THE DARK REEF INTERIOR

1987



Principal Investigator

David R. Kobluk

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EARTHWATCH

EARTHWATCH

THE ORGANIZATION

History and Operations

As far back as Columbus, explorers have had trouble financing their expeditions. First royalty, then wealthy patrons financed most of the exploration of the New World. In recent times, government agencies, universities, research institutions, museums, and corporations have assumed most of this funding responsibility. But competition is fierce for such grants, which are subject to political whims and shifting priorities.

Earthwatch began as a new solution to this old problem. We call our mode of research support "participant funding": a distinctive combination of patronage and participation that mobilizes field expeditions and provides contributing volunteers as research staff.

Earthwatch was born out of a sense of excitement about exploration. Today the search for knowledge is not just an adventure; it's a need. As society depends more and more on science and technology, it is in danger of relying on fewer and fewer voices—those of the experts. As knowledge becomes more and more specialized, even the experts cannot communicate with one another about issues of social concern. Their isolation undermines public discussion and debate on important policy issues.

Ralph Waldo Emerson thought scholars ought to take time from their studies to discourse with the public. Earthwatch makes that happen. Whereas field research traditionally has been restricted to scholars and their apprentices, we have opened that experience to the public, who contribute—in addition to funds—labor, insight, and, often, useful ideas.

This collaboration between scholars and amateurs benefits both. It helps communicate to the public the range, methods, ends, and nature of research. It helps inform public judgments about research aims and uses. It links scholars to their fellow citizens, scholarship to other aspects of culture, and issues encountered in the field to the concerns of citizens' daily lives. Participants return from the field with firsthand experience in "knowing how to know." Scholars return enriched by sharing their work with concerned, motivated citizens.



Earthwatch hands

With four pilot projects in 1971, our organization opened its doors to scholars who needed funding and labor. The first decade yielded such good fruit that Earthwatch now is mobilizing over 2,500 volunteers a year on 100 research projects. Altogether, Earthwatch has provided more than $9.3 million in funds and equipment for 830 expeditions in 75 countries. Today Earthwatch is the third largest private source of field research funding in the country. So far as we know, we are the only national organization offering members of the public the opportunity to invest directly in scientific research.

We are delighted you have decided to join us in the field. Welcome to the adventure of Earthwatch, to an ancient aristocratic pleasure now democratically open to all.

Planning and Launching Expeditions

Earthwatch's small staff now numbers about 48 people, including full- and part-time volunteers, who recruit proposals, scientists, and volunteers and prepare them for the field.

The Center for Field Research, an affiliated organization that solicits and screens inbound proposals from scientists, reviews about 400 projects a year. Its network of senior scientists, advisers, and peer reviewers assists the Center staff in their evaluation of each expedition plan and recommends to Earthwatch those with the greatest potential for scientific contribution and valuable participatory experience.

Once a program of expeditions is approved, Earthwatch announces the projects in its quarterly magazine and newsletter, which are mailed to all members. At the same time a briefing is prepared for each project. Our Public Affairs Department sends information to newspapers, magazines, and radio and TV contacts. Our best publicity, however, is from the recommendations veteran volunteers make to their friends.

The Field Operations Department matches volunteers with researchers and mobilizes teams. Your expedition coordinator provides you with all the information you need to prepare for the field, including this briefing, and keeps you abreast of any logistical changes before you leave. Once you reach the field, the scientist takes over. As a member of a research team, you work directly for him or her.



The staff of Earthwatch and the Center for Field Research

Sources and Allocation of Funds

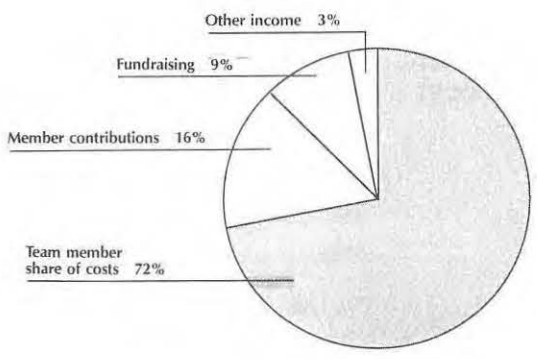
Volunteers who join Earthwatch scientists in the field finance about half our expeditions solely through their contributions. To finance others we combine your contributions with support from the researcher's affiliated institution or a grant from an agency such as the National Science Foundation.

Your "share of costs" consists of two parts. One is the per-capita grant that goes directly to the principal investigator to pay for your project's food, shelter, freight, field transport, and tools and equipment. The amount of this grant varies from project to project depending on location, the amount of the principal investigator's supplemental funding, necessary field costs, and the requested number of volunteers. In 1986, $1.7 million went directly to researchers in the field, reflecting from 40 to 100 percent of the share of costs, depending on the project.

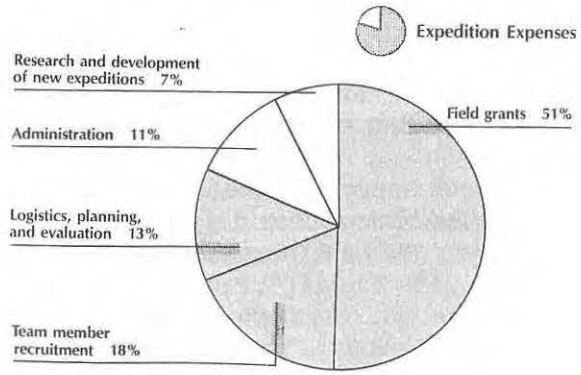
The other part is your contribution to the entire Earthwatch expedition enterprise—finding and screening research proposals, publicizing the projects, recruiting volunteers, processing applications and preparing teams for the field, publishing research news about finds in the field, organizing training conferences for the principal investigators, and providing logistical support wherever possible. In 1986, roughly 30 percent of team members' shares of costs was allocated to recruiting, screening, and deploying a research corps of 2,500 people; another 7 percent went toward finding and developing new expeditions. The remaining 11 percent helped pay a portion of the general administrative cost of Earthwatch. Of course, some projects cost more to launch than others. So your contribution is essential to mobilizing all of our research expeditions in addition to this one you will soon join in the field.

Earthwatch raises 9 percent of its funds from foundations, corporations, and individuals to support the expenses of the administrative staff in Watertown and special programs. We have received development grants for continuing education, career training for students and teachers, program development, international exchange, and public understanding of science. Many members also make annual tax-deductible contributions, beyond their dues, to further these special programs. Our list of corporations who match members' contributions is growing.

Sources of Funds, 1986



Uses of Volunteer Share of Costs, 1986



Tax Deductibility

You are considered a volunteer, providing your time and services to a tax-exempt activity: scientific research. As a volunteer, your out-of-pocket expenses are fully tax-deductible. This includes not only your contribution to Earthwatch on behalf of the expedition but also your transit costs to and from the staging area.

Tax laws are being revised by the Congress of the United States. Currently, the value of your time and your services is not tax-deductible; nor are any personal expenses unrelated to the expedition. For example, if you stop off to visit someone or sightsee en route to or from the project, then your transit costs must be pro-rated accordingly. Sample: 15 days with the team, divided by 20 days away from home, multiplied by your airfare, is the tax-deductible share of your transportation cost.

If you plan to seek academic credit for participating, then your volunteer status may be questionable and your share of costs taxable as tuition. On the other hand, professionals (such as teachers) joining Earthwatch to improve or maintain their career standing should be able to claim a business deduction even if they do obtain academic credit.

If the volunteer is not the taxpayer (a parent paying his child's share of costs, for instance), the Internal Revenue Service may disallow the deduction. You should consult a tax adviser in this case.

Membership

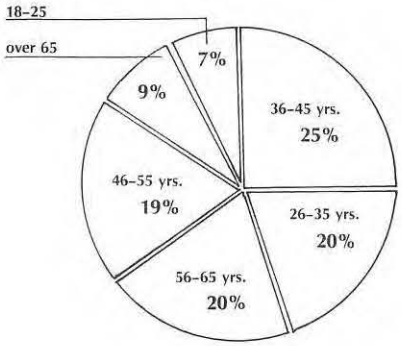
Canadians, Australians, and Europeans are adding to our growing membership. Increasingly, we are finding our strength in the levels of energy and commitment you give not only to the principal investigators but also to us in spreading the word. As our membership climbs toward 30,000, so too have our efforts to improve the benefits and quality of service to each of you. This has meant more magazines, newsletters, and expedition planners to provide timely information on newly accepted projects, and the Expedition Alert–Advance Notice system that matches individual interests with future opportunity. We have invested in staff and computers to drive the whole process.

Member Profile

A good part of the richness of an expedition stems from the diversity of you, the volunteers. Truck drivers, grandmothers, nuclear physicists, nursing students, corporate lawyers, and artists may all converge on a small island off Georgia to explore the remains of the Spaniards' northernmost outpost on the eastern seaboard.

A recent survey showed that Earthwatch members defy pigeonholing. But as impressed as we were with the differences between you, we noted a few common threads. You are fairly evenly distributed between the ages of 26 and 65. More than half are single; most have college degrees, and nearly half hold

Age Distribution of Members



advanced degrees. A prime attraction in choosing Earthwatch, members said, is the opportunity to learn by doing, although many also cite the personal challenge involved, the unique vacation aspect, and the chance to meet interesting people as motivating factors in joining an expedition. The last is virtually guaranteed. Be prepared to meet anybody on an expedition.



Steve Benjamin

Taking a lunch break while tracking orangutans in a Bornean rain forest.

Earthwatch Reaches Out

- Many local, national, and international institutions have put us in touch with their members; others have contributed to our expeditions and our scholarship programs; all have become members of our Cooperating Institutions program. In return, Earthwatch supplies speakers for membership gatherings, press releases to complement newsletters, and even funds to those institutions that recruit team members for Earthwatch expeditions. In some cases an institution may become a cosponsor of a research project.

- Recognizing the importance of a vital teaching force, Earthwatch has sought contributions from corporations, foundations, and individuals to support the participation of teachers and students on projects.

  Increasingly, full and partial grants have been awarded to secondary and elementary teachers through our Research for Renewal Program. Teachers are returning to the classrooms and school communities in a position to share newfound knowledge and renewed enthusiasm, thereby leveraging our grants many times over.

  Our Career Training Program offers a limited number of scholarships for secondary school students—our future scientists—to become apprentices to professionals in the field.

- Earthwatch has field representatives in most major U.S. cities and in several foreign countries—volunteers like you who are helping to coordinate our outreach efforts in their local areas. We would love to put you in touch with a local field rep when you return, or if there is no rep nearby perhaps you can help us get started in your town. When you return from the field, fill out your evaluation form

so that we can keep track of what happened to you. Since Earthwatch staff can cover very few expeditions, we need to hear your comments and stories in order to improve our expeditions from year to year. And we need the chance to share in what you have learned and accomplished. There are many ways to stay involved. The simplest is to tell your friends about us, and, if you'd like to help, call the field rep coordinator when you return.

Thanks to Special Friends

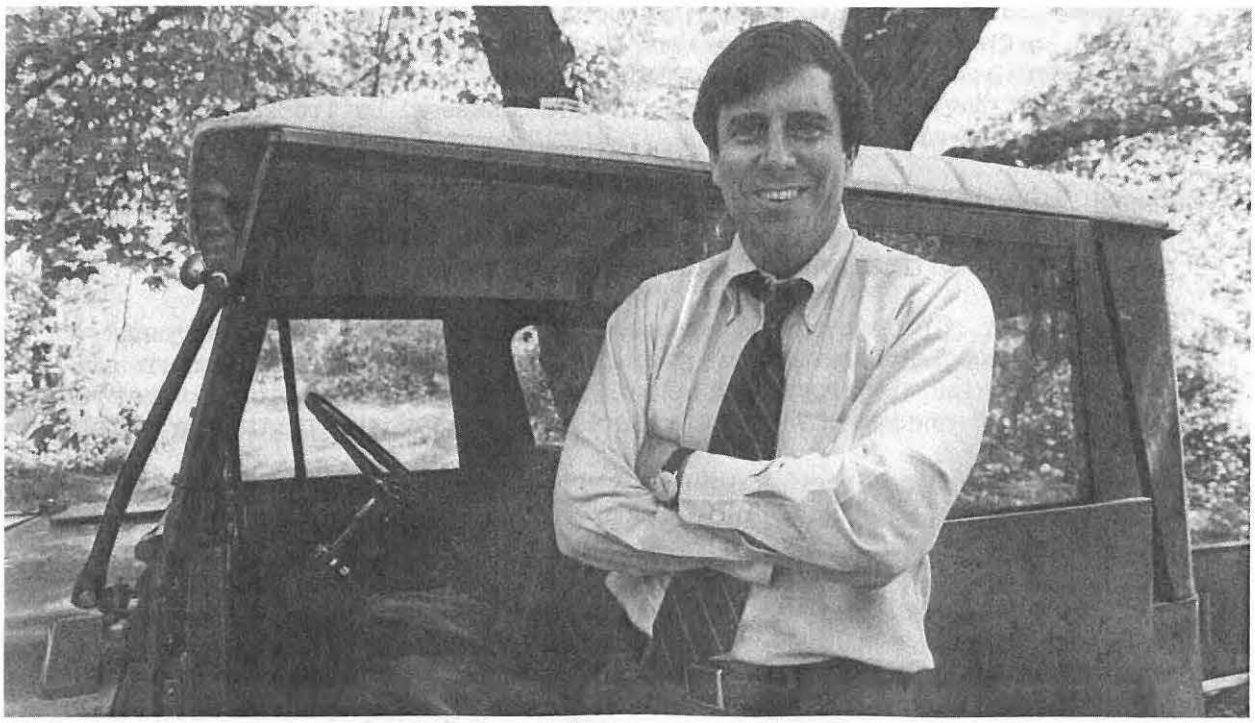
Without the aid and advice of many people and institutions we would not be where we are today. Special thanks to some who have brought us to this point:

Mr. and Mrs. George Argabrite from Los Angeles, the DeWitt Wallace Fund of the Readers Digest, and the Mead Foundation for establishing Earthwatch's first endowment for youth; and likewise the Leonhardt Foundation for our teacher endowment.

The Atlantic Richfield Foundation, TRW, Union Bank, Bank of California, Boston Globe, R & B Wagner, Frank Arensberg, and Polaroid for annual support of the Career Training Program for students.

The Edward John Noble Foundation, the Lyndhurst Foundation, Exxon Education Fund, the Klingenstein Foundation, Cabot Family Trust, the Phil Hardin Foundation, Raytheon, Marty Timken, Geraldine R. Dodge Foundation, and the Mustard Seed Foundation for annual support of teacher fellowships.

Special thanks to Alice Reynolds-Tatum, the Rosewood Company, and the AKR Meyer Foundation for support of the Texas Field Office; to the Myer Fund, Wang Australia, and Esso Australia for support of the Australia Field Office; to Mrs. Jefferson Patterson for a lead gift in support of Earthwatch Washington D.C.; to the Mead Foundation and the MacIntosh Foundation for their support of Earthwatch California.



Lilian Kemp

Brian Rosborough, Earthwatch President

And the Lounsbery, Phipps, Vetlesen, Tinker, and Hunt foundations, the Bayne Fund, and Ms. Zack de Zutel for their support of program development and operations.

Special thanks to all who helped make a move to new headquarters and technology upgrade possible with in-kind gifts: Hewlett-Packard, Printronix, Raytheon, WrightLine, John Hancock, and many others.

As Earthwatch grows, our need for support correspondingly increases. As a member of the Earthwatch family you will be asked for help from time to time. There is still work to be done. Just pick up the telephone and call.

The Future

From its modest origins in 1971 Earthwatch has gained the recognition and respect of the scientific community. Earthwatch volunteers have worked, for instance, with such noted primatologists as Alison Jolly (lemurs in Madagascar) and Birute Galdikas (orangutans in Borneo).

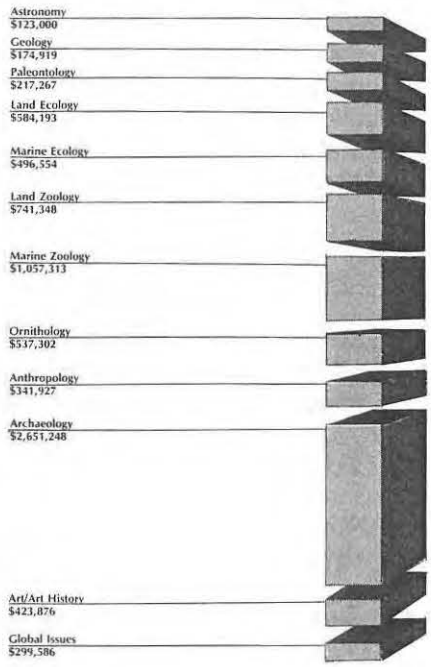
Several television programs have highlighted particular expeditions as part of their series. These include NOVA, SURVIVAL, ODYSSEY, Smithsonian World, and National Geographic. The BBC has filmed several expeditions for its Chronicle series.

In developing and developed countries Earthwatch operates as a scientific peace corps. Currently we are applying the participant funding model to a broader range of problems: monitoring endangered species, saving rain forests, and ethnography—exploring the nature of human cultures. Global issues—evaluating nutritional problems and testing agricultural improvements in developing nations—occupy a small but growing portion of our program. Among respondents to our member survey, agriculture, nutrition, and medicine ranked as the most popular "new fields" for Earthwatch to explore.

To aid service and expansion we have set up field offices in Washington, D.C., Dallas, Los Angeles, London, and Sydney. This year we are sending over 2,500 volunteers on 95 projects to the field. Earthwatch is still growing, but to ensure a good experience for volunteers and scientists alike we are leveling off our program at 100 projects per year.

You have made our work possible. Thank you. We hope your time in the field will be as rewarding and fruitful for you as it is to your principal investigator.

Grants by Discipline 1971-1985



Total grants, 1971-1985: $7,648,534

The rest of this briefing is to prepare you for your experience in the field.

THE EXPERIENCE

Field Research Is Improvisation

Before you begin, you must balance your romantic notions about field research with the realities of scientific discovery. Yes, it is always exciting to go somewhere you have never been and gain new insights to share when you return. But in the middle of that pursuit, the weather can be unpredictable, schedules can collapse, field food can range from unimaginative to peculiar, and the day-to-day work can be repetitious and difficult.

So be prepared for anything. Carefully laid plans are adapted in the field to meet the conditions at hand. Field research is improvisation. A good first rule is to expect the unexpected. Second is to be tolerant of trial and error. A third, and most important, is to find humor in difficult situations. If you can remember those three things you will have the time of your life.

Expeditions Are Teamwork

Although there are exceptions, such as archaeology projects, Earthwatch expedition teams are usually small, about 6 to 12 members. Many of us are not used to the close living of field conditions, and the ability to get along with others is of paramount importance. All the labors, like cooking and portage of equipment, become team assignments to be shared and enjoyed as much as the research itself.



Steve Benjamin

En route to an early man site in Zaire

Food, Shelter, and Clothing

Earthwatch expeditions have been based in every situation imaginable, from sleeping in bed rolls on flatbed trucks and jungle platforms to old English cottages with fine wines and tea service. As a rule, conditions are modest, and the food simple but plentiful. Your imagination, enterprise, and ability to improvise make it fun and interesting.

Field research is work, so dress accordingly. Bring your most comfortable, loose-fitting clothes, to conform to the weather on location. Your Expedition Plan sets out specific requirements and suggestions. Experienced participants will have learned how much more comfortable it is to be prepared for all eventualities.

Carry your luggage in a side-zippered canvas or nylon duffel bag. Everything is available, instead of out of reach at the bottom of your bag, and you avoid the storage problem presented by suitcases in tight quarters. You'll be glad for the soft bags on your first long, bumpy ride to the research site.

Ambassadors-at-Large

When overseas, you are viewed as ambassadors of this country. Courtesy and respect for local customs are important. Customs clearance and government permits are critical to continuing research in foreign nations. Possession of illegal drugs by one team member, for example, would jeopardize the entire mission of this and future expeditions. Each year more governments close their doors to foreign researchers. Your professionalism and general demeanor, under the watchful eyes of host countries, are important to Earthwatch and to all researchers who will follow you. It is likely that you will be exposed to aspects of a different culture not accessible to tourists. It is this added dimension that requires your extra sensitivity, discretion, and adaptability.

Field Notes and Photography

Your expedition is a search for information, which, we hope, will help resolve unanswered questions. Volunteers' observations and field notes can be just as important to the research team as those gathered by more experienced staff members. Everything you see, hear, and do has value.

Accordingly, you should bring the means to record your observations daily as well as take notes of the briefings and discussions held in the field. A simple spiral-bound notebook is most commonly used by scientists. If it fits in your pocket, so much the better. Whether you can draw or not, sketches of your observations will help you explain your experiences when you return home. If you have a camera, bring it, though sometimes working conditions will compete with your opportunities to use it.

The Earthwatch photo collection depends almost entirely on our volunteers, many of whom are talented amateur photographers. We can put your photos to good use in Earthwatch and other publications and in our slide shows. Volunteer artists are also encouraged to share their drawings, watercolors, cartoons, and illustrations.

Our publications department welcomes accounts of your expedition for use in expedition briefings and in our magazine and the News. Occasionally some of our volunteers write articles for our publications. If you are interested in setting up a specific assignment, please call our editor before you go.



Tom Newman

Volunteer and migratory golden eagle

Advance Preparation Helps

Your project will have a reading list that can shorten your training time in the field. Some hard-to-find articles may be included in this briefing.

Extracurricular study and physical exercise are also recommended. You might start walking several miles a day, learning to observe what is around you in a way that you have never done before.

Like most things in life, your experience with Earthwatch will be as good as what you put into it.



Investigating an Icelandic volcano

QUESTIONS AND ANSWERS

We have tried in this briefing to give all the information available in helping you plan for your expedition. Read it carefully and don't hesitate to call or write us if you have any questions.

The following questions are most frequently asked by those joining expeditions for the first time.

When do I know I am accepted on the team?

Your expedition coordinator screens volunteer applications according to the needs of the principal investigator. Most participants are notified of acceptance within one or two weeks. Very popular projects fill up immediately. In this case, Earthwatch will notify you of placement on a waiting list, to stand by for an opening. Having a second choice when you apply assures you the opportunity of joining an expedition.

Who is the expedition coordinator and will I meet him/her on the project?

Six expedition coordinators handle over 400 teams each season. They answer myriad questions and generally help prepare you for your field experience. Though you will probably not meet your coordinator in the field, (s)he will certainly be with you in spirit. Always feel free to call your expedition coordinator with questions, and don't forget to send a postcard from the field when you have a chance.

Does Earthwatch handle travel arrangements and hotel accommodations?

Earthwatch has a travel coordinator who can make transportation arrangements. The coordinator needs your completed travel form, provided in your acceptance packet, well in advance to assure you confirmed seats at a reasonable price. Principal investigators prefer to have teams arrive in a group, so our travel coordinator needs to know your itinerary in order to coordinate rendezvous and keep track of volunteers in transit.

Are there many people on my team? How will I recognize them on arrival?

Team size and demography vary, depending on the needs of the project and its popularity. A team list of participants and their backgrounds will be forwarded to you one month before the departure date. Past teams have ranged from 2 to 40 members. The average size is 8 to 10. Wear your Earthwatch patch and use your Earthwatch stickers (provided with the team list) so that you and other team members will be readily identifiable to each other.

How much baggage should I bring?

As little as possible, yet all that's necessary. Storage space is usually at a premium. Soft carry-on luggage and shoulder bags are recommended. You must be able to carry all your own baggage. You will find a specific list of clothing suggestions in the Field Logistics section of this briefing.

What about travel requirements and insurance?

Visas, inoculations, passports, and travel and medical insurance are your responsibility. We do have specific recommendations for travel insurance and have sent you the necessary information. Be resourceful, but call us if you have any problems or questions.

Do I really need a medical examination?

Yes. Earthwatch requires that your doctor complete a Health Statement. If (s)he is familiar with your general health and physical condition, of if you have had a check-up in the last 12 months, this should not require a special physical. We are simply looking for some assurance that your health is not going to be a problem for your participation. In addition, the principal investigator needs to know of any allergies or previous illnesses that might affect you while in the field. Some projects are more strenuous than others and do require specific skills and physical abilities. Read the "Value of Volunteers" and "Physical Conditioning" sections of this briefing carefully to find out if this is an appropriate expedition for you.

Will I need shots and inoculations?

For most projects, yes. We provide a list of recommended and required shots and inoculations. We also suggest that you contact the Center for Disease Control in Atlanta, 404-329-2572, for the most up-to-date recommendations regarding shots and inoculations for the area you will be visiting. You should also discuss your specific medical needs with your physician.

What out-of-pocket expenses can I expect beyond my share of costs?

Participants cover all travel costs between home and the staging area. No additional money is required; however, most participants bring pocket money for film, reading material, gifts, liquor, souvenirs, etc. While on expedition, all costs are covered, except spontaneous events and nights on the town.

May I bring my children?

Children under 16 are rarely allowed on expeditions. Children 14 or 15 are sometimes permitted in cases where the son or daughter is mature enough to share responsibilities of the project. We do have quite a few families, husband-and-wife teams, and father-son or mother-daughter combinations.

Can I bring special equipment or cameras, or conduct my own experiments?

Yes. Special interests are encouraged but alert your expedition coordinator first. If your independent project might interfere with any scheduled assignments, it should be cleared first in a letter to your scientist.

Can I bring back any souvenirs or artifacts from the expedition?

Generally, anything of value is retained by the principal investigator or left with the host country. These expeditions are not treasure hunts, but rather research investigations. There are occasions, however, to bargain for souvenirs in the field. Ask your principal investigator what's appropriate.

Can I get academic credit for joining the expedition?

Frequently. First check with your college or university to ascertain what might be required for granting academic credit.

Do you really think I am qualified to join the team? I have no previous experience.

Yes. That's what Earthwatch is all about. You learn as you go.

Good luck.
Brian Rubright

EXPEDITION PLAN

EXPEDITION PLAN

University of Toronto

Erindale Campus
Mississauga, Ontario
Canada L5L 1C6

Earth and Planetary Science
(416) 828-5361

Welcome to The Dark Reef Interior 1987

This is the 8th field season in Bonaire for this project, and I hope that it will be as successful as the previous seasons.

We have accomplished some exciting things during this on-going project, many of which we will talk about on-site in Bonaire. Among these, however, has been the production of 4 contiguous very detailed maps of the coral reef surface which were designed to census the reef surface-dwelling biota; this census provides a tight framework with which to contrast and compare the cavity-dwelling biotas living below the surface. The actual mapping is now complete and as a result the map work has shifted to the laboratory. In the lab, our computer has become our prime tool - the organism data derived from the maps is being analysed statistically. We are looking at various aspects of population dynamics, including species associations.

Below the surface, inside the reef cavities, we are concentrating upon the biota in a piecemeal fashion - to date sampling has been completed on the diatoms, and the bryozoans (colonial moss-animals). The bryozoan collection to date is approaching 10,000 specimens, each one of which is being identified to the species level.

This year our work will revolve about detailed sampling of the cavity biotas and the wall rock that lines the cavities. The collection will be a sizeable one, and will be made at 10 ft. depth increments down to 120 ft at several sites along the west coast of the island. A great deal of what we have been finding in the reef cavities is new and certainly is exciting ... but we'll talk about it all in Bonaire.

David R. Kobluk
Associate Professor
of Geology


ORIENTATION MAP
THE BAHAMAS
ATLANTIC OCEAN
CUBA
HAITI
DOMINICAN REPUBLIC
PUERTO RICO (U.S.)
GREATER ANTILLES
INSET A
Anguilla (U.K.)
Saint Martin
SABA
SINT EUSTATIUS
Antigua (U.K.)
Guadeloupe (Fr.)
NETHERLANDS ANTILLES
Martinique (Fr.)
CARIBBEAN SEA
INSET B
ARUBA
CURAÇAO
BONAIRE
SARB.
TRINIDAD and TOBAGO
COLOMBIA
VENEZUELA
GUYANA
Statute Miles
Kilometers
INSET A
Anguilla (U.K.)
SAINT MARTIN (Fr.)
Phillipsburg
SINT MAARTEN
Saint Barthélemy (Fr.)
WINDWARD ISLANDS
The Bottom
SABA
SINT EUSTATIUS
Oranjestad
Saint Christopher (U.K.)
Nevis
INSET B
ARUBA
Oranjestad
CURAÇAO
BONAIRE
KLEIN BONAIRE
Kralendijk
WILLEMSTAD
(also insular capital of Curaçao)
VENEZUELA
NETHERLANDS ANTILLES
National capital
ARUBA Insular community
Insular community capital
Administrative center
International airport
Statute Miles
Kilometers
Staging Area/ Research Site

PRELIMINARY PROPOSAL

PRINCIPAL INVESTIGATOR: Dr. David R. Kobluk

TITLE/POSITION/DEGREE: Associate Professor and Associate Chairman of Geology, B.Sc, M.Sc., Ph.D.

ADDRESS: Earth and Planetary Sciences, Erindale Campus, University of Toronto, Mississauga, Ontario, Canada, L5L 1C6

OFFICE TELEPHONE: (416) 828-5363; (416) 828-5335

PROJECT TITLE: Coral Reef Population Census, Population Dynamics, and Interactive Coral Reef Simulation Modelling.

DISCIPLINES: Geology, Ecology, Marine Geology, Marine Biology, Computer Science, Conservation

GEOGRAPHIC LOCALE: Bonaire, Netherlands Antilles.

TIME PERIOD: May 20, 1987 to June 2, 1987, June 5, 1987 to June 18, 1987, and June 21 to July 4, 1987.

PROJECT SUMMARY:

See accompanying project research proposal and briefing manual for a detailed summary.

SUMMARY OF RESEARCH OBJECTIVES:

1) Detailed coral reef mapping to quantificy the abundance, distribution, and surface area coverage of important reef-dwelling organism groups (e.g. sponges, corals, hydrozoans,gorgonians, etc.).
2) Document in a very detailed fashion, zonations of reef-dwelling organisms with increasing depth down the forereef front.
3) Use population statistics gathered by reef mapping to help in the development, and testing, of a holisticcomputerized coral reef simulation.

NEED FOR VOLUNTEERS:

Team 1: 6 - 8 volunteers, May 20-June 2, 1987
Team 2: 6 - 8 volunteers, June 5-18, 1987
Team 3: 6 - 8 volunteers, June 21-July 4, 1987

SCUBA divers are required for the construction of underwater grid systems and the detailed mapping of reef surface-dwelling organisms.

STAFF COMPOSITION:

Dr. D. Kobluk - Principal Investigator.
M.A. Lysenko - Research Assistant: Erindale Campus, University of Toronto, Mississauga, Ontario - Coral Reef Specialist.

INTRODUCTION TO THIS PROJECT MANUAL

In Bonaire we are focusing upon a major frontier in coral reef research: the ecology and geology of the reef interior. There are many major groups of plants and animals that are an integral part of the reef environment that have representatives living in reef interior cavities. We know that the reef cavity ecosystem is very old, indeed almost as old as the record of reefs themselves. Work investigating the communities of living reef cavities and fossil reef cavity systems gives us a glimpse of an only poorly known realm of shade-loving and shade-tolerant animals and plants.

Earthwatch teams have been assisting in the study of reef cavities in Bonaire now for 8 field seasons, and have helped contribute to a general understanding of how very complex and exciting these cavity communities are. We have, to date, for example, completed the most detailed large scale map of the surface of a coral reef ever attempted, which serves to give us an accurate perspective and framework with which to compare the reef interior communities. A comprehensive survey of the cavity-dwelling corals in Bonaire has also been completed, as has a detailed study of the molluscs living in reef cavities. A large scale survey of the cryptic bryozoans in the Bonaire reef is currently being completed as well; the field work over 2 field seasons has produced a collection of about 9500 bryozoan specimens from cavities over the depth range 1 m to 73 meters (240 ft.). Many other aspects of the reef cavity system have also been tackled in Bonaire over the years, and some of them are outlined in this manual.

This project manual is designed to do 3 things: 1) introduce you to the general geology of the island of Bonaire, and aspects of its marine ecology that are of interest geologically, 2) outline some of the results of work to date on our project in Bonaire, and 3) introduce you to the overall plan and logistics of this coming season's field work. You will probably find some of the reading to be heavy going if you have no geological and/or biological training; I therefore recommend a geological dictionary or a good Oxford or Webster's dictionary to be at hand when you do read it. If, even after reading it, you have difficulty with some of the concepts or some of the terminology, do not hesitate to ask for help or a special seminar after you arrive in Bonaire.

An outline of the contents of this manual in the order in which you will encounter them is as follows:

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- LOCATION AND CLIMATE
- NOTES ON THE EARLY HISTORY OF BONAIRE
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- PLEISTOCENE REEF AND EROSIONAL TERRACES
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LOCATION AND CLIMATE

Bonaire comprises 2 islands, the main island of Bonaire itself, and to the west smaller Klein Bonaire nestled in the protected lee of the island. The main island is centered about latitude 12°12'25.2" north and longitude 68°18'25.0" in the southern Caribbean, 85 km due north of the coast of Venezuela. It is one of a series of east-west-trending islands, cays, and shoals referred to as the La Blanquilla-Aruba chain that parallels the South American coastline. Immediately to the east of the island are the Las Aves Islands (Venezuelan) and to the west (40 km) is Curacao; further west (115 km from Bonaire) is Aruba, which together with Bonaire and Curacao, form the 'ABC' island chain of the Netherlands Antilles.

Bonaire is graced by a remarkably pleasant and stable climate; the mean annual temperature is 27°C with little variation over the year. The daily temperature varies an average of only 4°C. Mean annual rainfall is about 500 mm with a mean annual relative humidity of 75%. The rainy season is from October to January, but it is a "dry" rainy season compared to that of other Caribbean islands north and east. The island is semi-arid in character due largely to its denuded surface which has no true forest cover, little humus soil, and widespread cactus and scrub brush growth. The semi-aridity results more from this lack of soil-stabilizing vegetation than to lack of rainfall. The mean wind velocity is 5 m/sec from due east. Bonaire is not in the normal path of hurricanes, which rarely hit the island. Generally they pass to the north, but even these have effects on the island, including strong winds from the west or south, heavy seas, and rainfall. The reefs and coast on the west and southwest side of the island are particularly vulnerable to strong seas and other abnormal weather conditions.

The people of Bonaire are friendly and speak Papiamentu, Spanish, and Dutch, but English is widely spoken; one can get along quite comfortably in English.

Bonaire presents a nearly virgin tropical desert island environment with magnificent near-shore coral reefs. Forests of cactus and several hypersaline lakes predominate (it does not rain very much). The southern part of the island is flat, and the north is mountainous. Troublesome animals and insects are not found, with the exception of very small scorpions and centipedes, which do not present any problem, as they are never encountered. Sharks are very rare; barracuda are small, uncommon, and present no hazard. Bonaire is famous for it s rare birds (about 120 species plus pink flamingoes).

NOTES ON THE EARLY HISTORY OF BONAIRE

Bonaire was first visited by Europeans in September of 1499 when the navigator of the Spanish Ojeda Expedition, Amerigo Matteo Vespucci, landed there during an exploration of the north coast of South America from Trinidad. The island was named Isla de Palo Brasil (Dye-Wood Island) after the forests of dye-wood that then covered Bonaire. A few

years later the island was renamed by the Spanish following a phonetic translation of the Indian name for it: Bojnaj. Through the centuries the name was gradually modified to its modern form. The original meaning of the Indian name for Bonaire has been lost, but it most certainly does not mean "good air" following the French, as much popular literature would have it.

The island was inhabited already when the Spanish arrived by a Stone Age tribe of Arawak Indians called the Caiquetios; their cultural realm included Aruba, Curacao, and Bonaire, as well as part of north-central Venezuela west of present day Caracas. Their cultural origins appear to have been the Columbian Andes. Caiquetios pictographs are still found at several localities on Bonaire: some of the best examples are on an open cave roof at Onima on the east coast. The pictographs cannot be dated, and their meaning is unclear, although some of the symbols such as hands, lizards, cactus, snakes, etc., can be recognized.

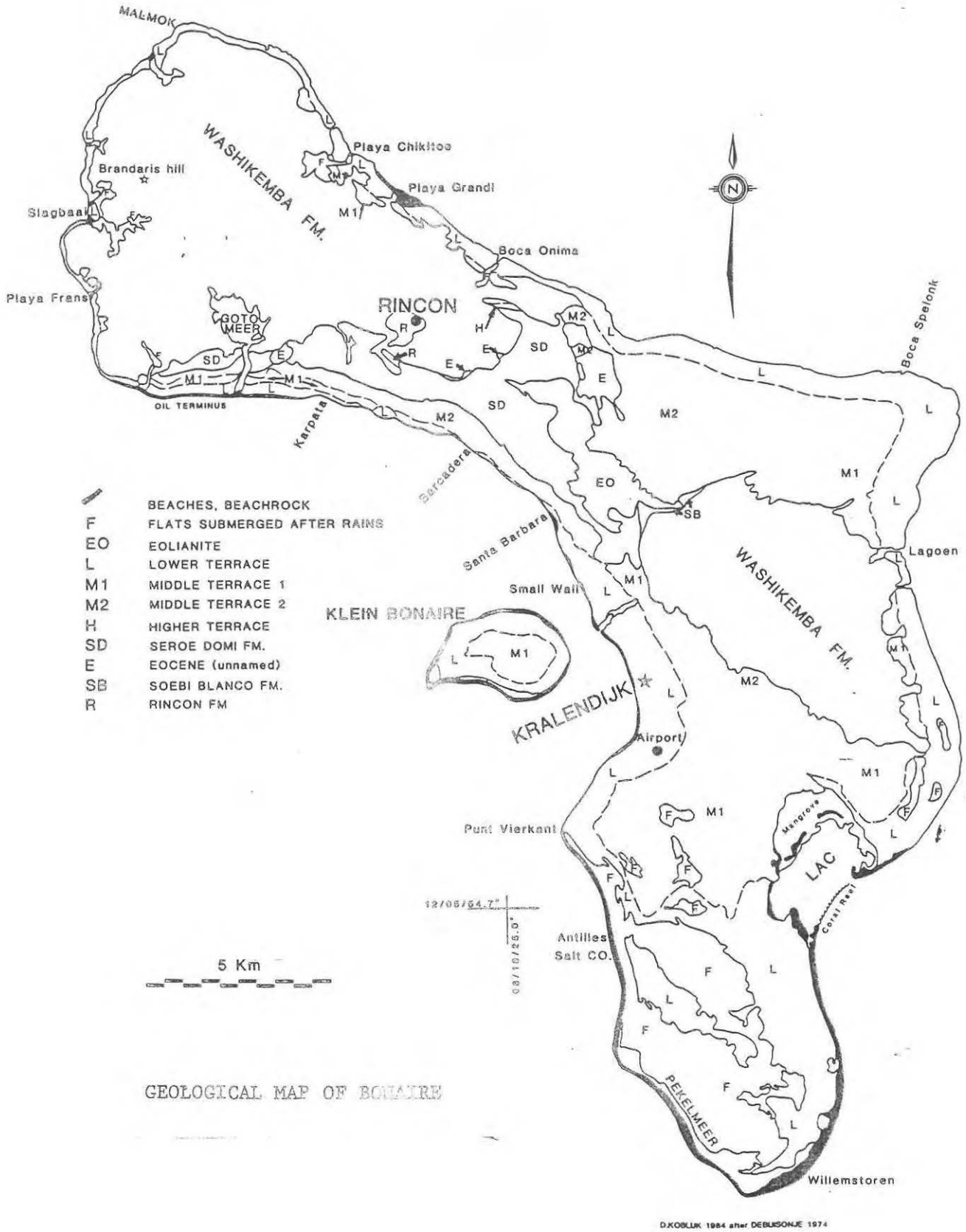
The aboriginal Caiquetios were deported from Bonaire in 1513 to 1515 to Hispaniola by the Spanish to provide slave labour for the copper mines there. The Spanish settled the island about 1527, and founded a village at the present site of Rincon in the north-central part of Bonaire. The first domesticated animals (pigs, horses, sheep, donkeys, etc.) arrived with them.

The Dutch occupied neighbouring Curacao in 1634 and took Bonaire in 1636 from the Spanish to secure the eastern approach to Curacao. Bonaire was used in this period almost exclusively for meat production to support the Curacao colony.

In 1639 the Dutch West India Company took total control of Bonaire and under its Economic Development Project For Bonaire And Aruba began to develop an agricultural plan for the island based upon the production of salt, maize, and stock-breeding. At first labour for these projects was provided by using the surviving Caiquetios Indians on the island. However, by 1662 the appearance of a large African slave market in Curacao provided the Dutch West India Company with a source of African slaves for slave labour on their Bonaire agricultural and salt projects; by 1700 there were 97 slaves in Bonaire.

Gradually the salt industry became paramount; the slaves who were unfortunate enough to be working the salt pans at Blauwe Pan on the southwest coast (site of the ancient Blue Obelisk) were housed in Rincon in the north of the island. The slaves were marched overland twice weekly between Rincon and the salt pans. At first they slept in the open on the rocks, but by the early nineteenth century an attempt was made to provide them with shelter. The slaves were given a choice of on-site temporary work housing either in small huts or in a large barracks. They opted for the smaller huts which still stand. Rincon was used as a "slave breeding place" where families of the slaves were kept - this unpleasant practice was common and apparently was considered acceptable at the time. The Caiquetios Indian population on the island declined steadily throughout this period until by 1816 there were no full-blooded Indians left on the island.

Lumbering on Bonaire for dye-wood continued for centuries, but never became a mainstay of the economy. Dye-wood was being harvested as early at 1639, and possibly before that, although there are no earlier records surviving. The impact this minor industry has had has far outweighed its size, as much of the present denuded surface of the island is due directly to uncontrolled lumbering and associated soil erosion.



GEOLOGICAL MAP OF BONAIRE

GENERAL GEOLOGY OF BONAIRE

Considering the small size of the island of Bonaire, its geological structure and stratigraphy are complex (see Figure). The island is separated from the Venezuelan shelf to the south by the 1700 meter deep Bonaire Trench, and stands on an oval 1000 meter deep platform-like structure which is elongate to the southeast.

Major east-west-trending faults to the north and south border the La Blanquilla-Aruba chain of which Bonaire is a part. The fault to the north passes through Nicaragua in Central America and extends to the east into the Atlantic past the Lesser Antilles between Tobago and Barbados. Relative movement of the southern block containing the La Blanquilla-Aruba chain is to the west. South of Bonaire a major fault crosses through the Paranguana Peninsula of Venezuela and the Bonaire Trench, progresses to the east, and enters the Atlantic north of Trinidad. Relative movement of the island chain along this fault has been toward the east. The geological history of Bonaire is related in part to movement along these faults.

The entire La Blanquilla-Aruba island chain has a mid-Eocene to Holocene history of relative stability, with an earlier history through the Cretaceous and early Tertiary of submarine volcanism; reduced volcanic activity and increased tectonism were taking place by the early Tertiary (Beets and MacGillavry, 1977).

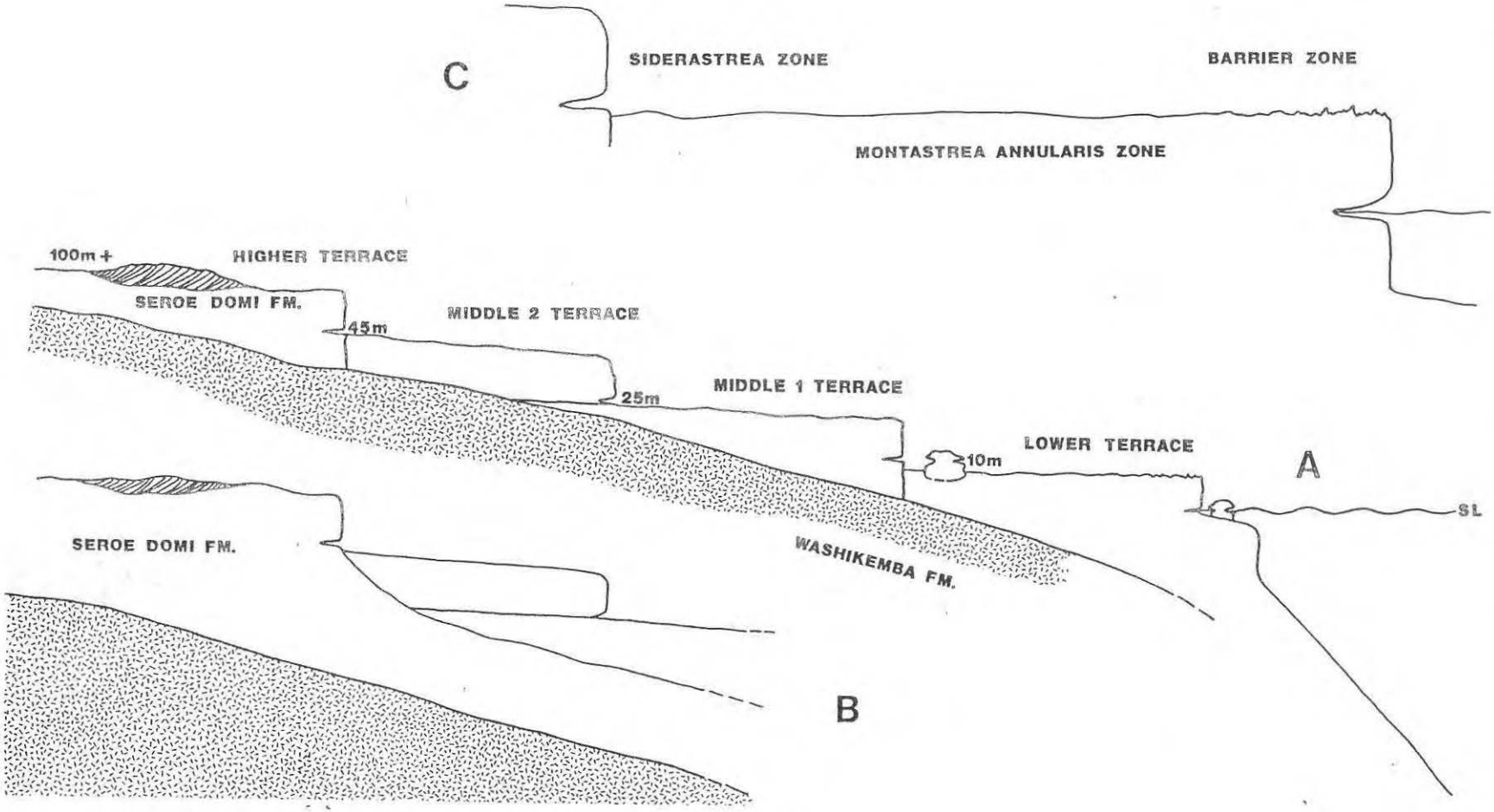
PLEISTOCENE REEF AND EROSIONAL TERRACES

Limestone terraces in the southern Netherlands Antilles are grouped into accumulation terraces and erosional terraces. From the oldest to the youngest, these terraces are:

1) Highest Terrace
2) Higher Terrace
3) Middle 1 Terrace
4) Middle 2 Terrace
5) Lower Terrace

Higher Terrace

In Bonaire the Highest Terrace is missing (eroded). The Higher Terrace outcrops at the highest points on Bonaire. It is an erosional terrace, with a steep scarp facing the sea produced by coastal erosion during deposition of the Middle Terrace (see Figure). The Higher Terrace is capped in places by eolianite (wind-blown) deposits comprising 2 types: 1) those with preserved foreset (sloping) lamination, and 2) those with horizontal lamination. The reef deposits in this terrace have a low siliciclastic (quartz and clay) content. They are best developed and preserved along the higher parts of the windward side of the



PROFILE THROUGH THE REEF TERRACES, BONAIRE

island, and have a high point generally at 50 to 80 meters elevation with a knickpoint (wave notch) at about 70 meters. Above the knickpoint, the terrace comprises lagoonal deposits with common Siderastrea and in situ bivalves. Below, the rocks represent a forereef facies with preserved in situ Acropora palmata and scattered A. cervicornis. At the seaward cliff edge of the Higher Terrace is a preserved wave notch. This notch developed in a period of static relative sea level during deposition of the Middle Terrace.

Middle Terrace

The Middle Terrace consists of 2 distinct subdivisions referred to as Middle Terrace 1 (older, lower elevation) and Middle Terrace 2 (younger, higher elevation). The Middle Terrace 2 limestones were deposited on and above Middle Terrace 1 limestones against the seaward edge of the Higher Terrace (see Figure).

The Middle Terrace 2 generally is the widest; its average width is 300-500 meters, but it may reach several kilometers (De Buisonje, 1974). The top of this terrace (erosional plane) dips toward the sea from an elevation of 45 meters where it meets the older Higher Terrace, to 25 meters elevation at its seaward leading edge. The exposed Middle Terrace 1 is narrower than Terrace 2, and reaches a width of 400 meters. At the seaward edge a cliff commonly is developed; this was formed by coastal erosion during deposition of the Lower Terrace (see below, and accompanying Figure). In some places where Terrace 2 rests on Terrace 1 this cliff comprises both Middle Terrace 1 and Terrace 2 limestones; this represents extreme landward erosion of the coastal cliff during deposition of the Lower Terrace (De Buisonje, 1974).

De Buisonje (1974) presents a 3-part scheme for deposition of the Middle Terrace limestones:

1) Transgressive Stage - deposition of lagoonal carbonates (limestones) over a zone about 400 meters wide, and the formation of Middle Terrace 1.

2) Sea Level Stability Stage - sediments deposited offshore as Middle Terrace 1 are not exposed, but wave action erodes the Higher Terrace and produces a planation surface and cliff. Some eolian dune (windblown) deposition takes place.

3) Final Transgressive Stage - rapid relative rise of sea level preserves the cliff at the seaward edge of the Higher Terrace; Middle Terrace 2 limestones are deposited offshore over Middle Terrace 1 deposits. There is deposition of carbonate dunes landward on the Higher Terrace.

Table . Fossils documented from Middle Terrace deposits (After De Buisonje, 1974).

MIDDLE TERRACE 2

Montastrea annularis
Siderastrea sp.
Strombus gigas
Homotrema rubrum
Coralline algae
Unidentified bivalves

MIDDLE TERRACE 1

Siderastrea Zone	Montastrea Annularis Zone
Siderastrea siderea	Montastrea annularis
Siderastrea radians	Montastrea cavernosa
Acropora cervicornis	Acropora palmata
Strombus gigas	Acropora cervicornis
Coralline algae	Diploria labyrinthiformis
	Diploria strigosa
	Diploria clivosa
	Meandrina meandrites
	Strombus gigas
	Coralline algae
	Colpophyllia natans

Where Middle Terrace 2 limestones directly overlie Middle Terrace 1 deposits, there is no clear erosional or depositional break, as the Terrace 1 sediments were not exposed to erosion; the two Middle Terraces are separated by a clear and distinct change in sediments. There is, however, a clear erosional disconformity at the base of Middle Terrace 2 where it overlies the Seroe Domi Higher Terrace or older rocks.

Middle Terrace 1 Sediments

A reef barrier was developed, but was not preserved (removed by coastal wave erosion during deposition of the Lower Terrace). The remaining limestones are zoned into a seaward Montastrea annularis zone (300 meters wide) and a landward Siderastrea zone (De Buisonje, 1974). The zonation is similar to that in the Lower Terrace (see below), but coral growth forms differ. M. annularis colonies show large scale columnar growth, often reaching a height of several meters. This is interpreted by De Buisonje (1974) as a response to deepening water and rapidly accumulating sediment during the Middle Terrace 1 transgression.

The Siderastrea zone is distinguished by its abundant colonies of Siderastrea and its landward position in the terrace relative to the Montastrea zone. Although in general this is a narrow zone, in Bonaire at Terra Corra, Lima, Wanapa, and Bacuna it reaches several kilometers in width; there the Siderastrea zone was deposited over a Middle Terrace 1 planation surface that had progressed far inland. The sediments deposited over this extensive planation surface are notably thinner than elsewhere (De Buisonje, 1974). Fossils of Strombus gigas (conch) are very common in some parts of the Siderastrea zone (eg: at Wanapa to Bacuna); where this occurs, coral fossils are rare. De Buisonje (1974) interprets this environment to have been similar to that existing in the modern Lac Lagoon.

Middle Terrace 2 Sediments

These deposits are clastic carbonates (erosional deposits derived from limestones and skeletons) with variable amounts of siliciclastic (quartz and clay) material. The siliciclastic content reflects the composition of nearby older rocks that were being eroded during deposition of the Middle Terrace 2. Siliclastic sediments occur as silt- to cobble-size clasts, often rounded to well rounded; in some areas they occur in thin conglomerate beds within the Terrace 2 limestones. Several origins for these conglomerate beds are possible. They may, for example, represent lag or storm deposits of size- and density-sorted material, or sudden deposition of terrestrial material offshore from roois (dry washes) during flash floods accompanying severe rainstorms.

In some areas, the Terrace 2 limestones resemble Terrace 1 limestones; in general, however, there is little similarity between the two. In Middle Terrace 2, corals are only rarely found in growth position, and the limestones have an overall poorly sorted, unbedded and

unzoned, almost chaotic character. Coral colonies often are found fragmented and abraded. Coarse calcarenite commonly fills primary shelter voids between overturned corals in areas where deposition was close to the seaward cliff of the Higher Terrace (De Buisonje, 1974). In other areas, calcarenite (lime sand) may occur in extensive irregular beds where the limestones are not bounded on the landward side by Higher Terrace deposits - De Buisonje (1974) interprets these as reef-derived sands.

Eolianites at Seroe Largo, and between Montagne and Columbia, are associated with Middle Terrace 2. The eolianites were deposited as dunes with preserved steep westerly-dipping foresets (30^{o}); De Buisonje (1974) speculates that the steep foresets may indicate little stabilizing vegetation cover, and therefore an arid or semi-arid climate.

Conditions during deposition of Middle Terrace 1 and Terrace 2 differed dramatically. Terrace 1 sediment accumulated in a normal reef environment similar to those developed during deposition of the Lower Terrace and some of the modern reefs. Middle terrace 2 deposits reflect shallow water, wave surge, and strong currents; the environment was generally strongly agitated.

Lower Terrace

The Lower Terrace is the youngest of the elevated limestone terraces on Bonaire. Carbon14 radiometric age dates (on aragonite from conchs of Strombus gigas) give an age of 30,000 to 40,000 yrs. B.P. for the lower part of the terrace currently above water (De Buisonje, 1974). Molengraff (1929) and De Buisonje (1974) mention the occurrence of Pre-Ceramic Indian rubbish and artifacts in uppermost Lower Terrace lagoonal limestones. These are dated archeologically at 3000 to 7000 B.P. (Heekeren, 1963; De Buisonje, 1974). If this age for the uppermost Lower Terrace is correct (which seems likely), it has important implications for the maximum age of the Holocene reef around Bonaire. However, Focke (1978) has indicated as much as 16 meters of Holocene reef accumulation at Bullenbaai Curacao, and about 14 meters at the Solar Salt Works on southwestern Bonaire. An age date (C^{14}) on a sample 10 meters inside the reef (22 meters below present sea level) was about 6010 yrs. B.P. (Focke, 1978). Extrapolations by Focke (1978) give an estimate of 10,000 to 11,000 yrs B.P. for the oldest post-Lower Terrace accumulation in these areas. An age of 3000 to 7000 yrs. B.P., therefore, for the top of the Lower Terrace based on archeological dates seems very improbable.

Lower Terrace deposits fringe the entire island of Bonaire and Klein Bonaire (Klein Bonaire also has Middle Terrace deposits). The width of the terrace varies dramatically from several hundred meters to several kilometers in the south of the island. The top of the terrace is planed flat, with the elevation of the edge of the planation surface varying from about 1 meter (south Bonaire) to 15 m above present sea level; in general the planation surface is 4 to 15 m above sea level (De Buisonje, 1974). Almost everywhere on Bonaire the Lower Terrace faces the sea as a vertical cliff (the area around the Pekelmeer at the south

of the island is anomalous in this respect). An active wave notch is developed in the Lower Terrace cliff at present sea level; below sea level the terrace continues to slope seaward for a few meters to 100 meters or more. Almost everywhere the submerged Lower Terrace is covered by Holocene reef deposits, but north of Bachelor's Beach (southwestern coast) the submarine planation surface is exposed at the bottom or is covered by only a few centimeters of sand. Along the west coast the submerged terrace surface slopes at a few degrees seaward to a depth of 10 to 12 meters where it drops at an angle of 20^{o} to 50^{o}. Between Bonaire and Klein Bonaire the bottom levels out at about 35 m depth but continues to slope seaward at about 5^{o}. This slope continues to at least 76 m depth (verified by SCUBA diving). Throughout the 35 to 76 m depth interval on the platform no terrace limestones are visible. They are covered by medium sand to fine mud with scattered small coral-sponge bioherms at about 50 m. Well rounded short sticks of A. cervicornis are scattered about on the surface and are buried in the sediment. At about 55 m depth at one location north of the Hotel Bonaire, conical piles of well rounded sticks and algal nodules up to 0.5 m high and 1 meter in diameter were found; their origin is unknown, but the common scattered sticks of A. cervicornis on the plateau at this depth may be the remnants of fields of living A. cervicornis that were alive at a low sea level stand during the last eustatic sea level rise. Similar fields of A. cervicornis grow on the coastal submarine terrace to about 3 to 10 m depth today along much of the west side of Bonaire.

At a few locations along the west coat the Lower Terrace limestones outcrop below a depth of 10 m. At Cliff (north of the Hotel Bonaire), for example, the Lower Terrace is exposed as a vertical cliff from 10 to 18 m depth. This represents a submerged coastal cliff (subaerial karst is still visible beneath a very thin cover of coralline algae on much of the wall). A 0.5 m high indentation of the wall at the bottom of the wall near the center of the exposure may be a preserved wave notch.

Subaerial karst is also preserved on the submarine planation surface where it is exposed near Bachelor's Beach at 1 to 3 meters depth. The karst consists of the lower parts of eroded kamenitzas, narrow solution-widened joints, an undulatory surface, and in some areas preserved small scale pitting. This karst probably formed during the last low sea level stand, but its presence suggests that the 0 to 12 m submerged erosion surface on the Lower Terrace could not have been produced by planation during the last sea level rise or more recently by Holocene coastal erosion. It must pre-date the final stages of the last eustatic sea level rise; this planation surface may represent a previous high water stage during which planation occurred at about present sea level, with a subsequent drop perhaps to the level of the submerged wall (about -20 meters) during which karstification took place. Eustatic sea level rise to the present level must then have occurred quickly in order to preserve the karst on the submerged Lower Terrace planation surface and on the face of the submerged cliff.

Preserved Wave Notches

Where the Lower Terrace meets the vertical cliff face at the seaward edge of the Middle 1 Terrace a deep notch is preserved in the Middle Terrace at about 10 meters above present sea level. The notch is very narrow and very deep, suggesting that it is a solution notch rather than a wave notch such as the one currently forming at sea level around the island. The presence of preserved Lithophaga borings (bivalves that bore into rock) in the cliff face at this level at several locations (eg: near Hato) demonstrates that the solution notches are marine (see also: De Buisonje, 1974); they therefore represent quiet water and narrow tidal ranges during at least part of Lower Terrace deposition. These conditions could have resulted from the presence of a seaward barrier that produced lagoonal conditions or a different wind pattern from that present today: the solution notches are developed on both the present leeward and windward sides of the island.

Zonation

Lower Terrace limestones are subdivided into 3 zones (Fig. 2C):

1) Barrier zone
2) Montastrea annularis zone
3) Siderastrea zone

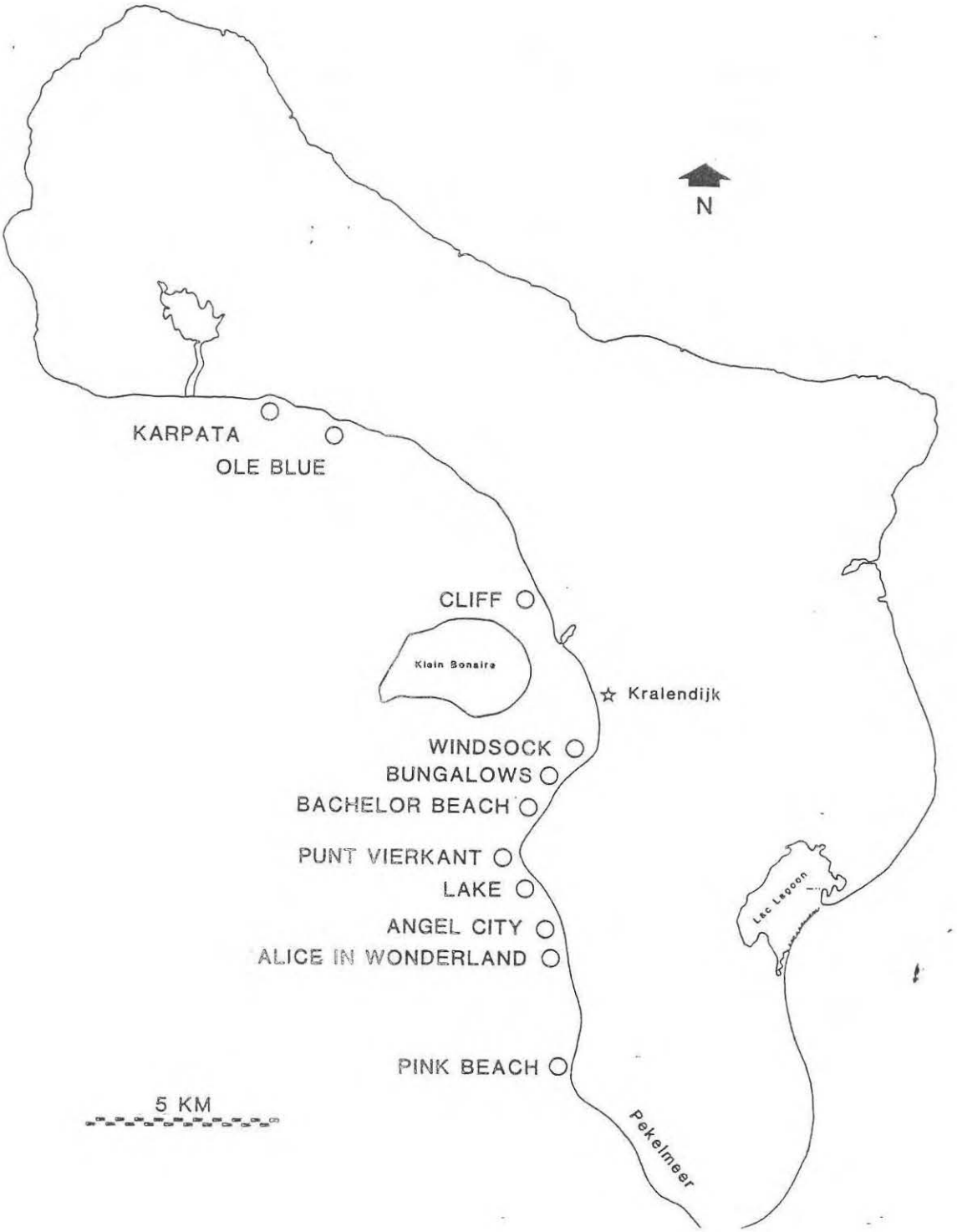
The Barrier zone is about 10 meters wide at present. The original width is unknown. It represents the offshore reef during deposition of Lower Terrace sediments, and comprises a framework of coralline algae, Acropora palmata, Diploria, and Meandrina.

The Montastrea annularis zone is a 400 meter wide complex of in situ very large colonies of M. annularis, large patches of Acropora cervicornis, and A. palmata calcirudite. The calcirudite in this zone often shows seaward-dipping imbrication of boulders and cobbles of A. palmata (De Buisonje, 1974). Sticks of broken A. cervicornis show no preferred orientation; De Buisonje (1974) uses such evidence to interpret this zone as lagoonal in character, with an absence of strong unidirectional currents. The shallow living reef on the west coast of the island shows similar patches of broken A. cervicornis sticks even near wave base; the sticks are unoriented largely due to binding by sponges and algae.

Furthest landward is the Siderastrea zone; it may reach several hundred meters in width. De Buisonje (1974) interprets quiet water conditions for this zone similar to the M. annularis zone. It differs from the M. annularis zone by the dominance of Siderastrea siderea and S. radians and common bivalves and gastropods (eg: Strombus).

On the windward side of Bonaire the latest stage in the development of the Lower Terrace Siderastrea zone consists of extensive beachrock deposits. These accumulated seaward over the Siderastrea zone sediments and eventually over the M. annularis zone (De Buisonje, 1974). The beachrock deposits are thin (maximum 1 meter) and are finely laminated with the laminae dipping seaward at a maximum of 5°. Lower

Terrace beachrock represents a marine regression, but it is not developed on the leeward side of the island. Deposition of the beachrock probably occurred rapidly: they become cemented in only a few years or decades today.



AREAS REFERRED TO IN THE TEXT

CORAL REEFS

General Structure

Focke (1978) studied an excavation in the modern reef off the Solar Salt Works on the southwest coast of the island and found that modern reef accumulation has been at least 16 m, and that the reef is developed upon 2 irregular fossil reef terraces. A similar reef thickness was found in an excavation in Curacao; carbon14 dates from the deepest parts of the reef excavation at Bullenbaai gave ages of 5485 and 6010 yrs. B.P. (Focke, 1978). In Curacao, 16 m inside the reef at 28 meters below present sea level, the framework contains a coral assemblage similar to that presently growing on the reef surface above. This suggests that water depth has remained more or less constant over that part of the reef for at least 6000 years.

Holocene reef accumulation is not as thick everywhere around Bonaire as in the area of the Solar Salt Works; for example, Pleistocene bedrock crops out through the modern reef at Cliff and at other localities. This probably is due to both the irregularity of the Holocene/Pleistocene unconformity and also to the steepness of the slope below 10 meters depth. The steepness of the reef slope appears to be an important control on the thickness of the reef deposits by controlling the density of accumulation of corals and other skeleton-secreting organisms. This is supported by Roos (1971) and Scatterday (1974) who note that the most prolific reef growth in the M. annularis zone (see below) is where the slope is most gentle. Even vertical walls have some reef growth, but it is usually sparse, with large areas of coralline algae-covered Pleistocene bedrock between corals. As the slope decreases, reef cover increases (at least in the deeper reef), until on the most gentle slopes as on the south coast of Aruba, coral cover is almost continuous (Roos, 1971).

The profile of the Holocene reef around much of Bonaire consists of a narrow seaward-sloping shelf from shore to 7-12 meters depth where there is a drop-off at which the bottom slope changes sharply. The reef slope in most areas is quite steep, and is in the range of 20^{o}-45^{o}. In the northwest and north of the island the reef slope continues to 70-80 meters depth at which there is a second drop-off to 80-90 meters; below the second drop-off is a sandy plain (Bak, 1975). Along parts of the south west coast and between Klein Bonaire and the main island is a sand plain beginning at 30-38 meters depth, and which is marked by a sharp decrease in slope from the reef. This plain slopes seaward at 5^{o}-15^{o} and is sand-covered over most of its extent.

Small sponge-coral bioherms were found at about 50 m depth at the Cliff locality on the sand plain. At 83 m depth between Klein Bonaire and Bonaire the plain comprises silt, mud, and sand, with scattered rounded coralline-algae-encrusted coral cobbles. Crinoids are found occasionally on the sand plain and appear to have moved out there from the reef above. Garden eels are also very common in some areas, and form fields between the base of the reef (at about 38 mdepth) and 50 m depth. Their burrows may reach an estimated density of 10 to 15 per m^2. Other

Table. Scleractinians and stony hydrozoans reported from the coral reefs of Bonaire (after Scatterday, 1974).

ORDER SCLERACTINIA
Suborder: ASTROCOENINIINA
Family: ASTROCOENIIDAE

Stephanocoenia michelini

Family POCILLOPORIDAE

Madracis decactis
Madracis mirabilis
Madracis pharensis

Family ACROPORIDAE

Acropora cervicornis
Acropora palmata
Acropora prolifera

Suborder FUNGIINA
Family AGARICIIDAE

Agaricia agaricites
Agaricia fragilis
Agaricia lamarcki
Agaricia tenuifolia
Leptoseris cuculata

Family SIDERASTREIDAE

Siderastrea radians
Siderastrea siderea

Family PORITIDAE

Porites astreoides
Porites branneri
Porites furcata
Porites porites

Suborder FAVIINA
Family FAVIIDAE

Favia fragum
Diploria clivosa
Diploria labyrinthiformis
Diploria strigosa
Manicina areolata
Colpophyllia natans
Montastrea annularis
Montastrea cavernosa
Solenastrea bournoni

Family RHIZANGIIDAE

Astrangia solitaria
Colangia immersa

Family MEANDRINIDAE

Meandrina meandrites
Dichocoenia stellaris
Dichocoenia stokesi
Dendrogyra cylindricus

Family MUSSIDAE

Mussa angulosa
Scolymia cubensis
Scolymia lacera
Scolymia cf wellsi
Isophyllia sinuosa
Isoplyllastrea rigida
Mycetophyllia aliciae
Mycetophyllia danaana
Mycetophyllia ferox
Mycetophyllia lamarckiana

Suborder CARYOPHYLLINA
Family CARYOPHYLLIIDAE

Eusmilia fastigiata
Desmophyllum riisei (?)

Family FLABELLIDAE

Gardineria minor

Suborder DENDROPHYLLIINA
Family DENDROPHYLLIIDAE

Tubastrea coccinea

ORDER MILLEPORINA

Millepora alcicornis (formae alcicornis, complanata, squarrosa)

ORDER STYLASTERINA

Stylaster roseus

fish are not common, although groups of goatfish and single rays and juvenile puffers have been seen; turtles, small sharks, and tarpon rarely are seen cruising at the boundary between the sand plain and the coral reef. There is also a diverse ichnofauna developed on the sand, comprising the traces of small hermit crabs, gastropods, fish markings, and others. These traces have not been studied in any detail to date. In addition, the surface is often cratered with ray pits, some of which may reach 1 meter across and 30 cm deep; they have been found as deep as 83 m and may be spaced as closely as 1 m apart; they may occur even deeper. In some areas these pits create a lunar-like landscape.

Algae play a minor sediment-binding and stabilizing role on the sand plain by forming thin, patchy, dark filamentous mats; they have been found as deep as 75 m north of the Aquahabitat Hotel. These mats may form large patches, which can cover up to several tens of m^2 each. The patches are separated by stretches of many meters of unbound sand. These mats do not bind sediment as firmly as most intertidal mats. They are easily disrupted by a diver moving over the bottom, and the floating pieces carry adhering grains with them when they are torn up. However, unlike intertidal algal mats, they do not appear to accumulate: excavations show no lamination, or any trace of buried mats. This may be due to the apparently slow sedimentation rates on the sand plain, and the absence of cyclic sedimentation, allowing dead parts of the mats to decay before they can be buried.

The M. annularis zone and the deeper Agaricia-M. cavernosa zone (see below) are characterized along much of Bonaire's leeward coast by small steeply-sloping sand gullies separating coral prominences; these vaguely resemble poorly developed examples of the sand channel and buttress system seen on other Caribbean reefs. Sediment and rubble moves down these gullies, and in some areas (eg: Karpata and south end of the island) the sediment is very unstable, generating impressive turbidity currents at the flip of a diver's foot. Bak (1975) mentions that gravity slides may occur along the slope over a width of up to 10 meters, cleaning the slope of organisms.

Reef Zones

The reef around Bonaire may be divided into the windward and leeward reef, of which the windward reef has not been studied extensively. The leeward reef on the protected west side of the island is well-zoned, and may be divided into the following:

1 - Shore Zone
2 - Nearshore Reef Zone
3 - Barren Zone
4 - Acropora cervicornis Zone
5 - Montastrea annularis Zone
6 - Agaricia-Montastrea cavernosa Zone

Shore Zone

This is a very narrow zone occurring immediately adjacent the shore in front of either a limestone cliff or a beach (usually cobbles). Filamentous algae and urchins are common, as are extensive fields of encrusting coralline algae. The zoanthid Palythoa mammillosa also is common, whereas corals are generally sparse, small, and encrusting. Encrusting Millepora may also occur in some areas.

This is a high stress environment, and is subject to constant wave activity and tidal influence; the substrate is usually rocky and may comprise coral boulders, loose blocks of Pleistocene limestone, or exposed Pleistocene bedrock. In some areas there is a shifting blanket of carbonate sand on the bottom.

Nearshore Reef Zone

Scatterday (1977) recognizes 3 types of shallow water nearshore reef on Bonaire:

1 - Acropora palmata reefs: present in turbulent water areas, generally on the windward coast.

2 - Montastrea annularis reefs: leeward coast quiet water reefs that are permanently under water.

3 - Diverse, periodically emerged reefs: exposed at very low tide or during periods of abnormally low water.

These shallow water reefs fringe the coast very closely, and along the leeward coast, types 2 and 3 (above) may be as close as 1 or 2 meters from shore. These reefs are not developed everywhere along the leeward coast, but as Scatterday (1977) notes, they occur sporadically, and in sum fringe about 50% of the coast. Where these reefs are absent, and seaward of where they are present, a more typical Caribbean reef assemblage and zonation is developed.

Diplora clivosa - Acropora palmata Zone

This zone may extend 20-30 meters from shore and reach a depth of 2-3 meters. No reef framework is developed. Acropora palmata may be common at the seaward edge, along with scattered A. prolifera and A. cervicornis. Also common is D. strigosa which is mixed with the slightly more abundant D. clivosa.

Barren Zone

In many areas a barren zone exists between the seaward edge of the shallow nearshore reef zone, or the D. clivosa zone and the Acropora cervicornis zone. There is no reef growth and very little coral growth. The bottom comprises broken plates and boulders of A. palmata, plates of transported Millepora, and broken and abraded sticks of A. cervicornis, with a thin cover of shifting sand. Scattered colonies of Porites astreoides, Madracis mirabilis, other corals, and Millepora may occur, along with some sponges (eg: Neofibularia). The shifting sand effectively prevents large scale colonization. The most diverse biota is cryptic, living in small shelter cavities under broken coral rubble.

Acropora cervicornis Zone

This zone comprises dense intergrowths of A. cervicornis with contributions from M. annularis, D. strigosa, D. labyrinthiformis, and other corals. Millepora, which is very common in the shallow reefs is often present as well, but most commonly in its encrusting form. The production of rubble and sand in this zone is high. Storms, bioerosion by endolithic (boring) algae and sponges, and other agents produce short broken sticks of A. cervicornis that commonly are bound into the substrate by encrusting sponges, Millepora, and complex entanglement (Scatterday, 1974). At the cliff locality infaunal and endolithic sponges have been found very firmly binding this rubble to a depth of 15 cm below the surface so effectively that a SCUBA diver has great difficulty breaking into it. The same type of sponge binding is also found in the Barren Zone. In this kind of bound substrate, sponges are covered by loose sand and silt and commonly are overgrown by thin felts of green filamentous algae that also trap and bind the sediment to the top of the sponges. Sponge oscula protrude through the algae-sediment cover with a density of about 12-15 per 100 cm2.

Montastrea annularis Zone

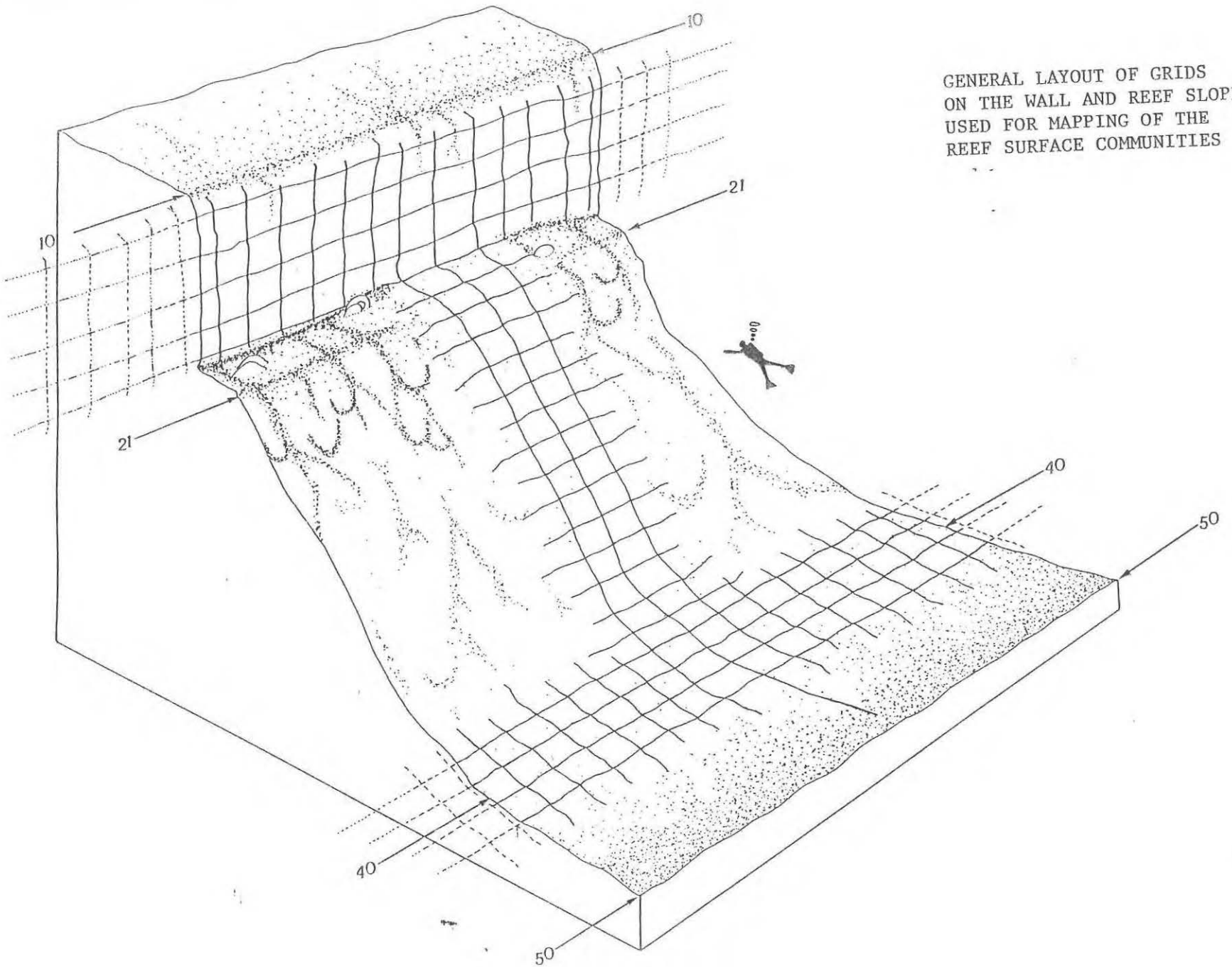
Seaward of the A. cervicornis zone, beginning at 7-12 meters depth and continuing to about 30-35 meters depth, is the Montastrea annularis zone. On the leeward side of Bonaire, 10-12 meters depth marks the edge of the reef slope, a pronounced change in slope of the bottom from only a few degrees above to as much as 45° or more below. This zone has the greatest coral diversity and usually the greatest density as well; it is dominated by large colonies of M. annularis. Also important are M. cavernosa, D. strigosa, D. labyrinthiformis, S. siderea, S. radians, and Agaricia spp. In Bonaire sediment may cover as much as 60% of this zone (see below).

Along the west-central and southwest coast of the island where the shallow subtidal shelf is very broad (to 10 m depth), the uppermost M. annularis zone and lowermost A. cervicornis zone is commonly dominated by large fields of gorgonians; these are so abundant in some areas that it seems reasonable to invoke an informal Gorgonian Zone between the A. cervicornis and M. annularis zones.

Agaricia - Montastrea cavernosa Zone

Below about 35 m depth, coral diversity and density decreases rapidly to the base of the second drop-off at 80-90 m depth where the deep sand plain begins. This zone is dominated by Agarica spp. and Montastrea cavernosa. Four species of Agaricia are present and one of Leptoseris (cuculata), along with scattered small colonies of Siderastrea siderea (even at 77 m depth at Karpata). Desmophyllum cf riisei, previously unreported from Bonaire was recovered from a growth framework cavity at 73 m depth at Karpata (D.R. Kobluk, unpublished).

With increasing depth in this zone, the corals become smaller and more widely scattered. At 76 m depth, colonies of M. cavernosa and S. siderea are only 10-20 cm in diameter; Agaricia is very flat, and almost encrusting. At these depths the substrate between corals (as much as 1 m apart) is either thinly dusted with silt and sand, or is encrusted by coralline algae.



GENERAL LAYOUT OF GRIDS ON THE WALL AND REEF SLOPE USED FOR MAPPING OF THE REEF SURFACE COMMUNITIES

REEF POPULATION CENSUS: PRELIMINARY RESULTS OF THE 1978 TO 1982 BONAIRE CORAL REEF MAPPING PROJECT

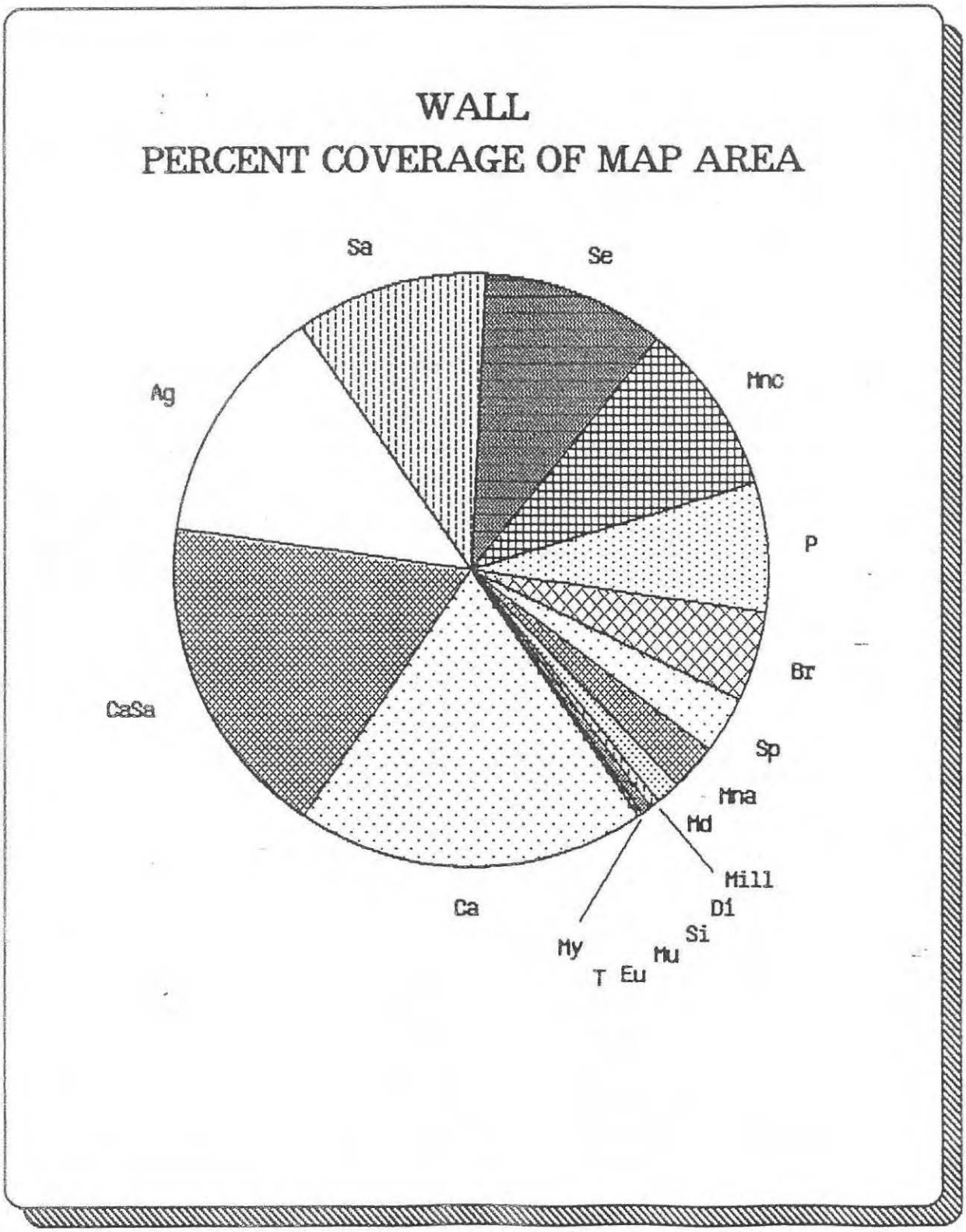
Over the 5 year period 1978 to 1982 a large scale reef mapping project was undertaken with the aim of producing an accurate map of a portion of the Bonaire coral reef slope near the Aquahabitat on the leeward side of the island. The project was designed to produce very detailed maps showing the distribution of sediment on the reef, the size, accurate shape, and area covered by each individual organism, the exact position of each organism relative to neighbours, etc. These maps have been completed and provide a huge database from which to study organism interaction and distribution on the reef. Some of the preliminary results of the ongoing analysis of these maps are presented below.

Methods

Large contiguous grids laid out in square meters were constructed over the reef at 4 sites that covered the entire reef surface within the limits of the grids; the grids spanned the depth range 10 to 40 m and covered a total of 226.4 m^2 of the reef. Three of the four grids were constructed over the normal reef slope and provided a continuous grid cover over the entire 10 to 40 m depth range from the slope break to the base of the reef at 40 m where it meets the sand-covered platform. One grid was built over the entire exposure of a vertical wall (the Cliff site) immediately adjacent to the other 3 grids. The top of the wall is at 10 m depth and its base is at 20 m depth (see accompanying Figures for a summary of the organism distribution on the wall). The data presented below is for the reef slope.

Over the span of the field work 110 SCUBA divers operating in successive teams of 8 to 10 divers logged a total of almost 4000 dives and 2300 hours underwater constructing the grids and mapping the reef. Each of the 4 grids were mapped by hand on site underwater on a square-meter-by-square meter basis by dividing each meter into 4 quadrats and very accurately drawing and identifying each colony, individual organism, patch of algae, patch of sediment, etc., and recording vagrant benthic organisms such as urchins, in accurate position and scale on a calibrated plexiglass slate. On land the portion of the map on each slate was traced and the individual square meter maps assembled into a mosaic; discrepancies in the fit of the mosaic were corrected from a photomosaic of the entire grid or by re-mapping selected areas. The assembled mosaic was traced onto acetate, photographed, and reduced to a manageable scale. The maps were divided into equal-sized sample blocks for processing. Measurements of organism size and distribution were carried out directly from the maps using a HiPad digitizer interfaced to an Apple III microcomputer.

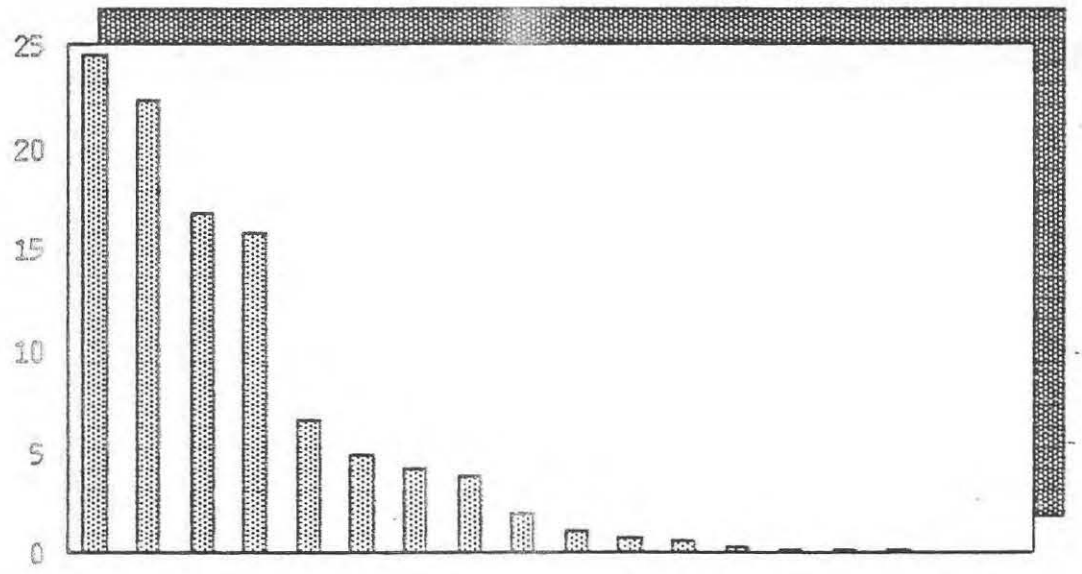
DATA FROM THE MAP OF THE VERTICAL WALL, BONAIRE



DATA FROM THE MAP OF THE VERTICAL WALL, BONAIRE

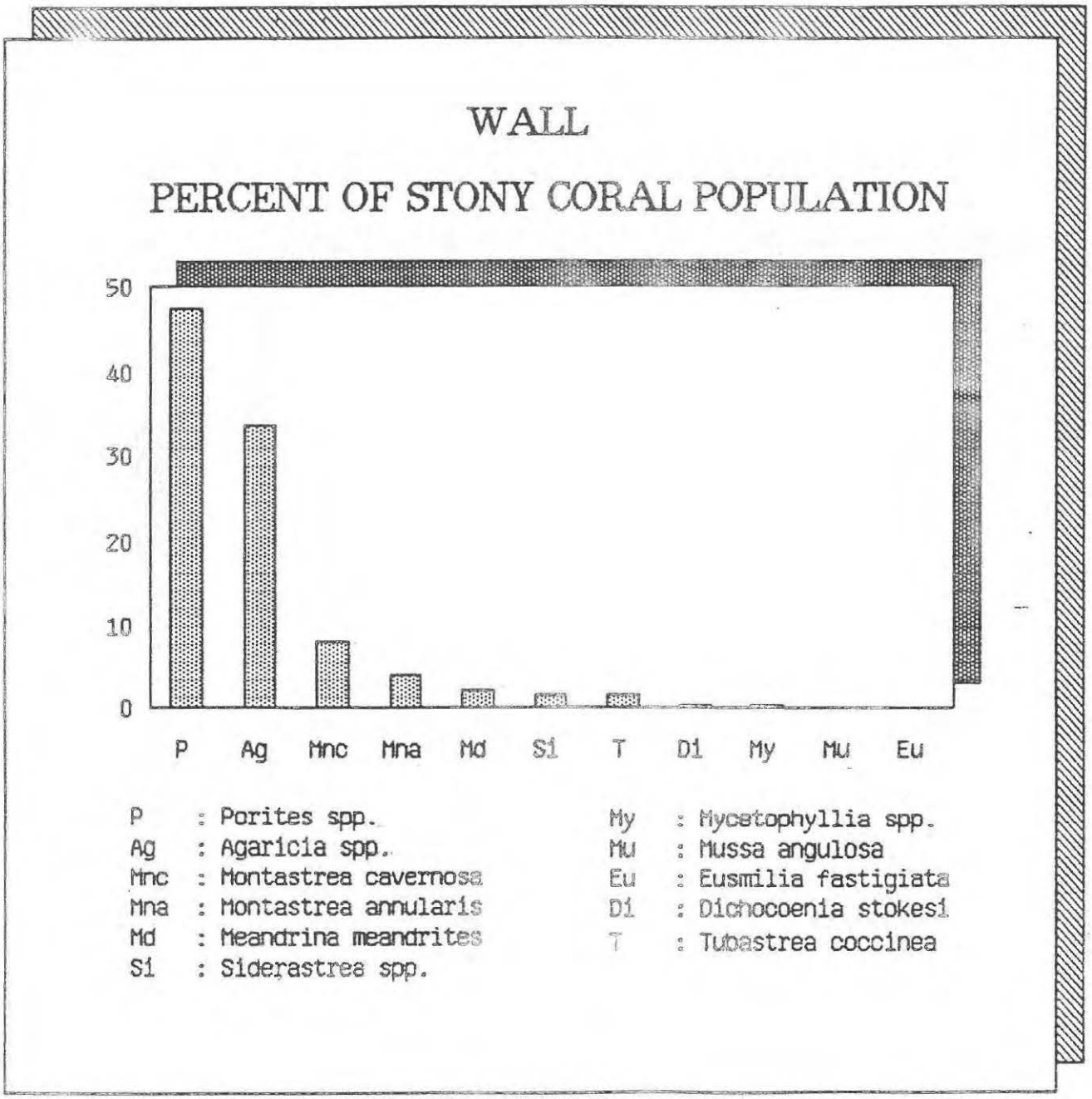
WALL

PERCENT OF POPULATION OF BENTHIC METAZOA

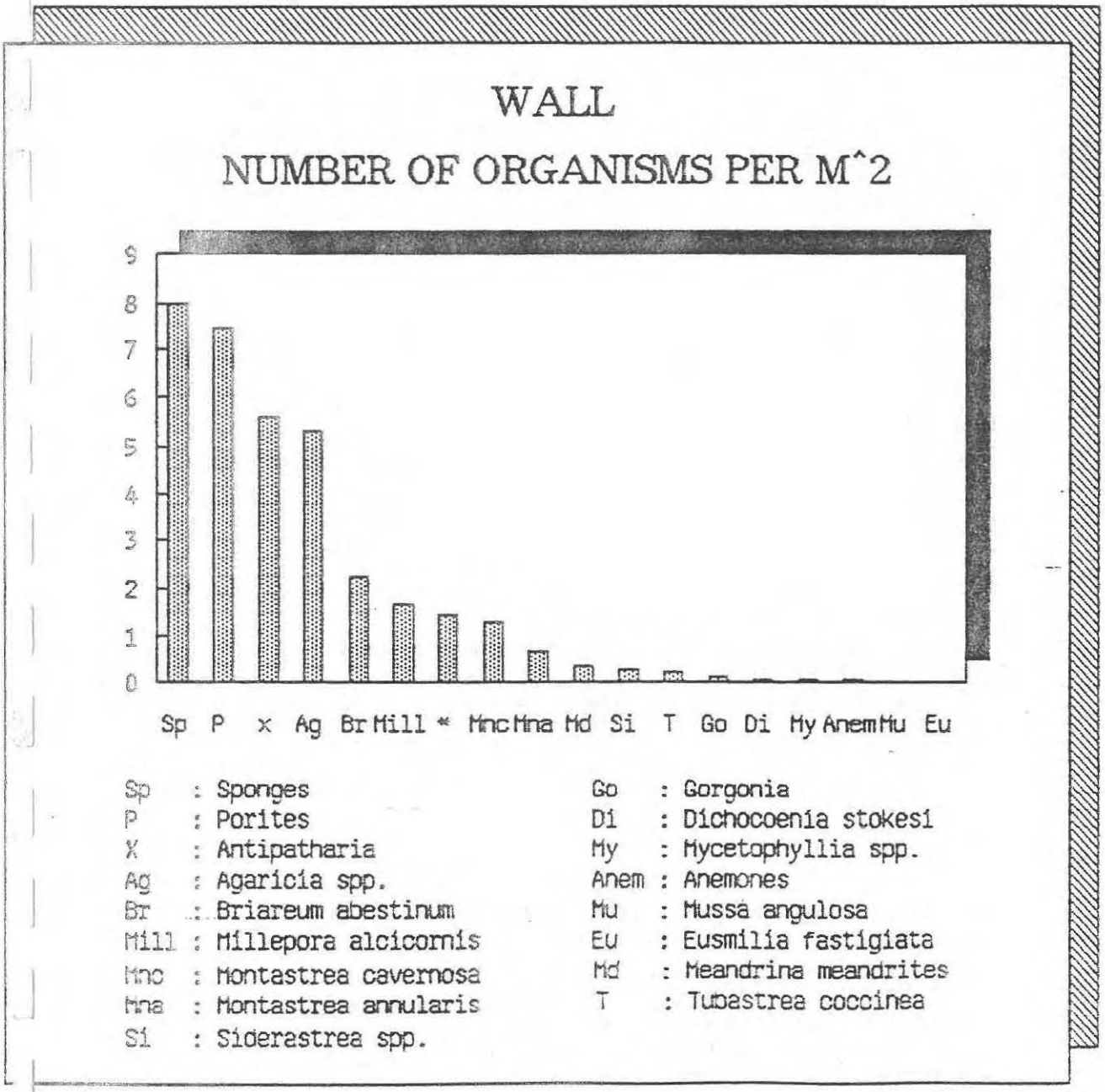


Sp : Sponge
P : Porites spp.
X : Antipatharia
Ag : Agaricia spp.
Mill: Millepora alcicornis
* : Urchins
Mnc : Montastrea cavernosa
Mna : Montastrea annularis
Md : Meandrina meandrites
T : Tubastrea coccinea
Go : Gorgonia
Br : Briareum abestinum
Di : Dichocoenia stokesi
My : Mycetophyllia spp.
Anem : Anemones
Mu : Mussa angulosa
Eu : Eusmilia fastigiata
Si : Siderastrea spp.

DATA FROM THE MAP OF THE VERTICAL WALL, BONAIRE



DATA FROM THE MAP OF THE VERTICAL WALL, BONAIRE



Identification of Organisms Underwater

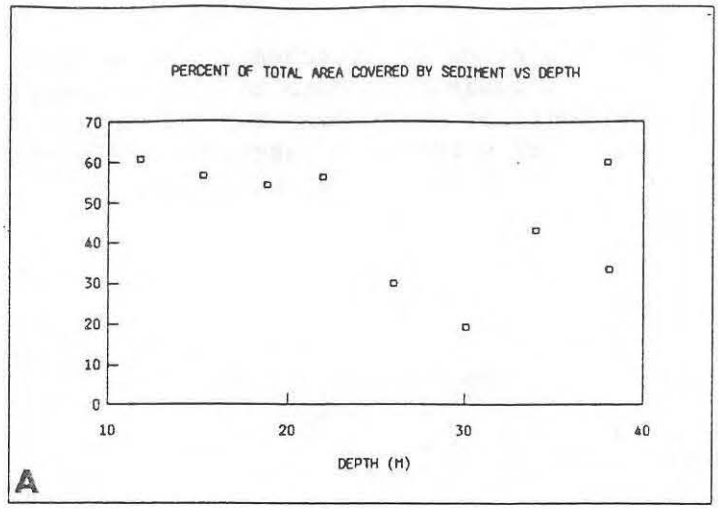
Accurate identification of many organisms can only be accomplished in the laboratory. In addition, the taxonomy of some groups at the species level, such as the corals, and even at the genus level in some cases, is still in a state of flux. This makes the precise identification of some organisms in situ underwater difficult to impossible. Because the nature of this mapping project involved the recording of in situ undisturbed populations distributed over a large area in a legally-protected coral reef, large numbers of specimens could not be removed for verification or identification at the surface. The identification procedures that were used therefore had to take all of these factors into balance. Before mapping each grid, the area was surveyed and firm identifications of the organisms present were made using representative samples and colour photographs. During mapping organisms were classified to the level that was most reliable underwater while still providing the most useful geological information. This resulted in the following list which contains all the organisms and groups of organisms found within the map grids and the level to which they were identified:

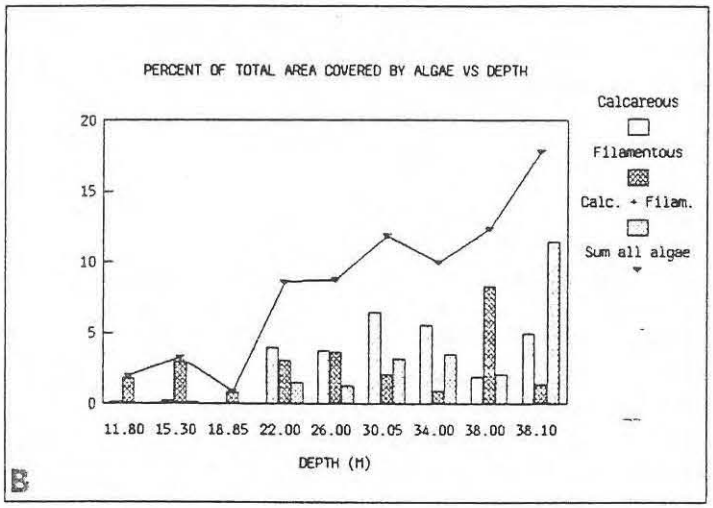
Sediment
Soft filamentous algae
Anemones
Crinoids
Millepora alcicornis
Gorgonia
Hydroids (macroscopic)
Worm tubes
Montastrea annularis
Agaricia spp.
Eusmilia fastigiata
Dichocoenia stokesi
Stephanocoenia michelini
Scolymia cubensis
Siderastrea spp.
Madracis spp.
Leptoseris cuculata
Calcareous algae
Mixed soft algae+calcareous algae
Urchins
Sponges
Antipatharia
Briareum abestinum (encrusting)
Zoanthids
Tubastrea coccinea
Montastrea cavernosa
Porites spp.
Diploria spp.
Favia fragum
Solenastrea bournoni
Mycetophyllia spp.
Meandrina meandrites
Colpophyllia natans
Mussa angulosa

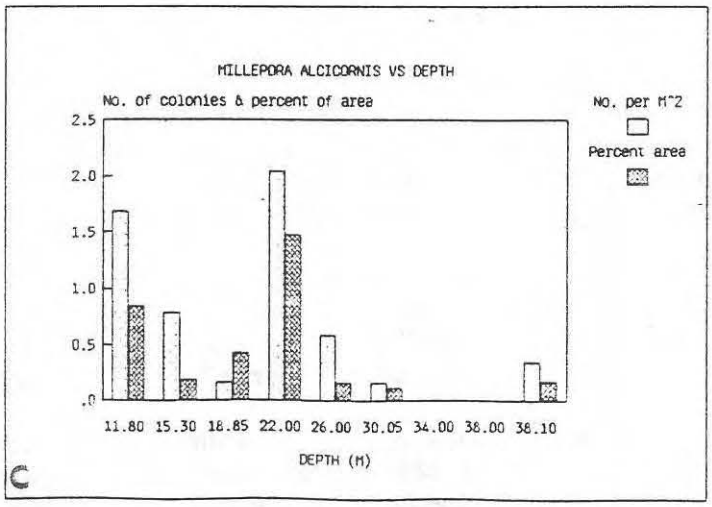
Processed Data

To date the data we have gathered from the maps includes the number of organisms and colonies, the surface area of the reef occupied by each organism or colony, the surface area covered by sediment, and the area covered by patchily-distributed groups of organisms such as fields of filamentous algae and calcareous algae. From these data have been calculated: 1) minimum and maximum size found in the population of each taxonomic group, 2) mean surface area of the reef covered by the population of each taxononomic group, 3) percent area occupied by each organism and by each taxonomic group, 4) the percent of the total coral population made up by each coral species or genus, 5) the percent of the

DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE







entire population of attached organisms made up by each group, 6) the number of organisms of each taxon per square meter of reef surface, 7) total numbers of individual vagrant organisms such as crinoids, anemones, and urchins, 8) skewness and standard deviation of the size distribution of each taxononic group.

Sediment

The percent of the surface of the reef covered by sediment is 50% to 60% over the depth range 10 m to 22 m; from 22 to 30 m depth sediment cover drops to as low as 20% (Fig. 3A) but below 30 m the percent cover rises steadily. Sediment is constantly moving down the slope of the reef by slow creep and in sudden pulses triggered by slope instability, moving fish, or other disturbances. The pronounced drop in the sediment cover at the reef surface in the 22 m to 30 m depth range can only be accounted for by movement of the sediment into cavities below the area of maximum coral coverage (see below), sediment piled-up in small screes can be seen at the openings of growth framework cavities and inside cavities where tunnels open into larger cavities.

Algae

Coralline algae reach their peak of abundance (7%) when measured as a percent of the reef surface area in the 30 to 40 m depth range; patches of filamentous algae are generally most important (up to 4% of reef cover) in the upper part of the reef slope (see Figure), except unaccountably at 38 m depth where they reach 7%. The percent of the reef covered by all algae, however, shows a steady increase with depth (se Figure), reaching 17% at about 38 m depth. There is no correlation between sediment cover and the abundance of algae.

Urchins, Anemones and Crinoids

Urchins are not abundant in the map area during the daytime (when the mapping was carried out); there is a relation between the mean number of urchins per m^2 and depth (see Figure). The decline in the abundance of urchins with depth is in direct contrast to the steady increase in the percent cover of algae, one of their food sources.

Anemones are less abundant than urchins, and reach a maximum abundance of 0.34 per m^2 (about 3 per 10 m^2). Their greatest abundance is in the shallowest water of the reef slope, and they exhibit a steady decline in the mean number per m^2 with increasing depth (see Figure).

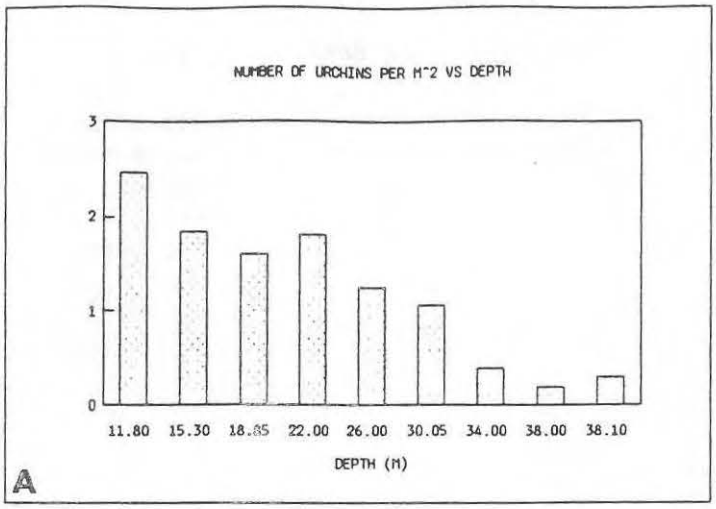
Crinoids show a peak of abundance at 22 m depth (see Figure). They were not found in the map area below 34 m depth, although they do occur in Bonaire much deeper than 34 m. Their apparent absence is due to their low population density (less than 1 per 10 m^2) below these depths.

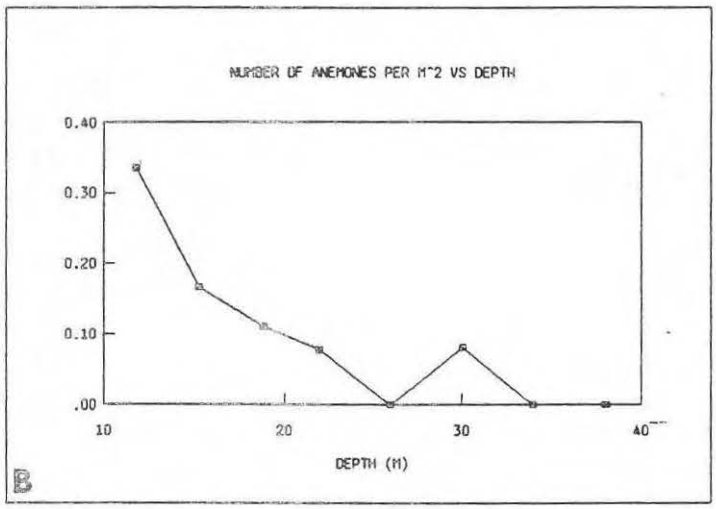
Table. Sponges reported from Bonaire (after Soest, 1981).

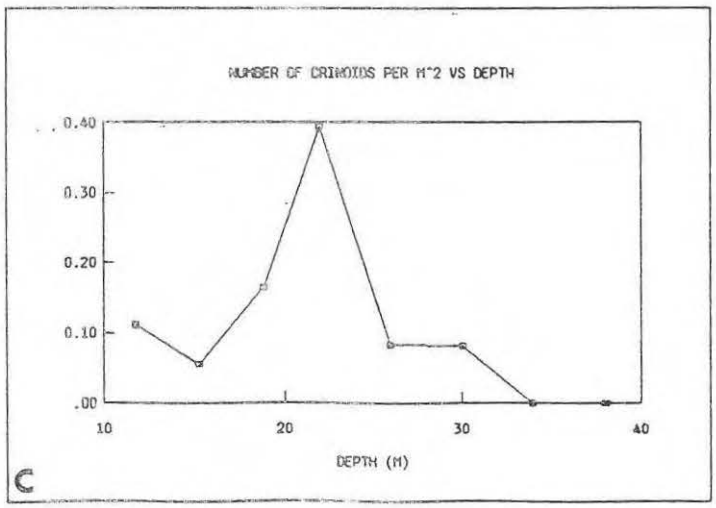
Goedia gibberosa	Jaspis udica
Cinachyra alloclada	Spheciospongia vesparia
Cliona caribboea	Cliona delitrix
Timea sp.	Tethya cf seychellensis
Terpios fugax	Aaptos bergmanni
Chondrilla nucula	Chondrosia collectrix
Ulosa ? ruetzleri	Ectyoplasia ferox
Hemiasterella sp.	Agelas dispar
Agelas clathrodes	Agelas conifera
Agelas screptum	Halkichondria cf magniconulosa
Mycale microsigmatosa	Mycale laxissima
Biemna tubulata	Didiscus flavus
Iotrochota birotulata	Desmapsamma anchorata
Neofibularia nolitangere	Ulosa funicularis
Lissodendoryx isodictyalis	Tedania ignis
Aplysina fistularis	Aplysina archeri
Aplysina fulva	Aplysina lacunosa
Verongula rigida	Pseudoceratina crassa
Rhaphidophlus schoenus	Rhaphidophlus minutus
Rhaphidophlus irodictyoides	Rhaphidophlus oxeotus
Rhaphidophlus raraechelae	Haliclona hogarthi
Haliclona molitba	Adocia implexiformis
Niphates erecta	Niphates amorpha
Callyspongia fallax	Callyspongia pallida
Callyspongia vaginalis	Callyspongia plicifera
Xetospongia sp.	Petrosia weinbergi
Spongia obliqua	Spongia tubulifera
Hyattella cf intestinalis	Hyrtios violacea
Ircinia felix	Ircinia campana

Merlia normani (first report: found by D.Kobluk, 20 m depth)

DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE







Sponges

Sponges are common on the reef in the mapping area, reaching a mean abundance of over 10 per m^2 at 22 m depth. Their abundance in relation to depth, however, is complex (see Figure): they show an increase in the mean number of sponges per m^2 from 10 m to 22 m depth, with a sudden drop to only 3 per m^2 at 26 m depth, followed by a steady rise in abundance to 38 m. Crinoids show a similar peak in abundance at 22 m depth, and as both groups are filter feeders, they may be reflecting an abundance of available food at about 22 m depth.

Antipatharia

No antipatharians were found in the map area at 10 m to 12 m depth. Below that depth the mean number of antipatharians per m^2 increases to a maximum of about 7 per m^2 at 38.1 m (see Figure). This is to be expected, as antipatharia are generally most abundant at depth on reefs.

Gorgonia

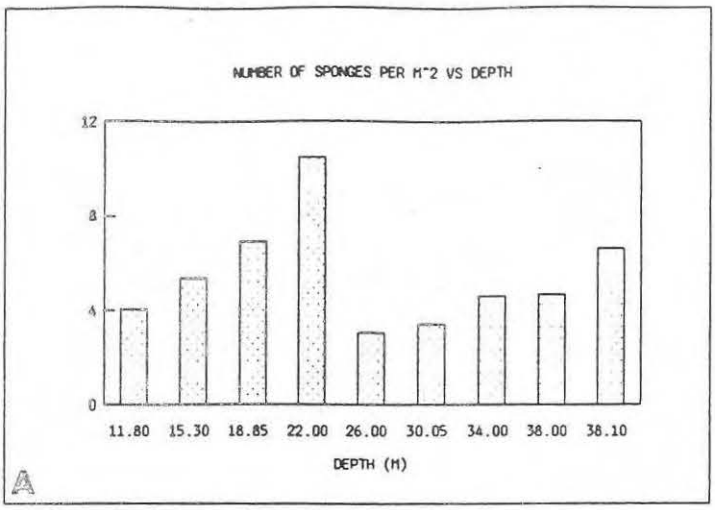
The abundance of gorgonians is greatest at the shallowest depths in the map area (mean of 6 per m^2) at 10 m to 12 m depth (see Figure). This drops sharply to 22 m depth and remains low (mean of 1 or less per m^2) to 38 m depth. The number of colonies of Briareum abestinum per m^2, an important encrusting gorgonian in the area, also shows a decrease with depth (see Figure). The importance of Briareum lies in its percent coverage of the reef surface: on the wall nearby it covers almost 5% of the total surface area.

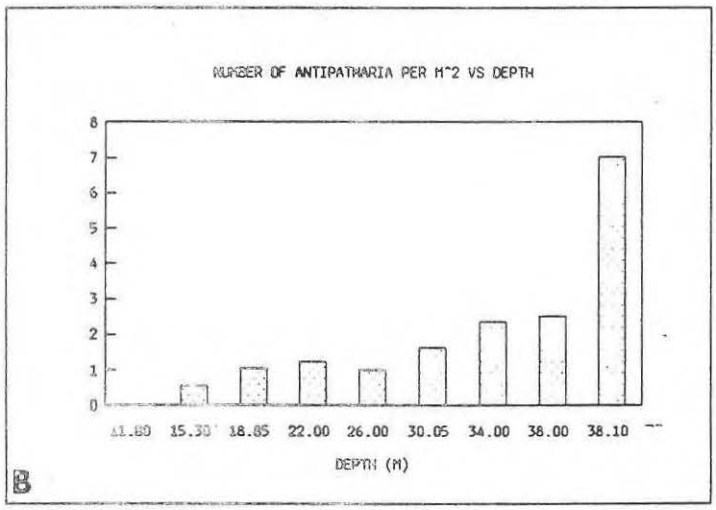
Millepora

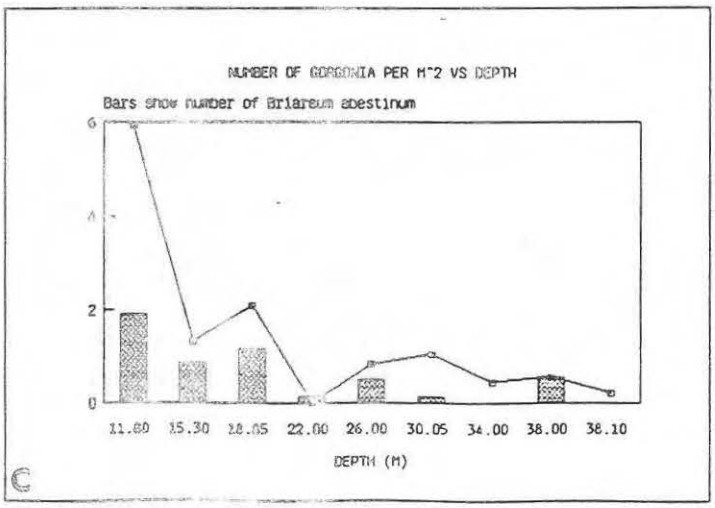
This skeletal hydrozoan is most prominant in Bonaire in the shallow water nearshore reefs and in the barren zone. However, on the reef slope it is also significant, having 2 peaks of abundance, one at 10 m to 12 m depth, and the other at 22 m (see Figure). Almost all of the Millepora at these depths is encrusting. It is found encrusting almost every type of substrate, including antipatharians. In the shallowest water of the map area it has a mean abundance of about 1.7 colonies per m^2 and covers just under 1% of the reef surface. At 22 m depth its abundance is about 2 colonies per m^2 covering an average of 1.5% of the reef.

Scleractinian Corals

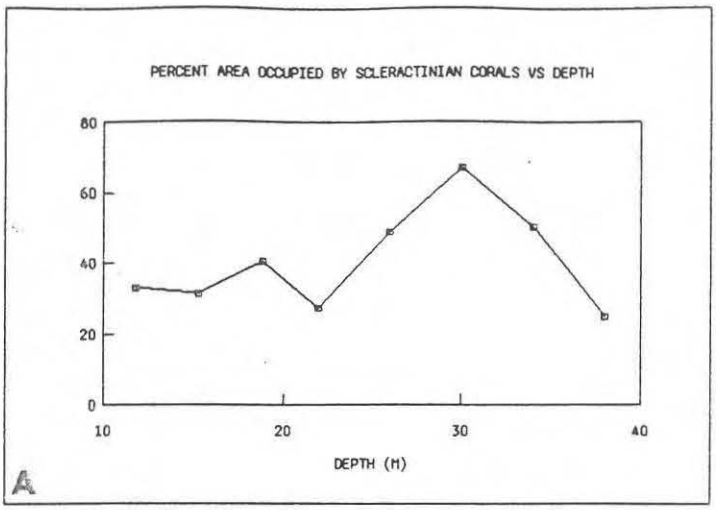
DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE

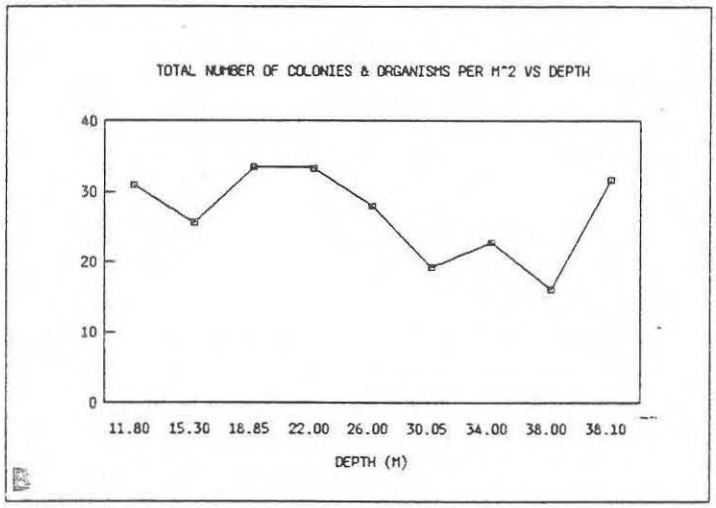


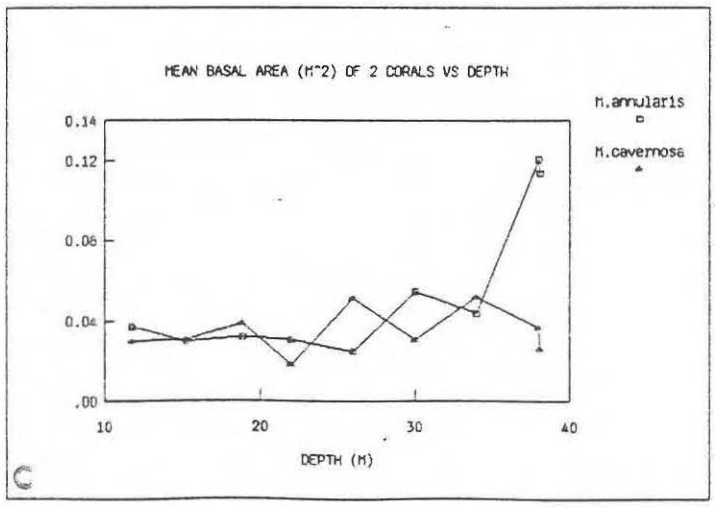




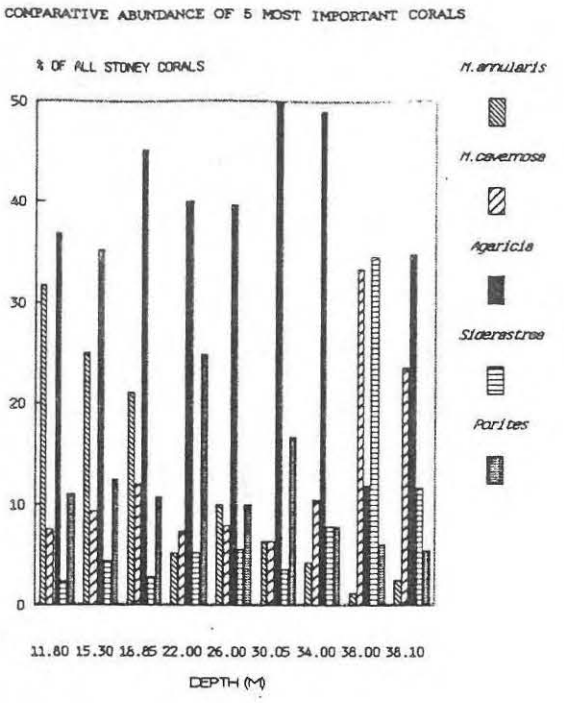
DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE

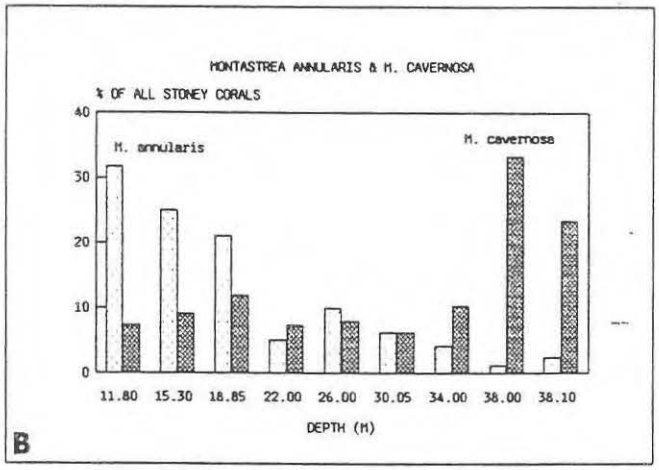


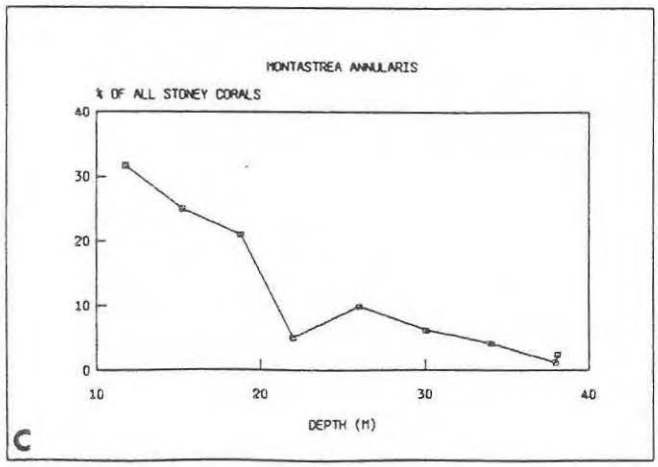




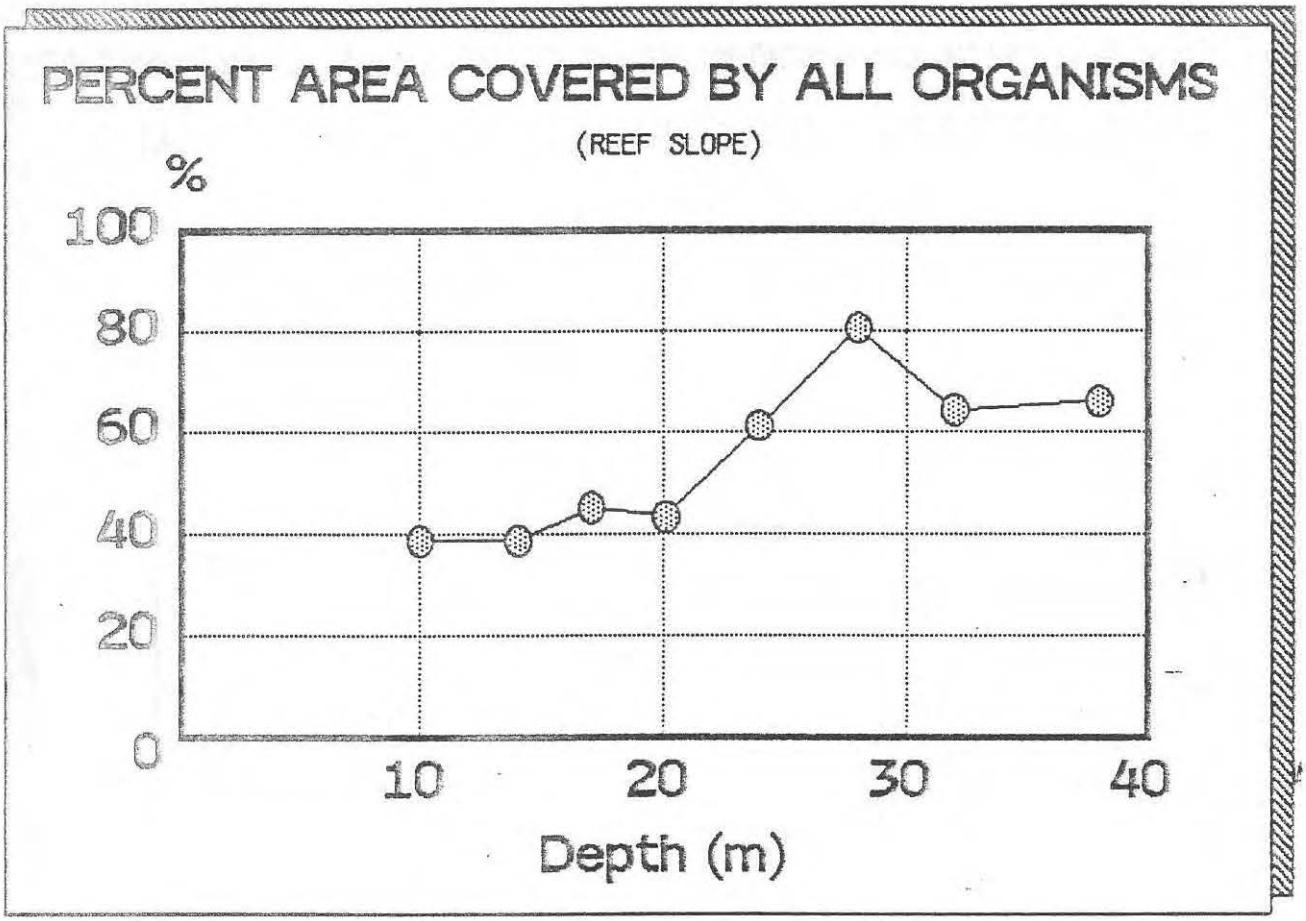
DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE



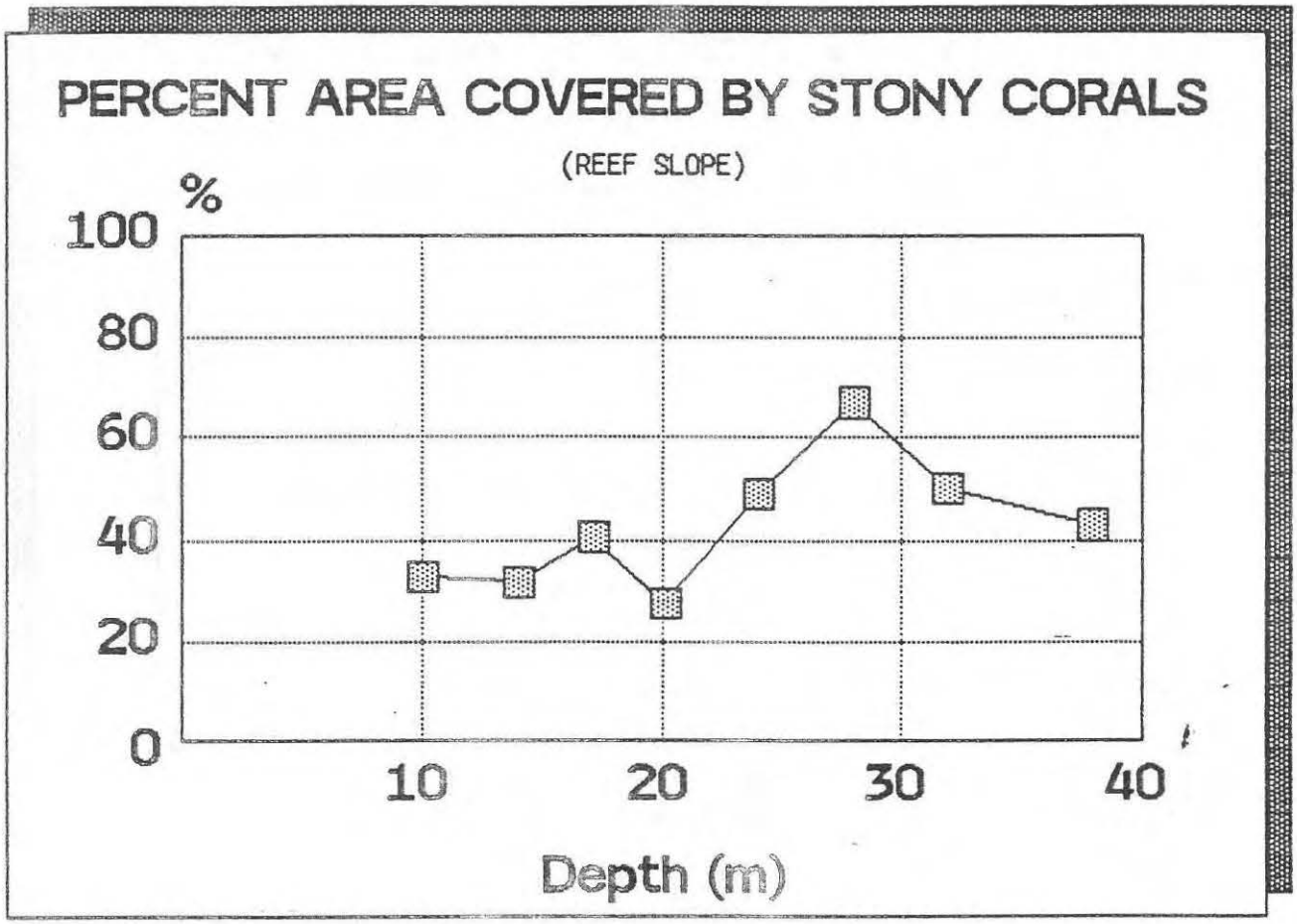




DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE



DATA FROM THE MAP OF THE REEF SLOPE, BONAIRE



Above 22 meters depth all scleractinian corals cover between 30% and 41% of the reef surface (see Figure). From 22 m to 30 m the percent areal coverage increases to a maximum of 68% of the reef. The lowest coverage is about 25% at both 22 m and 38 m depth. Scleractinian corals clearly dominate the reef in the 30 meter depth range (see Figure). The most abundant corals are Montastrea, Agaricia, Siderastrea, and Porites at all depths, with Agaricia being generally the most abundant. At 30 to 34 m depth Agaricia comprises about 50% of all corals (see Figure). The distribution of all corals over the depth range of the mapping with abundances (expressed as number of colonies per m^2) is shown in the accompanying figure.

Montastrea annularis and Montastrea cavernosa illustrate the behaviour of 2 species with depth in the map area. M. annularis shows a steady decline in importance with depth (see Figure), whereas M. cavernosa shows a coincident increase in importance (see Figure). Although at most depths one or other of these 2 corals is more important in terms of percent of the total population of scleractinian corals (a reflection of the number of colonies), their sizes do not differ significantly except at the very base of the reef slope where colonies of M. annularis are significantly larger (see Figure).

Total Organism Population

The mean total number of all colonial and solitary attached benthic organisms per m^2 is shown in the accompanying figure. This is a sum total of all coral colonies, antipatharians, sponges, etc. In the shallowest water of the reef slope the mean number is about 31 per m^2; the number is highest in the 18 m to 22 m depth range where it reaches 34 per m^2. Below 22 m depth there is a gradual decline in the mean number of organisms to a low of about 18 per m^2 at 38 m. Below 38 m depth to the edge of the sand plain at about 40 m the number of organisms reaches over 30 per m^2.

Considered alone, these data give the impression that the reef is comparatively depauperate between about 30 and 38 m depth. However, the percent area coverage by corals is highest in this depth range, indicating that while there are fewer colonies, they are larger and actually occupy more of the reef than at any other depth.

REEF CAVITIES

Cavities are a prominent feature of Bonairean reefs, and comprise 3 main types: 1) growth framework cavities, 2) shelter cavities, and 3) secondary solution cavities. In terms of size they may be grouped into 1) caves, 2) macrocavities, and 3) microcavities. Caves are considered those cavities large enough for a diver to enter, whereas macrocavities are those too small for a diver to enter yet larger than 10 cm in their maximum dimension; microcavities are defined as those with a maximum

dimension smaller than 10 cm. These size limits are arbitrary, but do provide a convenient terminology for discussing these cavities.

Caves are rare in the reefs of Bonaire, and are known at only a few localities along the north coast of the island (eg: off Playa Benge). For example, at Playa Benge in the National Park, caves at 5 tol5 m depth may reach several meters in width and tens of meters in depth; some form tunnels connecting at both ends to the reef surface.

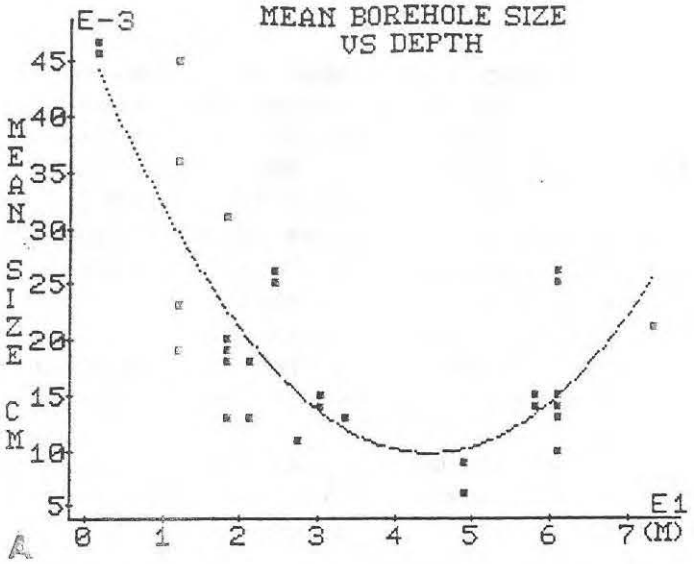
Macrocavities falling into each of the open, gloomy, and dark categories are known in Bonaire, but by far the most easily accessible are open cavities. Among these growth framework cavities are most prominent and abundant; they are small, and only rarely exceed 1 m^2 in volume. Small secondary subaerial solution cavities in submerged terrace limestone are important locally, but overall are not significant. Shelter cavities under overturned corals and other rubble are very common in the shallow reefs and barren zone, and in some areas on the reef slope. Larger shelter cavities under overturned blocks on the reef foreslope in many areas are common largely because of the inherent instability of parts of the reef and the ease with which corals and chunks of the reef move downslope and are overturned. In some areas (eg: Cliff site) very large pieces (over 1 meter across) of reef may be rocked back and forth by a diver with little effort, and may be dislodged and overturned accidentally in some cases unless care is exercised.

Cavity Structure

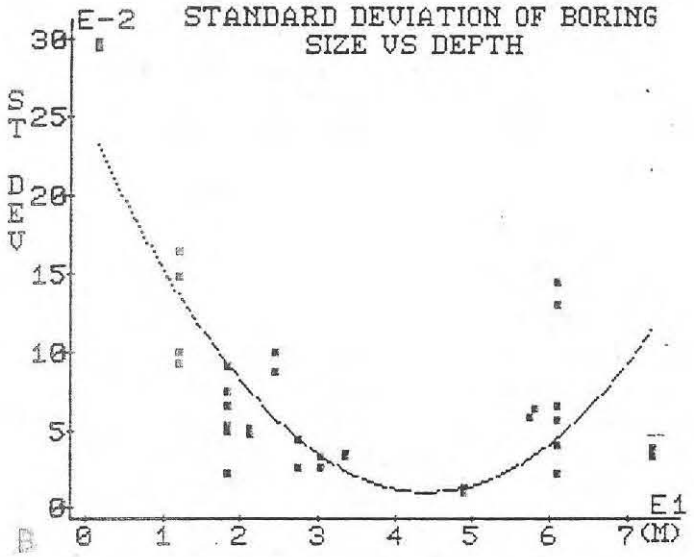
The growth framework macrocavities are of limited extent and consist of a roof, wall, and well-defined floor; the entrance is most commonly wide in relation to the size of the cavity (from about 50% to 100% of the width of the cavity interior). Most cavities have smaller peripheral openings which connect to the reef surface or to other cavities. The roof and walls of many cavities were found to be well cemented (thin section and SEM observations) and encrusted living organisms (see below). A U/Th radiometric age date of a sample of the back wall of a cavity at 20 meters depth at the Cliff site gave an age of 500 +— 100 yrs. B.P. The floor is almost invariably covered in sediment which may reach over 30 cm in depth (determined by probing). Cavity roofs comprise the underside of corals, often a single large colony; M. annularis and A. fragilis are the most common cavity roof corals.

Internal Bioerosion

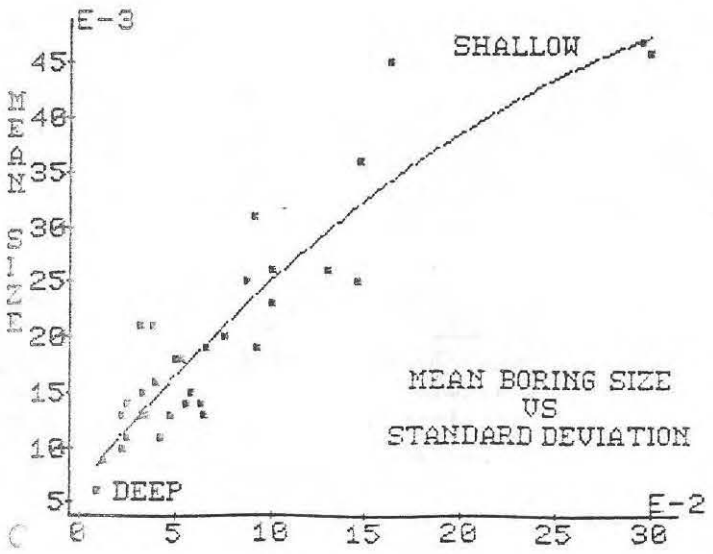
Along a transect from 1.5 to 33.5 m depth at the Cliff site Kobluk and Kozelj (1983) found a relationship between depth and macroborings in the walls of open growth framework cavities (see Figure). The macroborings are produced by diverse groups, including sponges, polychaetes, sipunculids, and bivalves; in the study all borings greater


MEAN BOREHOLE SIZE
VS DEPTH
E-3
MEAN SIZE CM
45
40
35
30
25
20
15
10
5
E1
0 1 2 3 4 5 6 7 (M)

A


STANDARD DEVIATION OF BORING
SIZE VS DEPTH
E-2
ST DEV
30
25
20
15
10
5
0
E1
0 1 2 3 4 5 6 7 (M)

B


E-3
MEAN SIZE
45
40
35
30
25
20
15
10
5
SHALLOW
DEEP
MEAN BORING SIZE
VS
STANDARD DEVIATION
E-2
0 5 10 15 20 25 30

C

than 300 microns in diameter were measured. A total of 7076 macroborings in 22 samples from 11 cavities were measured for cross-sectional area. The number of borings and the percent area bored in each sample (intensity of boring) each showed no relation to depth. However, the mean borehole size (measured as cross-sectional area) in the samples did show a decrease with increasing depth (correlation coefficient 0.82). The standard deviation of borehole sizes (cross-sectional area) in each sample shows a similar decrease with depth (correlation coefficient 0.95). The mean borehole size (area) and the standard deviation of borehole size show a close relation in which both decrease simultaneously with increasing depth (correlation coefficient 0.96).

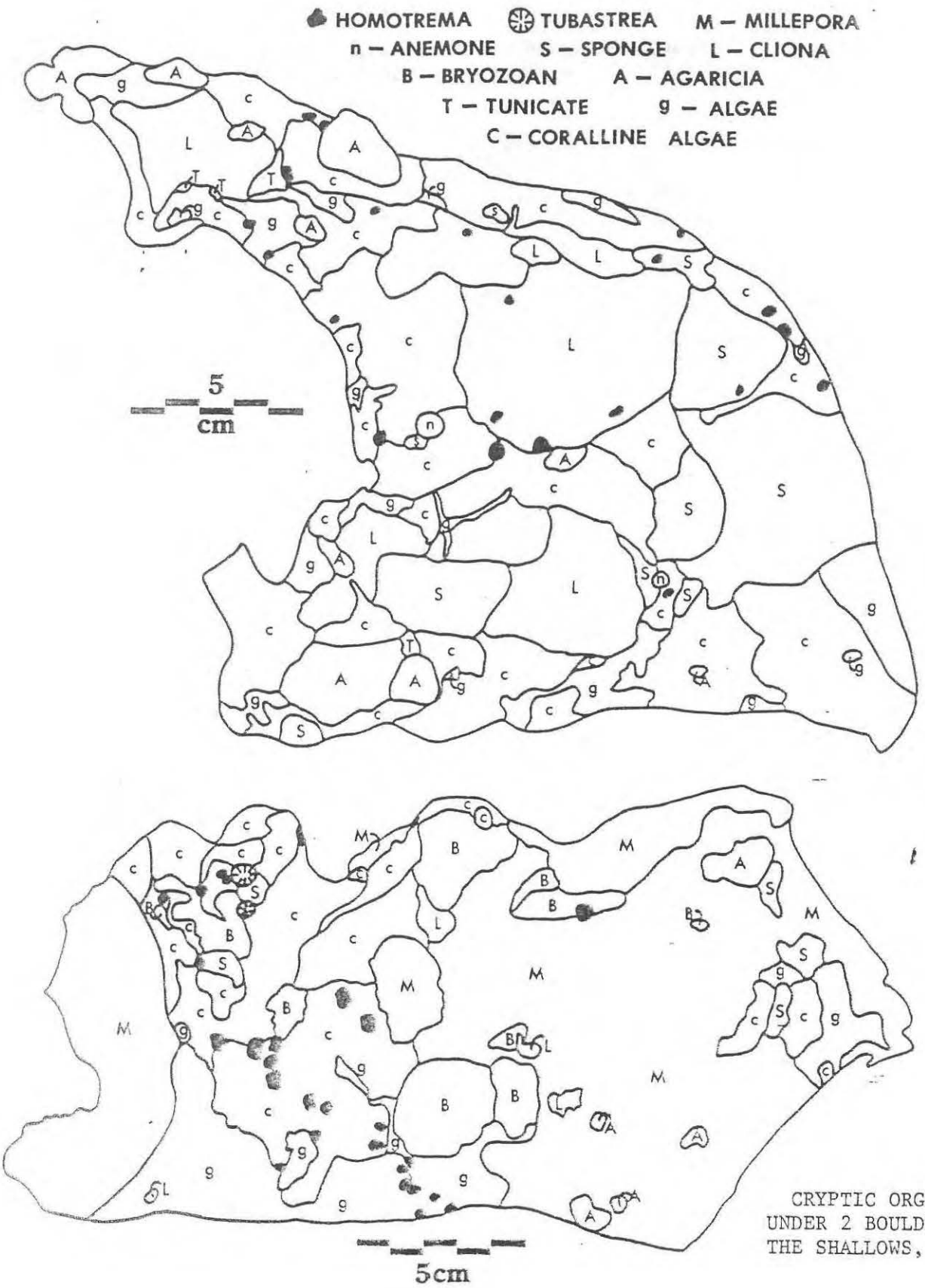
The factors controlling the relation of borehole size to depth in Bonaire are unknown, but to speculate, it may be due in part to changing dominance of endolithic species with depth. In the 1.5 to 33.5 m depth range large macroborers appear to become less important with depth; the size of boreholes becomes closer to the mean borehole size (cross-sectional area) with depth. This may be related to both decreasing size and decreasing diversity of macroborers in cavity walls, so that fewer different borers produce a smaller range of borehole sizes. Whether or not there is actually a decrease in diversity of macroborers in cavity walls with depth is not known, however.

Shelter Cavities

At all depths from the shore zone to at least 73 m on the front of the reef dislodged blocks of reef, overturned corals, and other rubble produce shelter cavities; they vary in size from only a few centimeters to almost 1 meter. The greatest density of shelter cavities along the west coast of the island is in the Nearshore Reef and Barren Zones where very commonly broken plates of *Millepora alcicornis* lie scattered about. At greater depths, particularly in the *Montastrea annularis* and *Agaricia-Montastrea cavernosa* Zones broken and transported *Agaricia* plates produce shelter cavities.

In shallow water (1 to 10 meters depth) where the shelter cavities have been studied (D. Kobluk, unpublished), the upper surfaces of *Millepora* plates (photo-positive surface) are covered by a dense mat of filamentous algae that traps (?) and binds sand-size material; some upper surfaces are encrusted by *Millepora* (see accompanying Figure). The undersides (photo-negative surface) house a diverse encrusting and attached biota comprising:

Homotrema rubrum
Tubastrea coccinea
Agaricia agaricites
Tunicates
Coralline algae
Serpulids
Millepora alcicornis
Sponges (encrusting)
Cliona sp. (endolithic)
Filamentous algae
Bryozoa (35 species)



CRYPTIC ORGANISMS
UNDER 2 BOULDERS FROM
THE SHALLOWS, BONAIRE

The accompanying figure shows 2 examples of cryptic biotas on the undersurfaces of Millepora plates from the Barren Zone at the Airport Beach locality.

Some shelter cavities are buried completely by sand up to 2 centimeters deep and still support a living encrusting biota comprising bryozoans, sponges, serpulids, and rare anemones. Apparently enough water circulates through the sand to keep the assemblage alive.

Mobile organisms are present even in very small shelter cavities in the Barren Zone, Juvenile fish, crabs, shrimp, bristle worms (Hermodice), small eels (Myrichthys acuminatus), small urchins, nemertean worms, and stomatopods were observed moving in-and-out through small openings above the sand, or were found after lifting plates (see Table).

Table. Vagrant organisms observed living in, or moving through, reef cavities in Bonaire (Observations 1978 to 1983).

VERTEBRATES

Myrichthys acuminatus	(Sharptail Eel)
Gymnothorax funebris	(Green Moray Eel)
Gymnothorax vicinus	(Purplemouth Moral Eel)
Gymnothorax moringa	(Spotted Moray Eel)
Scarus vetula	(Queen Parrotfish)
Sparisoma viride	(Stoplight Parrotfish)
Eupomacentrus partitus	(Bicolor Damselfish)
Holocanthus tricolor	(Rock Beauty)
Gramma loreto	(Fairy Basslet)
Ocyurus chrysurus	(Yellowtail Snapper)
Epinephelus cruentatum	(Graysby)
Epinephalus guttatus	(Red Hind)
Epinephalus fulvus	(Coney)
Epinephelus striatus	(Nassau Grouper)
Lactophrys sp.	(Trunkfish)
Equetus acuminatus	(Cubbyu)
Equetus lanceolatus	(Jacknife Drum)
Bodianus rufus	(Spanish Hogfish)
Canthigaster rostrata	(Pufferfish)
Diodon hystrix	(Porcupinefish)
Diodon holocanthus	(Balloonfish)
Haemulon chrysargyreum	(Smallmouth Grunt)
Coryphopterus glaucofraenum	(Bridled Goby)
Chromis cyanea	(Blue Chromis)
Scorpaena plumieri	(Scorpionfish)
Lutjanus apodus	(Schoolmaster)
Lutjanus griseus	(Grey Snapper)
Lactophrys triqueter	(Trunkfish)
Chaetodon capistratus	(Foureye Butterflyfish)
Muraena miliaris	(Goldentail Moray Eel)
Myripristis jacobus	(Blackbar Soldierfish)
Holocentrus ascensionis	(Longjaw Squirrelfish)
Flammeo marianus	(Longspine Squirrelfish)
Chorististium rubre	(Swissguard Basslet)
Rypticus saponaceus	(Soap Fish)
Pempheris schomburgki	(Copper Sweeper)
Priacanthus cruentatus	(Glasseye)
Apogon lachneri	(Whitestar Cardinalfish)
Abudefduf saxatilis	(Sergeant Major)
Clepticus parrai	(Creole Wrasse)

INVERTEBRATES

Ophiuroids	Holothurians
Diadema antillarum	Unidentified polychaetes
Shrimp	Stomatopods
Arrow crabs	Amphipods
Rock crabs	Panulirus
Bristle worms	Hermit crabs
Crinoids	Gastropods

FRAMEWORK CAVITY BIOTAS

Organisms inhabiting growth framework cavities in the 10 to 80 meter depth range are grouped into:

Endolithic - in the walls and roof
Encrusting - on the walls and roof
Attached - on the walls and roof
Infaunal - within sand on the floor
Vagrant - live in, or move through cavities

The endolithic organisms have not been studied in detail, but preliminary work shows that the biota comprises filamentous algae and fungi, bivalves, polychaetes, sipunculids, and sponges (Cliona, etc.). All skeletal material recovered from growth framework cavities over the 80 m depth range had been bored, often very intensively; this indicates that bioerosion in these cavities is important and ubiquitous (Kobluk and Kozelj, 1983).

Attached and encrusting organisms are very abundant in the cavities; they cover every surface, and in some cases their skeletons form crusts up to several centimeters thick. Of particular interest is the very diverse bryozoan assemblage that comprises 75 species over the 1.5 to 73 m depth range. This is the second most diverse Atlantic bryozoan assemblage known, after the Bermuda fauna (Kobluk, Cuffey, and Fonda, in preparation). The cryptic Bryozoa are summarized in the accompanying Table.

Microorganisms are ubiquitous on the walls and roof of framework cavities (Kobluk, 1981a). Loricate peritrichous ciliates, amoeboid testaceans, diatoms, filamentous algae and fungi, vorticellids, encrusting red algae, bacteria (filamentous, bacillus- and Microcyclus-types), very small polychaetes, Homotrema rubrum, and other foraminifers (Globorotalia, Eponides, Reophas, Rosalina, Cibicides, Cassidulina, Rotorbinella, Asterigina, among others) have been found in the 18 to 80 m depth range. The diatoms comprise a diverse flora (including pennate forms) that occurs both in cavity sediment, and on the walls and roof; they are currently under study by T. Sawa and D. Kobluk.

The deepest cavities in the 64 to 74 m depth range contain a diverse organism assemblage (Kobluk, 1981b). Calcareous red algae and green algae together with attached and encrusting sponges and dendritic hydrozoans dominate. Scleractinian corals (Agaricia sp., M. cavernosa, Desmophyllum riisei (?), and Solenastrea bournoni) are present though not common. More common are small ahermatypic corals, branching and encrusting bryozoans (43 species), and antipatharians. Sabellid and serpulid worm tubes occur in all cavities, as does encrusting Homotrema rubrum. Vagrant organisms are not common at these depths, but are

Table. List of cryptic bryozoan species occurring on the leeward side of Bonaire over the depth range 1.5 meters to 73.1 meters (From Kobluk, Cuffey, and Fonda, in preparation; identifications by R.J. Cuffey and S.S. Fonda). Species are listed in order of first occurrence (read from left to right with increasing depth).

Lichenopora radiata
Beania intermedia
Trematooecia turrita
Rhynchozoon rostratum
Steginoporella magnilabris
Trypostega venusta
Smittipora americana
Parellisina curvirostris
Diaperoecia floridana
Celleporaria albirostris
Parasmittina munita
Exechonella antillea
Hippopodina feegeensis
Scrupocellaria cornigera
Smittoidea cf marmorea
Microporella ciliata
Aimulosia uvulifera
Mastigophora pesanseris
Aeta anguina
Thalamoporella mayori
Scrupocellaria bertholetti
Hippoporidra aff. edax
Trematooecia pertusa
Tremogasterina rugosa
Schizomavella auriculata
Reginella floridana
Mastigophora porosa
Alderina irregularis
Cleidochasma contracta
Aeta ligulata
Acanthocella clypeata
Retevirgula tubulata
Microporella marsupiata
Floridina antiqua
Stephanocella rugosa
Acanthodesia arborescens
Chaperia galatea
Hippaliosina rostrigera
Smittina smittiella
Parellisina latirostris
Tremogasterina mucronata
Bugula cf avicularia
Trypostega venusta
Trematooecia tubulosa
Rhynchozoon ? aff. larreyi
Drepanophora tuberculata
Cleidochasma porcellana
Synnotum aegyptiacum
Bugula minima
Hippopodina irregularis
Onychocella sp.
Cranosina coronata
Phylactellipora collaris
Cribrilaria radiata
Stylopoma spongites
Trematooecia protecta
Thalamoporella distorta
Parasmittina spathulata
Reptadeonella violacea
Exechonella spinosa
Tremogasterina malleola
Rimulostoma signata
Crepidacantha longiseta
Crepidacantha poissonii
Retevirgula caraibbea
Bellulopora bellula
Scrupocellaria frondis
Hippothoa flagella
Membraniporella petasus
Antropora granulifera
Aimulosia floridana
Microporella pontifica
Petraliella bisinuata
Canda retiformis
Vibracellina goesi
Halophila johnstoniae

represented by small gobies, arrow crabs, and rare small urchins (only 1 live urchin has been found). Carbonate mud, silt, and sand cover all ledges, the cavity floor, and adhere to the walls and roof. The source of much of this sediment probably is from upslope on the reef: the sediment at these depths is very unstable on the steep reef slope, and can be dislodged with the touch of a diver's flipper (small turbidity currents are often produced in this way). Filamentous algae, long small diameter worm tubes, and dendritic hydroids bind much of the cavity sediment and allow it to drape over ledges and hang suspended from the cavity roof.

CRYPTIC CORALS IN BONAIRE FRAMEWORK CAVITIES

The corals in shaded habitats are of interest because they are an extension into the reef interior of a reef surface biota that plays an important role in reef construction, and because their common presence on both the reef surface and in cavities provides an opportunity to compare directly some aspects of the cavity and reef surface habitats.

Corals are known from cryptic habitats in the Pacific, Atlantic, and elsewhere (e.g. True,1970; Garrett et al.,1971; Jackson et al.,1971; Bonem,1977; Dinesen,1982,1983), although very few studies have treated the scleractinian corals of shaded habitats in detail. Dinesen (1982,1983) studied the cryptic scleractinians of the Great Barrier Reef from caves, tunnels, and overhangs, and found a very diverse assemblage comprising 150 species. Vasseur (1974) mentions ahermatypic corals and stylasterines in cavities in reefs of Madagascar, and True (1970) and Zibrowius (1976) found scleractinians in Mediterranean submarine caves. In the Atlantic Wells (1972) reported 4 species of ahermatypic corals from cryptic habitats in Bermuda, and Garrett et al. (1971) noted the presence of only one species of hermatypic coral in cavities in Bermuda patch reefs. Logan (1981) recorded 8 corals in caves in Grand Cayman and 2 in Bermuda caves (Logan et al. 1984). Zibrowius (1976) also recorded cave-dwelling scleractinians from the coast of Portugal, Madeira, the Canary Islands, and the Azores. In general reports of corals from reef cavities are scattered. There have been no previous comprehensive studies of cryptic corals from Caribbean reef cavities, and there have been no previous studies of cavity-dwelling corals that have attempted to relate the distribution of these corals to water depth over a substantial depth range (see Kobluk and Lysenko, 1985a).

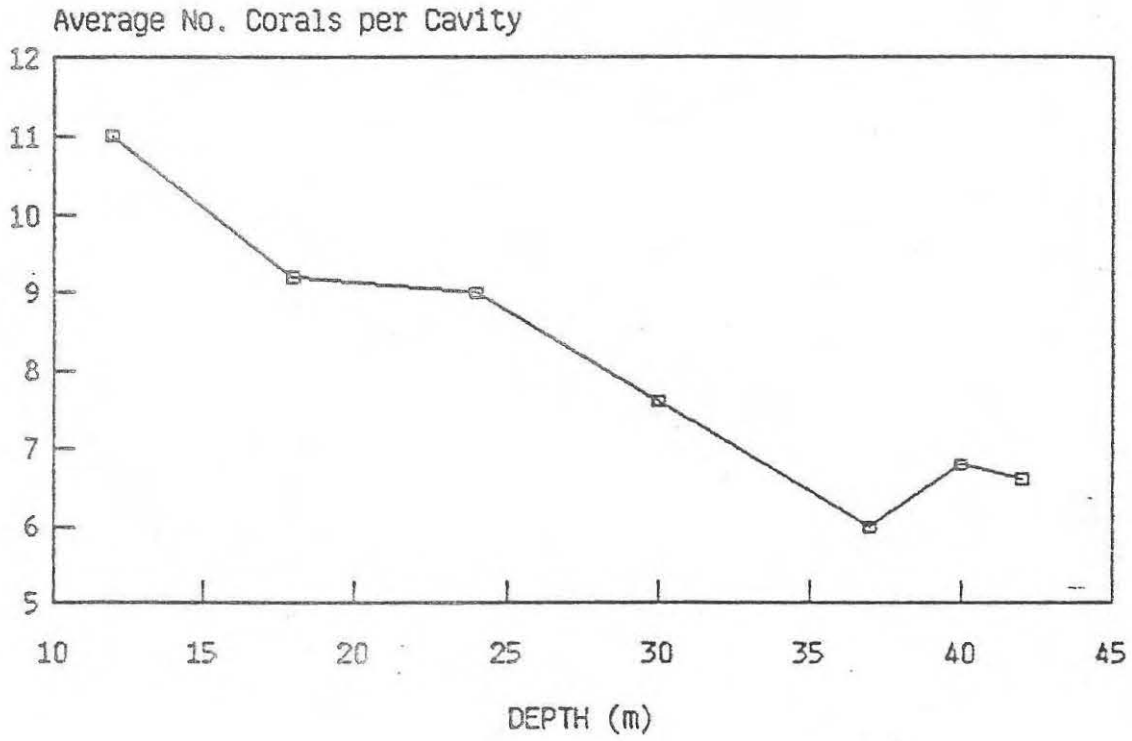
Methods

A total of 2474 living coral specimens from 284 growth framework cavities were identified and counted. All of the corals and Millepora found in the cavities were included in the study, with the exception of small, solitary ahermatypic corals (e.g. Gardineria). The small ahermatypes were not included because of the impossibility of finding all of them within each cavity without removing the wall and roof rock from every cavity. The sample includes all of the corals living on the walls and roofs of cavities, as well as all those living on the sand of the cavity floor. The definition of a cavity - dwelling coral used here includes all corals within the volume of the cavity delimited by a vertical plane from the roof to the floor across the cavity opening. The cavities selected for study were those that conformed most closely to an ideal well-enclosed cavity with well-defined walls, floor, and roof (see below). An attempt was made to select cavities of about the same size: 0.5 to1 m high and 0.5 to1 m deep with an opening under 1 m wide. The size of cavity selected was governed by the necessity of a uniform size distribution to allow comparison of data between cavities, as well as the practical limitations of allowing a diver to have access to the interior and sufficient room to permit the gyrations of the diver necessary to see all the interior surfaces.

Table. Abundances of cavity-dwelling corals with depth in Bonaire.

TAXA \ DEPTH(M):	12	18	24	30	37	40	42	TOTAL %
Stephanocoenia michelini	37.3	41.0	43.3	38.7	42.2	47.1	45.5	40.3
Agaricia spp.	11.6	14.1	13.3	12.2	21.1	11.8	15.2	13.1
Millepora alcicornis	11.6	14.4	11.4	21.9	7.8	8.8	9.1	14.1
Madracis spp.	8.2	8.6	8.3	10.3	7.8		21.2	8.77
Eusmilia fastigiata	0.6	1.4	1.2					0.77
Montastrea annularis	6.9	2.7	5.5	2.8	2.2	2.9	3.0	4.49
Montastrea cavernosa	3.2	4.3	4.3	4.1	6.7	5.9	3.0	4.08
Leptoseris cuculata	0.6	0.9	0.9	0.4				0.65
Porites astreoides	5.5	3.1	4.8	4.3	7.8	20.6		4.77
Porites spp.	3.9	2.7	2.6	1.2			3.0	2.55
Siderastrea siderea	2.0	1.0	1.2	2.0	2.2	2.9		1.58
Solenastrea bournoni	0.2	1.7	1.2	0.8	1.1			0.93
Mycetophyllia spp.	0.2	0.3	0.3					0.20
Mussa angulosa	0.2	0.3						0.12
Diploria strigosa	0.2							0.04
Diploria labyrinthiformis		0.2						0.04
Tubastrea coccinea	7.7	0.5	0.3					2.22
Scolymia lacera	0.3	0.3	0.9	1.2	1.1			0.65
Dichocoenia stokesi				0.2				0.04
Unidentified coral		2.4	0.3					0.65

AVERAGE NUMBER OF CRYPTIC CORAL COLONIES IN REEF FRAMEWORK CAVITIES, BONAIRE



All of the data was gathered at 11 sites along the leeward (western) side of Bonaire (See Figure). At each site transects oriented perpendicular to shore and running down the reef slope were used; at some sites 2 transects were made, for a total of 13 transects. Observations were made at 6 meter depth intervals by SCUBA divers beginning at a depth of 12 meters where the reef "barren zone" ends and the reef slope begins (see Scatterday, 1974 and Kobluk and Lysenko, 1984). Most of the 11 transects covered the depth interval 12 meters to 30 meters; 2 transects extended to 37 meters depth, but at the Karpata site observations were made from 12 to 42 m depth (12m, 24m, 30m, 37m, 39m, 42m depth stations); at all of the other sites except Karpata, reef growth stops at about 30 meters depth, where the reef is replaced by a sand-covered terrace. At each depth station on each transect 5 cavities were studied, and all of the corals in each cavity were identified and counted.

Not all of the corals could be reliably identified to the species level *in situ* within the cavities. The Bonaire reefs are protected by law, so that large numbers of corals could not be removed for identification. Therefore, in cases of taxa where identification to the species level was dubious without removing the specimens from the cavity, they were identified to the genus level; examples include *Agaricia* and some *Porites*.

All of the cavities studied were well-enclosed growth framework cavities comprising the basic elements of a rigid, self-supporting roof and walls, a sediment-covered floor, and a central water-filled void space. The main aperture is generally large compared to the largest dimension of the cavity interior and opens directly onto the reef surface. Most cavities have secondary openings in the walls or roof that are much smaller than the main opening, and that connect to the reef surface or to other cavities; sediment and water enter through these openings.

Light levels within cavities vary greatly. Qualitative measurements using a hand-held light meter show that the highest intensity is at the floor at the cavity aperture. The lowest light levels are within crevices and subsidiary cavities within larger cavities, at the roof, and also at the back of cavity where the wall meets the roof.

Cryptic Coral Biota Composition and Abundance

A total of 20 taxa of scleractinian coral, which includes 1 unidentified form, plus the hydrozoan *Millepora alcicornis* were found in the cavities over the depth range of this study. These are:

Agaricia agaricites
Leptoseris cuculata
Madracis decactis
Scolymia lacera
Diploria strigosa
Stephanocoenia michelini
Madracis pharensis
Madracis mirabilis
Dichocoenia stokesi
Diploria labyrinthiformis

Solenastrea bournoni	Porites porites
Siderastrea siderea	Mycetophyllia spp.
Mussa angulosa	Eusmilia fastigiata
Montastrea annularis	Montastrea cavernosa
Millepora alcicornis	Tubastrea coccinea
Unidentified coral	

Agaricia lamarcki, Agaricia fragilis, Agaricia grahamae, and Agaricia tenuifolia also occur at the apertures of cavities, but generally not as cavity-dwellers. They form sheets that may cover part of the aperture, and may have a portion of the colony projecting a short distance into the cavity aperture. For this reason they may be referred to as very marginally cavity-dwelling. Agaricia agaricites is, however, the common cavity-dwelling agariciid; in the discussion to follow A. agaricites and the other agariciids are grouped into Agaricia spp. Madracis pharensis is the important cavity-dwelling species of Madracis. However, M. mirabilis and M. decactis? do occur at the cavity aperture, and are referred to hereafter as Madracis spp. The flabellid coral Gardineria minor and the rhizangiid corals Astrangia solitaria and Colangia immersa also occur on the walls and roof of cavities, but they are not included in this study.

By far the most common coral in all of the cavities over the entire depth range is Stephanocoenia michelini (996 colonies = 40.3% of the total sample); the least common are Dichocoenia stokesi (1 colony = 0.04%), Diploria labyrinthiformis (1 colony = 0.04%), Mussa angulosa (3 colonies = 0.12%), and Mycetophyllia spp. (5 colonies = 0.2%). S. michelini, Agaricia spp., Madracis spp. and Millepora alcicornis are the most important taxa, and together make up 76.3% of the cavity coral samples. The other taxa account for the remaining 23.3% of the sample. The abundances of the various taxa as a percentage of the coral biota at each depth station and for the entire population at all depths are shown in the accompanying Table and Figure.

Location Of Corals In Cavities

In most cavities corals are most abundant near the entrance, where the light level is highest. In the shallowest cavities where higher intensity light is reflected from the white sand floor to the roof and back walls, corals are also common further back in the cavity. Corals on the cavity roof depend almost entirely upon light reflected from the white sand floor or scattered through the cavity by the water; little is reflected from the walls as these are generally dark in colour. Because the aperture of the cavity is the only source of light, and because corals generally decrease in size and abundance into the cavity, the cavity aperture provides the most realistic and convenient reference to which the distribution of corals can be related.

In general Bonaire cavity-dwelling corals may be divided into 3 groups defined on the basis of their locations in cavities and as a corollary on their level of shade-tolerance:

1) corals tolerant of slightly reduced light levels found generally near the entrance to a cavity.

2) corals tolerant of, or adapted to, significantly reduced light levels that are found well within the cavity on the walls or where the wall meets the floor.

3) corals tolerant of, or adapted to, the lowest light levels in the cavity that are found on the roof or at the top of the back wall.

Some organisms are generalists in that they can be found almost anywhere within the cavity, whereas others have specific preferences for certain locations. Corals tolerant of the lowest light levels and restricted to the cavity roof and walls (group 3 above) are: Leptoseris cuculata, Madracis pharensis, Stephanocoenia michelini, Scolymia lacera, and Tubastrea coccinea. Those found within the cavity at significantly reduced light levels on the floor or near the base of the walls (group 2 above) are: Solenastrea bournoni, Porites porites, Siderastrea siderea, Agaricia spp., Mycetophyllia spp., Mussa angulosa, and Montastrea annularis. Those found at only slightly reduced light levels, generally near the entrance to the cavity (group 1 above) are: Dichocoenia stokesi, Diploria strigosa, Diploria labyrinthiformis, Eusmilia fastigiata, Madracis decactis, and Madracis mirabilis. Millepora alcicornis is ubiquitous in the cavities, and Montastrea cavernosa and Agaricia agaricites occur on both the floors and walls, but are not found on cavity roofs.

The cavity habitat as well may be divided into 4 distinct areas on the basis of the nature of the substrate, light levels, and location and orientation of the substrate surface. These areas and their assemblages consist of:

1) cavity roof
   - Stephanocoenia michelini
   - Madracis pharensis
   - Tubastrea coccinea
   - Millepora alcicornis
   - Porites astreoides

2) cavity walls
   - Montastrea cavernosa
   - Scolymia lacera
   - Agaricia agaricites
   - Porites astreoides
   - Millepora alcicornis
   - Madracis pharensis
   - Stephanocoenia michelini
   - Leptoseris cuculata

3) cavity floor at the base of the walls
   - Montastrea cavernosa
   - Millepora alcicornis
   - Agaricia spp.
   - Solenastrea bournoni
   - Mycetophyllia spp.
   - Siderastrea siderea
   - Porites porites

4) cavity floor at the cavity aperture
   - Porites astreoides
   - Agaricia spp.
   - Diploria labyrinthiformis
   - Siderastrea siderea
   - Diploria strigosa
   - Mycetophyllia spp.

Table. Growth forms of cavity-dwelling corals in Bonaire.

Stephanocoenia michelini	sheet-like encrusting
Agaricia agaricites	massive to encrusting
Other Agaricia	foliaceous to sheet-like
Millepora alcicornis	encrusting
Madracis spp.	branching
Madracis pharensis	encrusting
Eusmilia fastigiata	branching
Montastrea annularis	massive
Montastrea cavernosa	massive, low-dome
Leptoseris cuculata	sheet-like to tabular
Porites astreoides	massive encrusting
Porites spp.	branching
Siderastrea siderea	massive to low-dome
Mycetophyllia spp.	massive platey
Mussa angulosa	massive
Diploria strigosa	massive
Diploria labyrinthiformis	massive
Tubastrea coccinea	open clusters of corallites
Scolymia lacera	solitary plate-like
Dichocoenia stokesi	massive
Solenastrea bournoni	massive to sheet-like encrusting
Unidentified	massive to sheet-like encrusting

Mussa angulosa	Porites porites
Eusmilia fastigiata	Montastrea annularis
Madracis decactis	Madracis mirabilis
Solenastrea bournoni	Dichocoenia stokesi
Montastrea cavernosa	Millepora alcicornis

Growth Form

The growth forms of the cavity-dwelling corals are summarized in the accompanying Table. In general, corals living close to the aperture have massive, branching, or foliaceous growth forms typical of their form on the reef surface. The further into the cavity that a coral occurs, the more likely the colony is to be an encrusting, tabular or sheet-like form. Corals also tend to be smaller inside cavities than they are outside. Normally massive forms such as Montastrea annularis and Montastrea cavernosa are also massive inside cavities, but the colonies are small and tend to develop a low-domed growth form. Siderastrea siderea is also low-domed in cavities, and may even begin to approach sheet-like in form if it occurs far inside the cavity. Branching forms such as Madracis mirabilis and Eusmilia fastigiata are rare inside cavities away from the aperture; Madracis mirabilis and related branching species appear to be replaced by encrusting or low-lying thin massive colonies of Madracis pharensis inside cavities.

Several workers have noted that the spacing of corallites tends to increase in some corals as light levels decrease (Wijsman-Best,1974; Scatterday,1974; Lasker,1977; Highsmith,1979; Dinesen, 1983). Dinesen (1983) noted this in several species of cavity-dwelling corals from the Great Barrier Reef (e.g. Leptoseris, Echinophyllia, Porites, Galaxea, Cyphastrea, Montipora). Scatterday (1974) also noted this in reef surface corals in Bonaire. In the Bonaire cavities, increased corallite spacing was seen in some colonies of Montastrea cavernosa, Solenastrea bournoni, and Madracis pharensis, but it was not common.

Cryptic Coral Depth Ranges

Seven of the 21 cavity-dwelling taxa (33%) occur throughout the entire 12 to 42 m depth range of this study. Of the remaining corals, with the exception of Siderastrea siderea, which extends to 40 m, all the other cavity corals are found to 37 m or less in depth. Tubastrea coccinea, Eusmilia fastigiata, Mycetophyllia spp., and the unidentified form are found only to 24 m depth. Mussa angulosa is even more restricted, with a depth range of 12 - 18 m. The 3 least common corals, Diploria strigosa, D. labyrinthiformis, and Dichocoenia stokesi have been found at only one depth; this apparently short depth range, however, is due to their rarity in cavities and the infrequency with which they are encountered. They are found only at the entrances of cavities, and may therefore be only occasional coelobionts, occurring rarely in cavities under special conditions.

On the basis of depth range, the Bonaire cavity coral biota may be divided into a deep assemblage and a shallow assemblage. There is no specific depth at which the assemblages change character; rather, there is a progressive disappearance of taxa over a depth interval of 7 m from 30 m to 37 m (tension zone: see below). The shallow assemblage occurs between 12 m and 30 m depth and contains all of the corals recognized in the cavities. The deep water assemblage begins to appear at 30 m and extends to 42 m and probably deeper; it comprises Stephanocoenia michelini, Agaricia spp., Millepora alcicornis, Madracis spp., Montastrea annularis, Montastrea cavernosa, and Porites spp. The corals Porites astreoides, Siderastrea siderea, Solenastrea bournoni, and Scolymia lacera may also be found at the shallow end of the deep assemblage. The deep assemblage contains no unique corals, but rather is characterized by the disappearance of forms that are present in shallower water.

Coral Abundance vs Depth

Coral abundance in cavities was measured by counting the number of colonies of each species in every cavity, and also by calculating the abundance of the species at each depth station as a percentage of all the specimens found at that depth.

The abundance of the entire coral population in cavities with increasing depth (the mean number of colonies per cavity at each depth) shows a decline from 12 m to 37 m depth, with a slight increase below 37 m to 42 m (see Figure). Although systematic size measurements were not made on all the transects, it was seen that colonies generally become smaller in size with depth as well as less common in the cavities. At 37 m, 39 m, and 42 m depth no colonies were found larger than 10 cm in diameter in 25 sampled cavities, whereas at 12 and 18 m depth some colonies reach 40 cm in diameter.

Stephanocoenia michelini shows a general decrease in the mean number of colonies per cavity, but an overall increase in its percent abundance with increasing depth. Agaricia spp. also shows a general decrease in the mean number of colonies per cavity, but with a sharp increase at 40 m depth; its percent abundance is relatively constant with depth except at 40 m where it increases to over 20% of the cavity coral population. The mean number of colonies of Millepora alcicornis per cavity also shows an overall decrease with depth, but with a peak of abundance at 30 m depth. Its percent abundance is almost constant with depth but shows a dramatic increase in abundance at 30 m. Both the mean number of colonies per cavity and the percent abundance of Madracis pharensis is constant over almost the entire depth range except at 42 m where it increases. Montastrea annularis is most abundant in shallow water cavities and shows an overall decrease in percent abundance and in the mean number of colonies per cavity; there is a peak of abundance at 24 m depth. Montastrea cavernosa has a peak in its percent abundance at 37 and 40 m depth. The mean number of colonies per cavity is almost constant over the depth range, with a sharp drop 42 m depth. Porites astreoides shows a similar trend to that of Montastrea cavernosa.

Diversity vs Depth

Although there is a very general decrease in abundance of cavity corals as depth increases, the mean number of taxa per cavity versus depth shows a more erratic distribution than the overall abundance of colonies.

The sample diversity, measured as the maximum number of taxa found at each depth shows a relationship to depth wherein the highest sample diversity increases to 18 m depth (18 taxa), and decreases steadily with depth to the low at 39 m and 42 m, where 7 taxa are found. This is a decrease of 61 % in sample diversity over the 30 m depth range of the study. However, sample diversity has an important drawback when attempting to measure diversity because it treats each species as equally important, even if it is a rare species and contributes little to the total population. For example, rare Dichocoenia stokesi is given the same importance in the calculation of the sample diversity as Stephanocoenia michelini, the most abundant coral.

To attempt to reduce the influence of rare or uncommon corals in showing diversity trends in the populations the following additional diversity and equitability indices were calculated for the cavity-dwelling coral populations at each depth:

1) Odum Diversity
2) Average Evenness
3) Margalef Diversity
4) Simpson Diversity

The values for the Odum diversity (number of species / number of individuals) are almost constant to 30 m depth and thereafter increase dramatically down to 42 m. This shows that to 30 m depth the number of species in cavities and the number of individual corals representing them on a population basis shows little change; below that depth the number of taxa decreases steadily (shown by the decrease in sample diversity), but the number of corals representing these species decreases at a much slower rate.

Average evenness (number of individuals / number of species) represents the average number of individual corals per species in the population; it shows a small decrease from 12 m to 18 m and then rises to 30 m depth; at 30 m there is a sharp drop in evenness to 42 m depth (see Figure). At 30 m depth an average of 39 corals per taxon was found, compared to only 5 at 40 and 42 m depth.

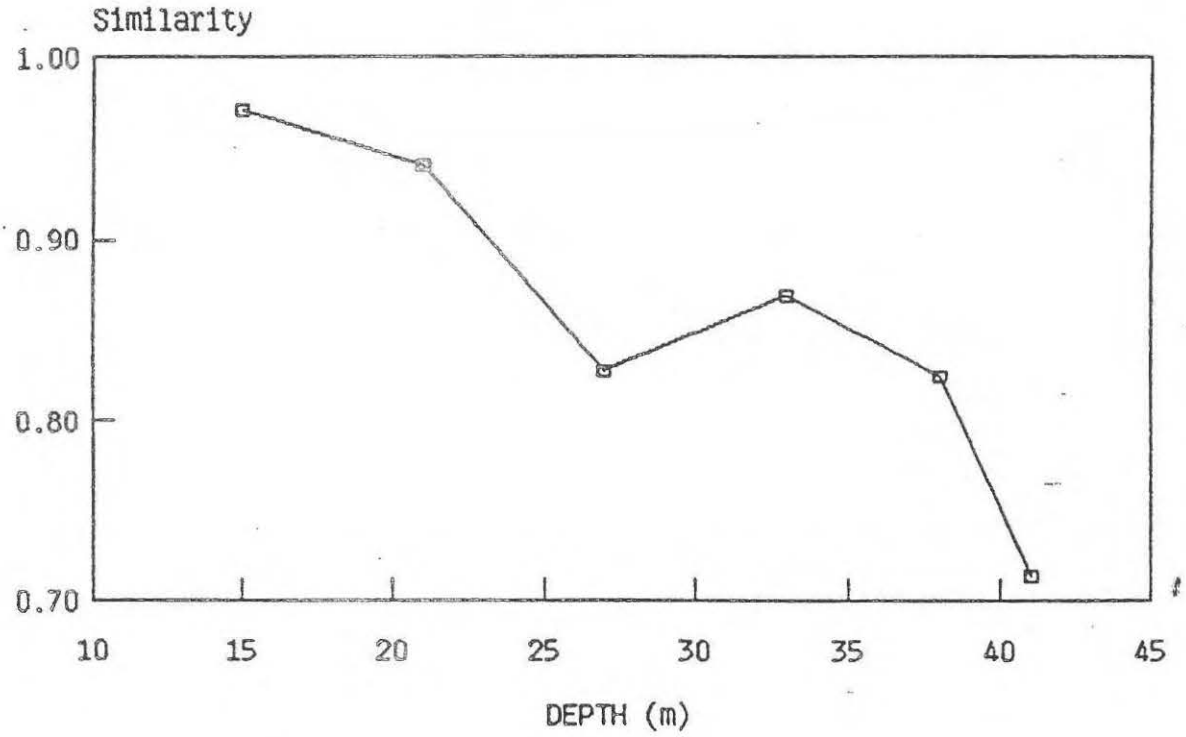
Simpson diversity values (sum of the square of the number of corals in each taxon / sum of all corals) show a general increase over the entire depth range with a minor drop at 30 m.

Margalef diversity is calculated as the number of species at each depth (minus 1) divided by the log of the number of specimens

Table. Comparison of surface-dwelling and cavity-dwelling coral populations.

TAXA	SURFACE-DWELLING	CAVITY-DWELLING
Stephanocoenia michelini	x	x
Madracis pharensis	x	x
Madracis decactis	x	x
Madracis mirabilis	x	x
Acropora cervicornis	x	
Acropora prolifera	x	
Acropora palmata	x	
Agaricia agaricites	x	x
Agaricia lamarcki	x	marginal
Agaricia grahamae	x	marginal
Agaricia fragilis	x	marginal
Agaricia tenuifolia	x	marginal
Leptoseris cuculata	x	x
Siderastrea siderea	x	x
Siderastrea radians	x	
Porites astreoides	x	x
Porites furcata	x	x
Porites porites	x	x
Porites branneri	x	
Favia fragum	x	
Diploria strigosa	x	x
Diploria labyrinthiformis	x	x
Diploria clivosa	x	
Manicina areolata	x	
Colpophyllia natans	x	
Montastrea annularis	x	x
Montastrea cavernosa	x	x
Solenastrea bournoni	x	x
Meandrina meandrites	x	
Dichocoenia stokesi	x	x
Dichocoenia stellaris	x	
Dendrogyra cylindricus	x	
Mussa angulosa	x	x
Scolymia lacera	x	x
Scolymia cubensis	x	
Scolymia cf wellsi	x	
Isophyllia sinuosa	x	
Isophyllastrea rigida	x	
Mycetophyllia spp.	x	x
Eusmilia fastigiata	x	x
Tubastrea coccinea	x	x
Millepora alcicornis	x	x

SIMILARITY INDEX VERSUS DEPTH FOR CRYPTIC CORAL POPULATIONS IN FRAMEWORK CAVITIES, BONAIRE



(individuals) in the sample (log N). Margalef diversity values are almost constant from 12 m to 30 m depth; below 30 m there is a pronounced decrease in the diversity values as depth increases; this index is useful in this situation as a small number of taxa account for a large proportion of the individuals at each depth. The Margalef index uses the empirically-derived assumption that the greatest number of species in the population shows the minimal abundance, which is taken into consideration in the calculation by using the log of the total number of specimens. The values of Margalef diversity versus depth may therefore be the best representation (among those used here) of the taxonomic diversity of the cavity coral populations with increasing depth.

Similarity

A useful measure of both similarities and differences between populations of cavity-dwelling corals with increasing depth is the use of a simple similarity index in which the presence or absence of coral taxa in cavities at each sampled depth is compared with that in cavities at the next shallower or deeper depth. The index is a measure of the number of taxa shared in common, and has values that range from 0 (no similarity whatever; no taxa occur in common) to 1 (complete similarity; all taxa occur in common). The formula used here is:

$$\text{Index of Similarity} = 2C / (A + B)$$

where C = number of taxa occurring in both populations
A = number of taxa occurring in population 1
B = number of taxa occurring in population 2

In this study successive pairs of cavity-dwelling coral populations with increasing depth were compared; for example, a similarity index value was calculated comparing the populations at 12 and 18 m depth, then 18 and 24 m, etc.

Over the depth range of the study similarity indices show a general decline with depth (see Figure), indicating that the number (and proportion) of coral taxa occurring in common within cavities at successive depths decreases. The shallowest cavities have very high similarities, and the deepest ones significantly lower similarities. The drop in the similarity index at 24 to 30 m depth coincides closely with the change from the shallow to deep cavity assemblages (see above), and appears to be a tension zone (Curtis, 1959; Krebs, 1978) representing the distributional limits of some species.

Comparison With Surface-Dwelling Corals

All of the corals found in the cavities (with the exception of the small ahermatypes mentioned above) also occur on the reef surface. Among

them, only Tubastrea coccinea appears to be preferentially cavity-dwelling.

If depth range is used to compare surface and cavity-dwelling corals, the cavity corals may be divided into 4 groups:

1) Corals with the same depth range as surface-dwelling forms within the depth range of the study:

Stephanocoenia michelini	Agaricia spp.
Madracis spp.	Montastrea cavernosa

2) Corals with a shallower depth range in cavities than on the reef surface:

Siderastrea siderea	Scolymia lacera
Solenastrea bournoni	Leptoseris cuculata
Eusmilia fastigiata	Mycetophyllia spp.
Mussa angulosa	Diploria strigosa

3) Corals with a deeper depth range in cavities than on the reef surface:

Montastrea annularis	Porites spp.
Porites astreoides	Tubastrea coccinea
Millepora alcicornis	

4) Corals occurring in cavities over an intermediate part of their reef surface depth range:

Dichocoenia stokesi	Diploria labyrinthiformis

The controls governing the distribution of cavity-dwelling corals within cavities and in comparison with their surface-dwelling counterparts are not known with certainty. However, light levels are almost certainly a significant factor (Jaubert and Vasseur,1974; Lasker,1977; Dinesen,1983;, as are space limitations and competition between corals and with other organisms for that limited space (Jackson,1977a,b; Jackson and Buss,1975). Water circulation as a control on oxygenation and the supply of nutrients may be important in restricted cavities, but those studied in Bonaire had wide openings and were not deep, so that circulation within cavities and exchange with the surface should not be restricted greatly.

Hermatypic corals subjected to reduced light intensities commonly develop a low-lying to flattened or encrusting growth morphology, with the colony surface oriented toward the impinging light (Goreau,1963; Roos,1967; Dustan,1975; Graus and Macintyre,1976; Jaubert,1977). This is also true of hermatypic corals in reef cavities, where light levels are lower than at the surface, as has been noted by some authors (Jaubert and Vasseur,1974; Dinesen,1983).

In the Bonaire reef cavities, corals living on the floor at the cavity aperture have growth forms typical of the open reef surface habitat. Further back in the cavity, where light levels decrease, the colony form tends to become flattened to encrusting. The requirement of many corals to adapt to low light levels by flattening their growth form may explain why some of the cryptic species in Bonaire are restricted in their locations in cavities. Eusmilia fastigiata, Madracis decactis, Madracis mirabilis, and Porites porites are all branching corals that grow as open bushes; growth of the colonies tends to be upward and outward, and they appear to be incapable of producing encrusting or flattened colonies; their ability to adapt to the low light levels of the deep cavity interior and roof by flattening colony form is therefore probably limited. Mussa angulosa probably is similarly restricted by its typical robust dichotomous colony form and upward growth. Corals that grow as massive colonies on the open reef surface appear to have a variable ability to adapt to the cavity interior. Diploria strigosa, Diploria labyrinthiformis, Solenastrea bournoni, Siderastrea siderea, Dichocoenia stokesi, Agaricia agaricites, Montastrea cavernosa, and Montastrea annularis are all capable of flattening their colony form to produce variably low domes to almost plate-like forms in some cases (e.g. M. annularis). The observation that of these only Agaricia agaricites and Montastrea cavernosa occur in the darker recesses of the cavity back walls may reflect differences in tolerance for reduced light levels. Montastrea cavernosa, for example, is thought to be able to adjust to low light levels by adjusting its colony form as well as by increasing the spacing of corallites which serves to increase the proportional area of coenosarc containing zooxanthellae for photosynthesis (Scatterday,1974; Lasker,1977).

Porter's (1976) suggestion that corals with small polyps compensate for inefficiency in capturing zooplankton by having a high surface area to volume ratio to increase photosynthetic efficiency may have bearing upon the overall adaptive ability of corals to cavities. The ability of corals to adapt to shaded cavities may be related in part to the ability of species to either increase overall photosynthetic efficiency as light levels drop by modifying the shape and of the colony to make use of available light, or become increasingly heterotrophic. For example, Tubastrea coccinea which does not require light, has large polyps that should be efficient at gathering food; Scolymia lacera can use light, but in cavities it is successful by orienting its surface toward the impinging light and by having a large polyp. Stephanocoenia michelini, the most abundant cavity coral, has intermediate size polyps, but is presumably gathering light by having a flattened and encrusting form and by being oriented toward the cavity aperture. Corals that are capable of increasing light gathering efficiency or growing as flattened or encrusting colonies but that are not common or are absent from

cavities may be excluded by an inability to compete for space in the cavity competitive network (Jackson and Buss,1975).

Summary of Bonaire Cryptic Corals

A total of 2474 corals living in 284 growth framework cavities over the depth range 12 m to 42 m at 11 sites on the west coast of Bonaire were identified and counted. The population comprises 20 taxa of scleractinian coral plus the hydrozoan Millepora alcicornis. The assemblage is dominated overwhelmingly by only 3 corals (Stephanocoenia michelini, Madracis, and Agaricia) and Millepora alcicornis, which together make up 76.3 % of the population, while accounting for only 20 % of the taxa. Of these, Millepora is not a coral and Stephanocoenia is the most significant (40.3 %) of the 3 most important corals. If 2 % abundance is selected as an arbitrary cut-off level, then the significant taxa in the Bonaire reef cavities in order of importance are: Stephanocoenia michelini, Millepora alcicornis, Agaricia spp., Madracis spp., Porites astreoides, Montastrea annularis, Montastrea cavernosa, Porites spp., and Tubastrea coccinea. Of these, only S. michelini and T. coccinea are preferentially cryptic; only S. michelini occurs throughout the depth range of the study.

One third of the coelobiontic taxa occur through the entire depth range of this study; the remainder have variable depth ranges. On the basis of depth range, the cavity corals may be divided into deep and shallow assemblages, with a 7 meter deep tension zone in-between, that is reflected in a plot of similarity indices with depth.

There are differences in depth distribution if surface- and cavity-dwelling taxa are compared; these differences are complex, and the controls governing them are not understood. Differences between surface and cavity coral populations are also reflected in the reef sands, wherein the percentage of coral grains in cavity sediments is generally higher than in sediments from the reef surface, even though coral is more abundant on the reef surface.

The abundance of cavity-dwelling corals decreases into the cavities, and is probably related to decreasing light levels, so that the greatest abundance and diversity in most cavities is near the entrance. Many corals within cavities show preferences for certain locations and as a result the cavities are divisible into 4 areas, each with a recognizable assemblage of corals; some of the corals are restricted to these areas, while others are generalists and may occur in two or more areas.

Coral growth forms tend to be encrusting, tabular, or sheet-like within cavities; the size of colonies also shows a tendency to decrease into cavities.

Taxonomic diversity measured as the Sample Diversity shows a decrease with depth. Other measures of diversity, including Average Evenness, Simpson Diversity, Odum Diversity, and Margalef Diversity show variable relationships with increasing depth.

CAVITY-DWELLING MOLLUSCS IN BONAIRE

Gastropod and bivalve molluscs have long been known as reef coelobionts, but they have not been systematically collected and studied from growth framework cavities over a substantial depth range on any one reef tract. Gastropods are important predators, carnivores, scavengers, and herbivores, and the bivalves are a major group of filter, suspension, and deposit feeders in reef systems. Their presence in reefs suggests that they may be important in these roles in cavities as well, but not enough is known at present to indicate what their role within cavity systems might be, or even if they are numerically important elements in cavity biotas (see Kobluk and Lysenko, 1985b). Both bivalves and gastropods are well documented from reef surface environments and the sediment infauna in the Caribbean and elsewhere (eg: Kohn, 1964, 1967, 1968; Robertson, 1975). Shallow water reef-dwelling molluscs living in small holes and under rocks have been best studied, but these reports usually consist of taxonomic lists accompanied by short statements of habitat preference of individual taxa. Although very useful ecologically, these studies give little hint of the potential abundance and diversity of molluscs in deeper water reef cavities. A few studies of reef caves and cavities in deeper water have recorded some molluscs, but the lists appear to be incomplete.

Methods

Samples were collected by SCUBA divers from 60 open growth framework cavities (terminology following the usage of Garrett, 1969) in reefs on the leeward (west) side of Bonaire through the depth range 3 m to 61 m. Most samples were collected at the Cliff site (also referred to as the Aquahabitat site) to a depth of 40 m. Because reef growth stops at 40 m at that site, two other areas referred to locally as Ole Blue and Karpata were selected for sampling of deeper cavities; the deepest samples were from Karpata.

An attempt was made to select cavities of uniform size for sampling. These were 0.5 to 1 m deep, and of similar height and width. The openings were generally slightly narrower than the cavity itself, but had to be wide enough to allow a diver to see and reach inside. Their small size makes collecting molluscs <u>in situ</u> from the walls and roofs difficult, so that collecting had to be carried out in two ways: 1) by removing individual molluscs that could be seen in the cavities, and 2) removing pieces of the wall and roof of the cavity interior by hammer and chisel. Rock samples from the cavities were carried to the surface in buckets, and the molluscs on the samples removed; the rocks were also broken into small pieces and all molluscs hidden in crevices or within boreholes were collected. The cavities were thoroughly sampled by the divers, an attempt being made to collect all of the endolithic and epilithic molluscs in each cavity.

Mollusc Biota

A total of 610 specimens (almost all alive) comprising 34 gastropod species and 40 bivalve species (including endolithic bivalves), were collected from the 60 cavities (see Table). In

Table. Summary of molluscs reported from Caribbean and subtropical Atlantic reef cavities.

BERMUDA	FLORIDA	JAMAICA	ST. CROIX
Spondylus sp.	Lithophaga nigra	Spondylus sp.	Ostrea sp.
Spondylus americana	Lithophaga antillarum	Pseudochama sp.	Chama sp.
Chama macerophylla	Petricola lapicida	Chama sp.	Isognomon? sp.
Isognomon radiatus	Gastrochaena hians	Lithophaga nigra	
Lithophaga nigra	Botula fusca	Spengleria rostrata	
Lithophaga bisulcata	Barbatia domingensis		
Lithophaga sp.	Isognomon radiatus		
Ostrea frons	Ostrea permollis		
Pseudochama radians	Plicatula gibbosa		
Arca spp.	Chama florida		
Gastrochaena hians	Spiroglyphus sp.		
Chlamys sp.	Pseudochama sp.		
Barbatia domingensis	Spondylus sp.		
Vermicularis sp.	Chama sp.		
Dendropoma sp.	Spengleria rostrata		
Pinctada radiata			
Pteria colymbus			
Spengleria rostrata			
Malleus candeanus			

SOURCES: Bermuda - Garrett (1969); Garrett et al. (1971); Scoffin (1971); Ginsburg & Schroeder (1973); Scoffin & Garrett (1974). Florida - Bonem (1977); Choi & Ginsburg (1983). Jamaica - Bonem (1977); Jackson et al. (1971). St. Croix - Rasmussen (1983); Grand Cayman - Logan et al.(1984); Belize - Macintyre et al.(1982).

GRAND CAYMAN	BELIZE
Barbatia domingensis	Barbatia domingensis
Lithophaga bisulcata	Chama congregata
Lithophaga nigra	Chama macerophylla
Malleus candeanus	Gastrochaena sp.
Spondylus americanus	Lithophaga nigra
	Gregariella coralliophaga
	Coralliophaga coralliophaga

Table. Cavity-dwelling gastropods in Bonaire reef cavities.

Family: Atyidae
- Atys sp.

Family: Cerithiidae
- Cerithium litteratum
- Cerithium sp.

Family: Columbellidae
- Nitidella laevigata
- Nitidella sp.

Family: Conidae
- Conus sp.

Family: Coralliophilidae
- Coralliophila caribaea
- Coralliophila abbreviata

Family: Costellariidae
- Vexillum pulchellum

Family: Crepidulidae
- Cheilea equestris

Family: Chitonidae
- Chiton sp.

Family: Cymatiidae
- Cymatium pileare

Family: Eulimidae
- Balcis intermedia

Family: Fasciolariidae
- Latirus ? sp.

Family: Fissurellidae
- Diodora cf variegata
- Diodora sp.
- Emarginula pumila
- Hemitoma emarginata

Family: Littorinidae
- Littorina ziczac
- Nodilittorina tuberculata

Family: Marginellidae
- Marginella avena
- Marginella sp.

Family: Mitridae
- Pusia gemmata

Family: Muricidae
- Muricopsis oxytatus

Family: Olividae
- Olivella nivea
- Olivella sp.

Family: Potamididae
- Seila adamsi

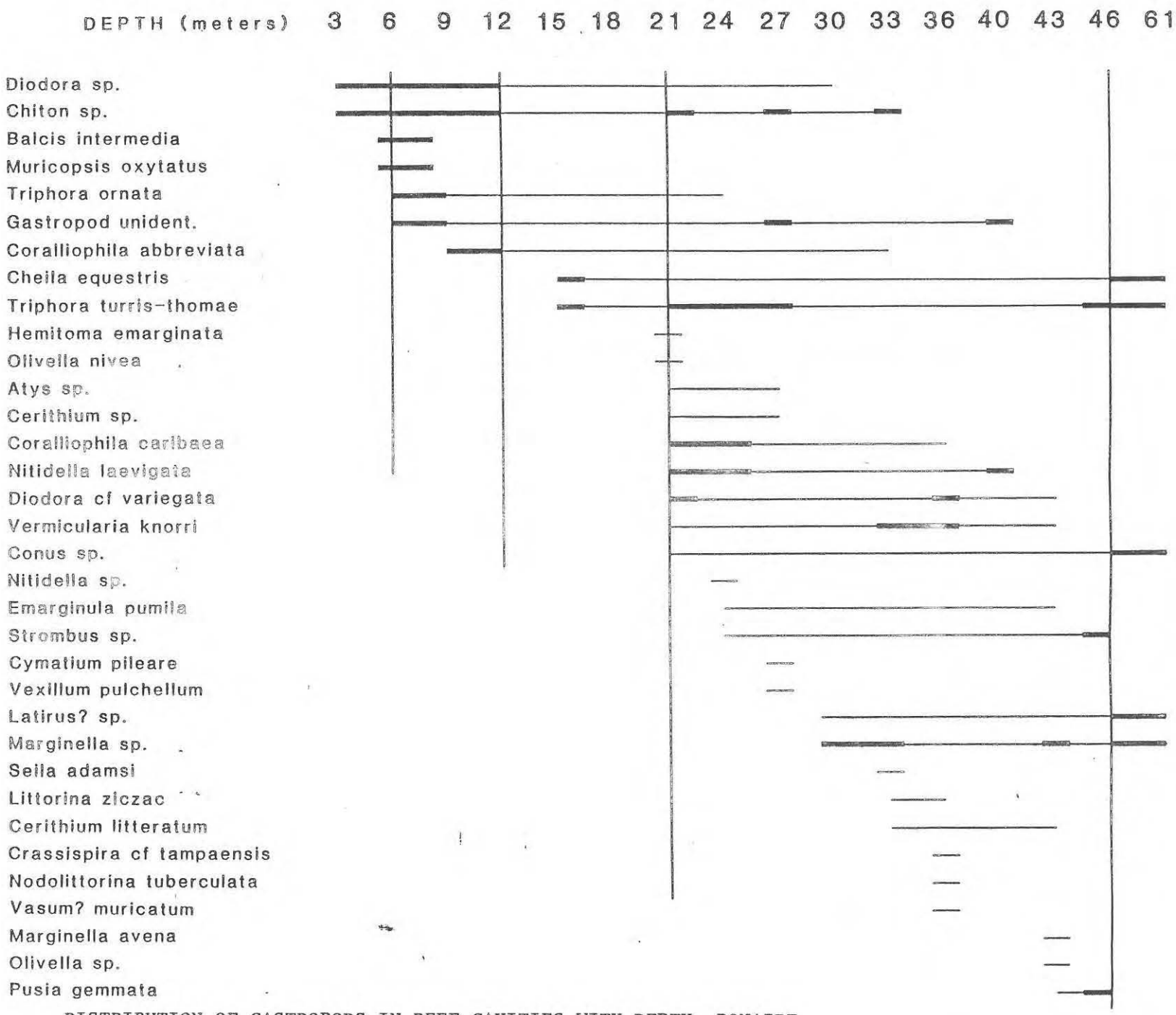
Family: Strombidae
- Strombus sp.

Family: Triphoridae
- Triphora ornata
- Triphora turris-thomae

Family: Turbinellidae
- Vasum ? muricatum

Family: Turridae
- Crassispira cf tampaensis

Family: Vermetidae
- Vermicularia knorri



DISTRIBUTION OF GASTROPODS IN REEF CAVITIES WITH DEPTH, BONAIRE

comparison with mollusc populations normally seen in reef surface environments this is neither an abundant nor a very diverse mollusc biota (average of 10.2 specimens per cavity).

The mollusc population can be divided into several life habit groups on the basis of the relation of the organisms to the cavity roof and wall substrate (see Table): 1) vagrant forms, 2) loosely attached benthic forms (eg: by byssal threads), 3) firmly attached cemented or encrusting forms, 4) swimmers, 5) endoliths (borers), 6) chasmoliths (live in vacated boreholes or crevices in the walls and roof). All the specimens were found on, or in, the walls and roofs of the cavities; no live gastropods or bivalves were found on the cavity sediment.

Gastropods

Over the entire depth range, the gastropod fauna is dominated by Chiton sp. (8.9% of all specimens), Triphora turris-thomae Holten (8.9%), Vermicularia knorri Deshayes (8.1%), and an unidentified high-spired form (11.4%). No single gastropod species clearly dominates the assemblage, although the above four most important forms together make up 37.4% of the sample population (123 specimens).

The largest number of specimens and the highest species diversity came from cavities in the depth range 21 to 36 m (see Figure). Using range-through data, the number of species shows a dramatic increase in the 20 to 36 m depth range. The smallest number of species is found in the shallowest and in the deepest cavities (see Figure).

None of the species occurs over the entire depth range studied, and only 7 species (20.6%) are found through a depth range of 30 m or more (see Figure). The gastropods with the greatest depth ranges are: Chiton sp., Marginella sp., Cheilea equestris Linnaeus, Triphora turris-thomae, Conus sp., Latirus sp., and the unidentified form.

The gastropod assemblage represents 24 families, of which the most abundant are the Chitonidae, Fissurellidae, Triphoridae, and the Vermetidae. The families with a bathymetric range of 30 m or greater are the Triphoridae (55 m), Coralliophilidae (52 m), Crepidulidae (46 m), Conidae (40 m), Marginellidae (31 m), Fasciolariidae (31 m), and the Chitonidae (30 m) (see Figure). Using range-through data the number of gastropod families in cavities increases to a maximum at 36 m depth over the range 3 to 36 m; below 36 m the number of families declines steadily (see Figure).

Bivalves

The six most abundant species of the forty bivalve species found in the cavities comprise 72.6% of all bivalve specimens (total of 487 specimens). The most important bivalves and the percentage of the bivalve sample population they make up are: Lima scabra Born (31.8%), Ostrea equestris Say (13.7%), Coralliophaga coralliophaga Gmelin (7.4%), Lithophaga bisulcata Orbigny (7.0%), Gastrochaena hians Gmelin (6.6%), and Chama sp. (5.3%).

Table. Cavity - dwelling bivalves in Bonaire reef cavities.

Family: Arcidae
- Anadara lienosa floridana
- Arca zebra
- Arca sp.
- Barbatia cancellaria
- Barbatia candida

Family: Cardiidae
- Americardia media

Family: Chamidae
- Chama macerophylla
- Chama sp.
- Pseudochama radians

Family: Gastrochaenidae
- Gastrochaena hians
- Spengleria rostrata

Family: Isognomonidae
- Isognomon radiata
- Isognomon sp.

Family: Limidae
- Lima scabra

Family: Lucinidae
- Anodontia cf philippina

Family: Mytilidae
- Botula fusca
- Gregariella coralliophaga
- Gregariella opifex
- Lithophaga bisulcata
- Lithophaga nigra
- Lithophaga antillarum
- Lithophaga sp.
- Modiolus americanus
- Modiolus sp.

Family: Ostreidae
- Lopha frons
- Ostrea equestris
- Ostrea sp.

Family: Pectinidae
- Chlamys cf sentis
- Chlamys sp.

Family: Pinnidae
- Atrina cf seminuda

Family: Pteriidae
- Pinctada radiata
- Pteria sp.

Family: Spondylidae
- Spondylus americana

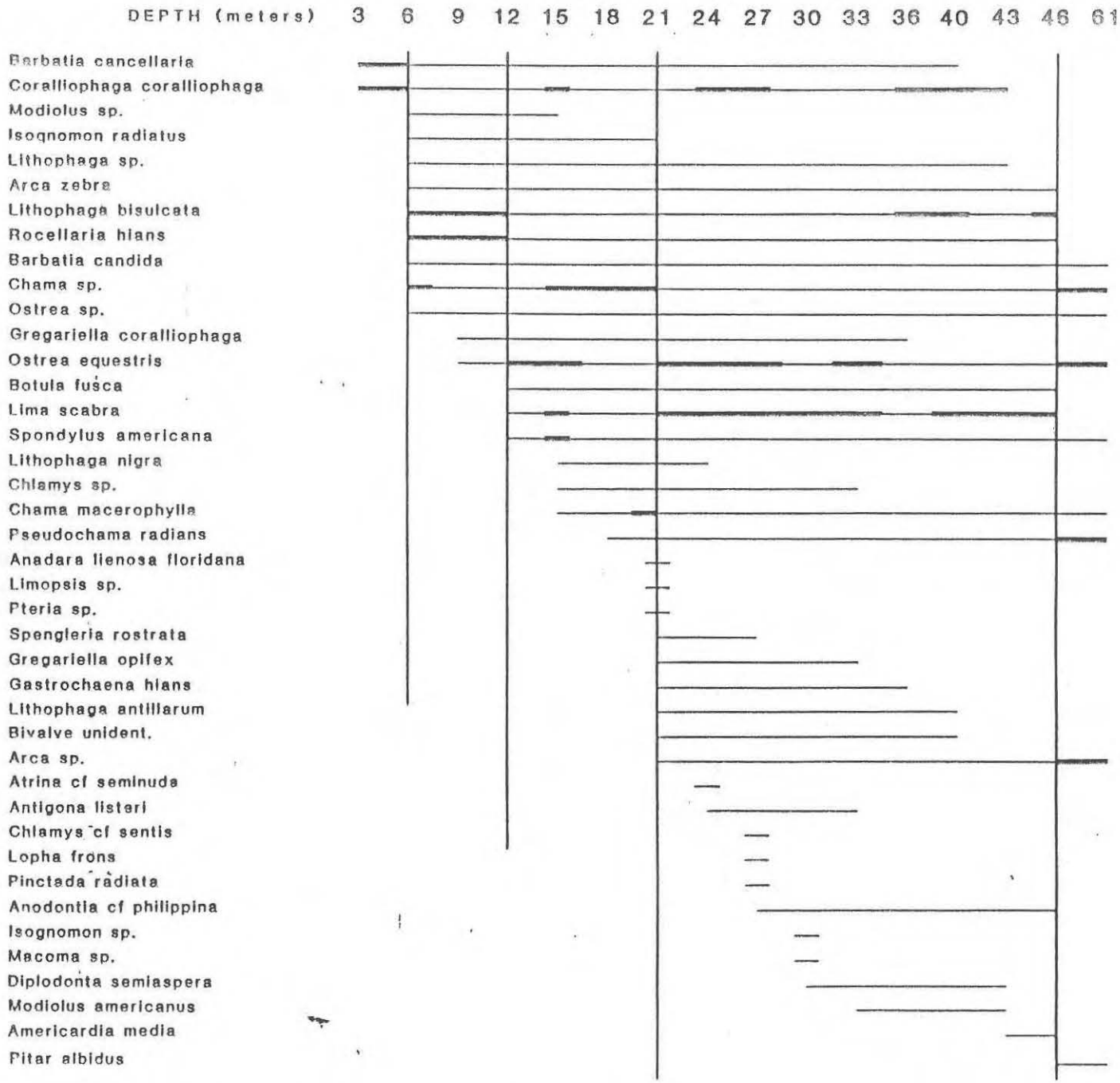
Family: Tellinidae
- Macoma sp.

Family: Trapeziidae
- Coralliophaga coralliophaga

Family: Ungulinidae
- Diplodonta semiaspera

Family: Veneridae
- Antigona listeri
- Pitar albida

Family: Limopsidae
- Limopsis sp.



DISTRIBUTION OF BIVALVES WITH DEPTH IN REEF CAVITIES, BONAIRE

Bivalves are most abundant in the depth range 21 to 46 m (see Figure). The greatest number of species in cavities is found over the depth range 20 to 40 m based on the raw data; using range-through data, the bivalves show an increase in the number of species present from 3 to 20 m, and a steady decline in the number of species below 30 m depth (see Figure).

The endolithic (boring) bivalves comprise 22% of all bivalve species within cavities. The number of species of borers increases steadily with depth to a peak of 9 species at 21 to 24 m depth, and then declines steadily with increasing depth (see Figure). From 6 to 36 m depth, the borers make up an almost constant percentage of all the bivalve species present, with only a slight increase at 21 to 24 m depth. Below 36 m, the borers decline in importance. The longest-ranging borers are the two most abundant endoliths, Lithophaga bisulcata and Gastrochaena hians (6 to 46 m).

With increasing depth from 6 to 21 m there is a progressive addition of new species to the endolithic assemblage; below 21 m depth Lithophaga nigra Orbigny, Spengleria rostrata Spengler, Gregariella opifex Say, Gastrochaena hians, Lithophaga antillarum Orbigny and Gregariella coralliophaga Gmelin disappear progressively from the endolithic assemblage as depth increases to 40 m (see Figure).

A total of sixteen bivalve species (40%), of which four species are endoliths (10%), range 30 m or more in depth. The percentage of bivalves with large bathymetric ranges is almost twice the percentage of gastropods showing equivalent ranges.

Twenty bivalve families are represented in the cavities, of which the most abundant are the Limidae, Ostreidae, Mytilidae, Chamidae, Trapeziidae, Gastrochaenidae, and Arcidae. The families with a bathymetric range of 30 m or more are the Trapeziidae, Arcidae, Mytilidae, Gastrochaenidae, Chamidae, Ostreidae, Limidae, and the Spondylidae. All of the most abundant families also have among the largest bathymetric ranges. Using range-through data, the number of bivalve families found in cavities shows an increase from 3 to 30 m, and a steady decrease below 30 m.

Exotic Elements

Seven bivalve species found in the cavities normally are found as infauna in sands in shallow to deep water; these include: Atrina cf. seminuda (1 specimen), Macoma sp. (1 specimen), Americardia media Linnaeus (2 specimens), Antigona listeri Listeri (2 specimens), Pitar albida Gmelin (2 specimens), Diplodonta semiaspera Philippi (5 specimens), and Anodontia cf philippina (8 specimens). They are very uncommon, and together amount to only 4% of all bivalve specimens. Although some individuals may have been transported into the cavities from other environments, all of the specimens of these normally infaunal bivalves were found alive in the cavities. They occur wedged into small crevices or within pores (as chasmoliths) in the walls or roof, always with an opening directly to the cavity interior and appear to be indigenous to the cavities. It is not clear how Macoma, which normally

is an infaunal deposit feeder would feed in such a habitat, although it is possible that it is able to make use of sediment falling into the cavities through openings without the shelter provided by burial in sediment.

Comparison of Bivalve and Gastropod Distribution

The ratio of the number of gastropod specimens to bivalve specimens (relative abundance) versus depth shows a general decline with increasing depth; this indicates that in progressively deeper cavities, the bivalves become more abundant relative to the gastropods. Based upon range-through data, the ratio of the number of gastropod species to bivalve species (ratio of species richness or sample diversities) declines down to 12 m depth and then rises to 21 m. The species (richness) ratio is almost constant below 21 m depth.

The number of bivalve species (species richness) at any given depth is consistently higher than the number of gastropod species by an approximate factor of 2. However, both bivalves and gastropods show the same general declining trend in the number of species versus depth.

Species richness (Sample diversity) has the drawback of giving rare species the same weight or relative importance as very abundant ones when attempting to show the diversity for the mollusc populations. Some of the rare species represented by a few individuals could be accidental migrants or have been transported into the cavities by currents or some other mechanism. Species richness does not in any way take into account rare occurrences of this kind and gives them the same importance in measuring population species diversity as much more abundant and clearly indigenous forms. In an attempt to show changes in cavity mollusc species diversity with depth by reducing the effects by including rare or accidental species occurrences, four other diversity indices were calculated from the bivalve and gastropod data: 1) average evenness, 2) Odum diversity, 3) Log-richness diversity, 4) Margalef diversity. Each of these takes the sample size (N) into consideration in the calculations.

The average evenness (number of individuals/number of species) is consistently higher for the bivalves than for the gastropods. The difference in the index for the two populations is smallest in shallow water and increases slightly with increasing depth. Gastropod evenness is low and almost constant with depth, whereas bivalve evenness shows an erratic but general increase.

The Odum diversity (number of species/number of individuals) is highest for the gastropods, and as is the case for average evenness, shows an increased separation of the gastropod and bivalve populations with increasing depth. When related to depth, the gastropod Odum diversity is erratic, but the bivalve Odum diversity generally decreases with increasing depth.

The gastropod log-richness diversity index (calculated as the log of N, the sample size) versus depth shows the largest values in the depth range 21 m to 36 m. The relation to depth is erratic, but as is

DISTRIBUTION OF GASTROPOD AND BIVALVE FAMILIES WITH DEPTH, IN REEF CAVITIES, BONAIRE

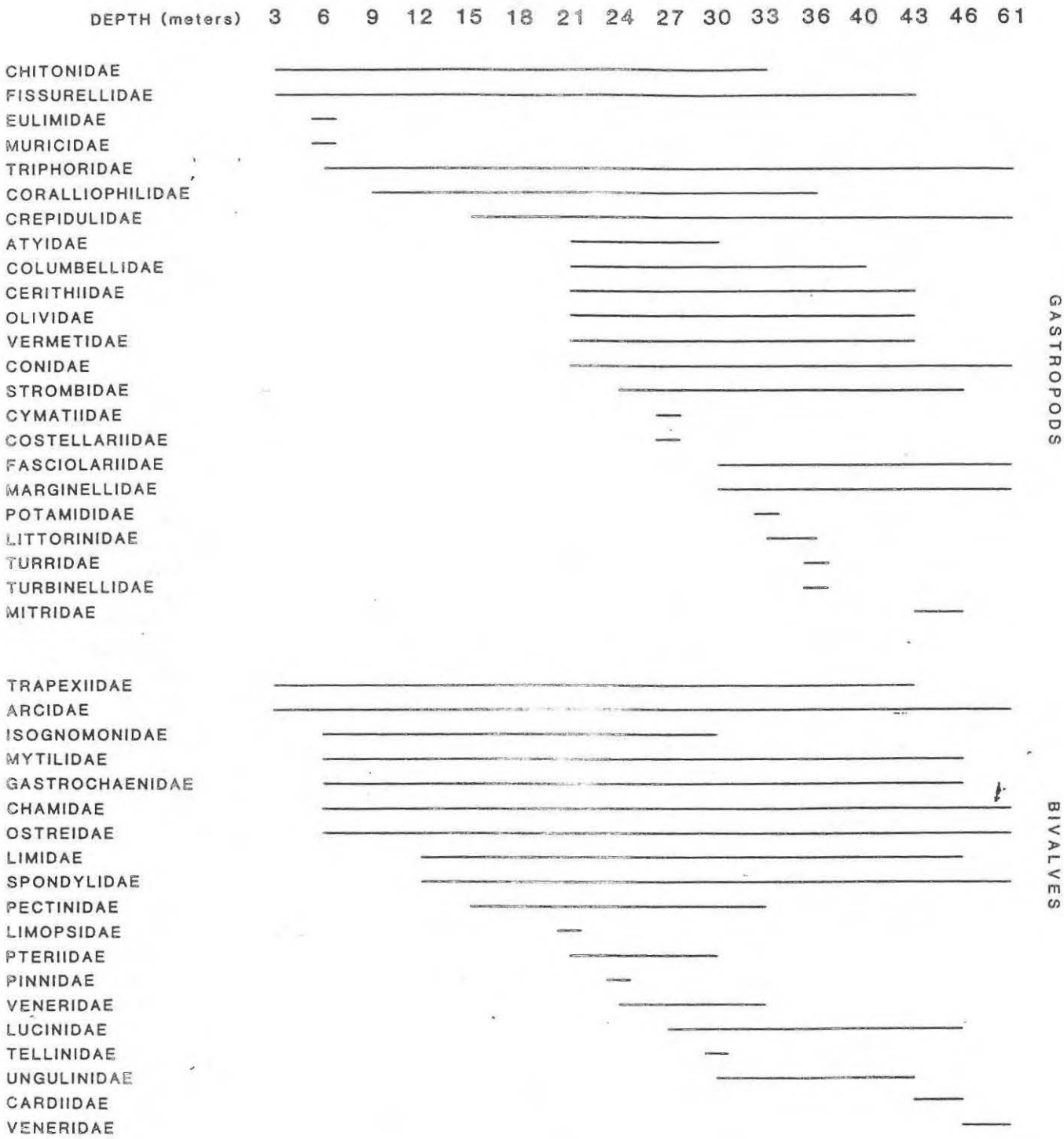


Table. Summary of gastropod and bivalve life habits in Bonaire reef framework cavities. END. = endolithic; SWIM. = swimmer; VAG. = vagrant; LOOSE ATT. = loosely attached; CEM. = cemented; CHASM. = chasmolithic.

Gastropods:

	END.	SWIM.	VAG.	LOOSE ATT.	CEM.	CHASM.
Atys sp.		X	X			
Balcis intermedia			X			
Cerithium litteratum			X			
Cerithium sp.			X			
Cheilea equestris				X		
Chiton sp.			X			
Conus sp.			X			
Coralliophila caribaea			X			
Coralliophila abbreviata			X			
Crassispira cf tampaensis			X			
Cymatium pileare			X			
Diodora cf variegata			X			
Diodora sp.			X			
Emarginula pumila			X			
Hemitoma emarginata			X			
Latirus ? sp.			X			
Littorina ziczac			X			
Marginella avena			X			
Marginella sp.			X			
Muricopsis oxytatus			X			
Nitidella laevigata			X			
Nitidella sp.			X			
Nodilittorina tuberculata			X			
Olivella nivea			X			
Olivella sp.			X			
Pusia gemmata			X			
Seila adamsi			X			
Strombus sp.			X			
Triphora ornata			X			
Triphora turris-thomae			X			
Vasum ? muricatum			X			
Vermicularia knorri					X	
Vexillum pulchellum			X			

Bivalves:

	END.	SWIM.	VAG.	LOOSE ATT.	CEM.	CHASM.
Americardia media						X
Anadara lienosa floridana						X
Anodontia cf philippina						X
Antigona listeri						X
Arca zebra				X		X
Arca sp.				X		X
Atrina cf seminuda				X		X
Barbatia cancellaria				X		
Barbatia candida				X		
Botula fusca	X					
Chama macerophylla					X	
Chama sp.					X	
Chlamys cf sentis		X				
Chlamys sp.		X		X		
Coralliophaga coralliophaga						X
Diplodonta semiaspera						X
Gastrochaena hians	X					
Gregariella coralliophaga	X					
Gregariella opifex	X					
Isognomon radiata				X		
Isognomon sp.				X		
Lima scabra		X				
Limopsis sp.				X		
Lithophaga bisulcata	X					
Lithophaga nigra	X					
Lithophaga antillarum	X					
Lithophaga sp.	X					
Lopha frons					X	
Macoma sp.						X
Modiolus americanus				X		
Modiolus sp.				X		
Ostrea equestris					X	
Ostrea sp.					X	
Pinctada radiata				X		
Pitar albida						X
Pseudochama radians					X	
Pteria sp.		X		X		
Spengleria rostrata	X					
Spondylus americana					X	

seen in the bivalves, there is a significant increase in the index at 21 m depth. In general the log-richness index is highest for bivalves and shows less variation with depth than for gastropods, especially below 21 m depth.

The Margalef diversity index is a measure of the amount of order in the system. It is calculated as the number of species (minus 1) in each sample (at each depth in this study) divided by the log of the number of specimens in the sample (log N). Bivalves show a slightly higher Margalef diversity index than the gastropods at almost every depth. Although the indices for both populations are variable when related to depth, there is an increase at 21 m depth similar to that seen using the other diversity indices.

Both the Log-richness and Margalef diversity indices are based upon log(N) in each sample. Underlying them is the empirically-derived assumption that the greatest number of species in the population shows the minimal abundance. Although this is not true in every community, it is true in the Bonaire cavity mollusc populations, where a small number of species account for a large proportion of the individuals at each depth.

Mollusc Depth Zones

Five mollusc depth zones are defined subjectively on the basis of: 1) the coincident appearance and disappearance of numbers of species, 2) coincident rapid increases and decreases in the relative abundance of several species, and 3) the dominance of one or more species over a given depth range. The boundaries between the depth zones are placed at 3 m, 12 m, 21 m, and 46 m depth; the lower most depth zone boundary is poorly defined due to the large sampling gap at that depth. The zones are shown in the accompanying figures.

Mollusc Taphonomy

Because all of the molluscs found in the cavities are shelled, the overall potential for preservation is high. However, the potential for preservation in the fossil record of a mollusc assemblage recognizable as having lived in cavities is dependant upon the percentage of the whole assemblage that is likely to be preserved *in situ*. Molluscs that fall to the cavity floor after death will either become mixed with shells transported into the cavities or will be removed from the cavities in the migrating sediment; it is not likely that the mixed assemblage of shells found in cavity sediment could be separated into surface-dwelling and cavity-dwelling populations in the fossil state. The bivalves and gastropods that are most likely to be preserved *in situ* as recognizable coelobionts are those living in small holes and cracks in cavity walls and roof, endoliths, and those cemented to the substrate. The accompanying tables summarize the various life habits of the cavity molluscs, and show those that are most likely to be preserved *in situ* based upon whether they live attached to the substrate, or within small holes from which they are unlikely to be removed. Of the 34 gastropod species, only *Vermicularia knorri* is cemented to the substrate; all the others are vagrant, so that only 3% of the entire

Table. Molluscs likely to be preserved in situ in fossilized cavities based upon their life habits in modern framework cavities in Bonaire.

Vermicularia knorri
Anadara lienosa floridana
Antigona listeri
Chama macerophylla
Coralliophaga coralliophaga
Gastrochaena hians
Gregariella opifex
Lithophaga nigra
Lithophaga sp.
Macoma sp.
Ostrea sp.
Pseudochama radians
Spengleria rostrata
Arca zebra
Americardia media
Anodontia cf philippina
Botula fusca
Chama sp.
Diplodonta semiaspera
Gregariella coralliophaga
Lithophaga bisulcata
Lithophaga antillarum
Lopha frons
Ostrea equestris
Pitar albida
Spondylus americana
Arca sp.

gastropod species assemblage is likely to be recognizable as coelobiontic in a fossil reef. The bivalves show a higher percentage (66%) of potentially recognizable coelobiontic species (see Logan, 1974 for a discussion of the preservation potential of S. americanus).

The fossilized assemblage would be dominated overwhelmingly by bivalves (97% of all species), with the gastropods grossly under-represented (3% of all species), so that the preserved assemblage would appear to be dominated by filter and suspension feeders. The relative abundance of endolithic bivalves and their contribution to species diversity also would increase significantly. All of the information on coelobiontic molluscan scavengers, vagrant herbivores, and predators (all vagrant gastropods) would likely be lost.

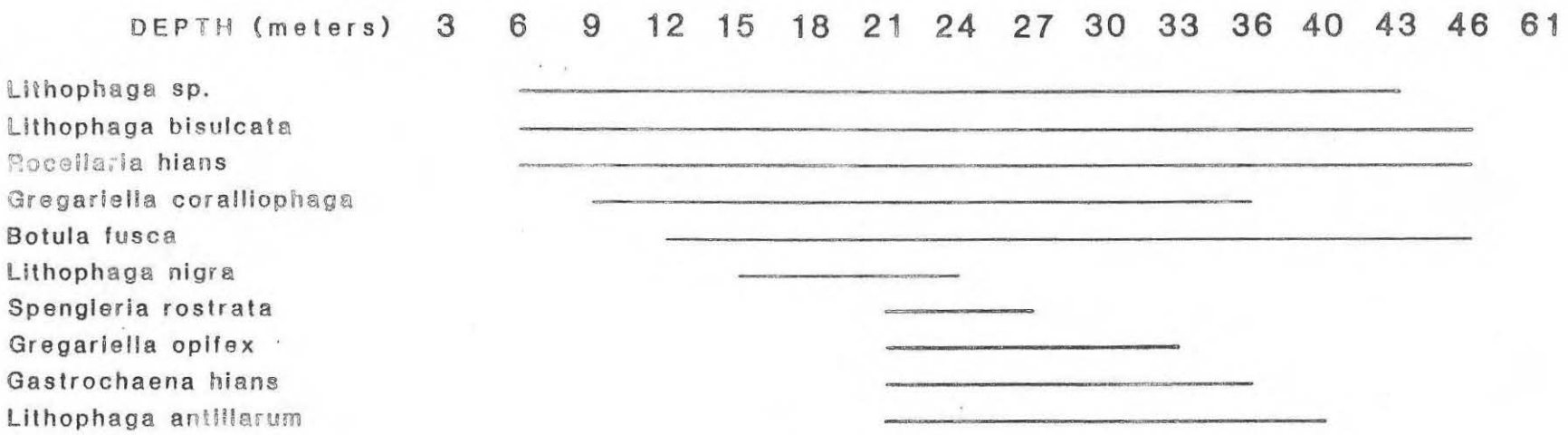
Summary of Cryptic Mollusc Distribution

A total of 34 gastropod and 40 bivalve species from a collection of 610 specimens were found in 60 growth framework cavities over the depth range 3 m to 61 m on the reef slope at 5 localities on the leeward side of Bonaire, Netherlands Antilles.The gastropod assemblage is dominated by Chiton sp., Triphora turris-thomae, Vermicularia knorri, and an unidentified form; the bivalves are dominated by Lima scabra, Ostrea equestris, Coralliophaga coralliophaga, Lithophaga bisulcata, Gastrochaena hians, and Chama sp.

The highest species diversity and greatest abundance of specimens among the gastropods is in cavities from 21 to 30 m depth; the number of species shows a dramatic increase in the 20 to 30 m depth range. The bivalves are most abundant in the 21 to 46 m depth range, with the greatest number of species occurring from 20 to 40 m depth. At any given depth, the number of bivalve species present is consistently higher than the number of gastropod species by a factor of about 2, although both groups show the same general trend in the number of species versus depth.

Most gastropods have a narrow depth range: of the 34 species found, 7 have a depth range of 30 m or more. This contrasts with 16 of the 40 bivalve species that have a depth range of 30 m or more. The coelobiontic gastropod assemblage therefore has a theoretically greater potential than the bivalves as a water depth indicator in ancient reefs because of the greater proportion of species with narrow depth ranges. However, only 3% of the gastropod assemblage is likely to be preserved in situ (1 species) in cavities and therefore be recognizable as coelobiontic, as contrasted with 66% of the bivalve assemblage likely to be recognized as coelobiontic in fossil cavities. The resulting fossil assemblage derived from a living community such as found in the Bonaire reef cavities would comprise 97% bivalve species and 3% gastropod species, which contrasts dramatically with the living proportions of 46% gastropod species and 54% bivalve species. In studying ancient reef cavity systems in which gastropods and bivalves are preserved, it should be noted that the coelobiontic gastropod assemblage is likely to be greatly under-represented, and the bivalve assemblage over-represented.

DISTRIBUTION OF ENDOLITHIC (BORING) BIVALVES IN REEF CAVITIES, BONAIRE



SEDIMENT

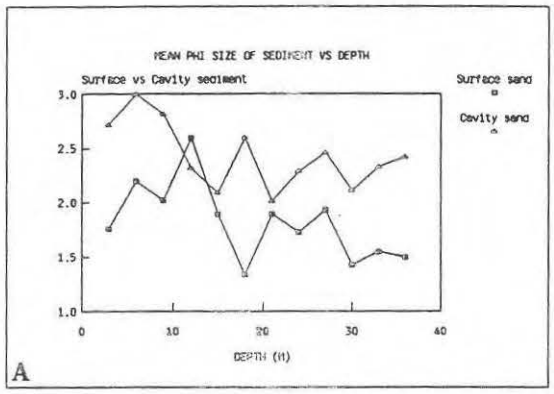
Study of the distribution of carbonate sediment on the leeward reef of Bonaire has focused upon similarities and differences between sediment exposed at the surface of the reef and that in open growth framework cavities. Samples were collected at 3 meter depth intervals over the depth range 3 meters to 36 meters along a transect off the Aquahabitat area. The samples were dried, impregnated with epoxy under vacuum, and thin sectioned. All the grain parameters reported here were measured from 48 thin sections of samples from 12 cavities and 12 surface sample stations outside of, and immediately adjacent to, each sampled cavity. Four hundred grains from each sample were studied, and for each grain, the following were determined: grain size, grain composition, grain angularity and the percent of each grain converted to micrite. The resulting data base comprises 38,400 measurements from 9600 grains.

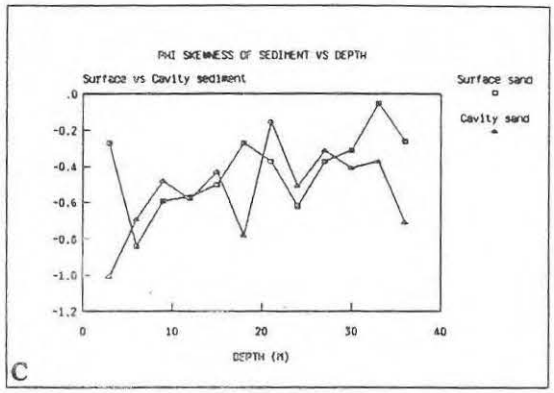
Grain Size

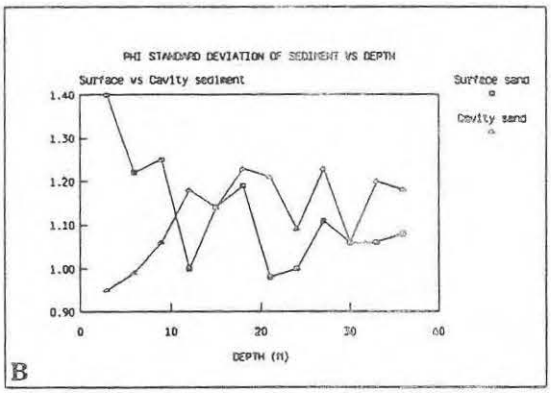
Sediment from the surface of the reef and from cavities shows an overall coarsening with increasing depth; on the reef surface sediment becomes finer to a depth of 12 meters before coarsening with depth. Cavity sediment (range 2.01 Phi to 3.03 Phi) is finer than sediment at the surface (range of mean size 1.3 Phi to 2.2 Phi) so that over the entire sample depth range there is a clear size difference between surface and cavity sediment (Fig. 11A).

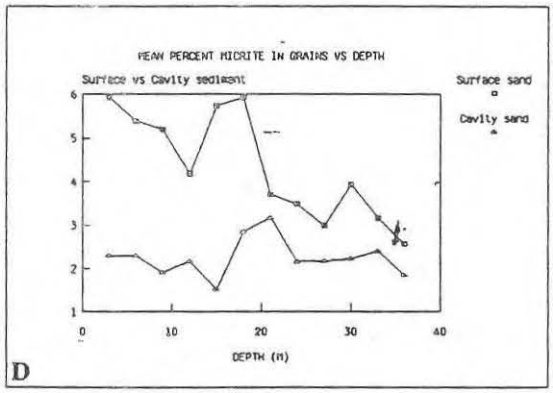
At depths shallower than 12 meters the Phi standard deviation of surface sediment (range 1.22 to 1.4) is greater than that of cavity sediment (range .95 to 1.06). This indicates that sediment in cavities is slightly better sorted than sediment at the reef surface; this surprising observation cannot be explained at present. Below about 12 meters depth this changes, so that cavity sediment tends to have a marginally larger Phi standard deviation (se Figure). The 10 to 12 meter depth where this occurs corresponds to the break where the reef slope beings. The Phi standard deviation of surface sediment shows a general decrease with increasing depth, which is the reverse of the trend shown by cavity sediment. As a result, on the reef slope surface sediment becomes increasingly better sorted with depth, whereas cavity sediment becomes more poorly sorted.

There is little evidence of a separation of cavity and surface sediment over the 3 m to 36 m depth range if Phi skewness is related to depth (see Figure). All skewness values are negative, and show a decrease with increasing depth, indicating that in shallow water the sediment tends to be skewed to the coarse grain sizes, and changes to increasingly less coarse grain skewness as depth increases. This may be due to the deposition of fine sediment washed into the deeper water of the reef slope from the more agitated shallow barren zone. In the









Computer-generated graphs of grain size parameters and micritization in surface and cavity sediments.

shallowest surface and cavity samples (3 m depth) as well as in the deepest samples (30 m to 36 m) surface sand is less negatively skewed than cavity sand, indicating that sediment within cavities at these depths is skewed less to coarse grain sizes.

In summary, sediments on the surface of the reef and in reef cavities show different size distributions and trends with increasing depth. In the shallow water on the barren zone surface sediment is coarser than cavity sediment and shows poorer sorting, with a greater skewness toward coarser grains. With increasing depth both surface and cavity sediments show a decrease in mean Phi size (coarsening), with cavity sediment tending to become finer than sediment on the surface. Both surface and cavity sediments show a reduction in skewness toward coarse grains with increasing depth; cavity sediment becomes increasingly more poorly sorted with depth, whereas surface sediment shows increased sorting.

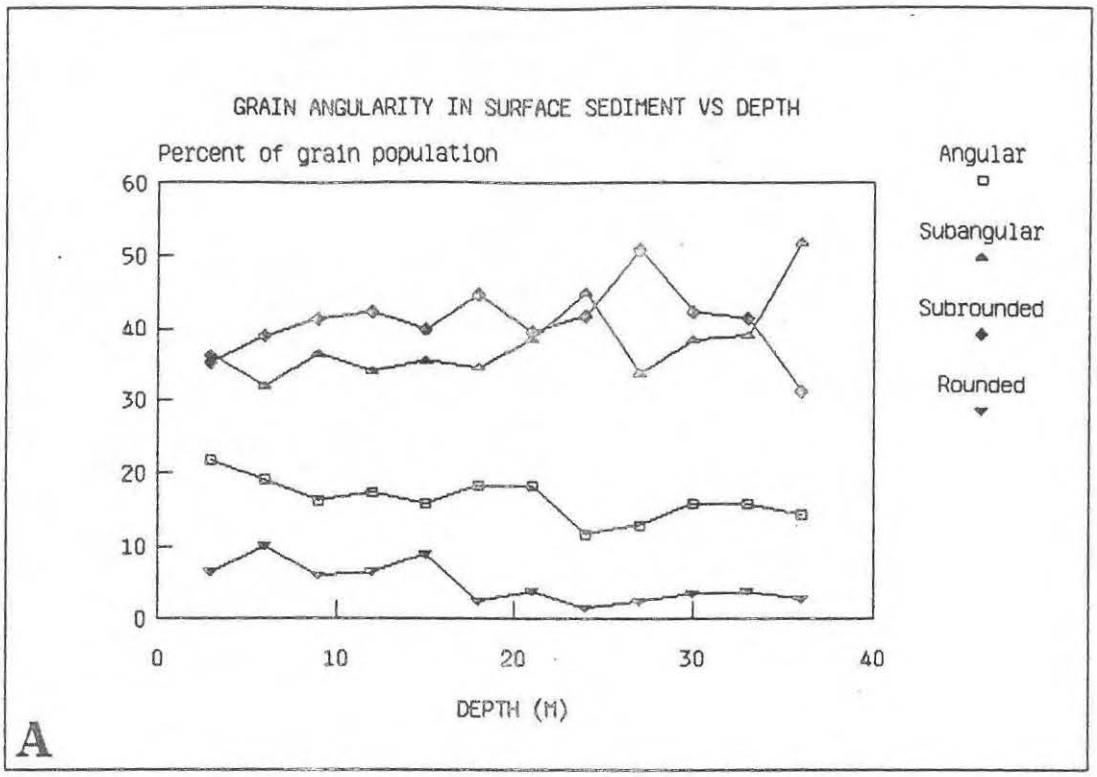
Angularity

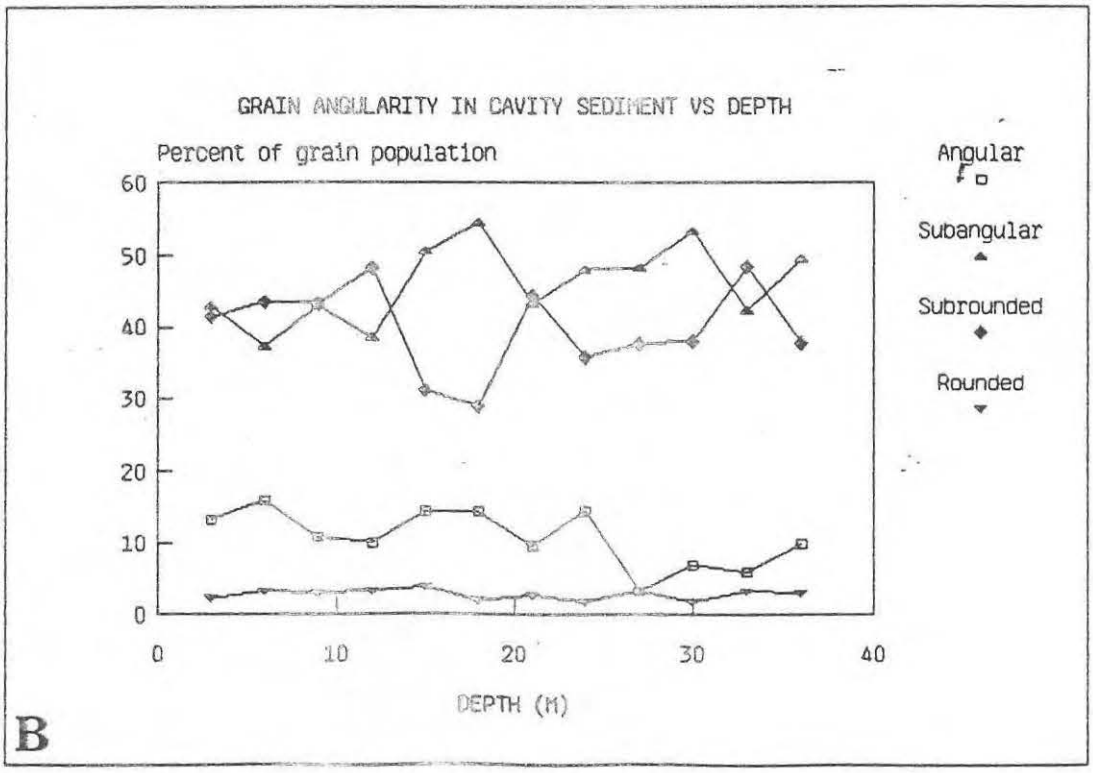
Between 60% and 80% of the grains at all depths in both surface and cavity sediments are subangular to subrounded; rounded grains are least abundant. In surface sediments, the percentage of both rounded and angular grains decreases with increasing depth, whereas in cavity sediments the percentage of rounded grains shows no relation to depth; the percentage of angular grains shows only a very poorly correlated decrease with depth (see Figure).

In general, surface sediments have more rounded and angular grains than do cavity sediments, so that grains in surface sediments tend to be more broadly distributed across all 4 main angularity classes than in cavity sediments. As a result, it is possible to distinguish between surface and cavity sediments on the basis of grain angularity.

Micritization

Grain micritization was measured as the percentage of each grain made up of micrite. Almost all of the grains encountered in thin sections were skeletal, and the micrite was the result of destructive micritization by algae and fungi. The degree of grain micritization can therefore be used as a measure of micro-endolithic activity. Grains in surface sediments show more intensive micritization than do grains in cavity sediment (see Figure); the difference is most pronounced in shallow water where the mean percent micrite content of grains at the surface of the reef is 4% to 6% whereas grains in cavities show 2% to 3% mean micrite content. Surface sediment shows a decrease in the mean percent micrite in grains with increasing depth, but cavity sediment shows no decrease with depth (see Figure). At depths of 30 m to 36 m the mean micrite content in both surface and cavity sediment grains is almost equal.

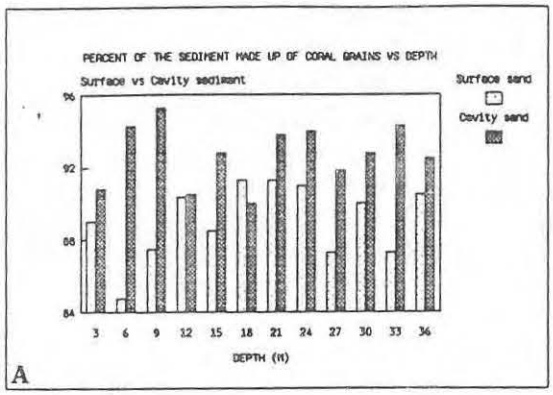

GRAIN ANGULARITY IN SURFACE SEDIMENT VS DEPTH
Percent of grain population
60
50
40
30
20
10
0
0
10
20
30
40
DEPTH (M)
Angular
Subangular
Subrounded
Rounded
A

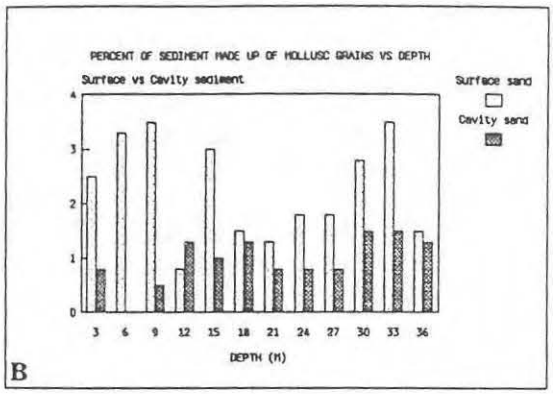

GRAIN ANGULARITY IN CAVITY SEDIMENT VS DEPTH
Percent of grain population
60
50
40
30
20
10
0
0
10
20
30
40
DEPTH (M)
Angular
Subangular
Subrounded
Rounded
B

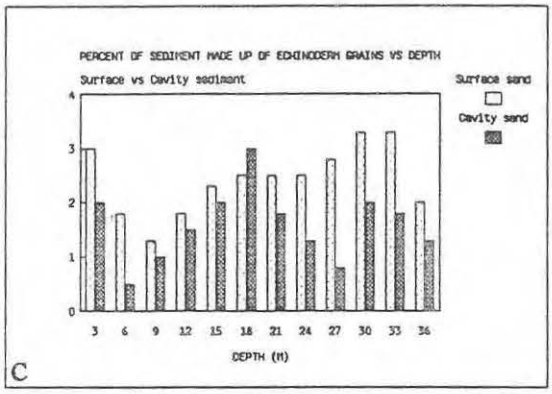
The decreasing micrite content of grains in surface sediments can be correlated with decreasing light intensity and altered light spectral composition with depth, which affect the rate at which algae bore and their species distribution. Cavities are shaded habitats even in very shallow water, so that micro-endolithic activity should be less than in surface environments receiving direct illumination. This in part accounts for the lower mean micrite content in cavity sediment grains at all depths; however, the light levels in cavities also decrease with increasing depth, so that it should be expected that the mean percent micrite content of cavity grains would decrease with depth as it does in surface sediments. It is not known at present why this decrease does not occur. To speculate, it is possible that as light levels decrease, in the cavities a declining endolithic algal population is replaced more rapidly by fungi (not light-dependent) than at the surface as light levels decline.

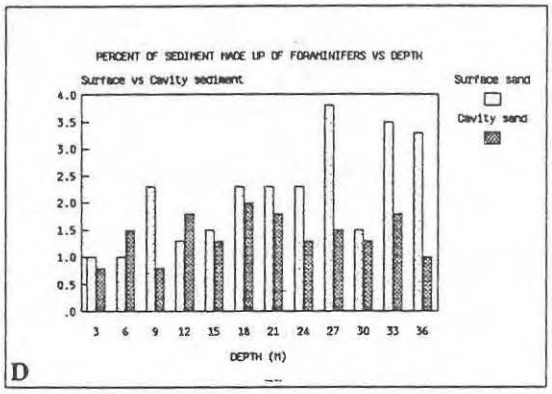
Sediment Composition

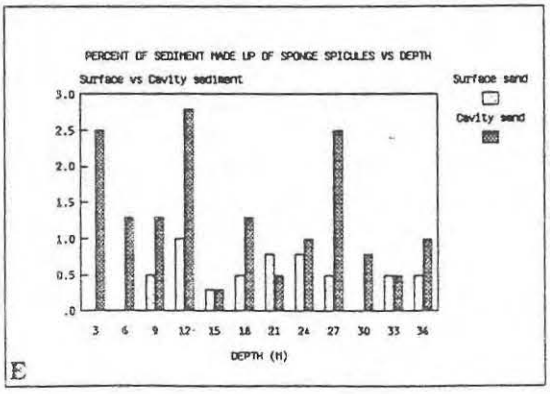
The sediment both inside and outside of cavities is composed dominantly of the following: coral and mollusc fragments, calcareous algae and echinoderm fragments, foraminifers, sponge spicules, fragments of arthropod carapace, worm tubes, other rare grains such as quartz and feldspars, and ascidian and gorgonian spicules. Scleractinian coral debris comprises 84% to 95% of all the grains; these grains are more common in cavity sediments where they make up 90.0% to 95.3% of the sediment. In surface sands coral grains are less abundant, making up 84.8% to 91.3% of the sediment (see Figure). Mollusc grains (bivalve and gastropod) are most abundant in surface sediments compared to cavity sediments but tend to decrease in abundance in the 18 m to 27 m depth range on the reef surface (see Figure). Echinoderm grains generally are slightly more abundant in surface sediments than in cavities, but show a peak of abundance in cavities at about 18 m depth (see Figure). Foraminifer tests are most abundant in surface sediments where they show a general increase in abundance with increasing depth; in cavity sediments the abundance of foraminifers shows no relation to depth (see Figure). Sponge spicules are most abundant in cavity sediments at almost all depths, and reflect the great abundance of sponges in cavities in the Bonaire reefs (see Figure).











Computer-generated graphs showing comparisons of the 5 most abundant grain types in reef surface and reef cavity sediments versus depth.

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RESEARCH PLAN

Purpose and Perspective

The overall purpose of this research project is to investigate coral reef cavity-dwelling biotas (also termed coelobionts) from a geological and ecological perspective.

Very little is known of organisms that inhabit the interior of reefs, and almost nothing is known of their fossil history and evolution. Only recently has the very great age of the cavity-dwelling community been realize. Kobluk and James (1979) have found coelobionts in well preserved fossil reef cavities almost 530,000,000 years old from the coast of southern Labrador; even older (about 535 x 106 years) coelobionts have more recently been described from reef cavities exposed in fossil reefs in western Nevada (Kobluk, 1981). Clearly, the fossil record of this community is very ancient. Much of what we are learning from the study of the modern reef cavities in Bonaire is being applied directly to the interpretation of these and similar fossil reef cavity ecosystems.

Although none of the fossil forms found in the ancient cavities are extant, many of the major groups they represent are (e.g. in the fossil reef cavities there are extinct representatives of crustaceans, foraminifera, algae, brachiopods, echinoderms, etc., all of which have living representatives in modern reef cavities). The structure of the organism community (i.e. the structure of the cavity ecosystem, including feeding types and organism interaction) is essentially similar to what we find today even in the most ancient of fossil reef cavities. The modern and fossil organisms found in cavities are not the same, but their roles are the same: there are modern filter feeders in cavities just as in ancient cavities, etc.. An analogy would be that of an apartment building: through time the building (i.e. cavities in the reef) stays basically the same, but the families (organisms) inhabiting the apartments continually change.

Modern coral reefs abound in cavities, which may make up to 40% of the volume of the reef. These can be classified in many ways, but one of the more useful classifications is made on the basis of light reaching the interior of the cavities:

1. Dark cavities - these cavities are open to water circulation, but receive no light; they are open to the surface indirectly through long tunnels or by being interconnected with other cavities. An observer must use a light.

2. Gloomy cavities - cavities which are dark, but receive enough light to enable the observer to perceive shapes. It is like being outside at night on a particularly well moonlit night.

3. Open cavities - not as light as the reef surface, but light enough to plainly see objects; a light is not required by the observer.

Each of these cavity types, produced by the upward growth of the reef, contain distinct and different organism communities. In living reefs, the dark cavities commonly are accessible only by blasting. The open gloomy cavity types usually are accessible from the reef surface and may be studied directly.

The effects that coelobionts have upon the geological structure of a reef are not fully understood; some that are known, however, include:

1. Production of internal reef sediment by the action of endolithic (boring) organisms boring into the walls of the cavities.

2. Enlargment of reef cavities and the enhancement of permeability in reefs through boring.

3. Reduction of reef porosity and permeability by encrustation of cavity walls and roof by organisms.

Cavities also may function as "broods" in which juvenile organisms find protection until they are able to survive in the surface environment on their own. Cavities also serve as a refuge for some organisms that even in adult or large form, may not be able to compete with other more successful or better adapted organisms on the outside. Such an example is found in the cryptic sponge and brachiopod communities discovered in caves and cavities in Jamaican reefs.

Only a portion of the community inhabiting reef cavities has been described in the scientific literature; this is due to the new-found interest among geologists and biologists in this field, a relatively sudden and recent awareness of the great significance of these communities, and the

small number of researchers currently working in this field. Clearly, by not understanding the reef coelobiontic community in modern reefs, we are overlooking a key piece in the mosaic of the coral reef. Until we gain a clear picture of the role of coelobionts and the structure of the cryptic community in reefs, there is little hope of fully understanding the complex history of development of coelobiontic faunas and floras over the last half billion years.

RESEARCH OBJECTIVES

This project is designed to povide basic information relating to the ecology and geology of the "open" and "gloomy" reef cavity systems (see above). The ultimate aim is to produce a "base line study" from which an understanding of ancient cavity-dwelling organisms may be gained by applying directly or indirectly to ancient reef cavities what is known of modern ones.

Our work is long-term, so that each year a new aspect of the cavity system is tackled. For example, in the past we have mapped a large portion of the reef surface to provide us with a baseline with which to compare the cavity communities. We have sampled many organism groups from cavities at all depths, including sponges, hydroids, gastropods (snails), bivalves (clams), diatoms, worms; in 1984 we studied the cavity-dwelling corals. Still to be done are surface area and size measurements of corals and other cavity-dwelling organisms such as sponges, encrusting hydrozoans (Millepora), algae, and others.

Among the problems this project will address are:

1. What is the nature of the transient cavity fauna (i.e. what animals move through, between, or within cavities).

2. What sort of preservable traces do these mobile organisms produce, and what effects do they have on the sediment.

3. What is the rate and nature of infestation of cavity walls and roof by endolithic (boring) algae and fungi, and larger organisms such as worms and bivalves.

4. What is the rate of establishment of new cavity encrusting organisms on hard surfaces in cavities.

5. What is the composition of the fauna and flora encrusting the walls and roof of cavities of different types at various water depths. This involves extensive collecting and in situ observation of organisms living in cavities.

Geologists are keenly interested in how the composition of reef communities changes with depth. This applies to communities within reef cavities as well, but we are still at the stage of attempting to demonstrate that some groups of cavity-dwellers vary with increasing water depth. Because of this critical emphasis on depth most of our collecting and observations are stratified by depth: for example, 5 pairs of divers will be sent at one dive locality to depths of 10, 20, 30, 40, 50 ft. or 10, 30, 50, 60, 80 ft., etc. to observe or collect.

APPLICATION OF RESULTS

There is the continuing hope among reef researchers that many of the classic problems in coral reef studies finally may be resolved eventually. However, with every problem solved, new problems arise of which we were not even aware previously. There is still a very great deal to be learned about the functioning of the coral reef ecosystem. That geologically important organisms live their entire lives within the reef is quite new to geological thinking, and has wide application in many areas; among them are problems of porosity and permeability modification in reefs (related to petroleum and gas reservoir development and exploration), cementation processes (production of rock from loose sediment), sediment production within reefs, and a host of problems related to understanding the roles of very ancient organisms in fossil reefs. Applications in paleontology and biology are greatest in increasing our understanding of the evolution of several important groups of organisms, and perhaps in the discovery of the very origins of some.

The results of this work in Bonaire are being applied directly within the context of a more general study of the early geologic history of reef coelobiontic organisms in fossil reefs in Labrador, Ontario, Quebec, Virginia, Poland, and California/Nevada.

METHODS AND LOGISTICS

In Bonaire this year, the field work will focus upon detailed mapping of the reef, together with sampling of reef cavity-dwelling organisms.

The work will involve SCUBA diving, at depths from 2 to 35 meters. The actual depth at which an individual works will depend upon his or her diving experience. One dive will be in the morning, and the other dive will be in the afternoon. Each second day will involve only one dive. We do not use boats on this project because of the ideal access to the reefs available in Bonaire from shore. This helps reduce our diving costs

Participants will be given introductory talks and seminars to introduce them to the organism types they will be describing, and other more general aspects of reef ecology and geology. In addition, participants will be brought up-to-date on the work of the past teams and the interpretation of data gathered to date.

ACCOMMODATION

Accommodation will be in 2 convenient adjoining private bungalows with an ocean front view on the southern outskirts of Kralendijk, the island capital. The houses provide all the modern conveniences including beds, linens, gas stove, refrigerator, running water, shower, ocean view, etc.

We will have 2 radios on hand for entertainment, but there is no telephone at the houses.

PHYSICAL CONDITIONING

Conditions will be challenging, rarely difficult. Participats should be in good general physical condition, without specific physical handicap. Expect periods of 1/2 hour to 1 hour in the water, and very short hikes over easy terrain.

Each participant is given ample opportunity for independent and responsible work, and after proper introduction and training will be asked to carry on some operations independently. Among these will be specimen collection, and observation, and possibly some other diving operations (in pairs and only after suitable familiarity with the reef has been gained).

All the participants must be good swimmers and comfortable in the water. All must be capable snorkelers. All of the research team must be qualified SCUBA divers, with NAUI, PADI, ACUC, or similar certification. It is not essential to have had previous tropical reef experience, though the diver should have done some open water diving.

INSTRUCTIONS AND BRIEFINGS

Three teams, of 6-8 participants each, will operate in Bonaire for 2 weeks each, one following the other.

Each team will receive an informal talk dealing with the organisms to be expected in the cavities, basic reef ecology, structure, and geology, and the history of reefs over geologic time. There will be guidebooks on hand, as well as specialized identification guides to aid participants in the identification of some of the organisms that will be encountered.

You will find that the approach to briefings used on this project is very informal; apart from 1 formal session on the morning of your first day, there will be no planned formal seminar or discussion sessions. Instead, we want you to ask questions, initiate discussion, or ask for discussion sessions when you feel you want them. The best times are after dives and after dinner each night, or during the non-work afternoons. Please feel free to bring up discussions at any time and always ask questions - ask a lot of them, and try to get as much out of your participation as you possibly can.

Our attitude to this expedition is that it is both a research and learning experience. We like to talk geology and reef ecology, so try to give us a chance to do it.

You should leave the project with a basic understanding of the southern Caribbean region, its coral reef structures and organism communities, and the general and detailed significance of the work you are carrying out.

STAGING AREAS AND ITINERARY



Bonaire: Kralendijk (Bonaire) international airport (Flamingo Airport); May 20, 1987 for team 1; same location for departure of team 1 on June 2, 1987. Team 2 arrives at Flamingo Airport on June 5, 1987, and departs on June 18, 1987; Team 3 arrives June 21, and departs July 4. The principal investigator will meet all participants at the airport in Bonaire upon arrival. Please be certain that Earthwatch knows your arrival schedule well before you are due to arrive in Bonaire. Transportation to, and from, the airport will be provided. Please do not arrive in Bonaire before your due date, as *accommodation will not be available on the site until the starting dates for each team.*

MEDICAL

A routine physical examination is strongly recommended for all persons SCUBA diving. Although passports technically are not required for entrance to Bonaire, one cannot travel to Bonaire from any other Caribbean island without one. General rule: bring your passport. No special vaccinations are required for U.S. or Canadian citizens departing from points in the U.S. or Canada. Visas are required for stays longer than 14 days.

Persons having serious reactions to certain organisms such as sponges, fire coral, or urchins, salt water, heat or sun, or who suffer from claustrophobia, are not encouraged to participate. Persons abnormally subject to severe sinus infections, ear infections, or the like also are discouraged from participating. Insect repellants generally are not required; your favourite sun tan or sun screen oil may or may not be available in local stores. A doctor is available in nearby Kralendijk. Persons of excessive weight should be aware that work in the open field in the tropics may cause physical hardship.

FIELD SUPPLIES

Required for surface work:

- shorts
- long pants (optional)
- running shoes or sandals with secure straps
- sunglasses, or polaroids
- sunscreen oil or similar product

Required & recommended for underwater work:

- regulator (essential)
- underwater watch (essential)
- depth gauge (essential)
- scuba tank submersible pressure gauge (essential)
- wet suit jacket (optional)
- T-shirt to prevent sunburn (essential if not using a wet suit)
- light gloves (optional, but recommended)
- mask, fins, snorkel, inflatable vest (essential)
- weight belt without weights
- tanks are supplied with backpacks
- submersible dive tables (strongly recommended)

Dress during the day is highly informal, and almost anything is suitable; dress for comfort. However, people are expected by the locals to dress properly and modestly when in town: although you will occasionally see tourists in bikinis and skimpy bathing suits wandering around town, this is regarded in Bonaire as tasteless, and depending upon the "exposure index", offensive. For those interested in the limited night life, short-sleeved leisure suits or colourful shirts, trousers and slacks, etc., in bright colours are worn by men. Women generally in slacks and sleeveless colourful top in local spots; dress or dress slacks in the hotels or night club.

Mail service to Bonaire from North America is slow. Mail (always use airmail) and telegrams may be directed to: c/o General Delivery, Kralendijk Post Office, Kralendijk, Bonaire, N.A. In the Dutch West Indies, overseas calls are made via the cable office (Lands Radio Co., Kralendijk) from which cables may be sent. Therefore, no phone number is available for Bonaire. Telegrams, addressed c/o General Delivery, Kralendijk Post Office, are fast and the best way to be certain of receipt of important communications.

April 30, 1986

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Birth Date: February 4, 1949

Citizenship: At Birth - Canadian; Current - Canadian

Additional: G-Class Driver's Licence; NAUI Certified Scuba Diver

EDUCATION

High School	- St. Thomas High School, Pointe Claire, Quebec Graduated, Junior Matriculation, 1966
University	- McGill University, Montreal, Quebec Bachelor of Science, Geology, 1971
Graduate School	- McGill University Montreal Quebec Master of Science, Graduated 1973 Thesis, Geology
	- McMaster University, Hamilton, Ontario Ph.D. Program, Geology 1976
Postdoctoral Fellow	- Memorial University Department of Geology St. John's, Newfoundland 1976-1977
Additional	- Business Management Courses Two year correspondence course with LaSalle Extension University, Chicago, Ill. Diploma in Business Management - Computer Programming Extension Course at McMaster University in computer programming with Fortran IV, 1974. - Common Law Three year correspondence course with LaSalle Extension University, Chicago, Ill. Credit toward Ontario Bar examination; in California recognized as sufficient training in law for admission to the bar.

- Principles of Benthic Community Analysis Course at University of Miami, Florida, given by A.M. Ziegler, K.R. Walker, E.J. Anderson, E.G. Kaufman and R.N. Ginsburg, November, 1974.

BACKGROUND

University and Graduate School

Extracurricular Activities
- Graduate Study Committee, McMaster University, 1974-1975
- Committee member, speakers selection committee, Geology, McMaster University
- Chairman of Speakers Committee, Adams Geology Club, 1973
- Certified NAUI Scuba Diver, 1973
- Member, Adams Geology Club, 1971-1973
- Member, Monteregian Geology Club, 1966-1972
- Vice-President, Monteregian Geology Club, 1969-1970
- Editor of Monteregian Geology Club publication,1970
- Chairman of the Undergraduate Curriculum Evaluation Committee, 1969-1970
- Student undergraduate representative to the Faculty, 1970
- Member, CNRA Archery Club, 1968-1969
- Photography, both hobby and commission basis

Honours, Awards
- Institute for Marine Sciences Assistance Fellowship, 1976
- McMaster University Research Assistantship. 1975-1976
- Ontario Graduate Scholarship, 1975-1976
- McMaster University Research Assistantship, 1974-1975
- McMaster University Research Assistantship, 1973-1974
- National Research Council Research Assistantship, 1972-1973
- National Research Council of Canada Bursary, 1971-1972
- R.P.D. Graham Scholarship, 1968-1969
- Logan Scholarship, 1967-1968

Grants
- McMaster University Research, Travel Grant, 1976
- McMaster University Dept. Geology Travel Assistance Grant, 1976
- Geological Society of America Penrose Bequest Research Grant, 1975
- McMaster University Dept. Geology Travel Assistance Grant, 1975.
- Geological Society of America Penrose Bequest Research Grant, 1974
- Grant-in-Aid, University of Miami, 1974

Post University

Professional Affiliations
- Association of Geoscientists for International Development
- American Association of Petroleum Geologists
- American Geological Institute
- Canadian Society of Petroleum Geologists
- Society of Economic Paleontologists and Mineralogists: both Paleontology and Sedimentary Petrology Sections
- Paleontological Association (Britain)

Grants
- National Research Council Operating Grant, 1986-87
- Earthwatch Research Grant (2 grants), 1986
- Earthwatch Research Grant (2 grants), 1985
- National Research Council Operating Grant,1984-85
- Earthwatch Field Research Grant (2 grants), 1984
- National Research Council Operating Grant, 1981-83
- National Research Council Operating Grant, 1980
- Earthwatch research grant, 1980
- Earthwatch research grant, 1978
- Sigma XI Society research grant, 1977
- Earthwatch research grant, 1977
- Memorial University operating grant, 1977
- National Research Council Operating Grant, 1978
- University of Toronto Advisory Comm. on Educational Development grant, 1978
- University of Toronto Connaught Commonwealth Research Award, 1978
- Erindale College Internal Grant, 1977
- Erindale College Internal Grant, 1978
- Earthwatch research grant, 1979
- National Research Council Operating Grant, 1979
- Erindale College Internal Grant, 1979
- Earthwatch Field Research Grant, 1981
- Earthwatch Field Research Grant, 1982
- Earthwatch Field Research Grant (2 grants), 1983
- Erindale College Internal Grant, 1982

Appointments and Committees
- Chairman, Senate Ph.D. defense for E.T. Meddings, Univ. of Toronto,1986.
- Chairman, Search Committee, to fill tenure track Petrology position, Dept. of Geology, 1986.
- Associate Chairman of the Department of Geology (Erindale), 1984-1987.
- Appointment to the School of Graduate Studies faculty

University of Toronto, 1978
- Earth Sciences representative to Erindale College Library Committee, 1979 to 1986
- Committee on teaching assistantships and graduate awards, 1979 to 1986
- Department of Geology council, 1979-80-81
- Earth and Planetary Sciences representative to the Erindale College Centre B Research Committee, 1978-79
- Earth Sciences Representative to Academic Affairs Committee, Erindale College, 1978-79
- Appointed Associate of the Institute for Environmental Studies, University of Toronto, 1981-present
- Committee on Plagiarism and Cheating, Erindale College, 1981-82.
- International Assoc. Sedimentologists Field Trip Organizing Committee, 1981-82.
- Graduate Scholarships Committee (Geology) 1980-86.
- Graduate Affairs Committee (Geology) 1983-86.

Functions
- Co-organizer of Peel County Geography Teachers Professional Development Conference, Nov. 30, 1978.
- Organizing and mounting Bonaire '79 expedition, Aug. 15-30, 1979
- Co-leader, "Carbonate Rocks and Paleoenvironments of Ontario" fieldtrip, for the International Association of Sedimentologists Conference, Hamilton, Ontario, 1982.
- Leader, "Carbonate Rocks and Coral Reefs of Bonaire, Netherlands Antilles" fieldtrip, for the Geol. Assoc. of Canada annual Mtg., London, Ontario, 1984.

Honours
- Election as a Fellow to the Explorers Club of New York, 1980
- Included in Who's Who in the East, 1983.
- Professional papers and career biography added to the collections of the American Heritage Center, Univ. of Wyoming, Laramie, 1984.

PUBLICATIONS

THESES

Kobluk, D.R., 1973, The paleoecology of stromatoporoids from the southeast margin of the Miette carbonate complex, Jasper National Park, Alberta: M.Sc. Thesis, McGill University, Montreal, Quebec.

Kobluk, D.R., 1976, Boring and cavity-dwelling algae: effects on cementation and diagenesis in marine carbonates. Ph.D. Thesis, McMaster University, Hamilton, Ontario.

PUBLICATIONS IN REFEREED JOURNALS

Kobluk, D.R., 1974, The orientation of Amphipora ramosa fragments and their potential for use in paleocurrent studies in Devonian carbonate complexes: Bull. Canadian Petroleum Geology, v. 22/3, p.353-356.

Kobluk, D.R., 1975, Stromatoporoid paleoecology of the southeast margin of the Miette carbonate complex, Jasper Park, Alberta: Bull. Canadian Petroleum Geology, v. 23/2, p. 224-277.

Kobluk, D.R., and Risk, M.J., 1974, Devonian boring algae or fungi associated with micrite tubules: Candian Jour. Earth Sci., v. 11/11, p. 1606-1610.

Kobluk, D.R., and Hall, R.L., 1976, Preserved colour patterns in Ormoceras westonense from the Middle Ordovician of Quebec: Canadian Jour. Earth Sci., v. 13/10, p. 1479-1481.

James, N.P., Kobluk, D.R., and Pemberton, S.G., 1977, The Oldest macroborers: Lower Cambrian of Labrador: Science, v. 197/4307, p. 980-983.

Kobluk, D.R., Bottjer, D., and Risk, M.J., 1977, Disorientation of Paleozoic hemispherical corals and stromatoporoids: Canadian Jour. Earth Sci., v. 14, p. 2226-2231.

Kobluk, D.R., and Risk, M.J., 1977, Algal borings and framboidal pyrite in Ordovician brachiopods: Lethaia, v. 10, p. 135-144.

Kobluk, D.R., and Risk, M.J., 1977, Calcification of exposed filaments of endolithic algae, micrite envelope formation, and sediment production: Jour. Sedimentary Petrology, v. 47/2, p. 517-528.

Kobluk, D.R., and Risk, M.J., 1977, Micritization and carbonate grain binding by endolithic algae: Bull. Amer. Association Petroleum Geologists, v. 61/7, p. 1069-1082.

Kobluk, D.R., and Risk, M.J., 1977, Rate and nature of infestation of a carbonate substratum by a boring alga: Jour. Exp. Marine Biol. Ecol., v. 27, p. 107-115.

Kobluk, D.R., 1978, Reef stromatoporoid morphologies as dynamic populations; application of field data to a model and the reconstruction of an Upper Devonian reef: Bull. Canadian Petroleum Geology, v. 26/2, p. 218-236.

James, N.P. and Kobluk, D.R., 1978, Lower Cambrian patch reefs and associated sediments: southern Labrador, Canada: Sedimentology, v. 25, p. 1-35.

Kobluk, D.R., Pemberton, S.G., Karolyi, M., and Risk, M.J., 1977, The Silurian-Devonian disconformity in southern Ontario: Bull. Canadian Petroleum Geology, v. 25, p. 1157-1186.

Kobluk, D.R., James, N.P., and Pemberton, S.G., 1978, Initial diversification of macroboring ichnofossils and exploitation of the macroboring niche in the Lower Paleozoic: Paleobiology, v. 4/2, p. 163-170.

Pemberton, S.G., and Kobluk, D.R., 1978, The oldest brachiopod burrows: Lower Cambrian of Labrador: Canadian Journal of Earth Sciences, v. 15/8, p. 1385-1389.

Kobluk, D.R. and Kahle, C.F., 1978, Geologic significance of boring and cavity-dwelling marine algae: Bull. Canadian Petroleum Geol., v. 26, no. 3, 362-379.

Kobluk, D.R. and James, N.P., 1979, Lower Cambrian cavity-dwelling organisms in archaeocyathid patch reefs from southern Labrador: Lethaia, v. 12, p. 193-218.

Kobluk, D.R., 1979, A new and unusual Lower Cambrian skeletal organism : Canadian Journal of Earth Sciences, v. 16, p. 2040-2045.

Pemberton, S.G., Kobluk, D.R., Yeo, R. and Risk, M.J. 1980. The boring Trypanites at the Silurian-Devonian disconformity in southern Ontario: Jour. of Paleontology, v. 54, p. 1258-1266.

Kobluk, D.R., 1980, Upper Ordovician (Richmondian) cavity-dwelling organisms from southern Ontario: Canadian Jour. Earth Sciences, v. 17, p. 1616-1627

Kobluk, D.R., 1981, The record of cavity-dwelling (coelobiontic) organisms in the Paleozoic: Canadian Jour. Earth Sciences, v. 18, p. 131-190.

Kobluk, D.R., 1981, Cavity-dwelling biota in Middle Ordovician (Chazy) Bryozoan mounds from Quebec: Canadian Jour. Earth Sciences, v. 18, p. 42-54.

Kobluk, D.R., 1981, Earliest reef cavity-dwelling organisms, Poleta Formation, Nevada. Canadian Jour. Earth Sciences, v. 18, p. 669-679.

Kobluk, D.R., 1981, Lower Cambrian cavity-dwelling endolithic sponges. Canadian Jour. Earth Sciences, v. 18, p. 972-980.

Kobluk, D.R., 1981, Middle Ordovician (Chazy Group) cavity-dwelling boring sponges. Canadian Jour. Earth

Sciences, v. 18, p. 1101-1108.

Kobluk, D.R. and Nemcsok, S., 1982, The macroboring ichnofossil Trypanites in colonies of Middle Ordovician Prasopora: population behaviour and reaction to environmental influences. Canadian Journal of Earth Sciences, v. 19, p. 679-688.

Kobluk, D.R., 1982, First record of Labyrinthus soraufi Kobluk 1979 from the southern Appalachians: Upper Shady Dolomite, Virginia. Canadian Journal of Earth Sciences, v. 19, p. 1094-1098.

Kobluk, D.R., 1983, Earliest cavity-dwelling organisms (coelobionts), Lower Cambrian Poleta Formation, Nevada: Reply. Canadian Journal of Earth Sciences, v. 20, p. 1350-1351.

Kobluk, D.R., 1984, A new compound skeletal organism from the Rosella Formation, Atan Group, Cassiar Mountains, British Columbia. Journal of Paleontology, v. 58, p.703-708.

Kobluk, D.R., 1984, A procedure for digitizing small scale geologic features directly from hand sample or core using a microcomputer system. Bull. Canadian Petroleum Geology, v. 32, p. 335-336.

Kobluk, D.R., 1984, Archaeotrypa Fritz 1946 (Cambrian, problematica) reinterpreted. Canadian Journal of Earth Sciences, v. 21, p. 1343-1348.

Kobluk, D.R., 1984, Coastal paleokarst near the Ordovician-Silurian boundary, Manitoulin Island, Ontario. Bull. Canadian Petroleum Geology, v. 32, p.398-407.

Kobluk, D.R., 1985, Cambrian coelobiontic (cavity-dwelling) biota in Epiphyton mounds, Upper Shady Dolomite, southwestern Virginia. Journal of Paleontology, v. 59, p. 1158-1172.

Kobluk, D.R. and Kozelj, M., 1985, Recognition of a relationship between depth and macroboring distribution in growth framework reef cavities, Bonaire N.A. Bull. Canadian Petroleum Geology, v. 33, p. 462-470.

Kobluk, D.R. and Lysenko, M.A., in press, Distribution of molluscs in open growth framework cavities, leeward reef of Bonaire, Netherlands Antilles. Bulletin of Marine Science.

Kobluk, D.R., in press, Halftone illustration of specimens by microcomputer. Bull. Canadian Petroleum Geol.

Kobluk, D.R. and Noor, I., in press, Interactive input, storage

and modification of maps on a microcomputer. Geobyte.

PAPERS SUBMITTED TO REFEREED JOURNALS OR IN PREPARATION

Kobluk,D.R. and Lysenko, M.A. submitted, Impact of two sequential hurricanes on sub-rubble cryptic corals: the possible role of cryptic organisms in maintenance of coral reefs. Jour. Paleontology.

Kobluk, D.R., in preparation, Cryptic reef faunas: Ecology and Geologic importance.

Kobluk, D.R., Cuffey, R.J., and Fonda, S., in preparation, Distribution of reef-dwelling cryptic bryozoans, Bonaire Netherlands Antilles.

Kobluk, D.R.and Lysenko, M.A., in preparation, Caribbean cryptic scleractinian corals: The modern Caribbean cryptic coral assemblages.

Kobluk, D.R., in preparation, Devonian cavity-dwelling organisms, Formosa Reef Limestone, Ontario

BOOKS AND GUIDEBOOKS

Kobluk, D.R., and Brookfield, M.E., 1982, Lower Paleozoic Carbonate Rocks And Paleoenvironments In Southern Ontario: International Association of Sedimentologists Field Excursion Guidebook for Excursion 1 2A, Hamilton, Ontario, 62 p.

Kobluk, D.R. and Lysenko, M.A., 1984, Carbonate Rocks And Coral Reefs Bonaire, Netherlands Antilles. Geol. Assoc. Canada - Mineral Assoc. Canada Field Trip Guidebook for Trip 13, London, Ontario, 67p.

SEMI-POPULAR AND POPULAR ARTICLES

Kobluk, D.R., submitted, Inside The Reef. Sea Frontiers Magazine.

ABSTRACTS (REFEREED)

Kobluk, D.R., 1975, Destruction and alteration of carbonates by boring (endolithic) algae: Geol. Soc. Amer. Abstracts with Programs, v. 7/6, p. 798.

Kobluk, D.R., 1976, Micrite envelope formation, grain binding, and porosity modification by endolithic (boring) algae in calcarenites in modern and ancient reef environments: Geol. Assoc. Can., Program with Abstracts, v. 1, p. 78.

James, N.P., and Kobluk, D.R., 1977, Internal stucture of Lower

Cambrian archaeo-cyathid reefs: northern Maritime Appalachians: Bull. Amer. Association Petroleum Geologists, v. 61/5, p. 799.

Kobluk, D.R., Pemberton, S.G., and James, N.P. 1977, Possible origin of the reef macroboring fauna: diversification and radiation of lower Paleozoic hardground borers: Geol. Soc. Amer. Abstracts with Program s, v. 9/3, p. 285-286.

Kobluk, D.R., Pemberton, S.G., Karolyi, M.S., and Risk, M.J., 1977, Small scale paleokarst: utility in the recognition of Paleozoic subaerial surfaces in carbonate sequences: Geol. Soc. Amer., Abstracts with Programs, v. 9/3, p. 286.

Kobluk, D.R., and Risk, M.J., 1977, Girvanella, a reinterpretation: Geol. Soc. Amer. Abstracts with Programs, v. 9/5, p. 615.

Kobluk, D.R., and James, N.P., 1978, Cavity-dwelling organisms (coelobites) in Lower Cambrian reefs, Labrador: AAPG-SEPM National Mtg., Oklahoma City, Apr. 1978.

Pemberton, S.G., Kobluk, D.R., Yeo, R., and Risk, M.H., 1978, Silurian macro-borers and macroboring organisms: AAPG-SEPM National Mtg., Oklahoma City, Apr. 1978.

Kobluk, D.R., and Karolyi (Bourque), M.S., 1978, Early Exploitation of the Reef Cavity Habitat by Micro- and Macroborers: Geol. Soc. Amer., Abstracts with Programs, v. 10, No. 6, p. 259.

Pearce, G.W., Kobluk, D.R., and James, N.P., 1978, Preliminary paleomagnetic estimate of the latitude of southern Labrador in the Lower Cambrian: EOS, v. 59, no. 12, p. 1034.

Pemberton, S.G., and Kobluk, D.R., 1978, Paleozoic expansion and decline of shallow and deep water lingulids: competition during the rise of the siphonate bivalves: Geol. Soc. Amer. Abstracts with Programs, v.10/7, p. 469.

Pemberton, S.G., James, N.P., and Kobluk, D.R., 1979, Ichnology of the Labrador Group (Lower Cambrian) in southern Labrador: AAPG-SEPM national mtg., Houston, 1978.

Kobluk, D.R., 1979, Boring algae: rates of infestation and time to initial infestation of calcite in shallow reef environments, Discovery Bay, Jamaica: Geol. Soc. Amer. Abstracts with Programs, v. 11, no. 1, p. 20.

Kobluk, D.R., and Karolyi (Bourque), M.S., 1979. Modern platy algal mounds from Bonaire: modern analog for phylloid algal mounds?: Geol. Soc. Amer. Abstracts with Programs, v. 11, no.

5, p. 233.

Kobluk, D.R., and Karolyi (Bourque), M.S., 1979. Hardground encrusters and cavity-dwelling organisms from Bonaire, Dutch West Indies: a modern analog for an ancient habitat: Geol. Soc. America Abstracts with Programs, v. 11, no. 4, p. 185.

Kobluk, D.R., 1980, Cavity-dwelling (coelobiontic) organisms in the Paleozoic: Geol. Soc. Amer. Southeastern Sect. Mtg., Birmingham, Alabama.

Kobluk, D.R., 1980, Origins of color patterns in Paleozoic shelled and carapaced invertebrates: Geol. Soc. Amer., Northeastern Sect. Mtg., Philadelphia, Pa.

Kobluk, D.R., 1980, Reef cavity-dwelling biota (coelobionts) from Ordovician (Chazy Fm.) bryozoan mounds near Montreal, Quebec. Geol. Soc. Amer., Northcentral Mtg., Bloomington Indiana, April 10.

Kobluk, D.R., 1981, Cavity-dwelling organisms (coelobionts) in archaeocyathid patch reefs, Lower Cambrian Poleta Fm., western Nevada: Geol. Soc. Amer., Cordilleran Mtg., Sonora Mexico, March 25-27.

Kobluk, D.R., 1981, Coelobiontic (cavity-dwelling) biota from open cavities, 64-74 meter (210-240 ft) deep forereef zone, Bonaire, Netherlands Antilles: Geol. Soc. Amer., Northcentral Mtg., Ames, Iowa, May 1.

Kobluk, D.R., 1981, Coelobiontic (cavity-dwelling) microorganisms in open and gloomy reef framework cavities, 18-80 meter depth zone, Bonaire, Netherlands Antilles: Geol. Soc. Amer., Northeastern Mtg., Bangor Maine, Apr. 9-11.

Cuffey, R.J., Zimmerman,L.S., Hewitt, M.S., and Kobluk, D.R., 1985, Modern Bonaire reef-crest bryozoans as paleoecological models - abundances, diversity, and sampling scales. Geol. Soc. Amer. Abstract with Progs., v. 17, no. 1, p. 14.

Kobluk, D.R. and Lysenko, M.A., 1985, Modern reef cavity-dwelling molluscs from Bonaire and their potential for preservation in a fossil reef. Geol. Soc. Amer. Abstracts with Progs., v. 17, no. 1, p. 28-29.

Kobluk, D.R. and Lysenko, M.A., 1985, Reef framework cavity-dwelling corals (12-42 mdepth) leeward fringing reef, Bonaire, Netherlands Antilles. Geol. Soc. Amer. Abstracts with Progs., v. 17, no. 5, p. 296.

Kobluk, D.R., 1986, The cryptic habitat in reefs as a community preserve. Fourth North American Paleontological Convention,

Boulder Colorado, Invited paper for Hard Substrates Symposium.

Noor, I. and Kobluk, D.R., 1986, The Shadow Lake rocks in Ontario: reflection of Ordovician continental influence, Islands, bays and shallow nearshore sedimentary environments. G.A.C.-M.A.C. Annual Meeting, Ottawa, Ontario, May 18-21, 1986.

Kobluk, D.R., 1986, Early reef and mound cryptobionts. Fourth North American Paleontological Convention, Boulder Colorado, Invited paper for History of Reef Communities Symposium.

PUBLICATIONS IN CONFERENCE PROCEEDINGS

Kobluk, D.R., 1975, Endolithic algae in carbonates from the Caribbean: Eastern Canada Paleontology and Biostratigraphy Seminar, Toronto, Ontario, Nov. 21-22.

Kobluk, D.R., 1976, Calcification of endolithic algal filaments, micrite envelope formation, and the binding of sediment grains in the tropical reef environments of Jamaica and Barbados, W.I. (abstract): Geobotany Conf. Proc., Bowling Green, Ohio, Feb. 1976.

Kobluk, D.R., Pemberton, S.G., Risk, M.J., and Karolyi, M.S., 1976, The Silurian Devonian disconformity in southern Ontario: a bored hardground and paleokarst: Eastern Canada Paleontology and Biostratigraphy Seminar, Windsor, Ontario, Oct. 22-23.

Kobluk, D.R., 1977, Calcification of filaments of boring and cavity-dwelling algae, and the construction of micrite envelopes: In GEOBOTANY, ed. R.C. Romans, Plenum Publ., New York, p. 195-207.

James, N.P., and Kobluk, D.R., 1977, Internal structure of Lower Cambrian archaeocyathid reefs, northern Maritime Appalachians: Eastern Canada Paleontology and Biostratigraphy Seminar, Waterloo, Ontario, Oct. 21-22.

Kobluk, D.R., and James, N.P., 1977, Lower Cambrian cavity-dwelling organisms (coelobites) from Labrador: Eastern Canada Paleontology and Biostratigraphy Seminar, Waterloo, Ontario, Oct. 21-11.

Pemberton, S.G., James, N.P., and Kobluk, D.R., 1977, Ichnology of the Labrador Group (Lower Cambrian) in southern Labrador: Eastern Canada Paleontology and Biostratigraphy Seminar, Waterloo, Ontario, Oct. 21-22.

James, N.P., and Kobluk, D.R., 1978, Paleoecology of a Lower Cambrian reef-associated benthic community from southern

Labrador, Canada: Geol. Soc. Amer. Northeastern Section Mtg., Symposium "Ediacaran-Early Cambrian Life of Eastern North America, Boston, Massachusetts, March 8, 1978.

Kobluk, D.R., 1980. A middle Lower Cambrian cavity-dwelling biota from Nevada compared to a late Lower Cambrian cavity biota from Labrador: Canadian Paleontology and Biostratigraphy Seminar, Fredericton N.B., Sept. 27. IN, Maritime Seds. and Atlantic Geol. v. 17, No. 1, p. 60.

Kobluk, D.R. and Kozelj, M. 1983, Distribution with depth of macroborings from growth framework cavities, forereef of Bonaire Netherlands Antilles. Canadian Paleontology and Biostratigraphy Seminar, Univ. of Toronto, Sept. 23-25.

SEMINARS AND COLLOQUIA

University of Manitoba, Department of Geology, 1976: Invited speaker,

1) Paleoecology of the Devonian Miette reef Jasper Alberta : a view from the Caribbean.
2) Macroboring algae, powerful agents in tropical reef construction and destruction: a diagenetic perspective.

Purdue University, Department of Geology, West Lafayette, Indiana, 1976: Invited speaker:Boring microphytes:influence on early carbonate diagenesis in modern and ancient tropical reef environments.

University of Oklahoma, Department of Geology, Norman, Oklahoma, 1976: Invited speaker:Binding of sand grains, micrite envelope generation, and the calcification of endolithic algal filaments in tropical reef environments.

University of Cardiff, Department of Geology, Cardiff, Wales, U.K., 1977, Invited speaker: Microboring and cavity-dwelling plants as diagenetic agents in tropical reefs: Jamaica and Barbados.

National Museum of France, Institute of Paleontology, Paris, France, 1977,

1) Paleoecology and sedimentology of the Upper Devonian Miette carbonate complex, Jasper, Alberta.
2) Boring microphytes in modern and ancient coral reefs of Jamaica, Barbados, and Curacao. Invited Speaker.

University of Toronto, Department of Geology, Toronto, Ontario, 1978, Lower Cambrian shallow marine paleoenvironments, southern Labrador and western Newfoundland.

Bowling Green State University, Bowling Green, Ohio, 1978, A reef ecosystem of Lower Cambrian age, Labrador, Canada.

Hope College, Department of Geology, Holland, Michigan, 1978, A Lower Cambrian reef ecosystem.

Erindale College, University of Toronto, 1978, Reef studies in Bonaire, Netherlands Antilles.

Erindale College, University of Toronto, 1979, Processes of Growth in Caribbean Coral Reefs.

University of Nevada (Las Vegas), Department of Geology, 1979, Paleoecology of Lower Cambrian Reefs and Associated Environments, Labrador, Canada.

University of Buffalo, Department of Geology, 1980: Invited speaker: Modern and ancient tropical reef cavity dwelling organisms.

Erindale College, University of Toronto, 1980, Coral Reef Research in Bonaire, Netherlands Antilles.

McMaster University, Dept. of Geology, 1980: New frontiers in coral reef research: organisms of the dark reef interior.

University of Toronto, Dept. of Geology, 1980: Tropical reef cavity systems - exploring the reef interior.

Erindale College, University of Toronto, 1983, FIJI.

Erindale College, University of Toronto, 1983, Microcomputer applications in Paleontology.

University of Toronto, Dept. of Geology, 1983, Developments in the study of coral reef cavity systems.

Scarborough College, Department of Biology, University of Toronto, 1983, Exploration of the coral reef interior: Bonaire Netherlands Antilles and Fiji Islands South Pacific.

Earthwatch Conference, Boston, Massachusetts, 1984, Cavity dwelling biota, Bonaire, Netherlands Antilles.

Erindale College, University of Toronto, 1984, Recent developments in the Bonaire and Fiji Coral Reef Projects.

Earthwatch Conference, Boston, Massachusetts, 1986, 1) Expedition Safety Management, and 2) The Fiji Coral Communities Project.

OTHER SPEAKING ENGAGEMENTS, POPULAR TALKS

University of Toronto, Senior Alumni Association, 1979: Coral Reef Research and Oil in Canada.

Rotary Club, Clarkson Branch, Mississauga, Ontario, 1979: Coral Reef Research And Oil Exploration.

University of Toronto, Women's Club, 1979: Modern and Ancient Caribbean Coral Reefs.

Deep River Underwater Club, 1980: Living Coral Reef Environments and Ancient Reefs in Canada.

University of Toronto, Hart House Scuba Diving Club 1982: The Hole Reef Story: The Reef Interior Bonaire.

Port Credit Rotary Club, 1982: Coral Reef Research: Interpretation of Fossil Oil-Bearing Reef Structures.

21 McGill, Toronto, 1983: The Inside of the Reef.

Clarkson Secondary School, Mississauga, Ontario, 1983: Careers as a Geologist.

Erindale College, University of Toronto, 1984, Advances in the study of coral reef cavity systems.

Second Mile Club, Toronto, 1985: Scientific exploration of South Pacific and Caribbean coral reefs.

North American Assoc. Geology and Geography Teachers Annual Mtg., Toronto 1985: Keynote address - Uniformitarianism as a Tool in Geology Teaching and Field Research.

Senior Alumni Assoc., University of Toronto 1985: Recent - Exploration of the Coral Reef Interior, Bonaire, Dutch West Indies.

Morning Star Secondary School, Mississauga, Ontario 1986: The Coral Reef.

RESEARCH UNDERWAY

1) Benthic marine diatoms from surface and cavity reef habitats, 3-45 meter depth zone, Bonaire, Netherlands Antilles. Begun 1981, cooperative with T. Sawa, Botany Dept., University of Toronto.

2) Coelobionts in Lower Cambrian Shady Formation (middle Member) archaeocyathid mounds, Austinville, Virginia. Begun 1981.

3) Paleokarst in the Keyser Formation, Lewisburg,

Pennsylvania. Begun 1981, cooperative with E. Cotter.

4) Cavity-dwelling organisms in cavities in a Jurassic hardground, Poland. Begun 1980, cooperative with M. Gruszczynski, Polish Academy Sciences, Warsaw.

EMPLOYMENT SUMMARY

- July 82 to present
  Associate Professor Univ. of Toronto Erindale Campus

- Dec. 77 to July 82
  Assistant Professor Univ. of Toronto Erindale Campus

  DUTIES - Teach paleontology undergraduate and graduate courses.

- Nov. 76 to Dec. 77
  Post Doctoral Memorial University Supr: Dr. N.P. James,
  Research Fellow Assoc. Prof. of Geology

  DUTIES - Research into paleontology and paleoecology of Lower Cambrian reef communities.

- Sept. 75 to Apr. 76 McMaster University Supr. Dr. M.J. Rick

  Demonstrator Prof. Marine Geology

  DUTIES - Teach undergraduate introductory geology laboratory.

- Sept. 74 to May 75 McMaster University Supr: Dr. R.G. Walker

  Demonstrator

  DUTIES - Teach undergraduate laboratory in earth history.

- May 74 McMaster University Supr: Dr. H.D. Grundy
  Demonstrator Dr. M.J. Risk

  DUTIES - Assist in teaching field school group at field camp area on north shore of Lake Huron, Ontario.

- Sept. 73 to May 74 McMaster University Supr: Dr. M.J. Risk
  Prof. Marine Geology

  DUTIES - Direction and supervision of undergradaute geology laboratory; includes lecturing, make-up and corrections of exams, laboratories, etc.

- Jan. 73 to May 73 McGill University Supr: Dr. R. Hesse
  Demonstrator Prof. Stratigraphy

DUTIES - Direction and supervision of the undergraduate invertebrate paleontology laboratory.

- Sept. 72 to May 23 McGill University Supr: Dr. E.W. Mountjoy
  Demonstrator Prof. Stratigraphy

DUTIES - Direction and supervision of the undergraduate stratigraphy and sedimentation laboratory.

- May 72 to Aug. 72 Soquem Supr: Mr. F. Feldor
  Party Chief Ste. Foy, Quebec, Canada Proj. Manager

PROGRAM - Party chief of geological/geochemical exploration party in the Grenville Series north and south of the Saquenay Basin in Quebec.
- Three geological environments surveyed: Anorthosite body near Chicoutimi; Orthogneiss structure south of Chibougamau; Orthogeneiss/ Paragneiss series near Tadoussac.
- Discovery of two Cu-Ni and one Molybdenite showings.
- Production of reports, maps, and recommendations for future work.

- Jan. 72 to May 72 McGill University Supr: Dr. R. Hesse
  Demonstrator Prof. Stratigraphy

DUTIES - Direction and supervision of the undergraduate stratigraphy and sedimentation laboratory, as well as the undergraduate paleontology laboratory.

- May 71 to Sept. 71 Soquem Supr: Mr. M. Tauchid

  Party Chief Ste. Foy, Quebec, Canada Proj. Manager

PROGRAM - Party chief of geochemical/geological exploration program in the Eastern Townships of Quebec.
-Regional in scope, included direction of regional stream sediment sampling, regional and detailed soil sampling, detailed and regional geological mapping, and rock geochemical surveys.
-Direction of radiometric, electromagnetic (E.M. 16 and 17), magnetometer, and I.P. surveys.
-Production of maps, reports, and recommendations for future drilling and exploration.
-Discovery of several showings in copper, one in arsenic-gold, one in lead-zinc, and one in bismuth. Copper discovery of major importance.

- Jan. 71 to May 71 McGill University Supr: Dr. R. Hesse
  Demonstator Prof. Stratigraphy

DUTIES - Direction and supervision of paleontology laboratory. Responsibilities similar to those described above.

- May 70 to Sept. 70 Soquem Supr: Mr.J.Descarreaux

Party Chief Ste. Foy, Quebec, Canada Proj. Manager

PROGRAM -Party chief directing a base metal exploration program in the Chapais area of the Chibougamau Camp.
-Detailed geological mapping of the 57 claim property, direction of Magnetometer survey, rock geochemical survey, boulder tracing survey, and line cutting under contract.
- Development of operational structural theory for the property.
- Production of colour aerial photographic survey of the property.
- Recommendation of future work and production of report.

- Jan. 70 to Apr. 70 McGill University Supr: Dr. R. Hesse
Demonstrator Prof. Stratigraphy

DUTIES -Direction and supervision of undergraduate paleontology laboratory. Correcting and marking papers.

- May 69 to Aug. 69 Soquem Supr: Mr. M. Vallee
Party Chief Ste. Foy, Quebec, Canada Proj. Manager

PROGRAM -Party chief of four to eight man field party and drilling crew in the LaTuque area.
-Final stages in the evaluation-development of a copper-nickel ore body in the Grenville series.
- Detailed geological mapping.
- Rock geochemistry.
-Direction, supervision, logging and positioning of diamond drill operation (2 rigs, 6 men, 24 hours per day).
-Direction of surveying crew in production of topographic map.
-Production of maps, drill profiles, and topographic mapping (1" = 200 ft.) of 75 square mile project in the Eastern Townships of Quebec.

- May 69 Quebec Dept. Natural Resources Supr: Dr. T.H. Clark
Field Assistant Prof. Emeritus McGill University

DUTIES -Assist in the geological mapping of Ordovician series of sediments in the St. Lawrence Lowlands of Quebec.

- Dec. 68 to Apr. 69 McGill University Supr: Dr. R.H. Grice
Research Assistant Prof. Engineering Geology

DUTIES -Detailed analysis of the stratigraphy of the Black River Group (Ord.) in and around Montreal.
-Use of computers in the storage of geological data and the production of variable scale geological maps and engineering geology maps.
-Construction of a tailored lithological classification for rocks in the Black River System amenable to computer map production.

- May 68 to Sept. 68 McGill University Supr: Dr. R.H. Grice
Research Assistant Prof. Engineering Geology

DUTIES - Same as described above.

- Jan. 68 to Mar. 68 St. Thomas High School Supr: Staff

DUTIES -Full time laboratory technician responsible for setting up experiments and classes and supervising laboratories for high school chemistry, biology and physics classes.

- Sept. 67 to Dec. 67 McGill University Supr: Dr. R.H. Grice
Research Assistant Prof. Engineering Geology

DUTIES - Same as described above.

- June 67 to Sept. 67 Terratech Ltd. Supr: Mr. F. Tordon

Test Pit Inspector Montreal, Quebec, Canada Proj. Manager

DUTIES -Test pit inspector engaged in the exploration for and evaluation of gravel and sand deposits for the construction of retaining dykes for Churchill Falls Power Project, Central Labrador.
-Direction of four men, two pieces of heavy machinery (D-6 bulldozer and Go-Tract machine) and one helicopter.

CONSULTING

-International Mines Services Ltd., Toronto.
Consultation on reef-associated uranium prospect in Windsor Basin of Nova Scotia, Canada, 1978.

ADDITIONAL FIELD RESEARCH EXPERIENCE

Bermuda
1972 -Field work aimed at a reconnaisance study of reef environments and faunas. 1 week. Nov. 72.

Barbados, W.I.

1973 -Field work studying reef environments and faunal relationships as well as Pleistocene facies and limestone diagenesis. 2 weeks.
Mar. 73.

Maritime Provinces, Canada
1973 -Reconnaisance study of Appalachian stratigraphy, structure, and classic paleontological localities in Gaspe, New Brunswick and Nova Scotia. 2 weeks. June 73.

Florida, U.S.A.
1973 -Study of reef communities and reef destruction by endolithic algae and fungi in the reef front area of the Upper Florida Keys near Key Largo. 1 week. Oct.Nov. 73.

Jamaica, W.I.
1973 -Assist in the construction and monitoring of artificial reefs in Discovery Bay. Aimed at study of the potential for the enhancement of commercial fish and lobster populations. Additional investigation of endolithic algae and fungi in corals and calcareous substrates and their degradational effects. 2 weeks. Dec. 73.

Jamaica, W.I.
1974 -An in-detail study of endolithic algal and fungal infestation in modern coral reefs. 5 weeks. May-June 74.

Barbados, W.I.
1974 -Field work studying endolithic algal and fungal infestation of modern and Pleistocene coral reefs. Research aimed at and understanding of the role endolithic microphytes play in the erosion and micritization of skeletal components. 2 weeks. July 74.

Alberta, Canada
1974 -Study of micritization in the Devonian Miette reef complex in the Alberta Rocky Mountains. Supported by Amoco Petroleum Co. Ltd., Calgary, Alberta. 3 weeks. Aug.-Sept. 74.

Jamaica, W.I.
1974 -Study of communities in reefs with particular emphasis on bioerosion by endolithic microphytes. 2 weeks. Nov. 74.

Jamaica, W.I.
1974 -Study of endolithic microphytes in the marine environment. 2 weeks. Dec. 74.

Bermuda
1975 -Assist in a geochronological study in Bermuda caves; also reconnaisance study of the feasibility of setting up a study of endolithic microphytes in Bermuda waters. 1 week. Jan. 75.

Bonaire, N.A.
1975 -Study of recent reef communities and of Pleistocene reef exposures. 1 week. Jan. 75.

Curacao, N.A.
1975 -Reconnaisance study of recent reef communities and Pleistocene reef exposures. 2 weeks. Jan. 75.

Jamaica, W.I.
1975 -Field work on the reefs at Discovery Bay and the late Pleistocene exposures at Rio Bueno and Oracabesca. A study of endolithic microphytes in the modern and ancient reef environment. 2 weeks. Feb. 75.

Jamaica, W.I.
1975 -Study of endolithic microphytes in the modern reef environment at Discovery Bay; Pleistocene at Rio Bueno. 11 weeks. April-July 75.

Bonaire, N.A.
1975 -Study of recent supratidal environment, including recent dolomites, crusts, and stromatolites. 1 week. July 75.

Curacao, N.A.
1975 -Study of reef environments and subaerial diagenesis in Pleistocene exposures. 2 weeks. July 75.

Barbados, W.I.
1975 -Work on the recent reefs at Bellairs, and the Pleistocene rocks of the north coast. 1 week. Aug. 75.

St. Lucia, W.I.
1975 -Study of the geology of the island and of the fringing reefs at Vigie. 1 week. Aug. 75.

Jamaica, W.I.
1975 -Study of endolithic algae and fungi in the modern reef environment. 2 weeks. Aug. 75.

Jamaica, W.I.
1975 -Placement of substrate plates on the reefs and monitoring of previous installations at Discovery Bay. Additional field work on the forereef community and

collection of sample materials. 2 weeks. Sept. 75.

Florida, U.S.A.
1975 -Survey of Florida Bay algal mat communities; research on overturning of coral heads in back reef and reef crest environments; sampling for a study on endolithic algae and fungi in Pleistocene and Recent reef carbonates. 1 week. Nov. 75.

Jamaica, W.I.
1976 -Placement of substrate installations on the reefs at Discovery Bay; monitoring of existing installations; sampling and survey of specific lagoon and backreef environments. 1 week. Feb. 76.

Florida, U.S.A.
1976 -Synsedimentary and early diagenesis in carbonate calcarenite sand muds. Florida Keys. 1 week. April 76.

Alberta, Canada
1976 -Study of stromatoporoid overturning in the Upper Devonian Miette reef complex, Jasper, Alberta. 3 days. May 76.

Jamaica, W.I.
1976 -Study of micritization of the Jamaican Pleistocene reef terraces, and the reef at Discovery Bay. 2 weeks. June 76.

Labrador, Nfld.
1976 -Paleoecology of Lower Cambrian archaeocyathid reefs, biostromes, and interreef clastic sequences. 3 weeks. Aug. 76.

Paris, France
1977 -Study of archaeocyathid taxonomy, systematics, and paleoecology with Dr. Francoise Debrenne at the Institute of Paleontology of the National Museum of France in Paris. 3 weeks. Feb. 77.

Labrador, Nfld.
1977 -Study of the paleoecology and paleontology of Lower Cambrian archaeocyathid reefs. 6 weeks. June-July 77.

Jamaica, W.I.
1977 -Study of activity of boring algae and fungi in modern and Pleistocene reef environments. Earthwatch supported expedition.
7 weeks. Aug.-Sept. 77.

Bonaire, N.A.
1978 -Leader of a field trip to study the ecology of Bonairian living reefs, and paleoecology of fossil Pleistocene reefs. 1 week Mar.78.

Jamaica, W.I.
1978 -Co-instructor of a field course on Jamaican coral reef geology and ecology, with Hope College, Holland, Michigan, at Discovery Bay.
3 weeks. May-June 78.

Jamaica, W.I.
1978 -Field work on modern reef cavity systems, Discovery Bay. 4 days, July 78.

Bonaire, N.A.
1978 -Field research into modern reef cavity systems. Earthwatch supported field program. 7 weeks, July-Aug. 78.

Bonaire, N.A.
1978 -Leader of field trip to study modern reef environments of Bonaire.
1 week, Oct. 78.

Jamaica, W.I.
1978 -Research on modern marine cave faunas at Rio Bueno, Jamaica North coast. 1 week, Oct. 78.

Nevada, U.S.A.
1979 -Reconnaisance study of Lower Cambrian patch reefs and associated cavities. 3 days, Mar. 79.

Bonaire, N.A.
1979 -Island reconnaisance of living and Pleistocene coral reefs. 1 week, May 79.

Jamaica, W.I.
1979 -Study of cave-dwelling marine faunas and floras at Pear Tree Bottom and Rio Bueno. 1 week, May 79.

Bonaire, N.A.
1979 -Research into modern cavity-dwelling flora and fauna in coral reefs. Earthwatch supported. 5 weeks, June-July 79.

Bonaire, N.A.
1979 -Leader and organizer of Bonaire '79 expedition of 65 participants to study modern coral reef geology and ecology. 2 weeks, Aug. 79.

Fiji Islands, South Pacific

1979 -Reconnaisance study of the geology of Viti Levu Island and the surrounding coral reefs. 2 weeks, Nov. 79.

Fiji Islands, South Pacific
1980 -Reconnaisance study of the geology of the south coast of Viti Levu. 1 week, Feb. 80.

Bonaire, Netherlands Antilles
1980 -Study of Halimeda algal bioherms in Lac Lagoon. 2 weeks, March 80.

Bonaire, Netherlands Antilles
1980 -Study of coelobiontic organisms in Bonairian reefs near Kralendijk. 4 weeks, May/June 80.

Tobago, B.W.I.
1980 -Reconnaisance survey of island geology and reefs. 1 week, May 80.

Bonaire, Netherlands Antilles
1980 -Leader of Bonaire 80 educational expedition to Bonaire, to study the ecology of coral reefs and tropical island geology. 3 weeks, July 80.

Virginia, U.S.A.
1981 -Fieldwork on Middle and Upper Cambrian part of the Shady Dolomite series, looking for coelobionts in cavities in Epiphyton algal mounds. 1 week, May 81.

Bonaire, Netherlands Antilles
1981 -Fieldwork into reef cavity-dwellers. 6 weeks, May-June 81.

Fiji Islands, South Pacific
1981 -Design, marketing, teaching and leading a field course for the public on coral reef ecology and geology. 2 weeks, July 81.

Bonaire, Netherlands Antilles
1982 -Fieldwork investigating reef cavity-dwellers. 9 weeks, May-June 82.

Bonaire, Netherlands Antilles
1983 -Study of reef cavity-dwelling invertebrates, 10-50 meter depth zone. 5 weeks, May-June 83.

Fiji Islands, South Pacific
1983 -Study of reef cavity systems in back reef and lagoon environments, Malololailai Island. 5 weeks, July-August 83.

Bonaire, Netherlands Antilles

1984 -Study of coral reef cavity-dwelling corals, sponges, and hydroids. 5 weeks, May-June 84.

Fiji Islands, South Pacific
1984 -Study of intertidal coral reef flat cryptic corals and molluscs, Malololailai Island. 6 weeks, July-September 84.

Bonaire, Netherlands Antilles
1985 -Study of coral reef cavity-dwelling corals. 5 weeks, May-June 85.

Fiji Islands, South Pacific
1985 -Study of coral reef intertidal cryptic corals, Malololailai Island. 7 weeks, July-September.

MARY ALEXANDRA LYSENKO

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Phone: (416)828-5335

BIRTH DATE: DECEMBER 30, 1954

CITIZENSHIP: AT BIRTH - CANADIAN; CURRENT - CANADIAN

HEALTH: GOOD

STATISTICS: HEIGHT - 5 FT. 5 IN. (164 CM);WEIGHT - 110 LBS. (50 KG)

LANGUAGES SPOKEN: ENGLISH, UKRAINIAN.

EDUCATION:

University - University of Toronto
Toronto, Ontario
1974 - 1982
Bachelor of Science, Degree Awarded, 1980.

High School - Parkdale Collegiate Institute
Toronto, Ontario. Arts and Science Program, 1973 - 1974;
Graduated, 1974.
- Central High School of Commerce
Toronto, Ontario
Arts and Science Program, 1969 - 1973;
Junior Matriculation, 1973

Theses Sedimentology Of Siliciclastic And Carbonate Grains In A Reef At Malololailai Island, Fiji Islands, Southwest Pacific. University of Toronto, Dept. of Geology, Erindale Campus; Honours B.Sc. 1985.

Additional Courses
- Natural Science Illustration Workshop
Wilfred Laurier University Waterloo, Ontario N2L 3C5 Dept. of Biology; Dr. W.Y. Watson
October 22 - 23, 1983
- Basic Programming for Computers
University of Toronto, Erindale Campus Continuing Education Programme 1982, Fall Semester
- Ukrainian Language Institute 1961 - 1971; Diploma, 1971.

PROFESSIONAL AFFILIATIONS
- American Association of Petroleum Geologists, May 1984 -present
- Geological Association of Canada, 1982 - present
- Geological Society of America, Member, 1981 - present
- International Oceanographic Foundation, Member, 1980 -present

HONOURS AND AWARDS
- Princess Poltava Pavilion, Metro Toronto Folk Arts Council Caravan, 1975

EXTRACURRICULAR ACTIVITIES
- Scuba Diver: PADI Certification; Needlepoint, Cultural Museum Work, Malacology.

MEMBERSHIPS AND CLUBS

- Coleman Geology Club, Member
- Erindale Campus Geology Club, Member, 1981.
- Ukrainian Museum of Canada - Eastern Branch, Member and Executive Member: Correspondence Secretary, 1977 - 1979
- Vesnianka Ukrainian Folk Dance Ensemble, 1973 - 1977
- Student Administrative Council (SAC) Representative, University of Toronto, 1975 - 1976
- University of Toronto and Erindale Campus Ukrainian Clubs, member, Secretary and Social Convener, 1975 - 1977
- Community Folk Arts Council, Metro Multicultural Caravan, volunteer, 1973 - 1975

PUBLICATIONS

- Kobluk, D.R. and Lysenko, M.A. 1984. Carbonate Rocks and Coral Reefs, Bonaire, Netherlands Antilles. GAC - MAC Field Trip Guidebook No. 13, Geological Association of Canada, Mineralogical Association of Canada Annual Meeting, London, Ontario, 67 p.

- Kobluk, D.R. and Lysenko, M.A. Submitted. Reef-dwelling molluscs in open-framework cavities, Bonaire,N.A., and their potential for preservation in a fossil reef. Bulletin of Marine Science.

- Kobluk, D.R. and Lysenko, M.A. Submitted. Cavity - dwelling corals in a Caribbean fringing reef. Bulletin of Marine Science.

- Kobluk, D.R. and Lysenko, M.A. 1985. Modern Reef cavity-dwelling molluscs from Bonaire, N.A. Geol. Soc. of Amer. Abstracts with Programs, Northeastern Section Mtg.,Vol. 17,No. 1.

- Kobluk,D.R. and Lysenko, M.A. 1985. Reef framework cavity-dwelling corals (12-42 m depth), leeward fringing reef, Bonaire, Netherlands Antilles. Geol. Soc. of Amer. Abstracts with Programs, North central Section Mtg., Vol. 17, No. 5.

- Kobluk, D.R. and Lysenko, M.A. Submitted. Impact of two sequential Pacific hurricanes on sub-rubble cryptic corals: the possible role of cryptic organisms in maintenance of coral reef communities. Journal of Paleontology.

- Kobluk, D.R. and Lysenko, M.A. Submitted. Caribbean cryptic Scleractinian corals: comparison with the southwest Pacific, and the origins of modern Caribbean cryptic coral assemblages. Palaios.

PRESENTATIONS AT PROFESSIONAL MEETINGS

- Earthwatch Conference; Belmont, Mass. Feb. 24 - 26, 1984. Intertidal Reef Flats of Malololailai Island, Fiji.

CONFERENCES AND FIELD SEMINARS

- "Carbonate Rocks and Coral Reefs, Bonaire,N.A." Geol. Assoc. Canada - Mineral Assoc. Canada Annual Meeting, Field Trip 13, London, Ontario. Assistant in running GAC-MAC Fieldtrip to Bonaire and co-authour for D. Kobluk; May, 1984.

- Canadian Paleontology and Biostratigraphy Seminar, Toronto, Ont., Sept. 1983. University of Toronto.

- "Lower Paleozoic Carbonate Rocks and Paleoenvironments in Southern Ontario". Inter. Assoc. of Sedimentologists Field Excursion 12A, Hamilton, Ont. Field Assistant on carbonate field trip to D. Kobluk, co-leader. D. Kobluk and M. Brookfield. August, 1982.

- Canadian Paleo. and Biostratigraphy Seminar, Manitoulin Island, Ont., Sept., 1981. Field Trip given by P.G. Telford.

- Earthwatch Principal Investigator Conference, Belmont, Massachusetts; Participant 1984, 1985.

RESEARCH ACTIVITIES

- Taxonomy and documentation of Indo-Pacific and Caribbean Mollusc faunas; compositional sand analysis.

- CORAL REEF POPULATION DYNAMICS: Study of reef surface populations, involving mapping, census, statistical data entry and testing as parameters for comparison to cavity-dwelling biotas in subtidal and intertidal reef structures. Computer-processed areal mapping, frequency data, spatial relationships and growth parameters of modern reef biota and sediment are used to further a comparative model and analysis to reef structure and sediment. Bonaire, N.A.

- ECOLOGY AND GEOLOGY OF SHALLOW WATER REEF CAVITIES: INTERTIDAL REEF FLATS OF MALOLOLAILAI ISLAND, FIJI ISLANDS: Reconnaissance survey of the cavities and cavity biota, and the ecology and geology of the shallow water intertidal and immediate subtidal (backreef) cavity habitat. Population study of cavity - dwelling corals in backreef and lagoonal environments, and compositional analysis of surface sands.

- CAVITY-DWELLING ORGANISMS IN REEF FRAMEWORK CAVITIES IN BONAIRE, N.A.: The focus of this mapping project is to document the community composition of a leeward fringing reef in Bonaire, N.A. The aim of a computer-based statistical population study of the surface is to compare and contrast cavity communities and sediments. Documentation of cavity corals of the forereef zone; population dynamics of reef surface community.

- BIOEROSION IN REEF FRAMEWORK CAVITIES IN BONAIRE, N.A.: A survey of the depth distribution and character of reef interior cavity bioerosion on the forereef slope on the west coast of Bonaire, N.A.

EMPLOYMENT SUMMARY

University of Toronto
Erindale Campus
Mississauga, Ontario

September, 1979 - Present
Position Title: Research Assistant
Supr.: Prof. D. Kobluk (Geology)

DUTIES: Research assistant, laboratory work, curatorial, map and data preparation, field assistant; computer data entry and processing of field data; seminar preparation.

University of Toronto
Erindale Campus
Mississauga, Ontario

September, 1980 - Present
Position Title: Curator of Paleontological Collections and Teaching Assistant.
Supr.: Prof. D. Kobluk (Geology)

DUTIES: Curate Paleontology and Carbonate teaching collections; classification and cataloguing, and assist in teaching, preparation of undergraduate course materials.

Sears Ltd.
108 Mutual St.
Toronto, Ontario

September 27, 1980 - Present
Position Title: Telephone Salesclerk
Supr.: B. Forgrave
(Manager: Mr. L. Roth)

DUTIES: Telephone and mail order sales department; computerized order entry of telephone orders, customer sales and service, switchboard, clerical and typing. Part-time.

Robarts Library-
University of Toronto
130 St. George St.

September 28, 1982 - 1985.
Position Title: Student Assistant
Supr.: Mrs. Mignon (Circulation Dept.) Mrs. Joan Williams

DUTIES: Duties include signing-out and renewal of books, sortation to bookstacks,general information in public service-oriented routine. Part-time.

University of Toronto
Erindale Campus
Mississauga, Ontario

January 4, 1983 - May 16, 1983
Position Title: Teaching Assistant
Supr.: Dept. of Earth Sciences

DUTIES: Teaching assistant for first year undergraduate course (EPS 115S) in historical geology, evolution and paleoecology, with an emphasis on marine organism-substrate relations with a modern - ancient analog approach. Responsibilities; grading of tests, term papers, exam and teaching assistance with course materials.

University of Toronto
Erindale Campus
Mississauga Ontario

January 10,1982 - February 7,1982
Position Title: Graphics Assistant
Supr.: Prof. D. Kobluk (Geology)

DUTIES: Preparation of art work for Paleontology Laboratory Manual.

University of Toronto
Erindale Campus
Mississauga, Ontario

January 4, 1982 - April 8, 1982
Position Title: Teaching Assistant
Supr.: Dept. Of Earth Sciences

DUTIES: Teaching assistant for first year undergraduate course (EPS 115S) in historical geology, evolution and paleoecology.

Robert Simpson Co. Ltd.
176 Yonge St.
Toronto, Ontario

October 7,1973 - September 27,1980
Position Title: Telephone Salesclerk
Supr.: Mrs. F. Tongue
Mrs. Webb

DUTIES: Telephone Operator, telephone order department for Simpsons-Sears and Simpson Co. Ltd.; customer sales and service. Part - time.

T.Shevchenko Ukrainian School
(Toronto Board of Education)
404 Bathurst St.
Toronto, Ontario

September, 1975 - May, 1981
Position Title: Teacher; Grades 2 and 3
Supr.: Mrs. A. Foty

DUTIES: Teacher in private school immersion program and bilingual curriculum under Heritage Program: reading, writing, grammar, literature, culture and folklore.

Clarke Institute of Psychiatry
250 College St.
Toronto, Ontario

June, 1977 - September, 1979
Position Title: Office Clerk
Supr.: Mrs. A. Doherty (Accountant)

Comptroller's and Financial
Business Office

DUTIES: Clerk, Accounting Dept. of Comptroller's Office; Accounts Payable and Receivable; some secretarial duties: typing; Payroll on computerized system; petty cash, bank deposits, inventory control; Grant Ledgers.

Canadian General Electric
24 Ward St.
Toronto, Ontario

August 25,1976 - September 1,1976
Position Title: Clerk
Supr.: Miss C. Bailey

DUTIES: Clerical: inventory control: verifying computer listings versus stock reports. Temporary assignment for Temporary Opportunities Agency.

SKILLS

- Typing, microcomputers, bibliographic research, technical and scientific writing and presentation, computerized data entry.

FIELD RESEARCH EXPERIENCE

Bonaire,N.A.

- Jan. 7 - 14, 1985.

Research and field teaching assistant to Dr. Kobluk. Pleistocene and tropical island geology and reef ecology.

Fiji Islands, South Pacific

- July 21, 1986 - September 7, 1986.
-.July 22, 1985 - September 5, 1985.
- July 27, 1984 - September 7, 1984.
- July 22, 1983 - September 4, 1983.

Malololailai Island Earthwatch Research Team Logistics Co-ordinator and Research Assistant to Dr.D. Kobluk. Reconnaissance survey and mapping of cavity biota, ecology and geology of shallow water (intertidal and subtidal) reef flat cavity habitat from shoreline to the reef crest of an atoll.

Bonaire, Netherlands Antilles

- May 16, 1986 - July 5, 1986.
- May 27, 1985 - July 3, 1985.
- May 23, 1984 - July 1, 1984.

Earthwatch Research Team.Fieldwork investigating cavity - dwelling reef biota, coelobiontic sponges, corals, hydroid; field seminars, data collection; areal mapping of reef surface biota for computerized and statistical processing. Logistics co-ordinator and research assistant for Dr. D. Kobluk. Scuba-diving, photography, teaching field seminars.

Bonaire, Netherlands Antilles

- May 23, 1983 - July 1, 1983

Earthwatch Research Team. Research Assistant to Dr. D. Kobluk. Study of reef cavity ecosystems, cavity organisms, organisms-substrate relationships and reef communities. Documentation of in situ cavity biota on the forereef slope of the leeward fringing reef. Field seminars aimed at teaching reef ecology and geology, photography, Scuba diving.

Bonaire, Netherlands Antilles

- May 23, 1982 - July 18, 1982
- May 22, 1981 - July, 1981

Earthwatch Research Team. Research Assistant to Dr. D. Kobluk. Studying cavity-dwelling communities in the leeward coral reefs of Bonaire; sediment sampling, photography of cavities; detailed sampling and measurement of temperature, water flow, cavity sediments, and observation of cavity biota in the depth range of 2 - 40 m (6 - 120 ft.). Detailed mapping of a leeward fringing coral reef from 10 - 27 m (30 - 80 ft.); teaching of reef organisms, invertebrates, general ecology of reef ecosystems; sampling of cavities. Scuba diving.

Pennsylvania, U.S.A.

- August 11 - 14, 1981

Lewisburg
Fieldwork on Silurian - Devonian disconformity and paleokarst. Dr. D. Kobluk.

Fiji Islands, South Pacific
- July 10 - 26, 1981
Suva City; Malololailai Island
Assisted in a field course aimed at teaching geology and ecology of coral reef ecosystems, modern reefs; Scuba diving. Reconnaissance study of lagoon, backreef and reef flat environments. Research and field assistant to Dr. D. Kobluk.

Virginia, U.S.A.
- May 1 - 8, 1981
Blacksburg
Field assistant to Dr. D. Kobluk. Fieldwork on Upper Cambrian Shady Dolomite bioherms; fieldwork and sampling aimed at a study of Cambrian cavity-dwelling organisms.

Manitoulin Island, Ontario
- December 27 - 29, 1980
Field and research assistant to Dr. D. Kobluk. Fieldwork, sampling, observations of stratigraphy of the Ordovician - Silurian disconformity, paleokarst surface at Kagawong.

Labrador, Newfoundland
- October 4 - 13, 1980
Research Assistant to Dr. D. Kobluk. Field-trip to study the Lower Cambrian archaeocyathid patch reefs of the Forteau Fm., exposed on the Straits of Belle Isle, Labrador, near Pt. Amour.

Bonaire, Netherlands Antilles
- July 2 - 20, 1980
Assisted on Bonaire '80: a field courses aimed at the teaching of the geology and ecology of a modern fringing coral reef and tropical island geology. Scuba diving.

Bonaire, Netherlands Antilles
- May 24 - June 28, 1980
Earthwatch Research Team Research Assistant to Dr. D. Kobluk. Fieldwork: detailed mapping of a leeward fringing coral reef from 10 - 50 m; observations of cavities and cavity-dwelling organisms. Scuba diving, photography, sediment-sampling.

Tobago, West Indies
- May 17 - 24, 1980
Reconnaissance study of a fringing coral reef and island geology. Scuba diving.

Bonaire, Netherlands Antilles
- March 28 - April, 1980
Research Assistant to Dr. D. Kobluk. Reconnaissance study of a fringing reef and the lagoon biota in the Lac Lagoon; *Halimeda* algal bioherms. Scuba diving, photography, sampling of sediment and algae.

Nevada and California, U.S.A.
- November 11 - 16, 1979
Goldfields area, Nevada.Field and research assistant to Dr. D. Kobluk. Lower Cambrian archaeocyathid bioherms and cavities; fieldwork to study the Lower Lower Cambrian archaeocyathid patch reefs in the Poleta Fm. Sampling and photography aimed at a study of the cavity biota.

Bonaire, Netherlands Antilles
- May 19 - 26, 1979
Field assistant to Dr. D. Kobluk. Reconnaissance study of a reef on the leeward side of the island of Bonaire.

PAST PARTICIPANTS

Furney Hemingway

Tommy Tinker

Fiske Field

EARTHWATCH Team Dives Deep Into Bonaire's Underwater World

The Atlanta Journal, August 12, 1984

Earthwatch team dives deep i

Research expeditions let you talk to dolpl

By Furney Hemingway
Staff Writer

BONAIRE, Netherlands Antilles — The water below gradually deepens, staghorn coral replacing the elkhorn on the narrow apron of sand surrounding the island of Bonaire, to be replaced in turn by clumps of boulder coral as the edge of the dropoff looms.

The bottom turns abruptly downward, darkening, mysterious, a steep hillside completely covered with living things, stoney corals, soft corals, false corals, sponges, with every nook and crevice sheltering other living things, lurking fish, octupuses, feathery crinoids, britle stars, moray eels — a wall of life.

We are here to study some of that life, a team of eight Earthwatch divers led by a scientist and his assistant.

Well beyond the point where the bottom slides into the deep, Lew, a retired Air Force pilot, raises his head out of the water and asks, "Ready?" "Ready," I reply. Regulators replace snorkles, air is let out of buoyancy vests and down we go, into the cool, green world beneath the sea, slowly drifting downward away from the world of glaring sunlight, harsh noise and relentless gravity into a realm of subdued light, silence and weightlessness.

At 80 feet we slow, checking our gauges. At 100 feet we stop, signaling each other that this is it, our assigned depth.

We swim to the wall, find a cavity eroded beneath a large coral boulder and begin identifying and counting corals growing inside the shady cavity, marking our discoveries on a slate. Taking turns with the slate, we probe five cavities, recording the various species of coral growing in the dark recesses.

Twenty minutes go by and that is about all the time allowed at that depth without going into decompression procedures. Lew jerks his thumb upwards, I answer with a similar gesture and a nod and we begin a slow swim up the side of the hill toward the surface.

Another Earthwatch research dive comes to an end.

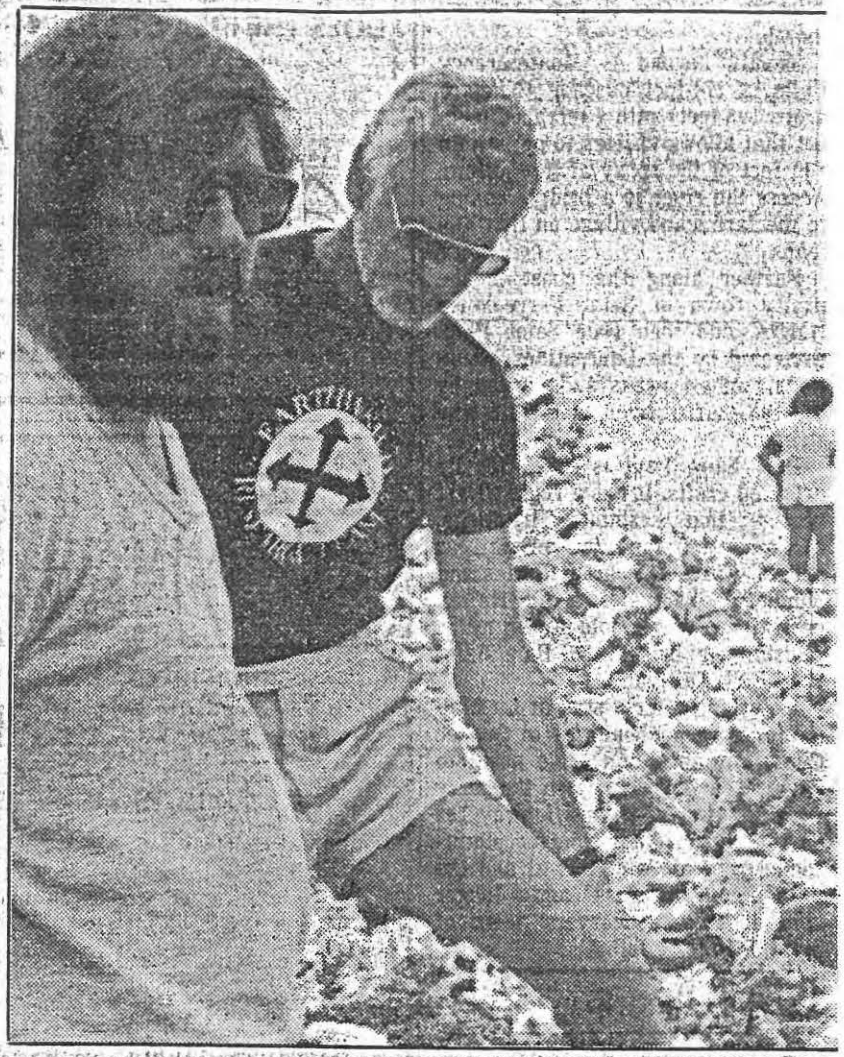
Earthwatch, a nonprofit organization with headquarters in Belmont, Mass., sponsors more than 80 research expeditions a year to sites on six continents and about a dozen islands. The projects include talking to dolphins in Hawaii, tracing the Nazca lines in Peru, saving Leatherback turtles on St. Croix, searching for traces of early man in Africa, Britain and Majorca, digging for fossiles in Nevada, recovering a Revolutionary War ship off Yorktown, Va., and excavating a city built by King Herod of Judea.

The projects are paid for, in part, by volunteers who do the research work under the direction of scientists.

The scientists get free and enthusiastic, if unskilled, labor. The volunteers get an unusual vacation, a chance to take part in actual scientific field research, an opportunity to meet people with interests similar to their own, and a break on their income taxes. All contributions to Earthwatch, plus all out-of-pocket expenses, including transportation to and from the research site, are tax deductible.

This expedition is to Bonaire, one of the Netherlands Antilles just off the coast of Venezuela, an island inhabited by about 8,000 people, 10,000 flamingos, 20,000 goats and several hotels full of North American Scuba divers. On the western side of the island, the trade winds are reduced to gentle breezes, the sea is always calm, the reefs lush and the underwater visibility ranges from good to unbelievable — up to 200 feet. It is one of the three best places to dive in the Caribbean and among the top 10 spots in the world.

Dr. David Kobluk, a geologist and a marine biologist, has been leading Earthwatch projects on Bonaire for the past six years. After mapping an area of the surface of the reef, with a census of surface-dwelling organ-



SHELL STUDY: Geologist Dr. David Kobluk (left) instructs Earthwa

nto Bonaire's underwater world

ins, save turtles, dig into mankind's history



FURNEY HEMINGWAY/Special

tch team on marine life.

isms, he concentrates research on caves and cavities and the plants and animals that live in them.

The oil industry is interested, hoping a better knowledge of reef communities past and present will reduce the cost of drilling. Petroleum, it seems, lurks in ancient reefs buried miles below the surface of the earth.

In addition to taking census of corals growing in cavities, volunteer divers this summer gathered hyroids, little animals resembling two-inch-high trees that grow inside the cavities and chiseled-off bits of the walls and roofs of the dark recesses. The rock samples would be examined later by specialists for their microscopic inhabitants.

Dives were to 40, 60, 80 and 100 feet, with careful records kept as to what was done at which depths. Two dives a day was the norm.

Since you have a task to perform and a limited amount of time to do it, especially at deeper depths and on second dives, research diving is more strenuous than sport diving. Safety first was the order, with careful checks kept on time and depth to avoid the bends. With your head in a cavity, it is hard to see where tender knees land, so fire coral and razor-sharp lettuce leaf coral take their toll.

No resort diving, this. There is no one to carry your tanks, no one to lead you about underwater. Dive sites are not selected for beauty or adventure, but to further the research project. Divers more accustomed to sightseeing underwater discover how time flies and air disappears when you are engrossed in a project.

But if the sea is sometimes a hard taskmaster, it is a never-ending source of beauty and wonder. While working below, I had these experiences.

■ I was attacked by a fearless four-inch damsel fish when I invaded its territory, putting my hand in its algae garden.

■ I encountered an octupus squeezed into an impossibly small crevice, with only one eye and a row of suckers showing.

■ I saw parrotfish eating coral, gobies eating parasites off a tiger grouper, goatfish stirring up dinner in the sand, and big baraccudas just waiting around, eying the possibilities for their next meal.

■ I was followed around by angelfish, mobbed by yellowtail snappers and accompanied on a swim by a dozen trunk fish, triangular shaped, slow swimming comic beggars.

■ I saw a wall of coral with a thousand living Chinese pagodas stretching from the sunlit surface to the black depths.

■ I saw a reef named Alice-in-the-Wonderland and instantly knew why. Castles of the deep were flanked by 12-foot-high mushrooms and other fantastic shapes carved out by the eternal struggle between life and death on the reef.

All was not work, however. There were afternoons off for pleasure diving, trips into town, reading and resting and a full day off for a tour of the island.

Earthwatch expeditions offer a bit of adventure, something real in a world increasingly flooded with fake experiences and a chance to make a small contribution to science.

"I'm with the Earthwatch group," a volunteer said at the dive shop where she wanted an air fill. "Honey, a woman who watches the Earth is here," sang out the shop owner's wife.

The Earth needs watching. You can do it, too.

Tips for the trip

■ **Information:** For complete information on all of Earthwatch's research programs, contact Earthwatch, 10 Juniper Road, Box 127, Belmont, Mass. 02178. Dues are $20 a year; expedition costs vary. ■

Sitting on the bungalow patio looking out towards Klein Bonaire, my eyes and mind are focused on the dark blue line where "our" reef starts its seemingly endless drop to 110'. I spent 90 minutes on that reef today, one dive this morning at 0900 to 70', and again at 1400 to 40'. It's also fairly certain that tonight at about 2100 Brent, Don, Carolyn or Barbara will remember that there is more than 1500 lbs. of air in some of the tanks and start bugging me to "do" a night dive. By that time this glass of wine and perhaps another, plus the huge steak that Dane is presently preparing to barbecue, will take my mind away from that reef world I find so intriguing now. I may balk but will eventually agree to go, no need to get off the dive tables yet. I've been a slave to them for the last 24 hours - why quit now?

This is actually the most relaxing part of our day. Brent and Lisa have kitchen duty, Howard and Carolyn are hauling tanks down to be filled, and of course David and Mary never have time off, but the rest of us are free for the remainder of the day.

Team I is 10 days into our adventures and I think we have slipped into the life style quite nicely. The eight of us have been paired into four teams. Sally is my partner, not only in diving, but for the twice-a-week kitchen and tank duty. We get along great. She's a fine diver, gets to remind me when our alloted time is up (those nagging dive tables). We have finally become competent

enough with our coral identification that we can each just about complete the drawing of our assigned square meter of reef in one dive. In the kitchen, Sally would rather wash than dry (like Jack Sprat and his wife), and on tank duty she hauls as many as I.

Before these two weeks are up, I will have completed 24 dives, helped in the rescue of two young flamingo chicks that were blown into the sea, had my knowledge of geology increased tenfold, and gained seven pounds (Mary's cooking). A superb experience!

Tom Tinker

16904 Kennedy Road
Los Gatos, CA 95030

8/3/86

Comments from Fiske Field, Team III, 1986.

Coinciding with your return home from Dark Reef Interior, you will receive an evaluation form from Watertown, MA, asking you to supply a 1-5 numerical rating to about 15 aspects of David Kobluk's project, from food and lodging to the professional quality of the experience. I think you will find it difficult to go below a 5 and that you'll wish you could give 10's.

On the back of the page you have an opportunity to suggest future changes for the good of the cause and yet-to-come D.R.I. teams. I wrote that the only change I could recommend was to lengthen the time from 2 to 2-1/2-3 weeks.

It's more than that good. The environment, the challenge, the fulfillment, the comfort level--in terms of physical amenities, Kobluk-hammered conch chowder and incredible free-time activities as well as a Kobluk-Lysenko-inspired confidence vis-a-vis the mission--are extraordinary.

You might find some of the following observations helpful, reassuring or whatever:

1. Everyone in Bonaire speaks English and at least 3 other languages, and they're quite happy to accept American money. It's easy to make telephone calls stateside if you want to.

2. David's gear list is all you really have to have, but you might want to pack an underwater light with a recharger (David has a good -- adapter) and a handful of light sticks. The sport diving at night is fantastic, and the nights themselves are so dark that the stars come all the way down to your ankles.

3. The experienced divers on our team all seemed to wear blue jeans or full, lightweight wetsuits or skins, plus booties, to protect against fire coral. Good idea, as I learned the hard way.

4. In terms of washing and drying clothes, jobs I have previously left to the Maytags in the basement, no problem. A lovely lady and her daughter come in to clean the cottages twice a week, and they're glad to do your laundry too--in by 10, out by 2 the same day, and donations are accepted.

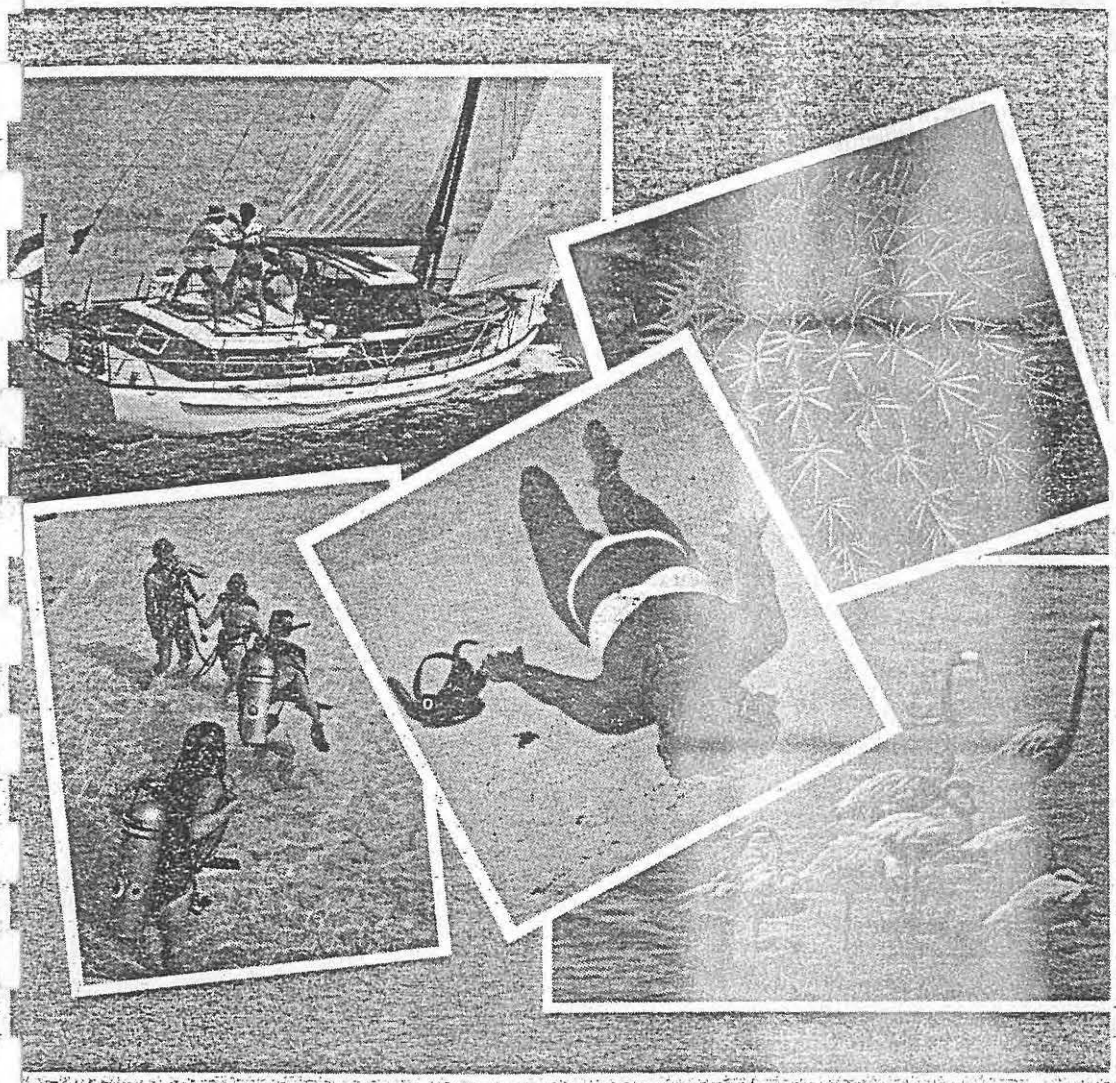
5. Bring a camera. In fact, if you have both an underwater and regular camera, bring two, and more film than you think you can possibly shoot. The coral reefs and fish and the grid you're mapping will be much more impressive if you have slides or prints to go along with your verbal superlatives, and Bonaire's other scenery, which you'll enjoy on your free time, is highly photogenic.

Some of David's briefing in the green binder was pretty heavy for this pension consultant, but a substantial amount of it fit into place surprisingly quickly. David is an extraordinary teacher, and the odds of your asking him a question he can't answer with at least 1,000 (interesting) words are higher than winning $15 million in the lottery.

Though I am inclined to share more, I will resist that temptation. All of the surprises are fun and I know you are in for 2 of the most pleasing and meaningful weeks you've ever had.

bonaire holiday!

FREE official guide to vacation fun and best buys



the main event

It started as a wager between a few friendly fishermen. Nineteen years later the Bonaire Sailing Regatta has grown into a world class event with participants and vessels of major stature in the world of ocean racing.

These and boats of every description move in for the chase as the island gears up for the frenzied week in October of activity that marks the high point of its year.

The challenging course tacks around Bonaire and Klein Bonaire, fighting the South Caribbean trade winds and the rugged North coast. Smaller vessels compete in Kralendijk Bay. What makes this regatta so special is that it still includes the original fishermen's race. Manned by a picturesque collection of hardened island fishermen, the sloops fight their way to their own cup, taking the same course as the larger vessels.

The après sail scene offers the latest in hair-raising stories, brew and bitters. To crew on Bonaire you must be made of strong, strong stuff. The same goes for getting a hotel reservation. Try now. A limited number of rooms is available. Contact the Bonaire Tourist Bureau. (See Fact File below).

tact file

RFIELD:
00 feet paved runway.

AIRLINE OFFICES:
ALM/KLM Tel. 8300 ext. 20, 21, 22. ekdays after 5:30 and Sunday call 01. ASNA: Air Services Netherlands tilles (charters) Tel. 8600.

AIRMAIL RATES:
US & Canada: letters NAf. 1.— st cards NAf. 0.60.

RPORT TAX:
$5.75/NAf. 10. Inter island tax: $2.75/ NAf. 5 per person over 2 years of age.

NK HOURS:
30—12:00 & 2:00—4:00 Mon—Fri.

CLIMATE:
temperature 82° F. Rainfall 22" ndspeed 16 mph. Water temp. 80°F early averages.

CREDIT CARDS:
may be subject to limitations. Check with hotel desk to avoid delay on ecking out. Proper identification quired. American Express, Diners, aster Charge and Visa.

CURRENCY:
S $: NAf. 1.77. The N.A. florin or ilder, is a sound currency backed gold and foreign exchange.

DRINKING WATER:
deliciously distilled and purified seawater.

DRIVING LICENSE:
foreign and international licenses accepted.

ELECTRICITY:
127/220 VAC/50 cycles.

ENTRY REQUIREMENTS:
for US & Canadian citizens: proof of citizenship and return or continuing ticket.

EVENTS AND HOLIDAYS:
New Year's Day; February: Carnival dancing and parades, Carnival Monday; Good Friday; Easter Monday; Coronation Day, April 30; Labor Day, May 1; Ascension Day; Celebration of Dia de San Juan (St. John's Day), June 24, folkloric dances in various villages; Celebration of Dia de San Pedro (St. Peter's Day), June 28, folkloric dances & songs in Rincon; Bonaire Day, Sept. 6; Annual Sailing Regatta, mid-Oct.; Christmas, December 25 and 26.

GAS STATIONS:
Mon. thru Sat. 7am—9pm. Kralendijk Station open Sun. 9am—3:30pm.

INVESTORS INFO. OFFICE:
Dept. of Economic Development, Government Office Building. Tel. 8330 Netherlands Antilles Economic Commission: 1114 6th Ave., NYC 10036, Tel. (212) 719-4601.

KLEIN BONAIRE:
1,500 acre flat, rocky and uninhabited islet half a mile offshore. White sandy beaches, great snorkeling, picnics.

LANGUAGES:
Papiamento and Dutch. English and Spanish widely spoken.

LOCATION:
50 miles north of Venezuela, 30 miles east of Curaçao, 86 miles east of Aruba and 1,720 miles from New York at 12°05' north latitude, 68°25' west longitude, outside hurricane belt.

POPULATION:
10,012.

RADIO BROADCASTS IN ENGLISH:
Trans World Radio: Mon—Fri 8:30am. Daily 1, 7:30am, 5:45, 10:59pm. 800 kHz. n.w. Radio Nederland Wereldomroep daily. 4:30pm. 21.640 kHz. s.w. 10:30pm, 1:30am, 61.65 kHz. s.w. 3:30 and 4:30am. 97.15 kHz.

SIZE:
24 miles long, 3—7 miles wide, 112 square miles. Highest elevation is Brandaris Hill, 784 ft.

STORE HOURS:
8—12:00 and 2:00—6:00pm Mon. thru Sat. When cruise ships are in port on Sundays or holidays tourist shops open for a few hours. For information call: 8322/8649.

TELEVISION:
TeleCuraçao channel 11. Daily 5pm—midnite. Mon—Fri. CNN Take Two 12—2pm, Moneyline 11pm, Sports News 11:30pm.

TIME:
Eastern Standard Time, all year round.

TOURIST BOARD OFFICES:
Bonaire: Kaya Grandi. Tel. 8322/8649. New York Representative: Bonaire Tourist Information Office, 1466 Broadway, Suite 903, New York, N.Y. 10036. Tel. (212) 869-2004. Toronto, Ontario: 815-A Queen Street East. M4M 1H8. Tel. (416) 465-2958. Caracas: Torre Maracaibo, piso 15-E, Avenida Libertador. Tel. 723460/723583.

TRAFFIC:
on the right, international road signs.

customs regulations

CUSTOMS EXEMPTIONS FOR U.S. RESIDENTS RETURNING FROM A VISIT TO THE NETHERLANDS ANTILLES.

Significant benefits for international travelers are included in the Customs Procedural Reform and Simplificant Act of 1978. Highlights of the law, as of January 27, 1983 are outlined below:

1. NOW, you may bring home, free of duty, $400 worth of articles based on the retail value in country of acquisition. FORMERLY, your duty-free personal was $300. (plus $25 worth of Edam or Gouda cheese for personal use).
2. NOW, the number of cigarettes which you may include in your duty-free exemption is 200 (1 carton). FORMERLY, the quantity of cigarettes was specified as being a quantity suitable for personal use.
3. Duty-free liquor is 1 quart per person over 21 years of age within the $400 exemption. However, substantial savings can be realized when taking back more than 1 quart, because even with the duty it comes out cheaper than at the corner liquor store in the U.S. This is especially so on higher priced brands.
4. NOW, articles accompanying you, in excess of your personal $400 exemption, up to $1,000, (thus $600) will be assessed at a flat 10% rate of duty based on the fair retail value in country of acquisition. These articles must be for personal use or for use as gifts and not for resale. This provision may be used once every 30 days, excluding the day of your last arrival. FORMERLY, goods acquired in excess of your personal exemption were dutiable at various rates of duty.
5. NOW, members of a family residing in one household traveling together on their return to the U.S. will group articles acquired for application of the flat duty rate regardless of which member of the family may be the owner of the articles. For example, an eligible family of four would have their articles grouped for a total of $2,400 (see point 4) fair retail value for entry at the flat rate of duty. FORMERLY, there were no provisions for flat rates of duty.
6. NOW, if you cannot claim your personal $400 exemption because you have used it in the preceding 30 days or you were out of the country for less than 48 hours (Mexico and the Virgin Islands excluded from this time limitation), you are allowed to bring in $25 worth of articles acquired for your personal or household use. FORMERLY, the allowance was $10.
7. NOW, in addition to the $400 exemption, each traveler can mail an unlimited number of gifts valued at $25 to friends and relatives back home, provided the addressee does not receive more than one gift parcel in a day. FORMERLY, the gift parcel exemption was $10. No declaration is required and no tax is levied. No liquor or tobacco is permitted.
8. FREE OF DUTY are foreign photographic film, original paintings, drawings and sculptures, foreign language books, antiques, caviar and truffles. Under the U.S. program of trade concessions to developing regions, your gold and silver jewelry could qualify as original works of art if made in the Netherlands Antilles. Be sure to obtain a certificate from the place of purchase that your jewelry was made here. Locally made souvenirs & handicrafts are duty-free also.
9. You may not bring in merchandise which originate from North Korea, North Vietnam, Rhodesia or Cuba. Goods from China are allowed.
10. NOW, if you understate the value of an article you declare or otherwise misrepresent an article on your declaration, you may have to pay a penalty in addition to payment of duty. Under certain circumstances the article can be seized and then forfeited if the penalty is not paid. FORMERLY, the article or its value was liable to forfeiture and duty had to be paid even if the article was seized.
11. Residents returning to Puerto Rico may only take back 1 qt. of liquor and 1 carton of cigarettes within duty exemption (additional carton: $0.80 duty).

Regulations covering the Virgin Islands, American Samoa and Guam, are different than for the Netherlands Antilles. Check with those islands or with U.S. customs.

OF COURSE, customs clearance and exemptions for both U.S. residents and visitors are subject to the same restrictions and requirements as in the past; e.g., agricultural items, endangered species, air pollution and safety control for vehicles. These are covered in leaflets issued for international travelers:

"Know before you go—Customs hints for returning residents"
"Customs hints for visitors (non-residents)"
"Customs highlights for government personnel"
"Customs trademark information for travelers"
"Customs tips for visitors"

Copies may be obtained from U.S. Customs, P.O. Box 7118, Washington, D.C.

CURRENCY

The currency of the Netherlands Antilles is the NAf (guilder). The official rate at which the banks accept US dollar banknotes is NAf 1.77; checks at 1.79. Travellers checks accepted everywhere. The rate of exchange granted by the shops and hotels ranges from 1.75 to 1.80. Under present circumstances the above rates are subject to change.

The guilder is divided into 100 cents, and there are coins of 1 cent, 2 1/2 cents, 5 cents (square nickel), 10 cents, 25 cents, and the 1 and 2 1/2 guilder coins. Banknotes are issued in denominations of 1, 2 1/2, 5, 10, 25, 50, 100, 250 & 500 guilders.

ponaire thumbnail sketch

Getting there by air: From
YC daily on American Airlines
Curaçao or Aruba. ALM (Antillean Airlines) flights: via Curaçao on Wednesday and Sunday.
om Miami: ALM weekdays via
raçao; direct on Thurs. & Sat.
Eastern Airlines daily via Curaçao.
ALM provides connections beeen Aruba, Curaçao & Bonaire
ily. For further info contact one
of the airlines or your travel agent.

By boat: from Curaçao weekly
its by Isidel III. On occasions a
ger ferry makes the trip, leaving from Brion Warf. For further info
contact your travel agent.

Entry requirements: transits (including cruise visitors) need proof of identity for a 24-hour
r less) stay on the island. Temprary stay U.S. and Canadian citizens can do without a passport. They do need a birth certicate, affidavit, naturalization
rtificate, alien registration card or even a voter's registration card as proof of citizenship.

Climate and clothes: warm all
ar round with lowest annual temperature of about 75° and the
sun shines every day. Trade winds
r the air, bringing fresh breezes
om the sea. Nights are cool. Dress is very casual. Cottons are favorites with men and women
ke. Bathing suits are fine for
ach and pool areas.

History: Bonaire was discover-
d in 1499 by an expedition unr Amerigo Vespucci. Indian
awings can be seen today in several places, some dating back
centuries before the discovery
the island. In 1527 the Spanids started their colonization which lasted for little more than a century. In 1634 the Dutch occupied the island of Curaçao as a maritime base in their war against Spain. Once settled, they were forced to occupy the neighboring islands. In 1636 Bonaire became a Dutch colony. The Dutch West India Company drew up an economic development project in 1639. Salt production, corn planting and stock breeding were developed. Salt production gradually became Bonaire's most important source of revenue. An ever increasing number of slaves were brought to the island to work in the saltpans.

Between 1800 and 1816 Bonaire suffered from the activities of French and British pirateers. The British also occupied the island for some time, and not knowing what to do with it, they leased it to a NY merchant, including its 300 slaves, for about $2,400 annually. In 1816 the Dutch took over again and set up a system of government plantations (Brasil wood, aloës, cochenille, etc.) and the saltpans. After the abolition of slavery in 1863, the government operations turned out to be unprofitable and the island was parcelled out and sold.

Faced with an economic recession till about 1926, Bonaireans began to migrate to Curaçao and Aruba where they found work in the oil industry. Having left their wives behind, the men mailed their earnings home. This period is known as the era of "money order economy". Automation of the oil industry in the late fifties seemed disastrous and many unemployed Bonaireans returned to their native island. Happily, during these last few years, international tourism discovered the Caribbean and eventually, also the scenic beauties of Bonaire. The first hotel opened in 1951. Since then, others have been completed and condominium and hotel construction plans are on the drawing board. A marina has been added and further development of this kind is warmly encouraged. Tourism has remained the most favored industry. The Bonaireans, however, would prefer to keep tourism on their paradise island low-key and tranquil, rather than swinging and frantic.

With the Netherlands Antilles autonomy in 1954, Bonaire was allocated some outside resources to improve economic prospects for the island. The saltpans were modernized and became one of the most environment-conscious plants in the world employing solar energy.

A small ready-made clothes factory made a modest beginning. Making use of shark bone, coral, wood, leather and other natural products native to the island, "Fundashon Arte Industria Bonairiano", a non-profit foundation to promote handicrafts, has set out to train young people in this field. An enlarged power plant and airport were built to accommodate the budding contracts with the outside world. With the advent of Bonaire Petroleum Corporation (BOPEC) in September 1975, the island acquired a terminal receiving oil for transfer from giant to smaller tankers. This process in no way affects the clean balmy air. Indeed, determined to protect their natural resources, Bonaire was the first of the Antilles to enact stringent environmental legislation on land and sea, to reserve a national park and safeguard flamingoes in a wildlife sanctua In 1964 "Trans World Radio", super powered (500,000 W.) Pr testant missionary station beg broadcasting over the entire We ern Hemisphere, the Middle Ea North Africa and even behind t Iron Curtain. In 1969 "Rad Nederland Wereldomroep", t Dutch World Broadcasting C started their own shortwave i stallation, and its programs ha become popular in this part the world.

Government: Bonaire with population of 10,012 is the seco largest of the 6 Netherlands A tilles islands... Aruba, Bonai Curaçao, St. Maarten, Saba & S Eustatius, of which, since Janua 1986, Aruba no longer forms pa The Netherlands Antilles is autonomous part of the Kingdo of the Netherlands. Its form administration is a parliamenta democracy. A governor, appoir ed by the Queen of the Neth lands, represents the Crown. Bo aire has a Lieutenant Governo Mr. G. Soliana, residing in Krale dijk, the island's capital. There a Legislative Council, call "Staten" (Parliament), an Exec tive Council and Advisory Cou cil. The seat of the Centr Government is in Willemsta Curaçao. Each island territory h its own Legislative and Executi Body called an Island Counc Senator Mr. Ch. L.R. Ellis is Bo aire's representative in "Staten



If you find, wh strolling throu town, that you need some information or assistance, ask Caicai Cecilia, the Bonaire Tourist Bureau courtesy guic Caicai will be glad to help yo


To: Bonaire Beach Hotel & Casino; Buddy's Dive Resort; Captain Don's Habitat; Colombian Consulate; Den Laman Bar & Restaurant; Sand Dollar Condo; Trans World Radio
kralendijk
shopping center
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To: Achie Tours
To: ASNA; Bonaire Sunset Villas; Budget Rent-A-Car; Flamingo International Airport; Antillean International Salt Co.; Milton's Tax & Duty Free Shop.
Consales
ALM 28
Algemene Bank Nederland 8
Aries Boutique 12
Beefeater Restaurant 10
Bistro Des Amis 36
Bonaire Sightseeing 29
Bonaire Trading 29
Boncar 29
Boolchand's 13
BOPEC (Admin. Off.) 22
Buddy's Dive Resort 14
Budget Rent-A-Car 29
Busi Construction 4
China Garden Restaurant 20
Consales Bonaire 5
Ennia Caribe N.V. (Insurance Co.) 7
Flamingo Beach Hotel & Casino 1
Happy Chappy Rentals 2
Hotel Rochaline 3
Kralendijk Trading Co. 29
Littman Jewelers 11
Maduro & Curiel's Bank 24
Optica Antillana 17
Poseidon Nemrod 2
Rendezvouz Bar & Café Rest. 25
Spritzer & Fuhrmann 15
Things Bonaire 9
Zeezicht 16
Cable Office B
Catholic Church Q
Children's Playground N
Customs G
Fish Market L
Government Offices D
Hospital P
Instituto Folklore (museum) C
North Pier H
Police Station F
Post Office E
Protestant Church J
Ro-Ro Pier R
South Pier A
Tennis Court O
Tourist Bureau M
Venezuelan Consulate K
bejolha
CONSTRUCTION

The inside story

The beautiful world of coral reefs seen and photographed by most visitors to Bonaire hides another world, one rarely seen, tucked out of sight... and out of mind. Small openings in the reef under coral ledges or algal overgrowths, lead below the reef surface into a dark maze of tunnels and cavities which are a feature of all reefs. Reefs are porous, like a Swiss cheese... a cheese of corals, algae, and limestone with large spaces, sometimes amounting to 40% of the volume of the reef. Deep inside the porous interior, over many millions of years, animals and plants have adapted to a life in a quiet, dark environment. Throughout their lives, many of these animals never see the light of day, living in the dark interior cavities and caves. Called coelobionts, animals and plants living inside Bonaire's reefs belong to one of the most poorly understood and yet one of the most ancient of ecosystems.

Dr. David Kobluk, of the Department of Geology at Canada's University of Toronto, has been studying the ecology and geology of the interior of Bonaire's reefs for some years now, as part of a large project in which he is investigating the geological history of reef cavity ecosystems. Dr. Kobluk selected Bonaire for his study because of the pristine quality of the reefs, the excellent scuba diving services on Bonaire, and the easy access to most of the coastal reefs. The Bonaire government's wise protection and management of its irreplaceable coral reef resource, has kept Bonaire's reefs among the finest in the Caribbean.

Dr. Kobluk has visited Bonaire often over the years, sometimes with as many as ten research scuba divers to assist in the cavity ecosystem project. Some of these research expeditions have been coordinated through Earthwatch of Belmont, Massachussetts, a non-profit organization based in the United States.

Over the first four years, 51 research scuba divers have travelled to Bonaire to work with Dr. Kobluk on this project, studying the ecology of the reef interior and mapping its exterior to provide a framework within which to compare the ecology inside the reef. The mapping phase of the project is complete, and 240 square meters of coral reef from the surface to forty meters in depth have been mapped painstakingly by hand to produce the largest detailed map of a coral reef yet produced anywhere, even the individual tubeworms, a centimeter in diameter are included in this picture of the coral reef. The underwater mapping part of this project alone required 1,940 scuba dives and 410 man hours under water to complete.

Why all this research and underwater work? In order to properly protect and manage coral reefs, we must understand them as fully as possible. "By not understanding the ecology of the reef interior we are missing a very large and important part of the whole reef picture".

"Reefs have been in existence for about 550,000,000 years... but even in some of the oldest of known fossil reefs from the coast of Ecuador, Canada, animals and plants that once lived below the reef surface in cavities, are found fossilized in place. If we look back at some of these half billion year old fossil reefs and the preserved organisms fossilized inside the cavities, the amazing thing we find is that, although species of cavity dwellers have changed, the basic organization of the cavity ecosystem has not. When we look into cavities inside Bonaire's reefs, what we see is a modern example of one of the oldest living ecosystem structures known to man; it does not appear to have changed in its basic organization in over 530,000,000 years".

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Bonaire Beach Bungalows:
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Bonaire Sunset Villas:
1 and 2 bedrm cottages w/airco. Tel. 8291. Belnem.

Carabela Bungalows:
1 & 2 bedrms, complete kitchen, maid service. Tel. 8065.

Carib Inn:
5 rms w/airco. Tel. 8819. J.A. Abraham Blvd.

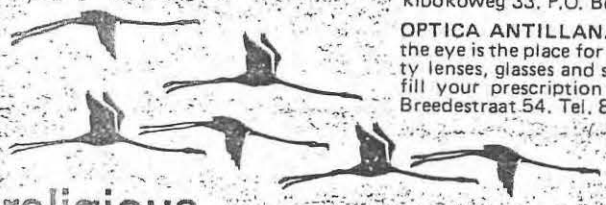
Coral Villas:
2 apts w/ 2 beds; 1 house w/ 4 beds. Tel. 8428. Belnem.

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OPTICA ANTILLANA at the sign of the eye is the place for optician's quality lenses, glasses and sunglasses. They fill your prescription at the store on Breedestraat 54. Tel. 8815.



religious services

EVANGELICAL ALLIANCE MISSION: Nrd. Saliña. Sun 9am worship service; mass: 7:30pm. Wed. prayer service: 7:30pm. Tel. 6245.

JEHOVA'S WITNESSES: Antriol. Tues. 7:30pm; Fri. 7:15pm; Sun. 7pm.

NEW APOSTOLIC CHURCH: Nrd. Nikiboko 220. Tel. 8483. Sun. 9:30 till 10:30am. Wed. 8 till 9pm.

OUR LADY OF COROMOTO R.C.: Antriol. Sat. 7:30pm. Sun. 9am and 6pm. Tel. 4211.

SAN BERNARDO CHURCH, R.C.: Kralendijk. weekdays 6:45pm; Sun. 8:30am and 7pm. Tel. 8304.

SAN LUDOVICO CHURCH, R.C.: Rincon. Sun. 6 and 9am, 7:30pm. Weekdays 7:30pm. Tel. 4254 / 4621.

SEVENTH DAY ADVENTIST CHURCH: Sat. 9am. Sun. and Wed. 7:30pm. Antriol and Rincon. Tel. 4254.

TRANS WORLD RADIO FELLOWSHIP: Sun. 11am; 6:30pm; Sunday school 9:30am. Tel. 8800.

UNITED PROTESTANT CHURCH: For information call 8086.

club meetings

The service clubs of Bonaire extend a cordial welcome to out-of-town members to attend local club meetings.

JAYCEES: meets last Wednesday of the month. For information call 8285.

KIWANIS: meet every Thurs. at Bonaire Beach Hotel 7pm. For more info call 8299.

LIONS: meet twice monthly. For more info call 8546.

ROTARY: meets every Wed. for lunch at Bonaire Beach Hotel. Tel. 8448.

ROUND TABLE INTERNATIONAL: for info call 6218.

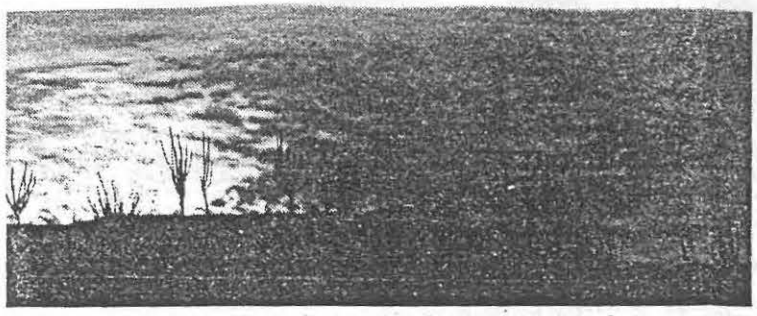
YOGA: Mon. 8—9pm, Hatha Yoga. Wed. 7—9pm, Siddha Yoga. Sun. 6:30—7:30am chanting every two weeks, teaching of Siddha Yoga. Road to Lagoen. Tel. 4291.

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many animal species are unique to bonaire

Cut off from contact with other land masses, Bonaire developed a number of unique animal species. Although Venezuela is but 60 miles away, the fauna in many respects is quite different. Even common birds like the Bananaquits and the Parroquets are colored differently. On Bonaire the Bananaquit has a yellow breast, on the mainland its breast s greyish. The mainland Parroquet has a yellow throat.

On Aruba, the yellow head area is longer, on Curaçao most is yellow, but on Bonaire the head and breast are bright orange-yellow. Many other bird species are Bonaire originals too.

Lizards too are unique. The big blue lizards belong to a true endemic Bonairean species. The Anolis, a tree lizard with a beautiful yellow dewlap, is also a Bonaire native. This Anolis is not even related to its Venezuelan neighbors but to some Windward Islands Anolis species. Some other reptiles, birds and land snails show closer relationship to the far-off northern Windward Islands than to nearby mainland. Scientists think this came about because Bonaire was a volcanic island, long ago, with closer ties to the large Caribbean island group than to Venezuela.

Conservation is important not just for the beauty of the fauna but because it's irreplaceable. Most species are not currently endangered. One of the exceptions is the Bonairean "lora", a parrot much larger than the parroquet. These parrots used to be considered a pest, especially during the dry season when they visited the plantations and devoured the mangos, papayas and other fruits, alongside the long caffercorn millets, sorghum).

In later years, their natural habitat has diminished, and their population has been reduced by the capture of nestlings that are sold— although this is prohibited by law. The population may have reached a critical stage now. This year, two biologists are trying to make a census of the lora population and investigate their food habits. They will try to promote the growth of the trees and shrubs that are important to the loras. Good progress is being made. They are cooperating with The Washington/Slagbaai National Park management to prevent extinction of the Bonairean parrot.

Data by Dr. I. Kristensen from the Caribbean Marine Biological Institute

SEE BONAIRE'S UNIQUE SCENIC BEAUTY, THE FLAMINGOES, SLAVE HUTS, CONCH SHELLS, GOTO LAKE, INDIAN INSCRIPTIONS, FISH MARKET, HANDI-CRAFT CENTER, etc. IN OUR COMFORTABLE SIGHTSEEING BUSES...

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touring the island

Rent a car, hire a taxi or join one of the scheduled bus tours and see why Bonaire is called unique in the Caribbean. You might take a hat, a camera and refreshments.
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scenic tour south

When taking the two hour tour of the island, you'll notice that it varies not only in direction from the northern part, but also in its content and nature. Soon you'll see the Trans World Radio antennae towering over you from 500 feet.

Further on you'll come upon the historic salt pans which have been reactivated by Antilles International Salt Co. N.V. after many years of non-use. The snow-white hills of salt sparkle like diamonds in the sun. Then there are the stone slave huts built around 1850 to shelter the slaves when working the pans, and the three 30 ft. obelisks built in 1838 to guide the salt ships to their moorings.

The flamingoes feed in a number of the salt pans and use less saline water of the Pekelmeer for bathing and drinking. The brown and pinkish color of the pans is caused by algae and bacteria. Some flamingoes can usually be seen in the pans and the Pekelmeer near Pink Beach. Amidst the salt pans lies the 55 Ha (135 acre) flamingo sanctuary, the exclusive breeding ground for the southern Caribbean flamingo population, counting some 10,000 birds.

The flamingo nest measures about 12 to 15 inches high and approximately 2 feet across at the bottom, tapering off to concave tops caused by the flamingoes smoothing the clay with their beaks; each nest holding one egg. Since breeding flamingoes are extremely sensitive to disturbances, access to the sanctuary is strictly prohibited and we recommend Gotomeer and the Washington-Slagbaai Park for watching the daily take-off of flamingoes to Venezuela at sunset. This can best be seen from the slave huts at Rode Pan.

Heading on you'll come to the Willemstoren, which having been built in 1837, is the oldest lighthouse on Bonaire. Next are Sorobon Beach and Boca Cai at landlocked Lac Bay, two of the most attractive spots on the island, with aquarium-like marine life and conch shells stacked up on the beaches. On the road back to Kralendijk you'll pass through the village of Nikiboko, where you might stop for refreshments.

scenic tour north

When you take the Northern tour, which also runs for about two hours, it almost seems as if you're going to disappear into the hills. After passing Bonaire Beach Hotel and the water distillation plant you'll soon come to the transmitting site of Radio Nederland Wereldomroep (Dutch World Radio). All along this road, which will eventually bring you into Rincon, there are delightful little paved paths which angle closer to the coast on the left and then back towards the caves on the right, for cycling or strolling.

As the road winds and curves you'll see the storage tanks of Bonaire Petroleum Corporation N.V. (BOPEC) which has kept nature in mind when planning the installation as they are quite environment conscious. The road leads upward to Gotomeer which is Bonaire's most beautiful inland region. This is one of the best places to watch the flamingoes. There are commonly hundreds of flamingoes in Gotomeer, some even quite close to the road. Photographers stay in your cars for best results.

Further on down the hill the road comes to what looks like an oasis with many palm trees and vegetation. This area is called "Dos Pos" or Two Wells. When reaching the crest of the following hill one stops almost breathlessly at the sight of a small township nestled at the bottom of the other side of the hill; Bonaire's oldest village, called Rincon. The crest where you stop to take in this view is aptly called "Para Mira", Stop and Look. Past Rincon on a side road are the Arawak Indian inscriptions reputed to be over 500 years old. Further along is Seru Largu with its fabulous view of Kralendijk and the sea. Then through the village of Noord Saliña head back to Kralendijk.

Washington / Slagbaai National Park

This 13,500 acre game preserve is the first of its kind in the Netherlands Antilles. As you can see on our island map, the park occupies almost all of the north western portion of the island. The park is open 7 days a week from 8am to 5pm. Entrance only NAfl. 3.62 ($2) per person, children under fifteen NAfl. 0.50. An excursion guide booklet to the park is available for NAfl. 7.50 ($ 4.15) at the gate. The best bird watching time is in the morning. No hunting, fishing or camping allowed. Visitors are requested not to frighten the birds or animals nor to damage or remove anything from the grounds. Two routes are laid out through the park: a 24 km (15 mile) "short" route and a 35 km (22 mile) "long" route, marked by the yellow and green arrows respectively. As befits a wilderness sactuary, the roads are a bit rugged... and as such they force one to drive slow enough to really see and appreciate the birds and terrain. The European Common Market has recently financed an extensive road improvement program within the park, which was presented and executed by the Bonairean Government.

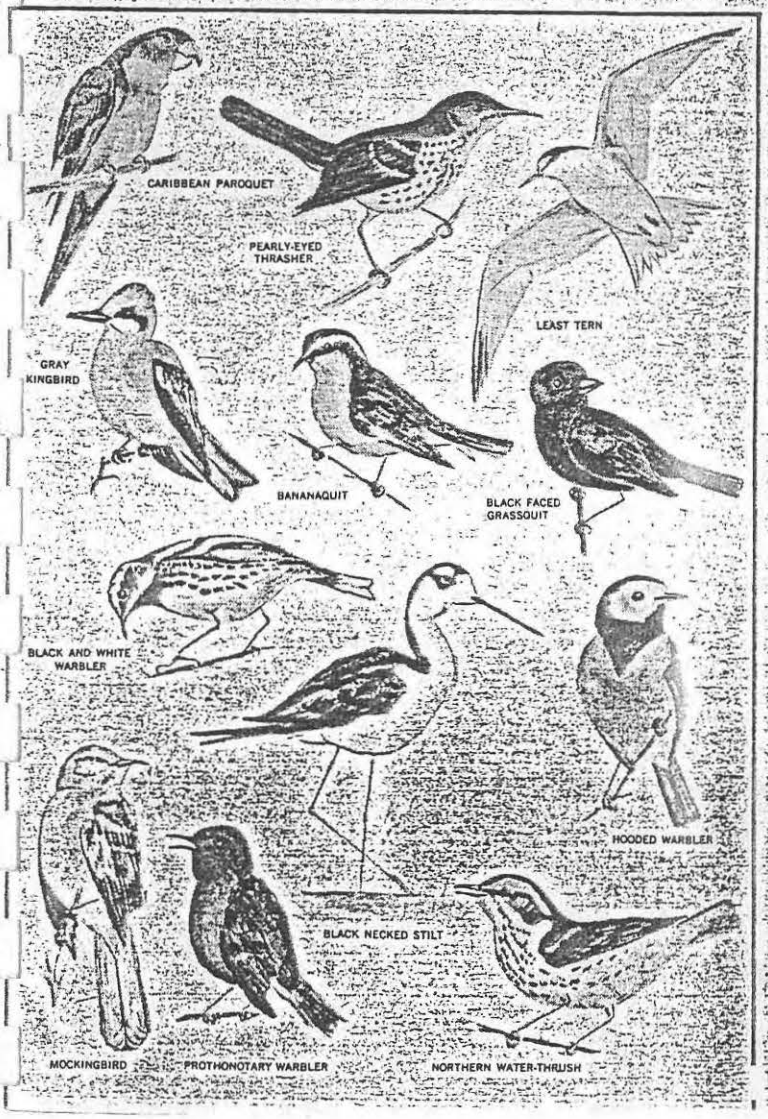
tour of the park

Entrance tickets to be purchased at the gate. The first stop after leaving the gate house is Saliña Mathijs, a salt flat where flamingoes may be seen during the rainy season. After the water in the pan has evaporated a white salt crust covers the saliña (salt pan).

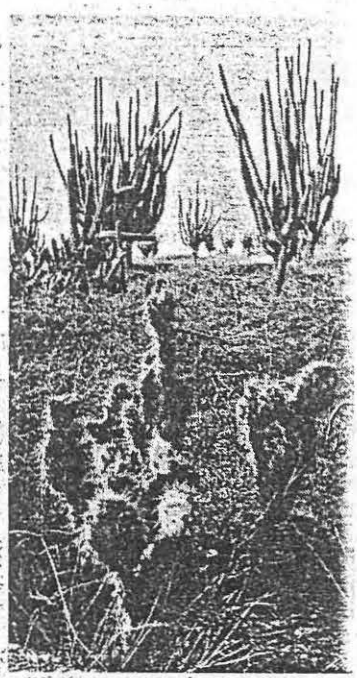
A few kilometers further on, a side road to the right leads to Playa Chikitu, a lovely beach with a strong, high surf. More appropriate for sunbathing and body surfing than for swimming. Stay in the middle of the beach since the undertow, especially on the left, is rather strong. Avoid swimming out far and keep a close watch on your children.

"Seroe Bentana" (Window Hill) and its lighthouse are a few kilometers down the road. Here you'll see the boulders that nature formed into a "window" through which you can look out onto the sea.

A good bird watching post is Poos di Mangel, a watering place where many birds gather in the mornings and late afternoon to drink. Poos di Mangel is off on a road to the left, West on the way to Boca Bartol. At Boca Bartol the road runs across the flats between the sea and large inland saliña of Bartol. You're now heading south with Mount Brandaris looming up directly before you. A right at the fork takes you to Playa Funchi where you'll find one of the best snorkeling spots on the island.



Flamingoes also frequent the saliña behind the beach. A left turn at the fork leads you to Bronswinkel Well. Here, at the foot of the Brandaris, where hundreds of birds come to drink, you'll see blue pigeons, yellow breasts and once in a while screeching parakeets. Here and on the trip back to the gate you'll see 10, 15 and 20 foot high cacti. Bonaireans, you may know, make a delicious soup from this type of cactus. With tongue in cheek they will remind a stranger that the thorns must be removed, of course.



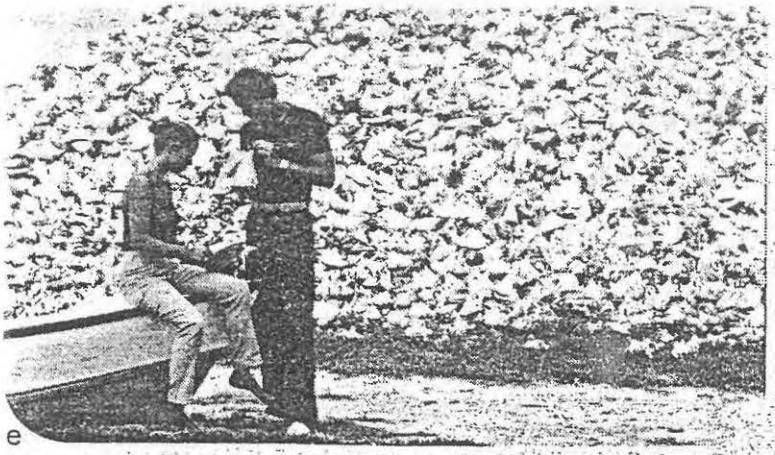
If you continue your trip to Slagbaai, leaving Playa Funchi you first drive on a cliff along the ocean. In between Playa Funchi and Wayaka you have a good chance to see some 3–4 ft. iguanas on the edge of the cliff. The road leads you around the saliña Wayaka at the foot of the Brandaris and to Boca Slagbaai. This is a good place to rest, picnic, swim and snorkel. From Boca Slagbaai the road takes you back to the park gate, with a possible side trip to a beautiful panorama of Gotomeer with its flamingoes. On the way to the gate, before crossing the Juwa Hills, there are some magnificent lignum vitae trees.

If you haven't signed the guest book at the gate on your way into the park, remember to do so as you leave. The purpose of the park is, of course, to conserve for posterity its untouched nature with all its flora and fauna, its beautiful hills and bays, beaches and coastline. Thus our descendants can see how the land looked formerly. Thank you for visiting the park and for your donation. Your help, together with the immense help from the Dutch and Antillean governments and nature lovers of the Antilles, have made this park possible.

history of the park

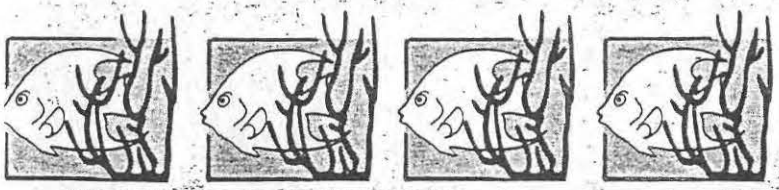
Slightly over one hundred years ago the Government of the Colony of Curaçao sold what is now Washington Slagbaai National Park to several individuals, namely Dr. Moises Jeserun and three Neuman brothers. It was later sold to Jean Luis Cadieres and Jean Jacques Debrot in 1892 who in turn sold the northern part to the Herrera brothers in 1920. They named it America and subsequently Washington. As the years went by the property became a plantation and produced under the Herrera family divi-divi, aloë, charcoal and goats. It prospered somewhat from the 1940's until the end of the 60's when the final private owner Boy Herrera passed away. Not wishing to see the land exploited he negotiated with the Netherlands Antilles Government to purchase it with the express condition that the land remain in its natural state. Thus "Washington" became the first sanctuary in the Netherlands Antilles.

Recently, in 1978 the Beaujon family, who had acquired the southern portion of the property, sold it to the N.A. National Parks Foundation who in turn added it back to the northern portion thereby enlarging the Washington National Park of 1974 to the Washington/Slagbaai National Park of 1978. Thus the land has come full circle... back to Caesar and back to nature.



e

BONAIREANS LOVE CONCH... especially pickled and peppery. Conch, which is similar to abalone, is fished up at Lac. After the meat is extracted, the shells are piled along the shore.



Bonaire Marine Park

A UNIQUE VENTURE IN REEF MANAGEMENT

The Bonairean Government's positive approach towards conservation can hardly be better illustrated than by its development of the Marine Park. It was agreed that the park would consist of all the coral reefs around Bonaire and Klein Bonaire. This is roughly the entire coastline from the highwater tidemark down to a depth of 60 meters (200 ft.).

"Marine Park" is translated as an area for which certain restrictions and regulations hold forth in order to attain the best possible balance between protection and utilization. An area that is being managed properly, because future generations will also want to benefit from the reefs, whether it be by scuba diving or by harvesting food from the reefs. This is why the World Wildlife Fund (WWF) in 1979 funded a project to establish the Bonaire Marine Park and why marine biologist Eric Newton, along with assistant Franklin Winklaar, are working hard on a reef management program under the aegis of the Netherlands Antilles National Foundation. (Better known under its Dutch acronym STINAPA). A program that is being developed in close harmony with dive operators because they are well aware of relationship between proper reef management and a successful dive business.

Managing a coral reef requires a lot of basic information that must be gathered through research. Biologists of the Caribbean Marine Biological Institute (CARMABI) in Curaçao, have collected a substantial portion of this information and are continuing their efforts in this field. For example, Fleur van Duyl is conducting a reef mapping survey of the leeward side of Bonaire, using aerial photographs to draw basic maps and subsequently checking this data underwater using a diver propulsion vehicle (DPV). In addition, the park's staff is conducting long-term monitoring in an attempt to determine if and how the ever increasing number of divers affects the health of the reefs. Management also includes policing the area and providing certain facilities for park visitors. Such as the unique system of 32 public moorings, that will, if properly used, reduce to almost zero the damage inflicted by boat anchoring.

If you'd like to know more about the Bonaire Marine Park, there is a dive guide available in bookstores and at dive operations. Please follow these basic park rules while diving and snorkeling on our reefs:

do not spearfish

do not take shells or coral (any kind of coral, dead or alive) from the reefs

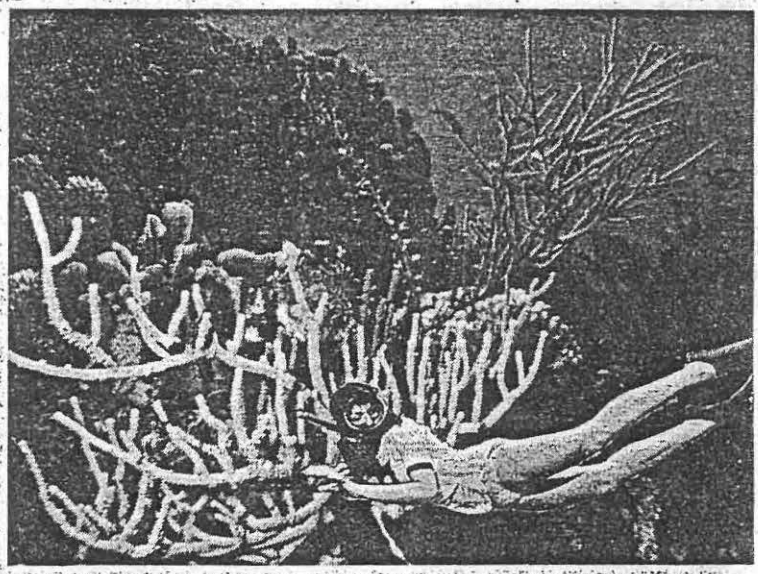
do not damage the reefs by stepping or resting on coral heads. They are living animals!

do not litter the reef and its adjacent coastal area

do not anchor on the reef outside the Kralendijk harbor area, do use the public moorings.

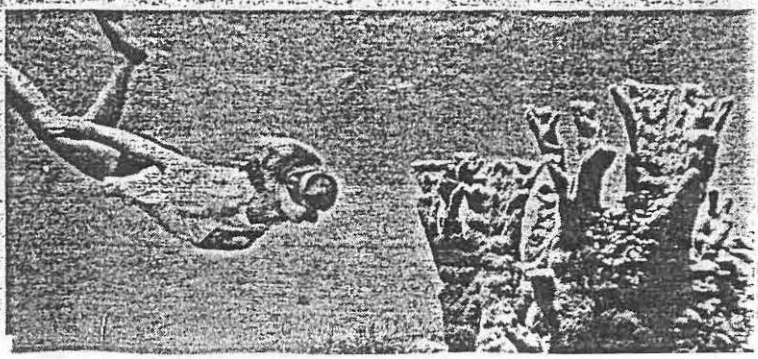
There's a program that has become a tourist attraction in addition to generating an exciting island enterprise. It has long been recognized that the once plentiful conch found on the ABC islands has become one of the endangered species. The combined governments of these islands have found a solution and have initiated a large scale conch farm next to Habitat. This project is being headed up by Robbie Hensen, a marine biologist from Curaçao who explains that the raising of conch in captivity, using modern technology, can improve nature's yield by a thousand times or more. For example, a single conch will lay during her life span approximately six million eggs of which only three or four will reach maturity. Because of this low rate of survival and the extreme fishing pressure, conch has become almost extinct. Thousands of cultivated conch have been released in nature since 1982. Natural survival has been exellent.

To get an idea of the popularity of conch on Bonaire, one only has to visit Lac Bay where small mountains of the discarded shells stand. In the future maybe even the shell will be of economic value. Experiments are also being done to cultivate shirmp, edible and exotic fishes. One can always drop in but please call beforehand for a guided tour. Tel. 8595 / 8836.



Underwater slide shows

Bonaire has some little publicized but much enjoyed evening entertainment for divers and non-divers alike: slide shows. Captain Don's Habitat hosts two each week. Wednesday at 8:45 Habitat's photo pro André Nahr does his unique slide show. On Monday nights at 8:45 as well, dive guide Dee Scarr presents "Touch the Sea.., a slide experience dealing with tactile sensations and interactions with Bonaire's marine creatures... including individual fish personalities. For non-divers Captain Don also presents a view of Bonaire "Above the Plimsoll Mark" on Friday 9pm. Bonaire Scuba Center presents a slide show on Wednesday nights at Bonaire Beach Hotel & Casino at 9:30pm. New 24-min. underwater video "Discover the Caribbean" on Sunday night at 9:30pm at the Flamingo Beach Hotel & Casino. More information on these entertaining and educational evening activities can be obtained by inquiring at the individual hotels. Of course all of the slide shows are provided free of charge by the hotels for your enjoyment!



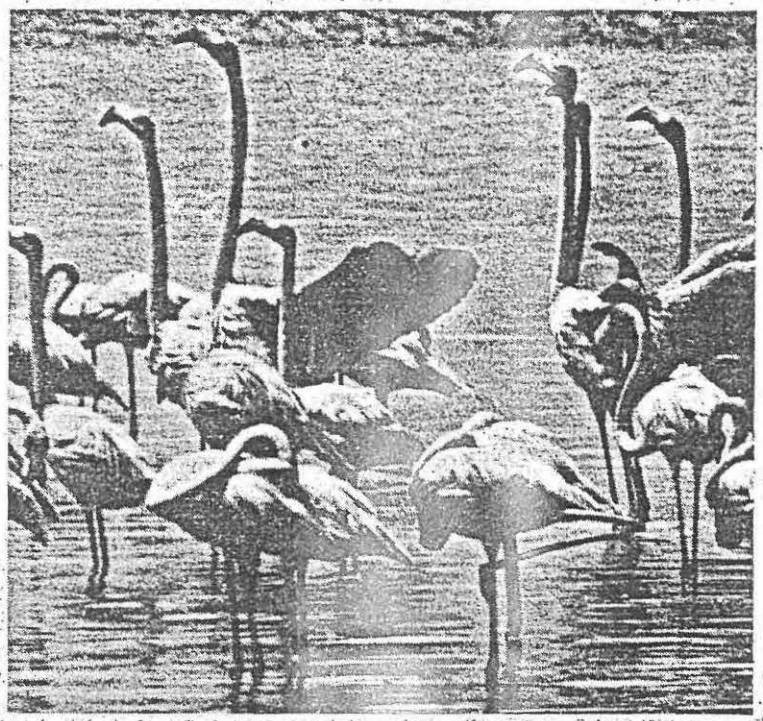
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saltman spare that bird

On Bonaire ornithology and technology were involved, in preserving a species before it was endangered. As a result hundreds of flamingoes now live peacefully in the midst of an industrial operation which is essential to the economy of the island, the solar manufacture of salt. It's the story of an enlightened company, Antilles International Salt, and the Bonaire government, and what they did to spare the island's fragile birds.

The Salt Company contracted to reactivate and expand the long dormant salt industry, but required the use of the old salt pans where the flamingoes had built hundreds of their conical mud nests. The question was whether or not the company could conduct its operations without disturbing the bird population; but company engineers agreed to redesign their original plans, at an additional cost of $100,000 in order to bypass the famous breeding sanctuary. The birds seemed apprehensive with the sudden activity, but eventually settled down to a surprising peaceful coexistence. During the breed time the population grows to thousands. Each flamingo nest has a depression in the top just large enough for a single egg. The graceful, longlegged birds wade among the salt pans, feeding on small snails. As far as Bonaire is concerned, a bird in the pan is definitely worth its salt.

With its constant sunshine, trade winds, and scant rainfall, Bonaire is ideally suited for the solar manufacture of salt, a method used by the Chinese more than 2,000 years ago. Sea water is pumped into a series of concentrating ponds where the brine content of the water is raised to the saturation point. The brine is pumped to crystalizer ponds where the evaporative power of the sunshine and trade winds cause crystals to form as the pond dries up. This is salt in its crudest state. These crystals are removed mechanically from the pond bed and pass through a washing plant to be cleaned of impurities. The washed crystals are put out to drain and dry in huge mounds. Three months later the salt crystals, cleaned and thoroughly dried, are ready for shipment. They are loaded on great mechanized conveyor belts and moved at the rate of 2,000 tons per hour to ocean going freighters at the company's deepwater pier.

Sponsored by the Antilles International Salt Co. N.V., a wholly owned subsidiary of International Salt Co., which is part of AKZONA Incorporated.

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ADVANCE PREPARATION

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PREPARATION

READING LIST

The reading list following is designed to give you a selection of a wide range of popular to technical articles to prepare your background for the Bonaire project. The articles and books listed vary from the very easy to the highly technical, so that you should be able to find some articles in this list to suit your particular background level. It is not expected that you will read all of them, or even be able to find all of them; however, some attempt should be made to gain as much background as possible in at least the generalities of coral reef ecology and theory before arriving in Bonaire.

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THE EVOLUTION OF REEFS

The community of plants and animals that builds tropical reefs is descended from an ecosystem of two billion years ago. The changes in this community reflect major events in the history of the earth

by Norman D. Newell

To a mariner a reef is a hazard to navigation. To a skin diver it is a richly populated underwater maze. To a naturalist a reef is a living thing, a complex association of plants and animals that build and maintain their own special environment and are themselves responsible for the massive accumulation of limestone that gives the reef its body. The principal plants of the reef community are lime-secreting algae of many kinds, including some whose stony growths can easily be mistaken for corals. The chief animal reef-builders today are the corals, but many other marine invertebrates are important members of the reef community.

This association of plants and animals in the tropical waters of the world is the most complex of all ocean ecological systems; as we shall see, it is also the oldest ecosystem in earth history. Its closest terrestrial counterpart, in terms of organization and diversity, is the tropical rain forest. Both settings evoke an image of exceptional fertility and exuberant biomass. Both are dependent on light in much the same way; the sunlight filters down through a stratified canopy, and the associations at each successive level consist of organisms whose needs match the available illumination and prevailing conditions of shelter. There is even a parallel between the birds of the rain forest and the crabs and fishes of the reef. Both play the part of lords and tenants, yet their true role in the history and destiny of the community is essentially passive.

It is a common belief that a reef consists principally of a rigid framework composed of the cemented skeletons of corals and algae. In reality more than nine-tenths of a typical reef consists of fine, sandy detritus, stabilized by the plants and animals cemented or otherwise anchored to its surface. Physical and biochemical processes that are little understood quickly convert this stabilized detritus into limestone. The remains of dead reef organisms make a substantial contribution to the detritus. This major component of the reef, however, has a fabric quite different from the upward-growing lattice of stony algal deposits and intertwined coral skeletons that forms the reef core.

The Reef Community

The interaction of growth and erosion gives the reef an open and cavernous fabric that in an ecological sense is almost infinitely stratified and subdivided. In the dimly lit bottom waters at the reef margin, rarely more than 200 feet below the surface, caves and overhanging ledges provide shelter for the plants and animals that thrive at low levels of illumination. From the bottom to the surface is a succession of reef-borers, cavern dwellers, predators and detritus-feeders, each living at its preferred or obligatory depth, that includes representatives of nearly every animal phylum. Near and at the surface the sunlit, oxygen-rich and turbulent waters provide an environment that contributes to a high rate of calcium metabolism among the myriads of reef-builders active there.

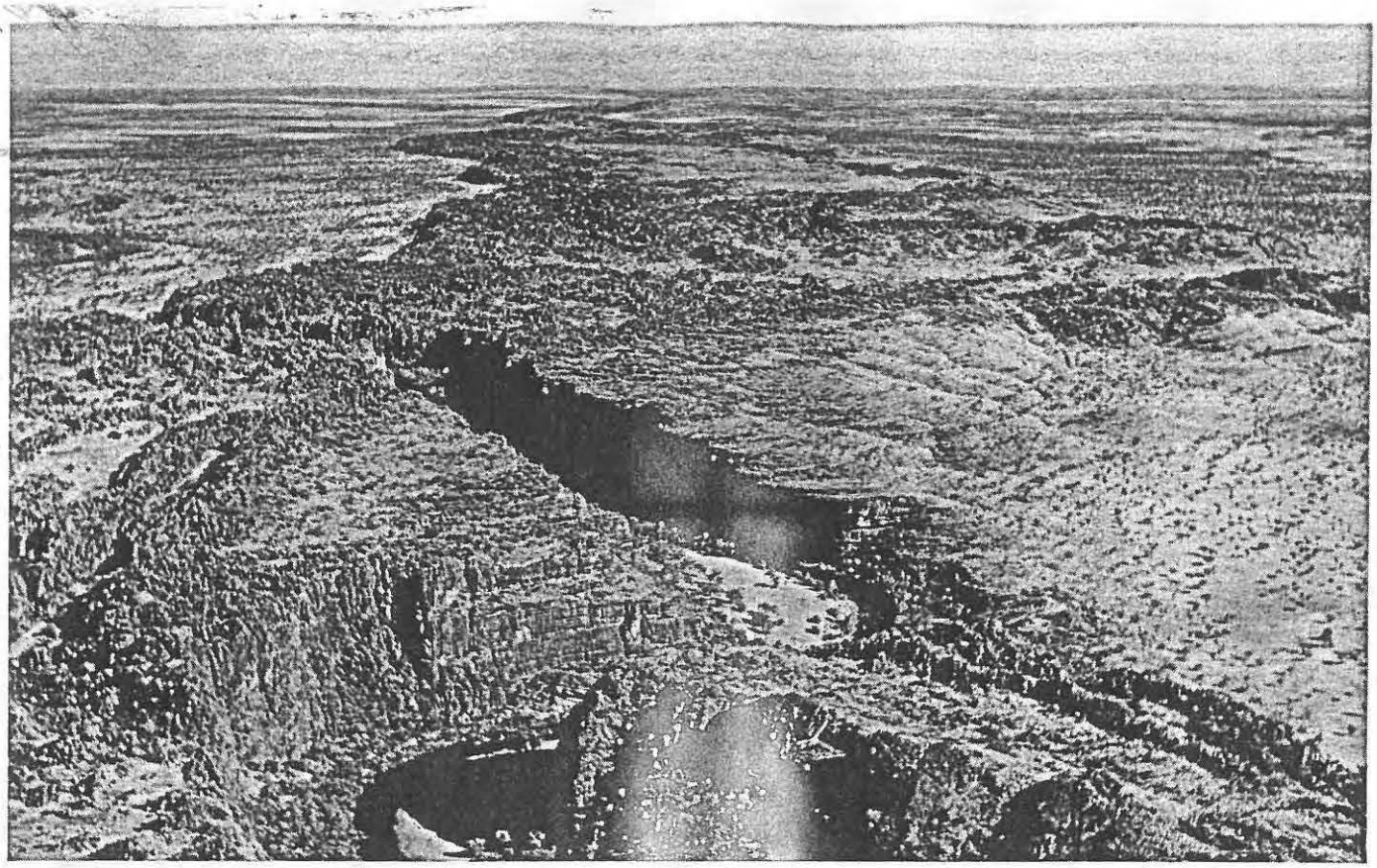
The most familiar of the reef animals, the corals, are minute polyps that belong to the phylum Coelenterata. The polyps live in symbiosis with zooxanthellae, microscopic one-celled plants embedded in the animals' tissue, where they are nourished by nitrogenous animal wastes and, through photosynthesis, add oxygen to the surrounding water. Experiments show that the zooxanthellae promote the calcium metabolism of the corals. The corals themselves are carnivores; they feed mainly on small crustaceans and the larvae of other reef animals.

The limestone-secreting algae—blue-green, green and red—are the principal food base of the reef community, just as the plant life ashore nourishes terrestrial herbivores. The algae are distributed across the reef in both horizontal and vertical zones. The blue-green algae are most common in the shallows of the tidal flat, an area where red algae are absent. The green algae are predominantly back-reef organisms and the reds are mostly reef and fore-reef inhabitants [*see illustration on page 64*].

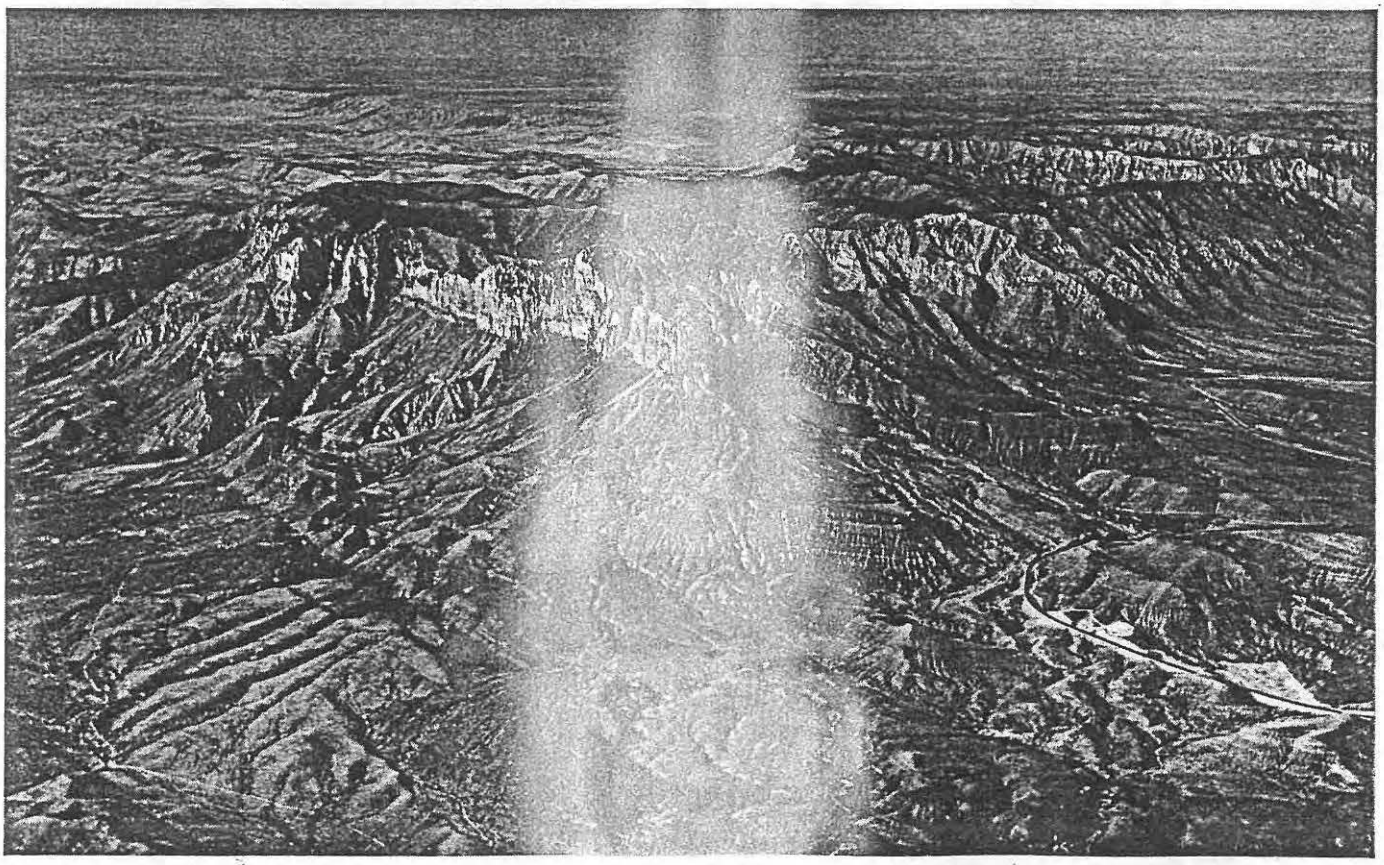
The other important members of the reef community are all animals. Next in significance to the corals as reef-builders are several limestone-secreting families of sponges, members of the phylum Porifera. The phylum Protozoa is represented by a host of foraminifera species whose small limy skeletons add to the deposits in and around reefs. Several species of microscopic colonial animals of the phylum Bryozoa also contribute their limestone secretions, as do the spiny sea urchins and elegant sea lilies of the phylum Echinodermata, the bivalves of the phylum Brachiopoda and such representatives of the phylum Mollusca as clams and oysters, all of whose accumulated skeletons and shells contribute to the reef limestones.

Many organisms in the community do not add significantly to the reef structure; some burrowers and borers are even destructive. The marine worms that inhabit the reef are soft-bodied and thus incapable of contributing to the reef mass. The hard parts of such reef dwellers as crabs and fishes are systematically consumed by scavengers. A few fragments may escape, but except for such passive and minor contributions to the reef detritus these organisms are not reef-builders.

The reef community is adapted to a low-stress environment characterized



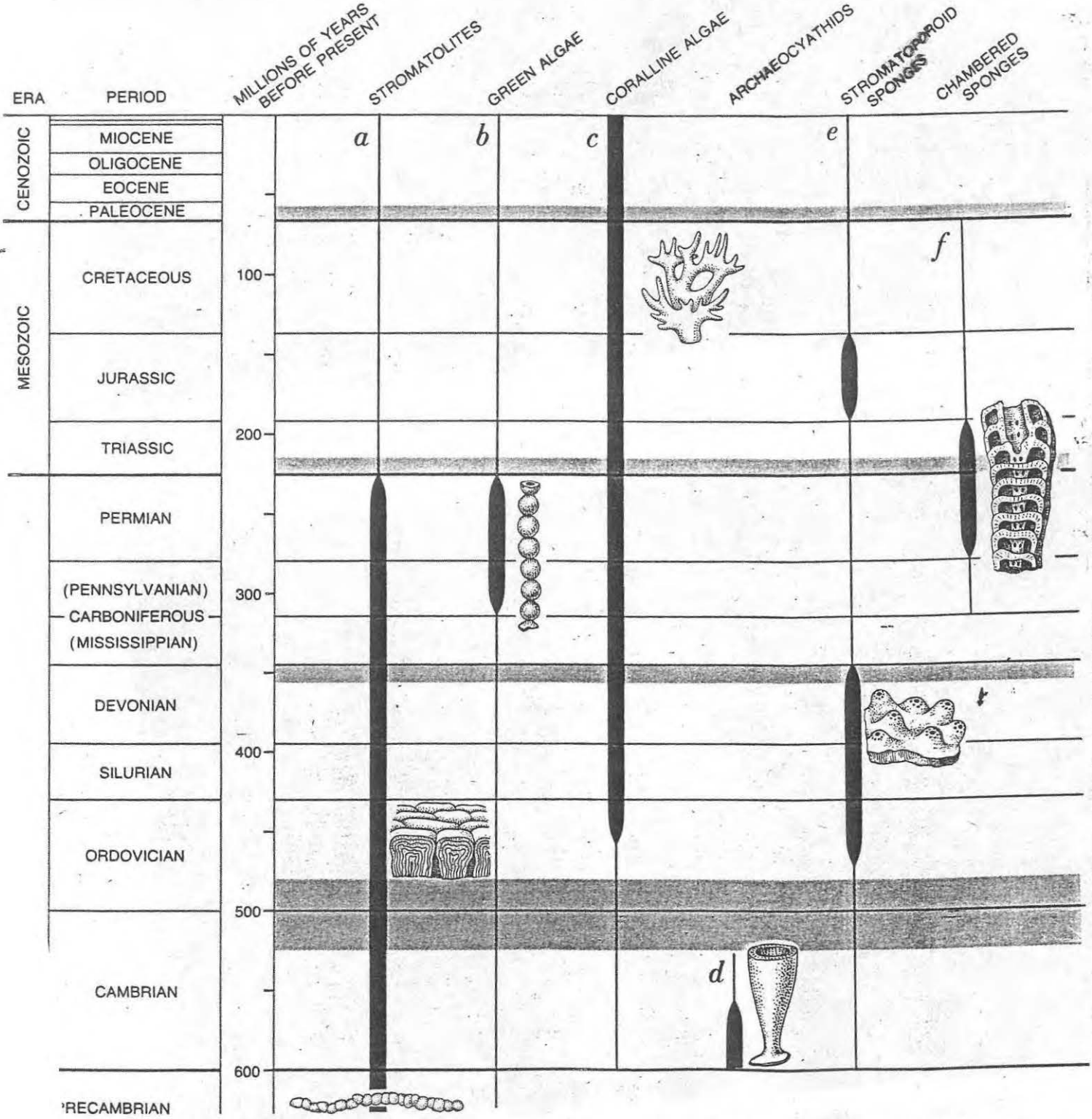
FOSSIL BARRIER REEF was built in upper Devonian times by a community of marine plants and animals living in the warm seas that covered part of Australia more than 350 million years ago. Exposed by later uplift and erosion, the reef now forms a belt of jagged highlands, known as the Napier Range, in Western Australia. A stream has cut a canyon (*foreground*) through the reef rock.



YOUNGER FOSSIL REEF, built some 250 million years ago in the Permian period, forms a rim of rock 400 miles long surrounding the Delaware Basin (*right*) on the border between Texas and New Mexico. Most of the reef is buried under later deposits, but one exposure forms this 40-mile stretch of the Guadalupe Mountains. El Capitan (*foreground*), a part of the reef front, is 4,000 feet high.

by the absence of significant seasonal change. The mean winter temperature of the water where reefs grow is between 27 and 29 degrees Celsius and the difference between summer and winter monthly mean temperatures is three degrees C. or less. The water is clear (so that the penetration of light is at a maximum), agitated (so that it is rich in oxygen) and of normal salinity. Even under these ideal circumstances many reef organisms (for example corals) do not grow at depths greater than 65 feet. This adaptation to freedom from stress makes the community remarkably sensitive to environmental change.

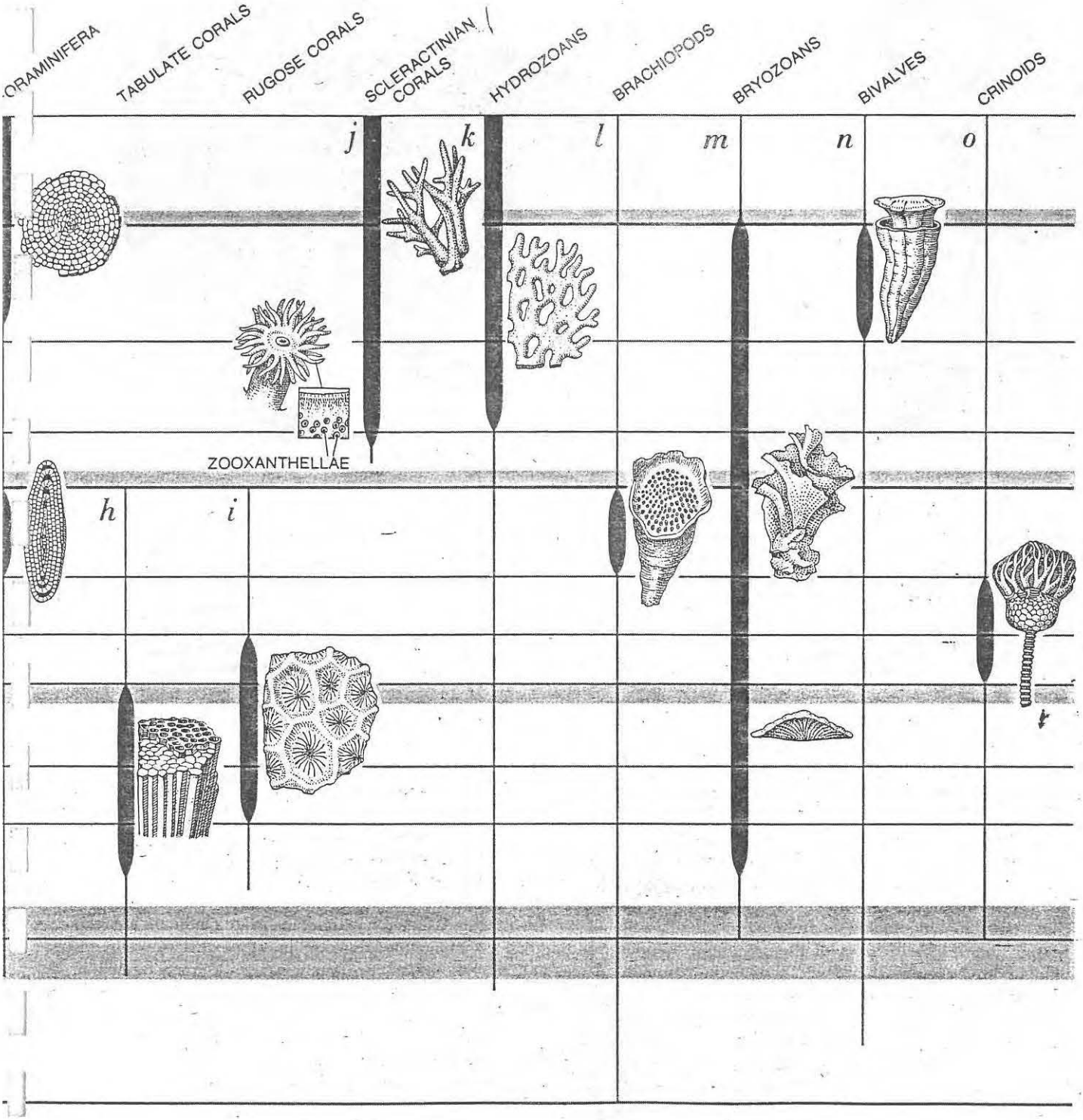
The fossil record documents hundreds of episodes of sweeping mass extinction, some continent-wide and others worldwide. These times of ecological disruption have simultaneously affected such disparate organisms as ammonites at sea and dinosaurs ashore, the plankton on land and the protozoans afloat among the



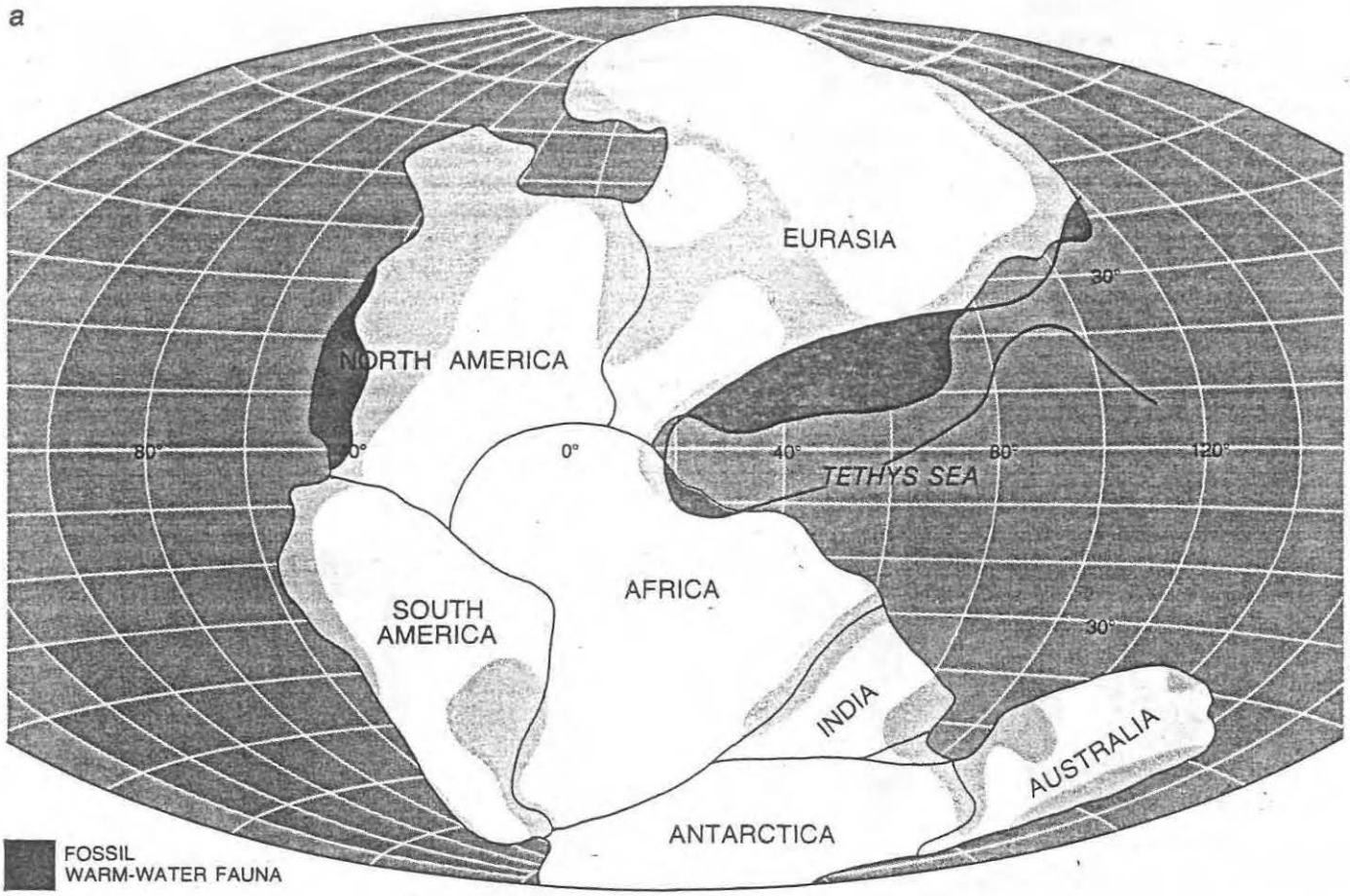
OLLAPSES (*bands of color*) have altered the composition ef community since the initial association between plant al reef-builders was established nearly 600 million years was when a group of spongelike animals, the archaeocya- appeared among the very much older reef-forming algal tes (*a*) at the start of the Paleozoic era. In less than 70 million years the archaeocyathids became extinct; their demise marks the first community collapse. A successor community arose in mid-Ordovician times. Its members included coralline algae (*c*); the first corals, tabulate (*h*) and rugose (*i*); stromatoporoid sponges (*e*), and communal bryozoans (*m*). The group flourished [illegible] the end of the Devonian [illegible]

oceanic plankton. The causative phenomena underlying the disruptions must therefore be unlike the ordinary, Darwinian causes of extinction—natural selection and unequal competition—that tend to affect species individually and not en masse.

For generations, in a reaction to the biblical doctrine of catastrophism that dominated 18th-century geology, scholars have viewed the apparent lack of continuity in fossil successions with skepticism. The breaks in the record, they proposed, were attributable to inadequate collections or to accidents of fossil preservation. At the same time, certain pioneers—T. C. Chamberlin and A. W. Grabau in the U.S. and Hans Stille in Germany—saw the breaks in fossil continuity as reflections of real events and sought a logical explanation for them. These men were eloquent proponents of a theory of rhythmic pulsations within the earth: diastrophic move-



time of the second collapse. Its successor, some 13 million years later, contained a new sponge group (*f*) and increased numbers of green algae (*b*), foraminifera (*g*), brachiopods (*l*) and crinoids (*o*). These reef-builders flourished until the end of the Paleozoic era and the third collapse. The next resurgence occupied most of the Mesozoic era. It was marked by the appearance of modern corals (*j*) and a dramatic upsurge of a mollusk group, the rudists (*n*), that became extinct at the time of the fourth community collapse some 65 million years ago. Draining of shallow seas during the Cenozoic era produced cooler climates and led to formation of the Antarctic ice cap. Both developments have been factors in restricting the successor community in diversity and distribution.



TWO FACTORS that have affected world geography and climate are the movement of the continental plates and their greater or lesser invasion by shallow seas. The status of both factors during three key intervals in earth history is shown schematically here and on the opposite page. Near the end of the Paleozoic era (*a*) the continental plates had gathered into a single land area. Many of the reef-building species were then pantropical in distribution. By the end of the Mesozoic era (*b*) sea-floor spreading had separated the continental plates. The Atlantic Ocean had become enough of a barrier to the migration of reef organisms between the Old and New World to allow the evolution of species unique to each region. At the end of the Mesozoic era the shallow seas encroaching on the continents were drained completely. Early in the Cenozoic era (*c*) the shallow seas had been reestablished in certain zones, but the total continental area above water was larger than in the Mesozoic. The change resulted in a trend toward greater seasonal extremes of climate; the distribution of tropical and subtropical organisms, however, remained quite broad, as palm-tree fossils show.

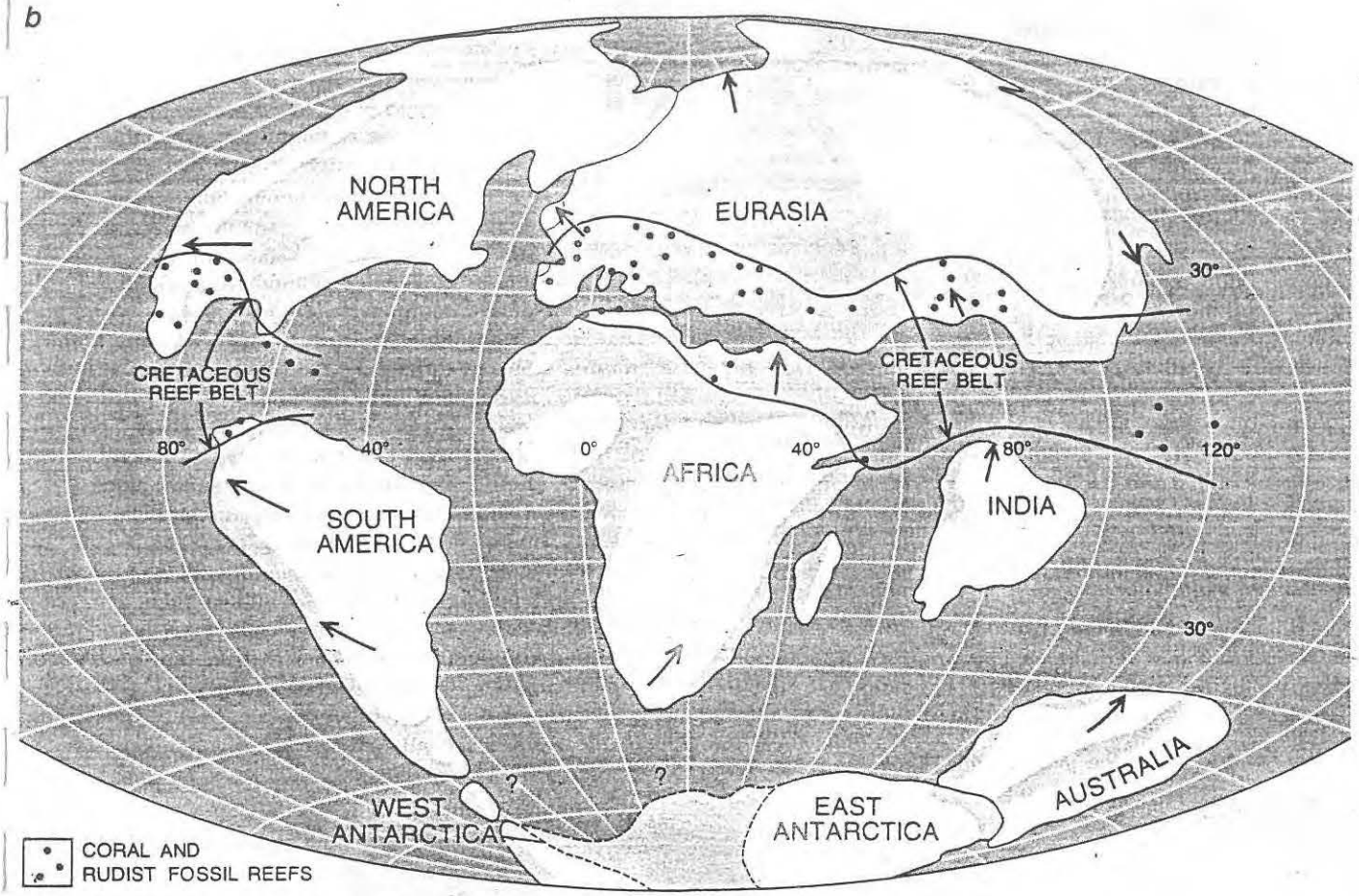
ments that had been accompanied by significant fluctuations in sea level and consequent disruptive changes in climate and environment.

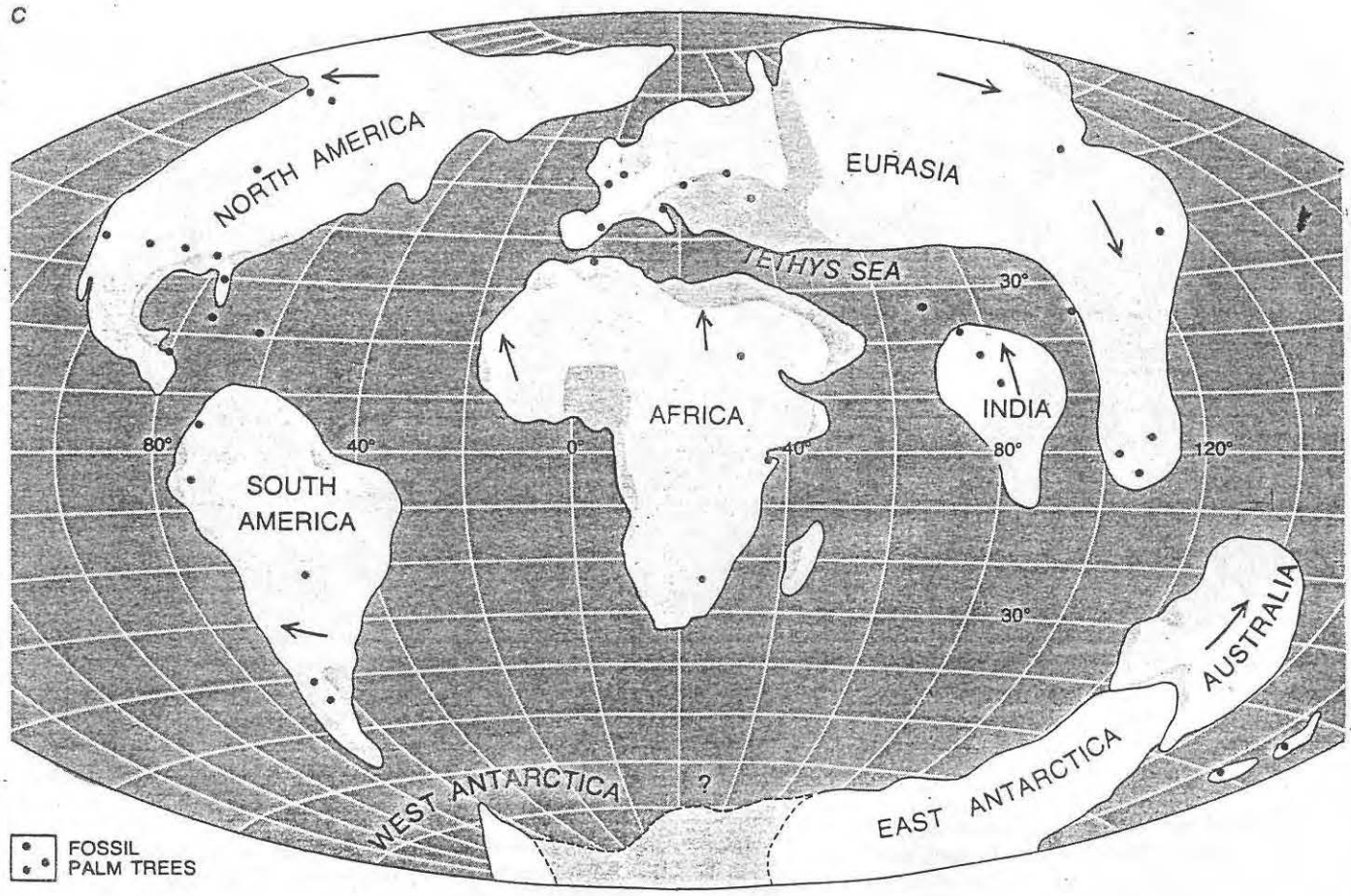
The lack of any demonstrable physical mechanism that might have produced such simultaneous worldwide geological revolutions kept a majority of geologists and paleontologists from accepting the proposed theory of the origins of environmental cycles. Today, however, we have in plate tectonics a demonstrated mechanism for changes in sea level and shifts in the relative extent of land and sea such as Chamberlin and his colleagues were unable to provide [see "Plate Tectonics," by John F. Dewey; SCIENTIFIC AMERICAN, May]. Significant changes in the volume of water contained in the major ocean basins, produced by such plate-tectonic phenomena as alterations in the rate of lava welling up along the deep-ocean ridges or in the rate of sea-floor spreading, have resulted sometimes in the emergence and sometimes in the flooding of vast continental areas. The changing proportions of land and sea meant that global weather patterns alternated between mild maritime climates and harsh continental ones.

Now, reef-building first began in the earth's tropical seas at least two billion years ago. As we have seen, the modern reef community is so narrowly adapted to its environment as to be very sensitive to change. It seems only logical to expect that the same was true in the past, and that changes in reef communities of earlier times would faithfully reflect the various rearrangements of the earth's land masses and ocean basins that students of plate tectonics are now documenting. The expectation is justified; whereas many details of earth history will be clarified only by future geological and paleontological research, the record of fossil reef communities accurately delineates a number of the main catastrophic episodes.

As one might expect, the oldest of all types of reef is the simplest. Algae alone, without associated animals, are responsible for limestone reef deposits, billions of years old, that were formed in the seas of middle and late Precambrian times.

The Precambrian algae produced extensive accumulations of a distinctively laminated limestone that are found, flanked by aprons of reef debris, in rock formations around the world. Geologists call these characteristic limestone masses stromatolites, from the Greek for "flat" and "stone." The microscopic organisms that built the stromatolites are rarely


b
NORTH AMERICA
EURASIA
CRETACEOUS REEF BELT
CRETACEOUS REEF BELT
80°
40°
0°
40°
80°
120°
30°
30°
AFRICA
SOUTH AMERICA
INDIA
AUSTRALIA
WEST ANTARCTICA
EAST ANTARCTICA
?
?
CORAL AND RUDIST FOSSIL REEFS


c
NORTH AMERICA
EURASIA
TETHYS SEA
30°
AFRICA
INDIA
80°
40°
0°
40°
80°
120°
SOUTH AMERICA
30°
AUSTRALIA
WEST ANTARCTICA
?
EAST ANTARCTICA
FOSSIL PALM TREES

preserved as fossils, but they must surely have been similar to the filamentous blue-green algae that form similar masses of limestone today.

The accomplishments of these Precambrian algal reef-builders were not inconsiderable: individual colonies grew upward for tens of feet. They did so by trapping detrital grains of calcium carbonate and perhaps by precipitating some of the lime themselves. The resulting fossil bodies take the form of trunklike columns or hemispherical mounds.

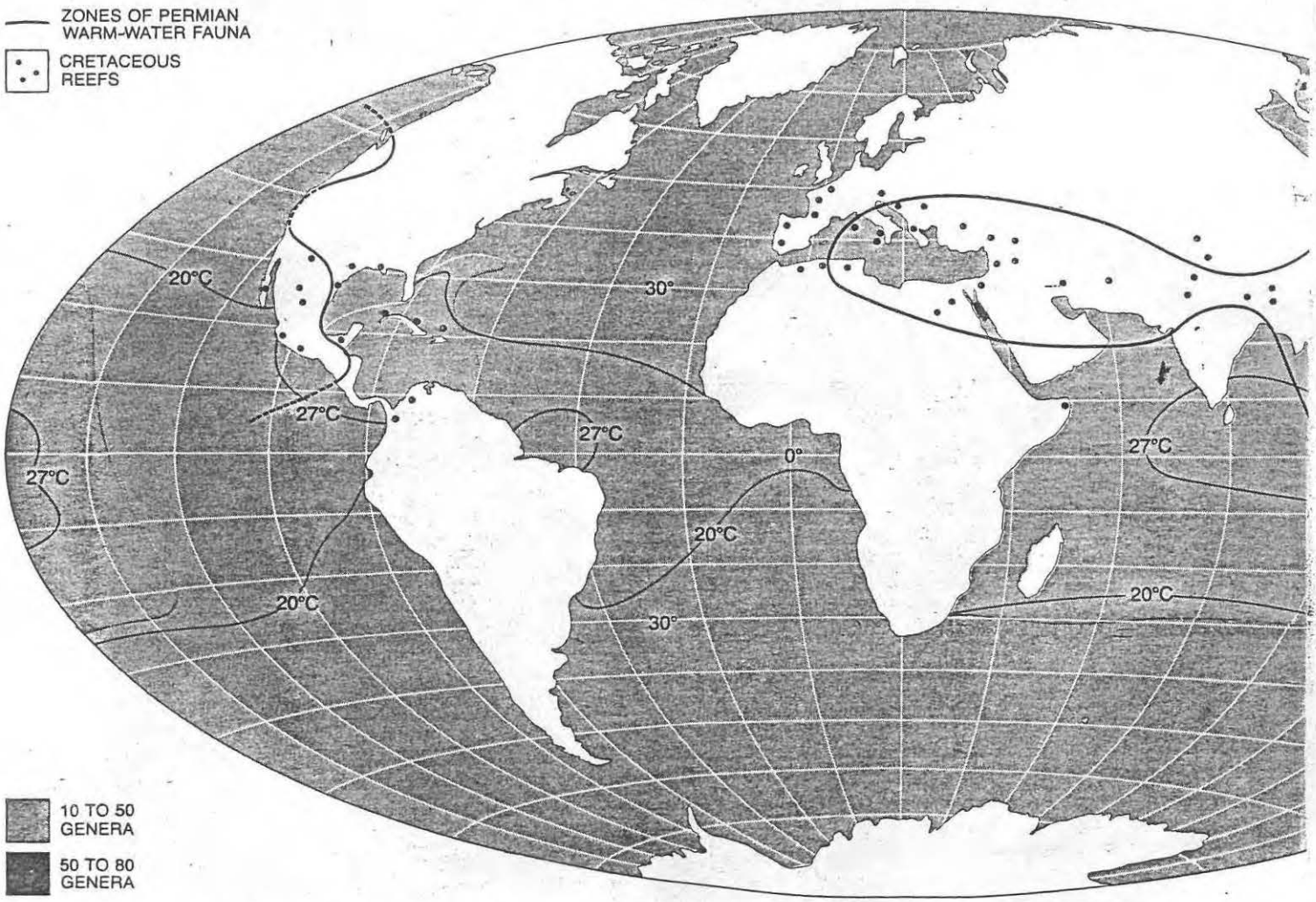
As I outline the evolution of the reef community the reader will note that I often speak of first and last appearances. This does not mean, of course, that the organism being discussed was either instantly created or instantly destroyed. Each had an extensive evolutionary heritage behind it when some chance circumstance provided it with an appropriate ecological niche. Similarly, the decline and extinction of many major groups of organisms can be traced over periods of millions of years, although in numerous instances the time involved was too short to be measured by the methods now available.

Enter the Animals

The long Precambrian interval ended some 600 million years ago. The opening period of the Paleozoic era, the Cambrian, saw the first establishment of a reef community. The stromatolites' first partners were a diverse group of stony, spongelike animals named archaeocyathids (from the Greek for "ancient" and "cup"). In early Cambrian times these stony animals rooted themselves along the stromatolite reefs, grouped together in low thickets or scattered like shrubs in a meadow. It is not hard to imagine that the vacant spaces within and between these colonies provided shelter for the numerous bottom-feeding trilobites that inhabited the Cambrian seas. Not every reef harbored archaeocyathids, however; some reefs of early and middle Cambrian times are composed only of stromatolites.

By the end of the middle Cambrian, some 540 million years ago, the archaeocyathids had vanished. No single cause for this extinction, the first of the four major disasters to overtake the reef community, can be identified. One imaginable cause—competition from another reef-building animal—can be ruled out completely. The seas remained empty of any kind of reef-building animal throughout the balance of the Cambrian and until the middle of the Ordovician period, some 60 million years later. All reefs built during this long interval were the work of blue-green algae alone.

Fossil formations in the Lake Champlain area of New York, a region that lay under tropical seas in middle Ordovician times some 480 million years ago, contain the first evidence of a renewed association between reef-building plants and animals. The community that now arose was a rather complex one. Stromatolites continued to flourish and a second kind



REEF-BUILDERS TODAY are confined to a narrow belt, mainly between 30 degrees north and 30 degrees south latitude (*light gray*), and even within this belt the greatest number of species are found where the minimum average water temperature is 27 degrees Celsius. Paleozoic and Mesozoic reef fossils, however, are found in areas far outside today's limits (*black lines and dots*). This suggests that the true Equator in those times lay well to the north of the equators shown on the maps on the preceding pages. The asym-

of plant life appeared: the coralline red alga *Solenopora*, a direct progenitor of the modern coralline algae. Colonial bryozoans, previously insignificant in the fossil record, now assumed an important role in the expanding reef community. Animal newcomers included a group of stony sponges, the stromatoporoids, some shaped like encrusting plates and others hemispherical or shrublike in form. These calcareous sponges were to play a major role in the community for millions of years. The most significant new animals, however, in light of subsequent developments, were certain stony coelenterates: the first of the corals. The intimate collaboration between algae and corals, apparently unknown before middle Ordovician times, has continued (albeit with notable fluctuations) to the present day.

These new arrivals and the other corals that appeared during the Paleozoic era were mainly of two types. In one type the successive stages of each polyp's upward growth were recorded as a series of parallel floors that subdivide the stony tube sheltering the animal; these organisms are called tabulate corals. The conical or cylindrical stone tube that sheltered the second type has conspicuous external growth wrinkles on its surface; these corals are called rugose.

A little more than 350 million years ago, near the end of the Devonian period, worldwide environmental changes caused a number of mass extinctions. Among the victims were many previously prominent marine organisms, including several groups in the reef community. That community now underwent a major retrenchment. Up to this point the tripartite association between algae, sponges and corals that first appeared in Ordovician times had proliferated for 130 million years without significant disturbance. The environmental alterations that nearly wiped out the reef community at the end of that long and successful period of radiation remain unidentified, although one can conjecture that a change from a mild maritime climate to a harsh continental one probably played a part. In any event the episode was severe enough so that only scarce and greatly impoverished reef communities, consisting in the main of algal stromatolites, survived during the next 13 million years. Not until well after the beginning of the Carboniferous period was there a community resurgence.

Some 115 million years passed between the revival of the reef community in Carboniferous times and the end of the Paleozoic era; the interval includes most of the Mississippian and all of the Pennsylvanian (the two subdivisions of the Carboniferous) and the closing period of the Paleozoic, the Permian. The revitalized assemblage that radiated in the tropical seas during this time continued to include stromatolites, numerous bryozoans and brachiopods and a dwindling number of rugose corals. Except for these organisms, however, the community bore no great resemblance to its predecessor of the middle Paleozoic. Both the stromatoporoid sponges and the tabulate corals are either absent from Carboniferous and Permian reef deposits or are present only in insignificant numbers.

Two new groups of calcareous green algae, the dasycladaceans and codiaceans, now attained quantitative importance in the reef assemblage. As if to match the decline of the stromatoporoid sponges, a second poriferan group—the calcareous, chambered sphinctozoan sponges—entered the fossil record. At the same time a group of echinoderms—the crinoids, or sea lilies—assumed a larger role in the reef community. As the Paleozoic era drew to a close, the crinoids and the brachiopods achieved their greatest diversity; their skeletons preserved in Permian reef formations number in the thousands of species.

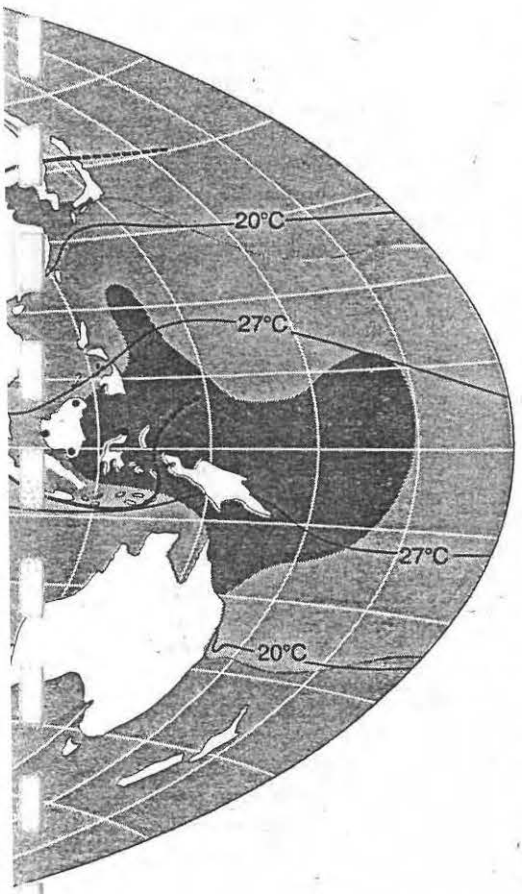
The Third Collapse

Half of the known taxonomic families of animals, both terrestrial and marine, and a large number of terrestrial plants suffered extinction at the end of the Paleozoic era. The alteration in environment that occurred then, some 225 million years ago, had consequences far severer than those of Devonian times. In the reef community the second successful radiation—based principally on a new tripartite association involving algae, bryozoans and sphinctozoan sponges—came to an end; reefs are unknown anywhere in the world for the first 10 million years of the Mesozoic era.

What was the cause of this vast debacle? There is little enough concrete information, but analogy with later and better-understood events encourages the conjecture that once again unfavorable changes in climate and habitat were major factors. In late Paleozoic times all the continents had come together to form a single vast land mass: Pangaea. Continental ice sheets appeared in the southern part of this supercontinent, a region known as Gondwana, in Carboniferous and early Permian times. These glaciers are concrete evidence of cooler climates; paleomagnetic studies show that the glaciated areas were then all located near the South Pole. Any relation between these early Permian ice sheets and the widespread late-Permian extinctions, however, is not yet evident. What is probably more significant is evidence that, at least during a brief interval, all the shallow seas that had invaded continental areas were completely drained at the end of the Paleozoic era. Serious climatic consequences must have resulted from the disappearance of a mild, primarily maritime environment.

In late Paleozoic times a wide tropical seaway, the Tethys, almost circled the globe. The only barrier to the Tethys Sea was formed by the combined land masses of North America and western Europe, which were then connected. The tongue of the Tethys that eventually became the western Mediterranean constituted one end of the seaway. The opposite end invaded the west coast of North America so deeply that great Permian reefs arose in what is now Texas.

The Mediterranean extremity of the Tethys Sea was the setting for a signifi-



metry of the fossil-reef belt with respect to the present belt suggests that much of a once wider array has been engulfed by subduction along continental-plate boundaries.

cant development when, after 10 million years of eclipse, the reef community was once again revitalized. There, in mid-Triassic times, a new group of corals, the scleractinians, made its appearance. The scleractinians were the progenitors of the more than 20 families of corals living in the reef community today. At first the new coral families, six in all, were represented in only a few scattered reef patches found today in Germany, in the southern Alps and in Corsica and Sicily. Even by late Triassic times, some 200 million years ago, the new corals were still subordinate as reef-builders to the calcareous algae.

The Mesozoic Community

During the 130 million years or so of Jurassic and Cretaceous times the reef community once again thrived in many parts of the world. The stromatoporoid sponges, all but extinct since the community collapse of Devonian times, returned to a position of some importance during the Jurassic. The new coral families steadily increased in diversity and reached an all-time peak in the waters bordering Mediterranean Europe during the Cretaceous period. In that one region there flourished approximately 100 genera of scleractinians; this is a greater number than can be found worldwide today. The reef community in this extremity of the Tethys Sea was also rich in other reef organisms. It included the two groups of sponges and such reef-builders as sea urchins, foraminifera and various mollusks. In addition a hitherto minor group of coralline red algae, the lithothamnions, now began to play an increasingly important role. By this time the stromatolites, important reef-builders throughout the Paleozoic, were no longer conspicuous members of the reef community.

Early in the Cretaceous period, some 135 million years ago, there was an unfavorable interval: reefs are unknown in the fossil record for some 20 million years thereafter. This pause merely set the stage, however, for a further efflorescence. Both in the Mediterranean area and in the waters of the tropical New World, hitherto unknown or insignificant coral families appeared. The present Atlantic Ocean was just beginning to form. Regional differences between reef communities in the Old World and the New that appeared at this time testify to the growing effectiveness of the Atlantic deeps as a barrier to the ready migration of reef organisms.

An extraordinary evolutionary performance was now played. Certain previously obscure molluscan members of the reef community, bivalves known as rudists, abruptly came into prominence as primary reef-builders. The next 60 million years saw a phenomenal rudist radiation that brought these bivalves to the point of challenging the corals as the dominant reef animals. Along the sheltered landward margins of many fringing barrier reefs rudists largely supplanted the corals. Their cylindrical and conical shells were cemented into tightly packed aggregates that physically resembled corals, and many of the aggregates grew upward in imitation of the coral growth pattern. Before the end of the Cretaceous period some 65 million years ago the rudists had attained major status in the reef community. Then at the close of the Cretaceous they quite abruptly died out everywhere.

Ever since the pioneer days of geology in the 18th century the end of the Cretaceous period has been known as a great period of extinctions. Nearly a third of all the families of animals known in late Cretaceous times were no longer alive at the beginning of the Cenozoic era. The reef community was not exempt; in addition to the rudists, two-thirds of the known genera of corals died out at this time. Forms of marine life other than reef organisms were also hard hit. The ammonites, long a major molluscan group, had suffered a decline during the final 10 million years of the Cretaceous; by the end of the period they were all extinguished. The belemnites, another major group of mollusks, declined sharply, as did the inoceramids, a diverse and abundant group of clams that had previously flourished worldwide. Among the foraminifera, the free-floating, planktonic groups suffered in particular.

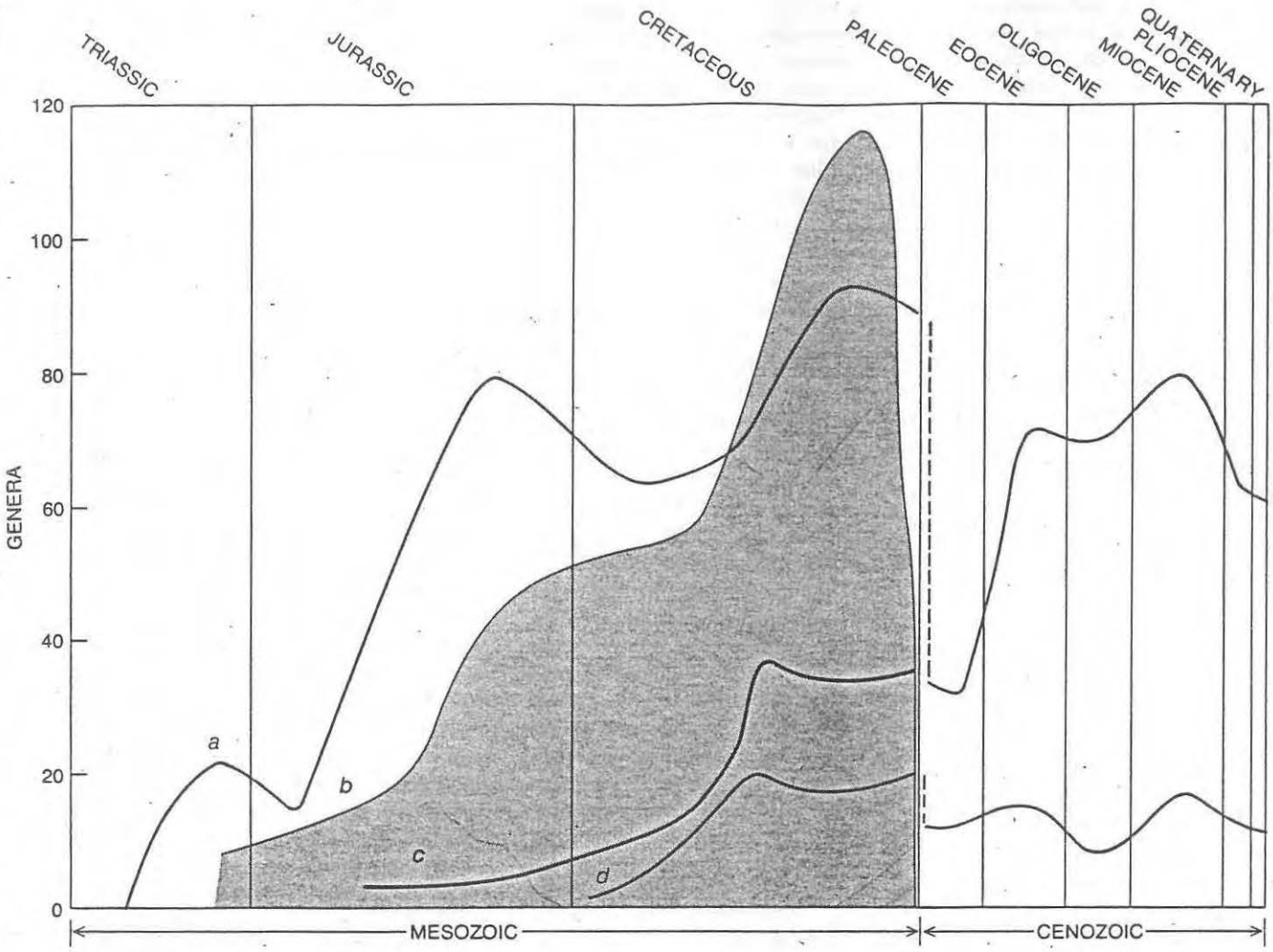
The environmental changes that devastated life at sea also took their toll of land animals. Perhaps the most spectacular instance of extinction ashore involved the group that had been the dominant higher animals during most of the Mesozoic era: the dinosaurs. Of the 115-odd genera of dinosaurs found in late Cretaceous fossil deposits, none survived the end of the period. The concurrent breakdown of so many varied communities of organisms clearly suggests a single common cause.

What was the source of this biological crisis? We have now come sufficiently close to the present to have a better grasp of the evidence. Throughout almost all of Mesozoic times life both on land and in the sea seems to have been remarkably cosmopolitan. A broad belt of equable climate extended widely in both directions from the Equator and there was no very evident segregation of organisms into climatic zones. The earth has always been predominantly a water world; the total land area may never have exceeded the present 30 percent of the planet's surface and has often been as little as 18 percent. In the late Cretaceous almost two-thirds of today's land area was submerged under shallow, continent-invading seas. It appears that during times of extensive inundation such as this one there was nothing like the blustery global circulation of air and strong ocean currents of today.

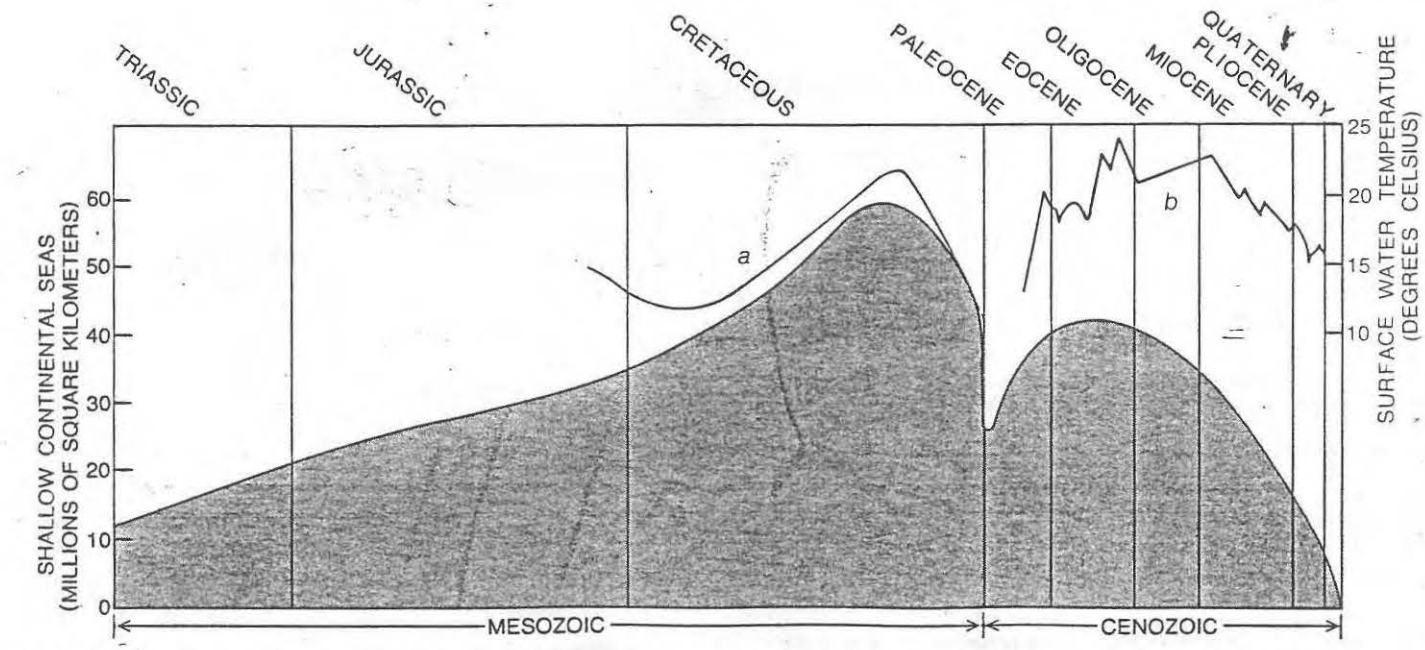
Paleoclimatology reveals the contrast between contemporary and Cretaceous conditions. By measuring the proportions of different isotopes of oxygen present in the carbonate of fossil foraminifera and mollusks it is possible to calculate the temperature of the water when the animals were alive. Today the temperature of deep-ocean water is about three degrees C. Cesare Emiliani of the University of Miami has shown that early in the Miocene epoch, some 20 million years ago, the bottom temperature of the deep ocean was about seven degrees C. He finds that in the Oligocene, 10 million years earlier, the temperature was about 11 degrees and that in late Cretaceous times, 75 million years ago, it was 14 degrees. He suggests that the onset of cooling may have been lethal to dinosaurs. In any event it is clear that cold bottom water has been accumulating in the deep-ocean basins since early in the Cenozoic era.

The accentuated seasonal oscillations in temperature and rainfall at the end of the Cretaceous period, a trend that evidently started when the shallow continental seas began to drain away into the deepening ocean basins, have been credited by Emiliani and also by Daniel I. Axelrod of the University of California at Davis and Harry P. Bailey of the University of California at Riverside with the simultaneous reduction in numbers or outright extinction of many other animal and plant species at that time. Genetically adapted to a remarkably equable world climate over millions of years, many of these Mesozoic organisms were ill-prepared for the extensive emergence of land from under the warm, shallow continental seas and the climate of accentuated seasonality that followed. Perhaps we should be surprised not that so many Cretaceous organisms died but that so many managed to adapt to the new conditions and thus survived.

Near the end of the Paleocene epoch, some 10 million years after the great



MESOZOIC INCREASE in the diversity of ocean and land animal genera reached a peak in the Cretaceous period. It was followed both by extinctions and by severe reductions in the number of genera that chanced to survive. At sea the explosively successful rudists (*c*) and ashore the long-dominant dinosaurs (*b*) became extinct. Corals (*a*) and globigerine foraminifera (*d*) fell in numbers.



SHRINKING OF SEAS that had invaded large continental areas (*gray*) began near the end of the Mesozoic era and accelerated in the Miocene epoch. Oxygen isotopes in belemnite (*a*) and foraminifera (*b*) skeletons show that the ocean has become progressively cooler since early in Miocene times (*color*). A relation seems to exist between a larger land area and greater seasonal extremes in climate.

Cretaceous collapse, a reef community sans rudists reappeared in the tropical seas. The following epoch, the Eocene, saw a new radiation of the scleractinian corals. Several genera that now appeared worldwide were unknown earlier in the fossil record; many of them are still living today.

The Cenozoic Decline

A sharp reduction in coral diversity that began in late Eocene times and lasted throughout the Oligocene epoch seems to reflect a continued increase in seasonality of climate and a substantial lowering of mean temperatures over large areas of the globe. Nonetheless, communities built around a bipartite association of corals and coralline algae continued to build extensive reefs in the Gulf of Mexico and the Caribbean area, in southern Europe and in Southeast Asia. Continued sea-floor spreading and deepening of the Atlantic basin, which enhanced the effectiveness of the Atlantic as a barrier to migrating corals, are evidenced in increasing differences between Caribbean and European coral species in late Oligocene fossil deposits.

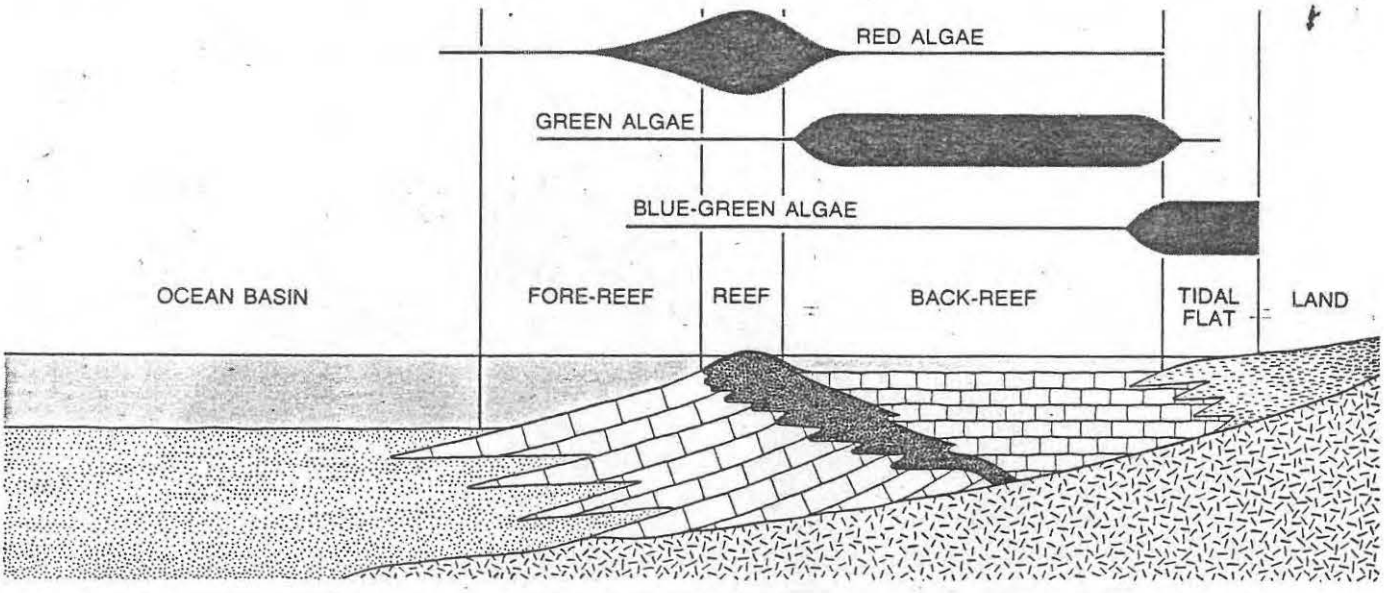
By now the earth had been free from continental glaciers for almost 200 million years, but a change in the making was to have profound consequences for world climate: the Antarctic ice cap was becoming established. Fossil plant remains and foraminifera from nearby deep-sea deposits both testify that even in early Miocene times the climate in much of the Antarctic continent was not much different from the blander days of the early Cenozoic, when palm trees grew from Alaska to Patagonia. At this time, moreover, Antarctica was some distance away from its present polar position. Nonetheless, mountain glaciers had begun to appear there millions of years earlier, in Eocene and Oligocene times. Sands of that age, produced by glacial streams and then rafted out to sea on shelf ice, are found in offshore deep-sea cores. The cooling trend was well established before the end of the Miocene epoch. In the Jones Mountains of western Antarctica lava flows of late Miocene age overlie consolidated glacial deposits and extensive areas of glacially scoured bedrock.

With the formation of the Antarctic ice cap some 15 to 20 million years ago a factor came into being that strongly influences world weather patterns to this day. The ice cap energizes the world weather system. In the broad reaches of open ocean surrounding Antarctica the surface water is aerated and cooled until it is too heavy to remain at the surface. The cold water sinks and spreads out along the sea floor, following the topography of the bottom. The result is a gravity circulation of cold water from Antarctica into the world's ocean basins, with a consequent lowering of the mean ocean temperature and cooling of the overlying atmosphere. The energetic interactions of the atmosphere above with the ocean and land below, in turn, strongly influence global wind patterns and worldwide weather. Today's climate is the product of a long cooling trend, marked by ever greater seasonal extremes; the trend became strongly accentuated when the Antarctic ice cap came into being late in the Miocene epoch.

This event and others in the Cenozoic era are faithfully recorded in terms of changes in the reef community. For example, in spite of the development of new barriers to the migration of reef organisms during the Mesozoic era, such as the Atlantic deep, the reef community had remained predominantly cosmopolitan up to the close of the Cretaceous. By Miocene times, however, what had once been essentially a single pantropical community was effectively divided into two distinct biogeographic provinces: the Indo-Pacific province in the Old World and the Atlantic province in the New World.

In the Old World the increasingly unfavorable climate had eliminated the reef community in European waters. It was during Miocene times, when Australia reached its present tropical position, that the Old World reef-builders first began to colonize the shallows of the Australian shelf; in terms of maximum diversity, the headquarters of the Indo-Pacific province today lies in the Australasian region where seasonal contrasts in water temperature are minimal.

Like the Atlantic deep, the deep waters of the eastern Pacific formed a generally effective barrier to the migration of reef organisms from the Indo-Pacific province into the hospitable tropical waters along the west coast of the Americas, principally around Panama. In Miocene times this Pacific coastal pocket was still connected to the reef-rich Caribbean, the headquarters of the At-



REEF ANATOMY centers on a rigid core (*color*) composed of the cemented skeletons of algae and corals. In this diagram growth of the core began at right and continued upward and outward. Most of the bulk of the reef consists of wide areas of stabilized detritus that are continuously being converted into the limestone that comprises the fore-reef and back-reef. The sandlike detritus is stabilized by the growth of the animals and plants in the reef community. The zones occupied by different algae are indicated here.

lantic province. Contact between the Atlantic province and the small Pacific enclave continued until the two areas were separated during the Pliocene epoch by the uplifting of the Isthmus of Panama.

The Pliocene saw a further contraction of the world tropics. The community of reef-builders gradually retreated to its present limits, generally south of 35 degrees north latitude and north of 32 degrees south latitude. Rather than serving as a center for new radiations, this tropical belt essentially became a haven. The epoch that followed, the Pleistocene, was marked by wide fluctuations in sea level and sharp alternations in climate that accompanied a protracted series of glacial advances and retreats. Oddly enough, the reef community was scarcely affected by such ups and downs; the main reasons for this apparent paradox seem to be that neither the total area of the deep tropical seas nor their surface water temperature underwent much change during the Pleistocene ice ages.

Is a fifth collapse in store for the most complex of ocean ecosystems? It would be foolhardy to respond with a flat yes or no. If, however, the past is prologue, the answer to a collateral question seems clear. The question is: Will a reef community in any event survive? The most significant lesson that geological history teaches about this complex association of organisms is that, in spite of the narrowness of its adaptation, it is remarkably hardy. At the end of the long interlude that followed each of four successive collapses, the reef community entered a new period of vigorous expansion. Moreover, without exception each revitalized aggregate of reef-builders included newcomers in its ranks.

The conclusion is inescapable that even during the times most unfavorable to the reef ecosystem the world's tropical oceans must have had substantial refuge areas. In these safe havens many of the threatened organisms managed to adapt and survive while others seem to have crossed some evolutionary threshold that had prevented their earlier appearance in the community. Today the Atlantic and Indo-Pacific provinces are two such refuge areas.

As long as the cooling trend that began in Cretaceous times does not entirely destroy these tropical refuge areas, one long-range conclusion seems firm. Any collapse of the present reef community will surely be followed by an eventual recovery. The oldest and most durable of the earth's ecosystems cannot easily be extirpated.

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An Outline History of Tropical Organic Reefs[1]

By Norman D. Newell[2]

ABSTRACT

Organic reefs, especially shallow-water coral reefs of warm seas, are built by stable communities of organisms in a narrow adaptive zone of low stress. They have an extraordinarily good fossil record that may be applied to broad problems of evolution of the tropical marine biota and ancillary questions about past climates and changing distributions of land and sea over more than one-half billion years of earth history. This essay is an attempt at a synopsis through the eyes of a paleobiologist of some of the exciting episodes in the history of the world's oceans and their organisms. The reef community is well suited for a leading role in this history.

THE REEF ECOSYSTEM

Living tropical coral-algal reefs and rain forests epitomize segregated, highly independent communities and distinctive ecosystems. Intricately organized and immensely diverse, they evoke an image of exceptional fertility and exuberant biomass. This aspect results, however, not so much from high productivity as from relative environmental uniformity, freedom from seasonal interruptions, and other sources of stress in life processes.

The environments of both ecosystems are so dominated by the inhabitants that, in a very real sense, they constitute habitats created and maintained by the organisms themselves. Here, the physical factors of environment are so buffered that the most evident selection relates to interspecific accommodations in space, nutrition and shelter, and ever increasing narrowness of adaptation.

In general, their microhabitats are created by the physical arrangements of the associated organisms and by their physiology and behavior (fig. 1). The correlated increase in taxonomic diversity through geologic time has resulted in proliferation of new adaptive opportunities and niches. Environmental resources of these communities are shared among the inhabitants with varying degrees of coadaptation and with little sign of reaching any ultimate limit in subdivision short of failure of some essential external condition of the environment, as has frequently occurred in the history of reefs.

The reef ecosystem with its plankton and many benthonic plants and plantlike animals shares many similarities with rain forests of the tropics. Both are phototropic and they have adopted the same method for controlling and filtering sunlight through a stratified canopy. Like man-built cities, the reefs are densely populated and commonly surrounded by contrasting, more sparsely inhabited areas. The specific diversity of a modern tropical coral reef probably exceeds by one order of magnitude the diversity of the most nearly comparable other marine community, the littoral and neritic rocky bottom biota. Judged from the fossil record, a similar disparity in diversity between the two probably has obtained since the middle Paleozoic.

To press a metaphor further, reef communities are outstandingly adapted to cope with problems of a city, such as crowding, ventilation, nutrition, and waste disposal. And, of all marine communities, reef organisms alone have the capability of building their rocky substrate laterally and upward in opposition to the processes of attrition. They create and maintain favorable substrate, food, and shelter by a kind of community homeostasis. Their organisms are superlatively coadapted.

Because of insufficient observations and experimentation, much about living coral reefs remains poorly understood. Even today, after much work, there is uncertainty about the energy avenues and ultimate sources and amounts of inorganic nutrients needed by teeming coral atolls which characteristically are surrounded by comparatively sterile wastes of shallow tropical waters. The external contributions of plankton to the reef community are still to be measured (Yonge, 1963, p. 254).

[1] I am indebted to John W. Wells, Cornell University, for sharing with me some of his great knowledge of scleractinian systematics. Several of my colleagues at the American Museum of Natural History, as well as Robert S. Dietz, Atlantic Oceanographic and Meteorological Laboratories, Miami, and Ernst Mayr, Harvard University, have critically read and discussed with me many of the ideas here set forth. But, of course, they are not accountable for my shortcomings.

[2] Chairman and Curator, Department of Invertebrate Paleontology, the American Museum of Natural History.

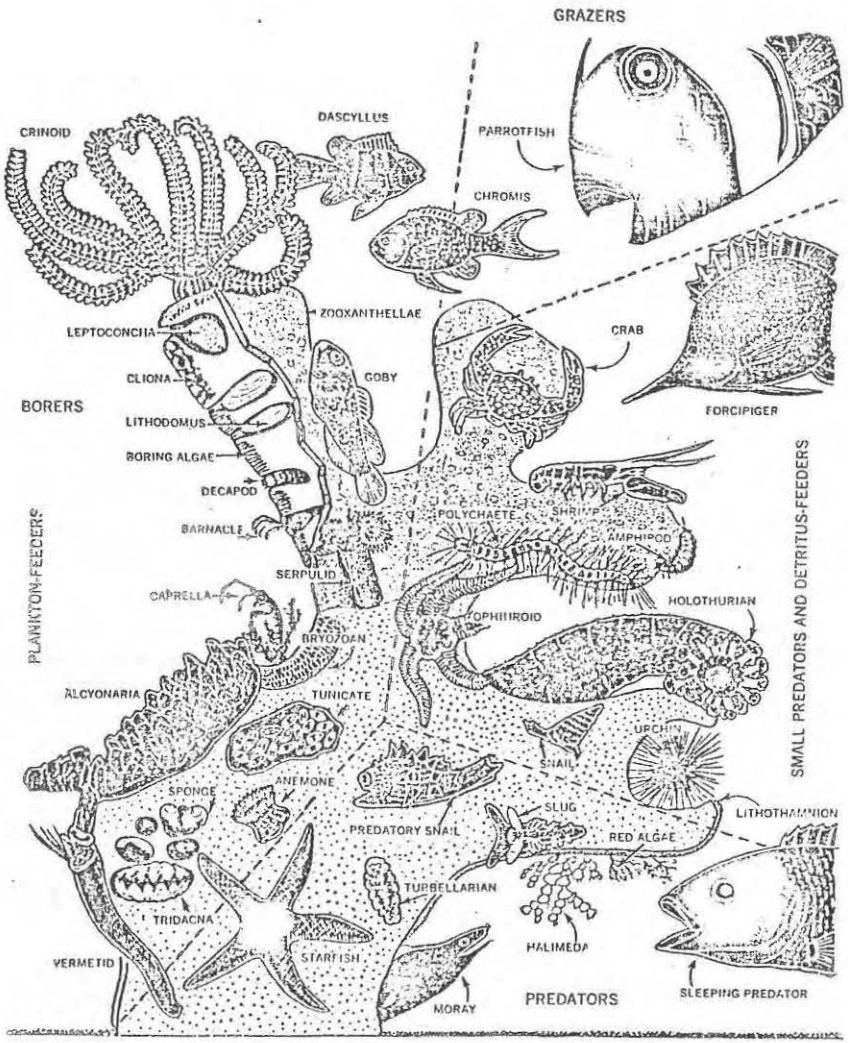


FIG. 1. Some of the varied constituents of the coral reef community. Stippled area with rosettes, living corals and zooxanthellae. Stippled area without rosettes, dead corals and perforating blue green algae (data from Gerlach, 1960).

As with the tropical rain forest, most of the nutrition of a reef community probably is stored in living protoplasm of the standing crop. Income and losses are small and therefore difficult to assess. One external increment of nutrients is the guano of roving sea birds that roost on sand cays and rocky

islets of coral reefs. Another is the dissolved salts in the runoff from neighboring land masses and their terrestrial vegetation.

The distribution of coral reefs with respect to islands is of interest in this connection. The most flourishing reefs commonly lie near, but not too near, the most extensive lands. On the other hand, wholly submerged shallow banks farthest away from lands ordinarily are only sparsely or not at all colonized by living reefs. Some of the so-called drowned atolls of the Pacific apparently have been abandoned by the reef community. Although a number of these lie well within the euphotic zone and are in proximity to actively growing atoll reefs, they tend to be poor in reef builders.

Mogami Bank and a dozen or so drowned atolls west of Namonuito, in the eastern Caroline Islands (Shepard, 1970), and Alexa Bank (Fairbridge and Stewart, 1960) northwest of Fiji, are examples of such shallow, atoll-shaped banks without active coral reefs. All are alike in being devoid of supra-tidal lands and nitrogen-fixing land vegetation. It is, of course, possible that their reefs have been killed by biological causes, for example, by an irruption of a predator such as *Acanthaster planci*, or a nonselective parasite. But they may also be starved for nutrients. In any case, the shallower examples can hardly have been drowned by rapid submergence.

The most conspicuous, but not necessarily the most important, organisms of the reef community are animals, not plants, and the most evident animals, the corals, are microphagous carnivores. This fact is noteworthy when the reef community is compared with most terrestrial communities in which the visible herbivores vastly outnumber the carnivores. Undoubtedly, the zooxanthellae and the benthic algae are primary producers but the exact role of phytoplankton in the economy of coral reefs remains uncertain.

The food web of the reef ecosystem has been assessed in an admirable preliminary study by Hiatt and Strasburg (1960). But this survey was directed primarily to the fishes. These investigators recognized five successive trophic levels ranging from the algal primary producers to small and large herbivores, algal and detritus feeders, omnivores, and successive grades of carnivores. Their interpretation of the food web, with fourteen major feeding categories is a useful qualitative analysis of the industry of some of the reef organisms.

THE CONTRIBUTION OF GEOLOGY

The reef community, with its multitude of species and microhabitats, clearly is remarkably efficient in exploitation of space and conservation of energy. Intuitively, one might suppose that a well-integrated reef biocoenose must be the product of a very long evolutionary history of accom-

modation and niche subdivision. The fossil record abundantly confirms such an estimate.

The ecosystem of organic reefs is certainly the oldest for which there is a preserved record. Remains of reef assemblages scattered through geologic time provide evidence of increasing diversity since the early Paleozoic, very long before modern reef organisms appeared on the scene. These records tell much about oscillations in physical environments through geologic time, on a local and worldwide scale.

Throughout reef history, the leading role, in fact a dual role, has been played by the algae. They have been the primary producers and certainly were always important limestone reef builders. First the blue-green filamentous forms appeared; later they were joined by green and red algae and at some unrecorded date by those remarkable symbionts, the zooxanthellae, essential partners in any hermatypic union. Phytoplankton are conspicuously lacking from fossil reef deposits.

After the organization of the oldest animal reefs in the early Paleozoic, the stony coelenterates and calcareous sponges commonly were more conspicuous than the algae, but the corals, possibly deriving benefits by diffusion from the zooxanthellae, nonetheless are obligate carnivores high in the food web of the ecosystem (Yonge, 1963).

Massive contributions to the reef limestones also have been supplied by diverse encrusting and interstitial bryozoans, foraminifera, brachiopods, echinoderms, and molluscs, all of which, by the accumulation of their skeletons, have added greatly to the bulk of calcareous deposits in and around the reefs.

Hundreds of pages have been written about classification of reefs based mainly on their physical form and inner rock fabric (Stoddart, 1969). However, much of the resulting terminology, based on mature living reefs, has little meaning in the over-all understanding of their genesis. In the total life history of an individual reef it is certain that a reef community is prerequisite to the reef structure, and an upward growing reef may originate in sheltered waters many meters below the surface of the sea. So, the ecology of a reef must change with reef growth. These changes are reflected in chronological and ecological successions of genera and species.

Geologists have been preoccupied with the problem of distinguishing and analyzing long-past reef environments in the records of ancient marine sedimentary rocks. In spite of repeated and meticulous descriptions of living reefs based on surface observations and borings into reef limestones, a persistent misconception remains that organic reefs are mainly composed of a wave-resistant framework of rigidly cemented *in situ* skeletons of corals and algae (Achauer, 1969; Dunham, 1970).

Many reefs living today are structural complexes more than nine-tenths of which are composed of detrital sand bound together by cemented and anchored organisms and quickly converted without exposure to air, I believe, to friable limestone by biochemical and physical processes. In fossil reefs contemporaneous lithification is indicated by the abundance of reef talus of angular fragments composed of cemented grains, and by fossil epibiota of hard bottoms unlike the burrowing faunas of sand banks. Thus, the distinction is paleoccological rather than lithologic and an organic reef is best considered a complex of many kinds of rocks and sediments generated by a reef community of organisms. It is not limited to the rigid frame of *in situ* skeletons.

Not all reef organisms add significantly to the reef structure. Many are neutral inhabitants, or even reef destroyers. Characteristically, many polychaetes, most of the arthropods, and nearly all the fishes of the reefs are without any fossil record because their skeletal remains are systematically destroyed by scavengers that abound in this strongly oxidizing environment. Consequently, the history of coral reef crabs and fishes and some other groups must be inferred from the evidence provided by other preserved groups and the circumstantial evidence of inferred relationships. For the most part, the arthropods and fishes probably have always stood in relation to the reefs much as do the birds of the tropical forest, lords and tenants with but subordinate roles in the history and destiny of the whole community of which they form a small part.

Throughout geologic history, many sessile reef-dwelling invertebrates and plants have been characterized by (a) the ability to grow upward rapidly under stress of crowded conditions so that they maintain an artificial surface in agitated waters above the floor of accumulating sediments, and (b) by their high rates of calcium metabolism. These functions certainly have been aided by symbiotic zooxanthellae (Yonge, 1963), and the essential presence of the zooxanthellae may be inferred when these conditions are demonstrable in the fossil record.

One characteristic aspect of reef building has been the production of bottom prominences of open-textured and cavernous limestone with great potentialities for production of varied microhabitats. This open-textured substrate is multitiered and stratified in the ecologic and geologic sense. It shelters and supports an astonishing variety of cryptic borers and cave dwellers representing nearly every animal phylum, and many kinds of algae, most of which exist very well at quite low levels of illumination.

The work of making taxonomic and ecologic inventory of coral reefs has only been started, and many of the most obvious questions of environmental dynamics of living and fossil reefs still are matters for speculation.

Consequently, we can take only the broadest view of trends in community succession. Certainly, the communities responsible for living reefs as we now find them, represent the latest stage in an evolutionary history. They are of comparatively late origin, from a geological point of view.

In summary, through their life activities organic reef communities have created the most complex and one of the oldest habitats in the sea. But the history of these communities is not simply a quiet and gradual proliferation of lineages passively living together within this habitat. Rather, their history involves dramatic and disconnected episodes, repeated radiations, stagnation, replacement of dominant groups by ecologically similar but unrelated groups, selective extinction, and even worldwide obliteration of entire communities, leaving ecological vacuums for millions of years. Present distributions are rarely reliable indications of past distributions. Surely, these events faithfully reflect significant environmental vicissitudes on a vast scale, especially climatic and diastrophic changes among which sea-floor spreading and continental drift are assuming ever more emphasis among students of earth history.

The following remarks summarize some highlights of this story. Details must await further geological and paleontological research.

EARLY FOSSIL REEFS

When, where, and how did the earliest reef communities arise? These questions, of course, cannot be answered directly, but geology and paleontology provide many clues.

Limestone accumulations of algal stromatolites flanked by fragmental reef debris are known over the world in Precambrian rocks two billion years or more old, (see, for example, Knight, 1968). By analogy with modern stromatolites (Ginsburg, 1967), it may be supposed that those ancient deposits were built by filamentous blue-green algae. But there are no traces of associated animals in the Precambrian reefs. Indeed, it is quite probable that animals were not yet in existence when the earliest reefs were formed (Cloud, 1968).

We may surmise that natural selection was already working on a basic problem of benthic marine organisms, that is, most effective utilization of substrates in areas that supplied other requisites for habitation. Individual algal colonies of some Precambrian reefs grew upward several feet by entrapping calcium carbonate grains or by precipitation of calcium carbonate to form hemispherical masses and trunklike columns of limestone that rose above the sediment floor.

Organic mounds, "bioherms," of Cambrian age show little advancement. Some were built by stromatolites. In others, stromatolites were joined by stony spongelike organisms, the extinct archaeocyathids (Okulitch, 1955) assembled in low thickets or meadows. Doubtless, unfilled spaces within and between the animal colonies provided shelter for trilobites and naked invertebrates without aptitude for preservation. By the close of the Middle Cambrian, the archaeocyathids had vanished and widespread limestone seas of the Upper Cambrian and Lower Ordovician (Canadian) were left for an extended time without comparable animal reef builders. Only small bioherms or reef mounds of algal stromatolites date from this time.

In mid-Ordovician (Chazyan) time a complex algae-invertebrate reef community appeared in North America (Pitcher, 1964, 1971) and the adaptive zone vacated by the archaeocyathids came to be occupied by coralline red algae (*Solenopora*), stony bryozoans, stromatoporoid sponges, and tabulate and rugose corals (Hill, 1956). These constructed the oldest known "coral reef" community, progenitor of an algal-coral association which evolved and proliferated through a long chronological succession spanning 130 million years, until unidentified environmental changes wiped out the reef community near the close of the Devonian Period (Frasnian-Famennian interval) in a worldwide episode (McLaren, 1970; Jamieson, 1971). This was followed by a well-defined interval (beginning in the Famennian and continuing into the earliest Lower Carboniferous) of impoverishment of the reef community throughout the world marking, no doubt, an environmental event that eliminated the middle Paleozoic reef community.

Many of the middle Paleozoic reefs grew in shallow agitated waters, as indicated by sedimentary and paleontologic contexts (Lowenstam, 1957; Playford and Lowry, 1966), encouraging speculation that some of the reef builders of those times enjoyed symbiotic union with zooxanthellae.

The late Paleozoic (Mississippian, Pennsylvanian, and Permian periods) was characterized by scattered shelf-edge organic sand banks and reef complexes stabilized and consolidated by stromatolites, cemented and anchored brachiopods, bryozoans, sphinctozoan (chambered calcareous) sponges, red and green algae (solenoporoids, dasycladaceans, and codiaceans) with local contributions of great quantities of scree and debris from echinoderms, brachiopods, foraminifera, and molluscs of a highly organized community that bore little resemblance to mid-Paleozoic reef builders. Through middle and late Paleozoic times reef commensals, such as brachiopods and crinoids, became increasingly varied in taxonomic diversity and, in limited parts of the geologic column (e.g., Cooper, 1946; Grant, 1971), attaining hundreds or even thousands of species.

During the Permian Period, a pantropical seaway, Tethys, extended nearly around the globe (fig. 4). Because of the extraordinary diversity of invertebrate faunas in Tethyan Permian deposits it may be supposed that this seaway was a low latitude circumtropical belt distinguished from temperate to cold waters of higher latitudes (Newell et al., 1953), a conclusion subscribed to by Stehli (1957).

The tropical marine Permian faunas of the Americas represent the extreme eastern outpost of the marine tropics of the time. The preserved Permian to Miocene deposits of Tethys now are mainly limited to the great orogenic belt that extends from the Mediterranean region on the west, across the Middle East, south Asia, and Indonesia, to Japan in the east.

In any case, when the scleractinian corals first appeared in Middle Triassic rocks of western Tethys in south Europe and the Mediterranean region, they were moving into an important ecological zone that had been unoccupied or only sparsely inhabited by coelenterates since the catastrophic decline of the tabulate corals and stromatoporoid sponges in the middle Paleozoic. The superficially similar rugose corals of the Paleozoic in most cases favored quiet, frequently turbid, waters. Generally, they were not primary reef builders although they formed thickets in some cases.

The first scleractinian corals, progenitors of the modern reef community, appear in Middle Triassic rocks (Anisian-Muschelkalk) of Germany, the southern Alps, Corsica and Sicily, where they are represented by scattered reef patches containing six distinct families. Gradually, these six families evolved in well-documented stratigraphic sequences over the world into a score or more of still living families and a dozen extinct families (fig. 2) that span Mesozoic and Cenozoic history (Wells, 1956).

By Late Triassic time the scleractinians played an important, but still subordinate, role in reef building. Especially in the southern Alps there are magnificent displays of Late Triassic reefs in which sphinctozoan sponges, bryozoa, and algae played leading roles. Although Triassic coral colonies generally are quite small as compared with living hermatypic corals, some alpine examples of the genus *Thecosmilia* exceed one meter across (A. G. Fischer, personal commun.).

The known latitudinal range of Upper Triassic reefs is different from that of modern reefs, from latitude 60° N. to 10° S. (fig. 3), suggesting that geographic conditions may have been unlike those of today (fig. 3).

Southern Europe and lands marginal to the Mediterranean contain the best records of Jurassic and Cretaceous coral reefs. In this region of western Tethys the reef community underwent continued diversification from mid-Jurassic time until the close of the Cretaceous (fig. 2). Besides

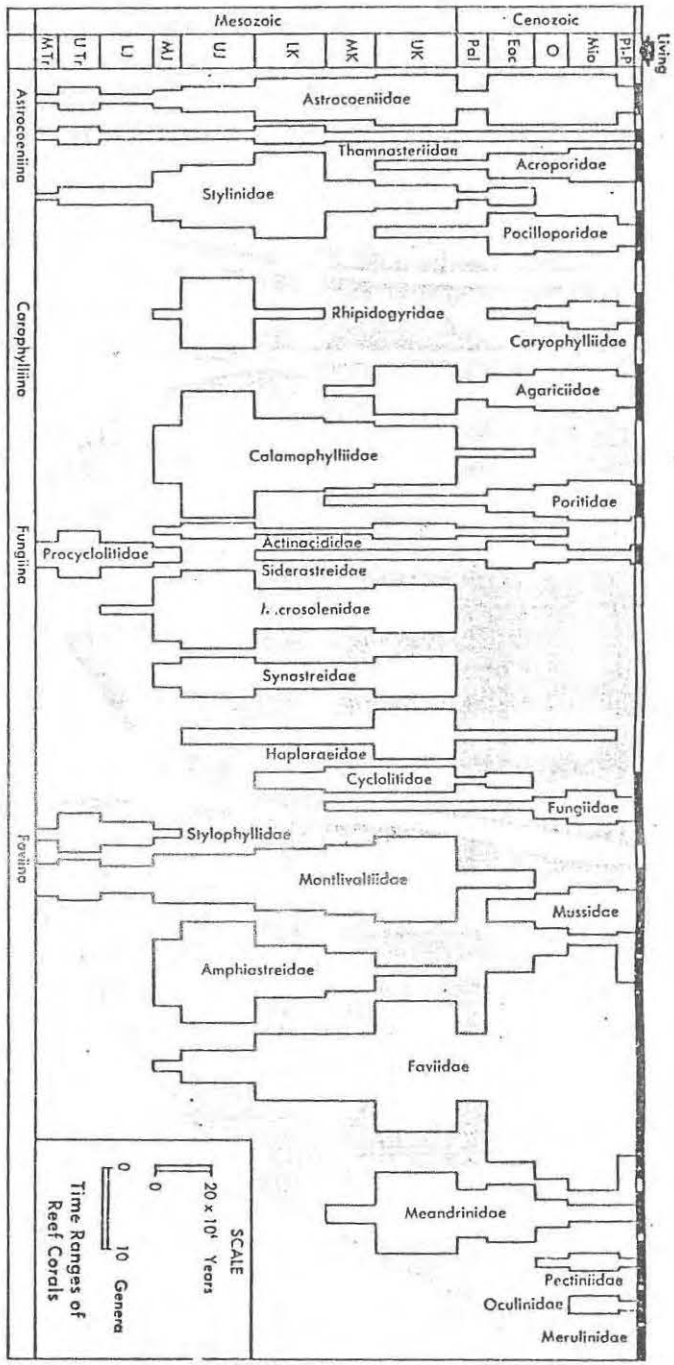


Fig. 2. Fluctuations in diversity of reef (hermatypic) corals through geologic time. Note marked retrenchment in the Paleocene (data from Wells, 1956).

being one of the richest known coral assemblages of all time (in generic diversity), the community consisted of lithothamnian algae (Wray, 1971), organisms very like stromatoporoids (LeCompte, 1956), sphinctozoans (Rigby, 1971), and a very diverse assemblage of molluscs, echinoderms, and other commensals.

Little or no reef development is known anywhere in earliest Cretaceous rocks, reflecting, no doubt, one of many epochs of unfavorable world conditions. But a worldwide epoch of reef building began a little later

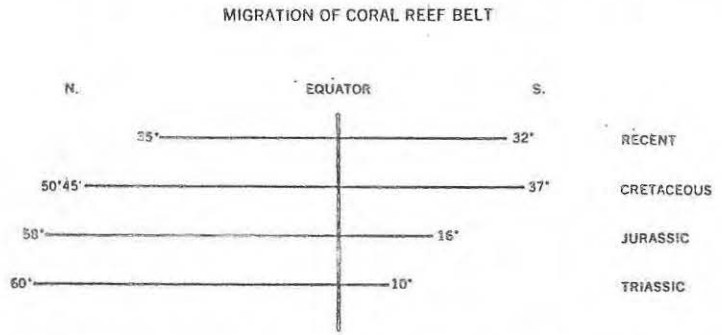


FIG. 3. Latitudinal range and displacement of coral reefs through time, possibly an effect of northward drift of fossiliferous deposits (data from Wells, 1956).

(Urgonian episode of the Barremian and Aptian), near the present tropical belt. Many new families of corals and other members of the reef community appeared in western Tethys and tropical America. Although these regions clearly lay within a circumtropical zone, regional differences are evident and the influence of the deep Atlantic, as a barrier to migration, was well established.

A previously obscure group of marine bivalve molluscs, the rudists (Coogan, Dechaseaux, and Perkins, 1969), underwent a remarkable evolutionary radiation during the Cretaceous Period and at times challenged the dominance of the corals among reef animals. The rudists successfully competed with, and even largely supplanted, the corals along the sheltered inner margins of fringing and barrier reefs, but the corals generally maintained dominance along the seaward margins of the reefs (B. F. Perkins, personal commun.). Many of the rudists developed tightly packed aggregates of cylindrical or conical cemented shells that grew upright in many cases simulating solitary corals. The rudist-coral reefs are limited to low latitudes and this distribution suggests that the northern limit of the tropical zone of Cretaceous times lay not far from the present

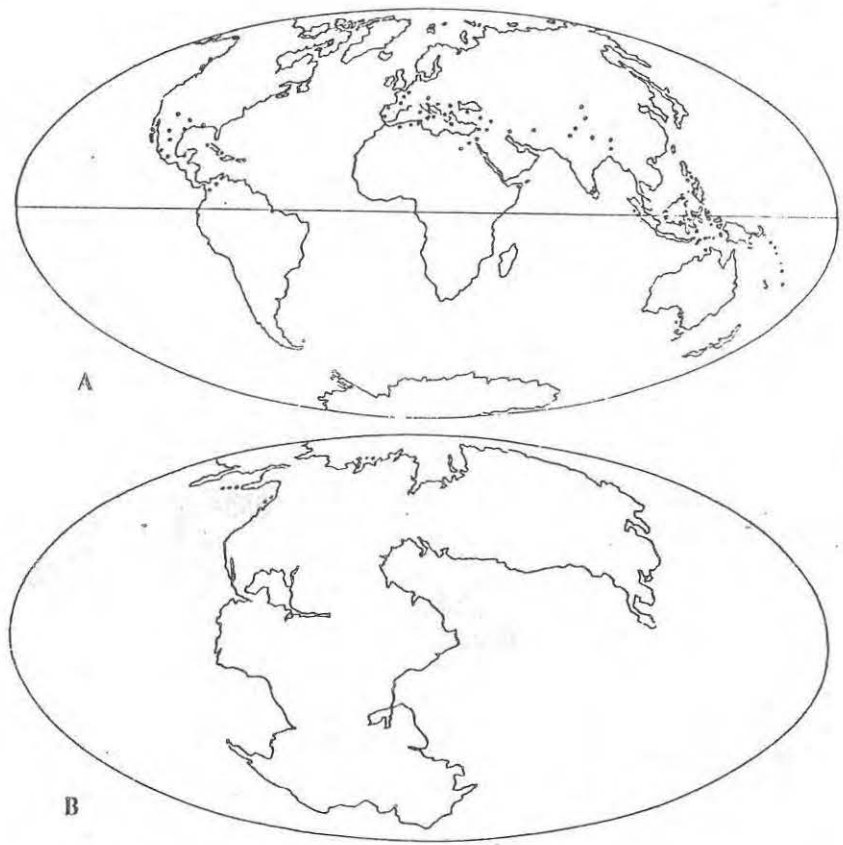


FIG. 4. A. Present distribution of fossil tropical faunas of Permian (stippled) and Cretaceous (circles) ages in the Tethyan orogenic belt. The former is based on distributional area of neoschwagerine fusulinids and richthofeniid brachiopods; the latter indicates most important localities of the rudist-scleractinian reefs (data from Dacqué, 1915; Joleaud, 1939; Stehli, 1957; and B. F. Perkins, personal commun.). B. Permian paleogeography showing an interpretation of Tethyan seaway (based in part on Wilson, 1963).

tropics (fig. 4). At the very close of the Cretaceous Period the rudists became extinct over the world, leaving no descendants, and this extinction was concurrent with disappearance of the dinosaurs and ammonites and with a sharp decline in diversity of reef corals and many other great groups of animals (fig. 5) of the time (Newell, 1966).

Coral Reefs and Continental Drift

In the past few years converging lines of evidence from studies of paleomagnetism, stratigraphy, and paleontology have supplied increasingly compelling evidence that the southern continents and India were joined together in late Paleozoic times in a single great continent, Gondwana, and at least for part of this time (during the Carboniferous and Permian periods), this continent supported ice sheets presumably near the geographic south pole (fig. 4). The deep Atlantic Basin did not then exist and North America and Eurasia were joined by more or less continuous land. The complete lack of evidence of Triassic ice caps is an enigma which also involves the remarkably cosmopolitan distributions of terrestrial and marine biotas that display hardly any evidence of climatic zonation. Gondwana was ice-free by Triassic time, and for long thereafter the whole earth apparently was relatively ice-free.

The precise time, or times, of separation of the several continents is still under debate (Funnell and Smith, 1968) but the proto-Atlantic Basin as a broad oceanic barrier to faunal migrations is clearly discernible in the distribution of Atlantic marine strata of Cretaceous age and in the endemic character of many Caribbean fossils of this age (Hallam, 1967).

Evidence from paleontology generally is not in conflict with these interpretations. Permian and Mesozoic reefs and other tropical elements are mainly (but not wholly) limited to the orogenic regions that form a belt at low latitudes across southern Eurasia and America, roughly parallel with, but generally somewhat to the north of, the present tropics (fig. 4).

Before the Cenozoic, the southern continents generally lay at higher latitudes than their present locations and it is not surprising, therefore, that fossil hermatypic corals are lacking in the nuclear land masses of South America, Africa, Australia, India, and Antarctica. Shifting of the continents in response to sea-floor spreading clearly has involved a northward component. Africa and India moved across the ancient ocean floor (Tethys) against the southern flanks of Eurasia, crumpling, and displacing tropical deposits of mid-Cenozoic Tethys. Probably, it is because of this global tectonism that the marine tropical record of Permian to Miocene times occupies an east-west belt not much broader than, but well to the north of, the present tropics (figs. 3 and 4).

Early Cenozoic (Paleogene) Reefs

Worldwide collapse and reorganizing of very many animal communities at the close of the Cretaceous Period plainly is written in the fossil record (Newell, 1966, 1967). The immediate causes of this biological revolution

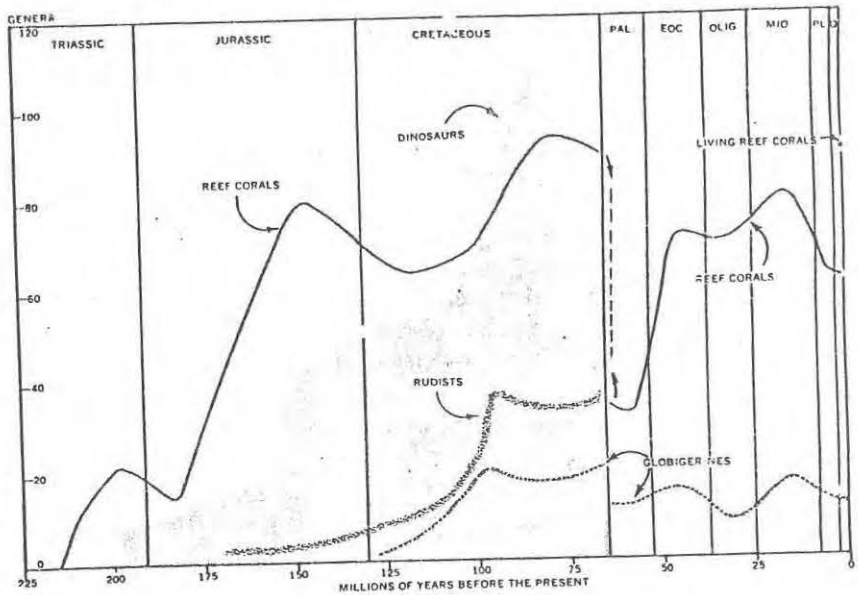


Fig. 5. Mesozoic-Cenozoic fluctuations in generic diversity of some important fossil groups as evidence of a post-Cretaceous faunal revolution. Shaded area represents dinosaurs. Late Cretaceous diversity peaks correspond closely with the time of maximum spread of epicontinental seas and maritime climates. Discrepancy between Pleistocene and Recent corals indicates insufficient collecting and provides some evidence bearing on reliability of evidence (data from Newell, 1966, and Treatise on Invertebrate Paleontology, R. C. Moore, ed.).

are uncertain but they probably stem from ecological dislocations that originated in sweeping geographical and climatic changes at the end of the Mesozoic. Some of these have been long known and substantially documented (Hallam, 1963).

The terrestrial vertebrates were greatly decreased as a result of the elimination of the dinosaurs, which were still dominant land animals until near the end of the last stage of the Cretaceous (fig. 5). Extinctions depleted many elements of the marine fauna. The rudists, diverse and abundant until near the close of the Maastrichtian Stage, became extinct in a remarkably short time, from a geological viewpoint. These various changes were concurrent (but may have proceeded at different rates) in the last part of the Cretaceous Period (Newell, 1966, 1967). Altogether, nearly one-third of the families of Upper Cretaceous animals failed to survive this episode of extinction. Although some of these groups started to

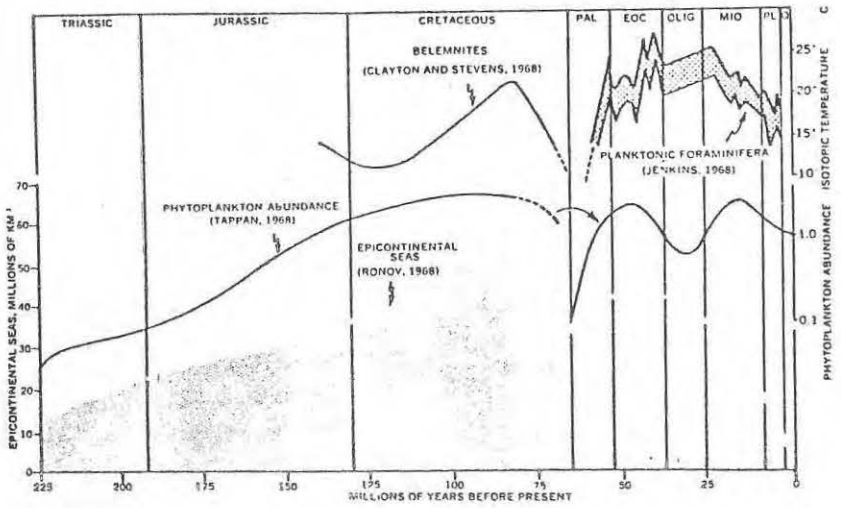


FIG. 6. Parallel trends in isotopic paleotemperatures (New Zealand), phytoplankton abundance (diversity), and areas (shaded portion) of epicontinental seas.

decline 10 or 15 million years before their extinction, others were diverse, cosmopolitan, and numerically abundant shortly before their disappearance. The Paleocene opened with an impoverished fauna composed of slightly modified survivors from much more diverse Cretaceous faunas.

The reef community participated in, and for at least 10 million years, did not recover from, this episode of world extinctions. Coral reefs are unknown in Paleocene rocks over most of the world. The hermatypic coral genera were survivors from the Cretaceous Period and not a single genus is known to have originated in the Paleocene.

Sweeping changes in planktonic foraminifera and a notable decline of phytoplankton at the end of the Cretaceous also underscore the universality of the factors responsible for this biological revolution (figs. 5, 6).

One probable cause of the biological crisis near the Cretaceous-Paleocene boundary may have been the onset of seasonal oscillations in temperature and rainfall to which the Cretaceous organisms were not adapted (Axelrod and Bailey, 1968). This was a time of drainage of epicontinental seas from the continents, caused, presumably, by ocean basin subsidence, a trend that continued through the Cenozoic (fig. 5).

A new radiation of hermatypic corals populated the tropical seas of the Eocene with genera unknown in older rocks and many of these have survived until today. But for unknown reasons Eocene reefs generally are sparse and poorly developed. Planktonic foraminifera likewise experienced

early Cenozoic radiations, one in the Paleocene, another in the Eocene (Cifelli, 1969), followed by sharp reduction of diversity in late Eocene and Oligocene times correlated with climatic oscillations (fig. 5).

Oligocene reduction also is evident in the hermatypic corals, molluscs, and phytoplankton over much of the world. This trend, together with supporting evidence of paleotemperature estimates from oxygen isotopes, has suggested an episode of cooling (figs. 6, 7), or at least greater seasonal range of temperatures at intermediate latitudes during the Oligocene (Fleming, 1967; Devereaux, 1968; Edwards, 1968; Gill, 1968; Hornibrook, 1968; Jenkins, 1968; Tappan, 1968; Addicott, 1969). However, the hermatypic corals and coralline algae locally built extensive fringing and patch reefs in the Gulf of Mexico, the Caribbean area, southern Europe, and southeast Asia (Wells, 1956). The Caribbean fauna of latest Oligocene age shows heightened isolation from Europe, probably an effect of the spreading of the Atlantic Basin.

GEOLOGIC BASIS OF CENOZOIC CLIMATIC TRENDS

The volcanic foundations of many Pacific coral atolls are known to be of Cretaceous and early Cenozoic age having subsided many hundreds and even thousands of meters since they lay exposed at seal level (Menard, 1964). The vast volumes of oceanic rocks involved in lateral transport probably are sufficient to account for subsidence over great areas of the ocean basins and withdrawal of marine waters from the continents during the past 60 or 70 million years. Such withdrawal is plainly recorded by coastal belts of marine rocks of Cenozoic age that girdle many of the continents.

Ronov (1968) has estimated from the present, and inferred, from original distributions of marine strata on the continents, that the land areas have progressively increased by about 65 per cent since the great inundation of the Cretaceous Period. At the Cretaceous maximum transgression the coverage of the earth by marine waters must have been around 90 per cent (fig. 6). The remarkable recession of the seas since the Cretaceous, and especially since the early Miocene (Tanner, 1968), has affected the later history of coral reefs in particular, and all life in general, by altering the areal extent of habitats and by influencing world climates. Stratigraphic geology provides many records of the former, and analysis of the fossil record supplies documentation of the latter.

Bottom waters of the present oceans are heavy because they are cold. In each ocean bottom water, cooled and aerated at the surface around Antarctica, spreads out meridionally and zonally along the bottom accor-

ing to bottom topography. Very little oceanic bottom water is of Arctic origin (Defant, 1961). This gravity circulation of ocean waters from Antarctica into the ocean basins of the world provides ventilation and lowers the mean temperatures of the oceans and overlying atmosphere (Kremp, 1964).

Emiliani (1966) has shown that oxygen isotope ratios of deep-sea benthonic foraminifera indicate a decline of around 12° C. since late Cretaceous time some 75 million years ago (fig. 7). From this we may deduce that contributions of very cold water from Antarctica are of fairly recent

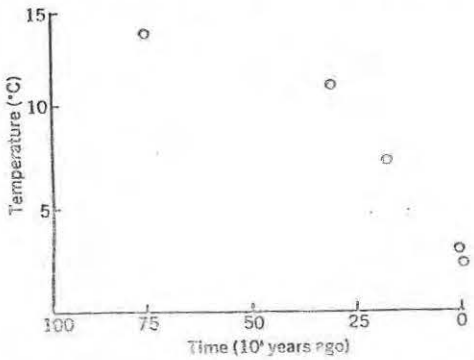


FIG. 7. Secular cooling of deep ocean waters, as indicated by oxygen isotope analyses of benthonic foraminifera (data from Emiliani, 1966).

date, geologically. Oxygen isotope determinations of fossil invertebrate skeletons, and faunal and floral analyses from many parts of the world (fig. 6) provide compelling indications of increasingly sharp climatic zonation and seasonality through the Cenozoic. More direct evidence bearing on the history of the Antarctic ice cap is coming to light in field work now in progress.

Tertiary floras from the Antarctic Peninsula indicate temperate climates through the Lower Miocene (Adie, 1964). Extensive glacial pavement and tillite below lava in the Jones Mountains of western Antarctica are dated by potassium-argon as also probably Miocene, presumably Late Miocene (Rutford, Craddock, and Bastien, 1968; Denton, Armstrong, and Stuiver, 1970).

Isotopic paleotemperatures and paleontologic data over the world converge to indicate a climatic amelioration during the early Miocene, followed by cooling in later Miocene concurrently with the establishment of the Antarctic ice sheet and complex glacial oscillations of Quaternary times (Dorf, 1957; Dawson, 1968; Tappan, 1968; Addicott, 1969; Bandy, Butler and Wright, 1969; Denton and Armstrong, 1969). Margolis and Kennett (1970) reported ice-rafted sands as old as Eocene and Oligocene

age in sub-Antarctic deep-sea cores. This evidence suggests at least alpine glaciation in Antarctica during the early Cenozoic.

Axelrod (1967) and Axelrod and Bailey (1968) have called attention to the probably deleterious effects of heightened seasonality on breeding patterns of animals long adapted to equable climates. They had in mind mass extinctions of Cretaceous dinosaurs and late Pleistocene and early Holocene mammals, but the principle might well apply to aquatic animal extinctions. Bretsky and Lorenz (1970) presented a persuasive argument based on the principle that an over-all increase in environmental stress will be selectively lethal to groups of organisms that have previously undergone a long period of homoselection in stable environmental settings (*op. cit.*, p. 2454). Unquestionably, the rate of onset of such environmental perturbations influences the result. Slow changes may be compensated by adaptation.

MIOCENE ORIGINS OF THE MARINE BIOGEOGRAPHIC PROVINCES

Ekman (1953) more than any other marine biogeographer understood the historical origins of present organism distributions in the sea. His grasp of this subject led him to penetrating analysis and conclusions that provide part of the basis for the following summary.

During Permian and Mesozoic times, east-west marine connections at low latitudes via Tethys were comparatively open and a pantropical biota was distributed across southern Eurasia, reaching the Americas first from the Pacific, later by way of the Atlantic. Provincialism is evident in the Western Hemisphere in the Permian and Cretaceous periods (fig. 4) and later, but many of the Triassic and Jurassic marine faunas are remarkably cosmopolitan.

Climatic belts were poorly defined throughout the Mesozoic and Paleogene when the earth was essentially ice-free and the temperate and tropical zones were much broader than they now are. Fossil palm trees of Paleogene age are scattered over more than 100 degrees of latitude, from Alaska to Patagonia, and their occurrence in India suggests that this continent had moved far northward from its Permian location near the south pole (fig. 8) while the position of the equator remained constant.

Prevailing mild climates gave way to cooler and more seasonal climates in mid-Miocene times with the birth of the Antarctic ice cap. Western Tethys became blocked by the northward movement of the African land mass which came to separate the Indian Ocean from the Mediterranean, and the latter thenceforward became an Atlantic sea (Gignoux, 1955).

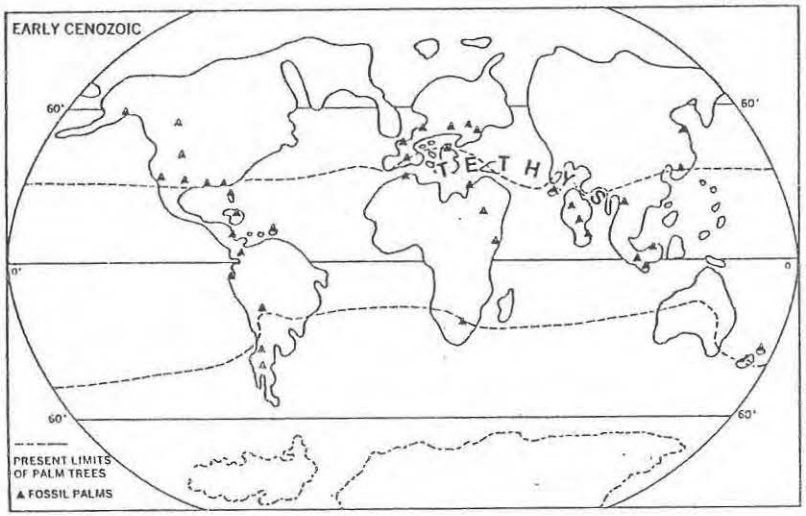


FIG. 8. Early Cenozoic tropical belt deduced from distribution of fossil palm trees (data from Kremp, 1964).

The tropical seas became sharply differentiated after the early Miocene into the present Atlantic biogeographic province, with headquarters in the Caribbean, and an Indo-Pacific province, (fig. 9), with its center of diversity in the Australasian region. Western Tethyan genera, already in decline in the Paleogene, became relicts in the Caribbean (fig. 10).

From the early Cenozoic the eastern Pacific had been a broad and deep obstacle to migrations of shallow-water invertebrates and fishes which had earlier followed the warm northern margin of the Pacific Basin between Asia and North America and had utilized volcanic island stepping stones across the central Pacific. Migrations were now impeded by a filter-barrier of open ocean (fig. 11). After separation of the Americas from Eurasia, migrations between the Americas and Tethys were mainly across the Atlantic. During the Neogene, the most favorable climatic and hydrographic conditions of tropical seas centered in the Caribbean and Australasian areas.

NEOGENE HISTORY OF CORAL REEFS

Elements of the Indo-Pacific coral faunas now extend over an enormous area (117×10^6 km.^{2}) almost equal to one-third of the oceans of the world. They were naturally more diverse from the outset than those of the Caribbean province and this disparity also pertains to other, associated groups of marine organisms. The hermatypic fauna of the European

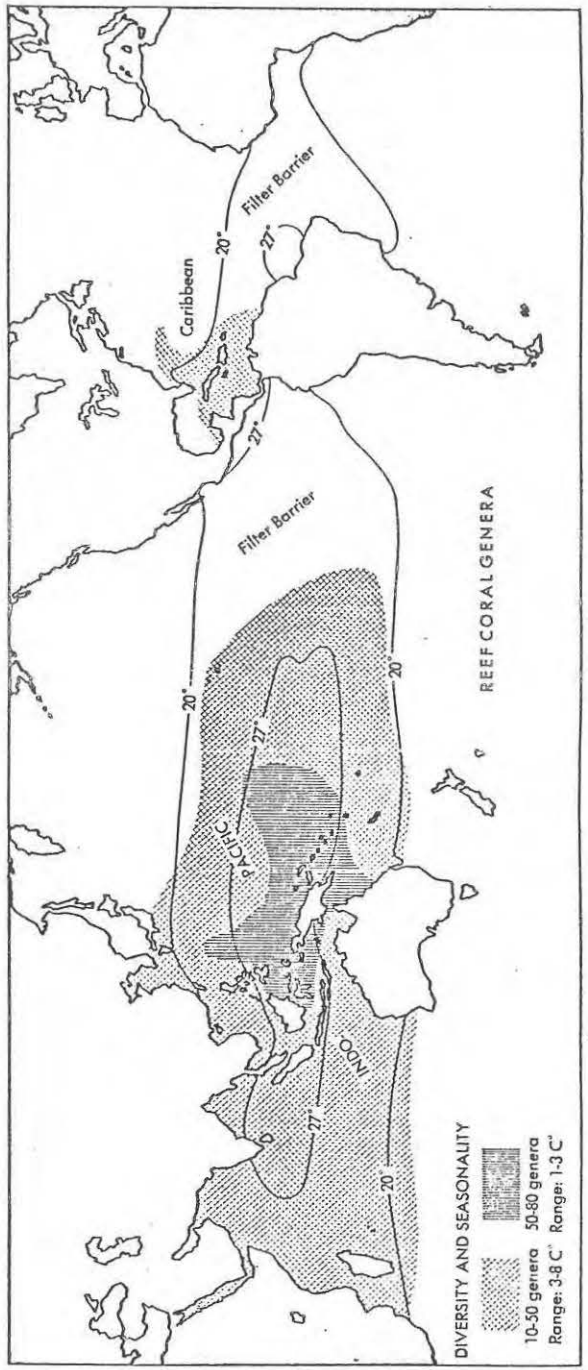


FIG. 9. Approximate limits of the tropical Indo-Pacific and Caribbean marine biotic provinces as defined by reef (hermatypic) coral genera and compared with minimum average temperatures (isocrymes). Approximate mean summer-winter temperature range along the 20° C. isocryme is 6° C., along the 27° C. isocryme, 3° C. (temperatures from U. S. Navy Hydrographic Office, 1944, and Hutchins and Scharff, 1947; coral data from Wells, 1954).

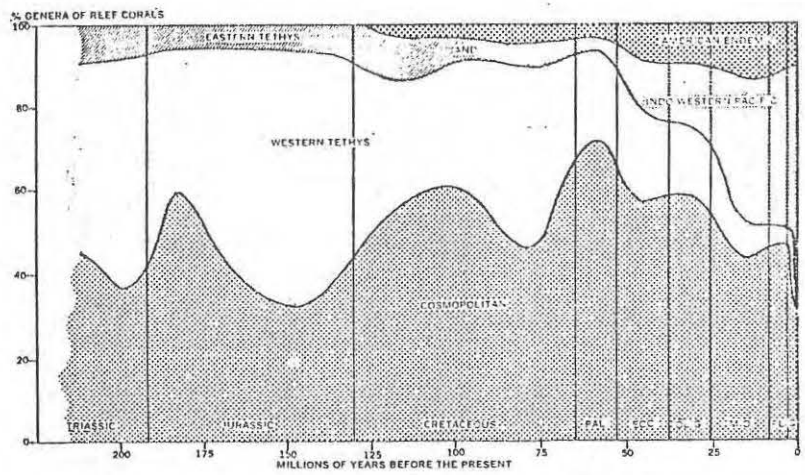


FIG. 10. Percentage distribution of reef coral genera through time with respect to zoogeographic origin (data from Wells, 1956, and personal commun.).

Miocene contains genera related to both Indo-Pacific and Caribbean faunas. However, because of unfavorable climate, reef corals soon disappeared permanently from that region. It was in the Miocene that coral reefs began to colonize the shelf of Australia.

Contraction of the tropical belt in Pliocene time compressed the limits of reef corals to approximately present-day distribution between about latitude 35° N. and 32° S. Pleistocene glaciation and resulting great eustatic fluctuations of sea level had only a limited effect on hermatypic corals, possibly because surface temperatures in the deep tropics were little affected and habitats were scarcely altered either as regards sedimentation or available area. Furthermore, the reef community had long been excluded from inland seas and had achieved great homeostatic stability.

The Isthmus of Panama rose out of the sea in the Neogene isolating the marine outpost species of the Panamic region from their haven base in the Caribbean. Several Paleogene cosmopolitan and Caribbean genera of the eastern Pacific died out leaving a few niches to be recolonized from the west. With these events of the latest Cenozoic, the corals along the Pacific coast of the Americas have assumed an Indo-Pacific complexion (fig. 10).

ZOOGEOGRAPHY OF LIVING REEF BIOTAS

Diversity Gradients

From the foregoing conclusion it seems clear that time and events of geologic history are major determinants in the spatial relationships of

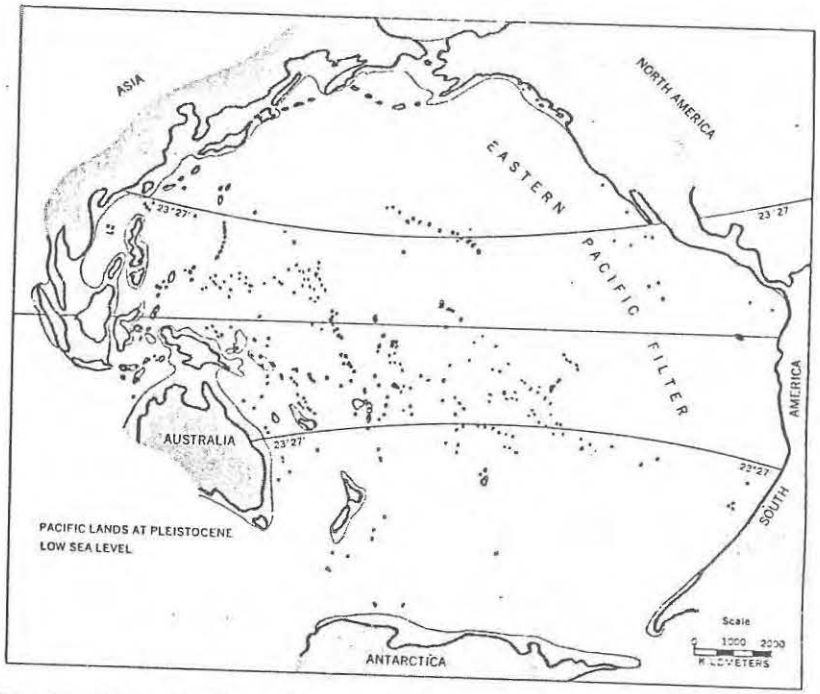


FIG. 11. Pleistocene map of the Pacific Basin to illustrate island stepping-stones and the Eastern Pacific filter-barrier as geographic factors in Cenozoic dispersal of the Indo-Pacific marine biota (data from Durham, 1963).

reef corals, as with other creatures. However, organisms live wherever they can. With changing environmental conditions, their facilities for modifying or extending their geographic ranges often are astonishingly effective.

The fact that mature corals are sessile has not prevented some species from maintaining gene flow over linear distances of more than 10,000 kilometers from the east coast of Africa across the Indo-Pacific to the Americas. Dispersal with these, as with other shallow-water invertebrates, is accomplished by floating larvae, which may be carried for immense distances throughout the tropical seas both by surface and submerged currents. Their dispersal has been essentially random.

Broad deeps are not absolute barriers to migrations of these forms. Many kinds of larvae are equipped with sensors for detecting the proximity of shallow bottoms. These larvae tend to remain in the meroplankton until an opportunity is presented for descent to a favorable shoal on the sea floor. Laboratory observations on larval longevity, therefore, can hardly

be reliable for assessing dispersal capabilities of a species, as has been assumed (Thorson, 1961, p. 469).

A small percentage of the larvae of any population may survive trips of weeks or months across deep waters. Of probable significance, perhaps even more important than larval longevity, may be the biological and physical environments available after a long passage by living larvae over deep waters (Hertlein and Emerson, 1953; Emerson, 1967).

The breakup of Tethys, and climatic events in the Miocene, were accompanied by and probably responsible for the decline in the Atlantic biota and its eastern Pacific outpost, and the uplift of the isthmian barrier completed the isolation of the Caribbean fauna. The consequent dropout of many Caribbean genera and species in the Pacific-Panamic area then freed many microhabitats for new occupancy by a few hardy Indo-Pacific immigrants. So, the Pacific-Panamic region, not especially favorable for reef corals because of upwelling cool waters and narrow shelves, displays increasing influence from the west, not so much because of biogeographic pressures from the Indo-Pacific biota, but because of the disappearance there of several reef corals derived in earlier times from the east.

According to Wells (1954), the Indo-Pacific reef corals are remarkably homogeneous at the generic level. Few, if any, display well-defined morphological clines. The most conspicuous regional change in community composition is the dropping out of genera toward the periphery in all directions radiating outward from the Australasian region. The same genera drop out in characteristic sequence and the most widely distributed genera include only those that are also found more centrally. The more restricted genera virtually are limited now to the East Indian archipelagoes and northeastern Australia. However, this restriction for many genera is geologically recent. Many clearly are relicts. Wells (1954, 1955), has tabulated the Indo-Pacific coral genera in ascending order of tropicality. Among the Indo-Pacific genera, only 57 per cent are now or were in the past restricted to the Indo-Pacific province, and only 20 per cent are apparently endemic to the Australasian area. However, as most of the second category are not yet identified in the fossil record, the present restriction of a genus to the central area of the Indo-Pacific is not compelling evidence that it originated there. The Indo-Pacific genera may further be analyzed, as follows (data from Wells, 1954, 1955, 1956):

	Number	Per Cent
Known only in central area	15	20
Quaternary, greater Indo-Pacific only	22	25
With long history, greater Indo-Pacific only	9	12
With history both without and within the Indo-Pacific	31	43
Totals	77	100%

Similarly, among the modern tropical American coral genera, only about 10 per cent are unknown elsewhere. Probably few, if any, of these originated in the areas to which they now are apparently restricted.

Geologic history and present environments are responsible for the modern limits of the biogeographical provinces. Within these provinces, ecological barriers (temperature, depth, turbidity, salinity, edaphic conditions) define subprovinces.

Temperature Minimum

The Indo-Pacific coral gradients closely parallel temperature gradients, and this and other illustrations of high correlation of temperature with taxonomic diversity has led Stehli (1968) and others to stress the limiting controls of temperatures. The correlation is good, but it is not perfect. Generally, the coral reefs lie within the 20° C. mean winter minimum isotherm (isocryme) and the greatest number of genera lie close to the 28° C. isocryme, but there are some notable exceptions. For example, a diverse reef biota follows the Kuroshio Current northward from the Philippines to Japan along a temperature drop of several degrees (fig. 9). Possibly this biota is being maintained by continuous recruitment from the south (Wells, 1954). A small relict haven of high diversity also occurs in the Red Sea where 58 genera are now known from the northern half (J. W. Wells, personal commun.). All these also occur elsewhere.

The best-known reefs and greatest-known taxonomic diversity of the Caribbean biota are found around Jamaica. This is an area that is considerably cooler (24° C. in the winter) than the most tropical parts of the Atlantic Ocean (fig. 9) which are otherwise unsuitable for reef growth.

Seasonality

As with tropical forests (Stebbins, 1950) or deep-sea benthos (Sanders and Hessler, 1969) stability of the physical environment characteristic of reefs insulates the reef community and frees it from many of the stresses that affect communities of more seasonal climates. Stability favors accumulation of phyletic lines and consequent multiplication of organism niches and microhabitats (Fischer, 1960; Dunbar, 1960; Pianka, 1966; Goulden, 1969; Bretsky and Lorenz, 1970).

"Where physical conditions are easy, interrelationships between competing and symbiotic species become the paramount adaptive problem. The fact that physically mild environments are as a rule inhabited by

many species makes these interrelationships very complex. This is probably the case in most tropical communities." (Dobzhansky, 1950.)

Even within the tropics, where seasons may be ill-defined, the coral reef community shows a sensitive relationship between diversity and temperature range. It commonly is assumed that minimum temperatures limit these distributions even where the temperatures remain well above the absolute minimum for healthy coral reefs (Wells, 1954).

Probably a more significant aspect of seasonality is temperature range which may be taken as one measure of specificity of physiologic adaptation. In the tropics, this may influence reef diversity even more than minimum temperatures.

The Australasian headquarters of the Indo-Pacific biota is characterized not only by the highest marine isocrymes in the world (27°–28° C.) but the annual range of mean monthly temperatures is minimal, only about 1°–3° C. (U. S. Navy Hydrographic Office, 1944). Average minimum temperatures in tropical seas elsewhere are lower and the mean annual range is greater. That is, the seasonal fluctuations away from the Australasian area are more marked and generic diversity is proportionally diminished (fig. 9).

By contrast, the range of mean monthly temperatures of surface waters in most of the Caribbean province is 3° to about 8° C., and the isocrymes range from about 18° to 27° C. (U. S. Navy Oceanographic Office, 1967). These characteristics of the Caribbean province stem from influence of nearby continental masses.

Habitat Dimensions

A large area should support a more diverse biota than a small area of like environment, because a large area can sustain larger, hence more varied, gene pools and provide more refuges at times of exceptional stress. Where the environments are not uniform, ecological conditions are likely to be more varied in a large than in a small area and the historical backgrounds of the inhabitants more diverse in the large area. Consequently, area of occupancy (geographic range) of species and higher categories provides a rough measure of diversity. It follows that extinction rates are higher in small than in large areas of comparable habitat (Mayr, 1965). These relationships are dramatically illustrated by the birds of ecologically similar tropical islands (fig. 12) of differing sizes.

Quantitative data for marine invertebrates are by no means as complete or detailed as for island birds but comparison of the Indo-Pacific biota with that of the Caribbean suggests that the same relationship applies.

The greater diversity of the Indo-Pacific biota simply reflects its greater area of favorable environments.

The Indo-Pacific province covers about 117.4 x 10^6km.^{2} and the Caribbean province, 5.7 x 10^6km.^{2} (fig. 10). The former includes approximately one-third of the area of marine waters of the earth and more than 20 times the area of the Caribbean province.

Of course, the coral-reef biota does not occupy more than a fraction of the total areas of these provinces. A map by Joubin (1912) showing world distribution of living coral reefs provides a useful, if generalized, measure of the extent of the reef habitat. My estimates, based on this map, indicate about 1,250,000 km.^{2} for Indo-Pacific reefs and about 250,000 km.^{2} for those of the western Atlantic, in ratio of five to one (fig. 13).

Taking into account inaccuracies of Joubin's map and gross exaggeration resulting from the small scale, we may assume that the estimates given above are probably too high by one order of magnitude. In any case, they suggest that diversity may be roughly proportional to area of occupancy. Inaccuracies become insignificant if we adjust diversity to equal areas. If we compare some of the better known taxonomic groups, we have the following estimates of diversity of shallow-water organisms in the two provinces. Note that the species/genus ratio of reef corals in the Indo-Pacific is about twice that of the Caribbean.

	Indo-Pacific	Caribbean	Ratio
Area of habitat	125,000 km.^{2}	25,000 km.^{2}	5/1
Reef corals (genera)	80	20	4/1
Reef corals (species)	500	65	7.7/1
Shelled molluscs (species)	5000	1200	4.2/1
Cidarid echinoids (species)	75	13	5.8/1
Fishes (species)	2175	600	3.6/1
Cypraeid gastropods (species)	121	13	9/1

Dispersal Centers or Refuges?

It has always been tempting to regard regions of comparatively high diversity as centers of outstanding evolutionary activity and it has been agreed that the often cited correlation between diversity and climate indicates that evolutionary rate is temperature-dependent (Stehli, Douglas and Newell, 1969). We may ask: have the more tropical regions of the past been centers of origin and dispersal of taxa? Or, can we consider the present tropical biota a shrunken relict of a more widely distributed biota of, say, Eocene time? I am inclined to give a qualified yes to both questions.

Of course, more speciation takes place in the tropics because there are more evolving phyletic lines there and trophic resources are continuously

available. However, it is not necessarily true that phyletic lines evolve more rapidly in the tropics than elsewhere. So far as I am aware, there is no evidence from genetics that greater input of solar energy at low latitudes is translated into accelerated evolution. The mode of evolution probably has not consisted of a one-way outward movement of new taxa from the tropics into high latitudes. And paleontology does not supply compelling evidence of systematic displacement of more primitive, less

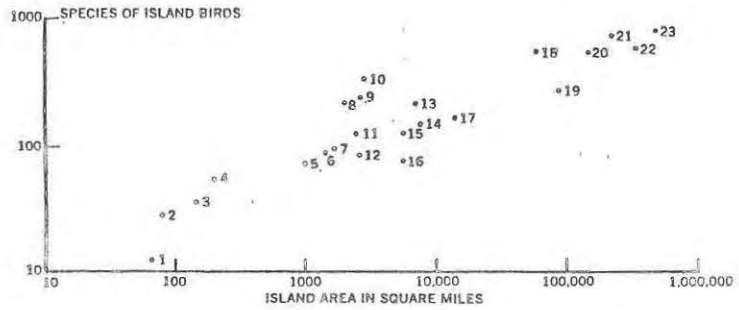


FIG. 12. Correlation between area of habitat and diversity of island birds within similar environments (data from Carlquist, 1965). 1, Christmas; 2, Bawean; 3, Engano; 4, Savu; 5, Simalur; 6, Alors; 7, Wetar; 8, Nias; 9, Lombok; 10, Bali; 11, Billiton; 12, Mentawei; 13, Flores; 14, Sumbawa; 15, Sumba; 16, Bangka; 17, Timor; 18, Java; 19, Celebes; 20, Philippines; 21, Sumatra; 22, Borneo; 23, New Guinea.

successful groups away from the tropics into regions of lower diversity (as implied, for example, in the arguments of Matthew, 1915; Ekman, 1953, p. 18; Briggs, 1966, 1967; Stehli, 1968; MacArthur, 1969, and others).

Coral genera and species and their associates of the peripheral regions also thrive in the central areas. They have not left the central areas. These are simply the taxa with broad environmental tolerances and dispersal facilities adequate to enable them to occupy most of a province rather than their being restricted to refugia of minimal stress.

Thus, I favor an ecological over a genetical explanation of the relatively high diversity of more tropical as compared with less tropical biotas, in agreement with a conclusion reached by Mayr (1969) for distribution of birds.

In short, it appears probable that organisms of more tropical climates, with their narrow specificity of adaptations, infrequently invade and adapt to less tropical conditions of heightened stress and develop adaptations

that necessarily are more generalized, such as the ability to survive in the broader spectrum of conditions of more seasonal climates.

Quite likely, larval dispersal has been random in direction if not in frequency (fig. 15), as suggested in Ladd's (1960) thought that the atolls have been favorable sites for the development of new genotypes in isolated small populations. Frequently cited ecological heterogeneity of the central areas, from the standpoint of the reef biota, is more apparent than real, and in any case, ecological variety does not provide the kind of geographic separation required by the theory of allopatric speciation.

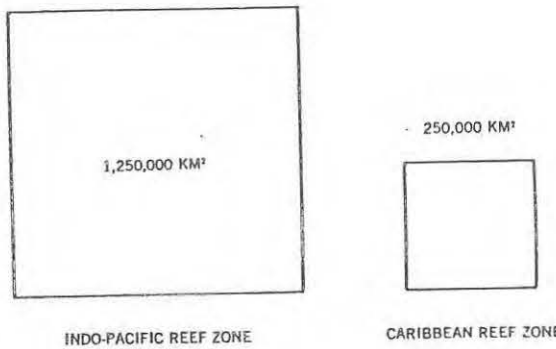


FIG. 13. Comparative areas of occupancy of coral reefs in the Indo-Pacific and Caribbean provinces. Actual areas of living reefs are less, possibly one-tenth the indicated areas.

The evidence is compatible with a conclusion that the high generic diversity of reef biota of the Australasian and Caribbean areas is mainly an effect of the accumulation of relicts and low extinction rates as compared with the peripheral areas. The many "living fossils" of these and contiguous areas (e.g., limulids, *Nautilus*, and *Neotrigonia*) are testimony to the importance of ecological factors in the present shrunken distribution of their biotas.

SUMMARY

The organisms of tropical coral reefs have achieved the highest level of community integration and stability. Stages in the evolutionary history of reef organization are recorded in a long and distinguished fossil record that reaches in time far back into the Precambrian, thus antedating other well-defined ecosystems for which there are direct records. By mid-Ordovician time small reef patches were being built by a coral-algal

association. The outline of subsequent history of reefs involves two iterative stages: (1) colonization and evolution more or less within habitat, each community eventually achieving marked stability; and (2) revolutionary world episodes of loss of homeostasis, selective extinction and organization of new, significantly different reef communities that appeared in the fossil record after long time intervals without known reefs.

An algal-coral-stromatoporoid association including a great diversity of commensal shelled invertebrates can be traced in ancestor-descendant sequence through some 140 million years of the early and middle Paleozoic (Chazyan-Frasnian).

This community was eliminated in latest Devonian time probably by an unfavorable climatic episode, and earliest Lower Carboniferous strata lack reef communities. When a reef community reappeared later in the Lower Carboniferous, it had a strikingly new composition marked by absence of stromatoporoids and subordinate role of corals. The reefs were built largely of skeletal detritus of crinoids and brachiopods trapped and consolidated in biohermal mounds by algae and bryozoans. In the Upper Carboniferous (Pennsylvanian) and Permian, chambered calcareous sponges (Sphinctozoa) and cemented and spiny brachiopods joined the community to produce some of the greatest reef structures of the Paleozoic. This widely distributed community for a time disappeared near the close of the Permian Period.

Examples of organic reefs and reef communities are unknown anywhere in rocks of early Triassic age. The Scleractinia, dominant corals of modern reefs, made their first appearance in the Middle Triassic, gradually replacing sphinctozoan stragglers in Upper Triassic reefs. By Jurassic time, the lithothamnion-scleractinian community was well established.

The ecological role of the scleractinian reef corals was challenged during the Cretaceous Period by an aberrant and enterprising order of bivalve molluscs, the rudists, which underwent an extraordinary radiation and produced many hermatypic entrepreneurs. This community, highly successful and widespread until the very end of the Cretaceous, collapsed in sweeping extinctions, and the succeeding epoch, the Paleocene, was without a recognized reef community.

This episode of extinction coincides with a major biological revolution over the world probably stemming immediately from climatic deterioration and ultimately from draining of the epicontinental seas.

Lithothamnion-scleractinian reef organisms underwent a second major radiation during the Eocene, and subsequent history has been one of waning and waxing of the reef community in harmony with oscillations of world climates.

From the Mesozoic Era until the present, changes in the diversity and distribution of reef organisms have sensitively reflected world trends in physical environments: restriction of the epicontinental seas, shrinkage of the tropical belt, differentiation and increasing seasonality of climate. In addition, major diastrophic events of the later Cenozoic, connected with sea-floor spreading and the thrust of the southern continents against the northern continents, caused sweeping changes in oceanic circulation patterns. These geographic and climatic changes further interrupted the circumtropical continuity of the marine biota, broken in the Western Hemisphere even before the late Mesozoic by intervening land barriers and the deep eastern Pacific.

From the mid-Miocene to the present there has been a universal shrinking in range of the tropical neritic and reef biotas, both of which have tended to become segregated into geographically separated refugia over the shallow shelves of the western Pacific and the Caribbean. As these centers of diversity harbor many relict genera with originally much wider distributions, the present centers of high diversity should be regarded as havens rather than principal source areas of dispersal. They harbor relict biotas somewhat remindful of the great tropical forests of the world. Generic diversity gradients among living corals reflect present extensive areas of favorable habitat and minimal climatic stress (seasonality).

Uplift of the isthmian link between the Americas, beginning in the latest Miocene and completed in the Pliocene, segregated a fringe Panamic subprovince from the Caribbean area and subsequent isolation has resulted in considerable specific divergence. Generic differentiation between these and other areas, however, results mainly from differential and selective extinctions of genera and the slow spread of Indo-Pacific elements into the Panamic subprovince.

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