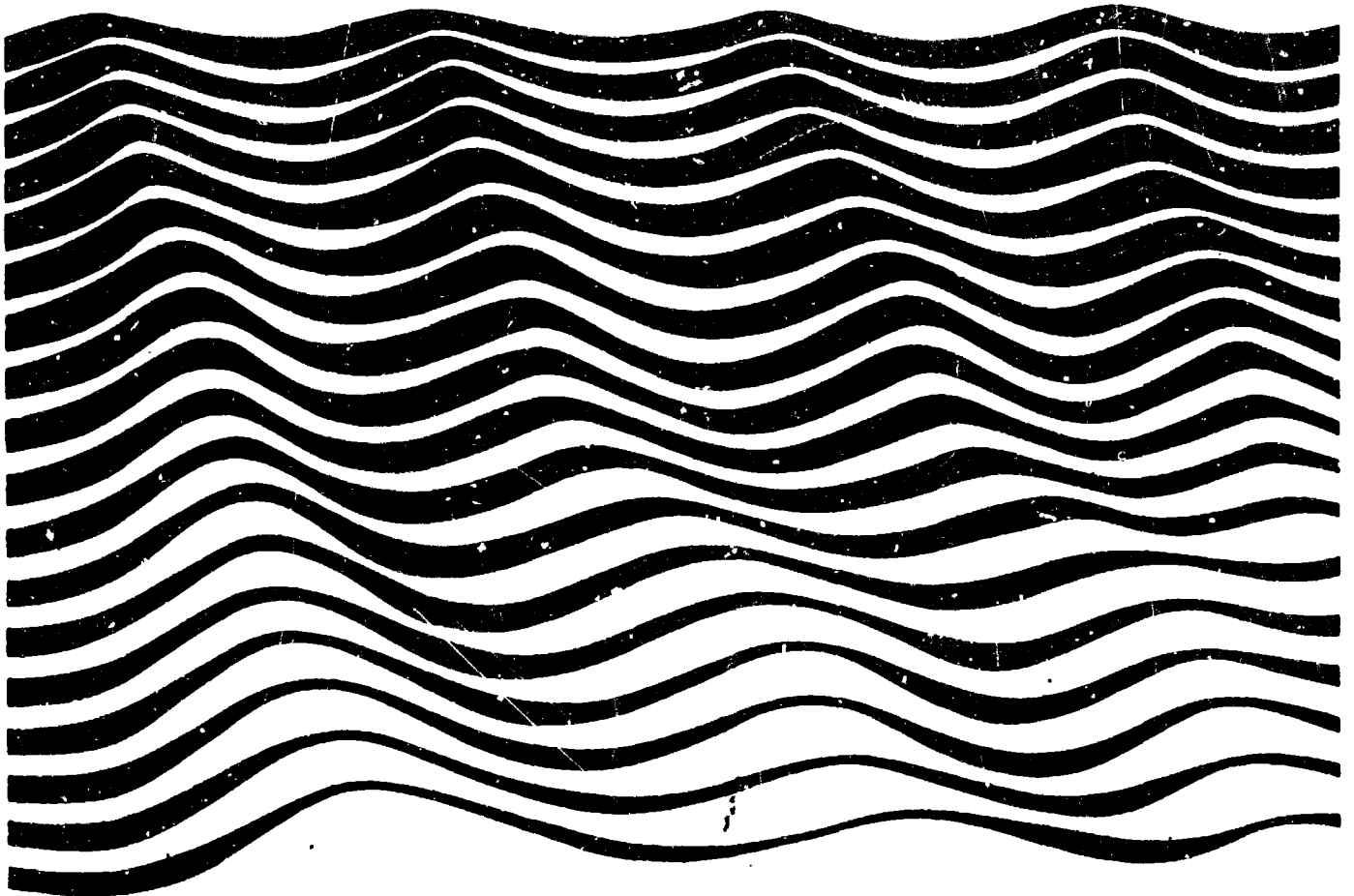


Caribbean coastal marine productivity

Results of a Planning
Workshop at Discovery Bay Marine
Laboratory
University of the West Indies
Jamaica, November, 1985



Unesco, 1986

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22 Guidelines for marine biological reference collections Prepared in response to a recommendation by a meeting of experts from the Mediterranean Arab countries Available in English, French and Arabic	1983	39 Development of marine sciences in Arab Universities Meeting of Experts held at the Marine Science Station Agaba, Jordan 1-5 December 1985 Available in Arabic, English, French	1986
23 Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean Report of a workshop held at West Indies Laboratory, St. Croix, U.S. Virgin Islands, May, 1982 English only	1983		

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Edited by:

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Elizabeth H. Gladfelter

with the editorial assistance of the
CARICOMP Steering Committee

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PREFACE

Unesco Reports in Marine Science are designed to serve specific programme needs and to report on developments in projects conducted by the Unesco Division of Marine Sciences, including those involving collaboration between the Division and the Intergovernmental Oceanographic Commission.

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ABSTRACT

The present document contains the results of a planning workshop held at Discovery Bay Marine Laboratory, University of the West Indies, Jamaica, in November 1985. This workshop, sponsored by Unesco and the National Science Foundation (USA), was an activity organized within the framework of Caribbean Coastal Marine Productivity (CARICOMP), a multinational and multidisciplinary approach to research, training, and management in a tropical regional sea environment.

Discussions, during the workshop, focused on factors influencing biological productivity in the Caribbean coastal zone, and resulted in a framework for the development of a regional research programme to investigate this subject.

RESUME

Le présent document contient les résultats d'un atelier de planification qui s'est tenu en novembre 1985, au Discovery Bay Marine Laboratory de l'University of the West Indies (Jamaïque). Organisé sous l'égide de l'Unesco et de la National Science Foundation (Etats-Unis), il constituait une des activités du projet CARICOMP (productivité des eaux côtières de la mer des Caraïbes), qui est fondé sur une approche multinationale et multidisciplinaire de la recherche, de la formation et de la gestion concernant une mer régionale des Tropiques.

Les participants ont essentiellement examiné les facteurs qui influent sur la productivité biologique de la zone côtière des Caraïbes et ont ainsi élaboré un cadre pour la mise au point d'un programme régional de recherche sur cette question.

RESUMEN

El presente documento contiene los resultados de un seminario de planificación celebrado en el Laboratorio Marino de Discovery Bay, University of the West Indies, Jamaica, en noviembre de 1985. El seminario, patrocinado por la Unesco y por la National Science Foundation (Estados Unidos) se organizó en el marco del proyecto de Productividad Marina Costera del Caribe (CARICOMP), iniciativa multinacional y multidisciplinaria de investigación, formación y gestión en un medio marino regional tropical.

Los debates celebrados durante el seminario se centraron en los factores que influyen en la productividad biológica en la zona costera del Caribe y crearon el marco para el desarrollo de un programa regional de investigación sobre el tema.

РЕЗЮМЕ

Настоящий документ содержит результаты учебно-практического семинара по планированию, состоявшегося в Морской лаборатории залива Дисковери, Вест-Индский университет, Ямайка, в ноябре 1985 г. Этот учебно-практический семинар, проведенный при финансовом участии ЮНЕСКО и Национального научного фонда (США), явился мероприятием, организованным в рамках Прибрежной морской продуктивности Карибского бассейна (КАРИКОМП), с обеспечением многонационального и междисциплинарного подхода к исследованиям, подготовке кадров и управлению в тропической региональной морской окружающей среде.

В ходе учебно-практического семинара обсуждения были сосредоточены на факторах, воздействующих на биологическую продуктивность в карибской прибрежной зоне, и послужили основанием для развития региональной научно-исследовательской программы по изучению этого вопроса.

خلاصة

تضم هذه الوثيقة نتائج حلقة العمل التخطيطية التي عقدت في مختبر ديسكوفري بي البحري، بجامعة جزر الهند الغربية، جامايكا، في نوفمبر/ تشرين الثاني ١٩٨٥. ونظمت هذه الحلقة تحت رعاية اليونسكو والمؤسسة الوطنية للعلوم (الولايات المتحدة الأمريكية، في إطار البرنامج الخاص بإنتاجية المياه البحرية الساحلية في منطقة الكاريبي (كاريكومب)، وهي تمثل نهجا مشتركا بين عدة أقطار وعدة تخصصات في مجالات البحث والتدريب والإدارة في بيئة بحرية مدارية.

وقد تركزت المناقشات، أثناء حلقة العمل، على العوامل المؤثرة في الانتاجية البيولوجية في المناطق الساحلية من البحر الكاريبي، وأسفرت عن مخطط لوضع برنامج بحوث اقليمي لاستقصاء هذا الموضوع.

摘 要

本文件系1985年11月在牙买加西印度群岛大学迪斯卡弗里贝海洋实验室举行的一期规划讲习班的成果。由教科文组织和国家科学基金会(美国)主办的这个讲习班,是在“加勒比沿海地区海洋生产力(CARICOMP)”范围内组织的一项活动,旨在通过多国和跨学科的方法解决热带地区海洋环境的研究、培训和治理问题。

讲习班集中讨论了影响加勒比沿海地区生物生产力的各种因素,为制订一项目的在于这一问题进行调查研究的地区研究计划奠定了基础。

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FOREWORD

The rational utilization and management of coastal zone habitats and marine resources is a major challenge to modern, high energy consuming societies. Conflicting uses, over-exploitation of resources, and partial or total destruction of habitats, are urgent problems that confront managers and decision makers. The solutions to these problems are confounded by a lack of information about how different coastal marine ecosystems function, what interactions exist between different ecosystems, and how resistant individual and connected ecosystems are to perturbations.

CARICOMP is a pilot project of the COMAR Regional Project for Research and Training on Coastal Systems of Latin America and the Caribbean and their relations with the continental shelf (COSALC). COMAR, in turn, is a major interregional UNESCO project for research and training to the integrated management of coastal systems. The National Science Foundation (NSF), Division of International Programs has provided partial funding for planning of the pilot project.

The present document contains the results of the planning workshop held at Jamaica in November 1985. Discussions, during the workshop, focused on factors influencing biological productivity in the Caribbean coastal zone, and resulted in a framework for the development of a regional research programme to investigate this subject. It represents a multinational and multidisciplinary approach to research, training and management in a tropical regional sea environment.

BACKGROUND

During 3-9 November 1985 a research planning workshop, sponsored by UNESCO and the U. S. National Science Foundation (NSF), was held at the Discovery Bay Marine Laboratory of the University of the West Indies, Jamaica. A multinational, multidisciplinary group of 33 marine scientists was brought together to discuss: "Factors influencing organic productivity in the Caribbean marine coastal zone", and to draft a framework for the development of a regional research program to investigate this subject. A major goal of the program would be the participation and training of local scientists and technicians to increase the scientific expertise of the nations of the region.

The Workshop followed on the recommendations of a previous workshop on coral reef, seagrass, and mangrove interactions in the Caribbean, held in June 1982 at the West Indies Laboratory of Fairleigh Dickinson University, St. Croix, U. S. Virgin Islands¹.

The Workshop began with a series of short lectures on the first and second days designed to introduce the subject of organic productivity from different scientific approaches and within different ecosystems. The extended abstracts of these presentations may be found in Part VI of this report. In the evening of the first day, the Workshop participants divided into working groups. The remainder of the week consisted of working group discussions which generated the major working hypotheses, and writing sessions in which sections of the present document were drafted. Each day at least one plenary meeting was held to share ideas from the smaller working groups with the entire Workshop.

The Workshop participants, divided by working groups are listed below. Their addresses may be found in Part VII.

Physiology Working Group

Dr. Henry Blackburn	U. Aarhus, Denmark
Dr. Chris D'Elia	U. Maryland, USA
Dr. Elizabeth Gladfelter*	West Indies Lab, FDU, USA
Dr. Rosario Fraino Pannier	U. Central Venezuela
Dr. James Porter	U. Georgia, USA
Dr. Alina Szmant-Froelich	RSMAS, U. Miami, USA
Dr. William Wiebe	U. Georgia, USA
Dr. Susan Williams	West Indies Lab, NURP, USA

¹Ogden, J. C. and E. H. Gladfelter. 1983. Coral reefs, seagrass beds and mangroves: Their interaction in the coastal zones of the Caribbean. UNESCO Reports in Marine Science 23. 133p.

Ecology Working Group

Dr. Peter Bacon	UWI, Jamaica
Dr. Rolf Bak	NIOZ, Netherlands
Dr. Robert Carpenter	Smithsonian, NHM, USA
Dr. Jorge Cortes	CIMAR, Costa Rica
Dr. Jeremy Jackson	STRI, Panama/USA
Dr. Eric Jordan	UNAM, Mexico
Dr. Euna Moore	UWI, Barbados
Dr. John Ogden*	West Indies Lab, FDU, USA
Dr. Pablo Penchaszadeh	INTECMAR, USB, Venezuela
Dr. Jeremy Woodley	DBML, UWI, Jamaica

Systems Working Group

Dr. Idelisa Bonnelly de Calventi	UASD, Dominican Republic
Dr. Juan Gonzales	U. Puerto Rico, USA
Dr. Ivan Goodbody	UWI, Jamaica
Dr. Stephen Head	UWI, Jamaica
Dr. Dennis Hubbard	West Indies Lab, FDU, USA
Dr. Barry Jupp	UWI, Jamaica
Dr. Michael Kemp	U. Maryland, USA
Dr. Bjorn Kjerfve	U. South Carolina, USA
Dr. Victor Klemas	U. Delaware, USA
Dr. Sergio Martinez	CIP, Nicaragua
Dr. Peter McRoy	U. Alaska, USA
Dr. Eugene Ramcharan	IMA, Trinidad
Dr. Victor Scarabino	ROSTLAG/UNESCO, Uruguay
Dr. Marc Steyaert	UNESCO, France
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* Organizers

ACKNOWLEDGEMENTS

The organizers and the editors are grateful for the support of the UNESCO Division of Marine Sciences, especially Dr. Marc Steyaert. The U. S. National Science Foundation, Division of International Programs (Grant # INT 8418474) provided travel funds for U.S. participants in the Jamaica Workshop. We particularly thank Ms. Christine French of NSF. Dr. Jeremy Woodley, Dr. Brian Keller, Ms. Johnston and the staff of the Discovery Bay Marine Laboratory were ideal hosts. Finally, the organizers depended upon the cheerful assistance of the faculty and staff of West Indies Laboratory, especially Ms. Dorothy Rowe for her help in administrative tasks and in producing the final report.

SUMMARY

The Caribbean Coastal Marine Productivity (CARICOMP) project:

- 1. is a 5-year multinational cooperative investigation of comparative aspects of productivity in Caribbean coastal ecosystems;**
- 2. is a multidisciplinary investigation of ecological processes in mangrove forests, seagrass beds, and coral reefs throughout the Caribbean region;**
- 3. is a project which integrates basic scientific investigations, emphasizes training and scientific exchange, and aims to develop coastal management strategies for the Caribbean;**
- 4. is a regional network of marine laboratories and institutions addressing common scientific and management questions;**
- 5. aims to develop an understanding of the factors that influence biological productivity in the Caribbean coastal zone;**
- 6. serves as a mechanism to acquire a coherent scientific data set to be used for comparative analysis, hypothesis testing, and to develop rational management strategies;**
- 7. implements scientific training of personnel at Caribbean research sites, assists in the development of local research skills, and plays a role in the scientific education of Caribbean scientists.**

I. INTRODUCTION

During the next decade, the Caribbean region will undergo significant changes. Population is expected to increase and forest resources to decrease dramatically, while regional food and fish production has reached its maximum level or is already over-exploited. Given the limitations of technology in many parts of the region, the Caribbean will continue to have an overall deficiency in food supply. In addition, increased urbanization and associated pollution are expected to reduce the overall quality of life in the region.

The dominant ecosystems in Caribbean coastal areas are mangrove forests, seagrass beds, and coral reefs. Generally, these ecosystems are among the most productive in the world. Each has evolved mechanisms to overcome the basic nutrient limitations of tropical seas. As the productivity of these ecosystems is the basis of the potential yield of shallow water marine resources in the Caribbean region, the goal of this research plan is to determine the factors most responsible for regulating the variability of organic productivity.

Further, the role of terrestrial influence on the productivity of coastal marine ecosystems is poorly understood. To elucidate the potential coupling between coastal development and productivity, along gradients of land influence, would enhance our ability to manage Caribbean coastal resources wisely. Thus, the scientific focus of this project deals with the linkages between the dominant ecosystems on one hand, and the role of terrestrial input on productivity and ecosystem responses, on the other hand.

Many Caribbean coastal ecosystems are already experiencing increased environmental stress. Mangroves are being cut down for lumber and agricultural/urban development; deforestation of hillsides and wetlands is causing sediment stress on reefs due to erosion of denuded land; and coastal fish stocks are becoming overfished. Governments throughout the region are aware of the need for conservation and restoration, but they lack sufficient understanding of how the coastal ecosystems work to develop sound management strategies.

The problem is complicated because diverse ecosystems in the coastal Caribbean often exist adjacent to each other, but we do not know to what extent they depend on each other or interact. For example, are coral reefs and seagrass beds functionally independent; what are the consequences of reducing or eliminating a mangrove forest; should mangroves and reefs be managed as separate, independent units? The CARICOMP project has been developed to acquire the information base and technical competence to give answers to questions of this nature.

II. GOALS

A. Scientific Goal

The goal of CARICOMP is to understand the factors influencing biological productivity in the Caribbean coastal zone in order to facilitate rational use and proper management of its living resources. Productivity, in this context, encompasses the nature and extent of development of the ecosystems within which primary and secondary production of organic resources occur.

We hypothesize that productivity of mangrove, seagrass, and coral reef ecosystems is influenced by 1) interactions between adjacent systems and 2) the nature and quantity of terrestrial runoff. Interactions and inputs vary widely throughout the Caribbean, and create large scale gradients which strongly affect the development of coastal ecosystems. The implementation of this program requires cooperation of investigators, laboratories, and governments, spanning the entire Caribbean region.

B. Training

Training and personnel exchange are emphasized as integral components of CARICOMP. The ultimate success of the project, on all levels, depends on local involvement throughout the Caribbean. Training and personnel exchange are necessary to assure the full and continued commitment and participation of local research scientists and institutions. These scientists, in turn, are committed to help train junior scientists and students as a part of their project involvement. Examples of this training might range from the direction of theses or dissertations to arrangement of local workshops, training sessions, and individual consultations.

CARICOMP provides a mechanism to help improve scientific and management expertise, especially in less developed countries. By providing funds and direction, employment and training of young scientists can be accomplished. The training and exchange of personnel are especially encouraged for small Caribbean island countries, to enable them to participate fully in the CARICOMP project. While benefiting this project directly, such training will also assure continuation of research and analysis capability for the future. One form of support might include regional scholarships for research study at the postgraduate level.

C. Scientific Information Exchange

Recognizing that recent, updated bibliographic materials are lacking in many Caribbean countries, a literature exchange system will be established for each activity within CARICOMP. In order to develop the CARICOMP project as rapidly as possible, several sub-projects have been authorized by the Steering Committee and funded by UNESCO.

One of these projects aims to develop an up-to-date reference list and bibliography pertaining to the three major coastal ecosystem types in the Caribbean. This project has two components. The first component is to compile a comprehensive reference list by utilizing computerized reference searches, reference lists of experts in the field, and requests to Caribbean researchers and laboratories. The reference lists will be published as a UNESCO Report in Marine Science. The second component is to assemble a set of reprints for each of the three Caribbean ecosystem types. These reprints will consist of approximately 30 key papers for each ecosystem type, primarily focused on the Caribbean. Once assembled, these papers will be made available to researchers and laboratories in the area.

D. Management

Planning for rational management of Caribbean coastal zone habitats is complicated by the presence of several quite different ecosystems and by the competing pressures for uses of a region. The CARICOMP project will increase our understanding of the mechanisms controlling the structure, function, regional variability, and interaction of these coastal marine ecosystems. This will provide a basis for linking the organic productivity potential of the ecosystem to the management of the resources.

An important goal for the CARICOMP project is to provide a scientific data base and rationale for management of mangrove, seagrass, and coral reef ecosystems. However, methods and mechanisms commonly used in coastal zone management decision-making to convert these data and allow economic cost/benefit analysis, have yet to be developed. Therefore, a permanent interaction between field researchers and resource managers must be guaranteed at each research site throughout the project domain. This will enable the reconciliation of demands for economic benefits from coastal areas with the principles of sustained management.

PROJECT STRATEGY

A. Main Hypotheses

This program consists of a series of investigations to be carried out at sites throughout the Caribbean. Although there is scope for a variety of different projects at each site, they are united by a common theme. They include a number of identical components for testing of specific scientific hypotheses. A few general working hypotheses serve to focus the project, and for each general working hypothesis, it is possible to formulate a series of testable scientific hypotheses. The first general working hypothesis can be stated:

- * The structure and productivity of Caribbean coastal marine ecosystems are influenced by the nature and magnitude of terrestrial input.

Potential adjacent ecosystems will modulate the effects of terrestrial or oceanic inputs on one another. This idea can be framed as a second general working hypothesis:

- * Where one ecosystem type is adjacent to another, the productivity and structural development of each will be obligately interdependent.

To a large extent, Caribbean nations are ultimately concerned with the secondary productivity of their ecosystems. This focus can be framed as a third general working hypothesis:

- * The secondary productivity of each coastal ecosystem will vary as a function of its structural development.

A common concern is that secondary productivity has been reduced as a consequence of natural or human disturbance to the coastal marine ecosystems or adjacent watersheds. This can be rephrased in a fourth general working hypothesis:

- * It is possible to predict how the structural development and secondary productivity of each ecosystem is altered by environmental changes.

B. Research Objectives

The CARICOMP project is designed to refine the general working hypotheses concerning the three major coastal ecosystems in the Caribbean. Because of regional diversity, it is necessary to examine numerous sites. The basic objective of the project is to undertake a comparison between different locations along gradients of latitude, climate, and watershed influence, and to examine the interactions that exist between mangrove, seagrass, and coral ecosystems. Caribbean marine research institutions are invited to participate by collecting a basic set of coordinated measurements at appropriate locations in their vicinity. They are also encouraged to develop other research programs within the framework of CARICOMP.

The basic research program at each site consists of a minimum set of structural and dynamic components. Minimum structural components include:

1. Site description and mapping of biotic communities, geomorphology, and bathymetry.
2. Biomass estimates of major ecosystem components and measurements of community composition and diversity.
3. Characterization of the means and variability of physiochemical factors at each site, including air and water temperatures, wind speed and direction, tide, turbidity, and levels of nutrients and suspended sediment in the water.

In addition, several dynamic components are to be examined for each ecosystem type and site, as follows:

1. Estimation of the system autotrophy and heterotrophy through measurements and determinations of P/R and net primary production.
2. Assessment of nutrient and organic matter fluxes, using differential upstream/downstream analysis, enclosed chambers, or another appropriate techniques.
3. Measurements of growth rates of at least one major organism within each of the three ecosystem types.
4. Continuous time series measurements of physiochemical variables, and recording of meteorological events.

It is possible that contemporary ecosystems exist in a perturbed state, with present terrestrial inputs and productivities different from those under which the ecosystem developed. For this reason, it would be useful to have some indication of growth rates of, for example, mangroves and principal coral species over a period of years. The Caribbean flora and fauna are relatively uniform and the species that dominate the three ecosystems tend to be similar throughout the region. This simplifies the comparison of growth rates at different sites.

Further, resource components will be analyzed as follows:

- assessment of quality and quantity of coastal and related offshore resources harvested at each site;
- investigation of the relationship of the harvested populations with one or several ecosystems;
- analysis of the harvesting techniques (modern versus traditional), seasonality, frequency, customs and regulations.

The specific details of the research plan will be formulated at a later time as one of the functions of the CARICOMP Steering Committee.

IV. PROJECT IMPLEMENTATION

A. Steering Committee

A CARICOMP steering committee was formed with the following terms of reference:

- To supervise and coordinate the project implementation;

- To assign particular work tasks to its members and establish working groups to meet the objectives of the program.
- To supervise the execution of specific research programs and advise, as necessary, towards maintaining the goals of the project;
- To coordinate the activities of the project with related ongoing national programs in the different participating countries;
- To evaluate progress and modify emphasis of activities as required for effective achievement of the fundamental objectives of the project.
- To coordinate project information exchange and dissemination of results.

The initial meeting of the Steering Committee was held at Discovery Bay Marine Laboratory, Jamaica, 3-9 November 1985, followed by a second meeting at the West Indies Laboratory, Fairleigh Dickinson University, Teague Bay, St. Croix, U. S. Virgin Islands, 20-23 May 1986. The following decisions were made:

Methods Manual: A Methods Committee was established to produce a Methods Manual for mapping and monitoring of biological and physical parameters at each study area. The Methods Committee is made up of persons with expertise in either one of the three ecosystem types or shallow-water oceanographic processes. The committee consists of Peter Bacon, Chairman (University of the West Indies, Jamaica; mangroves); Susan Williams (West Indies Laboratory, St. Croix; seagrasses); James Porter (University of Georgia; coral reefs); Björn Kjerfve (University of South Carolina; oceanography); and Jeremy Woodley (University of the West Indies, Jamaica; coral reefs).

Literature Updating and Exchange System: A current literature exchange system will be established for the project scientists. This will be accomplished by establishing a photocopy account at a central university library serving the region. Interlibrary loans and computerized literature searches will be available for regional scientists involved in the CARICOMP project. Photocopying and distribution to designated recipient institutions of data sets, manuals, and reference materials will be another element of the exchange system. Individuals involved in the CARICOMP project are encouraged to provide reprints and bibliographies that may contribute to the project goals. J. C. Zieman (University of Virginia) was designated by the Steering Committee to organize this Literature Updating and Exchange System, assisted by Rolf P. M. Bak (NIOZ, Netherlands) and Peter Bacon (UWI, Jamaica).

B. Study Area Network

Selection of Study Areas: CARICOMP research will be conducted throughout the Caribbean. The Steering Committee will invite participation from marine research institutions and individual scientists. It is expected that responses will be in the form of proposals. These should detail institutional capabilities, along with required funds, equipment, and/or training necessary before the institution meets the minimum requirements of the CARICOMP project. Institutions and individuals can submit proposals to be included within CARICOMP project activities. Institutions will be required to collect and contribute specified data for common use. This procedure will ensure wide participation in the project, and maximal geographic coverage.

Study Area Coordination: The Steering Committee will establish a Secretariat at one of the study sites to coordinate CARICOMP project research activities.

Data Analysis: Chief scientists will be placed in charge of each of the components of the research objectives listed in III B. It will be their responsibility to assume a leadership role in the analysis of data from all of the laboratories and sites. In addition, all data sets will be reviewed during annual meetings.

V. LOGISTICS

A. General Budget and Time Frame

The CARICOMP project is projected to last for 5 years and to have a budget of USD 5 million. A detailed budget and the specific logistics of the project are presently being formulated.

VI. EXTENDED ABSTRACTS OF GENERAL LECTURES

INTRODUCTION

Seven of the participating scientists presented short papers highlighting some important concepts to consider while formulating a research plan to assess "Factors influencing organic productivity in the coastal zone of the Caribbean." These presentations were given in three sessions: (1) Physiology, (2) Ecosystem Structure and Function, and (3) Physical Processes and Remote Sensing.

Dr. C. D'Elia began the first session by suggesting a classification scheme for Caribbean shallow water ecosystems based on different rates of allocthonous nutrient supply. Dr. J. Porter then followed with a discussion of "Patterns of productivity in tropical coastal zones," presented as a series of testable hypotheses.

The second session focused on ecosystem structure and function. In his paper on the Mangrove ecosystem, Dr. P. Bacon emphasized the rapid seral succession to climax and replacement readily observable in long-term ecological studies of these systems. Dr. J. Zieman illustrated the distinct and discernable patterns present in Seagrass ecosystems of the Caribbean, and he discussed the environmental factors which correlated most strongly with these patterns. Finally, Dr. R. Bak concluded this session with an analysis of the complexity of structure and function found in the Coral Reef ecosystem. He discussed the physical and biological factors most important in effecting the observed zonation patterns.

Dr. B. Kjerfve began the final session by emphasizing the importance of using correct temporal and spatial scales in taking measurements of physical and biological processes. Dr. V. Klemas concluded the formal talks by outlining the necessary field measurements to quantify remote sensing data.

The extended abstracts of these 7 papers follow:

GRADIENTS IN FACTORS LIMITING PRIMARY PRODUCTIVITY

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INTRODUCTION

The evaluation of gradients in productivity of Caribbean shallow water, coastal marine systems will inevitably lead to consideration of the role of nutrients. The following is a brief overview of important facets of nutrient-productivity relationships for coral reef, seagrass and mangrove communities; I will focus particularly on coral reefs with which I am most familiar. The aim in this report, is to provoke thought about the design and implementation of comparative nutrient-productivity studies for the Caribbean basin.

PRODUCTIVITY AND NUTRIENT REGIMES

Unlike most temperate shallow-water systems, Caribbean shallow-water systems are typically characterized by high levels of benthic, but not water-column productivity. Moreover, nutrient concentrations in offshore marine waters tend to be extremely low - often an order of magnitude less than in their temperate counterparts. The extremely low nutrient standing stocks severely limit the net productivity of the water column primary producers, so accordingly, phytoplankton biomass is low and water clarity is high. Table I presents a brief comparison of productivities and productivity-related features that are typically considered.

Despite the low concentrations of nutrients available to reef and seagrass communities, large amounts of nutrients may be conserved or supplied to them by a variety of mechanisms. For example, it is conventionally assumed that coral reefs are characterized by high rates of nitrogen fixation (Capone, 1983) and nutrient recycling (Johannes et al., 1972). Moreover, because the benthic communities are fixed in space relative to the water overlying them, advection of offshore sea water can supply the communities with large quantities of nutrients albeit at low concentrations. High advective supplies of nutrients at low concentrations favor the predominance of benthic productivity over water-column productivity.

There are undoubtedly differences in the prevailing nutrient regimes to which coral reefs, seagrass beds and mangroves are exposed. It thus may be possible to divide each type of Caribbean shallow water system into groups based on different rates of allochthonous nutrient supply. Such systems have not been classified with respect to prevailing nutrient regimes, although classification schemes based on other features have been developed (e.g. Lugo and Snedaker, 1974).

Differences in nutrient supply rates are an unknown, but represent a potentially important determinant of productivity. There have been few studies for any shallow-water marine tropical systems that attempt to construct the nutrient and energy budgets necessary to evaluate nutrient-productivity relationships. Table II lists major factors that determine the rate of allochthonous nutrient inputs to shallow water, benthic Caribbean systems and that should be taken into consideration in developing such budgets. While we might surmise that differences in allochthonous nutrient inputs substantially affect productivity of coral reefs and seagrasses, there are, in fact, no studies documenting differences in productivity between systems with different input. Clearly, such studies would be worthwhile.

EFFECT OF INCREASING NUTRIENT INPUTS

In temperate neritic systems, increases in nutrient loadings have generally been associated with increased water-column productivity. Although the species composition of the phytoplankton may change in response to nutrient enrichment, in general, the bulk of the primary production in the system is planktonic, and the system response to nutrient enrichment does not mean a drastic shift in the location of most primary production. On the other hand, increasing nutrient inputs to coral-reef and seagrass communities, which are dominated by benthic primary producers, may have much more noticeable effects on the location of primary productivity and on what organisms account for it. Nutrient-stressed coral-reef and seagrass communities have been shown to be dominated first by epiphytic microalgae, and then by increased numbers of planktonic producers (cf. Smith et al., 1981; Twilley et al., 1985). Relaxation of nutrient stress can have rapid effects on the recovery of these systems (Smith et al., 1981). More studies of benthic community response to gradients in nutrient input rates are needed to understand better the processes involved.

EVALUATING NUTRIENT METABOLISM AND BUDGETS

Most studies to date in shallow water, tropical ecosystems have focused on autecological measurement of nutrient exchange and productivity (e.g. D'Elia, 1977; Muscatine and D'Elia, 1978; Roffman, 1968), the identification and quantitation of specific processes in nutrient cycles (cf. Capone, 1983), or on Eulerian measurements at windward and leeward boundaries of benthic ecosystems (e.g. Webb et al., 1974; Rogers, 1979). Studies employing Lagrangian methods, those that follow changes in nutrient or oxygen concentration in given water masses, have seen less attention (Barnes, 1983). Likewise, few experimental studies have been done dealing with community response to nutrient enrichment (Kinsey and Domm, 1974) or relaxation of nutrient stress to entire systems. Research has begun to evaluate the coupling between different tropical marine systems (e.g. Ogden and Zieman, 1977; Meyer and Schultz, 1984), but much remains to be done. Processes such as denitrification have received much less attention than opposing processes such as nitrogen fixation (Seitzinger and D'Elia, 1985). There have been no comparative studies designed to assess gradients

in productivity in systems with different nutrient regimes using standardized techniques. Moreover, although studies on nutrient exchange and productivity have considered Caribbean systems, most studies of coral reefs have focused primarily on Pacific and not Caribbean systems.

CONCLUSIONS

A great deal more is known about the nutrient dynamics and productivity of shallow water, marine tropical ecosystems than was known even a decade ago. Large gaps in our knowledge still exist about community responses to gradients in nutrient input, particularly for coral reefs and seagrasses. Little is known about the coupling between coral reefs, seagrasses communities and mangroves, or about how these systems respond to nutrient stress. Virtually no comprehensive nutrient budgets exist for these systems. Comparative studies of ecosystem function in the Caribbean basin could help greatly in filling in the gaps in our knowledge.

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Feature	Relative Amount or Rate		
	Coral Reef	Sea Grass	Mangrove
Benthic Productivity			
Gross	High	Moderate-High	High
Net	Low	Moderate	High
Water Column Productivity			
Gross	Low	Low	Variable
Net	Low	Low	Variable
Biomass	Moderate	Moderate-High	High
Optimal Nutrient			
Concentration	Low	Low	Variable
Inputs	Low-moderate	Low-moderate	Moderate-high
Recycling	High	Moderate	Low
Resistance to Overenrichment	Low	Moderate	High
Water Clarity	High	High	Variable

Table II. Factors that determine the rates of nutrient inputs to shallow water, benthic Caribbean systems.

Factors Promoting Low Allochthonous Nutrient Inputs

Proximity to Low Islands
Proximity to Dry Islands
Low Advection of Sea Water

Factors Promoting High Allochthonous Nutrient Inputs

Proximity to High Islands
Proximity to Wet Islands
High Groundwater Inputs
High Riverine Inputs
High Anthropogenic Inputs
High Advection of Sea Water
Proximity to Upwelling of Nutrient-Rich Water

PATTERNS OF PRIMARY PRODUCTIVITY IN TROPICAL COASTAL ZONES

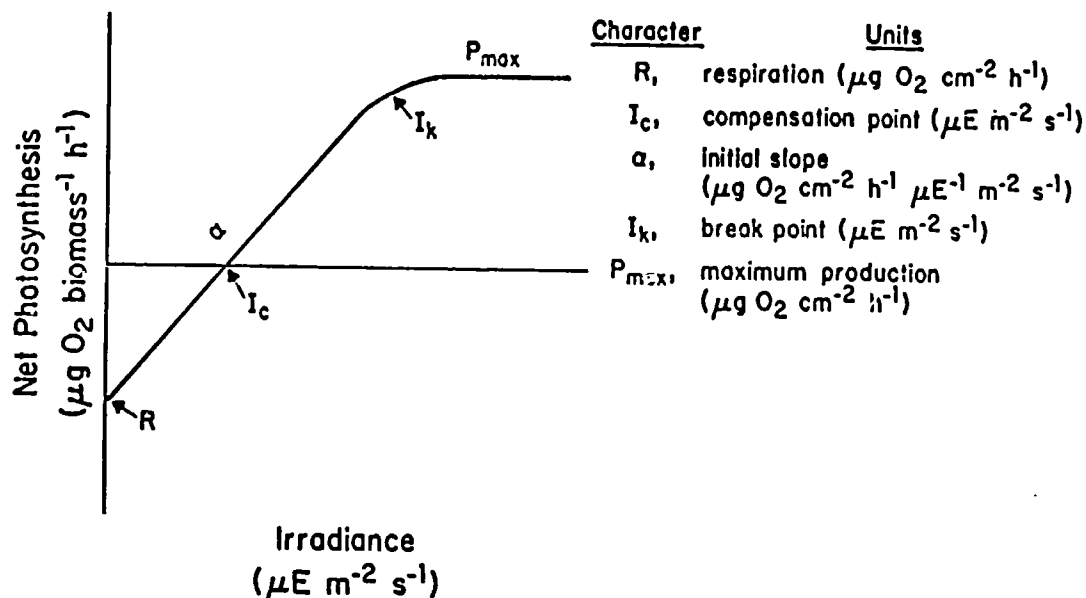
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INTRODUCTION

Sensitive measures of primary productivity have allowed us to quantify patterns of production on reefs and to understand the biological and physical controls influencing productivity rates and totals. In this extended abstract, I will (1) present a brief description of one approach to elucidating productivity patterns and processes, (2) outline some of the primary relationships between production and (a) depth, (b) shade, (c) pollution, (d) herbivorous grazing and (e) allelochemical defenses and (3) list testable hypotheses that would address some of the major themes of this workshop, mainly, factors regulating productivity in tropical near-shore environments.

Testable hypotheses presuppose enough observational and preliminary quantitative work to be able to ask interesting questions. With recent rapid advances in the quantification of reef production (Lewis, 1977; Kinsey, 1977; Porter, 1980; Muscatine, 1980; and Carpenter, 1985a) we are in the phase where good questions can be rigorously posed. Using the hyperbolic tangent function to mathematically define the relationship between production and irradiance, this generalized P vs. I curve (Fig. 1) can be used to observe changes in independent

P:I Curve



characteristics such as respiration rate (r), the initial slope (α) the light compensation point (I_c), the half saturation point (I_k), or the maximum production rate (P_{max}). These quantities have metric units as listed (Fig. 1) and utilize any appropriate biomass unit (surface area or chlorophyll a content, for example). They can be compared statistically for what they might reveal regarding an experimental manipulation or growth situation.

PATTERNS IN PRODUCTIVITY

Studies on the relationship between production and light reduction caused by depth for both reef corals and algae reveal highly predictable patterns. With increasing depth, chlorophyll a content per zooxanthellae or per surface area rises, with the effect that sensitivity to low light (α) also rises. Concomitantly, P_{max} , I_c , I_k , and respiration fall. These trends are significant regardless of the normalizing biomass unit used (Porter et al., 1986). The ecological effect of these complimentary modifications is to keep productivity high even in deep water. For instance, while there is a 93% drop in integrated surface irradiance, from $28.42 \text{ E m}^{-2} \text{ d}^{-1}$ at 1 m to $2.04 \text{ E m}^{-2} \text{ d}^{-1}$ at 50 m, gross production in *Montastrea annularis* drops by only 66% from $1,025 \text{ g C m}^{-2} \text{ y}^{-1}$ at 1 m to $293 \text{ g C m}^{-2} \text{ y}^{-1}$ at 50 m (Porter, 1985).

These observations suggest several testable hypotheses:

- H⁰ Through photoadaptation, production will not correlate well with irradiance over depth for any of the major photosynthetic reef organisms.
- H⁰ Due to their existence for most of the day in the light-saturated (P_{max}) portion of the P:I curve, and conversely due to their existence throughout most of the day in the light-limited (α) portion of the P:I curve, shallow water photosynthetic organisms are nutrient-limited, whereas deep water ones are light-limited.
- H⁰ Unlike most deep water temperate environments, deep water tropical marine environments can contribute substantially to local productivity.
- H⁰ Respiration decreases with depth, possibly as a result of lower nutritional contributions from photosynthesis.

Productivity patterns in response to light reduction due to shading rather than depth are similar if calculated on the basis of surface area, but different if calculated on the basis of chlorophyll a content (Porter et al., 1984; Muscatine et al., 1984; McGloskey and Muscatine, 1984; Porter et al., 1986). When the photosynthetic characteristics of the P:I curve are calculated on the basis of chlorophyll a, α is actually lower in shade-adapted corals, i.e. shade-adapted colonies are less sensitive to low light. The reason for this is probably self-shading of densely packed chlorophyll molecules (Dubinsky et al., 1984).

The alternative explanations for adaptation to low light are (1) chlorophyll a pigment increase per cell or (2) accessory photosynthetic pigment increases per cell. Corals appear to do both.

H⁰ Photoadaptation to light reduction due to depth or shade involves different mechanisms based in part on whether or not a spectral shift accompanies the irradiance reduction.

In examining oxygen flux patterns of corals growing on a control reef upstream from a sewage outfall pipe in St. Croix, we noticed that 10 m specimens of the brain coral Meandrina meandrites from the outfall had all of the photosynthetic and respiratory characteristics of specimens of this same species growing at 20 m.

H⁰ Due to the accompanying turbidity increase and its effect on photosynthesis, organic pollution may be more destructive to tropical nearshore communities than to temperate communities.

By using algal fouling plates grown at one depth and subjected to different kinds and intensities of grazing (Carpenter, 1985a and 1985b) or by using fouling plates grown at different depths between the surface and 40 m subjected to natural variation in depth-related grazing intensity (Adey and Steneck, 1985; Porter et al., unpublished), several trends on the causal relationship between grazing and primary production (Ogden, 1976) have become clear. As grazing intensity increases, the productivity per unit area drops due to the removal of algae. The productivity per plant biomass, however is highest under natural levels of grazing. Several hypotheses can be advanced to explain this:

- H⁰
- a) By removing scenscent plant material, grazing stimulates algal production.
 - b) By removing algae with low Production/Biomass ratios, grazing stimulates algal production.
 - c) By nutrient regeneration, grazing stimulates algal production.

Finally, in an exciting new area of research, Dr. Nancy Targett (Univ. of Delaware) and I have observed that plating corals in the genus Agaricia sitting next to sponges of the genus Plakortis have increased respiration rates and lowered production rates relative to corals not in association with sponges. Lowering of the P/R ratio can also be accomplished by exposing corals to Plakortis mucus. These sponges are extremely common; this leads to a potentially startling possibility:

H⁰ Through its effect on zooxanthellae viability and coral tissue respiration, sponge exudates may significantly reduce coral ecosystem productivity below 10 m.

SUMMARY

Recent advances in conceptualizing controls over coral reef ecosystem function and advances in the ease and accuracy of measuring productivity have poised coral reef scientists for rapid and significant advance in understanding the mechanisms and controls over patterns of productivity in ecological time.

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MANGROVE ECOSYSTEM RESPONSES TO GRADIENTS IN FACTORS LIMITING PRIMARY PRODUCTIVITY IN THE CARIBBEAN

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INTRODUCTION

The opportunistic nature of mangrove colonisation results in the development of mangrove communities (mangals) in a wide range of coastal systems. Basically, wherever sheltered, low energy conditions exist on mainland or insular Caribbean coastlines these permit the settlement and germination of propagules. Thus, mangals may occur round bays, behind protective reef or sand barriers, in estuaries and in lagoons. The further development of a mangal will be determined by the physical conditions existing at the site; so that variations in geomorphology and hydrodynamics are fundamental to understanding mangrove productivity - particularly as these effect nutrient supply to the plants. A certain amount of nitrogen fixation occurs in mangals, but they are dependent largely on external sources of nutrients, other than carbon.

Different types of mangroves are recognised, and related also to site location characteristics, and show a gradient of productivity from highest levels in Riverine Mangals (more properly "estuarine") with good supply of land-derived nutrients, to low productivity in Dwarf Mangals which are generally isolated from sediment supply and tidal flushing. Within these types, different mangrove species show differential productivity, with Rhizophora > Avicennia > Laguncularia. Species composition of the stand will determine overall primary productivity. Species composition is a function of colonisation history, substratum type and maturity of the mangal. In a well developed mangrove stand there is frequently a distinct zonation of species, with the Rhizophora zone more productive than the Avicennia zone which is in turn more productive than the Laguncularia zone or mixed landward zone. The NPP in a mangal will be found to vary from zone to zone and with the degree of development of each zone. Furthermore, the position of a stand or a zone within an estuary may affect productivity, with optimum levels in the middle of the estuary.

Mangals, like other wetland systems, evolve and change their structure and functions over time. This is perhaps a significant difference from seagrass and coral reef systems, which do not show such obvious seral succession to climax and replacement. Immature, mature and senile mangals can be expected to show gradients of primary productivity. Similarly, some of the littoral environments in which mangroves occur are evolving rapidly, so that conditions regulating mangrove productivity will show a time series related to the stage of development. Evolving lagoon structures on the dynamic south coast

of Jamaica exhibit differentially productive mangrove communities, with aging of the lagoon - salt pond - salina sequence leading to reduced productivity and, presumably, greater reliance on in situ nutrient generation.

In summary, the rate of primary production of mangals is dependent on their site and stage of development. These must be taken into account when searching for gradients in limiting factors. Consider a series of mangrove areas on the Jamaican coast (Fig. 1); all are expected to exhibit different degrees of primary productivity, as well as other characteristics.

LIMITING FACTORS FOR PRIMARY PRODUCTION

Analysing these gross differences of site and maturity results in a list of limiting factors for primary production, such as that shown in Table I. Included are physical, biological and natural stress factors, plus human influences on most areas of the Caribbean coastlines. The wide regional distribution of the same few mangrove plant species suggests that latitudinal and gross geographical effects should be superimposed over local geomorphologically regulated situations. If a comparison were made between Jamaica and Trinidad, for example, higher NPP would be expected in Trinidad - which is at lower latitudes, with higher rainfall, greater tidal range and high ambient water nutrient levels due to that island's situation relative to continental drainage. However, it is probable that, although some stands of mangroves are more productive per se in Trinidad, regional differences are obscured by marked local differences in the sites of mangal development. Figure 2 shows that, as in Jamaica, Trinidad has highly productive estuarine, and dwarf mangrove communities. Comparisons made between mangrove forest structure in Florida, Mexico, Costa Rica and Puerto Rico (Pool, Snedaker & Lugo, 1977) showed more marked differences between north and south coast Puerto Rican sites than latitudinal differences. In Puerto Rico the marked differences in productivity were related to rainfall and land-derived nutrient effects. The nature of the site of mangal development, particularly the type of associated water bodies and hydrodynamic characteristics, will determine the nature and degree of development of associated benthic and plankton algae. The ratio of mangrove forest to channel area determines the relative contributions of mangrove and algal species to the total NPP of a mangal.

Regionally, mangroves are best developed in environments not conducive to seagrass or coral growth. Mangrove dependence on these communities would appear to be minimal therefore. In these typically fluviatile, deltaic and lagoonal situations associated flora and fauna are euryhaline, whether permanent residents or migratory species. Species using mangals for nursery are typically those of nearby coastal waters, such as peneids, rather than distant reef inhabitants. The rhizophore fauna may be of typically estuarine species, including some found only in mangrove environments. Away from sources of terrestrial run-off, where mangroves grow under more marine conditions, the fauna contains an increasing number of species common to seagrass beds and

reefal habitats. There is more likelihood of interchanges of larvae and adults between systems the more similar the environmental conditions become. Identified interactions include transfers of nutrients by organisms moving between these ecosystems, largely from mangroves to the other communities. However, when growing away from terrestrial nutrient inputs, mangroves require a supply of nutrients from sources other than the seawater itself, and it is possible that faunal interchanges between coral reefs, seagrass beds and mangroves are important in this regard. Even within a mangal, the role of the resident fauna in nutrient exchanges which support mangrove production is not well understood.

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Table I. Factors Controlling Mangrove Productivity
(After Odum et al., 1982)

Water Chemistry	Species composition of the stand
Depth of the substratum	Age of the stand
Substratum type	Presence of competing species
Nutrient content of substrate	Degree of herbivory
Nutrient content of overlying water	Presence of disease or parasites
Salinity of the soil	Presence of roosting or nesting birds
Transport efficiency of oxygen root system	Periodicity of severe stress to (fire, hurricanes, etc.)
Amount of tidal flushing	Time since last severe stress
Relative wave energy	Inputs of toxic compounds or nutrients from human activities.
Characteristics of ground water	Human influences by ditching, dyking.

Figure 1. Influence of site location on mangrove community types on the south coast of Jamaica

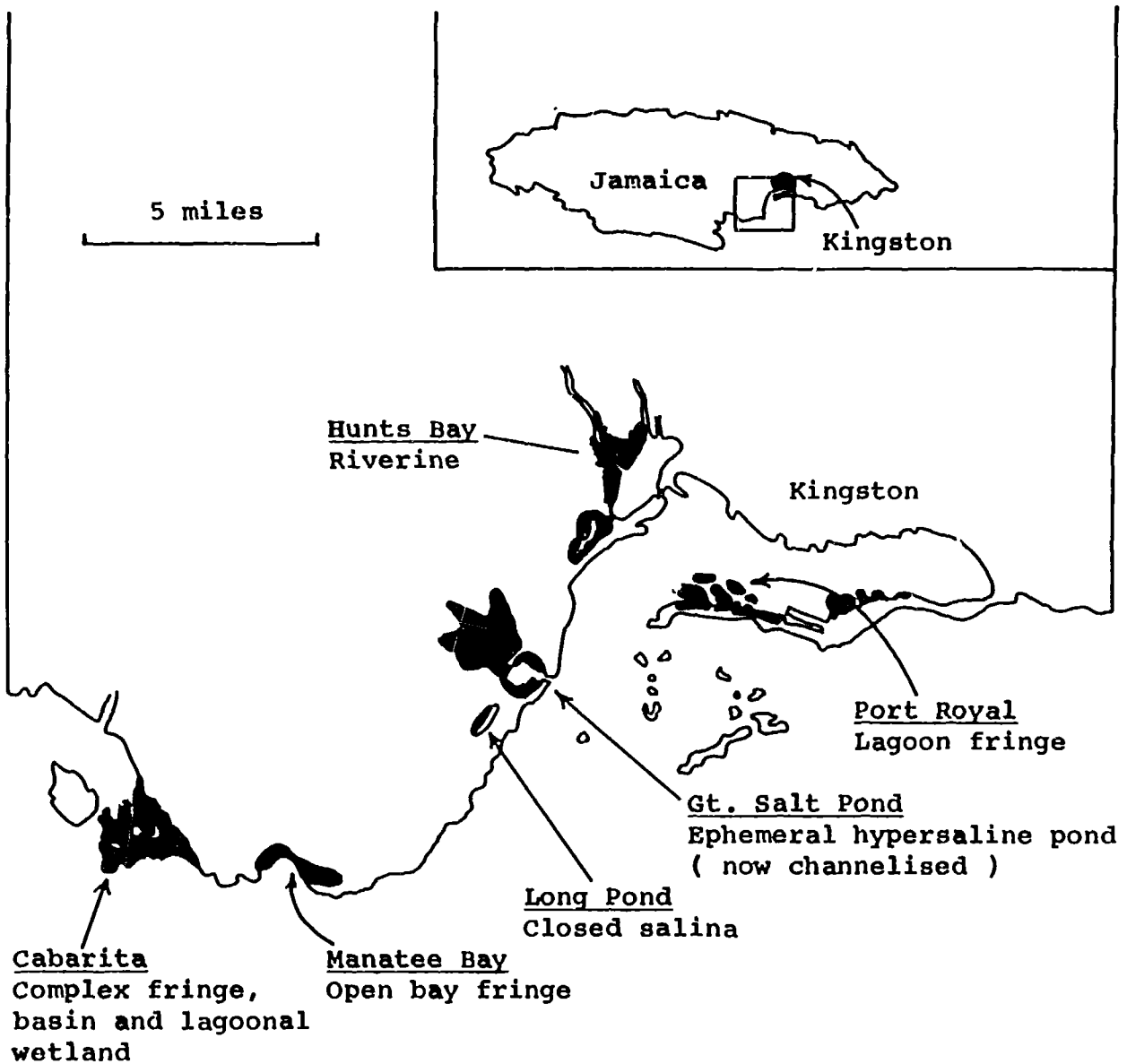
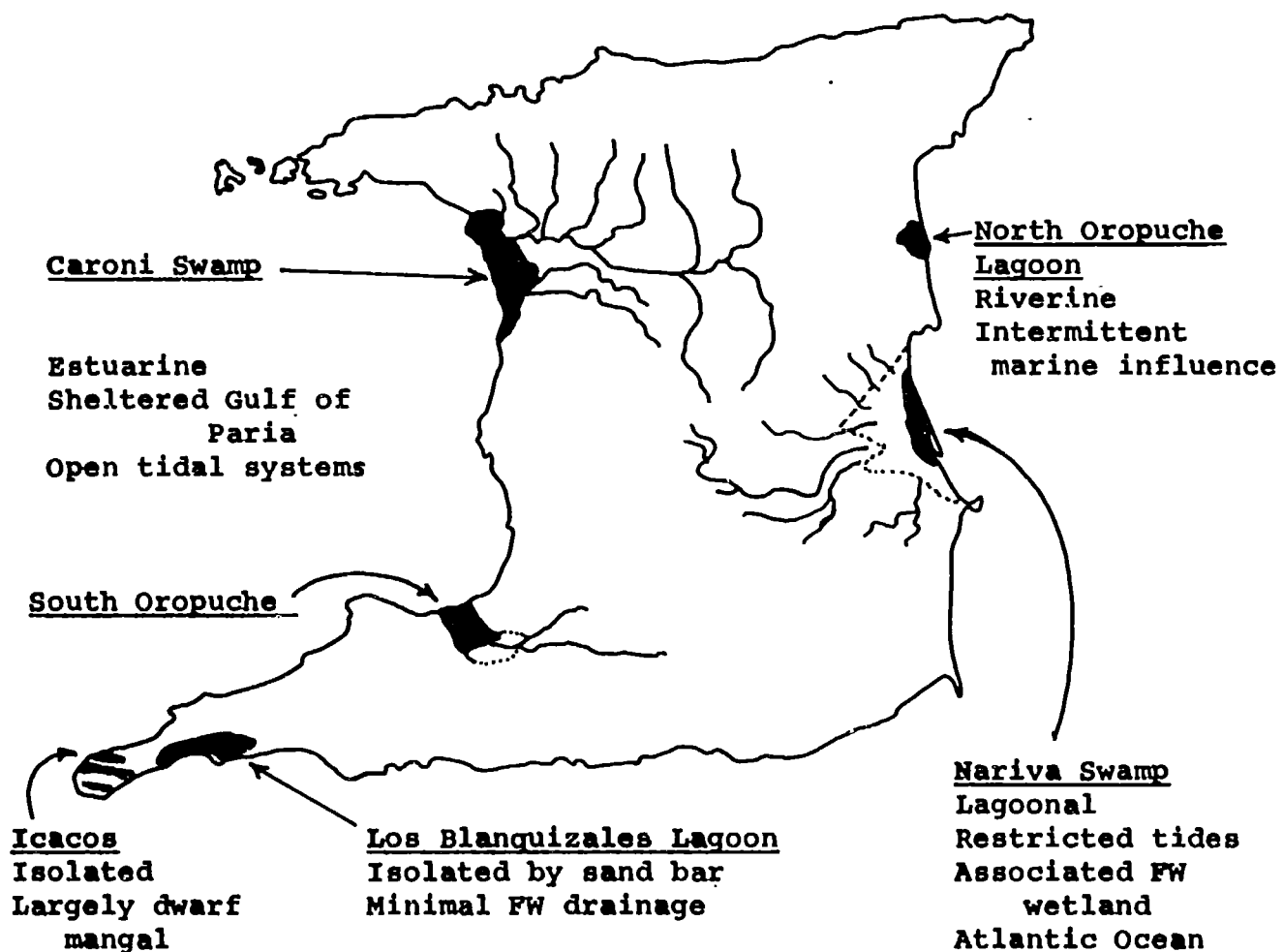


Figure 2. The range of mangal types in Trinidad



GRADIENTS IN CARIBBEAN SEAGRASS ECOSYSTEMS

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INTRODUCTION

Seagrass meadows are highly productive, faunally rich and ecologically important habitats found throughout the shallow coastal waters, estuaries, and coastal lagoons of the tropics. The complex structure of the meadow represents living space and protection from predation for large populations of invertebrates and fishes. The leaves, stems and rhizomes of the seagrass plants and associated macro- and micro-flora yield diverse microhabitats which support grazing and detrital food webs. The combination of plentiful shelter and food results in seagrass meadows being among the richest nursery and feeding grounds in shallow tropical waters. In addition, many species within mangrove, coral reef and continental shelf communities are linked with seagrass beds. Often these species are of commercial and sport fisheries importance or of significant ecological importance.

THE FUNCTION OF SEAGRASS ECOSYSTEMS

Seagrasses perform a variety of diverse and necessary functions in the shallow marine waters as a result of their physiology and morphology and the way they interact with the physical as well as biological environment. Ronald C. Phillips stated that "...by their presence on a landscape of relatively uniform relief, seagrasses create a diversity of habitats and substrates, providing a structured habitat from a structureless one." Because of their roots and rhizomes, the seagrasses have the ability to modify their environment to an extent not equalled by any other fully submerged organism. The resulting community is enhanced in productivity, environmental stability and shelter to a degree not possible without these plants. These functions of seagrass systems are summarized:

High Production and Growth

- 1) The ability of seagrasses to exert a major influence on the marine seascape is due in large part to their extremely rapid growth and high net productivity. The leaves grow at rates typically 5 mm per day, but growth rates of over 10 mm per day are not uncommon under favorable circumstances.

2) Food and Feeding Pathways

The photosynthetically fixed energy from the seagrasses may follow any of three general pathways: direct grazing of

organisms on the living plant material, utilization of detritus from decaying seagrass material, primarily leaves, and the export of seagrass material, both living and detrital to a location some distance from the seagrass bed.

3) Shelter

Seagrass beds serve as a nursery ground, that is a place of both food and shelter, for the juveniles of a variety of finfish and shellfish of commercial and sportfishing importance.

4) Habitat Stabilization

Seagrasses stabilize the sediments in two ways: the leaves slow and retard current flow to reduce water velocity near the sediment-water interface, which promotes sedimentation of particles as well as inhibiting resuspension of both organic and inorganic material. The roots and rhizomes form a complex, interlocking matrix with which to bond the sediment and retard erosion.

5) Nutrient Effects

The production of detritus and the promotion of sedimentation by the leaves of seagrasses provide organic matter for the sediments and maintain an active environment for nutrient recycling. Epiphytic algae on the leaves of seagrasses have been shown to fix nitrogen, thus adding to the nutrient pool of the region. In addition, seagrasses have been shown to pick up nutrients from the sediments, transporting them through the plant and releasing the nutrients into the water column through the leaves, thus acting as a nutrient pump from the sediment.

The greatest development of seagrass systems is found in less than 5 m of water although well-formed beds occur to cover 10 m and seagrasses have been recorded in the Caribbean to 42 m. The principal factors determining distribution in deep waters are light and pressure, while exposure and dessication are limiting in shallow waters.

In the Caribbean and Atlantic regions, the diversity of the seagrasses is relatively low and the species show distinct and discernable zonation patterns. These patterns are definitely not repeatable at all localities, but are broadly reproducible. The following would be a typical gradient observed throughout clear waters in south Florida and the Caribbean. In turbid water areas the same pattern would be expected, but the ranges of the various species would be attenuated.

Halodule is generally found in the shallowest water. It appears to be more tolerant of exposure than the other species, and the

relatively high flexibility of its leaves allow it to conform to the damp sediment surface during periods of exposure, thus minimizing the leaf surfaces available for dessication. Thalassia is found in waters nearly as shallow as Halodule. The shallowest Thalassia flats are commonly exposed on spring low tides, frequently with much leaf mortality.

Throughout the range of 1 to 10 m, all of the species may be found, singly or mixed, however, Thalassia is the unquestionable dominant in most areas, frequently forming extensive meadows that stretch for tens of kilometers in length. Although the absolute depth limit of the species is deeper, mature meadows of Thalassia are not found below 10-12 m. At this depth Syringodium replaces Thalassia and forms meadows down to the region of 15 m. Past the maximum for Syringodium development, Halodule will often occur, but it rarely develops extensively at depth. Past the point at which the major species occur, fine carpets of Halophila are found extending to past 40 m in depth.

More severe mortalities of organisms in seagrass meadows of the sub-tropics are caused by severe cold rather than heat, as extreme cold water temperatures are a more irregular and much wider spaced phenomenon than extreme high temperatures. The chill tolerance of populations of Thalassia, Syringodium and Halodule is related to their source location. Within a species, plants from lower latitudes had less chill resistance than those from higher latitudes, and those from shallow exposed bays showed greater tolerance than those from deeper waters of the same latitude. Colonizing species such as Halodule seem to be more eurythermal than those from the more mature community stages, and to have greater chill tolerance.

Mature seagrass beds can usually tolerate considerable salinity fluctuations, but most seem to have an optimum range near, or just below, the concentration of oceanic water. Thalassia has been found in waters varying from 3.5 o/oo to 60 o/oo, but can tolerate these extremes for only short periods of time. The optimum range for Thalassia has been reported to be from 24 o/oo to 35 o/oo.

While the standing crop of leaves is quite significant, the major portion of seagrass biomass is in the sediments, especially in the larger species. Thalassia typically has about 15-20% of its biomass in emergent leaves although published values range from 10-45%, with the rest being in roots, rhizomes, short shoots, and sheathing leaves (Zieman, 1975; 1982). The leaf to root and rhizome ratios of Thalassia increased from 1:3 in fine mud, to 1:5 in mud, and 1:7 in coarse sand (Burkholder et al., 1959), an increase of over twice the belowground material found in the coarser sand sediments. This can be interpreted either to indicate the positive effect of the richer fine muds supporting more robust plant development, or to indicate the need for a more developed root network for nutrient absorption in the coarser sediments, which tend to be lower in nutrients and organic matter.

Seagrass production and biomass are both strongly influenced by water current velocity as the diffusion gradients around the leaves are reduced by water motion. In the tropics, the densest stands of seagrasses with bright, long leaves are commonly found in tidal channels separating the mangrove islands.

The seagrasses, with their well developed root structure have the ability to take up nutrients through their roots or their leaves, although root uptake is the main pathway. Most studies of nutrient supply have been directed to the source and rate of supply of nitrogen. While phosphorous is in very low concentration in tropical waters, it is relatively abundant in the sediments and estimates on turnover time range from one to two turnovers per year to once every few years.

For the south Florida region productivity values of less than 0.5 to 16 g C/m² have been reported. Environmental conditions and seasonal programming vary throughout the range of the seagrasses, and this has a pronounced effect on their annual productivity and biomass cycles. Both productivity and standing crop vary seasonally, with high values in the warmer months and low values during winter. In south Florida the highest standing crop values were about 2.5 to 3 times the winter minimum. This seasonality varies latitudinally with a maximum to minimum leaf standing crop ratio of 1.2 to 2.5 on the northwestern coast of Cuba, 2 to 3 generally in south Florida, and 6 to 8 for the northwest coast of Florida. Table 1 lists some of the parameters seen to vary latitudinally in the Gulf and Caribbean.

Another latitudinal gradient exists in the relative food value of the leaves of seagrasses for consumers. In the more temperate waters Thalassia leaves have a high concentration of relatively indigestible structural carbohydrates and are lower in protein content (Table 1). In full tropical waters, in part due to the higher turnover rates, the protein content doubles and the structural carbohydrate content decreases, yielding a much higher grade food source.

**TABLE I. LATITUDINAL VARIATION IN SOME PARAMETERS OF
 THALASSIA TESTUDINUM**

LOCATION	STANDING CROP (Max/Min)	TURNOVER RATE (% / Day)	PROTEIN (% DW)	CARBOHYDRATE (Insoluble %)
NORTH FLORIDA	6 - 8	2.0		
TAMPA BAY		1.8	13	53
BISCAYNE BAY				
FLORIDA KEYS	2 - 3	2.0	16	47
JAMAICA		2.5		
ST. CROIX	1.2 - 2.5	2.8 - 3.5		
BELIZE			25	34

VARIATIONS IN CORAL REEFS IN RESPONSE TO GRADIENTS LIMITING PRIMARY PRODUCTION

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INTRODUCTION

Definite patterns in reefs and coral communities occur in relation to gradients in environmental factors. Over reef profiles or along coasts, physical factors are important at the extremes (shallow or deep and wave exposed or sheltered, respectively) and biological factors in intermediate situations. There is variation in the life history strategies among corals over the environmental gradients. The most obvious role of such variation in biological characteristics is in spatial variation. The characteristics of the algal community (biomass, primary production) appear not to respond to simple factors (e.g. nutrients), but to react in as complex a way as the coral community and to the same three sets of physical, biological and historical factors.

THE MESSAGE OF GENERAL PATTERNS

There are definite patterns in the occurrence of reefs, reef communities and reef organisms in response to environmental gradients. An obvious example is the general zonation of Caribbean reefs, from shallow to deep water, with a Shore zone, an Acropora palmata zone, an Acropora cervicornis zone, a Head coral zone, and a Slope zone. The factors that are operative along such a gradient are largely the same as those along the gradients limiting primary production.

Factors such as wave energy and turbulence are important in the formation of morphological features like spur and groove systems and are clearly related to the occurrence of the highly productive algal pavements (Wanders, 1976; Lighty, 1981). Examples of the influence of wave energy on the level of the organism are the change in depth of Acropora palmata colonies, with colonies growing deeper in more exposed conditions (Bak, 1976), and variations in the distribution of the Acropora palmata belt or of Gorgonia communities with wave exposure along the coast (van Duyl, 1985).

The influence of light is demonstrated where deep water coral species occur in shallow water in crevices and caves. It also shows a significant influence on the shape of the colonies (Roos, 1967). Light becomes a limiting factor for coral in deeper water. Turbidity is related to light as well as to sedimentation (Bak, 1978). The effects of sedimentation depend on sediment grain size and on quantities (Hubbard and Pocock, 1972; Bak and Elgershuizen, 1976). There are significant differences in the effect of sediments on coral species; consequently,

sedimentation influences coral community organization (Cortes and Risk, 1985). Of course sedimentation means different things at different depths: resuspension in shallow water, transport at medium and greater depths, and transport and sedimentation in deep water.

Other environmental factors are probably less influential over the profile of Caribbean reefs, e.g. temperature, salinity and oxygen are close to optimum values. Nutrients are a factor important in primary production and may locally affect the distribution patterns. This factor is often mixed with others, as in sewage discharge, and generally results in a deterioration of the coral communities and small colony size (van Duyl, 1985).

BIOLOGICAL VERSUS PHYSICAL IMPACT ON COMMUNITY

The patterns that emerge in the distribution of communities can be explained as the distribution of communities that are more or less physically or biologically accommodated. For example if physical factors are largely responsible for community organization then recruitment may take place mainly through fragments of colonies broken up during storms, or survival of corals may be controlled by sedimentation. In communities that are organized by biological forces, interactions between organisms are decisive, e.g. the small maximum colony size in a community is the result of high densities of grazing, rock-eroding organisms.

A model of the influence of physical versus biological factors with depth shows physical factors to be of importance in shallow and deep water (Fig. 1a). Factors involved are water movement, resuspended sediments (shallow water) limiting light levels, collapse of substratum, sedimentation (deep water). At intermediate depths there is a wealth of competing organisms; interactive mechanisms such as predation, overgrowth and bio-erosion are operative.

A similar model can be used along coasts from very exposed to very sheltered conditions (Fig. 1b). At the extremes, physical factors such as wave action and scour, respectively, turbidity and light will be the structuring forces. In intermediate situations there will be increased interactions between relatively high densities of bottom dwelling organisms.

THE RELATION BETWEEN CORAL LIFE HISTORY STRATEGY AND ENVIRONMENT

The reaction of corals to environmental stimuli is intimately related to the characteristics of the different life history strategies of the species. The usual view of corals has been that of very stationary animals, slowly growing, reaching large size and high age. Species such as Montastrea annularis, M. cavernosa and Agaricia lamarcki correspond to this picture. They allocate a relatively large part of the available energy to survival and as a result show good regeneration of lesions, a low production of settlers and a low mortality (Bak and Engel, 1979; Hughes and Jackson, 1985).

There are species that show much the opposite characteristics. For example Agaricia agaricites and Leptoseris cucullata are very mobile as bottom components. They regenerate wounds poorly, have high numbers of settling larvae and high mortality rates. Another distinct group are the branched corals such as Acropora palmata and A. cervicornis which are very well adapted to turbulent, wave exposed habitats. Colonies will break up but survival of the resulting fragments is good. Growth is rapid and regeneration rates are very high. Less energy is channelled into sexual reproduction and the production of larvae is low (or at most sporadic) through the years (Bak, 1983).

If we ask the question "How important are such biological characteristics in community organization?" we find the answer is, "They are very important in spatial organizations in the rate of rearrangement of the bottom components." Other questions such as, "Are biological characteristics related to competition important as a structuring force in community organization?" are much more difficult to answer. Of course, there is no doubt that species such as Montastrea annularis become dominant in some reefs and there is evidence for space monopolization on reefs over time (Porter et al., 1981). The problem is that the mechanisms that are actually operative remain so obscure. Potential mechanisms, such as mesenterial digestion by superior aggressors or attack by elongated sweeper tentacles have been studied (Lang, 1970; Bak et al., 1982; Logan, 1984), but these interactions are probably not responsible for the elimination of many colonies on the reef. Only small margins of colonies are killed and reversals in the aggressive hierarchy obstruct the process of space monopolization (Bak et al., 1982).

SPATIAL VARIATION

Biological factors such as settlement rates, growth and survival play a much more obvious role in structuring communities through spatial rearrangement. Even if, in terms of cover, a reef surface remains virtually unchanged over a period of time there can be a considerable rearrangement of the bottom components in space (Bak and Luckhurst, 1980).

In such a rearrangement it will appear that Montastrea annularis has hardly changed position, while Agaricia agaricites has disappeared in many spots to appear in many new positions. The component "bare rock" may not change in percentage cover over time, but if rock is continually covered and cleared, by sediments and organisms, new space will continue to be available. This is of particular importance for settlement of larvae and spores, and as such for community structure and primary production.

Spatial variation occurs at least on three scales. At the micro-scale, variation over a few square meters is caused by the differential mobility of species, the collapse of substratum and the shifting of sediment rivulets. Variation on the mini-scale is correlated with the patchiness of coral stands along a coast, e.g. the discontinuous

distribution of stands of Madracis mirabilis or Acropora palmata (van Duyl, 1985). At the macro-scale we find variations over large stretches of reefs caused by large scale phenomena such as hurricanes and intrusions of cold and turbid waters (Woodley et al., 1981; Porter et al., 1982).

In all scales there is a historical component. The presence of a particular substratum, relief or species, in reaction with the particular character of the disturbing agent, determines the result of a process. For example the occurrence of the white band coral disease will only result in a rubble bottom if Acropora was present to be affected by the disease (Gladfelter, 1982; Bak and Criens, 1981).

FACTORS IN OPERATION

The factors briefly discussed above and their gradients, and the variations in processes and structure are not only relevant in coral community organization but also relate to the occurrence of reef algae and to primary production. There are striking parallels in the characteristics of the algal community and primary production with the other processes on reefs (Fig. 2). What the actual relationships or what the mechanisms involved are may remain obscure because of the complexity of the interactions in the system. For example, the relatively low algal biomass at intermediate depth (Fig. 2) may be the effect of a higher abundance of available space for settlement in shallow and deep water, or it may be caused by higher densities of grazers at intermediate depth.

When reef substrata are protected from grazing there is an immediate increase in algal biomass, indicating that biological interactions rather than limited nutrient supplies are operative. Space appears to be a limiting resource for filamentous algae on reefs. Algae are the most common organisms on coral colony margins at these depths (Bak et al., 1976) and with reduced grazing pressure algae overgrow corals (Ruyter van Steveninck and Bak, 1976). Depending on life history strategy, some coral species are more susceptible to algal competition than others. There are other indications of the potential of active biological mechanisms at this level, e.g. the inhibitive effect of an exudate of the anemone Condylactis gigantea on filamentous algae (Bak and Borsboom, 1984). Herbivores are attracted to the physical structure of the reefs and their densities will not only influence algal biomass but also increase primary production (Carpenter, 1985).

SUMMARY

Variations influencing primary production are caused by the same gradients in the same three sets of factors, physical, biological and historical, that are identified as being operative in coral community organizations.

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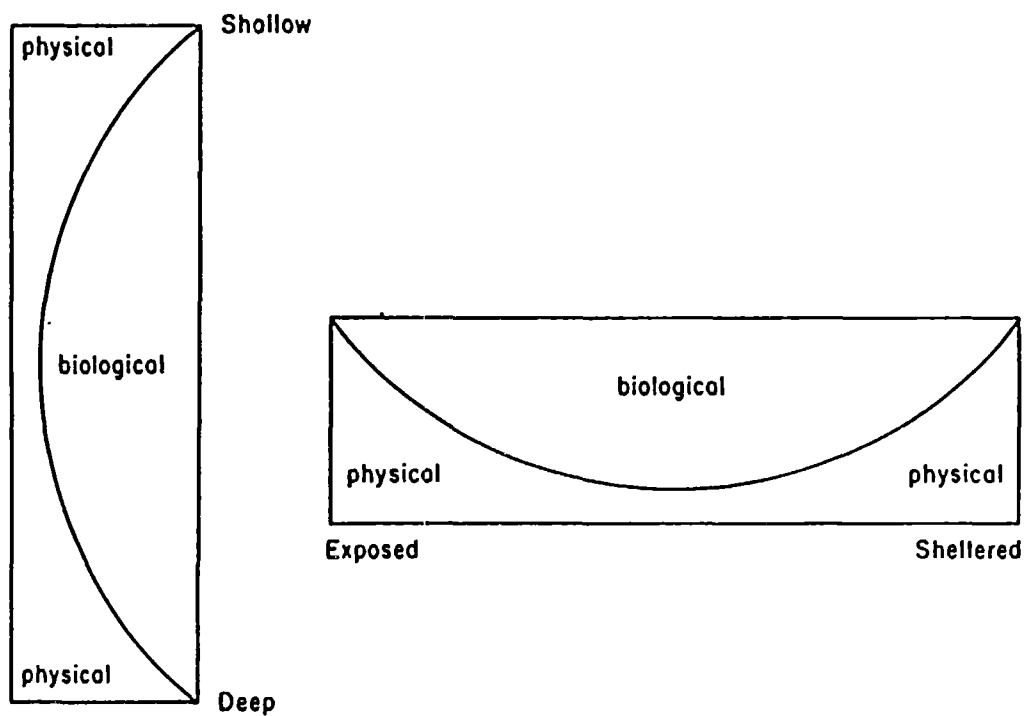


Fig. 1. Model of relative importance of physical and biological factors in coral community organization. A, from shallow to deep water. B, from wave exposed to sheltered conditions.

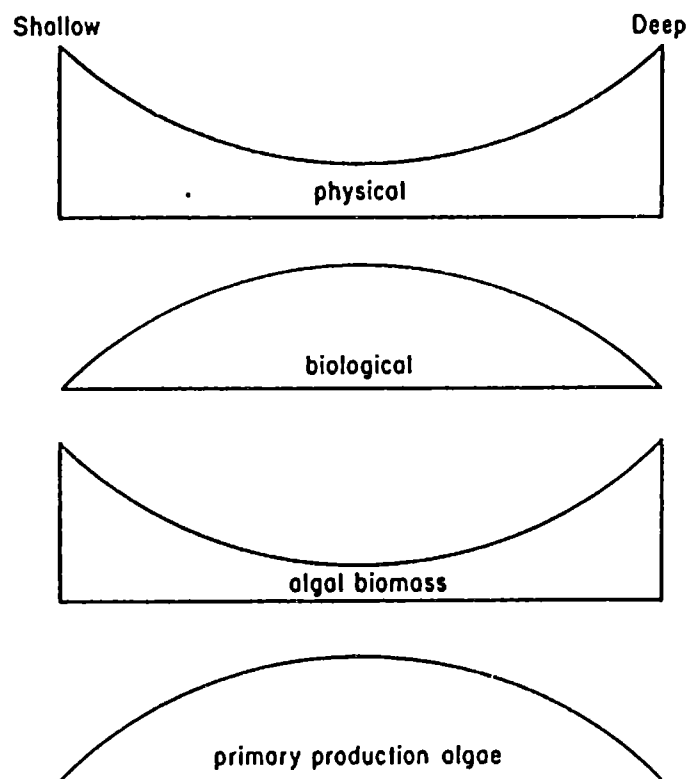


Fig. 2. Distribution of gradients in physical and biological factors over the reef (shallow-deep) in relation to algal biomass and primary production.

PHYSICAL FLOW PROCESSES IN CARIBBEAN WATERS OVER A RANGE OF SCALES

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INTRODUCTION

Flow processes impact on productivity in the coastal marine environment. Any study of productivity would need to include aspects of freshwater input, currents, mixing characteristics, and residence times. Thus, a physical oceanographer has a role to fill in most ecosystem studies. It is essential to characterize the coastal environment from a physical point of view, as well as to assess the temporal and spatial variability of both the physical forcing functions and the ecological responses within the system.

SAMPLING: SPATIAL AND TEMPORAL CONSIDERATIONS

Proper sampling rate and strategy are essential for the success of a comparative study of ecosystem productivity as well as in any study. In selecting study units, it is desirable to identify environmental areas exhibiting a minimum amount of variability. Differences in system response between units can then be assessed with greater certainty. Also, it is essential to sample at a frequent rate to avoid aliasing the data set. If sequential data are sampled at a rate, $1/\Delta t$, any significant variability at frequencies greater than the cut-off frequency, $f_c = 1/2\Delta t$, will contaminate or alias the data set. This point is demonstrated in Fig. 1, showing the variance spectrum sampled correctly and incorrectly. Once data have been measured at too slow a sampling rate relative to frequencies containing significant variance, in general, little can be done to correct for this error.

Ecological processes, as well as the physical forcing functions, operate over a spectrum of process scales (Table 1). Large space scales are typically associated with long time scales, and small space scales with short time scales. These so called process scales can be defined as the time/space scale over which a signal is coherent or recognizable.

In making comparisons between ecosystem processes, care should be taken to compare processes on the same scale. Rather than trying to relate the Caribbean circulation to productivity within a single seagrass bed, the local currents and exchanges within that particular seagrass environment should be related to each other. Data to be used for cross-reference should always be collected on the same scale, and preferably at the same rate. As an example, in making advective flux computations, velocity and concentration data are cross-correlated and should thus be measured simultaneously and at the same location.

Processes occurring on a large scale (e.g. macro) can be considered as a far-field forcing function to a process occurring on a smaller scale (e.g. meso). In this sense, it is possible to downscale, i.e. move from a larger scale (Table 1) to a smaller scale. The larger scale, for example the flow of a major ocean current, can sometimes effectively be assessed using remote sensing data, e.g. satellite thematic mapper imagery. On the other hand, the large scale process is often deducted from a series of local measurements. This may yield errors. Integrating a local process for an entire ocean basin, i.e. upscaling, is not likely to yield reliable estimates of the process on the larger scale because of integration errors. Thus, in coastal ecosystem studies where flow processes are hypothesized to influence productivity (of mangrove, seagrass, and coral reef environments), it is necessary to keep in mind that the biogeochemical and physical processes need to be evaluated at the same scales.

The Caribbean is a mediterranean sea, entirely located within the tropics, and having a surface area of 2.51×10^6 km² or approximately 3% of the area of the Atlantic Ocean. It consists of a series of deep basins (Fig. 2), has a maximum depth of 7,680 m (200 km WNW of Jamaica), and an average depth of 2,600 m. It connects to the Gulf of Mexico through the Yucatan Channel, and to the Atlantic Ocean in the east and northeast between the leeward and windward islands. However, these passages are relatively shallow and the greatest sill depth is 1,815 m in Anegada Passage, 200 km east of Puerto Rico (Stalcup and Metcalf, 1973).

The surface currents in the Caribbean (Fig. 3) are an example of a macroscale process. The characteristic current wind flows from east to west at 0.1-0.3 m/s is a continuation of the Guiana Current, and is largely wind-forced. Seasonal variability exists but does not alter the general flow pattern (Fig. 3). Two persistent cyclonic gyres exist in the Bight of Honduras and in the southwestern extreme of the Caribbean Sea. A persistent upwelling system occurs along the continental landmass near the Colombia-Venezuela border. Surface temperatures vary from 24 to 27 °C during the winter and from 26 to 29 °C during the summer. The surface salinity is high, typically from 35 to 36 ‰ away from river plumes and the coastal area.

The tide in the Caribbean sea is either mixed or diurnal (Fig. 4). Although the range is everywhere less than 0.5 m (Kjerfve, 1981), typically 50% or more of the current variability near the coast and in fringing reef areas varies at the tidal frequency. Thus, although the tide is small compared to many other coastal areas of the world, it is still a major forcing function for coastal currents and exchanges in the Caribbean.

The predominant wind distribution (Fig. 5) in the Caribbean area is the trade winds which generally blow 4-8 m/s from the northeast from December to May. Occasional "norte" events cause strong blows from the north and northwest at 5-15 m/s, and are usually the remnant of a North American frontal system, which typically propagates from

west to east anywhere from October to March. Most of the region surrounding the Caribbean Sea can be classified as tropical humid with the exception of a portion of the Colombia-Venezuela coast and some of the lower islands. A large portion of the Caribbean Coast from southern Belize to central Panama experiences rainfall in excess of 5 m annually, heaviest from July to September. Orinoco is the largest river of the region with an annual discharge of 25,200 m³/s. Although it debouches into the Atlantic Ocean, its discharge impacts the extreme eastern Caribbean Sea.

The western Atlantic experiences an average of ten tropical storms or hurricanes annually. Most of these occur from August to October. They start in the eastern Atlantic as "easterly waves" and travel to the west at 5-10 m/s. Most of these tropical storms/hurricanes enter the Caribbean at the windward islands and continue either to the Yucatan Channel or across the Greater Antilles (Fig. 5). The region just south of the western tip of Cuba has experienced 100 tropical storms/hurricanes in the past 100 years (Gentry, 1971). A hurricane will generate surface wind speeds 35-100 m/s; coastal sea level rise as high as 6 m, and storm waves which in coastal areas may have wave heights as great as 15 m at the time of breaking. Storm-induced upwelling-mixing will decrease surface water temperatures on the order of 5 °C in the path of the storm. Cumulative coastal effects due to hurricanes can be dramatic and destructive to the coastal ecosystems. In addition, coastal water turbidity may increase significantly as a result of terrestrial runoff and wave-resuspension and thus further affect coastal primary productivity.

The oceanographic conditions occurring on the north coast of Jamaica will serve to illustrate a mesoscale physical oceanographic process (Fig. 6). During typical trade wind conditions, the fetch-limited waves will arrive from the northeast, typically with a period of 4-7 s and a deep-water height less than 1 m. The wind drives a coastal current parallel to the fringing reef, and existing within at least 1 km of the reef. The current flows steadily 0.03-0.15 m/s towards the west. The dynamics of this current causes an offshore-directed Ekman flux and an associated weak nearshore upwelling. These conditions are typically associated with minimal rain/runoff and thus very low turbidity.

On the other hand, during a "norte", the wind and waves pick up. It often rains at this time, causing the Rio Bueno to discharge turbid waters into the nearshore. The shore-parallel current reverses directions almost instantly. The westward current carries the turbid plume of Rio Bueno along the fringing reef, extending it across the entrance to Discovery Bay 6 km away, and dramatically cutting down on underwater visibility along the Discovery Bay forereef. Upwelling ceases during these times and the water level within Discovery Bay may rise 0.6 m or more in response to the changing dynamic conditions. Obviously, this level of understanding of the physical characteristics impacts greatly on the local ecosystems and measurements/interpretations of biogeochemical processes.

An example of a milliscale physical oceanographic process in coastal Caribbean waters is the wave-induced flow across a fringing reef (Fig. 6) as exemplified by data from Carrie Bow Cay, Belize. When the mean water level is below the reef crest, the breaking waves pump water across the reef crest into the adjacent shallow lagoon. The reef crest is cut across the shallow (0.5-1.5 m) microgroove channels in five locations along this reef. The flow in the microgrooves is seaward when the mean sea level is below the reef crest and wave-pumping occurs. However, when the tide increases to the point that mean sea level is above the crest, wave-pumping is less of an effect. At such times, the flow in the microgroove oscillates with the waves and shows no net flow direction.

SUMMARY

Clearly, knowledge of physical processes on various scales affect the interpretation of other ecological processes.

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Table 1. Spectrum of process scales which are defined to be the scale over which a "signal" is coherent or recognizable.

Name	Space Scale	Time Scale	Example
Global	Earth	> Year	Thermohaline circulation; El Niño.
Macro	Basin	Week-year	Basin-wide ocean and atmospheric circulation.
Meso	System	Hour-month	Upwelling; fronts; wave refraction; sea land breezes.
Milli	Patch	Minute-hour	Flow around coral head; breaking waves.
Micro	Organism	Second	Molecular diffusion and turbulence.

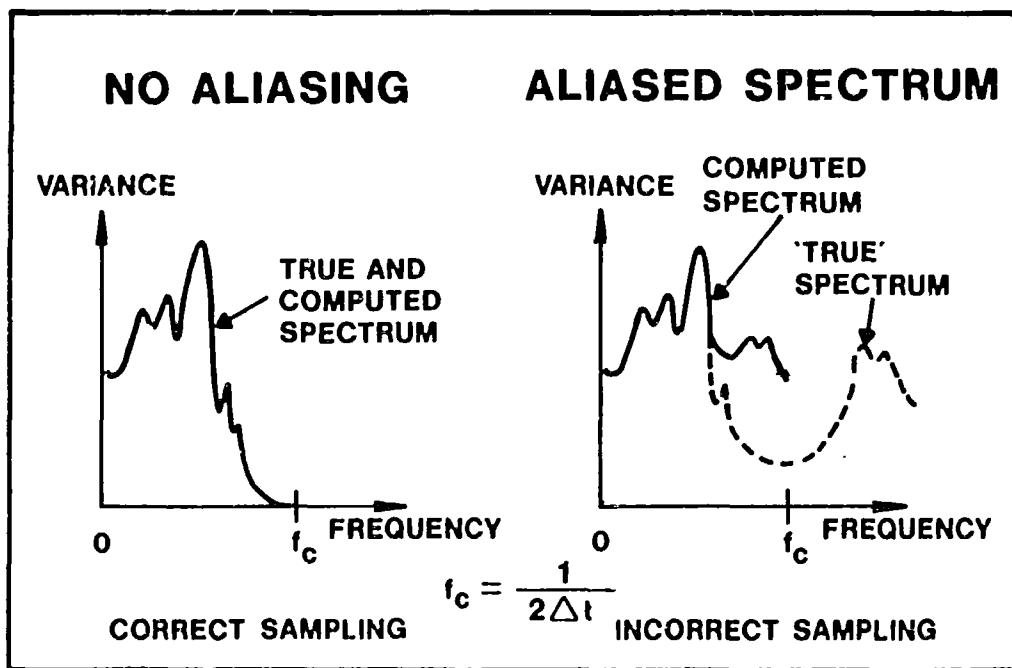


Fig. 1. Illustration of how an incorrect sampling rate may result in erroneous conclusions because of aliasing into the computed spectrum.

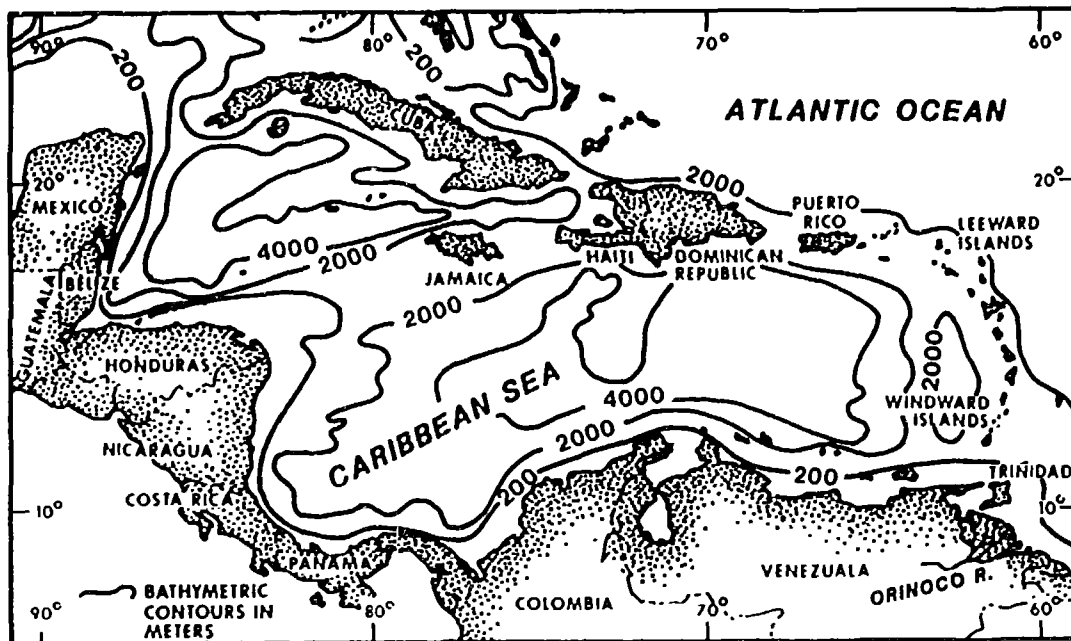


Fig. 2. Bathymetry of the Caribbean Sea.

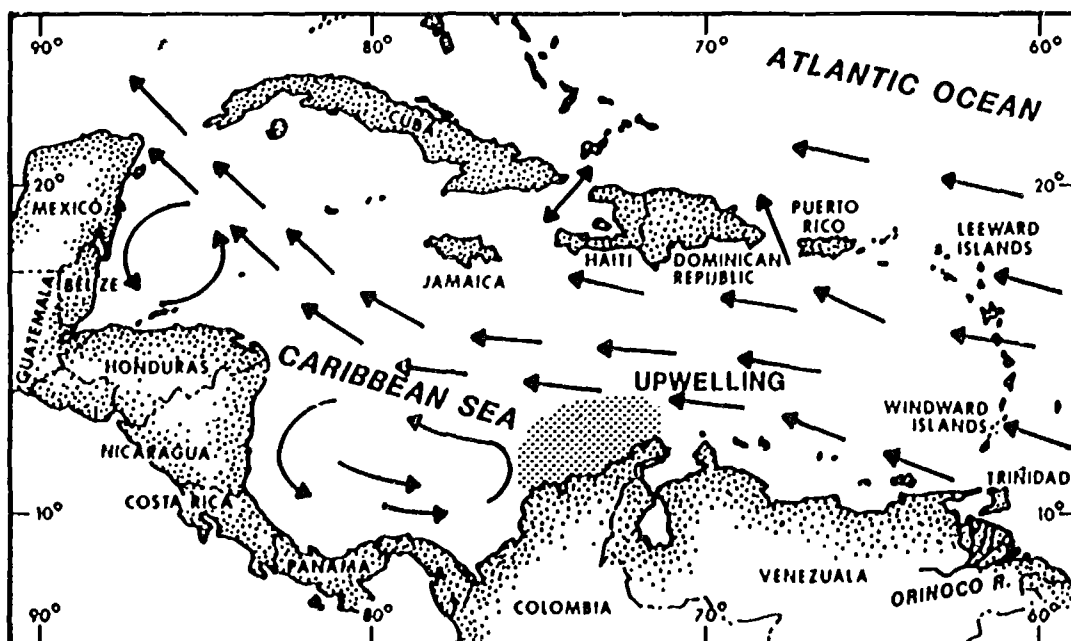


Fig. 3. Schematic representation of Caribbean surface currents.

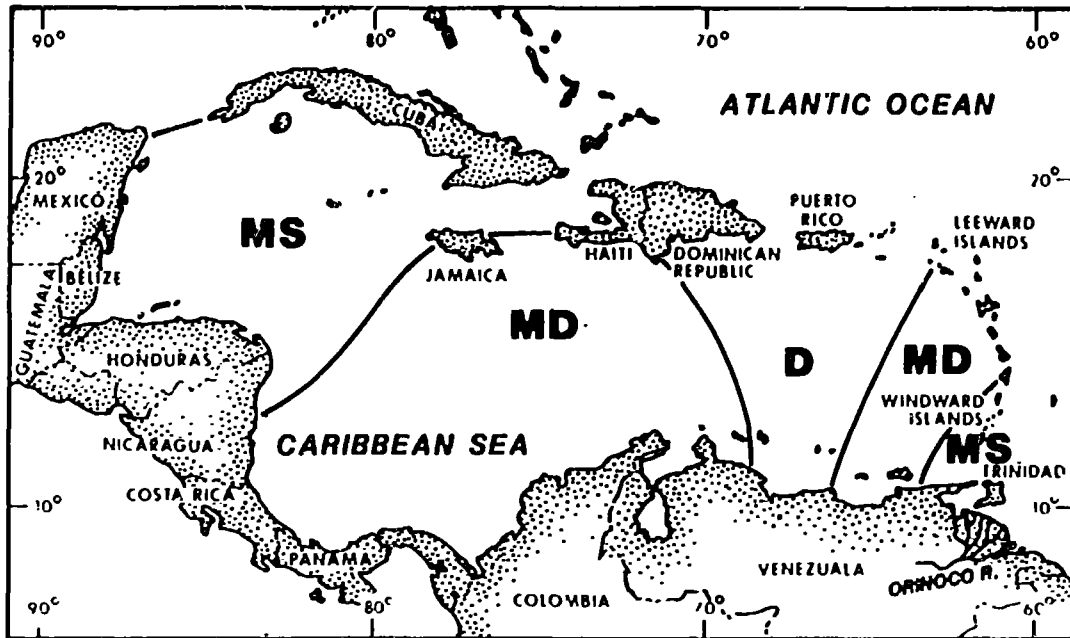


Fig. 4. Distribution of tidal type as represented by the form number (F), where MS is mixed tide, mainly semidiurnal; MD is mixed tide, mainly diurnal; and D is diurnal tide.

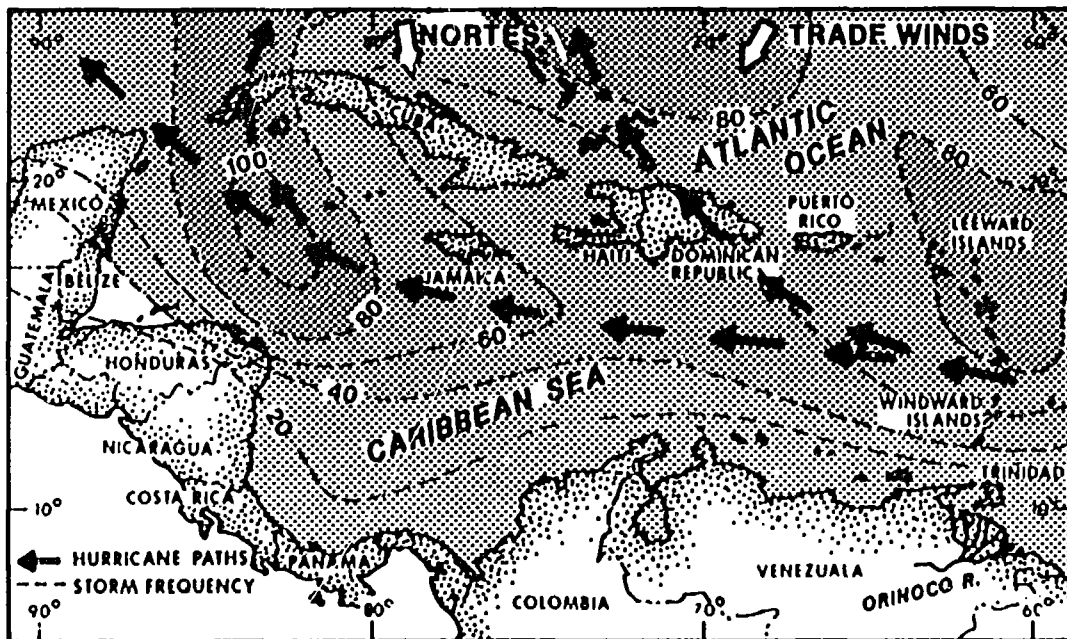


Fig. 5. Schematic illustration of predominant winds (trades and nortes) and the most common paths of hurricanes across the Caribbean. The underlying isopleths indicate the probable number of hurricanes or tropical storms per 100 years (after Gentry, 1971).

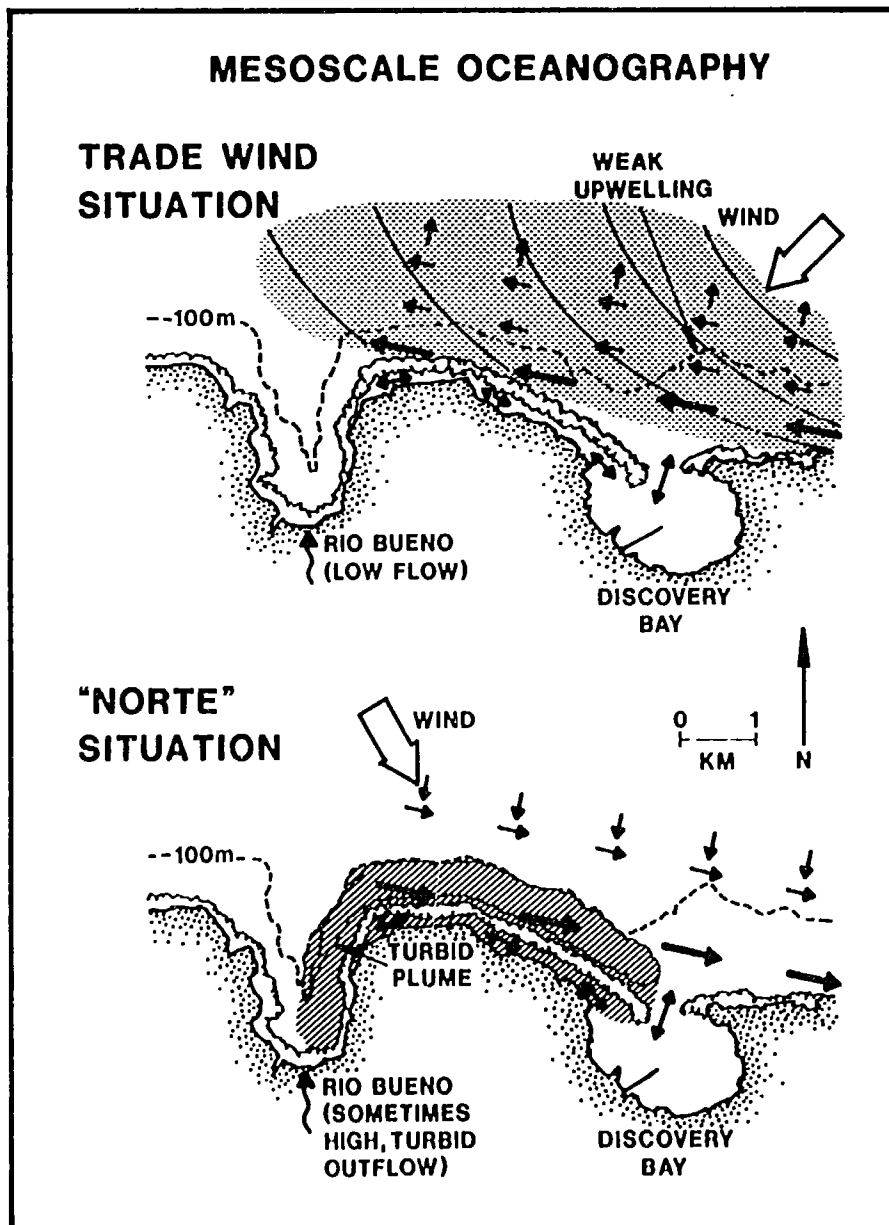


Fig. 6. Illustration of mesoscale oceanographic processes affecting a coastal system and the variability introduced by changing weather conditions.

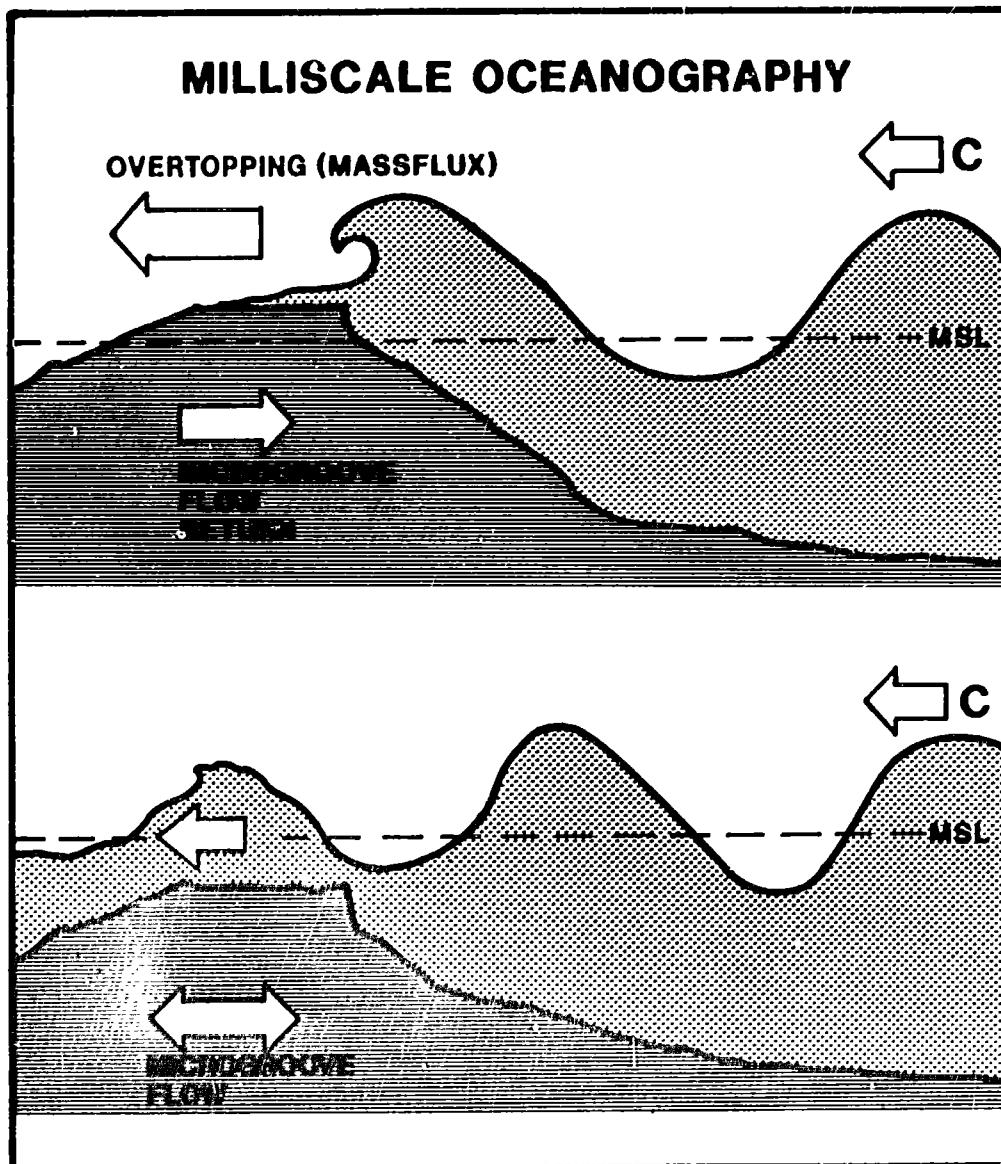


Fig. 7. Illustration of milliscale oceanographic processes, in this case the overtopping of the coral reef crest by breaking waves.

REMOTE SENSING OF TROPICAL COASTAL ECOSYSTEMS

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INTRODUCTION

There is a wide range of remote sensing systems available for observing tropical coastal ecosystems, including aerial film cameras for detailed mapping of mangroves, seagrass and coral reefs; multispectral scanners for mangrove/seagrass biomass and coastal water property studies; thermal and infrared scanners for mapping surface water temperatures and currents; microwave devices for salinity or wave measurements; and underwater cameras and acoustic systems for benthic observations. The recent appearance of low-cost microcomputers with user-friendly software for analyzing satellite imagery is enabling more investigators to use satellite data. The availability of high resolution Thematic Mapper and SPOT imagery is also important to coastal investigations. However, to meet both spatial and temporal resolution requirements, data from several satellites will have to be combined with aircraft and ship data in a cost-effective way. In this paper, we attempt to summarize the state of the art of remote sensing of coastal properties, and to point out user requirements for studies of tropical coastal ecosystems.

STATE OF THE ART OVERVIEW

Table 1 summarizes the present capability of aircraft and satellite remote sensors to provide data on coastal land and water properties. Even though the ratings assigned are somewhat subjective, depending on environmental conditions, availability of ground "truth" and mode of operation, this table provides a good idea of the relative ease or difficulty for remotely sensing coastal and oceanographic features which will be discussed in this paper.

As shown in Table 1, the species composition and condition of coastal vegetation can be mapped from aircraft or satellites using color films or multispectral scanners. With digital analysis of Landsat Multispectral Scanner (MSS) data, the classification accuracy of coastal vegetation types can be raised above 90%, especially if images from two different seasons are employed. Identical techniques apply to land use change mapping (Klemas et al., 1975).

Vegetative biomass of both Spartina marshes and mangrove swamps can be determined using ratios and differences of Landsat MSS or Thematic Mapper (TM) red and near infrared bands. For instance, the MSS band 7/band 5 ratio was found to correlate strongly with Spartina alterniflora (Bartlett and Klemas 1979, 1980, Butera 1983). Variations in biomass in salt and brackish marshes were also highly correlated with spectral

radiance expressed as the vegetation index or infrared index, based on differences and ratios of TM bands 3, 4 and 5 (Hardisky et al., 1983a, b).

Coastal erosion and coastal geomorphology have been studied successfully using aircraft film cameras and Landsat (Dolan 1973, Dolan et al., 1977, Stafford and Langfelder, 1971). The advantage of aircraft photography is that it provides the high resolution required for accurate measurement of beach erosion or accretion. Landsat MSS, however, can provide a geologic overview of an entire coastline, including underwater features. Bathymetric maps have been successfully prepared by extracting water attenuation and bottom reflectance from digitally processed Landsat MSS data (Rogers et al., 1982, Lyzenga 1978, 1979).

As shown in Table 1, water depth can also be measured by the time difference between laser pulses from the water surface and the bottom. Such laser profilers use green wavelengths which penetrate reasonably clear waters (Hoge et al., 1980). Visible images from aircraft or satellites can help provide relative depth profiles which may then be calibrated with airborne laser profilers. Even though powerful laser pulses penetrate the water column to several Secchi depths, a major limitation is their inability to reach bottom in turbid coastal waters.

Suspended sediment concentrations are of interest to marine geologists and biologists, since sediment relates to coastal erosion/siltation, affects sunlight penetration and marine productivity. With appropriate surface "truth" data, suspended sediment concentrations have been mapped from aircraft and satellites (Johnson, 1975; Moore 1978; Munday and Alfoldi, 1979; Maul et al., 1974). To enable one to calibrate the imagery in terms of suspended sediment load, one must obtain not only concentration measurements on the ground, but also data on the grain size distribution. Atmospheric corrections are required for both sediment and chlorophyll concentration mapping (Wilson et al., 1978). On the other hand, if one is looking only for suspended sediment patterns (qualitative information), film photography with appropriate filters and Landsat MSS bands 4 and 5 can be quite useful. The same discussion applies to mapping pollutant concentrations in coastal waters (Whitlock et al., 1981). To map pollutant concentrations, good ground measurements are required and fairly sophisticated data analysis techniques may have to be used with multispectral scanner data (Philpot and Ackleson, 1981; Klemas and Philpot, 1981).

Chlorophyll concentration strongly influences ocean color and is a good indicator of ocean productivity. The Coastal Zone Color Scanner (CZCS) on Nimbus 7 has been used with considerable success to map ocean color and chlorophyll-a concentrations over open ocean areas (Hovis, 1977; Wilson and Austin, 1978). Despite difficult atmospheric corrections, chlorophyll-a concentrations have been mapped with a factor two accuracy. In turbid coastal waters, it is more difficult to map chlorophyll concentrations using passive techniques. Water masses

dominated by dissolved carbon, particulate carbon and inorganic sediment have been differentiated with aircraft multispectral scanners (Klemas et al., 1981).

Chlorophyll and other pigments have been detected in turbid coastal waters using laser fluorosensing techniques. Chlorophyll concentrations and dispersed oil can be determined using low-altitude airborne lasers operating in the fluorosensing mode (Jarrett et al., 1979; O'Neil et al., 1980).

Thermal infrared scanners have been very effective for mapping ocean surface temperatures with about $\pm 1^\circ\text{C}$ accuracy and for studying coastal surface currents (Legeckis, 1975, 1978). Thermal infrared scanners on NOAA satellites together with multi-spectral scanners, such as the AVHRR and CZCS, have been used to study coastal upwelling and estuarine properties (Gagliardini et al., 1984; Karszenbaum et al., 1983). Estuarine fronts and their effects on oil dispersion have also been investigated with Landsat (Klemas, 1980). Several aircraft and ground-based radar techniques are being developed for measuring currents (Shuchman et al., 1979). Currents can also be measured using dyes and drogues tracked from shore or from aircraft (Klemas et al., 1974; Klemas et al., 1977). There are also photogrammetric methods for surveying tidal currents (Keller, 1963).

Large area measurements of coastal salinity are of considerable value to oceanographers investigating the coastal zone. However, salinity is one of the most difficult properties to sense remotely. L-band microwave radiometers employed from low altitude aircraft have been able to map salinity (Swift, 1980; Swift and McIntosh, 1983) with an accuracy of less than one part per thousand at 25°C . Such accuracy is useful for estuarine studies where large salinity gradients can be found. Open-ocean salinity sensing requirements are more stringent by at least one order of magnitude.

As shown in Table 1, sea state and wave spectra are best obtained using laser profilers from aircraft, radar mappers (SAR) and radar altimeters (Panicker, 1974; Ross et al., 1970; Born et al., 1979; Schule et al., 1971). Imagers such as synthetic aperture radar or film cameras are particularly effective for wave studies if the data is analyzed using Fourier analysis techniques (Stilwell, 1969). Since surface winds induce capillary waves which influence microwave emission and reflectance, microwave sensors, particularly radar scatterometers such as the one on Seasat, have been tested for surface wind determinations (Born et al., 1979). Seasat sensors were particularly designed for measuring and mapping ocean waves, surface winds, currents and other features (American Geophysical Union, 1983).

REMOTE SENSING REQUIREMENTS FOR TROPICAL COASTAL ECOSYSTEM STUDIES

In order to be able to use satellite and aircraft remote sensing techniques to compare the productivity and other important properties of coral reefs, seagrass beds and mangrove swamps, certain optical,

physical and biological properties of the vegetation, water column and the bottom will have to be measured. These measurements should ideally be conducted to give us an indication of both temporal and spatial variabilities. Within limited funding and time constraints, the best strategy seems to have one long-term, well-instrumented site, and several others where experiments of shorter duration and with less instrument complexity can be conducted. For instance, if three sites are chosen based on their susceptibility to land run-off, the one with the greatest variability might be best for long-term observations (e.g. several years continuously), while the other two are studied over shorter time periods (e.g. one month during rainy and dry seasons each).

Spectral observations of mangrove systems enables us to estimate aboveground biomass from satellites. To do this, however, we need to develop physical models which relate land area, density, geometry, etc., to spectral reflectance for each mangrove type, height and density range during rainy and dry seasons. To further improve the model, litter should be collected and root/stem biomass related to total leaf biomass. This effort will require a permanent activity, twelve months per year, at the primary, long-term test site.

Seagrass beds require "a priori" information on spectral properties of the bottom and each grass type, plus their texture, distribution and depth. The optical properties of the water column and bottom material should be measured over long periods under varying turbidity conditions, as a function of season (rainy versus dry), wind and weather, and run-off variations or resuspension due to other causes. Spectral transmission and light level measurements performed at the primary site should then be related to optical measurements at other sites, where simpler instruments (e.g. Secchi disks) may be used. The optical measurements over coral reefs will be similar to those over seagrass beds, except that even more emphasis will have to be placed on texture and detailed spatial variability.

All test sites will benefit from aerial photography conducted from small aircraft and low altitudes (1000-3000 meters) using inexpensive cameras with color, color-infrared and panchromatic films with appropriate filters. The primary test site should be overflown with sufficient frequency to catch variations in visible properties, e.g. degree of turbidity or visibility of coral reef, over a wide range of precipitation/run-off, wind, wave and current conditions.

Once the remote sensing models have been developed, the productivity of the other two sites and new sites will be mapped in order to test the reliability of the remote sensing techniques developed. Since remote sensors can measure only a limited number of properties (e.g. chlorophyll concentration in the upper portion of the water column, extent and total leaf biomass of mangroves, size and type of coral reef, etc.), it will be necessary for the biologists/ecologists to develop models which permit estimation of relative productivity of new sites from these limited measurements. Individual sites will be studied with Landsat MSS, TM and aircraft sensors. To extrapolate results to the entire Caribbean, we would have to depend on NOAA/AVHRR and Nimbus/CZCS data as well.

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Table 1. Performance of Remote Sensors for Estuarine Studies.

Sensor	Plat- form	Veg.& Land Use	Biomass & Veg. Stress	Coast- line Erosion	Bottom Feat. SAV	Depth Profiles	Susp. Sed. Ptrns.	Susp. Sed. Concen.	Chloro- phyll Concen.	Oil Slicks	Surf. Temp.	Water Sal.	Curr. Circ. Ptrns.	Wave Spectra	Surf. Winds
Film Cameras	A	3	1	3	3	2	2	1	1	2	0	0	2	2	1
	S	2	1	2	2	1	2	1	1	1	0	0	2	2	1
Multispectral Scanners	A	3	2	3	3	2	3	2	2+	3	0	0	2	2	1
	S	2	1	2	2	2	3	2	2	2	0	0	2	2	1
Thermal IR Scanners	A	1	1	1	0	0	1	0	0	3	3	1	2	0	1
	S	0	0	0	0	0	1	0	0	1	3	0	2	0	1
Laser Profilers	A	0	0	1	3	3	1	0	0	1	0	0	0	3	1
	S	0	0	1	1	1	0	0	0	0	0	0	0	2	0
Laser Fluorosensors	A	1	0	1	0	1	1	2	3	3	1	1	1	0	0
	S	0	0	0	0	0	0	1	1	1	0	0	0	0	0
Microwave Radiometers	A	1	0	1	0	0	1	1	1	3	3	2	2	1	3
	S	0	0	0	0	0	0	0	0	1	2	1	1	0	2
Imaging Radar (SAR or SLAR)	A	2	1	3	0	1	1	0	0	3	1	1	2	3	2
	S	1	0	2	0	1	0	0	0	2	0	0	1	2	1
CODAR (Radar)	G	0	0	0	0	0	0	0	0	0	0	1	3	2	2
RADS(Acoustic)	G	0	0	2	3	2	2	1	0	1	0	0	2	1	0
UW Camera	G	0	0	2	3	2	2	1	1	1	0	0	1	0	0

Rating

3 - Reliable (Operational)
 2 - Needs Additional Field Testing
 1 - Limited Value (Future Potential)
 0 - Not Applicable

Platform

A - Aircraft (Medium or Low Altitude)
 S - Spacecraft (Satellite)
 G - Ground (Boat or Field)

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