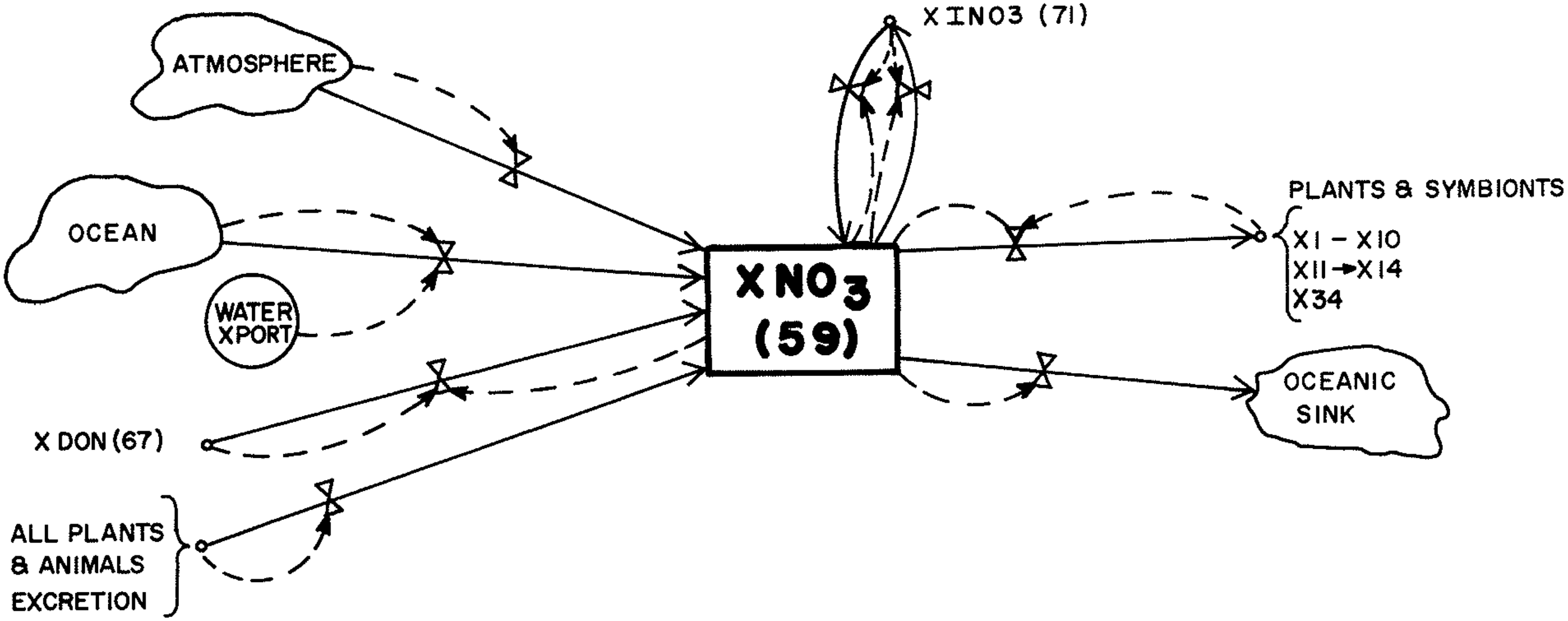


Figure 6. Diagram representing the dissolved nitrate compartment and its relation to other compartments.

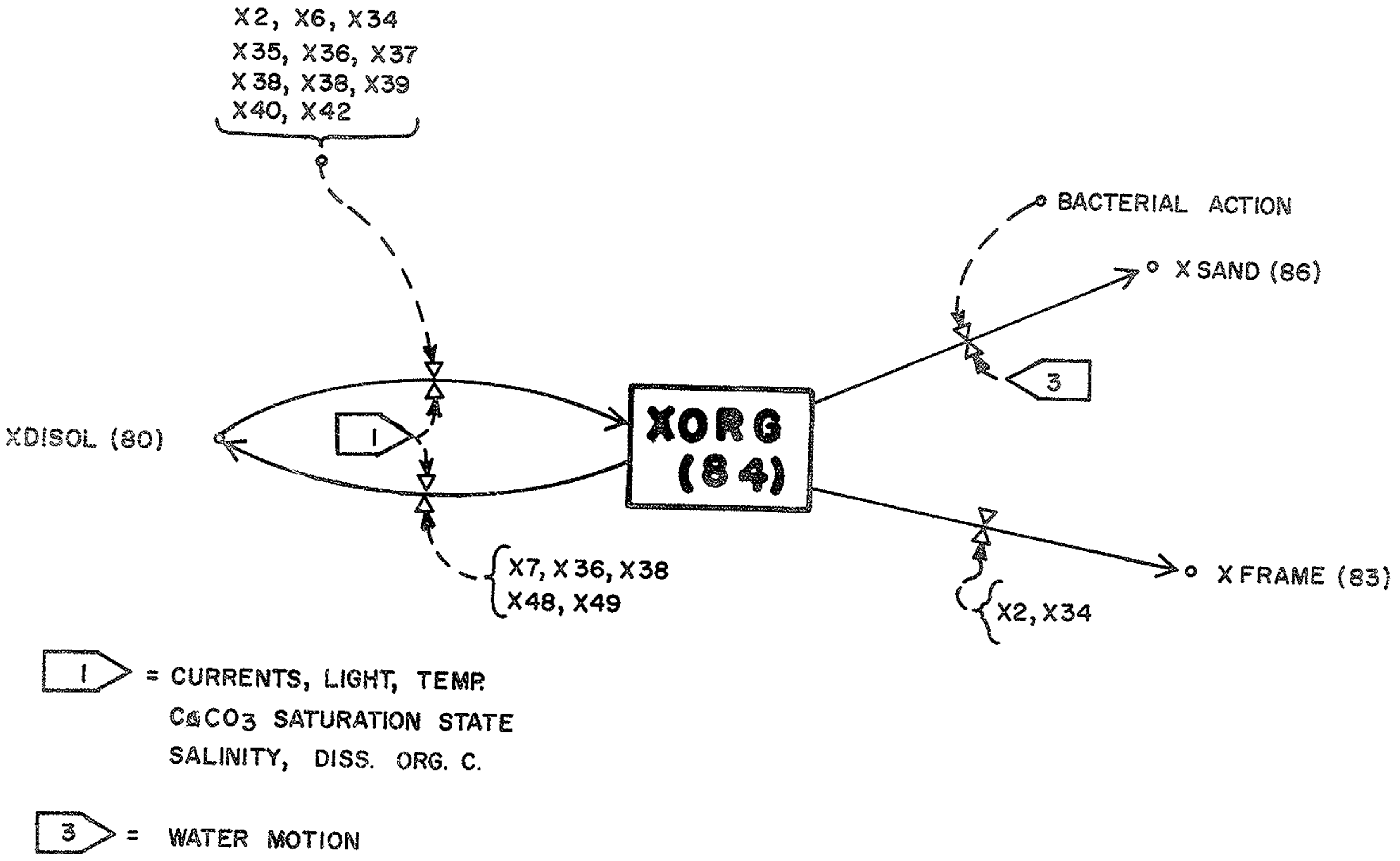


Figure 7. Diagram representing the non-frame/non-sediment $CaCO_3$ compartment and its relation to other compartments.

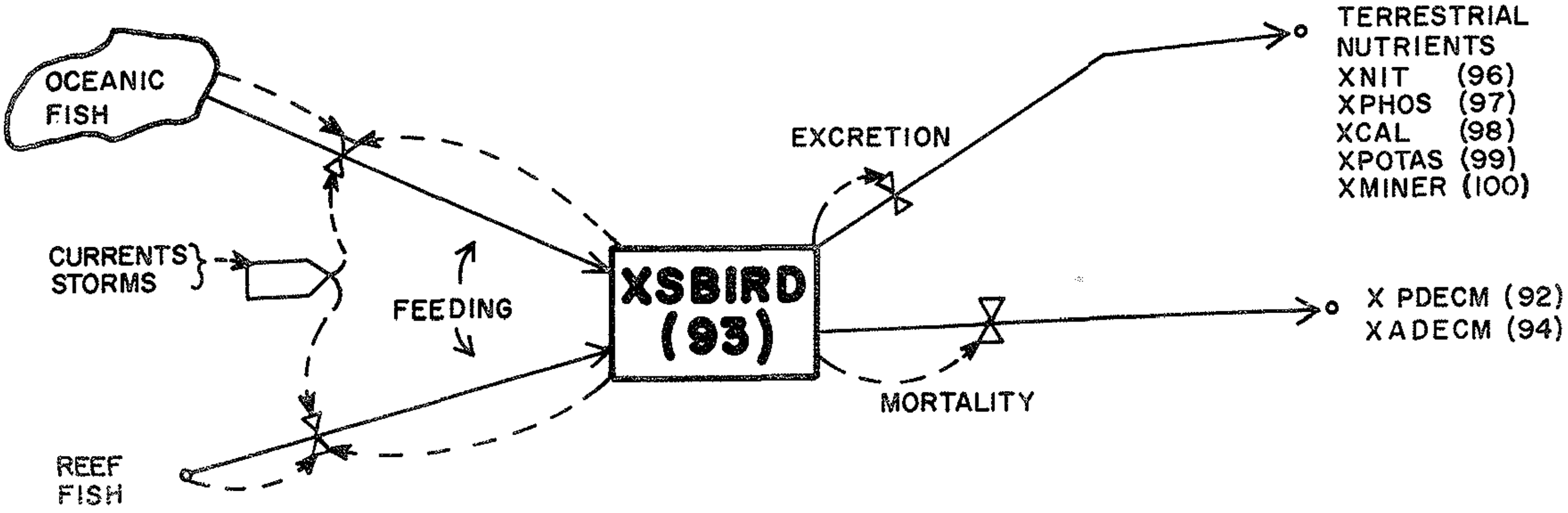


Figure 8. Diagram representing the seabird compartment and its relation to other compartments.

Figure 9. CITRE preliminary ecosystem matrix; reef-flat submodel. The dots indicate carbon or carbon-equivalent flows from compartments on the left to compartments along the top. Blanks indicate no connectivity, and the question marks indicate possible carbon flow between various organic compounds and benthic plants.

A COMPARATIVE SURVEY OF CORAL REEF RESEARCH SITES*

Arthur L. Dahl, Ian G. Macintyre, and Arnfried Antonius

The complexity of coral reef environments has long attracted scientific interest, but as yet few if any research programs have compared reefs from different areas or oceans with a view to understanding the overall functioning of a reef ecosystem. Plans for such programs recently were initiated at the Smithsonian Institution, and it was found that in the undertaking of an interdisciplinary investigation of reef ecosystems, the first critical step is to choose research sites that can meet stringent scientific criteria.

The Smithsonian's comparative information on potential reef research sites in both the Caribbean and Pacific is being presented here in the hope that other investigators will find it useful in planning future reef studies. The data were originally compiled as a report on the research site selection process for the Smithsonian programs, and this has largely determined the present format. The observations are primarily qualitative in nature, presenting a broad view of comparative reef structure and composition. Their value lies in their common perspective, having been compiled by a closely integrated site selection team whose members, within a short time, visited many coral reef areas throughout the Caribbean and much of the Pacific, applying common criteria to achieve a common goal.

The site search was conducted for two programs of the Smithsonian Institution. The first, Investigations of Marine Shallow Water Ecosystems (IMSWE), was organized within the National Museum of Natural History with the support of the Smithsonian Environmental Sciences program to conduct an integrated biological and geological analysis of coral reef communities. The second was to be a much larger, multi-institutional program, the Comparative Investigations of Tropical Reef Ecosystems (CITRE), developed under the auspices of the Smithsonian Office of Environmental Sciences with a planning grant from the International Decade of Ocean Exploration Office at the National Science Foundation. The plans for the CITRE program included the development of a complete systems analysis model of the reef ecosystem based on energy and material flows through various reef components. For both programs, the scientific advantages and greater research potential of a scientifically "ideal" reef site were given first priority, with purely logistical considerations

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* Investigations of Marine Shallow Water Ecosystems (IMSWE) contribution No. 3; supported in part by the Comparative Investigations of Tropical Reef Ecosystems project under NSF Grant No. GX-28676 as part of the International Decade of Ocean Exploration program.

considered secondarily, and thus a fresh look was taken at many potential reef research areas with the context of the programs in mind. An "ideal" reef was considered to be one that is subject to little external stress, and that is characterized by as many of the scientific criteria as possible.

Since the criteria by which sites were judged have a crucial bearing on the conclusions of the site analysis, they are outlined below in some detail:

1. Ample development of all characteristic reef zones, from the "reef flat" to deep water communities in depths of 50 to 100m.

2. A steep fore-slope, to facilitate field observations by telescoping the zonation.

3. Vigorous reef growth where interactions with the surrounding water mass can be measured and with a good geological record of past development.

4. Unidirectional current flow for periods long enough to permit cross-reef metabolic studies of the type successfully used at Eniwetok (Johannes _et_ _al_. 1972).

5. No overriding unique characteristics with respect to the reefs in the same area.

6. Freedom from major terrestrial, human, or natural catastrophic influences in the present or recent past.

Some practical criteria could not be ignored:

1. Sufficient accessibility to meet the needs of a large program.

2. A harbor and some accommodations and facilities, or the possibility of developing these at reasonable cost.

3. Availability of research vessel support.

4. Probability of a stable government with a favorable attitude towards the program.

5. Suitability for research needs such as multiple sampling, monitoring with shore-based instrumentation, drilling for geological samples, etc.

Since the published literature has only scattered information on many of these features, a questionnaire (Fig. 1) was developed and sent to numerous scientists with field experience in the Caribbean and the tropical Pacific. The response was generally good, particularly for the Caribbean, and provided many suggestions for potential coral reef research sites. Following preliminary evaluation of the questionnaires, survey teams were sent to the most promising reef areas to investigate their appropriateness in terms of the established criteria. The standardized reports of the survey teams, based primarily on their first hand observations, make up the body of the present paper. For the sake of brevity, no attempt has been made to cite the many earlier published reports on the areas described.

Reef descriptions were compiled from field notes and photographs. At least one, and generally two or more of the authors participated on all survey teams in order to provide a basis for valid comparative judgements. In all instances the surveys focused on the set criteria although additional details included in the reports may reflect the special interests of individual team members rather than the unusual prominence of a particular group. The conclusions in terms of site preference, were conditioned by the criteria for the proposed ecosystem programs, and would differ if other factors were to be included.

Charges for facilities or transportation, where given, are those at the time of the surveys (generally 1971) and are included only where such information is difficult to obtain to give a rough measure of practicality.

For convenience and clarity, and Caribbean and Pacific sites are treated separately. The Pacific survey was inevitably less thorough, and many other areas warrant detailed examination. The Indian Ocean and more distant Pacific areas such as Australia were excluded as being impractical for a U.S.-based program.

CARIBBEAN AREA

Until recently, Caribbean coral reefs were generally considered inferior to their Indo-Pacific counterparts, mainly because previous studies concentrated on the southern Florida and northern Bahama area (e.g. A. G. Mayor; T. W. Vaughan), which is noted for its marginal coral-reef development. Recent investigations, however, indicate that this earlier assessment of Caribbean reefs is not altogether accurate. Although reef growth in the Caribbean is accomplished by considerably fewer coral species than in the Indo-Pacific, the reef construction processes are comparable. In other words, the same variety of reef types occur in both oceans, as well as an overall similarity in zonation with depth.

Data on potential research sites were compiled for the Caribbean Sea and areas to the north. Regions of coral growth in the southwestern Atlantic, south of the barren area of heavy sedimentation off the Orinoco and Amazon rivers, were excluded from consideration owing to logistical problems and lack of scientific justification (see Laborel, 1967). Three sources of data were used: (a) the literature; (b) standard questionnaires sent to experienced workers in the Caribbean region; and (c) report from the site-survey teams. Information from the questionnaires is condensed in Table 1.

From accumulated information and the personal reports of program members, a number of sites were selected for detailed field examination, including Acklins Island (Bahamas), St. Croix (U.S. Virgin Islands), Discovery Bay (Jamaica), Glover's Reef (British Honduras) and the San Blas Islands (Panama). The data in Table 1 incorporate the conclusions of the survey team reports, which follow.

Acklins Island, Bahamas*

The reefs off the north and east coast of Acklins Island (22°30'N 74°00'W) in the eastern Caribbean were surveyed during two visits; the first on Oct. 20-24, 1970 by a two-man team, and the second from April 13-23, 1971 by an eight-man team.

Acklins Island is part of the Crooked Island District of the Bahamas, but in fact is separated from Crooked Island by "The Going Through", a tidal channel (Fig. 2). The nearest populated center is Nassau, and from there access to Acklins is by small plane or boat. An old airport at Pinefield Point will soon be replaced by the new one under construction at Pompey Bay. At present, charter airlines land on a road near this bay. Apart from this service, two weekly flights are available from Nassau to Crooked Island. The trip to Acklins is completed by taxi and ferry (small outboard).

A 27 m vessel based in Chester on northern Acklins is used primarily for shipping and ferrying from Nassau to Chester, but would be available for charter at $100/day, and it could feasibly be considered for a floating hotel or ferry for reef diving. Small boats are readily available, but outboards are not.

The population of Acklins is sparse and scattered along the western and northern coasts. Only a few settlements can be called communities. The cost of living is very high because nearly all commodities are imported. Local facilities for visitors are few and also expensive (e.g. a small cottage with barest essentials costs $11(US)/day/person, and a half-ton truck $24/day with driver). A research team would probably have to bring "bed and board" with it.

The island is composed of Pleistocene calcarenite, apparently predominantly oolitic material. Its topography is relatively flat but a series of striking "fossil dune ridges" (up to 30 m relief) parallel the present coastline. The water table is close to the surface (2-3 m) so that fresh water is readily available. The soil is very thin except in some depressions. Most of the vegetation is a heavy growth of low brush, generally about six to ten feet high, but there are a few scattered trees (coconut, mahogany, casuarina and tamarind). Mangrove swamps are well developed on the northern end of the Bight of Acklins.

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*Field survey: October 20-24, 1970, by W. H. Adey, and I. G. Macintyre. Second field survey: April 13-23, 1971, by W. H. Adey, A. Antonius, A. L. Dahl, P. M. Kier, I. G. Macintyre, M. E. Rice, and T. R. Waller.

First Visit: October 20-24, 1970

The eastern and northern areas of Acklins were investigated as well as the central lagoon area (Bight of Acklins). Heavy swells created rough weather conditions and turbidity for two days, a condition common in the area from October to April. The following sites were examined:

1. West side of Atwood Harbour, north coast of Acklins Island.

The patch reef here is no more than 15 m from shore, and it abounds with fish; a hawk's bill turtle also was observed in the area. Much of the reef surface is covered with crustose coralline algae, especially of the genera Porolithon and Neogoniolithon but large growths of Montastrea annularis, Acropora palmata, Millepora, Porites astreoides, and Porites porites were also present.

The sandy bottom of the harbor, where examined, had well-developed Thalassia beds with large heads of Neogoniolithon strictum. In the southwest where the current was strong only a thin sediment cover was present over the rock ledge and small heads of Siderastrea radians and Favia fragum occurred.

2. Patch reef directly shoreward of bank barrier reef off east coast of Acklins Island, opposite Golden Grove.

The reef here is about one and a half kilometers offshore. The abundant patch reefs in this area are surrounded by a sandy bottom and have about 6 m of relief. A very high percentage of the reef surface is covered by Porolithon, Neogoniolithon and other corallines. No large caverns were observed as described elsewhere on the Bahama Banks (Storr, 1964), but there were "overhangs" here and there. Large colonies of Acropora palmata and Millepora were observed along with abundant but small colonies of Agaricia agaricites. Additional common corals include three species of Diploria, Dichocoenia stokesii, Porites astreoides, and Montastrea annularis. A great abundance of alcyonarians was also noted.

3. Inner edge of bank barrier reef, northeast coast of Acklins Island off Pinefield Point.

Going seaward from the patch reef there is a zone of abundant Montastrea annularis and Diploria coral heads leading to the turbulent inner edge of the reef flat, where there are large overturned growths of Acropora palmata (some were live growths) and large growths of Millepora. Rock surfaces and coral debris are heavily coated with coralline algae. Fish were abundant, including a number of different types of parrot fish, some quite large, which seem to inhabit an open network of small tunnels under the coral-rock floor.

4. Off Spring Point on the west coast of Acklins Island in Acklins Bight.

For a distance of about 150 m from shore a very thin layer of sediment covers the smooth rock pavement. Rich algal growths of Halimeda, Penicillus, Batophora and Acetabularia were observed, along with two species of corals: Siderastrea radians and Flavia fragum. A few colonies of Manicina areolata were also noted.

TABLE I: Questionnaire Response - Caribbean Area

Site	Reef Structures*	Undisturbed	Accessible	Local Facilities	Political Status+
Colombia					
Islas del Rosario	-	+	0	-	-
Santa Marta	-	0	+	+	-
Curacao	+	0	+	+	+
Venezuela					
Los Roques	-	+	-	0	-
Cubagua, Coche, Margarita, Los Frayles Islas	-	+	-	-	-
Lesser Antilles					
Dominica	+	+	-	-	0
Puerto Rico					
Mona Island	0	+	0	-	+
Virgin Islands					
St. Croix	±	±	+	+	+
Hispaniola					
St. Domingo area	+	0	+	0	-
Jamaica					
Discovery Bay	+	-	+	+	0
Barrier Reef and Cays, Pedro Cays, Pedro Bank Banner Reef	+	+	+	-	0
Grand Cayman	+	+	+	0	0
Bahamas					
Acklins Island	-	+	0	0	+
Andros Island	+	+	+	0	+
Bimini	-	-	+	+	+
Bermuda	-	0	+	+	+
Mexico					
Islas de Lobos	-	+	-	-	0

Site	Reef Structures	Undisturbed	Accessible	Local Facilities	Political Status
British Honduras					
Barrier Reef	+	±	+	-	+
Turneffe Island	-	±	+	-	+
Lighthouse Reef	+	±	+	-	+
Glover's Reef	+	+	+	0	+
Colombian Islands (off Nicaragua)					
Serrana Bank	+	+	-	-	-
Roncador Bank	+	+	-	-	-
Old Providence Island	0	+	-	-	-
St. Andrews Island	-	+	-	-	-
Courtown Cays	+	+	-	-	-
Albuquerque Cays	+	+	-	-	-
Great Corn Island	±	+	-	-	-
Panama					
Holandes Cays, San Blas Islands	±	+	-	-	+

Key + = favorable or present 0 = unknown or possible - = unfavorable or impractical

± = variable

* see selection criteria above, p.

\+ basically the anticipated government attitude towards a large U.S. funded program

Questionnaires and equivalent information on Caribbean sites were supplied by the following: W. H. Adey, A. Antonius, R. W. Bauer, A. L. Dahl, R. F. Dill, J. Geister, P. W. Glynn, L. S. Land, J. C. Lang, I. G. Macintyre, J. D. Milliman, J. L. Munro, R. Pfaff, J. K. Rigby, and K. Ruetzler.

Second Visit: April 13-23, 1971

5. Atwood Harbor, North Coast of Acklins Island (see Fig. 3)

Back Reef

This area is characterized by small patch reefs scattered on a rock platform which generally has a thin sand cover. These protected patch reefs have a relatively dense coral growth consisting primarily of Acropora palmata, Montastrea annularis, Porites astreoides, Agaricia agaricites, Dichocoenia stokesii, Dichocoenia stellaris and Porites porites.

Reef Crest

Coral composition on the lee side of the reef crest is almost identical to that of the patch reefs. However, the remainder of the reef crest is dominantly composed of Acropora palmata and Montastrea annularis which form an open framework marked by the common occurrence of dead overturned coral communities.

Upper Fore-Reef Slope

The dominant characteristic of this area of the reef is a gently dipping rock pavement. The two distinct zones observed are a) barren zone 1.5-6 m and b) grooved zone 6-18 m.

Barren Zone: Predominantly a knobby rock bottom with a thin covering (2 cm) of benthic algae and fine to coarse carbonate sand. Crustose corallines generally are thriving under this algal-sediment cover. Small coral colonies scattered over the rock surface include Diploria strigosa, Siderastrea siderea, Siderastrea radians, Dichocoenia stokesii, Montastrea cavernosa, Montastrea annularis, Agaricia agaricites, Porites astreoides, Porites porites, Colphyllia natans, Isophyllia sinuosa, Meandrina meandrites. Sargassum sp., gorgonians, and Millepora sp. increase noticeably in depths less than 4 m and large patches of boring sponges are common. Scattered shallow (1 m) depressions in the rock pavement have a well-rippled coarse sand or rubble bottom. A few Diadema sp. occur under ledges in the walls of these depressions.

Grooved Zone: The most striking feature of this depth zone is the grooves which are clearly visible in aerial photographs. Off Atwood Harbour they are generally less than 30 m apart and are commonly about 60 m long. The gently dipping rock pavement transected by these grooves is encrusted with a variety of tropical-reef corals, but the colonies are generally small, well-spaced and therefore do not form an interlocking framework. Dominant corals include the following species: Diploria strigosa, Porites astreoides, Siderastrea siderea, Dichocoenia stokesii, Dichocoenia stellaris, Montastrea cavernosa, Montastrea annularis, Favia fragum, Meandrina meandrites, Diploria labyrinthiformis, Colpophyllia natans, Stephanocoenia michelinii. Gorgonians and sponges are also abundant in this depth zone.

The groove system begins in a general depth range of 5 to 10 m as an indistinct labyrinth of channels between the scattered coral growth. In our limited observations we did not find grooves originating as "spoon-shaped incisions" or "erosional pits," as reported for similar features off Andros Island (Newell et al., 1951, p. 25) and off Saipan Island (Cloud, 1959, p. 406).

These indistinct channels coalesce to form a well-defined u-shaped groove which is relatively straight and has a smooth sediment-free surface covered with a thin algal growth and corals here and there. These u-shaped grooves, which are about 10 to 15 m long, widen from 15 cm wide and 15 cm deep to 1 m wide and 1 m deep where they open out into a still deeper and wider sediment-filled groove. In some places, up to three separate u-shaped grooves were noted to be feeding into the same broad sediment-filled one.

The sediment-filled sections are generally about 50 to 60 m long with a maximum width of about 10 m. The lower sediment-filled sections tend to taper into a series of lobes at the outer limit of the grooves. The thickness of accumulated sediment in the troughs was not established; however, at the head of the sediment-filled sections the walls were 2 to 2.5 m high and gradually diminished in relief to about 1 m at the terminus. It is interesting to note that the grooves investigated were completely enclosed with no ready outlet into deeper water for the sediments.

At the head of the sediment-filled sections there is a band 5 m wide of coral rubble which grades down-slope into a well-rippled sand (wave length, 60 to 150 cm, amplitude, 12 to 15 cm). This is an extremely coarse to medium-grained skeletal calcarenite with gravel size material collecting in the ripple troughs. Texture gradation of the sediments continues down the groove so that about half-way down, the gravel is absent and there is simply a poorly sorted, extremely coarse to medium-grained skeletal calcarenite, which in turn grades into a well-sorted medium to coarse-grained skeletal calcarenite at the terminus of the groove.

Without subsurface data it is difficult to establish whether these linear features have been formed by erosion or differential accumulation of organic limestone. Newell et. al. (1951) found that grooves off Long Cay in the Bahamas cut into oolite bedrock, which clearly indicated an erosional origin.

Lower Fore-Reef Slope

This area starts at depths ranging from 12 to 18 m, where the slope of the sea floor increases markedly, and continues to the depth limits of our observations, approximately 40 m.

Large areas of well-developed and diverse deep-water coral communities are predominant in the upper section of this area. Sediment chutes that traverse the coral communities here and there coalesce at depths of 20 to 25 m to form an extensive sand flat. Below this sand flat the corals do not show any appreciable change in species composition but tend to construct large coral mounds covering areas of up to 220 sq. meters with approximately 3 m of relief above the surrounding sand slope.

The dominant corals of the lower fore-reef slope consist of the following species, in order of their abundance: Montastrea annularis, Agaricia agaricites, Montastrea cavernosa, Mussa angulosa, Diploria labyrinthiformis, Meandrina meandrites, Eusmilia fastigiata, Mycetophyllia lamarckiana, Colpophyllia natans, Porites astreoides, Stephanocoenia michelinii, Dichocoenia stokesii, Dichocoenia stellaris, Porites porites, Isophyllia sinuosa, and Diploria strigosa.

East Coast of Acklins Island

6. Off Pinefield Point

The area observed begins at a depth of 20 m where there is a distinct sand flat. Coral heads are sparse and widely scattered, but gorgonians and benthic algae are very common.

Below a depth of 20 m the slope of the sea floor increases and coral growths tend to be restricted to linear ridges which are separated by sand and gravel-filled grooves generally 3 m wide and 1 m deep. The coral assemblage is similar to that of the deep-water coral communities noted on the lower fore-reef slope off Atwood Harbour. Corals give way to a sand and gravel slope at depths of 35 to 40 m.

7. Misconception Rock

Misconception Rock consists of a small (100 sq. m), relatively flat rock pavement (well-sorted fine to medium calcarenite) in the reef tract that is exposed at low tide. It is approximately 1 kilometer north of Creek Point off the east coast of Acklins Island.

The rock surface is heavily pitted and etched, the characteristic erosional form of limestones in the splash zone (Newell et. al., 1951), and the outer edges are covered with a heavy algal growth. Many large gastropods (Livona pica), Diadema sp., and chitons were observed in numerous shallow depressions.

As found in other areas of the Bahamas (Newell et. al., 1951) the bank barrier reefs off eastern Acklins Island appear to be a Holocene reef veneer over pre-existing sand ridges that are exposed above sea level in places.

8. South of Golden Grove

The broad (12 m) platform which is a characteristic feature of the insular shelf off the east coast of Acklins Island separates the reef crest and fore-slope communities by distances of over 1.5 km.

The bottom is a smooth rock pavement which has a thin (1 cm) sediment-algal cover, consisting of a dense benthic algal layer with trapped sand- to silt-sized sediment.

Small coral mounds, having relief to less than 1 m are widely spaced on the rock pavement. Coral heads, for the most part dead, are scattered over this rock surface. Dominant live corals are _Diploria strigosa_, _Eusmilia fastigiata_, _Agaricia agaricites_ and _Dichocoenia stokesii_. Rich epifaunal and infaunal assemblages occur under the live and dead coral material, including the bivalve _Barbatia domingensis_, the gastropod, _Tegula fasciata_, and the echinoids, _Eucidaris tribuloides_, _Arbacia punctulata_ and _Echinoneus cyclostomus_.

Gorgonians are common and some are encrusted by _Millepora_ sp.

Summary

Atwood Harbour would be an excellent location for a base station as it is a good harbour for boats, and the Bahamian government is willing to cooperate with scientists working in their territory. The northeast corner of Acklins Island, east of Atwood Harbour and North of Pinefield Point, is Crown Land and arrangements could probably be made to set this area aside as a research site. The reefs have been relatively unaffected by human activity. Fishing appears to be a minor occupation carried out in a primitive fashion on an occasional basis.

When the new airstrip is completed, accessibility to Acklins Island will be improved with regular weekly flights scheduled for the near future. Bi-weekly flights to Crooked Island are currently available from Nassau.

A number of vacated small houses on the island might be used as accommodation facilities. They might be rented at reasonable rates, but it should be recognized that amenities are lacking.

Apart from some of the small patch reefs, the reefs on the insular shelf are not well developed. The exposure of calcarenite in the reef tract off the east coast (Misconception Rock) indicates that many of the reefs may be veneers over Pleistocene sediment ridges. The shallow reef crests are commonly separated from the fore-reef slope coral communities by a very broad rock platform.

Rough seas common during the months of October through April would prevent work on the reef crest and fore-reef slope during these months.

St. Croix, U.S. Virgin Islands*

St. Croix (17°45'N, 64°40'W) is the largest of the U.S. Virgin Islands, having a surface area of 22 sq. km (45 km long and up to 11 km wide; see Fig. 4). Its population is about 35,000, and apart from

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*Field survey: January 26-28, 1971, by I. G. Macintyre, assisted by H. G. Multer.

tourism, the island supports a few other industries such as bauxite refining, oil refining, and the assembly of wrist-watches.

This island is readily accessible as it is served by several major airlines. Transportation on the island is available through car rental at about $12/day or scooters at $7/day. Boats may be chartered, or rented less expensively through the Fairleigh Dickinson Laboratory. Hotel accommodations are costly, particularly during the winter season, but the marine laboratory has some rooms at reasonable rates for visiting scientists.

Terrestrial Conditions

The topography of St. Croix is "hilly" (maximum relief 355 m, Mt. Eagle). The island is composed of rocks having diverse origins and compositions, primarily Upper Cretaceous volcanic sandstones and mudstones, tuffaceous sandstones, Upper Oligocene montmorillonitic mudstones, and Lower Miocene argillaceous and sandy coral limestones. Despite the abundance of volcanic debris, no volcanoes are present on St. Croix; however, two small igneous bodies (a diorite and a gabbro) intrude the Cretaceous sedimentary rocks. Numerous small dikes are also present in the hilly ranges occurring on the eastern and northwestern sections of the island (Whetten, 1966).

St. Croix Reefs

Although St. Croix has a variety of reef types that would be excellent for scientific study, there appears to be no evidence of a reef marginal to deep oceanic waters, a serious drawback to the selection of St. Croix as a primary site.

1. Bank Barrier Reefs.

As expected, the best developed reefs occur off the eastern or windward coast, and the most striking developments are the bank barrier reefs on the landward edge of the insular shelf; these reefs parallel the northeastern and southeastern coasts for distances of over 5 km.

The bank barrier reef off Tague Bay (Fig. 2, Site 1) has about 5 m relief off the shoreward edge and is approximately 90 m wide. This reef is dominated by Acropora palmata, but an indistinct zonation was noted around the inner edge of the reef, where the base is characterized mainly by Montastrea annularis; the edge by Acropora palmata and large mounds of Porites porites (up to 2.5 m high and 4.5 m wide); and the top by Acropora palmata, Diploria sp., and Millepora sp.

The seaward edge of this reef was not investigated during this brief visit; however the transect (Fig. 6) based on information received from Dr. Multer indicates that this seaward slope drops off to a depth of 14 m and gives a graphic representation of the dominant coral distribution across the reef.

2. Algal Cup Reefs

There was not enough time to investigate the fringe reefs common around most of the promontories along the northeastern coast of St. Croix. However, the nearshore "algal cup reefs" occurring around Cottongarden Point were investigated (Fig. 5, Site 2).

These reefs, which are characterized by pronounced rims and over hangs, have a relief of about 2 m. Their upper surfaces are covered by fleshy algae including *Sargassum* sp. and a few flat colonies of *Porites astreoides*. Chips from these algal reefs, broken off with great difficulty, revealed a dense agglomeration consisting mainly of crustose coralline algae and the distinctive red encrusting foraminifera, *Homotrema* sp.

An unusual occurrence of *Acropora prolifera* in an area of high agitation was noted next to these algal reefs. Abundant algae are present on the sea floor surrounding the cup reefs, notably *Penicillus* sp. and *Halimeda* sp. (sediments are particularly rich in *Halimeda*-derived debris).

3. Buck Island Trail

A rapid survey of the Buck Island National Trail (Fig. 5, Site 3) indicated that this is a well-developed "palmata reef." Although separated from shore by a narrow sandy belt, it can be considered a form of fringe reef.

4. Deep Patch Reef

A deep patch reef directly east of Buck Island (Fig. 5, Site 4) consists of an area of large open frameworks, primarily *Acropora palmata*. This patch reef has a relief of about 8-9 m above its base, which is covered with large heads of *Montastrea annularis*, *Diploria* sp., *Montastrea cavernosa*, and surrounded by a great abundance of alcyonarians. *Millepora* was found coating some of the dead alcyonarian branches.

5. Shelf Edge North of Buck Island

This area was investigated in order to determine whether a shelf-edge reef exists at this location (Fig. 5, Site 5). The reconnaissance was carried out by a towed swimmer, and all observations were made from the surface of the water.

Although no evidence of a shelf-edge reef was found, an interesting transition in bottom characteristics was noted: at depths of about 30 m a series of sediment chutes traverse a relatively steeply dipping (about 10-20°) rock surface that is covered by alcyonarians, sponges, algae and scattered coral heads. From the surface, there appeared to be little relief between the sediment chutes and intervening rock surfaces. The sparsity of corals suggests that reef framework construction was not occurring at this depth. Although a spur and groove system appeared to be present at this location from the air survey, firsthand observations showed that the "buttress systems" described off Jamaica by Goreau (1959) are not present in this area off St. Croix.

Shoreward, the sea floor gradually grades into a rocky bottom having sand patches and scattered alcyonarians, sponges, algae and coral heads. Around depths of 15 m, large scattered colonies of Acropora palmata appear, and directly shoreward there is a zone of Millepora. Abundant colonies of Acropora palmata are present in depths of 3-6 m along with other corals such as Montastrea annularis and Diploria sp.

6. Other Reefs off St. Croix

During the R/V Eastward cruise, two other reef types were investigated in this area: inactive and submerged reefs.

The most prominent reef type off St. Croix is the inactive reef, of which Lang Bank is the best example. Inactive reefs are reefs that occur within depths of potential vigorous coral growth, but which are characterized by an absence of reef framework construction. Lang Bank, situated at the shelf edge east (windward) of St. Croix (Fig. 5) at depths of around 9-12 m, is ideally located for active barrier reef development. From limited bottom photographs, however, it is evident that an interlocking reef framework does not occur on this ridge which is covered with abundant alcyonarians and sponges and large sand patches, but only scattered coral heads. Dredge hauls from this area contained abundant alcyonarians, sponges, and small colonies of Porites porites, Porites astreoides, Diploria sp., Agaricia agaricites, Stephanocoenia michelinii, Acropora cervicornis, and Millepora sp. Coral debris heavily encrusted by coralline algae was also abundant. Meyerhoff (1926) suggested that the topography of the eastern St. Croix insular shelf is related to subaerial erosion of a Tertiary reef complex.

Submerged ridges were noted on bathymetric profiles off the southern coast of St. Croix, established at depths of about 40 m. These ridges are interpreted to be submerged reefs that were established in relation to a pre-existing lower sea level, and that occur in depths greater than are commonly associated with vigorous growth of tropical reef corals. They appear to be common features off most eastern Caribbean islands (Macintyre, 1972).

Pollution

Extensive pollution of the marine environment is occurring off the southwestern coast of St. Croix, where a garbage dump, bauxite plant and oil refinery are located (see Fig. 4). It is expected that pollution levels will rise in the near future because sewage will be piped from Christiansted (the island capital) over to this side of the island. Despite the unfortunate aspects of this circumstance, it would offer an opportunity for detailed comparison between polluted reefs off this coast and the non-polluted reefs to the east. Such studies might yield valuable information on the degrees of stress imposed on reefs by pollution, and how well they survive it.

West Indies Laboratory of Fairleigh Dickinson University

The West Indies Laboratory is located on Tague Bay, on the northeastern coast of St. Croix, and it overlooks Buck Island National Park (Fig. 5). This laboratory offers scientific facilities for researchers as well as some accommodations, when available. There are 4 small laboratories equipped with aquaria, and an outdoor aquarium area supplied by a dual saltwater system.

The Laboratory also owns two 4.9 m (16') Boston whalers and three 5.8 m (19') Rabollo boats which may be rented by visiting scientists at a minimal cost. Owing to an extensive summer program, visiting scientists are advised to plan visits for less crowded periods of the year.

An affiliate program is gradually being developed which will permit outside universities to have faculty and research space as well as teaching space privileges on the basis of a yearly charge.

Summary

Apart from the polluted reefs on the south coast of St. Croix, the coral reefs around this island have been relatively untouched by man because there is little need to exploit them for food. However, the absence of a reef marginal to deep water in the region is a drawback, as is the general lack of well-developed reef-flat zones on the shelf reefs (a distinct disadvantage in drilling operations).

On the other hand, the numerous advantages of this location make St. Croix worthy of consideration as a research site, particularly for a smaller scale program. The cooperation and available facilities of W.I.L. would make operational costs on St. Croix considerably lower than elsewhere in the Caribbean; at the same time, W.I.L. would probably facilitate detailed and sophisticated experimentation which might be difficult to undertake and complete at less well-equipped sites. Following is a brief outline of the merits of St. Croix as a study site:

1. Facilities of the West Indies Laboratory, notably;
   a. inexpensive accommodations;
   b. fish pens;
   c. outdoor and indoor aquaria supplied by all P.V.C. non-toxic dual saltwater systems and backed up by independent emergency power unit;
   d. laboratory and office space; motor boats;
   e. reference library with microfilmed periodicals and print-out service;
   f. radiocommunication with field units;
   g. monitoring service which W.I.L. intends to establish off northwestern coast.

2. The laboratory staff would be able to assist in servicing field equipment. Technicians working on Navy projects on western St. Croix might also be enlisted to aid with electronics problems.

3. Jet airport with daily flights to Washington, Miami, and New York costing less than $200 return. San Juan, P. R., is 45 minutes away by hourly scheduled flights.

4. A variety of reef types are present, including fringing, bank barrier, inactive, submerged, algal cup, polluted and non-polluted reefs.

5. Because St. Croix is an American territory there should be a minimum of red tape involved in having a section of reef tract set aside for scientific investigation; ground has already been broken with the Buck Island National Underwater Park.

6. There would be less difficulty in shipping equipment to a U.S. island, and financial advantages of a duty-free island in the purchase of equipment.

Discovery Bay, North Coast of Jamaica*

Jamaica, an independent member nation of the British Commonwealth, is a large tropical island located in the northwestern Caribbean Sea at the extreme northwest tip of the Nicaraguan Rise. It is 140 miles long and 60 miles wide and has mountain peaks in excess of 7,000 feet above sea level. Fringe reefs extend discontinuously along the north coast and are noted for their coral species diversity (Goreau and Wells, 1967).

Discovery Bay (18°30'N, 77°25'W), the site of the Discovery Bay Marine Laboratory, is located about midway along the northern Jamaica coast, and it lies adjacent to a well developed section of the fringe reef (Fig. 7). The reefs in Discovery Bay (Fig. 8) generally may be divided into the following major zones (after Kinsey, 1970; J. Lang, personal communication, 1971).

Lagoon Zone: This zone is about 400 to 500 m wide, and about 1 to 3 m deep. It has a submerged sinkhole 25 m deep, but the walls and bottom are mud covered and there are no rock exposures. Loose sand is the main constituent of the floor in the lagoon zone, and this precludes development of sessile benthic epifauna. Here and there, bare rock patches and coral heads occur with scattered gorgonians. Corals and rocks become more abundant seaweed, toward the rear zone.

Rear Zone: The inshore face of the reef crest makes up this zone, which is about 0.3 to 2 m deep. Apart from the reef flat, this is the only reef area strongly affected by tidal fluctuations and characterized by strong water movement. Bottom types range from calcareous sand, and sand and coral fragments, to bare coral-rock exposures. Living coral is

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* Field survey 21 to 28 July 1971 by I. G. Macintyre, assisted by P. Dustran, E. A. Graham, L. S. Land, and J. C. Lang.

common but never covers the bottom entirely. Richest coral growth occurs in the area abutting the shoreward face of the reef flat.

Reef Flat: The reef flat comprises the area just submerged at low tide. It is subjected to strong breaking wave action as well as occasional exposure to air and rainwater. The main component is a reticulate ridge-like structure 5 to 20 m wide, composed of dead colonies of *Acropora palmata*, which separates the lagoon from the sea. The unconsolidated skeletons of *A. palmata* form a lattice-like structure. Protected areas within the reef are locations for a restricted gorgonian fauna. Channels and pools in the reef flat may reach a depth of 2 m.

Palmata Zone: This narrow zone, 5 to 10 m wide, abuts the seaward face of the reef flat and extends seaward to a depth of 4 to 6 m. The full force of wave action occurs in this zone where *Acropora palmata* is predominant. The bottom consists of coarse sand and sand-scoured coral rock littered with dead and fallen *A. palmata* colonies.

Barren Zone: A band of reduced coral diversity occurs seaward, and it can be up to 20 m wide, ranging from 5 to 8 m in depth. The most common organism, *Diadema antillarum*, which grazes on the bottom, may be responsible for the scarcity of sessile organisms. Isolated colonies of *A. palmata* occur along with small heads of *Diploria strigosa*, *Montastrea annularis*, and *Millepora complanata*.

Buttress/Mixed Zone: In the Ocho Rios area studied by Goreau (1959) as well as other areas along the northern coast, the buttress zone merges abruptly with the barren zone. Although the component species remain the same, Discovery Bay differs slightly in architecture from the other areas in that the normal buttress zone becomes flatter, with a gradual increase in coral species and coral size. This "mixed" zone is 15 to 40 m wide, and slopes from 6 to 15 m in depth. *Montastrea annularis*, one of the dominant corals in the buttress formations, occurs in Discovery Bay in the form of huge rounded masses scattered in fields of *A. cervicornis*. Diploria spp. is also common, along with *Dendrogyra cylindrus*, *Agaricia agaricites*, *Porites* spp., and *Colpophyllia natans*. This is an area of rich gorgonian diversity.

Cervicornis Zone: *A. cervicornis* becomes dominant seaward, and *M. annularis* reduced to small patches. This zone, which is 30 to 100 m wide and 20 to 25 m deep, is characterized by huge mounds of *A. cervicornis* 15 to 40 m wide with their long axis normal to the axis of the reef crest. These reefs (1 to 5 m relief) are separated by sand channels 3 to 50 m wide. Upper surfaces of these reefs are generally level, and they gradually slope to about 10 m in depth at their seaward extremity, where they drop abruptly to sand level at about 20-25 m on their seaward face. Consolidated coral rubble covered with living *A. cervicornis* is typical (Land and Goreau, 1970). Other coral species appear on the steep seaward faces and lateral reef flanks adjacent to the sand areas, including *Porites astreoides*, Mycetophyllia sp., and *Montastrea cavernosa* as well as *M. annularis*. In Discovery Bay the *A. cervicornis* reefs drop steeply at the seaward edge to a zone of sand about 40 to 60 m wide.

Upper Sill Reefs: A series of elongate but discontinuous reefs are established at 40 to 50 m depths, and rise to about 25 m depths. Platy colonies of Montastrea annularis are dominant along with a mixed coral community composed primarily of Agaricia lamarcki, Mycetophyllia sp., other species of Agaricia, Scolymia sp., fleshy algae, sponges and antipatharians.

Fore Reef Slope: The platy growths of Montastrea annularis along with Agaricia sp. and abundant sponges, gorgonians and antipatharians continue down the reef fore slope to a depth of 50 m, below which either Agaricia sp. dominate, or mixed coral growths occur consisting of Agaricia sp., Madracis sp., Montastrea cavernosa, and Mycetophyllia sp.

Lower Sill Reefs: This zone, at depths of 60 to 70 m, is characterized by either elongate ridges having less than 10 m relief or isolated rocky outcrops. Corals occurring on these features include Agaricia sp., Montastrea cavernosa, Madracis sp., and Mycetophyllia sp. Sponges and antipatharians are also abundant.

Deep Fore Reef Slope: Scleractinian corals become increasingly sparse with depth, and the dominant benthic organisms are sclerosponges and demosponges.

The Discovery Bay Laboratory

The Discovery Bay Laboratory is jointly operated by the Marine Sciences Research Center of the State University of New York, and the University of the West Indies. The Laboratory site consists of .06 sq. kilometers (15 acres) of coastal property.

Facilities have been designed primarily for coral-reef research with emphasis on on-site investigations (SCUBA facilities) rather than for training programs. Therefore, only limited space is available to visiting scientists and there are no dormitory accommodations.

The new central building consists of an air-conditioned research unit housing four small laboratories, a large "wet" laboratory, a dark room, instrument store, museum and two offices. The "wet" lab is subdivided into six semi-enclosed research bays provided with all services including seawater and central tables for aquaria and sorting and holding tanks. A separate reading and conference room is nearby. Support facilities include a machine shop, a boat and wood workshop, and a diving locker. Three boats are available a 6.7 meter (22-foot) twin outboard-motor vessel, a 4.6 meter (15-foot) work boat, and a 3.7 meter (12-foot) inflatable boat that can be carried by car to remote sites. A landrover and Volkswagen bus serve to transport equipment as well as personnel.

The laboratory is equipped with a glass-distilled water supply, dissecting and compound microscopes, histological apparatus, drying oven, pH meter, top loading and analytical balances, photographic equipment and darkroom facilities, refrigerator, freezer, centrifuge, collecting gear, etc. The diving facility contains two high-capacity air compressors, a recompression chamber with air bank, SCUBA tanks, regulators and auxiliary diving equipment.

Summary

The reefs off Discovery Bay Laboratory probably are some of the most extensively studied reefs in the world, and the data already available would be a distinct asset to a research program.

The Discovery Bay reefs are rich and well developed both in shallow and deep water. Since they occur very close to the coast, their location would facilitate close monitoring of various parameters. Moreover, the relatively narrow horizontal extent of the reef biotope would be advantageous in instrument monitoring, as well as in on-site investigations.

This site is readily accessible from the U.S. mainland, and accommodations are available locally at inexpensively priced guest houses (ca. $7/day single) for as many as 40 scientists.

On the other hand, there is a significant but as yet undetermined terrestrial influence on the reef ecosystem in this area. The internal sediment found in association with the present reefs is characteristically brown owing to the presence of bauxite or iron oxide that has been incorporated from terrestrial sources.

From 1964 to 1967, a ship channel was dredged and blasted into Discovery Bay to permit docking of large ocean-going vessels in this bay. The channel is about 300 to 400 m from some of the key areas of potential research. The construction of this channel as well as frequent visits of large ships into the bay provide negative influences on the reef ecosystem in this area.

The paucity of larger reef fish is notable in Discovery Bay. Although fish populations are sparse, fish traps are still used extensively, and therefore this location has limited potential for any proposed fish studies in association with the reef ecosystem. The poor development of a buttress zone in the area is an additional drawback.

The Discovery Bay Laboratory is not eqippped to handle large coral-reef study programs because of its relatively small size. Research projects might also be hampered by customs delays and the need for import licenses owing to the problem of bringing onto the island scientific equipment and material from another country.

Glover's Reef, British Honduras*

A first reconnaissance visit to British Honduras, 17-22 January 1971, included several diving stations along the barrier reef and

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*Preliminary survey: January 17-22, 1971 by A. Antonius and J. N. Weber.
Field survey: June 20-27, 1971 by A. Antonius, A. L. Dahl, and K. Ruetzler.

Turneffe Island, and an air survey of the barrier reef, Turneffe Island, Lighthouse Reef and Glover's Reef. The information obtained strongly suggested that an extensive diving survey be focused on Glover's Reef, and this was conducted 20-27 June.

Description of Reefs

Glover's Reef (16°50'N, 87°50'W) is the southernmost of the three British Honduras atolls, about 75 km SE of Belize City, 45 km E of the mainland and 25 km E of the barrier reef. It is elongated in NNE-SSW direction, about 28 km long and 10 km wide. The atoll (Fig. 9) is surrounded by deep water (350-1000 m) within 1-2 km from the intertidal peripheral reef. The well developed surface-breaking atoll reef flat (mainly coral and coralline algae) is interrupted by two major openings: NE-entrance and SW-entrance (12 m deep). On its SE part, it supports a chain of six cays which are distributed over a distance of 10 km. The cays vary between 150 m and over 1 km in length and are more or less covered by coconut palms. The lagoon, in contrast to the other two British Honduras atolls, is rather deep, 8-15 m in most parts, with hundreds of patch reefs rising to the surface.

Of the six cays on Glover's Reef, only Long Cay and adjacent Little Cay are permanently inhabited. Both islands are used as a resort for diving-oriented tourists.

From the seaward margin of the peripheral reef a gradually sloping reef-front extends to the drop-off. The reef front varies in width from about 400 m (SW cays) to 1.5 km (Long Cay) and is about 500 m wide on the leeward side. The edge of the drop-off occurs at a depth of 15-25 m. A system of deep parallel grooves runs perpendicular to it. These grooves are particularly well-developed on the windward (E) side of the atoll. Sediments produced in the breaker zone are transported down the grooves permitting undisturbed coral growth in between. The leeward reefs are considerably more influenced by sediments which are driven out of the lagoon by wind generated currents.

The windward side shows a dominating, lush, growing reef-coral community including sponges and gorgonians (Fig. 10). No attempt was made to gain a complete list of species during the survey, but the general appearance of the reef and the unparalleled size of most of the coral and sponge specimens observed strongly suggest that all of the known Caribbean species can be found there. On the sketches of the reef transects only dominant species are listed.

Compared with the windward reef, the leeward side shows a slight decrease in number of scleractinian species and is slightly less populated, probably due to sedimentation (Fig. 11). The coral cover ends around 45 m and gives way to a sand slope.

The fore-reef slope is very steep at NE Cay, almost vertical at Long Cay and vertical to overhanging at SW Cay. It was explored at five different locations to a depth of 60 m. There, and as far down as one could see in the clear water (horizontal visibility at least 50 m), lush coral, sponge and algal growth continues.

The patch reefs rise to the surface from the lagoon floor, which is generally covered with sand and *Thalassia*. These reefs are mainly of *Acropora palmata* and *A. cervicornis* structure on top and *Montastrea annularis* below, with coral growth occurring to a depth of 3-4 m and occasionally 10 m. Every patch reef is a small individual reef-entity and ideal for a variety of experiments.

The winds in the vicinity of the British Honduras atolls blow steadily from the East for most of the year, being replaced between November and February by occasional Northern winds, which occur only a few times every winter and last four or five days at a time. Thus, the wind-generated western currents in the atoll area are by far predominant over the main Caribbean current, which impinges on the British Honduras atolls in a northerly or southerly direction, and regularly changes its direction several times a year.

Water temperatures at the surface vary between 25°C in winter and 31°C in the summer (open water); no significant temperature decrease was noticed during the dives (for detailed information on climatic, biologic and geologic features of Glover's Reef, see Stoddart, 1962).

Summary

British Honduras is a politically stable country, and its official language is English. Relations between the government and resident North Americans or Europeans are cordial. The British Honduras government seems to look favorably upon educational and research projects, and duty exemption for all scientific and educational equipment and materials has already been granted.

The remoteness of Glover's Reef makes it likely that it will remain undisturbed; still, there is good accessibility to Belize by air, and the atoll can be reached in any weather by boat because two-thirds of the trip takes place in a sheltered lagoon between the mainland and the barrier reef. There are no research facilities on the atoll at present, and it is not always possible to make satisfactory arrangements for an extended scientific program using tourist-oriented facilities.

Glover's Reef is well suited for direct comparison with Indo-Pacific atolls as there are no land influences, no pollution, or other human disturbances; yet the large barrier reef, and two comparable but physiographically different atolls are readily accessible. While Glover's Reef is the only one of the three atolls which was not hit by the devastating hurricane Hattie in 1961, there is a hurricane potential; a small one passed over the atoll in November 1971 without causing major damage.

In contrast to the other reefs surveyed in the Caribbean area, Glover's Reef atoll appears to offer the greatest variety of reef types and the optimum reef development in terms of population density and species diversity of reef corals and associated organisms.

San Blas Islands, Panama*

The San Blas Islands (9°39'N, 78°45'W) lie off the Caribbean coast of Panama between San Blas Point and Cape Tiburon (Fig. 12). During the Spanish conquest of Panama, the Cuna Indians were driven from the mainland to find refuge on these islands. Today, they have title to over 365 islands and a strip of land along the adjacent coast. They have jurisdiction over agreements to buy, settle or establish any forms of business on their islands.

Standard access to the San Blas Islands is by means of light plane or small boat. The islands are about 110 km east of Colon, and it takes about 8 hours from there by boat. There are scheduled flights to several San Blas localities from Panama City, and a float plane service from Colon.

One serious problem to be considered concerning travel by sea is that rough waters are common during the months of December to April, so the islands generally are not accessible by boat. Airstrips such as at Carti on the mainland (see Fig. 12) are accessible year round to light aircraft that can transport passengers to and from Panama City at a cost of $9.25 per one-way trip. Although this provides a rapid and inexpensive form of transportation to the area, and could be used by scientists when the islands are inaccessible by water, this air carrier cannot always operate on a specific schedule owing to the frequency of poor weather conditions. In addition, the short and uneven dirt airstrips preclude the use of larger aircraft so that only four or five passengers and light baggage loads can be accommodated on any one flight.

The only housing facilities presently available in the area are located on Picofeo Island, which is the only privately owned San Blas island. These facilities consist of several sheds and some machinery (including a 6-volt generator) that are part of a disused copra-processing plant. One building serves as the Picofeo Hotel which is operated by Jose Garcia, one of two Panamanian brothers who own the island and its buildings. The hotel, which is an old wooden structure, offers minimal accommodations to visitors, who are expected to bring their own food supplies at $2.50/night. Extended stays can be arranged at cheaper rates. Outsiders are generally discouraged from setting up reisdence in the other islands. However, a few tourist resorts are now being developed in the San Blas Islands, which should provide for improved access and accommodations.

A short initial visit confirmed the potential of the area, and

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*Preliminary survey: May 1-2, 1971 by A. L. Dahl and A. Childs. Field survey: August 3-7, 1971 by A. Antonius, J. C. Land, and I. G. Macintyre (assisted by C. Birkeland, D. Meyer, M. McCosker, W. K. Sacco).

located some sites for further study. Ten locations were then visited during the four-day survey. These areas are marked on maps redrawn from sections of HO chart No. 2771, San Blas Point to Concepcion Bay (Figs. 13, 17, and 22). Following are brief descriptions of the areas in the order that they were visited:

1. Off Sail Rock, Profile A-A'

Sail Rock is an exposed rock knob marking an isolated reef not far from Porvenir Island, where there is a very short airstrip (Fig. 13). The water was very turbid during the survey of the reefs in this area (less than 2 m visibility at a depth of 20 m) and there was a marked thermocline at a depth of about 3 m. The zonation across the profile is given in Fig. 14. Points worth noting in this area are the dominance of *Agaricia* sp. corals at the edge of the shallow platform and the lack of coral growth below about 20 m where the accumulation of fine sediments (rich in organic material) apparently prevents corals--other than the bladed *Agaricia tenuifolia*--from growing.

2. Picofeo Island

The Picofeo Hotel is set on piles over the water at the north end of Picofeo Island (Fig. 13). This area is characterized by typical back-reef coral communities (Fig. 15) dominated by *Porites porites*. As was found at Sail Rock, the outer edge of the platform is marked by a rich *Agaricia* sp. coral community. The reef terminates in a shallow sand flat at a depth of about 6 m.

3. Off Sardingan Point, Profile B-B'

Sardingan Point is on the mainland near San Blas Point and west of Picofeo Island (Fig. 13). The reef in this area drops off steeply to a depth of about 30 m (Fig. 16). An interesting aspect of this reef is that *Agaricia* sp. corals tend to dominate throughout the depth zones except in very shallow water, where *Porites porites* is the most abundant coral.

4. Off Salar, Profiles C-C', D-D', and E-E'

The group of islands at Salar are among the inner San Blas Islands north of Macolla Point (Fig. 12). As names for the individual islands were not available, they have been numbered from southwest to northeast (Fig. 17). The survey concentrated primarily on the area between islands 2 and 3. Several dives were completed in this area of vigorous coral growth, spectacular drop-offs, and overhangs which are described in profiles C-C' (Fig. 18), D-D' (Fig. 19), and E-E' (Fig. 20). The general zonation of the reef flat of island no. 3 is also shown in a diagramatic sketch (Fig. 21).

5. Off Ogopuquip, Profile F-F'

Three different sites were visited in the Holandes Cays (Fig. 22).

The first was at Ogopuquip on the southern side of the keys, where a profile (F-F') was prepared off the southwest point of Ogopuquip Island (Fig. 23). This area had the greatest diversity of coral species of any site visited in the San Blas Islands.

6. Holandes Cays Algal Ridge, Profile G-G'

The distinctive structure of the northern reef around the Holandes Cays is illustrated by profile G-G' (Fig. 24). This reef has a prominent algal ridge that has been described in more detail elsewhere (Glynn, in press).

7. Off Holandes Cays, Profile H-H'

Beyond the algal ridge off the east end of Holandes Cays, there is a broad rock platform similar to that observed off many of the Bahamian Islands (profile H-H', Fig. 25). The survey did not extend to the drop-off which, according to the chart, probably occurs 200 m beyond the outer end of the profile.

Summary

Some reef areas, in particular the reefs off Salar Island, meet the scientific criteria established above for a research site including: well-developed reefs, steep fore-reef slope, lack of disturbance by human activity, and a close proximity to shore. The well-developed algal ridge off the Holandes Cays offers an opportunity to make comparative studies with similar reef structures in the Pacific.

Buildings are available for conversion into research facilities. However, they are not located adjacent to well-developed reefs. Smithsonian Tropical Research Institute maintains marine laboratories and a research vessel elsewhere in Panama, and conducts research in the San Blas Island area.

Two atypical characteristics of San Blas reefs, in comparison with other Caribbean reefs, are the predominance of _Agaricia_ sp. corals in all depth zones, and the presence of a well-developed algal ridge off Holandes Cays.

The inaccessibility of this area by boat for five months of the year and the limited air transport service offered present a serious logistical problem in transporting personnel and material in and out of the San Blas area. As facilities on Picofeo Island are too distant from good reef development to be useful, it would become necessary to negotiate lease arrangements with the Cuna Indians for one of the uninhabited islands.

PACIFIC AREA

In the Pacific Ocean, coral reefs are scattered over a vast geographic area. The only safe generalization about Pacific reefs is that no two reefs are identical. However, in spite of the great diversity in form and composition that characterizes these communities, a number of features demonstrate the underlying relationships within this assemblage. The coral fauna is remarkably uniform throughout the Indo-Pacific (Wells, 1969), with the highest diversity and the center of evolutionary radiation in the western tropical Pacific (Stehli and Wells, 1971). This fact frequently leads to the statement that reefs in the western Pacific are "rich" while those to the east are "impoverished." Whether this applies to all elements of the flora and fauna, however, has yet to be demonstrated. The atoll reef form is another common Pacific feature, although involving many structural variations on the basic theme. The presence of a *Porolithon* algal ridge is often believed to be characteristically Pacific, and is certainly common there, while it rarely occurs on Atlantic reefs.

The great number and diversity of tropical Pacific reefs has made the search for data on research sites very difficult. Information was compiled from many sources on reef structure and composition, and on logistic and practical arrangements. Most published descriptions of Pacific Islands include only terrestrial geography; specific local descriptions are rare, and only the shallow reef is mentioned. Charts from the U. S. Army Map Service and the Navy Hydrographic Office indicate with fair accuracy the presence or absence of shallow reef structure, and sometimes the nature of the offshore slope and the depth to which coral development might be expected. A few scientific papers include reef descriptions of some sort, but not for the deeper areas important to a complete reef program, and generally in localities that are otherwise unsuitable. Most of the past research on Pacific reefs was conducted either by ship-borne expeditions to otherwise inaccessible islands, or in areas that have since been disturbed by development. Also, published information tends to be too dated to be reliable for current reef conditions; much of it predates World War II.

While many questionnaires were returned by Pacific reef specialists, their information did not always meet program requirements, perhaps because of the great size and complexity of the area. Personal experience tended to be limited to a few sites and to what could be seen from above the water. Areas of field experience and interpretations of reef quality depended on the respondant's special interest (an interesting reef to a coral specialist would not necessarily be selected by a bird or sea-snake expert, for example). Also, the information was often too generalized, referring to island groups rather than to specific reefs. The areas recommended and a summary of the questionnaire responses for the Pacific area are listed in Table II.

TABLE II: Questionnaire Response - Pacific Area

Site	Reef Structures*	Undisturbed	Accessible	Local Facilities	Political Status+	Number of Recommendations
Caroline Islands						
Palau	+	±	+	+	+	6
Helen Reef	0	+	-	-	+	1
Yap	+	±	+	0	+	1
Ulithi Atoll	+	±	+	0	+	2
Woleai	+	+	0	0	+	1
Ifaluk Atoll	0	+	-	-	+	1
Truk	+	-	+	0	+	1
Ponape	+	-	+	0	+	4
Ant Atoll	0	+	+	0	+	1
Pakin Atoll	0	+	+	0	+	1
Kapingamarangi	0	+	-	-	+	2
Marshall Islands						
Majuro	+	-	+	0	+	2
Arno	+	±	+	0	+	2
Ailuk	0	+	-	-	+	1
Eniwetok	+	±	+	+	-	2
Ellice Islands						
Funafuti	+	-	-	-	+	2
Phoenix Islands						
Canton Island	0	±	0	0	+	2
Fiji Islands						
Lau	0	+	-	0	+	1
Viti Levu	+	±	+	+	+	1
Samoa Islands						
Samoa	0	±	+	0	+	3
Rose Atoll	0	+	-	-	+	1

Site	Reef Structures*	Undisturbed	Accessible	Facilities	Political Status+	Number of Recommendations
Cook Islands						
Hervey Islands (Manuae)	0	+	-	0	+	1
Line Islands						
Christmas Island	0	±	0	0	+	1
Fanning Island	0	+	0	+	+	2
Society Islands						
Tahiti	+	+	+	0	-	1
Other						
New Caledonia	+	±	+	+	-	1
Port Moresby, Papua New Guinea	+	±	+	+	+	1
Ashmore Reef, Timor Sea	0	+	-	-	+	1
Heron Island, G.B.R.	+	+	+	+	+	1
Low Isles, N. Queensland	0	+	+	0	+	1
Aldabra, Indian Ocean	-	+	-	+	+	1

Sites suggested by name only: Saipan, Marianas Islands; Nukuoro, Caroline Islands; Wotho, Marshall Islands; Onotoa Atoll, Gilbert Islands; Butaritari Atoll (Makin), Gilbert Islands; Phoenix Islands; Buka, Bougainville, Solomon Islands; Rabaul; New Britain; Bismarck Archipelago.

Key: + = favorable or present 0 = unknown or possible - = unfavorable or impractical ± = variable

* see selection criteria above, p. 38

\+ basically the anticipated government attitude to a large international but U.S. funded program

Questionnaires and equivalent information on Pacific sites were returned by the following: A. Antonius, A. L. Bloom, A. L. Dahl, M. S. Doty, F. R. Fosberg, R. Hagemeyer, H. Heatwole, R. Johannes, H. S. Ladd, E. G. Menez, H. A. Rehder, R. W. Schreiber, J. Sieburth, W. A. Starck, D. R. Stoddart, J. N. Weber, C. M. Yonge, and University of Hawaii.

It was obvious from the questionnaires and the other information available that data on the reef state and structure, and on current logistic arrangements, could only be obtained by actual site visits by scientists familiar with the basic criteria for a research site, as was done in the Caribbean. As it would have been physically impossible to visit every potential site, it was necessary to select from those on which some data were available the areas with the best prospects for a satisfactory site. One important role of the questionnaires was to help pinpoint such areas for more detailed examination. Inevitably other areas which might be ideal have been overlooked because they were not sufficiently well known, often because they are more remote. Transportation in the Pacific however is improving rapidly, and will make more such areas logistically practical.

A number of islands in the Pacific have recently been recommended for preservation as "Islands for Science" (Elliott, 1971). These were selected for their lack of human disturbance, and in many cases, have excellent coral reef development. A number of them were in fact considered at an early stage in the screening process. However, they are undisturbed precisely because they are inaccessible, and thus logistically impossible for a major research program.

Site Screening

An initial screening of possible sites in the Pacific reduced to a more manageable number the list of areas being considered although many excluded areas have characteristics that might be of great interest for more specialized programs. The following criteria were applied in the screening. Because of the need to find a reef with as few complicating external influences as possible, preference was given to atolls or barrier reef areas far from high island influences. For a large program, the need for regular air service or an immediately adjacent airstrip for possible charter service eliminated many less accessible sites. The possibility of acquiring or constructing and maintaining a facility for at least 20 people at reasonable cost was also considered important. All French territories were omitted from consideration because of uncertainties concerning long-term cooperation with government authorities. Great distance or travel time from the United States was also considered to be less desirable. The results of the screening are given below by island group, with the reasons for inclusion or exclusion from further consideration.

Excluded from further consideration:

a. Hawaiian Islands--Reef structure and diversity inadequate. Disturbed.
b. Mariana Islands--High islands. Reefs marginal in quality. Serious disturbance by war and Acanthaster.
c. Guam--Reefs seriously disturbed.
d. Line Islands--Poor accessibility. Far from center of coral diversity.
e. Phoenix Islands--Inaccessible. Canton disturbed.

f. Tokelau Islands--Inaccessible.
g. Tonga--Poor accessibility.
h. Cook Islands--Poor accessibility.
i. Bismarck Archipelago, Solomon Islands, New Hebrides--High islands or inaccessible.
j. New Caledonia, French Polynesia--French administration.
K. Great Barrier Reef and other Australian reef areas--Great distance.

A further breakdown was made of those areas not excluded. Those discussed in more detail later in this paper are marked with an asterisk (*).

Caroline Islands

U. S. administration, good air service to district centers, many atolls, in center of coral diversity.

1. Palau*. Many recommendations. Greatest biological diversity in Pacific Islands. Regular air service. Some facilities. Considerable barrier reef area and one small atoll (Kayangl).
2. Helen Reef. Rich and undisturbed, but inaccessible.
3. Yap*. High island. Regular air service. Some rich reef areas.
4. Ulithi Atoll*. Airstrip and weekly Coast Guard flight, large atoll. Some disturbance during World War II.
5. Woleai Atoll*. Small, undisturbed atoll with abandoned airstrip. Excellent reefs.
6. Ifaluk Atoll. Very small atoll, inaccessible.
7. Truk. Accessible but reefs seriously disturbed.
8. Ponape*. Regular air service. High island with barrier reef. Some reef disturbance.
9. Ant Atoll*. Near Ponape, undisturbed except for recent Acanthaster damage.
10. Pakin Atoll*. Near Ponape, undisturbed.
11. Nukuoro. Inaccessible.
12. Kapingamarangi Atoll, Heavily populated, inaccessible.

Marshall Islands

U. S. administration. Many large atolls, mostly either disturbed or inaccessible.

1. Majuro*. Regular air service, disturbed.
2. Arno*. Near Majuro, undisturbed.
3. Wotho. Inaccessible.
4. Ailuk. Undisturbed but inaccessible.
5. Eniwetok. Accessible. Excellent facilities, disturbed. Clearance for foreign participants difficult to obtain.

Gilbert and Ellice Islands

Soon to have improved regular air service.

1. Funafuti. Serious World War II damage and heavily populated.

State of other reefs unknown.

Fiji Islands

Large high islands accessible. Rich reefs in outlying areas, no information on possible specific sites.

Samoa Islands

Accessible. Good fringing reef development.

1. Tutuila*. Reefs disturbed in more populated areas.
2. Manua Islands*. Undisturbed.
3. Rose Atoll. Small and totally undisturbed. Accessibility difficult.

On the basis of the initial screening, a number of areas most likely to offer suitable sites were selected, including Palau, Yap, Ulithi, Woleai, Ponape (including adjacent Ant and Pakin), Arno, and Samoa (including Rose Atoll). A survey team was therefore sent to examine these areas. Fiji and the Gilbert and Ellice Islands also have great potential, but too little information was available on which to plan a site visit, and time did not permit the more lengthy survey that would therefore be required.

U.S. Trust Territory*

Of the enormous number of reef areas scattered throughout the Marianas, Caroline and Marshall Islands, most were too inaccessible to be considered, but even the accessible areas include vast reef tracts with innumerable potential sites.

The experience and reports of the *Acanthaster* surveys conducted in Micronesia by the University of Guam (Tsuda, 1971) and the *Acanthaster* control teams operated by the U.S. Trust Territory Administration were of particular value in selecting promising areas for the survey team visits.

Transportation in Micronesia is improving. Continental Airlines--Air Micronesia now serves all the district centers (Koror, Yap, Saipan, Truk, Ponape, and Majuro) 2 to 3 times per week. In addition, Air Pacific has a charter service available for $180/hour (7-passenger airplanes), and there is a new charter service by Island Aviation, Inc., (rates around $120/hour). However, flying by other than Navy seaplanes is still restricted to those few islands with airstrips. Vessels service outlying islands at intervals of two weeks to several months.

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* Field survey: August 14-September 5, 1971 by A. Antonius and A. L. Dahl [assisted by R. Randall (Palau and Yap), R. T. Tsuda (Ponape) and B. Sablan (Majuro and Arno)]

Local transportation is difficult, although small motor boats can usually be hired. The Acanthaster control teams have diving compressors and good motor boats at Palau, Truk, Ponape, and Majuro, and provided much of the logistic support for the survey team. There is an excellent marine laboratory and staff at the University of Guam, and the U.S. Trust Territory Government is highly cooperative. There is some resistance from the local populations to outside interference but in general they appeared favorably disposed towards scientific as opposed to commercial or tourist activities.

There are small hotels in the district centers, but in outlying areas it is necessary to depend on the hospitality of the local people.

Palau

Palau (7°30'N, 134°30'E) is considered to have the richest reefs of any Pacific island area. The archipelago of volcanic and high and low limestone islands contains a complex of fringing and patch reefs partly surrounded by a barrier reef (Fig. 26). A small atoll occurs immediately north of the barrier reef. After a detailed examination of charts and consultations with local specialists, a number of sites ranging throughout the archipelago were chosen for detailed examination. This was a wholly inadequate sample of the diversity of sites available, so no generalizations should be made from the few descriptions presented here.

1. Ngeregong Island

The first dive was at Ngeregong Island, on the windward (east) side of the barrier reef about 32 km south of Koror (Fig. 26). Ngeregong has an abandoned Japanese airstrip that, if restored, could simplify logistic arrangements. The outer reef slope, on the SE side of the island consists of a gentle sandy slope, with scattered coral growth, becoming even sandier with depth. The reef was poorly developed.

2. Angaur

Angaur Island lies 40 km beyond Ngeregong, at the southern end of Palau, beyond the barrier reef (Fig. 26). It has an excellent Coast Guard airfield serviced weekly from Guam. The island, formerly an important source of phosphates, lacks major reef development except on the south and west sides. The team dived on the west (leeward) side of Angaur (Fig. 26), in the center of reef development. There is a smooth rocky flat with small scattered corals extending 700 m offshore to a depth of 5 m, followed by a gentle slope 200 m wide and going down to 8 m, with larger, more abundant corals. A steeper slope, 100 m wide with lush living coral coverage, extends down to 38 m, where it is interrupted by a sand flat 30 m wide. A slope with patches of coral interspersed with sand continues down from 40 m at 1 km offshore. The water was warm and clear. The lack of diverse coral habitats, the amount of sediment, and the extended zonation interrupted by terraces were considered undesirable for a research site.

The Ngemelis Islands are 40 km SW of Koror on the western barrier reef (Fig. 26). The islands are parts of a slightly elevated coral platform, and front on the outer reef margin on the west and a sheltered channel on the southeast, as well as the lagoon to the north. The islands can be reached from Koror by boat without going outside the barrier reef. Two dives were made, first on the SE side, off a vertical drop-off going down to 240 m, and then on the sloping west side.

3. Ngemelis Islands, SE

On the sheltered SE side of Ngemelis (Fig. 28), the shallow reef flat is 300 m wide, with few corals inshore, increasing to dense coverage of the reef edge at 0.5 m depth, with soft corals predominant. Beyond the edge is a vertical slope, mostly overhanging, dropping to 260 m. Alcyonarians dominate down to 30 m, with scleractinians and gorgonians equally represented. The slope begins to project outward at 40 m, collecting calcareous sediment; corals are scarce and appear not to grow beyond 30-60 m. The water temperature decreases with depth. The drop-off is spectacular, but soft corals are dominant, and there is apparently a constant flow of sediment.

4. Ngemelis Islands, W

The west (leeward) side of the Ngemelis Islands (Fig. 29) has a broader reef flat 500 m wide with stony corals dominant at the seaward edge (0.5 m depth). There is a steep drop-off to 12 m with good coral coverage, with big buttresses dominated by *Porites* heads and rubble-filled chutes extending down to 20 m. A gentle slope extends down to 40 m with *Pachyseris* dominant, after which the slope becomes increasingly sandy and corals dwindle. Again water temperature decreased with depth. The site has high species diversity and a good drop-off, but sedimentation limits coral growth at around 50 m. At both sites the drop-offs are very near the surface, and sponges are almost completely lacking. Current patterns in the area appeared quite complex, and this, together with the inadequacies in the reef structure, would rule this area out for certain types of reef research.

Kayangl Atoll is several hours away by small boat, traveling up inside the western barrier reef, and then beyond the northern tip of Palau (Fig. 26). Kayangl would generally be accessible from Koror except in rough weather. There was some difficulty at first because of a recently instituted village policy of charging all visiting Americans $50, but the requirement was waived after the District Administrator explained the value of the research program to the islands. Three dives were made on Kayangl; in the shallow lagoon, and on the outer leeward and windward slopes.

5. Kayangl lagoon

The first dive was on the west (leeward) side of the lagoon near the entrance channel (Fig. 30). The sandy bottom, 4-6 m deep, becoming shallower toward the reef, separates the abundant patch reefs and coral heads. These are coral-covered from top to bottom, and show very great species diversity. The area is typical of shallow Pacific lagoons.

6. Kayangl leeward outer reef

The leeward outer reef of Kayangl (Fig. 30) is topped by a 50 m wide flat of calcareous algae, leading to a reef edge with lush coral growth. There is a steep drop-off to 10 m depth, still with very good coral coverage and high species diversity, followed by a gentle slope to 40 m with Pachyseris dominant. The slope flattens between 40 and 50 m, and becomes very sandy beyond 50 m. The temperature decreases markedly with depth, and the water becomes increasingly murky. The living reef ends between 50 and 60 m.

7. Kayangl windward outer reef

The east side of Kayangl is very exposed, making it impossible in most weather to anchor a small boat. The windward outer reef (no diagram) commences off the islands with a broad algal-turf-covered flat, and then drops to a platform about 1000 m wide and 7-10 m deep with little coral growth. This was not followed to the drop-off.

The lack of a developed windward coral community and the shallow lagoon prevent this from being as desirable a site as logistics and diversity might indicate.

Yap

Yap (9°30'N, 138°05'E), as a district center, is accessible (3 flights per week from Guam), and has excellent fringing reefs, especially on the northwest side, with some lagoon development inside the reef (Fig. 31). It is a high island, so that there are considerable terrestrial influences, and the reefs have experienced some Acanthaster infestation. In four dives on the west side, a superficial count of corals by R. Randall yielded over 100 species. Profiles from the dives on different parts of the reef have been combined to yield a composite section (Fig. 32).

8. Off Gorror

Two dives were made in the lagoon, on the SW side, between the reef and Yap Island. The first, off Gorror, was in a shallow sand flat area with turtle grass and occasional coral patches of high coral diversity (approximately 50 species). The water was rather murky.

9. Off Nif

The second dive, off Nif, was in one of the deep lagoon areas. The surrounding reef walls are covered with large corals down to the sandy bottom at 10 m. The reef top is exposed at low tide, with an algal turf cover and only small specimens of Favites.

10. Off Okau

The leeward outer reef off Okau begins with a rocky fore reef flat, 1500 m wide, cut by long surge channels 2 m deep and 1-2 m wide. Coral coverage increases to the reef edge at a depth of 7 m, with only a few species less than in Palau. The slope then drops steeply to 25 m with good coral growth, beyond which a more gentle slope is dominated by Pachyseris. The water changes at around 20-25 m; above it is warm and clear, below cool and turbid. Coral growth seems to end at around 40 m.

11. Mil Entrance

A final dive was made in the Mil Entrance (no diagram) on the west side between Yap and Rumung Islands. The reef flat on the north side of the channel extends down to 2 m with good coral coverage. There is a drop-off with good coral growth down to 10 m, and a gentle slope with turtle grass deeper down. A strong current of turbid water was moving out of the channel, which contained many large sharks.

Although the reef quality observed was high, the terrestrial influences, distance of the reef front from shore, and shallow limit to coral development are major disadvantages. There is also more chance of antagonistic feelings against Americans on the part of the local population in district centers.

Ulithi and Woleai

It was not possible during the short survey to arrange transportation to Ulithi or Woleai Atolls in the Yap district, but from other evidence and from conversations with chiefs from both areas, some useful information was collected.

Ulithi (10°00'N, 139°45'E) is a large atoll northeast of Yap. It has an airstrip with weekly Coast Guard flights from Guam or the possibility of charter flights ($500-$650 for 5-7 passengers, one day round-trip). There is also ship service from Yap every two weeks. There are some sunken ships in the lagoon, and other remnants of war damage, as well as an increasing ciguatera problem, but with the large size of the atoll undisturbed areas must remain. This is one of very few relatively undisturbed atolls directly accessible by plane.

Woleai (7°20'N, 143°45'E) is a small, totally undisturbed atoll presently inaccessible but with an abandoned Japanese airstrip. If the airstrip were ever repaired this could be an important site to consider, even though logistics would be somewhat more difficult. Earlier suggestions that the airstrip might be restored soon have not been confirmed. A.Antonius dived on the reefs during the 1969 Acanthaster survey, and they appeared to be well developed.

Ponape

Ponape (7°00'N, 158°00'E) is another district center, consisting of a large volcanic island and several smaller islands surrounded by a barrier reef (Fig. 33). The reefs are generally subjected to considerable terrestrial influences. There are three flights weekly from Guam to Ponape and two from Hawaii, making this the most accessible of the Caroline Islands.

Not far from Ponape, however, are two small atolls, Ant and Pakin. Ant is an atoll of moderate size only 10 miles from Ponape, while Pakin, somewhat smaller, is 30 miles away. Both can be reached by small boat from Ponape within 3 hours. One dive was made on the outer slope of each atoll, and both had excellent reef development.

12. Ant

The dive was on the leeward side just beyond the northern tip at the northernmost islet (Fig. 33). The reef crest at this point is 100 m wide, with a fore reef flat 200 m wide, extending down to the reef edge at 10 m (Fig. 34). Coral growth begins at 2 m depth, 30 m offshore, increasing to 90 percent coverage at 50 m offshore, and 100 percent at 100 m out. From the reef edge there is a steep slope down to 30 m depth with a coral cover of over 100 percent because of the overlapping table *Acroporas* which are dominant. The slope continues down to 50 m with interspersed sand cover increasing to 50 percent, although coral development continues much deeper. The water was warm and clear, with no change in temperature. Ant is an excellent reef, with a deep entrance, a good drop-off, and deep coral development.

13. Pakin

The dive site at Pakin was near the center of the northern reef (Fig. 33), in an exposed though not windward area. The 80 m wide reef crest merges with a sloping fore reef 50 m wide and 7 m deep at the edge (Fig. 35). The first 20 m is bare of coral cover, but coral density increases to the rugged edge, with headshaped *Porites* dominant. From there an almost vertical slope descends as far as could be observed, with a good coral cover of large specimens and a considerable amount of algae. Sand patches begin at 50 m, but at 60 m the coral cover is still 30 percent and continues to the limit of visibility. Again there was clear warm water with no temperature change with depth. The reef is excellent for research, with a steep drop-off and coral development to beyond normal SCUBA range. Six gray sharks were observed.

Ant has a single owner, an ardent conservationist, which might make arrangements for a long-term project difficult. Pakin has no channel into the lagoon at present, but there are government plans to open one and to build a pier in the lagoon. There would not appear to be any difficulty in locating a facility there, and logistical and construction support on Ponape seems excellent. One dive was also made on the Ponape barrier reef (see below), but it was disappointing.

14. Mant Passage

The brief dive in the Mant Passage, a northeast entrance through the windward wide of the Ponape barrier reef revealed a smooth rocky flat at 4 m depth with 20-30 percent coral coverage and low species diversity. The water was rather turbid, and one gray shark 2.5 m long was seen. The frequent heavy rainfalls in Ponape might cause technical problems for a research program, as well as affecting the reef.

Arno and Majuro

Majuro (7°05'N, 171°10'E) and adjacent Arno (7°05'N, 171°45'E), two large atolls in the southern Marshall Islands, are the only accessible atolls in the area without government entry restrictions. Majuro has two weekly flights from Hawaii, and Arno can be reached easily from Majuro. Majuro has been reported as being disturbed, while Arno is relatively untouched but dives on both atolls revealed rich reefs with an excellent configuration.

15. Kinajon (Arno)

The outer reef off Kinajon on Arno is on the sheltered south side (Fig. 36). The rocky fore reef flat 100 m wide develops good coral coverage and surge channels towards its edge at 10 m depth (Fig. 37). A steep slope with Porites heads dominant drops to 30 m where the angle of slope lessens and sand patches appear. Pachyseris then becomes dominant. At 60 m the coral cover is still 20 percent and continues as far as can be seen. The water was warm and exceptionally clear (the water surface was visible from 60 m), with no change in temperature. The reef in general seemed excellent; on the other side where the deep entrance is, it is reportedly even better developed.

16. Laura (Majuro)

On Majuro the reef was surveyed off Laura, a sheltered location on the southwest side (Fig. 36). The 60 m wide fore reef consisted of 20 m of bare surface, 20 m with a dense algal cover, and 20 m with corals, mainly Acropora, leading to the rugged reef edge at 5-8 m depth (Fig. 38). Deep surge channels cut into the reef. There is no real drop-off, but a gently rounded slope with valleys and ridges perpendicular to the shore, and also many shore-parallel steps. The coral cover decreases from 90 percent at the edge (5-8 m) to 60 percent at 12 m, to 50 percent at 20 m with increasing algal cover. The slope gets steeper with depth, becoming vertical at 40 m, where the coral cover is 20 percent. This site is accessible by road from Majuro, and has good reef features and clear water. Fishes were very abundant, but no sharks were observed.

AMERICAN SAMOA*

The Samoa Islands (14°15'S, 170°00'W) are a chain of volcanic

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*Field survey: September 7-12, 1971 by A. L. Dahl and A. Antonius (assisted by S. Ritterbush).

islands with fringing coral reefs in the South Pacific. While rather far from the center of coral diversity, their ready accessibility by direct flight from Hawaii and the strong interest of the local government warranted detailed examination of the reefs. The Manua Islands are remote from the main island of Tutuila and can be reached by government or commercial boat in about 8 hours. There has also been an intermittent float plane service. Because transportation is difficult it was only possible to dive on the reefs in the vicinity of the main anchorage of each island. Since the reefs in the Manua Islands were not transected no diagrams are given.

17. Tau (Manua)

At Tau the dive was made off the northwest side (Fig. 39), a leeward but exposed area, about 300 m offshore. There is a rocky flat with huge boulders at 20-25 m depth. Few coral species are present, mainly *Porites* and *Pocillopora*, and specimens are small and scarce.

18. Olosega (Manua)

The dive off Olosega was on the sheltered leeward (west) side about 200 m offshore, at 20-25 m depth (Fig. 39). The bottom is rocky, with huge blocks, forming valleys and ridges. Coral cover is more extensive and with more species than Tau, with huge coherent colonies of table-like *Acropora* and *Porites* (*lobata?*). Many alcyonarians are also present.

19. Ofu (Manua)

The anchorage of Ofu is on the west side in a very sheltered location (Fig. 39), 200 m offshore from Alaufau, where the water is 10-20 m deep. The bottom has marked topographic relief, with small corals and red algae on top of the elevations, dense coral cover and good species diversity on the walls, and white sand in the bottoms of the troughs. The water was clear and warm. Fishes were abundant, but no sharks were observed.

Two dives were made on the fringing reefs on the north and south sides of Tutuila, the main island of American Samoa.

20. Leone Bay (Tutuila)

At Leone Bay on the windward south west side (Fig. 39), the reef was surveyed out to 350 m from the shore near Logologo Point (Fig. 40). The reef structure is irregular, somewhat resembling a spur and groove system, with a shallow reef flat, and then large reef patches in deeper water, extending down to 25 m. The coral cover is very variable, sometimes almost 100 percent, as at Ofu, but many helioporas are also present. A large flat of white completely detritus-free coarse sand occurs at 15 m depth. The water was warm and clear, with many fishes and no sharks.

21. Ogegasa Point (Tutuila)

On the north side of Tutuila, at Ogegasa Point (Fig. 39), there is a vertical basaltic rock slope from the surface to 3 m, followed by a rocky flat with small scattered corals extending 50 m offshore to a depth of 7 m (Fig. 41). From here a slope with spur and groove configurations drops to 15 m and then a very steep slope down to 30 m, ending in an extensive sand flat. This slope has the best coral coverage and richest species diversity of all the Samoan sites observed. The water was warm and slightly turbid, perhaps from a recent rainfall. Again the area was rich in fishes but lacked sharks. Apparently there are no good near-shore drop-offs around the islands of American Samoa.

It was not possible to reach Rose Atoll, as the seaplane was damaged shortly before our arrival, and time and weather precluded boat transportation. Discussions with the Office of Marine Resources which recently surveyed the atoll, indicated that the land area was inadequate for any facility, so that it could only be used for short visits.

CONCLUSIONS

The overall evaluation of the site information leads to the following conclusions for the Smithsonian-planned programs. In the Caribbean, the logistic problems and unique character of the San Blas Islands, the disturbance and political problems at Discovery Bay, and the poor reef structure of St. Croix and Acklins Island left Glover's Reef, British Honduras as the preferred site. In the Pacific no final decision was possible without further field surveys, but several areas showed good potential, including Pakin, Ulithi, and Arno. Ulithi was not visited by a survey team, and so requires further examination. A more detailed study of areas in Fiji and the Gilbert and Ellice Islands could also be productive. However, once the scientific suitability of a site was determined, it would still be necessary to negotiate with the local inhabitants for space and permission to work on their reefs.

It is important to remember that the areas reported on here were selected and described in accordance with the specific program criteria listed in the introduction, not all of which would necessarily apply to other projects. We hope that others searching for a suitable location for a coral reef research program will be able to use this information, with due caution for its limitations, in selecting a site most appropriate to their needs.

ACKNOWLEDGEMENTS

We should particularly like to acknowledge the support of the Environmental Sciences Program at the Smithsonian Institution and of the International Decade of Ocean Exploration office of the National Science Foundation (Grant GX-28676). In addition, the cooperation and support of the governments of the Bahamas, British Honduras, the U.S. Trust Territory and American Samoa were greatly appreciated, as was the assistance of the West Indies Laboratory of Fairleigh Dickenson University on St. Croix, the Discovery Bay Marine Laboratory on Jamaica, the Smithsonian Tropical Research Institute in Panama, and the University of Guam. The individuals who cooperated in this survey, either as participants on survey teams, contributors of questionnaires or site suggestions, members of the CITRE and IMSWE programs, or suppliers of local advice and support are too numerous to mention although many are acknowledged at appropriate places in the report.

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Site name ______________________ Ocean area ______________

General location ______________________________

Longitude ____________ Latitude ____________

Charts ______________________________

General references ______________________________

☐ Island; ☐ Continental; ☐ Atoll; ☐ Fringing reef on ☐ volcanic or ☐ other base;
☐ Barrier reef.

Description of site ______________________________

Features:	Yes	No	Notes
Adequate comparable reef area for sampling (perhaps 1 km frontage)	☐	☐	
Well developed reef flat for drilling	☐	☐	
Reef development to at least 50 m depth	☐	☐	
Width across reef less than 300 m	☐	☐	
Reef near enough to shore to permit shore-based instrumentation	☐	☐	
Reef undergoing active construction	☐	☐	
Considerable species diversity	☐	☐	
Reef not obviously unique	☐	☐	
Major terrestrial influences absent	☐	☐	
Reasonably continuous reef accumulation	☐	☐	
Current and tidal flow patterns permitting cross-reef metabolic studies	☐	☐	
Variety of subsidiary site types in area	☐	☐	
Undisturbed by development, catastrophic storms, war, or pollution	☐	☐	
Probability of remaining undisturbed	☐	☐	
Weather permitting year-round work	☐	☐	
Accessible, within 1 day's travel of a major airport and harbor facility	☐	☐	
Anchorage and landing for work boats	☐	☐	
Accommodations available	☐	☐	
Research space available	☐	☐	
Buildings available for conversion	☐	☐	
Electricity	☐	☐	
Fresh water	☐	☐	
Local suppliers (food, fuel, building materials)	☐	☐	
Research vessels available in general area	☐	☐	

Governmental authority ______________________________

Possible attitude toward project ______________________________

Previous scientific work (include references) ______________________________

Aerial Photographs (Source) ______________________________

Other notes ______________________________

Information supplied by ______________________ Date ______________

A sketch map on the reverse would be helpful. Indicate scale or approximate distances if possible. (Also idealized cross sections with reef zonations)

Figure 1 - QUESTIONNAIRE FOR SITE SURVEY

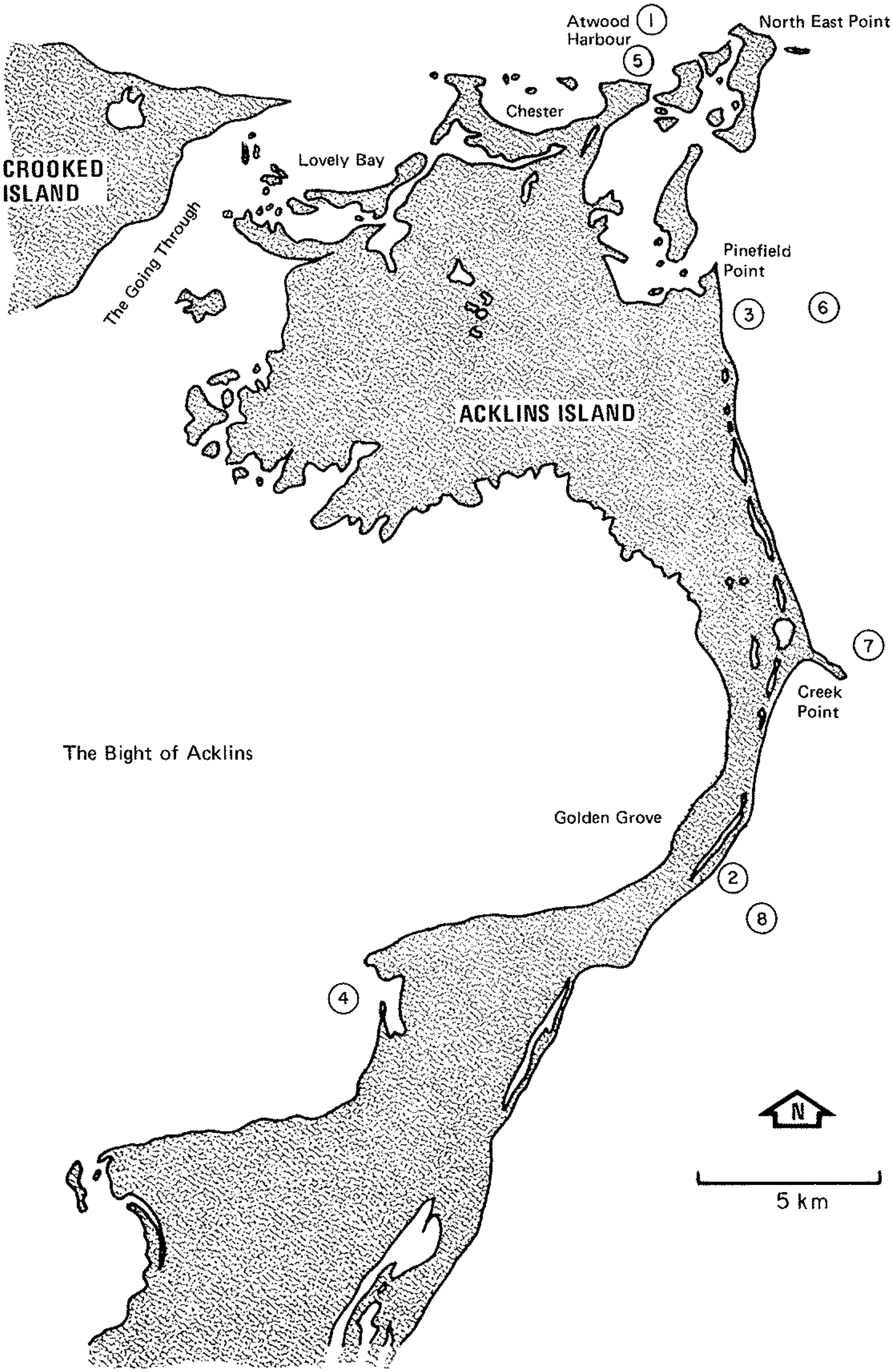


Figure 2 – ACKLINS ISLAND
22°30′N 74°00′W

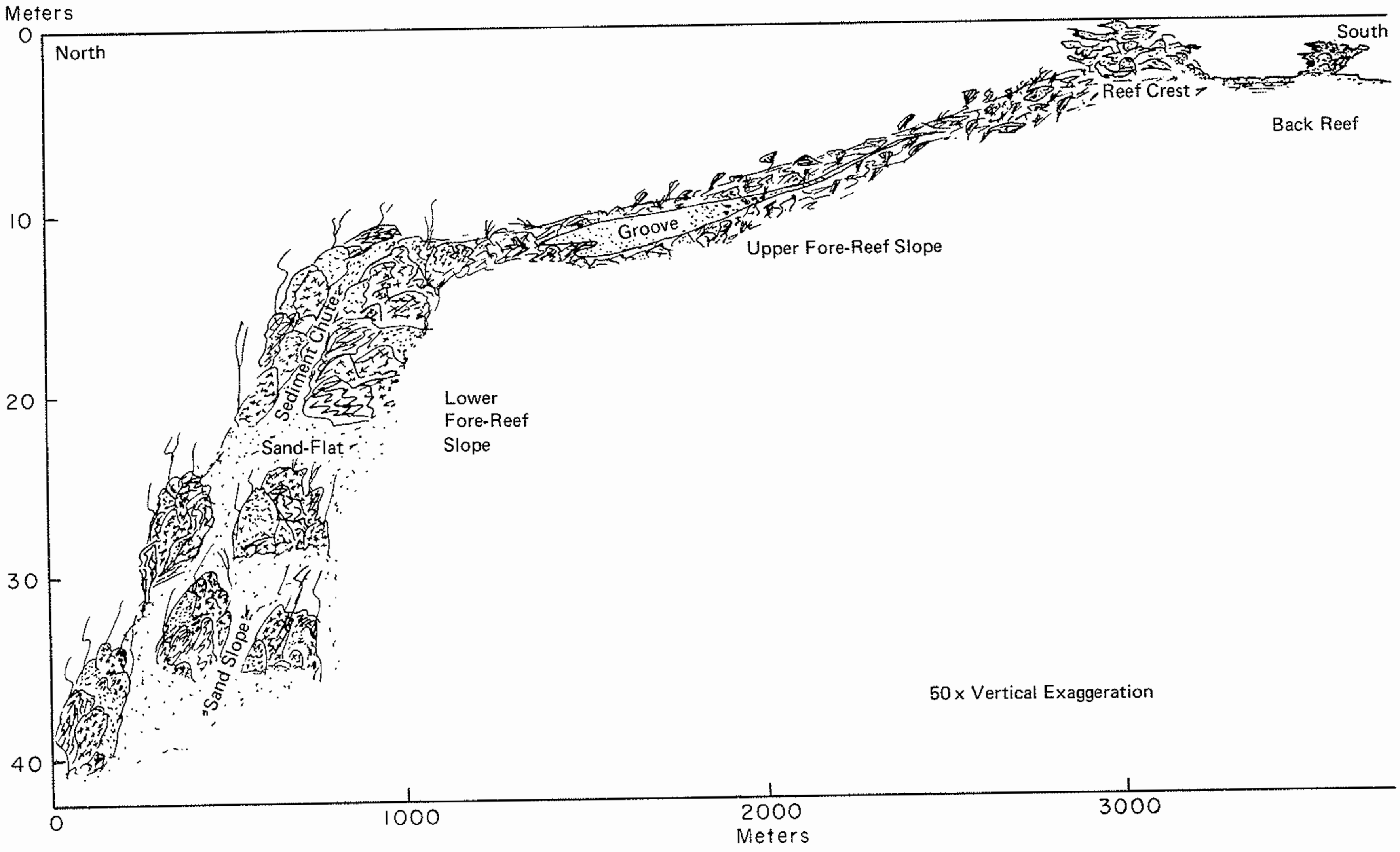


Figure 3 – SITE 5 - ATWOOD HARBOR

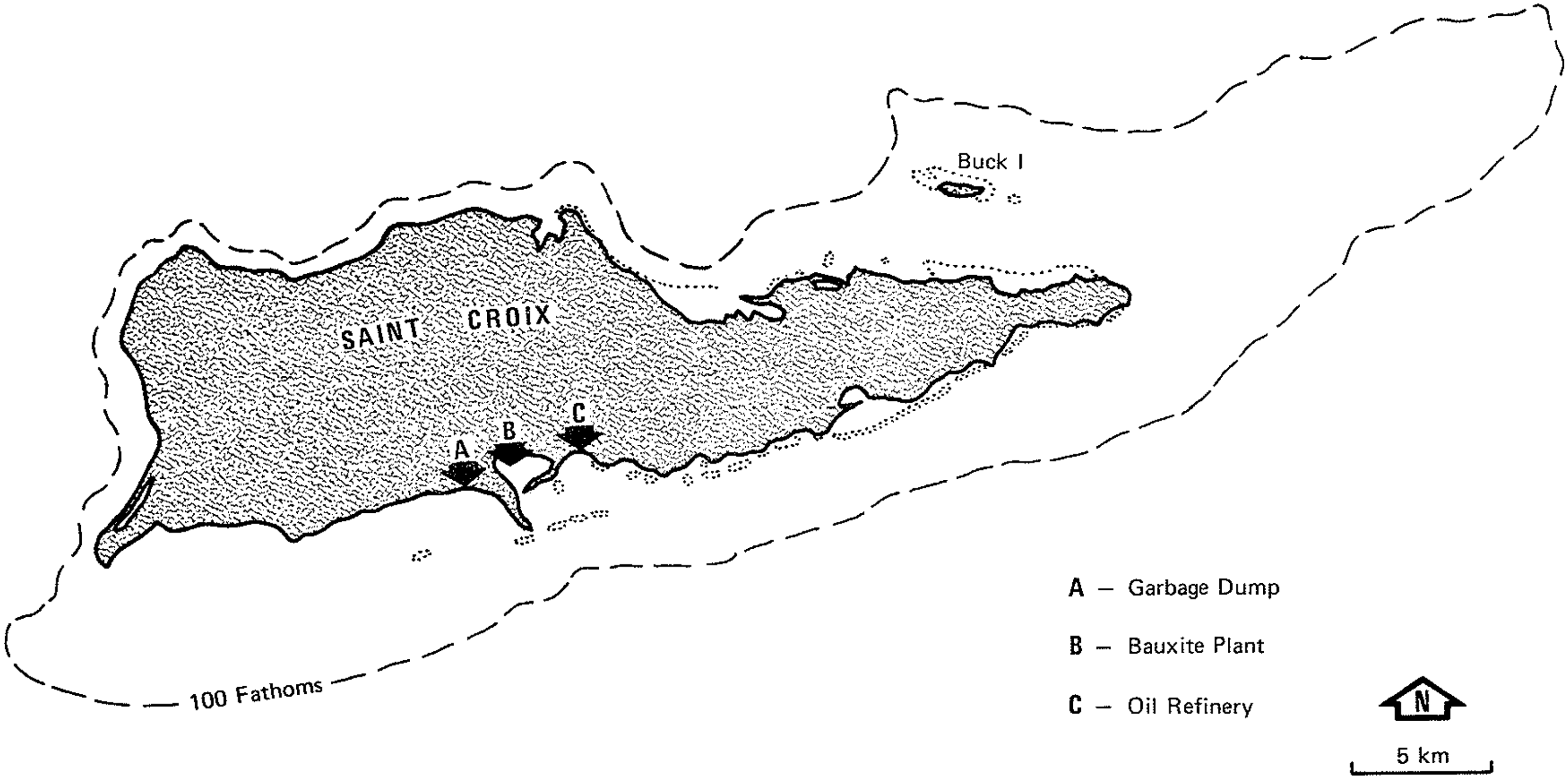


Figure 4 — ST. CROIX
17°45'N 64°40'W

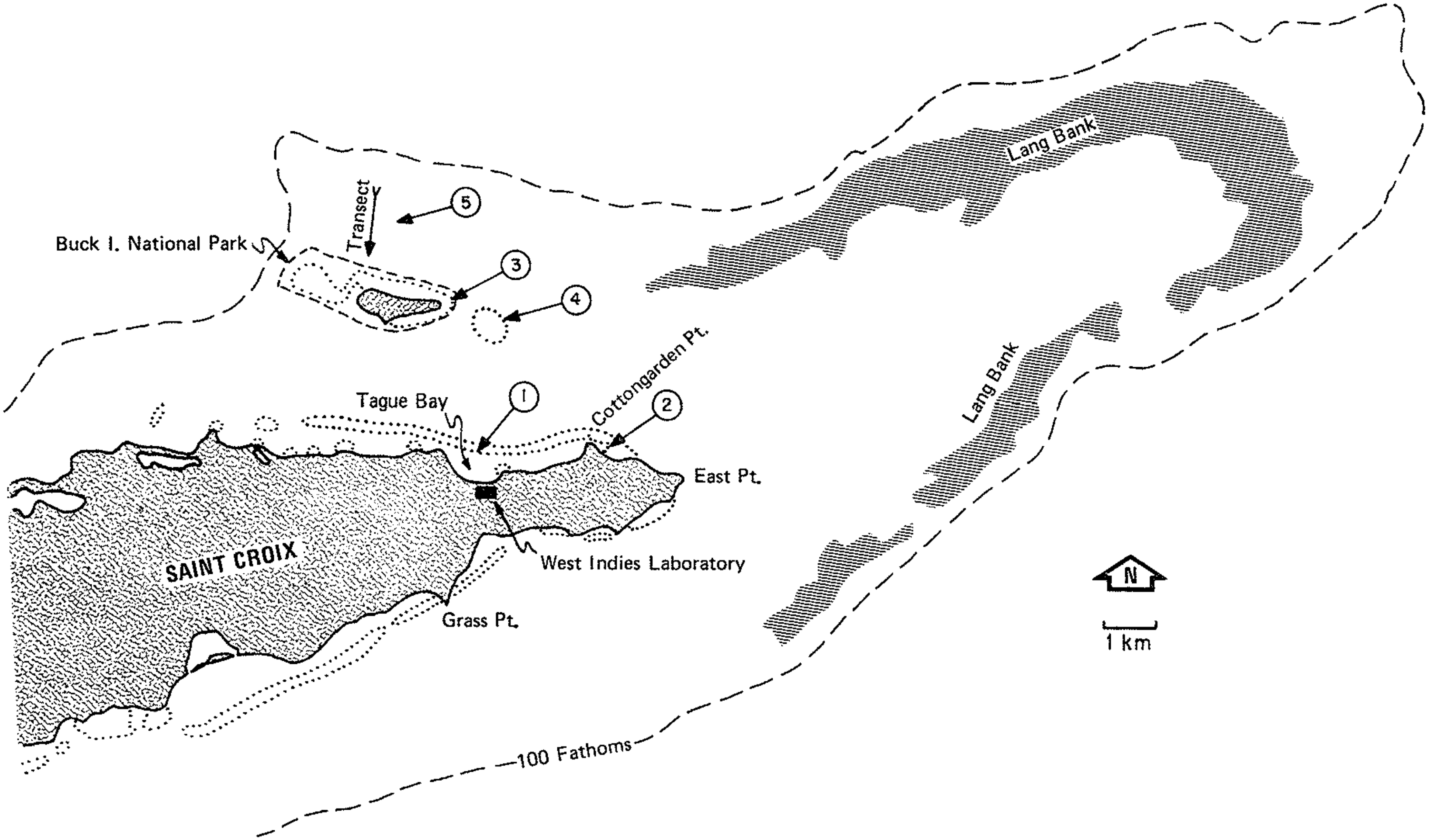


Figure 5 – EAST END OF ST. CROIX SHOWING DIVING SITES

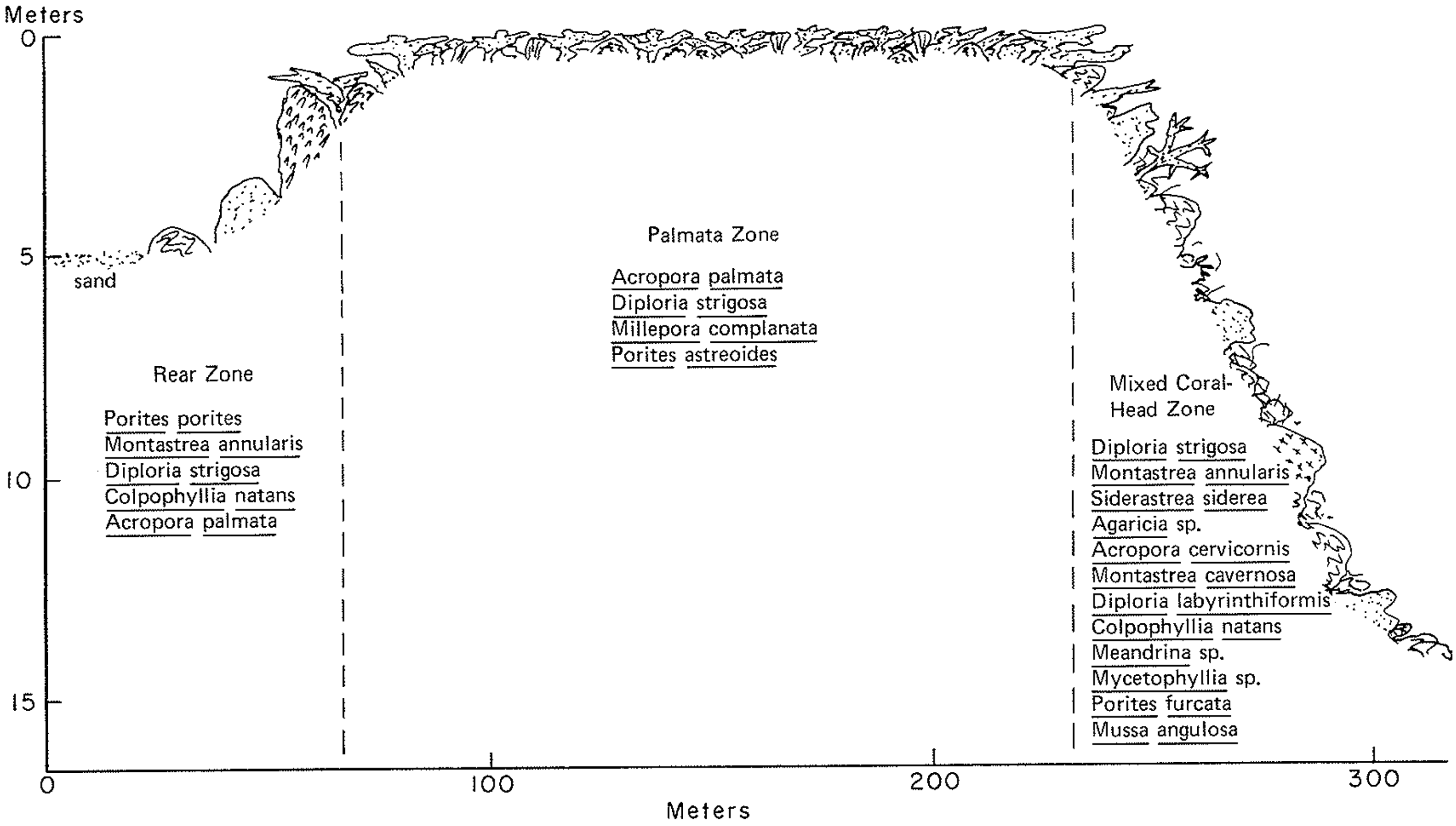


Figure 6 — ST. CROIX - SITE 1 - BANK BARRIER REEF OFF TAGUE BAY
(data supplied by L. Firth, D. Jennus and N. B. Ogden)

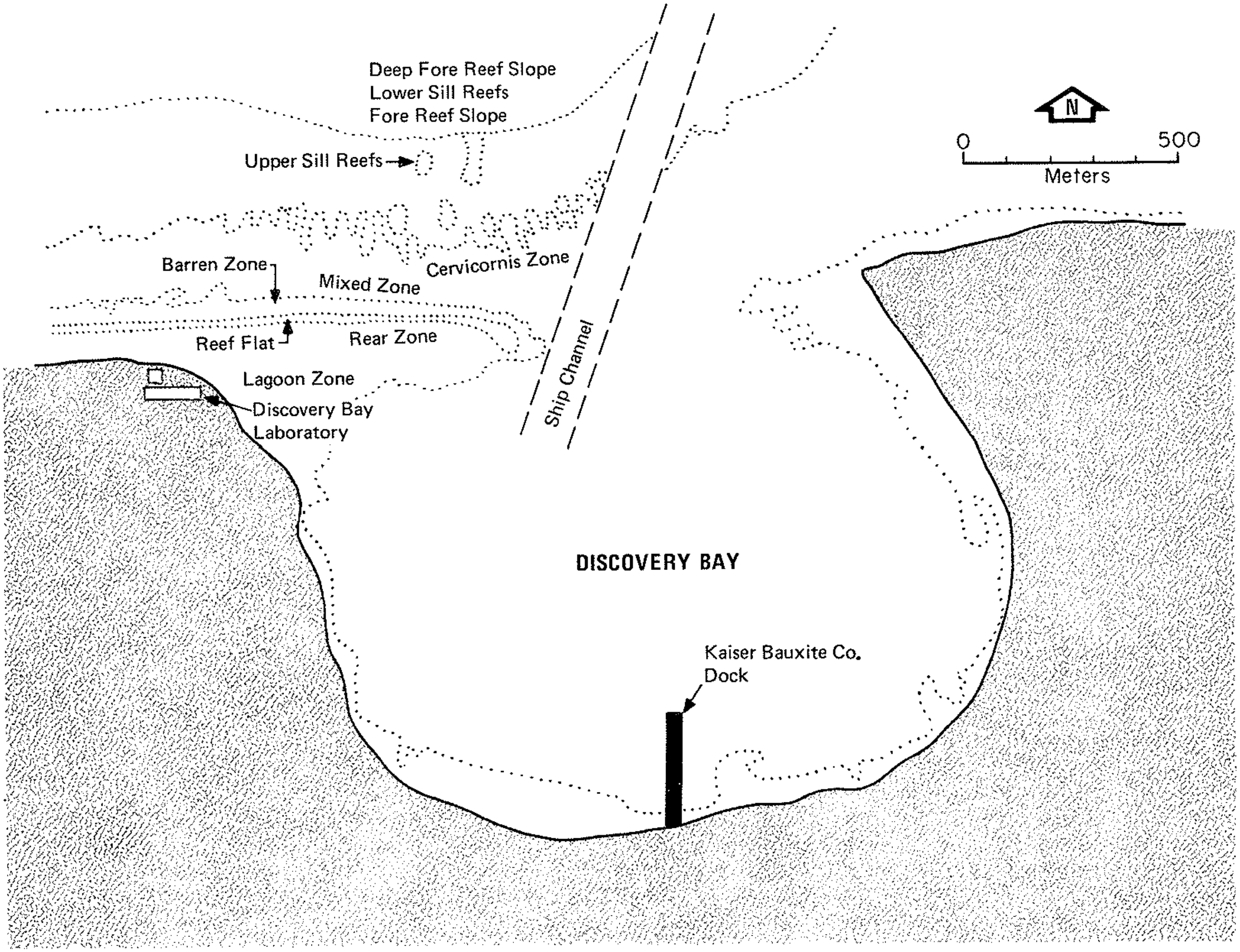


Figure 7 – DISCOVERY BAY (after Land, unpublished)
18°30′N 77°25′W

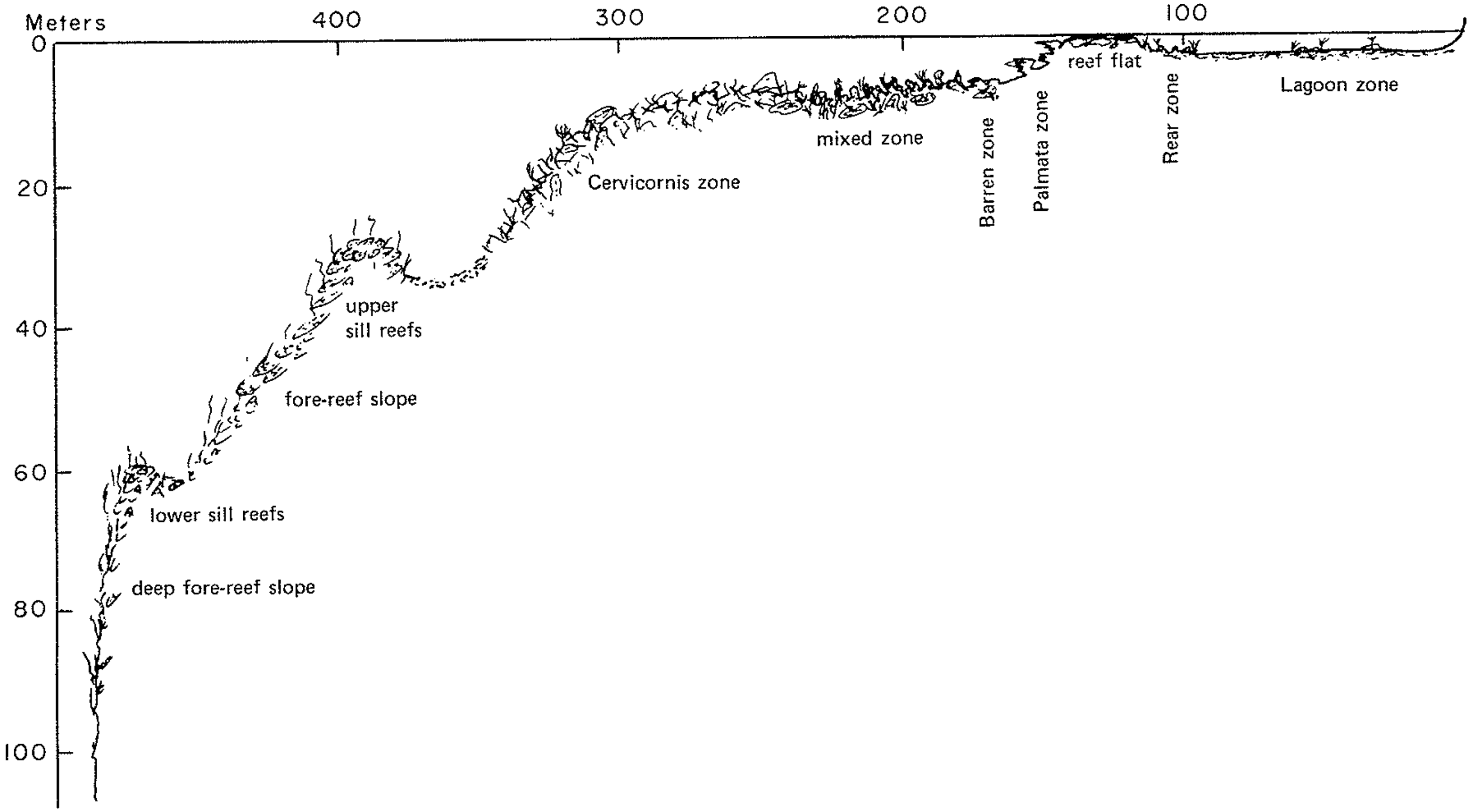


Figure 8 – DISCOVERY BAY, JAMAICA

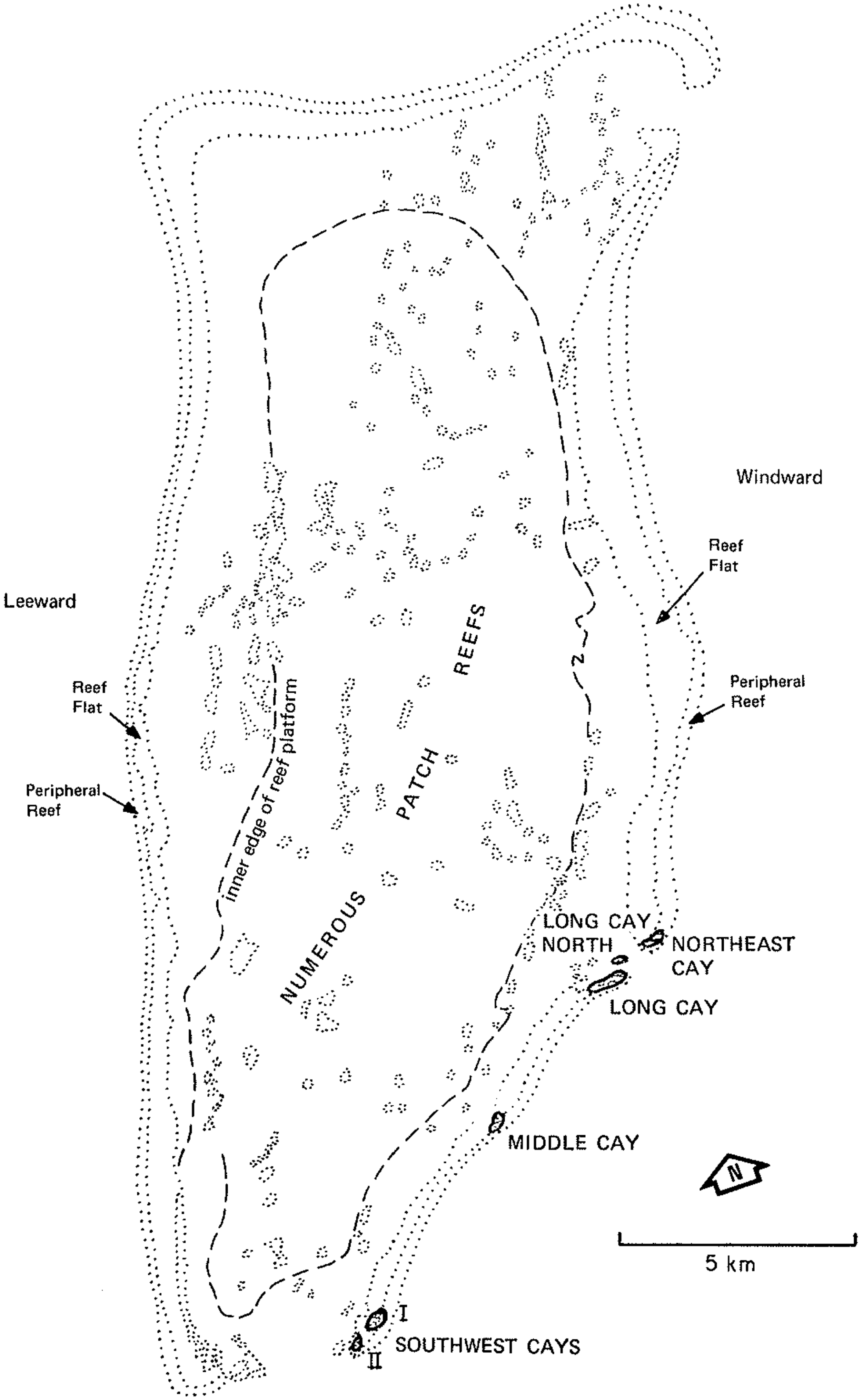
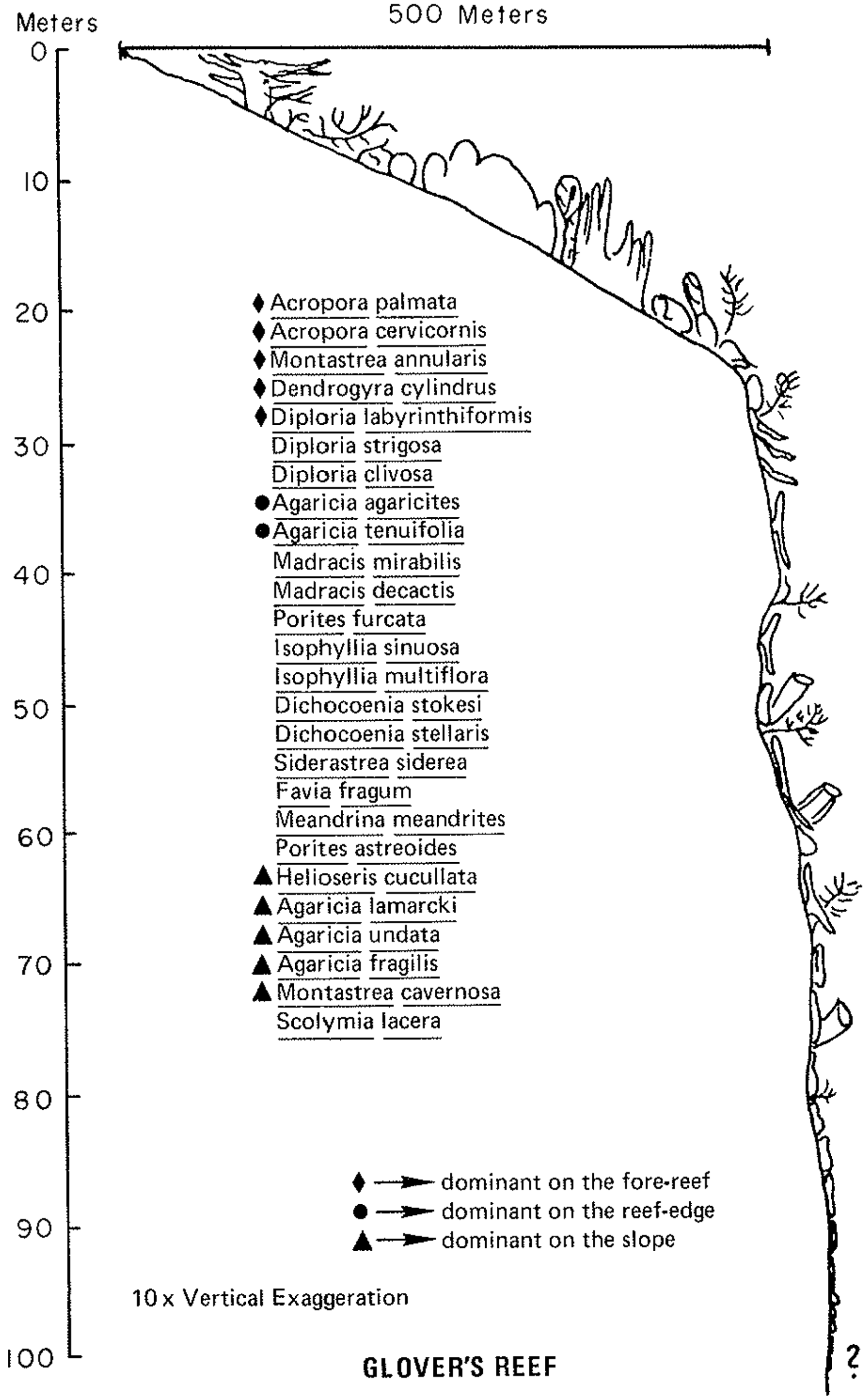
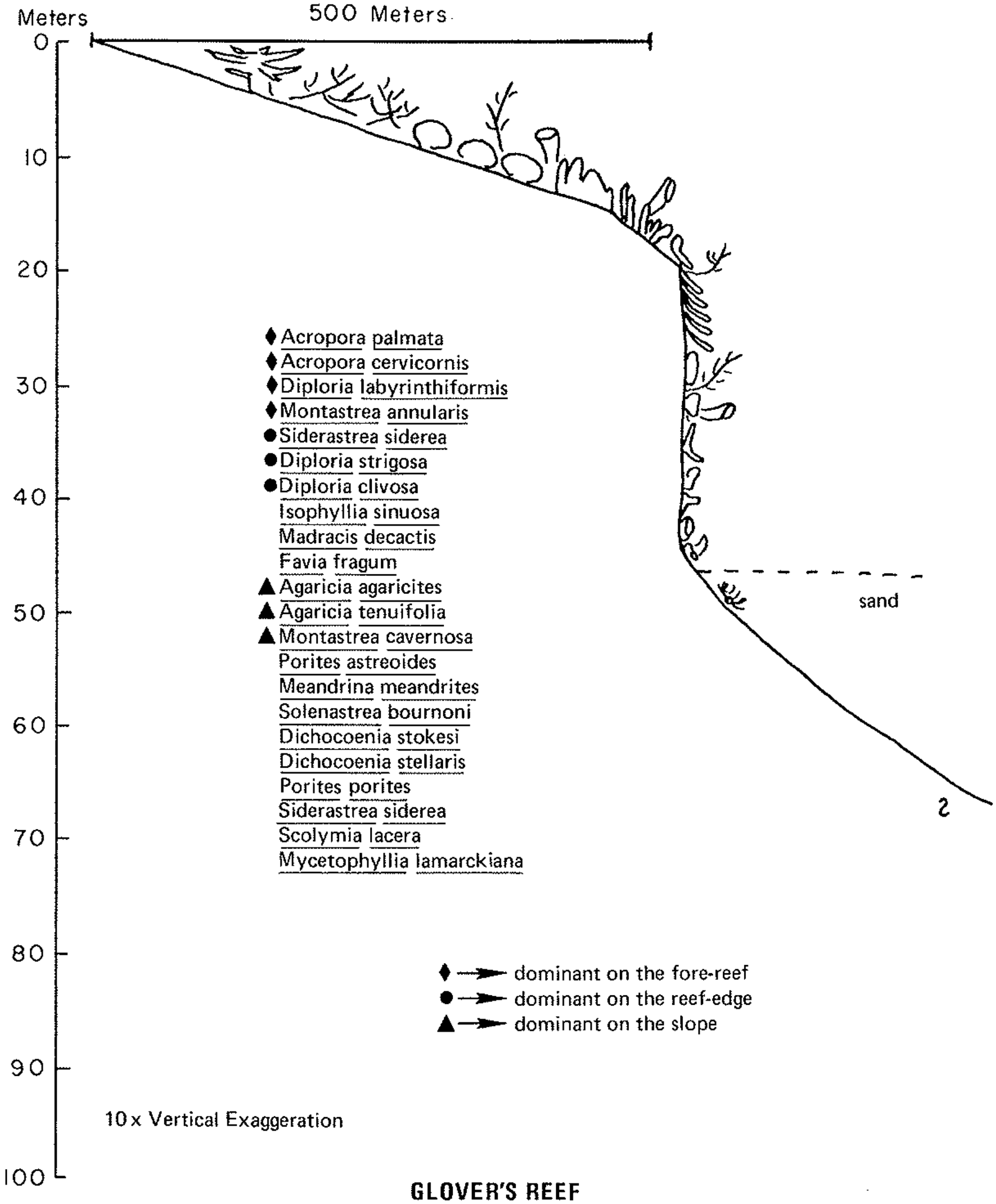


Figure 9 – GLOVER'S REEF (modified after Stoddart, 1962)
16°50'N 87°50'W



GLOVER'S REEF

Figure 10 – TYPICAL WINDWARD REEF



GLOVER'S REEF

Figure 11 – TYPICAL LEEWARD REEF

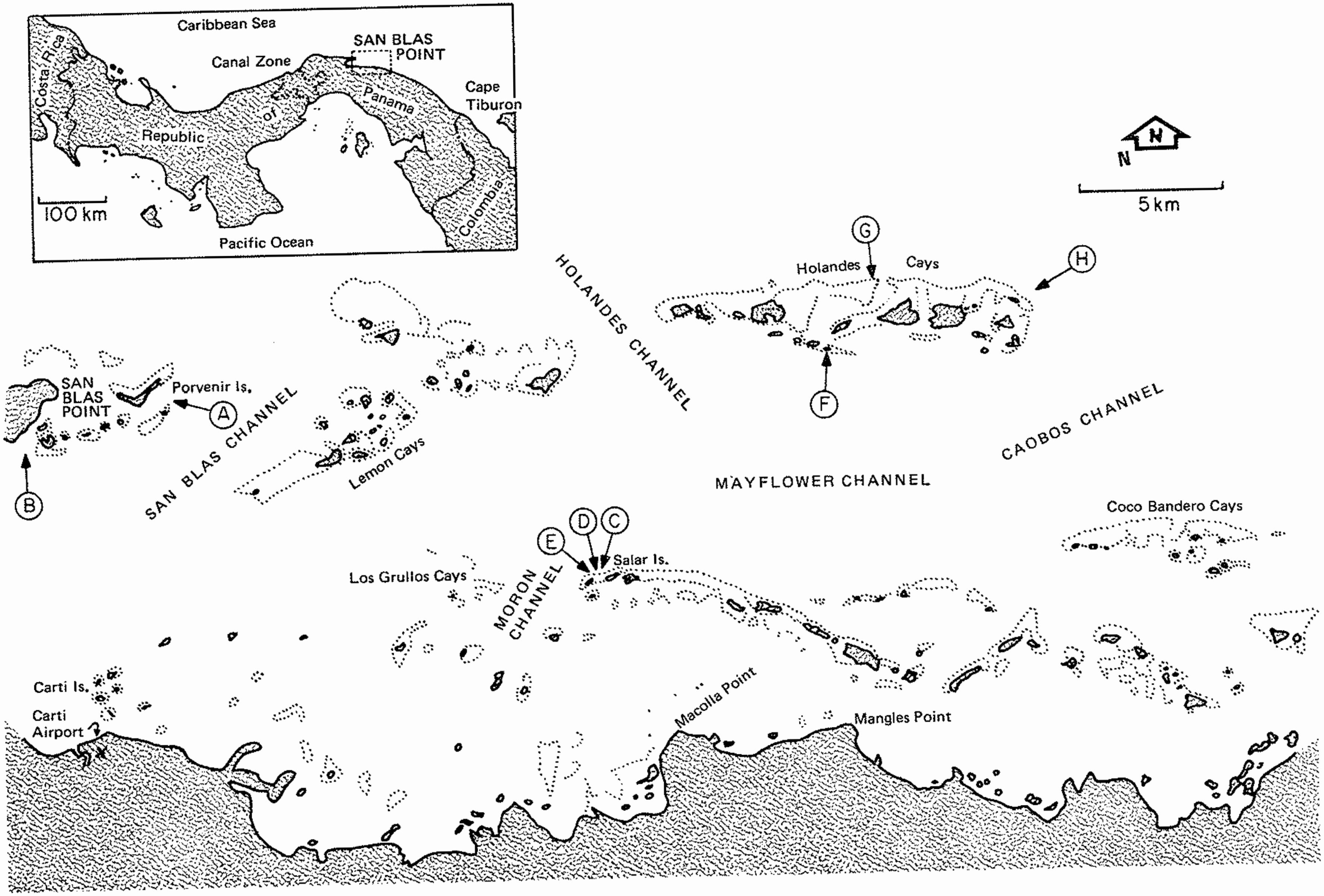


Figure 12 – WESTERN SAN BLAS ISLANDS
9°30′N 78°45′W

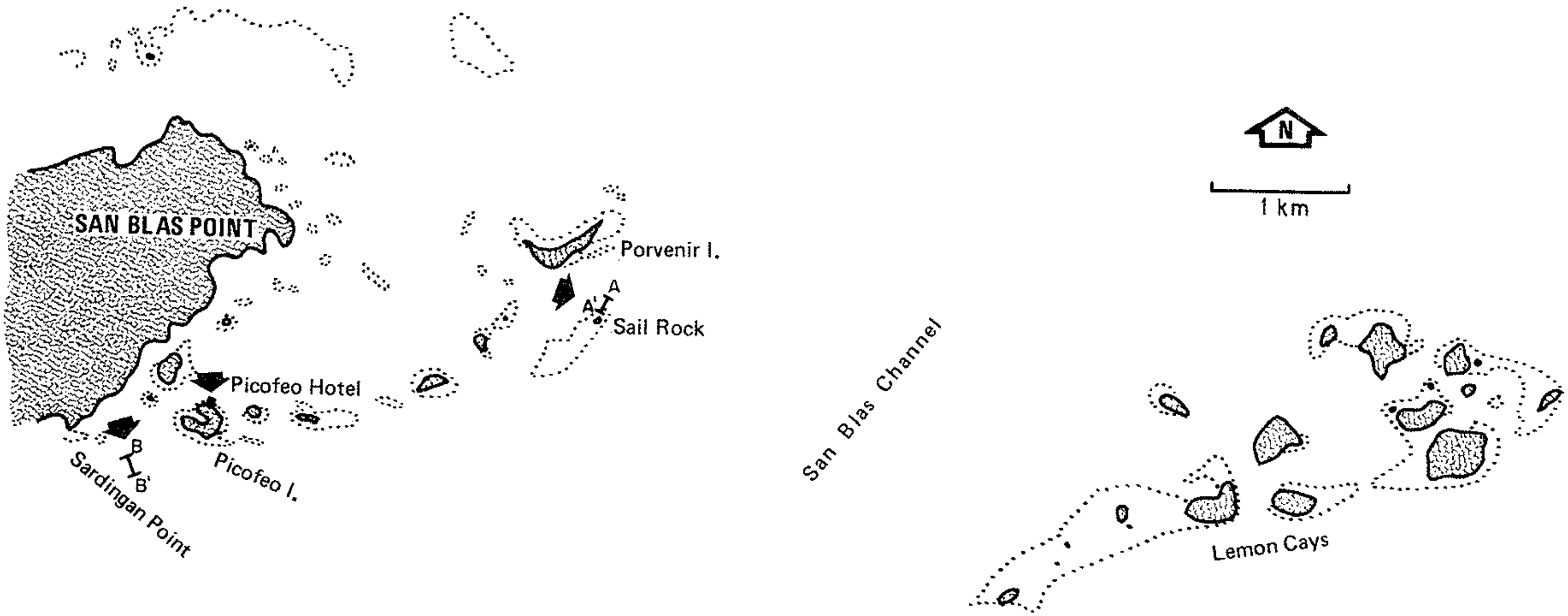
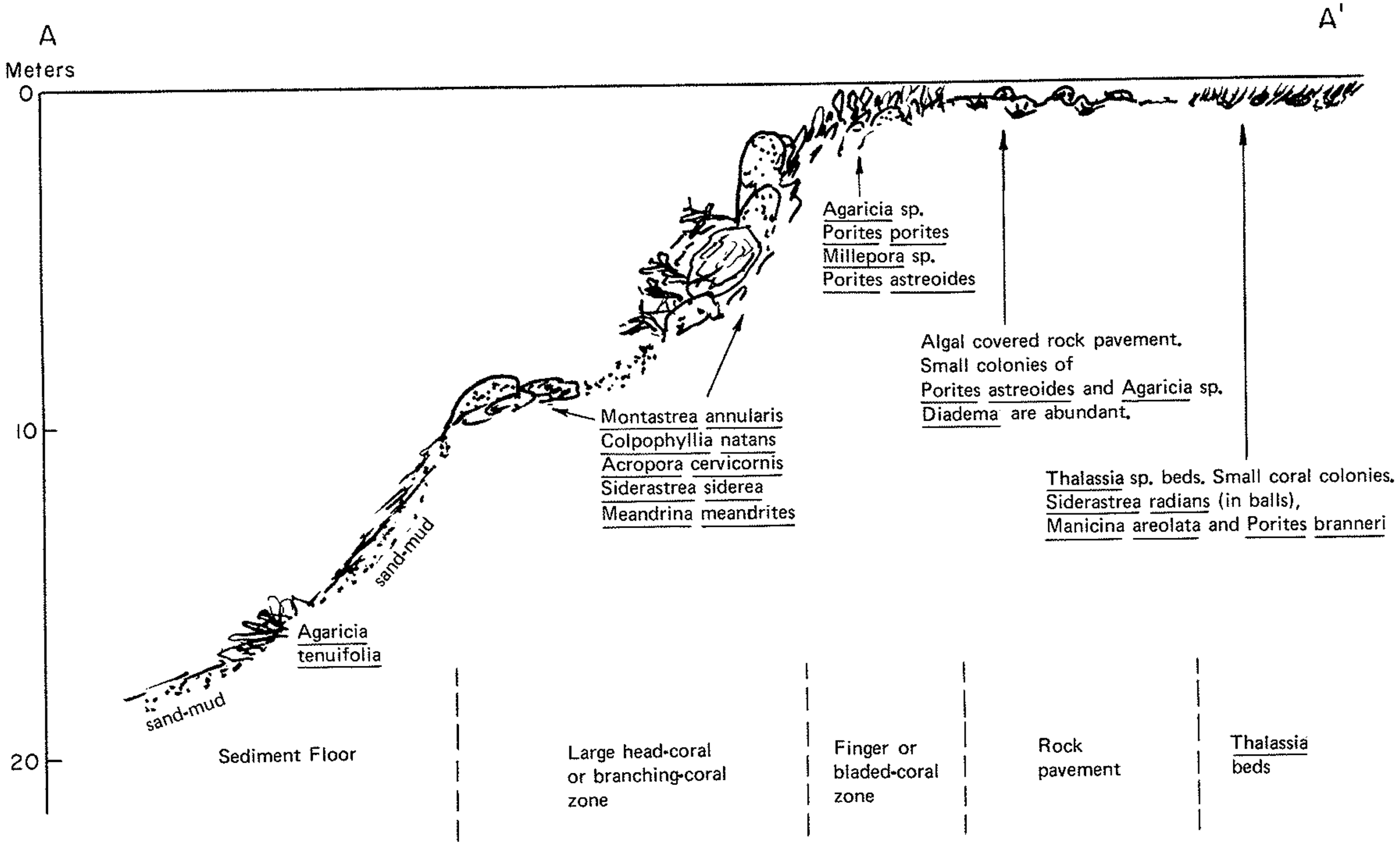
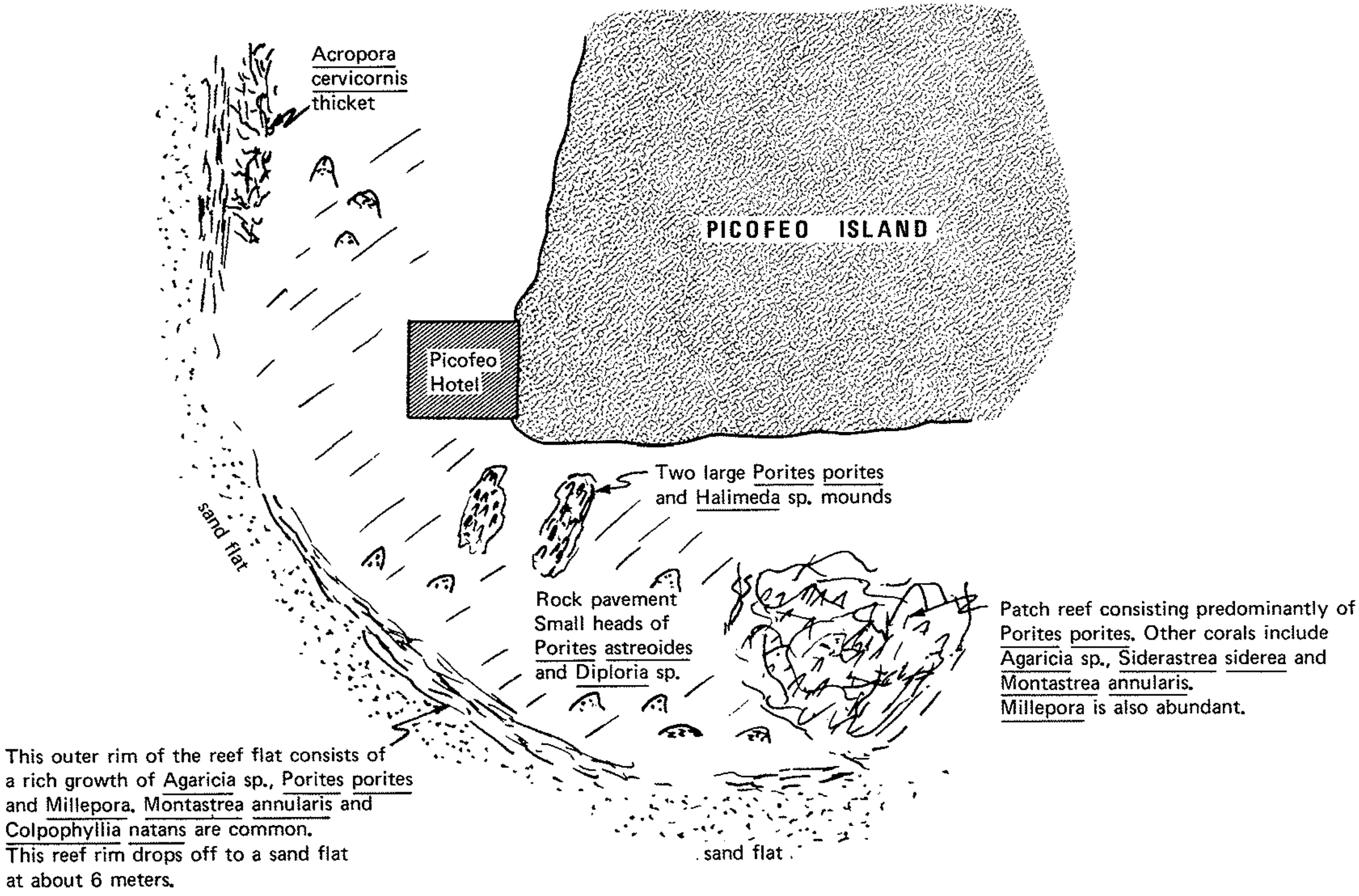


Figure 13 – SAN BLAS ISLANDS
9°30'N 78°55'W



SAN BLAS ISLANDS, PANAMA – OFF SAIL ROCK

Figure 14 – PROFILE A–A'



Acropora cervicornis thicket

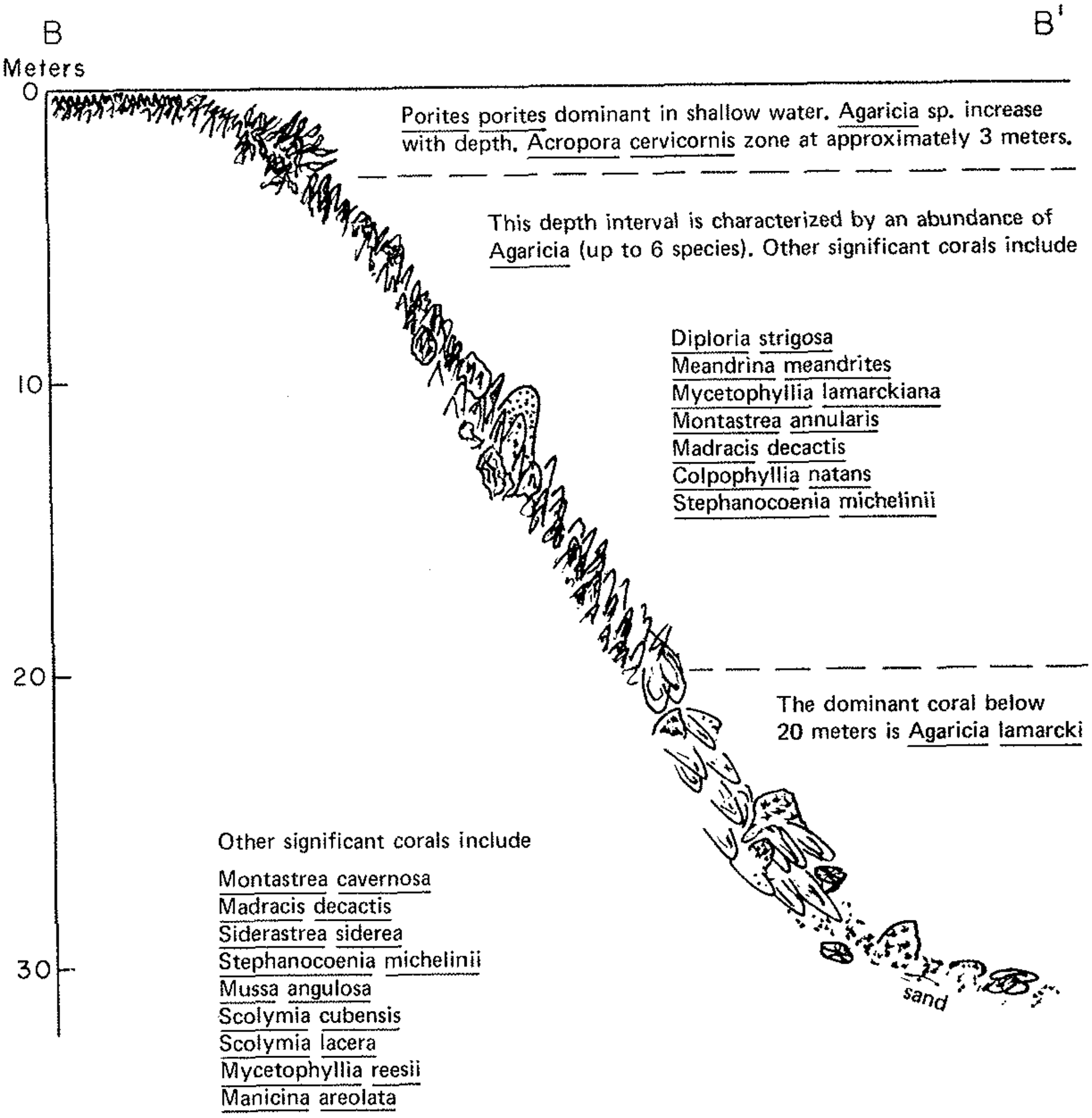
Two large Porites porites and Halimeda sp. mounds

Rock pavement
Small heads of Porites astreoides and Diploria sp.

Patch reef consisting predominantly of Porites porites. Other corals include Agaricia sp., Siderastrea siderea and Montastrea annularis.
Millepora is also abundant.

This outer rim of the reef flat consists of a rich growth of Agaricia sp., Porites porites and Millepora. Montastrea annularis and Colpophyllia natans are common.
This reef rim drops off to a sand flat at about 6 meters.

Figure 15 – DIAGRAMATIC SKETCH (plan view) OF REEF IN THE VICINITY OF PICOFEO HOTEL



SAN BLAS ISLANDS, PANAMA – OFF SARDINGAN POINT

Figure 16 – PROFILE B–B'

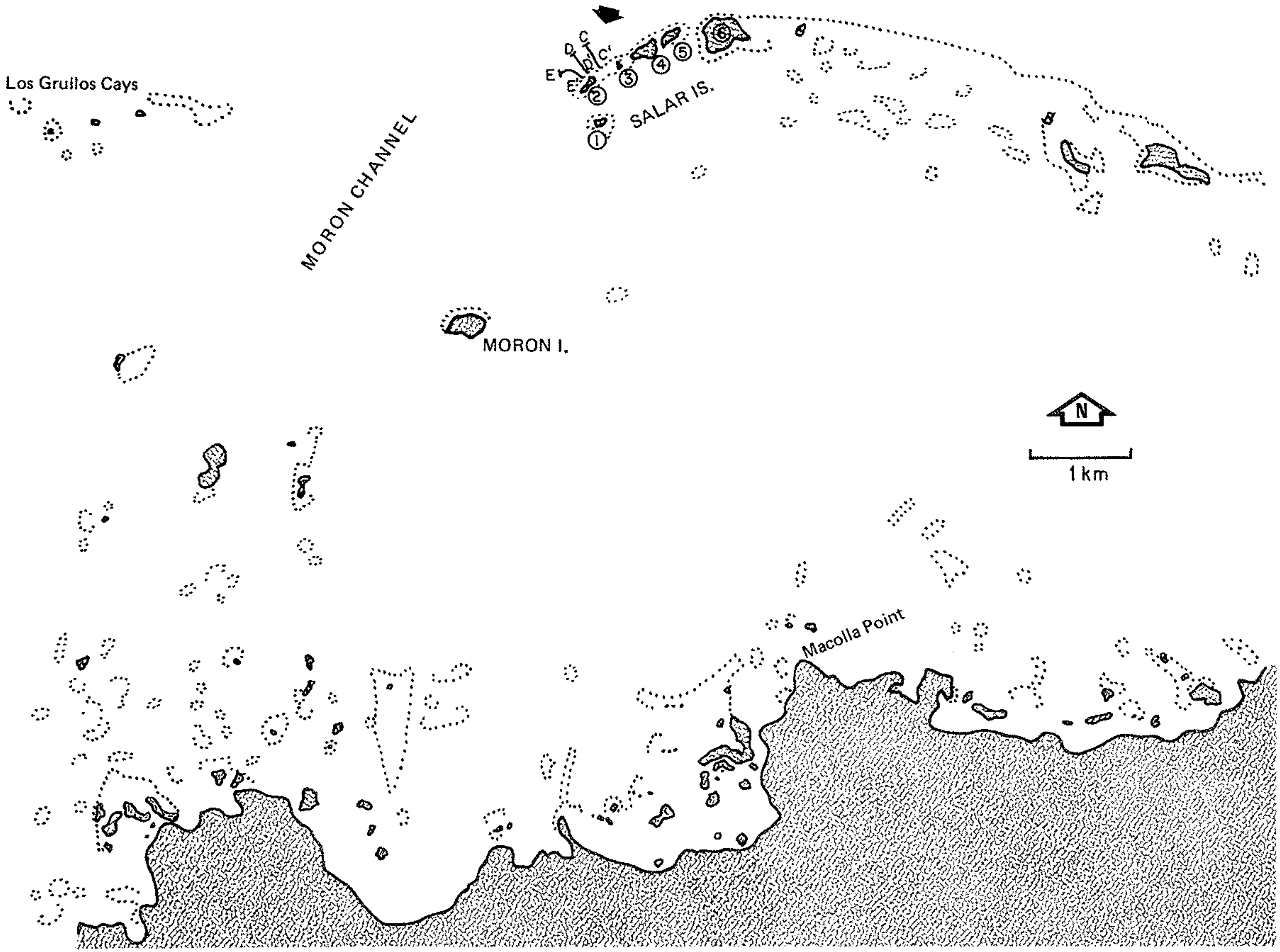
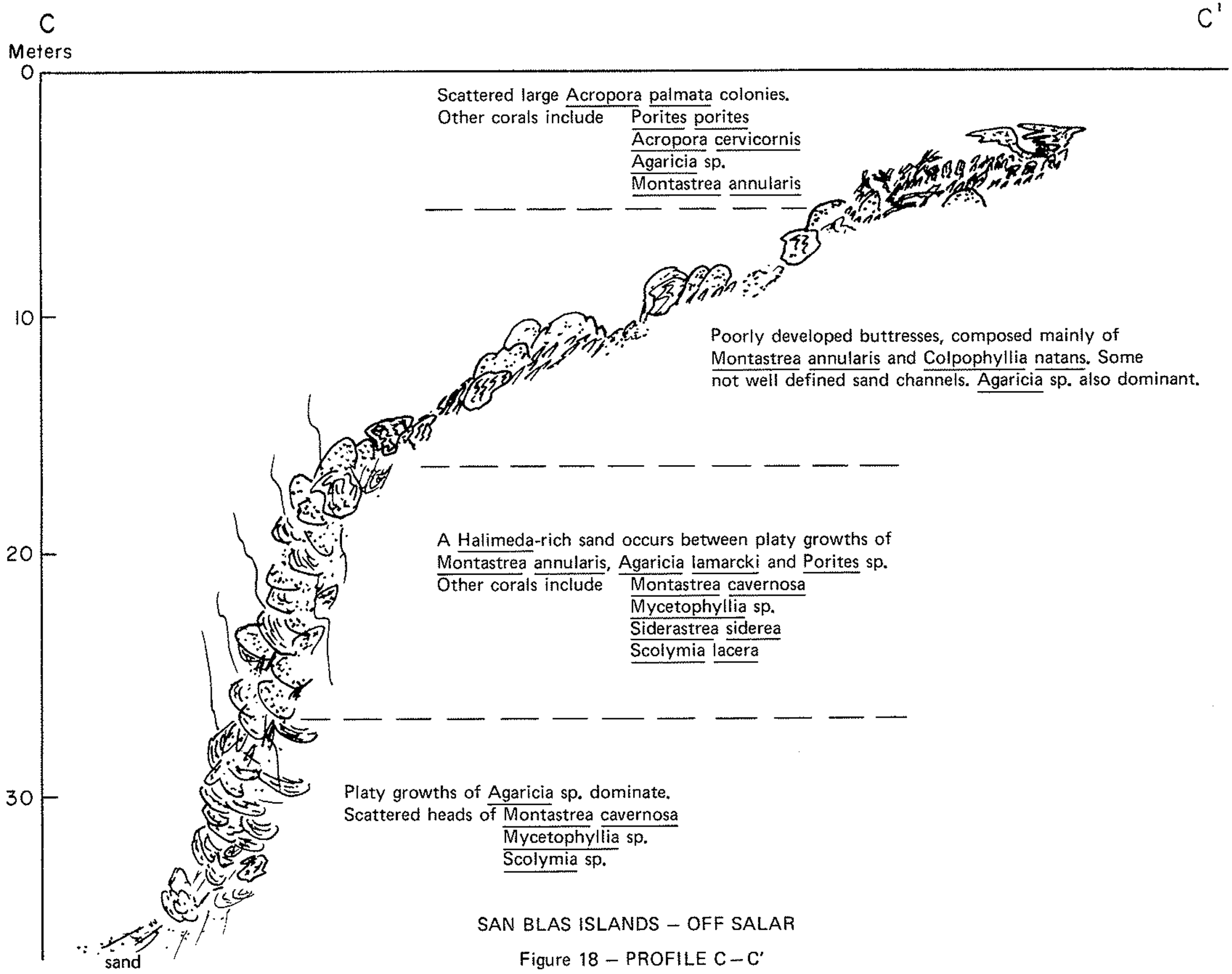
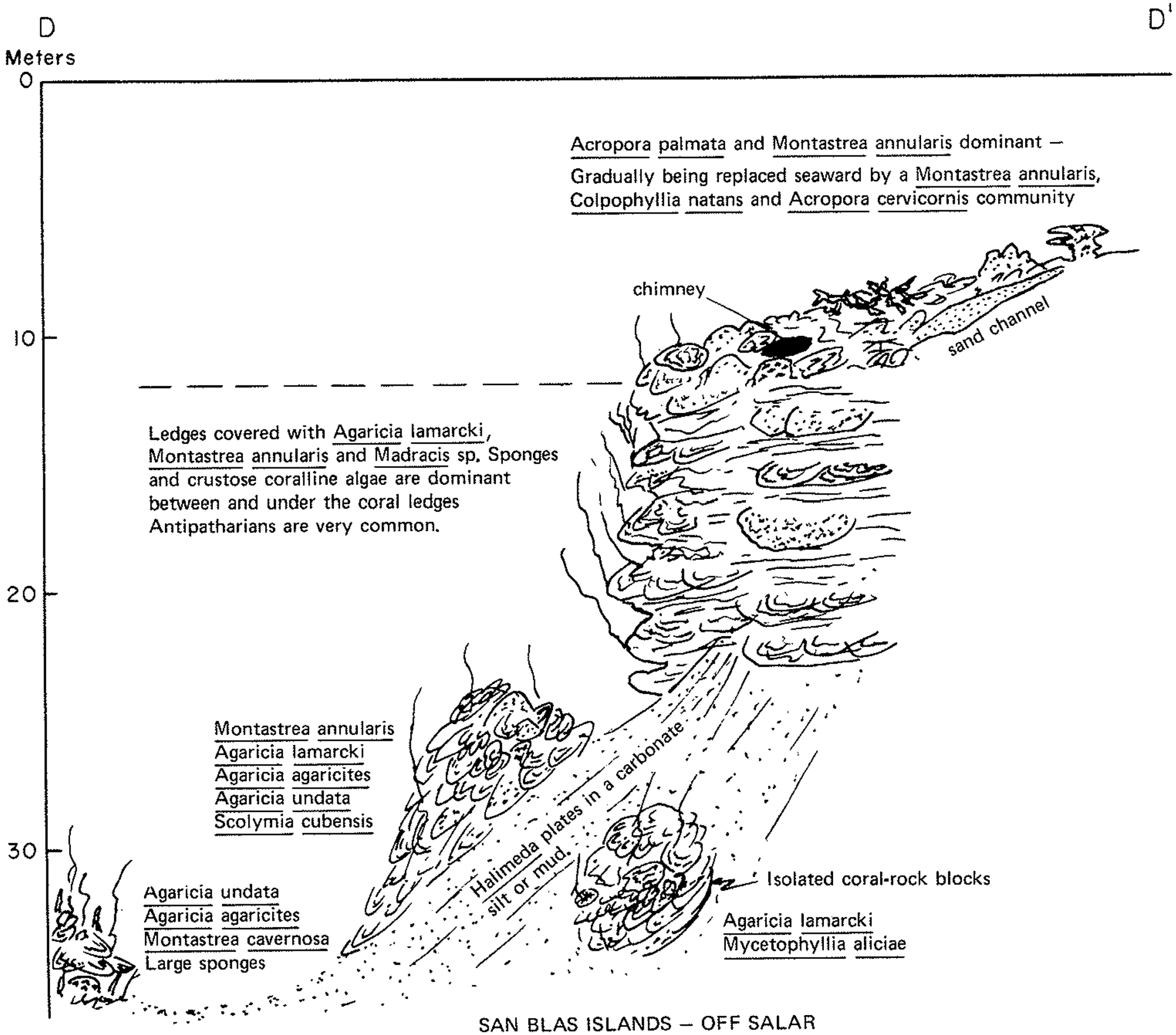


Figure 17 — SAN BLAS ISLANDS
9°30'N 78°48'W



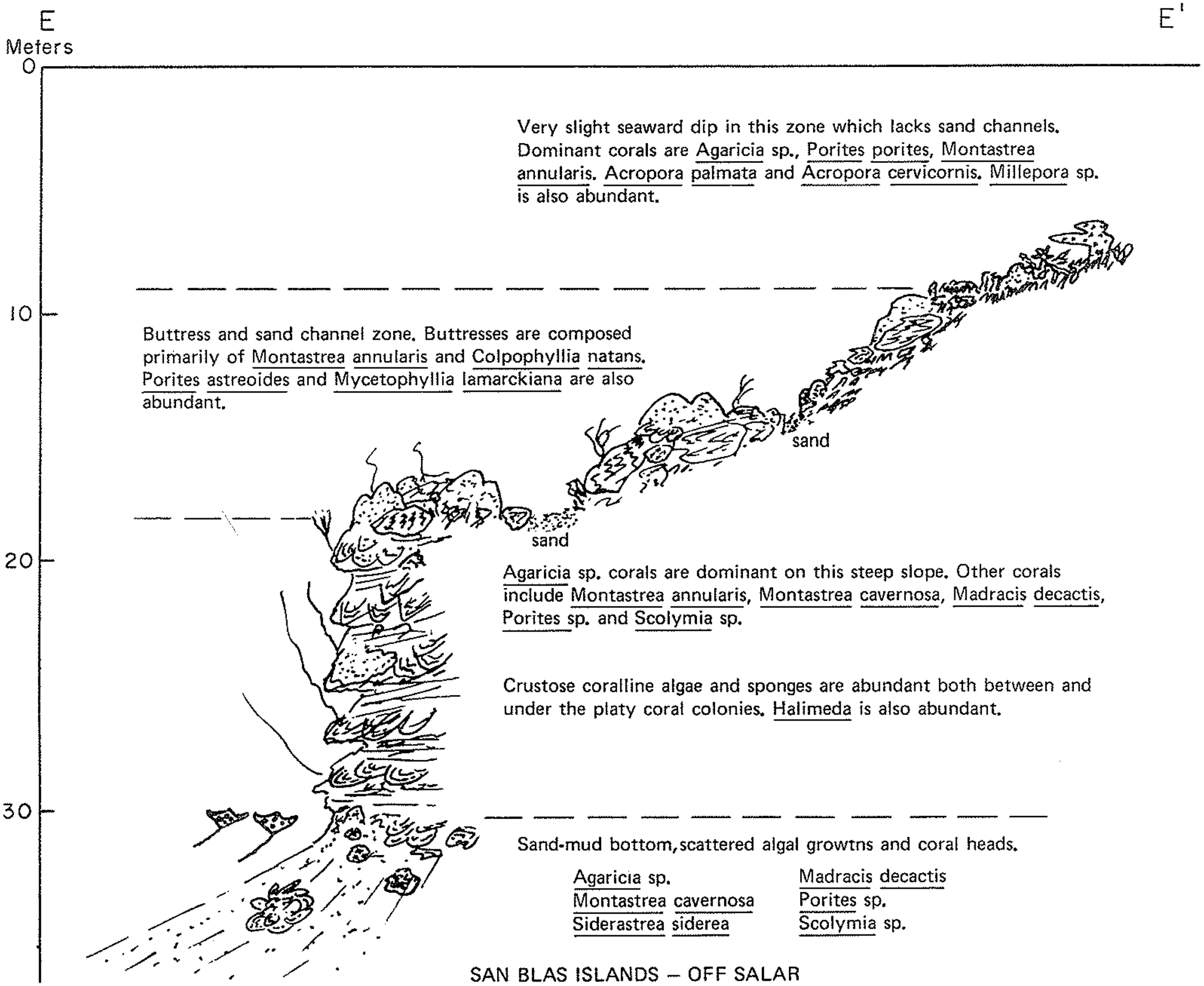
SAN BLAS ISLANDS – OFF SALAR

Figure 18 – PROFILE C – C'



SAN BLAS ISLANDS — OFF SALAR

Figure 19 — PROFILE D — D'



Very slight seaward dip in this zone which lacks sand channels. Dominant corals are Agaricia sp., Porites porites, Montastrea annularis. Acropora palmata and Acropora cervicornis. Millepora sp. is also abundant.

Buttress and sand channel zone. Buttresses are composed primarily of Montastrea annularis and Colpophyllia natans. Porites astreoides and Mycetophyllia lamarckiana are also abundant.

Agaricia sp. corals are dominant on this steep slope. Other corals include Montastrea annularis, Montastrea cavernosa, Madracis decactis, Porites sp. and Scolymia sp.

Crustose coralline algae and sponges are abundant both between and under the platy coral colonies. Halimeda is also abundant.

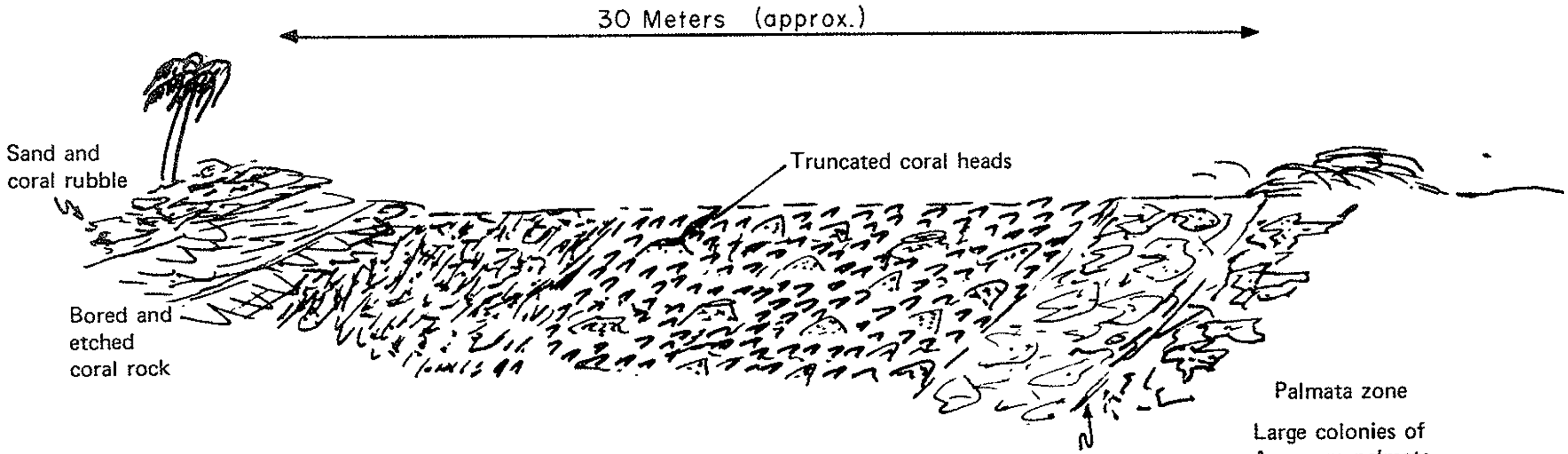
Sand-mud bottom, scattered algal growtns and coral heads.

Agaricia sp.
Montastrea cavernosa
Siderastrea siderea

Madracis decactis
Porites sp.
Scolymia sp.

SAN BLAS ISLANDS – OFF SALAR

Figure 20 – PROFILE E – E'



Algal zone

Thick growth of brown and green algae. Small colonies of *Siderastrea radians* and *Porites porites*

Porites zone

Thick growth of *Porites porites* with scattered heads of *Porites astreoides* *Siderastrea siderea* and *Diploria* sp. *Halimada* sp. is abundant.

Palythoa zone

Heavy encrustations of *Palythoa* sp.

Palmata zone

Large colonies of *Acropora palmata*

Figure 21 – REEF FLAT OFF NORTHWEST COAST ISLAND NO. 3
SALAR – SAN BLAS ISLANDS

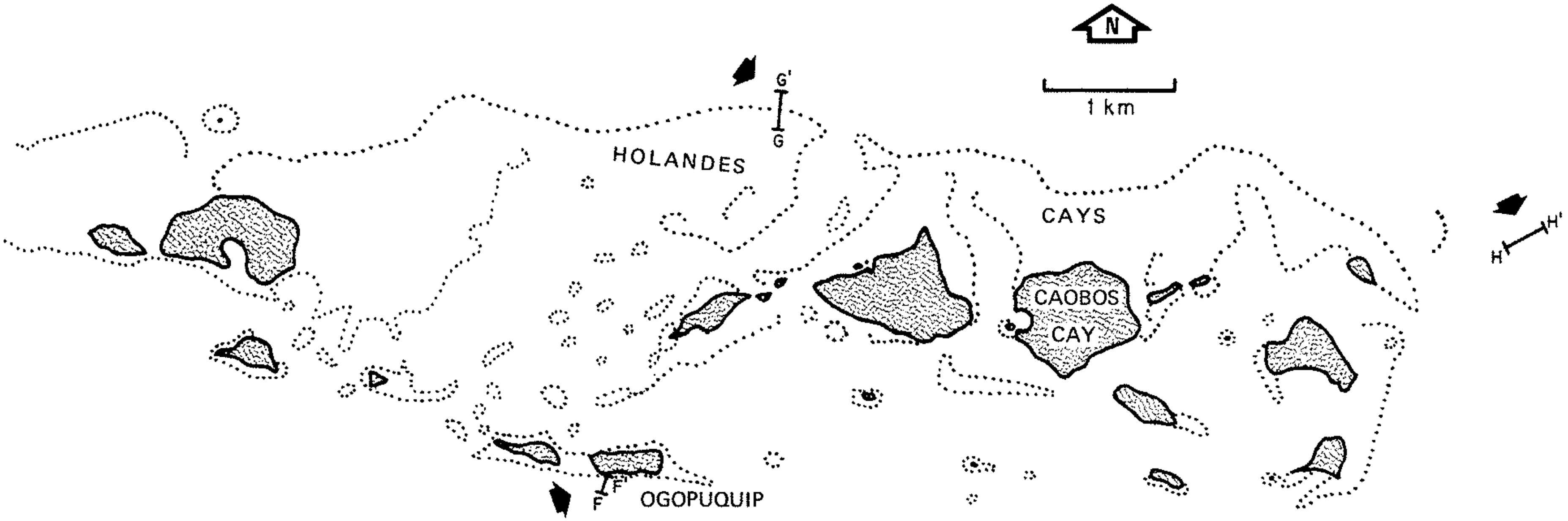
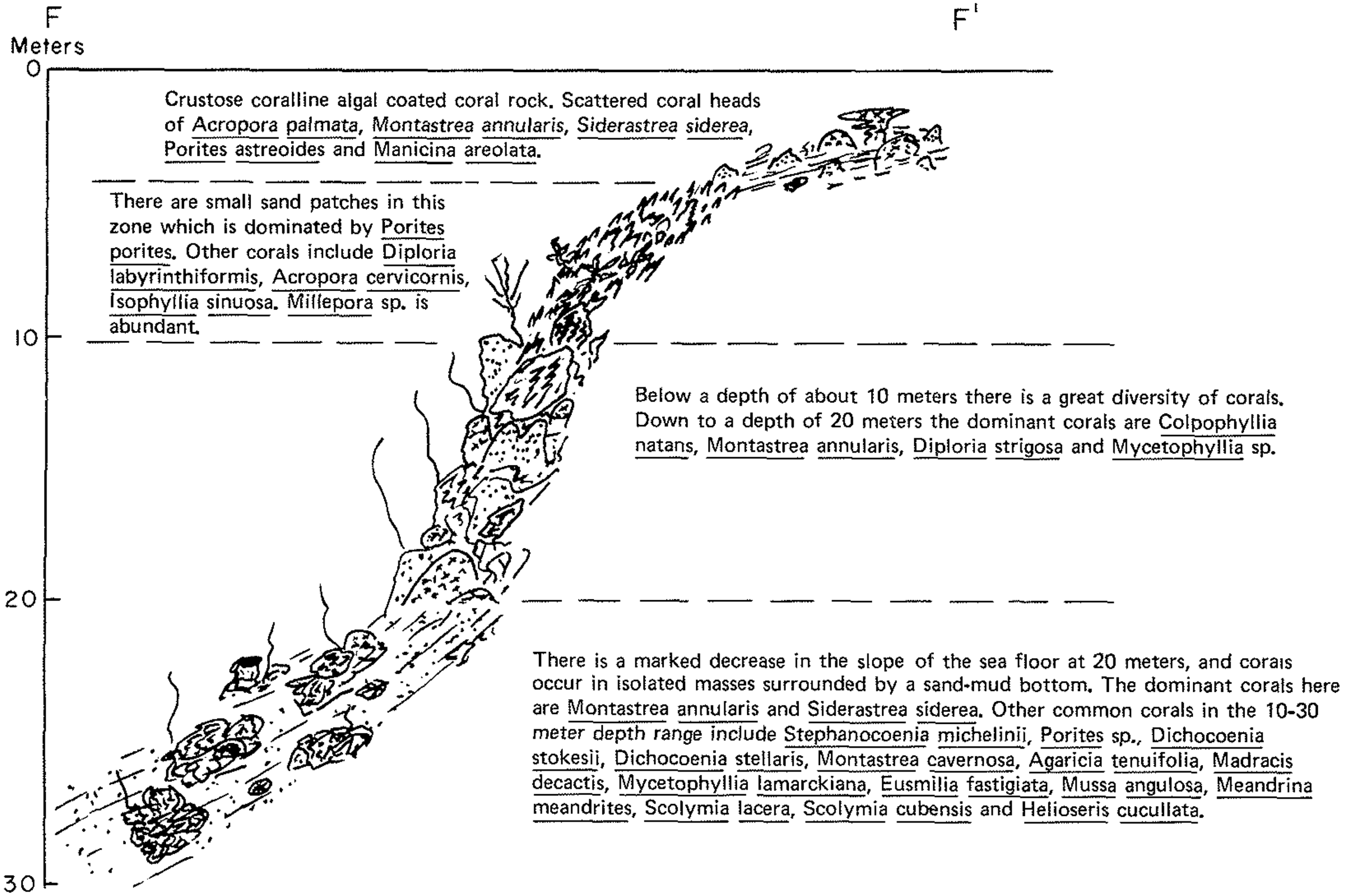


Figure 22 – SAN BLAS ISLANDS
9°35'N 78°43'W



Crustose coralline algal coated coral rock. Scattered coral heads of Acropora palmata, Montastrea annularis, Siderastrea siderea, Porites astreoides and Manicina areolata.

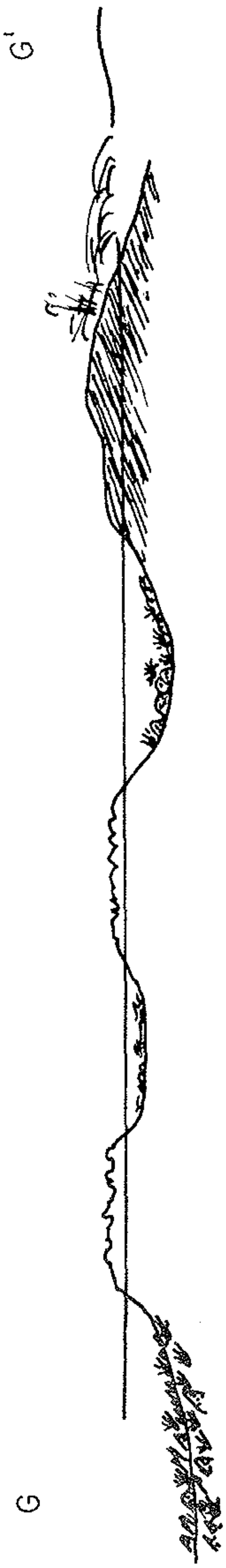
There are small sand patches in this zone which is dominated by Porites porites. Other corals include Diploria labyrinthiformis, Acropora cervicornis, Isophyllia sinuosa. Millepora sp. is abundant.

Below a depth of about 10 meters there is a great diversity of corals. Down to a depth of 20 meters the dominant corals are Colpophyllia natans, Montastrea annularis, Diploria strigosa and Mycetophyllia sp.

There is a marked decrease in the slope of the sea floor at 20 meters, and corals occur in isolated masses surrounded by a sand-mud bottom. The dominant corals here are Montastrea annularis and Siderastrea siderea. Other common corals in the 10-30 meter depth range include Stephanocoenia michelinii, Porites sp., Dichocoenia stokesii, Dichocoenia stellaris, Montastrea cavernosa, Agaricia tenuifolia, Madracis decactis, Mycetophyllia lamarckiana, Eusmilia fastigiata, Mussa angulosa, Meandrina meandrites, Scolymia lacera, Scolymia cubensis and Helioseris cucullata.

SAN BLAS ISLANDS, PANAMA – OFF OGOPUQUIP

Figure 23 – PROFILE F – F'



Algal Ridge. Nodular on sides and smooth on the surface (nodular growths coalesce to form the smooth surface). Distinct surge channels and blow holes. Exposed about 0.6 meters above the low tide sea level.

Outer Trough. In deep areas there are abundant corals (*Porites astreoides*, *Agaricia* sp. and *Diploria* sp.) and *Diadema* sp. In shallow areas the bottom is covered with *Padina* sp.

Middle Ridge. The surface, which is about 0.3 meters above sea level at low tide, is extensively pitted and etched. This is in marked contrast to the smooth rock floors of the troughs or tidal pools. Sampling indicated that this ridge is dominantly composed of crustose coralline algae.

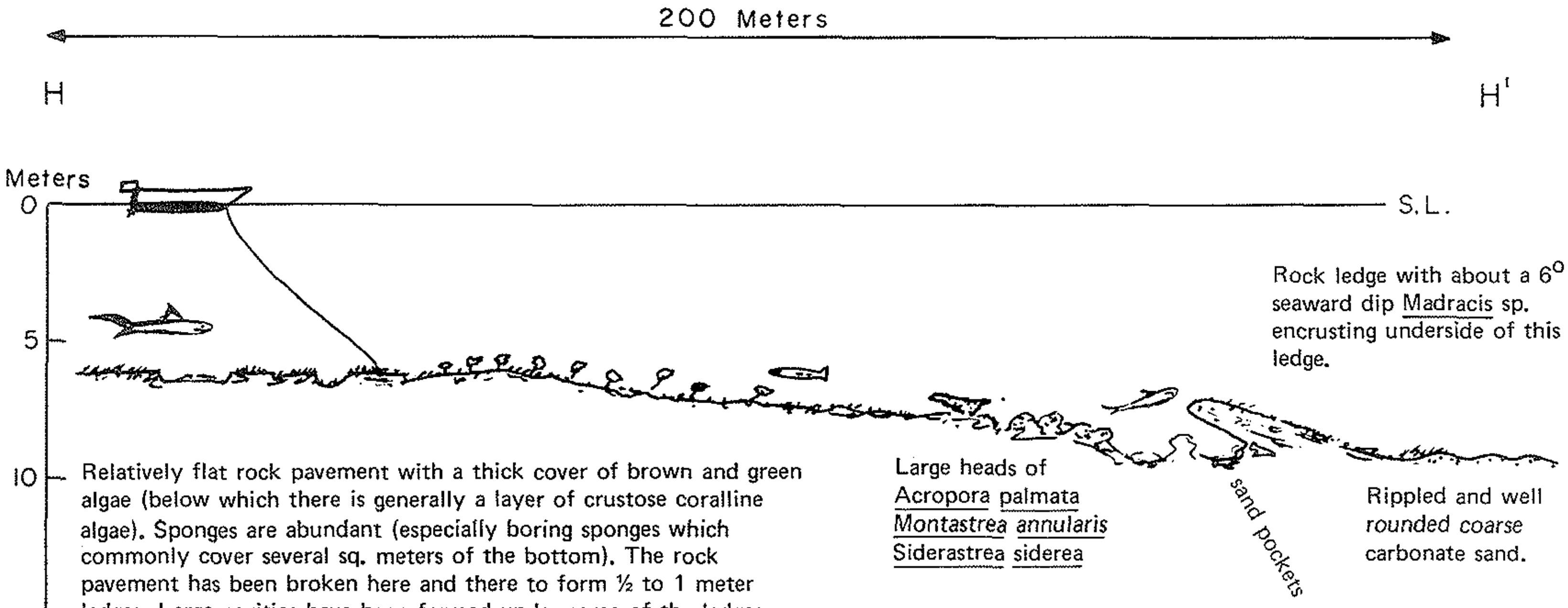
Inner Trough. Shallow rock bottom covered with algae, mainly *Caulerpa* sp. and *Halimeda* sp. over crustose corallines. *Porites porites* is common.

Inner Ridge. As in the case of the Middle Ridge the surface is extensively etched and pitted. However, this ridge is composed, for the most part, of corals in a coarse calcarenite matrix.

Back-Ridge Area. Corals (*Porites porites*, *Porites astreoides*, *Agaricia* sp.) *Millepora* sp. and *Diadema* sp. thrive in these shallow waters shoreward of the ridges. Most coral debris has a heavy crustose coralline coating.

(For a detailed description of this algal ridge see Glynn, in press.)

SAN BLAS ISLANDS, PANAMA – HOLANDES CAYS ALGAL RIDGE
Figure 24 – PROFILE G – G'



Rock ledge with about a 6° seaward dip *Madracis* sp. encrusting underside of this ledge.

Large heads of
Acropora palmata
Montastrea annularis
Siderastrea siderea

Rippled and well rounded coarse carbonate sand.

Relatively flat rock pavement with a thick cover of brown and green algae (below which there is generally a layer of crustose coralline algae). Sponges are abundant (especially boring sponges which commonly cover several sq. meters of the bottom). The rock pavement has been broken here and there to form ½ to 1 meter ledges. Large cavities have been formed under some of the ledges. Gorgonians are abundant but small.

Coral colonies are small and widely scattered. They include *Diploria clivosa*, *Diploria strigosa*, *Porites astreoides*, *Favia fragum*, *Agaricia* sp. *Siderastrea siderea*, *Manicina areolata* and *Acropora palmata*.

Rock consists of coral debris in a coarse calcarenite. Fresh nature of skeletal components suggests that this is Post Pleistocene in age.

SAN BLAS ISLANDS – OFF HOLANDES CAYS

Figure 25 – PROFILE H – H'

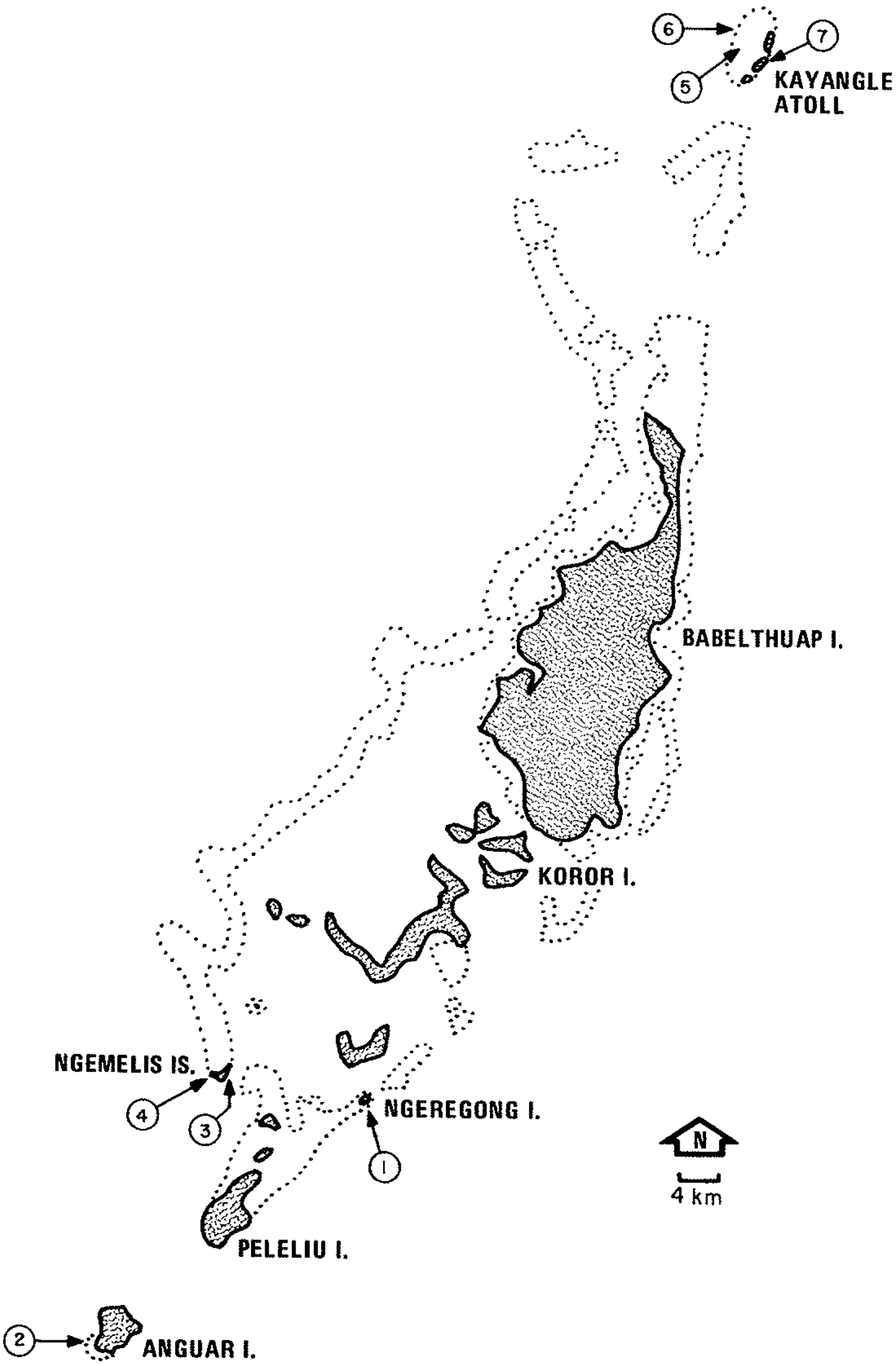


Figure 26 – PALAU
7°30′N 134°30′E

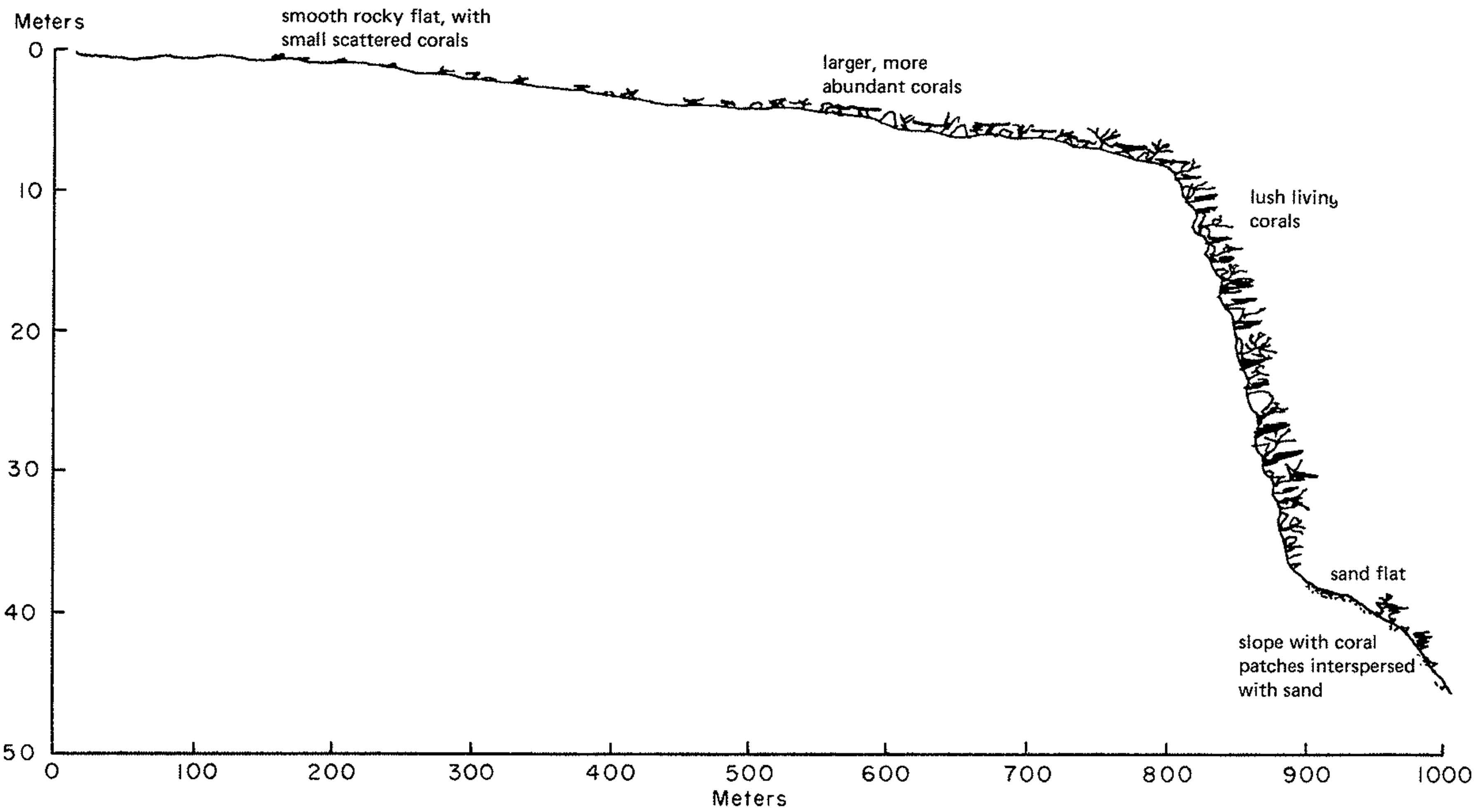


Figure 27 – SITE 2 - ANGAUR

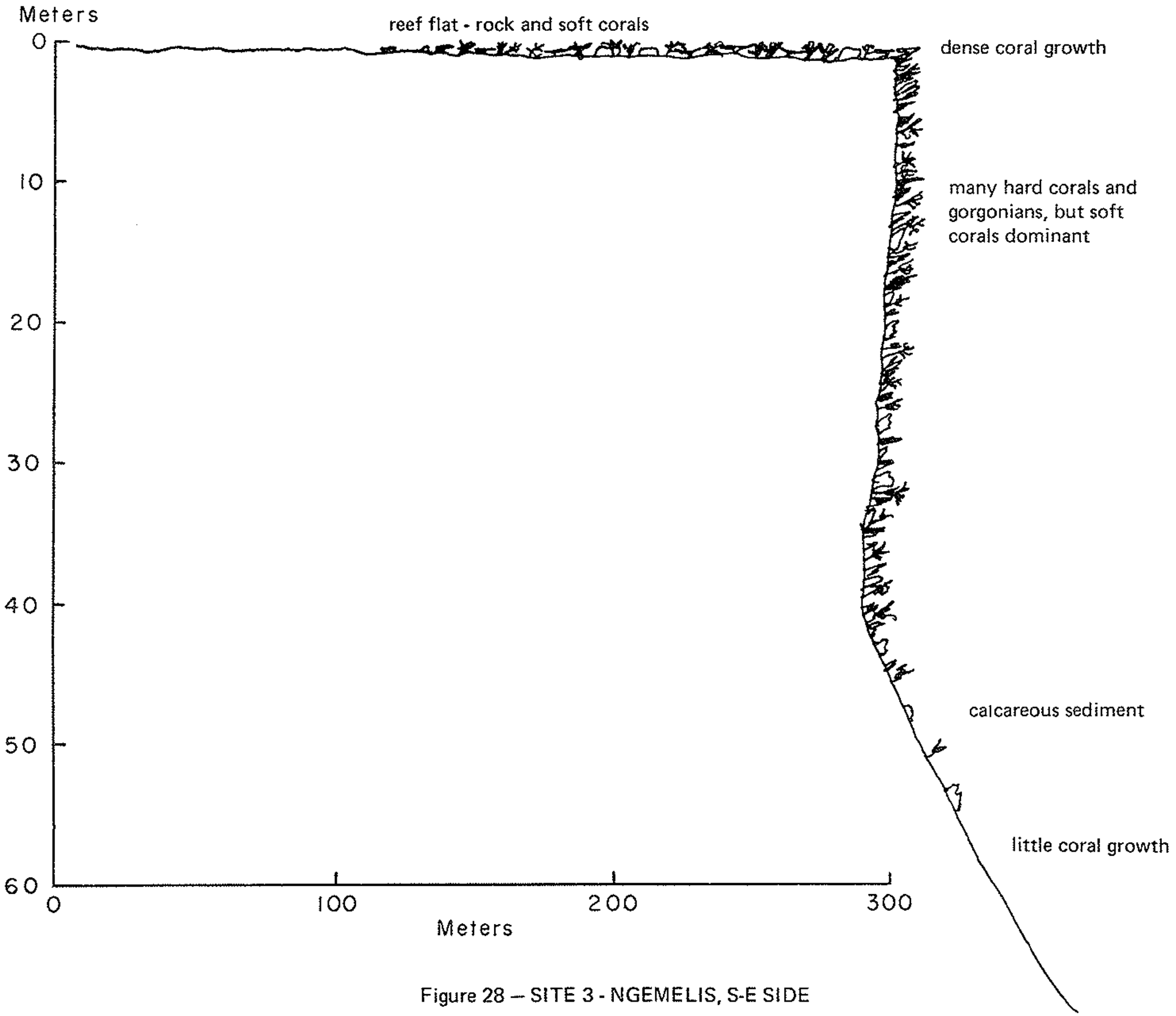


Figure 28 — SITE 3 - NGEMELIS, S-E SIDE

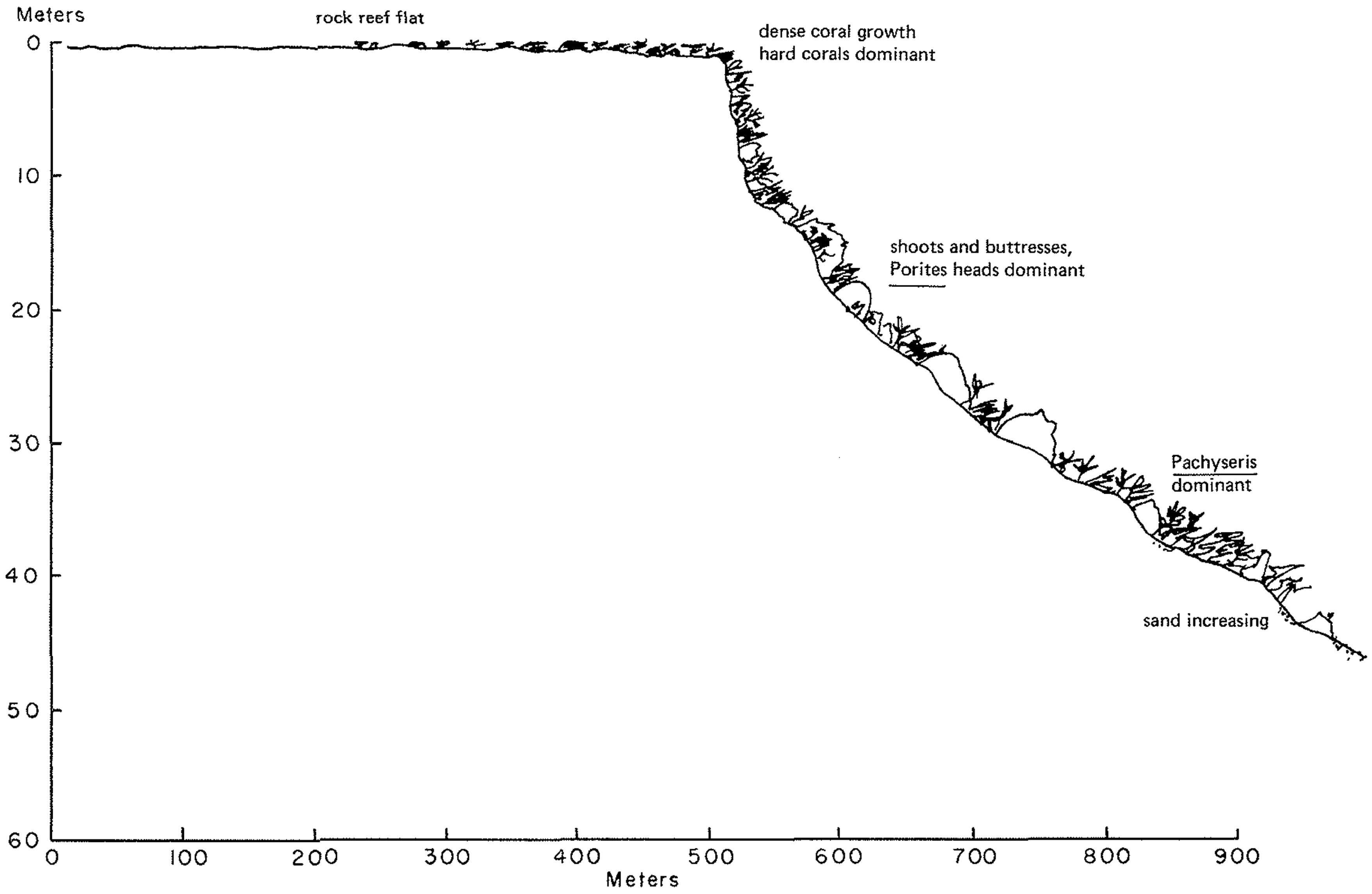


Figure 29 – SITE 4 - NGEMELIS, WEST SIDE

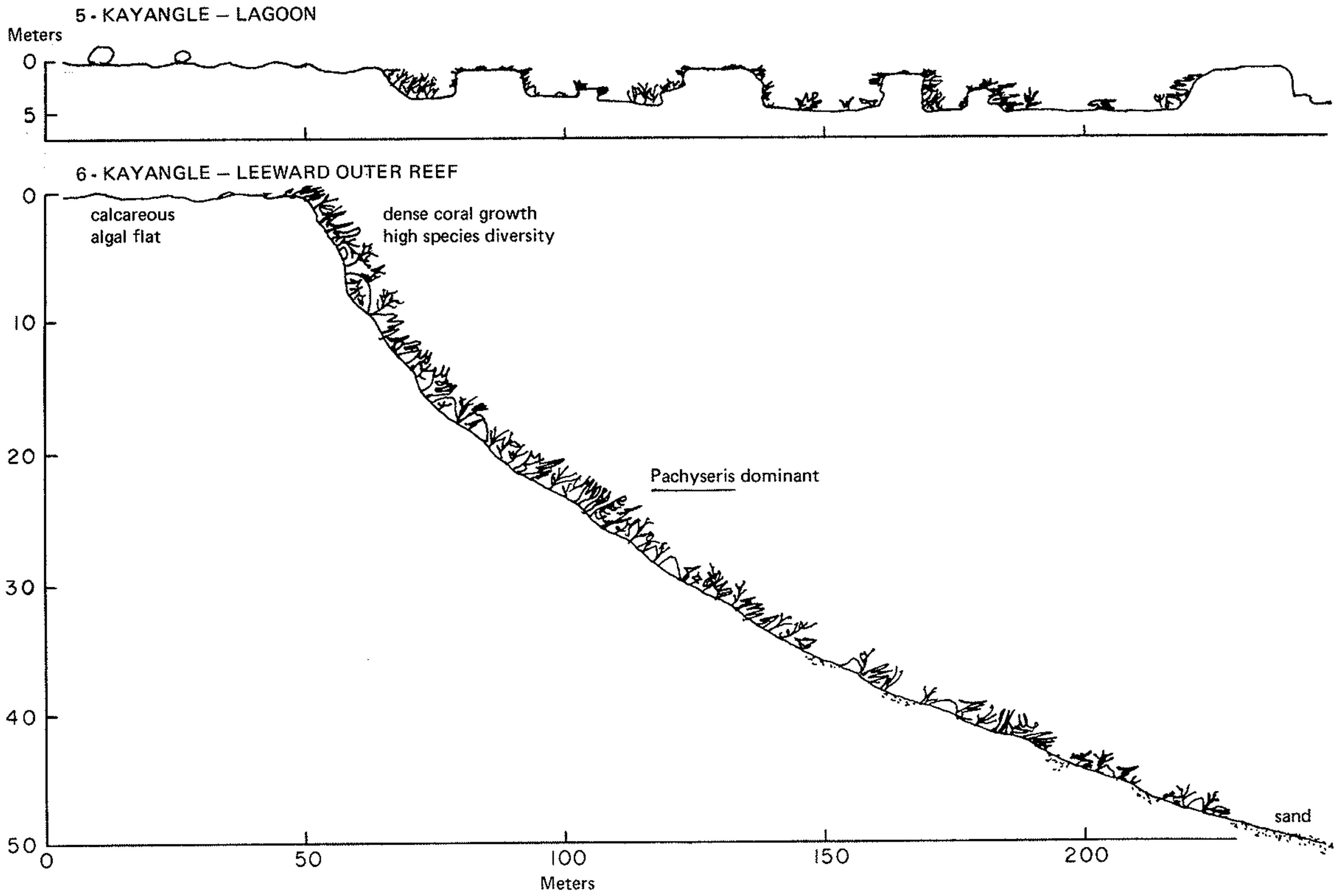


Figure 30 – SITES 5 & 6 - KAYANGLE

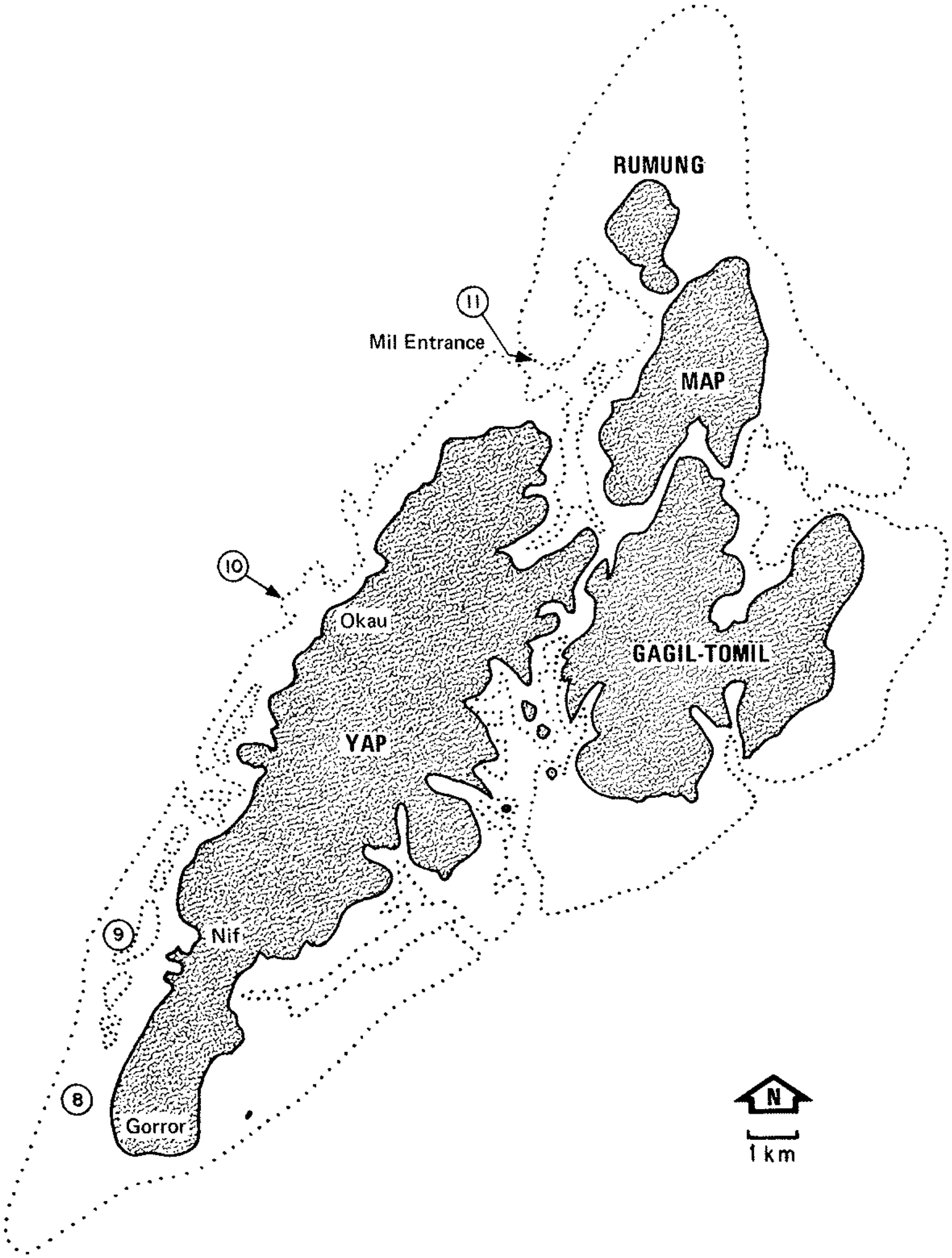


Figure 31 – YAP
9°30′N 138°05′E

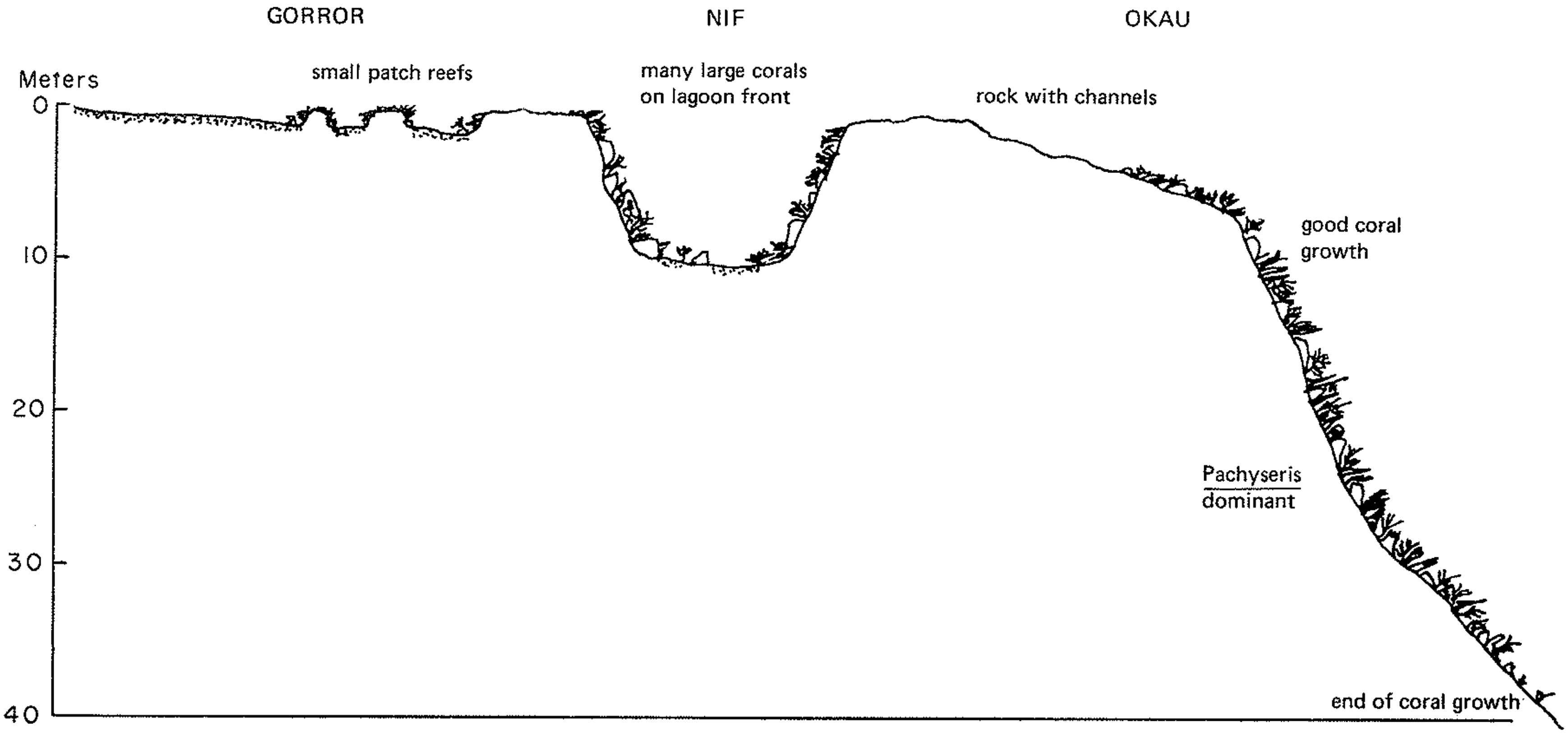


Figure 32 – SITES 8-10 - YAP – COMPOSITE SECTION

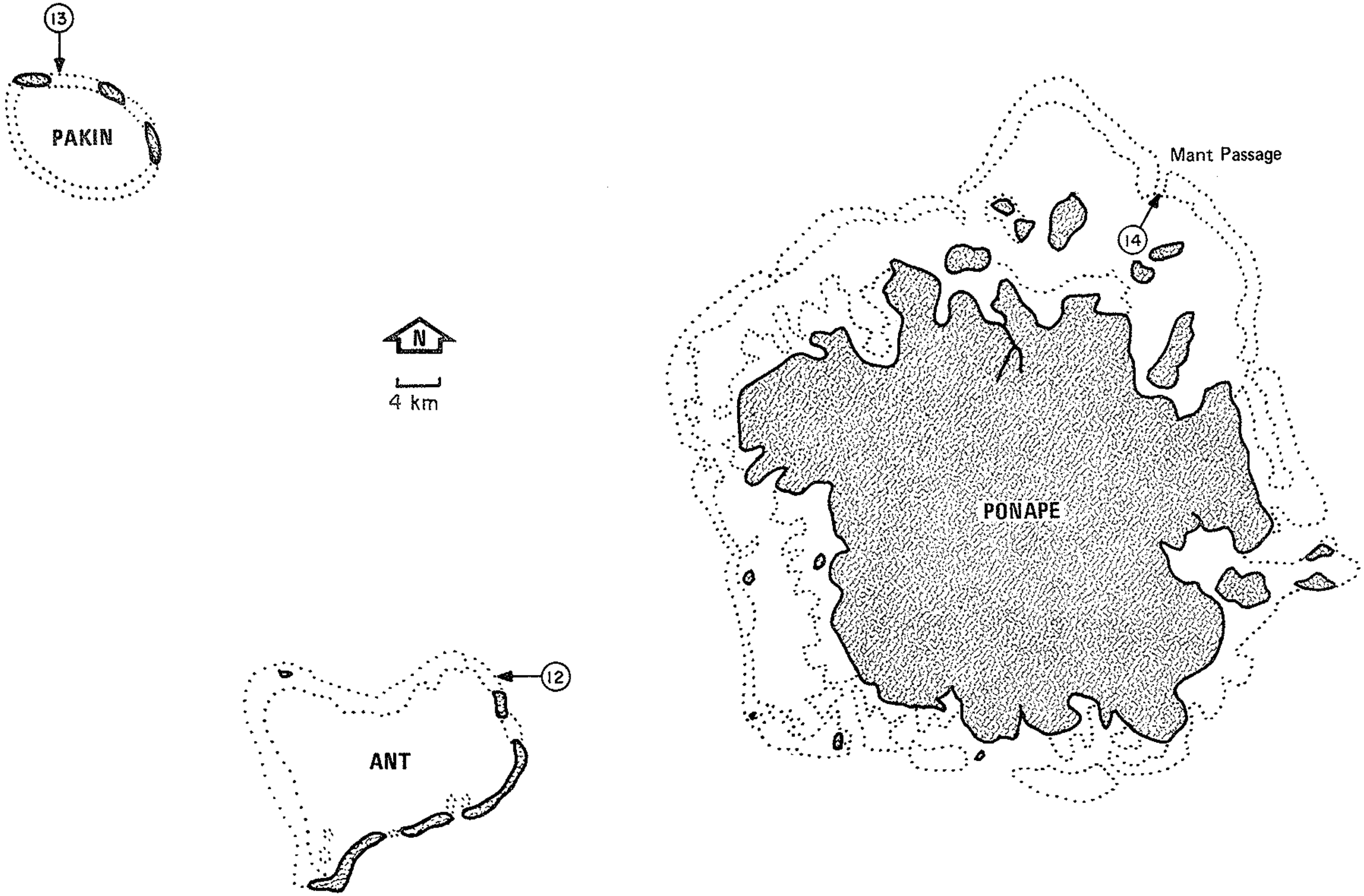


Figure 33 – PONAPE, ANT & PAKIN
7°00'N 158°00'E

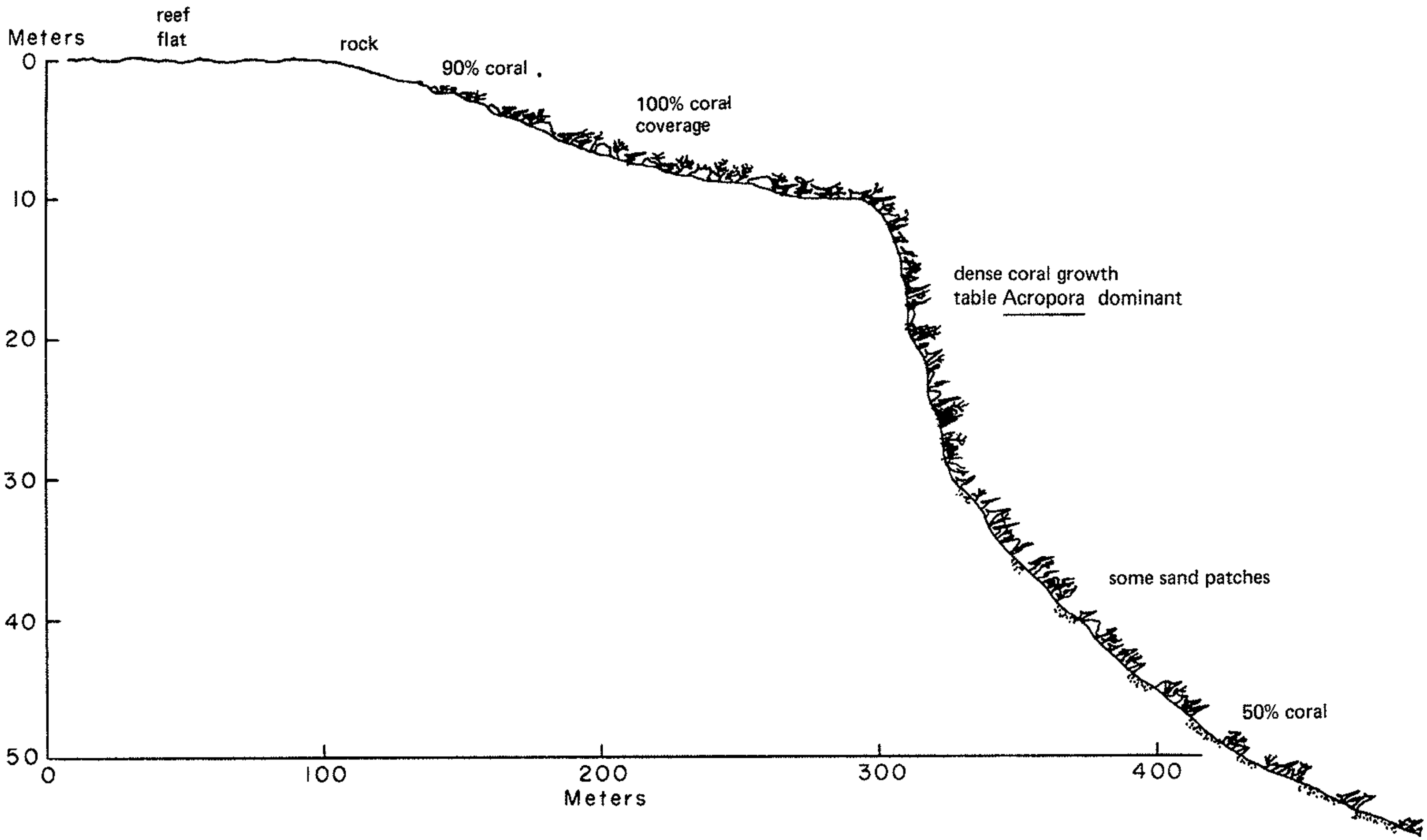


Figure 34 – SITE 12 - ANT

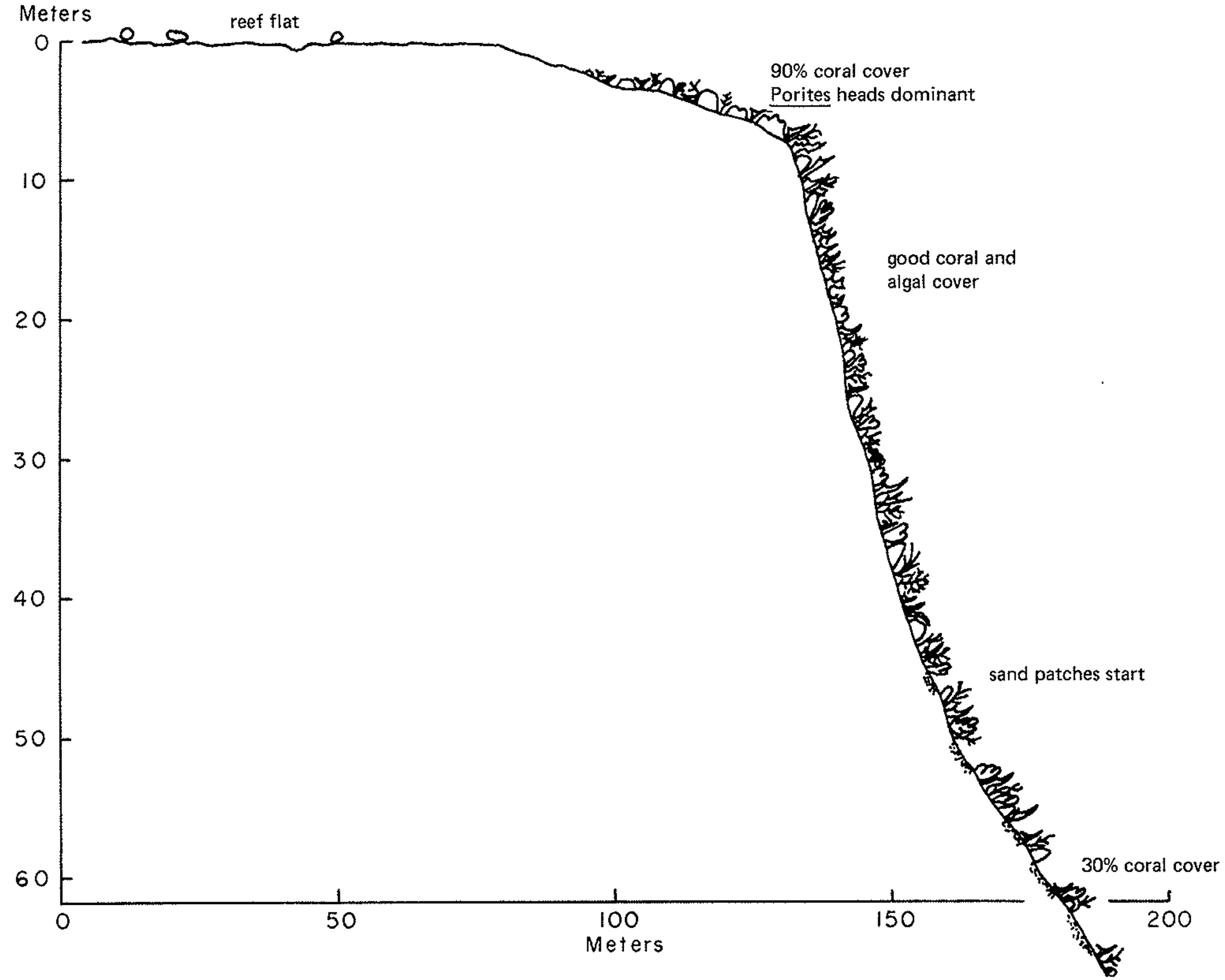


Figure 35 — SITE 13 - PAKIN

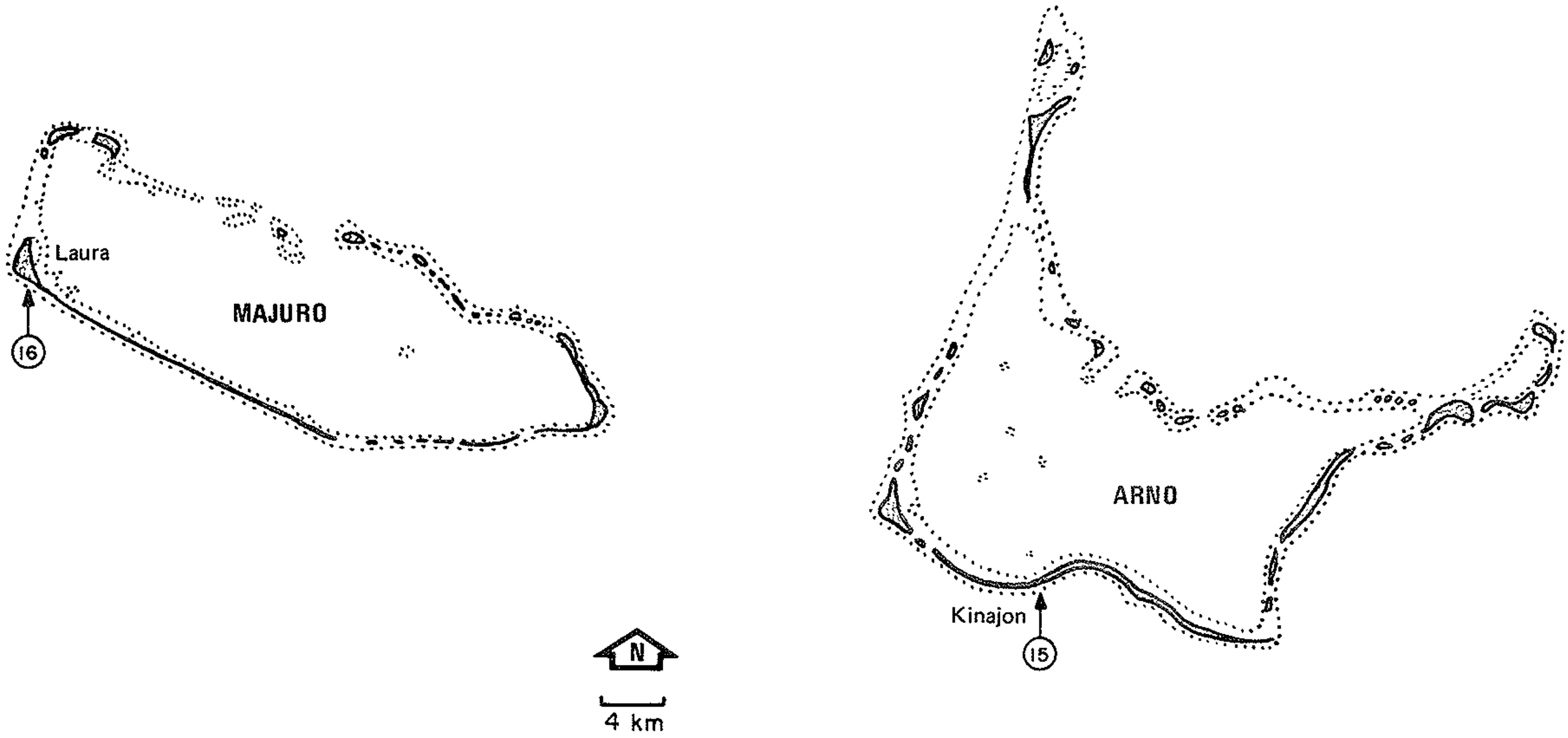


Figure 36 – ARNO & MAJURO
7°05'N 171°30'E

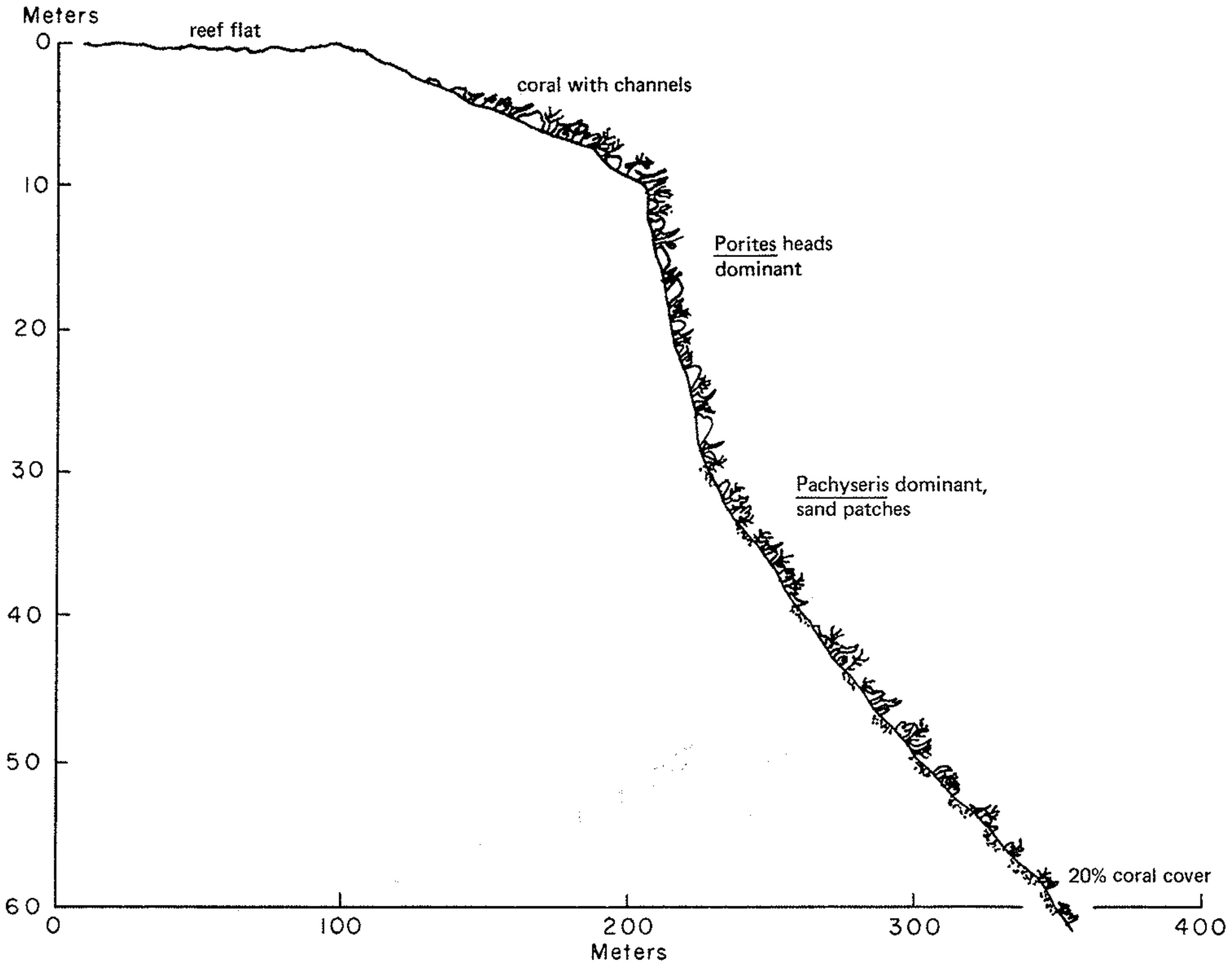


Figure 37 — SITE 15 - ARNO

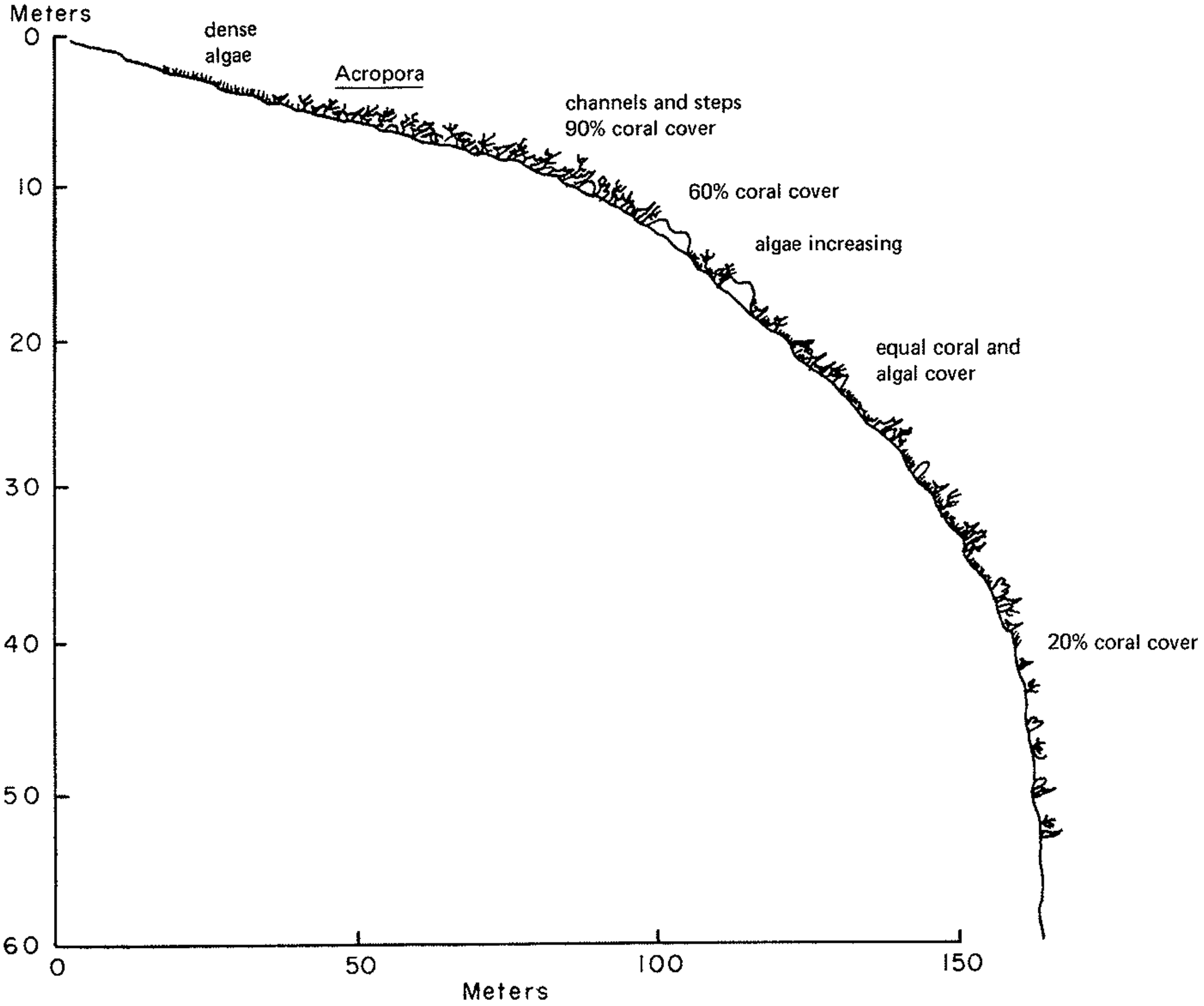


Figure 38 – SITE 16 - MAJURO

Figure 39 – AMERICAN SAMOA
14°15'S 170°00'W

Figure 40 – SITE 20 - LEONE BAY, TUTUILA

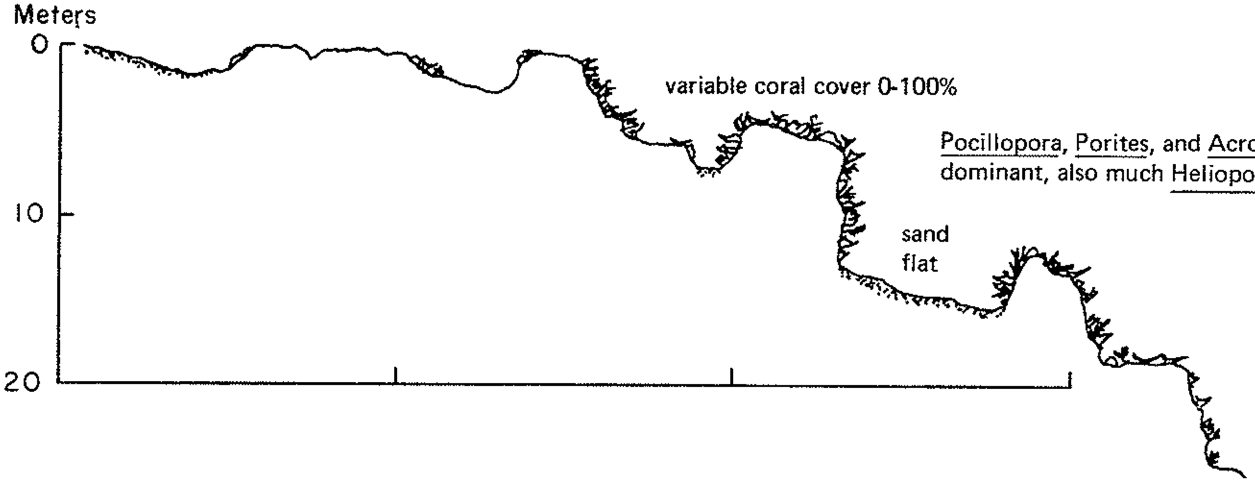
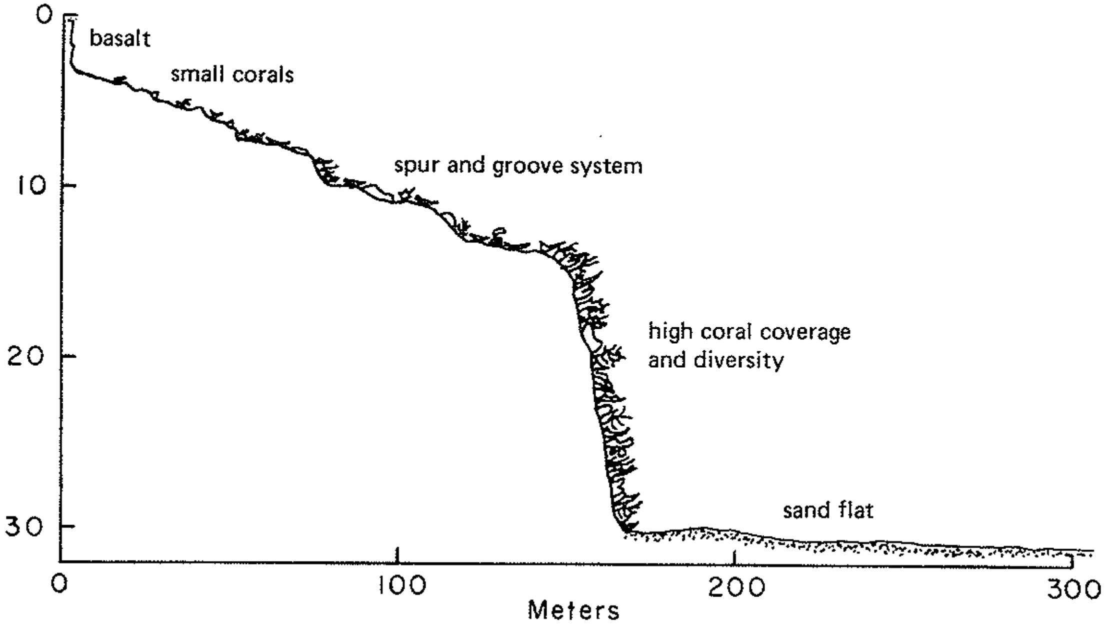


Figure 41 – SITE 21 - OGEGASA POINT, TUTUILA



STATE OF KNOWLEDGE
OF CORAL REEFS AS ECOSYSTEMS

Marie-Hélène Sachet

INTRODUCTION

The following brief review of current knowledge about coral reefs as ecosystems was written early in 1972, mostly from material furnished by the CITRE working groups. It attempts to describe the status of reef ecology papers which are particularly relevant to the modeling approach. No information on the systematics of reef biota is included in this summary, although inventories are obviously fundamental to any bio-ecological work. This review has become out-of-date in certain respects and should, ideally, be thoroughly revised. Time for this is not available, and only a certain amount of updating has been done. The bibliography has been gone over very carefully, corrected and very much enlarged. I acknowledge with thanks the work of Dr. Bryce Decker in this matter, and the help of former CITRE participants, especially those working in the Smithsonian.

In its present form, and with apologies for its shortcomings, I believe this review may still be of value, especially to readers not thoroughly familiar with the coral reef field, or those familiar with other aspects of coral reef research, e.g. systematics.

Since the November 1971 workshop, and the January 1972 completion of the CITRE proposal, the results of a number of Symposia and Seminars have been published, as well as several special issues of journals, devoted largely to coral reef research. They demonstrate how active and varied such research is, and should be consulted for topics outside the scope of this review, for details of studies only briefly mentioned here, and for more recent developments not covered here. Among such volumes can be cited the Proceedings of the 1969 "Mandapam Symposium" issued in 1972 (Mukundan and Pillai, eds.), those of the 1972 International Helgoland Symposium, "Man in the sea," assembled in a whole volume (24:1973) of Helgoländer wissenschaftliche Meeresuntersuchungen, the March and June 1973 issues of the Bulletin of Marine Science, containing 17 papers "In Memory of Dr. Thomas F. Goreau," and a recent issue of Atoll Research Bulletin (166-170) devoted to five papers on _Acanthaster_ infestations.

(Manuscript completed March 1974)

The results of an Acanthaster symposium at the Second Inter-Congress meeting in Guam, May 1973, have just been published in Micronesica (Dec. 1973). Also just received is the first volume of the long awaited treatise on Biology and geology of coral reefs (Jones and Endean, 1973). Several other symposia and review volumes are still in press, including the results of the "Floating Symposium" (2nd International Symposium on Coral Reefs, Great Barrier Reef), June 1973. Hot off the press at the time of the Glover's Reef workshop and the preparation of the CITRE proposal were Regional Variation in Indian Ocean Coral Reefs (Stoddart and Yonge, 1971) and the Supplement to Island Bibliographies (Sachet and Fosberg, 1971).

BACKGROUND

Following Charles Darwin's description and theory of atoll origin (1842, 1962), a growing controversy over the "coral reef problem" (i.e. origin of atolls and reefs) led to vigorous debates based mainly on information collected from published bathymetric charts and insufficient field data (e.g. Daly, 1910, 1915; Vaughan, 1916a, 1916b; Davis, 1928). An exception was the results of the Funafuti expeditions of the Royal Society (1904) and of the Australian Museum (Hedley, 1896-1900). Over the past 20 years, the "coral reef problem" controversy has abated, particularly since drilling techniques have made it possible to establish that atoll formation is indeed associated with subsidence--notably in studies by Ladd and co-investigators (Ladd et al., 1953; Ladd and Schlanger, 1960; Ladd et al., 1967).

The enormous volume of work carried out on reefs and atolls in the earlier periods and in recent years is summarized in literature reviews such as those of Stoddart (1969a), Ladd (in press) and Glynn (in press). Major topics discussed in previous reports include reef formation (Ladd and Tracey, 1949), geology of reefs (Ladd, 1961; Fairbridge, 1950; Newell, 1959), biological zonation of reefs (Wells, 1954, 1957a, Goreau 1959), and coral physiology (Yonge, 1940, 1963, 1968) to list but a few. In addition, several bibliographies of coral-reef studies have been compiled recently (Pugh, 1950; Sachet and Fosberg, 1955, 1971; Wells, 1957b; Ranson, 1958; Milliman, 1965).

As in the early expeditions, most of the work on specific atolls in the last 20 years has consisted of detailed descriptions and inventories (Ladd, ed. 1954-date; Sachet 1962b; Direction des Centres d'Expérimentations nucléaires, 1969). A qualitative description of the coral atoll ecosystem was prepared in 1957 by Fosberg (1961, 1963b). These descriptions furnish an excellent baseline for comparative studies and a starting point for the quantitative observations needed for model construction. It can be safely stated that neither the qualitative constitution nor the role of a single functional component has been completely elucidated in any one reef environment. Ecological processes on tropical reefs have been estimated on occasion by projecting data from long-term or detailed studies of temperate marine communities (Paine and Vadas, 1970; Newman, 1970). An aspect of reef ecology which has hardly been developed as yet is any work permitting an estimation of carrying capacity for exploitation by human populations.

GENERAL REEF SURVEYS

Since Darwin's reef studies, there have been many important general investigations of the nature of these structures from various viewpoints. Some of these were one-man enterprises, such as those of Alexander Agassiz at the end of the 19th century aboard the ALBATROSS, in all the major reef areas of the world, those of J. Stanley Gardiner in the Indian and Pacific Oceans in the first part of the twentieth century, that of Wood-Jones on Cocos-Keeling, results published in 1909 and 1910, and that of Gibson-Hill, also on Cocos-Keeling just before World War II. David Stoddart made three detailed geomorphological studies of the British Honduras reefs and cays between 1959 and 1965.

Notable were a substantial number of cooperative investigations involving people with different interests and backgrounds. Among these have been the Royal Society's and the Australian Museum's expeditions to Funafuti, Ellice Islands, reported on by David and Sweet in a volume published by the Royal Society of London in 1904 and in papers edited by Hedley (1896-1900); the Great Barrier Reef Expedition in 1928-1929, under the leadership of C.M.Yonge (1930a, 1930b, 1931); the Carnegie Institution of Washington's Coral Reef Program, with work especially at the Dry Tortugas Laboratory and in American Samoa and Tahiti in the first third of this century. Involved in this were especially Alfred G. Mayor (Mayer), W.A. Setchell, and T. Wayland Vaughan; some of their publications are listed in the references.

After World War II came a comprehensive program of work on Bikini and Eniwetok Atolls in connection with the atomic weapons tests there (Ladd, 1973). This work is published as an enormous series of papers collectively known as USGS Professional Paper 260, parts of which are still appearing. The USGS-Army Map Service Far East survey of the Northern Marshall Islands in 1951-1952 led to many papers, especially the Military Geography of the Northern Marshall Islands and Atoll Research Bulletin 113 (Fosberg et al., 1956, Fosberg and Carroll, 1965), and a review by MacNeil (1972).

During the 1950's the Pacific Science Board's Coral Atoll Program sent multi-disciplinary expeditions to Arno Atoll, Onotoa Atoll, Raroia Atoll, Kapingamarangi Atoll, and Ifaluk. In 1958 and 1960, under this same program were two expeditions to Jaluit Atoll to study the effects of Typhoon Ophelia. Reports were published in the Atoll Research Bulletin. ORSTOM, the French overseas research organization, sponsors a multidisciplinary study of coral reefs around Nosy-Bé, Malagasy. From 1967 to the present time the Royal Society has sponsored continuing work on Aldabra Atoll and other southwest Indian Ocean coral islands and reefs. A small research station is now maintained on Aldabra to continue this work. Preliminary results are presented in Philosophical Transactions of the Royal Society of London vol. B, 260, 1971. A comprehensive discussion of the geology of Aldabra has been published recently (Braithwaite et al.

1973). The Fondation Singer-Polignac during the 1960's sponsored a number of expeditions to New Caledonia and French Polynesia, and maintained a research vessel in the area for this purpose. Results are published in Cahiers du Pacifique and in a series of beautifully illustrated Mémoires. In connection with the nuclear tests on Mururoa, Tuamotus, the French government sponsored an extensive series of investigations in the Tuamotus, especially Mururoa, and in Clipperton Island. Reports are published in Cahiers du Pacifique and in a series of duplicated papers on Clipperton Island. In 1971, a small research station ("Antenne de Tahiti") of the Muséum National d'Histoire Naturelle, Paris, was created in Moorea, near Tahiti, to continue such research, and an impressive list of papers is already available, several of which are cited below (Chevalier, Denizot, Salvat, etc.) The marine station of Endoume-Marseille has for some years sponsored coral reef investigations at the marine station at Tulear, Malagasy, comprehensive reports have been published in special issues of the Recueil des Travaux series and later of Téthys. A general description of the reefs of Madagascar was presented by Pichon (1972).

The University of Hawaii recently acquired a station on Fanning Island in the Line Islands and during 1969 staged a broad-scale NSF-sponsored investigation of the Fanning Islands reefs. The results have been published in Pacific Science (April 1971) and in a special report issued by the Hawaii Institute of Geophysics (Chave, ed., 1970); this is a continuing program, and further results can be expected. Since 1968, a University of Hawaii Sea Grant project to study various quantitative aspects of reefs and reef biota in Kaneohe Bay, Oahu, has been underway. The first results of that program have been published (S.V. Smith et. al., 1973).

The work of several other surveys is mentioned throughout the following sections though the present discussion is by no means exhaustive.

PHYSICAL ENVIRONMENT

Much of the oceanographic work carried out in the tropical seas in the past, and especially in the last 25 years, is a source of environmental data on coral reefs. One example is work on surface currents, of significance in the distribution of reef and island biota. Specific research on atolls and reefs, however, has been pursued only by a small number of investigators and with a limited scope. Work at Bikini Atoll (von Arx, 1954; Munk and Sargent 1954) has delineated the circulation pattern within the lagoon that is established in response to prevailing winds and influenced by tides, waves, and local ocean currents. The Bikini study, as well as the research at Fanning Island (Gallagher et.al., 1971), provides volumetric estimates of exchanges of water between lagoon and ocean. Fanning Island investigations also produced measurements of salt and heat fluxes. The waters of the Great Barrier Reef have been studied by Brandon (1973). These studies and others devoted to specific physical parameters on reefs can contribute guidelines for an ecosystem model, but the majority of oceanographic projects on reefs have not included coordinated studies of interactions of the physical environment with the biological reef communities; see for instance the work of Van Dorn, and Vastano and Reid, on Wake Island.

Atoll meteorology was mostly limited, prior to World War II, to sporadic weather records (see for instance those used by Sachet, 1957), observations on storms and hurricanes, and the like. With World War II action, and the atomic tests in the Pacific, as well as the increase in geophysical research generally, much more information in meteorology and climatology has become available. Weather data are more complete and collected from more stations. Summaries such as those of R. C. Taylor (1973) and Zipser and Taylor (1968), and volumes of data such as those prepared for U.S. Joint Task Force Seven, are a few examples among many, which supply important data in the study of atoll ecosystems. See also studies by Montgomery (1973) and Quinn and Burt (1970), and the very detailed work of Blumenstock and Rex (1960) on Eniwetok. Even more closely related to the ecosystem approach are papers describing hurricanes, typhoons and other storms, and their effects on reefs and islands. The work of Blumenstock and others (1958, 1961) on Jaluit, that of Stoddart on the British Honduras reefs (1963, 1969d), and the Solomon Is. (1973), of Sachet relative to Clipperton (1962b) are a few examples.

More general work on hurricanes and other meteorological phenomena is included in the work of Ramage and others, in the U.S. Navy Atlases (1956-68) and many other useful sources.

Atolls have also been used as "observation platforms" (Lavoie, 1963) in atmospheric and other studies, notably by the Hawaii Institute of Geophysics and the U.S. Joint Task Force Seven (e.g. McCreary 1959).

GEOLOGY

The geological record of fossil reefs has been the subject of exhaustive studies, especially by petroleum geologists, and some of the reviews and bibliographies cited above are concerned with fossil reef studies, including paleoecology. Those references will not be detailed here (but cf. Ladd, 1957; Laporte 1974). Suffice it to say that a vast amount of knowledge of fossil reefs has accumulated, from which studies of modern reefs can derive data as well as ideas (Hedgepeth, 1957). To a certain extent, of course, the fossil and modern reefs cannot be separated. The modern sections of the reef are considered here to be material deposited in relation to present sea levels, approximately during the last 5,000 years.

Since the late 19th century, modern coral reefs have been studied by geologists primarily to provide information on pre-existing environmental conditions documented in the lithological record of the geological column. With few exceptions these studies have concentrated on descriptions of reef components rather than on the processes responsible for component formation. However, much attention has been paid to the influence of sea level changes on the nature of present-day reefs (Fairbridge 1958; cf. Stoddart 1971).

Studies of reef morphology (reviewed by Stoddart, 1969a) generally have included mapping bottom topography at intermediate scales (1:50,000) and describing topographical zonation and size of features in such terms as mean reef width, knoll dimensions, etc. (e.g. Emery et al. 1954). There have been few quantitative studies of reef features, apart from the work in Kaneohe Bay, Oahu, by Roy (1970a), at Fanning Island by Roy and Smith (1971), and in the Maldives and elsewhere by Stoddart (unpublished).

Many studies concern the mineralogy, composition, and texture of reef and near-reef sediments with a view to understanding sequences in the geological record (e.g. Ginsburg, 1956; Neumann, 1965, Macintyre, 1970). Recent trends have been to examine $CaCO_3$ budgets in areas of carbonate sedimentation (Stockman et al., 1967; Neumann and Land, 1969; Land, 1970; S.V. Smith et al., 1970, 1971; S.V. Smith 1971a, 1973; Chave et al., 1971). Such studies have only considered some (or even only one) of the components in the budget; or they have integrated the components of the budget across a very restricted environment; some have not even dealt with tropical reef systems. What is needed now is the generation of a total carbonate budget through time, in order to describe the relationships among reef development, sediment generation, sediment transport, and subsequent deposition.

Little information is available on former zonations in various stages of reef development, yet work on specific problems associated with coral reefs has indicated that significant data may result from exposing internal reef structures: Shinn (1963) investigated the origin of spurs in reefs off Florida and subsequently (Ginsburg et al., 1967) studied marine cementation and internal sedimentation within reefs off Bermuda. To date, rather little coring has been attempted (Mayor, 1924; Cary, 1931; Ladd and Schlanger, 1960; Stoddart 1971) on modern coral reefs, with the result that the internal structures and limestone facies of these reefs are largely unknown. Most of this work has involved only one or a few core holes per reef. More detailed drilling with a submersible drill that can penetrate 2 meters into the reef is underway on reefs of Jamaica (L. Land, personal communication, 1970).

It has been suggested that living coral reefs consist of a thin veneer of modern reef growth over older foundations which generally dictate their present-day morphology (Newell, 1962; Stoddart, 1969a, 1973). However, modern reef construction has been shown to form massive wave-resistant frameworks, notably in Jamaica (Goreau, 1961b, Goreau and Land, 1974) and in British Honduras (Purdy, 1974).

Numerous workers have investigated growth rates (e.g. Vaughan, 1915; Mayor, 1924; Shinn, 1966) or calcium carbonate deposition rates (e.g., Kawaguti and Sakumoto, 1948; Goreau 1959; Goreau and Goreau, 1959; Goreau, 1961a) or general reef $CaCO_3$ production rates (e.g. Chave et al. 1971; S.V. Smith et al., 1971, S.V. Smith, 1973, Glynn et al. 1971), as well as skeletal framework destruction by mechanical (Stoddart, 1963; Glynn et al., 1965; Ball et al., 1967; Perkins and Enos, 1968) and biological means (Duerden, 1902; Otter, 1937; Yonge, 1963; Goreau and

Hartman, 1963; Bakus 1964, 1967; Neumann, 1966). However, concurrent investigations of most of these processes have not been carried out at a single reef site in order to determine the relative importance of the various parameters controlling the net accumulation of modern reef framework.

The success of framework construction depends largely on the growth rate of reef organisms. Other factors affecting construction include predation, competition between corals and other organisms, variation in distribution of coral and other species, biological erosion of skeletal framework and of frame-cementing agents, mechanical erosion, and the rate of sea level change. Cement infilling and lithification of internal sediment in various cavities tend to negate the destructive action of coral borers. For example, some coral heads collected from submerged reefs in the eastern Caribbean have been almost completely altered--through repeated boring, infilling, and lithification--to a dense micritic limestone (Macintyre, 1972).

Biota have long been thought to be the major frame-cementing agents, but in recent years extensive Mg-calcite cementation of reef framework and inner framework has been recognized (summarized in Bricker, 1971). The relation, if any, of biological agents to this cementation is not altogether clear. The origin of magnesian calcite cement remains unexplained, but chemical analysis of reef interstitial waters may offer some clues to the processes responsible for its precipitation.

Within the reef ecosystem, interactions between waters and solid $CaCO_3$ appear to be largely the result of biological calcification processes, or interactions between biogenic rock, detritus, and waters separated from open ocean waters--e.g., the waters within the interstices of skeletal fragments or the reef frame itself.

Direct chemical precipitation and solution reactions of $CaCO_3$ in seawater appear to be inhibited or prevented by interactions of dissolved organic compounds in sea water with $CaCO_3$ mineral surfaces (Chave, 1965; Chave and Suess, 1967, 1970; Suess, 1970). Chemical reactions between seawater and carbonate minerals may occur, for example, in the formation of ooliths, grapestone, whitings, and beachrock; but these reactions are, at best, minor in a coral-reef ecosystem, if they are inorganic at all.

Two interactions between reef waters and biogenic carbonates appear to be important when considering the flow of carbon in a reef ecosystem. First, recent reports indicate that chemical or biochemical precipitation of $CaCO_3$ within the reef is as important, or even more important, than biogenic calcification with respect to binding the components to form a rigid, wave-resistant framework (see Bricker, 1971). The second interaction between reef waters and biogenic carbonates is the removal of dissolved carbonate from interstitial waters of sediments and deposition of $CaCO_3$ within the sediment components (see Bricker, 1971). The importance of this interaction is not only that it represents a flow of carbon from seawater into the reef ecosystem but that the result of this flow directly affects the character and hydraulic properties of the sediment.

In order to understand fully the processes responsible for the precipitation of $CaCO_3$, both in the framework and within sediment grains, it is necessary to investigate the whole reef $CaCO_3$ system--namely both water and rock chemistry. By studying the whole chemical system, it should be possible to determine whether the cementation process involves only an internal cycling of $CaCO_3$, or whether significant amounts of $CaCO_3$ are derived from external sources.

The CO_2 system in seawater provides a unique link between geochemical and biological processes. The link is particularly important in coral reefs, where both calcification and organic carbon production-consumption greatly affect the system. The organic carbon transfer should be mentioned; it is sufficient for this paper to point out that (as discussed in some detail by Park, 1969) measurement of two parameters in the marine CO_2 system is sufficient to partition the system changes into inorganic $CaCO_3$ precipitation-solution and organic C production-respiration.

Separating changes in deep ocean CO_2 into solution and oxidation has been undertaken by several authors (e.g. Park, 1968; S.V. Smith, 1971a). Both S.V. Smith (1973) and Kinsey (unpub. data and personal comm.) have studied diel variability in the CO_2 system in coral reefs. S.V. Smith (1973) has related this variability to organic carbon production and utilization and to calcification.

The present major limitation of these short-term studies is the small amount of change in the marine CO_2 system caused by inorganic chemical processes and organic metabolic activities of the reef communities. Kinsey's studies were performed on water which "aged" over several hours and consequently experienced easily measurable changes in the CO_2 system. Smith's studies dealt with water "aged" less than one hour therefore showing barely measurable perturbations in the CO_2 system.

BIOTIC ENVIRONMENT

The biotic components of the surrounding sea should not be ignored. Perhaps most important is the plankton, which is a significant food supply of the corals and many other reef animals. This has been studied with relation to reef animals by A.R. Emory (1968).

Small pelagic fish and fry are also food for reef-dwelling carnivorous fish, as well as for sea-birds. Predaceous pelagic fish visit the reefs and prey upon the reef fishes. The same is true of porpoises, other small cetaceans and pinnipeds.

Detritus of organic origin brought to the reefs by water movement is also an important input into the reef system (N. Marshall 1965). All these biotic components are discussed in more detail below.

TERRESTRIAL ECOSYSTEM

To the best of our knowledge, the only attempt at a generalization of the functioning of the terrestrial coral atoll ecosystem is the description written in 1957 by Fosberg (1961, 1963b). That description attempts to conceptualize the system in abstract, non-quantitative, non-mathematical terms, and to indicate functional groups of entities in the system which can be studied in terms of their relationships to the whole. This work was not followed up except for extending it to high islands. It resulted logically from the general program for atoll studies proposed at two coral atoll research symposia sponsored in 1951 by the Pacific Science Board (cf. papers in Atoll Research Bulletins 1, 2, 1951, Fosberg ed.). Five expeditions planned to provide comparable descriptive and inventory data on atolls of different types were carried out (to Arno, Onotoa, Raroia, Kapingamarangi and Ifaluk). Their results, as well as those of many other studies of land (and marine) aspects of atolls were published over the next 20 years in the Atoll Research Bulletin and elsewhere. An attempt at bringing together this great mass of data was made by Wiens (1962), but it was not entirely successful in representing the world atolls as an ecosystem. Other qualitative descriptions of the island ecosystem are included in Numata (1967) especially those papers by Jackson, and Sachet. See also Stoddart, 1969c. An idea of the enormous amount of basic information available on the terrestrial aspects of coral atolls may be gained by perusing the 261 pages devoted to this subject in Island Bibliographies and 236 in its supplement (Sachet and Fosberg 1955, 1971).

From this wealth of data, and citing only a few specific references, we can derive a fair idea of components and processes involved in the terrestrial or cay ecosystem and influences on the adjacent submerged reef ecosystems. Some components and processes, such as nutrient content of ground water, salt spray, rain water, animal and plant bodies, and sediments, have never been quantified but can be measured by standard analytical procedures. Standing crops of the macroscopic organisms present no problem, but again, there are no quantitative data for coral islands. Estimates can be reasonably made by simple sampling, counting, and weighing procedures. Imports of organic matter (fish, squid, etc.) by seabirds and shore and wading birds into the terrestrial atoll ecosystem have never been estimated.

Some observations have been made on the ground water of atolls, beginning with Charles Darwin (1839), but mostly within the last few years (Fosberg, 1959; Cox, 1951; Arnow, 1954, 1955; Tracey _et al_., 1961). The general nature of the atoll ground water lens has been established, but detailed studies of its behavior under varying conditions of geological structure and rainfall amounts and regimes, as well as of tidal ranges and regimes, are still required.

The terrestrial geology of certain atolls has been studied by a number of expeditions and individuals (e.g. Royal Society, 1904; Wentworth, 1931; Fosberg _et al_., 1956, Newell, 1956; Fosberg, 1957a; McKee, 1958, 1959; Fosberg _and Carroll_, 1965; Sachet 1962b; Stoddart, 1962, 1969b). Very few quantitative measurements of sediments are available.

Fairly detailed soil studies are available for a few Pacific atolls (Stone, 1951; Fosberg, 1954; Fosberg _et al_., 1956; Fosberg and Carroll, 1965; Tercinier 1956, 1969) as well as a general discussion of atoll soils (Stone, 1953). Most of the atoll soil types are very widespread and the patterns rather simple. There has been no systematic investigation to determine if Caribbean atoll soil types correspond to those in the Pacific.

The occurrence and origin of atoll phosphate rock in the central Pacific atolls were elucidated by Fosberg (1957b); and further observations have been reported by Stone (1953), Fosberg et al. (1956), Niering (1961, 1963), and Roy (1970b). Similar rock was described for the Indian Ocean atolls by Piggott (1968) and recently was found on Glover's Reef, British Honduras by Fosberg. Hutchinson (1950) deals in great detail with background information on phosphate accumulation.

Substantial information is available on atoll floras and vegetation (Fosberg 1949; Hatheway, 1953, 1955; Fosberg, 1953; Fosberg et al. 1956; Fosberg, 1957; Sachet 1962a; Stoddart, 1962; etc.) Pure stands of certain trees and shrubs are frequently found, an unusual occurrence in the tropics.

The land animals of coral islands are reasonably well known, but information, except for that on birds, is mostly scattered in monographs and papers on the groups concerned. A few papers specifically on atoll faunas are found in the Atoll Research Bulletin series and in the reports of the British Indian Ocean expeditions (Percy Sladen, etc.) of the early twentieth century. There is an extensive literature on atoll birds (listed and annotated by Sachet and Fosberg 1955, 1971). The atoll bird data have never been reviewed as a whole, but the Smithsonian field guides (Watson et al. 1963; King, 1967) and a number of regional papers (Amerson, 1959; Baker, 1951; Pelzl, ms.) are steps in this direction.

Atoll insects, as well as the insects of high islands, are discussed in the Pacific Insects and Insects of Micronesia series (Gressitt, ed.). Papers that deal with the interactions of atoll faunas are available for Arno atoll (Marshall, 1951) and the Tokelaus (Hinckley, 1969). Data on the consequences to the rest of the atoll ecosystem of the presence of large numbers of seabirds are brought together by Hutchinson (1950).

No work has been done on either terrestrial primary productivity or nitrogen fixation on atolls, nor is there much information on terrestrial food chains, predation or decomposition of organic matter under atoll conditions. Extrapolations may be made from other ecosystems, but it would be important to know just how well these extrapolations correspond to actual atoll patterns.

HUMAN INFLUENCES

The complex of human influences on and interactions with the cay ecosystem and the total reef ecosystem is quite apparent but difficult to characterize and summarize satisfactorily (Johannes 1970-71). The pesticide or, better, biocide, component is of general importance and is very probably pervasive in all parts of the system. This particular problem is dealt with specifically below. The nature of changes brought about by human activity varies from obvious (Stoddart 1968a) and easily measured to very obscure and hard to estimate, but the importance of these changes to the system may not necessarily be proportional to their obviousness. Pollution in terms of addition of human wastes (sewage, etc.) can be estimated from standard figures and tables. The amounts and effects of solid-waste pollution are probably in proportion to amount of human activity on the cays and within the lagoon, with a substantial addition from drift materials washed in from the open ocean. An FAO conference on Marine Pollution (Ruivo, ed., 1972) included several accounts of pollution of reefs, atolls and lagoon (see especially Johannes, Chan, Bagnis). Increased sedimentation is another frequent result of man's activities, as exemplified by Kaneohe Bay, Oahu (Roy, 1970a). This latter problem is likely to be more severe on high islands than on atolls.

One of the most significant effects of human activity is the destruction and/or alteration of habitats of other organisms (Sachet, 1963; Jackson, 1967). The replacement of natural forest by coconut plantation is a good example (cf. Stoddart, 1968). Except for simple measurement of area, we know of no way to measure such changes or their effects, or, in many cases, even to assign specific effects to particular causes. This does not in any way minimize their importance. A volume edited by Fosberg (1963a), deals with islands including atolls, with special reference to man's role in their ecology.

The presence of a marine laboratory in Kaneohe Bay, Oahu, Hawaii, has led to a large number of studies concerning various aspects of human effects on the barrier and fringing reef complex there. Among the papers dealing with that bay are Bathen (1968); Roy (1970a); Smith et al. (1970, 1973); Smith (1971b); Caperon et al. (1971); Clutter (1972); and Johannes (1970,1972). These papers have dealt primarily with the high nutrient level and rapid deposition rate in the bay.

Pollution of the biosphere by man-made chemical compounds has reached a level such that all faunal elements of the earth are contaminated (Risebrough et al., 1970). These compounds are of two types: 1) biocides (primarily chlorinated hydrocarbons) manufactured and distributed specifically to eradicate or control "pest" organisms; and 2) chemicals manufactured for and used in industrial processes which "escape" from their intended area of use (primarily polychlorinated biphenyls and heavy metals). The accumulated literature on the distribution of these compounds is extensive but only recently have their physiological effects on metabolic processes begun to be elucidated. New information on induction or inhibition of various enzyme systems and chemical reactions by man-made chemicals becomes available with each edition of the pertinent journals. These physiological effects are especially relevant to marine organisms, since accumulation and biological concentration occur most readily in aquatic systems.

While biocides have been detected by all studies thus far designed to investigate their presence or absence, few such studies have been carried out on coral atolls; and little investigation has been made of biocide accumulation in any level of the food web of a coral atoll. To our knowledge, the only non-marine data available for a tropical island are in unpublished information on Sooty Tern eggs from the Dry Tortugas, Florida, in which DDE and PCBs were present in all samples (W.B. Robertson, Jr. pers. comm.).

By an accident of geography, atolls have been the most numerous sites of atomic and nuclear atmospheric bomb-tests and, inevitably, the sites of pollution by radionuclides. Between 1946 and 1958, more than 59 tests took place at Eniwetok and Bikini atolls (Welander, 1969). Later Christmas and Johnston Islands were involved, and more recently, Mururoa and Fangataufa Atolls in the Tuamotus.

In the Marshall Islands, a survey of the ecosystem had been carried out prior to any tests (Ladd, 1973), and periodic resurveys followed. They gave rise to an enormous literature much of it in classified or hard-to-get AEC reports. Only after many years did papers appear in scientific journals of more general distribution, as well as in proceedings of conferences and symposia (see for instance papers by Beasley, Beasley and others, Held, Held and others, Nelson and Evans, Templeton _et al_, and many others). Such information has not yet been integrated as a whole picture of radionuclide pollution on coral reefs and atolls, but much data continues to be accumulated. There is much less easily available information on Johnston Island, Christmas Island (Palumbo et al., 1966) or the Tuamotus.

In the Marshalls, as the result of a catastrophic incident (Operation Castle, 1954) the effects of exposure to radiation on atoll human population became available for study. Detailed medical surveys of the exposed islanders have been carried out and repeated at regular intervals. See for example papers by Conard et al., Robbins et al. and Lisco and Conard. The sociological effects of the Castle disaster, as well as those of the displacement of the Eniwetok and Bikini populations are other aspects of human interference with the coral island ecosystem (Stoddart 1968a). Many others, the impact of war on atolls, of organized migration, of changes in economic patterns, could be mentioned, but cannot be detailed here. This type of information is beyond the scope of this review, but it is obvious that anthropology and history can furnish evidence relevant to the total picture of coral island ecosystems.

MARINE BIOTA: BENTHIC PLANTS

Benthic marine algae make major contributions to primary productivity, nitrogen fixation, community structure, organism distribution, carbonate production, and reef consolidation and destruction. Setchell (1926, 1928) was probably the first biologist to recognize fully the variety and importance of these roles of algae in coral reefs, and much work has followed his pioneer effort.

Setchell (1928) described zonation of algae across the reef, as have Kanda (1944), Doty and Morrison (1954), Gilmartin (1960), Doty

(1967, 1970) and Tsuda (1970). Seasonal occurrence has been described by Bernatowicz (1952) and Denizot (1969), and measured on Guam by Tsuda (1972), and Dahl (1972) has analyzed community structure of Samoan algae. Dahl (1971) has also demonstrated that certain benthic algae are useful as ecological indicators and can even provide a continuous record of environmental conditions.

Studies on temperate and subtropical algae have demonstrated their importance in ecological investigations and have developed techniques for surveying field populations. Line transects can provide a useful basis for describing community structure and measuring seasonal variations, as in the work by Neushul (1967) on subtidal vegetation in western Washington, and the recent survey of subtidal ecology off southern California (Neushul et al., 1967; Clarke and Neushul, 1967). Experimental techniques can add considerably to the field data on community composition and ecology (Neushul and Dahl, 1967).

Crustose coralline algae (Melobesioidae) may be at least as important as corals in the development of reef structures (Setchell, 1926; J.H. Johnson, 1961; Gross et al., 1969). These algae have been especially noted in the Pacific, where they have given their name to the "Lithothamnion ridge," a striking but misnamed topographic feature of Pacific atolls; however, the importance of coralline algae to reef construction in general is probably greater than the extant reef literature would indicate (Denizot, 1972). In many areas of the Pacific (e.g. Ladd et al., 1970; J.H. Johnson 1961) as well as in the Tethys Seaway (e.g. Lemoine, 1939; J.H. Johnson, 1965) and even in the Atlantic (Iams, 1969) encrusting coralline algae have been important or even the primary contributors to sedimentary formations. Considering the widespread occurrence of encrusting coralline algae, their importance in determining the nature of the substratum-water interface, and their presence in the Fossil record, they have been rather neglected. They are considered to be a difficult group (see for example W.R. Taylor 1960; Adey 1970) and have often been treated as part of the "dead" substrate. Adey has underway a detailed study of the role of coralline algae in the reef ecosystem.

Calcareous green algae (mostly Halimeda spp.) contribute greatly to loose sediments in certain areas of the reef, especially certain zones of lagoons (Chapman, 1901; Emery et al., 1954; Hoskin, 1963). Stockman et al. (1967) and Neumann and Land (1969) have also shown the importance of the genus Penicillus in the formation of lime muds in Florida and the Bahamas. Land (1971) has studied the importance of sediment production by Melobesia, a red alga which commonly encrusts sea grasses.

The roles of boring algae and microbenthic algae have yet to be delineated in respect to calcium carbonate breakdown though Nesteroff (1956) and others ascribe to them a major responsibility for intertidal erosion.

Some attempts at including crustose coralline algae in regional studies of calcium carbonate budgets (S.V. Smith et al., 1970, 1972a) and in investigations of primary productivity (Marsh, 1970; Littler, 1971 have been undertaken. The results are preliminary, however, as there is likely a variation by several orders of magnitude in growth and metabolic rates, as a function of light, temperature, species, and even part of an individual plant considered (Adey and McKibbin, 1970). Some preliminary productivity measurements have also been made on reef algae by Doty (1971) and Soegiarto (1972). Recent studies have indeed shown that the alga-covered reef flat, a visually unimpressive and often ignored component of the reef community (Dahl, 1972), was in fact, twice as productive as areas of rich coral cover and supported large roving populations of herbivorous fishes (Johannes et al., 1972).

Symbiosis, or the occurrence of zooxanthellae within living coral tissues has long been known, but only recently has their role as nutrient acceptors been demonstrated (Goreau and Goreau, 1960; Muscatine and Hand, 1958). The zooxanthellae also play a significant role in the calcification of some corals (Goreau, 1961a, Goreau and Goreau, 1960). There is still considerable debate over the interaction between plant and animal components. Recent work has only begun to explore the variety of marine symbiotic relationships (see for example, D.L. Taylor 1969a, 1969b, 1971).

Information on grazing of algae by reef herbivores includes general observations on predation upon algae via studies of gut contents and results from caging; herbivore densities have not been reported beyond presence or absence, nor have the plant communities in which the experiments were carried out been rigorously defined (Randall, 1961, 1965; Mathiesen et al., 1972; Earle 1972). The slate-pencil urchin, Heterocentrotus mammillatus, has been observed to feed heavily on Porolithon sp. on the algal ridge of Bikar Atoll in the Marshall Islands, and to have a significant influence in the erosion of the reef edge (Fosberg, pers. comm.).

"Sea grasses" are locally important in tropical nearshore environments. In his monograph, den Hartog (1970) summarizes under each species what is known of its biology, its role as food for herbivores (e.g. Randall, 1965), and its function as a substratum stabilizer. Recently, the echinoid Diadema has been shown to graze heavily on Thalassia in certain situations in the Caribbean (Ogden et al., 1973). There have been rather few quantitative studies on the productivity of turtle grass (Thalassia testudinum), one of the more abundant and the best known species. Early studies were made by Pomeroy (1960), Odum (1957), and Jones (1968) on productivity measured by the O_2 method. However, closer inspection by Zieman (1968) has shown that this method is suspect for Thalassia productivity, as the leaves have the capacity to expand and store gasses in interstitial lacunae. This phenomenon has also been demonstrated by Hartman and Brown (1967) for the fresh-water species Elodea canadensis and Ceratophyllum dimersum.

INVERTEBRATES

It is impossible here to discuss the individual roles of the numerous groups of invertebrates in the reef ecosystem, or the enormous amount of available work basic to an integrated study of the system. Many pertinent papers on invertebrates have appeared in Cahiers du Pacifique, which also include bibliographies of certain groups, and in recent Symposium volumes cited pp. 1-2. This review will only touch on a few highlights of recent research on invertebrates in their functions in the system. Since coral reefs are almost entirely the result of biological activity, an analysis of reef development may be approached by examining structural activities (construction, maintenance, and destruction) and the contribution of the various biota involved (calcification by hermatypes, binding and baffling properties of some soft-bodied species, and biodegradation by a variety of invertebrates).

Work on growth rates or calcium carbonate deposition rates has been mentioned in previous sections. The minimal energy requirements of corals were investigated by Coles (1969), who concluded that three common reef species are capable of capturing and ingesting sufficient zooplankton to account for daily maintenance under laboratory conditions. Yet it was determined from a field study in Bermuda that the energy needs of corals were of an order of magnitude greater than could be met by the supply of drifting net zooplankton (Johannes _et al_., 1970). Obviously these metabolic studies are not conclusive

Further studies of coral metabolism should include examination of coral feeding and digestive mechanisms and the relation of these mechanisms to coral morphology and food type.

Hartman and Goreau (1970) have called attention to the sclerosponges as an important constructional element besides scleractinian framebuilders in the sub-reef and deeper reef framework. It is also clear that many benthic reef invertebrates play an important role in maintenance processes. An example is that of the sponge _Mycale laevis_, which protects the lower surfaces of some massive corals from the destructive effects of boring sponges (Goreau and Hartman, 1966).

Although corals are commonly the principal animal contributors of skeletal materials to the framework and loose sediments that make up the reef, several other invertebrate groups can make substantial additions (especially mollusks, echinoderms, and Foraminifera). The latter, in addition to their commonly recognized role as stratigraphic markers, are frequently a prominent component of loose sediments. Some entire atoll beaches in the central Pacific are made up of the worn tests of _Calcarina_ and _Baculogypsina_, two genera that inhabit windward reef flats. _Hometrema_ forms conspicuous dark red crusts on the coral fragments seen on Glover's Reef and other atolls.

Skeletal framework destruction by biological means has been discussed above. Some processes are direct and obvious, such as the feeding of fishes, crabs, worms, snails, etc. on living corals. Notable also is the recent population explosion of Acanthaster planci which feeds upon and locally devastates reefs in Pacific areas (Antonius 1971a, Chesher, 1969; Newman 1970; Randall 1972; Atoll Res. Bull. 166-170, 1973; Micronesica, 9(2), Dec. 1973; and numerous other recent papers). Feeding of fishes on invertebrates, e.g. corals and sponges, was studied by Randall (1967), Randall and Hartman (1968), and Bakus (1967). Many endolithic boring and burrowing forms are also known (e.g. sponges: Goreau and Hartman 1963, and Ruetzler, 1971; sipunculids: Rice, 1969; mollusks: R. Robertson, 1970, and rates of destruction have been calculated for some of them (Neumann, 1966; Glynn et al. 1971).

Interactions involving invertebrates have been summarized for Western Atlantic reefs by Glynn (in press). Lang (1970, 1971) obtained information on the interspecific aggressive behavior of hermatypic corals, representing a feedback loop within a single functional component.

Research on the role of small interstitial animals in the coral reef ecosystem has lagged behind other areas of study. Preliminary sampling has indicated, for example, that groups such as Turbellaria, Nematoda, Polychaeta, and Crustacea are abundant in reef sediments, raising the possibility that they may provide a significant food resource for deposit feeders and possibly grazers and browsers (Renaud-Mornant, et al., 1971; Thomassin 1972; papers presented at the "Floating Symposium" (see p.2) by Thomassin, J.F. Grassle and other participants).

FISH (AND OTHER VERTEBRATES)

The place of fishes in the budget of the reef ecosystem seems to have been elucidated perhaps in more detail than that of most other vertebrate groups. Except for the green turtle, the biology of which is being studied in various parts of the tropics (e.g. Frazier ms.; Ehrenfeld 1974), little consideration has been given to such other vertebrates as seals or sea-snakes, which are only locally significant. Sea birds have already been mentioned with respect to the terrestrial part of the ecosystem.

Estimates of fish biomass have been made by Odum and Odum, 1955 (425 kg/hect.); Bardach, 1959 (450 kg/hect.); Randall, 1963b (1590 kg/hect.) Brock, 1954 (1850 kg/hect.); and Goldman and Talbot, in press (200-2100 kg/hect. from different reef areas). These widely different estimates may be due in part to different sampling techniques and in part to the variation that is now known to occur between different parts of a single reef. As yet, there is no good information on differences between widely separated reefs, particularly from ocean to ocean. Some of the factors in fish biology which affect biomass may be detailed as follows:

Habitat selectivity is marked in reef fishes. Distribution is obviously affected by depth, shelter, food availability and competitive interactions. Various areas of the reef have different specificity in many zones. Up to 25 per cent of species may be restricted to single areas of the reef (Talbot, unpublished information).

From the work done on the movements of fishes on coral reefs (Springer and McErlean, 1962; Randall, 1961, 1962, 1963a; Bardach, 1958; C.L. Smith and Tyler, 1972; Moe, 1969; Winn and Bardach, 1960; Reese, 1964) it seems that the majority of reef fishes are restricted to a reef or even individual patch reefs, at least for long periods. Many species are territorial. Some few pelagic species such as some scombrids, carangids, and sharks, apparently move between reefs (Tester and Wass, personal communication). These species feed mostly on reef fishes.

Within their territories, many fishes have different feeding and resting areas and may move up to a mile or even more on daily feeding migrations (Winn and Bardach, 1960; Randall and Randall, 1963; Randall, 1963; Bardach and Menzel, 1957). Some fishes may have daily breeding migrations. Others may rest in caves down the deep reef front and feed on the reef flat or rest on patch reefs by day and feed over Thalassia beds at night. Some diel changes in distribution have been documented by Hobson (1965, 1968, 1972), Starck and Davis (1966), and Collette and Talbot (1972).

The food habits of West Indian and Pacific coral fishes have been studied by a number of workers, and this information forms a solid qualitative basis for further study (Hiatt and Strasburg, 1960, Suyehiro, 1962, Randall, 1967; Plessis 1972; Starck, Emery, personal communications). Few data on feeding efficiency and conversion are available for coral reef fishes, but a fair amount is known about metabolic rates in temperate freshwater and marine fishes. It appears that conversion factors could be used to calculate the metabolism of coral reef fishes. Some further work is needed, however, on selected species of different sizes, activity patterns, and feeding habits for accurate ecosystem modeling.

Most investigators who have worked on the problem of age and growth rates have found that conventional techniques are not always applicable to tropical fishes. Recent work (Moe, 1969) has shown, however, that otoliths can be used for some species, and size-frequency techniques as well as aging population dynamics may yield data for representative species (Gulland, 1970).

Relatively little is known of the reproductive biology of coral reef fishes (Breder and Rosen, 1966). Fishes exhibit a wide variety of reproductive mechanisms, from extreme parental care (e.g. mouth breeding) to random scattering of eggs. A few species have been shown to undergo daily or annual breeding migrations (Randall and Randall, 1963; Reinboth, 1973; C.L. Smith and Tyler 1972). Sex ratios are greatly variable, and several types of hermaphroditism are common

Fecundity, recruitment, and egg and larvae losses are perhaps most poorly known.

Reef fishes can also play a role in reef destruction. Bardach (1961) has documented the role of destruction by fishes on Bermudian reefs, while Glynn et al. (1971) have done likewise for fishes on the Pacific reefs of Panama. Grazing by parrot-fishes and some other reef fishes is commonly observed on reefs in all areas.

PLANKTON

At present, the quantitative contribution of phyto- and zooplankton to the reef ecosystem is unknown. Estimations of the standing crop of zooplankton around coral atolls and in the lagoon areas can be found in M.W. Johnson (1949, 1954), Gilmartin (1958), Mahnken (1966), Barnett (ms.), O.A. Mathisen (1964), Odum and Odum (1955), and A.R. Emery (1968). Most investigators have found that the biomass of zooplankton in the vicinities of reefs and atolls and inside coral reef lagoons is higher than the biomass in the open ocean at the same latitudes, yet the reef zooplankton biomass has probably been underestimated due to the inadequate sampling of epibenthic (hovering above the water-bottom interface or within the coral heads) and neustonic (near surface) forms. Present estimates of zooplankton biomass, however, are orders of magnitude (Odum and Odum, 1955) smaller than estimates of benthic organism and fish biomass.

The standing stock of phytoplankton has been expressed by chlorophyll-A values (N. Marshall), but conversion of these values into carbon is unrealistic without further analysis.

The literature does contain information on such necessary inputs to tropical phytoplankton as light, nutrients, and trace metals (Strickland, 1960; Jeffrey, 1968). One common component of the coral reef water column, Trichodesmium, has been studied extensively (Prabhu et al., 1966; Calef and Grice, 1966; Goering et al., 1966; Ramamurthy and Seshadri, 1966a, 1966b; Ramamurthy and Krishnamurthy, 1967).

It is obvious that many reef organisms feed on zooplankton. Quantity of plankton utilized by one reef assemblage in Puerto Rico was determined by Glynn (ms). Glynn (in press and ms.) has also given quantitative data on feeding activity of fishes and invertebrates on zooplankton as well as data on zooplankton recruitment (Glynn, in press).

NUTRIENTS AND DETRITUS

Studies of total community metabolism on atoll reef flats situated in largely unidirectional currents were initially developed by Sargeant and Austin (1949, 1954). Their method has been applied in a number of later studies (e.g. Odum and Odum, 1955; Kohn and Helfrich, 1957; Gordon and Kelly, 1962; Milliman and Mahnken, 1961; Qasim and Sankaranarayanan, 1970; Odum et al., 1959). The method was first used in a comprehensive manner at Eniwetok in 1971 during Project Symbios (Johannes et al., 1972). That project proved without doubt the efficacy of this approach; for instance, the symbios studies explained why reef communities are so productive biologically though bathed in waters very low in plant nutrients. Nitrogen fixation and unusually efficient recycling of phosphorus within the community are apparently responsible. These two phenomena, therefore, should now be focused upon at the subcommunity and species levels. Random searching, species by species, would probably not have revealed the great quantitative significance of these processes.

Net reef photosynthesis and total nighttime respiration can be determined by measuring the increase in the oxygen concentration in the water as it crosses the reef during the day, and its decrease at night. Another method which can help monitor community productivity and respiration uses changes in the CO_2 system (S.V. Smith, 1972). The system was analyzed according to some of the calculations outlined by Park (1969). This approach has a number of advantages (cf. S.V. Smith, 1973; Smith and Marsh, 1973; Kanwisher, 1963).

Still another approach to community metabolism consists of measurements made in fenced enclosures with the water surface open to the atmosphere; it has been successfully used to a depth of 1 m on the Great Barrier Reef by Kinsey (1972, and unpublished observations).

The reef imports organic matter from upstream in the form of zooplankton and exports it downstream in the form of mucus aggregates and algal detritus (N. Marshall, 1965; Johannes, 1967, Johannes et al., 1972). This transfer is likely to be of great significance in lagoon ecology and potential aquaculture.

A curious result of recent studies at Eniwetok (Pilson and Betzer, 1973) has been to demonstrate that levels of dissolved phosphorus change remarkably little across the reef. The mechanism by which this constancy is maintained is by no means clear as yet. It may be that organisms paving the reef constitute a significant phosphorus sink and that exchange between this sink and the overlying water constitutes a mechanism for buffering phosphorus levels in the water. Such a mechanism has been demonstrated between sediments and the overlying water in salt marshes by Pomeroy et al. (1965, 1967, 1971).

ECOSYSTEM ANALYSIS

Interest in a mathematical representation of ecological phenomena developed early in connection with the dynamics of populations and epidemics. Names such as Malthus, Pearl, Merhulst, Lotka, and Volterra will always be cited in any history of mathematical ecology. At the present time, much active research centers on extensions and elaborations of the original Lotka-Volterra competition equations. This approach is particularly popular in population ecology.

In community and ecosystem ecology, the dominant models currently used are compartment models. They deal with storages and flows of energy and materials in systems and have been usefully complementary to chemical and radiobiological techniques developed and utilized in ecology during the last twenty years. They will continue to be important, despite suggestions that ecologists expand their mathematical horizons (e.g. Clymer, 1972) precisely because of this compatibility with current and prospective experimental methodology. The current status of systems modeling in ecology is summarized by Patten (1971, 1972). A model from a geological view point is presented by Macintyre et al., 1974.

The International Biological Program (IBP) has been instrumental in accelerating the pace of development of total ecosystem modeling (in particular with the Analysis of Ecosystems Project of the U.S. IBP). All the Biome Programs (Grassland, Deciduous Forest, Desert, Tundra, Coniferous Forest, etc.) are committed to some form of mathematical ecosystem analysis. Progress to date has been variable, and the degree of emphasis also differs from program to program. The Grassland Biome Program is explicitly engaged in total ecosystem modeling (cf. Bledsoe et al., 1971). Others (e.g. Deciduous Forest, Desert) are emphasizing process models as potential modules for eventual total ecosystem models.

The general philosophy and methodology of the ecosystem analysis approach as developed for reefs at the Glover's Reef workshop are described elsewhere in this issue by Dahl et al.

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