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# Coral reefs, seagrass beds and mangroves: Their interaction in the coastal zones of the Caribbean

Report of a Workshop held at
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# PREFACE

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## I. INTRODUCTION

The Caribbean Sea is a small, deep, and oceanographically diverse body of tropical water which is bounded to the east and north by a series of islands of widely varying size (Fig. 1). To the west and south its margins are the coasts of Central and South America. Currents driven by the North Atlantic gyre move through the islands of the Lesser Antilles from east to west at speeds of up to 1.5 knots, sweeping across the whole expanse of the Caribbean. The water column is vertically stratified with little upwelling of deeper water to the surface, except along the north coast of South America. The stratification keeps nutrient-rich waters locked into the depths and the resulting clear surface water, very poor in nutrients and phytoplankton, has been called a "biological desert" and is typical of many tropical seas.

Almost paradoxically, within this "biological desert" are some of the most productive and diverse ecosystems known in the world: coral reefs, seagrass beds, and mangroves. The apparent paradox is resolved when one examines the mechanisms whereby these ecosystems have overcome the critical nutrient limitations of tropical surface waters. The coral reef has evolved a very close coupling of animals and plants typified by the symbiosis between reef corals and their zooxanthellae. The mangroves and seagrasses exploit the rich nutrient sources that build up in shallow nearshore areas. As dominant features of the Caribbean coastal zone, these three ecosystems, individually and as an integrated web, are the basis of the potential yield of shallow water marine resources in the region.

There are more than 150 million people living in the Caribbean region. Included are population densities among the highest and most rapidly growing in the world, and incomes among the lowest in the world. The economy of the region until recently has been based largely upon subsistence level fishing and agriculture. Many areas have developed very rapidly in the last two decades, mostly in the area of petroleum resources, fisheries, forest products and agriculture, but much of this development has been for export. Going along with export of resources, an increase in tourism has served to emphasize further the constrast between the "haves" and the "have nots". In the face of almost exaggerated problems of development, an emerging focus for future exploitation for much of the Caribbean is the nearshore marine resources.

### A. Background to Workshop

The Workshop is an activity of the UNESCO Major Interregional project on Research and Training leading to the integrated management of coastal systems. This project began at the 21st Session of the General Conference of UNESCO (1980). The Workshop was sponsored by UNESCO, the Intergovernmental Oceanographic Commission for the Caribbean and Adjacent Regions, and by West Indies Laboratory, Fairleigh Dickinson University.

The three major tropical coastal ecosystems: coral reefs, seagrasses, and mangroves, have been subject to a good deal of research attention in the recent past. Coral reefs have been most intensively investigated and have been the sole subject of 4 international symposia over the past 12 years, most recently the 4th International Coral Reef Symposium in Manila in May, 1981, sponsored by UNESCO. Seagrasses were a major project under the International Decade of Ocean Exploration in the U. S. National Science Foundation, with almost 10 years of research support and much international collaboration. They have been subjected to increasing attention as major contributors to coastal zone productivity and the research output is increasing. The most recent international symposium on seagrasses was held in August, 1981, as part of the 13th International Botanical Congress in Sydney. Phillips and McRoy (1980) have recently collected a series of review papers in seagrass research. Similarly, mangroves have attracted increasing attention in the past decade. It is known that mangrove-dominated coastal zones are areas of high productivity and are important nurseries for marine organisms. A working group of UNESCO and the Scientific Committee on Oceanic Research (SCOR) is currently devoting its efforts to 1) produce a general scientific framework for mangrove ecosystem studies and 2) prepare a mangrove research handbook. The 1974 International Symposium on the Biology and Management of Mangroves was held in Hawaii, and in 1980 UNESCO organized an Asian Symposium on the Mangrove Environment in Malaysia.

In spite of this level of attention, scientific studies have concentrated on single ecosystems and have generally neglected interconnections between them. The development problems of the coastal zone transcend the boundaries of narrow scientific concerns. Interactions between the three major tropical coastal ecosystems have been perceived (e.g. Ogden and Zieman, 1977), but have rarely been investigated. As a first step in what we hope will be an increased research effort, we propose to examine these ecosystems with particular attention to their interaction.

The characteristics of these potential interactions are quite varied. As a matter of convenience ecosystems may be characterized as "open" or "closed" in the manner in which their plant-based productivity is exploited. Coral reefs, for example, might be called "closed" systems as their productivity is locked in the symbiosis between zooxanthellae and the reef corals, gorgonians, and other coelenterates they inhabit. At the level of consumers however, reefs are open systems: a great many fishes and invertebrates on coral reefs are involved in movements or migrations from the reef to other ecosystems (Randall, 1965; Ogden *et al.*, 1973; Ogden and Ehrlich, 1977). In contrast, seagrass beds are open systems. Plant productivity is exported in a variety of directions by the diel movements of feeding organisms, the direct transport of leaf material elsewhere, even to the deep sea, or by serving as a nursery for organisms which move elsewhere later in life. Mangroves, another open system, provide a rich source of particulate organic material which is utilized by a variety of organisms elsewhere and are also important nursery grounds for many species (Odum, 1970).

## B. Workshop Format

The Workshop convened at the West Indies Laboratory in St. Croix, U. S. Virgin Islands from 23 to 30 May, 1982. Participants representing working coastal zone scientists of the region were invited from 15 Caribbean countries (Appendix III). Lecturers (Appendix III) were invited to present plenary papers on each major coastal zone ecosystem to provide a background for discussions.

After an introduction, the plenary papers were presented and followed by a division of the participants into 3 working groups: coral reefs, seagrasses, and mangroves. These discussions concerned the major features of each system and critical limiting factors. Summaries of these separate discussions were given in plenary session.

Working group sessions then continued on potential interactions between the three systems. The group recognized two kinds of expertise at the Workshop, system specialists and regional specialists. It was agreed to divide along these lines with the system specialists providing a framework for the regional specialists to describe their particular region.

Finally, the group in plenary session agreed on a general format for a final document summarizing the Workshop and this was then drafted by several groups. The group sanctioned this document in outline form at a final session.

Discussions and plenary sessions were complemented by three field trips to types of ecosystems forming the theme on the conference.

## C. Acknowledgements

The idea for this Workshop was originally conceived by Dr. Marc Steyaert of UNESCO (Paris) and he was a guiding force in its successful completion. The Editors wish to thank Dr. Euna Moore and especially Dr. Gilberto Cintron for able assistance in the preparation of this report. The staff of the West Indies Laboratory contributed freely, often on their own time, to insure the comfort and support of the workshop participants. The UNESCO Regional Office for Science and Technology for Latin America and the Caribbean (ROSTLAC) in Montevideo, especially Serge Caschetto, was very helpful in financial and publication arrangements. Special thanks to Ms. Dorothy Rowe for managing logistic details of the Workshop and for typing the various drafts and ultimate final report.

## D. Literature Cited

Odum, W. E. 1970. Utilization of the direct grazing and detritus food chains by the striped mullet *Mugil cephalus*. *In*: J. H. Steele (ed.). Marine Food Chains - *University of Calif. Press* pp. 222-240.

Ogden, J. C., R. Brown, and N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: Formation of halos around West Indian *patch reefs.* Science 182: 715-717.

Ogden, J. C. and J. C. Zieman, 1977. Ecological aspects of coral reef seagrass bed contacts in the Caribbean. Proc. Intl. Coral Reef Symp. 3: 377-382, Miami.

Ogden, J. C. and P. R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). Mar. Biol. 42: 273-280.

Phillips, R. C. and C. P. McRoy (eds.) 1980. Handbook of Seagrass Biology: An Ecosystem Perspective. Garland STMP Press, NY 353p.

Randall, J. E. 1965. Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. Ecology 46: 255-260.

UNESCO, 1978. Coral reefs research methods. UNESCO monograph on oceanographic methodology. No. 5.

UNESCO, 1981. Bibliography on mangrove research. UNESCO.

UNESCO. Asian Symposium on Mangrove Environment Research and Management, 25-29 August, 1980. In preparation by the University of Malaya, Kuala Lumpur.

UNESCO. Mangroves: research methods. In preparation, UNESCO monograph on oceanographic methodology.

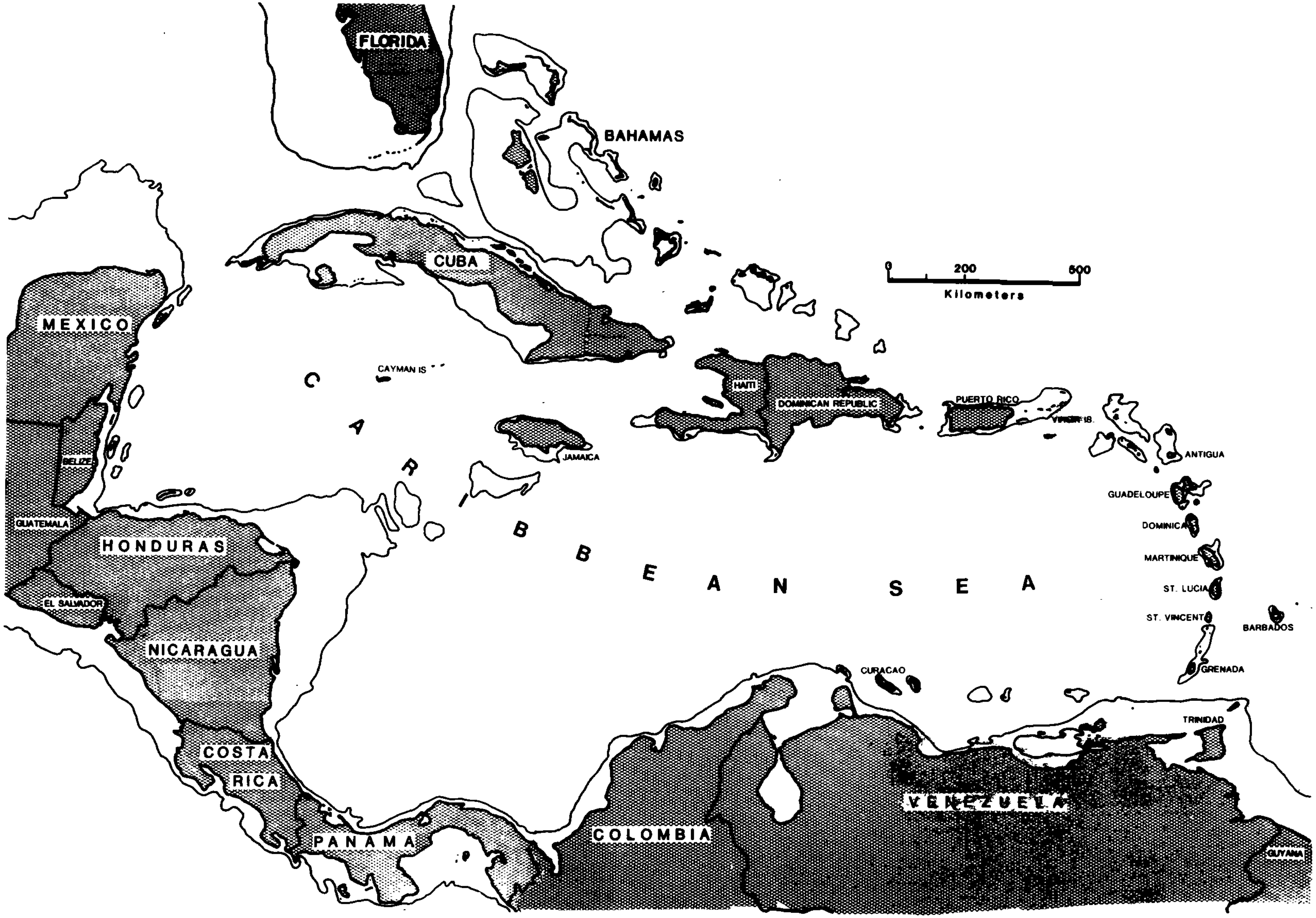

Fig. 1. A map of the Caribbean Sea, identifying the principal land masses defining its limits.

# II. CORAL REEFS, SEAGRASSES AND MANGROVE ECOSYSTEMS: THE CONNECTIONS

## A. Introduction

The participants in the discussion group on ecosystem interactions included scientists with knowledge of coral reefs, seagrasses and mangroves who represented regions of the Caribbean ranging from continental coasts to oceanic islands.

The first meetings of the group developed detailed conceptual models of processes that occur within each type of ecosystem. These led to more complex models of possible interactions between any combination of two or all three types of ecosystems considered (for example, Fig. 1). The subsequent discussions took into account regional examples which emphasized the complexity of interactions and their geographic variability. In spite of this, the group was able to classify the interactions into five major types (Figure 2). The following statements describe in some detail each of these interactions and their potential effect on the ecosystems involved.

## B. Physical Interactions

Coral reefs, seagrasses, and mangroves interact physically in a number of ways. Reduction of water energy, sediment relationships and flow regulation are all important. Seagrasses and mangroves are highly dependent on hydrodynamic barriers such as coral reefs which dissipate wave energy. The seagrass and mangrove communities are enhanced in structure when these barriers are present.

Reefs are active producers of carbonate skeletal material. Their high rates of carbonate production allow the construction of complex and massive calcareous structures. Rates of upward growth of reefs may be as high as 20-40 cm/100 yrs. The resultant structures are effective barriers which dissipate wave energy and create low energy environments in their lee. The reef also reduces the action of currents on shorelines, thus preventing erosion in those areas.

Large amounts of skeletal materials are constantly produced in the reef front, broken up by abrasion and ground into smaller fragments. Biological activities by fishes, urchins, and boring sponges are also important in the breakdown of these calcareous materials. These processes lead to the formation of gravels, sand, and silts, some of which are transported by waves and currents into the lower energy depositional environment behind the reef front. Molded by waves and currents, the sediments form shoals and islands and accumulate as sediment aprons which become the reef lagoon. They eventually may be colonized by seagrasses and mangroves. A living reef, growing faster than it is being eroded ensures the maintenance of this barrier to wave energy and thus the presence of a lower energy environment favorable for seagrasses and mangroves.

There are two ways that activities of the seagrass community influence other communities. Seagrasses 1) trap and stabilize sediment, and 2) produce sediment. Trapping and stabilizing sediment is important for adjacent coral reefs because it prevents abrasion or burial of reefs during storm conditions. It can be a disadvantage, however, in areas where lagoonal deposition exceeds removal of sediment so that the lagoon encroaches upon and buries the back reef areas. Seagrasses also produce sediment, by the activity of the associated calcareous algae, epiphytes and infauna. In some areas, this carbonate production can exceed the contribution made by reefs to sediments.

Mangroves develop in low lying coastal areas bathed by saline water. The fringe and basin forests act as depositional basins and are effective binders of sediments. As a result the sediment loads into coastal waters are reduced, and normally there is little if any resuspension of fines as a result of shoreline erosion or scour by waves.

Fringe and basin forests also regulate fresh water flows into coastal areas. Fresh water stored in the forest may be lost to evapotranspiration; the rest dissolves and dilutes excess salts accumulated in the inner fringes during periods of drought. Thus the volume of undiluted fresh water reaching the coast is reduced. It is also discharged over a longer time period, and as a result salinity changes are probably buffered.

## C. Nutrients

The inorganic nutrients phosphorus and nitrogen are essential to the primary producers of all ecosystems. In most marine systems nitrogen is considered to be the most limiting nutrient, and this is probably the case for coral reefs, seagrasses and mangroves. Each of these systems utilize dissolved nutrients and hence reduce the concentration of these nutrients as water passes through the system. This would be true for oceanic waters flowing across a coral reef or for river runoff flowing through a mangrove swamp.

In terms of absolute nutrient requirements, however, it is probable that the systems would rank in the order: mangroves > seagrass beds > coral reefs. Mangrove forest structure is positively correlated with high nutrient inputs; seagrasses in turn tolerate a higher level of eutrophication than coral reefs, while reefs are basically oligotrophic systems least tolerant of nutrient enrichment. The best coral reef development is always found on the driest and most nutrient-poor Caribbean coasts. The close linkage of producers and consumers already described for the coral reefs is typical of the kind of tight mineral and energy pathways found in all oligotrophic ecosystems, whether terrestrial or marine.

Mangrove and seagrass systems tend to "leak" or export nutrients. Some of the nutrient excess may also be tied up as peat in each system: but a sizeable fraction of the surplus may leave these systems as dissolved and particulate organic matter (D.O.M. and P.O.M.), some of which may in turn nourish reef organisms.

Animals also transport nutrients between these ecosystems. Any creature, from birds to invertebrates, that resides in one ecosystem but feeds in an adjacent different system has the potential for moving nutrients. For example, birds that nest in the mangroves and feed in seagrasses move nutrients into the mangroves by defecating there after returning from feeding.

### D. Dissolved Organic Matter (D.O.M.)

D.O.M. is a normal component of runoff from land. It is derived from leachate from the leaves, stems and roots of living plants, decomposing plant litter, soil organic matter and animal wastes. D.O.M. is often a complex mixture of compounds, some of which are less soluble in sea water than in fresh water. When fresh water runoff with a high D.O.M. content mixes with sea water some of the D.O.M. is precipitated as a floc, which can be fed upon by some marine organisms. In addition, decomposition of the organic matter may release inorganic nutrients. Mangrove runoff, and to a lesser extent, water flowing out of seagrass beds, often have appreciable D.O.M. content.

Coral reefs produce D.O.M. as mucus exudate from polyps. Exudates are also produced by reef plankton and bacteria. Physical abrasion, breakage and crushing of reef components by wave action promotes the release of D.O.M. on the reef. Although all three systems produce D.O.M., there is a pattern of net export in the direction mangroves → seagrass beds → coral reefs. D.O.M. concentrations are higher in mangroves than in other systems.

### E. Particulate Organic Matter (P.O.M.)

Large amounts of particulate organic matter enter the sea in estuaries as flocculated D.O.M. (see previous section) and as partially decomposed mangrove and seagrass leaf detritus. Mangroves export a large portion of their net production as leaf and woody litter. Much of this material is transported elsewhere by water currents, as it is being acted upon by micro-organisms, zooplankton, ciliates, nematodes, and other organisms. These organisms break the detritus into ever smaller fragments. A small detritus particle (with its associated microbial community) constitutes a protein rich food source for larger marine organisms.

Seagrasses can also contribute considerable quantities of leaf detritus to the water column, rivaling mangroves in their leaf production rates. Since the grass blades remain floating for long periods, the P.O.M. originating in seagrass beds may disperse far from source areas.

Coral reefs produce considerable amounts of mucus which mixes with other organic substances to create "snow-like" particulates nearly always found in reef areas. The presence of schools of fish nibbling on algae growing on the reef proper generates organic particulates by the abrasive action of the fish as well as the result of the production of fecal material.

Zooplankton communities within the three ecosystems produce fecal pellets that, upon breaking down, contribute to the production of particulates. Finally, all these organisms (phytoplankton, zooplankton, various invertebrates and vertebrates) contribute to organic exudates that end up in P.O.M. after being subjected to physical-chemical processes.

Autochthonous P.O.M. is scavenged by suspension and detritus-feeders within each system to differing extents; more escapes from mangroves and seagrass beds, less from coral reefs.

## F. Animal Migrations

Animal migrations form an important link between coral reefs, seagrass beds and mangroves. The different kinds of migrations can be schematized in terms of gain or loss of energy for an ecosystem. Two types of migrations are known: (1) Short-term feeding migrations which are either diel or seasonal; (2) Life-history migrations between systems. The net result of both is a transfer of energy from the system where feeding or development occurs to the system which shelters the adults.

### 1. Oceanic Interactions

The major organic input from the pelagic system is in the form of plankton. The input takes two forms. First, that which is consumed directly by planktivorous fishes, the principal concentration of which is on or above the seaward site of reefs. In suitable areas the numbers and biomass of such fishes can be considerable. Also of importance are fishes such as *Harengula* spp. which utilize lagoonal areas such as docks or shore-fringing reefs or mangroves for diurnal shelter and undergo nocturnal foraging migrations to feed on oceanic plankton. Such schools may consist of thousands of individuals. The second major form that such input takes is larvae, produced outside a particular coastal system, which are successfully recruited to a given system from the plankton. This may include economically important species with long larval lives such as lobster or many fishes or it may include forms consumed after recruitment including a wide variety of prey items. In addition some seabirds which typically roost within the coastal system (above fringing reefs, in mangroves, or rock shores) such as boobies or frigate birds feed on small fishes offshore thus providing energetic input into the coastal system. Vast numbers of adult shrimp (*Peneus* sp.) move offshore from mangrove lagoons and estuarine areas for spawning.

### 2. Adults

Energy transfer by organisms which utilize separate systems for shelter and feeding is recognized as being a potential net transfer between the systems. This relationship can be divided into two obvious strategies: (1) Edge (peripheral) feeders and (2) Migratory feeders.

Edge (peripheral) feeders are those organisms which utilize a system for shelter and also may feed there to some degree but travel away from the sheltering system to feed on nearby sources. Their normal migration is of short distance. Urchins (*Diadema*) and parrotfish (Scaridae) demonstrate this strategy around coral reefs to produce the obvious edge effect or "halo" around Caribbean reefs. A similar type of feeding strategy may be used by organisms which utilize mangroves for shelter.

The second strategy of migratory feeding is utilized by organisms which normally travel a greater distance for resources. Again these organisms utilize one system for shelter but have developed strategies for long migrations usually during specific periods to avoid predation (usually at night). Coral reef dwellers such as grunts and snappers are known to actively feed on seagrass beds at night and return to the coral reef for shelter. Green turtles are known to feed actively on seagrass beds and have been observed to occupy the coral reef between feeding bouts. Other organisms such as the barracuda and lobster actively feed between ecosystems. Migration of mangrove dwellers is not well known but is also a potential exchange.

The transfer of energy between ecosystems by organisms should be considered significant and may enhance other pathways of energy flow. For example, secondary production may be stimulated by periodic nutrient pulses provided by migrating organisms.

### 3. Juveniles

Coral reefs are known for the diversity and abundance of their fish and invertebrate faunas. Seagrass beds and mangrove areas are recognized as important nursery areas for many important commercial and forage organisms as well as some of the reef species.

The nursery function of the mangroves and seagrasses is due mainly to the availability of shelter for juvenile organisms and to an abundant supply of organic detrital food. Numerous and abundant organisms have their earlier life stages in the seagrass or mangrove regions and later move away from these systems or migrate offshore. Among the better documented cases are the spiny lobster, *Panulirus argus*, the pink shrimp, *Penaeus duorarum*, and various grunts and snappers (Haemulidae and Lutjanidae).

After lobster spawn, the larvae have a protracted pelagic existence and settle among the roots of mangroves or in seagrass beds. As the juveniles grow and the mangrove roots or holes in the seagrass meadows no longer provide sufficient shelter, they move off to the deeper surge channels and reefs where they generally hide by day and emerge at night to feed.

Post-larval grunts and snappers initially recruit to the inshore regions of seagrass and mangroves. The snappers are more dependent on the mangrove than the grunts. The small juveniles then move into the mangrove roots and seagrass canopy, but quickly form small schools around any available shelter in these areas. As they grow, they show more of a schooling habit and might form schools over rocks, patch reefs, and other forms of shelter. Here they also adopt the feeding habits of the adults, living in schools around the shelter by day and migrating to forage in the surrounding grassbeds by night. As their size increases, they move to larger outer reefs or to other areas.

Pink shrimp spawn in deeper waters often on the same grounds where commercial fishing occurs. Although they have a larval existence, it is relatively short compared with that of a lobster encompassing only a few weeks. The juveniles live in seagrass meadows and mangrove areas where they have abundant detrital food, shelter, and reduced salinity. As they grow larger they will bury in the sand by day and move into the seagrass meadows or other vegetated areas to feed at night. As they continue to grow they progressively migrate offshore and then into deeper water where the major commercial fisheries occur.

In this way, the mangroves and seagrass beds act as nurseries, providing food and shelter for these juvenile organisms. However, the organisms are forced to migrate as they mature, because they become sufficiently large that the mangroves and seagrasses can no longer supply sufficient protection. In fact it is due to these juveniles and their migrations that seagrass meadows and mangrove regions are also excellent fishing grounds for larger predatory fishes such as redfish, tarpon, snook and other high carnivores that forage on the juveniles in these regions.

### 4. Plankton

Extensive epiphytic growth is known to cover mangrove roots. Main components generally are molluscs, sponges, hydroids, bryozoans and ascidians as well as macro-algae. The larger part of these epiphytes are restricted to this habitat. These organisms produce planktonic larvae; a certain part of these larvae will be carried by water-movements to the other systems and serve as a potential food source there. On the other hand, this fauna largely consists of filter-feeders which will benefit from planktonic larvae produced in the reef or in seagrass meadows; the extent of this exchange is unknown.

Gradients of organic material (fine particulates, etc.) emanating from mangroves adjacent to seagrass beds provide a source of food which enhances growth of suspension-feeders close to the mangroves.

### 5. Seasonal Movements

Seasonal movements are not well documented but must be considered as a potential and perhaps important interaction between components of the Caribbean coastal system. Most of these movements probably involve seasonal spawning movements from one area to another. Fishes such as tarpon and snook are believed to move from their respective foraging grounds on seagrass beds or mangrove to spawn over reefs. The goby (<u>Gobionellus oceanicus</u>) moves into mangrove lagoons to breed. Perhaps to ensure better dispersal of their spawn in some areas, spiny lobster, Panulirus argus, migrate (seasonally?) across seagrass beds and other flat bottom communities providing an exchange both between different reefs and between reefs and intervening grassbeds. Diurnal resting schools of Harengula spp. seasonally shift their location potentially moving between and through components of the coastal system. Large sea urchins (Astropyga sp.) are believed to make migrations from deep flats into shallower seagrass beds, perhaps on seasonal spawning migrations.

## G. Human Impact

It is conceivable that in a properly managed Caribbean coastal zone, human activities could be so directed as to have beneficial effects on the three component ecosystems. Generally, however, human impacts disturb the systems to varying degrees, ranging from trivial amounts to complete destruction. Disturbing factors may be physical, chemical or biological (for example, tree-felling, nutrient pollution or over-fishing) but each can cause disturbance in the other modes and thus affect any of the flows between the systems. In particular, they may affect the sediment control function, the release of dissolved and suspended nutrients or the migrations of economically important animals.

In the case of mangrove and seagrass communities, extreme disturbance means destruction; there are no alternative systems. Coral reefs, are more sensitive and may be transformed to other hard-bottom communities, usually dominated by algae.

Known impacts on the systems are as follows:

### 1. Mangroves

Direct, deliberate, physical disturbance included logging and stripping bark for tanning. The ultimate, all too common, is destructive disturbance in clear-cutting and filling to create dry land. Other disturbances which may result in the death of mangroves include oil spills and thermal effluents. At lower intensities they will reduce secondary productivity. Detrimental chemical pollution may result from garbage dumping as well as from the concentration of pesticides. Direct biological disturbance takes the form of fishing which, as in all systems, can be excessive, resulting in the depletion of fisheries stocks.

### 2. Seagrasses

Physical disturbance includes anchor and propellor damage, but complete destruction is common in the form of dredging and sand mining. Other coastal engineering works may so alter currents that seagrass beds are destroyed. Seagrasses, like mangroves, can show reduced productivity or death as a result of pollution by heat, oil, other chemicals or excessive organic material such as sewage effluents.

The animal communities of seagrass beds are readily over-fished because of their accessibility and visibility. Beach-seining for little fishes is very destructive. Conch (Strombus spp.) and edible echinoid populations (Tripneustes sp. ) have been drastically reduced in some parts of the Caribbean.

### 3. Coral Reefs

Coral reefs are biologically more complex than the other systems. Members of the community respond to differing degrees of stress so that the reef may be progressively (and impercebtibly) transformed from a "healthy" reef, to a "sick" reef, to "dead" reef. In the last instance, although most of the corals may be dead, certain algae may yet flourish. Reefs are killed in this sense more often than they are physically destroyed, although this does happen in coral mining and in some coastal engineering works.

The best documented human impact on coral reefs is through activities which deposit unusual loads of sediment on them. Island soil erosion through careless agricultural practices, destruction of mangroves and seagrasses, dredge-and-fill operations and other coastal engineering works can all have this effect. Sediment reduces illumination, physically interferes with feeding and respiration, and drains energy in cleansing activities of corals; the stress is often too much for them.

Corals, due to their symbiotic algae, are adapted to live in water containing very little inorganic nitrogen and phosphorous. Free-living plants do not flourish in such waters. Nutrient enrichment, which can be due to sewage or fertilizers, will encourage the growth of free-living algae which may then successfully compete with corals for space and light. This is especially likely in enclosed bodies of water but could happen on open coasts. The detrimental effects on reef communities of other chemical pollutants such as oil and pesticides have been documented.

Over-fishing can easily occur in coral reefs. In many Caribbean localities changes in the fish populations have been documented; reduction in abundance, mean size and size composition have occurred in many areas. Large deep-bodied fishes such as the queen triggerfish (Balistes vetula) and angelfish (Pomacanthidae) are especially susceptible but most important carnivore and herbivore populations suffer. It is highly probable that the benthic community will change in consequence.

## H. Consequences of Destruction and Disturbance

### 1. Mangroves

In the case of riverine mangroves, destruction will allow terrigenous sediments to flow onto seagrass beds and coral reefs, possibly causing temporary damage to the former and permanent damage to the latter. In the case of fringing mangroves there would be less effect as only superficial runoff is involved. There will be an excessive outflow of particulate and dissolved organic matter which may cause smothering, shading and eutrophication. Later, nutrient inputs to other systems will be reduced; seagrasses, at least, will be less productive. Finally, refuges and nursery grounds for various fishes and invertebrates will be destroyed and secondary productivity on seagrass beds and reefs will be reduced.

### 2. Seagrasses

Sediments rendered unstable by removal of seagrasses can be shifted by currents or storms and may have a deleterious impact on adjacent seagrass beds, mangroves, coral reefs, beaches or navigational channels. There will no longer be a supply of P.O.M. exported to other systems and secondary productivity will be reduced. A nursery and feeding ground for reef fishes and invertebrates will have been destroyed.

### 3. Coral Reefs

There are two levels of "destruction". A reef community may be killed, or the reef framework might be destroyed. The actual removal of the reef framework might remove physical protection from wave energy and allow erosion of sediments from the coastal zone. "Killing" a reef does not have such as immediate effect, but it may allow reef erosion to occur. In any case, the increased biomass of algae and grazing organisms may produce more sediment. The small stock of nutrients stored in the reef community would be lost to adjacent systems, but would have little direct effect on them. The macrofauna of adjacent systems would be changed; some young fishes would have nowhere to go, and secondary productivity would be reduced.

### 4. Summary

All three systems are inter-connected in numerous ways but in undisturbed systems, different pathways are more important. Thus, a flow of dissolved nutrients from mangroves has been shown to enhance primary productivity of seagrasses. Seagrass beds and mangroves enhance secondary productivity of coral reefs by providing alternative feeding sites. Sediment control functions are more cryptic and their importance becomes apparent when the systems are disturbed. In practical terms, the more critical impacts flow from land to sea; it is more common for reefs to be damaged by impacts on the other systems than *vice-versa*.

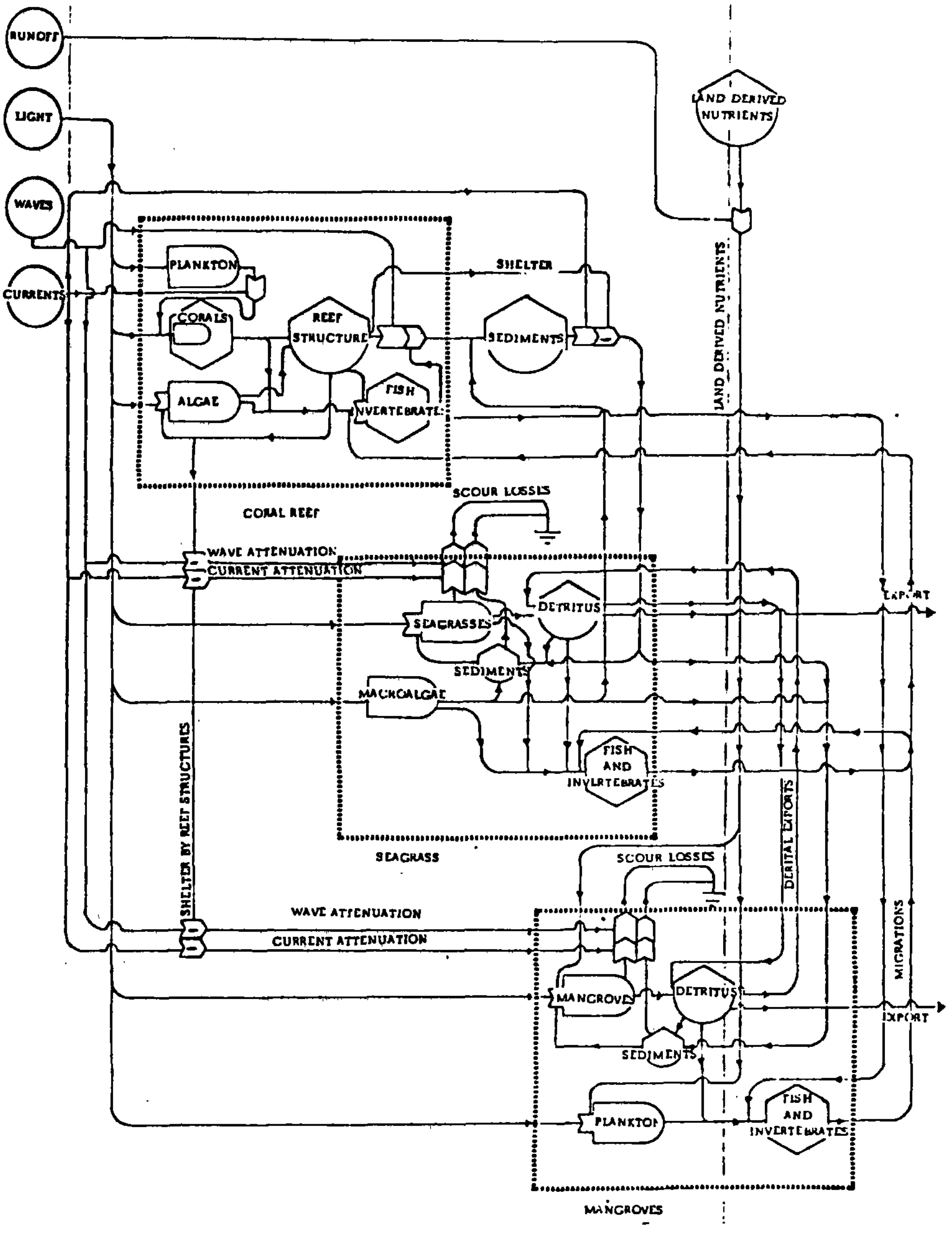

Fig. 1 (from Dr. Gilberto Cintron). Complex ecosystem circuit diagram showing potential connections between coral reefs, seagrasses, and mangroves in the Caribbean coastal zone.

The three ecosystems, isolated by heavy dashed lines, consist of plant (⊂⊃ ), animal ( ⬡ ), and accumulations of structure or material ( ⬠ ) as major compartments. Flows between the compartments of each system are regulated by functions ( Σ▷ ), or valves, often controlled by external factors shown as open circles. This complexity can be reduced conceptually to much more simple terms.

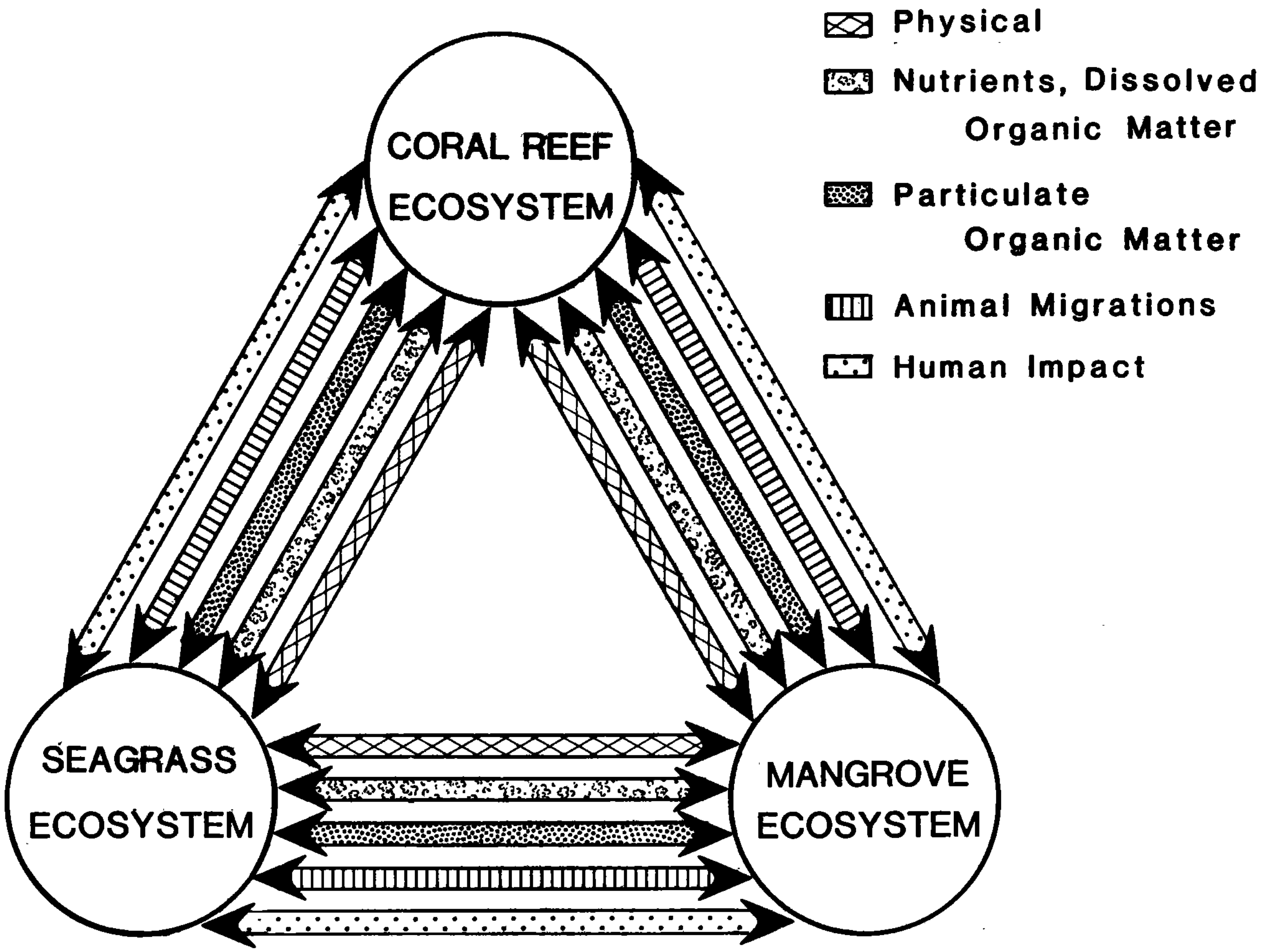

Fig. 2. Major types of interactions between tropical marine ecosystems.

# III. INVENTORY OF COASTAL ECOSYSTEMS AND EXISTING RESEARCH AND TRAINING FACILITIES

Participants in the Workshop were asked to write a short discussion of the state of knowledge of the coastal zone in their region. The extent of this knowledge, a necessary first step in understanding the functioning of the coastal zone, is dependent upon the existence of research and training facilities. Clearly some countries are much more capable in this area than others. It was agreed by the participants that a suitable goal would be to spread scientific knowledge through the region. This would best be done by exporting of scientists and research and training expertise from the more developed to the less developed countries rather than sending students from less developed countries to foreign educational research institutions.

Table I shows the extent to which the coastal zone is known among the diverse regions of the Caribbean with an indication of the marine research facilities and support capability within the particular country. Table 2 gives a summary of the principal fisheries in each country.

## A. MEXICO - Dr. Eric Jordan

The Atlantic coastline of Mexico can be roughly divided in two parts: the Gulf of Mexico and the Caribbean coast. The Caribbean coast of Mexico is formed of carbonate bedrock in which there are no rivers, and therefore very little runoff. Along the shoreline there is a more or less continuous barrier/fringing coral reef that extends for about 300 km. from the Belize border to Cancun Lagoon on the NE Yucatan Peninsula.

Between the reef and the coastline a reef lagoon is present, with an average width of about 3 km. The floor of this lagoon is covered with seagrasses, principally *Thalassia testudinum*. Mangroves are restricted to bays or coastal lagoons, although they may cover enormous areas mostly in the southern Mexican coastline. Their full extent is not presently known. The contact between these ecosystems is mostly between coral and seagrasses, as the mangrove systems are quite isolated in coastal lagoons.

Mexico has developed its research and training capability extensively on the Caribbean coast in recent years, but the level of knowledge of the coastal zone is still only moderate and considerable effort in the inventory of the coastal zones will be required.

## B. GUATEMALA - Prof. Carlota Monroy de Gomez

The Atlantic coastal ecosystems in Guatemala have not yet been studied. There is a rich mangrove area that will be surveyed within a short time. To study seagrasses and coral reef ecosystems, we need well trained experts that will help us in the basic inventory. The use of remote sensing techniques would make the work easier. Capability in the marine sciences is not well developed in Guatemala. It is necessary that Guatemala join a Regional Project concerning the investigation of these ecosystems and seek the training of scientists to undertake their management.

## C. NICARAGUA - Sr. Sergio C. Martinez

Most of the Caribbean coast of Nicaragua is a high energy area with an extensive estuarine mangrove system, especially red mangrove which supports a large amount of life. Many species of fishes occur here and all commercial shrimp species spend part of their lives in the numerous coastal lagoons. At the moment, we don't know the extent and distribution of mangroves. Nicaragua has extensive seagrass beds which are the natural feeding grounds of the green turtle and also support a large and unexploited population of conch (*Strombus* sp.).

Coral reefs are scattered about the Nicaraguan shelf in more or less isolated patches but not forming a solid reef structure. Some recent research showed a large rocky area on the shelf covered with coral. This formation is called "Cordillero o Sierra Central." Bathymetry and pieces of coral in nets suggest an extensive coral formation, but this formation is as yet unexplored.

Nicaragua needs extensive assistance in the development of inventories of the coastal zone, in the assessment of interactions between the major components, and in the eventual management of coastal marine resources.

## D. COSTA RICA - Dr. Manuel M. Murillo

### 1. Shoreline Morphology and Dynamics

The Caribbean coast of Costa Rica is predominantly a straight line extending from the Nicaraguan to the Panamanian borders. Along this line there are several estuarine zones, associated with the mouths of major rivers which alternate with a few small indentations and peninsulas. The coast is basically sandy with limited rocky patches and flats dominated with terrigenous sediments.

The high energy characteristics of this coastline are associated with a narrow platform and the prevailing strong currents moving in a north to south direction. In the inland area, parallel to the coast, a series of natural channels and small lagoons serve as the limiting barrier for shore vegetation. Although the shores are mostly sandy, there has been a recent input of terrigenous sediment due to human-induced changes along the Atlantic lowlands, basically for agricultural purposes. This sediment load is assumed to play an important role as a limiting factor for the development of some reefs and seagrass beds.

### 2. Major Coastal Ecosystems

a. Coral Reef - There is only one well-developed reef formation along the Costa Rican Caribbean coast. This coral reef is located south of Limon, at Cahiuta. Sparse, isolated coral growths occur elsewhere between Limon and the Panamanian border.

b. Seagrass beds - Several large patches of *Thalassia*-dominated seagrass beds occur from the northern Tortuguero area to the southern part of the coast. Associated *Thalassia* and coral reefs occur at Cahuita.

c. Mangrove - Conditioned by the high energy shoreline and the freshwater channels which run along most of the Caribbean coast of Costa Rica, mangrove growths are basically of the fringing type, alternating with riverine types occurring along the mouths of the major rivers.

### 3. Ongoing Research

Research efforts are basically oriented to describe the structure, and to provide information regarding the dynamics of coral reefs and mangrove systems. Only recently has attention been given to the study of seagrass beds.

### 4. Research Needs

Need for extensive studies of the three types of coastal ecosystems has been recognized due to the foreseable impacts of human-induced changes and long-term chronic effects of accumulated chemicals. In recognizing the importance of protecting these vulnerable ecosystems, the Government of Costa Rica has declared the Tortuguero seagrass beds and adjacent shoreline and the coral reef at Cahuita a national park and national monument respectively. Research projects incorporating components of structure, function, and interaction of these ecosystems are to be intensified. As a condition to do so, the training of appropriate scientific and technical personnel is desirable.

### 5. Ecosystem Exploitation

Coral Reef: Tourism, popular and scientific is the main activity, although fisheries (fish, lobster, molluscs) of the artesanal type are done by local people.

Seagrass beds: Turtle fisheries are common outside the limits of the Tortuguero National Park and in the *Thalassia* beds associated with the coral reef at Cahuita.

Mangrove forests are exploited as wood and lumber sources. Fisheries mainly of a subsistence artesanal type are common.

## E. PANAMA - Sr. Luiz D'Croz

The Republic of Panama has 600 kilometers of coastline along the Caribbean Sea. The continental shelf is narrow, with dominance of hard bottoms (mainly corals and sands). Three types of coastal communities are common: coral reefs, turtle grass beds and mangrove swamps.

Coral reefs are composed of at least 50 species of hermatypic and 16 species of ahermatypic scleratinians, and 4 species of Millepora. Coral reefs in the area generally extend down to 45 meters, however, isolated patches have been reported to 70 meters of depth. Distribution of coral species is in some cases very peculiar. Species like Acropora palmata are generally found not deeper than 5 meters, while the highly dominant Agricia agaricities is found to 70 meters. Productivity of these reefs has been estimated at 1,400 - 2,000 gC/m$^2$/year, based on chlorophyll content in corals.

Thalassia testudinum and other spermatophytes form large patches from the lower intertidal zone to depths of about 10 meters. Preliminary estimates of the Thalassia leaf biomass are around 96 ± 15 grams of dry weight/m$^2$ in unsheltered areas. An associated biota of 96 species of animals has been collected by the author over the seagrass beds and nearly half of them were fishes. However, other investigations have reported about 100 species of invertebrates in turtle grass meadows. Turtle grass mean primary productivity has been assessed in nearly 1,500 gC/m$^2$/year, according to the oxygen metabolism of the plant.

Observations on the biota associated with mangrove swamps showed a fish community with dominance of juveniles of mojarras, mullets and grunts. Diversity estimations have been made for this community. Research on mangrove crustacean decapods reported about 17 species. Among the most abundant species of mangrove decapods are Panopeus herbstii, Uca rapax and Sesarma curacaoense.

Panama has a research and training capability in the University and through a strong association with the Smithsonian Tropical Research Institute which has maintained a laboratory with numerous investigators on the Atlantic coast for the past 15 years.

## F. VENEZUELA - Dr. Frederico Pannier

The Venezuela coast offers excellent conditions to perform integrated mangrove-seagrass-coral reef research. One quarter of the total coastline is covered by mangroves according to a recent inventory made by the Ministry of Environment. An inventory of seagrass bed and coral reef areas has yet to be performed. Major coastal problems are related to sedimentation, hydrological and salinity changes and pollution.

Sedimentation problems can be specifically located in coastal lagoons and in the coasts of the Golfo de Venezuela. There are two major cases. The Laguna de Counetas in the frontier with Colombia offers a case of rapid sediment filling, in which mangrove takes a major role. This is a case of a lagoon in an extreme climatic zone. All the three ecosystems are present in a very restricted area. The mangroves of the Cienaga Los Olivitos, at the northeastern coast of the Golfo de Venezuela are degrading thanks to the blockage of natural flushing channels due to heavy sedimentation from geomorphological changes occurring in the Western coast of the Golfo de Venezuela.

Hydrological and salinity changes are of great importance in portions of the coastal zone dominated by rivers. Climatic fluctuations of fresh water runoff in estuaries of the Maracaibo basin and the Orinoco River leads to changes in populations of organisms and primary productivity in each of the involved estuarine and near-estuarine ecosystems. The construction of river dams in the western and central coastal zone will have great potential impact. How this fresh water diversion will affect the ecosystems in the coastal zone is worthy of intensive study.

The principal pollution problems in the Venezuelan coastal zone are industrial effluents, the impact of oil exploration, drilling, and spills and contamination from oil refineries, and domestic and industrial effluents into low circulation coastal lagoons.

### G. SURINAM - Mrs. Dorothy Resida

Geographically the Surinam coast forms a part of the Guiana coast consisting of the nearly 2000 km muddy and sandy shore of the Atlantic Ocean between the mouths of the Amazon and Orinoco Rivers. The coast of Suriname consists mainly of vast tidal mud flats covered on the higher parts with mangrove forests. The mud flats alternate in space and time from an accretion coast to an erosion coast. As a result of the rapid succession of accretion and erosion the coast has a rather unstable shoreline.

Landward, the coastal fringe is bordered by a wide zone of shallow lagoons and brackish herbaceous swamps, broken by several sand and shell ridges lying parallel to the coast. These ridges mark sites of previous shorelines. The lagoons are former mangrove forests in which the Avicennia has died after a prolonged inundation by seawater, either as a result of the lack of oxygen for the roots or as a result of the raised salinity caused by strong evaporation during long periods of drought. The mangrove vegetation covers about 2400 km$^2$. The black mangrove is mostly found along the coast above high tide level. The red mangrove is found along the stable banks of the brackish-fresh water rivers and the white mangrove grows along the brackish creeks.

The estuarine zone is being threatened by expanding ricefields, cattle meadows, the use of pesticides, sanddigging on the narrow beaches by building contractors and bad road construction. To limit unwise usage of this area and to manage it optimally, it is necessary to proclaim it as a Special Management Area. Such a Special Management Area will enable decision makers to plan development for the best suitable destination purposes while preserving the integrity of this coastal ecosystem. In this way the Estuarine Zone and the way it functions will be preserved. It may then be possible to increase the natural production. Part of the coast is already protected by three nature reserves: Coppename Reserve (100 $km^2$), Wia Wia Reserve (360$km^2$) and Galibi Reserve (40 $km^2$).

Dr. Tom Van't Hof

## H. NETHERLAND ANTILLES - Dr. Rolf Bak

Extensive fringing reefs exist in Aruba, Bonaire and Curacao. The major part of these reefs is situated along the southwestern leeward coasts of these islands. Reefs are locally well developed along the windward coasts although algal pavements (Sargassum and crustose coralline) are dominating here.

In Bonaire and Curacao nearly all seagrass meadows and mangrove stands are limited to a few land locked bays. Because of the aspect of these bays, the direction of the prevailing winds and the limited run off, exchange of P.O.M., D.O.M., and nutrients between these systems and the reef may be limited. The migratory aspects of interaction, such as movements of juvenile fish, are at least locally of importance.

Larger seagrass meadows exist along the leeward coast of Aruba. The best developed meadows are in a position down current of the major reef development and the possible pathways that may exist between these meadows, the reefs and a mangrove forest at the central part of this coast have not been investigated.

For the Netherland Windward Island Group reef development appears to be restricted to scattered coral communities. Seagrass meadows are present along the coasts of Saba, St. Eustatia and St. Maarten but significant mangrove stands occur only in St. Maarten.

The impact of man on the reefs has locally been considerable, especially along parts of the coasts with urban and industrial development. Seagrass meadows and mangroves have locally suffered from the same interference as well as from recreational activities. However, the whole underwater environment of Bonaire is conserved and managed as a National Park. For Aruba and Curacao the larger part of the reef is flourishing although spearfishing is a matter of concern in these islands.

Because of the dominance of the coral reefs, research carried out by the Caribbean Marine Biological Institute (CARMABI) has focused on this system. The inventory phase of the research, which included mapping of the main components, is largely finished. The results of extensive descriptive and experimental ecological studies are being used in the management of the reefs.

## I. TRINIDAD AND TOBAGO - Dr. Eugene Ramcharan

Trinidad is essentially an estuarine island with the nearshore marine environment heavily influenced by freshwater discharge from the Orinoco River. Mangrove ecosystems occur on all coasts with the greatest development being along the sheltered, low-energy Gulf of Paria shoreline. Here the mangroves are open to the sea as opposed to the communities on the other coasts which are delimited from the sea by sand bars.

Isolated and widely separated coral communities occur along the north coast and in the channels between the islands separating Trinidad from Venezuela. These have not been found near to any mangrove community. Along the gulf shoreline of the northwest peninsula, where the substrate is coarse and granular, seagrass (Thalassia testudinium) and sponge communities are common.

Tobago, on the other hand, experiences more oceanic conditions than Trinidad and the environment supports numerous reefs and reef systems, the largest being at Speyside/Charlotteville in the northeast of the island and at Buccoo/Bon Accord in the southwest. While the latter lies adjacent to a large fringing mangrove, the same cannot be said for the former.

Description of and distribution studies of these coastal ecosystems is essentially complete. The local linkages and/or interrelationships between these ecosystems, where they occur, are as yet unclear.

Occupying coastal lowland and nearshore localities which are in the path of human development, these environments are probably no longer pristine but in various stages of alteration. Wetlands are being reclaimed for agriculture and settlement and the reef organisms are removed in increasingly large numbers. Because of the active development both of the sea margins and hinterlands there are increases in the amounts of suspended inorganic materials in addition to larger amounts of domestic and industrial effluents.

The research needs of the country vis-a-vis these ecosystems revolve around the following:

a. Description of the detritus transport mechanisms - mangroves.
b. Assessment of the role of mangroves in fisheries.
c. Assessment of the alternative uses of wetlands.
d. Mangrove-coral reef interrelationship in the Buccoo/Bon Accord area of Tobago
e. Hydrological and nutrient characteristics of wetlands (mangrove-marsh) soils.

## J. BARBADOS - Dr. Euna A. Moore

Barbados, the easternmost of the Lesser Antilles, is 21 miles long and 11 miles at its widest, and 166 sq. m. in area. It is covered for its largest part by Pleistocene reef limestone. The limestone cap rises by a series of terraces to a height of 1104 ft. It has a quite regular coastline with no offshore islets. There are long stretches of coral-derived calcareous sand beaches around most of the island except at the northern end and some southern strips.

Actively growing reefs fringe most of the western coast forming crescent shaped bands fronting promontories along the coast. Shallow bays with sand or rubble bottom lie between each of the promontories and the associated reef. No actively growing reefs are found on the other coasts. Off the southern coast there are extensive rubble banks of calcareous rock but these support at present only widely scattered coral patches. The reefs along the eastern and northern coasts are composed of dead coral rock which supports only secondary growth of coral. Upwards of 33 scleractinian species have been identified in the reefs of Barbados.

In the reef flat zone the macroalgae Sargassum spp., Dictyota spp. and Padina spp. may be found, and in a few places turtle grass, Thalassia testudinum.

Inshore there were once intermittent patches of mangroves fronting the reefs, most often associated with drainage canals or streamlets. The largest mangrove stand, Grahame Hall Swamp, is found on the southwest corner of the island, with an outlet not too far removed from the greater seagrass beds in the Oistins and Silversands areas.

Associated with the seagrass bed is the local sea urchin or sea-egg (Tripneustes sp.) fishery. Other local fisheries include seaweeds, flying fish, snapper and dolphin. These are much prized for local consumption.

Over the last 15 years there has been considerable tourist development on the west and south coasts which has involved beach cleaning, emplacement of groynes, and removal of sand bars. In addition, reef dredging for building purposes and blast fishing on the reefs have provided new water channels that significantly affect the inshore current patterns. The immediate and very noticeable effects of these events is considerable beach erosion resulting in felling of trees of more than 50 years of age, undermining of building structures, and disappearance of animal populations from the reef flats, chief among them being the sea urchin (Tripneustes sp.). Coincidentally there has been a sharp decline in the seaweed and flying fish enterprises.

Despite their obvious detrimental effects, other developments on the coast are proceeding. These include sewage plants with seaward outfall areas, more extensive hotel plants, and a cement plant.

That this coastal area is stressed is obvious, and there are no proper estimates of its carrying capacity. In general, environmental and organismic tolerance levels in the area have been investigated only at the one factor level. For management purposes, there is therefore urgent need to assay environment tolerance limits at the multi-factorial level. Of no less importance, though the import may be less obvious, are the biogeochemical importance of the mangrove-seagrass-coral reef interrelationships in land formation and maintenance of coastal stability.

## K. GUADELOUPE - Drs. Claude and Yolande Bouchon
Mr. Max Louis

Guadeloupe is actually composed of two islands separated by a narrow channel. The windward island is an elevated carbonate platform of low altitude. This island possesses a discontinuous belt of fringing reefs but no seagrass beds or mangroves of noticeable importance. The leeward island is volcanic, elevated (1500m) and has, in general, a very abrupt coast. This coast is cut by the mouths of numerous rivers and is almost devoid of coral reef formations, seagrasses and mangroves. These three ecosystems are gathered in the Grand Cul de Sac Marin, a major embayment in the north, situated at the junction of the two islands. This bay has a thick coastal belt of mangroves (about 5 km wide) protected seawards by a coral reef barrier. This barrier reef encloses a lagoon (10 km wide, 30 m deep) largely occupied by seagrass beds.

Since 1977, a research program involving the participation of several French research institutions has been developed on the mangrove ecosystem of the Grand Cul de Sac Marin. Participants include Centre Universitaire Antilles - Guyane, Ecole Pratique des Hautes Etudes, Institut National de la Recherche Agronomique, Office de la Recherche Scientifique et Technique d'outre mer, Museum National d'Histoire Naturelle, Universite de Montpellier.

The main topics studied were:

- the physical environment of the mangrove area,
- the plant and animal communities of the mangrove ecosystem,
- Biomass and energy flux,
- the mangrove swamp as a nursery (birds, fishes, crustaceans).
- the nuisances resulting from the mangrove area (mosquitoes, parasitism, various diseases).
- the impact of pollution on the mangrove (sand dredging, the use of pesticides, heavy metals).
- the possible resources of the mangrove for utilization by man (wood, fishes, crustaceans, molluscs).

In this large program, the Laboratory of Biology and Animal Physiology of Guadeloupe University has more particularly studied the aquatic environment:

- the chemical and physical parameters of the water
- population dynamics of the fish communities
- population dynamics of the crab communities (Callinectes and Cardisoma).
- infauna of the mangrove swamp bottoms.

This program has involved the participation of 50 scientists and the field work is now finished. A final synthesis is planned to be published next year.

As soon as these studies are completed, the University of Guadeloupe will develop its research in two directions. First, in order to complete the knowledge of the coastal ecosystems of Guadeloupe, a comprehensive study will be carried out on the coral barrier reef and the lagoon seagrass beds situated in front of the mangrove zone, previously investigated. This coral reef will be studied by quantitative methods on a transect common to all the scientists involved in the project. The transect will run from the seaward limit of the mangrove to the outer barrier reef slope. At the moment, the mapping of this reef by aerial color photography has been completed and, in April 1982, a study of the algal communities started.

A second research project will deal with sea farming, which is now quickly developing in the French West Indies. The previous studies on the fish communities of the mangrove have shown the possible interest of local species for farming. The biology and ecology of the species which appeared to be the most suitable for that purpose will be studied in detail. These species belong to the families Pomadasyidae, Carangidae and Lutjanidae. These researches will concern: the estimation of the stocks, their turnover and the recruitment of juveniles; the growth of the species; their feeding behavior and their reproduction.

The laboratory of the University of Guadeloupe can provide accommodations and research facilities for foreign scientists interested in working on the marine ecosystems of Guadeloupe.

### L. U. S. AND BRITISH VIRGIN ISLANDS - Dr. John C. Ogden
### Dr. William MacLean

The northern Virgin Islands consisting of St. Thomas and St. John as well as Tortola and the diverse islands of the British Virgin Islands are situated on a large contiguous shelf over 300 km long shared with Puerto Rico. The only substantial bank barrier reef in this region is at Anegada in the NE British Virgin Islands. Other reef development is confined to very small fringe reefs or to corals and carbonate accumulation over often exposed bedrock. Seagrasses are well-developed along shallow sandy shelves and are often associated with mangroves or with protected waters between rocky headlands. Mangrove development is confined to only a few rather small and isolated areas as much of the terrain is steep and rivers and streams are absent. The most extensive mangrove is in Mangrove Lagoon on the south coast of St. Thomas. Much of the shelf surrounding the islands is deep (from 20 to 40 m) algal plain covered with macroalgae and several species of corals.

St. Croix to the south is isolated from the northern islands and is geologically distinct. The shelf area here is quite small and approximates that of the land (400 $km^2$). Bank barrier reefs are well-developed and form long unbroken structures protecting the coast from heavy wave action. Associated with reefs in lagoons and covering the deeper sandy portions of the shelf are extensive seagrass beds. Mangroves are nearly absent, being confined in their present natural state to one small bay, Salt River on the north central coast. A former large mangrove lagoon on the southwest coast has been taken over by industrial development.

The Virgin Islands are quite a small area and are presently well inventoried through research efforts at the College of the Virgin Islands (CVI), CVI's Caribbean Research Institute, and Fairleigh Dickinson University's West Indies Laboratory. The extent and significance of interactions between components of the coastal zone system are unknown. The area does provide, on a small scale, excellent opportunities to study interactions as the major systems may be found in virtual isolation or in nearly all possible combinations.

### M. PUERTO RICO - Dr. Juan G. Gonsalez
### Dr. Gilberto Cintron

Puerto Rico is the largest island on the extensive shelf area containing the northern U.S. and British Virgin Islands. The submerged shelf surrounding Puerto Rico is a relatively narrow band with large extensions to Culebra and Vieques Islands to the east and Mona Island to the west. Bank barrier reefs are limited in development, concentrated in the east near Culebra and Vieques, but coral reefs are extensive along the southern coast. Inshore the south coast of Puerto Rico is dominated by mangroves, especially in the bays that are scattered along the coast. Extensive gradients of mangrove development occur here and many areas are heavily influenced by man, mostly through large factories, power plants and harbors. Facing these mangrove areas are large seagrass beds with Thalassia testudinium growing in extremely dense single species. This 'climax' development of seagrass beds is unknown on the smaller islands of the Antilles.

Puerto Rico has extensive capability in marine sciences research and training through several large fisheries laboratories, a very active marine division in the Department of Natural Resources, and in several branches of the University of Puerto Rico, particularly the Department of Marine Sciences at the Mayaguez campus.

The Institute of Marine Biology, the forerunner of the Department of Marine Sciences of the University of Puerto Rico, was established in February 1953. Right from its inception, the department has devoted its efforts to the understanding of marine biota in the Puerto Rico area. Earlier research was concentrated on the classification of biological assemblages and taxonomic identification of the species present. Consequently, most of the initial published research is of a descriptive nature. References on marine copepods, algae, diatoms, coral, fish, invertebrates, etc. proliferated during that period. Mangrove and seagrass ecosystems have been studied to some extent but more research is needed on their function and interactions.

As a graduate entity of the Faculty of Arts and Sciences of the University of Puerto Rico, the department continues on its mission of training professionals in the field of marine biology and oceanography. Recently, a new phase of research was incorporated: Mariculture. This aspect has added a new dimension to the interests of scientists and Caribbean peoples as well.

## N. BAHAMAS - Mr. Edison Deleveaux

The Great Bahama Bank, while technically not a part of the Caribbean is the largest bank area in the region stretching from Grand Bahama Island (near Florida) over 1000 km to Great Inagua Island. This vast area with its myriad of islands, cays, reefs, and great shallow stretches of sand is only partially known. Fisheries in the region include lobster, reef fishes, conch, and turtles and are still in excellent condition, although use of chemicals such as bleach in fishing is having a local impact.

The area affords an excellent opportunity to study interactions between Caribbean ecosystems. For example areas protected by reefs develop extensive seagrass beds and fringing coastal mangroves while unprotected areas have only sparse seagrass and mangrove development.

Marine science capability in the Bahamas is presently limited to the field work done through the Department of Fisheries. Extensive survey work is necessary before more complex questions involving system interactions and management problems can be approached.

## O. DOMINICAN REPUBLIC - Dr. Idelisa Bonnelly de Calventi

The Dominican Republic needs an inventory and analysis of coastal resources which would permit establishment of a program of coastal management. At present the country's coastal environments are under intense pressure, given the development of tourism, industry (thermo-electric, etc.), construction of dams, and inadequately controlled fishing.

Inventory of coastal ecosystems has been initiated- mainly in reference to mangroves and reefs, but hardly any work has been done on seagrass beds. The fisheries of the principal invertebrates are located in these systems - conch (*Strombus gigas*), lobster (*Panulirus argus*), and land crabs (*Cardisoma*) - and it must be pointed out that they have declined in recent years, necessitating a study of causes.

A basic nucleus of scientists exists on relatively scant support, carrying out this work in different departments, but technical assistance is needed to complete basic aspects and accelerate the process. Training of an expanded personnel is also important to be able to understand the functioning of these systems and as an immediate step toward a solution to the problems of delineating the ecosystems and their interrelationships.

It is recognized that priority zones will have to be established (areas requiring protection, multiple use, etc.) by way of pilot studies. These zones are projected where the three principal ecosystems will be represented. In specific zones mixtures will be found, in others not necessarily. Expansion of fisheries and mariculture is one of the goals. Rational utilization of the mangroves is one of the problems.

An international mechanism could be established to collaborate in the study of these pilot programs in which research will go along with training and the search for solutions to problems. This mechanism could be useful to other countries with similar problems.

## P. JAMAICA - Dr. Jeremy D. Woodley

Jamaica, 240 km long and 80 km wide, is a high island; the forested Blue Mountains, in the East, rise to 2,250 m and the rest of the island has a mean elevation of about 500 m. Rivers drain to the north and south.

The submarine shelf of the north coast is narrow, about a kilometer wide or less, and drops steeply to the deep ocean. It supports well-developed fringing coral reefs and intermittent beds of turtle grass in the back reef zones. Extensive mangroves occur only in the sheltered embayments at Montego Bay and Falmouth.

Fringing reefs also occur on the south coast, but are less extensive. South of the Blue Mountains is a steep alluvial slope. To the west, reef development is interrupted by a shallow shelf extending 20 km offshore. Deep reefs occur on its outer edge, and intermittent shallow reefs along the shore. On the eastern part of the shelf are numerous patch reefs and two scattered groups of coral islands; the Port Royal Cays and the Old Harbour Cays. Seagrass beds occur in their vicinity, but the extent of seagrasses and patch reefs on the rest of the southern shelf are not well known. Mangroves occur in Kingston Harbour; on both sides of the Portland Bight; and as riverine formations in the Black River Morass.

To the East and South of Jamaica are a number of small 20-fathom banks or guyots, and two groups of islands; the Morant Cays, 60 km south-east, and the Pedro Cays, 80 km south. The latter are situated on the Pedro Bank, which covers about 8,000 $km^2$ and ranges in average depth from about 20 m in the east, where coral reefs are frequent, to 40 m in the west.

Reef fishes, pelagic fishes, lobster and conch are actively fished for with traps, nets, lines and spears, on an artisanal basis. Estimated catches in 1981 were 4,800 tons from the island shelves (three-quarters from the southern shelf) and 2,500 tons from the offshore banks. Catches have declined in recent years and many stocks have been over-fished; especially on the narrow northern shelf. Controls have been introduced; size-limits for lobsters, increased mesh size on traps, protection of nursery grounds and the licensing of fishermen.

Development in some form threatens most wetlands in Jamaica; cutting for firewood; garbage and sewage disposal; drainage, filling and construction; excavation of peat. On the credit side, a mariculture procedure for mangrove oysters has been developed. Coral reefs on the north coast were severely damaged by Hurricane Allen in 1980. All nearshore reefs are suffering some degree of stress from sedimentation and pollution, especially near to rivers and centers of population. In addition, the gross changes wrought by fishing on the reef-fish community may now be affecting the relative abundance of benthic organisms.

Research and monitoring in the coastal zone are carried out for the Government by the Natural Resources Conservation Department. Fisheries are monitored and managed by the Fisheries Division of the Ministry of Agriculture. Research on fish and fisheries is carried out by the Fisheries Division and by the Department of Zoology in the University of the West Indies. Research on other marine systems is done by that and other science departments of U.W.I., including the Discovery Bay Marine Laboratory, which, located in the center of the north coast, is particularly concerned with coral reefs and seagrass beds. U.W.I. undergraduate courses include some on marine biology, in which it also has a graduate program.

Table 1. Inventory of Coastal Ecosystems: Level of Information and Research Facilities/Support Capability (from R. R. Lankford).

| Poorly Known | Partially Known | | Well Known | |
|---|---|---|---|---|
| Guatemala | Dominican Republic | | Trinidad-Tobago | (**) |
| Nicaragua | Costa Rica | | Cuba | (*) |
| Haiti | Panama | (*) | Puerto Rico | (**) |
| Honduras | Bahamas | | U.S.Virgin Islands | (**) |
| Guyana | Venezuela | (**) | Jamaica | (*) |
| | Mexico | (**) | Netherlands (Aruba, Bonaire, Curacao) | (*) |
| | Surinam | | | |
| | Colombia | (*) | French Departments | (**) |
| | Belize | | Cayman Islands | (*) |
| | British Virgin Islands | | Barbados | (*) |
| | Turks & Caicos | | Bermuda | (*) |
| | Netherlands (Windward) | | U. S. A. | (***) |
| | Antigua + Barbuda | | | |
| | St. Kitts-Nevis | | | |
| | Anguilla | | | |
| | Montserrat | | | |
| | St. Lucia[1] | | | |
| | St. Vincent + Grenadines | | | |
| | Grenada | | | |

Marine Research Facilities/Support Capability

(***) = Maximum

(**) = Medium

(*) = Minimum

(No mark indicates complete lack of facilities)

1 = A laboratory is "on paper" - mainly oriented to Public Health/Water Quality.

Table 2. Major Fisheries of the Caribbean Coastal Zone (number refers to priority order)

| COUNTRY | FISHERY | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | SEAWEEDS | SEA URCHINS | CONCH | SHELLFISH | SHRIMP | LOBSTER | REEF FISHES | MANGROVE FISHES | PELAGIC FISHES | AQUARIUM FISHES | TURTLES |
| MEXICO | | | 5 | | 1 | 2 | 3 | | 4 | | |
| GUATEMALA | | | | | 1 | 2 | | | | | |
| HONDURAS | | | | | 1 | 2 | | | | | 3 |
| NICARAGUA | | | | | 1 | 2 | | | | | 3 |
| COSTA RICA | | | 5 | | 1 | 2 | 3 | | 6 | | 4 |
| PANAMA | | | 4 | | 1 | 2 | 3 | 5 | | | |
| VENEZUELA | | | | | 1 | | | 2 | | | |
| NETHERLANDS ANTILLES | | | | | | | 1 | | | 2 | |
| TRINIDAD/TOBAGO | | | | | 2 | | | | 1 | | |
| BARBADOS | 4 | 2 | | | | | 1 | | 3 | | |
| GUADELOUPE (French W.I.) | | | 2 | | | 3 | 1 | 4 | | | |
| U. S. AND BRITISH VIRGIN ISLANDS | | | 4 | | | 2 | 1 | | 3 | | |
| PUERTO RICO | | | 3 | | | 2 | 1 | | 4 | | |
| BAHAMAS | | | 3 | | | 1 | 2 | | | | 4 |
| DOMINICAN REPUBLIC | | | | | 2 | | 1 | | | | |
| JAMAICA | | | 4 | | | 1 | 2 | | 3 | | |
| CAYMAN ISLANDS | | | 2 | | | 1 | | | 4 | | 3 |

## IV. RECOMMENDATIONS OF THE WORKSHOP

Given the findings of this workshop that the three predominant ecosystem types: coral reefs, seagrass beds and mangroves have different attributes and dimensions on continental shelves and island coasts; and

Given the conclusion of the workshop that there are definite interrelationships between these ecosystems which affect the physical, chemical and biological components and their contribution to ecosystem stability; and

Given also that the state of knowledge regarding the structure and function of these ecosystems and their interactions in the Caribbean area range from the very well known to those that have not even been inventoried; and

Given that because of the increasing human impact and the possible far-reaching deleterious effect of improperly planned usage due to development pressures on these resources, time has become a critical factor for acquisition of the appropriate knowledge for the management of these systems; and

Given also that there is significant range, both qualitatively and quantitatively in the regional expertise available and required to provide the necessary scientific information to influence and guide decisions on the use and management of these resources;

A. It is hereby recommended that UNESCO through its Division of Marine Sciences and its International Oceanographic Commission and their regional associations, assign high priority to the implementation of research programs aimed at providing basic inventories of these three systems, the evaluation and quantification of the interactions between them, and further to assess the impact of human activities on these ecosystems and their interrelationships, for the ultimate but urgent purposes of better management of these resources, with the following provisos:

1. that these research programs be conducted with the full participation of the available regional scientific and technical human resources;

2. that projects be designed around the training needs of the region, to use as much as possible the identified training areas and available expertise, keeping always in mind the goal of strengthening the scientific and management capabilities of the region;

3. that there be incorporated into the project designs provisions for the updating and standardization of technologies and techniques used in the investigations to improve their compatability and regional usefulness;

4. that various aims of the research program could be most expeditiously achieved by implementation of a resource assessment study of the region by satellite imagery and other remote sensing techniques in conjunction with the ground truthing at the national level;

5. that support incentives be given to studies on the assessment and dynamics of fishes in the mangroves-seagrass-coral reef continuum; these studies to include basic research on the life history, reproductive biology and larval dispersal and recruitment strategies of these organisms, as well as determination of the sustainable yields from these ecosystems.

B. The following are the specific proposals:

1. In recognition of the differences between the continental and islandic coastal systems, and the needs described above, it is proposed that there be specific pilot projects embarked on with the greatest urgency; these pilot projects should have the following features:

a. Study of these ecosystems with emphasis on their interactions in undisturbed and highly exploited and/or stressed (e.g. hurricane damage) areas on the continental coast and on island coasts.

b. That these pilot projects be sited (in the first instance) where the appropriate infrastructure and training facilities are available.

c. That these pilot projects be models for other national or sub-regional projects necessary for completing the regional inventory and informing the regional scientific and management agencies.

2. As a first step toward achieving these goals it is proposed that there be a methodology workshop, for the short-term training of regional personnel in the current techniques in applied ecology and resource assessment and that this workshop be organized in a country with access to the three systems, and that manuals of standard research techniques be developed for use in the region.

3. For facilitating the early completion of the inventory grid, it is proposed that there be regular meetings of the scientists participating in studies of coastal zone ecosystems. The purposes of these meetings would be to exchange information resulting from these studies, and to coordinate continuing and future research programs.

4. It is also proposed that a Caribbean Coastal System Management Handbook be prepared as soon as possible. This would incorporate all presently available information on Caribbean coastal dynamics and production systems, likely stress impacts, and provide practical guidelines for systems management. There should also be provision for regular updating of the handbook by addition of case studies and interpretations of data.

APPENDIX I. A. Dr. Elizabeth H. Gladfelter

## The role of scleractinian corals in the trophodynamics of the reef ecosystem.

## ABSTRACT

Coral reefs are among the most productive natural ecosystems. For more than 30 years we have known that reef benthic primary producers fix carbon at rates one to two orders of magnitude greater than the surrounding tropical oceans. Yet the trophodynamics of coral reefs is still not well understood. Because corals are a dominant reef life form, and important both as primary producers and reef framework constructors, this paper will focus on present knowledge of the trophodynamics of individual corals with the aim of obtaining a better understanding of the reef system as a whole.

Reef corals are intimate symbioses between an animal and dinoflagellates (=zooxanthellae) which live within the animal tissue. They are thus polytrophic, functioning simultaneously as primary producer, primary consumer and secondary consumer. They also secrete the three dimensional reef framework which provides space for other reef dwelling organisms.

The quantitative trophic relationships between coral animals and their zooxanthellae are currently under investigation. The zooxanthellae function _in situ_ as primary producers. They exhibit a typical P vs. I curve, saturating at high irradiance and showing no inhibition at the highest natural light levels. Much of the fixed carbon is translocated to the cnidarian host, and provides a significant portion of the coral's daily carbon requirement for maintenance respiration. This results in the coral acting as a herbivore (and thus functioning as a primary consumer). Corals, through the activities of zooxanthellae, efficiently scavenge inorganic nitrogen from the environment, showing the ability to take up both ammonia and nitrate. They also retain rather than release excretory ammonium. The zooxanthellae can utilize inorganic nutrients to make organic molecules, some of which (alanine) can be transferred to host tissue. In turn, the latter break down protein to form ammonium which is taken up by the algae. Corals also function as secondary consumers; many species feed on zooplankton, often at night, but this alone is believed to be insufficient to meet daily energy requirements.

Reef habitats are not uniform; corals from different environments show intraspecific morphological and physiological differences. Corals respond to shade and depth in a variety of ways: 1) they change colony form and algal to animal biomass, 2) they exhibit changes in P vs. I curve, saturating at lower irradiances and thus increasing light capture efficiency, and 3) they show a decrease in respiration rate with depth.

To further our understanding of the trophodynamics of reef corals, we need a better quantitative view of the sources and sinks of organic and inorganic nutrients within the reef ecosystem. We also need to ascertain the relationship between irradiance, productivity and skeletal morphology.

## INTRODUCTION

Coral reefs are among the most productive natural ecosystems. Estimates of reef gross primary productivity are 300-5000 g $C.m^{-2}.y^{-1}$. These high rates contrast with those of the tropical waters surrounding reefs where productivity is only 20-50 g $C.m^{-2}.y^{-1}$ (Lewis 1977). Benthic producers including dinoflagellates (occurring in the tissues of cnidarian hosts), macroalgae and microalgae (forming extensive "turfs" on dead coral) are responsible for this high rate of reef primary production. Although studies of community productivity have shown that the ratio of reef primary production to reef respiration is close to unity, our knowledge of the trophodynamics of the coral reef ecosystem is still fragmentary (Lewis 1977). One approach to an understanding of the mechanisms which drive reef production in nutrient poor waters is to study the trophodynamics of reef corals.

Reef corals are an intimate symbiosis between a plant and an animal; they function simultaneously as primary producers, primary consumers and secondary consumers. In addition they construct the framework of the reef, by the continual growth of their skeletons. This paper is intended to provide the basis for a discussion of the trophodynamics of reef corals, with emphasis on the intraspecific adaptations in morphology and physiology observed in corals growing in different habitats. If we can understand the mechanisms by which these adaptations occur, we should be able to predict the possible effect of various perturbations on reef structure and trophodynamics. Exhaustive reviews of coral physiology are found elsewhere (cf. Lewis 1977, reef organic productivity; Trench 1979, plant-animal symbiosis; Muscatine 1980a, productivity of zooxanthellae; Muscatine 1980b, nutrient recycling).

### Morphology of the Coral Symbiosis

Reef corals (Cnidaria: Scleractinia) have two tissue layers, ectoderm and endoderm. There are functionally two types of ectoderm: 1) an outer protective layer adjacent to the surrounding sea water, and 2) an inner secretory layer responsible for depositing the calcium carbonate skeleton (Johnston 1980). Between these ectodermal layers, and separated from them by a thin mesoglea, lies the flagellated endoderm. This forms the lining of the coelenteric cavity; this cavity is contiguous throughout the coral colony, and thus joins the individual polyps. Zooxanthellae (Pyrrophyta: Dinophyceae) lie within the cells of the endoderm, especially in that layer of endoderm lying beneath the outer ectoderm. One can think of the zooxanthellae as lying in a two dimensional sheet conforming to the surface of the coral skeleton; the zooxanthellae occur in densities of ca. $10^6.cm^{-2}$ of colony surface. Some species of corals are simply sheets of tissues covering the surface of a compact skeleton, as is seen in the Pacific genus, *Pocillopora* (Johnston 1978). In other corals, however, the tissue ramifies throughout the interstices of a porous skeleton, as is seen in the circumtropical genus *Acropora* (Gladfelter 1982). We can see that photosynthetic tissue (i.e. the layer with zooxanthellae) occurs at the surface of a coral colony while respiring tissue may be just at the surface (e.g. *Pocillopora*) or deep throughout the colony as well (e.g. *Acropora*). This difference in tissue conformation will have important implications when we consider the entire carbon budget for the coral.

## TROPHODYNAMICS OF REEF CORALS

### Corals as Primary Producers

Zooxanthellae are the primary producers of the coral symbiosis; they behave as oligotrophic phytoplankton (Muscatine 1980a). Primary productivity in phytoplankton is often expressed as the amount of carbon fixed per unit chlorophyll a per unit time (Parsons and Takahashi 1975). Coral productivity is expressed in the same way and also as a function of colony surface area. Both kinds of values are found in the literature (cf. Muscatine 1980a). In the intact symbiosis (in vivo) or in isolated suspensions (in vitro), zooxanthellae show a photosynthetic response to irradiance (P vs. I) which saturates at high irradiances and has no tendency towards photoinhibition at the highest natural light levels (Muscatine 1980a). There are two important parameters to note when one is analyzing a P vs. I curve (Fig. 1a): 1) the initial slope, $\Delta P/\Delta I$, which will indicate the efficiency of light absorption at low irradiances, and 2) Pmax, the photosynthetic capacity, or that level of irradiance at which the photosynthetic system is saturated. The difference between the in vivo and in vitro systems is illustrated in Fig. 1. In the intact symbiosis (Fig. 1b) there are two compensation points: 1) the level of irradiance at which zooxanthellae productivity is equal to zooxanthellae respiration (as would be seen in the in vitro situation or in free living dinoflagellates) and 2) the level of irradiance at which zooxanthellae productivity is equal to coral respiration (i.e. both the algal and animal portion). When measuring productivity by oxygen production, the latter compensation point would be when the coral neither consumes nor releases oxygen.

There have been a number of investigations of coral productivity whose data are usually derived from short term incubations, ca. 1 hr (cf. Muscatine 1980a). More desirable are data on daily productivity of a coral measured continuously rather than extrapolated from discrete short term incubations. Muscatine et al.(1981) and McClosky and Muscatine (manusc.) have measured the daily productivity of corals in situ, by enclosing a coral in a chamber and monitoring changes in the $O_2$ level. The diel patterns of oxygen exchange, illustrated in Fig. 2, can be used to construct P vs. I curves as well as to determine the gross primary productivity of the coral over the 24 hour period. The data show generally that shallow water corals produce more carbon than they consume, but that this pattern changes with depth.

### Corals as Primary Consumers

Photosynthetic products are translocated from the zooxanthellae to the animal host (cf. Trench 1979; Muscatine 1980 a, b). Since these products are assimilated and metabolized by host tissue, the coral can be viewed as an herbivore, functioning as a primary consumer. The fact that the zooxanthellae release a substantial fraction of their daily production to the host results in substrate limitation for the growth of the algal population. Growth of zooxanthellae is thus regulated but the mechanisms responsible for regulating algal numbers in animal hosts are not yet fully understood (Muscatine and Pool 1979). We do know, however, that organic products which might have gone into algal population growth are redirected into coral growth.

## Translocation of Organic Carbon

How important are zooxanthellae in providing a nutritional source for corals? In 1977, Lewis stated that until recently many reef workers doubted whether corals derived a "significant" portion of their energy requirements from zooxanthellae. Porter (1976) suggested that some corals (especially branching forms such as *Acropora*) functioned as autotrophs, while other corals (especially massive forms such as *Montastrea*) functioned primarily as heterotrophs. Obviously to resolve this controversy, we need data on "the contribution of zooxanthellae to animal respiration," i.e. CZAR which equals $P_Z.T/R_a$ (where $P_Z$ = gross carbon fixation over 24 hours, T = % translocation of fixed carbon from zooxanthellae to host, and $R_a$ = animal respiration over 24 hours). CZAR is a term devised by Muscatine *et al.* (1980), who have provided a model by which one could determine this value for any coral. They used this model to determine CZAR for two Hawaiian species. First, they measured diel productivity (Fig. 2) as described above. They then determined the proportional biomass of algal tissue when compared to the whole coral: 8.9% for *Pocillopora damicornis* and 3.2% for *Fungia scutaria*. They made the assumption that biomass ratio reflects algal: animal respiration ratio. Finally they determined the percentage of photosynthetically fixed products translocated to the host. Translocation is measured by incubating the coral in the light in $^{14}C$-bicarbonate. The labelled carbon is incorporated photosynthetically by the zooxanthellae. After an appropriate time, the animal and algal fractions are separated; the amount of labelled products are determined for each. The amount of fixed carbon occurring in the animal fraction divided by total fixed carbon is equal to % translocation. In *P. damicornis* ca. 40% of the fixed carbon was translocated to the animal host, while in *F. scutaria* ca. 25% was translocated. Knowing the diel pattern of $O_2$ exchange, the biomass ratio of algal to animal tissue, and the % translocation, Muscatine *et al.* (1980) were able to compute the following levels of CZAR: 63.2% for *P. damicornis* and 68.5% for *F. scutaria*. Thus in these species, at least, the zooxanthellae play a significant role in coral nutrition; corals are clearly primary consumers.

The nature of the translocated products has also been investigated by determining what translocated $^{14}C$ labelled products are found in the animal fraction. These include glycerol, glucose and alanine (Trench 1979; Muscatine 1980 a, b). Release of these products from freshly isolated zooxanthellae is stimulated by host tissue (Muscatine and Cernichiari 1969). There is strong evidence that at least some of these products are used as precursors in a number of metabolic pathways in the host. A variety of labelled products is eventually found in the host tissue (Schmitz and Kremer 1977). The $^{14}C$ labelling experiments which have just been described can detect only those products which have recently been in the photosynthetic pathway of the alga. Products synthesized by other pathways would remain undetected. Patton *et al.* (1977) have provided evidence that host derived acetate is transferred to the zooxanthellae where it is converted into fatty acids. The energy for this synthesis would be the excess ATP and NADH generated in the chloroplast in the light. The fatty acids are then translocated back to the host where they are found in wax esters and triglycerides.

There is thus ample evidence that some corals derive a large fraction of their daily caloric requirement from products translocated from the zooxanthellae. In addition, it appears that the rates of synthesis of other products (such as fatty acids) might be enhanced by acetate recycling between host and zooxanthellae.

## Nutrient Recycling

Inorganic nutrients (nitrogen and phosphorus) can be limiting factors in phytoplankton productivity (Parsons and Takahashi 1975). Nitrogen is usually considered to be the limiting factor in coral growth, and thus it has been the focus of most investigations (Muscatine 1980b) although the importance of phosphorus is not really known. During the following discussion we will concentrate on what is known about nitrogen and reef corals.

Muscatine (1980b) has reviewed the subject of nutrient flux in a number of algal-invertebrate symbioses. Although much of the research was conducted on systems other than corals, the following picture is beginning to be assembled. Nitrogen sources for a coral include both organic nitrogen from ingested food (Johannes et al. 1970; Johannes 1974) and inorganic nitrogen in the form of nitrate (Franzisket 1973, 1974; D'Elia and Webb 1977; Wiebe and Webb 1978) and ammonia (Kawaguti 1953; Muscatine and D'Elia 1978). There is no evidence for nitrite uptake. Ambient levels of these nutrients are usually low: 1.0 µM nitrate and .02 - 0.8 µM ammonia at most reef sites except for inner bays where measurements are twice these values (Muscatine 1980b). Because corals have $K_s$ values for the uptake of ammonia and nitrate of less than 1.0 µM, Muscatine (1980b) suggests that they are functioning as oligotrophic phytoplankton. In addition, at ambient concentrations of these two sources of inorganic nitrogen, the rate of uptake of ammonia is twice that of nitrate (D'Elia and Webb 1977). This suggests that ammonia is probably the more significant of the nitrogen sources (Muscatine 1980b) as is true of many marine phytoplankters (Parson and Takahashi 1975).

Corals retain rather than release inorganic nitrogen. Muscatine and D'Elia (1978) observed that in 2 hr incubations in the light or in the dark, Pocillopora damicornis showed no net release of ammonia. They hypothesized that if light energy were required for the uptake and retention of ammonia, a long dark incubation would result in release, but during a shorter dark incubation the coral might have sufficient fuel reserves to delay the release of ammonia. Tests showed that if the coral was maintained in a long dark incubation (18 hr), it released ammonia, but the light of a natural diel cycle was sufficient to enable the coral to retain ammonia during the natural dark period.

Direct evidence for the transfer of nitrogen from animal to zooxanthellae is lacking for corals, but experiments by Marian (cited in Muscatine 1980b) showed that sea anemones fed zooplankton which were labelled with $^{15}N$ protein, later had the $^{15}N$ label in the algal fraction. Thus corals can scavenge inorganic nutrients from the environment, and inorganic nitrogen can be transferred from animal to algae. The completion of the cycle, i.e. transfer of nitrogen from zooxanthellae to animal host tissue also occurs. There are two lines of supporting evidence: alanine shows up as a translocated product in the $^{14}C$ experiments (Trench 1979 and discussed above) and Marian (cited in Muscatine 1980b) demonstrated that $^{15}NO_3^-$ taken up by the zooxanthellae of the reef coral Pocillopora damicornis, accumulates in the organic form in the animal. Lewis and Smith (1971) demonstrated that the amount of $^{14}C$ incorporation by animal tissue as alanine was increased if the medium was spiked with 5 mM ammonia.

The evidence for internal recycling of nitrogen within the animal-zooxanthellae symbiosis is strong but not yet complete. The mechanism of recycling enables the coral to retain much of the nitrogen (either in the organic or inorganic form) to which it is exposed. The total nitrogen budget of a coral, and the essential amino acids which are required are still largely unexplored (Muscatine 1980b).

### Corals as Secondary Consumers

Corals are active carnivores. They feed by a variety of mechanisms utilizing tentacles, ciliary mucus tracts, and extracoelenteric extrusion of gastric filaments (Lewis and Price 1975). Johannes et al. (1970) and Johannes (1974) sampled available zooplankton and concluded that this was insufficient to meet the daily caloric needs of the coral community. They pointed out, however, that the zooplankton could serve as a source of nitrogen and phosphorus for the corals. Porter (1974) carefully sampled gut contents of individual polyps of Montastrea cavernosa. He demonstrated that feeding could supply only a small fraction of the daily energy requirement, even in this species with large polyps that apparently is adapted for eating larger zooplankton. Alldredge and King (1977) and Porter et al. (1977) provided evidence that the largest component of the potential food supply for corals is the demersal plankton which emerges from the reef and sand intertices at night. Monthly plankton samples taken inside and outside reefs (Glynn 1973; Gladfelter et al. 1980) show annual peaks of zooplankton (with shorter term lunar cycles imposed on these). Apparently, zooplankton is an unpredictable source of nutrition, being more abundant at some times than at others. Corals might adopt a feast or famine strategy; i.e. when large quantities of zooplankton are available the corals feed heavily, storing some of this material for less favorable periods. Corals do store large energy reserves in the form of lipids (Patton et al. 1977); the lipid content of symbiotic cnidarians can be greater than 30% by dry weight (Bermann et al. 1956).

In summary, corals probably do not depend on secondary consumption for their total daily caloric needs. They do, however, probably rely on feeding to supply nitrogen and perhaps phosphorus to the system. They might also feed heavily when food is available and then store excess food in the form of lipids. Other heterotrophic food sources, such as organic debris, bacteria and dissolved or particulate organic carbon (DOC, POC) have not been investigated very thoroughly (Lewis 1977).

## INTRASPECIFIC ADAPTATIONS BY CORALS TO DIFFERENT ENVIRONMENTS

Corals in different habitats may experience differences in light quality and quantity, and differences in water movement. Of particular interest are the adaptations of corals of the same species to different habitats. A number of recent investigations have focused on intraspecific adaptations of corals, and the results can be summarized as follows below:

Falkowski and Dubinsky (1981) observed that colonies of *Stylophora pistillata*, a small branched species in Eilat, Red Sea, grow in the full sunlight and in the shade. The shade corals were darker and had a more club-like morphology than those which grew in the sun. The shade coral had a different P vs. I response (Fig. 3), showing the classic "shade" adaptations of 1) a steeper slope, indicating more efficient light absorption at low irradiances and 2) a lower Pmax. The shade coral had an equal density of zooxanthellae but 3.8 times more chl a per cell. The number of photosynthetic reaction centers ($P_{700}$) did not change, but the size of the photosynthetic unit (PSU) increased (i.e. there were more accessory pigment molecules per $P_{700}$). By making repicrocal transplants, Falkowski and Dubinsky (1981) were able to demonstrate that these adaptations to different irradiances could be reversed quite rapidly. Shade corals took only 4 weeks to adapt to sun conditions, while sun corals took 6-8 weeks to adapt to shade conditions. These experimental durations were too short to detect changes in colony morphology.

To determine if colony morphology is genetically programmed or environmentally induced, Foster (1979) working in Jamaica made reciprocal transplants of *Montastrea annularis* and *Siderastrea siderea* to several different reef habitats. After one year she examined the microstructure of the skeleton and was able to clearly demonstrate that the skeletal morphology in these species was very dependent on the habitat in which the colony lived, and not on local genetic strains growing in different habitats.

McCloskey and Muscatine (ms.) compared the trophodynamics of shallow (3m) and deep (35m) *Stylophora pistillata*. The deep coral had a different colony morphology, a shade adapted P vs. I curve, a lower density of zooxanthellae but with 3.8 times as much chl a per cell, a lower % translocation and a lower respiratory rate than the shallow coral. Most importantly, McCloskey and Muscatine (ms.) demonstrated that CZAR declined from 63% in shallow colonies to 9% in deep colonies. In addition if the total carbon budget is computed, the deep coral required exactly the same caloric input from sources other than zooxanthellae as the shallow coral. Thus within one species, there is the transition from a great dependence on translocated products from zooxanthellae as a carbon source to a very low dependence, while the coral's dependence on an external energy source remains the same. The zooxanthellae in the deep coral are functioning below the zooxanthellae compensation level much of the 24 hours. How this affects light enhancement of calcification has not yet been addressed.

Some corals show two distinct colony morphs living side by side in the same environment. Lasker (1981) divides *Montastrea cavernosa* into diurnal morphs which are expanded by day and night and nocturnal morphs which expand only at night. The diurnal morphs have a higher zooxanthellae density, and higher rates of both production and respiration. Respiration in both morphs was higher when polyps were expanded than when polyps were contracted. This is not surprising because the surface through which diffusion occurs is much greater in an expanded polyp. Although Lasker (1981) was unable to show a direct relationship between colony energetics and phenotype, his study points out the importance of coral behavior in affecting rates of both production and respiration. Environmental perturbations which cause an abnormal behavior pattern for a coral might severely influence the trophodynamics and colony form of that coral. Coral trophodynamics cannot be inferred from colony form, as was suggested by Porter (1976). Wellington (1982) assessed the relative contribution of light and zooplankton to the skeletal growth of three Pacific corals: a branching form, *Pocillopora damicornis* and two massive forms, *Pavona clavus* and *P. gigantea*. After one year manipulative field experiments, he found that *Pocillopora* grew independent of zooplankton supply, but was affected by shading. *Pavona clavus* (which has ca. 2 mm. wide polyps) was affected by shading, but this was minimized when zooplankton was available. *Pavona gigantea* (with 3 mm. wide polyps) was dependent on both light and zooplankton. Thus even corals which are apparently adapted for "heterotrophic" existance (i.e. with large polyps) are very dependent on light for skeletal growth.

Three investigations have asked how *Montastrea annularis*, a dominant Caribbean coral changes along a depth gradient: Dustan (1975) examined morphological differences, Davies (1980) looked at changes in respiratory rate, while Battey and Porter (ms.) examined changes in productivity. There are some similarities and some differences between *M. annularis* and the patterns observed in *Stylophora pistillata*, discussed above. *M. annularis* is a massive form showing a characteristic flattening of colony form in shaded or deep reef areas (Dustan 1975). Davies (1980) found that in this species, as well as in several others, the rate of respiration decreased with depth, as was also seen in *Stylophora*. *M. annularis* showed the following adaptations to depth (Battey and Porter, ms.): different colony morphology, decrease in zooxanthellae density, increase in chl a per surface area and per zooxanthella, and a decrease in primary productivity. All of these adaptations were also found in *Stylophora*. *Montastrea*, unlike *Stylophora*, however, shows no change in % translocation with depth. Because the productivity rate declines so rapidly with depth in *Montastrea*, CZAR might well decrease with depth; this has not yet been determined.

To summarize some intraspecific adaptation observed in colony morphology and physiology:

1. Coral colonies show morphological and physiological adaptations to different habitats; some species have morphs with different morphological and physiological characteristics in the same habitat.

2. Corals can adapt to a new habitat, showing a characteristic morphology and physiology associated with that habitat, given an appropriate amount of time.

3. Adaptations to depth (shade) include a change in P vs. I response, an a higher concentration of chl a per zooxanthella; in the "shade" coral, there was an increase in size but not number of PSUs.

4. Respiration of corals decrease with depth.

5. The % translocation of carbon from zooxanthellae to host tissue can decrease with depth or shows no change.

6. CZAR decreases with depth.

Adaptations of corals to different habitats include both a change in colony morphology and a change in the trophodynamics of the coral. The relationship between these two adaptations is intriguing. Many new investigations await formulation.

## SUMMARY

Corals are polytrophic organisms (Fig. 4), receiving organic (zooplankton) and inorganic nutrients from the external environment, having a high rate of productivity, showing a tight recycling of nutrients within the system. We have not discussed the contribution corals make to the secondary productivity of the reef; except for a recent study by Lewis (1981), this subject has not been investigated (Lewis 1977). The same questions we have posed for reef corals could be asked for the reef system as a whole: i.e. what are the trophodynamics of the system, and most importantly what are the sources and sinks of nutrients? How important are exchanges with other ecosystems?

We have also seen that corals can adapt rather quickly to a change in reef habitat. Reef corals have a finely tuned recycling mechanism which enables them to exist under a variety of nutritional regimes; i.e. higher or lower irradiances; more or fewer zooplankters; higher or lower nutrient concentration. However, we must consider: first, the limits to this plasticity and second, how a change in external reef environment which exceeds these limits will affect not only coral growth, but also coral skeletal growth. There is some evidence that algal-invertebrate symbioses which are apparently oligotrophic in nutrient requirements, can become severely disrupted if nutrient levels become too high (Muscatine and Neckelman 1981). The algae can actually overgrow and kill the host. A sharp decline in light levels on reefs, due to turbidity for instance affects community structure (Rogers 1979), probably by differentially affecting the trophodynamics of different species, and eventually skeletal form as well.

Future investigations on reef corals should concentrate on trying to understand the mechanisms by which these adaptations are effected. If the mechanisms are better understood, our ability to predict the effect of perturbations on the coral reef ecosystem will be greatly enhanced.

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## LITERATURE CITED

Alldredge, A. L. and J. M. King. 1977. Distribution, abundance, and substrate preferences of demersal reef zooplankton at Lizard Island Lagoon, Great Barrier Reef. Mar. Biol. 41: 317-333.

Battey, J. F. and J. W. Porter. A preliminary examination of the data collected for an explanation of photo-adaptation as a whole organism response in Montastrea annularis. Ms. in prep.

Bergmann, W., S. M. Creighton and W. M. Stokes. 1956. Contributions to the study of marine products. XL Waxes and triglycerides of sea anemones. J. org. Chem. 21: 721-728.

Davies, P. Spencer. 1980. Respiration in some atlantic reef corals in relation to vertical distribution and growth form. Biol. Bull. 158: 187-194.

D'Elia, C. F. and K. L. Webb. 1977. The dissolved nitrogen flux of corals. Proc. 3rd Intl. Coral Reef Symp. 1: 325-330.

Dustan, P. 1975. Growth and form in the reef-building coral Montastrea annularis. Mar. Biol. 33: 101-107.

Falkowski, P. G. and Z. Dubinsky. 1981. Light-shade adaptation of Stylophora pistillata, a hermatypic coral from the Gulf of Eilat. Nature 289 (5794): 172-174.

Foster, A. B. 1979. Phenotypic plasticity in the reef corals Montastrea annularis and Siderastrea siderea. J. Exp. Mar. Biol. Ecol. 39: 25-34.

Franzisket, L. 1973. Uptake and accumulation of nitrate and nitrite by reef corals. Naturwiss. 12: 552.

Franzisket, L. 1974. Nitrate uptake by reef corals. Int. Revue ges. Hydrobiol. 59: 1-7.

Gladfelter, E. H. 1982. Skeletal development in Acropora cervicornis: I. Patterns of calcium carbonate accretion in the axial corallite. Coral Reefs 1: 45-51.

Gladfelter, E. H. and W. B. Gladfelter. 1980. Environmental studies of Buck Island Reef National Monument. U. S. Dept. Interior, Natl. Park Ser. Report, 116 pp.

Glynn, P. W. 1973. Ecology of a Caribbean coral reef. The Porites reef flat type: Part II. Plankton community with evidence for depletion. Mar. Biol. 22: 1-21.

Johannes, R. E. 1974. Sources of nutritional energy for reef corals. Proc. 2nd Intl. Coral Reef Symp. 1: 133-137.

Johannes, R. E., S. L. Coles and N. T. Kuenzel. 1970. The role of zooplankton in the nutrition of some scleractinian corals. Limnol. Oceanogr. 15: 579-586.

Johnston, I. S. 1978. Functional ultrastructure of the skeleton and skeletogenic tissues of the reef coral Pocillopora damicornis. Ph.D. Diss. Univ. Calif. LA.

Johnston, I. S. 1980. The ultrastructure of skeletogenesis in hermatypic corals. Int. Rev. Cyt. 67: 171-214.

Kawaguti, S. 1953. Ammonium metabolism of the reef corals. Biol. Jour. Okayama Univ. 1: 171-176.

Lasker, H. R. 1981. Phenotypic variation in the coral Montastrea cavernosa and its effects on colony energetics. Biol. Bull. 160: 292-302.

Lewis, D. H. and D. C. Smith. 1971. The autotrophic nutrition of symbiotic marine coelenterates with special reference to hermatypic corals. I. Movement of photosynthetic products between the symbionts. Proc. Roy. Soc. Lond. B. 178: 111-129.

Lewis, J. B. 1977. Processes of organic production on coral reefs. Biol. Rev. 52: 305-347.

Lewis, J. B. 1981. Secondary production of reef corals. 4th Intl. Coral Reef Symp. Abstr.: 37.

Lewis, J. B. and W. S. Price. 1975. Feeding mechanisms and feeding strategies of Atlantic reef corals. J. Zool. Lond. 176: 527-544.

McCloskey, L. R. and L. Muscatine. Depth related changes in production and respiration in the Red Sea coral Stylophora pistillata. Ms. in prep.

Muscatine, L. 1980a. Productivity of zooxanthellae. In Primary productivity in the sea. (Ed. by P. G. Falkowski) pp. 381-402. New York: Plenum Publ. Corp.

Muscatine, L. 1980b. Uptake, retention and release of dissolved inorganic nutrients by marine algae-invertebrate associations. In Cellular interactions in symbiosis and parasitism. (Ed. by C. B. Cook, P. W. Pappas and E. D. Rudolph) pp. 229-244. Columbus: Ohio Univ. Press.

Muscatine, L. and E. Cernichiari. 1969. Assimilation of photosynthetic products of zooxanthellae by a reef coral. Biol. Bull. 137: 506-523.

Muscatine, L. and C. F. D'Elia. 1978. The uptake, retention and release of ammonium by reef corals. Limnol. Oceanogr. 23: 725-734.

Muscatine, L., L. R. McCloskey and R. E. Marian. 1981. Estimating the daily contribution of carbon from zooxanthellae to animal respiration. Limnol. Oceanogr. 26(4): 601-611.

Muscatine, L. and N. Neckelman. 1981. Regulation of numbers of algae in the Hydra-Chlorella symbiosis. Ber. Deutsch. Bot. Ges. Bd. 94: 571-582.

Muscatine, L. and R. R. Pool. 1979. Regulation of numbers of intracellular algae. Proc. Roy. Soc. Lond. B. *204*: 131-139.

Parsons, T. and M. Takahashi. 1975. *Biological oceanographic processes*. New York: Pergamon Press. 186 pp.

Patton, J. S., S. Abraham and A. A. Benson. 1977. Lipogenesis in the intact coral *Pocillopora capitata* and its isolated zooxanthellae: Evidence for a light-driven carbon cycle between symbiont and host. Mar. Biol. *44*: 235-247.

Porter, J. W. 1974. Zooplankton feeding by the Caribbean reef-building coral *Montastrea annularis*. Proc. 2nd Intl. Coral Reef Symp. *1*: 111-125.

Porter, J. W. 1976. Autotrophy, heterotrophy and resource partitioning in Caribbean reef-building corals. Amer. Nat. *110*: 731-742.

Porter, J. W., K. G. Porter and Z. Batac-Catalan. 1977. Quantitative sampling of Indo-Pacific demersal reef plankton. Proc. 3rd Intl. Coral Reef Symp. *1*: 105-112.

Rogers, C. S. 1979. The effect of shading on coral reef structure and function. J. Exp. Mar. Biol. Ecol. *41*: 269-288.

Schmitz, K. and B. P. Kremer. 1977. Carbon fixation and analysis of assimilates in a coral-dinoflagellate symbiosis. Mar. Biol. *42*: 305-313.

Trench, R. K. 1979. The cell biology of plant-animal symbiosis. Ann. Rev. Plant Physiol. *30*: 485-531.

Webb, K. L. and W. J. Wiebe. 1978. The kinetics and possible significance of nitrate uptake by several algal-invertebrate symbioses. Mar. Biol. *47*: 21-27.

Wellington, G. M. 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia *52*: 311-320.

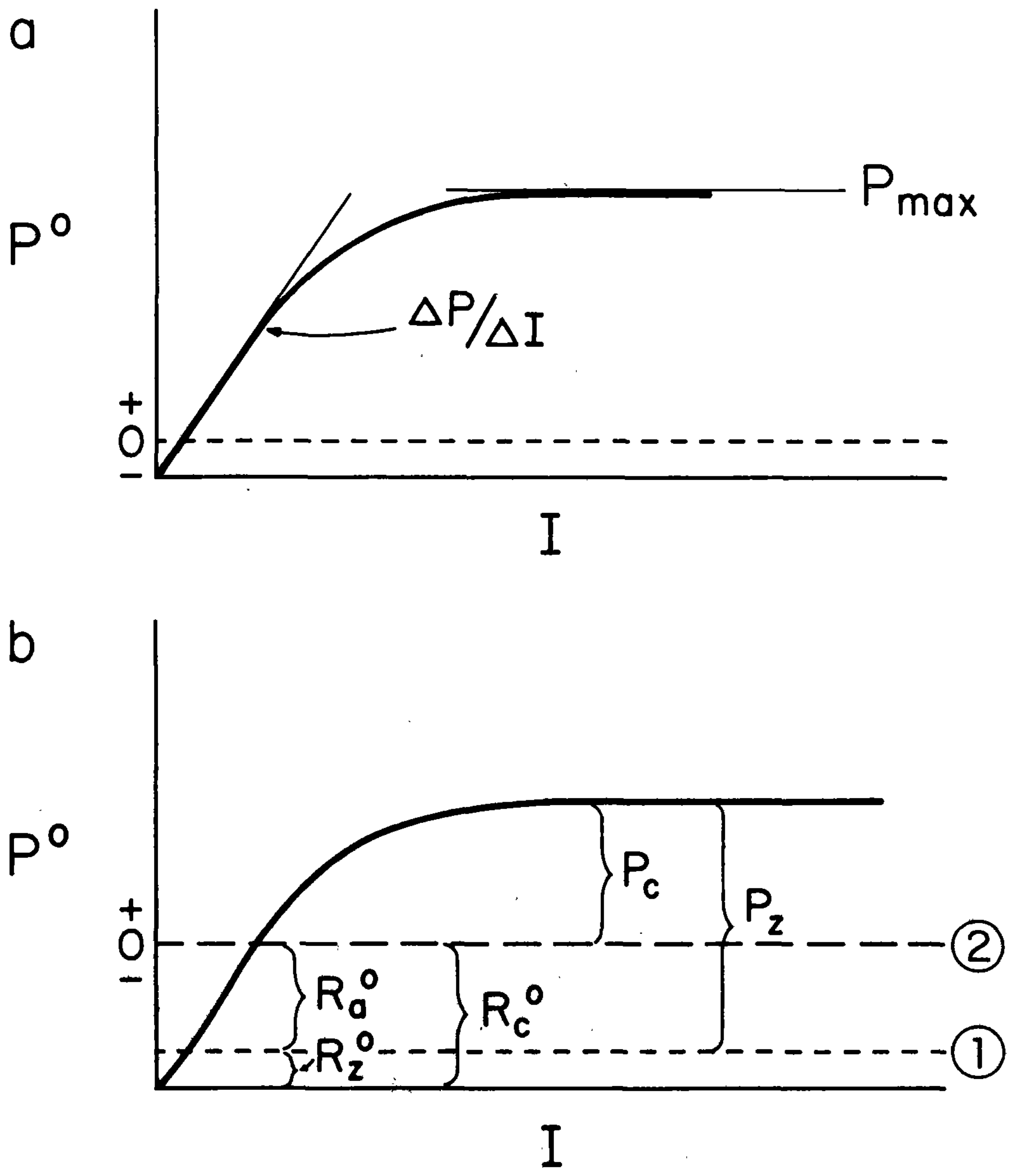

Fig. 1. Photosynthetic response (as measured by $O_2$ evolution) of zooxanthellae to an increase in irradiance; i.e. a P vs. I curve.

1a. A P vs. I curve for isolated zooxanthellae or free-living dinoflagellates. Photosynthetic rate (P°) increases with an increase in irradiance. Note ΔP/ΔI, the initial slope which shows the alga's ability to absorb light at low irradiances; $P_{max}$, the maximum rate of photosynthesis which is reached at a light level lower than ambient; and the compensation level (---), at which $O_2$ evolution by photosynthesis is equal to $O_2$ consumption by respiration.

1b. A P vs. I curve for an intact coral. Note that there are now two compensation levels: (1) zooxanthellae compensation level, at which zooxanthellae respiration rate ($R_z^{\circ}$) is equal to zooxanthellae productivity ($P_z$); and (2) coral compensation level at which coral respiration rate ($R_c^{\circ}$) is equal to coral productivity ($P_c$). Coral respiration has two components: zooxanthellae respiration ($R_z^{\circ}$) and animal respiration ($R_a^{\circ}$).

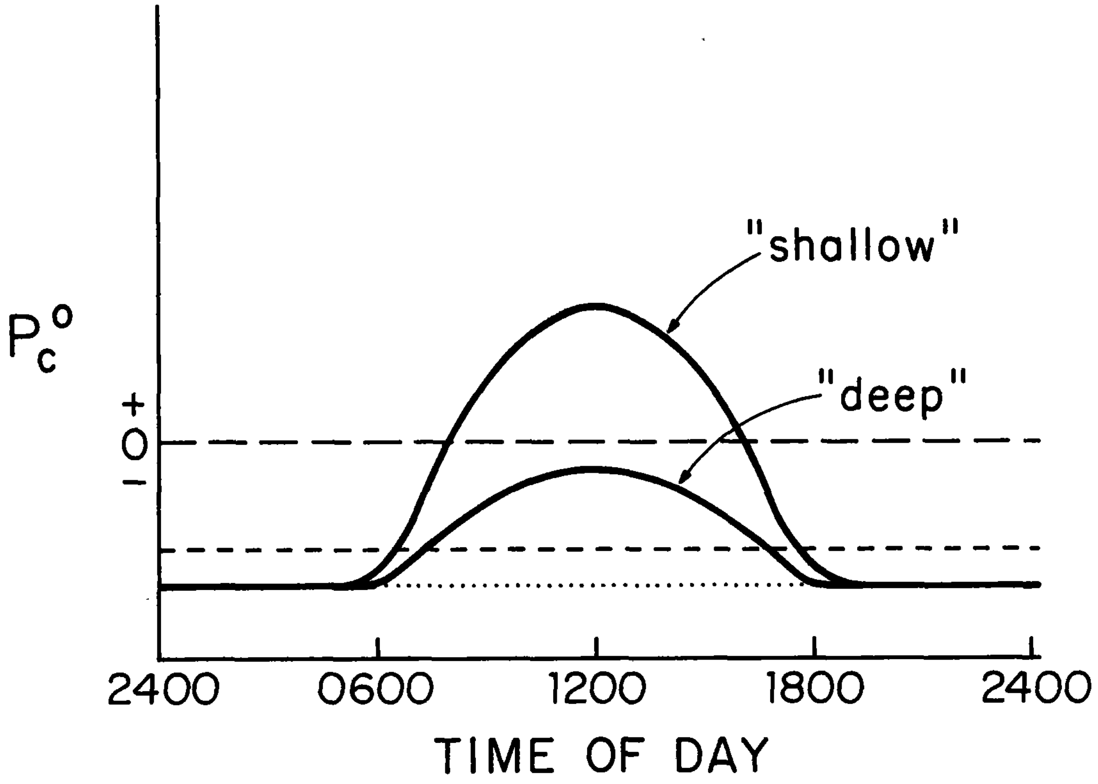

Fig. 2. Diel patterns of $O_2$ exchange of an intact coral, showing both the zooxanthellae compensation level (---) and the coral compensation level (— — — ). A "shallow" coral shows $O_2$ evolution during the day (corresponding to production by the algae greater than consumption by respiration of the coral). "Deep" corals never show $O_2$ evolution, but merely a decrease in $O_2$ consumption during the day.

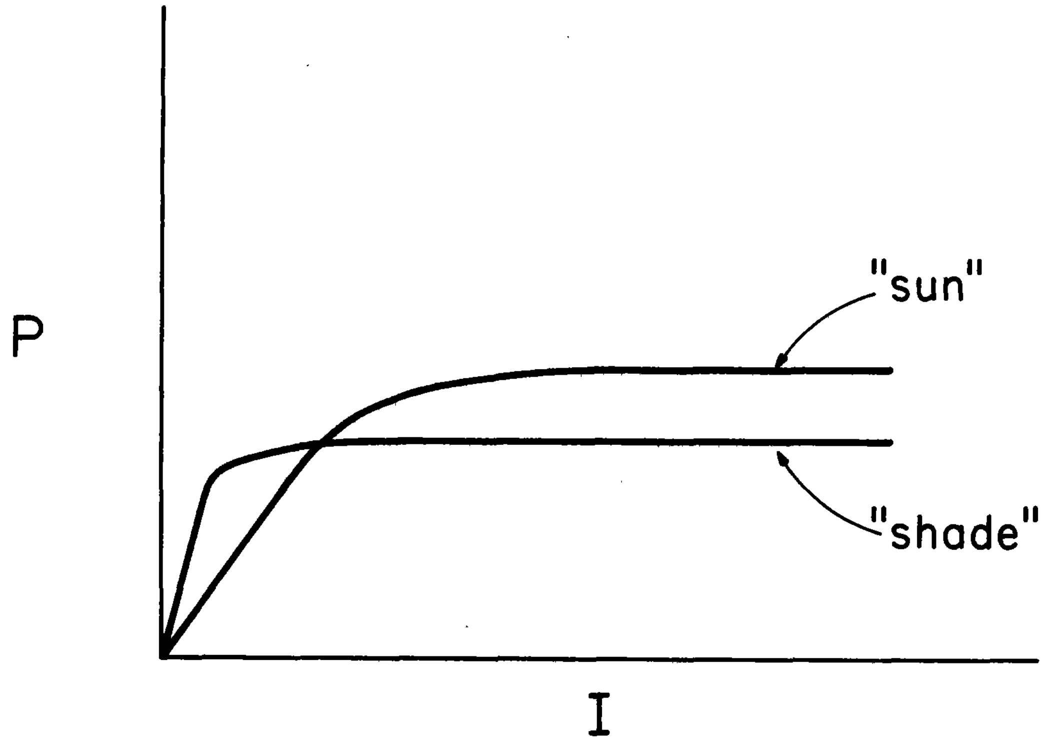

Fig. 3. A P vs. I response changes with a coral's position on the reef. A "shade" or "deep" coral shows a greater ability to absorb light at low irradiances (as indicated by a steeper initial slope) and has a lower $P_{max}$.

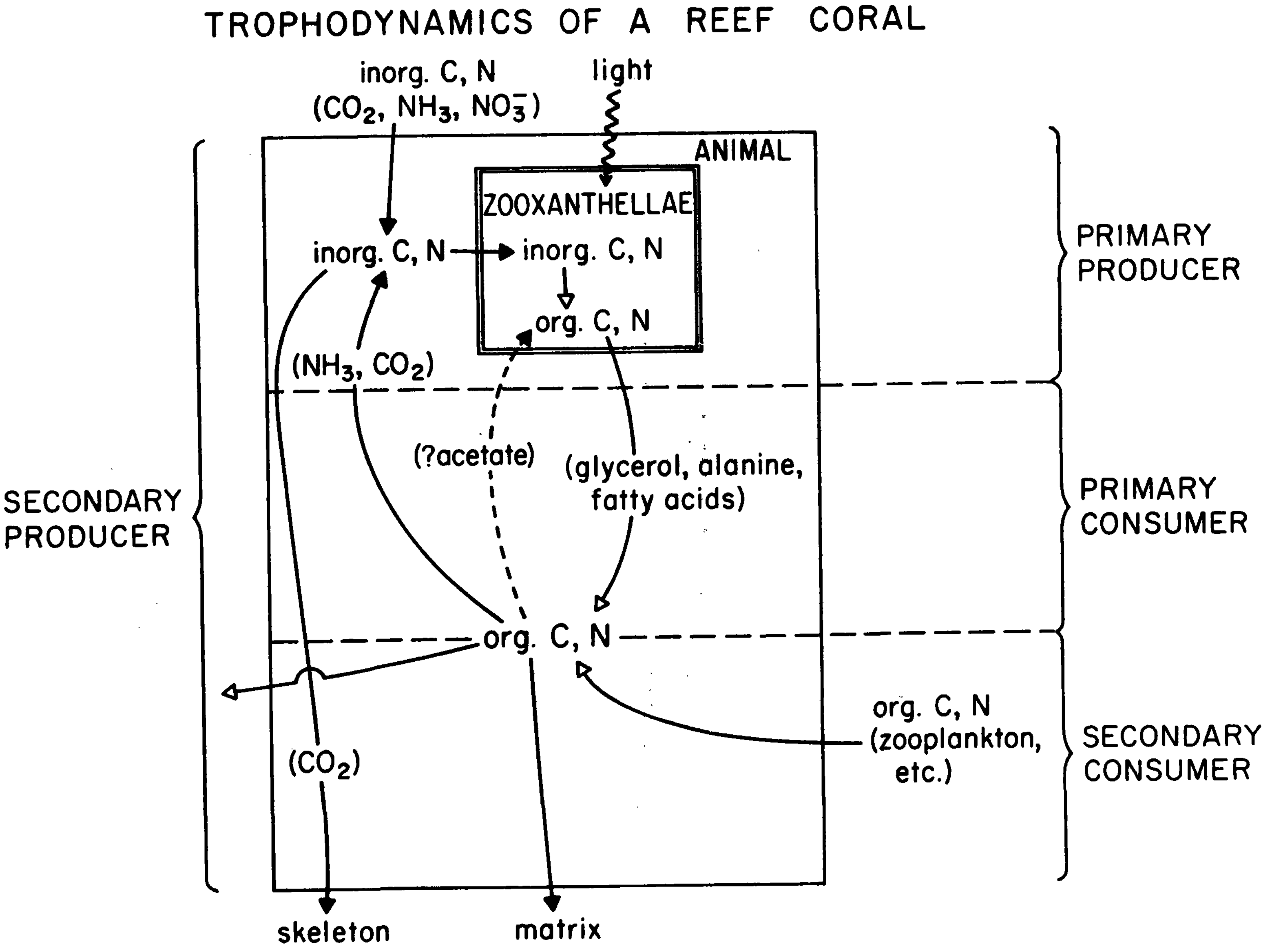

Fig. 4. A summary of the trophodynamics of reef corals: see text.

APPENDIX I. B. Dr. Rolf P. M. Bak

# Aspects of community organization in Caribbean stony corals (Scleractinia).

## ABSTRACT

Stony corals (Scleractinia) are the ecological dominants on Caribbean coral reefs. These organisms are distributed in distinct zones over the reef profile. This pattern has been explained as the result of physiological demands but increasing emphasis is laid on ecological differences between the coral species and the predictability levels of the various habitats. However, striking anomalies are found in the occurrence of coral species and of reefs. These are in part caused by the diverse reactions of corals to the temporal and spatial heterogeneity of their environment. The continuity of the habitats is interrupted by factors such as epidemic disease, storms, outbreaks of competitions and human activities, the effect of which in turn depends on the composition of the coral community. The variations in coral response are caused by the evolution of different life histories such as displayed by *Agaricia*, *Montastrea*, *Acropora* and *Madracis*. These species differ in the way they reproduce, survive, regenerate, compete for space, their growth rates etc. Reefs and their distributive patterns are far from fully understood but the interaction of physiological requirements, life history characteristics, heterogeneity and recent history of the habitat, is of major importance in the explanation of community composition and the stage of reef development.

## INTRODUCTION

Coral reefs are wide-spread throughout the Caribbean, ranging from Panama and Tobago in the south to Florida and the impoverished reefs of Bermuda in the north. Most Caribbean nations, the islands as well as the countries bordering on this sea, have reefs at least along parts of their coasts. Such coral reefs are increasingly exploited in commercial activities such as fisheries and tourism. Over-exploitation of the animal communities of reefs and damage through pollution and coastal development pose a serious threat to the continued existence of these systems.

Caribbean reefs are among the best developed in the world in terms of structure. The high accumulation rates of reefs, up to 12m/1000 years (Macintyre *et al*. 1977), allows them to considerably alter the relief of the sea bottom. The carbonate build-up of reefs results in various reef types which are traditionally called fringing reefs, barrier reefs and atolls, depending upon the distance to the shore or the presence of an island land mass. Recently (Adey and Burke 1977) the terms bench reefs and bank barrier have been introduced, based upon the geological history of the reef and its preexisting basement. Apart from differences in the major structure, there are smaller details in the physiognomy of a coral reef that vary from reef to reef. Over the reef profile, sloping from the shore to the base of the living reef, features such as buttresses, sill reefs (e.g. Jamaica, Goreau and Goreau 1973), reef crests, spurs and grooves (e.g. Belize, Rutzler and Macintyre 1982) develop. The terms are not well defined but buttresses and canyons as well as spurs and grooves are arrangements of high coral ridges alternating with lower sand canals. Such series of ridges project into the sea at right angle with the reef crest or shore line. They are not the result of pre-existing structure or erosion but are constructional features (Shinn *et al.* 1981, 1982) built by the corals and associated organisms. Their occurrence appears to be related to the exposure of shallow reefs to wave energy (Burke 1982).

Many organisms partake in building the reefs but, although groups such as crustose coralline algae (Corallinaceae, Adey 1978) and hydrozoans (Millepora, Milliman 1969) can be locally significant, the contribution of the stony corals (Scleractinia) is of paramount importance. Reef-building coral communities extend from sea level to depth of 70 m (James 1977), while individual corals continue to greater depth of 80-100 m (Lang 1974, Bak 1975). At these great depths sclerosponges may become a constructional component (Lang *et al.* 1975).

The prominent role of stony corals in reefs is such that they must be termed ecological dominants on Caribbean reefs. They are of vital importance and the reef and other reef organisms cannot exist without the corals. Corals are important in a trophic sense (Gladfelter, this volume), in the distribution and conservation of energy (= food, nutrients). Corals are certainly keystones in a structural sense. They built the habitat and are the environment for the other reef species.

## CORAL DISTRIBUTION

Corals are distributed over reefs in certain patterns from shallow to deep water. Such a zonation of a Caribbean reef will show the following features:

1. Shore zone: In very shallow water occur a few hardy species with respect to temperature, salinity changes and dessication (Mayor 1918, 1924; Vaughan 1919; Wells 1932). The colonies are encrusting or semispheroid.

2. *Acropora palmata* zone: This is a zone of considerable wave action and the shape and size of the large branched *A. palmata* colonies will depend on exposure to wave force (Graus *et al.* 1977). The depth range of this species is influenced by water movement and it will occur in deeper water (to 12m) in more turbulent conditions (Glynn 1973, Bak 1975). Possible regulating mechanisms are exchange of gases, nutrients, waste products and (animal) food (Chamberlain and Graus 1975).

3. *Acropora cervicornis* zone: Seawards of the wave swept *A. palmata* zone loose sediments accumulate and this zone is dominated by a species particularly suited to such an environment. Little water movement is sufficient to prohibit the build-up of sediment on the tissues of the spindly branched *A. cervicornis*. The colonies grow in self-supporting clumps commonly resting on dead bases of branches, over the sandy substratum.

An interesting approach to zonation studies (Robert 1977) showed that the border between the *A. palmata* and the *A. cervicornis* zone coincided with the change from a wave force to a current force dominated reef habitat.

4. Head coral zone: Often dominated by *Montastrea annularis*.

5. Slope zone: Dominated by flattened shingle-shape colonies.

What the exact physiological requirements of the corals in these zones are or the limits of their physiological niche, is not very well known. The response of these corals to factors such as salinity or dissolved oxygen is not relevant to an explanation of the distribution, because such factors do not vary much and are rather uniformly distributed on the deeper reefs (Ott 1975, Dana 1976, Ohlhorst 1980). Food availability (zooplankton) is a possibly regulating factor. But recent studies showed no correlations between nutritional requirements of coral species and zonation pattern (Wellington 1982), and zooplankton densities appear to be spatially unpredictable over the reef (Ohlhorst 1980). The absence of such relations may be explained by the dependence of corals on other nutritional sources such as organic carbon produced and translocated by their endosymbiotic algae (zooxanthellae). Recent studies have concentrated on the interactions of the coelenterate coral host with these uni-cellular algae and the response of the coral algal unit to different light levels (see Gladfelter, this volume). Variations in the characteristics of the algae may be correlated with coral distributional patterns.

The zonation and occurrence of corals has traditionally been explained as the result of the physiological demands and the metabolic requirements of the particular coral species. But lately more emphasis has been laid on the ecological differences between species and the predictability level of the environment. Differences in life history characteristics between coral species, such as reproduction and regeneration rates, result in a variety of responses to stimuli of the biotic and abiotic environment. The variation in life history strategies is very well suited to elucidate the differences that are encountered between coral communities and is treated in more detail below.

The general coral zonation pattern appears obvious but there are striking exceptions in zonation and in the occurrence of coral reefs. Sometimes these can be related to the role of the corals in their environment and thus help to understand community organization. Or they are explained by the physiological response of the coral to a certain environment factor. An example of this is the occurrence of deep reef corals in turbid water at depths of only 1 m but at light intensities comparable to deep water (Roos 1971). But sometimes these deviations are as yet inexplicable. A most intriguing example of the last catagory is the abrupt change from coral reef to non-coral reef rocky bottom. Such discontinuities occur on the north coast of Curacao and the same phenomenon has been described from Jamaica (Goreau 1969). In Curacao the reef, densely populated with corals and crustose coralline algae seems to engulf a rocky pavement. The pavement is only covered with crustose corallines, *Sargassum* and a few scattered corals. There is no difference in environmental factors such as depth, water movement etc. on the reef and on the neighboring hard bottom. Why the hard bottom has not been colonized by dense coral growth is unknown. Goreau (1969) suggested that a certain "critical mass" must be reached before a true reef can develop. In Curacao the situation seems to indicate that the reef has internal controls which do not exist on the hard bottom a few meters away. How the critical mass concept has to be applied or what internal controls allow reef community development is not known.

Other variations to the general zonation model are in the discontinuity of coral communities along a coast: the *Acropora cervicornis* zone is absent at the southwest coast of Aruba where the *Acropora palmata* zone borders seawards on a dense growth of *Montastrea annularis*. But no *M. annularis* community is present at the eastern tip of the island where at the depth of the presumed head coral zone only scattered gorgonians and small corals occur. At Curacao and Bonaire the *Acropora cervicornis* zone is locally developed, alternating with long stretches of sandy bottom populated with gorgonians and few scattered corals.

Coral communities also differ in the mean size of coral colonies and in the dominance of coral species; on some reefs, species such as *Montastrea annularis* reach large size, up to 4 m in diameter and height, while in another area along the coast all colonies are smaller than 1 m. The head coral zone is usually dominated by *M. annularis* but *A. agaricites* may be dominant or a consortium of other species. Patchiness appears to be a characteristic of reefs, reef corals and other reef organisms.

Some of the existing variation can be explained when we assume the reef habitat to be an unpredictable environment, subjected to disturbances of a varying frequency and intensity. In such a habitat the communities are unbalanced, not in equilibrium and the presence of species depends on the regulating impact of disturbance (see Connell 1976, 1978). When a pattern of succession (a change in species composition through time) of coral species and coral communities unfolds on a reef, disturbances will interrupt this process and cause a change in community composition. Succession on a reef would consist of two sequential phases:

1. a phase with an increase in species richness through time caused by the settlement of new species,

2. followed by a decrease in species numbers through factors such as competition.

Interruptions during the first phase will result in an abnormal low species number, while interruptions during the second phase will result in an abnormally high species number. The effect of a particular disturbance will depend on the characteristic of the corals such as on skeletal morphology or sediment rejection efficiencies. The mechanisms regulating a decrease in species number are uncertain (e.g. Bak *et al.* 1982, Bradbury *et al.* in press) but such impoverishment on *older* reefs has been observed (Grigg and Maragos 1974).

## DISTURBANCE ON REEFS

*Storms*. the effects of storms is strongest in the shallow part of the reef and branched or otherwise fragile corals are more susceptible than others. *Acropora palmata* and *A. cervicornis* will in particular suffer through breakage. After breaking the living surfaces of the fragments will often die through mechanical damage and scouring of sand and rubble. The chance of survival is related to fragment size (Highsmith *et al*. 1980) and many fragments may survive.

*Diseases.* Most of the documented diseases of corals fall into one or two catagories called: blackband diseases and whiteband diseases. Blackband disease affects mainly head corals such as *Montastrea annularis* and *Diploria* species. It seems to be more common in stressed habitats and outbreaks of this disease may be related to degradation of the environment (Antonius 1977). Whiteband diseases are epidemic in character. The disease sweeps over the reefs, affecting a high proportion of the colonies and killing most of these. It especially affects *Acropora* species. It is interesting to note that during a recent outbreak in some areas (Virgin Islands, see Gladfelter 1982) *A. palmata* was the main victim while on other islands (Bonaire, Curacao, Bak & Criens in press) the epidemic killed most of the *A. cervicornis* leaving the *A. palmata* reefs intact. There is evidence that the impact of this disease is enhanced by environmental stress. But epidemics certainly occurred in unstressed areas.

*Competition.* The importance of competition on reefs as a structuring force in community organization is a subject of current research. Some forms of composition such as with algae for space and light are undeniable and sometimes operate as disturbance. Under certain conditions, possibly changes in nutrient levels, algae can overgrow pristine reefs as shown by the occurrence of dying colonies of *Agaricia agaricites* under mats of the alga *Dictyota* (San Blas island, Bak pers. obs.). Of course similar phenomena have been documented for polluted reefs (Fishelson 1973, Banner 1974).

*Predation.* The influence of predators on corals in the Caribbean is disputed. No phenomena similar to the outbreak of *Acanthaster planci*, the crown of thorns, in the Indo-Pacific region have occurred. It is known, however, that common predators such as the fireworm *Hermodice carunculata*, the snail *Coralliophila abbreviata* and the sea urchin *Diadema antillarum* have a preference for certain coral species as favorite prey (Ott & Lewis 1972, Bak & van Eys 1975). The potential for an effect on community composition is present. It has been suggested that *Coralliophila* was important in the massive mortality of *Acropora cervicornis* in Jamaica following the passage of hurricane Allan (Knowlton *et al*. 1981).

*Bioerosion.* This is not only an important factor in the general accumulation of reef bodies and sediments but also in the survival and mortality of coral colonies. The sea urchin *Diadema antillarum* is an important eroder of bases of living corals. While the dead base is eroded the living part is continuing to grow and increase in mass and the result is weakened structure. Such colonies are much easier dislodged and destructed. They will not reach the size of intact colonies. Because *Diadema* populations can vary strongly in density along coasts (e.g. Bauer 1980) and because certain species such as Montastrea annularis and Colpophyllia natans (which grow potentially to large size) are conspicuous victims of their grazing behavior they exert a strong influence on colony size in coral communities (Bak unpubl. obs.).

Human Interference. The activity of man covers a large spectrum of disturbing influences on reefs (Johannes 1975). Human interference may result in the death of reefs, or may stress reef communities so much that diseases and bacterial infections or changes in the biology of coral species such as in fecundity, may change the community structure (e.g. Dodge & Vaisnys 1977; Bak 1978; Ducklow & Mitchell 1979; Loya & Rinkevich 1980). The impact of pollution can vary through the year with changing environmental conditions. For example, thermal pollution will be most effective during the months with highest sea temperatures. Of course the impact of agents of pollution varies with depth, the shallower zones being generally most affected.

However, to mention that disturbing agents, such as those listed above do halt community development, set back successional sequences and change the structure of coral populations is only to illuminate one side of the interaction strucutre. On the other side there is a characteristic feedback from the coral population. To what degree a disturbance affects a coral community and in which direction the change will be, depends not only on the disturbing agents but on the species composition and the constructional qualities (e.g. size of colonies) of the affected community.

## LIFE HISTORY CHARACTERISTICS IN CORALS

It is obvious that corals react differently to disturbances. At a certain disturbance level, e.g. a moderate storm, a community of branched or otherwise fragile corals would be much more affected than a community consisting for hundred percent of large Montastrea annularis colonies. To understand this spectrum of reactions we can consider the changes in a fairly typical Caribbean reef community consisting of a mixed coral assemblage of some 15 to 20 species. These changes are caused by small disturbances, occurring while environmental factors are considered stable, over a five year period. Table 1 shows the spatial change of the main bottom components of the reef. Spatial change is expressed as $I_R$ and reflects the extent to which a component remained at the same place or changed position on the bottom. The values of $I_R$ range from 0 (= no change in position over 5 years), to 100 (= all positions changed, see Bak & Luckhurst 1980 for details). It appears that the coral species vary highly in their "mobility", some are subjected to much more change than others. Such characteristics are indicative for the different life histories employed by the different species in the community. For example Agaricia agaricites proved to be an unstable coral in the community (Table 1, $I_R$=56) and the same study showed that this was related to the extraordinary high mortality in this species. Over 5 years 64% of the larger A. agaricites died (Table 2, Bak & Luckhurst 1980). These values are in marked contrast with those of Montastrea annularis which is spatially stable (Table 1, $I_R$= 13.6) and has a low mortality (Table 2). But while A. agaricites may be relatively easily wiped out, it is very abundant as a small colony. This is a consequence of the survival of small remnants of larger colonies

(Lewis 1974, Bak & Engel 1979, Bak & Luckhurst 1980, Hughes and Jackson 1980), but is mainly caused by its extreme efficiency as a recruiter through sexually produced larvae (Table 3). Of course this prolific settlement complements the extensive mortality resulting in the pattern of high spatial mobility. The abundancy of *A. agaricites* as a juvenile recruit is balanced by a relatively great vulnerability. *A. agaricites* is poor in sand sediment removal from its horizontal surfaces (Bak and Elgershuizen 1976) and lesions in the living tissue regenerate badly, especially if the skeleton is damaged, and such prolonged lesions carry a higher risk of invasion by organisms such as excavating sponges (Bak *et al.* 1977; Bak & Steward-van Es 1980). In *A. agaricites* energy appears to be allocated to reproduction and settlement rather than to maintenance and survival. Within the species this strategy is carried to the extreme limits by the form *humilis* (van Moorsel 1981).

The strategy of *Montastrea annularis* is in many aspects the opposite: *Montastrea* has few recruits (Table 3) but survival is good as shown by regeneration efficiency, (Bak *et al.* 1977), mortality is low (Table 2) and colonies can reach a high age and a great size. This view of *Montastrea* is confirmed by its spatial stability on the reef, having an Index of spatial change four times as low as *Agaricia agaricites* (Table 1). Under the current conditions both species can persist in the same habitat. This is shown by the lack of change in cover over the 5 year period (Table 4). The environment is changing (unpredictable) enough for *A. agaricites* to persist through colonization. Table 1 shows bare rock, a necessary resource for settlement, to be a spatially changing bottom component, while Table 4 demonstrates the continuity of this resource through time. This means that there is continually new rock uncovered and available for settlement by an opportunistic species such as *A. agaricites.* On the other hand, the habitat is not so unpredictable that a stable coral such as *M. annularis* cannot persist.

Distinctively different life histories are employed by the branched *Acropora* species. *A. palmata* is rare as a sexually produced juvenile (Table 3) but it is successful in asexual proliferation (Bak & Criens in press). This is in accordance with the high regeneration rate of lesions (Bak unpubl.) and the high growth rate (Bak 1976; Gladfelter *et al.* 1978). Such characteristics are easily understood with regard to the habitat of *A. palmata* on the shallow reef. Colonies are very exposed to turbulence and breakage of parts of colonies occurs under normal conditions (Bak 1976, Fig. 7). Occasionally storms will destroy colonies and whole *A. palmata* assemblages, but *A. palmata* is well-adapted to such disturbances and may actually need these to survive locally (van Duyl in prep.). *A. cervicornis* is more fragile and occurs in deeper water than *A. palmata* but the life strategy is very similar.

In these coral species extensive fragmentation with subsequent regeneration of colonies will result in a decrease of genetic variation in the population. This may be a double-edged sword: it facilitates survival of the species through enhanced chances of cementation to other fragments, which will result in greater stability. On the other hand it may be the reason why the *Acropora* species are so susceptible to epidemic diseases. Vegetative reproduction in *Acropora* increases the chance of local maintenance of a population but the potential to colonize other reefs is reduced.

Local persistence is also enhanced by the lack of antagonistic reactions (e.g. Hildemann et al. 1975) between the two species (Bak & Criens 1982). Fragments of A. palmata and A. cervicornis fuse easily. Well-developed communities of the two species are highly co-occurrent (van Duyl in prep.) and intra-generic fusion will be of advantage in survival.

Madracis mirabilis resembles the Acropora species in some respects. Living in deeper water as assemblages of clumped colonies or in nearly monospecific fields, this fragile branched species is less susceptible to wave action. But even in the absence of storms the colonies are subjected to considerable disturbance and the species can suffer a 50 percent reduction in cover over a few years (Bak & Luckhurst 1980). Continuing observations show the survivorship of colony fragments to be good (Bak & Criens in press; Bak pers. obs.). This despite the relatively low growth rate and although the fragments of M. mirabilis cannot enhance their stability through fusion. Stability is increased through the interference of the characteristic sponge fauna of M. mirabilis. These organisms cover the lower, dead, parts of the branches and their attachment to the substrata gives the Madracis fragments a reasonable stability in the relatively calm water conditions of this habitat.

A potentially important life history aspect in corals is their ability to compete with other coral species for space, because they vary in their competitive abilities such as extra-coelenteric digestion of neighbors through the mesenterial filaments. They can be ranked in an aggressive hierarchy (Lang 1970, 1971, 1973), with dominant species killing subordinate species: e.g. Montastrea annularis would kill Acropora palmata which would kill Agaricia agaricites which would kill Madracis mirabilis. If such a process could unfold on the reef, one species or a few species would persist through time while the subordinates would be eliminated. This would ultimately, when not interrupted, result in a climax community of dominant agressive species. However, subordinates may maintain themselves through rapid growth and overgrow the more agressive species. Competition through overgrowth and shading has shown to be of importance in rapidly growing corals on shallow Pacific reefs (Connell 1976, 1978). Recently the existence of yet another coral interaction mechanism, sweeper tentacle development, has been demonstrated (Richardson et al. 1979; Wellington 1980; Bak et al. 1982). Such elongated tentacles are developed in response to extra-coelenteric attack and used in counter-attack. Employing sweeper tentacles subordinate corals are able to reverse the initial dominance-subordinate relationship. An additional complicating factor in interspecific coral interactions is the role of epifauna. Vagile animals such as small crabs can occupy the lesions resulting from the coral interaction and damage the unaffected attacker (Bak et al. 1982). Reversal of interaction patterns in Caribbean corals is shown in Fig. 1.

It appears that many variables interfere in competition for space and the ultimate result of superior competitors, domination of the coral community and monopolization of space, will be a very time consuming process. Indeed the time scale involved for competition to become a structuring force in communities may easily exceed the time interval between larger and smaller disturbances.

## CONCLUSION

The interaction of environmental factors, coral physiology, interruptive forces and life history characteristics determines the character of a coral community *in situ*, is of necessity a general statement. We do recognize some of the effects of these factors in coral reefs. However, their variations in magnitude and interaction level over the reef and along the coast, are still not well understood. In view of this incomplete understanding of coral reefs, the world-wide degradation of reefs should concern us gravely. Research on these vulnerable systems must be encouraged while prudence should be a key word in the management of reefs.

## LITERATURE CITED

Adey, W. H. 1978. Coral reef morphogenesis: a multidimensional model. Science *202*: 831-837.

Adey, W. H. & R. B. Burke. 1977. Holocene bioherms of lesser Antilles - Geological control of development. AAPG Stud. Geol. *4*: 67 - 81.

Antonius, A. 1977. Coral mortality in reefs, a problem for science and management. Proc. Third Int. Coral Reef Symp. *2*: 617-623.

Bak, R. P. M. 1975. Ecological aspects of the distribution of reef corals in the Netherlands Antilles. Bijdr. Dierk. *45*:181-190.

Bak, R. P. M. 1976. The growth of coral colonies and the importance of crustose coralline algae and burrowing sponges in relation with carbonate accumulation. Neth. J. Sea Res. *10*: 285-337.

Bak, R. P. M. 1978. Lethal and sublethal effects of dredging on reef corals. Mar. Pol. Bull. *9*: 14-16.

Bak, R. P. M. and G. van Eys. 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. Oecologia (Berl.) *20*: 111-115.

Bak, R. P. M. and J. H. B. W. Elgershuizen. 1976. Patterns of oil-sediment rejection in corals. Mar. Biol. *37*: 105-113.

Bak, R. P. M., J. J. W. M. Brouns and F. M. L. Heys. 1977. Regeneration and aspects of spatial competition in the scleractinian corals *Agaricia agaricites* and *Montastrea* annularis. Proc. Third Int. Coral Reef Symp. *1*: 143-148.

Bak, R. P. M. and M. S. Engel. 1979. Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar. Biol. *54*: 341-352.

Bak, R. P. M. and B. E. Luckhurst. 1980. Constancy and change in coral reef habitats along depth gradients at Curacao. Oecologia *47*: 145-155.

Bak, R. P. M. and Y. Steward-van Es. 1980. Regeneration of superficial damage in the scleractinian corals *Agaricia agaricites* f. *purpurea* and *Porites astreoides*. Bull. Mar. Sci. *30*: 883-887.

Bak, R. P. M. and S. R. Criens. 1982. Experimental fusion in Atlantic *Acropora* (Scleractinia). Mar. Biol. Lett. *3*: 67-72.

Bak, R. P. M., R. M. Termaat and R. Dekker. 1982. Complexity of coral interactions: Influence of time, location of interaction and epifauna. Mar. Biol. *69*: 215-222.

Bak, R. P. M. and S. R. Criens. Survival after fragmentation of colonies of *Madracis mirabilis*, *Acropora palmata* and *A. cervicornis* (Scleractinia) and the subsequent impact of a coral disease. Proc. Fourth Int. Symp. Coral Reefs, Manila 1981 (in press).

Banner, A. H. 1974. Kaneohe Bay, Hawaii: urban pollution and a coral reef ecosystem. Proc. Second Int. Symp. Coral Reefs *2*: 685-702.

Bauer, J. C. 1980. Observations on geographical variation in population density of the echinoid *Diadema antillarum* within the Western North Atlantic. Bull. Mar. Sci. *30*: 509-515.

Bradbury, R. H., W. T. Williams and P. C. Young. The race and the swift revisited, or is agression in corals important? Proc. Fourth Int. Symp. Coral Reefs, Manila 1981. (in press).

Burke, R. B. 1982. Reconnaissance study of the geomorphology and benthic communities of the Outer Barrier Reef Platform Belize. *In*: The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I (eds. K. Rutzler and I. G. Macintyre) Smithsonian Press, Washington pp. 509-526.

Chamberlain, J. A. and R. R. Graus. 1975. Water flow and hydromechanical adaptations of branched reef corals. Bull. Mar. Sci. *25*: 112-125.

Connell, J. H. 1976. Competitive interactions and the species diversity of corals. *In*: G. O. Mackie, ed. Coelenterate ecology and behavior. Plenum Press, New York and London. pp. 51-58

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs. Science *199*: 1302-1310.

Dana, T. F. 1976. Reef-coral dispersion patterns and environmental variables on a Caribbean coral reef. Bull. Mar. Sci. *26*: 1-13.

Dodge, R. E. and J. R. Vaisnys. 1977. Coral populations and growth patterns: Responses to sedimentation and turbidity associated with dredging. J. Mar. Sci. *35*: 715-730.

Ducklow, H. W. and R. Mitchell. 1979. Bacterial populations and adaptations in the mucus layers of living corals. Limnol. Oceanogr. *24*: 715-725.

Fishelson, L. 1973. Ecology of coral reefs in the Gulf of Aqaba (Red Sea) influenced by pollution. Oecologia *12*: 55-67.

Gladfelter, E. H., R. K. Monahan, and W. B. Gladfelter. 1978. Growth rates of five reef-building corals in the northeastern Caribbean. Bull. Mar. Sci. 28: 728-734.

Gladfelter, W. B. 1982. White-band disease in Acropora palmata: implications for the structure and growth of shallow reefs. Bull. Mar. Sci. 32: 639-643.

Glynn, P. W. 1973. Aspects of the ecology of coral reefs in the Western Atlantic region. In: Biology and geology of coral reefs, Vol. 2. pp. 271-324. Eds. O. A. Jones and R. Endean. New York: Academic Press.

Goreau, T. F. 1969. Post Pleistocene urban renewal in coral reefs. Micronesica 5: 323-326.

Goreau, T. F. and N. I. Goreau. 1973. The ecology of Jamaican coral reefs. Geomorphology, zonation, and sedimentary phases. Bull. Mar. Sci. 23: 399-464.

Graus, R. R., J. A. Chamberlain, and A. M. Boker. 1977. Structural modification of corals in relation to waves and currents. pp. 135-153. In: S. H. Frost, M. P. Weiss, and J. B. Saunders, eds. Reefs and related carbonates-ecology and sedimentology. American Association of Petroleum Geologists, Studies in Geology No. 4.

Grigg, R. W. and J. E. Maragos. 1974. Recolonization of hermatypic corals on submerged lava flows in Hawaii. Ecology 55: 387-395.

Highsmith, R. C., A. C. Riggs, and C. M. D'Antonio. 1980. Survival of hurricane-generated coral fragments and a disturbance model of reef calcification/growth rates. Oecologia 46: 322-329.

Hildemann, W. H., D. S. Linthicum and D. C. Vann. 1975. Immuno incompatibility reactions in corals (Coelenterates). In: Immunologic phylogeny, (W. H. Hildemann and A. A. Benedict, eds.) pp.105-114.Plenum Press, New York.

Hughes, T. P. and J. B. C. Jackson. 1980. Do corals lie about their age? Some demographic consequences of partial mortality, fission, and fusion. Science 209: 713-715.

James, N. P. 1977. The deep and the past. Proc. Third Int. Coral Reef Symp. 2: 25-27.

Johannes, R. E. 1975. Pollution and degradation of coral reef communities. In: Tropical Marine Pollution, E. J. F. Wood and R. E. Johannes eds.) pp. 13-51. Elsevier, Amsterdam.

Knowlton, N., J. C. Lang, M. C. Rooney, and P. Clifford. 1981. Evidence for delayed mortality in hurricane-damaged Jamaican staghorn corals. Nature 294: 251-252.

Lang, J. C. 1970.Interspecific agression within the scleractinian reef corals, 80 pp. Ph.D. thesis, Yale University. 80 pp.

Lang, J. C. 1971. Interspecific aggression by Scleractinian corals I. The rediscovery of Scolymia cubensis (Milne Edwards & Haime). Bull. Mar. Sci. 21: 952-959.

Lang, J. C. 1973. Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift. Bull. Mar. Sci. 23: 260-279.

Lang, J. C. 1974. Biological zonation at the base of a reef. Am. Sci. 62: 272-281.

Lang, J. C., W. D. Hartman and L. S. Land. Sclerosponges: primary framework constructors on the Jamaican deep fore-reef. J. Mar. Res. 33: 223-231.

Lewis, J. B. 1974. Settlement and growth factors influencing the contagious distribution of some Atlantic reef corals. In: Proceedings of the Second International Symposium on Coral Reefs, 2: 201-206.

Loya, Y. and B. Rinkevich. 1980. Effects of oil pollution on coral reef communities. Mar. Ecol. Progr. Ser. 3: 167-180.

Macintyre, I. G., R. B. Burke and R. Stuckenrath. 1977. Thickest recorded Holocene reef section, Isla Perez cave hole, Alacran Reef, Mexico. Geol. 5: 749-754.

Mayor, A. G. 1918. Toxic effects due to high temperature. Carnegie Int. Wash. Pub. 252: 172-178.

Mayor, A. G. 1924. Structure and ecology of Samson Reefs. Carnegie Inst. Washington Pub. 340: 1-25.

Milliman, J. D. 1969. Four southwestern Caribbean atolls: Courtown Cays, Albuquerque Cays, Roncador Bank and Serrana Bank. Atoll Res. Bull. 129: 1-26.

Moorsel, G. W. N. M. van. 1981. Different reproduction strategies in two closely related stony corals (Agaricia, Scleractinia) Proc. Fourth Int. Coral Reef Symp. Abstract pp. 43.

Ohlhorst, S. L. 1980. Jamaican coral reefs: important biological and physical parameters. Ph.D. dissertation, Yale University.

Ott, B. 1975. Community patterns on a submerged barrier reef at Barbados, West Indies. Int. Revue ges. Hydrobiol. 60: 719-736.

Ott, B. and J. B. Lewis. 1972. The importance of the gastropod Coralliophila abbreviata (Lamarck) and the polychaete Hermodice carunculata (Pallas) as coral reef predators. Can. J. Zool. 50: 1651-1656.

Richardson, C. A., P. Dustan, and J. C. Lang. 1979. Maintenance of living space by sweeper tentacles of Montastrea cavernosa, a Caribbean reef coral. Mar. Biol. 55: 181-186.

Roberts, H. H., S. P. Murray and J. N. Suhayda. 1977. Physical processes in a fore-reef shelf environment. Proc. Third Int. Coral Reef Symp. 2: 507-515.

Rogers, C. S., T. H. Suchanek, and F. A. Pecora. 1982. Effects of Hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U. S. Virgin Islands. Bull. Mar. Sci. 32: 532-548.

Roos, P. J. 1971. The shallow-water stony corals of the Netherlands Antilles. Stud. Fauna Curacao 37: 1-108.

Rutzler, K. and I. G. Macintyre, 1982. The habitat distribution and community structure of the Barrier Reef complex at Carrie Bow Cay, Belize. In: The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize I., Eds. R. Rutzler and I. G. Macintyre pp. 1-45, Smithsonian Press, Washington, D.C.

Shinn, E. A., J. H. Hudson, R. B. Halley, B. Lidz, D. M. Robbin and I. G. Macintyre. 1982. Geology and sediment accumulation rates at Carrie Bow Cay, Belize I., Eds. R. Rutzler and I. G. Macintyre pp. 63-76, Smithsonian Press, Washington, D.C.

Shinn, E. A., J. H. Hudson, D. M. Robbin and B. Lidz. Spurs and grooves revisited: Construction versus erosion, Looe Key Reef, Florida. Proc. Fourth Int. Coral Reef Symp. (in press).

Vaughan, T. W. 1919. Coral and the formation of reefs. Smithsonian Inst. Ann. Rept. for 1917, pp. 189-238.

Wellington, G. M. 1980. Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47: 340-343.

Wellington, G. M. 1982. An experimental analysis of the effects of light and zooplankton on coral zonation. Oecologia 52: 311-320.

Wells, J. W. 1932. Study of the reef corals of the Tortugas. Carnegie Inst. Washington Yearbook 31: 290-291.

Table 1. Spatial change of substratum components, with a mean cover of 5% or greater per depth, at 10, 20, 30 and 40 m. $I_R$ = index of relative spatial change.

| Components | Depth 10m $I_R$ | 20m $I_R$ | 30m $I_R$ | 40m $I_R$ |
|---|---|---|---|---|
| *Agaricia agaricites* | - | 56 | - | 0 |
| *A. lamarcki* | 0 | - | 14.4 | 11.9 |
| *Montastrea annularis* | 13.6 | - | 0 | 0 |
| *M. cavernosa* | 8.3 | - | - | - |
| *Meandrina meandrites* | 0 | 33.8 | - | 0 |
| Coral - other | 62.5 | 35.3 | 22.5 | 41.8 |
| Sponge | - | - | - | - |
| Invertebrates - other | - | 58.5 | 38.3 | - |
| Rock | 59.1 | 50.8 | 24.1 | 20 |
| Loose sediment | 60 | 56.7 | 37.4 | 25.4 |
| Deep sediment | 29.2 | 28.4 | 30 | 22.7 |
| Coral fragments | 51.6 | - | 0 | 0 |
| All living components | 43.2 | 41.3 | 25 | 22.6 |
| All corals | 37.4 | 38.3 | 18.9 | 18.4 |
| All non-living components | 47.4 | 49.9 | 29.1 | 21.7 |
| Total change per quadrat | 45.7 | 46 | 27.7 | 22 |

Table 2. Mortality of coral colonies ($\geq$ 30 cm maximum diameter) between December 1973 and December 1978. Values expressed as % of N for each component. Mortality-other, includes colonies with mortality of >>50% in living surface.

| Components | N | Catastrophic mortality | | Mortality-other | Total Mortality |
|---|---|---|---|---|---|
| | | disappearance between two consecutive censuses | skeleton still present | | |
| *Agaricia agaricites* | 11 | 27 | 0 | 36 | 64+ |
| *A. lamarcki* | 47 | 2 | 0 | 9 | 11 |
| *Montastrea annularis* | 22 | 14 | 0 | 0 | 14 |
| *M. cavernosa* | 22 | 5 | 0 | 9 | 14 |
| *Meandrina meandrites* | 21 | 10 | 5 | 24 | 38 |
| Coral - other | 38 | 21 | 0 | 21 | 42 |
| Total | 161 | 11 | 1 | 14 | 26 |

\+ Arithmetic discrepancies are due to rounding errors

Table 3 - Percentage of the juveniles of different coral species per depth in Curacao. Total gives for each species the percentage of total sample (n = 919).

| | DEPTH | | | | |
|---|---|---|---|---|---|
| Coral Species | 3-9m | 9-17m | 17-26m | 26.37m | % Total Sample |
| *Stephnanocoenia michelinii* | | 2.6 | 3.9 | 6.7 | 3.4 |
| *Madracis decactis* | | 2.6 | 0.5 | 2.6 | 1.4 |
| *Madracis mirabilis* | 0.8 | | | | 0.2 |
| *Madracis pharensis* | | 0.5 | 0.5 | 2.6 | 1.0 |
| *Acropora* sp. | 0.8 | | | | 0.2 |
| *Agaricia agaricites* | 77.8 | 61.7 | 45.6 | 39.9 | 56.1 |
| *Agaricia lamarcki* | | 1.0 | 2.4 | 12.7 | 4.5 |
| *Agaricia grahamae* | | | | 0.8 | 0.2 |
| *Leptoseris cucullata* | | 12.4 | 19.0 | 8.6 | 9.4 |
| *Siderastrea siderea* | 0.8 | | | 1.1 | 0.5 |
| *Porites astreoides* | 9.5 | 3.6 | 9.3 | 9.3 | 8.2 |
| *Porites porites* | 1.6 | 0.5 | | | 0.5 |
| *Diploria strigosa* | 1.2 | | | | 0.3 |
| *Manicina/Colpophyllia* sp. | 0.4 | 1.6 | 1.0 | | 0.7 |
| *Montastrea annularis* | 1.2 | | | | 0.3 |
| *Montastrea cavernosa* | | 0.5 | | 1.1 | 0.4 |
| *Meandrina meandrites* | 2.4 | 4.1 | 8.7 | 9.7 | 6.3 |
| *Dichocoenia stellaris* | | | | 0.4 | 0.1 |
| *Mussa/Scolymia* sp. | | | | 0.8 | 0.2 |
| *Mycetophyllia ferox* | | 0.5 | | | 0.1 |
| *Eusmilia fastigiata* | 0.8 | 5.2 | 8.7 | 3.4 | 4.2 |
| *Millepora* sp. | 2.8 | 3.1 | 0.5 | | 1.5 |
| Unidentified | | | | 0.4 | 0.1 |

Table 4 - Comparison of mean percentage cover by coral reef substratum components between December 1973 and December 1978. Cover determined over 108 $m^2$, at depths 10-40m.

| Components | '73 | '78 |
|---|---|---|
| *Agaricia agaricites* | 2 | 2 |
| *A. lamarcki* | 8 | 8 |
| *Montastrea annularis* | 3 | 3 |
| *M. cavernosa* | 3 | 3 |
| *Meandrina meandrites* | 2 | 1 |
| Coral - other | 13 | 10 |
| Sponge | 2 | 4 |
| Invertebrates - other | 4 | 6 |
| Rock | 28 | 28 |
| Loose sediment | 16 | 18 |
| Deep sediment | 13 | 12 |
| Coral fragments | 5 | 5 |
| All living components | 38 | 37 |
| All corals | 32 | 28 |
| All non-living components | 62 | 63 |

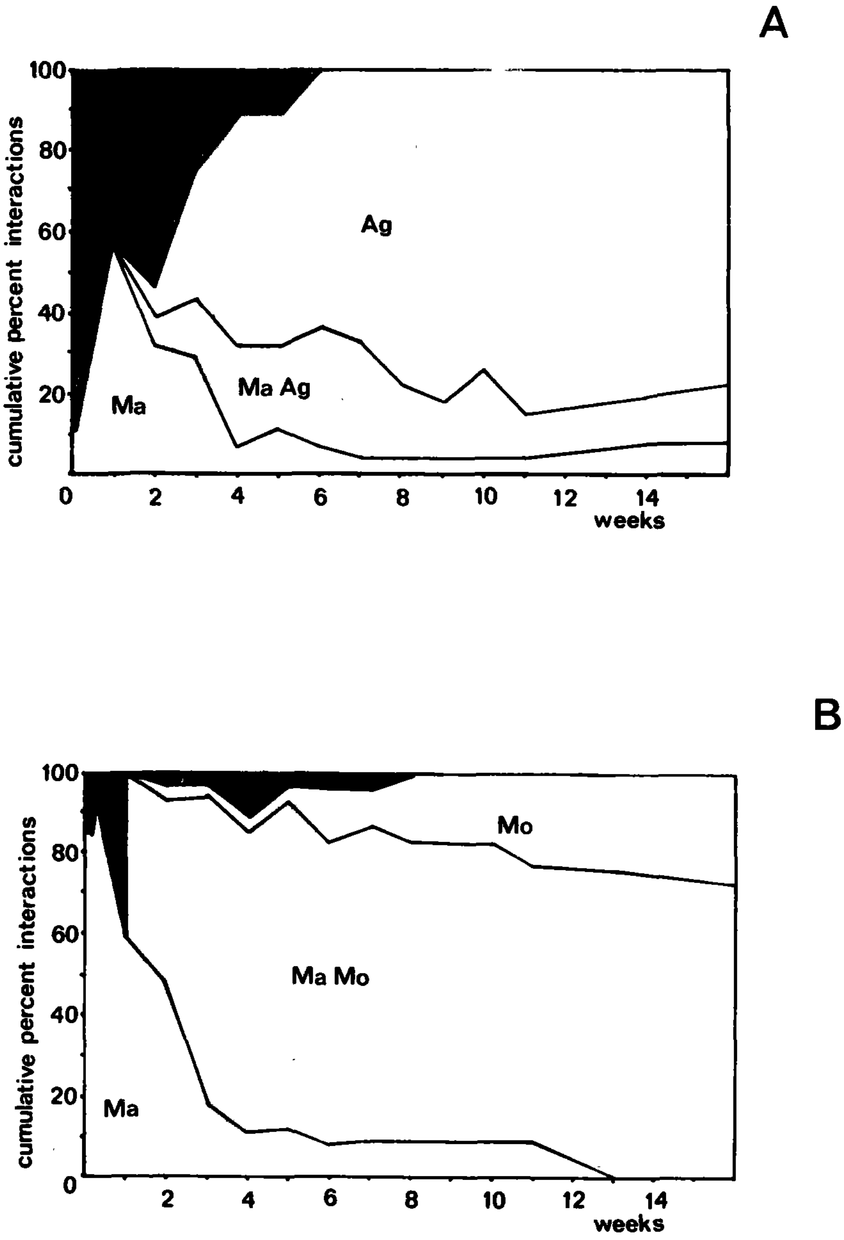

Fig. 1. Reversal of dominance-subordinate relationships in pairs of coral colonies. Shading indicates no interaction.

A. Madracis mirabilis suffers initial mortality in contact with Agaricia agaricites, but increasing mortality occurs in Agaricia after the first week. Ma= Madracis subordinate, Ma Ag = both species damaged, Aq = Agaricia subordinate, n= 28 pairs.

B. Initially mortality occurs only in Madracis mirabilis, but Montastrea annularis suffers increasing mortality after the first week. Ma = Madracis subordinate, Ma Mo = both species damaged, Mo = Montastrea subordinate. n = 29 pairs.

APPENDIX I. C. Dr. C. Peter McRoy

## Nutrient cycles in Caribbean seagrass ecosystems.

## INTRODUCTION

The cycling of the primary nutrients, nitrogen and phosphorus, is one of the major avenues of interaction within and between coastal ecosystems. In seagrass ecosystems in particular, the understanding of nutrient cycles is a key to understanding the distribution and abundance of seagrasses and how these systems are developed and maintained. Not all seagrass meadows are alike in function or structure nor, for that matter, are all Thalassia (turtlegrass) meadows. In many cases the differences in seagrass systems are the result of nutrient cycle processes; knowledge of these processes is crucial to predicting the response of a seagrass ecosystem to disturbance and hence useful to management strategies.

Tropical and temperate seagrass ecosystems can occupy a gradient of habitats that range, in terms of their nutrient status, from low nutrient conditions or oligotrophic habitats to high nutrient conditions or eutrophic habitats. In Caribbean coastal waters the interaction of seagrasses with coral reefs or mangroves can greatly affect the nutrient status of the system. Where a particular seagrass system falls on this nutrient gradient depends then on the processes that occur within the seagrass system as well as those between adjacent systems. Data to support these conclusions is limited for tropical seagrass systems in general and Caribbean seagrasses in particular, yet in combination with studies of temperate seagrass systems I consider it more than reasonable to speculate on the role of nutrient cycles in seagrasses and the interaction with other coastal ecosystems.

## NUTRIENT CYCLES IN TROPICAL SEAS

Tropical oceans such as the Caribbean are generally low in the concentration of dissolved nutrients in the water column (Morris et al. 1981). This is largely a consequence of a stratified water column maintained by the absence of a strong seasonal thermal fluctuation. In addition, coastal waters are nutrient poor due to the oligotrophic nature of the terrestrial soils as a sediment source (Jordan and Herrera 1981). The latter is a result of low geological activity in the recent geological past which due to the wet, warm climate has deeply weathered and leached the soil and coupled with low erosion has eliminated bedrock as a source of new nutrients. Furthermore, much of the marine sediment, particularly on the oceanic islands with little runoff, is derived from coral rubble which is primarily calcium carbonate and low in content of primary nutrients, nitrogen and phosphorus. In the Caribbean basin the highest nutrients occur in association with major population centers (Rodriquez 1981).

The lack of low winter temperatures in the Caribbean Sea has two major effects on nutrient cycles in coastal ecosystems. First, the absence of mixing below the permanent thermocline eliminates the water column as a major seasonal source of nutrients. Second, the absence of a thermal shock to sediment microbe populations results in continually high rate of organic matter decomposition. This latter point is a direct contrast to temperate coasts where organic matter can accumulate over winter due to low microbial activity. The consequence of these conditions is that tropical coastal ecosystems are expected to be skewed towards the oligotrophic end of a nutrient gradient. But this expected condition is not always the case and the variance from the expected condition is usually a result of interactions with other ecosystems.

## NUTRIENT CYCLES IN TROPICAL SEAGRASS MEADOWS

Seagrasses are rooted, vascular plants that depend primarily on nutrient resources in the sediments for growth (McRoy and Lloyd 1981). On the other hand, seagrass ecosystems although dominated by these vascular plants also contain many species of benthic and epiphytic algae that for the most part are only capable of utilizing nutrients from the water column; in a more limited way this latter nutrient source is also available to seagrasses (Short 1981). As a basis for considering nutrient cycles and interactions within seagrass ecosystems and between other coastal ecosystems I first describe some seagrass habitats in the Miskito Cays (from McRoy, Zieman, Short and Penhale, unpubl. data).

The Miskito Cays are a small group of mangrove islands on the large shallow shelf adjacent to Nicaragua. This bank constitutes the largest shallow water shelf in the Caribbean. It is a pristine area unaffected by the effluents of large population centers.

We sampled seagrasses and sediments from five stations on a transect that began in a shallow mangrove surrounded lagoon and ended in the waters of the open shelf (Fig. 1). Phillips *et al.* (1982) have described the marine plant communities in this area. The quantitative composition of these seagrass meadows varied greatly between the lagoon habitat (Station MT-1) and the shelf habitat (Station MT-5; Fig. 2). The inner two stations consisted of dense monospecific stands of turtle grass, *Thalassia testudinum* Banks ex König, and the shelf stations contained mixed *Thalassia* and *Syringodium filiforme* Kutz. and had lower overall biomass; a quantity of benthic macrophytic algae was present at all stations. The interstitial dissolved nitrogen, primarily as ammonium, was highest at the two lagoon stations and decreased to low levels in the shelf stations (Fig. 3). This trend was accompanied by a gradient of relatively low to high pH and high to low concentration of interstitial sulfide. The sediments in the lagoon stations also contained the largest quantity of plant detritus ('litter' in Fig. 2) and it was our conclusion that this gradient of detritus and associated decomposition processes was primarily responsible for the observed changes in the plant community, the sediment nitrogen concentration and other sediment parameters.

The transect of seagrass communities in the Miskito Cays represents a gradient of habitats from eutrophic in the lagoon to relatively oligotrophic on the shelf. The eutrophic end of the transect is the result of the protection from seas and currents afforded by the mangrove lagoon and concomitantly the subsidy of organic detritus to the sediments from mangrove leaves. Mangrove leaves, due to their high content of structural materials such as lignin and cellulose, are rather more resistant to microbial degredation than are the leaves of seagrasses (Rice 1982), hence this organic matter constitutes an additional reserve of nutrients for the seagrass meadows.

In a second example, Williams (1981) studied a gradient of seagrass meadows in habitats that ranged from oligotrophic to relatively more eutrophic on St. Croix in the U. S. Virgin Islands. The trends in the plant communities and the sediment conditions are in many respects similar to those in the Miskito Cays when examined with respect to this gradient (Table 1). Williams concluded that in very oligotrophic habitats seagrass ecosystems were represented structurally only by species of benthic algae, particularly the siphonous green macroalgae of the order Caulerpales. These rhizophytic algae have long been implicated as the colonizer species for seagrass ecosystems (den Hartog 1977) and Williams (1981) showed that these plants which anchor in soft sediments by root-like, rhizoidal holdfasts utilized interstitial nutrients from the sediments, a process similar to that in seagrasses. Williams also found that these algae could contribute a considerable quantity of organic detritus to the sediments in the early stages of system development and hence enrigh the nutrient pools.

## INTERACTIONS OF SEAGRASSES WITH OTHER COASTAL ECOSYSTEMS

The sequence of development of tropical seagrass ecosystems from bare sediment to rhizophytic algae through Halodule sp. and Syringodium to the climax species Thalassia testudinum (Fig. 4) was presented by a successional sequence by den Hartog (1977). Confirmation of this general scheme has come from studies of disturbed climax Thalassia beds and experimental transplants of various seagrass species (Taylor et al. 1973; Patriquin 1975; Zieman 1976; and Phillips 1980). The work of Williams (1981) is one of the few studies to deal with the nutrient processes involved in this successional scheme and she has added considerable functional detail to the outline presented by den Hartog. Furthermore, McRoy and Lloyd (1981) based on experience with temperate as well as tropical seagrass ecosystems, have postulated that the rate limiting step in this succession is the accumulation of sediment nutrients.

How are these processes affected by interaction with other coastal ecosystems? Coral reefs can affect the development of seagrass ecosystems and associated nutrient cycle processes in several ways. The primary function of a fringing or barrier reef is the creation of a physically protected habitat landward of the reef (Atkinson et al. 1981). This habitat is a trap that allows the accumulation of sediments and particulate organic matter - a necessary precondition for the establishment of a seagrass community. The degree of protection from waves and currents, particularly during storms, afforded by a reef can be a significant determinant in the subsequent succession of the seagrass system. For example, where the reef provides only minimal protection the sediment layer is thin (less than 3 to 4 cm) and the seagrass succession halts at the rhizophytic algae stage or that characterized by the shallow-rooted early seagrass colonizing species. Presumably this to the low accumulation of organic matter and nutrients in this sediment layer. This condition seems to be typical of the most leeward Caribbean islands (J. Ogden, pers. comm.). Where physical protection is greater and the sediment accumulation exceeds about 7 cm the successional sequence can proceed to the later stages of development, but what actually happens in any specific case will depend on the nutrient cycling processes.

Coral reefs (both fringing and patch) also affect nutrient cycles in adjacent seagrass meadows by providing a home for herbivorous fishes and invertebrates (Ogden 1980). Through food chains seagrasses provide nutrients to reef fauna and in many places the two systems are closely tied. An example of this relationship are the reefs and seagrass meadows in Tague Bay on St. Croix Island (Ogden 1976, Ogden et al. 1980). In cases of heavy grazing the herbivore community can indirectly control the seagrass nutrient cycles by increasing primary productivity and hence the successional stage of the seagrass system. Selective grazing by reef fishes has also been reported (Tribble 1981) and presumably this could also affect the nutrient status of the seagrass system.

Coastal mangroves can also provide some protection from water movements and hence create a sediment depositional habitat. Indeed, mangroves are well known to occur in thick, soft sediments and this was certainly the case in the mangrove-surrounded lagoon in the Miskito Cays. In addition, through the production of leaf detritus, mangroves contribute a considerable subsidy to the organic matter in the sediments and subsequently the nutrient pool. It is probable that the monospecific meadows of *Thalassia* found in the Miskito Cays are the consequence of this subsidy. For comparison, the 'climax' seagrass community described by Williams in Tague Bay consisted of mixed *Thalassia* and *Syringodium* plants as is the case for most seagrass meadows in the Caribbean. This mixed species community is probably actually a subclimax stage. It is likely that the final climax stage of these Caribbean seagrass ecosystems, that represented by monospecific *Thalassia* meadows, only occurs where there is a nutrient supplement to the sediments such as occurs around mangroves.

## CONCLUSIONS

Seagrass ecosystems occupy habitats that range from oligotrophic to eutrophic in Caribbean coastal waters. The developmental level of a specific seagrass community on this gradient depends on the balance between the accumulation and decomposition of organic matter in the sediments and the losses of organic matter from the system, i.e. the balance between nutrient supply and loss. All systems are imperfect and are constantly subjected to nutrient losses. Nutrient conservation mechanisms are a function of the living system hence any disturbance can result in rapid loss of nutrients and the system must recover through successional processes. The interaction with other coastal ecosystems can affect both nutrient accumulation and loss processes and thus affect the successional development of seagrass ecosystems. Few quantitative studies of these processes exist but such studies will contribute to the functional understanding of these systems necessary for conservation and management strategies.

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# LITERATURE CITED

Atkinson, M., S. V. Smith and E. D. Stroup. 1981. Circulation in Enewetak Atoll lagoon. Limnol. Oceanogr. 26: 1074-1083.

den Hartog, C. 1977. Structure, function and classification in seagrass communities, p. 89-121. In: C. P. McRoy and C. Helfferich (eds.), Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, N.Y.

Jordan, C. F. and R. Herrera. 1981. Tropical rain forests: are nutrients really critical? Am. Nat. 117(2): 167-180.

McRoy, C. P. and D. S. Lloyd. 1981. Comparative function and stability of macrophyte-based ecosystems, Chapt. 16. In: A. R. Longhurst (ed.), Analysis of Marine Ecosystems. Academic Press Inc., London.

Morris, I., A. E. Smith and H. E. Glover. 1981. Products of photosynthesis in phytoplankton off the Orinoco River and in the Caribbean Sea. Limnol. Oceanogr. 26: 1034-1044.

Morrison, J. M. and W. D. Nowlin, Jr. 1982. General distribution of water masses within the Eastern Caribbean Sea during the winter of 1972 and fall of 1973. J. Geophys. Res. 87(C6): 4207-4229.

Ogden, J. C. 1976. Herbivore-plant relationships on Caribbean reefs and seagrass beds. Aquat. Bot. 2: 103-116.

Ogden, J. C. 1980. Faunal relationships in Caribbean seagrass beds, pp. 173-198. In: R. C. Phillips and C. P. McRoy (eds.), Handbook of Seagrass Biology. Garland STPM Press, N.Y.

Ogden, J. C., S. Tighe and S. Miller. 1980. Grazing of seagrass by large herbivores in the Caribbean. Am. Zool. 20: 949.

Phillips, R. C. 1980. Responses of transplanted and indigenous *Thalassia testudinum* Banks ex Konig and *Halodule wrightii* Aschers to sediment loading and cold stress. Contr. Mar. Sci. Univ. Texas 23: 79-87.

Phillips, R. C., R. L. Vadas and N. Ogden. 1982. The marine algae and seagrasses of the Miskito Bank, Nicaragua. Aquat. Bot. 13: 187-195.

Rice, D. L. 1982. The detritus nitrogen problem: new observations and perspectives from organic geochemistry. Mar. Ecol.-Prog. Ser. 9: 153-162.

Rodriquez, A. 1981. Marine and coastal environmental stress in the wider Caribbean region. Ambio 10: 283-294.

Short, F. T. 1981. Nitrogen resource analysis and modeling of an eelgrass (*Zostera marina* L.) meadow in Izembek Lagoon, Alaska. Ph.D. Dissert., Univ. Alaska. 173 pp.

Tribble, G. W. 1981. Reef-based herbivores and the distribution of two seagrasses (*Syringodium filiforme* and *Thalassia testudinum*) in the San Blas Islands (Western Caribbean). Mar. Biol. *65*: 277-281.

Williams, S. L. 1981. *Caulerpa cupressoides*: the relationship of the uptake of sediment ammonium and of algal decomposition to seagrass bed colonization. Ph.D. Dissert., Univ. Maryland 77pp.

Table 1. A gradient in parameters of seagrass succession measured in Tague Bay Lagoon, St. Croix, U.S.V.I. (From Williams, 1981).

|  | Bare Sediments | Rhyzophytic Algal Community | Colonizing Seagrass Bed | Immature Seagrass Bed | *Thalassia* Seagrass Climax |
|---|---|---|---|---|---|
| # plants ($\bar{X}$)$\cdot$m $^{-2}$ | 0 | 254 | 981 | 3089 | 1533 |
| Biomass ($\bar{X}$ ) (g dry $^{-1}\cdot$m $^{-2}$) | 0 | 185 | 89 | 1244 | 2241 |
| # *Thalassia*:<br># *Syringodium*:<br># *Halodule* | 0:0:0 | 0:0:0 | 1:17:33 | 1:2:2 | 1:1:0 |
| Interstitial $NH_4$ ($\mu$M-N) | 0.0 | 1.0 | 3-4 | 3-39 | 6-200 |
| Adsorbed $NH_4$ ($\bar{X}$) ($\mu$M N$\cdot$g dry sediment $^{-1}$ ) | - | 0.63 | 2.50 | 3.05 | 12.82 |
| Sediment deoosition (g dry$\cdot$m$^{-2}\cdot$day $^{-1}$) | 240 | - | 2168 | - | 2941 |
| Detrital seagrass deposition (g dry$\cdot$m$^{-2}\cdot$week$^{-1}$) | - | - | 25.21 | - | 252.10 |

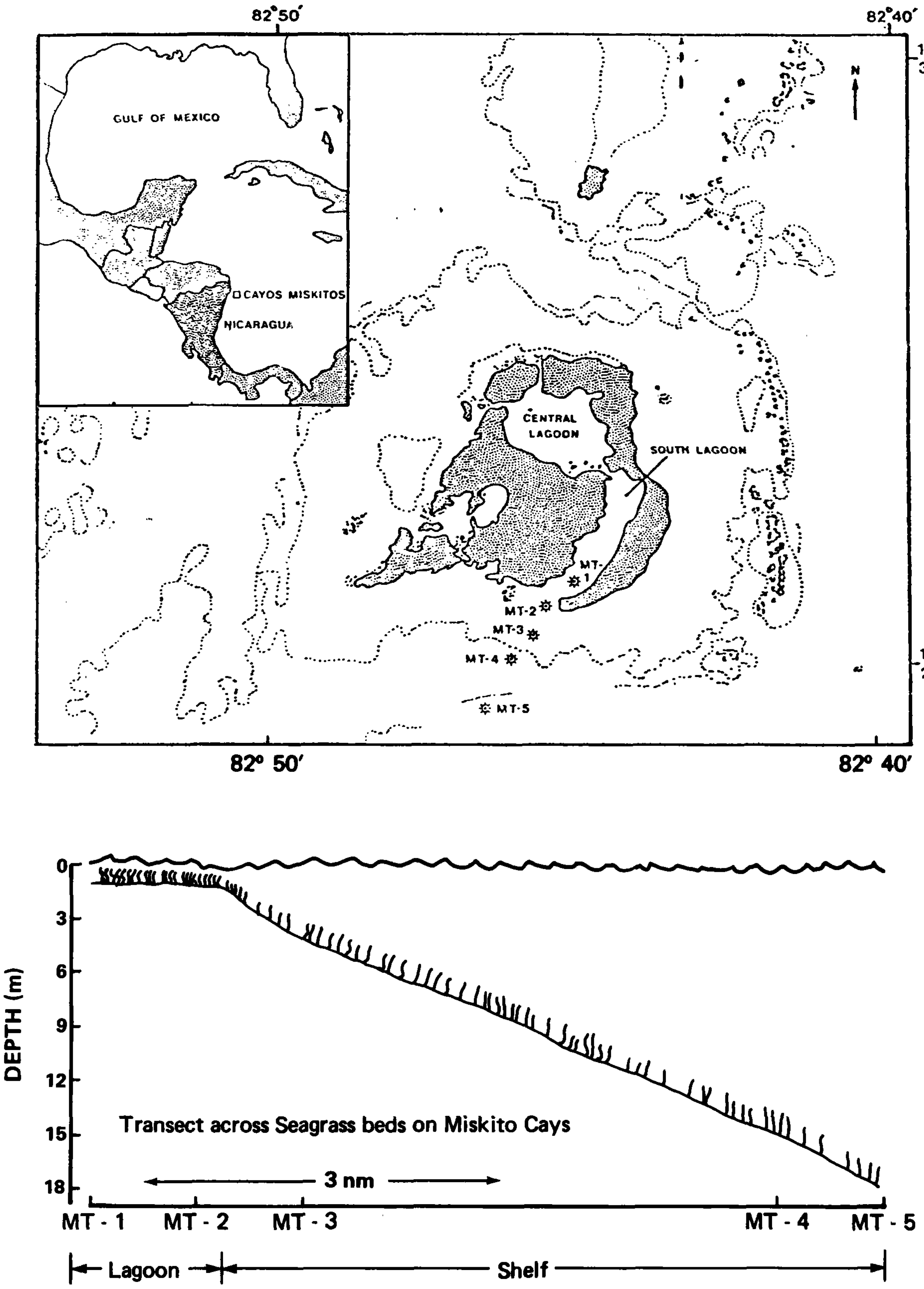

Fig. 1. Chart showing the location of the Miskito Cays and the seagrass transect stations (upper) along with a diagramatic representation of the transect (lower).

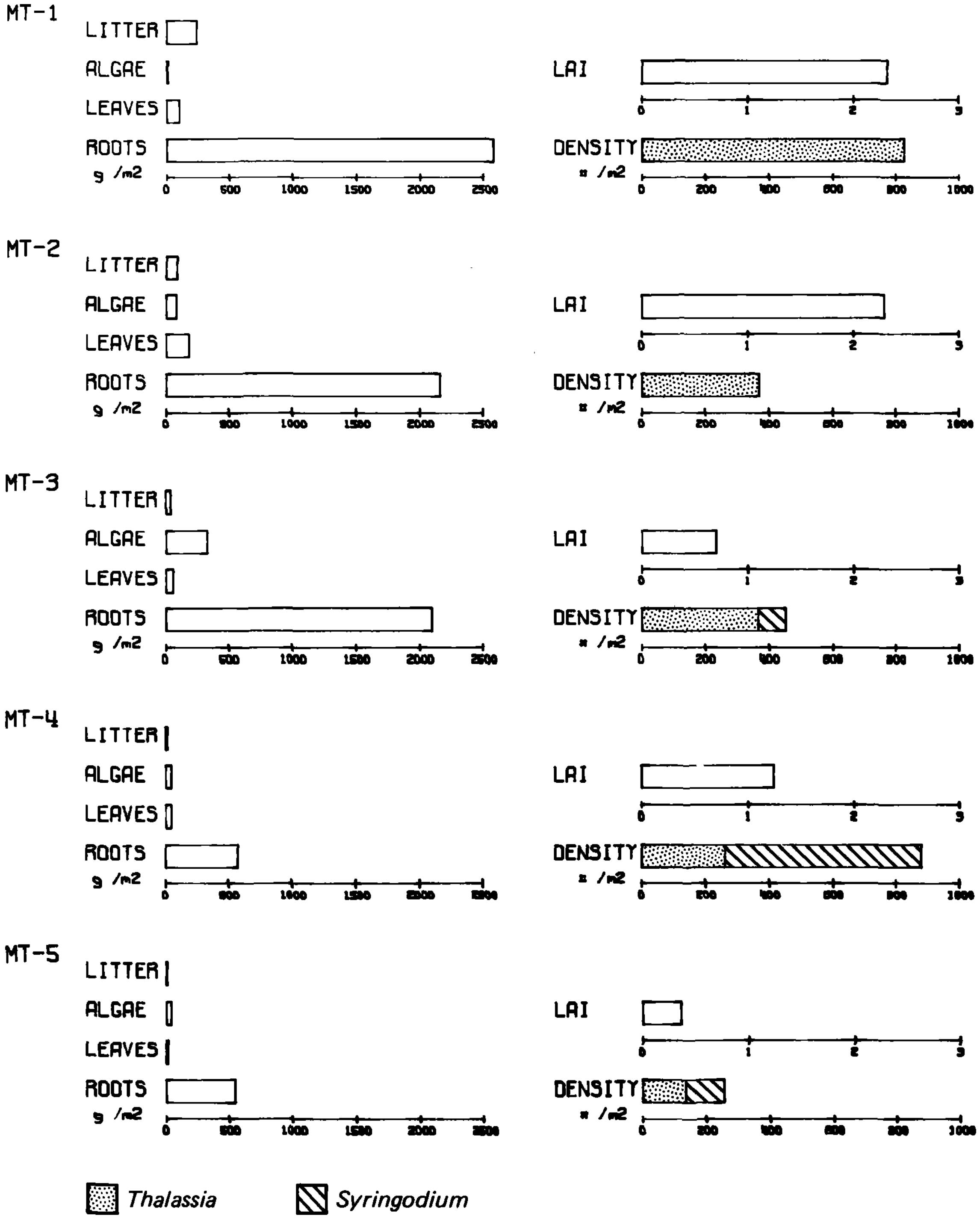

Fig. 2. Chracteristics of the plant community in the Miskito Cays seagrass transect (LAI refers to leaf area index).

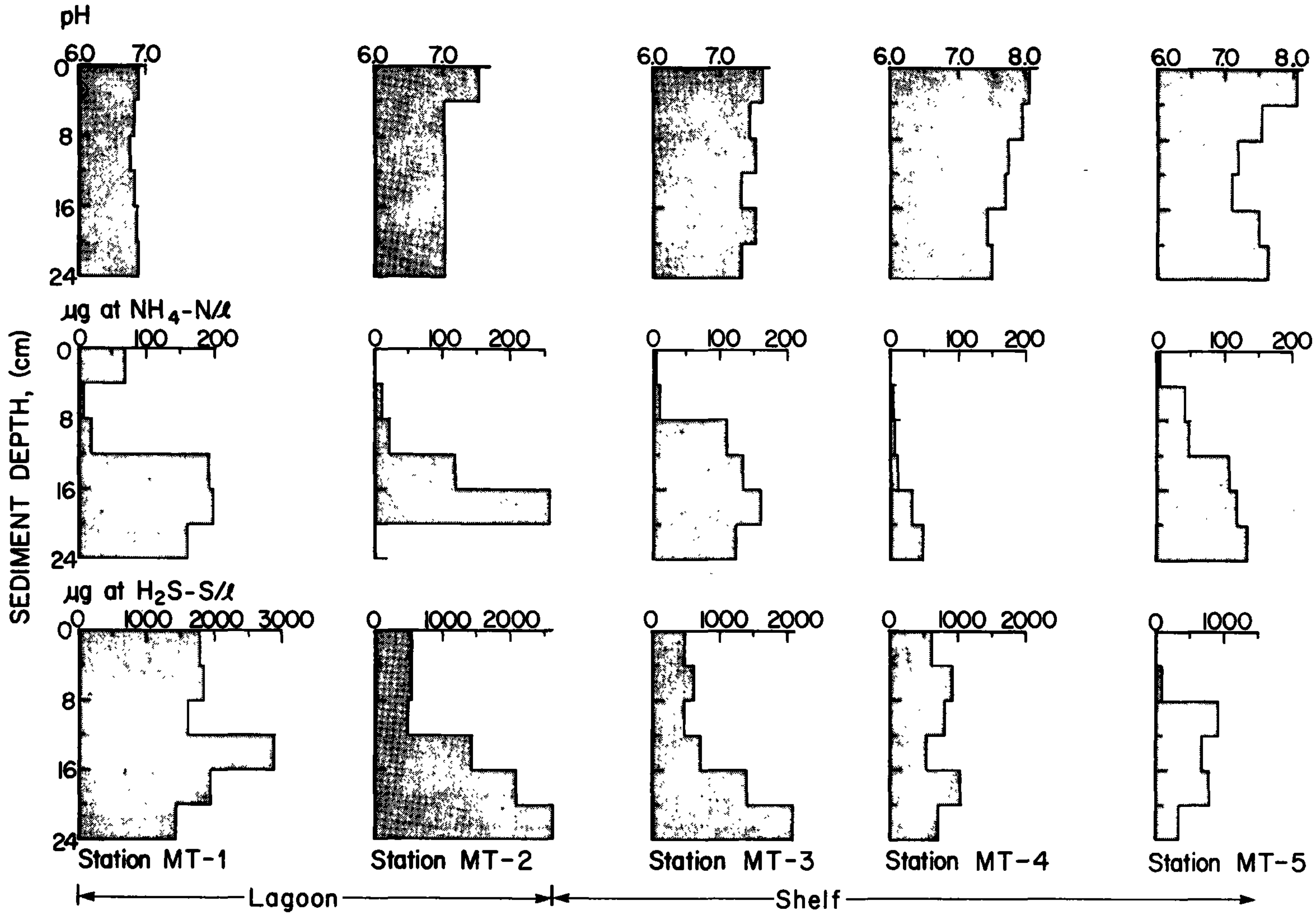

Fig. 3. Chemical characteristics (pH, interstitial ammonium and interstitial sulfide) of sediments associated with the Miskito Cays seagrass transect.

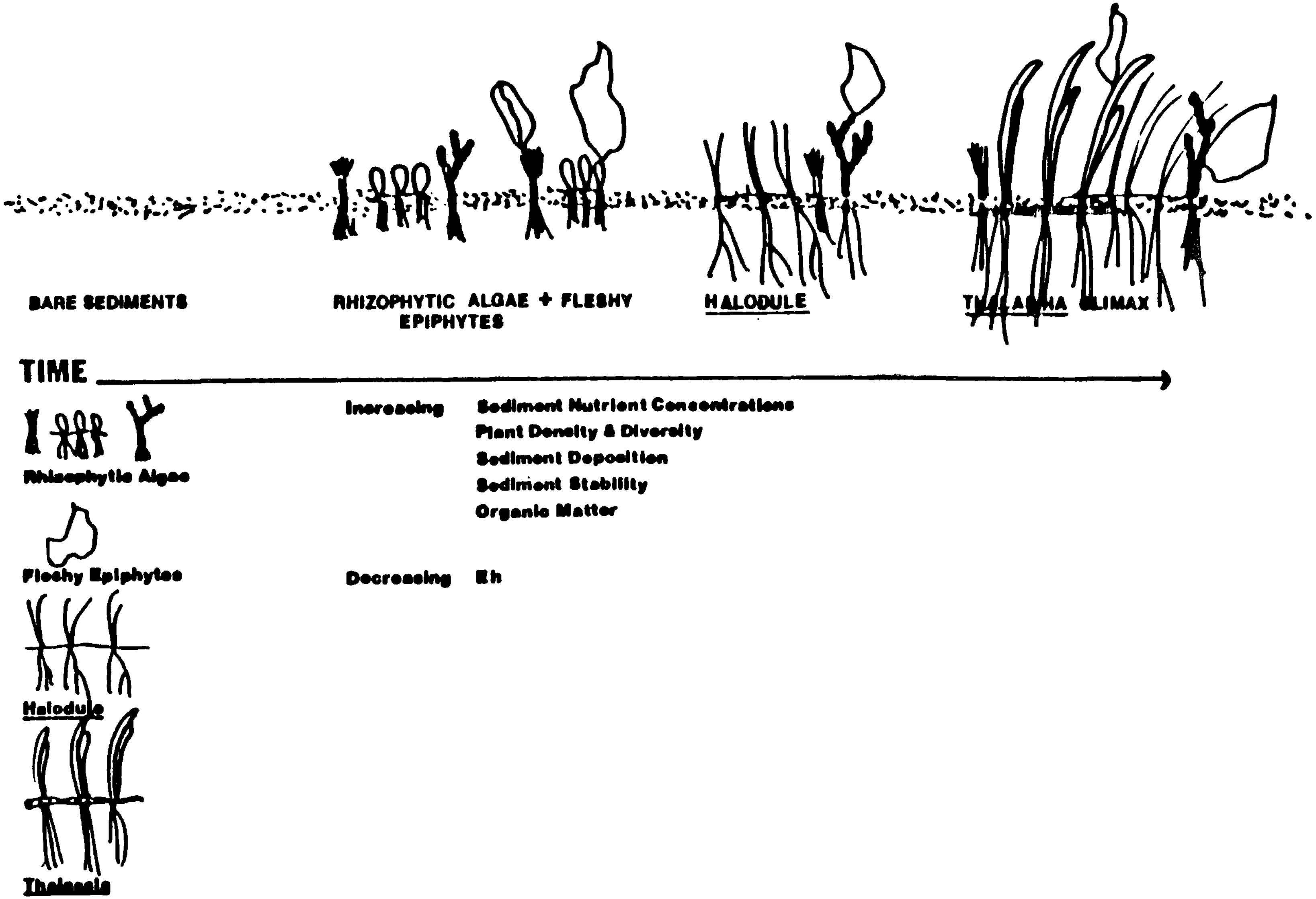

Fig. 4. Successional stages in the development of Caribbean seagrass ecosystems (after Williams, 1981). I consider the mixed species climax represented here to actually be a subclimax stage; the final climax stage would be a monospecific Thalassia community.

## APPENDIX I. D. Dr. Joseph C. Zieman

### Food webs in tropical seagrass systems.

## INTRODUCTION

Due to their distribution in shallow sublittoral and to some extent intertidal areas, seagrass systems are subject to stresses by the increasing human utilization of the tropical coastal zone. Seagrass beds are among the most productive of communities exceeding even phytoplankton production in upwelling areas off Peru (Ryther 1969; McRoy and McMillan 1977). These tropical seagrass beds support diverse and abundant fish and invertebrate faunas which often exceed populations in unvegetated portions of the system in both numbers and biomass.

Seagrass meadows act in several ways to control or modify the ecosystem, as shown in this classification developed by Wood et al. (1969):

1. They provide food for a relatively limited number of species such as the parrotfishes, surgeonfishes, Australian garfishes, the queen conch, sea urchins, and some nudibranchs. The green sea turtle formerly grazed heavily on the turtle grass, hence the name.

2. They serve as hosts for large numbers of epiphytes which are grazed extensively, by both invertebrates and fishes. These epiphytes may occasionally be comparable in biomass with the seagrasses themselves.

3. They produce large quantities of detrital material which serves as food for certain animal species and for microbes which in turn are used as food by larger animals.

4. They provide organic matter to initiate sulfate reduction and an activate sulfur cycle.

5. They tend to collect organic and inorganic material by slowing down currents and stabilizing the sediments.

6. The roots and rhizomes bind and stabilize the sediment surface. This also preserves the microbial flora of the sediment and the sediment-water interface.

7. The seagrasses have a rapid rate of growth and produce up to 10 g of dry leaf per $m^2$ per day.

A seagrass meadow produces a great quantity of organic matter and offers a substrate for epiphytic algae, microflora, and sessile fauna. Of the animal assemblage associated with above-ground portions of seagrasses, epifauna may have a close correlation with the bed while some infauna may be an extension of the benthic community of the surrounding area. In northwest Florida Hooks et al.(1976) found that greatest numbers of organisms of all of the habitats in several estuaries were found in seagrass beds, and that the highest abundances were associated with the densest vegetation, and concluded that many organisms are abundant in the grass beds due to (1) shelter and refuge from predation and high current velocities and (2) a food source, whether leaves, epiphytes or detritus. Similar observations and conclusions have been drawn from studies on temperate Zostera systems (Kikuchi 1961; Marsh 1973; Thayer et al. 1975). In Tampa Bay, Santos and Simon (1974) studied the abundance and distribution of polychaetous annelids in Thalassia, Halodule, and sand habitats, and found that different assemblages were not associated with different habitats, but that the Thalassia habitat had the greatest density of organism. This also appears true in most Zostera systems that have been studied (Orth 1971; Lappalainen 1973; Thayer et al. 1975).

Nekton species fall into three major categories: 1) some are permanent residents of the bed, 2) some reside in the bed only seasonally, and 3) some only use the bed during their daily foraging for food. Briggs and O'Connor (1971) and Adams (1976) have shown a greater density of fishes over seagrasses than in adjacent marine and estuarine waters. Adams (1976) presents data for seagrass beds in the Beaufort- North Carolina area which showed somewhat higher fish biomass than had been reported for Spartina marsh ponds, which are recognized as prime nursery area.

## GRASSBED UTILIZATION

The food webs formed among these organisms fall into three general categories: (1) direct herbivory, (2) detrital food webs within grass beds, and (3) detrital food webs of material that have been exported from the seagrass system. Classically the detrital web within the bed has been considered the main path of energy flow, and in most circumstances has been considered the only significant pathway. Studies in progress over the past several years have continued to show that this is the primary food web within a seagrass meadow, but that in some areas the other two pathways may be much more significant than previously suspected.

## DIRECT HERBIVORY

In the Caribbean region the major vertebrate consumers are green sea turtles (Chelonia mydas), West Indian manatee (Trichechus manatus), waterfowl, and fishes, waterfowl being less important than in the temperate region. While populations of the green sea turtle are low in many areas of the Caribbean, they are still regularly observed and may contribute conspicuously "mowed" areas of seagrass beds (Zieman, Iverson, and Ogden, ms. in prep.). The impact of turtle feeding on seagrass has never been fully evaluated. Manatees were once common in the mainland areas bordering the Caribbean, but were probably never important seagrass consumers in the smaller islands of the West Indies (Bertram and Bertram 1968). In the Chesapeake Bay region 20 species of waterfowl feed on one or another species of seagrass. The most common waterfowl species which feed extensively in grass beds (Stewart 1962) are Black brant, pintail, and scaup ducks. Previously, Cottam (1934) estimated that eelgrass constituted about 80 percent of the winter food of the black brant, while McRoy (1966) estimated that black brant and Canada geese consume about 17 percent of the standing crop of eelgrass in Izembek Lagoon, Alaska, during summer and fall. When nearly all of the eelgrass along the United States coast disappeared in the 1930's, the black brant all but disappeared.

The most studied vertebrates grazers in the tropical seagrass beds are fishes. Seagrass feeding in fishes is confined almost exclusively to the Caribbean (Randall 1965, 1967). Invertebrate consumers of seagrasses are most prevalent in tropical systems, and in temperate systems very few species feed directly on the living eelgrass blades.

In the West Indies and south Florida conspicuous halos surrounding coral reefs are caused by the grazing activity of herbivorous fishes and invertebrates. The primary grazers responsible for this zone are the sea urchin, Diadema antillarum (Ogden et al. 1973), and parrotfish and surgeonfish (Randall 1965). Both groups use the reef for shelter and protection, venturing into the relatively narrow (10m) zone where they may feed, but remaining near the protective cover of the reef.

The small grassbed parrotfish, Sparisoma radians, is a major seagrass consumer in the Caribbean and south Florida grassbeds. Ogden and Zieman (1977) showed that the parrotfish grazing in the vicinity of coral reefs form two distinct groups. The smaller parrotfish, Sparisoma radians, is a grassbed inhabitant and ventures to within about 20 m of a reef where its abundance decreases. Conversely, the larger parrotfish of the reef zone are highly abundant in the first 5 to 10 m from the reef but the number of these fish decreased greatly at 20 m distance. The canopy of the grassbed presents a three dimensional shelter for small (less than 15 cm) fishes, but is two dimensional to organisms greater than 20 cm which cannot hide in the leaves. Very large parrotfish, such as Scarus guacamia, are also seen in the grassbeds, but they are extremely wary, and the middle sized herbivores are confined to areas near the reef and its available shelter (Ogden and Zieman 1977). Occasionally mixed heterotypic schools include parrotfish, grunts, and snappers are seen foraging together in reef grassbeds (J. C. Zieman, pers. obs.).

In the Caribbean direct grazing now appears to be a more important pathway than previously suspected. Greenway (1976) found that 48 percent of the production of Thalassia in Kingston Harbor, Jamaica, was grazed by the extremely abundant urchin Lytechinus variegatus, while in St. Croix (Zieman et al. 1979) found that an average of 5 to 10 percent of the daily production of seagrasses was directly consumed by herbivores, with a maximum consumption of 15 to 20 percent. Seagrasses are not damaged by moderate grazing because the region of the leaf preferentially consumed is the outer portion which has ceased growing. This area of the leaf is senescent, but is often heavily colonized with epiphytic organisms.

## DETRITAL FOOD WEB IN GRASSBEDS

Classically, the detrital web in seagrass beds has long been considered the dominant pathway of energy flow and in many grassbeds is the only quantitatively significant path. Detritus formation consists of three primary processes; the initial rapid loss of soluble organic compounds, the colonization of the leaf substrate by bacteria, fungi, and protozoans, and physical and biological breakdown and fragmentation, as described in detail by Odum et al. (1973) and Thayer et al. (1978).

In addition to the living seagrasses, a complex community of microalgae, amphipods, rotifers, copepods and many other small organisms are mixed in with decaying grasses. Due to the basal growth pattern of seagrasses the leaves emerge from the short shoots clean and fresh, and become colonized by epiphytes from the oldest part of the leaf (the tip), downward, as the epiphytic community develops. This flourishing microcommunity becomes part of the litter layer. This community forms the basis of a microcarnivore food chain for a variety of juvenile fishes which use the beds as nurseries. Organisms that feed on this rich mixture may show some degree of selectivity in feeding, but are difficult to place into a conventional trophic scheme (Odum and Heald 1975).

## EXPORTED SEAGRASS

In recent years the amount of seagrass material exported from the beds and the potential importance of these leaves as food at distances and depths quite remote from the source grassbeds has been recognized. Menzies *et al.* (1967) found leaves and fragments of *Thalassia* in 3,160 m of water off the North Carolina coast, at densities of up to 48 blades per photograph, even though the nearest source was 500 to 1,000 km distant. Seagrass blades were observed in nearly all of 5,000 bottom photographs of the Virgin Island basin taken at an average depth of 3,900 m (Roper and Brundage 1972).

Greenway (1976) estimated that about 10 percent of the weekly production of *Thalassia* drifted out from Kingston Harbor, Jamaica after having been detached by urchin grazing.

The presence of seagrass leaves in remote locations is a result of grazing of herbivores, wave induced severing of leaves which are becoming senescent and the death of leaves due to tidal exposure on shallow flats. Storm waves also tear out healthy blades and rhizomes. Due to differences in morphology and size of *Thalassia* and *Syringodium* leaves, the effects of direct herbivory on the two species are quite different. *Thalassia* leaves are broad (typically 7-12 mm) and straplike, while *Syringodium* leaves are narrow (1-1.5 mm) and cylindrical. The bite of a parrotfish or urchin severs a *Syringodium* blade completely and the portion above the bite (commonly 2-4 cm) will float to the surface and drift away. The direct consumption of a small piece of leaf material releases a proportionately large amount of leaf material for export. Because of this mechanism in Tague Bay, St. Croix, 60 to 100 percent of the daily production of *Syringodium* is exported from (Zieman *et al.* 1979). Only a small portion of *Thalassia* is detached before senescence, as the heavier senescent turtle grass leaves normally remain in the bed in which they were formed and decompose. In Tague Bay, only about 1 percent of the *Thalassia* production is exported, and this material moves primarily by bedload transport as opposed to floating. Thus the two dominant tropical seagrasses of the Caribbean have quite different ecological functions. Retention of carbon and nitrogen within the grassbed and enhancing sediment development and recycling is promoted by *Thalassia*, a mature climax species. By comparison *Syringodium* which is not a climax species, does not contribute to the recycling and further development of the litter layer and its attendant organisms.

## HIGHER ORDER FEEDING RELATIONSHIPS

The lower level in the food webs consumers previously described provide a rich source of food for higher carnivores capable of exploiting the grassbeds. For small carnivores the primary restraint is the lack of shelter within the grassbeds. As a result much of the predation within grassbeds is nocturnal. Vast schools of snappers (Lutjanidae) in Florida, and grunts (Pomadasyidae) and squirrelfishes (Holocentridae) in the Virgin Islands, rest in the shelter of reefs by day and at night migrate large distances (.1 km or further) out into adjacent Thalassia beds to feed (Ogden and Zieman 1977; Starck and Schroeder 1969). At dusk the schools form into large streams at specific assembly points on the reef edge, and then migrate into the grassbed along routes that remain constant for several years. As the distance from the reef increases, the individual fish leave to feed alone in the grassbeds, returning along the same routes at dawn (Ogden and Zieman 1977).

The large and often pelagic top carnivores such as the jacks, tarpon, and barracuda constitute another identifiable group of organisms. Only the barracuda tends to be resident in a specific location, while most others roam over large distances in search of prey in the grassbeds and over the reef.

## SUMMARY

In tropical as well as temperate seagrass ecosystems, studies have indicated that the dominant pathway of energy utilization was through the detrital food web. More recent work and research in progress indicate that this is indeed the primary pathway for utilization of seagrass carbon, but suggest that other pathways, notably direct herbivory and export of material from grassbeds for remote utilization, are often significant in tropical systems. Further, energy is exported from seagrass beds via utilization by organisms that reside by day on coral reefs, but migrate to feed in grassbeds at night.

## LITERATURE CITED

Adams, S. M. 1976. Ecology of eelgrass, Zostera marina (L.), fish communities. I. Structural analysis. J. Exp. Mar. Biol. Ecology. 22: 269-291.

Bertram, G, C. L., and C. K. R. Bertram. 1968. Bionomics of dugongs and manatees. Nature 218: 423-426.

Briggs, P. T., and J. S. O'Connor. 1971. Comparison of shore-zone fishes over naturally vegetated and sand-filled bottoms in Great South Bay, New York, New York. N.Y. Fish and Game J. 18: 15-41.

Carr, W. E. S. and C. A. Adams. 1973. Food habits of juvenile marine fishes occupying seagrass beds in the estuarine zone near Crystal River, Florida. Trans. Amer. Fish. Soc. 102: 511-540.

Cottam, C. 1934. The eelgrass shortage in relation to waterfowl. Amer. Game Conf. Tanns. 20: 272-279.

Greenway, M. 1976. The grazing of Thalassia testudinum in Kingston Harbor, Jamaica. Aquat. Bot. 2: 117-126.

Hooks, T. A., K. L. Heck, Jr., and R. J. Livingston. 1976. An inshore marine invertebrate community structure and habitat association in the northeastern Gulf of Mexico. Bull. Mar. Sci. Gulf Caribb. 26: 99-109.

Kikuchi, T. 1961. An ecological study on animal community of Zostera belt in Tamioka Bay, Amakusa, Kyushu. I. Fish Fauna. Rec. Oceanogr. Works, Japan. 5: 211-223.

Lappalainen, A. 1973. Biotic fluctuations in a Zostera marina community. Oikos Suppl. 15: 74-80.

Marsh, G. A. 1973. The Zostera epifaunal community in the York River, Virginia. Chesapeake Sci. 14: 87-97.

McRoy, C. P. 1966. The standing stock and ecology of eelgrass, Zostera marina in Izembek Lagoon, Alaska. M. S. Thesis, Univ. of Washington, Seattle. 138 pp.

McRoy, C. P., and C. McMillan. 1977. Production ecology and physiology of seagrasses, pp. 53-87. In: McRoy, C. P. and C. Helfferich (eds.) Seagrass Ecosystems: A Scientific Perspective. Marcel Dekker, New York.

Menzies, R. J., J. Zaneveld and R. M. Pratt. 1967. Transported turtle grass as a source of organic enrichment of abyssal sediments off North Carolina. Deep-Sea Res. 14: 111-112.

Odum, W. E., and E. J. Heald. 1975. The detritus-based food web of an estuarine mangrove community, pp. 265-286. In: Estuarine Research, Vol. 1. Academic Press, Inc., New York.

Odum, W. E., J. C. Zieman, and E. J. Heald. 1973. The importance of vascular plant detritus to estuaries, pp. 91-114. In: Proc. 2nd Coastal Marsh and Estuary Management Symposium, Baton Rouge, Louisiana.

Ogden, J. C., and J. C. Zieman. 1977. Ecological aspects of coral reef-seagrass bed contracts in the Caribbean. Proc. 3rd Int'l. Coral Reef Symp. 1: 377-382.

Ogden, J. C., R.Brown, and N. Salesky. 1973. Grazing by the echinoid Diadema antillarum Philippi. Formation of halos around West Indian patch reefs. Science 182: 715-717.

Orth, R. J. 1971. Benthic infauna of eelgrass, Zostera marina. M.S. Thesis, University of Virginia, Charlottesville.

Petersen, C. G. J. 1918. The sea bottom and its production of food. Danish Biol. Stn. Rep. 25: 62 pp.

Randall, J. E. 1965. Grazing effects on seagrasses by herbivorous reef fishes in the West Indies. Ecology 46(3): 255-260.

Randall, J. E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. Miami 5: 665-847.

Roper, C. F. E., and W. L. Brundage, Jr. 1972. Cirrate octopods with associated deep-sea organisms: new biological data based on deep benthic photographs (Cephalopods). Smithsonian Contrib. Zool. 121: 1-46.

Ryther, J. H. 1969. Geographic variations in productivity in the sea, pp. 347-380. In: M. N. Hill (ed.) The Sea: Ideas and Observations on Progress in the Study of the Sea, Vol. 2. John Wiley and Sons, New York.

Santos, S. L., and J. L. Simon. 1974. Distribution and abundance of the polychaetous annelids in a south Florida USA estuary. Bull. Mar. Sci. Gulf Caribb. 24: 669-689.

Starck, W. A., and R. E. Schroeder. 1969. The biology of the gray snapper (Lutjanus griseus Linnaeus) in the Florida Keys. Stud. Trop. Oceanogr. Miami 10: 224 pp.

Stewart, R. E. 1962. Waterfowl populations in the upper Chesapeake region. U. S. Fish Wilds. Serv. Spec. Sci. Rep. No. 65.

Thayer, G. W., H. Stuart, W. J. Kenworthy, J. F. Ustach, and A. B. Hall. 1978. Habitat values of salt marshes, mangroves, and seagrasses for aquatic organisms. Wetland Functions and Values: The State of Our Understanding. Amer. Water Res. Assoc. Nov. 1978.

Thayer, G. W., S. M. Adams, and M. W. LaCroix. 1975. Structural and functional aspects of a recently established Zostera marina community, pp. 518-540. In: Estuarine Research, Vol. 1. Academic Press, Inc., New York.

Wood, E. J. F., W. E. Odum, and J. C. Zieman. 1969. Influence of seagrasses on the productivity of coastal lagoons, pp. 495-502. Lagunas Costeras, un simposio. Mem. Simp. Intern. Lagunas Costeras. UNAM-UNESCO, Nov. 28-29, 1967. Mexico, D.F.

Zieman, J. C., G. W. Thayer, M. B. Robblee, and R. T. Zieman. 1979. Production and export of seagrasses from a tropical bay, pp. 21-34. In: R. J. Livingston (ed.) Ecological Processes in Coastal and Marine Systems. Plenum Press, New York.

APPENDIX I. E. Dr. Gilberto Cintron and Dr. Yara Schaeffer-Novelli

## Mangrove Forests: Ecology and response to natural and man induced stressors.

## INTRODUCTION

Until very recently, mangrove swamps were seen as mosquito-infested wastelands, unfit for most uses, but convenient sites for open dumps and sewage discharges. Mangrove management meant "reclamation", either for agricultural purposes or housing developments. Mangrove forests are, however, among the most productive ecosystems on the planet. Their daily rate of organic matter fixation ( 20 g O.M./$m^2$ day) is about 70 times the maximum value reported for tropical oceanic waters and 6 times the mean for the rates reported for marine flagellate blooms in neritic waters in the Caribbean (Ryther 1969; Burkholder *et al.* 1967). Because of this high rate of production of organic matter, they are able to sustain important and valuable populations of fish, shellfish and wildlife and are prime breeding and nursery grounds for many species.

The main reason that mangroves have been consistently undervalued and poorly managed in our region is the lack of available information about the resource, its role and vulnerability. In this paper, we summarize some basic information about the ecology of these forests in our geographic region.

The word mangrove is employed to describe a group of plants adapted to colonize waterlogged anaerobic and saline soils. They grow as trees or shrubs along most tropical estuaries and sheltered shores. The term is also used to describe the complex assemblage of animals and other plants associated with this forest type.

## DISTRIBUTION

Mangroves are limited on a global scale by temperature and their lack of tolerance to frost. They extend latitudinally beyond the tropics, reaching in places to 29-30° in both hemispheres. At these latitudes, the mean monthly temperature for the coldest month is between 15 and 16°C, the mean annual temperature is 20-22°C and the annual temperature amplitudes range from 8-13°C. Frosts occur periodically at these areas and at the latitudinal limits the mangrove forests are poorly developed and grade into salt marshes dominated by herbaceous vegetation. Black mangroves (*Avicennia* sp.) are most frost tolerant and have the widest latitudinal range. Within the warmer portion of their range temperature is not limiting but the following other factors remain to be determinants or modifiers of their degree of development and areal coverage.

*Suitable physiography*: Mangroves develop in low lying areas subjected to saline intrusions. They develop best where topographic gradients are very small and saline intrusions penetrate far inland, for example on broad coastal plains.

*Presence of salt water:* Mangroves are not obligate halophytes but salt water removes the competition from plants that lack adaptations to deal with salt.

*Large tidal amplitude:* Tidal intrusions force salt wedges into the low lying areas. Where the tidal amplitude is large and the topographic gradient small, the mangrove belt may reach several kilometers in thickness.

*Precipitation in excess of evapotranspiration (P > PET):* Mangroves develop best in moist regions where there are fresh water surpluses. This results in abundant land drainage and extensive development of forests in the areas subjected to saline intrusions.

*River discharge:* Rivers are important geomorphic agents that shape the earth's surface and create deltaic features over which mangroves develop. In some regions their discharge may allow mangroves to develop in very dry regions where evapotranspiration greatly exceeds precipitation. In these areas, mangroves develop as riverine forests backed by extensive salt flats. Mangroves may develop in areas where there are no permanent river discharges (coastal fringes), but their development in these areas is limited. The absence of river discharges can be mitigated by the availability of runoff or fresh water upwellings.

*Shelter:* Mangrove seedlings and mature trees are vulnerable to uprooting by waves and current scour. They therefore develop best in low energy environments. They reach the sea only on protected segments of the coast, on the lee of offshore reefs, shoals or other protective structures. They line sheltered estuaries and coastal lagoons.

*Availability of allocthonous sediments:* Sediments from outside areas are essential for land building and encroachment. Terrestrially derived sediments bring nutrients that are incorporated by the plants. Although mangroves may develop in areas where there are very low allocthonous sediment inputs, the best developed forests are those of riverine environments that are subjected to periodic deposition of silts.

## SPECIES

In contrast to the Indo-Pacific region, where mangroves are thought to have originated, and where there are some 44 species, in the Caribbean region only seven species are present. These are the red mangroves *Rhizophora mangle*, *R. harrisonni*, and *R. racemosa*; the black mangroves *Avicennia germinans* and *A. schaueriana*; the white mangrove *Laguncularia racemosa*; and the buttonwood *Conocarpus erecta*. Of the red and black mangroves, only *R. mangle* and *A. germinans* are widely distributed in the Caribbean. The last two species, *L. racemosa* (white mangrove) and *C. erecta* (buttonwood) are found throughout the region. The buttonwood is considered a peripheral species and quite often is found in coastal nonmangrove associations.

## ADAPTATIONS AND ZONATION

Several environmental factors determine the position of individual species in a forest. For instance, in a fringe one may observe variations in terms of tidal exposure, salinity gradients and different soil types and textures with distance inland. Each species has adaptations that allow it to cope best with the site's factors with the least metabolic cost. This means that more energy can be alloted for growth and reproduction allowing that species to become highly competitive and ultimately dominant. This may lead to an observable zonation of species in a mangrove stand.

Red mangroves are usually found at the outer edges of a fringe or bordering tidal creeks and channels. This species has a large propagule (seed) that can reach some 30 cm long and weigh 30-40 g. Upon settlement the sapling quickly develops supporting roots that protect the young plant from washout. This prop root system is surprisingly responsive to the environment (Gill and Tomlinson 1977). Very complex prop root mazes develop in some fringe forests, possibly as a response to wind and wave stresses. The trees growing on more stable substrates often develop very erect boles and have proportionately fewer prop roots. These characteristics: the ability to become implanted in deeper water (up to 30 cm), and to withstand dislodgement by water movement, contribute to allow this species to become dominant in the outer fringes. Red mangrove has a low tolerance to high salinities. It actually develops best at low salinities (10-20$^{o}$/oo ) but will form forests, even where salinities reach 40-55$^{o}$/oo.These salinity levels are very close to the limits of its tolerance, and growth and development are poor under hypersaline conditions.

Black and white mangroves tolerate higher salinity levels and thrive in higher salinity substrates with a greater metabolic efficiency (Carter *et al.* 1973). These species are typical of the inner swamp where tidal flooding is less frequent and evapotranspiration contributes to accumulate salts. Black mangroves are the most salinity tolerant. Scrub forests are found in soils with interstitial salinities of 90$^{o}$/oo.Well developed forests are found where interstitial salinities are 60-65$^{o}$/oo.Although white mangroves are also fairly tolerant of high salinities, they seem to do best where these are not so high.

In general, in tropical areas, where there are ample fresh water flows and interstitial salinities are low, the white mangrove dominates. In areas where there are pronounced drought periods and salinities are high, black mangroves may be dominant.

The relative stagnation of water in basin forests requires special adaptations to allow ventilation of the root system. Black and white mangroves have adaptations to overcome this problem. They ventilate their root system by producing networks of chimney-like organs (pneumatophores). These arise from the root and project from the soil and the stagnant water surface. The surface of the pneumatophore has minute pores through which gas exchange takes place. In this way oxygen diffuses down to the root and carbon dioxide is vented out. These pneumatophores reach 10-30 cm in length depending on the site's flooding levels. They are never totally flooded for extended time periods since this would result in the eventual death of the tree.

These species also have small seeds. This is advantageous since the floating propagules can be disseminated by the weak water flows typical of these areas. The movement of small seeds is not as easily hampered by the profuse growth of pneumatophores.

Because of the smaller size of the propagule, the implantation depth is more restricted (10-15 cm). In general black mangroves appear to tolerate deeper and longer flooding than white mangrove. In this respect, black mangroves may be dominant in low salinity environments subjected to large seasonal changes in water level.

The buttonwood is a peripheral species. It has a low tolerance to salinity but can stand flooding by very brackish waters, usually where the salinity is less than 5‰ It does well in sandy or rocky substrates and may be found in areas that are not flooded. A few pure stands of *Conocarpus* occur in Puerto Rico in permanently flooded basins where salinity is less than 5 ‰

## ZONATION AND SUCCESSION

It has been suggested that the zonation observed in a mangrove swamp is the result of a succession of species (Davis 1940, Macnae 1968). According to Davis, the red mangrove is the pioneer species that prepares the way for the others. As this species progressively grows toward the sea, accretion takes place, and in the inner parts of the prograding fringe it is replaced by the black mangrove. Eventually, black mangrove is also replaced by the white mangrove, which gives way to buttonwood or fresh water swamps. This scheme suggests that mangroves are the 'casual' agent of coastal progradation. It now appears that mangroves are not the cause of the rapid accretion but that they are responding to coastal accretionary patterns. In this sense they contribute to stabilize rapidly accreting banks and shoals but the extent to which they promote accretion is uncertain (Bird 1976).

Davis' scheme is applicable only in some instances where sediment inputs are high and there is active coastal progradation and freshwater runoff, since in some areas the landward succession could be arrested by dry conditions. In areas where there are no large freshwater and sediment inputs, as in most of the dry portions of the Caribbean islands, mangroves develop over autocthonous peats. Progradation under these circumstances is very slow and may be surpassed by the known rise in sea level which is estimated to be some 3 mm/yr (Emery 1980 as cited by Etkins and Epstein 1982). In most instances, mangroves have retreated landwards due to the submergence of land masses during the Holocene transgression. Zonation patterns in these sediment starved areas are a response of the various species to environmental factors and do not necessarily 'recapitulate' successional patterns.

An analysis of old aerial photography (1936) to ascertain the patterns of establishment after a hurricane in southwest Puerto Rico (Cintron *et al*. 1980a) shows that there has been little or no peripheral accretion. Suitable areas were immediately recolonized and the present zonation pattern did not result from a succession of species.

## PHYSIOGRAPHIC TYPES

Mangrove forests vary greatly in their structural development. This structural variability is the response of the trees to the sum total of particular environmental factors, each of which can vary both in intensity and in frequency of recurrence. Individual forcing functions, or environmental factors, that control mangrove structure include tidal fluctuations (with daily, monthly and annual cycles), runoff and groundwater periodicity (usually over annual or longer cycles), nutrient inputs (usually tied to runoff hydroperiods), droughts (sometimes over periods of several years), soil salinity, etc. It is not usually possible to quantify all these factors to describe the so-called "energy signature" of each stand. Snedaker and Pool (1973) and Lugo and Snedaker (1974) developed a classification scheme that grouped mangrove forest types in units in which the major forcing functions operate at similar levels within each unit. Because of this, forest types within each unit share similar structural characteristics. Originally these authors recognized five types: (1) fringe forests, (2) riverine forests, (3) overwash forests, (4) basin forests (including hammocks) and (5) dwarf forests (Lugo and Snedaker 1974). More recently, after a review of all the available quantitative structural data available, we simplified the previous scheme by incorporating overwash forests as a type of fringe and considering dwarf forests a type of basin. The description of these forest types, taken from Cintron *et al*. (1980) and Cintron and Novelli (1981), follows:

### Riverine forests

Riverine forests develop along the edges of river estuaries, often as far inland as the toe of the saline intrusion. In this environment water flows and nutrient inputs are high. Flood waters bring in silts and mineral nutrients and these are rapidly incorporated into plant tissue. On the periphery of the forest, an area of high kinetic energy due to tidal motion and river discharge, the dominant species is *Rhizophora* sp., which develops a complex maze of adventitious roots. This root maze allows the establishment of well developed trees in spite of the strong water flows. Inland from the fringe one finds stands of *Laguncularia* sp. and *Avicennia* sp. Usually, riverine forests are most luxuriant in the lower and middle part of the estuary. Generally, interstitial salinities in these forests are lower than in the other types. They are lowest at times of flood when the salt wedge is driven seaward. During times of low flow, salt intrudes into the innermost parts of the estuary, raising the salinity temporarily. Usually interstitial salinities are in the range of 10-20‰or less.

### Fringe forests

Fringing mangroves develop along protected shores, over shoals or spits, often forming overwash islands. Fringes usually have pronounced gradients in topography, turbulence and tidal amplitude. Damping of the variation in tidal amplitude and turbulence inside the stand may result in high interstitial salinities in the inner parts of the fringe. There, the soil elevations are high and the terrain is less often flooded. In these inner portions *Avicennia* sp. may become dominant. On the outer edge where the levels of kinetic energy are high *Rhizophora* sp. dominates. Interstitial salinities in the outer fringe are just above ambinet sea water (39 ± 1.3‰), but increase to higher levels (59 ± 4‰) in the *Avicennia* sp. zone (Cintron *et al*. 1980a).

### Basin forests

Basin mangroves are characterized by sluggish laminar water flows over wide areas of very small topographic gradients. The water turnover rate is slow. Basins receive and store water seasonally. Because of the uniform sheet flows strong salinity gradients do not develop within the basin. Basin forests may be dominated by either *Laguncularia* sp. or *Avicennia* sp., although mixed stands may be found. Tidal creeks and drainage channels within the basin are often lined with *Rhizophora* sp. *Avicennia* sp. dominates in basin forests where high salinities prevail (> 50‰), whereas *Laguncularia* sp. dominates in low salinity basins. Mixed forests are found at intermediate salinities (30-40‰).

The structural characteristics of basin forests depend on the hydroperiod. Where flows are weak but constant, forests develop well. In stagnant basins there may be oxygen depletion, slow nutrient recycling and reduced growth.

### Dwarf forests

Dwarf forests occur where growth is limited by edaphic factors. Stands of dwarf *Rhizophora* mangle develop in some areas of the Caribbean over peat substrates in basins that do not receive substantial amounts of terrestrial runoff. Mature red mangrove trees in these basins are usually less than 2 m tall and often are about 1-1½ m in the inner parts of the stand. Dwarf stands of *R. mangle* develop over marl in Florida, USA. It appears that in both instances (growth over peat and marl) the plants are being subjected to nutrient deficient (oligrotrophic) conditions.

Dwarf stands of *Rhizophora* are known from Puerto Rico, St. Thomas (U.S.V.I.), and Paso de Catuan in the Dominican Republic.

Dwarfed black mangroves are often found on the landward side of fringes and basins in seasonally dry areas, immediately adjacent to salt flats or hypersaline lagoons. The dwarfing factor here is extremely high levels of salt in the soil.

## PRODUCTIVITY

Table 1 is a summary of productivity data from Lugo and Snedaker's (1974) review. The data have been converted from gC/m$^2$·day to grams of organic matter/m$^2$·day and presented by forest type. These numbers were obtained from gas exchange studies and represent total community metabolism. Riverine forests show very high rates of gross production (24g O.M./m$^2$·day), followed by basins (18g O.M./m$^2$·day), and fringes (13.2g O.M./m$^2$·day). Net production is the amount of organic matter left after metabolic losses are accounted for. This is the amount of organic matter available for growth, foliage and seed production. These rates are also high. Between 20 and 40% of net production is partitioned for the production of leaves, flowers, fruits and stipules, which constantly fall to the forest floor.

Litterfall rates (dry weight) are highest in riverine forests (2.94 - 3.96 $g/m^2 \cdot day$), slightly less in fringe forests (2.0 $g/m^2 \cdot day$) and intermediate in value in basins (1.9 - 2.3 $g/m^2 \cdot day$) (Pool et al. 1975). Well developed riverine forests in Puerto Rico have litterfall rates averaging 4.12 $g/m^2 \cdot day$ (Negron 1980). A monospecific black mangrove basin in Puerto Rico averaged 2.29 ± 0.30 $g/m^2 \cdot day$ (Negron and Cintron 1981). Litterfall rates in Avicennia sp., Rhizophora sp., and Laguncularia sp. stands in Guadeloupe were 3.56, 4.33 and 2.74 $g/m^2 \cdot day$, respectively (Febvay and Kermarrec 1978).

## DECOMPOSITION AND UTILIZATION OF LITTERFALL

It is now recognized that one of the primary reasons mangrove areas are so important is because of their high rates of productivity of organic matter as litter. This material falls to the forest floor where it starts to decompose. During this time soluble organics are leached out and the leaf surfaces are colonized by fungi and bacteria. In time a complex meiofaunal assemblage develops, grazing on the decomposers. The decomposing material, originally high in carbohydrates and low in proteins, becomes enriched with microbial protein. The C:N ratio of the plant material decreases during decomposition. In R. mangle the C:N ratio decreases from 90.6 to 40.7 during the first 70 days of the decomposition process (Cundell et al. 1979). These low C:N ratios indicate the greater nutritional value of the decomposing material. As a result of decomposition and the intense activity of grazing organisms the plant material is gradually reduced to very small particles. These detrital particles, enriched with microbial tissue, are consumed by detritivores. These derive their nutrition primarily from the microbial and meiofaunal assemblage associated with the detrital particle. Once consumed, the particle is stripped of its microbial and meiofaunal cover and egested. The undigested stripped particles may become recolonized by microbes, repeating the cycle anew until all the digestible components are utilized.

As stated earlier, the initial autolysis of the plant material releases large amounts of dissolved organic matter to the water. This DOM is an important component of the outflux from mangrove areas, especially from basins where tidal and freshwater flows are too weak to export particulate matter. Bacteria are known to be important in the uptake and utilization of DOM.

Prackash (1971) has shown that blooms of the bioluminescent dinoflagellate Pyrodinium bahamense are stimulated by humic substances from mangrove areas. These humic substances also enhance the productivity of other neritic diatoms such as Skeletonema costatum and Thalassiosira nordenskioldii (Prakash et al. 1973). Thus, there is evidence that the waters leaching from mangrove areas appear to be rich in biologically active substances which can stimulate or regulate phytoplankton production in adjacent waters.

## FISHERIES

Given the continuous availability of large amounts of nutritious organic matter in mangrove lined areas, it is not surprising that large numbers of organisms aggregate and utilize it. The sheltered nature of these areas also contribute to make them important as nurseries. Mangrove areas thus export protein to coastal areas in the form of aquatic organisms that use the mangrove areas for their early development and then migrate offshore. Well known are the massive migrations of mullets and shrimp from these areas. This is high quality protein that links mangroves directly to other coastal systems like coral reefs, seagrass beds, and ultimately to man.

A preliminary analysis of published lists of the fish fauna of mangrove areas in Florida (USA), the Caribbean and Brazil shows that there are more than 275 species of fish belonging to 66 families that are in some way associated with mangrove areas in these regions. Turner (1977) found a positive correlation between commercial yields of penaeid shrimp, the area of intertidal vegetation and latitude. The predicted annual yields per area of intertidal vegetation for the latitudinal range of 0° - 20° range from 39-159 kg/ha.

## CLIMATIC CONSTRAINTS ON DEVELOPMENT

Mangroves do not necessarily need rain water, since they extract fresh water from the sea, but the amount of rainfall influences the extent of mangrove development in two ways. First, rainfall determines the rates of soil weathering, erosion and transport, and thus the rate of formation of deltas and other shallow coastal sedimentary features. Since these areas are the optimal substrate for mangrove growth, their rate of formation can indirectly determine the extent of coastal mangroves. Second, high temperatures, causing overall high evapotranspiration rates in the tropics, would quickly lead to a salt build-up in the inner parts of mangroves, if it were not for the flushing and leaching of salts by rainwater. According to Macnae (1966, 1968), mangroves develop best in Australia in areas receiving more than 2,500 mm/yr. Below 1,500 mm/yr, salt flats begin to form.

### Precipitation and evapotranspiration

Rainfall in the Greater Caribbean is very low. Open sea areas receive only 800-1000 mm/yr. However, because of the large amount of solar radiation received at the surface there is a great deal of evaporation and moisture in the air. When the moisture laden air masses are lifted against the slopes of an island there is condensation and rainfall develops. The windward slopes of high islands are moist for this reason. Convection due to heating of the island mass is another important rain-producing mechanism. Since the land masses gain more heat than the surrounding seas, convection cells and rainstorms develop over the hot interior of islands often in the hot summer afternoons.

These rainfall producing mechanisms contribute more rain to the interior of the larger islands than to the coast. Furthermore, the "leading edge" of some islands can be drier than the "trailing edge" and the high islands may have a "rain shadow" zone because of the adiabatic heating of the subsiding air. Low and small islands get very little rain at all. On low islands, and in the "rain shadow" side of the larger islands there are commonly severe water deficits. During the year precipitation is much less than potential evapotranspiration. Under these circumstances, although there may be low areas influenced by salt water, mangroves may be unable to colonize there, due to excessive salt accumulations. The intense radiation turns these low flat areas into natural evaporation ponds. Salt crusts form at the surface and interstitial salinities are much beyond those tolerated by mangroves (> 90‰).

Under these circumstances mangroves develop as a fringe, quite often narrow, in which salinity levels are suitable. Because of the steep salinity gradient inland the landward trees quickly become scrubby and poorly developed. Between the swamp and higher ground one finds a hypersaline lagoon (often containing dead or dying trees) and salt flats.

Therefore, both rainfall and topography influence the development of basin and fringe forest types. Where precipitation is greater than evapotranspiration basin forests are well developed. The interstitial salinity in these basins is low and they may be dominated by the white mangrove. Where precipitation levels are less than evapotranspiration (> 1500 mm) basins begin to degrade until they disappear, giving way to the formation of broad salt flats and shallow hypersaline lagoons. In areas where precipitation is less than the potential evapotranspiration soil salinity becomes a dominant factor controlling the structural characteristics of the forests. Because of the limited amplitude of the tide in most of the Caribbean, high salt levels may be reached relatively short distances from the edge of the fringe.

## VULNERABILITY TO STRESSORS

A stressor may be defined as a condition that causes an energy drain and a loss of potential energy that could be used to do useful work in a system (Odum 1967). The sustained operation of a stressor (a chronic stressor) constitutes a constant energy drain and prevents the system from attaining high levels of development. A stressor may also occur periodically, causing transient episodes during which maintenance costs are increased. The resiliency of the system is its ability to respond to and recover from a stressor.

Mangrove areas are subjected to natural and man induced stressors both of which can impinge on the system in a chronic or acute mode. For instance, hypersalinity can be a chronic natural stressor in many areas of the Caribbean. Storms and droughts are examples of acute events. Some pollutants can be chronic stressors in polluted areas, or behave as acute stressors during a spill followed by effected cleanup. In general, it is obvious that in a rigorous environment the structural development of the forest will be arrested. In more optimum environments development will proceed further until the structure is limited by site characteristics such as nutrient availability, water turnover rate and climatic limiting factors such as hurricane recurrence rates.

In the following section some natural and man induced stressors are described and their impact on mangrove forests is discussed. The reader is referred to Odum and Johannes' (1975) excellent review for additional information.

## Natural Stressors

### Tropical Cyclones

Cyclonic disturbances develop in the north Atlantic, Caribbean, and Gulf of Mexico during the months of June through November, although they form outside of this "season" in rare instances. These cyclones have high sustained winds, which near their center reach speeds that range from 65 km/hr (40 mph) in a tropical depression to more than 119 km/hr (74 mph) in a hurricane. Mangroves are vulnerable to these disturbances due to their coastal location, their shallow root system (most of which is in the upper 30 cm of the soil), the poor cohesiveness or load bearing ability of most mangrove soils and their exposure to waves, surge and erosion by strong water flows.

Wind speeds greater than 93 km/hr can cause defoliation and winds in excess of 130-160 km/hr will bring down trees. Wadsworth and Englerth (1959) reported that during hurricane Betsy in a black mangrove forest in southern Puerto Rico, 59% of a sample of 62 trees had been overthrown. The maximum reported wind speed in San Juan, 21 km (13 miles) from the storm's center was 185 km/hr (115 mph). These trees were 26 years old and had diameters (DBH) between 10 cm and 30 cm (4 to 12 in). Black mangroves have very shallow root systems and lack prop roots. The canopy structure also appears to influence this type of forest's sensitivity to wind damage. Canopies of even height without emergents and gaps are more resistant. Mature low density black mangrove "orchard" forests appear to be very susceptible to windthrow.

Red mangrove forests, especially in exposed locations, develop an extraordinarily complex and dense root supporting system. This anchorage provides excellent protection from windthrow. Upright (straight bole) trees are only found inland in sheltered locations. At the fringes, however, wave scour may be a more severe problem than wind.

High wind speeds also cause extreme flexing of the stems and separation of the bark from the woody tissue. Violent rubbing between adjacent branches can cause girdling. Even if the tree is not defoliated these branches will die and the trees will appear "burned" after the storm. In an exposed location this type of damage will be more severe in the windward part of the forest.

Stoddard (1969) recorded the damages to mangrove areas during hurricane Hattie in British Honduras (Belize). Hurricane Hattie had winds gusting to 322 km/hr (200 mph). In this area there was absolute devastation within 1.6 - 3.2 km (1 - 2 miles) of the storm's track. The zone of almost complete destruction extended to 32 km (20 miles). In that zone, only small mangrove patches in the leeward portion of the largest islands survived.

During storms large amounts of sand and other materials may be dumped into the mangroves. The accumulation of these materials impairs gaseous exchange through lenticels and pneumatophores and may cause widespread mortalities. Usually defoliation ensues within 3-4 weeks. Børgesen (1909) described an instance where large amounts of sand and gravel were washed into Krausse's lagoon (St. Croix, U.S.V.I.) by the hurricane of 1899. Before the hurricane, the lagoon contained many mangrove islands with open water channels and bare flats.

Dense *R. mangle* forest occurred in the western landward side. After the storm, the vegetation died and the wood was used as fuel for a nearby sugarmill. Craighead and Gilbert (1962) and Craighead (1964) have similarly described post-hurricane mortalities due to marl deposition over roots in the Ten Thousand Island area in Florida.

Storm waves in Puerto Rico during hurricane David (1979) uprooted large tracts of seagrass beds in various areas. This material was deposited in large quantities ashore. In southwestern Puerto Rico, seagrass accumulations reached 2 m or more high in places, forming a dike in front of the mangrove fringe. Large amounts were carried inside the mangroves. These inordinate accumulations have caused dieoffs in the mangrove because of smothering and restrictions in tidal exchange, leading to hypersaline conditions. Tabb and Jones (1962) report similar occurrences in North Florida Bay as a result of Hurricane Donna.

When fringe trees die but remain standing they eventually lose their aerial roots and the associated root community (Tabb *et al*. 1962). In exposed locations whole cays and fringes may be scoured away by waves. Large boulders and limestone blocks were deposited by waves in some mangrove covered coral islands in southwestern Puerto Rico by Hurricane David. In Cayo Turrumote a boulder rampart 0.5-1 m in height was deposited against the mangrove forest. Recovery is determined by the after storm configuration of the coasts. In places sediment deposition may raise the level of the soil so much that the area cannot be successfully recolonized by mangroves. In other areas shoals and other structures may have been formed and become available for establishment. Recolonization is slow but ultimately the newly formed banks and shores become stabilized by seagrasses and mangroves, starting the forest development cycle anew. Forest development during the first years is slow and is a function of seed availability. The edges of channels and shorelines quickly develop thickets. The inner parts of the swamps usually develop more slowly since the entry of seedlings is impaired by debris and standing dead trees.

Alexander (1967) reported that extensive flooding by salt water (salinity 30‰) during Hurricane Betsy caused severe plant kills (scorching) of non-salt tolerant species in the southeastern Everglades. The damage was increased by impounding caused by man made dikes. The surface waters freshened slowly after the storm, taking about two months to revert to normal values.

### Tidal waves

Tidal waves are not frequent in the Caribbean but these destructive waves are known to have caused widespread damage in the past to low lying coastal areas, In 1946, a tidal wave destroyed a large mangrove forest situated at the head of Bahia de Samana in the Dominican Republic (Sachtler 1973). It is estimated that 4500 ha of a total of 6500 ha were destroyed. The surviving stands were those of black mangroves found in the innermost portions of the swamp.

The area recovered from this event rapidly. Presently basal area and density (for stems > 2.5 DBH) in the *R. mangle* stands are between 17.5-21.5 m$^2$/ha and 463-714 stems/ha, respectively. Mean diameter of the stand for this even aged forest (now 36 years old) is between 19.6 and 21.9 cm (Cintron and Alvarez, unpublished).

## Eustatic sea level rise and coastal erosion

Sea level is presently rising at the rate of 30 cm/100 years. This marine transgression has favored the expansion of mangroves over areas previously occupied by terrestrial plants. There is little doubt that this has induced a regressive movement in the seaward margin of mangroves in many years. Hoffmeister (1974) reports the erosion of a rock pavement of fossilized roots of black mangroves in Florida. Zieman (1972) has found circular beds of *Thalassia testudinium* growing over red mangrove peats. These peats were deposited in hammocks which were submerged by the sea level rise. Extensive areas within Card Sound (Florida) show severe fringe erosion. The shallow banks in front of the mangrove fringes are sand- or seagrass- veneered red mangrove peat deposits. In Puerto Rico, peat areas are found on the bottom of shallow embayments overlain by sand. In Bahia de Samana (D.R.) there is serious erosion of the fringe in considerable segments of the mangrove-lined bayhead shoreline.

## Hypersalinity

As discussed earlier, hypersalinity is a chronic stressor in most coastal areas of the Caribbean and is one of the dominant factors controlling the structural characteristics of these forests. Carter *et al*. (1973), Burns (1976), Hicks and Burns (1975), and Lugo *et al*. (1975) have demonstrated that there are increases in respiration and decreases in net productivity with increases in soil salinity. The higher maintenance costs are also associated with stunting. As interstitial salinities increase the canopy height decreases (Cintron *et al*. 1978, Fig. 1). The diameter of the trees also decreases as well as basal area, wood volume and complexity index (Martinez *et al*. 1981).

The control that salinity exerts over the physiographic characteristics of a stand in an arid environment is exemplified by some mangrove islands on the south coast of Puerto Rico (Cintron *et al*. 1975, 1978). The development of a mangrove island over time is shown schematically in Fig. 2. Initially mangroves colonize shallow banks, expanding laterally over them. The growth of the trees at the outer margins is more vigorous and these trees may attain greater heights. Circulation to the inner parts of the island may be reduced by active growth at the margins. Red mangroves in the core are replaced in time by black mangroves as salinities increase. If soil salinities remain high but stable an island will develop an outer ring of red mangroves and an inner core of well developed black mangroves. Where salinities are too high the core will consist of dwarfed blacks. If circulation is further restricted there will be a dieoff at the core leaving an annular island with a hypersaline lagoon as in step 5 of Figure 2.

Wave flushing at the windward edge of the island allows the red mangrove fringe to be thicker than on the protected side of the island (Fig. 3). In fact, where there is unimpaired circulation the island may remain in stage 1 or 2 indefinitely. The maturation process takes place in the islands in more sheltered localities.

Fringes may also suffer from a similar aging process. In time extensive areas of the inner swamp die and shallow lagoons and salt flats are formed. These diebacks occur following periods of drought. In dry regions, mangrove areas may be unstable with coverage fluctuating between periods of expansion (usually following storms or a succession of very wet years) and contraction (usually triggered by a succession of dry years). In very dry areas, basins may disappear altogether leaving only a thin red mangrove fringe backed by shallow bare hypersaline lagoons and salt flats.

These areas of dead mangroves are a common feature in dry coastlines. Bacon (1970) described the "Red Swamp," situated between the blue and Caroni Rivers in Trinidad. Examination of aerial photographs taken between 1942 and 1966 showed a gradual expansion of the dead areas. Reclamation work in the region may have been responsible for accelerating this dieoff by interfering with water movements.

Servant *et al*. (1978) report the characteristics of one of these hypersaline areas on the islet of Fajou in Guadeloupe. This area is separated by a porous bar from the sea. Seawater penetrates the basin and evaporates, concentrating salts within. Salinities are reduced transiently during episodes of heavy seas when water washes into the basin or when heavy rains leach some of the salts away. This stressful cycle is a common feature of many shallow hypersaline lagoons in the Caribbean area. In most of these arid areas the system is delicately poised and man's intervention by reducing water flows or impounding areas by structures such as causeways and roads often exacerbates these naturally occurring stressful conditions causing mortalities too.

## Man Induced Stressors

### Channelization, diversion of fresh water

Channelization and fresh water diversion schemes are extremely damaging. Mangroves are open systems and require continuous nutrient inputs to maintain their high rates of productivity and other ecosystem processes. Furthermore, in arid areas reduction of fresh water input quickly results in the onset of hypersaline conditions and mangrove dieoff.

### Impoundement

Impoundment is another stressor that leads to rapid deterioration and death of mangrove areas. Diking cuts off mangroves from nutrient flows, it may raise water levels or lengthen the hydroperiod, causing the lenticels and pneumatophores to become covered with water. This impairs or stops gas exchange. In other instances lowering water levels or reducing flows causes salinity to increase rapidly as salt water evaporates.

In 1965, the Department of Agriculture of Puerto Rico built a dike impounding a 177 ha mangrove stand and flooding it to a 1 m depth. The purpose was to artificially create a habitat for wading birds. A massive dieoff followed immediately. The area had contained an extensive and well developed black mangrove forest (DBH $\sim$ 10 cm). Only those trees on higher ground survived and then did so by producing extremely long pneumatophores (36.1 cm ± 0.5 as against 10-15 cm in normally flooded areas). There has been very limited natural restoration of the area. The dikes restrict tidal flushing so that during the dry season the impounded area dries up. The loss of the canopy exposes the impounded water and soil to the sun and extreme overheating during the dry season. Dissolved oxygen in the heated surface water (temperature > $30^{o}C$) drops below 0.5 mg/L.

White mangroves have recolonized some areas by becoming established over the stumps of fallen trees. The water depth reached during the wet season appears to limit the areas that can be colonized by mangroves.

Impoundment can also occur when roads are built through mangrove basins if care is not taken to preserve water flows. Patterson-Zucca (1978) has described the impact of road building on a mangrove swamp. In St. Thomas, construction of a road near Compass Point isolated and killed a small mangrove area. Hypersalinity may have been the cause of that dieoff.

### Sedimentation

Mangroves are adapted to high sedimentation environments, but sudden deposition of large quantities of sediments can cause mortality. Under natural conditions, excessive sedimentation occurs as a result of catastrophic phenomena like storm generated waves or floods. Man, however, is often the cause of severe sedimentation problems in some mangrove areas. Cintron and Pool (1976) reported that sand extraction from a coastal dune for airport construction reduced the dune height from 12 m to only 3 m. During 1967, storm waves overwashed the residual dune, carrying large amounts of sand into a mangrove forest. Sand deposition varied from more than one meter to a thin sand veneer more than 260 m inland. All the mangroves were killed where sand deposits were higher than 30 cm, and some trees died where the sediment depth was between 20 and 30 cm. The area covered by the sand wedge has been colonized by Australian pine (Casuarina equisetifolia).

Kolehmainen (cited by Odum and Johannes 1975) noted an area in Puerto Rico where fibrous waste from a sugar mill escaped from settling ponds and killed most of the trees in a black mangrove (A. germinans) stand.

Deposition of dredge spoils into mangrove areas will also cause large scale mangrove mortalities. During the late 1960's, dredged material was discharged into the Punta Picua peninsula on the north coast of Puerto Rico, causing the total destruction of a large mangrove tract. This area too has been extensively colonized by Australian pine.

Deforestation and loss of soil can increase the rate of sedimentation in low lying swamps, causing shallow lagoons to become salt flats and killing inner swamp trees.

### Thermal pollution

In shallow stagnant areas water temperatures may reach more than $43^{o}C$ ($110^{o}F$). These areas are not reseeded since temperatures may be limiting (Craighead 1964). McMillan (1971) reported that temperatures of $39\text{-}40^{o}C$ for 48 hours caused death of rooted but stemless A. germinans seedlings.

The cooling water plumes from electric generating plants often approach this temperature. In Puerto Rico, Banus and Kolehmainen (1976) have suggested that temperatures above 38°C (100°F) define the beginning of deterioration of mangrove trees. These stressed trees have small leaves (Lugo and Cintron 1975), are partially defoliated (only terminal leaves remain), chlorotic and produce dwarfed seedlings. The mangrove root community is much more sensitive to high temperatures than the mangrove trees (Kolehmainen et al. 1974). The species composition and biomass of mangrove root communities was unaffected by temperatures below 34°C (93°F). Between 34° and 35°C (93 and 95°F) the number of species decreased abruptly, and above 35°C (95°F) the number of species was inversely related to the water temperature. At higher temperatures, 37.5-39.7°C (99.5-103.5°F), blue green algae became common, forming floating mats in the water surface.

### Oil

Mangroves are extremely sensitive to oil pollution because of fouling of the gas exchange surfaces. Heavy coating of the intertidal root region or pneumatophores invariably causes death of the trees. In addition to acting as a mechanical barrier oil contains soluble toxic fractions. These compounds can be toxic to the roots and to the microbial populations in the soil.

The initial response of mangroves exposed to severe oil fouling appears to be defoliation. Defoliation may be partial or total, depending on the amount of oil remaining in the roots and substrate. Following the Peck Slip oil spill in eastern Puerto Rico, the heavily impacted areas lost 50% of the canopy in 43 days and 90% after 85 days (Cintron et al. 1981). Total loss of the canopy was irreversible in the oil stressed red mangroves. In the marginal areas where the trees were exposed to sublethal amounts of oil defoliation was followed by production of smaller, often deformed, new leaves.

Lugo et al. (1981) have suggested that different forest types exhibit different susceptibility to oil pollution. For instance, riverine forests appear to be least vulnerable to oil pollution since the surface freshwater flows move the oil slicks away. Oil spilled in the ocean has little chance of entering the river mouth since salt water enters as a bottom flow. The greatest vulnerability for this forest type would occur during the dry season when surface flows are reduced or if the spill occurs up river or inside the estuary. In exposed locations, sand bars formed in front of river mouths can hinder oil penetration.

Basin mangroves are most susceptible to stressors that originate inland and therefore are less vulnerable to seaborne oil. Often (but not always) basins are isolated from fringes by berm. Basins are most vulnerable during periods of spring tides. They can be severely impacted by spills that originate from inland facilities and pipelines. Since oil would be retained for a long time in a basin its effects would be devastating.

Fringe and overwash forests are the most vulnerable to seaborne oil. Oil enters the fringe and accumulates inside. In the outer edge of the fringe water motion assists in cleansing the root surfaces. For this reason, there may not be any defoliation of the trees in the outer edge and complete canopy loss inside. In very sheltered locations, however, defoliation may be total.

Presently, there are no practical means to remove oil from mangrove areas. For this reason, it is imperative to prevent the entry of oil by using booms and sorbent barriers. Oil tends to penetrate into the porous mangrove sediments and persist for very long time periods. Residual amounts of oil are still found in Bahia Sucia in southwestern Puerto Rico after a spill that occurred in 1973. In areas in which there are high rates of water exchange oil is leached out and seedlings are brought in so that recuperation from an acute event occurs quickly. Where large residual amounts of oil persist recovery may be considerably delayed. In fact, residual amounts of oil may impede the reestablishment of a well developed stand.

The "successful" establishment of red mangrove seedlings in an area impacted by oil does not mean that the site is on its way to recuperation. Red mangrove seedlings are very tolerant to stressors but this tolerance decreases as the plant develops and requires more from the external environment rather than from its ample storages. This independence is prolonged by the slow growth rate of the seedlings (0.4-0.5 cm/mo during the first months). This, and the continual replacement of dead seedlings by new arrivals gives the false impression that natural regeneration is occurring. It seems, however, that when significant amounts of oil remain in the sediment, seedlings dieoff as their initial high tolerance decreases. The development of saplings into mature trees may be dependent upon the rage at which oil is leached or degraded.

### Mining

There are no known mining activities currently occurring in mangrove areas of the Caribbean. The energy crisis has pressed consideration of the use of peats as energy sources and mining of these peats has been contemplated in the Negril's Great Morass in Jamaica.

In Puerto Rico, sand was mined from mangrove lined coastal lagoons during the 1960's. This activity created pits 18 m deep in places in lagoons whose original depth was only 1-2 m. These pits trap saline water and are depositional basins for organic sediments with high oxygen demands. As a result, the pits are persistently anoxic below 2 m, the $BOD_5$ in the bottom waters often exceeds 200 mg/L and $NH_4$ as (N) may be in excess of 15 mg/L (Ellis 1976).

## RECOVERY

Natural ecosystems have growth strategies and adaptations that allow them to recover from periodic natural perturbations. Because of this inherent resiliency, ecosystems will restore themselves spontaneously once the disturbance has subsided. Assuming that there are no residual effects left by the stressor(s) an ecosystem will normally revert to a state very similar to its pre-stressed condition. Under the influence of residual stressors and/or an increased recurrence rate of acute events, the system will only achieve a simpler level of organization (Odum 1981).

In general, then, human intervention in the restoration process could be limited to removing the stressor that is causing the degradation and allowing the system to restore itself. It is wasteful and useless to attempt to restore areas artificially if the stressor has not been removed or residual amounts are left.

In the case of mangroves, the rate of recovery in a benign environment is a function of the size and proximity to seed sources. The conservation of ample seed stocks insures quick and natural regeneration with minimal human intervention.

In some areas, it may be desirable to accelerate the recovery of a stand by preparing the terrain and insuring an even distribution of seedlings by planting. Pulver (1976) gives some preliminary guidelines for the transplant of saplings (0.5-1.5 m in height). Planting saplings, however, is more difficult and costly than planting seedlings and the saplings must be removed from natural stands. The following points should be considered before artificial restoration is attempted:

Select candidate sites carefully. If the area has contained mangroves before, determine the cause of loss and make sure the stressor has been removed. Naturally, "blank" areas may be hypersaline or too elevated for successful establishment.

Because of the ease of handling and planting, red mangroves are one of the most suitable species for restoration projects, but they may not always be appropriate. The selection of the species to plant should be made on the basis of the dominant species at nearby locations having similar elevation, hydroperiods and exposure.

Soil elevation should be low enough that the area is frequently flooded by tidal water, and there is adequate circulation. Stagnant areas tend to overheat.

Measure interstitial (soil) salinities. Areas with interstitial salinities above 50‰ are not suitable for restoration by red mangroves.

Areas must be sheltered from wave action and current scour.

Remove dead standing wood and clean-up the area. Floating or falling debris will uproot and damage planted seedlings.

Control the spacing of seedlings. Dense plantings result in stagnation (slow growth) due to excessive competition. For *Rhizophora* sp. the recommended spacing for seedlings is 0.6-1.2 m (Watson 1928).

Recently, fallen seeds may be collected from nearby mangrove areas or they may be collected from trees. Use only ripe seeds. For red mangrove, use those seeds in which the abscission layer has developed (these are easily detached from the parent tree). Select healthy seeds and discard malformed or damaged propagules. Maintain the collected material wet and avoid exposing it to overheating during transportation and before planting. Seeds can be carried in an inexpensive foam icebox or a wet burlap sack.

Red mangrove seedlings should not be inserted too deeply in the substrate. The seed should be planted deep enough so that it will not fall over Watson 1928). For a 20-30 cm seedlings the planting depth should be 4-7 cm.

Since initial growth rates and mortality of red mangrove seedlings are very low it is impossible to judge the success of a restoration project on the basis of a few month's observations. The restored area should be checked annually to replace dead saplings and/or remove unwanted new arrivals.

## CONCLUSION: CONSERVATION NEEDS

Island coastal marine ecosystems are in jeopardy in many areas of the Caribbean, due to high populations, mounting pressure to develop, a limited land base, and inadequate impact assessment procedures. In the small islands inland and coastal ecosystems are intimately linked. Inland activities like deforestation, agriculture on steep slopes, raising of domestic animals, road building and many others can increase sediment levels in estuarine and coastal waters, contributing to the degradation of coastal ecosystems. Protection of the marine resources depends on developing land use practices that will not impair the productivity of mangroves, seagrass beds and coral reefs.

Society derives direct benefits from the conservation of these coastal ecosystems. They are part of the resource base upon which islands depend. There are very practical reasons for their conservation, including the products they yield (fisheries) and their role in protecting the coasts from storm damage, as well as their more intangible values. Tourism, an important source of income, can be developed to take advantage of their uniqueness and great beauty. Natural reserves or parks can be established to protect especially important areas; these attract local as well as international tourism and also stimulate scientific research, all of which benefit the local economy. They are valuable educational assets.

On a more modest scale, small projects can be developed to take advantage of areas of particular scenic beauty. This kind of project, when designed for mangroves, needs to take into account the fact that mangrove areas are naturally prone to flooding; structures built in these areas are susceptible to recurrent damage by flood waters and storms unless they are constructed with flooding in mind. Because of the danger of storms, no permanent population centers should be encouraged to develop in mangroves, since the occupants would always be at risk.

In summary, mangroves are among the most productive coastal ecosystems known to science. In addition to their aesthetic and recreational values, they form an important part of the economic resource base of Caribbean islands because of their intimate ties to coastal fisheries, seagrass beds and coral reefs. In many areas they will evoke negative reactions, because of a lack of understanding of their importance. Though highly resilient in the face of natural stressors, mangrove forests are extremely vulnerable to many stressors caused by human activity, including sedimentation, channelization, diking, draining, and many kinds of pollution. An understanding of their role in coastal protection and the nurture of fish and wildlife should lead to more enlightened mangrove management practices throught the Caribbean.

## LITERATURE CITED

Alexander, T. R. 1967. Effects of Hurricane Betsy on the southeastern Everglades. Quart. J. Fla. Acad. Sci. 30(1): 10-24

Bacon, P. R. 1970. The Ecology of Caroni Swamp, Trinidad. Central Statistical Office, Trinidad. 68 pp.

Banus, M., and S. W. Kolehmainen. 1976. Rooting and growth of red mangrove seedlings from thermally stressed trees. Pp. 46-53. In: G. W. Esch and R. W. McFarland (eds.) Thermal Ecology II. CONF. 750425 Technical Information Center ERDA, Springfield, Va.

Bird, E. C. F. 1976. Coasts. An introduction to systematic geomorphology, volume 4, Australian National University Press. Canberra, 282 pp.

Bøergesen, F. 1909. Notes on the shore vegetation of the Danish West Indian Islands. Bot. Tidsskr. 29:201-259.

Burkholder, P. R., L. M. Burkholder, and L. R. Almodovar. 1967. Carbon assimilation of marine flagellate blooms in neritic waters of southern Puerto Rico. Bull. Mar. Sci. 17(1): 1-15.

Burns, L. A. 1976. A model of mangrove ecosystems, rationale, data analysis, and model formulation. Pp. 53-84. In: H. T. Odum (ed.) Guidelines for management of mangroves in south Florida. Contract No. 14-161004-426. Final Report to U. S. Dept. of the Interior. Center for Wetlands, Univ. of Fla. Gainesville, Fla.

Carter, M. R., L. A. Burns, T. R. Cavinder, K. R. Dugger, P. L. Fore, D. B. Hicks, H. L. Revells, and T. W. Schmidt. 1973. Ecosystems analysis of Big Cypress Swamp and estuaries. EPA 904/9-74-002, U. S. Environmental Protection Agency, Region IV, Atlanta. 478 pp.

Cintron, G., A. E. Lugo, D. J. Pool and G. Morris. 1975. Los manglares de las costas aridas de Puerto Rico e islas adyacentes. Memorias del Segundo Simposio Lationoamericano sobre Oceanografia Biologica. Universidad de Oriente, Cumana, Venezuela. 2: 137-150.

Cintron, G. and D. J. Pool. 1976. Efectos de la deposicion de arena e inundacion en un manglar en Puerto Rico. Tercer Simposio Latinoamericano de Oceanografia Biologica. San Salvador, El Salvador.

Cintron, G., A. E. Lugo, D. J. Pool and G. Morris. 1978. Mangroves of arid environments in Puerto Rico and adjacent islands. Biotropica 10(2): 110-121.

Cintron, G., A. E. Lugo, and R. Martinez. 1980. Structural and functional properties of mangrove forests. A Symposium Signaling the Completion of the "Flora of Panama," University of Panama. To be published in: Monographs in Systematic Botany, Missouri Botanical Garden.

Cintron, G., C. Goenaga, and A. E. Lugo. 1980a. Observaciones sobre la ecologia de las franjas de manglar en zonas aridas. Memorias del seminario sobre el estudio cientifico e impacto humano en el ecosistema de manglares. UNESCO, Montevideo. 405 pp.

Cintron, G., A. E. Lugo, R. Martinez, B. B. Cintron, and L. Encarnacion. 1981. Impact of oil in the tropical marine environment. Technical Publication, Division of Marine Resources, Dept. of Natural Resources of Puerto Rico.

Cintron, G. and Y. Schaeffer-Novelli. 1981. Introduccion a la ecologia del manglar. Seminario sobre ordenacion y desarrollo integral de las zonas costeras, Guayaquil, Ecuador, 18-27 May 1981. 20 pp. EC/80/006.

Craighead, F. C. 1964. Land, mangroves, and hurricanes. Fairchild Trop. Garden Bull. 19:5-32.

Craighead, F. C. and V. C. Gilbert. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. Quart. J. Fla. Acad. Sci. 25:1-28.

Cundel, A. M., M. S. Brown, R. Stanford, and R. Mitchell. 1979. Microbial degradation of *Rhizophora mangle* leaves immersed in the sea. *Estuarine and Coastal Marine Science*, 9:281-286.

Daivs, J. H. 1940. The ecology and geologic role of mangroves in Florida. Carnegie Inst. Washington Pub. 517:303-412.

Ellis, S. R. 1976. History of dredging and filling of lagoons in the San Juan Area, Puerto Rico. U. S. Geological Survey, Water Resources Investigations 38-76. U. S. G. S. Ft. Buchanan, P.R. 25 pp.

Etkins, R. and E. S. Epstein. 1982. The rise of global mean sea level as an indication of climatic change. Science 215(4530): 287-289.

Febvay, G. and A. Kermarrec. 1978. Formation de la litiere en foret littorale et en foret de montagne humide. Bulletin de Liaison du Groupe de Travail, Mangroves et Zones Cotiere, Guadeloupe 4:79-80.

Gill, A. M. and P. B. Tomlinson. 1977. Studies on the growth of the red mangrove (*Rhizophora mangle* L.). 4. The adult root system. Biotropica 9:145-155.

Hicks, D. B. and L. A. Burns. 1975. Mangrove metabolic response to alterations of natural freshwater drainage to southwestern Florida estuaries. Pp. 238-255. *In*: G. E. Walsh, S. C. Snedaker, and H. J. Teas (eds.). Proc. of the International Symposium on Biology and Management of Mangroves. East-West Center, Honolulu, Hawaii.

Hoffmeister, J. E. 1974. Land from the sea. University of Miami Press, Coral Gables, Fla. 143 pp.

Kolehmainen, S. E., T. O. Morgan, and R. Castro. 1974. Mangrove root communities in a thermally altered area in Guayanilla Bay, Puerto Rico. Pp. 371-390. *In*: J. W. Gibbons and R. R. Scharitz (eds.). Thermal Ecology. CONF. 730505. U. S. AEC. Augusta, Ga.

Lugo, A. E. and S. C. Snedaker. 1974. The ecology of mangroves. Ann. Rev. Ecology & Systematics 5: 39-64.

Lugo, A. E. and G. Cintron. 1975. The mangrove forests of Puerto Rico and their management. Pp. 825-846. In: G. E. Walsh, S. C. Snedaker, and H. J. Teas (eds.). Proc. of the International Symposium on Biology and Management of Mangroves. East-West Center, Honolulu, Hawaii.

Lugo, A. E., G. Evink, M. M. Brinson, A. Broce, and S. S. Snedaker. 1975. Diurnal rates of photosynthesis, respiration, and transpiration in mangrove forests of Florida. Pp. 335-350. In: F. B. Golley and E. Medina (eds.). Tropical Ecological Systems, Springer-Verlag, N.Y.

Lugo, A. E., G. Cintron, and C. Goenaga. 1981. Mangrove ecosystems under stress. Pp. 129-153. In: G. W. Barrett and R. Rosemberg (eds.). Stress Effects on Natural Ecosystems. John Wiley & Sons Ltd.

Macnae, W. 1966. Mangroves in eastern and southern Australia. Austral. J. Bot. 14:67-104.

Macnae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West-Pacific region. Advances Marine Biol. 6: 73-270.

Martinez, R., L. Encarnacion, G. Cintron, L. Cruz, and M. Aponte. 1981. Caracteristicas estructurales de los manglares de Puerto Rico. Proceedings VII Simposio Latinoamericano sobre Oceanografia Biologica. 15-19 Nov. 1981. Acapulco, Mexico.

McMillan, C. 1971. Environmental factors affecting seedling establishment of the black mangrove on the central Texas coast. Ecology 52:927-930.

Negron, L. N. 1980. La produccion de hojarasca en el manglar riberene del Espiritu Santo. M.S. thesis, Univ. of Puerto Rico, Rio Piedras, P.R. 73 pp.

Negron, L. and G. Cintron. 1981. Estructura y funcion del manglar de Laguna Joyuda, Mayaguez, Puerto Rico. Proceedings VII Simposio Latinoamericano sobre Oceanografia Biologica, 15-19 Nov. 1981, Acapulco, Mexico.

Odum, E. P. 1981. The effects of stress on the trajectory of ecological succession. Pp. 43-47. In: G. W. Barrett and R. Rosemberg (eds.). Stress Effects on Natural Ecosystems. John Wiley & Sons Ltd.

Odum, H. T. 1967. Work circuits and systems stress. Pp. 81-138. In: H. E. Young (ed.) Symposium on Primary Productivity and Mineral Cycling in Natural Ecosystems. Univ. of Maine Press. Orono, Maine.

Odum, W. E., and R. E. Johannes. 1975. The response of mangroves to man induced environmental stress. Pp. 52-62. In: E. J. Ferguson Wood and R. E. Johannes (eds.) Tropical Marine Pollution. Elsevier Oceanography Series, Amsterdam, Netherlands.

Patterson-Zucca, C. 1978. The effects of road construction on a mangrove ecosystem. M.S. thesis, Univ. of Puerto Rico, Rio Piedras, P.R. 77 pp.

Pool, D. J., A. E. Lugo, and S. C. Snedaker. 1975. Litter production in mangrove forests of southern Florida and Puerto Rico. Pp. 213-237. In: G. E. Walsh, S. C. Snedaker, and H. J. Teas (eds.) Proc. of the International Symposium on Biology and Management of Mangroves. East-West Center, Honolulu, Hawaii.

Prakash, A. 1971. Terrigenous organic matter and coastal phytoplankton fertility. In: J. D. Costlow (ed.) Fertility of the Sea. Proc. Int. Symp. Fertility Sea, Sao Paulo, Brasil. Gordon and Breach Science Publishers, London and New Yrok.

Prakash, A., M. S. Rashik, A. Jensen, and D. V. Subba Rao. 1973. Influence of humic substances on the growth of marine phytoplankton: Diatoms. Limnol. Oceanogr. 18:516-524.

Pulver, T. R. 1976. Transplant techniques for sapling mangrove trees. Rhizophora mangle, Laguncularia racemosa, and Avicennia germinans, in Florida. Florida Marine Research Publications No. 22. Florida D.N.R. Marine Research Laboratory, St. Petersburg, Florida. 14 pp.

Ryther, J. H. 1969. Photosynthesis and fish production in the sea. Science 166:72-76.

Sachtler, M. 1973. Inventario y fomento de los recursos forestales: Republica Dominicana, Inventario Forestal. PNUD/FAO FO:SF/DOM 8 Informe Tecnico 3. Roma.

Servant, J., N. Jean-Bart, and O. Sobesky. 1978. Le phenomene "Etang Bois-Sec": Une zone d'hupersalure en mangrove. Bulletin de Liaison du Groupe de Travail, Mangroves et Zones Cotiere, Guadeloupe- r:64-65.

Snedaker, S. C. and D. J. Pool. 1973. Mangrove forest types and biomass. Pp. C-1-C-13. In: The role of mangrove ecosystems in the maintenance of environmental quality and a high productivity of desirable fisheries. Final report to Bureau of Sport Fisheries and Wildlife. Contract No. 14-16-008-606, Center for Aquatic Sciences.

Stoddart, D. R. 1969. Post-hurricane changes on the British Honduras Reefs and Cays: Re-Survey of 1965. Atoll Res. Bull. 131:1-25.

Tabb, D. C., D. L. Dubron, and R. B. Manning. 1962. The ecology of northern Florida Bay and adjacent estuaries. Florida State Board Conserv. Tech. Ser. Pub. No. 39. 81 pp.

Tabb, D. C. and A. C. Jones. 1962. Effects of Hurricane Donna on the aquatic fauna of North Florida Bay. Transactions of the American Fisheries Society. 91(4): 375-378.

Turner, E. R. 1977. Intertidal vegetation and commercial yields of Penaeid shrimp. Transactions of the American Fisheries Society. 106(5):411-416.

Wadsworth, F. H. and G. H. Englerth. 1959. Effects of the 1956 hurricane on forests of Puerto Rico. Caribb. Forester 20:38-57.

Watson, J. G. 1928. Mangrove forests of the Malay Peninsula. Malayan Forest Rec. 6:1-275.

Zieman, J. C. 1972. Origin of circular beds of Thalassia (Spermatophyta: Hydrocharitaceae) in south Biscayne Bay, Florida, and their relationship to mangrove hammocks. Bull. Mar. Sci. Gulf Caribb. 22(3):559-574.

Table 1. Summary of primary productivity and respiration data for different mangrove forest types. Based on Lugo and Snedaker (1974) review.

| | g organic matter/m$^2$·day | | |
|---|---|---|---|
| Forest Type | Gross Primary Productivity | Total 24 hr. Respiration | Net Primary Productivity |
| Riverine | 24.0 | 11.4 | 12.6 |
| Basins | 18.0 | 12.4 | 5.6 |
| Fringes | 13.2 | 11.3 | 8.8 |
| Hammocks | 3.8 | 1.2 | 2.6 |
| Dwarf | 2.8 | 4.0 | -- |

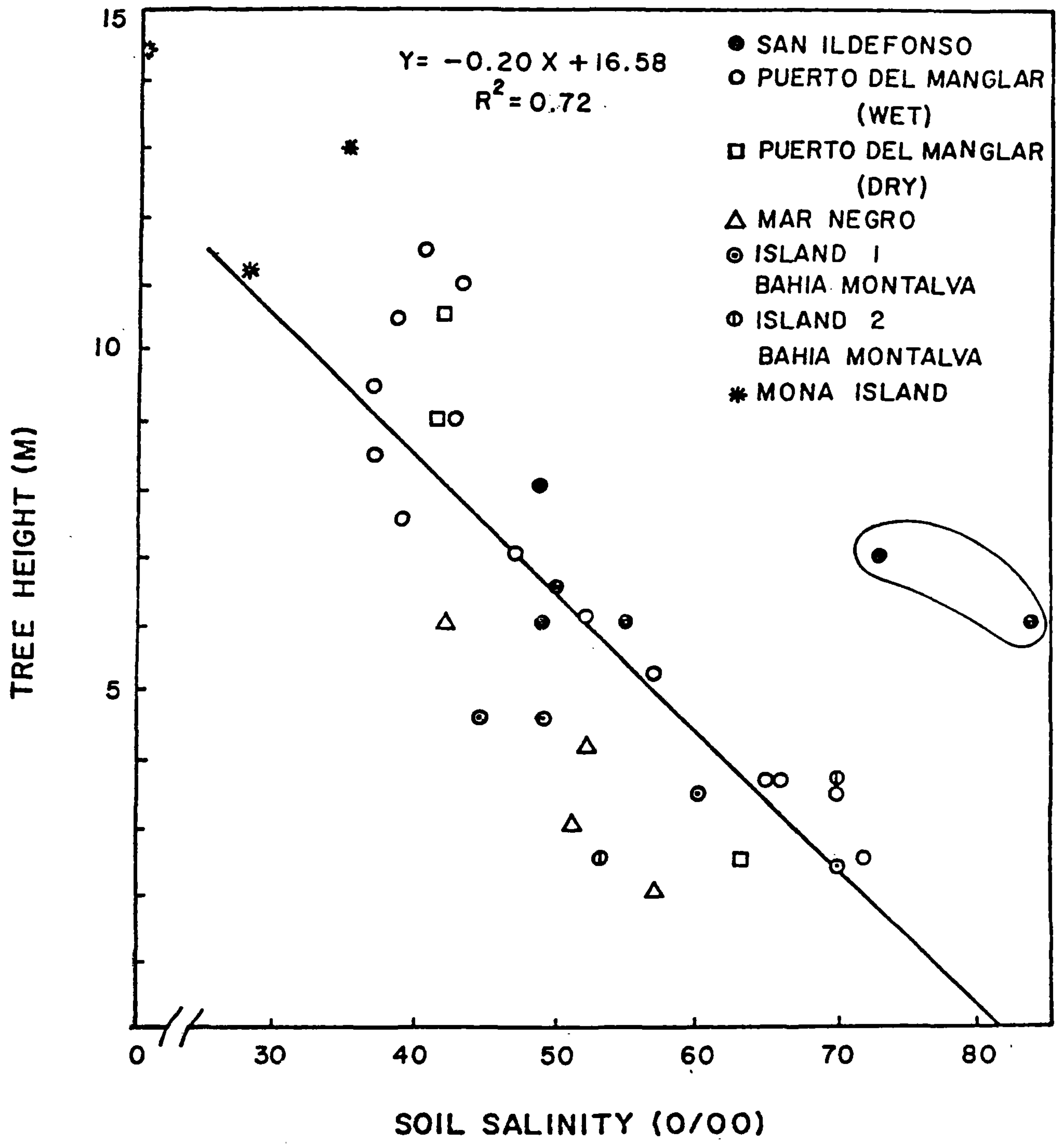

Fig. 1. Relationship between tree height and soil salinity in mangroves of arid coastlines of Puerto Rico and adjacent islands (Cintron *et al*. 1978)

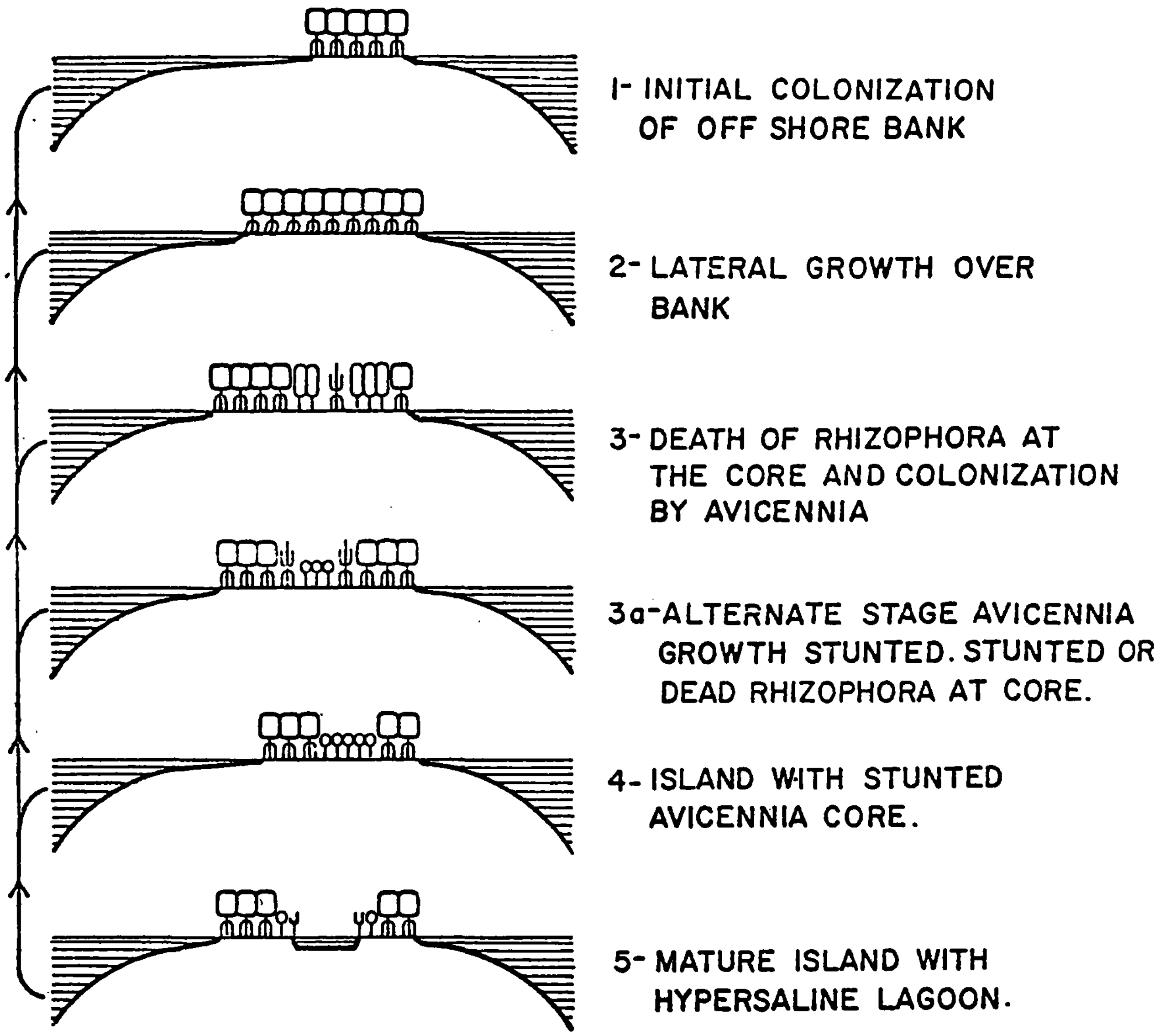

Fig. 2. Conceptual scheme of mangrove succession for mangrove islands in arid coastlines (Cintron *et al*. 1978)

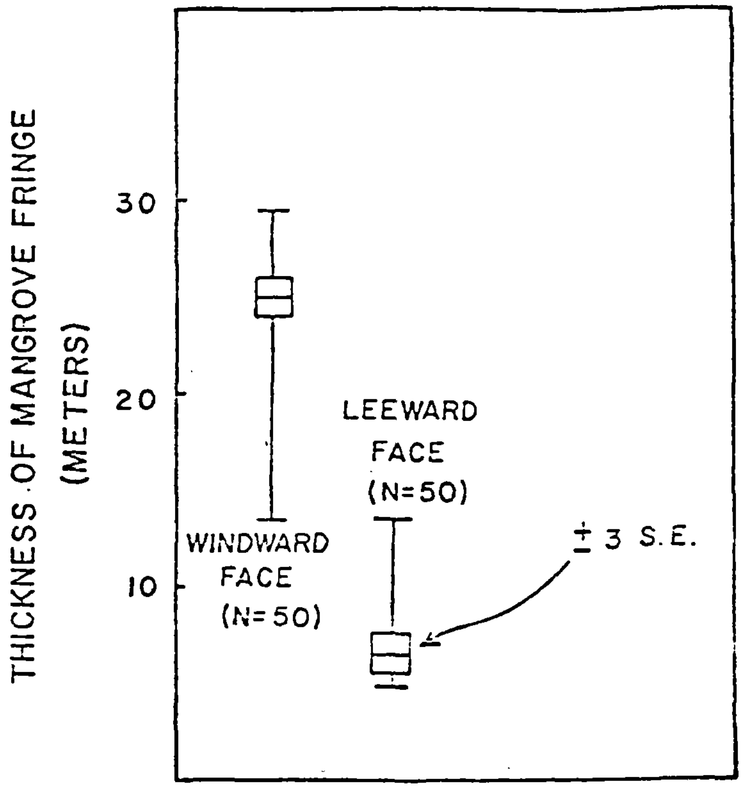

Fig. 3. Thickness of the red mangrove fringe in the mangrove islands of La Parguera (Cintron *et al.* 1978).

APPENDIX I. F. Dr. Mario D. Banus

## The effects of thermal pollution on red mangrove seedlings, small trees, and on mangrove reforestation

## INTRODUCTION

Mangrove trees are a major component of tropical coastal zones between latitudes 25° S and 25° N around the world (Chapman 1975). In many locations large areas of the trees have been removed to make land for agriculture, for industrial and residential sites and by warfare. In Puerto Rico, for example, the areas covered by mangrove trees have decreased from 24,300 ha. to below 4000 ha. as part of a government policy to upgrade "low-value" mangrove covered land (Lugo and Cintron 1975). Many of the remaining mangrove areas around the world are being affected by various pollutants such as sediment run-off, sewage, waste heat, hydrocarbons, and waste chemicals (Cintron 1982). Survival of some mangrove areas will depend on man understanding what these pollutants do to mangroves and taking action to prevent the harmful effects from occurring.

Waste heat, primarily emitted by electric generating plants, is especially damaging in tropical coastal zones because many organisms are living close to their upper thermal tolerance levels. Thus temperature increases of 5-10° C. above maximum summer ambient temperatures is generally fatal to plants and sesile animals. The devastation of a seagrass (Thalassia testudinum) community in Florida by the thermal discharge from the Turkey Point power plant has been well documented (Bader, Roessler and Thorhaug 1972). At Guyanilla, Puerto Rico, a 1100 mw (E) fossil-fuel electric plant dumps about 1000m$^3$/min of seawater heated to 41°C into a nearly totally enclosed lagoon of 19 ha (Fig. 1). The effects of this heated water on the mangroves and mangrove community have been described (Kolehmainen, Morgan and Castro 1974; Banus and Kolehmainen 1976 and Caney 1975). In spite of lagoon water temperatures as high as 40-41°C during the summer months, mature red mangrove (Rhizophora mangle) trees with a few white mangrove (Laguncularia racemosa) trees border two shores of this lagoon. The trees are obviously stressed and produce fewer and smaller seedlings (p. 46 and Fig. 1, Banus and Kolehmainen 1976).

The mangrove trees along the shore with water temperatures up to 41°C around their roots showed definite evidences of the effects of stress. The aerial-roots were very slender, about 2 cm diameter, and very numerous. Many were rotted off at the high tide level. The leaves were smaller and fewer as shown in Table 1. However, the chlorophyll content of the leaves suggests that their ability to carry out photosynthesis per unit area of leaf had not decreased.

The root communities associated with the prop-roots and aerial-roots are major sources of biomass and productivity in a healthy mangal. Elevated water temperature decreases the number of invertebrate species in the root communities from about 90 at ambient conditions to about 25 at 35°C to 10 at 37°C (Kolehmainen et al. 1974). At 38-40° there are few aerial-roots under water and no invertebrates or algae. The increase in temperature does not significantly decrease the number of algae species up to 37°C but does decrease the biomass.

Although the adult trees survive, with difficulty, around this heated lagoon, there are no growing seedlings or small trees in the shallow water areas. The smallest trees appeared to be 5-10 years old. However, their age was hard to judge due to unnatural growth caused by the thermal stress. Since the juvenile forms of many organisms have lower lethal temperature levels than their adult forms, it is possible that the temperature in this lagoon prevented the survival of seedling and small trees.

Reforestation of a mangal which has been under stress can occur if the propagules from the stressed trees will survive in stressed mangal or if propagules from outside the stressed area can enter, colonize and survive. If neither of these groups of propagules can survive and grow, older juveniles such as small trees could be planted and if they survive, reforestation can take place. A program of research was carried out over a period of 2½ years to evaluate the survival of the seedlings and small trees at various temperatures.

The elevated water and sediment temperatures in the mangal around this lagoon presented a natural laboratory to study the effects of elevated temperatures on red mangrove seedlings and small trees. However, the water temperatures in this lagoon varied annually due to fluctuating sea-temperatures and electrical demand at power plant as well as daily due to solar heating. Therefore laboratory experiments, at controlled constant temperatures, also were carried out to estimate the upper lethal temperature of small trees. The seedlings came from trees in Sites #2 and 3, Fig. 1 ("Thermal" Seedlings) and from trees in the Control area ("Ambient" Seedlings) at Pta. Ostiones on the west coast of Puerto Rico (see Banus and Kolehmainen 1976). Small trees were grown from seedlings from both sites under ambient conditions. (In this report, seedlings are propagules from abscission until roots are formed along with the first two pairs of leaves; when the third pair of leaves forms they are called small trees.). Under both field and laboratory conditions, the survival of "Ambient" vs "Thermal" seedlings and small trees were compared to determine if "Thermal" trees produced propagules that were better adapted to survive at elevated temperatures. Temperatures at the three field locations are given in Table 2 for the coldest and warmest months of the year; the means are based on daily thermograph recordings at the elevated temperature locations.

## SURVIVAL OF "AMBIENT" vs "THERMAL" PLANTS

### Seedling Survival in Field

The survival and growth of seedlings subjected to thermal stress under field conditions was evaluated by placing sub-batches of 100 seedlings, "Thermal" (from trees in the Thermal area), "Intermediate" (from trees in the Intermediate temperature area) and "Ambient" (from the Control area) in net cages in the three areas and observing their survival and growth for three months. The results are given in Table 3.

At the Thermal site both subbatches showed substantial mortality, while "Thermal" seedlings appeared to be rooting quicker. At the Intermediate site, there was a small mortality and the "Intermediate" seedlings appear to root and leaf faster. All survived, rooted, and formed leaves well under Ambinet conditions. After three months the seedlings were transferred to tubs of local sediments and kept at the same locations.

Within a month all the seedlings of both subbatches were dead (black and nonviable) at the Thermal site. The "Intermediate" seedlings at the Intermediate site appeared to do well at first, most formed roots in another month but the leaves and growing tips kept drying out and breaking off so that after 9 months (February) all were dead. The "Ambient" seedlings at this site appeared to do less well with only 50% getting roots and a few of these having leaves. However, once leaves were formed, most survived so that at the end of a year there were 17 small trees from the "Ambient" seedlings growing well while there were none of the seedlings from the trees in that very location which survived. Whether this was due to the moderate thermal stress on the parent trees or to other stresses (such as sediment hydrocarbon content) is not clear from this experiment.

### Survival of Small Trees in the Field

The batches of seedlings from the Thermal and Ambient locations which were studied for survival and rooting at the Ambient site provided large numbers of small trees for further tests. The seedlings with roots and leaves were grown to small trees in Ambient site sediments in 10x10x9 cm plastic boxes under flowing sea water outside the Laboratory until they had at least 4 pairs of leaves. Two sets of plantings were made at the Thermal and Intermediate locations, the first at the start of the high temperature period (1 June) at each location. The second planting was at the start of the minimum temperature period (3 December) and therefore was provided with four months of gradual temperature increase prior to the maximum temperature period.

The observed criteria for stress were loss of turgor of the leaves and growing tip; chlorosis, blackening, and abscission of the upper leaves. Yellowing of the first or second pair of leaves prior to abscission was not considered to be a sign of stress since this is normal and occurred for all small trees, both in the experimental sites and in the nursery tanks. Trees were considered dead when there were no leaves left and the growing tip was black with no green visible. The criteria for observing growth were the swelling of the terminal buds, the opening of a new pair of leaves, or the development of precicious branches at the leaf nodes. The results are given in Tables 4 and 5.

For the June planting, at the Thermal site all trees showed stress after a week, only a few showed temporary growth and there was a steady increase in mortality becoming complete after 119 days (Table 4). At both the Intermediate and Ambient locations all trees survived except for five which were planted in water so deep that they drowned.

The acclimation of several months provided by planting in December improved survival at the Thermal site, Table 5. During the first seven months (32°-37°C), 94% were surviving with 88% growing, new growth first observed after 2 months. During the period of maximum temperature (38-40°C), severe mortality again occurred but 13% (4 trees) survived and were growing well in the cooler November water (36-37°C). At the Intermediate site (45-37°C), 19% of the trees died but the balance grew well and sent out prop-roots. At both sites, the survival of "Ambient" small trees appears higher than for the "Thermal" trees, in agreement with the behavior of the seedlings.

## Survival and Growth of Small Trees at Constant Temperatures

It is difficult to set an upper lethal temperature from these field experiments due to fluctuations in water temperature, tidal cycles, and variation in sediment composition and contaminants between locations. Therefore laboratory experiments were made at carefully controlled sea water temperatures, at a constant water level and with the same sediments for all trees. The small trees were pot grown as described above from "Thermal" and "Ambient" seedlings which had rooted in cages at the Ambient site. Sub-groups of 10 small trees in individual plastic pots from each seedling source were held in 1 $m^2$ fiberglass tanks at 39°C, 37°C, 35°C and ambient temperature flowing sea water for 40 days. The water surrounded the pots so that the sediments were 0.4 - 0-6°C below the temperature of the water. The tanks were outdoors and subjected to typical western Puerto Rico sun, weather conditions and seawater.

Nearshore seawater was heated in an epoxy-coated concrete tank by tantalum heat exchanges and circulated to the tanks in an all plastic system. The individual tank temperatures were controlled by solenoid valves mixing seawater at 50°C with ambient seawater. The heated tanks had 1-2 l/min. of overflowing water and 8-19 l/min. of recirculating water to assure uniform temperatures. These temperatures were recorded using thermistors suspended among the small trees, a multichannel sequencing selector unit, and a millivolt recorder. The tank temperature (mean ± s.d.; (Range) ) were: 39.05 ± 0.22 (38.5-39.4); 37.04 ± 0.20 (36.1-37.5); 35.08 ± 0.31 (34.2-35.6); 29.5 ± 2.1 (24.8-33.4). Ambient temperature data were obtained 4-6 times/day using a referency mercury thermometer. Salinity: 31-33.5 Light levels: 0 (night) to 125-400 (rain and clouds) to 2200 (full sunlight) Einsteins/$m^2$/sec.

Small "Ambient" trees survived significantly better than "Thermal" trees at 39° and 37°C. At 39°C water temperature (Fig. 2A), "Thermal" small trees all showed signs of stress after 15 days and all were dead by 39 days. The "Ambient" small trees showed the effect of temperature stress at 28 days. However, three were still alive at 40 days, two dying during the subsequent recovery period.

At 37°C water temperature (Figure 2B) eight of the "Thermal" trees were stressed at 40 days and two of these were dead. Two more died subsequently during the recovery period. Initially, six "Thermal" trees started to grow but growth stopped for all but two before the end of the heating period. In contrast, only two of the "Ambient" trees showed signs of stress; neither died, with both recovering later at ambient temperatures. In addition, nine "Ambient" trees were growing after 28 days and continued to grow.

At 35°C and ambient water temperatures all trees survived. All 20 trees showed new growth after 35 days in the ambient tank and after 24 days in the 35°C tank.

At a constant 39°C sea water temperature, the $LT_{50}$ is 33 days for "Ambient" trees and 24 days for "Thermal" trees (Fig. 2A). The $LT_{50}$ times are both substantially shorter than the summer period in the lagoon when the water temperatures at the Thermal field location have daily maxima in the 38-40°C range (Table 2). These water temperatures were lethal to all twenty small trees at this location on 1 June in agreement with the laboratory results. A constant seawater temperature of 37°C has an LT50 of more than 40 days for "Thermal" trees and is probably lethal to "Ambient" trees only after several months: longer than the summer high water temperature period.

The "Thermal" small trees were more susceptible to thermal stress than "Ambient" trees in the laboratory tanks. Seedlings from the same parent trees showed the same comparative behavior in the field. Therefore, the elevated water temperatures cause adult trees to produce smaller and fewer seedlings, and these seedlings are less able to withstand elevated temperatures, both initially and when they have grown in ambient conditions to small trees. The physiological basis for the increased sensitivy of "Thermal" seedlings and small trees to thermal stress is not suggested by what is known about the effect of elevated temperatures on mangrove physiology, such as leaf DNA and chlorophyll content and the trees productivity at elevated temperatures (Miller 1974).

In the laboratory experiments there was no acclimation of the small trees. Seawater temperatures were raised from ambient to 35°, 37°, and acclimation is beneficial. In addition to acclimation, the diurnal thermal cycle of about 2°C and some days with temperatures below 37°C, apparently provided enough relief from the high temperature stress so that a small percentage of trees survived the summer water temperatures of 38°- 40°C in the field.

Since at ambient and 35°C water temperatures all the small trees survived and grew, the growth rates between these temperatures and for the two sources of small trees were compared. The values for the four sub-groups are given in Table 6. These data suggest that "Ambient" trees in 35°C seawater have the best growth rate with little difference among the other three sub-groups. There was an observable variation in growth habit among the individual trees which is obscured using mean values. Some trees grew only from the terminal bud either rapidly or slowly. Others grew primarily via the precocious branches which form just above a leaf pair. The growth morphology of Rhizophora mangle has been described by Gill and Tomlinson (1969). I observed that the trees on which the precocious branches are developing do not grow at the terminal bud until the branches are well developed. For example, for the sub-group "Ambient" trees in ambient water, the two trees with smallest increases in height, 8 and 9 mm each, had a pair of precocious branches with one and two leaf-pairs per branch respectively. Likewise, the two trees with least increase in height for "Ambient" trees at 35°C and "Thermal" trees at ambient temperatures had branches with up to three pairs of leaves per branch.

Therefore, a Growth Index was designed which arbitrarily set up a point system for various growth modes to account for these variations. These were assigned the following values: one point: for each cm of height increase, for each new main leaf pair, and for each branch, with one-half point for each branch leaf pair. The total points per tree varied from 1 to 9 and were summed for each sub-group to give the Index for the sub-group (Table 1). The Growth Index clearly confirms the superior growth for the "Ambient" trees at 35°C water temperatures. The "Thermal" trees in ambient water grew less rapidly than any other sub-group, while 35°C water improved their growth so that it became equivalent to the "Ambient" trees in ambient water. Thus, for small trees living in coastal waters with temperatures up to 33°C an increase in water temperature to 35°C appears beneficial but temperatures of 37°C and higher cause stress and mortality.

## MANGROVE REFORESTATION

These studies have shown that reforestation of an area of red mangroves, which have been partially or completely destroyed by excessive thermal pollution, can only be accomplished if the water temperature can be kept at or below 37°C for most of the time. Excursions up to 39°C can occur if limited to a few hours. Under these conditions, small trees grown from seedlings collected in unstressed areas have an excellent chance for survival. The survival is enhanced if there is a period when the water temperatures are below 37°C and the trees are planted during this period. If seedlings rather than small trees are to be the reforestation source then the water temperatures must be below 37°C for any appreciable survival and the seedlings must come from unstressed trees. These temperature limits would be applicable to reforestation where there was an existing mangal prior to the thermal stress and the small trees must have been grown in sediments similar to those of the mangal to be reforested.

Reforestation of seashore areas where red mangroves are scarce or not present has many problems. If there is a nearby source of seedlings, the area may be free of red mangroves because physical stresses other than thermal pollution may prevent the recruitment of new trees. The most obvious stress is wave action which removes the seedlings before they can take root, covers them by transporting sediments (beach building), or smothers them with beach wrack (grass blades, seaweed, trash, etc.). Any of these can occur at various times and the seedlings are vulnerable until they have grown to small trees with branches and even prop-roots. The sediment type is not critical to the survival of the seedlings although root formation and growth does depend on the sediments. Sand appears to accelerate root formation while soft anoxic muds such as found in mature mangals encourage leaf and branch growth. Rooting is slow in heavy clay sediments and in those with high $H_2S$ content.

The sediment characteristics are much more critical when transplanting small trees. They survive well when transplanted to sandy soil or to sediments similar to those in which they were raised. They do not survive in heavy, clay based sediments, in anoxic sediments with high $H_2S$ content nor in sediments where there is a lot of decaying organic matter (such as sea grass leaves), although seedlings can be started in these substrates with difficulty. This behavior suggests that their initial growth adapts to the substrate and drastic changes in substrate is lethal. This limits the activity of reforestation with small trees. However, in areas where there is wave and current motion and a suitable sediment, small trees are the preferred reforestation source although a great deal more effort is required to transplant them.

## ACKNOWLEDGEMENTS

I thank Dennis Corales for technical assistance in the laboratory and field and Mary Nutt for reviewing this manuscript.

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## LITERATURE CITED

Bader, R. G., M. A. Roessler and A. Thorhaug. 1972. Thermal Pollution in a Tropical Marine Estuary. Ch. 4. Marine Pollution and Sea Life, Ruive. M. (ed.). Fishing News (Books) Ltd. Surrey and London, England.

Banus, M. D. and S. E. Kolehmainen. 1976. Rooting and growth of red mangrove seedlings from thermally stressed trees. In: *Thermal Ecology* II. G. W. Esch and R. W. McFarlane (eds.). CONF 750425. Technical Information Center ERDA, Springfield Va. pp. 46-53.

Canoy, M. 1975. Diversity and stability in a Puerto Rican *Rhizophora mangle* L. forest. In: Walsh, G. E.,S. Snedaker and H. Teas (eds.) Proc. Int. Symp. Biol. & Mgmt. of Mangroves. U. Florida Press, Gainesville, Fla. pp. 344-356.

Chapman, V. J. 1975. Mangrove Biogeography. In: Walsh, G., S. Snedaker and H. Teas (eds.) Proc. Int. Symp. Biology and Management Mangroves. U. of Florida Press, Gainesville, Fla. pp. 3-33.

Cintron, G. 1982. Mangrove Forests: Ecology and response to natural and man-induced stresses. UNESCO/W.I.L. - F.D.U./IOCARIBE Report.

Gill, A. M. and P. B. Tomlinson. 1969. Studies on the growth of red mangrove (*Rhizophora mangle* L.) 1. Habit and general morphology. Biotropica *1*: 1-9.

Kolehmainen, S. E., T. O. Morgan, and R. Castro. 1974. Mangrove root communities in a thermally altered area in Guyanilla Bay, Puerto Rico. In: Gibbons, J. W. and R. R. Scharitz (eds.) Thermal Ecology: CONF. 730505, U. S. A. E. C., Augusta, Ga.

Lugo, A. E. and G. Cintron. 1975. The Mangrove Forests of Puerto Rico and their Management. In: Walsh, G., S. Snedaker and H. Teas (eds.). Proc. Int. Symp. Biology and Management Mangroves. U. of Florida Press, Gainesville, Fla. pp 825-846.

Miller, P. C. 1974. In: Proc. Symp. of Phys. and Biol. Effects on the Environ. Cooling Systems and Thermal Discharges at Nuclear Power Stations. 1 AEA-SM-187/17.

Table 1. Leaf Parameters vs Water Temperature Surrounding Red Mangrove Trees.

| Water Temp. °C | 28-35°C (4 locations) | 38-40°C (single locations) |
|---|---|---|
| Leaf Length | 11.12 cm | 9 cm |
| Width | 4.5 cm | 3.5 cm |
| Weight | 1.8 - 2.4 gm | 1.1 gm |
| (means of 100 leaves picked at random at each location) | | |
| Chlorophyll - a $\mu$ g/g tissue | 232-332 | 240-367 |
| Leaf Area Index (Canoy 1974) | 7.0 | 2.8 |

Table 2. Monthly Water Temperatures, °C at Field Experimental Locations (means of daily max. and min. values).

| Month | Thermal Site | | Intermediate Site | | Ambient Site | |
|---|---|---|---|---|---|---|
| | Max. | Min. | Max. | Min. | Max. | Min. |
| Jan. | 32.3 | 30.9 | 32.4 | 30.3 | | |
| Feb. | 33.2 | 32.0 | 32.6 | 30.3 | 27 | 26 |
| Mar. | 33.1 | 31.8 | 31.6 | 30.0 | | |
| Aug. | 39.0 | 37.6 | 37.5 | 35.9 | 32 | 30 |
| Sept. | 38.4 | 36.8 | 37.2 | 35.4 | | |
| Oct. | 38.6 | 37.7 | 37.0 | 35.1 | 30 | 28 |

Table 3. Seedling Behavior in Sea Water from 12 June to 12 September

| | Thermal Site | Intermediate Site | Ambient Site |
|---|---|---|---|
| Mean Max. Daily Temp.°C | 38.1 | 37.6 | 29 |
| Mean Min. Daily Temp.°C | 36.5 | 34.2 | |
| "Thermal" Seedlings | 81 alive-19 R* | | 100 R, 27 L** |
| "Intermediate" Seedlings | | 98 alive,<br>68 R, 12 L | 100 R, 50 L |
| "Ambient" Seedlings | 81 alive-3 R | 95 alive<br>31 R, 3 L | 100 R, 37 L |

* R with small roots

** L with leaves

Table 4. Behavior of Small Trees Planted in Thermally Stressed Areas.

| | Thermal Site | | | | Intermediate Site | | | |
|---|---|---|---|---|---|---|---|---|
| Date | Alive | Grow | Poor | Dead | Alive | Grow | Poor | Dead |
| 1 June | 20 | | | | 20 | | | |
| 7 June | 20 | - | 3 | 0 | 20 | - | 5 | - |
| 15 June | 19 | - | 5 | 1 | 19 | 1 | 4 | 1 *** |
| 22 June | 18 | 4 | 4 | 2 | 18 | 4 | 3 | 2 *** |
| 8 July | 16 | 5 | 3 | 4 | 15 | 12 | 0 | 5 *** |
| 20 July | 14 | 4 | 1 | 6 | 15 | 14 | 0 | 5 |
| 29 July | 14 | 5 | 4 | 6 | 15 | 15 | 0 | 5 |
| 5 Aug. | 13 | 4 | 4 | 7 | 15 | 15 | 0 | 5 |
| 24 Aug. | 13 | 0 | 6 | 7 | 15 | 15 | 0 | 5 |
| 3 Sept. | 8 | 0 | 7 | 12 | 15 | 15 | 0 | 5 |
| 16 Sept. | 2 | 0 | 2 | 18 | 15 | 14 | 1 * | 5 |
| 27 Sept. | 0 | 0 | 0 | 20 | 15 ** | 14 | 1 * | 5 |

* Top broken off

** These trees were alive and growing well with branches and prop-roots at the end of a year.

*** Set in water too deep for survival

Table 5. Survival and Growth of Small Trees Planted in December

| Source of Seedlings | Thermal Site | | | | Intermediate Site | | | |
|---|---|---|---|---|---|---|---|---|
| | Thermal | | Ambient | | Thermal | | Ambient | |
| | Total | Grow | Total | Grow | Total | Grow | Total | Grow |
| 16 Dec. | 20 | | 13 | | 20 | | 13 | |
| 22 Dec. | 20 | 0 | 13 | 0 | 20 | 0 | 13 | 0 |
| 8 Jan. | 20 | 0 | 13 | 0 | 20 | 3 | 13 | 1 |
| 4 Feb. | 20 | 14 | 13 | 10 | 20 | 17 | 13 | 12 |
| 10 Mar. | 20 | 16 | 13 | 11 | 20 | 20 | 13 | 13 |
| 26 Apr. | 19 | 17 | 12 | 12 | 14 * | 14 | 11 * | 11 |
| 15 June | 19 | 17 | 12 | 12 | 11 | 11 | 10 | 10 |
| 8 July | 19 | 15 | 12 | 10 | 9 | 9 | 9 | 9 |
| 29 July | 19 | 11 | 12 | 7 | 9 | 9 | 9 | 9 |
| 24 Aug. | 15 | 4 | 12 | 2 | 9 | 9 | 9 | 9 |
| 3 Sept. | 13 | 0 | 10 | 0 | 9 ** | 9 | 8 ** | 8 |
| 16 Sept. | 5 | 0 | 4 | 0 | 9 | 9 | 8 | 8 |
| 27 Sept. | 5 | 0 | 3 | 2 | 9 | 9 | 8 | 8 |
| 14 Oct. | 2 | 1 | 3 | 2 | 9 | 9 | 8 | 8 |
| 22 Oct. | 1 | 1 | 3 | 3 | | | | |
| 17 Nov. | 1 | 1 | 3 | 3 | | | | |

* Eight trees destroyed by floating tire

** Most have prop-roots starting

Table 6. Comparison of Growth of Small Mangrove Trees

| | Height* Increase Mean ± S.D. mm | Range mm | % Trees with New Leaves | % Trees with New Branches | Leaves per Branch | Growth Index |
|---|---|---|---|---|---|---|
| "Ambient" Seedlings | | | | | | |
| At 26-33°C | 20.3 ± 10.4 | 9.36 | 80 | 30 | 2.5 | 40 |
| At 35°C | 20.8 ± 13.4 | 0.42 | 90 | 60 | 3.8 | 55 |
| "Thermal" Seedlings | | | | | | |
| At 26-33°C | 11.4 ± 5.7 | 2.22 | 90 | 30 | 3.3 | 34 |
| At 35°C | 19.3 ± 20 | 2.65 | 90 | 20 | 2.6 | 39 |

* The height of the trees were measured from the top of the hypocotyl to the highest leaf node and did not include the terminal bud.

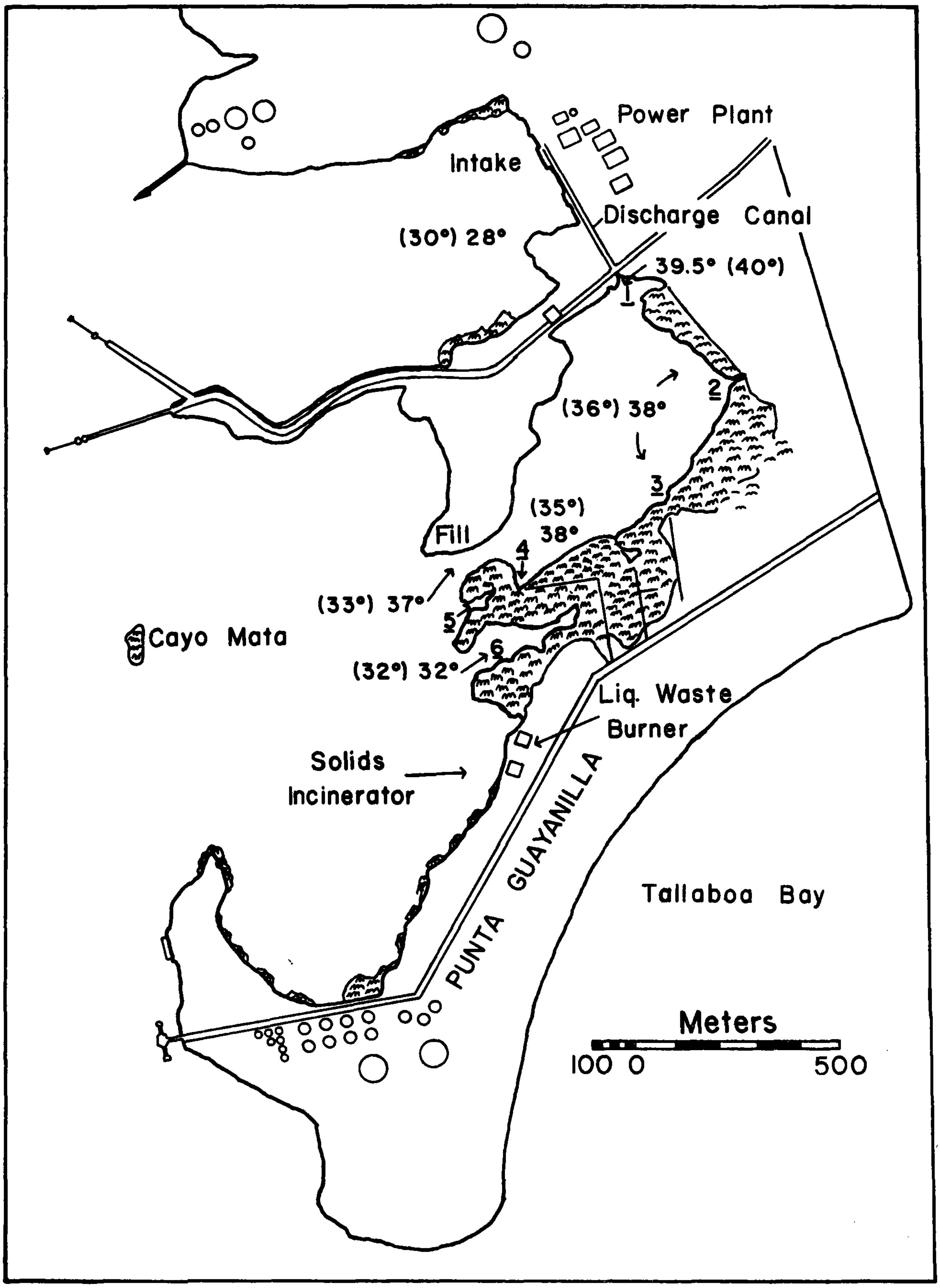

Fig. 1 Plan of Thermal Cove at Guayanilla, P.R. Site locations are underlined numbers. Water temperatures for April 1974 are compared with temperatures for October 1971 (in parentheses). "Thermal" seedlings were collected from trees at sites 2 and 3.

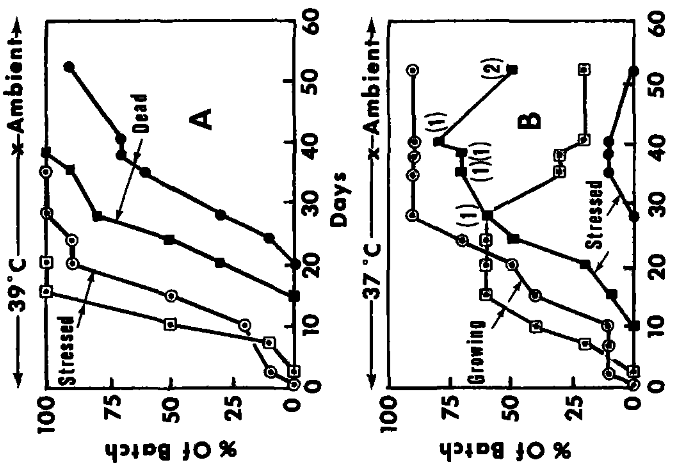

Fig. 2 Survival and Growth of Small Trees in Laboratory Tanks.

A. Trees at 39$^0$C. "Thermal" Trees: Stressed —⊡ : Dead —■
"Ambient" Trees: Stressed —⊙ : Dead —●

B. Trees at 37$^0$C. "Thermal" Trees: Growing —⊡ : Stressed —■
"Ambient" Trees: Growing —⊙ : Stressed —●

"Thermal" seedlings were 15 months old when used in these laboratory experiments and had been growing in sediments for 7 months. "Ambient" trees were from seedlings harvested from control trees at Pta. Ostiones, P.R. They were 10 months old and had been growing in sediments for 7 months when used. The mean tree height was the same for each source: 201.1 ± 46.5 mm. "Thermal" vs. 209.7 ± 48.5 mm. "Ambient". However, the "Thermal" trees had more leaves: 9.5 ± 2.1/tree vs. 7.9 ± 1.4/tree.

## APPENDIX IIA: Dr. Frederico Pannier

### Effects of the mortality and decomposition of a large fish population on mangroves in Venezuela.

On March 9, 1982 a massive fish mortality of spectacular proportions occurred inside the Bay of Carenero, near the coastal resort city of Higuete on the northeastern coast of Venezuela. About six to eight million fishes, primarily belonging to the species Entegraulis edentulus (Rabo amarillo), were found dead along a mangrove fringe which was 1.5 km in length. The dead fishes covered the space between the prop roots of the red mangroves.

The news of the fish kill produced an instantaneous reaction from the public who demanded an explanation of the possible causes of this phenomenon from the scientific community. The government, through the Division of Fisheries of the Ministry of Agriculture decided to create a technical commission. This commission was composed of representatives from the different Ministeries, universities and the Division of Toxicology of the Policia Tecnica Vadicial (PTV). The function of the commission was to elaborate and to analyze the information processed by each institution concerning the fish kill, and to establish the strategies to follow in the future. The results obtained by the commission's investigation were as follows:

1. Ichthyopathological symptoms (vibrosis, mixomatosis, etc.) which could explain massive mortality could not be observed;

2. No biotoxins (of the type produced by the red tide) could be extracted from either the plankton ingested by the fishes or the collected water samples;

3. Chromatographic analyses of water and dead fish samples did not show the presence of organochlorine or organophosphate compounds at levels above acceptable limits. Also, heavy metals were at levels under the usual limits;

4, No bronchial or dermal lesions of mechanical or caustic origin were observed;

5. No β-radioactivity in fish samples (blood, stomach contents and other organs) could be detected.

In fact, no apparent cause of mortality could be established.

With the gradual appearance of four more spots of high fish mortality, which occurred in intervals of 2-3 days, inside the channel system of the recreational development area, the situation became critical. These latter kills were evidently caused by oxygen depletion of the water due to the first fish kill. The following occurred:

- The National Guard tried to collect the dead fishes to bury them;
- The people of the region got preventitive vaccination; many moved temporarily away because of the intense odor;
- Political elements tried to produce local disturbances;
- The sale of fish in all of Venezuela dropped considerably for a time;
- The Congress invited the Ministers of the Environment and of Science and Technology, as well as representatives of the scientific community, to a hearing.

The initial fish mortality could have been due to:

(1) A high tide causing accidental stranding of the massive fish school in bay water which had a limiting oxygen content;

(2) Effects of domestic effluents containing herbivides;

(3) Dumping of highly toxic swimming pool cleaning products;

(4) Collateral effects of local and recent clearcuttings of mangroves, etc.

Not one of these hypotheses could be sustained.

A collateral effect of the fish mortality was the induction of mangrove degradation. After two weeks the following observations were made in the mangroves at the site of the first fish mortality:

- The canopies of the affected Rhizophora mangle fringe (8-10 m wide) were aporoximately 80% defoliated.
- The remaining leaves belonged mainly to the apical twigs of the canopy. Only one or two pairs of the terminal leaves of the verticillum remained attached.
- These leaves had lost their turgor, and became abcissed by the smallest movement of the twig.
- The cortex of the trees and of the secondary ramifications was apparently functional; it showed no abnormality of its characteristic hypodermal chlorophyll layer.
- The prop roots of the affected trees were covered (to a height of 50-60 cm above the lowest tide level) with a thick whitish greasy material.
- The surface of the mangrove soil was densely covered by spherical grease balls (3-10 cm in diameter) of a spongy consistency. These floated and dispersed in the area with the tidal water.
- Young Rhizophora seedlings (with 3-6 leaf pairs) seemed absolutely to not have been affected; their leaves remained turgid. Sporadically present adult individuals of Lanuncularia racemosa showed no visible abnormalities.
- Soils were infiltrated (to a depth of ca. 20 cm) with oil. They produced an exceptionally strong sulphur odor.
- Inner surfaces of the soil, exposed to the sun, were covered to a depth of 15-20 cm with dried fish, bones and spines.

- No dead, nor living birds were observed. Littorina, which normally live on prop roots and the lower parts of trunks, were found on the lower surfaces of the remaining leaves, at a height of 4 m above soil level.

From these observations, the following can be concluded:

(1) The observed defoliation pattern spreads from the base to the top of the trees, and from the base to the top of the twigs, suggesting an increasing water balance disturbance at the level of the water absorbant root system;

(2) The basal, more developed leaves of each verticillum are more vulnerable to water loss than the apical ones; they abciss earlier;

(3) Young seedlings of Rhizophora are not apparently affected by grease probably because propagules characteristically contain substantial nutritional reserves. Continued future observations of the affected mangroves will determine their capacity for survival.

In order to avoid future similar cases of diagnostic inconsistancy of the causes of massive fish mortality, the Venezuelan government has created a coastal monitoring and environmental protection system.

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