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Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological processes, and productivity

Results and scientific papers of a
Unesco/COMAR workshop University
of the South Pacific Suva,
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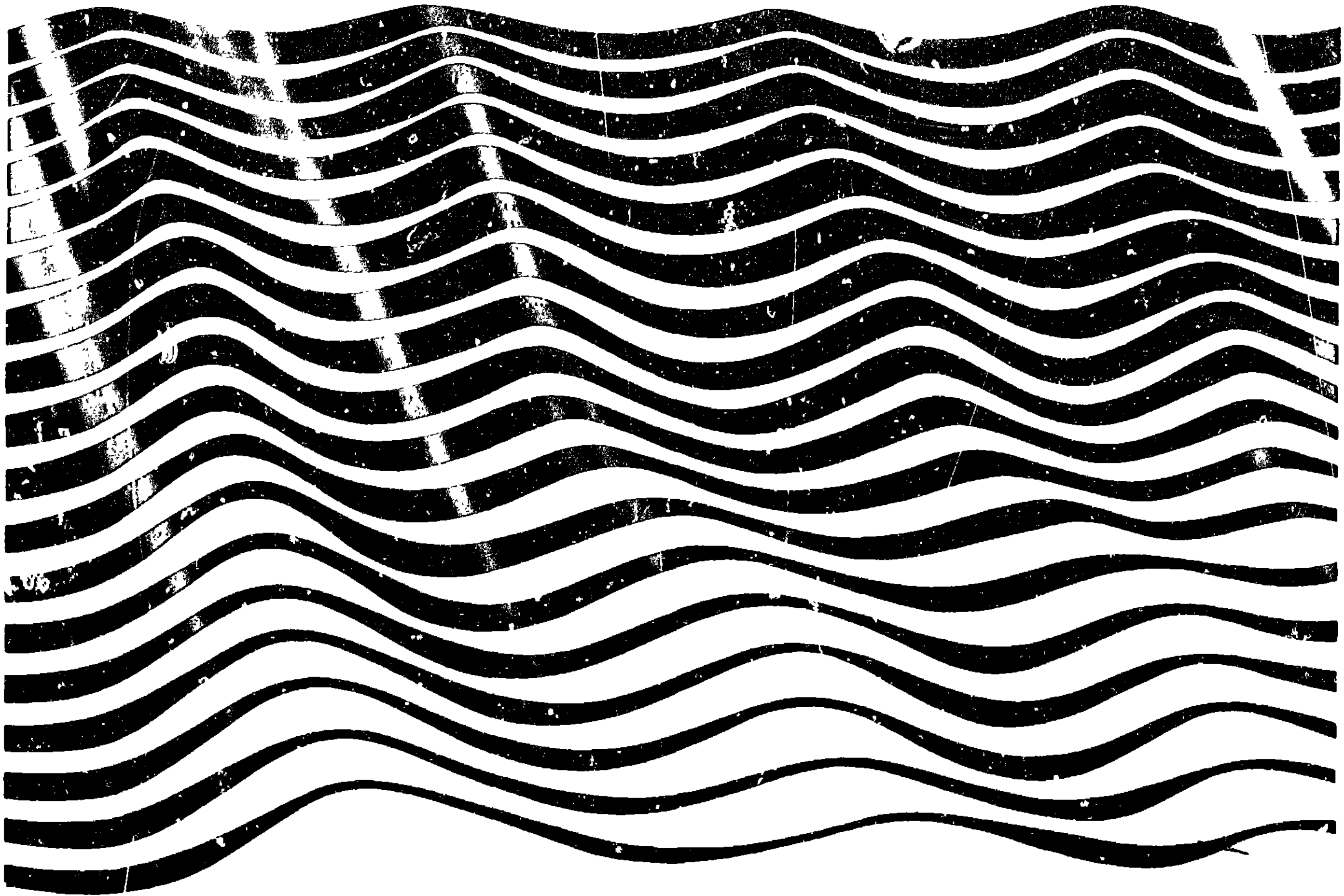

Unesco, 1987

UNESCO REPORTS IN MARINE SCIENCE

No.		Year
1	Marine ecosystem modelling in the Eastern Mediterranean Report of a Unesco workshop held in Alexandria, Egypt, December 1974 English only	1977
2	Marine ecosystem modelling in the Mediterranean Report of the Second Unesco Workshop on Marine Ecosystem Modelling English only	1977
4	Syllabus for training marine technicians Report of an IOC/Unesco workshop held in Miami, Florida, 22-26 May 1978 Available in English, French, Russian and Spanish	1979
5	Marine science syllabus for secondary schools Report of an IOC workshop held at United World College of the Atlantic, United Kingdom, 5-9 June 1978 Available in Arabic, English, French, Russian and Spanish	1979
6	Organization of marine biological reference collections in the Mediterranean Arab countries Expert meeting held in Tunis, 20-23 September 1978 Available in Arabic, English and French	1979
8	The mangrove ecosystem: Human uses and management implications Report of a Unesco regional seminar held in Dacca, Bangladesh, December 1978 English only	1979
9	The mangrove ecosystem: scientific aspects and human impact Report of the seminar organized by Unesco at Cali, Colombia, 27 November-1 December 1978 Available in English and Spanish	1979
10	Development of marine science and technology in Africa Working Group of Experts sponsored by ECA and Unesco, Addis Ababa, 5-9 May 1980 Available in English and French	1980
14	Marine science and technology in Africa: present state and future development Synthesis of Unesco/ECA survey missions to African coastal states, 1980 Available in English and French	1981
15	Fishery science teaching at the university level Report of a Unesco/FAO workshop on university curricula in fishery science, Paris, May 1980 Available in Arabic, English, French, Russian and Spanish	1981
16	Marine and coastal processes in the Pacific: ecological aspects of coastal zone management Report of a Unesco seminar held at Motupore Island Research Centre, University of Papua New Guinea, 14-17 July 1980 English only	1981
18	Coral reef management in Asia and the Pacific: some research and training priorities Report of a Unesco workshop held in Manila, Philippines 21-22 May 1981 English only	1982
19	Mareas rojas en el Plancton del Pacífico Oriental Informe del Segundo Taller del Programa de Plancton del Pacífico Oriental, Instituto del Mar, Callao, Perú 19-20 de noviembre de 1981 Spanish only	1982
20	Quantitative analysis and simulation of Mediterranean coastal ecosystems: The Gulf of Naples, a case study Report of a workshop on ecosystem modelling Ischia, Naples, Italy, 28 March to 10 April 1981 Organized by the United Nations, Educational, Scientific and Cultural Organization (Unesco) and the Stazione Zoologica, Naples English only	1983
21	Comparing coral reef survey methods A regional Unesco/UNEP workshop, Phuket Marine Biological Centre, Thailand, December 1982 English only	1983
22	Guidelines for marine biological reference collections Prepared in response to a recommendation by a meeting of experts from the Mediterranean Arab countries Available in English, French and Arabic	1983
23	Coral reefs, seagrass beds and mangroves: their interaction in the coastal zones of the Caribbean Report of a workshop held at West Indies Laboratory, St. Croix, U.S. Virgin Islands, May, 1982 English only	1983
24	Coastal ecosystems of Latin America and the Caribbean The objectives, priorities and activities of Unesco's COMAR project for the Latin America and Caribbean region Caracas, Venezuela, 15-19 November 1982 Available in English and Spanish	1983
25	Ocean engineering teaching at the university level Recommended guidelines from the Unesco/IOC/ECOR workshop on advanced university curricula in ocean engineering and related fields, Paris, October 1982 Available in English, French, Spanish, Russian, Arabic and Chinese	1983
26	Global survey and analysis of post-graduate curricula in ocean engineering English only	1984
27	Productivity and processes in island marine ecosystems. Recommendations and scientific papers from the Unesco/IOC sessions on marine science co-operation in the Pacific, at the XVth Pacific Science Congress, Dunedin, New Zealand, February 1983 English only	1984
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29	Eutrophication in coastal marine areas and lagoons: a case study of 'Lac de Tunis' Report prepared by Dr M. Kelly and Dr M. Naguib English only	1984
30	Physical oceanography of the Eastern Mediterranean: an overview and research plan Report of a workshop held in Lerici, La Spezia (Italy), September 1983 English only	1984
31	MABAHISS/John Murray 50th anniversary: Marine science of the North West Indian Ocean and adjacent waters Report of a symposium on the occasion of the 50th anniversary of the MABAHISS/ John Murray Expedition (1933/34), University of Alexandria, Egypt, 3 to 7 September 1983 English only	1985
32	L'estuaire et la mangrove du Sine Saloum Résultats d'un Atelier régional Unesco-COMAR tenu à Dakar (Sénégal) du 28 février au 5 mars 1983 French only	1985
33	Coral taxonomy Results and recommendations of a regional Unesco (COMAR)/UNEP Workshop with advanced training Phuket Marine Biological Centre Thailand, 10-26 February 1984 English only	1985
34	Bibliography on costal lagoons and salt marshes along the Southern Mediterranean coast (Algeria, Egypt, Libya, Morocco, Tunisia) Available in Arabic, English and French	1985
35	Physical oceanography of the Eastern Mediterranean (POEM): A Research Programme. Reports of the Organizing Committee Meeting, Paris, August 1984, and the Scientific Workshop, Lucerne, October 1984 English only	1985
36	Méthodologie d'étude des lagunes côtières. Résultats d'un atelier régional réuni à Abidjan du 6 au 11 mai 1985 French only	1986
37	Principles of Geological Mapping of Marine Sediments (with special reference to the African continental margin) Available in English and Russian	1986
38	Marine Sciences in CMEA countries Programme and results of co-operation Available in English and Russian	1986
39	Development of marine sciences in Arab Universities Meeting of Experts held at the Marine Science Station Aqaba, Jordan 1-5 December 1985 Available in Arabic, English, French	1986

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Edited by
Charles Birkeland

Sponsored by
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PREFACE

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

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ABSTRACT

This report presents the workshop conclusions concerning important differences among tropical seas in terms of ecological processes in coastal marine ecosystems, and the corresponding implications for resource management guidelines. They result from the presentation and discussion of nine review papers and three days of field surveys during the workshop. The report includes the review papers as well as four recommendations for follow-up.

RESUME

Ce rapport présente les conclusions de l'atelier relatives aux différences marquées relevées, d'une mer tropicale à l'autre, quant aux processus écologiques des écosystèmes marins côtiers, et à leurs conséquences pour l'établissement de principes directeurs concernant la gestion des ressources. Ces conclusions découlent de neuf études de synthèse qui ont été présentées et discutées au cours de l'atelier et d'excursions auxquelles trois journées ont été consacrées. Le rapport comprend les études de synthèse ainsi que quatre recommandations sur la suite à leur donner.

RESUMEN

En este informe se presentan las conclusiones del seminario sobre las grandes diferencias que existen entre los mares tropicales en cuanto a los procesos ecológicos en los ecosistemas marinos costeros y sus repercusiones en lo relativo a la fijación de normas para la gestión de los recursos. Dichas conclusiones son el resultado de la presentación y la discusión de nueve documentos recapitulativos y de tres días de estudio sobre el terreno, efectuados durante el seminario. En el informe se incluyen dichos documentos así como cuatro recomendaciones relativas a su aplicación.

ВЫДЕРЖКА

В настоящем докладе представлены выводы учебно-практического семинара в отношении серьезных различий между тропическими морями с точки зрения экологических процессов в прибрежных морских экосистемах, а также соответствующие последствия для руководящих принципов рационального использования природных ресурсов. Они являются результатом представления и обсуждения девяти обзорных докладов и трех дней проведения обследований на местах в ходе учебно-практического семинара. Доклад содержит обзорные доклады, а также четыре рекомендации в отношении последующих мер.

ملخص

يقدم هذا التقرير الاستنتاجات التى خلصت اليها حلقة العمل بشأن الفروق الهامة بين البحار المدارية من حيث العمليات الايكولوجية فى النظم الايكولوجية البحرية الساحلية ، وما يترتب على ذلك من حيث المبادىء الرائدة فى مجال ادارة الموارد . وجاءت هذه الاستنتاجات ثمرة عرض ومناقشة تسعة بحوث وقضاء ثلاثة أيام من الدراسة الميدانية أثناء حلقة العمل . ويشمل التقرير البحوث المقدمة وأربع توصيات تتعلق بالمتابعة .

摘　要

此项报告介绍了讲习班关于热带海洋中沿海生态系统方面的重要差别所取得的结论以及其对资源管理指导原则的相应影响。这些结论是在讲习班期间提出和讨论9篇考查论文及3天实地调查之后产生的。此报告包括所有考查论文和四项关于后续活动的建议。

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I. INTRODUCTION

Tropical coastal ecosystems are among the most productive ecosystems in the world in terms of gross primary productivity. A large number of countries in the tropics are on islands and over 90% of the protein in small island communities comes from coastal marine ecosystems. Most tropical countries are still developing their strategies of resource exploitation. As bases for policies of resource management and utilization, it is most important to have a fundamental understanding of the dynamics of ecosystem productivity and organization. Some basic differences exist between Caribbean, eastern tropical Pacific, and Indo-west Pacific coastal ecosystems, differences that have important implications for resource utilization. Because of the rapid development and population growth in tropical countries, it is an urgent matter to develop a theoretical framework which could be the basis for development of rational management programs for tropical coastal resources.

A. Objectives of the Workshop

Despite the practical importance and urgency of understanding fundamental differences in the organization and dynamics of tropical coastal ecosystems among different geographic regions, this matter has not been explicitly addressed. As a first step in developing our knowledge of this matter, UNESCO/COMAR organized a workshop on differences in community dynamics and productivity of comparable tropical coastal ecosystems among different geographic regions. The a priori objectives of the workshop were:

1. to identify important differences in productivity, community structure, and ecological processes in the tropical Atlantic, eastern Pacific, and Indo-west Pacific,
2. to identify mechanisms reponsible for these differences,
3. to identify implications of these differences for marine resource utilization by man, and
4. to develop a theoretical framework as a basis for rational management programs for tropical coastal resources.

B. Workshop Format and Venue

The UNESCO/COMAR workshop was held 24-29 March 1986 at the University of the South Pacific (USP) in Suva, Fiji, and at the Dravuni Island Research Station, about 40 km south of

Viti Levu, Fiji. A total of 9 participants came from Thailand, Guam, Australia, Hawaii and the continental United States. A representative of UNESCO and two representatives of USP also participated. The list of participants and their mailing addresses is given in Appendix 1.

Dr. J.R.E. Harger, Programme Specialist in Marine Sciences, UNESCO/ROSTSEA, Jakarta, Indonesia, presented the objectives of the workshop and stated his hopes that a substantive benefit towards the rational management of coastal ecosystems will emerge from this workshop. He also presented the benefits of developing a pantropical network of data compilation among research and academic institutions through exchange of data-base fragments on floppy disks, using a convenient data management system such as dBase-III. The full text is given as Appendix 2.

Each participant then presented his (her) own review paper on differences between tropical seas in terms of important ecological processes in coastal ecosystems. Group discussion followed each participant's presentation.

Following the presentations of papers, the workshop participants went to the USP marine research station 60 km south of Suva at Dravuni Island. Here we made dives at several sites in order for each of us to survey the same locations, then compare results and calibrate our scales of reference so that we could be confident that our discussions were from comparable points of reference. Although it would have been most efficient logistically to have worked on the outer reefs on our way in to Dravuni Island, in respect for local tradition and reef-tenure we went directly to Dravuni to meet with the chief and village elders to explain our intentions and ask permission to dive on their reefs. This formal ceremony is called the sevusevu. Miss Milika Naqasima, a participant from the School of Pure and Applied Science, USP, has written a description of the ceremony. This document is attached as Appendix 3.

Following our initial surveys of the reefs near Dravuni Island we noted that they were not as intensively overharvested as some other Pacific Islands, e.g., Truk and Guam. This may be largely a result of traditional control of reefs by the chiefs and elders of nearby villages. The night before we left Dravuni Island to continue our workshop back in Suva, we invited the chief and elders and their wives over to the research station for a dinner we prepared. During their evening visit we praised their adherence to traditional management of resources and expressed our hope that they will continue to use their resources wisely.

After three days of field surveys and evening discussions at Dravuni Island, the workshop participants returned to Suva for two days of intensive discussions. A summary of our collective findings as to significant differences between Atlantic and Pacific coastal ecosystems, the implications of these differences for tropical coastal resource management, and our recommendations for further research and for action by UNESCO are outlined below. The review papers and hypotheses of individual participants are then presented. It is hoped that they will be useful as a background for future research on this important subject.

C. Acknowledgements

At the end of the workshop, the participants expressed their appreciation to UNESCO/COMAR for taking an interest in this subject of regional differences in coastal marine ecosystems and for bring the participants together so that we could combine our information and work out a synthesis of our conclusions through direct discussion. We believe that this was a catalytic event that will produce printed results on several occasions in the future. We also thanked Dr. J.R.E. Harger, Programme Specialist in Marine Sciences at UNESCO/ROSTSEA, for coordinating the workshop. We acknowledged the University of the South Pacific (USP) for letting us use their facilities and Dr. Uday Raj, Director of the Institute of Marine Sciences (USP), for hosting the workshop. Particular gratitude was due Mr. Saran Singh who ably handled all the logistics, including the research vessel, our food and lodging for the 3-day fieldtrip to Dravuni Island, and the various office supplies and the conference room at USP.

Miss Milika Naqasima and Mr. Jon E. Brodie, both of the School of Pure and Applied Sciences (USP), participated in the workshop, and also facilitated our fieldtrip as guides and interpreter, by loaning us equipment, and by helping with logistics.

We particularly thank Angela Duenas for patiently typing the entire volume with additional corrections.

II. CONCLUSIONS OF THE UNESCO/COMAR WORKSHOP CONCERNING IMPORTANT DIFFERENCES AMONG TROPICAL SEAS IN TERMS OF ECOLOGICAL PROCESSES IN COASTAL MARINE ECOSYSTEMS

A. Rate of Nutrient Input

Geographic regions of the tropical seas can be characterized by a gradient of nutrient input with the regions highest in nutrient input influenced by upwelling (widespread in the eastern Pacific and found in areas off southern Indonesia, Somalia, and Venezuela), with the regions of intermediate characteristics being "continental" (the Caribbean and the S.E. Asian coast with a tongue extending out into the Pacific from the Malaysian Peninsula through Indonesia to include Papua New Guinea) and the regions of low nutrient input being the "oceanic" Pacific (Micronesia, tropical Polynesia, and eastern Melanesia). A transect on the Great Barrier Reef would probably fit on this gradient somewhere near "continental" (near the coast of Australia) and extend along the gradient towards "oceanic" (offshore reefs, e.g., Myrmidon). Enclosed lagoons of oceanic high islands obtain "continental" characteristics, perhaps because of increased residence time of water.

This quantitative gradient in rate of nutrient input among localities brings about qualitative differences among localities in the nature and relative importance of ecological processes such as recruitment, competition, predation and recycling which, in turn, bring about qualitative differences in the characteristics of the marine communities at different localities (reviewed by Birkeland, this workshop, with influences on an evolutionary scale reviewed by Vermeij and by Thresher, this workshop). These findings have important implications for resource management guidelines as will be noted in the next section.

A study of these differences among tropical seas could be developed as a circumtropical extension of the program conceived by the UNESCO/NSF workshop entitled "Factors influencing organic productivity in the Caribbean coastal zone: a research-planning workshop" which was held at Discovery Bay Marine Laboratory, Jamaica, 3-9 November 1985.

To directly assess the rate of nutrient input into coastal marine ecosystems by measuring water chemistry would be difficult because dissolved nutrients in the water column are ephemeral in time and localized in space. Comparing average nutrient levels or average levels of primary productivity may not give us useful information. The biological differences between high islands and atolls may result from occasional intense pulses of nutrients and concomitant pulses of productivity at the former, and not from average differences. These pulses may be very short, but the effects long lasting. For example, if a short pulse of nutrients stimulates a phytoplankton bloom that in turn facilitates a larger survivorship of larvae of Acanthaster planci, the second-order effect on the coral reef community of this plytoplankton bloom (and increase in larval survival of A. planci) may be evident for a decade or more. A forest fire may be easier to measure and more meaningfully measured by its effects than by direct measurement during its brief appearance.

The pulse of nutrients may occur briefly and not be detected by sampling. Rather than take water samples for nutrients or chlorophyll, it might be better to agree on some biological indicator that would integrate the effects of nutrients over time and incorporate any effects of brief pulses of nutrients that might occur during the time period. Some methods that may provide this sort of comparative measure would be an integration of the rates of biomass accumulations of fouling panels or an assessment of the growth of selected organisms (e.g., bivalve mollusks or ulvoid algae) that had been transplated to the sites under investigation. Fouling panels or selected organisms would have to be protected from grazing in order to assess the gross rate of growth. Unfortunately, the predator-exclusion cage adds a complicating factor because the "cage effect" is not a constant; it increases as a function of productivity (cages get fouled to a greater extent) and decreases as a function of grazing pressure (grazers can keep outer surfaces of cages clean). The grazing pressure could be assessed by having controls exposed to grazing.

Nutrients are also ephemeral in space insofar as being measurable as free reactive ions. The nitrates from groundwater seepage sometimes reach concentrations as high as 13.2 times the average concentrations in surrounding waters (FitzGerald 1978). But these nutrients are rapidly taken up by the biota or are diluted on the reef platform and these inputs are measurable on the reef platform no more than 10 m from the source (with instruments available at Water and Energy Research Institute, University of Guam, R. Clayshulte, pers. comm.). Although some nutrients are difficult to measure at low concentrations, the biological effects are easy to see. For example, the fan of Enteromorpha extending out from areas of groundwater seepage is obvious. Again, biological indicators such as fouling panels of selected organisms for growth in predator-exclusion cages may be more reliable than chemical analysis because of the ephemeral nature of dissolved nutrients in both time and space. Although they are ephemeral in their free state, the influence of a brief but substantial pulse may be felt for years. It might be suggested that we do not concentrate on averages from numerous spot-samples, but try to develop methods that integrate the effects of these irregular pulses into the measurements over longer periods of time.

In addition to fouling panels, methods of assay for productivity or rates of growth that integrate effects over time could include measurements of CNP in sediments, fluorescent light or x-ray examination of cores from corals, etc.

It was pointed out during discussion that we should recognize that the scale of effects of nutrient input are also along a continuum in time from the short-lived phytoplankton bloom in the water column, to succession of fouling communities, to community structure (large, slow-growing sponges or corals as compared to barnacles and filamentous algae), to effects over evolutionary time (such as egg volumes in confamilial fishes from different regions, cf. Thresher, this workshop).

Although the papers from different participants were from disparate scales of reference and independent topics, they each led to a common conclusion that fundamental differences between geographic regions of tropical seas may ultimately be linked through the common factor of nutrient availability. For example, geographic differences in nutrient availability may have strong influences on the evolutionary scale (e.g., differences in egg sizes of confamilial fishes in different oceans [cf. Thresher, this workshop] and as refuges from extinction for "highly escalated" species [cf. Vermeij, this workshop]), on the level of community structure and processes (e.g., intensity of predation, prevalence of species with r-selected vis-a-vis K-selected traits, and relative importance of the phytoplankton food-web in comparison with the benthic algal food-web [cf. Birkeland, this workshop]) and on the level of local variations in space and time (e.g., pulses of nutrient input can cause large fluctuations in abundances of species with planktotrophic larvae). By arriving at common causal mechanisms from disparate scales, perspectives, and approaches, the models were considered to be robust.

B. Temporal Instability (Unpredictability)

El Niño occurs on a frequency scale of tens to hundreds of years and its effects are felt across the tropical Pacific, most strongly in the eastern Pacific. The effects of El Niño are not as strong in the Caribbean as in the Pacific.

Typhoons (= cyclones, = hurricanes) appear to have greater effects on coastal marine communities in regions where typhoons occur less frequently. A supertyphoon (sustained wind speeds >150 miles hr^{-1} = 240 km hr^{-1}) with gusts in excess of 200 miles hr^{-1} (>320 km hr^{-1}) was documented to have had little effect on coral communities of Guam (Randall and Eldredge 1977; Ogg and Koslow 1978) where typhoons are relatively frequent, while typhoons at Belize, Jamaica, and the Great Barrier Reef have been found to cause severe damage to corals.

An examination of growth bands from coral cores may give comparative indications of environmental stability in different regions over a few decades.

On longer times scales, the central and western Pacific may be influenced to a lesser extent by glaciation as a result of the relatively large area and volume of the Pacific Ocean.

C. Size of Area

The tropical Pacific is over 10 times the area of the tropical western Atlantic. This buffers the spread of diseases (e.g., mass mortalities of Diadema and commercial sponges spread throughout the Caribbean, but mass mortalities of Echinothrix have been confined to the Hawaiian archipelago). The areal size of the tropical Pacific also buffers the effects of glaciation. There is less susceptibility to extinction in the Pacific because the populations are spread over a larger area and populations can be isolated, allowing pockets of survival when conditions change or a disease or a predator spreads.

D. Opportunity for Speciation

The large area of the tropical western Pacific compared with the tropical western Atlantic is perceived to be a major factor bringing about differences in rates of speciations and extinctions. The larger area of the Pacific water mass serves to buffer climatic changes and allows for isolation of populations. Isolation is important for speciation and also can buffer against extinction from biotic factors such as disease or predation. That the Malaysian, Indonesian and Philippine Archipelagoes are all interconnected on the continental shelf provides a mechanism for isolation and reconnection of biotas with changes in sea level. Oceanic archipelagoes may also undergo isolation and reconnection as current patterns change with changes in sea level. Greater rates of speciation and buffers against extinction produce a greater species diversity for most taxa in the Pacific.

E. Nature of Diversity

The within-habitat diversity (α diversity) of coral-reef fishes may not differ between the Caribbean and the central Pacific, but between-habitat diversity (β diversity) is greater in the central Pacific. There is less overlap between habitats in the Pacific. Although the α diversity (of fishes) may not be different between oceans, the β diversity is greater, so the total species diversity is considerably greater in the Pacific for most taxa.

The size of the tropical Pacific and the prevalent current patterns cause a decrease in diversity for many taxa from west to east across the Pacific. The relatively small area in combination with a consistent counterclockwise circulation pattern are considered important factors in causing the homogenity of the Caribbean biota.

F. Degree of Interconnection of Coastal Habitats

The literature implies that seagrass beds, coral reefs and mangroves have more trophic and population interconnections in the Caribbean than in the Pacific. This needs to be examined more thoroughly, especially in the Pacific. Is this another aspect of higher β diversity in the Pacific? The fewer interconnections between habitats in the Pacific is probably a major factor in bringing about a lower index of overlap in the Pacific.

There are no substantial seagrass beds in the eastern Atlantic, eastern Pacific, and south of the Amazon (except for *Syringodium*). Mangroves drop out eastward across Polynesia.

G. Degree of Coevolution

There are more kinds of close mutualistic associations in the Pacific than in the Caribbean (e.g., anemones with fish, bivalves with zooxanthellae, etc.). The degree of escalation between predator and prey is higher in the Pacific. Perhaps higher diversity and the factors favoring speciation are also favoring these aspects of community structure.

H. Taxa of Important Predators

Asteroids are influential predators of corals in the Pacific, but not in the Atlantic. Polychaetes (*Hermodice carunculata*) are predators of corals in the Caribbean, urchins (*Eucidaris thouarsii*) are very influential grazers on corals in the Galapagos, and fishes (*Arothron meleagris*), gastropods (*Jenneria pustulata*) and an asteriod (*Acanthaster planci*) are all influential in the eastern Pacific (except in the Galapagos).

Fishes are the most influential herbivores of macroalgae in the oceanic Pacific. Echinoids are often more influential in the Caribbean, but it is not certain whether this is a natural characteristic of the Caribbean or if this has been a relatively recent development, coming about as a result of overfishing by humans. Harger pointed out that echinoids are dominant grazers in continental regions of southeast Asia, particularly in regions of high nutrient discharges from major cities such as Jakarta.

I. Patterns of Reproduction

Reproductive patterns of marine organisms differ in some cases within species or within taxa in different geographic regions of the tropical seas. Many species of coral spawn synchronously in the Great Barrier Reef, but at separate times in the Red Sea (Richmond, this workshop). *Pocillopora damicornis* reproduces by fragmentation or by polyp bail-out in the eastern Pacific, but by planulation in the central Pacific (Richmond, this workshop). *Acropora* spp. generally recruit by fragmentation in the Caribbean, but frequently by planulation in the Pacific (Sammarco, this workshop). Confamilial fishes spawn smaller eggs in the Caribbean and mature at a smaller size in the Caribbean than in the Pacific (Thresher, this workshop). The nature of the reproductive processes in organisms has important implications for fisheries regulations and for methods of reestablishing populations in an area.

J. Traditional Rules of Exploitation by Humans

A previous UNESCO/COMAR workshop on traditional resource managment practices, held at the UNESCO/ROSTSEA in Jakarta, Indonesia, December 1983 (Ruddle and Johannes 1985) had noted (among other things) that traditional management of marine resources in the "continental shelf" part of Southeast Asia (eastern Indonesia and Thailand) appeared to be weaker than in the central Pacific. Exploitation of fishes, sea turtles, and other marine resources have been strictly controlled and managed by social protocol systems, traditional fishing rules, and reef tenure systems on atolls and high islands of Oceania. Traditional rules of reef tenure and coastal resource management may be stronger in the oceanic islands of the Pacific than in the Caribbean. Whether this is because European influences disrupted traditional systems in the Caribbean hundreds of years before their influences were felt at the smaller Pacific islands, or whether the traditional systems for marine resource management were not as strong in the Caribbean even before the European influence, is not known.

At the workshop discussion at Dravuni Island, Chansang pointed out that fisherman along the coast of Thailand, and perhaps along most of the coasts of S.E. Asia, had been exploiting the coastal resources in a free-for-all manner, not under a strong family or village coastal tenure system, for hundreds of years and perhaps always. Birkeland insisted that strict and complex systems of marine resource utilization are found on atolls such as Ulithi. It was becoming clear in the discussion at Dravuni that marine resources of continental coasts have long been used for barter for terrestrial produce while marine resources on atolls have traditionally been partitioned for their own sake by strict protocol. Thresher suggested turning this relationship around and considering a possible causal relationship between productivity and traditional management. Human societies may have evolved strict systems of tenure and protocol for management of marine resources in regions of low nutrient availability and recycling of materials, while societies have tended to evolve free-for-all systems of utilization and barter in regions of nutrient input (terrestrial runoff or upwelling) and high productivity. The "Dravuni Hypothesis", as it was subsequently called, is worth examining because it has important implications for marine resource management, sociology, and economics.

It may be that even in areas of higher productivity, fisheries rules are developed when human population pressure increases relative to the resource supply and when the economy becomes money-based. Japan has traditional coastal land tenure regulations. New reef tenure rules are being created in the Caribbean where reef resources are being exploited for trade.

Another way by which effects of increased human exploitation pressure could differ between geographic regions is by modification of fishing techniques. As human populations increase and large piscivorous fishes become overexploited on Caribbean reefs, local fishermen may tend to shift to obtaining benthic fishes by traps while in the western Pacific, fishermen may tend to shift to obtaining midwater column fishes by nets from the surface. The differing second-order effects of removing different components of the reef-fish communities in different geographic regions is important to assess.

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III. IMPLICATIONS FOR RESOURCE MANAGEMENT GUIDELINES

Fundamental differences in community dynamics of comparable coastal ecosystems in different geographic regions of the tropics have important implications for proper resource utilization. One cannot necessarily generalize successful resource management policies or guidelines from one geographic region to another. Because of the rapid population growth in tropical countries, it is an urgent matter to develop a theoretical framework which would be the basis for development of rational management programs for tropical coastal resources. It has been a general objective of science to find generalizations, but it could be a serious mistake to generalize management techniques where different ecosystem processes prevail.

A. Rate of Nutrient Input

Coral reefs have higher rates of productivity per unit biomass than do many other communities. Yet coral reefs are frequently and easily overfished. Although coral reefs are very productive, they cannot withstand much export of harvest. The problem appears to be that the rate of nutrient input into a coral reef ecosystem is low, at least at oceanic islands and the central Pacific atolls, and these nutrients are recycled, not exported. Nutrients are recycled at the physiological level in symbioses, at the community level in detrital food webs, and at the regional level by currents.

Resources may be commercially exploited from systems such as tuna fisheries where there is a regular input of nutrients by upwelling. Atolls can support a resident human population with a fisheries if the fishes are used for subsistence and waste products are recycled into the lagoon, but the atoll can be quickly overexploited if the resources are exported rather than recycled. Oceanic reefs, like tropical rain forests, should be pruned and recycled, not harvested and exported.

Dynamiting of coral reefs for fishes may have substantially greater long-term effects on oceanic reefs than on benthic communities near regions of upwelling because it may take a longer time for regions of damaged coral reef to build up a stock of nutrient materials.

Conversely, eutrophication via sewage may alter the normal system in atolls or oceanic reefs more than in lagoons of high islands, near mouths of rivers, or in regions of upwelling. Eutrophication could be expected to lead to an increase in the phytoplankton-based food-web at the expense of the benthic-algal-based foodweb and to increased growth rates of sponges and bivalves and to increased bioerosion rates of reef-building corals. An increased rate of nutrient input from terrestrial runoff may increase the frequency of red tides and outbreaks of creatures with planktotrophic larvae such as Acanthaster planci. It is important for planners to understand the local and regional effects of sewage output and land-clearing.

Large rivers are a major source of nutrient input and thus have a major influence on tropical coastal ecosystems.

When the Aswan Dam went into operation, the fisheries yield in the Mediterranean immediately dropped to 3.7% of its former level (Aleem 1972). Again, the effects of a river dam may differ between regions. The effects of the Burdekin Dam on the biota of the central Great Barrier Reef will be interesting to document.

B. Temporal Instability (Unpredictability)

An understanding of regional differences in susceptibility of coastal resources to disturbance by irregular events such as typhoons or El Niño events is important in estimating the degree of exploitation a resource can sustain. Disturbances such as El Niño and typhoons are periodic occurrences in some areas and must be considered in management plans.

C. Size of Area

Diseases ard introduced species are more likely to spread rapidly throughout the Caribbean and more likely to be restricted to separate archipelagoes in the central Pacific. This is because of the relative distances involved. Conversely, if a species is eliminated from a particular archipelago in the Pacific by disease or overexploitation, it may have less chance of becoming naturally reestablished because of distances from other populations.

D. Opportunity for Speciation

E. Nature of Diversity

F. Degree of Interconnection of Coastal Habitats

G. Degree of Coevolution

Ecological theory would predict that species introduced from regions with higher diversity, with greater predator-prey escalation, and with more complex associations would be more likely to be successful and to significantly affect communities in the region into which they were introduced. It might be predicted that introductions from the Pacific to the Atlantic (e.g., Acanthaster, sea snakes, etc.) would tend to have greater effects than introductions from the Atlantic to the Pacific. An alternate hypothesis is that the effects of introduced species can only be judged in terms of individual species and their region of origin is of no consequence. The latter hypothesis must not be ignored.

Populations in regions of lower β diversity or more interconnections of habitats might be able to recover more easily from catastrophic disturbances or local extinctions by immigration from surrounding habitats.

H. Taxa of Important Predators

A knowledge of which taxa are influential in a region is important for predicting effects of events. For example, if a disease causes mass mortality of regular echinoids in the Caribbean, there will be a significant increase in the standing stock of benthic algae; if a disease causes mass mortality of regular echinoids in Oceania, we might not expect an increase of comparable magnitude in the standing stock of benthic algae.

I. Patterns of Reproduction

Relative success of recruitment by asexual versus sexual processes is an important factor on coral reefs which exhibits regional differences. This factor is important to understand when an attempt to manage or reestablish a coral population is to be made. Differences in reproductive patterns among populations of confamilial fishes is important for developing fisheries management plans.

J. Traditional Rules of Exploitation Pressure by Humans

Relative merits of different systems of resource management under different environmental conditions need to be studied. It is probably unwise to attempt to generalize one system of resource management to be utilized in all tropical coastal regions. Local traditional systems of resource management should be studied for insight into their operational benefits before they are lost in the transformation to modern western societies.

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IV. RECOMMENDATIONS

Tropical coastal ecosystems are among the most productive ecosystems in the world in terms of gross primary productivity. A large number of communities in the tropics exist on islands, and 90% of the protein for small island populations comes from coastal marine ecosystems (Johannes 1977). Most tropical countries are still developing their strategies of resource exploitation. It is most important to have a fundamental understanding of the dynamics of ecosystem productivity and organization as bases for policies of resource management and utilization. Because of rapid development and population growth in tropical countries, the development of a theoretical framework is an urgent matter. It is to this end that UNESCO/COMAR sponsored this workshop.

The following are the major recommendations made to UNESCO by the participants in the workshop.

Recommendation 1: UNESCO should promote cooperative efforts among bilateral and international programs already in existence enabling these programs to integrate their resources into a project establishing rational management programs that take into account important differences in ecological processes among comparable habitats in different geographic regions.

This report presents an outline of findings which suggest that differences in ecological processes among tropical coastal regions require different management policies be applied to these different regions. These findings serve as a basis for developing a framework on which a number of large-scale bilateral programs already in existence could be integrated. We recommend that resources of these bilateral and international programs be coordinated in a cooperative effort to establish rational management programs for tropical coastal resources that take important differences in ecological processes among these regions into account. UNESCO is in an ideal position to promote cooperation between agencies dealing with the development of coastal resource management (e.g., international programs such as IOC and UNEP and countries such as the U.S.A., Australia, Canada and Japan which have bilateral programs). We strongly recommend that UNESCO take the lead in initating such cooperative programs.

Recommendation 2: UNESCO should initiate a broad-scale program in the Pacific complementary to the UNESCO program in the Caribbean.

In particular, UNESCO/NSF sponsored a research-planning workshop entitled "Factors influencing organic productivity in the Caribbean coastal zone" at Discovery Bay Marine Laboratory, 3-9 November 1985. In this workshop, a research plan was formulated to assess productivity gradients in the Caribbean, to identify mechanisms underlying differences in productivity along the gradients, and to assess the interconnectedness of coastal marine habitats. These gradients in productivity within the Caribbean are suggestive of the apparent gradients in nutrient input among the tropical seas of the world, except on a smaller domain. The nutrient input in the coastal waters of the Caribbean is probably less than that in the upwelling regions of the eastern Pacific or in the coastal waters of S.E. Asia, and is probably more than in the waters around the atolls in Oceania.

A cooperative program should be established at sites of elevated nutrient input (Gulf of Panama, Smithsonian Tropical Research Institute; Ambon Bay, Pattimura University; Ko Phi Phi Don, Phuket Marine Biological Center) and at sites of lesser rates of nutrient input. Now that the laboratory at Enewetak is closed, there are no laboratories in continuous operation on a true atoll. The University of Guam Marine Laboratory could monitor sites on an oceanic high island which probably receives less nutrients on the average than most regions of the Caribbean. Atolls in close proximity to the high island of Pohnpei, Truk, and Belau might be considered as areas to work from. The Museum National d'Histoire Naturelle, Ecole Pratique des Hautes Etudes, has a field station on the raised atolls of Takapoto in the Taumotu Archipelago, a region of low nutrient input.

Long-term comperative data sets are noticably nonexistent. All that are available now are "snapshots". These "snapshots" surveys have a high probability of representing atypical times. Conversely, even if the samples come at times that are typical and reflect average conditions, a short-term irregular event such as a nutrient pulse could have long-term second-order effects on community structure. Therefore, data should be collected with measurements that integrate effects of nutrient input over time.

Recommendation 3: UNESCO should utilize a widely accessible international data base for the compilation of the data for this program.

This matter is discussed in Appendix 2.

Recommendation 4: Information should be obtained on the traditional methods of resource management under different regional environmental conditions.

Are strict systems of reef tenure developed by societies in environments with low rates of nutrient input, while less structured systems of marine resource utilization are practised in areas with high rates of nutrient input into the coastal marine ecosystems? Are new systems of reef tenure and rules of resource utilization adapted to the particular environmental conditions of the region? How effective are different reef tenure and resource management schemes in providing a sustainable yield? How do factors such as nutrient input, resource exploitation and population levels affect resource availability? This effort must involve a long-term circumtropical study of not only traditional resource management practices by indigenous peoples, but also an investigation of the biological and physical factors that determine these patterns of resource utilization.

It is urgent that information be obtained on these matters. As populations of small islands grow and change from subsistence to money-based economies, the traditional management policies may become impractical and be abandoned. The successful traditional systems for resource management that have been refined over hundreds of years of trial-and-error may be appropriate for marine resources in the environment where the society exists. The new management policies being developed for monetary gain may be impractical. While we do not suggest that islanders should refrain from participating in the international economy as the opportunities arise, a reliance of an island economy on foreign markets is based on a faith in an expanding world economy. To abandon the traditional expertise of their elders in resource management and utilization policies would be a commitment and faith in a healthy world economy and a gamble that marine resources in their ecological setting could withstand their new exploitation strategies. This would be burning the bridges for returning to partial self-sufficiency of island communities if their faith in the world economy was not upheld and their resources could not sustain an export economy.

It is also urgent to obtain such valuable historical information from islanders before it dissipates as the elderly pass away. It would be wasteful for scientists to ignore the rich and sophisticated working knowledge of fishing and resource management practises that islanders have acquired over hundreds of years of use. Dr. R.E. Johannes, a widely recognized and productive marine biologists, stated that by interviewing local fishermen he "....gained more new (to marine science) information during sixteen months of fieldwork using this approach than.... during the previous fifteen years using more conventional research techniques" (Johannes 1981: page x).

All this new (to science) information helps to remind us that while the scientific method is the best procedure known for objectively testing hypotheses, it is a ponderous and usually biased procedure for generating hypotheses. If we try to obtain a new hypothesis by discerning new casual relationships through multifactorial analysis, stratified sampling, or controlled experiments, the relations we observe are restricted to those variables that we select ahead of time and between scales in time and space that we decided upon ahead of time. New hypotheses fit within established paradigms. We dismiss results as variance or as results of a poorly-run experiment when they do not seem to fit our a priori alternatives. The wisdom and expertise of artisanal fishermen evolved independently of science and the accuracy of their predictions have been tested by success in everyday life over hundreds of years. While we cannot formally accept them without rigorous testing, the generalizations obtained from local fishermen were derived unbiased by established paradigms of science and may be especially productive for providing new insights.

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NUTRIENT POOLS AND DYNAMICS IN TROPICAL, MARINE, COASTAL ENVIRONMENTS, WITH SPECIAL REFERENCE TO THE CARIBBEAN AND INDO-WEST PACIFIC REGIONS

by

W. J. Wiebe*

ABSTRACT

A review of the literature shows that our understanding of the nutrient dynamics of coral reefs, seagrass meadows, and mangrove forests is very incomplete. Our comprehension of the nutrient dynamics of tropical coastal ecosystems may be severely distorted by lack of data on temporal and spatial variability. Geographical breadth of investigation is lacking; a network of study sites is suggested for comparative studies to resolve conflicting results from different regions and to bring order to the field. Data available in the literature imply that there is only a limited exchange of nutrients between adjacent tropical coastal systems. Because coral reefs, seagrass meadows, and mangrove forests are often found in close proximity, it has been suggested that each requires the other in some way. It there is a necessary interaction, it is more likely to be one of buffering the upstream, ultimately the terrestrial, imports. Each system acts as a filter for the downstream one, essentially removing nutrients rather than exporting them. There are a number of mechanisms by which reef biota acquire fixed nitrogen and there is active internal recycling, including denitrification, within the reef lagoon. There is little evidence that nitrogen limits primary production on reefs, while under some hydrographic circumstances phosphorus may be limiting. Phosphorus increases may contribute more than nitrogen to eutrophication. Increased nutrients lead not to increased production by the resident biota, but rather to a successional shift to fleshy algae and a reduction in coral growth.

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*Department of Microbiology & Institute of Ecology
University of Georgia
Athens, Georgia 30602

INTRODUCTION

Tropical coastal ecosystems comprise roughly one-third of the shallow-water coastline of the earth (15% coral reefs [Smith 1978]; 9% mangroves [Rodin et al. 1975]; 9% tropical seagrass meadows [assumed equal to mangrove area]). These systems may exist in isolation or they may be associated with each other. Large human populations from mostly developing nations inhabit these areas. The coastal boundaries are exploited for urban development: industries (including shipping), tourism, and by the local populace (who use them for recreation, food and profit, e.g., shells, coral, wood). In most countries there is little management employed and little protection from these practices (see for example UNESCO Reports in Marine Science 8, 9, 16, 17, 18, 23, 24, 27; Gomez 1983; Thorhaug 1981; Thayer et al. 1975; Maragos 1985; Lal 1984).

One reason for the lack of sound management is that despite their quantitative significance, tropical coastal ecosystems have been inadequately studied individually and almost not at all as interactive systems. The result is that even where management is attempted, decisions must be made using grossly incomplete information. One important aspect of understanding how these systems function involves their biogeochemical cycling and inorganic nutrient status and transfers. In this paper I want to review what is known about the biogeochemical nutrient pools and dynamics in each of three systems (coral reefs, seagrass meadows, and mangrove forests), and examine what evidence exists that the systems, where they are physically associated, interact.

WHAT WE KNOW ABOUT NITROGEN, PHOSPHORUS AND OTHER NUTRIENT DYNAMICS IN TROPICAL COASTAL ECOSYSTEMS

A. General

Almost without exception, studies on all three systems have been conducted at few sites, on short-term expeditions. There is a noticeable deficiency of both replication and detail. We lack seasonal observations, statistical validation of data from individual sites and data from a range of sites. It is important to recognize these problems, because our view of these systems could be greatly distorted by these limitations.

B. Coral Reefs

Coral reefs have intrigued scientists for over a century. They thrive in tropical waters noted for their low nutrient concentrations and lack of planktonic biota. Yet the gross production of coral reefs is among the highest of any ecosystem, including agricultural ones. Nutrient studies have been concentrated on discovering how reefs acquire and maintain fixed nitrogen and phosphorus. As we shall see, this may have been a misleading approach.

The nitrogen cycle on coral reefs has been reviewed recently by Wiebe (1985, in press). Three processes, nitrogen fixation, nitrification and denitrification, appear to be the most likely processes that control nitrogen availability.

Nitrogen fixation is a major source of fixed nitrogen on almost all reefs that have been investigated. The geographical coverage of the data is probably better for this process than it is for any other process or system. Reefs examined include atolls and fringing reefs, reefs in the Indian and Pacific oceans and the Caribbean Sea, and across the latitudinal extent of reef growth. It is a ubiquitous process, occurring most intensively on the windward sides of atolls and the forereef of fringing reefs. One example of the complexity in the control of this process is provided by Wilkinson and Sammarco (1983), who demonstrated that fish grazing can affect the rate of nitrogen fixation.

In addition to nitrogen fixation we now recognize several other sources of fixed nitrogen for reefs. Tropical upwellings (Kimmerer and Walsh 1981), internal waves (Andrews 1983), terrestrial runoff (Marsh 1977), groundwater (D'Elia et al. 1981) and endo-upwelling (Rougerie and Wauthy 1986) can contribute fixed nitrogen to reefs. The importance of each of these sources depends upon the geographical and geomorphological setting of the reef.

Nitrification appears to be a major process in reefs, with nitrate increasing across windward reefs flats toward the lagoon or shore (e.g., Webb et al. 1975; Webb and Wiebe 1975; Adey and Steneck 1985). Recent studies on nitrogen recycling (Szmant-Froelich 1983) and translocation (Meyer et al. 1983) have suggested the importance of fish in nitrogen dynamics, including stimulation of nitrification.

Recently, denitrification has been identified as a quantitatively important process within some reef systems. Seitzinger and D'Elia (1985) found low rates of in situ denitrification in a reef lagoon in the Bahamas; however, they suggested that, given the size of the lagoon, these low rates could equal the rate of fixation. Smith (1984) argued from sediment N:P ratios that denitrification occurs in the several lagoons that he had studied and, given the size and configuration of the lagoons and the negligible output of fixed nitrogen from the systems, it probably balanced the nitrogen fixed.

In summary, there are a number of mechanisms for reef biota to acquire fixed nitrogen and there is active internal recycling, including denitrification, within the reef lagoon.

Phosphorus is the other elemental nutrient about which there is broad geographical information. Unlike nitrogen, there is no atmospheric source (other than anthropogenic) for phosphorus. Concentrations in tropical waters are generally very low (Crossland 1983). Upwelling, internal waves and terrestrial runoff are possible sources of phosphorus, as they are for nitrogen, but the actual magnitudes have not been well-documented (see D'Elia [in press a, b] for a recent review of phosphorus dynamics on coral reefs).

In contrast to nitrogen, Pilson and Betzer (1973) could find no net flux of phosphorus across the windward reef at Enewetak Atoll. These results tended to confirm and broaden earlier studies suggesting that there was a particularly well-adapted community retention and recycling of phosphorus. However, Pomeroy et al. (1974) at the same time examined the exchange of ^{32}P-phosphorus in a variety of the system components, including cyanobacterial mats, calcareous algae, rubble communities and several coral species. They concluded that there were no special mechanisms developed to deal with the low concentrations of phosphorus in reef waters, except that found in the symbiotic corals; the principal reef communities were not limited by the supply of phosphorus.

More recently, Atkinson (1981, 1983) has shown that uptake or release of phosphorus across a windward reef flat in Hawaii depended in large part upon the incoming concentration. Similarly, Johannes et al. (1983) found that phosphorus and some nitrogenous compounds showed net flux characteristics that were dependent upon the incoming concentration. Adey and Steneck (1985) also found variable fluxes for phosphorus in reef flats in St. Croix, Virgin Islands. Interestingly, corals may contain within their skeletons a history of the phosphorus concentrations in water (Dodge et al. 1984). This may be of value in ascertaining long-term trends of phosphorus concentrations. At high phosphorus concentrations, calcification is inhibited (Kinsey and Davies 1979), although the mechanism is unknown.

There has been considerable speculation and some investigation concerning nutrient limitations to primary production of reefs. Birkeland (1984), in discussing this problem, stated that "Essential nutrient materials, not energy, must be limiting". However, the most recent consensus suggests that in most systems neither nitrogen nor phosphorus is limiting. Crossland and Barnes (1983) examined the flux of nitrogen, phosphorus, silicate, organic nitrogen and organic carbon across the entire reef system at Lizard Island, Great Barrier Reef, Australia. They found essentially a zero flux of any of these materials. While there were local depletions or releases within the different subsystems, these were balanced by subsequent releases or depletions downstream. This study emphasizes one of the difficulties in dealing with flux measurements: often they are made on only part of the system and the results are extrapolated to the entire system.

Smith (1984) has examined nitrogen and phosphorus budgets for several entire reefs and concluded that "If hydrodynamic fluxes are small, then biochemical fluxes of nitrogen are likely to obviate any limitation, while phosphorus is exhausted. If hydrodynamic fluxes are large, then neither biochemical fluxes nor hydrographic supply of either nitrogen or phosphorus is likely to limit net ecosystem production of organic matter." Rayner and Drew (1983) reached a similar conclusion based on an examination of reef structure. Adey and Steneck (1985) examined nutrient dynamics on several transects across fringing reefs at St. Croix, U.S. Virgin Islands, over an entire year (January, May, August, October). They found that nitrate (+ nitrite) was exported across all reefs at all times of year except August, where mean values of fore and back reef stations were virtually identical, 0.572 and 0.599 µM NO_3+NO_2-N ℓ^{-1}, respectively. The yearly integrated means were 0.283 and 0.512 µM NO_3+NO_2-N ℓ^{-1} for fore and back reefs, respectively.

Phosphate showed a less consistent pattern, with one transect always showing a net release while the other three transects showed net uptake. There was some evidence that uptake or release was a function of incoming concentration. They concluded that phosphorus, although in low and variable concentrations, was not limiting primary production. Grigg et al. (1984) summarized their extensive study by suggesting that nutrient concentrations per se probably do not limit primary production of the French Frigate Shoals, Hawaii, system. Rather, these coral reefs are operating near their upper metabolic limit.

Recently Smith (in press) concluded that entire coral reef systems produce <u>new</u> carbon at a rate only slightly higher than the surrounding plankton communities and that coral reefs have very limited metabolic interaction with the surrounding ocean. This view is of particular importance, because it places coral reefs in the context of other shoal-water systems (see also Nixon et al., in press).

Thus, the picture that has emerged over the past 10-15 years is that coral reef systems function not in some unique metabolic way, but rather represent one end of a continuum of shoal-water systems. We will discuss some implications of this subsequently.

Several investigators have found that phosphorus, but not nitrogen, enrichments to reefs or reef microcosms increases instantaneous primary production rates, but changes the community to an algal dominated one (Kinsey and Domm 1974; Kinsey and Davies 1979; Evans 1977). These studies suggest that where nitrogen concentrations are naturally elevated, care should be taken to prevent phosphorus inputs. Interestingly, these authors found that the effects of phosphorus enrichment were maintained for a month or longer after fertilization ceased, suggesting that phosphorus is more tightly recycled than nitrogen.

Finally, a statement in UNESCO Reports in Marine Science (No. 23, 1983) deserves mention: "The best coral reef development is always found on the direct and most nutrient-poor Caribbean coasts" (page 7). While I do not believe that this statement has been rigorously tested, it probably represents the consensus of feeling among investigators; the accumulating evidence supports this idea.

In summary, there is little evidence that nitrogen limits primary production on reefs, while under some hydrographic circumstances phosphorus may be limiting. More importantly, phosphorus increases may contribute more than nitrogen to eutrophication. Increased nutrients lead not to increased production by the resident biota but rather to a successional shift to fleshy algae and a reduction of coral growth. One final point. As Entsch et al. (1983) have discussed, nitrogen and phosphorus are not the only possible limiting nutrients. These authors make an excellent case for iron limitation. While I am unaware of any subsequent studies, these data deserve consideration, along with an examination of other trace metals, e.g., Howarth and Cole (1985) suggested that a molybdenum deficiency in sea water is responsible for reduced nitrogen fixation.

C. Seagrass Meadows

Seagrasses consist of twelve genera of aquatic angiosperms. They are widespread from the tropics to the sub-boreal seas and rank among the most productive systems on earth. Much of the work on seagrass nutrient cycling has been done in temperate systems; this work will be discussed here only as it may relate to tropical situations.

Nitrogen studies of tropical seagrasses have focused on _Thalassia testudinum_ in the Caribbean. There is abundant evidence that nitrogen fixation can take place on leaves and within the rhizosphere (summarized by Capone 1983). As reviewed by Paerl et al. (1981), _Thalassia_ root and shoot nitrogen fixation rates range from negligible to greater than 100% of the plant requirements of nitrogen. Capone et al. (1979) found a direct relationship between nitrogen fixation and primary productivity in _Thalassia_ communities. They also suggested that leaves and roots may represent rather separate systems regarding nitrogen fixation. McRoy et al. (1973) reported zero to trace amounts of nitrogen fixation for *Syringodium filiforme* from Florida and very low rates for adjacent *Thalassia*. They concluded that nitrogen fixation could not supply the required nitrogen necessary for growth. It is not known whether these differences in results are caused by higher ambient inorganic nitrogen concentrations, advection of particulate material into the seagrass beds or some other factor.

As reviewed by McRoy (1982), there is a definite relationship between the depth of the organic sediment layer and the type of vegetation present in the Caribbean. In areas where the organic sediment is less than four cm deep, rhizophorous algae dominate. *Syringodium* requires about seven cm deep organic sediments, and *Thalassia* requirements are greater yet. Each system increases the root depth; this appears to be related to nutrient requirements and the modes of uptake. Blackburn (pers. comm.) showed that there is active recycling of ammonium in sediments of several types of seagrasses and that much of this material is retained within the system. Zieman et al. (1984a) found that ammonium concentrations within sediments of *Thalassia* beds were reduced by grazing of sea urchins and turtles. When the sediment values reach a level that reduced the nitrogen content in the leaves, grazing decreased dramatically. These studies suggest that at least in some regions, fixed nitrogen is important for seagrass growth.

Rates of denitrification in *Thalassia* sediments have been measured by Patriquin and Knowles (1974), but their technique does not permit extrapolation to the field. In Hattori's 1983 review of marine denitrification, no tropical seagrass sites are reported. It appears that the examination of this process needs urgent attention as does work on nitrification. Denitrification is likely to be important in *Thalassia* beds, since one requirement for their growth appears to be anoxic sediment (McRoy and Lloyd 1982); active sulfate reduction has been reported in *Zostera capricorni* beds (Moriarty et al. 1985).

Phosphorus has been shown to be taken up by both leaves and roots of *Zostera marina* (McRoy and Barsdate, 1970), but it appears that most of the phosphorus in *Thalassia* is taken up via the roots (e.g., Patriquin 1972). Given that sulfate reduction occurs in these sediments, there should be available inorganic phosphate. Of interest in this regard is the work of Zimmerman and Montgomery (1984). They found that transient drift algal mats of *Microcoleus* in the Indian River lagoon, Florida, were trapped within seagrass beds and raised pore water nutrient concentrations of ammonium to 300-900 $\mu M\ NH_4\text{-}N \cdot \ell^{-1}$ and 20-200 μM dissolved reactive phosphate $\text{-P} \cdot \ell^{-1}$. They suggested that these periodic inputs cause build-ups of nutrients that are exploited by the seagrasses over time and that these periodic buildups represent an important mechanisms for the grasses to acquire nutrients.

There has been considerable work done on the effects of added nutrients to seagrass systems. Modest enrichment appears to stimulate growth. However, high concentrations have a deleterious effect, partially explained by the reduction of light to the seagrasses. As Williams and McRoy (1982) have demonstrated for six seagrasses, including _Thalassia_, light saturation irradiances are greater than 40% of the surface irradiance. Thus, reduction of light by plankton and epiphytes could reduce seagrass growth. With the temperate, aquatic, vascular plants _Potamogeton perfoliatus_ and _Ruppia_ _marina_, Twilley et al. (1985) showed significantly reduced growth due to phytoplankton shading. Epiphytic shading has also been postulated to reduce seagrass growth (e.g., Cambridge and McComb 1984). In this sense seagrasses appear to do best in mesotrophic systems, where nutrients are higher than found in coral zones, but much less than those found in mangrove forests (see the next section).

In summary, what few data exist demonstrate that nitrogen fixation can take place in seagrass beds, but may not always do so, and that moderate or pulsed inputs of nutrients may stimulate plant growth while continuously higher concentrations act to reduce growth due to shading by the growth of epiphytes and plankton. With regard to shading, Phillips (1980) has noted that both _Thalassia_ and _Halodule_ can be debilitated by sediment accumulation with even modest dredging. Work is needed on denitrification rates in order to understand the dynamics of the nitrogen cycle in these systems. Perhaps even more than in coral research, work on seagrass nutrient cycling has suffered from short-term expeditionary examinations. S.L. Williams (West Indies Laboratory, St. Croix, U.S. Virgin Islands [pers. comm.]) is just finishing the first long-term (5-year) study of _Thalassia_ nutrient dynamics, including studies on fertilized plots. One significant result is that some effects of nutrient perturbations can take several years to see. We will discuss some implications of this observation later.

D. Mangrove Forests

Mangrove forests are found along most tropical coastlines. They represent a large group of plants: 35 families, 61 genera, and 108 species of mangroves have been identified (Chapman, 1984). They grow in intertidal zones that range from almost fresh water to hypersaline sea water. They are found as forests covering thousands of hectares and as isolated colonies of a few trees along the shore or on coral cays. It is thus difficult to generalize about these systems in any respect. Added to this, by far the major amount of work at all levels of organization has been done on two genera, *Rhizophora* and *Avicennia*. The study of microbial processes and biogeochemical cycles within these systems has been extremely sparse and the literature is scattered.

Mangroves live in highly reduced, anaerobic soils generally, although there are exceptions. Sediment nutrient concentrations tend to be higher than those in seagrass beds, but there is some overlap of values in the literature. A number of studies have been done on nitrogen fixation in these systems. Root and litter-associated nitrogen fixation have been found in *Avicennia marina* roots and rhizospheres in New Zealand (Hicks and Sylvester 1985), Florida (Zuberer and Silver 1978, 1979), Israel (Potts 1984) and Aldabra Atoll (Potts and Whitton 1977); on the roots of *Rhizophora mangle* in Puerto Rico (Coker and Gonzalez 1960); within the bark of *Bruguiera gymnorrhiza* in Japan (Uchino et al. 1984) and associated with decaying red mangrove (*R. mangle*) leaves (Gotto and Taylor 1976). There are not enough data to calculate the nitrogen contribution to the system, but the general consensus is that the effects are probably local rather than system-wide (Potts 1984).

While there have been measurements made of pools of nitrogen compounds in a variety of mangrove soils, very few studies have dealt specifically with the processes in the nitrogen cycle. Nedwell (1975) examined the effect of sewage effluent in a *Rhizophora mangle*, *Rhizophora stylosa* and *Bruguiera gymnorrhiza* mangrove forest in Fiji. He found that only ammonium was utilized in the water column and that nitrate was denitrified within the sediment. He suggested that mangrove forests might be used as "cheap tertiary treatment" plants to reduce coastal eutrophication. Boto and Wellington (1983) found that several *Rhizophora* species were nitrogen-limited at all elevations, while phosphorus limitation existed only at the higher elevations. They also found that mature leaves reflected the sediment nutrient status and that they might be useful indicators of overall nutritional status of the mangrove forests.

Boto and Wellington (1984) also found that good growth of several species of *Rhizophora* was positively related to extractable sediment phosphorus and to low redox, and negatively correlated with salinity. They found no relationship with ammonium concentration. However, Boto et al. (1985) found that *Avicennia marina* had a crucial requirement for nitrate. Seedings grown in pots for 63 days in $^{15}\mathrm{NH}_4^+$ enriched anaerobic soil showed a 50% reduced uptake of nitrogen when the nitrification inhibitor, N-serve, was added to the soil. While no explanation was given for these results, they certainly deserve further investigation in view of the widely held opinion that nitrate represents only a very minor source of nitrogen in anaerobic sediments. These data point out that we have much to learn about nutrient processes in anaerobic soils.

One major biogeochemical process that should occur in many parts of mangrove soils is sulfate reduction. Nickerson and Thibodeau (1985) found that the distribution of *Rhizophora mangle* and *Avicennia germinans* were closely related to the amounts of hydrogen sulfide in soil, with *R. mangle* confined to low to moderate concentration zones and *A. germinans* tolerating very high concentrations immediately beyond their root zones. There was evidence that *A. germinans*, but not *R. mangle*, could modify the H_2S concentrations immediately adjacent to their roots. There are few other measurements of H_2S concentrations and none on rates of formation of which I am aware. Certainly this microbial process deserves much further attention. Jacq (1981) has looked at mangrove sulfur metabolism from another standpoint, what happens when mangrove soils are used for rice culture? He found a rapid decrease in pH to ~ 3, due to the bacterial oxidation of pyrite and other reduced sulfur compounds, when the system became aerobic. This suggests that in addition to organic matter, reduced sulfur is also stored within the soil in significant concentrations.

There have been several studies of leaf decomposition. Fell and Masters (1980) found that a sequence of fungi occurred on decaying *Rhizophora mangle* leaves and that the fungi were responsible for nitrogen immobilization. Ulken (1984) has summarized the literature on this topic. Kuthubutheen (1984) reported over 40 fungal species associated with living leaves of *Avicennia alba* and *Rhizophora mucronata*. Matondkar et al. (1980) reported high numbers of bacteria and fungi in mangrove water and sediments that can serve as inocula for leaf decomposition. Benner and Hodson (1985) found that *R. mangle* leaves at Andros Island, Bahamas, leached rapidly upon death and that this material was mineralized by the microflora with a 30% efficiency aerobically. The lignocellulosic component was mineralized at one-tenth this rate. Under anaerobic conditions the rates decreased 10-30 fold. The results of Boonruang (1984) with *Rhizophora apiculata* and *Avicennia marina* leaves in Thailand, incubated under aerobic conditions, were essentially the same as those in Benner and Hodson (1985); 40-50% of the organic carbon was lost in 20-40 days. Similarly, van der Valk and Attwill (1984) measured a 50-60% loss of *A. marina* leaf dry weight in 50 days in a Westernport Bay, Australia mangrove forest. In summary, leaching over a period of about three to four weeks removes 40-60% of the dry weight of mangroves leaves. The remaining structural material decomposes much more rapidly under aerobic than anaerobic conditions.

There have been several studies of carbon and nutrient import and export from mangrove forests. It is a generally held belief that mangroves export inorganic and organic nutrients and that they are responsible for increased productivity of the downstream systems (e.g., see the discussion of this topic by Nixon et al. 1984). But this is not supported by the data. Golley et al. (1962) reported a P/R ratio for a Rhizophora mangle forest in Puerto Rico of 0.9 in May. There were no seasonal data and there are no other comparable data of which I am aware, but if the yearly P/R is ~ 1 there cannot be, by definition, much net organic matter export from the system. Boto and Bunt (1981) estimated a net export of organic C of approximately 1 g m^{-2} day^{-1} in a Rhizophora-dominated mangrove forest in Queensland, Australia. Various authors have estimated organic carbon losses from a variety of forests at about the same level. All authors agree that these values are very tentative.

If carbon export is low, nutrient losses appear lower yet. Boto (1980) calculated a 1.7 g m^{-2} yr^{-1} loss of nitrogen from a Queensland forest and commented on how small this value was compared to the internal pools. Interestingly, he also measured nutrient input from the freshwater and found these values also were very low, with concentrations of total N and P of 2 $\mu M\ \ell^{-1}$ and <1.0 $\mu M\ \ell^{-1}$, respectively. Boto and Bunt (1981) working in the same forest system, concluded that "comparison of the C, N and P levels in the exported material with those of the standing crop suggest that N and P are efficiently conserved within the mangrove system." Nixon et al. (1984) found that there was no evidence for outwelling in two Malaysian mangrove forests. These systems functioned as..." sinks for suspended solids, particulate organic carbon, nitrogen and phosphorus and for inorganic nitrogen, phosphorus and ...silica." Odum et al. (1982) summarized our understanding of nutrient cycling in mangrove areas by stating,... "knowledge of nutrient cycling in mangrove swamps is highly speculative. The ecosystems appear to act as sinks for many elements, including nitrogen and phosphorus, as long as modest input occurs." We will return to this point. Finally, Zieman et al. (1984b), in a study of a south Florida Bay mangrove and adjacent seagrass system, found that the $\delta^{13}C$ of consumers in each system was closely related to the dominant local carbon source. There was no evidence for major carbon subsidies by either system.

In summary, mangrove forests appear to act more as sinks for carbon and nutrients than as exporters for downstream systems. This relationship appears to break down only when the mangrove or terrestrial systems are disturbed (Pannier 1979). The role of mangrove forests is that of a buffer or filter of the terrestrial systems.

TWO COMMONLY HELD BELIEFS

There are two beliefs that have materially affected how we look at these tropical coastal systems: 1) nitrogen is the limiting nutrient for growth and 2) there is necessary and positive biochemical interaction between systems. Here I would like to examine the evidence for these beliefs.

A. The Limiting Role of Nitrogen

This belief stems in large part from a paper by Ryther and Dunstan (1971) and from studies that show that rapid additions of nitrogen can stimulate primary production. At the system level, however, there is little support for this view. As discussed in the above section on coral reefs, there is limited interaction of coral reefs with their surrounding systems and, in addition, coral reefs actively fix nitrogen. While there may be short term stimulation of primary production, there is no evidence for stimulation over the long term.

Seagrass meadows have not been examined to a great enough extent to generalize on this question. However, moderate nitrogen increases have been shown to have a limited effect on plant growth, while greatly elevated increases have been shown to be deleterious to seagrass growth by stimulating the growth of phytoplankton and epiphytes, and thus reducing light (see the above section on seagrass meadows). There is some suggestion that pulsed imports of nutrients are beneficial.

The growth of some mangroves are stimulated by addition of nitrate, but ammonium concentrations in at least one *Rhizophora* forest showed no correlation with plant growth. It is more likely that phosphorus is limiting in the long run, if any major nutrient is. There is evidence that increases in nutrients to coral reefs and seagrass meadows over the long-term result in succession to new community types. It is unclear whether mangroves are adversely affected by moderate to high nutrient enrichment.

B. Biochemical Interaction Between Tropical Coastal Communities

Birkeland (1984) stated that the study by Meyers et al. (1983) represented..."the first tangible documentation of the effect of nutrient flow between tropical coastal ecosystems." However, other effects were suggested by correlation. Red tides at Guam and fluctuations in *Acanthaster* populations have both been correlated with increased terrestrial runoff (Birkeland 1984). Zieman (1982) suggested that seagrass wrack might provide a subsidy to mangroves, while McRoy

(1982) speculated that mangroves might provide a subsidy to seagrasses.

There is very little evidence that strong, necessary connections exist between coral reefs, seagrasses and mangroves. The data reviewed in the section on what we know about nitrogen and phosphorus do not support the view that there are major nutrient or carbon fluxes between these three systems. Each of these systems exists in the absence of the others. It is clear then that no specific requirement exists between them. The question is, where they are adjacent, is there an obligatory relationship? I propose that the answer is yes. Mangroves are required to remove nutrients and sediment from terrestrial sources in order for seagrasses to flourish. Likewise, seagrasses further reduce these materials by metabolism and trapping, making adjacent coral growth possible. The driving force is the terrestrially exported material. If this is true, then one can easily see why each system can exist alone, yet under some circumstances require the others. The examination of the nature of linkages is, from both management and theoretical considerations, the most important system-wide area of research to undertake.

PACIFIC VS. CARIBBEAN COASTAL MARINE SYSTEMS

At a number of levels, as documented in this Report, there appear to be differences in the components of coastal marine systems of the Pacific as compared to those in the Caribbean. From a nutrient standpoint these differences are not so obvious. Certainly, from the few nutrient data that exist, it is not possible to demonstrate any clear differences. Further, data on concentrations alone can not provide an adequate answer to the question; flow-through must be considered, as is known from work on coral reefs, and pulses of imported materials must also be considered. These factors have been discussed in the Conclusions by the UNESCO/COMAR Workshop presented earlier in this Report. The suggestion in the Report that biological indicators, such as the ratio of autotrophic to heterotrophic sponges, growth of algae on fouling panels and growth of specific organisms, might be a more appropriate means of assessing nutrients rather than direct measurements is one that should be examined in any new study.

RECOMMENDATIONS: THE NEED FOR COMPARATIVE AND LONG-TERM STUDIES

While I have recommended several specific topics that need immediate examination, there are two general recommendations that are critically needed: comparative and long-term studies. In a recent paper, Nixon et al. (in press) have demonstrated the value and necessity of these two approaches.

A. Comparative Studies

Over the past century an enormous amount of ecological data have been collected. Theories have been developed (and mostly rejected) and subdisciplines within the field of ecology have been established. Most biological disciplines have followed a common development: identification of the field; increased research with increasingly conflicting results; comparative studies which bring order to the field; stemming from this, the examination of specific problems of similarity and dissimilarity and an expansion of the field. This progression has been true for biochemistry, physiology, anatomy, genetics, etc.; it is time that ecology advance consciously to the comparative studies stage. I propose that a network of sites be established within which a series of variables would be measured in a consistent fashion. The data should be placed in a computer-assisted format and be available to all participants. A board of directors should examine these data sets at least once a year; they should review the value of each measurement, suggest changes in techniques and facilitate data and synthesis exchange between participating groups. The sites initially should be existing laboratories that wish to participate; new sites, e.g., Man in the Biosphere Reserves, could be phased in. Such a program format already exists for the Caribbean area (CARICOMP Project, J. Ogden, West Indies Laboratory, St. Croix, U.S. Virgin Islands and Eric Jordan, UNAM, Cancum, Mexico, are co-chairman of the project) and could be expanded to form a global network.

B. Long-Term Studies

There is an appealing lack of long-term observations on which to base our understanding of short-term data. The need for sites that develop decades and centuries of data is critical. This is not a new idea. For example, Sir Maurice Yonge in 1968 (South Pacific Commission/RSCN/W p.9) in reference to the needs for coral reef research stated that, "Never has there been a laboratory with a permanent staff capable of conducting a programmed long-term observations to cover changes in environmental conditions and changes in the composition of the biota. Attempts at assessing productivity of reefs have been based on surveys lasting only a few weeks and without precise knowledge of the fauna and flora. Adequate work can only be conducted in large, well-equipped laboratories with adequate and highly qualified staff..."

Few long-term data sets exist for any marine environment. For individual variables, those of weather measurements and tide-gauge readings are probably most important and have lead to some remarkable predictions. Most of the permanent field laboratories are less than 30 years old and their programs are most often directed by the available funding. Thus, even in the older laboratories, long-term data sets are most often not available, except by accident. It is now recognized that catastrophic events often control ecosystem development over the long term. Hurricanes, droughts, floods, fire, etc., set limits on ecosystem developed and require systems to go through periodic successions. Callahan (1984) pointed out that one reason for the lack of long-term data is the short-term nature of research funding and that the National Science Foundation (U.S.) is now supporting a program in long-term ecological research. At a recent meeting of ecologists to consider future needs for environmental studies (Cooley and Golley 1984), there was unanimous agreement that both comparative and long-term ecological studies were critically needed.

I propose that a few, well-funded sites in various parts of the world be established to initiate long-term studies on the various properties of ecosystems. They should be permanent reserves, financed by multiple sources and protected from the oscillations of governments. They should have permanent facilities for a small research staff and larger technical staff and visiting investigators. A major activity of the permanent staff would be to collect and analyze data on a fixed set of variables. The choice of variables and the broad interpretation and publication of the data would rest with a board of governors. Visiting scientists would be funded from outside research grants. As many as possible of these sites should be placed in developing countries. This would facilitate regional training and would bring needed expertise to the areas. Such facilities would provide an essential, but at present totally missing, ingredient for the advancement of ecological research at both basic and applied levels.

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FACTORS DETERMINING THE DISTRIBUTION AND MORPHOLOGY OF CORAL REEFS AND MANGROVES IN SOUTHEAST ASIA

by

Hansa Chansang*

ABSTRACT

The distribution and variation of fringing reefs within 200 m depth of the continental shelf of Southeast Asia were surveyed. It was found that direction of monsoon wind plays an important role in determining the location of reefs. Reefs are sheltered from the effect of predominant wind wave action. In the Andaman Sea, reefs are located on the lee sides of the islands and in bays of the west coast of the mainland sheltered from southwest monsoon. Reefs along the east coast of Malay Peninsula are located along the west and southwest of nearshore islands sheltered from the northeast monsoon.

Types of reefs vary from shallow reefs with extensive intertidal reef flats and steep slopes which extend to 3 m depth in sheltered bays to reefs of extensive slopes down to 30 m depth on offshore islands. Reefs on offshore islands also exhibit a dominant growth form of plate and whirl patterns on the lower slope extending from 15 m down to the base of the slope. It is concluded that reef development varies according to the degree of exposure to wave action, depth of seafloor and water clarity. In different evironments, reef morphologies are different, but with relatively constant growth form and coral species within certain depth zones.

In addition, the linkage of 2 important coastal ecosystems, i.e., coral reefs and mangroves along the shoreline of Southeast Asia, as proposed in the Caribbean, is questioned due to their separate locations in this region.

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*Phuket Marine Biological Center
Department of Fisheries
P.O. Box 60
Phuket, Thailand

NUTRIENT AVAILABILITY AS A MAJOR DETERMINANT OF DIFFERENCES AMONG COASTAL HARD-SUBSTRATUM COMMUNITIES IN DIFFERENT REGIONS OF THE TROPICS

by

Charles Birkeland*

ABSTRACT

Despite taxonomic affinities among the species found in different tropical regions of the oceans around the world, differences prevail among these regions in terms of processes which structure the communities. These processes bring about differences in the elements of the species pool that predominate and thereby regional differences in community structure. It is proposed that nutrient availability is one of the major determinants of these regional differences. In particular, the phytoplankton food-web preempts the benthic algal food-web as nutrient input increases; success of recruitment of particular year-classes from planktotrophic larvae is occasionally facilitated by strong nutrient pulses and, because of this, competition for space and grazing pressure increase with nutrient input; heavy grazing pressure forces generalized diets and this compounds the grazing pressure; K-selected traits are favored in regions of low nutrient availability while r-selected traits are favored in regions of high nutrient availability or nutrient-pulse conditions. These processes are most influential on recent recruits or juveniles and much less on adults, so community structure is largely determined by factors influencing these early stages. Along a gradient of decreasing nutrient input, whether on a geographical or a local scale, the predominant occupants of primary substrata in shallow water change from heterotrophic suspension-feeders to benthic plants to phototrophic animal-plant symbionts.

This subject is of practical importance as a basis for rational management plans for tropical coastal ecosystems. Communities in areas of nutrient input from upwelling might be managed for an export economy, but coral reefs on atolls should be managed for local subsistence and as a service-oriented economy in relation to the world market. It is urgent that UNESCO encourage international cooperative studies on the mechanisms and effects of nutrient input into tropical coastal ecosystems because with modern technology, human activities such as construction of the Aswan Dam and coastal clear-cut logging can have international effects on fisheries and coastal resources.

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*Marine Laboratory
University of Guam
UOG Station, Mangilao, Guam 96923

INTRODUCTION

Orians and Paine (1983) expressed the concept that if community ecology is to become a predictive science, then we must expect to find that structurally and functionally similar ecosystems develop in regions with similar physical environments, even if the component species making up these communities are from different taxonomic origins. Similarities in life-history characteristics of such taxonomically unrelated organisms as tunicates and bivalves, when the species fill comparable functional roles in the marine communities, are heuristic examples for discussions of convergent evolution at the community level (Paine and Suchanek 1983; Orians and Paine 1983). In contrast, tropical nearshore hard-substratum communities from different geographic regions are characterized by taxonomic similarities and by fundamental differences in ecological processes and community structure. Coral communities (which include sponges, bivalves, fishes, algae, etc.) vary considerably in the dominance of heterotrophic versus phototrophic organisms as occupants of primary substrata, in the dominance of the phytoplankton versus benthic algal foodwebs, and in the victors of competition for space being long-lived colonial organisms or short-lived solitary species. A more appealing approach for the study of coral communities should be to examine the causes of differences rather than to look for similarities. I believe major determinants of the rates and relative importances of processes which in turn lead to differences in community structure are degree of nutrient availability and whether nutrients come in pulses or relatively steadily. The differences brought about by nutrient availability are outlined in Table 1.

If the nature of nutrient availability is an important factor in determining both the rates of ecological processes and, consequently, the organization and structure of tropical nearshore marine communities, then these relationships should be of practical importance towards designing rational strategies of resource management for tropical coastal marine ecosystems.

The obvious differences in coral-reef community structure among geographic regions that need explanation will be outlined in the next section. Each of the processes that bring about these differences will be presented in the following sections.

LIFE-FORMS OF BENTHIC COMMUNITIES

On a global scale, there are qualitative differences in the life-forms of comparable shallow-water marine hard-substratum communities of different geographic regions of the

Table 1. Trophic composition of complete reef fish communities in various oceanic regions. All entries are (1) percentages of the entire predator community by predator numbers (Pred. no.) or weight (Pred. wt.), or (2) percentages of all prey eaten by the community by prey numbers (Prey no.) or weight (Prey wt.). Except as noted, the divisions into categories are as made by the original author (source) or are computed directly from data presented therein. The lowest level categories are basically the guilds of Williams and Hatcher (1983).

<table>
<tr><th rowspan="5">LOCALITY</th><th rowspan="5">SOURCE</th><th rowspan="5">MEASURE</th><th colspan="5">←HERBIVORE→</th><th colspan="2">←OMNI-VORE→</th><th colspan="7">←CARNIVORE→</th></tr>
<tr><th colspan="5"></th><th>Sessile[a]</th><th>Plankton[a]</th><th colspan="7"></th></tr>
<tr><th colspan="4">←BENTHIC HERBIVORE→</th><th colspan="5">←PLANKTIVORE→</th><th colspan="3">←BENTHIC INVERTEBRATE FEEDER→</th><th colspan="2">PISCIVORE</th></tr>
<tr><th colspan="3">←Browser→</th><th>Grazer</th><th>Algal Planktivore[c]</th><th></th><th></th><th>Zooplankton[d]</th><th>Gelatinous Plankton</th><th>Coral</th><th>Sessile Inverts.</th><th>Mobile Inverts.</th><th>Facultative</th><th>Confirmed</th></tr>
<tr><th>Sucker[b]</th><th>Small Cropper[b]</th><th>Large Cropper[b]</th><th>Scraper[b]</th><th></th><th></th><th></th><th></th><th></th><th></th><th></th><th>Benthic Crustacea</th><th></th><th></th></tr>
<tr><td>Tanzania, East Africa</td><td>Talbot (1965)[ef]</td><td>Pred. wt.</td><td colspan="5">←19→</td><td colspan="2">←20[g]→</td><td colspan="7">←61→</td></tr>
<tr><td>" "</td><td>" " ef</td><td>Pred. wt.</td><td colspan="4">←19→</td><td></td><td></td><td></td><td colspan="2">←1→</td><td colspan="3">←69→
20[g]</td><td colspan="2">←11→</td></tr>
<tr><td>Tulear, Madagascar:</td><td>Harmelin-Vivien (1981)[ef]</td><td>Pred. no.</td><td colspan="5">←11→</td><td colspan="2">←26→</td><td colspan="7">←63→</td></tr>
<tr><td></td><td></td><td></td><td colspan="5"></td><td colspan="2"></td><td colspan="5"></td><td colspan="2">←3→</td></tr>
<tr><td>Full reef</td><td>" "[ef]</td><td>Prey wt.</td><td colspan="5">←17→</td><td></td><td></td><td colspan="2">h</td><td>4</td><td>~4</td><td>←~56→</td><td colspan="2">←19→</td></tr>
<tr><td>Tulear, Inner flat</td><td>Vivien (1973)[ef]</td><td>Pred. no.</td><td colspan="5">←7→</td><td colspan="2">←37→</td><td colspan="7">←56→</td></tr>
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</table>

Great Barrier Reef (central)	Williams & Hatcher (1983)[e]	Pred. no.	←8→ ←~42→ ←~50→
" "	" "[e]	Pred. wt.	←19→ ←~10→ ←~71→
" "	" "[e]	Pred. no.	←8→ .2 ←84→ ←7→ ←1→ 1 ~42 2 .3 4+ 9 .2
" "	" "[e]	Pred. wt.	←19→ ←54→ ←19→ ←6→ 3 ~2 ~8 3 ~1 15 4− 2+
One Tree Island, GBR	Goldman & Talbot (1976)[ef]	Pred. wt.	←18[i]→ ←10→ ←18→ 54
Cocos Lagoon, Guam	Jones & Chase (1975)[j]	Pred. no.	←45→ ←31→ ←23→ ←1→
Enewetak, Marshall Ids.	Gladfelter et al. (1980)	Pred. no.	←25→[k] ←32→ ←38→ ←5→ 20
Northwestern Hawaiian Ids.	Parrish et al. (1985)[ef]	Prey. no.	←11→ ←83→ ←6→ (Predator no. ←6[l]→)
" "	" "[ef]	Prey. wt.	←16→ ←8→ ←66→ ←10→ (Predator wt. ←19[l]→)
Kaneohe Bay, Hawaii	Brock et al. (1979)[e]	Pred. wt.	←8→ ←?—59→ ←31→ ←2→
" "	Stimson et al. (1982)[em]		13 and ←16[m]→
Florida Keys	Bohnsack (1982)[n]	Pred. no.	←~20→[k] ←~26→ ←48→ ←6→
U.S. Virgin Islands	Randall (1963)[ef]	Pred. wt.	←24→ ←16→ ←60→ ←5[o]→
" "	" "[e]	Pred. no.	←12[o]→
U.S. Virgin Islands	Gladfelter et al. (1980)	Pred. no.	←39→[k] ←5→ ←54→ ←2→ 9
Bermuda	Bardach (1959)[e]	Pred. wt.	←32[p]→[k] - - - - ←68→

[a] Sessile omnivores eat sessile invertebrates and some plant material. Plankton omnivores eat animal plankton and some plant material. The plant material is usually assumed to be benthic, although omnivory involving drift algae may occur. It was not clear in all studies whether full populations of plankton omnivores were included within the overall planktivore category, or whether the category included only their carnivorous feeding.

[b] The trophic classification is that of Hatcher (1982b).

[c] Feeder on drift algae (benthic-derived detritus in the water column).

[d] All animal plankton other than gelatinous forms, including resident and pelagic material, holo- and meroplankton (including many small crustaceans).

[e] In these studies, quantitative collections were made to contribute to estimates of the community composition. In all other studies, only visual census methods were used, and the cryptic fauna was certainly underestimated.

[f] These studies apparently made use of at least some significant amount of original, local data on diet of the populations studied. In all other studies, diet interpretations were based on literature.

[g] The "few facultative omnivores" found were "placed among the herbivores if their stomach contents were predominantly of algal matter" (Talbot 1965). In the present classification (following Harmelin-Vivien 1981), to create an omnivorous category, all coral feeders only were classed as omnivores.

[h] Mobile benthic invertebrates and planktonic invertebrates were not distinguished.

[i] Coral feeders and conventional herbivores were reported combined as 18% of the total fish biomass.

[j] Assigned to trophic categories in the present study based on community composition reported by Jones and Chase (1975), and using diet data from Hiatt and Strasburg (1960), Hobson (1974), Sano et al. (1984) and supplementary information.

[k] In all other studies it seems certain, or at least likely, that the methods used resulted in reporting drift algal feeding within total herbivory (although usually not identified as such). In these studies, it seems less certain, and such feeding may have been reported as part of another category.

[l] From Parrish et al. (1986).

[m] Calculated from data of Brock et al. (1979) by Stimson et al. (1982), with results that piscivores were 13% of biomass in the 1977 collection and 16% in the 1966 collection.

[n] Assigned to trophic categories in the present study based on community composition reported by Bohnsack (1982) and using diet data from Randall (1967) and supplementary information.

[o] Assigned to trophic category in the present study based on community composition reported by Randall (1963), and using diet data from Randall (1967) and supplementary information.

[p] Defined as "omnivores (mostly herbivorous)" (Bardach 1959).

Table 1. An outline of some of the differences in community processes brought about by strong nutrient pulses or greater levels of nutrient availability.

1-COMPETITION: r-selected traits favored in high-nutrient or nutrient-pulse conditions

K-selected traits favored in low-nutrient conditions

r-selected species are not necessarily ephemeral nor dependent upon disturbance; under nutrient-pulse conditions they can retain space over K-selected species by competition among juveniles

2-RECRUITMENT: success of recruitment by planktotrophic larvae is occasionally facilitated greatly by a nutrient pulse, after which the abundant recruitment brings about:

increased competition for space
increased grazing pressure

because of greater abundances of competitors and grazers

3-PREDATION: with increased grazing pressure because of increased populations of grazers, food resources are kept at lower levels by the grazers, grazers must generalize their diets,

generalized diets set back succession, favor r-selected traits in prey, i.e., rapid growth, promote increased biomass production per gram biomass

(specialized diets facilitate and accelerate succession, favor K-selected traits in prey, i.e., antipredatory mechanisms, promote decreased biomass production per gram biomass)

4-AMENSALISM: phytoplankton food-web preempts benthic algal food-web as nutrient input increases

5-COMMUNITY STRUCTURE: along a gradient of decreasing nutrient input, whether geographical (upwelling region to continental shelf region to oceanic reef) or local (lagoonal to open coast), the predominant occupants of primary substrata in shallow-water communities change from heterotrophic suspension-feeders to benthic algae or seagrasses to phototrophic animal-plant symbionts.

With increase in rate of nutrient input, space becomes predominantly occupied by smaller animals with greater rates of turnover.

tropical seas (Fig. 1). The substrata of open-coast coral reefs of Oceania (Polynesia, Micronesia, and the smaller islands of eastern Melanesia) are predominantly occupied by phototrophic organisms such as hermatypic corals, octocorals, tridacnid bivalves, didemmid ascidians with associated Prochloron sp. (Lewin et al. 1983), cyanobacteria-associated sponges (Wilkinson 1983), and algae, especially crustose coralline algae. For example, at the study site for Lewin et al. (1983) in Belau (Palau), Micronesia, the phototrophic animal-plant systems rivaled the plants for predominance. Prochloron - associated ascidians (Lissoclinum voeltzkowi and Didemnum molle) coated many blades of the seagrass Enhalus acoroides, Diplosoma virens coated may rhizophores of the Sonneratia (mangroves) bordering the seagrass, and the larger Lissoclinum patella coated rocks at the edge of the seagrass. The animal producing the greatest biomass in the seagrass bed appeared to be the cyanobacteria - associated sponge Dysidea herbacea. The other prevalent organisms at the site also involved phototroph - animal systems: the scyphozoan Cassiopeia, the bivalve Tridacna, and scleractinian and alcyonacean corals.

As with Prochloron - associated ascidians which "could make a major contribution to the productivity, especially in localized areas of tropical marine waters characterized by low nutrient levels and high irradiance" (Lewin et al. 1983: Abstract), all species of Tridacna require clear, high-salinity water. "T. derasa is restricted to oceanic environments and it is not found on fringing reefs adjacent to large land masses" (Munro and Heslinga 1982:2). Wilkinson (1986) showed that the proportion of heterotrophic sponges was greatest on inner shelf reefs of the Great Barrier Reef (GBR) while phototrophic sponges became more prevalent on outer shelf reefs of the GBR.

In the "continental" western Pacific (Thailand, Malaysia, Indonesia, Papua New Guinea, Philippines, and Taiwan) and in the Caribbean, heterotrophic benthic organisms such as massive sponges, boring sponges, ascidians without symbiotic prokaryotes, crinoids, burrowing bivalves (Highsmith 1980a), etc., become more prevalent. This contrast between life-forms of benthic communities on oceanic and continental reefs is depicted in Highsmith's (1980a) Figure 6. Massive sponges such as Xestospongia (Highsmith 1980a: Fig. 6B) are characteristic of coral reefs in "continental" regions such as Thailand, Malaysia, Indonesia (Ambon, Bali, Sulawesi), Papua New Guinea, the Solomon Islands, and the Caribbean, but not in Oceania.

In the relatively heterotrophic benthic communities of both the "continental" western Pacific and the Caribbean, and also in the relatively phototrophic benthos of Oceania, large sessile organisms occupy much of the primary substrata. In tropical regions with nutrient-rich upwelling waters such as

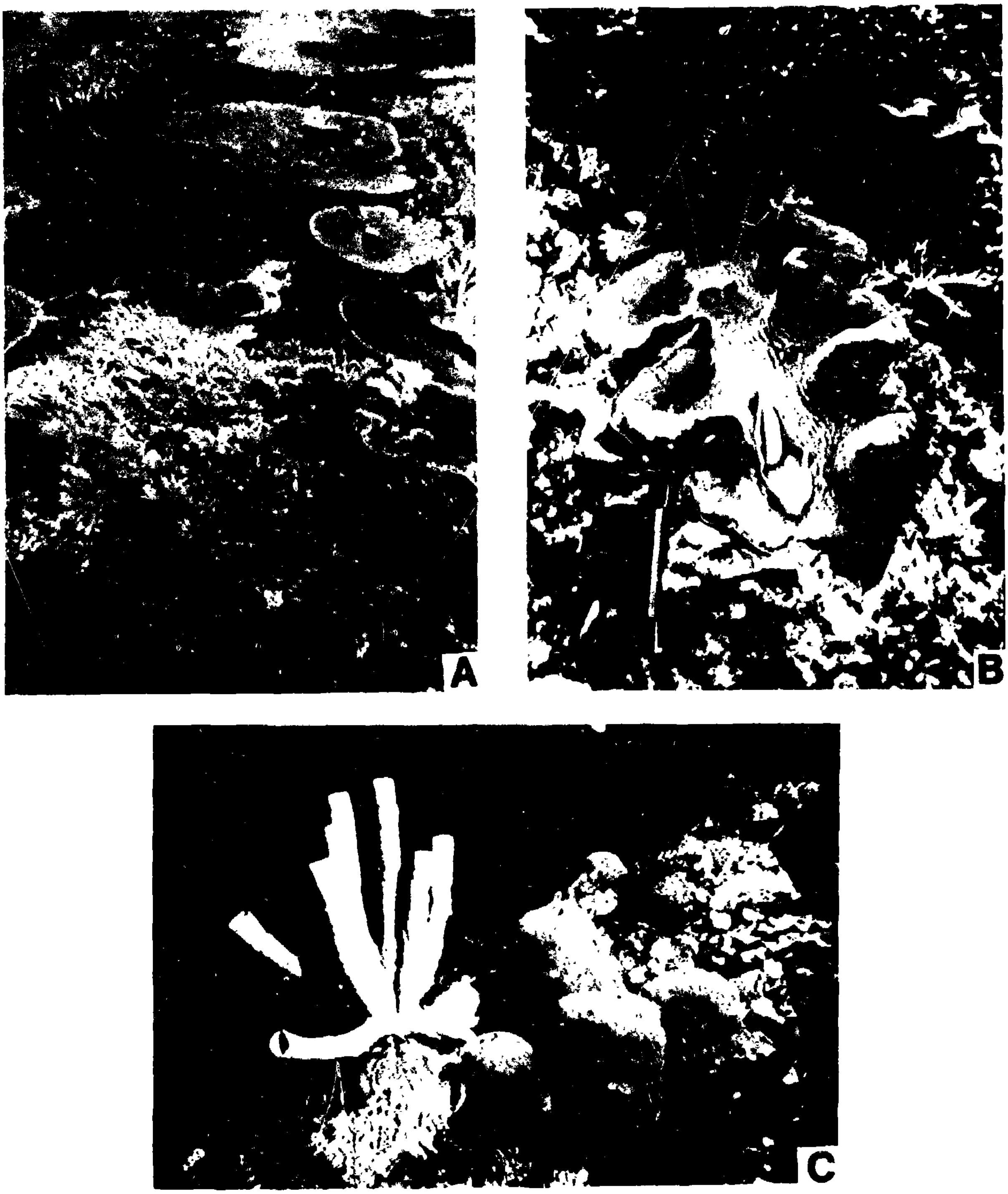


Fig. 1. Oceanic coral reefs dominated by phototrophs (A- Aunu'u Island, American Samoa; B- Kayangel Atoll, Palau) and a continental shelf coral reef dominated by heterotrophs (C- Menjangen Island, Bali).

the Gulf of Panama, there is even a greater proportion of substratum occupied by heterotrophic suspension-feeders. But there, sessile organisms such as small barnacles, hydroids, bryozoans, and small (usually $< 10\ cm^2$) encrusting sponges are prevalent; large sponges and corals are scattered in distribution and are not predominant (Fig. 2).

From an evolutionary perspective, Vermeij (1983) proposed that mutualisms are more likely to evolve in nutrient-poor regions than in areas of upwelling or periodic phytoplankton blooms. The variety of symbiotic associations with algae of didemnid ascidians, bivalves, scleractinians, and alcyonaceans in the Indo-West Pacific as compared with the eastern Pacific and the Atlantic supports Vermeij's hypothesis because nutrient-poor Oceania makes up a large portion of the area of the Pacific. However, much of the area of the western Pacific is "continental", with large amounts of nutrient input. Many, if not most, of the species with symbiotic associations with algae may be found in these nutrient-rich regions of the Pacific, although with less predominance. In this essay I will outline differences in rates of ecological processes which lead to qualitative differences in community structure, i.e., the effects of large and/or irregular inputs of nutrients from an ecological perspective. These ecological patterns are generally consistent with Vermeij's evolutionary patterns, but on a more fine-grained scale.

PREEMPTION OF LIGHT AND NUTRIENTS

Phytoplankton is able to react rapidly to a sudden impulse of nutrients because the component populations are made up mostly of single-celled plants. With large surface-to-volume ratios, they can efficiently absorb nutrients. Phytoplankton also absorb light in the upper water column. As nutrient input increases, phytoplankton can undergo a rapid population increase or "bloom" which can have profound effects on the benthic community. As phytoplankton becomes dense it can absorb essentially all the nutrients in the water column and take up much of the light. It has been calculated that if phytoplankton reaches a density of $2\ g\ m^{-3}$, a compensation depth originally at 100 m depth would be moved up to 3.5 m (Ryther 1963; Nybakken 1982). In effect, the benthic algal community and the food-web based on it would be eliminated below 3.5 m depth.

Nutrient input and eutrophication on coral reefs can, up to a point, stimulate the growth of benthic vegetation and increase rates of primary productivity (Kinsey and Domm 1974; Kinsey and Davies 1979). The increase in macroalgal growth can lead to overgrowth and sometimes even mortality of corals (Fishelson 1973; Banner 1974), and a general shift in dominance from corals to benthic algae. However, when

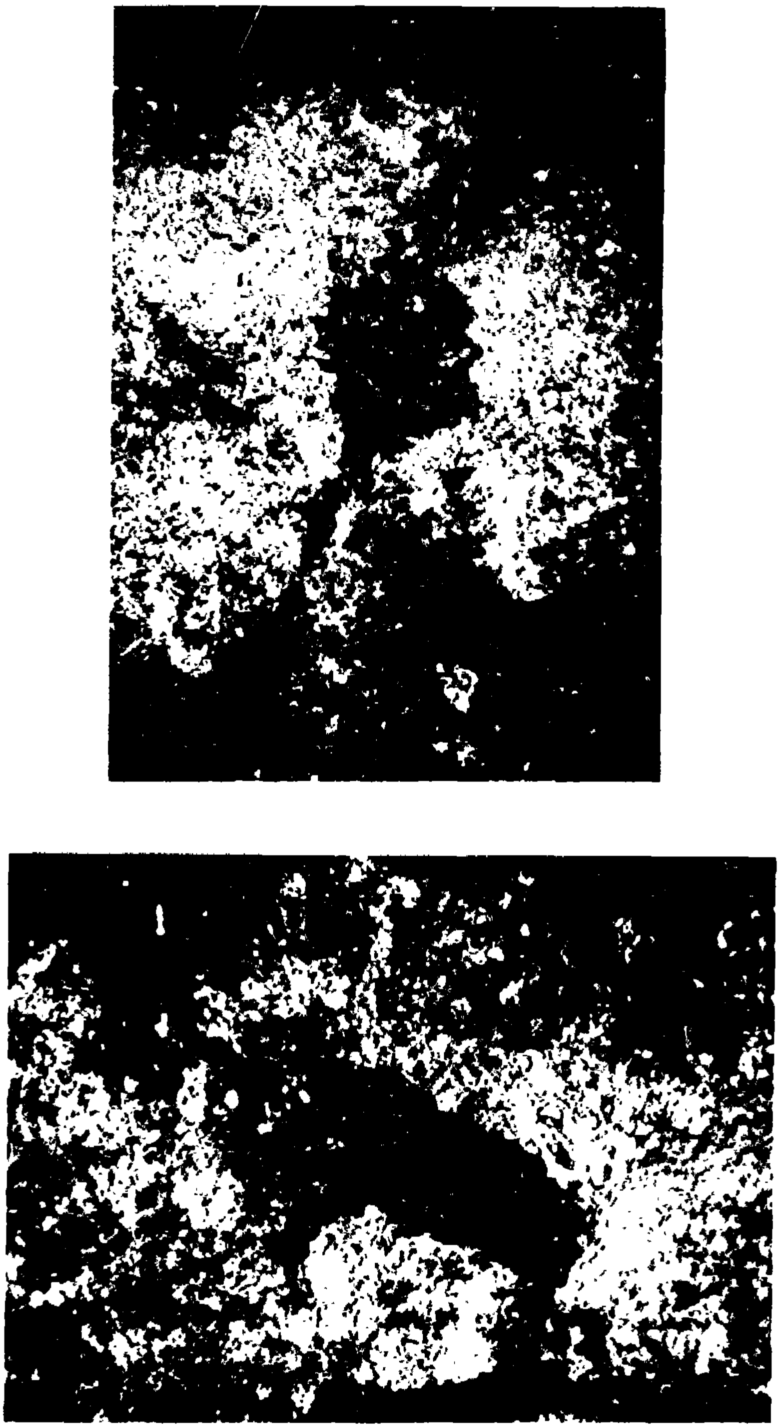


Fig. 2. *Pocillopora damicornis* ("*P. cespitosa*" form) often originate in crevices in areas subject to nutrient-rich upwelling. Note majority of substratum occupied by small heterotrophs: sponges, hydroids, bryozoans and ascidians.

nutrient input reaches even higher levels, shading by phytoplankton can significantly reduce the growth of benthic algae (Twilley et al. 1985; Wiebe 1987). Seagrasses, for example, appear to do best in "mesotrophic systems" where nutrient input is greater than on coral reefs but less than in mangrove forests (Wiebe 1987). As nutrient input increases, phototrophic animal-plant symbionts give way to benthic algae. If nutrient input increases even further, the heterotrophic suspension-feeders (part of a phytoplankton- or suspended detrital-based food-web) prevail over benthic algae. This shift in community structure along a gradient of nutrient input can be seen on both geographical and local scales of distance, and on both ecological and geological scales of time.

A. Geographic Gradients

This phenomenon is clearly observable when comparing the coral reef communities at the extremes of nutrient input, e.g., an oceanic atoll and a continental or high island coral community near large river drainages. At Micronesian atolls such as Kayangel and Pakin, crustose coralline algae and Halimeda were predominant well beyond 50 m depth (pers. observ.). Large populations of scarids and acanthurids were prevalent and siganids were common (pers. observ.). On islands near the coast of the Malaysian Peninsula in the northern Gulf of Thailand, an area which receives tremendous amounts of nutrient input from several major rivers, algae were sparse below 4 m (Kamura and Choonhabandit 1986; Tsuchiya et al. 1986) and schooling herbivorous fishes were absent (Menasveta et al. 1986). The coral community at this site consisted of 85 species of hermatypic corals, 21 of which were acroporids (Sakai et al. 1986). Corals grow slower than algae, but usually have several trophic mechanisms (Muscatine and Porter 1977) and this may explain how they are better able to survive than are algae in eutrophic, phytoplankton-dominated, situations.

The complete absence of schooling herbivorous fishes (scarids, acanthurids, siganids, and kyphosids) at the islands in the northern Gulf of Thailand was remarkable when considering there were 31 families of reef fishes present and the fish stock amounted to 832 kg ha^{-1}, an intermediate amount for coral-reef fish communities (Menasveta et al. 1986). Planktivorous fishes were prevalent. Likewise, suspension-feeding invertebrates were abundant: the bivalves (Arca ventricosa, Saccostea mordax, Dendrostrea crenulifera, Isognomon acutirostris, Beguina semiorbiculata, Lithophaga sp., Gastrochaena cuneiformis, Spengleria mytiloides and others), the barnacles (Tetraclita squamosa, Chthamalus stellatus), massive sponges (Xestospongia and others), and ascidians (Tsuchiya and Lirdwitayapasit 1986; Tsuchiya et al. 1986). The ordinarily herbivorous Diadema spp. were there, but their diet consisted largely of detrital material, sediment and diatoms, and the herbivore trophic level was weakly represented.

B. Local Gradients

This comparison can be repeated on a local scale. The high island of Pohnpei (Carolines, Micronesia) receives about 192 inches of rain per year on the coast, 350 to 400 inches per year at the higher elevations (NOAA 1978). The island is surrounded by a lagoon in which the nutrients from the terrestrial runoff collect. There are at least 215 species of coral on the reefs in the lagoon, but large sponges, suspension-feeding bivalves and planktivorous fishes are also prevalent (Fig. 3). Fouling panels in Pohnpei lagoon become dominated by heterotrophic benthic animals both inside and outside fish-exclusion cages. Ant Atoll, 9 km from the outer reef of Pohnpei, also has a diverse coral assemblage, but crustose coralline algae and herbivorous fishes are prevalent, and there are almost no sponges or suspension-feeding bivalves. Fouling panels become dominated by filamentous algae inside, and by crustose coralline algae outside, fish exclusion cages at Ant Atoll.

At Guam, the benthos in the nutrient-rich (nearly enclosed) Apra Harbor was dominated by corals and sponges. The fouling panels were dominated by heterotrophs (bivalves, sponges, ascidians, hydroids, and actinians). The benthos on the outer reef slope 2 km away was dominated by corals and algae. The fouling panels were dominated by algae.

At Ambon Bay in the Moluccas Archipelago of Indonesia, massive sponges, ascidians and planktivorous fishes are prevalent at the narrow inland head of the bay that receives enrichment from sewage and terrestrial runoff. Algae and herbivorous fishes become more prevalent towards the open mouth of the bay. Sponges are dominant on fouling panels at the head of the bay and fleshy algae are dominant on fouling panels at the mouth of the bay.

C. Changes Over Time

The above are examples of different trophic characteristics of coral-reef communities under different conditions of nutrient input between regions. At Kaneohe Bay, Oahu, we can observe the change in trophic characteristics of a community as the conditions of nutrient input change with time. From 1951 through 1977, increasing amounts of sewage were released into southeast Kaneohe Bay. The sewage was diverted from the bay in 1977 through early 1978. The total amount of particulate carbon decreased with distance from the sewage outfall and also decreased after sewage diversion (Smith et al. 1981). The abundance of phytoplankton was directly related to average nutrient input. Likewise, the biomass and numbers of zooplankton decreased

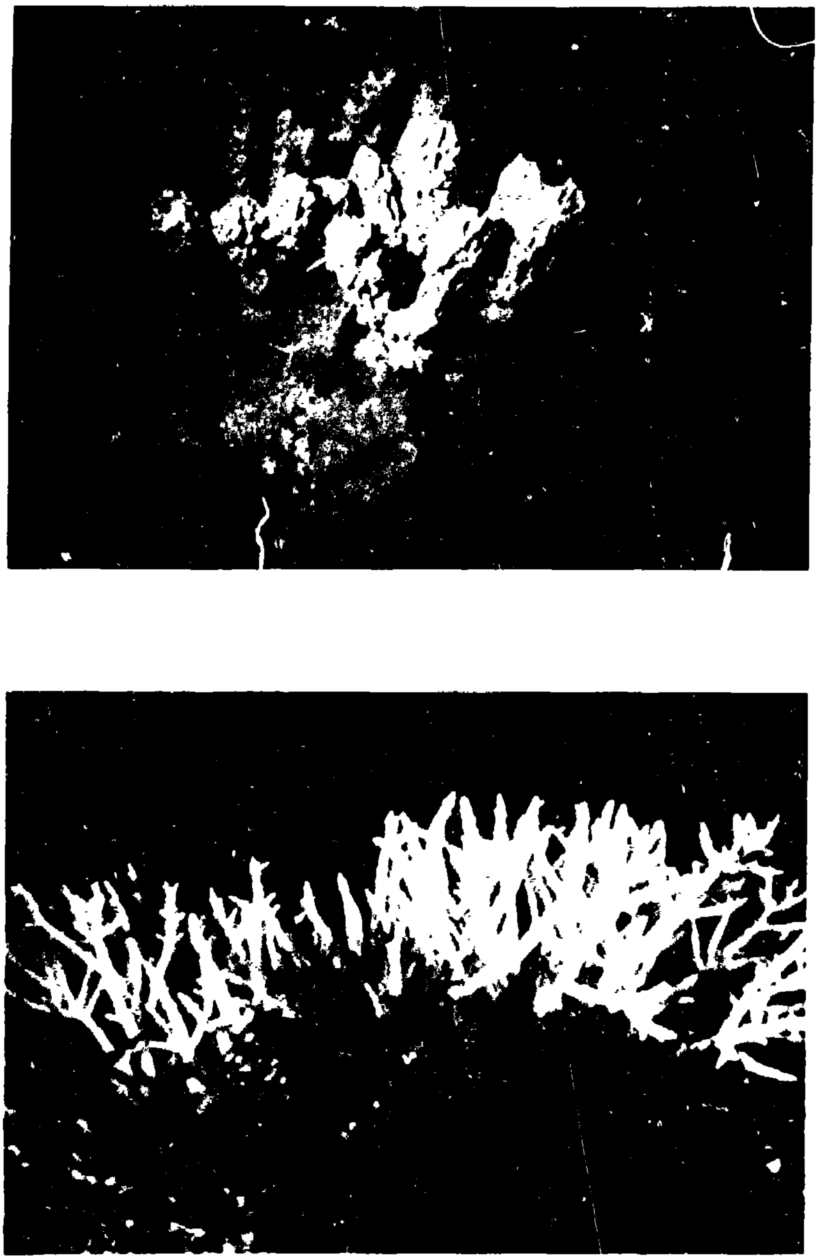


Fig. 3. Heterotrophs also prevail in Oceania in lagoons of high islands. The sponge-Acropora interaction (lower picture) was observed in 1979 and in 1985 and appeared to be static; no obvious change had come about over the 6-year period.

with distance from sewage outfall and also decreased after sewage diversion. Before sewage diversion, over half of the total benthic biomass of the bay was in the southeastern quarter of the bay near the sewage outfall. This rich benthos was predominantly composed of heterotrophic suspension-feeders: conspicuous sponges, tunicates, polychaetes, barnacles, and mollusks (Smith et al. 1981). The benthic biota further northwest in the bay was a typical coral reef community, composed predominantly of the phototrophs, algae and coral. When the sewage was diverted, the biomass decreased rapidly throughout the bay in both the plankton and the benthos. The decrease was greatest in the heterotrophic benthos of the southeast sector of the bay. The biomass decreased from 505 down to 145 metric tons dry weight in the community composed predominantly of suspension-feeders (Smith et al. 1981).

These sorts of changes in trophic structure of marine communities are also indicated to have occurred over geologic time. Hallock and Schlager (1986) found evidence in the geologic record that "drowned" coral reefs and carbonate platforms fall behind rises in sea level, or "drown", during periods of excess nutrient input. They proposed that increased nutrient input stimulates phytoplankton growth and thereby reduced water transparency, increasing competition for space and bioerosion by heterotrophs.

D. Standardized Comparisons

To standardize comparisons of communities which develop under different conditions of nutrient input, fouling panels were set out at various pairs of sites and compared after 77 days following the time they were set out as clean plates. All panels were set at 9 m depth. Fouling panels at the offshore side of Taboguilla Island in the Gulf of Panama during the dry season were exposed to nutrient input from upwelled waters. The panels exposed to upwelling were dominated by heterotrophic communities (barnacles, bivalves, bryozoans, sponges, ascidians, polychaetes, and hydroids) which had 12 times the biomass of phototrophic communities (algae and corals) on panels at islands offshore (6 to 14 km) of the Caribbean coast and 6 times the biomass of phototrophic communities on panels at the Caribbean coast of Panama (Birkeland 1977). This same pattern has been observed with fouling panels at Pohnpei and at Guam in the Pacific.

E. Community Amensalism

Sessile benthic heterotrophs and phototrophs can compete for space. However, benthic algae cannot compete with phytoplankton for light because benthic algae are attached to the bottom and the phytoplankton is in the water column. Furthermore, phytoplankton are generally unicellular and can absorb nutrients more efficiently and can multiply more rapidly in immediate response to a pulse of nutrients. Phytoplankton can make the environment less suitable for benthic algae and thereby replace the benthic algal food-web by amensalism rather than by competition.

Schooling herbivorous fishes can be totally (Menasveta et al. 1986) or nearly (personal observations at Ko Phi Phi Don, Andaman Sea) absent from a coral community and replaced by an abundance of planktivorous fishes. The opposite does not occur. Herbivorous fishes are abundant on oceanic atolls, but planktivorous fishes can be abundant also. Planktivorous fishes are not necessarily dependent upon a phytoplankton-based food-chain. They can feed primarily on demersal zooplankton which feeds largely on detrital organic material (Gerber and Marshall 1974a, b). Planktivorous fishes can also feed on reproductive products, fecal material (Robertson 1982), drifting algal scraps, or pelagic zooplankton when the primary productivity is low in the water column over a coral reef.

In summary, the phytoplankton can inhibit benthic phototrophs and the benthic phototrophic food-web by preempting light and nutrients in the water column, but the benthic algae and corals do not significantly inhibit the phytoplankton or the phytoplankton food-web.

RESPONSES TO NUTRIENT PULSES

The phytoplankton-based food-web, sessile suspension-feeders, and recruitment of organisms with planktotrophic larvae, are immediately affected by the magnitude of nutrient input into the coral-reef system. Growth rate, fecundity, and larval survival of marine animals have all been found to be associated with increased nutrient input or phytoplankton productivity.

The growth response of communities of heterotrophic suspension-feeders to nutrient input is rapid. A benthic community made up mostly of heterotrophic suspension-feeders dropped to 29% of its previous biomass well within the first year of sewage diversion from Kaneohe Bay (Smith et al. 1981). A demosponge population demonstrated a 5-fold increase in biomass following a 6-fold increase in bacterial biomass when a sewage outfall commenced operation off Grand Cayman Island (Rose and Risk 1985). The community of suspension feeders that developed within 77 days on fouling panels at Isla Taboguilla in the Gulf of Panama was 1.6 times larger (dry-weight biomass) in the dry season of upwelling than in the nonupwelling season, and 7.5 times greater than on the opposite side of the island which was not directly subjected to upwelling waters (Birkeland 1977).

Recruitment of marine organisms with planktotrophic larvae is strongly affected by nutrient pulses. Increases in population density of over 6 orders of magnitude in Acanthaster planci are correlated with terrestrial nutrient runoff (Birkeland 1982). Aleem (1972) reported that when the Aswan Dam was closed, the nutrient concentrations in the Nile flood water decreased, the phytoplankton blooms disappeared and, within a year, the fisheries catches for the eastern Mediterranean decreased to 3.7% of their former level. Ben-Tuvia (1960) and Chidambaram and Menon (1945) found positive correlations between abundances of juvenile sardines near the coast of India and rainfall during previous peak spawning season. Sutcliffe (1972, 1973) showed that commercial catches of fishes, bivalves, and lobsters are each correlated with the amounts of land drainage or river discharge as long as lag periods for growth to commercially harvested size are taken into account for each species.

Stage-one nauplii of Balanus balanoides appear in the plankton in the British Isles at about the time of the spring phytoplankton bloom (Barnes 1956). In the spring of 1950, the phytoplankton blooms were rich, cyprids of B. balanoides were abundant, barnacles recruited densely on intertidal rocks (Barnes 1956), and intraspecific competition was probably relatively intense. In 1951, there was no spring phytoplankton bloom, few barnacles recruited (Barnes 1956), and competition was probably of low frequency.

In Kaneohe Bay, the number of barnacle larvae in the water column decreased dramatically upon the diversion of sewage (Smith et al. 1981). Smith et al. (1981) attributed this decline in larval abundance to diminished adult fecundity. I would infer that larval food supply was also reduced. The rapid response of heterotrophic organisms with planktotrophic larvae is from at least two factors: a decrease in growth rate and/or gamete production of adults and a lower growth rate and/or survival rate of larvae.

EFFECTS OF STRONG RECRUITMENT

A. Competition in the Benthos

Strong nutrient pulses sometimes facilitate strong recruitment of species with planktotrophic larvae. When this occurs, the benthic community is exposed to more intense competitive and predatory pressures. The competitive pressures increase as strong recruitment fills up space. For example, in areas influenced by upwelling on the Pacific coast of Panama (Gulf of Panama), space on the upper surfaces of fouling panels were occupied by macroorganisms 3 to 6 times faster than space on fouling panels on the Caribbean coast of Panama (Meyer and Birkeland 1974). The biomass of fouling communities on the panels accumulated 6 times faster in the area of upwelling on the Pacific coast than on the Caribbean coast (Birkeland 1977). The intensity of competition for space (and perhaps for some other resources) increases with increased nutrient input both because of greater planktotrophic larval survival and subsequent successful recruitment, and also because of faster growth of juveniles and adults.

The nature of coral recruitment changes along a gradient as rate of nutrient input increases from oceanic reefs to continental shelf reefs to areas of upwelling. On oceanic reefs (Guam, Mariana Islands), corals recruited to fouling panels within 37 days and continued through 180 days (Birkeland et al. 1982). (These were the periods over which the panels were inspected; they probably actually started recruiting earlier and continued longer.) Corals tended to recruit to plates which had already been settled by corals, and so recruitment became significantly aggregated. After 180 days, representatives of up to 3 families of corals could be found on the same panel. Space on the panels was not filled after 180 days and no signs of competition for space were observed. The number of coral spat appeared to be limited mainly by the number of planulae in the water column, not by open space on the panels available to recruits, at both Guam and the Great Barrier Reef (Birkeland et al. 1982; Wallace 1985).

On Caribbean shelf reefs on the coast of Panama where there was probably more nutrient input by terrestrial runoff, the density of coral recruits as a function of time was similar to that at Guam, but competition with algae (and occasionally ascidians, sponges and bryozoans) was a problem for coral recruits if fish failed to graze over the panel (Birkeland 1977).

On panels in upwelling regions the survival of coral recruits was extremely low (Birkeland 1977). In nutrient rich upwelling waters, surfaces of panels were entirely occupied by barnacles, bivalves, ascidians, sponges, bryozoans, polychaetes, hydroids, etc., each of which grow more rapidly than scleractinian spat. Only 2 scleractinian coral recruits were observed on 251 panels in the region of upwelling, and these were clearly about to be overgrown at the time the panels were collected (Birkeland 1977). The 262 coral spat on 262 Caribbean panels and the 200 coral spat on 123 oceanic Pacific panels were not in immediate danger of being overgrown on panels exposed to grazing by fishes (Birkeland et al. 1982).

B. Reproduction of Corals

Hermatypic (phototrophic) corals are well adapted to nutrient-poor environments by means of efficient utilization and recycling of nutrients (Muscatine and Porter 1977); but for unknown reasons, corals are unable to take advantage of a pulse of nutrient input and the resulting plankton productivity as quickly and to the extent that small suspension-feeders are able. In fact, Wallace (1985) found that acroporid coral recruits grow much more slowliy than was previously inferred. Therefore, the first two or three years after settlement are especially risky for corals in regions of high nutrient input, but less so in oceanic regions where larval availability may be relatively important rather than space (Birkeland 1977; Birkeland et al. 1982; Wallace 1985).

Adult colonies of *Acropora*, however, can grow remarkably fast; branching colonies lengthen by up to 26 cm yr^{-1} (Buddemeier and Kinzie 1976) and tabular colonies extend by as much as 11 cm yr^{-1} (R.H. Richmond pers. comm.). In high nutrient conditions, broken branches which reattach may have an immediate refuge in size, thereby having a better chance of survival when subjected to competition with barnacles, sponges, algae, etc., than would coral recruits having recently undergone metamorphosis. One would naturally predict a greater proportion of successful reproduction by fragmentation in environments of high levels of nutrient input. This seems to be the case.

Richmond (1985, 1987) described how *Pocillopora damicornis* reproduces solely by fragmentation or "polyp bail-out" in the eastern Pacific and mainly by planulation in Oceania. Sammarco (1987) noted that *Acropora* spp. in the Caribbean reproduce mainly by fragmentation, but reproduce on the Great Barrier Reef mainly by planulation. Highsmith (1980b) told how even massive colonies reproduce and gain broader distribution by fragmentation. He further pointed out that fragmentation by bioerosion (grazing of the base or boring) and predation occur at greater frequencies in areas of higher productivity (Highsmith 1980a, 1982).

Richmond (1985, 1987) determined that colonies of *Pocillopora damicornis* in the eastern Pacific which do not produce planulae grow considerably faster than colonies at Enewetak which invest a large portion of their energy into production of gametes. This diversion of energy from gametes to colony growth enhances the ability of the colony to compete for space in the productive environment and to reproduce by fragmentation.

C. Competition Among Coral-Reef Fishes

Thresher (1987) noted that the ratio in proportion of resident juvenile damselfishes to adults appears to be greatest in the eastern Pacific, intermediate in the Caribbean, and least of all in the Indo-West Pacific. This alleged gradient in relative density of juveniles to adults is in the same pattern as the general pattern of productivity in the water column (Koblentz-Mishke et al. 1970). Thresher

(1987) further suggests that because of more abundant recruitment, populations of reef fishes may be closer to the carrying capacity of their habitat or more "tightly packed". This suggests that greater larval survival facilitated by higher productivity in the water column may be the ultimate explanation for the prevalence of papers on "niche partitioning" among coral-reef fishes from the Caribbean and papers on "recruitment limitation" or "lottery systems" for coral-reef fishes from the western Pacific (Thresher 1987). Papers in which larval availability or recruitment-limitation are taken to be an important factor in community dynamics on coral reefs are generally from the western Pacific (Doherty 1982; Birkeland et al. 1982; Wallace 1985).

The literature on both corals and coral-reef fishes suggest that competition increases along a gradient of increasing productivity from Oceania to the Caribbean to the Gulf of Panama. Fishes, however, may compete more strongly as a result of increased abundance through larval survival. Corals are under increased competitive pressure for space because of both greater survival of recruits of other phyla and greater growth rates of sessile suspension-feeders and algae.

D. Predation and Grazing Intensity

Degree of grazing and predation-pressure also increases with strong recruitment. Strong recruitment facilitates a strong age-class. A larger standing stock of fishes exerts a greater pressure on its food resource.

Nutrient-rich upwelling waters are associated with large recruitment of fishes. According to Ryther (1969), upwelling regions comprise no more than one-tenth of one percent (0.1%) of the ocean surface, yet produce about half (50%) the world's fish supply. The commercial fisheries is considerably greater in the Gulf of Panama than off the Caribbean coast of Panama. Whale sharks and manta rays are more common in the Gulf of Panama. The schools or aggregations of <u>Holacanthus</u> spp. in the eastern Pacific appear to be made up of fishes similar in size which suggests that large schools each represent year-classes that recruited successfully. The ratio in abundance of resident juveniles to adult damselfishes in the eastern Pacific appears to be greater than in the other tropical seas (Thresher 1987) which suggests that recruitment of fishes is more successful on the average in the relatively nutrient-rich eastern Pacific.

Great numbers of cormorants, frigate birds, pelicans and other seabirds were invariably seen at Isla Taboguilla on the Pacific coast of Panama; but in 5 years of living and working on the Caribbean coast of Panama, 55 miles (88 km) away, I never saw a single pelican or gull, and only one cormorant.

These are disparate biological indicators of local productivity in the marine habitats.

This general increase in abundance of marine fauna also can be seen in the water column over the coral reef. Carangids, scombrids and coryphaenids were frequently seen over eastern Pacific reefs. Solitary great barracuda (*Sphyraena barracuda*) were seen over most Caribbean reefs; large numbers of schooling barracuda were frequently seen over eastern Pacific reefs.

Although there are fewer species of browsing reef fishes in the eastern Pacific than in the Caribbean, their combined population densities are far greater. For example, *Holacanthus ciliaris*, *H. bermudensis*, and *H. tricolor* are found in the tropical western Atlantic; *H. passer* is the only member of the genus found widely in the tropical eastern Pacific. (*H. clarionensis* and *H. limbaughi* are only found on islands off Mexico, except the former which is also found near Cabo San Lucas). The average number of individuals of *H. ciliaris* and *H. tricolor* combined that I observed on six 30-minute observation periods at Galeta Point, in the San Blas Islands, at St. Johns, and at St. Croix was 2. In six 30-minute periods on two sides of Isla Taboquilla in the Gulf of Panama, I observed an average of 43 *H. passer*. Glynn et al. (1978) reported that coral-eating pufferfishes were nearly 5 times as abundant on eastern Pacific reefs as on Caribbean reefs.

Populations of some browsing or grazing reef fishes may be 5-20 times denser in the Gulf of Panama than are populations of their counterpart species in the Caribbean, but does this actually result in an increase in browsing pressure? To standardize the assessment of browsing intensity on sponges, we turned over and photographed rocks or coral slabs with a variety of sponges on their undersurfaces. We again photographed them after 24 and 72 hours (Fig. 4). The photographs were projected onto paper, traced, and surface areas of sponges were measured with a planimeter. When a rock was turned over in the eastern Pacific, fish were observed to begin to browse the freshly exposed sponges promptly, despite our presence. The browsing intensity was over an order of magnitude greater in the eastern Pacific than in Caribbean (Table 2). It should be noted that the standing stock of *Holacanthus* spp. was also over an order of magnitude greater in the eastern Pacific.

These findings of different browsing pressures on coral reefs in different geographic regions support the divergent views of both Bakus (1964) and Randall and Hartman (1968). Randall and Hartman (1968) pointed out that massive sponges are prevalent in exposed situations in the Caribbean despite the existence of at least 8 species of Caribbean reef fishes that feed extensively on sponges (Randall 1967). Bakus

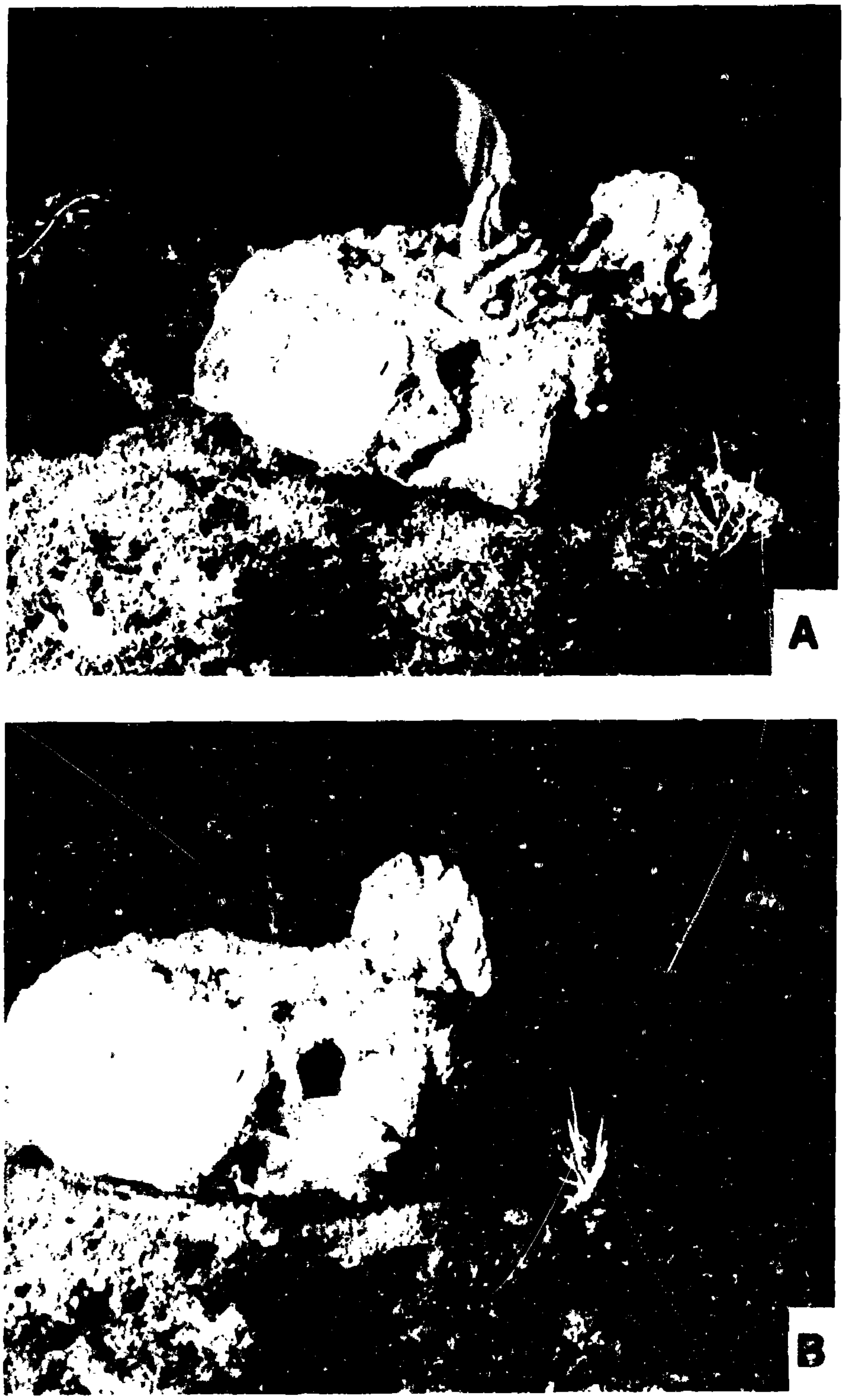


Fig. 4. Rock overturned at Isla Taboguilla, Gulf of Panama, to assess intensity of grazing on sponges by fishes. A - immediately after overturning; B - 3 days later.

(1964) pointed out that massive sponges are scarce in exposed situations at Fanning Island in the central tropical Pacific. When sponges were exposed by turning over rocks at Fanning Island, they were intensively browsed by fishes (Bakus 1964).

Glynn (1972) pointed out that predation on hydrozoan and scleractinian corals was far more intense in the eastern tropical Pacific than in the Caribbean. Earle (1972) commented that the standing stock of algae was far greater on the Caribbean coast than in the eastern Pacific, where only encrusting and fine filamentous forms were prevalent. She stated that it was quite likely that heavy grazing by herbivores was in part responsible for the low profile of algae in the lower intertidal. The high rates of nutrient input in upwelling regions suggest, however, that preemption of light by phytoplankton and intense grazing pressure may both contribute to the scarcity of algae and the prevalence of suspension-feeders on the subtidal substrata in the Gulf of Panama.

As the intensity of browsing or grazing increases as a result of frequently successful recruitments, the effects of increased browsing or grazing cause subsequent behavioral changes which compound the intensity. First, large numbers of fishes such as Holacanthus spp. tend to forage in schools. This compounds the browsing or grazing effects of large populations of fishes because each fish forages more efficiently when it is part of a school than when it is alone (Pitcher et al. 1982; Pitcher and Magurran 1983) and concentrated browsing by an aggregation of fishes has a more intensive effect than do fishes that are relatively evenly dispersed. Second, fishes have to broaden their diets as their population densities increase (Ivlev 1961).

Holacanthus spp. and Pomacanthus spp. are at relatively low population densities in the Caribbean and their prey (the common sponges) are large in size and prevalent, with a large standing stock biomass and slow growth (cf. next section). In contrast, Holacanthus passer and Pomacanthus zonipectus are abundant and their prey (sponges, bryozoans, hydroids, algae, crustaceans, gastropods, and plankters such as salps) are small in size, each of which has a relatively small standing stock biomass, but with a short turnover time. If abundant fishes must subsist on small standing stocks of prey, then the fishes must broaden their diets (Table 3). Refuges in patchy distribution or irregular abundance are not as effective against generalists because the generalist can continue to forage as it consumes alternative prey. Abundant generalists may exert greater browsing or grazing pressure than specialists.

Table 2. Removal of sponge tissue by grazing fishes over 3-day periods from overturned rocks or slabs of dead coral.

	No. rocks	No. sponges	No. eaten completely	No. damaged	No. left alone	Surface area removed (cm^2)	% Surface area removed
Caribbean							
Salar, San Blas Islands	5	390	7	3	380	72.1	1.9
Galeta, coast of Panama	5	175	2	1	172	85.3	3.1
Lameshur Bay, US Virgin Islands	10	89	9	16	64	54.6	1.0
TOTAL CARIBBEAN	20	654	18	20	616	212.0	1.76
Western Pacific							
Manado, Sulawesi (Celebes)	11	319	32	0	287	224	9.1
Motupore, Papua New Guinea	18	287	42	3	242	490	21.9
Guam - exposed coast	4	72	7	7	58	47	5.5
Guam - Apra Harbor	4	36	10	4	22	90	23.7
TOTAL WESTERN PACIFIC	37	714	91	14	609	851	16.5

Table 2. Continued.

Eastern Tropical Pacific							
Isla Toboguilla, Gulf of Panama	9	79	10	5	64	1706	61.3
Islas Secas, Gulf of Chiriqui	3	24	9	3	12	644	65.0
Playas del Coco, Costa Rica	11	86	36	9	41	1230	40.9
TOTAL EASTERN PACIFIC	23	189	55	17	117	3580	52.0

Table 3. Percent of diet consisting of sponge in several reef fishes. Information was taken from Randall (1967) and from Reynolds and Reynolds (1977).

Fish Species	% diet as sponge by volume	no. stations sampled	no. fish stomachs sampled
CARIBBEAN			
Holacanthus ciliaris	96.8	19	26
Holacanthus tricolor	97.1	12	24
Pomacanthus arcuatus	70.2	27	34
Pomacanthus paru	74.8	22	23
Chaetodipterus faber	32.7	22	29
Cantherhines macrocerus	86.5	7	10
Cantherhines pullus	42.8	19	27
Acanthostracion quadricornis	30.7	6	6
EASTERN TROPICAL PACIFIC			
Holacanthus passer	71-80	1	6
Pomacanthus zonipectus	53-60	1	6

In summary, rich nutrient inputs from upwelling or terrestrial runoff stimulate phytoplankton blooms which increase zooplankton production which, in turn, produces large stocks of predatory animals (Ryther 1969; Lasker 1975, 1978; Methot and Kramer 1979). The population densities of browsing and grazing fishes off the Pacific coast of Panama were about an order of magnitude (5 to 20 times) greater than on Caribbean reefs. The grazing pressure on sponges on overturned rocks was also an order of magnitude (about 25 times) greater off the Pacific coast of Panama (Table 2). As browsing and grazing fishes become more abundant, the grazing pressure increases. As the grazing pressure increases, the standing stock of sessile prey decreases and rate of turnover increases. As standing stock of prey decreases, the browsers and grazers are faced with less of any particular resource and so become more generalized in diet which, in turn, compounds the grazing pressure.

TURNOVER IN OCCUPATION OF SPACE

The interactions between corals, sponges, ascidians, and other sessile or sedentary organisms were observed at Punta Galeta on the Caribbean coast of Panama over a 5-year period (1970-1975). Competitive interactions occurred constantly in the Caribbean benthic communities, but the net effect on community structure was very little. A sponge would overgrow a parcel of a coral, then retract, leaving a small bare spot; the same sponge would again overgrow a different parcel of the coral, then again retract (Figs. 5, 6). In six permanent subtidal quadrats over a period of 5 years, the average change per 1-year period in occupation of the primary substratum was 15%.

Permanent quadrats were also established at Playas del Coco on the Pacific Coast of Costa Rica over a 1-year period, and monthly observations were usually made at a study site at Isla Taboguilla on the Pacific Coast of Panama over a 5-year period. At these sites in Panama and Costa Rica, the turnover in occupation of space was over 99% per year (Fig. 7).

These quadrats in both oceans were not subjected to any large irregular disturbances (e.g., hurricanes, slumping of substrata, El Niño effects, lava flows) and the effects of these large irregular disturbances (disasters or catastrophes) will not be considered in this study. Here we are assuming that only what are considered to be regular disturbances (predation, disease, competition, seasonal input of nutrients) have occurred, and they are assumed to be at their typical levels.

In the Caribbean quadrats, the competition for space was easy to observe, yet the net effect was very little.

Fig. 5. Interaction between a sponge (Mycale adhaerens) and a coral (Montastrea cavernosa) over a 52-month period. A-November 1970, B-September 1972, C-March 1974, D-March 1975.

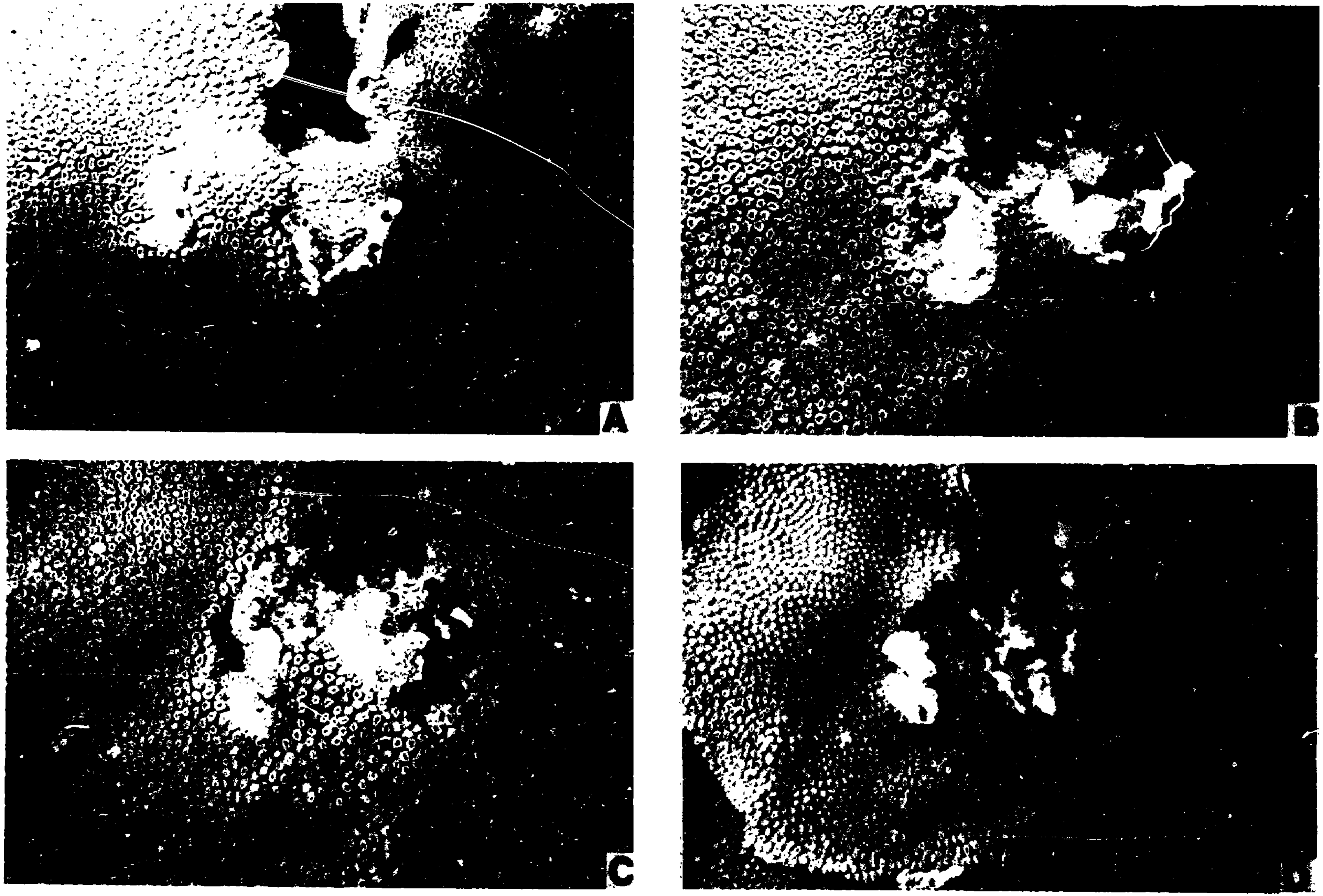
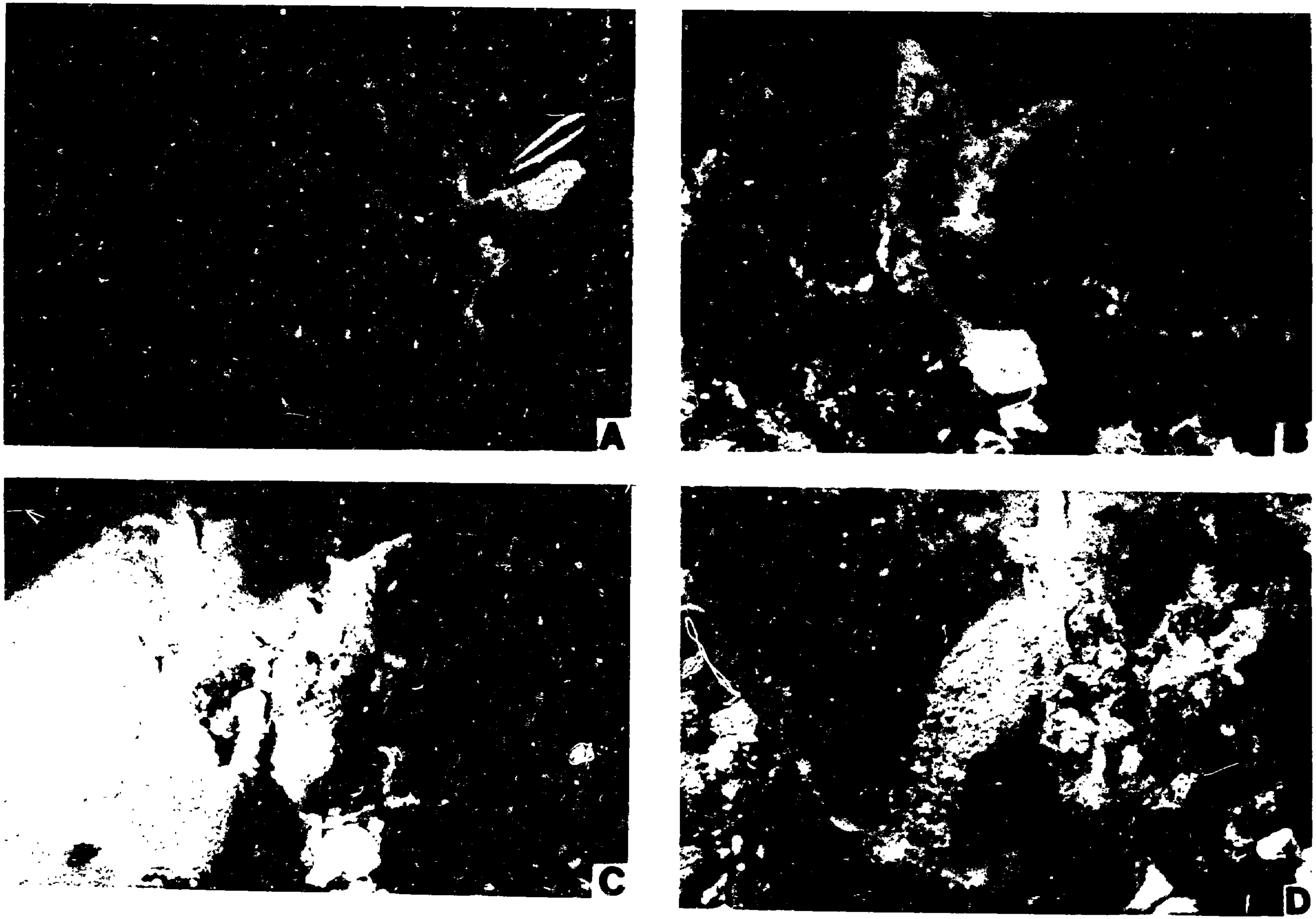


Fig. 6. Interaction between a sponge and a coral *Siderastrea sidera* over a 52-month period. A-November 1970, B-September 1971, C-March 1974, D-March 1975.



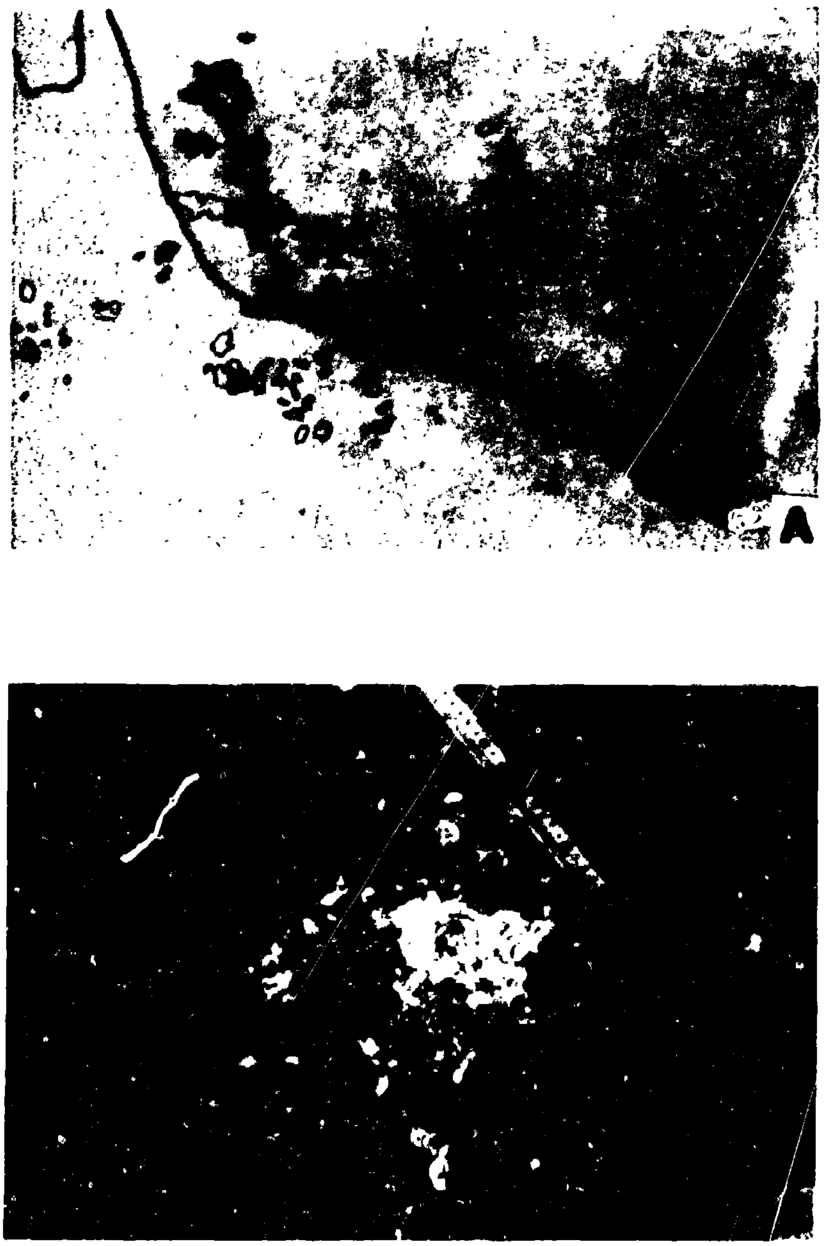


Fig. 7. Turnover of sessile benthic fauna in the tropical eastern Pacific. A - map of location of Polyandrocarpa (social ascidians) in February 1970 (open outlines) and February 1971 (lightly shaded patches); B - small barnacles, bivalves, sponges ascidians, bryozoans, and hydroids probably grazed by a balistid.

Similarly in Oceania, the competition for space among adult coral colonies was frequently observed (Fig. 8), but no evidence of signficant impact on community structure was obtained (Bradbury and Young 1982; Birkeland et al. 1982). Recent recruits and juvenile corals are often killed by competition from algae and colonial animals, but no adult coral colonies were observed to be completely killed by competition with other corals. In contrast, complete mortality of adult coral colonies from predation (by Acanthaster planci), competition with organisms from other phyla (Terpios sp.), or physical environmental stress have been documented. It may be suggested that the time scale of our observations may have been too short for competition between adult corals to be followed to completion; but I doubt this is an important factor because changes resulting from competition are frequently observed. Our time scale is adequate for observing back-and-forth changes by overgrowth. It is the net change that is minor.

Even in environments such as the Gulf of Panama with substantial input of nutrients, where successful recruitment of corals is rare and occurs mainly in crevices (Fig. 2), adult colonies can survive for long periods of time once established. About 35 adult colonies of Pocillopora damicornis ("P. cespitosa" form) were present at the Isla Taboguilla study site. They were in good health and apparently grew rapidly, but they changed shape without showing substantial net growth. Branches would be knocked off, apparently by physical forces, and so there was no obvious net gain in the population over the 5-year period of study (Birkeland 1977) despite their rapid growth rates (Richmond 1985, 1987). No successful recruitment of hermatypic corals was observed in the region of upwelling nutrient-rich waters during this study. The processes that influence recruitment have major long-term influences on benthic community structure. The success of coral recruitment is inversely related to rate of nutrient input into the habitat (Birkeland 1977). Interactions among established adult colonies have less net impact.

INFLUENCES OF GRAZING INTENSITY

Since heterotrophic animals grow fast in the Gulf of Panama and since they recruit frequently, then why are most of them so small? Although sponges in exposed situations in the eastern tropical Pacific were generally small or thinly encrusting, the sponges under rocks in the eastern tropical Pacific appeared to be just as large as sponges under rocks in the Caribbean.

A dead coral knob at Punta Galeta on the Caribbean coast of Panama was already encrusted with a large Placospongia intermedia in August 1970. The sponge remained essentially

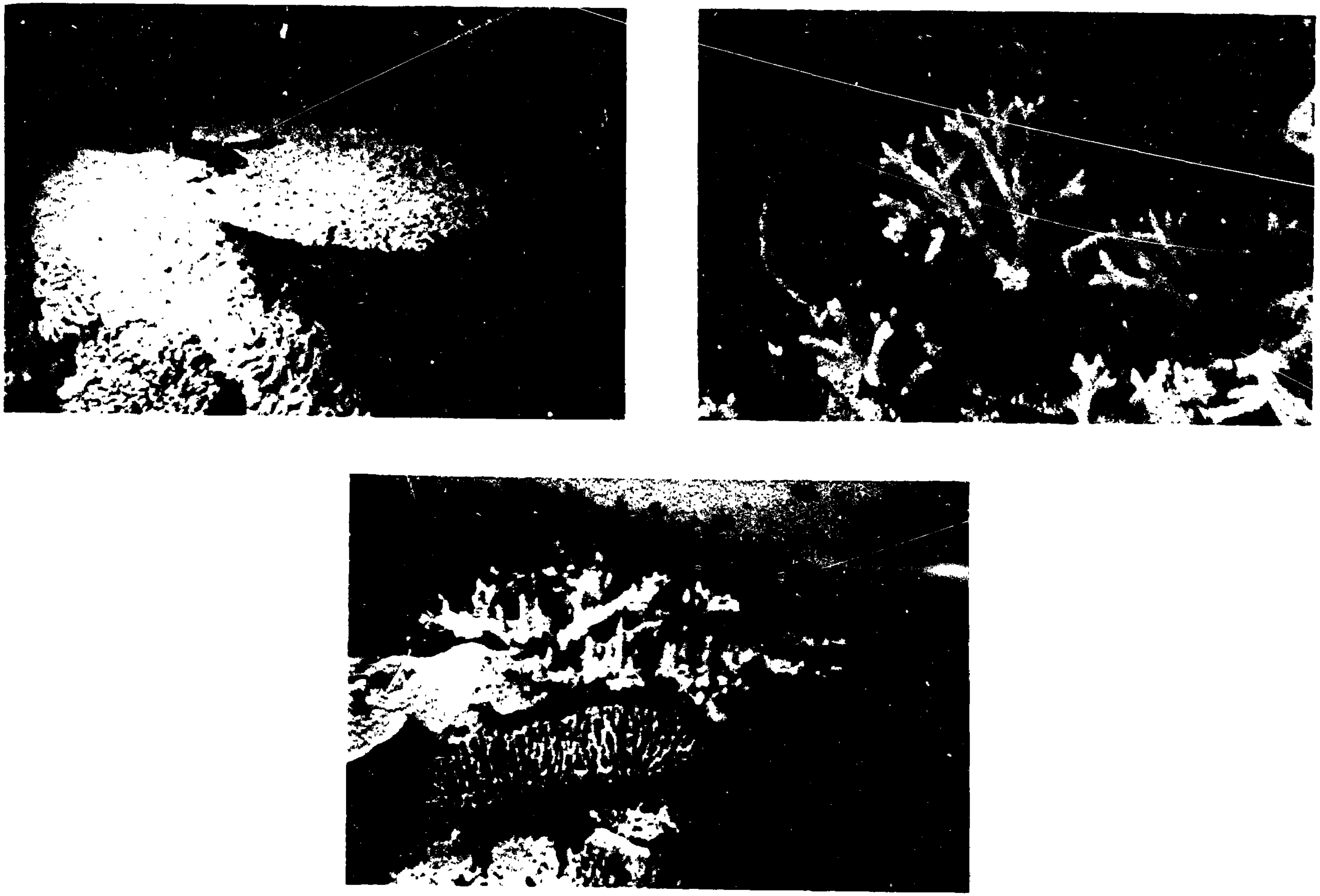


Fig. 8. Overgrowth of one coral colony by another at American Samoa. Damage to the colony beneath appeared to be negligible.

unchanged in its prominently exposed position through June 1975; it may still be there. Small (ca. 9 cm^2) *P. intermedia* have been seen in upward facing positions in the eastern tropical Pacific resembling shadows at the base of empty tests of barnacles or basal shells of oysters. Larger *P. intermedia* were occasionally found on the undersides of rocks in the eastern tropical Pacific. When the rocks were turned over, the *P. intermedia* were grazed by fish (*Pomacanthus zonipectus* and several damselfish) within a few hours.

To test whether sponges were physiologically capable of growing large on upward-facing surfaces in the eastern tropical Pacific, 5 rocks were placed in boxes made of plastic screen (Vexar) at Playas del Coco, Costa Rica, and at Isla Taboquilla, Gulf of Panama. Within 5 months the sponges grew up and covered the upper surfaces of the rocks (Fig. 9A). Other animals usually found under rocks, such as colonial ascidians and sabellid tubeworms, also grew up and around to the upper surfaces of some of the rocks. The plastic wire mesh certainly changed many physical and biological factors of the environment of the rock so the information available does not allow us to determine which factors were most important in stimulating the growth onto the upper surface. However, when the rocks were removed from the boxes at Isla Taboquilla, fishes such as *Pomacanthus zonipectus* began pecking at the sponges immediately. Within 3 days, the sponges were essentially gone, except for a few small patches (Fig. 9B). Although the cages may have influenced the patterns of growth of sponges, ascidians, sabellid tubeworms, and other organisms which usually live under rocks by changing the physical environment, intense grazing by fishes ultimately prohibits some species of large sponges and sabellids from living on exposed surfaces.

With abundant recruitment of grazing fishes, the grazing intensity is very great. Under heavy grazing pressure, the removal of sponges and other encrusting animals increases to the point at which the population consists of small individuals and has a rapid turnover time. The few exceptions are either organisms that have originated in a protected situation and have reached a refuge in size, or are organisms that have toxins or armature. The sponges and ascidians under rocks appear similar to those in the Caribbean. A few scleractinians reach a size large enough to afford the loss from grazing by fishes. Most of the *Pocillopora damicornis* colonies at the study site at Isla Taboguilla in the Gulf of Panama appeared to originate in small crevices (Fig. 2). The bright blue ascidian *Rhopalaea birkelandi* releases an acid ($pH \leq 2$) when slightly bruised, and its body contains about 610 ppm vanadium (Stoecker 1980). It is conspicuous, yet apparently not preyed upon.

The western tropical Atlantic fishes that feed on sponges are apparently relatively scarce and relatively

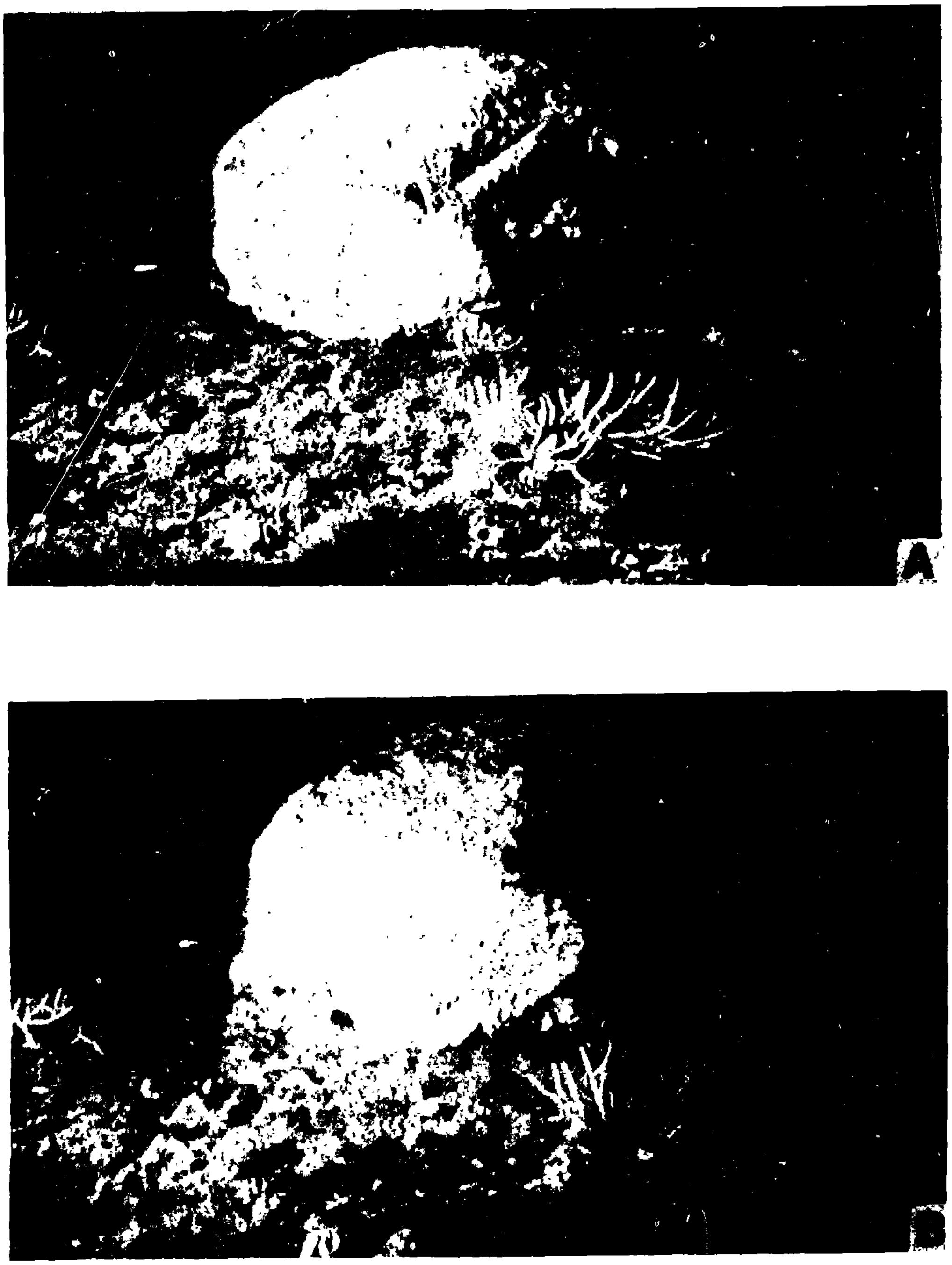


Fig. 9. A rock which was overgrown by a sponge while in a fish-exclusion cage at Isla Taboquilla, Gulf of Panama, was removed from the cage to determine impact of grazing by fishes. A - immediately after removing from the cage; B - 3 days later.

specialized on sponges. Holacanthus passer and Pomacanthus zonipectus in the eastern tropical Pacific are roughly an order of magnitude more abundant than their combined multispecific counterparts (Table 4) and their combined grazing pressure is roughly an order of magnitude more intense (Table 2). Under such grazing pressure, the sponges in locations exposed to grazing are small and are frequently removed. Under such conditions, there is probably not a sufficient standing stock of sponges to support the large fish population, so the fishes have to broaden their diet. If a large portion of fishes have broad diets, organisms in a large number of taxa have a small standing stock, a size distribution predominantly composed of small individuals, and a short turnover time. These community traits are characteristic of the shallow benthos in the eastern tropical Pacific (Table 4).

Predation could be considered a form of disturbance, but it is not disturbance alone that determines the predominance of species with r-selected traits. The greater rate of predation in the eastern tropical Pacific brings about a greater rate of turnover of space occupation in the benthic community, but despite the greater intensity of predation or grazing, substrata are occupied more rapidly in the tropical eastern Pacific than in the Caribbean. Nutrient input is probably an ultimate factor leading to the abundances of grazers and the concomitant grazing intensity, but it also facilitates abundant recruitment and rapid growth of sessile occupants of space. Species with r-selected traits are capable of taking the most effective advantage of a pulse of nutrients.

Specialized grazers tend to favor the survival of species with K-selected traits by selectively feeding on the species with r-selected traits (fast growth, fewer chemical and morphological defenses). In Oceania, grazing by fishes facilitates and accelerates succession towards a community characterized by a predominance of K-selected species with lower productivity per gram dry weight (Birkeland et al. 1985). The opposite occurs in areas of the tropical eastern Pacific which are subjected to upwelling. Nutrient input appears to lead to abundant recruitment of grazing fishes which exert a heavy pressure on their food resources. As most specific food resources undergo rapid turnover and small standing stocks, the fish must become more generalized in diet. Intense grazing by generalists sets back succession and favors prevalence of r-selected species with higher productivity per gram dry weight (Birkeland et al. 1985).

In summary, the rich nutrient input from upwelling has long been known to produce large stocks of fishes (Ryther 1969). Large stocks of fishes impose intense grazing pressures. Intense grazing pressures increase the rates of turnover. The increased turnover produces a small size

Table 4. Characteristics of coastal, shallow, hard-substratum benthic communities on the Caribbean and Pacific coasts of Panama.

	Caribbean	Gulf of Panama
% space occupied by same INDIVIDUALS after 1 year[1]	85	1
% space occupied by same SPECIES after 1 year[1]	86	3
time for clean substrata to resemble surrounding community[2]	several years	4-6 months
biomass of fouling community after 77 days[3]	27-54 g m^{-2}	41-306 g m^{-2}
body or colony size of exposed sessile animals	large	small
body or colony size of sessile animals under rocks	no difference	
occupants of majority of space on fouling panels after 77 days	algae	animals
number of individual *Holacanthus* observed per 30-minute period[4]	2	42
number of *Arothron* or *Diodon* observed per hour[5]	0.7	3.4

Table 4. Continued.

	Caribbean	Gulf of Panama
% sponge grazed from overturned rock per 3-day period[6]	2	52
competition for space by sessile animals	OFTEN OBSERVED relatively unimportant in determining community structure	NOT OBVIOUS, but probably very important in determining community structure by affecting recruitment

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1. Based on photographs of 6 permanent quadrats over a 52-month period at Punta Galeta on the coast of Panama, on 2 permanent quadrats over a 1-yr period at Playas del Coco on the Pacific coast of Costa Rica, and 4 permanent quadrats at Isla Taboquilla in the Gulf of Panama.
2. Observations on terra cotta and on cement construction blocks.
3. Birkeland 1977: Table 2.
4. Based on six 30-minute counts in each ocean.
5. Glynn et al. 1978.
6. Table 2, this paper.

distribution in prey populations which favors species with r-selected traits. The possibility of a species with K-selected traits reaching a refuge in size or becoming large enough for its toxic properties to be recognized become less. With small standing stocks of each species of benthic organism, the grazing fishes must generalize. With each grazer acting as a generalist, the intensity of grazing on most small organisms is increased. This scenario is consistent with the comparative characteristics distinguishing the Caribbean coral communities from the eastern tropical Pacific coral communities (Table 4).

NUTRIENTS SHIFT SUCCESSION FROM K-SELECTED TO r-SELECTED TRAITS

Textbooks on ecology present model systems in which species with r-selected traits are eventually outcompeted by species with K-selected traits. The r-selected species are said to depend on repeated disturbances for opportunities to perpetuate themselves. This appears to be true for low-nutrient and perhaps moderate-nutrient systems. As nutrient input increases the model is no longer appropriate. When nutrient input comes in large pulses, species with K-selected traits are not able to become established and species with r-selected traits perpetually prevail.

A. Outcome of Competition

Hermatypic corals and crustose coralline algae are examples of K-selected species. Their algal cells provide mechanisms for growing in nutrient-poor environments. Some species of corals grow huge and are apparently able to live for hundreds of years. Corals and coralline algae appear typical of species adapted to nutrient-poor environments in their ability to persist and in their inability to respond quickly and grow rapidly when a nutrient pulse occurs.

Filamentous algae, barnacles, ascidians, filter-feeding bivalves, etc., are r-selected species. They are able to respond quickly and grow especially rapidly when a nutrient pulse occurs. This favors r-selected species over K-selected species both in terms of competitive pressures and predation pressures. Corals have a difficult time recruiting by planulation in upwelling regions because filamentous algae, barnacles, ascidians and bryozoans grow so rapidly that the coral spat are overgrown, smothered by sediment between the algal fronds, or shoved off by barnacles.

The development of benthic communities under different levels of nutrient input, e.g., at coastal and offshore island locations on the Caribbean and eastern Pacific coasts of Panama, were compared by following the growth of sessile communities on fouling panels (Birkeland 1977). The benthic community in the region of upwelling on the Pacific coast accumulated over 10 times the biomass per unit time as compared to the amount accumulated at the offshore islands on the Caribbean coast (Tables 2 and 5 in Birkeland 1977). Sponges, ascidians, bryozoans and barnacles occupied the entire surface of the panels within 60 days at the eastern Pacific sites (Meyer and Birkeland 1974). In contrast, filamentous algae and crustose coralline algae were the principal occupants of space on panels on the Caribbean coast and, not considering microbes, 60 to 80% of the space on panels was still unoccupied after 60 to 70 days (Meyer and Birkeland 1974). While 262 hermatypic corals successfully recruited to 262 panels in the Caribbean (the average of exactly 1.0 is a coincidence; the recruitment was aggregated in distribution), only 2 coral recruits were observed on 251 panels in the region of the eastern Pacific subject to upwelling nutrient-rich waters. Barnacles in the upwelling region were able to attain basal diameters of 15 mm within 56 days and the two coral recruits, with basal diameters of 2 mm each, were doomed to be pushed off the plate by barnacles or overgrown by sponges, ascidians or bryozoans.

Similar results were observed on cement construction blocks and terra cotta tiles that were placed on the two coasts of Panama for over 3 years. At the offshore San Blas Islands in the Caribbean, we found 173 successful coral recruits of 12 genera on 6 cement construction blocks after 39 months (Table 4 in Birkeland 1977). At Punta Galeta on the Caribbean coast, a cement block was settled by 19 colonies of 4 species which together occupied 35% of the surface of the block within 4 years. In contrast, cement blocks set on a solid cover of living Pocillopora on the lee side of Isla Taboguilla in the eastern Pacific were never colonized by hermatypic corals. Their surfaces were quickly monopolized by tunicates, bryozoans, barnacles and algae. The Pocillopora on which the blocks were set began to grow up and around the blocks. After 2 years this gave the illusion that the blocks were gradually sinking into the reef. Established colonies and communities of adult corals do well in the eastern Pacific (disregarding disasters or irregular larger scale disturbances such as El Nino), but there was no noticeable recruitment at the study sites between 1970 and 1975.

Although successful larval recruitment of hermatypic corals was not observed in the Gulf of Panama during this 5-year period, there was repeated successful recruitment and population turnover of small sponges, barnacles, bryozoans, ascidians and hydroids, the predominant occupants of the primary substrata.

A hypothetical analogy to the situation of hermatypic corals in upwelling regions might be a tree in the rich soil of a sugarcane field. The tree may grow well and prosper;

once it is a tall tree, the sugarcane will not overgrow it. But getting started as a seedling in the fast-growing sugarcane would be very difficult.

Large colonial organisms appear to grow well and maintain themselves for years in both in the Caribbean and in regions of upwelling in the eastern Pacific (if there are no major disturbances). But while species of potentially large forms have been able to recruit periodically and thus have been predominant in the Caribbean, recruitment has been difficult for large colonial organisms in the eastern Pacific. Although adult large benthic sessile organisms survive and grow well in either ocean, successful recruitment in nutrient-rich upwelling waters is almost entirely by smaller heterotrophic colonial animals (e.g., bryozoans, colonial ascidians), heterotrophic solitary animals (barnacles, solitary ascidians, small encrusting sponges), and algae.

The success in recruitment of scleractinian corals is inversely correlated with rate of benthic biomass accumulation (Birkeland 1977). On the Caribbean and Pacific coasts of Panama, the gradient of prevalence of scleractinians in the benthic community was inversely correlated with the rate of biomass accumulation on fouling panels at the site. Offshore Caribbean reefs had the best coral cover, followed by continental coastal Caribbean reefs, followed by nonupwelling side of Gulf of Panama island reefs, followed by hard substratum communities in regions of upwelling. The rate of benthic biomass accumulation increased along the same sequence from offshore Caribbean to a region of upwelling in the Pacific (Table 2 in Birkeland 1977); therefore, there was a significant inverse correlation between hermatypic coral prevalence and rate of biomass accumulation ($r_s = -1.0$, $p < .05$).

I propose that as nutrient input increases, small, rapidly-growing organisms with r-selected traits prevail because they are able to respond more immediately and directly to a pulse of nutrients into the system. Nutrients are also favorable to the growth of organisms with phototrophic symbionts, but these organisms are adopted to efficient recycling of nutrients in nutrient-poor environments (Muscatine and Porter 1977) and they are not as capable of rapid growth in nutrient-rich environments, especially if nutrient input comes as a pulse. When nutrient input is great enough, organisms with r-selected traits (e.g., filamentous algae, barnacles, bryozoans) cover the substratum so rapidly that newly recruited organisms with K-selected traits (e.g., hermatypic corals) are overgrown or pushed off the substratum. As nutrient input decreases, the rate of biomass accumulation of the benthic community decreases and hermatypic corals have a greater chance of reaching a refuge in size from being overgrown.

The differences in rates of biomass accumulation between geographic locations at comparable depths is influenced by nutrient input. At a given locality, the rate of biomass accumulation of algae is related to light which decreases with shading and depth. Although hermatypic coral recruits grow faster on the upper surfaces of artificial substrata on coral reefs, survival is greater in the shade on vertical and under surfaces (Birkeland 1977). Growth of recruits is faster in shallow waters, but survival increases with depth, at least to 20 m, as the light decreases (Birkeland 1977).

B. Effects of Predation

Small rapidly-growing species are more successful than slowly-growing species when subjected to consistently intense grazing or browsing pressure, even if the slowly-growing species are distasteful or toxic and avoided by grazers. Observations indicate that this difference in success results from relative rates of growth to a critical size. Toxic algae are found in widely-scattered patches or clumps when grazing intensity is high. This is probably not entirely a result of patchy recruitment because algae cover fouling panels fairly uniformly when the panels are protected by fish-exclusion cages. It appears that when toxic or distasteful algae are very small, the grazing fishes do not distinguish them from other components of the algal turf and they are taken incidentally. If grazing is intense, the toxic or distasteful algae rarely reach a recognizable size. Once this size is reached, the algae is avoided by grazers and browsers and will persist as one of several isolated patches of the species. If grazing pressure is relatively low, many algae will reach the critical size and the toxic alga will form a more extensive stock.

The same is true of corals. Although fish can recognize and avoid biting corals as small as 2.5 mm diameter (Birkeland 1977), echinoids can harm recently settled corals indiscriminately (Schumacher 1974; Sammarco 1980) until the corals become large enough to be obstacles.

C. Summary

As nutrient input increases, species with r-selected traits are favored over species with K-selected traits in both competition and effects of predation. Species with r-selected traits are generally able to respond quickly and grow rapidly as an indirect result of strong nutrient pulses. Species with K-selected traits are not able to grow as rapidly and are swamped. In regions with frequent large inputs of nutrients, species with K-selected traits are rarely able to become established, so species with r-selected traits dominate. Likewise, as the intensity of grazing or browsing and degree of dietary generalization of grazers or browsers increase with nutrient input, relatively slow-growing species with K-selected traits such as chemical or structural defenses become increasingly unlikely to reach a size at which their defenses are effective. The species with rapid growth responses prevail.

PRACTICAL IMPORTANCE FOR RESOURCE MANAGEMENT

An understanding of sources and rates of nutrient input into coastal marine habitats on geographic and local scales, and a knowledge of how differences in the magnitudes and rates of nutrient input influence marine communities, is of more than academic importance. The practical importance of the subject in the past has been the nearly total (>90%) dependence of traditional human populations across Oceania on protein from the sea (Johannes 1977) and the influence of coastal processes on offshore as well as nearshore fisheries. An understanding of the influence of nutrient input into coastal marine systems is now of practical importance from an international perspective, and is urgent, because human population growth, urban or agricultural development in coastal regions, socioeconomic changes, and new technologies are causing rapid and widespread changes in patterns of nutrient input.

A. The International Perspective

The desirability of an international cooperative approach to these matters of nutrient input is that processes on the coasts of certain nations can affect the fisheries or general biology of another region. Ryther (1969) stated that regions of nutrient upwelling comprise no more than one-tenth of one percent (1/1000) of the ocean surface, yet produce about half of the world's supply of fishes. The nutrients, when taken up by phytoplankton, move downstream out of this relatively tiny area. Depending on the patterns of currents and gyres, the production from upwelling regions can cross boundaries of international waters. Likewise, the nutrient input by major rivers affects the coastal productivity on an international level. For example, when the Aswan Dam was closed, the nutrient concentrations in the Nile flood water decreased, the phytoplankton blooms associated with the floods disappeared and, consequently, the fisheries catches for the multinational eastern Mediterranean decreased to within 3.7% of their former levels (Aleem 1972). Alternatively, increased agricultural or urban development could increase the nutrients and sediments in a river discharge which could in turn affect the coastal habitats for hundreds of kilometers in terms of the sources and distribution paths of nutrients influencing productivity in coastal and oceanic waters. This is a subject of international cooperative interest.

The upwelling of nutrients directly affects the growth of phytoplankton, but it doesn't affect higher levels in the phytoplankton food-web until the phytoplankton increases its standing stock. Upwelling near the southeast edge of Taiwan enhances the fisheries of Okinawa, possibly because the concentrations of phytoplankton, then the standing stock of zooplankton and small fishes, increase as the Kuroshio Current flows northward from the site of the upwelling off Taiwan to the coast of Okinawa.

Sometimes the source of brood-stock for a species is also international. The dominant coral in the eastern Pacific (Pocillopora damicornis) was devastated by the 1982-83 El Niño event. Since P. damicornis does not produce larvae in the eastern Pacific (Richmond 1985), isolated populations may be dependent on larvae from the Line Islands, and/or small colonies attached to floating objects originating elsewhere in the Pacific, for genetic heterogeneity and, in some cases, for reestablishment of a local population (Richmond 1985). The unusual appearance of mangrove crabs in New Zealand was probably the result of a concentration of larvae transported by a coherent water mass from Australia (Dell 1964; Manikiam 1967). Yamaguchi (1987) describes how pseudopopulations of Acanthaster planci at high latitudes at Japan are established by larval transport. Both recruitment and over-winter survival of A. planci are determined by fluctuations in the Kuroshio Current.

Primary outbreaks of the crown-of-thorns starfish at Green Island may be partially a result of pulses of nutrients from the Burdekin river, 400 km to the southeast (Birkeland and Wolanski 1987), and secondary outbreaks may spread for hundreds of kilometers by transport of larvae southward by currents (Kenchington 1977).

Although the Pacific is partially interconnected by the transport of nutrients and larvae by major water currents, the Pacific is a mosaic of interacting areas, and not so completely interconnected as is the Caribbean. Diseases of echinoids or sponges spread throughout the Caribbean; a mass mortality of Echinothrix in the Pacific was limited to the Hawaiian Islands. Crinoids and most other taxa are distributed throughout the Caribbean, but a gradient of decreasing diversity runs from west to east in the tropical Pacific. Over 90 species of crinoids are found on reefs in Indonesia, about 30 are found in Palau, 6 at Guam, and none in French Polynesia. Even entire habitats, such as mangroves, decrease in prevalence from west to east across the Pacific. In the Pacific the question of regional isolation is of importance for barriers to the spread of disease and outbreaks of alien species, as is the question of interconnection for reestablishment of overexploited biological resources. All nations bordering the Caribbean should have a direct interest in any coastal resource management activities of all other nations in the Caribbean because all regions in the Caribbean are interconnected. The Pacific may be more of a mosaic of interconnected regions, partially isolated from other regions, and so resource management in the Pacific may be divided into subregions of international cooperative programs.

B. Implications for Differences in Resource Management Programs

People living on small islands in the Pacific, especially on atolls, are dependent upon the coastal marine habitats for sustenance. Over 90% of the protein for people living on atolls traditionally came from the sea (Johannes 1977). Residents of Pacific atolls become especially dependent upon the sea after typhoons, dependent for items with caloric value as well as protein. This is because the wind knocks down coconut palms, breadfruit and pandanas, and waves crossing the entire motu deluge the taro patches with seawater. It takes years after a typhoon for new trees to grow and for the salts to rinse out of the taro patch depression. In speaking of the effects of a typhoon at Jaluit Atoll in the Marshalls, Blumenstock (1958) noted that "the inhabitants report better fishing since the storm than there was before; but it is possible that they gain this impression through having to fish more intensively than before, since vegetable food is in short supply."

The soils of atolls are calcareous and, whether covered with volcanic materials or not, their fertility depends entirely on the organic matter content (Latham 1982). The organic matter can be high under natural vegetation but can decrease dramatically as a result of inappropriate cultivation techniques. The entire soil can be buried under coral rubble or scoured away during typhoons. The potential for commercial development of terrestrial resources has been limited to coconut plantations for copra production, an economy subject to vagarities of the world market and destruction by typhoons.

Residents of large high islands or coasts of continents need not be so totally reliant on the sea. If a taro patch near the shore is innundated by saltwater, the people can move inland to a suitable location for another taro patch. They also have more options for sources of protein and vegetable matter.

However, people on large high islands or continents have a greater potential of influencing productivity of large areas of coastal or even offshore habitats by increasing or decreasing nutrient input. The international effects of the Aswan Dam and the potential scale of influence of the Burdekin Dam are examples already mentioned. The effects of urban development and sewage discharge on nutrient input, and subsequent changes in marine community structure and productivity of Kanoeho Bay, Oahu, Hawaii, over a 30-year period has been well documented (Smith et al. 1981).

Gradual changes in Pacific coastal ecosystems over a larger scale in the western Pacific during the previous two decades may be resulting from human activities. Paralytic shellfish poisoning (PSP) was known from temperate Pacific waters for centuries, but not from the tropical Pacific. People have been dying and hospitalized from PSP at an accelerating rate since 1975 at Kalimantan, Papua New Guinea, Fiji, Solomon Islands, Indonesia, Phillippines, and both coasts of India (Maclean 1984). That dinoflagellate blooms have been increasing at a geometric rate in both frequency and magnitude has been documented since 1975 at Hong Kong (Maclean 1984, Holmes and Catherine 1985). I hypothesize that PSP and dinoflagellate blooms are indicative of an increase in frequency and magnitude of phytoplankton blooms in general, that these increases are brought about by increased nutrient input in continental and large-island regions (but not around atolls) and this widespread increase in nutrient input may be a result of a major increase in deforestation in coastal regions.

If increased nutrient input from deforestation and agricultural, urban and industrial development is increasing the frequency and intensity of phytoplankton blooms in the western Pacific, the subsequent changes will be multifaceted. Not only might we expect a greater frequency of human deaths and hospitalizations from PSP and an increase in numbers of coral reef fish mass mortalities, we can expect widespread changes in natural communities. If outbreaks of the crown-of-thorns starfish (Acanthaster planci) are partially a result of phytoplankton blooms (Birkeland 1982) which, in turn, are facilitated by land-clearing activities of humans (Nishihira and Yamazato 1974), then we might expect A. planci outbreaks to be increasing in frequency since the 1960s. An increase in frequency in A. planci outbreaks will bring about drastic changes in the benthic community (Endean 1973, Pearson 1981) and coral reef fish community (Sano, Shimizu, and Nose 1984; Williams 1986; Wass 1987) structure. Since the ultimate potential for harvest of reef fish in, for example Palau (Micronesia), is of about the same magnitude as is the offshore tuna harvest (Mitchell 1975, Johannes 1977), these potential effects of increased nutrient input on reef communities by PSP, A. planci outbreaks, and other factors resulting indirectly from increased nutrient input will influence the economies and subsistence of local peoples.

Although islanders are more dependent upon coastal marine resources for their livelihood and although these resources may be more vulnerable to overexploitation and nutrient depletion, only the peoples on the coasts of high islands and continents are in situations in which their actions which cause increased nutrient input could have more widespread, even international, repercussions. In order to rationally manage coastal resources, we must have both a better knowledge of the natural sources of nutrient input (Birkeland 1984) and the influence of human activities on creating new inputs or depletions of nutrients.

Over centuries or millenia, atoll dwellers and inhabitants of continental coastlines may have adapted their resource management traditions to their different local situations in ways that accommodate the differences in rates and magnitudes of nutrient input. "Possessing a fishery which was readily perceived as being limited, [South Pacific] islanders therefore viewed marine resources in a way fundamentally different from continental peoples who possessed abundant terrestrial resources of animal protein and who had access to wide continental shelves. Some Pacific islanders knew for centuries that their marine resources could be easily depleted and so had devised a variety of measures to guard against this eventually, including territorial use rights, closed areas or seasons and size restrictions" (Ruddle and Johannes 1985:3).

At the UNESCO/COMAR Workshop on Inter- and Intraoceanic Tropical Coastal Ecosystems (University of the South Pacific, Suva, Fiji, 24-29 March 1986), it was noted that traditional rules of reef tenure and coastal resource management may be stronger at the oceanic islands and atolls of the Pacific than in the Caribbean. Although territorial aspects of reef tenure systems develop in areas where resources are being exploited for commercial purposes, the restrictions on size, breeding season, spawning area, etc., may be controlled with more detailed regulations in oceanic island and atoll situations. An hypothesis was proposed at the workshop that human societies may have evolved strict systems of tenure and protocol for management of marine resources in regions of low nutrient availability and recycling of materials, while societies have tended to evolve free-for-all systems of utilization and barter in regions of nutrient input (terrestrial runoff or upwelling) and high productivity.

This gradient of nutrient input in different regions of the Pacific leads to a dichotomy of appropriate resource management and exploitation strategies. Although management and exploitation are complementary aspects of any system, the emphasis in nutrient poor environments tends to be on management in the recent past and present, while the emphasis in nutrient rich environments has been on exploitation. For example, the waters of Takapoto, an atoll of the Tuamotus, are extremely oligotrophic, both in the lagoon and in the oceanic waters surrounding the atoll (Sournia and Ricard 1975). Here, the main industry of Takapoto involves the production of pearls by filter-feeding bivalves. This is a labor-intensive industry in which only the pearls are exported. The meat is consumed and sewage and shells are returned to the lagoonal system. The export of organic material on a large scale from an atoll might cause nutrient depletion at a rate at which the system would be unable to replenish and maintain itself.

Regions of upwelling, such as the Gulf of Panama or the coast of Peru, are able to exploit and export large quantities of organic matter year after year because of repeated nutrient input on a large scale. At tropical atolls, the emphasis should be more on management and recycling. Like tropical rainforests, coral reef ecosystems may be able to withstand pruning and recycling but not the kind of mass harvest and export sustained by upwelling regions. The nature of nutrient input into the system therefore has fundamental influences on the operation of the natural communities which leads to basic differences in rational management strategies for human populations in these different regions. This hypothetical framework for regional differences in management plans is not established or recognized because of the anecdotal or fragmentary nature of the available information and data. An international coordinated cooperative approach is necessary to assess the validity of this theoretical framework for resource management in the tropical coastal regions of the Pacific.

C. The Urgency

It was not long ago when human populations in Oceania with subsistence technologies and with cultural regulations on harvest and exploitation were able to maintain renewable resource yields in harmony with the environment. Humanity has now progressed to the point at which it has the technology and abundance to change the CO_2 content of the entire earth's atmosphere, to reduce the productivity of the eastern Mediterranian by over 96%, and to cause the extinction of hundreds of species.

Major changes in coastal ecosystems of the Pacific region are probably already underway as a result of human influence on the distribution of nutrients, especially between terrestrial and marine coastal systems. These changes will affect the economies and the well-being of the peoples of the regions. Whether or not the increases in cases of PSP and in frequency and lengths of Acanthaster planci outbreaks are indicative of an increase in nutrient input from deforestation is conjecture at this time. This is because we do not have enough knowledge of the natural sources and distributions of nutrients in the coastal marine ecosystems in the Pacific region, nor do we have an adequate understanding of the influence of nutrient inputs on the functioning of marine communities. We do not have any direct information on the degree to which human activities such as construction of dams, creation of breakwaters, deforestation and urban development are altering the nutrient distributions. The inhabitants of the Pacific coasts are nouveau riche with modern technologies; we must obtain some understanding of the major effects of human activities on the nutrient availability in coastal marine ecosystems before the changes progress too far while remaining unrecognized.

The increased influences of humanity on coastal marine ecosystems are occurring because of at least three factors: increased populations, socioeconomic changes, and techonological advances. Human population increases affect coastal regions first and with the greatest impact because humans tend to settle first in concentrations in coastal areas with the richest resources. The river mouths and harbors were settled first because of the advantages for transportation and the richness of both terrestrial and marine habitats in these locations. These are the areas of greatest degree of interaction between terrestrial and marine ecosystems. Even the point of influence of erosion from land-clearing in highland country on marine ecosystems is at the river mouths and harbors. It is at these sites, however, where the activities such as reclamation of land from mangroves, dredging of channels, and construction of breakwaters may have the greatest effects on productivity of coastal marine habitats. So while coastal resources have been traditionally the resources most heavily utilized, they are also the areas which most directly and immediately feel the impact of man's activities. An understanding of how coastal ecosystems function and interact with each other and with the abutting terrestrial and offshore areas is of primary importance as a basis on which to make sound rational decisions in developmental and coastal zone resource and land management matters. These matters are becoming more urgent as human population growth increases these pressures on these critical regions.

Major socioeconomic changes that affect management of coastal ecosystems are the loss in authority of traditional regulatory guidelines for resource use and a switch to international monetary exchange. Traditional resource-use strategies had an emphasis on management and they tended to promote sustained yields. Modern monetary demands produce an emphasis on exploitations and they tend to promote high extractive yields.

The importance of a knowledge of the factors influencing organic productivity in tropical Pacific coastal ecosystems has two sides; we need to know how changes in population size and socioeconomic frameworks will affect these factors, and we conversely need to be able to decide on which resource utilization strategies are the most favorable for the local environment. Perhaps service-oriented economies are best for nutrient-poor atoll lagoons (e.g., pearl production at

Takapoto) and extractive exploitation is the best strategy for regions with nutrient upwelling (e.g., the sardine fisheries off the coast of Peru).

The general changeovers in socioeconomic frameworks that are occurring along with population increases are happening rapidly. A general assessment of the distribution of nutrients and coastal productivity in the tropical Pacific, the interrelations between habitats and regions, and how these are being affected by human activities must be undertaken now because large-scale environment changes may be happening already in the tropical Pacific if the PSP occurrences and Acanthaster planci outbreaks are indicative of changes in nutrient input. An assessment is urgent because rational guidelines are usually less expensive than corrective measures.

The final factor contributing to the recent and dramatic increase in the influence of human activities on nutrient flow in tropical Pacific coastal ecosystems is our rapid technological advancement. A century ago, errors in management would not have the breadth of impact shown by the Aswan Dam. Overexploitation by an individual fisherman with net and spear does not have the breadth of influence of overexploitation with dynamite and Clorox.

D. Summary

It is of immediate importance to understand the reciprocal interactions between humanity and the nutrient cycling in the tropical coastal Pacific. Human populations can possibly affect the nutrient-poor oceanic atolls by overharvesting and can affect the productivity of nutrient-rich nearshore habitats of continental and large island coasts by clearing forests, by reclaiming land from mangroves, and by damming rivers. Conversely, the natural nutrient-transport processes in the region should affect our economic strategies; perhaps communities in nutrient-poor environments (e.g., oceanic atolls) should emphasize management, recycling, and service-oriented economies, while communities in nutrient-rich environments (e.g., regions of coastal upwelling) might be able to emphasize exploitation and export-oriented economies. The assessment is urgent because wide-scale, long-term changes in coastal ecosystems are already underway, occurring rapidly because of recent accelerations of human population increases, socioeconomic changes, and advancements in technologies. A cooperative research effort and information exchange is necessary at an international level in the tropical Pacific because the distribution of nutrients in coastal ecosystems takes place on an international scale.

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SPONGE BIOMASS AS AN INDICATION OF REEF PRODUCTIVITY IN TWO OCEANS

by

Clive R. Wilkinson*

ABSTRACT

Sponges are long-lived filter-feeders that utilize organic matter in the seawater for nutrition. Surveys were undertaken of sponge biomass on the forereef slopes of reefs across the continental shelf of the Great Barrier Reef, at 7 different locations in the Caribbean Sea, and on a reef in Fiji. Sponge biomass was between 2 and 10 times larger on Caribbean reefs than on the Great Barrier Reef, with the greatest difference occurring among exposed, clean-water reefs. The amount of nutrient consumed by Caribbean sponge populations is considerably higher than the 2- to 10-fold difference in biomass. On clean-water reefs, many Great Barrier Reef sponges derive considerable nutrition from photosynthetic symbionts. Therefore it is concluded that more organic nutrient is available in Caribbean waters than in the West-Pacific region, probably as a result of considerably higher productivity.

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*Australian Institute of Marine Science
PMB No. 3
Townsville, M.C., Qld 4810
Australia

INTRODUCTION

Sponges are generally long-lived and derive their nutrition from the organic content of seawater. In this regard they are useful indicators of the long-term availability of dissolved and particulate organic matter. In some coral reef habitats, notably the Great Barrier Reef, there is another category of sponges, termed phototrophs, which derive 50% or more of their nutrition from the photosynthetic activities of symbiotic algae (Wilkinson 1983). This category of sponge has further accentuated the value of sponges as indicators of the trophic and productivity status of coral reef environments. For example, Wilkinson and Trott (1985) showed that sponge populations on nearshore reefs of the Great Barrier Reef were larger and almost totally heterotrophic as compared to smaller populations on reefs further removed from land-derived nutrients. Of these smaller populations, there was a considerable proportion (often greater than 50%) which had essentially phototrophic nutrition.

In this preliminary report, comparisons are drawn between the sponge populations of eleven sites in the Caribbean and those reported previously for the Great Barrier Reef. These comparisons are used in order to comment on differences in the trophic structure and productivity of two different oceanic systems: the Caribbean - western Atlantic Ocean and the Great Barrier Reef - southwest Pacific region.

LOCATIONS

The following 11 sites were surveyed for sponge populations between November 1985 and February 1986 using methods similar to those reported in Wilkinson and Trott (1985): Belize (Wee Wee Cay 13 km from the mainland, Southwater Cay adjacent to Carrie Bow Cay 18 km from the mainland, and Glovers Reef 52 km from the mainland); Jamaica (2 km west of the entrance to Discovery Bay); Puerto Rico (southwest corner near La Paguera); St. Croix (northern coast off Buck Island and west of Salt River Canyon); Barbados (west coast off Bellairs Research Laboratory and southeast coast off Sam Lords Castle); Exuma Cays (Lee Stocking Island east side); Key Largo (French Reef in the Marine Sanctuary). Additional surveys were conducted in Fiji on Great and North Astrolabe Reefs. Sites on the Great Barrier Reef (GBR) are those reported in Wilkinson and Trott (1985) surveying inner-shelf reefs (approximately 18 km from land), middle-shelf reefs (76 km), outer-shelf reefs (126 km) and Coral Sea Reefs (222 km).

RESULTS

A comparison of sponges on the eastern or southeastern faces of reef across the two most extensive barrier reef systems is presented in Table 1. These surveys were conducted at comparable latitudes (Great Barrier Reef between 17° 40' and 19° 00'S; Belize along 16° 45'N), however, the width of the continental shelves is different (GBR 126 km; Belize 18 km). The data show that sponge biomass is 2.1 to 11 times greater on comparable Belize reef sites than on the GBR, with the most marked difference on the ocean-influenced reefs of the outer-shelf (3.6 times) and open ocean (11 times).

Table 1. Mean sponge biomass as wet weight (g m^{-2}) on the fore reef slope at 20 m depth (15 m for inner-shelf reefs) of reefs across two continental shelves (Great Barrier Reef and Belize). Also listed is the proportion of sponge biomass with essentially phototrophic nutrition (deriving at least 50% of carbon nutrition from cyanobacterial symbionts: see Wilkinson 1983; Wilkinson and Trott 1985) and the proportion of species which have cyanobacterial symbionts (from Wilkinson, in press).

	Inner-Shelf		Middle-Shelf	Outer-Shelf		Open Ocean	
site	GBR	Belize	GBR	GBR	Belize	Coral Sea	Belize
no. of reefs	2	1	4	3	1	3	1
biomass g m^{-2}	484	1011	134	137	499	64	703
% phototrophs	0	0	47	38	0	64	0
% with symbionts	9	35	43	58	45	31	46

The proportion of sponges with significant phototrophic nutrition is high on GBR middle-shelf and outer-shelf reefs and on the Coral Sea reefs, whereas no phototrophic sponges were encountered during surveys of any Belize reefs (Table 1). There were, however, comparable numbers of species with photosynthetic symbionts on the Belize continental shelf. These sponges are not phototrophs as they derive only a small proportion of their nutrition from the low content of symbionts.

The marked difference in sponge biomass between the two regions is accentuated when the surveys of 8 sites at 6 other

Caribbean and western Atlantic Ocean locations are included (Table 2). The sites surveyed are listed in three subjective energy categories based on prevailing wind and wave direction and proximity of the nearest barrier to ocean waves. While these data have not been subjected to more detailed analysis it is apparent that sponge biomass on these reefs is markedly higher than on comparable sites on the Great Barrier Reef. For example low energy sites in the Caribbean have 2.6 to 5 times the sponge biomass as sites on the inner-shelf of the GBR (Table 1). Moderate energy sites, roughly comparable to middle and possibly outer-shelf sites on the GBR, contain 4.8 to 10 times the sponge biomass. High energy sites in the Caribbean have between 5 and 6 times the sponge biomass that is found on exposed reefs in the Coral Sea.

The sponge populations on the fringing reef off the north coast of Jamaica are apparently less than those found on the GBR. However, this is considered anomalous as the region was extensively damaged by a severe hurricane 5 1/2 years prior to these surveys (Woodley et al. 1981). This hurricane destroyed all large sponges at this site and all individuals surveyed were considered to be a maximum of 5 years old.

Table 2. Sponge biomass (g wet weight m $^{-2}$) at 20 m depth at 8 sites in the Caribbean as a mean of three 40 m^2 transects. The sites are listed in approximate energy zones relating to degree of exposure to oceanic waves. The Jamaica site is bracketed as it was recently exposed to a single large disturbance event, Hurricane Allen.

Low Energy		Moderate Energy		High Energy	
Reef	Biomass	Reef	Biomass	Reef	Biomass
Key Largo Sanctuary	1259	Puerto Rico southwest	792	Exuma Cays Lee Stocking Id	343
Barbados West Coast	2458	St. Croix north -Buck Island	654	Barbados east coast	368
		-Salt R. Canyon	1354	(Jamaica	97)

A comparison of another site in the southwest Pacific, off the south coast of the main island of Fiji, shows that sponge populations are comparable to, but smaller than, those on reefs in the Coral Sea. The estimated biomass on 3 sites on North and Great Astrolabe reefs was 45, 20 and 8 g m^{-2} whereas the biomass at 3 sites on the Flinders Reefs in the Coral Sea was 82, 57 and 54 g m^{-2}.

DISCUSSION

Coral reefs in the Caribbean - West Atlantic region have between 2 and 10 times as much sponge biomass as reefs in the Great Barrier Reef - southwestern Pacific region. The differences are most marked when reefs remote from large land masses are considered.

The inference is therefore drawn that the larger Caribbean sponge populations consume between 2 and 10 times as much organic matter as sponges on the Great Barrier Reef. Hence there is either a greater availability of organic matter or Caribbean sponges are more efficient in extracting the organic matter from the water column. When the larger populations of phototrophic sponges on the GBR are considered (approximately 50% of the biomass) the difference in nutrient removed by sponges in the two regions is further accentuated as there are no similar sponges in the Caribbean.

While it is possible that some sponges are as much as twice as efficient in removing organic matter from sea water it is unlikely that the Caribbean populations are more than twice as efficient. Therefore the conclusion is drawn that there is 5 to 10 times as much organic matter produced and made available in the water column in the Caribbean region than in the GBR region. The difference may be greater when reefs in Oceania, e.g., Fiji are considered. For example, the difference in sponge biomass between Glovers Reef, an atoll-like formation in the Caribbean, and the Astrolabe reefs of Fiji is approximately 30-fold.

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INTEROCEANIC DIFFERENCES IN ARCHITECTURE AND ECOLOGY: THE EFFECTS OF HISTORY AND PRODUCTIVITY

by

Geerat J. Vermeij*

ABSTRACT

Studies of the architecture of marine tropical organisms reveal striking differences in the degree of development of antipredatory and competition-related traits between the biotas of the major tropical regions. Armor in gastropods, the degree of specialization of shell-crushing predators, crinoid spine armature, and the extent of specialization in intimate associations between guests and hosts are greater in the Indo-Pacific than in the Atlantic, with the eastern Pacific usually holding an intermediate position. These patterns are interpreted to reflect geographical differences in escalation, the evolutionary process in which species adapt to cope with enemies as the latter increase their capacities to acquire and defend resources. Escalation is believed to have proceeded furthest in the Indo-West Pacific because this region has been characterized by low rates of extinction and high rates of species formation. The tropical Atlantic, on the other hand, has suffered high rates of extinction during the Pliocene and Early Pleistocene, during which time species which were highly escalated along with their enemies were especially susceptible to extinction. If additional data support these findings, they will imply the introduction of Indo-West Pacific species to other tropical regions would have more deleterious consequences for the recipient biota than would the introduction of Atlantic species to the Pacific. It is further suggested that areas of high productivity may be important as refuges for species during times of crisis, and that they may therefore be important in preserving highly escalated species. Because much research has been confined to clear-water coral reefs, it is especially important to study interactions among species in highly productive parts of the Indo-West Pacific (especially in southeast Asia) and the eastern Pacific.

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*Department of Zoology
University of Maryland
College Park, Maryland 20742

INTRODUCTION

It has been a central tenet of biogeography that physically similar environments support ecologically and architecturally convergent biotas. Wherever lowland tropical rain-forests grow, the constituent canopy trees are generally characterized by ovate leaves with entire margins and more or less drawn-out tips, and there are many high-climbing lianas among the smooth-barked trees (Richards 1952). Vegetation in areas of Mediterranean-type climate is dominated the world over by shrubs with small leathery evergreen leaves that are often strongly aromatic (Mooney and Dunn 1970). In the sea, wave-swept tropical coasts tend to support large populations of encrusting coralline algae and a diversity of thick-shelled gastropods and barnacles.

More detailed comparisons of physically similar environments usually reveal, however, that there are subtle but ecologically and architecturally important difference among resident biotas. These differences often pertain to the ways in which species interact with each other, and involve traits that enable individuals to cope with biological hazards in their environments.

The purpose of this essay is to review the evidence pertaining to interoceanic differences among shallow-water biotas in the marine tropics. The essay is an updated version by my 1978 book, in which I tried to show that species in the Indo-West Pacific region are in most respects more highly specialized to deal with their enemies than are ecologically similar species in the eastern Pacific and Atlantic. Here I shall try to show that the interoceanic differences arise from contrasting evolutionary histories of the biotas, and that these histories have been influenced by regimes of productivity. I shall also assess new evidence and point out inconsistencies, contradictions, and unresolved questions.

THE EVIDENCE

A. Gastropod Armor

Gastropod shells often function as effective fortresses of armor against a great variety of predators that accost the prey by shell breakage, shell drilling, swallowing whole, or extraction by way of the aperture. Particularly effective features promoting defense during the resistance phase of a predatory attack include large size, thick shell wall, high spire (associated with the ability to retract the food deep within the shell away from the apertural edge), tight coiling, a markedly elongated or thick-lipped aperture, an inflexible operculum forming a tight seal in the aperture, and strong external sculpture of spines, tubercles, knobs, or ridges (Vermeij 1978, 1982b, 1983b, 1987; Palmer 1979; Bertness and Cunningham 1981). Just how strong shells with these attributes can be is indicated by the fact that the Indo-West-Pacific thaidid Drupa morum, which commonly attains a length of about 35 mm, requires upto 5.5 kN of compressive force for the shell to be crushed between two flat metal plates, and that a 45 mm long Thais (Vasula) melones from the tropical eastern Pacific coast of Panama can take a load of 9.8 kN before shattering (Vermeij and Currey 1980).

Architectural studies of local assemblages of low intertidal and shallow subtidal gastropods from hard bottoms reveal that the incidence and degree of expression of armor (especially of narrow and constricted apertures, compact low spires, and strong sculpture) are highest in the Indo-West Pacific, intermediate in the eastern Pacific, and relatively low in the western and eastern Atlantic (Vermeij 1974a, b, 1978, 1979; Vermeij and Currey 1980). A similar pattern is seen among high intertidal assemblages (Vermeij 1974a). These interoceanic differences in architecture exist even within families. They have been documented in the Neritidae, Thaididae, Conidae, Trochidae, and Fasciolariidae (Vermeij 1978, 1979; Vermeij and Currey 1980).

Among gastropods from unconsolidated sandy and muddy bottoms, armor is again best developed in the Indo-West Pacific, but in contrast to hard-bottom gastropods there is no significant difference in armor between the Atlantic and the eastern Pacific (Vermeij 1978; Vermeij et al. 1980).

Repaired shell breaks provide additional clues to interoceanic differences in armor. During an unsuccessful attempt by a predator to break a shell whose outer lip is not internally reinforced, part of the outer lip and the adjacent shell wall are often damaged. The gastropod subsequently repairs this damage, but a record of the encounter is preserved as a scar whose course across the outer shell surface departs markedly from the growth-rings marking previous positions of the intact outer lip. The absence of scars on a shell indicates any of three possibilities: (1) all attacks by shell-breakers were successful (that is, mortal to the gastropod; (2) despite efforts to break the shell, the predator was unable to cause even minor damage, either because it was too weak or because it was unable to grasp the shell; and (3) shell-breaking predators were absent (Vermeij 1982b; Schindel et al. 1982; Signor 1985). If explanations (1) or (3) apply, there would be no unsuccessful attacks, and selection in favor of greater armor is unlikely. If scars are present, at least some attacks by shell-damaging predators (or other agencies) must have been unsuccessful, and the potential for selection in favor of increased armor exists. The higher the frequency of scars, (number of scars per shell in a population), the greater is this potential (Vermeij 1982, 1986).

Published surveys of the incidence of shell repair show that in the high-shore Neritidae, the highest frequencies occur in the Indo-West Pacific, followed respectively by the eastern Pacific and the western and eastern Atlantic (Vermeij 1978). In the sand-dwelling Terebridae, repair is most frequent in the Indo-West Pacific, with the eastern Pacific and tropical Atlantic coming relatively far behind (Vermeij et al. 1980). This finding was initially surprising in view of the fact that very slender terebrid species, in which the frequency of repair is significantly lower than in squatter species, are especially characteristic of the Indo-West Pacific region. Signor (1985) has argued that the aperture of these slender terebrids is so small that most shell-peeling calappid crabs, whose unsuccessful attempts to prey on the snails leave characteristic spiral scars, are unable to gain a purchase on the outer lip for peeling. If only squat species were compared among oceans, the interoceanic differences in the incidence of repair would be substantially greater than if all terebrid species were included (Vermeij et al. 1980).

I have surveyed four additional families of gastropods for interoceanic patterns in the incidence of shell repair. The Columbellidae (adult length 10 to 25 mm) and Planaxidae (adults 10 to 40 mm long) both show the lowest incidences in the western Atlantic (Tables 1 and 2). The Indo-West Pacific and eastern Pacific ranks highest, whereas in the Columbellidae, the highest rank is taken by the Indo-West Pacific region. In small epifaunal Cerithiidae (adults 10 to 40 mm long), in which no interoceanic difference in architecture is evident (Vermeij 1979), statistically significant differences in the incidence of repair do not occur among regions, although the data suggest that species in the eastern Pacific have higher incidences than those in the western Atlantic (Table 3).

The fourth family shows an apparently contradictory pattern. In the family Conidae, sand-dwelling as well as rock-dwelling species have the highest frequencies of repair in the western Atlantic (Figure 1). Frequencies in eastern Pacific species are either significantly lower (among sand-dwellers) or insignificantly different from those in the western Atlantic (rock-dwellers). Indo-West Pacific species generally have lower frequencies of repair. It is possible that the narrower apertures of most Indo-West Pacific conids (as compared to species in the New World [Vermeij 1976, 1979]) prevent lip fracture during attacks by predators, much as do the very small apertures of some Indo-West Pacific terebrids; but this hypothesis (or, to put it more bluntly, ad hoc explanation) still needs to be tested. In any case, the picture emerging from the new data is rather less

Table 1. Frequencies of repair (number of scars per shell) in rock-dwelling Columbellidae.

Region and Species	Locality	n	Freq.
Indo-West Pacific			
Columbella versicolor	Pujada Bay, Mindanao	12	0.50
	Dodinga Bay, Halmahera	13	0.31
Columbella sp.	Bagabag, P.N.G.	12	0.75
C. versicolor	Moti, Maluku	16	0.31
C. ocellata	Honduras Bay, Mindoro	20	0.10
Pyrene testudinaria	Ulang, Palau	11	0.18
P. deshayesi	Western Shoals, Guam	12	0.33
Western Atlantic			
Columbella mercatoria	Handikurari, Aruba	12	0
	Piescadera Baai, Curacao	9	0
	Santa Cruzbaai, Curacao	27	0.11
Eastern Pacific			
Anachis rugosa	Chepillo, Panama	10	0
A. boivini	Paitilla, Panama	10	0
A. varia	Playa Venado, Panama	11	0
A. fluctuata	Isla Perico, Panama	50	0.08
Anachis spp.	Paitilla, Panama	42	0.05

Table 2. Frequencies of repair of rocky-shore Planaxidae.

Region and Species	Locality	n	Freq.
Indo-West Pacific			
<u>Planaxis sulcatus</u>	Majuro Atoll	49	0.35
	Badisika, P.N.G.	16	0.13
	Dravuni, Fiji	15	0.13
	Piti Channel, Guam	27	0
	Jef Bie, Maluku	15	0.13
	Tajandu, Kai Islands	8	0
	Baclayon, Bohol	9	0.11
	Ravao Island, P.N.G.	12	0
	Tipalao Beach, Guam	22	0.14
<u>P. niger</u>	Ayem, Maluku	34	0
	Salafai, Pagan	12	0
	Pialama, Pagan	32	0.06
	Anatahan	24	0.04
<u>P. sulcatus</u>	Ngerchebal, Palau	9	0.22
	Pulau Subar Darat, Singapore	11	0
	Nasugbu, Luzon	11	0
	Salu, Singapore	8	0
	Malakal, Palau	10	0.10
	Eilat, Israel	8	0
	Ras Muhamad, Sinai	15	0.13
Western Atlantic			
<u>P. nucelus</u>	Picadera Baai, Curacao	9	0
	Playa Adaro, Venezuela	8	0
	Fort Randolph, Panama	12	0
	Cove Bay, Saba	11	0
	Fort Bay, Saba	9	0
	Cahuita, Costa Rica	11	0
	Rio Bueno, Jamaica	8	0
Eastern Pacific			
<u>P. planicostatus</u>	Naos Island, Panama	30	0.23
	Palaya Brava, Panama	10	0.40

Table 3. Frequencies of repair in epifaunal small Cerithiidae.

Region and Species	Locality	n	Freq.
Indo-West Pacific			
Cerithium columna	Pago Bay, Guam	10	0.20
	Majuro Atoll	13	0.23
	Majuro Atoll	13	0.15
	Majuro Atoll	11	0.18
	Pujada Bay, Mindanao	19	0.53
C. sejuctum	Pago Bay, Guam	16	0.19
C. zonatum	Piti Channel, Guam	89	0.04
	Majuro Atoll	30	0.23
	Pago Bay, Guam	17	0.12
C. suturale	Agat, Guam	15	0.13
	Agat, Guam	11	0.09
C. atromarginatum	Majuro Atoll	17	0.82
C. rostratum	Pago Bay, Guam	51	0.10
Clypeomorus nympha	Pago Bay, Guam	18	0.17
C. bifasciata	Baclayon, Bohol	33	0.76
	Pago Bay, Guam	15	0.20
	Piti Channel, Guam	11	0
	Aru, P.N.G.	11	0.18
	Pujada Bay, Mindanao	11	0.45
C. batillariaeformis	Ravao Island, P.N.G.	37	0.43
	Arakabesan, Palau	12	0.25
C. trailli	Arakabesan, Palau	12	0.33
Western Atlantic			
Cerithium lutosum	Cahuita, Costa Rica	13	0.46
C. literatum	Cahuita, Costa Rica	29	0.10
C. muscarum	Gasparilla, Florida	13	0.31
C. atratum	Blind Pass, Florida	11	0.45
C. eburneum	Runaway Bay, Jamaica	26	0.15

Table 3. Continued.

Eastern Pacific

Cerithium menkei	Anconcito, Ecuador	20	0.45
	Playa Brava, Panama	10	0.40
C. sterucsmuscarum	Paitilla, Panama	48	0.35
	Chepillo, Panama	22	0.64
C. adustum	Playa Brava, Panama	15	1.00

consistent than it was when only the data from Terebridae and Neritidae were available.

Some evidence from shell architecture suggests that there may be intraoceanic differences in Indo-West Pacific gastropods. Many species with large geographical ranges in the western Pacific have close relativies in the Central Pacific (eastern Micronesia and Polynesia). These oceanic offshoots usually have a smaller aperture and a higher spire than do the species from which they probably evolved (Vermeij 1978). Examples may be found in the species groups of Conus miliaris Hwass (Kohn 1978; Rehder 1980), Vasum turbinellus L. (Abbot 1959), Thais armigera Link, Astrea rhodostoma Lamarck, Drupa ricinus L., D. rubusidaeus Röding (Emerson and Cernohorsky 1973), Harpa harpa L. (Rehder 1973), Strigatella decurtata Reeve (Cernohorsky 1976), and Nassarius albescens (Cernohorsky 1984). Though exceptions may occur, I am unaware of any.

The significance of this regional difference remains unclear, but two hypotheses suggest themselves. First, the difference in architecture may be related to the capacities of predators. It is possible that predators in Polynesia and other parts of the tropical Central Pacific have been especially effective in selecting in favor of small apertures among shallow-water gastropods. The second hypothesis is that the morphology of Central Pacific species reflects conditions resulting in slow individual shell growth. Experiments have shown that spire height increases, and apertural width decreases, as growth rate decreases (Kemp and Bertness 1984). The low planktonic productivity that generally characterizes the central oceanic Pacific may therefore be reflected in a consistently higher spire and smaller aperture of endemic gastropod species. These two hypotheses are not mutually exclusive, and neither has been tested. A purely phenotypic explanation seems unlikely, however, because there is some geograpical overlap between the low-spired western Pacific and the higher-spired Central Pacific forms in some areas such as the Marshall Islands.

In addition to the intraoceanic differences in form, several sand-dwelling species groups show a greater development of axial sculpture in Micronesia and Polynesia than in the generally more continental Indo-Malayan and Melanesian areas. Examples include the Strombus erythrinus Dillwyn complex (Abbott 1960), Nassarius distortus (Cernohorsky 1984), Rhinoclavis fasciata Bruguiere (Houbrick 1978), and species of Casmaria (Abbott 1968).

B. Predators of Molluscs

If Indo-West Pacific gastropods are more heavily armored than those elsewhere in the tropics, predators there should be either more common or more powerful than their counterparts in the eastern Pacific and especially in the western and eastern Atlantic. The only predators for which this hypothesis has been evaluated even in part are shell-crushing brachyuran crabs, notably highly specialized members of Zanthoidea, Portunoidea, and Parthenopidae (Vermeij 1976, 1977; Abele et al. 1981). Comparisons among congeners reveals that Indo-West Pacific species of Carpilius, Eriphia, and Daldorfia are both larger in size and relatively larger-clawed than are eastern Pacific and Atlantic species. Eastern Pacific species of Eriphia and Ozius are larger and have larger claws than do congeners in the western Atlantic. No Atlantic or eastern Pacific portunid has claws as large or as specialized for crushing as does the Indo-West Pacific Scylla serrata. Whether these differences in fact reflect interoceanic differences in crushing performance has not yet been demonstrated, but the differences in claw size and form parallel patterns in gastropod shell architecture.

Comparative biogeographical studies of other predators (calappid crabs, shell-breaking fishes, and drilling and shell-entering gastropods) would be immensely desirable, but they have not yet been undertaken. It is noteworthy that many important genera of molluscivores (and even some species) have circumtropical or nearly circumtropical distributions. They may, therefore, be expected to show similar levels to predatory performance in the various marine biogeographical regions in the tropics. This is likely, for example, in the case of shell-peeling crabs of the genus Calappa, shell-crushing pufferfishes of the genus Diodon, shell-drilling gastropods (genera Natica, Naticarius, and Neverita), shell-entering gastropods (genera Cymatium, Gutturnium, Thala, and Thais), the shell-crushing loggerhead turtle (Caretta caretta), and various shell-crushing rays. In all these categories of predators, however, the Indo-West Pacific has by far the greatest diversity of any region, even at the local scale. Many genera have evolved and remained restricted in the Indo-West Pacific. Predation in which a gastropod inserts its proboscis into the prey via the aperture or between gaping valves is known throughout the tropics, but in the Indo-West Pacific it is practices by many endemic genera in which this mode of feeding appears to be quite specialized. One of the genera involved (the conid Cylinder) is known also from the eastern Pacific, but this range extension seems to have been very recent, and almost certainly represents a case of eastward migration from the Central Pacific. A similar range extension from the west occurred in the naticid taxon Mammilla, which typically attacks pelecypod prey by drilling at the valve margins.

In summary, evidence pertaining to interoceanic differences in predation of gastropods points to the development of greater armor of gastropods in the Indo-West Pacific. Data on the incidence of shell repair and on characteristics of molluscivores is more equivocal, that is, they do not point as clearly to a consistent interoceanic pattern. Much remains to be done on the comparative biogeographical level, particularly with respect to the predatory performances of molluscivores.

C. Habitat Specialization of Molluscs

With some exceptions, western Atlantic molluscs can be described as habitat generalists, whereas Indo-West Pacific and to lesser extent eastern Pacific species are more specialized to particular habitats. I shall illustrate this pattern with epifaunal molluscs.

Consider gastropods living on the blades of seagrasses. In the western Atlantic, grazing gastropods found on seagrasses are typically also found on the undersides of stones and on other hard substrata. Of 9 gastropods that I have collected on seagrass blades in the Caribbean region, only 1 or 2 are restricted to this habitat. At least 3 of the 9 species have very close relatives in the eastern Pacific, but in that region, where seagrasses are extremely rare and local in distribution (den Hartog 1970), these close relatives are found only on rocky substrata. The degree of habitat specialization among Caribbean grass-dwellers is low when compared to the Indo-West Pacific. Of 15 seagrass gastropods that I have collected in the Indian and western Pacific Oceans, at least 8 (53%) appear to be found only on seagrasses.

Mangrove forests represent another environment in which interoceanic differences in molluscan habitat specialization are evident. Among tree-dwelling species of the littorinid gastropod genus *Littoraria*, species specialized for life on leaves are found only in certain parts of the Indo-West Pacific and eastern Pacific (Reid 1985). In the tropical Atlantic, the single species present (*L. angulifera*) lives on branches and roots as well as occasionally on leaves. Many gastropods in the Indo-West Pacific and eastern Pacific are found in mangrove forests only on the trees themselves. Examples include species of *Nerita*, *Littoraria*, *Cerithidea*, and *Clypeomorus*. The only tropical Atlantic gastropods to be more or less restricted to the trees themselves are *L. angulifera*, and perhaps *Littorina flava*. Species of *Cerithium*, *Cerithidea*, and *Nerita* are found on trees as well as on rocks, sand, and mud, even in environments away from mangrove forests (Vermeij 1973).

Still other examples of interoceanic differences in habitat specialization come from epizoic limpets and from coral-associated commensals. These will be treated in a somewhat different context in the next section.

D. Sessile Organisms

Sessile animals and plants may show parallel geographical differences with molluscs. Indo-West Pacific comatulid crinoids, for example, have higher incidences of spinose arm bases (which may protect these animals from predators) than do species in the tropical western Atlantic (Meyer and Macurda 1977; Meyer 1985). Hay and Gaines (1984) attribute the rarity of large algae in the intertidal of the eastern Pacific to higher grazing intensities there than in the western Atlantic (see also Birkeland 1977). Indo-West Pacific and eastern Pacific corals are extensively eaten by fishes, gastropods, seastars, and (locally, at least) sea urchins. Not only is this predation apparently more intense than in the western Atlantic, but several major predators of corals (notably seastars, including Acanthaster, and pufferfishes of the genus Arothron, as well as many coralliophilid and other gastropods) are unknown in the western Atlantic (Glynn et al. 1972; Glynn 1982; Glynn and Wellington 1983). It is not yet clear if these differences in predation are reflected in coral morphology. Crabs and shrimps which defend host corals from attack by seastars and perhaps some other kinds of predators are common in the Indo-West Pacific and eastern Pacific, but they are unknown in the western Atlantic (Glynn 1976, 1983).

Limpet-like gastropods living epizoically on the shells of other animals (especially on living gastropods and hermit crabs) differ in the degree to which they excavate home scars on their hosts. In the Indo-West Pacific, the hipponicid Sabia conica (which is more or less specialized to live on the shells of gastropods and hermit crabs) excavates a pit on the shell exterior, where it is probably well protected against incidental grazing and from other disturbance. The eastern Pacific calyptraeid Crepidula incurva, which is also specialized for life on shells, does not make such excavations. Neither do species of Crepidula in the western Atlantic or West Africa, where the epizoic mode of life appears to be facultative (Vermeij 1978).

Intimate associations between small guests and large hosts are, on the whole, more numerous as well as more specialized in the Indo-West Pacific than in the western Atlantic. I reviewed this topic in detail in an earlier paper (Vermeij 1983a). A few examples will be mentioned here. Whereas ten fish species are facultatively associated with large stichodactylid sea anemones in the western Atlantic, a large number of pomacentrid clownfishes is obligately associated with these hosts in the Indo-West Pacific (Dunn 1981). Zooxanthella-bearing bivalves (Tridacnidae and the cardiid genus Corculum) are confined today to the Indo-West Pacific, as are coral-associated shell-dwelling sipunculans. Crabs and shrimps that guard corals against predators are found in the Indo-West Pacific and eastern Pacific but not the Caribbean; the eastern Pacific species are apparently identical to those of the Indo-West Pacific and probably came from the latter region along with many other reef species during the Pleistocene (Glynn 1983). Eulimid snails on the spines of Diadema sea urchins occur in the Indo-West Pacific but not the western Atlantic.

E. Variations Related To Productivity

Phytoplankton productivity varies widely within and between oceans, and probably has profound influences on the ecological and architectural composition of benthic communities. Highsmith (1980), for example, found that the degree to which living coral colonies were bored by lithophagine bivalves and other bioeroders declines sharply from continental shores to the less productive shores of oceanic islands, especially atolls. Because of widespread upwelling, bioerosion is particularly intense in the eastern Pacific. The dependence of bioerosion on planktonic productivity was investigated in detail in the eastern Pacific, where the incidence of lithophagines was found to be higher in areas affected by upwelling (Bay of Panama and parts of the Galapagos) than in less productive areas without upwelling (Gulf of Chiriqui and parts of the Galapagos) (Glynn et al. 1983; Glynn and Wellington 1983). No data are yet at hand to ascertain if these pattern also apply to bioerosion of molluscan shells.

Some modes of life are apparently far more common in productive areas than in unproductive ones, and therefore tend to be characteristic of only some biogeographical regions. Although the gastropod genus Calyptraea is distributed in most tropical oceans, this group of suspension-feeders, which often lives on the inside surfaces of clam valves, is wholly absent from the insular Caribbean and Indo-West Pacific regions. Species of Calyptraeidae specialized for life on the inner walls of gastropod shells occupied by hermit crabs are common in the upwelling areas of the eastern Pacific and western Atlantic, but are absent or very rare in the Gulf of Chiriqui.

THE HISTORICAL PERSPECTIVE: EXTINCTION AND SPECIATION

How did the architectural and ecological differences among the tropical shallow-water marine biotas come about? This is clearly a question of history. Although many details need to be worked out, the answer to this question seems to be that the Indo-West Pacific differs from the other tropical marine regions by having exhibited lower rates of extinction and higher rates of speciation over the last ten million years. Moreover, the processes of extinction and speciation have been selective with respect to the architecture and adaptations of species.

It may be useful to provide first a brief overview of the Cenozoic history of the tropical ocean. More detailed discussions may be found in the works of Berggren and Hollister (1977), Por (1978), and Hallam (1981a, b). During the Paleocene and Eocene, a more or less continuous belt of ocean surrounded the earth at tropical latitudes. Although the biotas in different parts of the tropics showed species-level differences, and some biotas were richer than others, there was far less heterogeneity than there is in the modern marine tropics. Tectonic events during the Neogene (Miocene, Pliocene, Pleistocene, and Holocene) led to the fragmentation of this continuous belt. During the Early Miocene, the connection between the Mediterranean region (Tethys Sea) and the Indo-Malayan region was severed by tectonic activity in southwestern Asia. Slight northward movement of Africa further constricted the Mediterranean region. The continent comprising Australia and New Guinea also moved northward, approaching southeast Asia as it did so, and creating a complex configuration of islands and narrow sea passages in the area of Indonesia and the Philippines. In tropical America, uplift in Central America at first caused the seaway between North and South America to become shallower during the Middle and Late Miocene. During the Pliocene, the uplift was completed, resulting in a complete separation of the marine biotas of the eastern Pacific and western Atlantic.

At least two events of biotic interchange have occurred in the tropics during the Neogene, but their effects have so far been minor compared to the effects of fragmentation. Perhaps as a consequence of the northward movement of the Line Islands in the Central Pacific, Indo-West Pacific molluscs and other reef-associated species have been able to colonize the eastern Pacific by means of planktonically dispersing larvae (Dana 1975; Glynn and Wellington 1983). In the Atlantic, some Indo-West Pacific and West African taxa have similarly colonized the east coast of tropical America during the Pleistocene, perhaps as a consequence of accelerated oceanic circulation (Petuch 1981).

The biogeographical regions that remained after the breakup of the continuous tropical sea belt had widely differing subsequent histories. Substantial episodes of extinction affected the western Atlantic during the Pliocene (Vermeij and Petuch 1986; Woodring 1966) and to a much lesser extent the eastern Pacific. About 32% of gastropod subgenera found during the Pliocene in the tropical western Atlantic became extinct in that region, whereas only about 15% of subgenera disappeared from the eastern Pacific. As far as I have been able to determine, no extinction at the subgeneric level took place among Indo-West Pacific molluscs. Instead, this region saw a substantial episode of diversification during the early Pliocene. The history of West Africa during the Neogene remains obscure owing to a poor fossil record there.

In tropical America, extinction during and after the Pliocene contributed in an important way to the architectural differences observed between the Recent eastern Pacific and western Atlantic molluscan faunas. Armored hard-bottom gastropods suffered relatively more extinction than did unarmored types in the western Atlantic, whereas in the eastern Pacific the impact of extinction was greater among unarmored than among armored hard-bottom gastropods. Thus, although the incidence of armor was the same in the eastern Pacific and western Atlantic during the Pliocene, differential extinction among hard-bottom gastropods was responsible (at least in part) for the observed difference in the incidence of armor in recent hard-bottom gastropods from opposite sides of tropical America (Vermeij and Petuch 1986).

We are still far from an understanding of how this selectivity of extinction was brought about, but it is possible that reductions in phytoplankton productivity were partly responsible. That such reductions in productivity have taken place and caused extinction is indicated not only by evidence from carbon-isotope studies of deep-sea sediments (Keigwin 1982), but also by the fact that the two areas in tropical America that have acted as refuges - areas where species with formerly much larger geographical regions have become confined - are characterized by upwelling or by extensive terrestrial runoff. These refuges are the eastern Pacific and the continental north coast of eastern Colombia and Venezuela (Vermeij and Petuch 1986). In the Indo-West Pacific, the islands of the Indo-Malayan arc have also served as refuges for taxa that had larger ranges during the late Neogene. These continental coasts are also characterized by upwelling and extensive terrestrial inputs of nutrients (Vermeij 1986). A reduction in phytoplankton productivity may lead to higher mortalities of larvae. It also results in decreased growth rates of post-larval individuals and probably in reduced individual fecundity as well. Whether and how these effects would be selective with respect to antipredatory architecture is not known.

Differential speciation has also played a decisive role in bringing about and accentuating the present-day differences in architecture and specialization. In contrast to tropical America, where very few (if any) subgenus-level molluscan taxa originated during the Pliocene and Pleistocene, a larger number of supraspecific groups in the Indo-West Pacific had post-Miocene origins. Not only are many of these groups unknown as fossils from the Miocene, but they are wholly unknown from the richly fossiliferous Miocene and Pliocene strata of Europe, an area with intimate biogeographical connections with the present-day Indo-West

Pacific. Continuing studies suggest that the incidence of very heavy armor among gastropods is exceptionally high in genera that originated in the Indo-West Pacific after the Miocene, and that many of these gastropods have achieved a very wide geographical distribution in the Indian and Pacific Oceans. Examples include Drupa, Lambis, Conomurex, Morula, Drupella, and various groups in the Cypraeidae, Mitridae, and Costellariidae. The coral-eating seastar Acanthaster likely also had a post-Miocene origin. Preliminary indications are that the Indo-West Pacific has been characterized by high rates of diversification during the last several million years (especially during the Early Pliocene), and that this diversification has especially affected heavily armored types among gastropods. It must be emphasized, however, that these statements are tentative, and that firmer conclusions must await the results of continuing studies.

EPILOGUE

It is abundantly obvious that great gaping holes exist in our understanding of the nature, magnitude, causes, and history of interoceanic differences in the architecture and ecology of tropical shallow-water marine organisms. We badly need systematically collected data on the absolute levels of performance of individuals with respect to such activities and attributes as locomotion, resistence against predators, growth rate and other competitive methods, grazing intensity, rate of feeding (handling time of predators), likelihood of encounters between predators and their enemies, and so on. Further studies of differential extinction and speciation are also needed. Intraoceanic differences, particularly in relation to planktonic productivity and its effects, deserve more attention than they have thus far received. Very little has been done on species and communities in environments other than coral-sand habitats and clear-water reefs. In view of the vast areas of coastal muddy habitat and continental shelf, which also support important commercial fisheries, these environments should be targeted for intensive, systematic, and comparative study.

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A COMPARISON OF SOME ECOLOGICAL PROCESSES ON CORAL REEFS OF THE CARIBBEAN AND THE GREAT BARRIER REEF

by

Paul W. Sammarco*

ABSTRACT

Major grazers and coral recruitment patterns have been compared between Caribbean coral reefs and the Great Barrier Reef. The major grazers in the Caribbean have generally been echinoids while fish have filled this niche on the Great Barrier Reef. The difference may be due to either the differential geological histories of the two regions and/or, in recent times, to higher levels of exploitation of Caribbean reef fishes by man.

Grazers play a key role in both regions, assisting in the success of coral recruitment. Biological disturbance to or predation upon newly settled corals is an important factor in influencing success of coral recruitment, as is competition for space with other sessile organisms. Grazers appear to mediate these processes in both system.

Coral recruitment patterns are different in the two regions, particularly with respect to the relationship of recruits to adults in dominant corals. Acropora is a dmoninant coral in the adult community of the Caribbean, accounting for major zonation patterns, yet is rare in the newly settled community of juveniles derived from planulae. On the Great Barrier Reef, adult Acropora are dominant on most reefs and their newly settled spat often represent 50-80% of the juveniles. It is suggested that most species of Acropora on the Great Barrier Reef are dependent upon recolonization by planular settlement while all species of Acropora in the Caribbean rely much more heavily on asexual reproduction via branch-breakage and recemmentation. It is predicted that reef recovery after a major environmental perturbation might also require longer periods of time in the Caribbean than on the Great Barrier Reef. The reasons for differences between recruitment-related strategies may be historical, particularly with respect to the different geological histories of the two regions.

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*Australian Institute of Marine Science
P.M.B. No. 3
Townsville M.C., QLD 4810
AUSTRALIA

The settlement patterns of coral larvae suggest that effects of predation or biological disturbance on coral spat may be more intense on the Great Barrier Reef than in the Caribbean. Under conditions of reduced grazing, coral spat are generally found in more cryptic positions on benthic surfaces on the Great Barrier Reef than in the Caribbean.

INTRODUCTION

Interoceanic comparisons between the Pacific and the western Atlantic have been an area of interest for ecologists and evolutionary biologists for many years. Many studies have dealt with comparisons of diversity (Stehi et al. 1967; Chesher 1972), productivity (Birkeland 1977; Vermeij 1978; Highsmith 1980a), and morphological characters of biota exemplifying convergent evolution. Some studies have concentrated on similarities in zonation and community organization in such well-studied habitats as the intertidal (Stephenson and Stephenson 1949, 1950, 1972; Knox 1960; Lewis 1964; Salvat 1970; Vermeij 1978).

Several studies have compared the eastern Pacific with the western Atlantic with specific reference to the Panamanian coasts. Earle (1972) and Glynn (1972) compared abundances and the general profile of algae in these areas and related them to relative intensities of grazing by fish. Glynn (1972) considered many aspects of the two regions, comparing taxonomic composition, physical regimes, biological processes, and interactions between species. Birkeland (1977) compared grazing intensities using direct experimentation and also examined comparative levels of coral recruitment. Palmer (1978), also using experimental techniques, compared relative levels of predation and adaptations of gastropods to such predation, relating differences to species diversity.

Direct comparisons between the western Pacific, particularly the Great Barrier Reef, and the western Atlantic have also been made. For example, Meyer and Macurda (1977) compared the predator-related adaptations of the Indo-West Pacific crinoids with those of the Caribbean. Goreau et al. (1979) have compared the maximum depths of well-developed coral growth and related it to differential predation intensities. Risk and Sammarco (1982) have compared the habits of boring sponges and also related them to differential levels of predation. Thresher (1982, 1984) has compared differences in the reproductive biology of coral reef fishes and examined their potential effects on recruitment and adult fish community structure. Williams et al. (1981) have compared the structure and composition of phytoplankton communities.

The most extensive and detailed ecological comparison of the Indo-Pacific and the Caribbean to date is that of Vermeij (1978). He compared morphological adaptations of gastropods and numerous other organisms, relating them to differences in ecological and evolutionary processes in the two regions. In particular, he along with Bakus (1966, 1969) provide evidence that the intensity of predation and grazing is higher in the Indo-Pacific than in the Caribbean.

Here I shall attempt to compare some processes related to grazing and coral recruitment in the two regions, expanding some ideas discussed earlier (Sammarco 1985a). In particular, I will be addressing the questions of whether grazing plays a similar role in the Caribbean and on the Great Barrier Reef and whether the major complement of grazers is similar. In addition, the relationship between coral recruitment and adult community structure will be compared. Finally, any differences which become apparent will be discussed with respect to their implications for reef generation in response to natural or man-made perturbations to the different systems. Clearly, important differences can result in varying directions and rates of secondary succession in the two respective regions, the character of new stable points reached by the respective coral communities, and the relationship of those new stable points to the previous ones.

MAJOR GRAZERS AND THEIR EFFECTS ON CORAL RECRUITMENT

A. Caribbean Grazers

In many parts of the Caribbean, although certainly not in all parts (Hay 1984), regular sea urchins (Echinodermata; Echinoidea; Regularia) have been among the major grazers (Lawrence 1975; Ogden 1976; Ogden and Lobel 1978; Lawrence and Sammarco 1982). Densities there can reach high levels. For example, on some lagoonal patch reefs in Discovery Bay, Jamaica, densities of *Diadema antillarum* Philippi alone have reached an average of 77 m^{-2} in 1973 (Sammarco 1978, 1980, 1982a). Total echinoid densities, including *Echinometra viridis* A. Agassiz, *Lytechinus williamsi* Chesher, and *Eucidaris tribuloides* Lamarck, averaged 99 m^{-2} (Sammarco 1982a). Forereef values were lower, averaging < 16-22 m^{-2} (Sammarco and Williams 1982; Kaufman 1977, 1979; Hughes 1986).

The grazing activities of echinoids, particularly *Diadema antillarum*, have been considered to be more important than those of fish in many parts of the Caribbean (Ogden and Lobel 1978). For example, Ogden (1977) has shown that in

Panama, D. antillarum and Echinometra lucunter each account for sediment production an order of magnitude greater than that caused by the striped parrotfish Scarus croicensis Bloch.

Densities of regular echinoids, particularly Diadema antillarum, can be variable through time. In 1983, a massive mortality of D. antillarum occurred throughout the Caribbean, extending from Panama and other parts of Central America through the West Indies, Netherlands Antilles, Greater and Lesser Antilles, and Florida (Lessios et al. 1983, 1984a, b; Bak et al. 1984; Vicente and Goenaga 1984; Hughes et al. 1985). Diadema is believed to be r-selected (Hendler 1977) and it is hoped that juvenile Diadema will soon recolonize these areas (Bak et al. 1984). It is not known whether this variability in ecological time is something which has occurred in the past in the Caribbean. In addition, it is not known whether populations of grazing vertebrates on the Great Barrier Reef experience such severe population fluctuations.

B. Grazers of the Great Barrier Reef

Little quantitative information has been published to date on regular echinoid densities associated with hard substrata on the Great Barrier Reef. In the central region of the Great Barrier Reef (Fig. 1), only three species of hard-bottom echinoids occur in measurable numbers - Diadema setosum Leske, Echinometra mathaei de Blainville, and Echinostrephus molaris de Blainville (Sammarco 1985a). Diadema occurs primarily in the inshore waters of the Great Barrier Reef lagoon, while Echinometra occurs at the mid- and outer-shelf, ~60 and 120 km offshore, respectively. On the whole, echinoid densities are negligible there, with average densities ranging from 0-1/m^2, as assessed by both diurnal and nocturnal surveys. Higher abundances of D. setosum have apparently been observed at Green Island (northern region of the Great Barrier Reef; K. Peterson pers. comm.). Sea urchins may also be found nocturnally on Lizard Island (northern region) at densities up to 1/m^2, including such species as Diadema savignyi Micheline, D. setosum, Echinometra mathaei, Echinothrix diadema, Heliocidaris erythrogamma Clark, H. tuberculata, and Centrostephanus rodgersi (Filmer-Sankey 1984, pers. comm.). On the whole, however, regular echinoids appear to be uncommon in those parts of the Great Barrier Reef which have been censused, and this concurs with results of other investigators reporting abundances for as early as 1929 (Clark 1938; also see McLean 1974). In addition, this situation is not unique in the Indo-Pacific, as low echinoid densities have also been reported for Guam (Randall 1978) and Belau (Birkeland et al. 1976; Randall et al. 1978; c.f. Birkeland 1984).

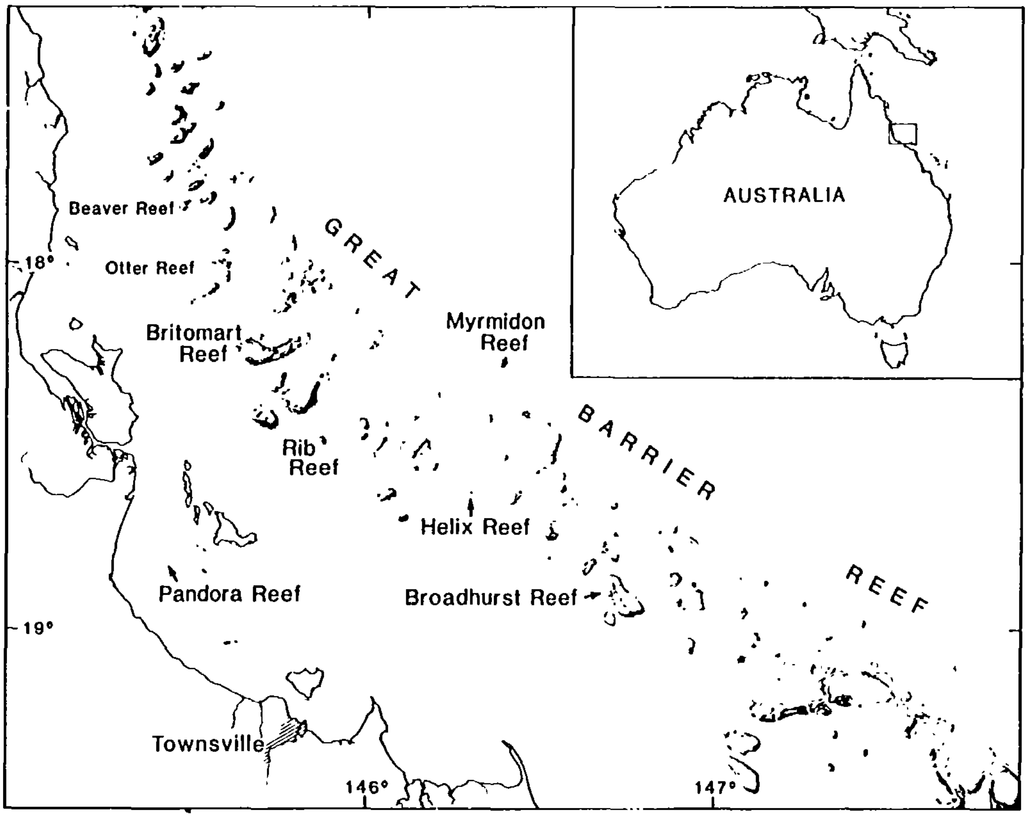


Figure 1. Map of central region of the Great Barrier Reef depicting several platform reefs of interest: Pandora, Britomart, Rib, Helix, Otter, Beaver, Myrmidon, and Big Broadhurst Reefs. Inset: Position of the central region of the Great Barrier Reef with respect to Australia.

With the assistance of time-lapse cinematography (both diurnal and nocturnal: Sammarco and Carleton 1982; Hatcher 1981, 1982; Sammarco et al. 1986, work in progress) and through the surveys of Williams (1982), Williams and Hatcher (1983), Choat (1983; pers. comm.) and Russ (1984a, b, c), it has become evident that fish are the major grazers on those portions of the Great Barrier Reef which have been censused-primarily of the Scaridae, Acanthuridae, and Pomacentridae. Similar conclusions have been reached by Stephenson and Searles (1960), Day (1977a, b), Borowitzka et al. (1978), and Borowitzka (1981). Nocturnal time-lapse cinematography has revealed that other benthic grazers not normally observed by divers during the day occur in abundance in the central region of the Great Barrier Reef. These include small, nocturnally active crustaceans of the galatheid (e.g., <u>Galathea subsquamata</u>), pagurid, and portunid families (Sammarco et al. 1986). The impact of these organisms on benthic reef community structure is believed to be relatively small.

C. The Relationship Between Grazing and Coral Recruitment in the Caribbean

In the Caribbean, <u>Diadema antillarum</u> is a source of biological disturbance for newly settled juvenile corals. While the urchin is feeding, it incidentally removes newly settled corals from the substratum (Sammarco et al. 1974; Schuhmacher 1974; Sammarco 1978, 1980, 1982a, 1985b, 1986a; Rylaarsdam 1983). It has been demonstrated experimentally that increased densities of <u>D. antillarum</u> cause a significant decrease in the success of coral settlement (Sammarco 1978, 1980, 1982a). Coral larvae are not excluded from settlement of abundant populations of filamentous algae, for the planulae settle in high numbers together with the algae. Optimal conditions for the survival of coral spat, however, occur at intermediate grazing pressures. Without grazing, algae and many sessile invertebrates which posses high growth rates rapidly outcompete many juveniles (and adult) corals for space (Dart 1972; Benayahu and Loya 1977; Birkeland 1977; Borowitzka 1981; Hughes 1986). Thus, a balance is achieved at intermediate grazing pressures between competition for space and biological disturbances (Sammarco 1975, 1978, 1980, 1982a, 1985b, 1986a; Lawrence and Sammarco 1982). A similar relationship between grazing by <u>Diadema setosum</u> and success of coral settlement has been suggested to occur in the Red Sea (Dart 1972; Schuhmacher 1974; Benayahu and Loya 1977).

These relationships make echinoid grazing a critical controlling factor for coral community structure in the Caribbean. This has been demonstrated by the recent mass mortalities of <u>Diadema</u>, the concomitant reduction in grazing pressure, and the resultant catastrophic adult coral mortality due to overgrowth by algae in Jamaica (Hughes 1986, pers. comm.; J. C. Ogden pers. comm.; L. Kaufman pers.

comm.). High mortality levels in coral spat may also be expected to occur (Sammarco 1982a).

D. The Relationship Between Grazing and Coral Recruitment on the Great Barrier Reef

The role of fish grazing in controlling success of coral recruitment has been examined on the Great Barrier Reef. An aggressive, site-attached damselfish (Hemiglyphidodon plagiometopon Bleeker) which specifically excludes herbivores from its territories (Lassuy 1980) was used as a vehicle for the study along with fish-exclusion cages and shade controls. Success of coral settlement was reduced significantly by 5-7 fold on substrata fully exposed to fish grazing in comparison to conditions of reduced grazing. As in the Caribbean, algae did not exclude coral planulae from settling. The experiment was inconclusive, however, in demonstrating that grazing regulated competitive interactions between coral spat and other epibiota. Nevertheless, grazing has been shown to have an effect in regulating competition between juvenile or adult corals and algae in other experiments on the Great Barrier Reef (Potts 1977; Sammarco 1980; Harriot 1983) and on the Pacific side of Panama (Wellington 1982). Similar conclusions have been reached by Brock (1979) about Hawaiian reefs and by Borowitzka (1981) and Day (1983) in their discussions concerning the Great Barrier Reef.

E. Discussion

It appears that there is a high variance in densities of grazing echinoids in the Caribbean in both space and time and very low densities with low variance in this same group on hard bottom on the Great Barrier Reef. In many parts of the Caribbean, echinoids, particularly Diadema antillarum, have been the dominant grazers, whereas fish have filled this major niche on the Great Barrier Reef, as has been suggested by Ogden (1976) and Hatcher (1983). One possible reason for this difference in recent times is human influence (Woodley 1977; Hay 1984). Commercial reef fishing in Jamaica is done with fish traps which are somewhat indiscriminate in the age of their catches, trapping both juvenile and adult fishes (Munro 1983a, b, c). Non-target fish or those too small to be of commercial value often expire in the time required to remove target fish from the traps (pers. obs.). The fruits and vegetables initially used as bait along with the dead fish serve to attract all types of fish - herbivores, carnivores, scavengers, etc., making the technique even more indiscriminate. Predators of echinoids such as balistid fishes may also be caught in the traps (Hay 1984). This may help to explain the high densities of echinoids observed at some Caribbean islands (Ogden et al. 1973; Woodley 1977) and the variance observed between islands (Randall 1974; Ogden and Lobel 1978; Hay 1981, 1984).

Fishing on the Great Barrier Reef is much more directed and has a lower impact on the overall reef community. Most fishing is done by baited hand-lines and trolling (W. Craik pers. comm.) which are more discriminating in their catch than traps. Predatory fish such as members of the Serranidae, Lutjanidae, and Lethrinidae serve as primary targets of the reef-fish industry. In addition, the level of human impact on fish populations appears to be lower on the Great Barrier Reef. For example, although the state of Queensland and the island of Jamaica have approximately the same populations (∼ 2 million in 1978), the population density in Jamaica is 164 times higher due to the difference in area (Black 1979; May 1980). Thus, the resultant demand on the natural resources of the Great Barrier Reef is much lower (Munro and Williams 1985). In addition, fishing activities on the Great Barrier Reef are well managed by a number of authorities at both the state and federal levels.

In comparing the distribution and abundance of grazers in these two regions, it is important to recall that the Caribbean has had a different geological history than the southwestern Pacific (see the section on Geological Perspective below). It is possible that echinoid densities have been naturally higher in the Caribbean than on the Great Barrier Reef through geological time. It may never be possible to separate these two confounding influences, but the answer may lie within future comparative sedimentological studies where density of spines in fossil sediments have been used to estimate paleodensities of echinoderms (Bathurst 1975; Frankel 1977).

It appears from available data that grazing plays an important role in controlling the success of coral recruitment in both the Caribbean and on the Great Barrier Reef. However, the processes are not, necessarily the same. In the Caribbean, biological disturbance of spat was evident due to the clear association of increasing levels of physical damage to juvenile corals with increased levels of grazing (Sammarco 1980, 1982a). This was not the case on the Great Barrier Reef. Proposed mechanisms of reduction of juvenile corals include differential settlement preferences in planulae, or planula-, or spat-specific, predation (Sammarco and Carleton 1982). In general, however, it appears that in both the Caribbean and on the Great Barrier Reef, grazing may help to balance success of coral settlement against subsequent competition for space. More research is requried in this area.

RECRUITMENT PATTERNS OF DOMINANT CORALS

A. The Caribbean

Two major zones typical of well-developed reefs in the Caribbean are the *Acropora palmata* Lamarck zone, occurring from the reef crest to a depth of 0-7 m, and the *A. cervicornis* Lamarck zone which can extend down to 7-20 m on the forereef slope (Goreau 1959; Goreau and Land 1974; Levinton 1982).

Extensive analyses of the distribution and abundance of newly settled corals on lagoonal patch reefs in Discovery Bay, Jamaica during 1973, 1974, and 1975 revealed that, despite its dominance as an adult (Fig. 2), *Acropora* was represented at consistently low levels in the juvenile portion of the coral community. This was found to be the case under conditions of both primary (Fig. 3) and post-primary (Fig. 4a, b; Sammarco 1980, 1982a) succession (i.e., on new and old reef substrata, respectively). The dominant coral recruits belonged to the genera *Agaricia* and *Porites*, with *Favia* reaching high numbers under conditions of reduced grazing.

Rylaarsdam (1983) found similar results while working on the forereef slope in Discovery Bay and commented on the rarity of *Acropora* in the spat community. During 1976, 1977, and 1978, its juveniles were uncommon or absent in her samples while *Agaricia* and *Porites* clearly predominated (Fig. 5).

The patterns exhibited by these six years of data from Jamaica are typical for the Caribbean. Bak and Engel (1979) found similar recruitment patterns on the islands of Curacao and Bonaire, Netherlands Antilles (Fig. 6). Rogers et al. (1984), who performed a detailed examination of coral recruitment patterns on the north coast of St. Croix, U.S. Virgin Islands, where both *Acropora palmata* and *A. cervicornis* constituted distinct zones, also commented on the rarity of *Acropora* juveniles in their samples; *Agaricia* and *Porites* along with several other genera were, again, common.

Birkeland (1977) examined the recruitment patterns of corals at Galeta Point in Panama. From his summary data and photographs it is evident that *Agaricia* and *Porites* were well-represented on his settlement plates. No *Acropora* recruited during his study (Birkeland pers. comm.).

In a recent study, Bright et al. (1984; also see Baggett and Bright 1985) performed an extensive examination of coral recruitment on the East and West Flower Garden Banks in the northern Gulf of Mexico, 107 nautical miles south of Galveston, Texas, U.S.A. These reefs are of special

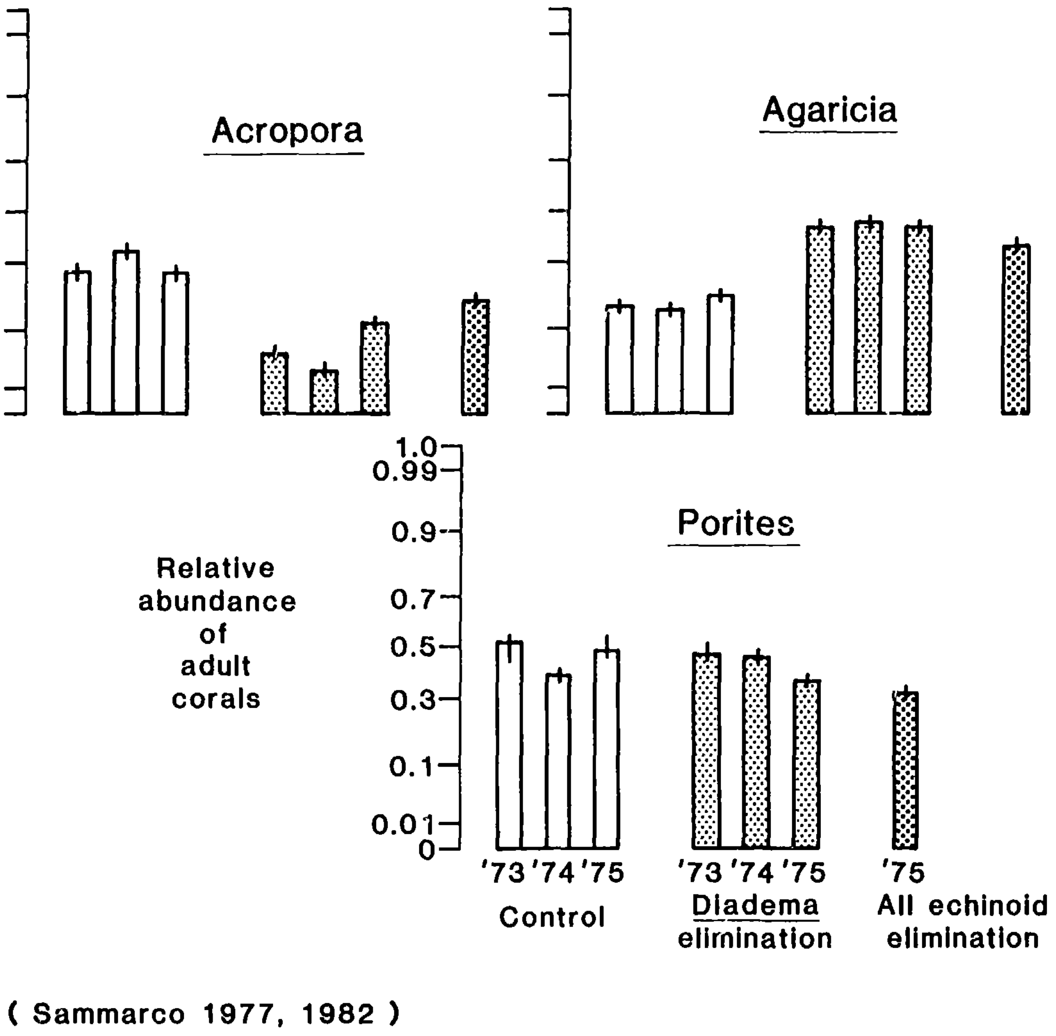


Figure 2. Percent-cover of live adult coral for three major genera - *Acropora*, *Agaricia*, and *Porites* - on lagoonal patch reefs in Discovery Bay, Jamaica, W.I. Data shown on 1973, 1974, and 1975 with 95% confidence limits under conditions of experimentally reduced echinoid densities: clear bars - control conditions with naturally high echinoid densities (averaging up to $99/m^2$); lightly stippled - all *Diadema antillarum* eliminated; heavily stippled - all echinoids eliminated. (Data derived from Sammarco 1978, 1982a).

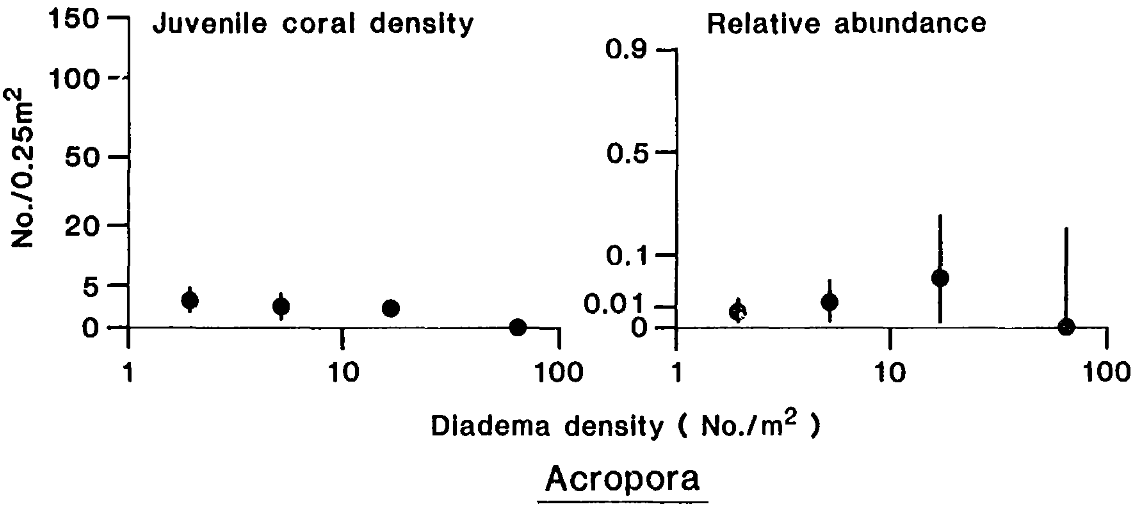


Figure 3. Density of newly settled spat of _Acropora_ as a function of experimental density of _Diadema antillarum_ in a lagoonal patch reef environment in Discovery Bay, Jamaica, W.I. Relative abundances also shown. Data are for 1974 under conditions of primary succession; shown with 95% confidence limits. (Data derived from Sammarco 1978).

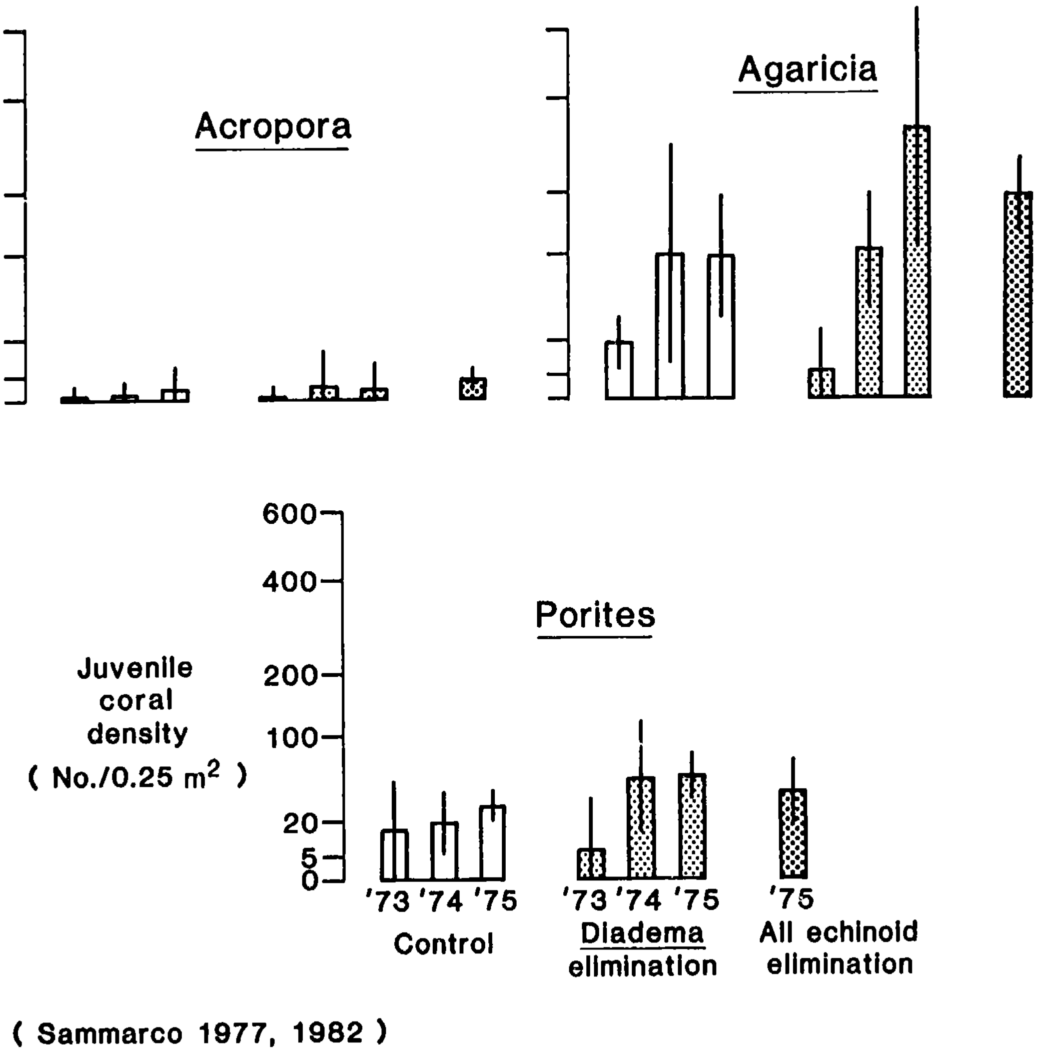
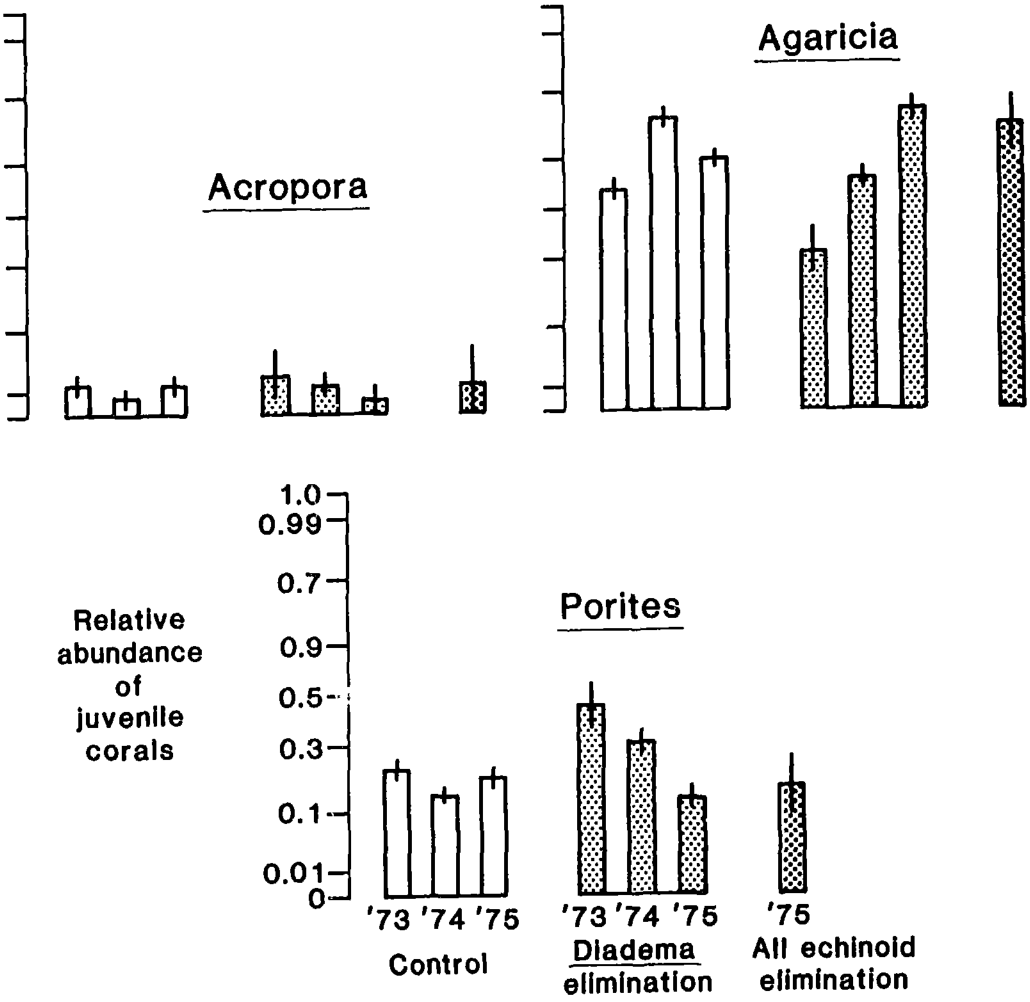


Figure 4a. Densities of newly settled coral spat of three major Caribbean genera - <u>Acropora</u>, <u>Agaricia</u>, and <u>Porites</u> - under conditions of experimentally varied echinoid densities. Samples from lagoonal patch reef environment in Discovery Bay, Jamaica, W.I., under conditions of post-primary succession; collected in 1973, 1974, and 1975. Treatments represent conditions of 1) natural echinoid densities (averaging up to 99/m^2), 2) elimination of all <u>Diadema antillarum</u>, and 3) elimination of all regular echinoids, including <u>Echinometra viridis</u>, <u>Lytechinus williamsi</u>, and <u>Eucidaris tribuloides</u>. Data shown with 95% confidence limits; derived from Sammarco (1977, 1982).



(Sammarco 1977, 1982)

Figure 4b. Relative abundances of newly settled coral spat of three major Caribbean genera - *Acropora*, *Agaricia*, and *Porites* - under conditions of experimentally varied echinoid densities. (See Fig. 4a for details).

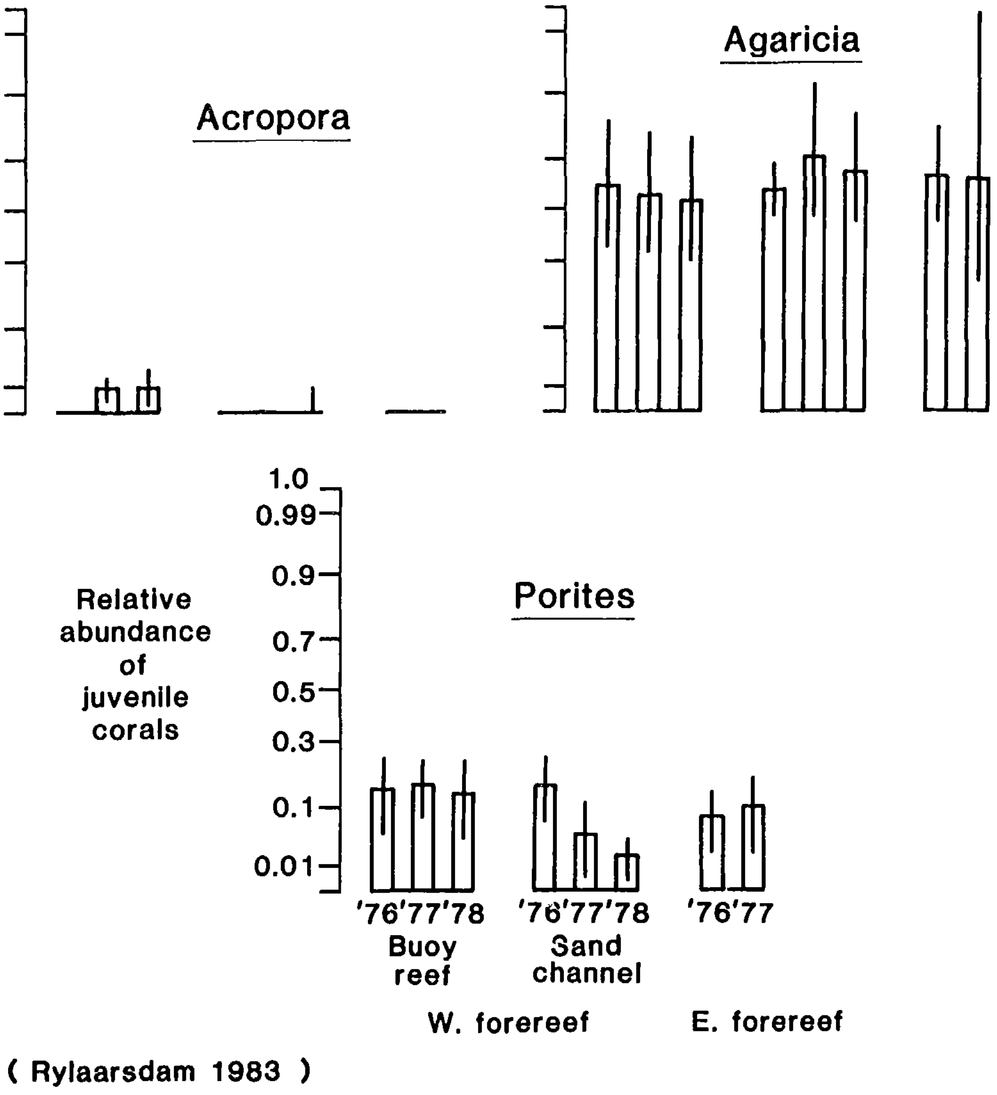


Figure 5. Relative abundances of juvenile corals of three major genera - *Acropora*, *Agaricia*, and *Porites*. Data from three separate sites on the forereef slope at Discovery Bay, Jamaica, W.I., collected in 1976, 1977, and 1978. Data shown with 95% confidence limits; derived from Rylaarsdam (1983).

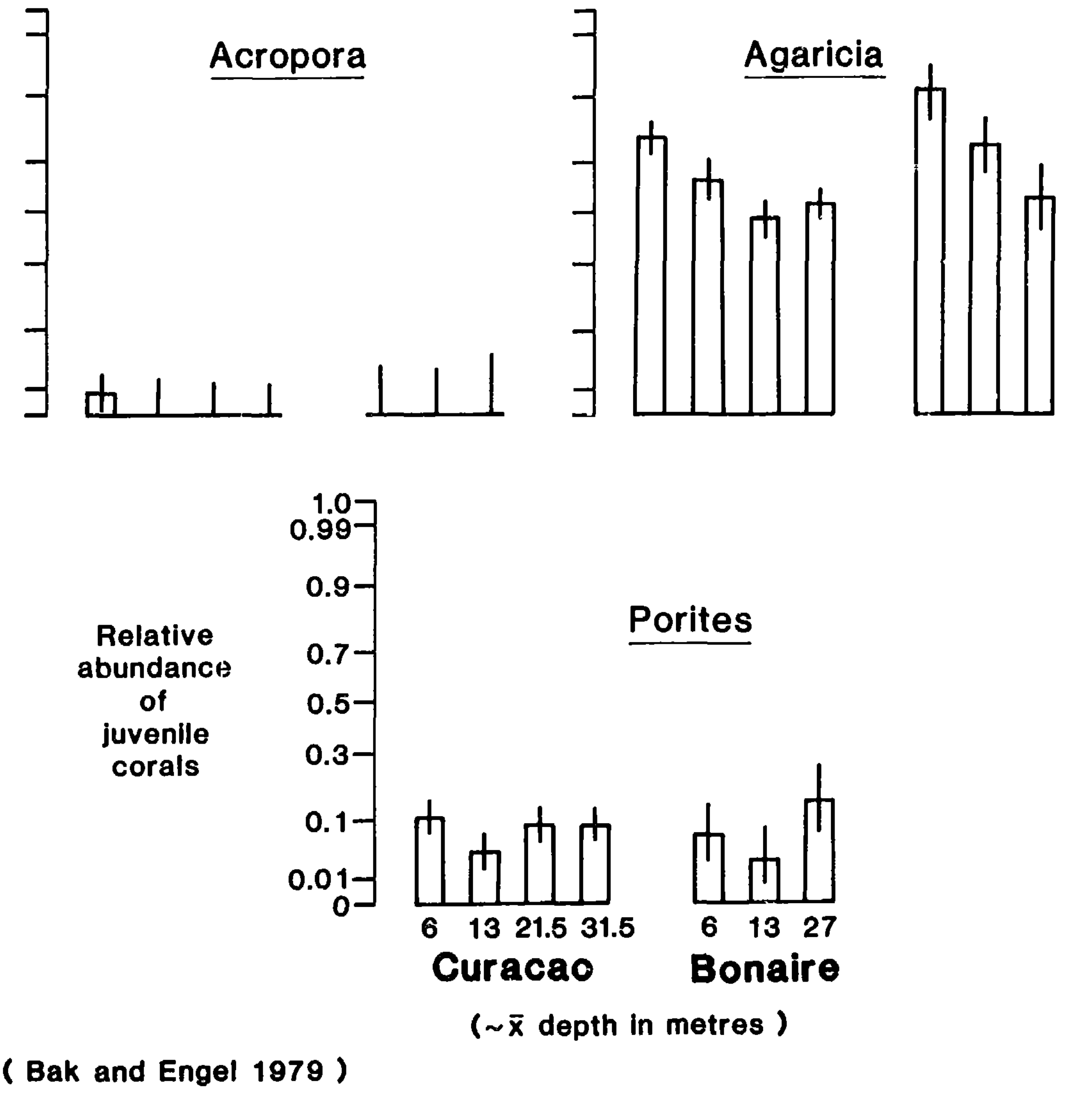


Figure 6. Relative abundances of juvenile corals of three major genera - Acropora, Agaricia, and Porites - in Curacao and Bonaire, Netherlands Antilles during 1975. Samples from depths averaging 6, 13, 21.5, and 31.5m on the forereef slope. Data shown with 95% confidence limits; derived from Bak and Engel (1979).

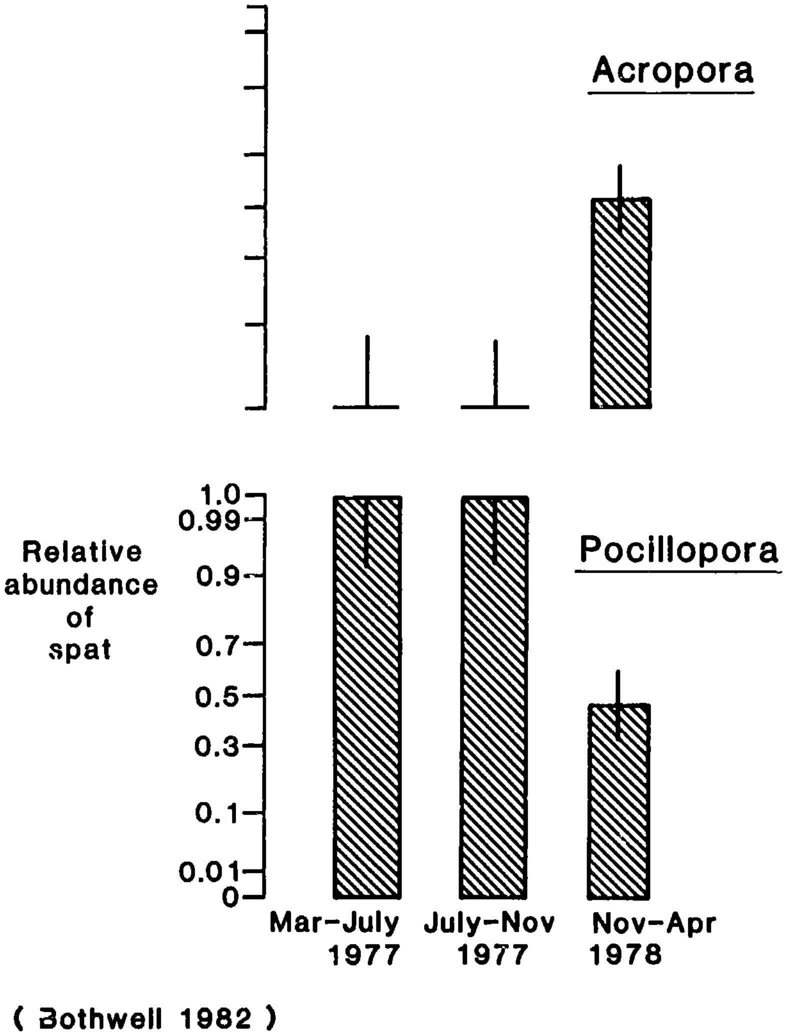


Figure 7. Relative abundances of spat of two major coral genera - *Acropora* and *Pocillopora* - in a shallow lagoonal environment on Heron Island, southern region of the Great Barrier Reef during 1977-1978. Data shown with 95% confidence limits; derived from Bothwell (1982).

interest, for they are well isolated by distance from reefs off Mexico, the west coast of Florida and the Florida Keys (Bright and Pequegnat 1974; McGrail et al. 1982; Rezak et al. 1983). Again, Acropora was absent as juveniles from all his samples while Agaricia and Porites consistently appeared as dominants.

B. The Great Barrier Reef

Acropora is a well-recognized dominant coral genus on the Great Barrier Reef. Its diversity is much higher there, having 70 species (Veron and Wallace 1984) as compared to three in the Caribbean (Bright et al. 1984). It is so prominent on the mid- and outer-continental shelf in the central region that platform reefs in this area have been termed "Acropora reefs" (Done 1982).

In striking contrast with the case in the Caribbean, Acropora was the predominant coral recruit on the Great Barrier Reef. It accounted for 70-80% of all coral spat examined in the damselfish experiment on Britomart Reef in 1979/1980 (Sammarco and Carleton 1982) and 1980/1981 (Sammarco, unpub. data). Acropora spat were also abundant along with spat of the genus Seriatopora, on various reefs at the middle and outer continental shelf. This was the case in 1981 and 1982 on Rib and Myrmidon Reefs (Sammarco 1983a, b; Sammarco, unpub. data) and in 1983/1984 on Helix Reef (Sammarco 1986a, b, c, d; Sammarco and Andrews 1986). On Helix Reef, ~60% to > 90% of all coral recruits examined at different sites from 15-18 m depth belonged to the genus Acropora.

Wallace and Bull (1982), Wallace (1985), and Wallace et al. (1986) have also found Acropora to be a dominant recruit on Big Broadhurst Reef, on the forereef as well as on the reef crest and reef flat. Acropora is also a major recruit in the southern Great Barrier Reef on Heron Island (Fig. 7; Bothwell, 1982). Bothwell found a distinct seasonal pattern of recruitment in this genus; this is not surprising in light of the highly seasonal reproductive activities recently discovered in species of this genus (Harrison et al. 1983, 1984).

C. Life-History Strategies in Acropora

Different species of Acropora on the Great Barrier Reef are now known to utilize a number of modes of reproduction, both sexual and asexual (Wallace 1985). The above recruitment data suggest that at least some species possess life-history traits and recruitment strategies that differ from those in the Caribbean. Acropora, Seriatopora, and Pocillopora appear to be among the "weeds" of this coral community, rapidly recolonizing reef habitats after a perturbation (see Loya 1976a, b). This contention is supported by long-term observations of recolonization on the Great Barrier Reef after the crown-of-thorns starfish outbreak in the 1960s. This corallivorous starfish (*Acanthaster planci* L.: Echinodermata, Asteroidea) devastated reefs through its predatory activities, and the reefs were later recolonized by *Acropora* species (Pearson 1974, 1975, 1981). A similar outbreak and recovery was noted on Guam (Colgan 1981, 1982).

On the other hand, recruitment to the community by the planktonic larvae of all three species of *Acropora* in the Caribbean - *A. palmata*, *A. cervicornis*, and *A. prolifera* Lamarck - is extraordinarily low, despite the prevalence of adults of the genus. It is now known that *Acropora palmata* use external fertilization and have planktonic development of planulae in much the same way as most Great Barrier Reef *Acropora* (Harrison et al. 1983, 1984). Yet from the recruitment data, it is clear that all three species of Caribbean *Acropora* are more heavily dependent upon asexual reproduction via breakage and recementation of branches, as suggested earlier (Sammarco 1978, 1982a). In addition, they have shown superior survival rates under conditions of reduced grazing and resultant competition for space with algae (Sammarco 1978, 1982a). This is not the case with Caribbean species of *Agaricia* or *Porites* (also see Stoddart 1974; van Moorsel 1983).

In summary, *Acropora* on the Great Barrier Reef and most likely other parts of the Pacific are heavily dependent upon recruitment from planulae dispersed in the plankton, while Caribbean *Acropora* are heavily dependent upon asexual reproduction through fragmentation.

D. Implications for Reef Recovery

The striking differences observed in coral recruitment patterns in the two geographic regions have strong implications for comparative recovery rates in their respective reef communities after a severe environmental perturbation. Many Indo-Pacific reefs, including the Great Barrier Reef, experience population explosions of the crown-of-thorns starfish, *Acanthaster planci* Lamarck. These corallivores devastate reefs by consuming much of the living coral cover, as was the case in the 1960s (Endean 1973). Some 10-15 years later, those reefs were recolonized primarily by *Acropora* spp. (Pearson 1981). This type of secondary community succession was observed both in Guam (Colgan 1981, 1982) and on the Great Barrier Reef. The coral recruitment data now available from various regions of the Great Barrier Reef (northern, central, and southern; see above section) help to explain this pattern of recolonization, for *Acropora* is now known to be a predominant recruit in these areas.

An Acanthaster outbreak has recently occurred again on the Great Barrier Reef in the central and northern regions (Done 1984; Endean 1984; Moran 1984; Moran et al. 1984; Wallace 1984) and many reefs have been reduced to 5-10% of their original levels of live coral cover. Under normal conditions, one could expect these reefs to again become recolonized primarily by Acropora within 15 years.

One of the factors which makes this relatively short recovery time possible is the lack of direct effects of Acanthaster predation on newly settled coral spat and juvenile corals (Colgan 1981, 1982). Small colonies would escape detection and thus predation by the starfish (also being of little nutritional value to it). These small colonies often comprise a high proportion of the total number of colonies in the coral community. Thus, even before a new settlement occurs after massive coral mortality due to Acanthaster, a substantial juvenile population would already be in the process of driving reef regeneration, making it possible for coral populations to rebound quickly.

Recovery from massive Acropora mortalities in the Caribbean, however, would require much longer periods of time. Acanthaster or an equivalent corallivore does not exist there, but hurricanes can have the same effect on live adult coral cover. For example, in 1981, the eye of the Hurricane Allen, now termed a "100-year hurricane", passed along the northeast coast of Jamaica with 285 km hr^{-1}. winds producing 12 m waves (Woodley et al. 1981) where 0.5-1.0 m waves are considered normal. This decimated the shallow Acropora palmata zones and much of the deeper Acropora cervicornis zones. Juvenile corals and newly settled spat would have suffered very high mortalities under conditions of heavy surge due to sand abrasion (Sammarco 1983a, b). The low recruitment rates of Acropora would further aggravate the situation and depress recovery rates. Thus recovery of Acropora-dominated zones from perturbations such as this would be much slower in the Caribbean than in the western Indo-Pacific (also see Stoddart 1974).

Under normal circumstances, branch-breakage is known to assist in proliferation of Acropora colonies through redistribution and recementation of fragments (Gilmore and Hall 1976; Shinn 1976; Tunnicliffe 1978, 1981, 1982; Highsmith et al. 1980; Bothwell 1982; Highsmith 1982; Rogers et al. 1982; also see Hein and Risk 1975; Highsmith 1980b). In fact, it is a recognized form of asexual reproduction in the coral. In the case of very severe physical disturbances such as Hurricane Allen, however, many of the broken fragments die either from direct abrasion or from a usually fatal infection termed "white band disease" (Antonius 1982a, b) which follows the perturbation by several weeks, killing many of the remaining fragments (Knowlton et al. 1981; Bak and Criens 1982). Thus, early scleractinian colonizers of disturbed reefs such as these would be comprised primarily of Agaricia and Porites colonies, not Acropora.

In the Indo-Pacific, one of the worst natural disturbances which could occur to a reef would be the combination of an Acanthaster outbreak and a cyclone. The Acanthaster would remove much of the adult coral cover while the cyclone would most likely kill a high proportion of the juveniles. Thus, estimated recovery times for reefs experiencing both of these perturbations could be expected to be much longer than those experiencing only one or the other. This recently happened to several reefs in the central Great Barrier Reef region - i.e., Otter and Beaver Reefs (Fig. 1), and I would predict that regeneration to pre-disturbance levels of coral cover might require, say, 40-50 years.

E. Geological Perspective

The comparative geological histories of the areas under consideration may help to explain the striking differences observed in recruitment-related strategies of the dominant coral genus Acropora. In J. E. N. Veron's recent review on corals of the Indo-Pacific (1986), he points out that the Tethys Sea was pantropical and continuous throughout most of the Tertiary (65-7 million years B.P., also see Van der Spoel 1983). This allowed circumglobal transport of tropical marine larvae, including those of corals. Marine climatic conditions were also more equable at this time on a global scale, enhancing the proability of successful widespread larval dispersal. In fact, he states that the coral fossil records are more similar for the Indo-Pacific and the Caribbean during this period than they are now. During the Miocene (25-7 million years B.P.), however, temperatures began to fall and the Antarctic ice cap formed. Somewhat later, during the Pliocene (5 million years B.P.), the Isthmus of Panama developed, segregating the Atlantic and the eastern Pacific oceans.

The last glaciation occurred approximately 20,000 years ago, and sea level dropped by 100 m (Bloom et al. 1974; Hopley 1982). Veron (1986) claims that massive extinctions of corals resulted, causing a severe genetic bottleneck in the Caribbean region. This concurs with Stanley's (1984) deductions concerning mass extinction in the oceans, particularly in the Caribbean at this time. When the climate warmed and the glaciers receded, physical conditions in this region once again became suitable for scleractinian corals. Veron (pers. comm.) believed that corals from the southwest Atlantic off the Brazilian coast were probably those which eventually recolonized the Caribbean.

These events in themselves by no means account for the specific selective factors responsible for shaping the evolution of the two recruitment-related strategies observed in *Acropora*. They do, however, demonstrate that present-day Caribbean species of *Acropora* may be the result of secondary colonization by a small subset of species. Thus, founder effect (Dobzhansky 1970; Mayr 1970) and vicariance (Nelson 1983; Valentine and Jablonski 1983) could help to explain differences we now observe in their life-history strategies.

COMPARISONS OF THE CRYPTIC NATURE OF CORAL SETTLEMENT

A. Cryptic Habits and Predation

The degree to which a sessile marine organism displays cryptic habits is believed to be at least a partial indicator of the amount of predation to which it has been subjected through evolutionary time (Newman 1960; Bakus 1964, 1966, 1969, 1971; Hatcher 1983; Day 1983). Location at settlement is a manifestation of the behavioral response of the larva exhibited at a critical stage of the life cycle - a point at which a mistake in the singular choice of a settlement site may be fatal to sessile organisms (Strathmann et al. 1981; Levinton 1982). (This problem may be circumvented in certain cases. For example, *Seriatopora hystrix* and *Pocillopora damicornis* are capable of "polyp bail-out" upon experiencing environmental stress [Sammarco 1981, 1982b, c; Richmond 1985]). A comparison of placement of coral settlement in the two oceans may then reveal information concerning their respective evolutionary histories with respect to predation.

In Jamaica, when grazing by *Diadema antillarum* was removed from the benthos, a shift occurred in the settlement exposure of juvenile corals. They shifted from 20% settlement on fully exposed benthic surfaces at *Diadema* densities of 64 m^{-2} to ~ 80% on exposed surfaces at 0-1 *Diadema* m^{-2} (Sammarco 1978, 1980). Thus, given the opportunity, and with a reduction in levels of biological disturbance, coral larvae exhibited a preference to settle in exposed areas.

On the Great Barrier Reef, the response appears to be different. In an experiment on Britomart Reef (Sammarco and Carleton 1982; Carleton and Sammarco, in press), ~28% of all coral spat were found in exposed positions under naturally high levels of grazing. When grazing was experimentally reduced within the territories of certain damselfish, this level did not change. Under conditions of reduced light levels within the territories and also within cages, however, 40-45% of the spat were found on exposed surfaces. Data on coral settlement from Pandora, Rib, and Myrmidon Reefs also followed this pattern (unpub. data). In many cases, coral spat were 100% cryptic. An exception to this was found in deeper water on Pandora Reef where, once again, light levels were relatively low. Wallace and Bull's (1982) data from Big

Broadhurst Reef are also supportive of this finding. They found that coral spat occurred in more exposed positions with increased depth, where light levels are known to be lower (Done 1982, 1983; Chalker 1983; Chalker and Dunlap 1983; Chalker et al. 1983; Drew 1983). Birkeland et al. (1982) have also found generally cryptic settlement of coral spat in shallow water in Guam, shifting to exposed positions with depth.

B. Discussion

Coral larvae seem to settle more cryptically on the Great Barrier Reef (and possibly in other parts of the Indo-Pacific) than in the Caribbean. This implies that the intensity of biological disturbance and/or predation in the former area has been greater through evolutionary time. This hypothesis is supported by the fact that both the diversity, abundance, and impact of corallivores is higher in the Indo-Pacific than in the Caribbean. While many species of fish are known to prey upon live coral in the Indo-Pacific, very few do so in the Caribbean (Hiatt and Strasburg 1960; Randall 1967, 1974; Glynn et al. 1972; Glynn 1973; Hobson 1974; Neudecker 1977, 1982; Frydl and Stearn 1978; Vermeij 1978; Brock 1979; Frydl 1979; Borowitzka 1981). Corallivorous gastropods, such as Drupella, Jenneria, Quoyula, and others are also more common in the Indo-Pacific (Vermeij, 1978), although it has been suggested that Coralliophila breviata can be an important predator of corals in the Caribbean (Robertson 1970; Brawley and Adey 1982; Glynn et al. 1978).

Asteriod predators of corals are only known from the Indo-Pacific. These include Nidorellia and Culcita as well as the better known Acanthaster (crown-of-thorns) (Vermeij 1978). Acanthaster, of course, can be responsible for massive coral mortalities on the Great Barrier Reef and other Pacific coral reefs (Endean 1973, 1974, 1982, 1984; Endean and Stablum 1973, 1975, 1977; Pearson 1981; Done 1984). In fact, predation on adult coral colonies may be an important factor influencing cryptic settlement, allowing the juvenile colony to grow into a size refuge that increases its probability of survival if preyed upon (Birkeland 1977; Sammarco 1978, 1982a; Brock 1979).

The conclusion that predation is more intense in the Indo-Pacific than in the Caribbean concurs with those of earlier investigators. Bakus (1966, 1969) concluded from his observations of the cryptic habits of sessile organisms that fish grazing was more intense in the Indo-Pacific than in the western Atlantic. Earle (1972) and Glynn (1972) deduced the same in attempting to acount for the scarcity and low profile of algae in the eastern Pacific as compared to the Caribbean. Birkeland (1977) demonstrated experimentally that eastern Pacific grazers could remove greater biomass from the benthos than Atlantic grazers in the same time period. Vermeij

(1978) noted that the predation-related adaptations of gastropods were more highly evolved in Indo-Pacific species than in those from the Atlantic, and he substantiated this claim with both descriptive morphological (Vermeij 1974, 1976, 1977a) and experimental (Vermeij 1976) data. He also noted that the claws of molluscivorous brachyuran, panulirid, and, in some cases, portunid crustaceans were larger and more powerful than their western Atlantic counterparts (Vermeij 1976, 1977b). Palmer (1978) demonstrated experimentally that eastern Pacific molluscivores were more effective than those from the western Atlantic. Meyer and Macurda (1977) noted that Indo-West Pacific crinoids possessed more highly evolved predator-related adaptations than those of the Caribbean.

Vermeij (1978), in reviewing a host of possible explanations for these observed differences, concluded that they could not be explained by differences in the physical environment, such as wave force, tides, or temperature, nor by differences in productivity. He and Palmer (1978), however, did note that the trend for increased levels of predation was associated with increased species diversity. This trend is reinforced with data derived from juvenile corals.

OVERVIEW

The effects of grazing on the success of coral recruitment are related in the Caribbean and the Great Barrier Reef. Biological disturbance to, or predation upon, newly settled corals is an important contributing factor in reducing success of coral settlement in both systems, as is competition for space with other sessile organisms. The effects of grazing seem to be similar, although the actual mechanisms involved may be different.

The major grazers seem to be different. In the Caribbean, echinoids were the major grazers (until recently), while fish fill the major portion of this niche on the Great Barrier Reef. This may be due, at least partially, to two causes: 1) the different evolutionary histories of the two regions, and 2) the more recent impact of man's exploitation of Caribbean reef fish populations.

Coral recruitment patterns are quite different in the two regions when considering the relationship of recruits to adults, particularly in the genus Acropora. Acropora is predominant in the adult coral community of the Caribbean, accounting for major zonation patterns; yet it is ill-represented and, indeed, rare in the juvenille community. This indicates that at least some species of Acropora on the Great Barrier Reef are heavily dependent on both asexual reproduction and larval dispersal for colonization while Caribbean species all rely primarily on asexual modes of reproduction, utilizing branch-breakage and recementation for colonization. These findings have major implications for differential reef recovery in the two areas after a severe environmental perturbation, probably requiring much longer periods of time in the Caribbean. These differences may be due to the different geological histories of the two regions.

Finally, the degrees of predation or biological disturbance on juvenile corals appears to be more intense on the Great Barrier Reef than in the Caribbean. This may be inferred from the comparative settlement patterns of the larvae under similar conditions, as coral spat will tend to settle more cryptically on the Great Barrier Reef than in the Caribbean.

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COMPARISON OF THE TROPICAL WESTERN ATLANTIC (CARIBBEAN) AND THE INDO-PACIFIC: HERBIVORE-PLANT INTERACTIONS

by

John C. Ogden*

ABSTRACT

Many of the apparent differences between the tropical western Atlantic (Caribbean) and the Indo-Pacific with respect to herbivore-plant interactions arise from studies of the spatial association and interrelationships of the three major tropical ecosystems: coral reefs, seagrass beds, and mangroves. In the Caribbean, these relationships are particularly evident and well-studied between coral reefs and seagrass beds as they are often closely associated. In the Indo-Pacific, atolls and submerged reefs may occur far from any contact with land, precluding the development of seagrass beds or mangroves.

Herbivores are a principal vector of ecosystem interaction, particularly in the Caribbean. The following general points are worthy of more attention:

1. Between Caribbean coral reefs and seagrass beds there are striking diurnal and nocturnal movements of fishes and invertebrates. Diurnal and nocturnal herbivores, particularly fishes and echinoids, move across the reef-seagrass boundary, graze, and create prominent halos. Halos are not as evident in the Indo-Pacific but have been noted in some locations (e.g., Belau). Nocturnal benthic-feeding fishes, such as haemulids and holocentrids, move from reefs to seagrass beds and may, along with herbivores, be significant vectors of nutrients, DOM, and POM from seagrass beds to coral reefs.

2. In the Pacific, direct consumption of seagrasses is limited to a few animal groups such as turtles, dugongs, and several families of fishes, particularly siganids. In the Caribbean, there is intensive herbivory in seagrass beds and many examples of over-grazing.

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*West Indies Laboratory
Fairleigh Dickinson University
Teague Bay, Christiansted
St. Croix, USVI 00820

3. In the Caribbean, coral reefs next to seagrass beds, or patch reefs isolated in seagrass meadows, show elevated fish biomass due mainly to the presence of herbivores and benthic feeders, such as scarids, haemulids, and holocentrids which use the reef for shelter and forage over seagrass beds for feeding.

4. Seagrass beds and mangroves have been implicated as nurseries for a variety of organisms which spend their adult life on coral reefs. This phenomenon has not been well-studied in either the Caribbean or the Indo-Pacific.

5. Export of detrital material from seagrass beds and mangroves to coral reefs and the deep sea has been documented in several locations in the Caribbean using stable carbon isotope ratios as natural food chain tracers. Studies in the Indo-Pacific are lacking.

6. Due to its small size, high population density in coastal areas, and intense fishing pressure, many areas of the Caribbean are already over-fished. This seems to be less of a regional problem in the Indo-Pacific. Thus, the Caribbean is rapidly changing and may now be quite different from its undisturbed, pre-Columbian state.

In the Indo-Pacific, coral reefs are distributed across a vast geographic region, larger than the ranges of distribution of many plants and animals. This creates a spatially and biologically complex set of associations. In contrast, the Caribbean is geographically small, with a relatively uniform flora and fauna. On coral reefs in both oceans, there are numerous similarities and differences which provide the basis for comparative studies of herbivores and plants in the Caribbean and the Indo-Pacific. For example:

1. Macroalgae in both regions are subject to 'blooms', either seasonally or when reefs are suddenly disturbed, as in the recent mass mortality of the echinoid Diadema, or when Acanthaster opens space on the reef for settlement.

2. Algal turfs (consisting mainly of blue-green algae and filamentous red algae) are prominent on coral reefs in both the Indo-Pacific and the Caribbean, but may be a greater component of overall reef productivity in the Caribbean.

3. Echinoids appear to be more abundant and more subject to population explosions and crashes in the Caribbean than in the Indo-Pacific. The relative

importance of predation in controlling echinoid abundance patterns should be studied.

4. Herbivorous fishes, while prominent in both oceans, make up a greater proportion of the fish biomass on coral reefs in the Caribbean compared to many Indo-Pacific reefs, particularly atolls and other reefs remote from land.

Circumstances prevented John Ogden from attending the workshop on which we are reporting here. Nevertheless, he contributed this expanded abstract for which we are grateful.

--The Editor--

CHARACTERISTICS OF FISH COMMUNITIES ON CORAL REEFS AND IN POTENTIALLY INTERACTING SHALLOW HABITATS IN TROPICAL OCEANS OF THE WORLD

by

James D. Parrish*

ABSTRACT

Coral reefs occur in a variety of situations in the Atlantic, Pacific and Indian Oceans, which involve great differences in the degree of isolation from surrounding shallow environments, e.g., seagrass beds, mangroves and unvegetated sediments. Mangroves and seagrass beds appear to offer attractive habitats for fish--including species commonly found on reefs--especially for settling postlarvae and developing juveniles. The extent and situation of these habitats are often such that they could effectively intercept large numbers of recruits, and these habitats may offer some advantages over coral reefs for early survival of young juveniles. However, many reef tracts that occur far from such habitats appear to experience adequate recruitment and survival. There is no clear evidence as to whether, in general, reefs situated favorably to the shallow, vegetated habitats experience any enhancement of these early life stages. Such adjacent, extensive, vegetated areas may act as accumulators of excess recruits, which may tend to smooth out the temporal patchiness of recruits available to reefs directly from the plankton. There are a few demonstrated mechanisms of movement of plant and animal material (alive, dead or reprocessed) between these shallow habitats, including recycling of reef organic production through an adjacent habitat and back to the reef. The absolute values of such fluxes that are assimilated by (or returned to) the reef may be small, but the transport mechanism or form in which the material is exchanged may be particularly suitable to enhance fish populations. Relative trophic patterns among the various shallow, demersal habitats and among the oceans of the world are not entirely clear. This is partly because quantitative fish community studies and trophic studies in seagrass and mangrove habitats are inadequate. Carnivores appear to dominate in all habitats in almost all situations; usually benthic invertebrates are the major prey group. In a few reported situations, primarily in the Pacific,

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*Hawaii Cooperative Fishery Research Unit
2538 The Mall, University of Hawaii
Honolulu, Hawaii 96822

planktivory appears to be the dominant trophic mode. Algivory is important in all situations, but almost never dominant, and its importance varies widely within (as well as between) oceans and types of situations. It may be most significant on the open coasts of some isolated islands and atolls. Seagrass is grazed directly by relatively few fish species anywhere, but it is eaten to some extent where it occurs in all oceans. This is best documented in the Atlantic. If important linkages occur among the shallow, adjacent, tropical habitats, they most likely involve fish recruitment and/or trophic processes involving invertebrates. Both are little-known subjects in these environments, that will require additional, focused research to clarify the nature and magnitude of any interactions that influence marine resources.

INTRODUCTION

Coral reefs occur widely in the tropical Atlantic, Pacific and Indian oceans, in a wide variety of situations. They are often surrounded by or adjacent to extensive shallow areas with other types of substrate that provide quite different habitat for biota. Tropical habitats that commonly occur extensively near reefs include seagrass beds and mangrove tracts, as well as open sandy flats. Both seagrass and mangrove habitats have high primary productivity, much of which seems to be available for export as dissolved or detrital organic material (Odum, Burkholder and Rivero 1959; Bakus 1969; Heald and Odum 1970; Odum and Heald 1972, 1975; Buesa 1974; McRoy and McMillan 1977; Ogden 1980; Cintron and Schaeffer-Novelli 1983). Both types of habitat contain dense vegetation of fairly high relief that provides suitable protective cover for many species of marine fish and invertebrates. It has long been suspected that there may be important ecological linkages between these diverse habitats in terms of flux of energy or materials, obligate use of a combination of the habitats in the life cycles of animals, or other interactions (Odum and Heald 1975; Ogden and Zieman 1977; Ogden and Gladfelter 1983; Birkeland and Ogden 1985). It has been suggested that the functioning of such linkages largely explains the persistence of extraordinarily high densities of biomass concentrated on the limited bottom area of reefs (Bardach 1959; Starck and Davis 1966).

The potential harvest from reef areas is considerable; Munro (1984) and Munro and Williams (1985) have recently suggested a theoretical potential world harvest from all coral reefs of 9 million tons per year. Much of this harvest (present and potential) is fish. Thus, there are important economic as well as scientific motivations to determine how the various shallow-water tropical habitats are used by fishes, and how their ecological interactions affect productivity of "reef" fish populations. There are undoubtedly important physical interactions among the major shallow-water habitats (e.g., effects of sediment production and movement, other effects of water circulation and wave energy), and some types of interchange of inorganic nutrients and other compounds, as well as separate interactions among invertebrate animals (Ogden and Gladfelter 1983). However, the present discussion will be limited to processes that involve fish production more or less directly. It will be concerned with the nature and importance of processes, the habitats involved, and the characteristics and extent of the processes in the various types of situations and oceanic regions where reefs occur.

FLUX OF MATERIALS AND ENERGY

Questions of the direction and amount of net flux of energy and materials between the major habitats are still open to conjecture, and it seems likely that the pattern is different in different situations. However, it is clear that shallow surroundings of almost any kind offer some opportunity for storage of detrital material leaving the reef. Reefs produce large quantities of such material that ranges from mucus to carcasses of dead animals (Glynn 1973; Johannes and Gerber 1974; Gerber and Marshall 1974a; Hobson and Chess 1978; Hatcher 1982a). Some reef-dwelling or reef-associated fishes that forage in the water column feed heavily on such material as it is washed from the reef, and thus return to the reef a portion of the potential detrital loss (Johannes 1967; Gerber and Marshall 1974a, 1974b; Hobson and Chess 1978), Behaviorally this feeding interaction may be viewed as planktivory, and such fishes are usually indiscriminately lumped with predators on live pelagic plankton as "planktivores" in most studies. However, the source of the material, representing reef productivity, creates an important distinction. Furthermore, since much of its biomass appears to be displaced reef benthic algae, such feeding represents herbivory on reef primary production, a very different trophic role from the typical carnivory on pelagic animals such as crustaceans.

Such algal "planktivory" has been best reported from Pacific oceanic atolls (specifically Enewetak). These atolls lie in extremely oligotrophic waters (Sargent and Austin 1949; Odum and Odum 1955; Taniguchi 1972) without the benefit of shallow-water surroundings (other than their lagoons). It is widely believed that they are among the most "closed" of ecosystems--i.e., they are organized for maximum retention and recycling of resources. Thus, it seems adaptive that this form of recycling of reef algal primary productivity should be most highly developed in such situations. The apparent high levels of algal productivity in these situations, together with the presence of effective agents to produce algal debris (heavy wave action on windward exposures and heavy benthic fish grazing) may lead to especially high occurrence and consumption of this drift algae. Studies of midwater feeding downcurrent of reefs in other situations have apparently not been done in ways that permit assessment of this trophic mode elsewhere. Its importance is beginning to be recognized, however (e.g., Williams and Hatcher 1983).

Reef debris that is not recaptured by reef planktivores will be most effectively retained in shallow surroundings that provide dense relief to reduce water motion and collect finer sediments. Both seagrass beds and mangroves provide such an environment. Once debris is stored in these habitats, return to the reef may occur by several mechanisms. Foraging fish, commuting from the reef may eat it directly, but diet studies of resident reef fishes do not suggest that this is a major mechanism. The major fish consumers of such benthic debris are probably a few generalized detritivores that associate rather indifferently with a variety of shallow habitats (e.g., Mugilidae). The net movement of materials or energy associated with their activities is uncertain.

Reef detritus may (1) be consumed directly in these surrounding habitats by a variety of resident invertebrates, or (2) it may sustain a microflora of detritivores which is consumed by these invertebrates, or (3) if reduced to basic nutrients, it may support plant growth within the habitat. In any case, the food web within the habitat produces an invertebrate fauna which may be abundant where the habitat provides sufficient protective cover. Such habitats as algal beds (Thomassin 1974), rubble flats (Alheit 1982), and sandy substrates with significant coverage of sessile invertebrates such as sponges and ascidians (Parrish and Zimmerman 1977) may provide the required cover. Certainly seagrass beds and mangroves are highly suitable habitats which often have large invertebrate biomass (O'Gower and Wacasey 1967; Heald and Odum 1970; Austin and Austin 1971; Abele 1974; Thomassin 1974; Brook 1975, Table 16; Heck 1977; Weinstein and Heck 1979; Wahbeh 1982).

Fish are probably the main agent for returning materials and energy of reef origin by this pathway, and they are one of the major animal agents of transport between the reef and its surroundings for flux of any origin. Some echinoids that reside on the reef also commute to surrounding areas and consume large quantities of vegetation, particularly seagrasses (Ogden 1976, 1980; Ogden and Zieman 1977). This is clearly a quantitatively important pathway in the Caribbean where such mobile urchins are abundant; it is probably of minor importance elsewhere (Ogden and Zieman 1977; Ogden 1980; Hatcher 1982a; Gates

1986).

Direct herbivory by fishes in surrounding areas is probably quantitatively important wherever reefs and vegetated habitats occur together. Seagrass, a resource unique to a specific habitat, provides one herbivorous pathway. The algae within grass beds and mangrove habitats (particularly algae epiphytic on grass blades and submerged prop roots) also represent a ready resource that is transported to the reef when consumed by herbivorous fishes (Bakus 1969; Rutzler 1969; Austin 1971; Earle 1972; Ogden 1980; Lobel and Ogden 1981; Harmelin-Vivien 1983).

The flux of benthic invertebrates from surrounding habitats to the reef is produced primarily by the activities of a guild of daily commuters that shelter on or near the reef by day and forage the surrounding habitats by night. The systematic groups of fishes involved appear to be rather different in the Caribbean as compared to other oceans. Apogonids and holocentrids (especially the Holocentrinae) probably fill this role to some extent in all oceans, and they are everywhere very abundant (Randall 1963, 1967; Starck and Davis 1966; Vivien and Peyrot-Clausade 1974; Ogden and Zieman 1977; Weinstein and Heck 1979). They probably have a shorter range than some other nocturnal commuters. Foraging at somewhat greater range, snappers of many species (particularly the smaller forms) are moderately abundant and function as important commuting predators in all oceans (Hiatt and Strasburg 1960; Starck and Davis 1966; Randall 1967; Starck 1971; Ogden and Zieman 1977; Weinstein and Heck 1979). Mullids also fill this role to some extent, as well as feeding close upon the reef (Randall 1967; Hobson 1973; Jones and Chase 1975; Ogden and Zieman 1977; Weinstein and Heck 1979). Some mullid species are more active diurnally, but others school passively by day near the reef and scatter widely over the surroundings at night (Hobson 1974; personal observation). Mullids are much more speciose and abundant in the Indo-Pacific.

In some parts of the Atlantic, some Sciaenidae and Muraenidae also forage in this way (e.g., Hobson 1975; Weinstein and Heck 1979), and several species of Haemulidae are particularly important commuters of much the same habits (Starck and Davis 1966; Randall 1967; Starck 1971; Ogden and Zieman 1977; McFarland 1979; Weinstein and Heck 1979). The abundant haemulids are especially conspicuous because they loiter by day on the reef in exposed schools of up to several hundred individuals. They are also rather large fish and fairly conspicuous visually by night as well. By comparison with more cryptic species such as holocentrids, the abundance and importance of the Haemulidae is likely overestimated. However, in the western Atlantic, they are unquestionably very important as transport agents from the surroundings to the reef in terms of abundance, diet, great foraging range, and dependence on the reef surroundings for food.

No haemulid commuters occur in other oceanic regions. However, throughout most of the Pacific and Indian oceans, various species of Lethrinidae occur and apparently fill a somewhat similar trophic role as wide-ranging commuters and agents of transport from the surroundings to the reef (Hiatt and Strasburg 1960; Talbot 1960; Jones and Chase 1975). They are nowhere as abundant as the largest concentrations of haemulids and they do not occur on western Atlantic reefs. Many less abundant reef species also forage the invertebrate fauna of grass beds, e.g., Serranidae (Randall 1963; Harmelin-Vivien and Bouchon 1976), Scorpaenidae (Starck and Davis 1966; Harmelin-Vivien and Bouchon 1976), Fistularidae (Weinstein and Heck 1979), and Aulostomidae (Weinstein and Heck 1979). Meyer et al. (1983) listed 15 families with species that "feed away from and then rest in or over coral heads."

The diel cycle of carnivorous feeding reported for grass beds at Tulear, Madagascar (Harmelin-Vivien 1983) appears to be considerably different from the Caribbean situation. In the Caribbean, there are significant influxes to the grass beds of nocturnal predators on benthic invertebrates. At Tulear the nocturnal invertebrate predators are almost entirely planktivores, and most predators on benthic invertebrates are diurnally active (and probably more nearly resident).

Material brought to the reef by commuting fish is incorporated into the reef trophic system through a number of mechanisms. Since the commuters are reef residents, this input from the surroundings that contributes to their maintenance, growth, and reproduction represents support of reef biomass. Commuting fish are also consumed by resident piscivores, e.g. serranids, lutjanids, muraenids and synodontids. In studies of community piscivory in the Northwestern Hawaiian Islands, Apogonidae comprised 16% of all fish prey individuals, Mullidae 12%, and Holocentridae 6% (Parrish et al. 1986). Similarly, Caribbean Haemulidae are major prey for resident snappers and other piscivores (Starck and Davis 1966; Randall 1967). In all areas studied, the wide ranging, demersal commuters appear to be a major staple in the diets of resident piscivores (Hiatt and Strasburg 1960; Talbot 1960; Randall 1967).

Not all that is consumed by commuter fishes is assimilated or utilized. Loss by defecation and excretion is usually of the order of 20% of consumption for carnivorous fishes (Mann 1969). However, this material is not necessarily lost to the reef. As a result of the diel feeding cycle and typical intervals for transit of food through the digestive tract, a good deal of unassimilated food is voided on the reef. Recycling can occur by direct coprophagy. Coprophagy by fish has frequently been casually observed and has recently been studied and quantified in some detail (Robertson 1982). There is every reason to believe that this practice is widespread and that it may recycle a significant fraction of the food imported but not directly assimilated. There are no quantitative data on natural coprophagy by reef invertebrates on fish feces. However, much of what is voided must be recycled in this way. Much of the reef food web is believed to be detrital, and all benthic community studies show large populations of invertebrates that seem likely scavengers of fish feces. Since most of these detritivores frequent the interstices of the reef substrate, feces reaching the reef surface would be accessible to them. The portion that persists on the bottom for any length of time is likely to accumulate an abundant microflora that results in increased nutritional value.

The potentially important effects of imported fish excretory products on sessile reef invertebrates (particularly corals) have recently been investigated (Meyer et al. 1983; Nelson 1985). Measurements showed elevated levels of dissolved nutrients in the water column and increased sedimentary feces on the bottom in the vicinity of large schools of haemulid commuters loitering on the reef after a night's feeding. Comparison of growth measurements of adjacent corals against controls, and experimental removal of a fish school from a coral gave somewhat ambiguous results, but suggested that increased coral growth from this fertilization process may be measurable where commuters are concentrated. Whether measurable by present methods or not, the mechanism is entirely credible and probably operates widely on reefs. Measurements are lacking to detect any effect of such fertilization on benthic algae, but there is every reason to believe it occurs widely also.

These fluxes between habitats may not be large by comparison with some other fluxes of productive shallow-water systems. However, they may be disproportionately important for several reasons. Oceanic inputs of energy to reefs are often very low due to oligotrophic waters, unfavorable flow patterns, and low retention times. Thus, even small direct fluxes from surrounding habitats are possibly important. To a large extent, reefs appear to maintain their high biomass and rate of productivity by internal recycling. To the extent that these external recycling pathways function, they enhance this trophic mode. For the mechanisms that involve fluxes originating in surrounding habitats, these habitats are highly productive, not only at the primary level, but at the level of benthic invertebrate forage animals (e.g., Rodriguez 1959; O'Gower and Wacasey 1967; Rutzler 1969; Heald and Odum 1970; Austin and Austin 1971; Thomassin 1974; Brook 1975, Table 16; Heck 1977; Wahbeh 1982). For several of the mechanisms described, the import or recycling occurs at a relatively high trophic level (or at least at a level that is close to direct support of fish populations), so the trophic efficiency is high. Even the import of inorganic nutrients (e.g., as completely reduced excreta) fertilizes benthic algae, much of which is consumed directly by fish on the reef.

Situations in which these pathways (other than gleaning of benthic algal drift from the reef) are important obviously are limited to those in which reefs are adjacent to extensive shallows. Atoll lagoons do store reef production and facilitate its recycling, but the area of shallow water is usually very limited. The constraints are much the same for small, high islands that represent the peaks of emergent oceanic mountains and are surrounded by steep slopes with limited shallows. Much of the reef in the central Pacific occurs in such situations, and in many of these areas seagrass beds and mangroves are absent or greatly limited in area and development. Thus, the mechanisms for trophic exchange and reproductive interaction (discussed below) are less effective in these regions. In portions of the western Atlantic, bathymetry and the occurrence of extensive vegetated, shallow habitats are favorable; important fish commuters occur in abundance; and sufficient research has been focused on the pathways that there is some direct evidence of their effectiveness. In other regions where bathymetry and surrounding habitats are favorable, the potential interactions have received less attention, and it is not clear that much direct evidence is available. A major, diurnally conspicuous commuter family (the Haemulidae) is missing, and the most abundant predators that are likely to fill the role have cryptic diurnal habits, and thus have been poorly assessed in all oceanic areas. It seems established that commuter fish foraging in habitats surrounding reefs is an important trophic mechanism in the Caribbean. A basically similar mechanism exists in generally similar areas of the Pacific and Indian oceans; it is not clear whether it is as important quantitatively.

MOVEMENT BETWEEN NURSERY AND ADULT HABITATS

Potentially important interactions related to reproduction and nurture of young fish occur between reefs and shallow surroundings. There is still considerable doubt about how adequately the larval supply from the plankton provides the reefs with postlarvae competent to assume demersal habits and ultimately maintain resident reef populations (Williams 1980; Leis 1982; Doherty 1982, 1983; Victor 1983; Munro and Williams 1985; Sale 1985). The young of almost all reef species go through pelagic stages, and it is not clear how effectively the postlarvae of any particular reef tract may be returned to it by ocean circulatory processes and behavioral adaptations (Johannes 1978; Munro and Williams 1985; Lobel and Robinson 1986).

Regardless of the parental source of larvae, many reefs are of very limited area and not favorably situated to receive abundant recruits. If reefs are prime habitat for many species (as seems to be the case), but a limited and difficult "target" for planktonic larvae to hit, then a strategy of settling nearby in a suitable nursery habitat and migrating to the reef later as a nektonic adult or subadult would seem adaptive for the individual. From a reef population or community perspective, such a nursery or "waiting room" would insure an adequate supply of recruits to the reef.

It may well be (as was long generally believed) that most reefs normally receive an oversupply of potential settlers. Reefs commonly have very high densities of fish, including young stages, and there are indications from many studies that the same general membership or composition is maintained over considerable periods of time. Certainly the impression is that reefs are crowded. From this perspective also, use of an adjacent nursery staging area might be adaptive for the recruit. In terms of community stability, even if pelagic recruits are normally superabundant, this "waiting room" would serve as as an accumulator or buffer to maintain recruitment in the face of occasional bad years. (There are certainly many stochastic elements in the parental stock-to-larval recruitment process.)

The shallow surroundings of reefs have the potential to serve the collector/accumulator/buffer function. They are often extensive in area, typically much more so than the reef. They are often more or less continuous over a considerable linear extent. For example, mangroves may occupy many continuous miles. These areas are often at or near a shoreline, where arriving planktonic larvae are more likely to be retained. As a net result, such areas may be especially effective at intercepting planktonic young that miss the reef directly. Where sampling has been done for recruits in the general vicinity of reefs, they appear to be present and to recruit to any suitable substrate as well as to the reef (Russell et al. 1977; Eckert 1985; Sale 1985; Schroeder 1985). Habitats such as grass beds and mangroves should attract and sustain settling recruits intercepted by these extensive features.

These nursery habitats may offer improved survival in contrast to settlement directly on the reef. Predation on reefs is believed to be particularly intense, especially on very young fish (Johannes 1978; Norris 1985). Parrish et al. (1986) found some fish parts in the gut contents of 52 fish species from a total of 126 examined from Northwestern Hawaiian Islands reefs. Most prey were juveniles. There is generally a lower total density of adult fish in grass beds, mangroves, and other surrounding habitats (Ogden and Zieman 1977; Blaber 1980, 1986). Some piscivorous fish that are abundant and actively predatory on reefs are absent or greatly reduced in numbers. Large piscivorous predators forage in these habitats, but they may produce a net positive effect on survival of young recruits by controlling the local occurrence of other fish of moderate size (Ogden and Zieman 1977; Ogden 1980). Seagrass (even artificial grass) has been shown experimentally to provide protective concealment for small and medium size macrocrustaceans (Main in press), and it is apparently similarly effective for small fish (Randall 1965; Ogden and Zieman 1977; Ogden 1980).

It seems, then, on theoretical grounds that there is a range of sizes from first settlement size to some juvenile stage during which surrounding habitats such as grass beds and mangroves would provide attractive shelter with improved survival for many fish species. At greater sizes, these habitats would remain suitable for relatively few species, and reefs would become more attractive. The composition of communities observed in the various habitats is consistent with this prediction (Austin 1971; Brook 1975; Weinstein and Heck 1979; Ogden 1980; Blaber 1980, 1986; Martin and Cooper 1981). The movement of maturing fish to reefs from surrounding nursery areas represents little direct transfer of biomass. However, since the material and energy input required to maintain them and grow them from settlement size to the size at migration has been supplied largely from sources other than the reef, this acquisition is also highly trophically efficient for the recipient reef.

Based on the data available, a good number of young "reef" fish are in fact found in these surrounding habitats. The data are difficult for several reasons. Relatively few quantitative assessments of whole fish communities seem to have been attempted in tropical seagrass beds and very few in mangroves. Logistical problems of sampling quantitatively close among mangroves are severe, and studies in those habitats tend to be not well quantified. Such assessments as there are were not all made near coral reefs nor even in regions where reefs occur. The proximity to reefs is not always reported.

Quinn and Kojis (1985) in Papua New Guinea made a direct, qualitative comparison of the fish fauna in a mangrove site near coral reefs and in a site remote from reefs, and detected little difference. They reviewed the few and sketchy available reports from the Papua New Guinea area and the study by Blaber (1980) in northeastern Australia. Based on these sources, they reported that the evidence did not suggest that the proximity of coral reefs significantly altered estuarine (mangrove) fish assemblages in the region, and that the mangrove areas studied served as nurseries for very few species of reef fish. However, Blaber (1980) collected a number of species that appear to be reef related in the mangrove estuary at Cairns (several kilometers from reef tracts on the Great Barrier Reef).

Their greater abundance in the mangrove estuary than in the open bay, together with the opposite trend in distribution of their adult predators, caused Blaber to conclude that the mangrove provided an effective nursery. Collections by Blaber (1986) in mangroves of the Dampier region of northwest Australia also contained the young of a number of species that appear to be reef related in some localities. The proximity to the reefs in this study is not clear. The site was judged a poorer nursery because of the abundance of adult piscivores well within the estuary and the apparent high level of predation.

Results of Lal et al. (1984) in Fiji indicated a high incidence of reef-related species among the fish in their mangrove collections. They concluded that the mangrove studied was important both as a nursery and feeding grounds for a number of species from the nearby coastal reefs. Austin (1971) and Austin and Austin (1971) also reported that mangroves in western Puerto Rico harbored the juveniles of a number of fishes common to the nearby reefs. They believed that the mangroves provided an important nursery for reefs in the area. Odum and Heald (1972) extensively collected the fishes of estuarine mangroves in the North River, inland of Cape Sable in south Florida. The site is at some distance from extensive coral development, but several reef-associated species were collected (some commonly or abundantly). Talbot (1960) reported that juveniles of several important species of lutjanids of the reefs off Tanzania, East Africa were abundant in mangroves of the area.

Ogden and Zieman (1977) indicated that seagrass beds at St. Croix, U.S. Virgin Islands contain juveniles of several species that occur (some prominently) in the adult fauna of neighboring reefs. They made estimates of the considerable density of some species as juveniles and reported the influx of huge aggregations of Diodon recruiting to the grass beds. The sequential use of habitats during the development of haemulids has been specifically studied by McFarland (1979) and Brothers and McFarland (1981) at St. Croix. This study documented settlement of postlarvae to grass beds, which were occupied as nurseries, followed by later recruitment of the matured juveniles to coral patch reefs.

In 22 quantitative chemical collections made in Thalassia and Syringodium grass beds near mangrove shores in southwestern Puerto Rico, Cooper (1974) and Martin and Cooper (1981) consistently found many fish species common to the neighboring coral reefs. They also reported that the fish community composition was demonstrably different in pure stands of these two different seagrasses. Brook (1975, 1977) made collections of whole fish communities throughout the year in seagrass beds among the coral keys just off the southeast coast of Florida. His collections contained a high percentage of juvenile fishes, many of which were reef-associated species, and seasonal influxes of juveniles were recorded. Weinstein and Heck (1979) attempted to collect the entire fish communities in seagrass beds in Caribbean coastal waters of Panama. All sites were apparently in the general vicinity of coral reefs, and 2 sites were specifically selected for their proximity to mangroves and coral reefs respectively. The authors reported that the faunas of all 4 sites contained about the same species, and that all had much in common with reef faunas (much more so than did seagrass faunas sampled in the northern Gulf of Mexico, remote from reefs). They concluded that the Panama grass beds act as an important nursery for reef fish, and that many fish treat reefs and grass beds as a single habitat.

Harmelin-Vivien (1983) made extensive collections of the fish communities in various grass bed habitats at the great reef at Tulear, Madagascar. She reported an abundance of juvenile fishes of many common groups of reef residents and commented on the major nursery role provided by the grass beds. Based on extensive underwater visual census work in a variety of habitats in Cocos Lagoon, Guam, Jones and Chase (1975) recorded large numbers of juveniles of several important reef fishes in grass beds. They concluded that the lagoon was "an invaluable nursery for many of the species," largely due to the "natural cover available."

There remains to be demonstrated in a quantitatively convincing way the extent to which fishery yields from reefs are a function of the presence and quality of these surrounding nursery habitats. Ecological wisdom and the evidence cited above would lead to a prediction of such a relationship. There are also qualitative observations that support such a conclusion. Ogden and Gladfelter (1983) pointed out that seagrass beds and mangrove regions are often excellent fishing grounds for larger (reef-related) predatory fishes. They attributed this fact to the presence of abundant prey in the form of juvenile fish and invertebrates that have outgrown the protection of these habitats. In some cases (e.g., Heald and Odum 1970), some major trophic pathways have been identified, estimates of flux at some points in the web have been made, and the existence and value of an apparently related fishery have been cited. However, problems remain in establishing and quantifying the direct link with the fishery, particularly for reef fisheries. Based on an examination of fishery yields from various types of coral reef situtions and their shallow surroundings, Marshall (1985) stated that "no suggestion can be offered as to the possible influence of mangroves," and that "the interaction of reef to adjacent shallows may not be as important as past interpretations have implied." Clearly there is a need for more focused comparative studies of the appropriate situations, and more direct, quantitative measurements of transfers between habitats in terms of specific high level trophic linkages, population size and life history parameters, and movements of fishes at the cohort or population level.

When recruitment and nursery interactions of the various habitats are considered in an oceanic regional perspective, many of the same physical constraints previously discussed also apply. Strong interactions would be expected in some areas of the western Atlantic with extensive adjacent shallow habitats, and there are reports to suggest that some occur. There is less information for other regions, but there is no reason to predict less interaction (particularly in the western Pacific and Indian oceans) wherever suitable physical conditions and habitats occur.

Transfers of either trophic or reproductive fluxes from surrounding shallows to reefs provide the reef ecosystem with some net gain in resources of materials and energy, as compared to an isolated reef system. However, there is an additional benefit from use of a resource in short supply on reefs--space. Reefs are typically crowded biotopes where competition for space can be intense. Regardless of the source of reproductive propagules or the food resource that young or adult fish consume, the fact that these activities of fish, that are currently or ultimately reef residents, can occur outside the reef, permits a higher standing crop of biomass and a more complex reef community with a higher level of total activity.

COMMUNITY COMPOSITION AND TROPHIC RELATIONSHIPS

The richness of the fish fauna is very different in various oceanic regions where coral reefs occur: about 520 species in the western Atlantic (Starck 1968; Goldman and Talbot 1976), at least 300 species in the eastern Pacific (Hobson 1968 based on Walker 1960), about 450 in Hawaii, 600-700 in the Marshall and Marianas Islands, at least 1500-2000 in areas of the Philippines, New Guinea and tropical Australia, and 700-900 in islands of the Indian Ocean (Seychelles and Madagascar) (Goldman and Talbot 1976). A similar trend is seen when only those species that can clearly be called coral reef fishes of individual large reef tracts are compared: about 400 species in the Florida Keys, 850 in the Capricorn group of the Great Barrier Reef, about 250 at Tutia reef off Tanzania (Starck 1968; Goldman and Talbot 1976). The effects of these large differences in species richness would be expected to persist down to some smaller scale of reef size or habitat diversity. As a general trend, the great majority of families are represented in all the major oceanic regions. Most species are not shared between the major faunal regions; however, there are many cognate species pairs between the regions.

There are major differences in the composition of assemblages of fishes in different microhabitats of any reef tract. "Habitat zones" within reef tracts and their individual fish assemblages have been extensively studied and defined in terms of depth, wave energy, type of substrate, relief or rugosity, and other variables (e.g., Hobson 1974; Goldman and Talbot 1976; Harmelin-Vivien 1981; Hayes et al. 1982). The great variability makes it difficult to define or quantify the composition of the community for an entire reef tract and to compare reefs within an oceanic region or between regions (Williams 1982; Williams and Hatcher 1983; Russ 1984a). Few rigorous quantitative comparisons have been attempted on large geographic scales, and the results are of little value for understanding the factors that control any differences among regions or major habitats.

In a few cases examined, the "within habitat" diversity of fish communities of reefs in widely separated oceanic regions was found to be similar, despite greatly different available species pools. Bohnsack and Talbot (1980) found essentially the same total number of families and species attracted to similar artificial reefs in the Florida Keys and at One Tree Island, Great Barrier Reef. Comparing 20 chemically collected samples from natural reefs in the Bahamas with 20 similar samples from reefs in the Society Islands, Smith (1978) found no significant difference between the mean number of individuals in a community (collection). The numbers of species, genera and families were significantly higher in the Bahamas. Sale (1980) examined the species richness (as a function of size of the collection) and found no significant differences between 20 patch reefs at One Tree Island and patch reefs at 13 Caribbean sites. Talbot and Gilbert (1982) compared species richness and number of individuals and weight of the total community for 4 locations (Solomon Islands, Lizard Island (GBR), One Tree Island, and Lord Howe Island) widely separated in latitude, at about the same longitude in the western Pacific. Relatively few statistically significant differences were found except for Lord Howe Island. Similar comparisons (except weight of individuals not tested) between Lizard Island and Tutia Reef, Tanzania showed no significant differences. Sale (1980) failed to find any significant latitudinal component of variability in species richness for several coral reef communities tested. However, he found species richness negatively correlated with the distance from the Philippine Islands (an assumed zoogeographical area of faunal origin).

These comparisons on the whole fail to evaluate "between habitat" diversity or overall diversity of reef tracts. In almost all cases, variability appears to be high within the data from each locale. For some of the published results, it appears that it may be too high for significant differences to be shown where they likely exist. Also, present sample sizes in most cases may be too small to permit assessing the variability at a locale adequately. Williams and Hatcher's (1983) warning about making generalizations on large geographic scales should be taken seriously. In light of these difficulties, any efforts to perceive oceanic regional or habitat trends in the following results must be viewed with cautious skepticism.

An interesting perspective, particularly for making oceanic regional comparisons, is gained by considering the trophic structure or composition of entire fish communities (or the closest approximations for which data are available). Results compiled or calculated from 12 studies of reefs are shown in Table 1. There are (few) results from all major oceans and various types of reef situations. Several overlapping or nested types of trophic classification are used. As much as possible, the original author's classification has been used, and additional classifications have been applied in some cases in an effort to make results more comparable. Thus, a single study may appear in 2 or more lines, classified differently.

Types of measurements vary as noted in the table and footnotes. Some results are based on numbers of individuals for each fish species ("Pred. no.") and some on total weight for each species ("Pred. wt."). Abundance of fishes was variously estimated by large-scale, quantitative collection using chemicals or explosives or by visual underwater census, or some combination of these methods. In all except 2 studies, the community trophic composition appears to have been estimated by assigning the population of each fish species to one or more trophic categories, based on separate diet data (from the local area or elsewhere) and then summing each category. In studies by Harmelin-Vivien (1981) in Madagascar and Parrish et al. (1985, 1986) in the Northwestern Hawaiian Islands, data on populations and diet of each species were taken more or less concurrently. Thus, the actual consumption of each trophic category was determined directly, and predation by each species fell into as many categories as were appropriate. For these studies, results appear in the form of the percentages of the total number and/or weight of prey eaten by the entire fish community ("Prey no." or "Prey wt.").

Table 1 probably contains results from all published studies in which the relative abundance of the species in a more or less complete fish community was quantified, and a broad range of original diet data was taken for it. These studies were supplemented by several others with detailed, well replicated quantification of the community, but lacking original diet data, and for which the author used diet information from the relevant literature. Table 1 may contain all such published studies. In 2 cases (Jones and Chase 1975; Bohnsack 1982), the quantification of the community appeared to be of comparable quality, but the authors did not assign the species to trophic categories.

These studies were done in interesting localities where other trophic results were lacking. The authors' results seemed sufficiently clear and detailed, and diet information in the literature appeared adequate to permit estimating the trophic composition. These results, prepared for this report, must be considered more approximate, since they involve the present author's interpretations in handling the data. The total results in Table 1 contain some interesting similarities and diversity, and provide a useful backdrop for considering the various trophic modes as they are practiced in various oceanic regions, habitats and reef situations.

A. Herbivory

Herbivory seems a priori the simplest and least ambiguous trophic category. However, on reefs and in surrounding shallow habitats, it entails several complexities. Endosymbiotic algae, particularly the zooxanthellae of scleractinian corals, pose a conceptual problem, which some workers have approached by lumping herbivores and coral feeders (Goldman and Talbot 1976, see Table 1). The possibility must be allowed that some fishes acquire significant nutrition directly from the algal symbionts in animal tissue. However, for operational purposes in the present discussion, trophic classification and interpretation is based on the host animal as prey. Reef fishes that are quantitatively the major consumers of other plant material do not appear to consume enough endosymbiotic algae to suggest that it represents a major direct food source for herbivores as a whole. Fish communities also consume plants by gleaning drift algae (covered elsewhere in this discussion) and by feeding directly on sea- grasses and attached benthic algae.

Seagrass feeding as a trophic mode does not fit neatly into any category of Table 1. Perhaps seagrass feeders are most nearly "large croppers" feeding external to the reef. Seagrass herbivory has very seldom been considered as part of the trophic scheme in quantitative studies of reef fish communities. Much of the available information is anecdotal or occurs among lists or tables of fish gut contents. Results from the two studies which permit considering seagrasses in a perspective of reef community trophics are compiled in Table 2. Clearly, a rather small fraction of all species ate seagrass at all, and very few species ate it regularly or as a large part of the diet. For most consumers, it was a minor (perhaps occasional or incidental) component.

The frequent consumers that used the reef as a primary residence were apparently all scarids and acanthurids in both the West Indies and Madagascar. These species were among the diurnal (usually short-range) commuters from nocturnal reef refuges to algal or seagrass

Table 2. Summary of direct herbivory by fishes on seagrasses in the Virgin Islands and Tulear, Madagascar (Modified from Tables VI and VII of Harmelin-Vivien 1983).

	LOCATION	
	U.S. Virgin Islands[1]	Tulear, Madagascar[2]
1. Number of species studied	212	142
2. Number (and %) of species that contained seagrass in guts	32 (15%)	14 (10%)
3. Number (and %) of species that ate seagrasses regularly	4 (1.9%)	2 (1.4%)
4. % of diet composed of seagrass for regular seagrass eaters (item 3)	45-88% by volume	54-78% by weight
5. % of diet composed of seagrass for all other seagrass eaters	0.1-17% by volume	0.1-5.5% by weight
6. Seagrass as % of total food consumed by the fish community		
Barrier reef grass beds[3]	-	1.9% by weight
Neighboring littoral grass beds[3]	-	2.4% by weight

[1] From Randall (1967)

[2] From Harmelin-Vivien (1979)

[3] Specimens for gut analysis were all collected from grass beds in two areas near the Great Reef at Tulear.

grazing grounds (Randall 1965; Earle 1972; Ogden 1976; Ogden and Zieman 1977; Weinstein and Heck 1979; Alheit 1982). Some species of several other families ate more than trivial quantities of seagrass: Sparidae, Monacanthidae, Tetraodontidae, Ostraciidae, Balistidae, and Hemiramphidae (Randall 1965, 1967; Austin and Austin 1971; Carr and Adams 1973; Ogden 1980; Harmelin-Vivien 1983). The latter family has mostly surface pelagic habits and thus is not truly a reef resident. Most of the seagrass eating species of the other 5 families also associate rather indifferently with reefs. At least traces of seagrass have been found in some species of Gerreidae, Cynoglossidae, Polynemidae and Kyphosidae, primarily also species that associate with reefs only incidentally. For several of these seagrass consumers, grass beds are a major habitat throughout the day.

There is considerable doubt concerning the relative importance of fish and echinoids as grazers on seagrasses in the Caribbean (Moore et al. 1963a, 1963b; Earle 1972; Ogden et al. 1973; Greenway 1976; Ogden 1976; Ogden and Zieman 1977; Hay 1981; Tribble 1981; Hay et al. 1983). It has been demonstrated in at least one Caribbean locality that the recent catastrophic mortalities of echinoids have resulted in increased consumption of algae by fishes (Carpenter 1985). A similar competition for the seagrass resource could be postulated. This line of reasoning has led to the question of whether the higher consumption of seagrass by echinoids in a few locations where it has been intensively studied is in fact a cultural artifact resulting from human activities that have depressed populations of their fish predators and of herbivorous fishes (Hay 1981, 1984; Hay et al. 1983).

Seagrass feeding has been most actively studied in the Caribbean, where conspicuous "halos" of heavily grazed seagrasses often surround reefs within grass beds (Randall 1963, 1965; Ogden et al. 1973; Ogden 1976; Ogden and Zieman 1977; Tribble 1981). The quantities of seagrass consumed by fishes in some Caribbean locations have been shown to be substantial (Ogden 1980; Tribble 1981; Hay et al. 1983). This activity results in a considerable effect on seagrass stands and a significant trophic transfer to reef habitats. Attempts to measure the linkage between the primary production of seagrasses and the nutrition of reef fish have produced ambiguous results (Weinstein et al. 1982), although stable isotopic similarities have been shown (Fry et al. 1982).

There has been little work on quantification of seagrass grazing in other oceanic regions, and a tendency has developed among ecologists to view seagrass feeding by fishes as a Caribbean phenomenon (Kikuchi and Peres 1977; Ogden 1980). However, halos and high estimated rates of consumption have been demonstrated at artificial reefs in a Guam sea grass bed (Gates 1986). Also, the results of

Harmelin-Vivien (Table 2) in Madagascar suggest that the general level of activity there may be of about the same order as indicated by diets of West Indian fishes. In general, it seems likely that seagrass feeding is somewhat more intense in the Caribbean than in other regions. However, more results are needed in other regions from localities with abundant grass beds.

Algivores represent an important trophic component of all reef fish communities and of most shallow surrounding areas. Unlike most trophic groups, they are heavily dominated by large populations of fishes from a few families. A very large fraction of all reef herbivores in all oceanic regions are Acanthuridae or Scaridae (Bouchon-Navaro and Harmelin-Vivien 1981). Some species of Pomacentridae seem to be important everywhere, and locally other groups may be prominent (e.g., Siganidae in Guam [Kami and Ikehara 1976] and the Great Barrier Reef [Stephenson and Searles 1960; Russ 1984a]). In the Atlantic, there are very few acanthurid species, but they are extremely abundant and widespread, and all appear to be almost entirely herbivorous. In the Indo-Pacific, the family is much more speciose. In any Indo-Pacific locality, smaller individual populations of several acanthurid species are likely to be present, feeding on algae with a variety of specializations (Jones 1968; Robertson et al. 1979; Hatcher 1982a; Williams and Hatcher 1983; Russ 1984a). A few Indo-Pacific acanthurids have also adopted other trophic roles, e.g., zooplanktivory (Jones 1968; Hobson 1974).

There are several common scarid species in the Atlantic, and even more in the Indo-Pacific. In reef habitats in all oceanic regions, most scarids seem to share a common, general feeding mode. They remove algae (usually short, fine forms) very close to the substrate, and often scrape the substrate surface, ingesting carbonate material and sometimes the endolithic algae of corals (Bardach 1961; Stephenson and Searles 1960; Randall 1965, 1967; Glynn et al. 1972; Hobson 1974). Observers have the impression that scraping of coral and other carbonate substrates by benthic algal grazers is more common and intensive in the Indo-Pacific than in the Caribbean (Bakus 1964, 1967, 1969; Randall 1974; Goldman and Talbot 1976). However, the comparative data that have been assembled (Bouchon-Navaro and Harmelin-Vivien 1981) suggest that scarids constitute a higher percentage of herbivores on Atlantic island reefs, and that acanthurids tend to be dominant on Indo-Pacific islands. More recent data from Hawaii (Hayes et al. 1982) are fully consistent with this result. Results of Bohnsack (1982) from the Florida Keys and Russ (1984b) from the Philippines are in agreement, but the difference is small in some cases. On the Australian Great Barrier Reef, Russ (1984a) obtained consistent results (but no great differences) at the more offshore reefs and opposite results closer inshore. Bakus (1967, 1969) observed the prevalence on tropical oceanic islands/atolls of the Indo-Pacific of mass movements of algal grazers on and off reef flats with the tide and believed that such feeding was less pronounced in the Caribbean.

Besides these roving benthic algivores, significant algivory may be produced by more stationary (usually territorial) benthic fishes. Pomacentrids are the most important of these on reefs in all oceanic regions. This is trophically a problem group because, in all regions, various species of this large and diverse family fill a variety of trophic roles (Hiatt and Strasburg 1960; Randall 1967; Hobson 1974; Gerber and Marshall 1974a; Hobson and Chess 1978; Sano et al. 1984). In most localities some species are predominantly herbivorous, some are mostly planktivorous, and often there are species that are significantly omnivorous. This mixture of feeding modes and the paucity of data on diets of many pomacentrids makes this the only one of the quantitatively dominant fish families practicing herbivory in reef communities that is often of uncertain trophic status. Robertson et al. (1979) cited the results in support of the idea that algivorous pomacentrids in the Caribbean hold a relatively more important place in the total herbivorous activity than in at least some Indo-Pacific localities. The Blenniidae are perhaps the only other herbivorous family that makes a major quantitative contribution to community herbivory everywhere, feeding primarily on short, filamentous algae. Their abundance (and herbivory) are poorly quantified in almost all localities, but it seems likely that they are of comparable importance on reefs in all oceanic regions and situations.

Many other reef related species practice herbivory. Of 212 West Indian species analyzed for diet (Randall 1967), 59 species from 16 families contained some plant material (more than 125 species of algae and 4 kinds of vascular plants). Some of these are omnivores or incidental consumers of algae. Several depend heavily on algae and are moderately abundant in some localities, e.g. some Kyphosidae, Chaetodontidae, Sparidae, Gobiidae, Balistidae and Monacanthidae. Most are not usually numerous enough in the community to produce a major trophic impact. However, the aggregate effect of these lesser algal consumers is probably considerable in all fish communities.

The community of algivores as a whole has been estimated for a number of locations both in terms of absolute density (Bouchon-Navaro and Harmelin-Vivien 1981) and as a fraction of the entire community (Table 1). Density values are extremely variable both within and between localities. As a fraction of the community, a range from at least 7% to nearly 40% by numbers is found, and a nearly equal range by weight. Some isolated oceanic islands of the Indo-Pacific show a very large herbivorous component (Odum and Odum 1955; Hobson 1974; Jones and Chase 1975;

Robertson et al. 1979; Hayes et al. 1982), but it is not clear whether there are any real overall differences between any of the major oceanic regions.

B. Planktivory

In all shallow tropical environments, there are significant numbers of fish that are surface or midwater pelagics. Many of these species live predominantly or entirely within shallow waters and may commonly occur near reefs, grass beds, mangroves or other surrounding habitats. However, their habitat is clearly the water column, and they may associate indifferently with the various benthic habitats. Some species loiter in large schools near reefs by day and move off into more open water to feed by night (Starck and Davis 1966; Hobson 1973, 1975). There must be some linkages with the benthic habitats, e.g., roving piscivores of this group prey on fishes of all the benthic habitats, and the pelagic Hemiramphidae eat floating grass blades from seagrass beds. However, such linkages are tenuous, poorly established by data, and blurred by the free movement of these pelagics among the surface waters over all benthic habitats.

Except for the relatively small populations of piscivores, such as the Belonidae, these pelagics are largely planktivorous. They include species of the Clupeidae (e.g.,_Harengula_, _Jenkinsia_, _Sardinella_, _Opisthonema_, _Spratelloides_), Atherinidae (e.g., _Hypoatherina_, _Atherinomorus_, _Pranesus_), Engraulidae (e.g., _Anchoa_), Hemiramphidae, and small carangids (scads) such as _Decapterus_ and _Selar_. These are all small-to-medium, schooling species, which tend to be somewhat patchily distributed, but locally abundant. Several are important bait fish for tuna pole-and-line fisheries. They are likely supported primarily by pelagic productivity, and will not be considered further in the discussion of fish communities relative to benthic habitats.

What is usually thought of as planktivory in tropical shallow-water systems, and particularly at reefs, involves at least 3 types of food resources. One form is debris washed directly from the source or indirectly stirred up from surrounding sediments by water motion. This is dead material; much of it is algal fragments or coral mucus (Johannes 1967; Benson and Muscatine 1974; Johannes and Gerber 1974; Gerber and Marshall 1974a, 1974b; Hobson and Chess 1978). From a trophic perspective, it is probably best to consider fish that feed on this drift material as e.g., algivores (see above), coral feeders, etc., regardless of where or in what conditions the food material is collected. As a practical matter, the separation can be difficult, and it has not been seriously attempted in most studies. All species that feed in the water column are often lumped as "planktivores," mixing consumers of food of sessile benthic origin with feeders on pelagic animals. This inaccuracy is not trivial in magnitude; of 16 zooplanktivores studied by Hobson and Chess (1978) at Enewetak, 6 species contained more than 20% drift algae (3 had more than 60%). Pomacentrids are the major, resident, diurnal planktivores in most oceanic regions, and their diets are often varied and poorly known (see above). Thus, there is often considerable uncertainly about the quantitative importance of planktivory (however defined) in a community. This is clearly an area where there is need for additional careful, quantitative work on certain quantitatively important "planktivores" in these fish communities.

A second major type of plankton is pelagic holoplankton, which has its origin and habitat in the water column, and to a large extent represents an import to the shallow-water habitats from surrounding waters. Even where holoplankton is produced locally in shallow waters, much of the input resources may come from outside the local shallow-water habitats, e.g., in the form of terrestrial runoff. In most localities, the major component of this plankton that provides food for adult fish is probably copepods, with other important groups of small, pelagic crustaceans as well, but also including edible gelatinous forms (Emery 1968; Tranter and George 1972; Johannes and Gerber 1974; Hobson and Chess 1978; Williams and Hatcher 1983). For small, isolated, oceanic islands without surrounding shallows (e.g., atolls), this plankton must be the major external food resource available to reefs.

The importance of "resident" or "demersal" meroplankton in shallow tropical environments (particularly reefs) is being increasingly recognized (Gilmartin 1958; Emery 1968; Tranter and George 1972; Johannes and Gerber 1974; Sale et al 1976; Alldredge and King 1977; Porter and Porter 1977; Hobson and Chess 1978; Walter et al. 1982; Ohlhorst 1982). This category includes not only larval or otherwise pelagic juvenile forms, but all other planktonic animals that are either in the plankton only briefly or that have a benthic habit during part of the day. This meroplankton is more or less resident within the shallows and is retained and probably nourished by processes different from those affecting the holoplankton (Sale et al. 1976).

Observations of several investigators (Emery 1968; Alldredge and King 1977; Porter et al 1977; Hobson and Chess 1978) suggest that the high relief topography of the reef contributes to maintaining high populations of this resident plankton. It can also be found in conspicuous abundance and concentrations in seagrass beds (Emery 1968) and apparently in mangroves (Steven 1961; Blaber 1980), where it is also eaten by fish. There appears to be no information about flux of "resident" plankton between shallow habitats. This plankton is dependent to a considerable degree on resources from the reef or surrounding shallows, e.g., space, source of propagules, and likely some level of primary productivity.

Systematically, this resident plankton also has a substantial component of copepods, but the taxa are often different from those of the pelagic plankton. Gelatinous forms are much reduced or absent, and several other bottom-related groups such as mysids, cumaceans, amphipods, polychaetes, and crustacean larvae are much more important (Emery 1968; Sale et al. 1976; Alldredge and King 1977; Hobson and Chess 1978).

There is some evidence that some plankton eating fishes specialize on either "resident" or pelagic plankton (Gerber and Marshall 1974a; Vivien and Peyrot-Clausade 1974; Hobson 1975; Alldredge and King 1977; Hobson and Chess 1978). As in the case of planktivory on reef drift material, it is important to identify such specializations. Since the "resident" meroplankton has major dependence on the shallow-water production system, and the pelagic holoplankton represents largely an import of external production, this separation would help clarify the total pattern of energy flux at higher trophic levels in these systems. Zooplanktivores are abundant enough in many localities that this distinction may affect a sizable portion of the utilization of locally produced biomass of some groups, occupying considerable local habitat.

There are indications from some collections that "resident" plankton may be more diverse and abundant than pelagic holoplankton at and near reefs (in contrast to adjacent deep open waters), even at an atoll and in other rather isolated reef situations (Gilmartin 1958; Bakus 1964; Sale et al. 1976; Alldredge and King 1977). The data are probably inadequate to permit generalization about the relative importance of these types of plankton. It would be of great interest to know whether "resident" plankton are more important on reefs associated with continents, larger islands, and extensive shallows than in small, isolated, oceanic reefs (e.g., atolls). Such a trend seems likely a priori. If it applies broadly, and if the resident plankton have short enough generation times and fast enough growth, this plankton might provide an effective mechanism for prolonging the effects of irregular and infrequent nutrient pulses resulting from events such as heavy storm run-off (Birkeland 1984). Such a mechanism could capture the effects of such events at a trophic level that would result in high trophic level responses locally, rather than permitting loss of all the nutrients by advection or diffusion.

As implied above, where diets of abundant species are in doubt, inappropriate lumping may occur which distorts the apparent importance of a trophic mode. It is likely that planktivory in a community is commonly estimated inaccurately by lumping pomacentrids excessively as either planktivores or herbivores. The problem is compounded by the fact that many species of (often very abundant) pomacentrids--especially those that use the water column--are highly conspicuous and easily censused visually. The same is true of some other very abundant diurnal planktivores such as caesionids. On the other hand, nocturnal planktivores can also be very numerous (e.g. Myripristinae, some Apogonidae, Pempheridae), and they are almost certainly always underrepresented in censuses, except possibly where chemicals or explosives are used. Many of the "resident" plankton appear to be in the water column primarily at night (Emery 1968; Hobson 1975; Alldredge and King 1977; Porter et al 1977; Hobson and Chess 1978). It seems likely that in common practice, adult planktivores as a fraction of the community may be somewhat overestimated; the number of nocturnal planktivores substantially underestimated; planktivory on "resident" plankton underestimated; planktivory on pelagic holoplankton overestimated; and the importance of drift material of benthic origin underrecognized.

An additional complication is that nearly all fish are planktivorous at some young life stage, and the degree of planktivory at various stages of development varies among species. The usual procedure in trophic studies is to deal only with the diets of adult fish, an approach which is conceptually simple and logical, but begs much of the question as regards understanding the trophics of entire communities. Similarly, common practice in quantitatively defining communities by census omits or grossly lumps juveniles, so that the abundance of these temporary planktivores, as well as their diet, is usually poorly known. These limitations probably apply to most or all of the results in Table 1.

One major difference between Atlantic and Pacific reefs that may apply rather generally is the higher abundance and larger portion of the community represented by zooplanktivores on Pacific reefs (Table 1). Planktivores appear to be important in the Pacific around extended or densely aggregated reef groups with extensive shallows (e.g. Williams and Hatcher 1983; Russ 1984b, 1985) as well as on some isolated, oceanic islands/atolls (e.g., Brock et al. 1979; Gladfelter et al. 1980). However, useful comparative studies are few, and not all results fit this pattern (e.g., Hayes et al. 1982; Parrish et al. 1985). The few Atlantic results include both island and continental habitats and show lower planktivore abundance. The pattern in the Indian Ocean is less clear, but planktivory is probably less prominent than in most of the Pacific areas reported.

There are considerably more planktivorous species in the Indo-Pacific, both within the families that are planktivorous in the Atlantic and in other families. The Indo-Pacific has at least 2 planktivorous acanthurids; some fairly abundant lutjanids such as *Pterocaesio* species that feed largely in the water column; abundant, small, plankton feeding Anthiinae (Serranidae); and the very populous, planktivorous Caesionidae. These abundant planktivore groups are less than balanced by the relatively few specializations to planktivory from unusual groups in the Atlantic (e.g., the single midwater labrid, *Clepticus parrai*; the planktivorous serranids, *Paranthias furcifer* and *Schultzea beta*; and the partly planktivorous lutjanid, *Ocyurus chrysurus*).

Quantitative plankton collections in the near vicinity of reefs are few and scattered. Meaningful measurements are hard to make because of the ecological and trophic diversity of the various types of plankton, and the difficulty of sampling quantitatively the component that is in the water column only part-time, or is patchily distributed, or very close to the reef structure (Emery 1968; Alldredge and King 1977; Hobson and Chess 1978; Porter & Porter 1977). It is unlikely that it could be demonstrated whether the total plankton density (or even the live zooplankton portion) is greater in one oceanic region than another. On evolutionary grounds it would be expected that larger and more diverse zooplanktivore guilds would have developed where more zooplankton is available. (Availability is affected by habitat and behavior of the plankton as well as abundance.) In much of the Indo-Pacific, zooplanktivorous fishes may experience more competition from corals than in the Atlantic for the plankton resources that occur. Major plankton consumption by corals has been well demonstrated in the Pacific, and on the average, Indo-Pacific reefs appear to have greater areal coverage of live corals.

Of all shallow benthic habitats, planktivory appears to be most intense at reefs. It is unlikely that any other habitat provides the shelter to maintain such large planktivorous populations. Also (as stated above) "resident" plankton appear to favor the high relief offered by the reef habitat. However, planktivory is common in grass beds and sand flats wherever sufficient cover can be found close to the feeding site. Often shelter is provided by burrows from which the planktivores either emerge a short distance to feed or maintain part of the body within the burrows while feeding: congrid eels such as *Nystactichthys halis*, *Taeniconger* and *Gorgasia*; tilefish such as *Malacanthus plumieri*; razor wrasses such as some *Xyrichtys* species; jawfish such as *Opistognathus aurifrons*; gobiids such as *Coryphopterus* species (some species of which also capture plankton from a reef habitat (Starck and Davis 1966; Randall 1967; Emery 1968; Davis and Birdsong 1973). Other reef-related fishes that eat plankton in grass beds include *Pomacentrus partitus* and juveniles of *Haemulon aurolineatum*, *Abudefduf saxatilis* and *Equetus umbrosus* (Emery 1968). The diets and the abundance and distribution of these planktivores from surrounding habitats have been poorly studied. It is known that they can occur locally in rather large aggregations. They seldom rival reef planktivores in density, but suitable surrounding habitat is very extensive compared to reef coverage in many areas. The total effect of their populations may be significant in the system utilization of the pelagic plankton in particular.

C. Omnivory and Other Complications

The remaining trophic categories are even more difficult to apply to the comparison of shallow tropical communities. The category of omnivory, used by some authors, is rather unsatisfactory conceptually for addressing the flux of materials and energy and the dependent relationships of groups of organisms. It often relates poorly to other ecological categories, and when a significant fraction of a community is assigned to such a heterogeneous category, major pathways in the food web may be obscured.

In Table 1, the assignment of the fish predator community to this category ranges from not made (because deemed inappropriate), through 1.5%, to over 40% (based on numbers of predator individuals). The great variability among values probably reflects (1) the ambiguity of definition of omnivores, (2) the difficulty of measurement (it is particularly difficult to assess quantitatively the relative abundance of animal and plant material in a fish gut), and (3) the latitude for a variety of different choices regarding such matters as unidentifiable food material. Since omnivores have the option to take either plant or animal prey, a problem to be expected in sampling is that the diet will vary temporally and spatially, depending on the availability of plant versus animal material. Sample collections are usually short-term, one-time programs, so the probability is high for bias in the results and differences in the results of different studies.

There are a fair number of species in all habitats and regions that take both plant and animal food in substantial amounts. In a few families, one or a few omnivorous species within a locality are fairly abundant, e.g., the Pomacentridae, Chaetodontidae, Balistidae, Monacanthidae, and Tetraodontidae. The extreme abundances seen for algivores and planktivores do not seem to occur anywhere.

In terms of understanding the life history and ecology of an individual species, it may be useful to consider the omnivorous habit. However, nothing appears to be gained by trying to define an omnivorous portion of the community and considering it in making habitat and oceanic regional comparisons. Where an omnivorous category has been created in community studies, the procedure apparently used by most workers is to determine that a species eats significant amounts of both plant and animal food and then assign its entire population (however estimated) to the omnivorous category. Thus, the effects of its consumption of plant and animal food are lost from the herbivorous and carnivorous categories, respectively. The trophic integrity of the important categories can be maintained approximately if good, quantitative diet data permit assigning portions of each species population (or of the population's food consumption) to each of these two categories, corresponding to the portions of the diet that are of plant and animal origin, respectively. This eliminates the omnivorous category and much of the ambiguity. In effect, this was done in the study of Parrish et al. (1985). For a number of the studies reported, adequate quantitative diet data apparently were not available, or not used, or it is simply unclear how assignments to categories were made.

For these reasons, it is more instructive to compare carnivory in the results of the various studies at lower levels of aggregation. Unfortunately, results of a number of studies are not broken down below the level of carnivory. In other cases, plankton are separated from benthos and nekton as diet categories, but benthos and nekton are not separated. This is particularly unfortunate, since the sources and trophic levels represented by these categories may be so diverse. The benthos may be of either local (e.g., reef) or surrounding origin. However, almost without exception, it and its sources of support are identifiable with benthic habitat, and no trophic ambiguity with the nekton is involved. In contrast, the nekton may include cephalopods, with somewhat more ambiguous affinities, and fish with a frankly ambiguous trophic position. (Fish in the diets of fish represent an internal recycling, and some of the fish in this prey category may in fact eat other fish.) It is therefore useful to examine the major subcategories of carnivory and consider the implications for habitat interaction and regional differences.

D. Piscivory

Community studies in which piscivory could be isolated have been recently reviewed by Parrish et al. (1986). Almost all these studies involved direct collections of populations and diet analysis. The major results appear in Table 1 along with results of a few additional studies in which collections were not made and diet information was taken from other sources. The range of values is considerable: 1-6% piscivores by number and about 6-54% by biomass. Some of the highest and lowest (and some intermediate) values come from the Australian Great Barrier Reef. There are also some moderately high values from coastal areas near large land masses in the western Indian Ocean and from smaller, isolated, oceanic islands in the central Pacific. The 2 studies from the Atlantic both lack direct diet data. One is from a small, fairly isolated, oceanic island and the other from a continental area. Their results are mixed.

The composition of piscivore taxa is strikingly different in some of the various areas without producing a discernible effect on the total piscivorous component. For example, groupers and snappers provide a major contribution to the piscivorous component in all oceans, except in the Hawaiian archipelago. But values from 2 widely separated localities in Hawaii are not greatly different from the estimate for Enewetak, nor lower than results from other regions.

Abundance of piscivorous fishes is particularly subject to the influence of human exploitation, since piscivores are often prized catches. Most of the studies considered here were conducted in localities exposed to relatively little fishing, and the level of fishing does not appear to bear any consistent relationship to the abundance of piscivores. For example, the localities with the greatest and the smallest piscivorous biomass component were both nearly pristine.

All the results considered together suggest some generalizations. Either there are grave problems with sampling by the various methods (a not unlikely possibility for this trophic group), or some communities have a drastically different trophic structure at the top levels. On the other hand, despite obvious sampling problems, some widely scattered and otherwise disparate habitats are not dramatically different at the piscivore level. Trends related to the habitat situation are not detectable (but not excluded). It seems likely that the piscivorous component is greater in the Indo-Pacific, but good, quantitative studies which include diet data and involve unexploited communities are lacking in the Atlantic.

A final complication is that all the studies examined are limited primarily (but not strictly) to more or less resident piscivores. However, most communities are affected by some important piscivores (e.g., sharks, large jacks, even the largest reef-resident predators such as snappers and groupers) that are more transient, or at least sufficiently uncommon and mobile that they present serious sampling problems. The variable success at sampling the full spectrum of piscivores--from the cryptic residents to the passing transients--will continue to affect interpretations at this trophic level. If an important component of the piscivory is imposed by wide-ranging, transient predators, even if their abundance were well quantified, interpretation of the trophic system would be more difficult.

E. Feeding on Benthic Invertebrates

The remaining major trophic category includes feeding on benthic invertebrate animals of all kinds. This feeding is often reported in one or another set of ecologically useful subcategories, but such subcategories vary and are often absent. What is important for the present comparisons, and often impossible to determine, is the source habitat of the benthos. Separating coral feeders is useful because the feeding mode and food source are distinctive. The source habitat, of course, is the reef, and this trophic mode may be altogether less dependent on the surroundings than most other modes. An evolutionary argument can be made that where less external sources of food are available, reef fish should evolve toward increased coral feeding. The data available suggest that coral feeding is indeed relatively intense in isolated reef situations with high coral cover (Randall 1974; Reese 1977). Higher coral consumption in the Indo-Pacific than in the Atlantic appears to be a common observation (Hiatt and Strasburg 1960; Randall 1967, 1974; Bakus 1969; Goldman and Talbot 1976; Neudecker 1977). This difference is discernible even on opposite sides of the isthmus of Panama (Glynn et al. 1972; Bakus 1975), and despite the fact that the eastern Pacific coastal region has high nutrient inputs. Coral feeding has not been well quantified in reports on trophics at the community level. It has occasionally been reported lumped with herbivory (e.g., Goldman and Talbot 1976) and is frequently lumped with other benthic prey of carnivores or omnivores.

The most abundant coral feeding fishes are certainly the Chaetodontidae, Pomacentridae, Labridae and Scaridae (Randall 1974). The first 3 of these eat soft tissue (i.e., browse without destruction of coral skeleton). The Chaetodontidae include many more species for which coral is a major food source, and they are abundant enough to represent a significant trophic component (Reese 1977; Harmelin-Vivien and Bouchon-Navaro 1982, 1983). Only a few pomacentrid and labrid species are involved, and the total trophic effect may be minor. It is not clear how commonly scarids eat live coral (Randall 1974). A small fraction of all scarid species have been implicated in scattered observations. But scarids are such abundant and active grazers on reefs and near live corals that the effects could be trophically significant. The fishes that take coral skeleton and soft tissue together as an important portion of their diets are primarily the plectognaths, especially the Balistidae, Monacanthidae, Tetraodontidae (including Canthigasteridae) and Diodontidae (Randall 1974).

Ecologically and behaviorally, predation on other sessile invertebrates is rather different from capture of mobile benthic animals. The former group is much easier to observe, census and quantify as to standing crop, although the degree of utilization as food for fishes may be harder to determine. Many exposed, conspicuous, sessile animals have structural or chemical defenses against predation (Randall and Hartman 1968; Bakus 1969, 1981; Neudecker 1985). However, not all these defenses are well known, and it is often not clear to what extent a sessile species is edible or eaten. Apparently a relatively small portion of the fish fauna anywhere has evolved effective specializations to exploit such prey (Randall 1967; Randall and Hartman 1968; Bakus 1969; Goldman and Talbot 1976; Neudecker 1985). The Pomacanthidae, some Chaetodontidae and Ephippidae, and certain plectognaths seem to be especially well adapted.

Sessile invertebrates other than corals are especially abundant on the hard substrates of reefs, but they are also well represented in shallow surrounding habitats, e.g., on mangrove prop roots, on patches of hard substrate or rubble, in seagrass beds, and even in open sand flats (Rodriguez 1959; Rutzler 1969; Parrish and Zimmerman 1977; Vacelet and Vasseur 1977). Despite unusual defenses, wherever they occur, they appear to be eaten to some extent by fishes.

Bakus (1964, 1969) noted the high intensity of fish predation on sessile invertebrates on Indo-Pacific reefs and concluded that many sessile species there have evolved cryptic habits in response. Vasseur (1977) also recorded a similar predominance of cryptic forms among the sessile fauna in Madagascar, but he believed that the effect of fish predation was not as evident there as in the Pacific (Vacelet and Vasseur 1977). In this regard, the reef would become a disproportionately important habitat for sessile benthos and their fish predators because of the protective cover which its interstices provide to the prey. Bakus (1969) concluded that feeding on sessile benthos was probably less intensive in the Atlantic, and that Atlantic species had evolved more structural and chemical defenses in response, rather than cryptic habits. Certainly large, exposed sessile forms such as sponges and ascidians are a more conspicuous element of the Atlantic fauna, although exposed forms with similar defenses occur in the Indo-Pacific as well (e.g., Bakus 1981). Solid, quantitative data on a whole community basis are sparse or nonexistent, but observational data suggest that sessile invertebrate feeding is a more important trophic mode in isolated, oceanic reef areas and particularly in the Indo-Pacific.

Feeding on mobile invertebrates is difficult to generalize. The range of taxa, life forms, sizes, habitats, habits and defenses is extreme. The echinoderms--one of the groups of largest and slowest moving animals--is especially patchily distributed on an oceanic regional basis. Echinoids are abundant in most western Atlantic tropical localities, where they are usually important herbivores.

They are variably abundant in certain eastern and central Pacific and Indian Ocean areas, and quantitatively unimportant in much of the western Pacific. Wherever they occur, they appear in the diets of a small portion of the fish fauna as a minor, but not insignificant prey. They include reef residents, seagrass inhabitants, and commuters between. Quantitative data may be totally lacking, but it seems probable that echinoids are a larger portion of the diet in the Atlantic because of their abundant occurrence in almost all localities and in a variety of habitats throughout the region.

Ophiuroids are strongly concentrated where sheltering interstices are plentiful, and thus they are especially abundant on reefs and rubble areas. There may be no useful data on the regional or major habitat distribution of this abundant but highly cryptic group. Some correlation has been found in the Florida Keys of ophiuroid abundance with available potentially habitable shelter area, and with abundance of seagrass for at least one species (Kissling and Taylor 1977). Holothurians are common and locally abundant in all oceanic regions, and often occupy rather open surrounding habitats, including sand flats. They do not appear to be an important prey of fishes in any region. Of the many remaining groups of mobile invertebrates, crabs, shrimps, stomatopods, gastropods and polychaetes appear to be common in all habitats worldwide and important in fish diets everywhere. Bivalve molluscs and some of the smaller crustacean groups such as amphipods, isopods and tanaidaceans are also common and widespread in all habitats. Different specific taxa occur in different regions and habitats, but important representatives of these groups occur in all.

For whole fish communities, there appear to be no data for making quantitative trophic distinctions among regions or habitats for these individual groups. In almost all community trophic studies, these groups--and certainly the benthic invertebrates as a whole--emerge as the most important single trophic category (Table 1). However, the homogeneity as a category is related more to the way in which predatory fish consume it than to its trophic level or the relationships of its components to other trophic groups. Even among the crustaceans, there is a variety of trophic levels, ranging from herbivores (e.g., some amphipods) to at least second level carnivores (e.g., stomatopods). Furthermore, it seems likely that a large portion of the trophic flux through this category involves detrital material at some stage, which introduces trophic ambiguity.

Groups within this category (crustaceans and others) are undoubtedly important in trophic transfers between habitats. For example, grapsid crabs from mangroves, portunids from grass beds, and calappids from open sand flats could be expected to be imported to the reef by commuting foragers such as lutjanids, haemulids and mullids. There has been no quantification of such transfers, and in fact it seems unlikely that all the functioning linkages among taxa involved have even been identified in any specific case. This seems a fruitful area for further work. At present, the major generalities that emerge for this benthic invertebrate group are probably its great quantitative trophic importance in all regions and all habitats, and the diversity (both systematic and trophic) of means by which it can function. Whether in fact the potential for diverse functioning in different situations is realized is an interesting ecological question.

DIRECTIONS FOR RESEARCH

This discussion has raised a number of questions that cannot be answered with present information, particularly in a quantitative sense. We wish to understand the exchange and interactions among shallow, tropical, marine habitats and their effects on fish communities. The processes and mechanisms proposed here are all credible, and some have been confirmed qualitatively. The important ecological questions are not primarily of the form, "Does such an interaction occur?" but rather, "Where and under what circumstances does it produce significant, perceptible effects, and what are they?" Are there measurably higher standing stocks of fish or higher rates of production by fish in a situation where the proximity of a mangrove tract results in a large net flux of detrital material to a reef? in a situation where reef resident fish commute to an adjacent grass bed and consume large quantities of secondary and higher level production that is supported by the primary production of the grass bed? in a situation where many fish larvae settle in a nearby grass bed or mangrove, develop there, and subsequently migrate to the reef? If so, which groups have the life history and trophic characteristics that are favored by these neighboring resources so that their abundance or production in the reef fish community is more enhanced? Such questions as these require that research be focused in new directions.

Several approaches seem appropriate for making a major improvement of our understanding of regional and habitat effects. Feeding in surrounding habitats by commuters from reefs seems a potentially important mechanism. Only recently have focused and somewhat quantitative studies of the phenomenon been pursued for haemulids in the Caribbean. The results have been rewarding. It is now known that commuter feeding in that situation for that family is important. But that situation is so much better known than any other, that useful comparisons are not presently possible. A necessary step is to identify and assess all the quantitatively important commuters in several localities and situations, identifying their feeding grounds and diel cycles and quantifying the sizes of commuting populations and their diets. Properly done, such a study would allow an estimate of transfer between the habitats. This assessment should include herbivores (probably all diurnal), but particular effort should be applied to the nocturnally active, diurnally cryptic (and usually abundant) species such as the Holocentridae and Apogonidae. Their roles in this context are presently poorly understood and poorly quantified, and probably underestimated. It seems likely that in different regions and situations, different commuters (and perhaps different prey) will be important. How different the overall effect may be on the entire community cannot be assessed with present data.

Feeding by fishes within grass beds in the tropical environs of reefs has been little studied. Of several studies cited in this review (and others extant) that report on diets of fishes from grass beds, most were either (1) from the subtropics, (2) from areas remote from reefs, or (3) where multiple habitats were available, feeding from the grass beds was not identifiable or separable. It would be particularly useful to know specifically what flora and fauna from grass beds contribute to the support of reef based commuters and grass bed residents, particularly the temporary juvenile fish residents.

Closely tied to the issue of herbivorous grazing by commuting reef fish is the question of echinoid commuting and grazing. Again, the subject has been much less developed outside the Caribbean. In fact, the occurrence and abundance of potential echinoid grazers appears not to have been widely reported. Clearly there are situations in the Indo-Pacific generally analogous to the patch reef-grass bed habitats studied in the Caribbean. Similar studies in these areas could establish the relative abundance of both major groups of potential herbivores on grass and algae and provide some estimate of their relative consumption or effect on plant biomass and/or production. There has been some work in the Indo-Pacific where echinoid populations are quantitatively unimportant. What is needed now is studies where they are significantly abundant.

The research thrusts proposed above should give particular emphasis to investigating non-Caribbean situations. The results may indicate that qualitatively different things are happening in different regions. If so, a likely cause would be a difference in the occurrence of the key fauna. If all the faunal components that appeared to be appropriate were present but simply not performing the same functions, the result could lead to some further interesting ecological studies to determine why structurally similar but functionally different systems have evolved in the different regions.

The following research thrusts are at least as important within a region as on an interregional scale. The evidence available to date for the proposed nursery function of surrounding habitats for juvenile fish is primarily of the type cited in that section of this review (above). It consists largely of the occurrence in the surrounding habitats of juveniles of species that occur as adults on reefs. Seldom if ever has a direct relationship been established between the juveniles in the nursery and the adults in the final habitat. Establishing such a relationship in any quantitative way that explains how the full adult population on a reef becomes recruited will not be easy. However, with state-of-the-art techniques, it may be feasible. Possible approaches might include well controlled, long-term body marking experiments, use of radioactive tracers or stable isotope analysis where diets in the habitats appeared significantly different, or examination of microstructure patterns deposited in hard parts (e.g. otoliths), particularly in the earliest stages near settlement. It would clearly be valuable to demonstrate for even a small number of cases that this recruitment interaction mechanism does or does not functiuon in a significant way.

Another important research approach bypasses the questions of mechanism and goes directly for the answers to questions close to those posed early in this section, i.e., "Where and under what circumstances is a significant effect (of a difference in the situation of habitats) perceptible? It would probably be feasible and instructive to simply select some particular sites, as similar as possible in all other respects, that differ in the types of habitats occurring together: reefs with and without grass beds, mangroves, and any other available combinations of common, shallow-water habitats. The key variables for comparsion (for the purposes of this discussion) would be the community composition (relative abundance of its species), population density (abundance) of the fish community, stability of the abundance and community composition over a period of several years, trophic composition, and fish production. (The latter 3 measurements could not be quickly made, and if done thoroughly, would probably represent increasingly greater effort.)

If sufficiently well controlled by wise selection of study sites and adequate sample sizes ("random" variability will be high), the results might strongly suggest that certain cooccurring habitats do or do not interact so as to affect fish populations in one or both. That indication alone would have major ecological and resource habitat management implications. Furthermore, the nature of the differences would likely give clues as to the mechanisms responsible. For example, relative species abundances might be different for known commuting foragers or for species known to use a surrounding habitat as juveniles. A difference in temporal stability observed over several years might well indicate the functioning of a surrounding habitat as an accumulator of recruits.

Thus, although such initial comparisons would not directly reveal mechanisms of interactions among habitats, they would indicate whether any were likely effective, and if so, they might suggest which should be further investigated. Field experiments such as removals of commuters or juveniles, blocking of commuting or migration paths, or reduction of shelter or food resources offer prospects for focusing on the effective mechanisms. Any of these experiments could simply be applied to selected habitats initially. However, the experimental program would likely be more efficient and better directed after such initial paired comparisons of natural situations. When (and if) some particular mechanisms of interaction have been demonstrated and studied within an environment (e.g. an oceanic region), it should be profitable to look for the mechanism in similar situations in other regions. If regional differences emerge, it should then be possible to identify them specifically at the level of the mechanism and associate such differences with the effects at the population and community levels.

This full line of inquiry will certainly be long, difficult and complex. It deals with some basic questions in marine ecology, involving complex interactions of individually complex systems. For exactly these reasons it is also of great importance to theoretical and applied ecology, and its resolution will be of great value to the management of habitats and living resources. Fortunately, the first important steps in this line of research involve modest cost, time and effort and can produce very useful results.

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INTEROCEANIC AND REGIONAL DIFFERENCES IN THE REPRODUCTIVE BIOLOGY OF REEF-ASSOCIATED FISHES

by

Ronald E. Thresher*

ABSTRACT

Sources of regional variation in the reproductive biology of reef-associated fishes include differences between major zoogeographic regions (e.g., western Atlantic versus Indo-Pacific), between latitudes, and between island groups within oceans. These variations are in three general areas: social behavior, early life history parameters, and adult reproductive morphology and physiology. No single factor is likely to be the cause of these diverse regional differences; rather, the factors involved are likely to include interoceanic differences in faunal diversity, in the geographic extent of reef habitats, and, possibly, in patterns of water column productivity. Hitherto unrecognized regional differences in the basic biology of reef fishes could underly some of the current controversy over the roles of competition and recruitment limitation in structuring reef fish assemblages, and may also have implications for the effective management of reef fisheries.

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*CSIRO Marine Laboratories
G.P.O. Box 1538
Hobart, Tasmania 7001
AUSTRALIA

INTRODUCTION

There exists a widespread, though often implicit, assumption that the overall biology of confamilial fishes on coral reefs in the tropical western Atlantic and Indo-Pacific is fundamentally the same (e.g., Ehrlich 1975; Smith 1978; Sale 1980). This assumption seems reasonable, given the broad taxonomic overlap between the two faunas. Few families are restricted to one region, and in most cases overlap is extensive at the generic level (Ekman 1953; Briggs 1974). Confamilials in the western Atlantic and Indo-Pacific are not only morphologically and behaviorally similar (e.g., Low 1971, versus Thresher 1976) but also interact with the reef in much the same way, e.g., algal "farming" pomacentrids are found in both regions (Brawley and Adey 1977; Lassuy 1980).

However, few direct, quantitative comparisons have been made of the behavior, ecology or physiology of fishes from the two regions. Three studies, Smith (1978), Bohnsack and Talbot (1980) and Gladfelter et al. (1980), have examined the composition of reef-fish assemblages on more or less comparable habitat units at sites in the tropical Atlantic and Pacific. Although procedures and specific results differ between the studies, all three conclude that, in essence, communities in the two regions are similarly structured and are presumably limited in similar ways, despite conspicuous differences between the two oceans in species richness. Sale (1980) analyzed species richness as a function of number of individuals present on patch reefs in the western Pacific and western Atlantic, and found no significant difference between the two regions. On this basis, he suggested cautiously that levels of Alpha (within habitat) diversity may be similar in the two regions.

Thresher (1982a) approached the problem of interoceanic comparisons somewhat differently, by comparing egg sizes produced by confamilial fishes in the two regions. Egg size is closely linked, in fishes as well as other taxa, with a suite of reproductive parameters, including fecundity, incubation period and size of offspring at hatching (e.g., Blaxter 1969). Consequently, regional differences in early life history, if they exist, are likely to be manifest in the eggs. Data for the regional comparison were sparse, but those available indicated that for at least some demersal spawning familes (i.e., those in which eggs are adhesive, heavier than sea water, and usually tended by one or both parents), western Pacific species produce eggs with an average volume of up to nearly an order of magnitude greater than those of western Atlantic confamilials. In contrast, egg volumes of pelagic spawning families (i.e., those in which the buoyant, usually spherical eggs are shed directly into the water column) are equivalent for confamilials in the two oceans.

The implications of this regional difference in reproductive biology are not yet clear. One evident and immediate implication, however, is that an automatic assumption of direct comparability of fishes in the two oceans is not warranted, at least for demersal spawning families. Work conducted since Thresher (1982a) has explored a range of potential differences between fishes in the Pacific and Atlantic, some of which have borne up under close scrutiny. These differences are of three general types: 1) patterns of reproductive and social behavior; 2) early life history parameters; and 3) elements of adult reproductive morphology and physiology.

INTEROCEANIC DIFFERENCES IN REPRODUCTIVE AND SOCIAL BEHAVIOR

Studies of the social and, particularly, reproductive behavior of reef fishes have proliferated in the last decade. Thresher (1984), for example, cited 99 papers that dealt wholly or partially with reproduction in the Pomacentridae (damselfishes) alone, even after excluding the extremely well studied subfamily Amphiprionae. These studies involve 11 genera and species in all of the major reef regions of the world. Work on other families is far less complete, and for the larger-bodied fishes that are of interest in recreational and commercial fisheries, in particular, data are often largely anecdotal (see reviews by Johannes 1978; Barlow 1981; Thresher 1984). Nonetheless, sufficient data are available on at least some families to indicate broad trends in reproductive behavior.

One such trend is evidence of regional differences in social behavior. The documented social systems of one of the more thoroughly studied families, the Pomacanthidae (angelfishes), are listed in Table 1. Data of varying degrees of completeness are available for 24 species globally: 18 from the Indo-West Pacific, 5 from the tropical western Atlantic, and 1 from the eastern Pacific. The basic social unit of the Indo-Pacific angelfishes varies little; of the eighteen species studied, all but one have been found to occur in harems consisting of, typically, one male and one to six females. In contrast, the relatively few species of Atlantic pomacanthids exhibit a wide range of social organizations, from Pomacanthus paru, which has never been reported found in anything other than stable pairs and is almost certainly monogamous, to Pomacanthus arcuatus, which is apparently promiscuous and, in some areas at least, forms explosive breeding assemblages. The sole eastern Pacific species thus far studied, Holacanthus passer, exhibits as wide a range of social organization as all of the Atlantic species combined (Moyer et al. 1983). In low density populations, it forms heterosexual pairs that are stable over

Table 1. Documented social organizations of pomacanthids in different regions.

REGION	SPECIES	SOCIAL ORGANIZATION	SOURCE
Western Atlantic	*Centropyge argi*	Paired Harem	Moyer et al. (1983)
	Holacanthus ciliaris	Harem	Moyer et al. (1983)
	H. tricolor	Harem	Moyer et al. (1983)
	Pomacanthus arcuatus	Paired, Promiscuous	Moyer et al. (1983)
	P. paru	Paired	Moyer et al. (1983)
Eastern Pacific	*Holacanthus passer*	Paired, "Leks", Promiscuous	Moyer et al. (1983)
Indo-West Pacific	*Centropyge bicolor*	Harem	J. Aldenhoven (in prep.)
	C. bispinosus	Harem	Thresher (1982b)
	C. flavissimus	Harem	Thresher (1982b)
	C. heraldi	Harem	J. Moyer (pers. comm.)
	C. interruptus	Harem	Moyer and Nakazono (1978)
	C. loriculus	Harem	Thresher (1982b)
	C. multicolor	Harem	Thresher (1982b)
	C. nox	Harem	J. Moyer (pers. comm.)
	C. potteri	Paired (?), Harem	Lobel (1978)
	C. shepardi	Harem	Moyer (1981)

Table 1. Continued.

C. tibicen	Harem	Moyer and Zaiser (1984)
C. vroliki	Harem	Thresher (1984)
Euxiphipops sexstriatus	Harem	J. Aldenhoven (pers. comm.)
Genicanthus lamarck	Promiscuous	Moyer (1984)
G. melanospilos	Harem	Moyer (in prep.)
Holacanthus trimaculatus	Harem	J. Moyer (pers. comm.)
Pomacanthus imperator	Harem	Thresher (1982b)
Pygoplites diacanthus	Harem	Gronell and Colin (1985)

long periods, and is probably monogamous; at higher densities, it spawns in lek-like aggregations, in which males compete for females at regularly frequented spawning areas; at highest densities observed, it occurs in very large aggregations which suggests the formation of either immense lek-like spawning aggregations or explosive breeding assemblages.

Differences in the social behavior of the Atlantic and the Indo-west Pacific pomacanthids are parallel, though less well documented, in some other families. Both the western Atlantic and eastern Pacific jawfishes (Opistognathidae) exhibit a range of behavioral and ecological diversity far exceeding those of their Indo-West Pacific relatives (pers. obs., W. Smith-Vaniz, pers. comm.). In the damselfishes, Pomacentridae, the six widely distributed western Atlantic species in the genus Stegates have a broader range of social organizations (Thresher 1977) than any single genus in the Indo-West Pacific. The Atlantic parrotfish, Scarus iserti, intraspecifically exhibits social organizations that range from single-male-dominated harems and lek-like spawning aggregations, both involving pair-spawning, to massed group-spawnings (see review by Thresher, 1984). This one Atlantic species exhibits virtually the entire range of social organizations thus far documented for the Pacific scarids as a whole.

The social systems of western Atlantic fishes are not always more diverse than those of their Indo-West Pacific counterparts, however. Labrids appear to have generally similar social organizations in the Atlantic, Indo-Pacific and eastern Pacific (although there seems to be a tendency for relatively more species to form harems in the Indo-Pacific), and the vastly greater species richness of the Indo-West Pacific fish fauna virtually guarantees some types of social and ecological behavior will occur in the Pacific, but not the western Atlantic. Conspicuous examples of the latter include the anemonefishes (Pomacentridae, Amphiprionae) and the sabre blennies (Blenniidae, Nemophidinae).

INTEROCEANIC AND REGIONAL DIFFERENCES IN EARLY LIFE-HISTORIES

Available data continue to support the hypothesis that egg volumes of tropical western Atlantic and western Pacific representatives of demersal spawning families are significantly different. Currently, data for more than 20 species are available for two reef-associated taxa: the Pomacentrinae and the Apogonidae; in both, interoceanic differences in egg volumes are significant at $p<0.05$. The average sized egg produced by a pomacentrin in the Indo-West

Pacific, for example, is 0.46 mm^3, as compared to an average of only 0.17 mm^3 for western Atlantic species. A trend for a similar interoceanic difference in egg in size is evident in other, less well studied, taxa of demersal spawning fishes, including the Blenniidae, Chrominae and pseudochromoids. The distinction between demersal and pelagic spawning families also remains supported. Despite additional data, there is no evidence of a regional difference in average egg volume for any of three pelagic spawning families examined to date: the Pomacanthidae, the Acanthuridae, and the Serranidae.

Testing for interoceanic differences in egg volume of demersal spawning fishes is complicated by other sources of regional variation. Two, in particular, have become evident as I have analyzed the available data on egg size. First, egg volume varies with latitude in some, but not all fish families (Thresher, in prep.). Again, the dividing line seems to be between demersal and pelagic spawners. All five of the six demersal spawning families examined show a strong positive slope between egg volume and latitude; in the five pelagic spawning families examined, however, latitude and egg volume do not correlate. The "latitudinal effect" on egg volume of demersal spawners not only complicates analyses of other sources of regional variation, but also accounts for the very different conclusions drawn from the literature regarding the relative egg volumes of demersal and pelegic spawning fishes at temperate (e.g., Barlow 1981) and tropical (e.g., Thresher 1984) latitudes.

A second source of geographic variation in egg volume is within ocean, regional effects. Data to test for such effects are extremely sparse, but nonetheless already show, for example, that eggs produced by Hawaiian endemic apogonids (cardinalfishes) are significantly smaller than those produced by confamilials on the Great Barrier Reef. Relatively small eggs for Hawaiian species are also suggested by limited data on larval durations. Within families, larval duration generally correlates negatively with egg volume. The duration of the pelagic larval stages of Hawaiian species in several families are longer than those of confamilials found elsewhere in the Indo-West Pacific (pers. obs.). Potential regional variation in egg volume is also suggested by blenniid species found along the continental coasts of the Indian Ocean; their eggs are generally smaller than those produced by blennies on the Great Barrier Reef or in Oceania (pers. obs.). Whether this trend will be supported by fishes in other families is not known. There are far too few data, as yet, to generate a comprehensive map of regional variations in life-history parameters for the Indo-Pacific. I am, however, currently examining one parameter, the duration of the pelagic larval stage of several demersal spawning species for possible regional variations.

Egg size correlates with a wide range of early life history parameters. Size cf newly hatched larvae, for example, is a strong positive correlate of egg size in every family of reef fish for which I have data. The newly hatched larvae of demersal spawning fishes in the Indo-West Pacific are therefore almost certainly larger than those of confamilials on western Atlantic reefs. Data to test this hypothesis are sparse, but are consistent with the prediction. In the Pomacentridae, for example, sizes of newly hatched larvae of Indo-West Pacific species range from approximately 1.8 to 4.5 mm Total Length (TL), and averages 3.2 mm TL; however, two western Atlantic species for which I have data are only 2.0 and 2.3 mm TL at hatching.

In contrast, I have found no evidence that within taxa size at which postlarvae settle on the reef differs significantly between oceans for either demersal or pelagic spawning families. Again, using pomacentrids as an example, the mean size of newly settled individuals of 7 pomacentrin species collected at One Tree island, on the Great Barrier Reef, by Brothers et al. (1983) was 11.4 mm Standard Length (SL), Standard Error = 0.23 mm. In comparison, the mean size of the smallest individuals of 7 western Atlantic pomacentrins reported by Emery (1973) or collected by E.B. Brothers (pers. comm.) at St. Croix, U.S. Virgin Islands, was 11.6 mm SL (S.E. = 0.46 mm). The means are not significantly different. Data for other families are sparse, but personal observations in the western Atlantic and Pacific suggest that regional differences in size at settlement are probably minimal for most families.

The combination of a difference between areas in size at hatching and a similarity in size at settlement implies that the planktonic larvae of Indo-Pacific reef fishes either spend less time in the water column or grow more slowly than do their western Atlantic counterparts. In collaboration with E. B. Brothers, I have examined otolith microstructure of species in several reef-associated families to determine the duration of the presettlement stage of the fishes (Brothers and Thresher, in prep.). For the two demersal spawning families examined, we found significantly fewer pre-transition daily growth increments in western Pacific than in western Atlantic species. We found no evidence, however, of a comparable regional difference in two pelagic spawning families. Our data suggest that the duration of the pelagic stage of the larvae of western Atlantic demersal spawning families is up to 45% longer than that of their Indo-Pacific confamilials.

In contrast, the average rates of larval growth appear to differ little between regions. Data for this comparison are still very sparse, since each datum requires information on average size at hatching, size at settlement and larval duration. So far, I have been able to assemble the largest data set for the pomacentrids. In this family at least, mean rates of larval growth appear to be similar in the two regions. Estimated growth rates for nine Great Barrier Reef species range from 4.2% to 6.1%/day as against 4.3% and 4.7% for two western Atlantic species.

INTEROCEANIC DIFFERENCES IN ADULT REPRODUCTIVE PHYSIOLOGY AND MORPHOLOGY

Aside from aspects of embryonic and larval development, other elements of reproductive ecology may also differ between confamilials in different locations. Three possible differences I have examined thus far are maximum adult size, size at sexual maturity, and fecundity.

Egg size and adult size correlate in numerous taxa, including fishes (Blaxter 1969). Consequently, regional differences in egg sizes, and perhaps other early life-history parameters that covary with egg size, may derive primarily from selection acting on adult size, rather than on the early life-history parameters themselves. This hypothesis was tested by determining, first, whether there is a difference in the mean size of demersal spawning confamilials in the western Atlantic and Indo-West Pacific, and second, whether egg size correlates with adult size in the families of interest.

In regard to the first question, analysis of maximum adult sizes reported in the literature does not support the hypothesis that these sizes differ consistently between the two reef areas. Again using pomacentrids as an example, the maximum adult size of western Pacific pomacentrins averages 9.2 cm SL (S.E. = 0.19 cm), compared with 11.8 cm (S.E. = 0.64 cm) for western Atlantic species. The difference between regions is not significant, for either the damselfishes or for any other demersal spawning taxa I have thus far examined. Nor does analysis of the relationship between adult size and egg size support the hypothesis that regional differences in egg size derive from selection for adult size. Adult size and egg size do not correlate in the Pomacentrinae, the Apogonidae, or any other demersal spawning family of reef fishes thus far analyzed. However, there is generally such a correlation in pelagic spawning families (e.g., Thresher and Brothers 1985), emphasizing again the fundamental difference between fishes in the two spawning modes.

The possibility of regional differences in size at sexual maturity has thus far been examined by only Grimes (in press) for the Lutjanidae. Grimes reviews the reproductive biology of snappers, a pelagic spawning family, and provides data from the fisheries literature on 13 western Atlantic species and 19 species from the Indo-West Pacific. Aside from data on maximum adult size and size of males and females at sexual maturity, each species is also classified on the basis of its depth preferences (greater than or less than 90 m), preferred habitat type (continental margin versus insular), and zoogeographic province (Atlantic versus Pacific). On the basis of an analysis of covariance, Grimes concludes that the size relative to its maximum length at which a lutjanid reaches sexual maturity differs significantly with habitat and depth, but not zoogeographic province.

Nonetheless, lutjanids in the Pacific reach sexual maturity at a higher proportion of their maximum adult length (58.7%) than do Atlantic snappers (48.3%). The difference between oceans is significant at $p<0.02$ (Mann-Whitney U-Test). At the same time, there are apparent regional differences in the sizes to which snappers grow. In a multiple regression analysis, two variables are significant predictors of lutjanid maximum sizes: habitat and zoogeographic province ($p<0.01$ for both variables), i.e., snappers tend to be larger on continental margins than around islands, and species in the Pacific tend to be smaller than those in the Atlantic, once the effects of habitat are taken into account. The mean maximum length of the Atlantic species analyzed by Grimes (in press) was 63.1 cm Fork Length (FL), as compared with a mean of 47.5 m FL for the Pacific species. It should be noted, however, that this analysis is based on only those species for which fisheries data are available, which is a minority of the species in both oceans.

Finally, interoceanic differences in egg size for demersal spawning families strongly suggest that relative (size-specific) fecundity also differs between the two regions (and between Hawaii and the rest of the Indo-Pacific), although critical data to test this hypothesis are still lacking. Individual fecundity in fishes is a function of both body volume and egg size (e.g., Mann and Wills 1979); hence, fecundity should be lower in Indo-West Pacific demersal spawners than in those in the western Atlantic. The variables of primary interest are the rate of reproduction and net lifetime fecundity, which depend on not only egg and adult sizes, but also on life span and frequency of spawning. Data on the latter variables are too sparse to draw firm conclusions. Intrafamilial regional variation in spawning frequency, however, has previously been documented for some reef fishes (Thresher 1982b) and there is an indication that the pattern of lunar periodicity of demersal spawning fishes may differ between two oceans. All five studies thus far conducted on spawning cycles of western Atlantic demersal spawners (Marraro and Nursall 1983 on the blenny Ophioblennius atlanticus, and De Boer 1978, Williams 1978, Pressley 1980, and Schmale 1981 on pomacentrids) report unimodal lunar spawning cyles, with peak spawning frequency during or immediately after the full moon. Indo-West Pacific demersal spawning fishes appear to be more variable, with spawning cycles ranging from apparently noncyclical (e.g., MacDonald 1976) to strong, unimodal lunar cycle (e.g., Moyer 1975). Indo-West Pacific fishes however, seem to tend towards a strong semilunar peak in activity (e.g., Doherty 1983a, Thresher and Moyer 1983).

FACTORS UNDERLYING INTEROCEANIC DIFFERENCES IN THE REPRODUCTIVE BIOLOGY OF REEF-ASSOCIATED FISHES

Given the variety of possible interoceanic and regional differences in reproduction, it is unlikely that any single "cause" of the difference exists. Several fundamental differences between the western Atlantic and Indo-West Pacific may bear on perceived differences in reproduction, and are possible candidates for a "global" causal factor. These can be stated as hypotheses.

1. There is no fundamental difference in the biology of the two areas, and all perceived differences in reproductive biology are strictly due to chance and the low diversity of western Atlantic fishes. Among demersal spawning fishes, regional differences in egg sizes in the Pomacentridae can be ascribed in part simply to the relative dominance of one genus, *Stegastes*, in the western Atlantic. Nine of the 12 pomacentrin species in the Atlantic belong to this genus, whereas it includes only 7 of 97 pomacentrins found in the tropical Pacific "South Seas" (Allen 1975). One might therefore expect a greater consistency of life history parameters among Atlantic pomacentrins. Moreover, even in the Pacific, *Stegastes* spp. have smaller eggs and longer larval durations than their Pacific confamilials. The "chance" dominance of *Stegastes* in the Atlantic could alone partly explain evident interoceanic differences in reproduction. Regional differences in reproduction are evident in a variety of genera, however, and, in most cases, numerous families. For example, eggs are smaller in the Atlantic for all demersal spawning families thus far examined, not just the pomacentrins or *Stegastes*. The available evidence suggests a pervasive factor of some kind is involved.

2. The relatively small geographic extent of the western Atlantic reef complex not only promotes panmixia (and hence reduced diversity = greater consistency) but also ensures that species are likely to encounter a wider range of habitats, selecting for flexibility of response. The relatively small geographic extent of the western Atlantic may not be the primary cause of regional differences in reproduction, but is quite

likely a contributing factor. The diversity of social organizations of some Atlantic families, such as the angelfishes, may primarily reflect a wide range of population densities in New World species. Local variations in population density clearly correlate with changes in the spawning system of the eastern Pacific angelfish, Holacanthus passer, for example, and similar shifts in social organization deriving from changes in population density have been demonstrated experimentally for two New World labrids by Warner and Hoffman (1980). This implies that whatever underlying variable constrains population density, whether environmental differences in carrying capacity or consistent spatial variation in settlement patterns (or both), it must vary more widely in the New World tropics than in the Indo-West Pacific.

Little is known about settlement patterns of pomacanthids, and almost no data relevant to an interoceanic comparison are available. Local environmental heterogeneity could well be greater in the New World tropics than in most of the Indo-West Pacific. It is likely that all of the major zoogeographic reef provinces consist of a comparable spectrum of reef habitats, from muddy, inshore patch reefs to highly diverse, densely structured reefs in clear oceanic conditions. The small geographic extents of the western Atlantic and eastern Pacific reef provinces and the relatively short distances between environmentally different reef structures in those provinces could mean that for many species, normal patterns of larval dispersal could carry siblings into any one of a range of habitats. By comparison, the greater extent of the Indo-Pacific reefs and the narrower range of habitats around, for example, Melanesian atolls, could make it less likely that larvae would routinely drift into habitats radically different from those of the parents. The social organizations of the Indo-Pacific representatives of some families, such as the pomacanthids, then, may be phenotypically less labile than those of their New World counterparts because the low probabilities of encountering marginal habitats has not selected for such lability. Alternatively, the consistency of documented social systems of Indo-Pacific fishes could derive from the relatively small range of habitats in which the species occur and in which they have been studied. It would be of interest to examine the social behavior of Indo-Pacific pomacanthid species in either marginal habitats or under conditions of excessively high or low population density.

3. The low faunal diversity of western Atlantic reef communities, relative to those in the Pacific, affects intensity of competition, rates of mortality, or similar

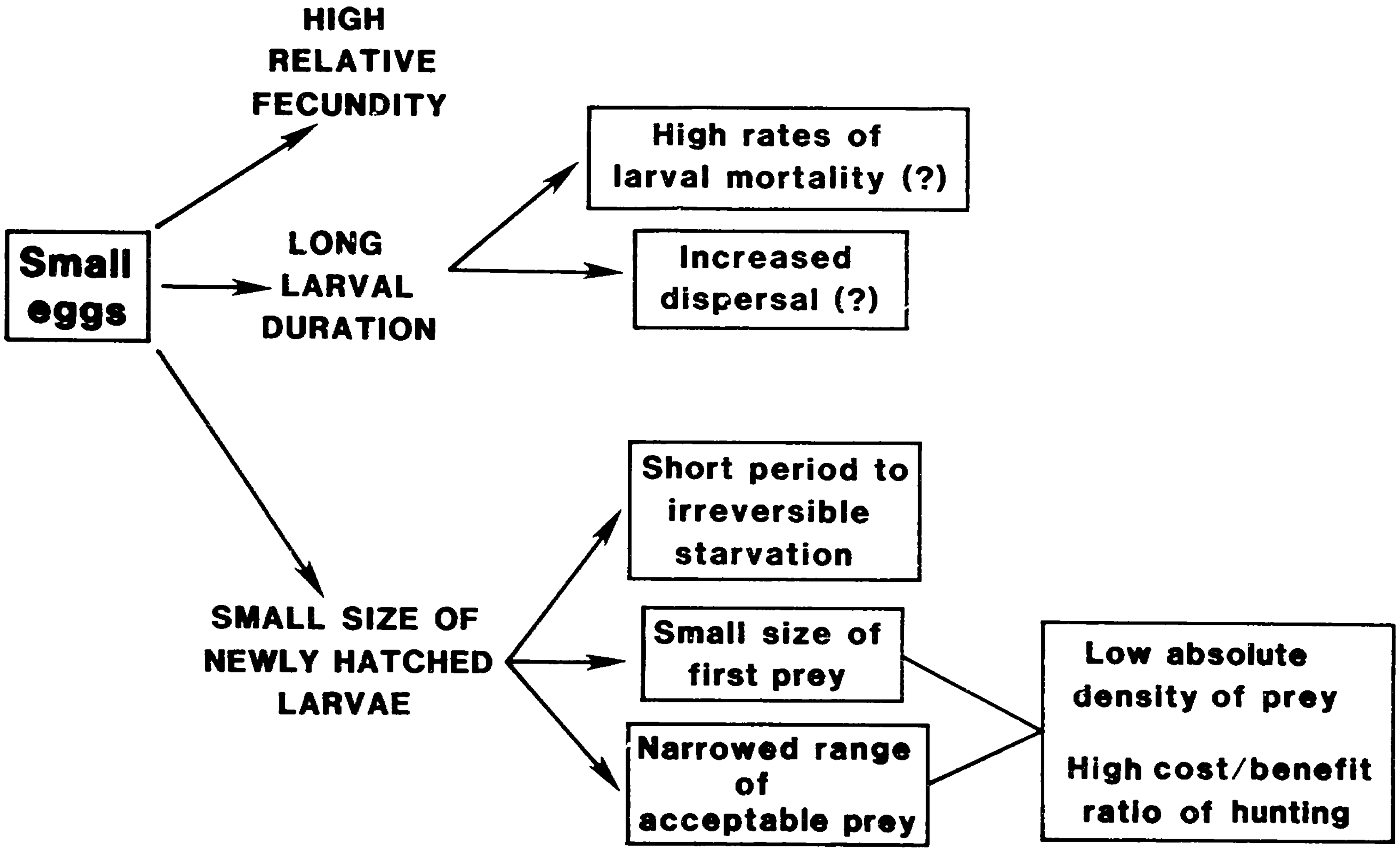
biotic factors at either the larval or postsettlement stage of existence, and selects for higher levels of parental investment in the Indo-West Pacific. This hypothesis is difficult to evaluate both because many factors may be involved and because their modes of operation are not clearly understood. There is too little information available on the levels and patterns of larval competition in the western Atlantic, for example, to determine to what extent it is affected by regional variations in parental investment.

Some insight into the factors underlying regional differences in early life-history parameters, at least, might be gained by considering, first, the logical consequences of the differences observed and, secondly, the systematic distribution of these differences. Small egg volume correlates with larvae that are small at hatching, and thereby with smaller size of prey that can be eaten at first feeding, a narrower range of potential prey sizes, and a shorter period to irreversible starvation by larvae should they fail to find food (Fig. 1). It also correlates with increased larval duration, which could lead both to increased rates of larval mortality and wider dispersal. The importance of the last two factors is unknown; work on the ecology of larval reef fishes is still very much in its infancy.

The consequences of producing larvae that are small at hatching, however, suggest that at first feeding, food for larvae is more abundant in the Atlantic than in the Pacific, a difference that may have permitted adults in the Atlantic to reduce their per capita investment in offspring and increase their fecundity. And secondly, there appear to be general distributional differences between larvae of demersal and pelagic spawning fishes, the principal point of separation between fishes that show regional differences in early life history and those that do not. Broadly speaking, the larvae of demersal spawning fishes tend to be found inshore of those hatching from pelagic eggs (e.g., Leis and Miller 1976). Consequently, the reproductive biology of demersal spawning fishes in general may be more closely linked to localized, coastal variations in productivity, current patterns, and the like than is the reproductive biology of pelagic spawning fishes, the larvae of which tend to be found in the geographically more uniform open oceanic conditions. This difference in larval distribution may explain why demersal spawning fishes seem to have a greater proclivity for regional variation in early life history parameters than do pelagic spawners.

The combination of this inshore-offshore difference in larval distributions and the apparent consequences of producing larvae that are small at hatching led Brothers and Thresher (in prep.) to suggst that the microzooplanktonic

CONSEQUENCES OF REDUCED EGG VOLUME



Small eggs

HIGH RELATIVE FECUNDITY

LONG LARVAL DURATION

High rates of larval mortality (?)

Increased dispersal (?)

SMALL SIZE OF NEWLY HATCHED LARVAE

Short period to irreversible starvation

Small size of first prey

Narrowed range of acceptable prey

Low absolute density of prey

High cost/benefit ratio of hunting

prey of first-feeding larvae are either more abundant in coastal regions of the western Atlantic than in the western Pacific, or are spatially or temporarily more predictable in occurrence. The limited data on global patterns of productivity (e.g., Koblentz-Mishke et al. 1970 [in Parsons et al. 1977]) seem to support this hypothesis, though more rigorous testing is clearly needed. Along similar lines, the temporal instability of the Indo-Pacific, e.g., El Niño-Southern Oscillation Events, seems to exceed greatly that of comparable portions of the tropical western Atlantic, which could affect the quantity of resources fishes have to invest in their offspring in order to ensure reasonable prospects of survival. In this regard, the pomacentrid genus Stegastes could prove a particularly interesting test case. Stegastes does not appear to exhibit the marked regional differences in early life history parameters otherwise apparently characteristic of demersal spawning fishes. If the hypothesis about regional differences in water-column productivity are correct, then I would predict that larvae of Stegastes are found farther offshore than those of other demersal spawning fishes, in areas more typical of the larvae of pelagic spawning families.

IMPLICATIONS OF INTEROCEANIC AND REGIONAL DIFFERENCES IN REPRODUCTION FOR COMMUNITY ECOLOGY AND FISHERIES MANAGEMENT OF TROPICAL COASTAL AREAS

Results of comparison of reproductive parameters between reef fishes in different oceans and between different areas within oceans are obviously still very tentative, pending availability of more data. If they are borne out, however, they are likely to have a number of implications for studies on the community ecology of reef fishes and the effective management of fisheries based on reef species.

First, very real differences between confamilial species on western Atlantic and Indo-Pacific reefs may bear on current controversies over the roles of resource limitation and recruitment rates as structuring factors of reef fish assemblages (for reviews of the field, see Helfman 1978; Sale 1980). Two schools of thought have developed: advocates of the "equilibrial hypothesis" have emphasized the importance of resource limitation and niche partitioning as structuring forces, whereas supporters of the "lottery" and "recruitment limitation" hypotheses emphasize the "sweepstakes" nature of competition for vacant living space and the chance processes associated with survival and dispersal of larvae (see Smith 1978; Sale 1980; and Doherty 1983b for reviews). Although many of the differences between these two schools may derive from conflicting interpretations of similar phenomena and data, it is striking that advocates of the equilibrial hypothesis have almost invariably worked in the western

Atlantic, whereas supporters of the "lottery" and "recruitment limitation" hypotheses have all worked on Indo-Pacific reefs. This difference in research locale may be irrelevant, but it may also suggest that there is some profit in examining the relevant biology of fishes in the two regions. At least one factor that could affect recruitment rates, individual fecundity, almost certainly differs for confamilial fishes in the Atlantic and Pacific. Logically, this difference could lead to differences in the relative importance of competition and recruitment limitation in structuring Atlantic and Pacific fish communities. The focus of field biologists on pomacentrids and other small, demersal spawning fishes as research subjects could have had the inadvertent effect of emphasizing regional differences in community dynamics.

In this regard, there is evidence, albeit qualitative and largely subjective, of interoceanic differences in settlement rates of reef-associated fishes. Personal observations of pomacentrid social organizations in the western Atlantic, eastern Pacific and Indo-West Pacific, for example, suggest there is a higher proportion of juveniles to adults in the New World tropics than in the western Pacific. In the eastern Pacific, in particular, habitats peripheral to those inhabited by adult damselfishes often support large numbers of juveniles and territories maintained by adults can routinely contain up to six coresident juveniles (Thresher 1984). By comparison, the number of juvenile Indo-West Pacific benthic damselfishes seems relatively low, though temporally variable (e.g., Doherty 1983b). Populations of reef fishes in the western Atlantic and, particularly, the eastern Pacific may well be more "tightly packed" into available habitat space than their Indo-West Pacific counterparts, and closer to carrying capacity.

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REPRODUCTION AND RECRUITMENT OF CORALS: COMPARISONS AMONG THE CARIBBEAN, THE EASTERN PACIFIC, THE INDO-WEST PACIFIC, AND THE RED SEA

by

Robert H. Richmond*

ABSTRACT

Detailed reproductive data are available for 92 of the approximately 400 species of scleractinian reef-dwelling corals, with additional observations recorded for species involved in mass spawning events on the Great Barrier Reef of Australia. Corals can be hermaphroditic (simultaneous or sequential, and in the latter case, protandrous or protogynous), gonochoric (dioecious), or sterile (51 species, 15 species and 4 species, respectively). Species may release brooded planula larvae (40 species), spawn gametes (153 species), or reproduce solely by asexual means. Characteristics of sexuality and mode of reproduction appear to be conservative within species, genera, and even families, yet there are reports of differences within each level, which may be adaptations to local environmental conditions. Acropora humilis, for example, has been reported to brood planulae at Enewetak, but spawns gametes on the Great Barrier Reef and in the Red Sea.

There appear to be several geographical trends in coral reproduction. Synchronous spawning of numerous species has been reported from the Great Barrier Reef, while asynchrony between species has been observed in the Red Sea. Sexual reproduction appears to be the means for successful recruitment for particular populations of Great Barrier Reef corals, while asexual processes (fragmentation, polyp bail-out) may be the sole means of recruitment for these same species in Hawaii and the eastern Pacific. Although our knowledge of coral reproduction and recruitment has grown substantially over the last few years, identification of additional patterns may still be premature. Regional differences occur among Caribbean, eastern Pacific, Indo-West Pacific, and Red Sea coral reefs, yet patterns of coral

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*Marine Laboratory
University of Guam
UOG Station
Mangilao, Guam 96923

reproduction and recruitment appear more dependent on variations in local conditions, which can range as widely within a region as between regions.

Recruitment success of the different reproductive strategies may vary within and between localities, and is mediated by both biotic (predation, competition) and abiotic (environmental variability, disturbance) factors. Data on reproductive patterns and recruitment success may be used for managing corals as a resource. In areas where juvenile mortality is high (eastern Pacific), transplantation of fragments ("asexual reproduction") is suggested to re-seed reefs, while in areas of relatively high adult mortality (Pacific atolls), introduction of planulating colonies is predicted to be most practical.

INTRODUCTION

Until recently, the majority of data on coral reproduction were anecdotal and incomplete observations based on short-term and sporadic studies. This is understandable, as the subject requires continuous monitoring of field populations, as well as histological and laboratory examination. Early generalizations (i.e., brooding is the common mode of reproduction) have since been proven false, as insufficent data were available to warrant such statements.

Within the last 5 years, the study of coral reproduction has advanced through numerous theses and dissertations, as well as from concerted group efforts, most notably on the Great Barrier Reef of Australia. These studies have provided data on coral sex (hermaphroditic vs. gonochoristic colonies), mode of reproduction (brooding planula larvae vs. spawning gametes), and timing (seasonality, periodicity, and synchrony). The major pattern that has developed is one of great variability. Corals are plastic both in growth form, and to an extent, in their life history characteristics. What appear to be members of the same species, can display different reproductive patterns at different geographical locations.

Detailed reproductive data are available on approximately one-third of the Caribbean reef-dwelling species, and on about one-fourth of the Pacific and Red Sea species. Certain patterns of reproduction and recruitment are discernable for these species, which enable a degree of generalization. In this paper, I review the data for 92 scleractinian species, and compare reproductive processes in the Caribbean, eastern Pacific, Hawaii, Central Pacific, Great Barrier Reef, and Red Sea. As more data become available, additional patterns and trends may emerge, which cannot be constructed from the present data base.

REPRODUCTION IN GENERAL

Reproduction is the process by which new individuals (or colonies) are formed from preexisting parent stock. Growth is an increase in size, and in scleractinian corals, includes both an increase in biomass, and the deposition of additional calcium carbonate.

A. Hermaphroditism vs. Gonochorism

Corals reproduce both sexually and asexually. Sexual reproduction is the result of gametogenesis and subsequent fertilization of eggs by sperm. Colonies may be hermaphroditic, with ovaries and spermaries developing on the same mesentery, on different mesenteries within the same polyp, in different polyps within the same colony, and at different times within the same colony (Harrigan 1972; Kojis and Quinn 1981; Bothwell 1982; Fadlallah 1983). Corals can be simultaneous hermaphrodites, with egg and sperm present at the same time, or sequential hermaphrodites, with gamete development occuring at different times (Bothwell 1982; Babcock 1984). Corals exhibit both protandry (male character develops first) and protogyny (female first) (Kojis and Quinn 1981; Babcock 1985). Gonochoristic (separate male and female) species also exist. Numbers of gonochoristic and hermaphroditic species at each site are summarized in Table 1. At all sites, hermaphrodites outnumbered gonochoristic species (Table 2).

Trends: On the Great Barrier Reef, and in the Red Sea, hermaphrodites greatly outnumber gonochorists for the data set available. Limited data from other sites make deductions tenuous.

Comments: Hermaphroditism is considered advantageous when the probability of finding members of the opposite sex is low, and self-fertilization is possible.

B. Brooding vs. Spawning

Fertilization may take place internally, within the polyp, or externally, after gametes are shed. Brooding (development of planula larvae within the parent polyps) occurs with a higher frequency in the Caribbean, Hawaii, and Central Pacific, than spawning (shedding of gametes with external fertilization), which occurs with a higher frequency on the Great Barrier Reef and in the Red Sea (Table 2). Overall, within the present data base, spawners outnumber brooders 153:40 (Table 2).

Trends: While the aforementioned difference in frequencies separates the Caribbean, Hawaii, and the Central Pacific from the Great Barrier Reef and Red Sea, the data base is limited, and incomplete. Szmant-Froelich (1984) generalized

Table 1. Coral reproduction

Caribbean

Coral	Sex	Mode	Season	Source
Acropora cervicornis	H(pg)	S	sr	1,6,29
Acropora palmata	H(pg)	S	sr	6,29
Agaricia agaricites	H	B	sp-yr	1,10
Agaricia fragilis	x	B	sr	13
Agaricia crassa	x	B	sp	13
Dendrogyra cylindris	G(pg)	S	sr	6,29
Diploria strigosa	H(pg)	S	sr	6,7
Favia fragum	H	B	sp-yr	1,6,10
Isophyllia sp.	G?	B	sp	1
Manicina areolata	H	B	sp	1
Meandrina sp.	x	B	sp	1
Montastrea annularis	H(pg)	S	sr	6,29
Montastrea cavernosa	G(pg)	S	sr	6,29
Mycetophyllia ferox	H(pg)	B	w-sp	6,29
Porites astreoides	H(s)	B	sp-yr	1,6,10
Porites porites	G?	B	w-sp	1
Siderastrea radians	G	B	yr	1,6,10
Siderastrea siderea	G	S	sr	6
	6G:9H:3?	11B:7S		

Pacific Corals

Hawaii

Acropora cytherea	H	*	*	12
Acropora humilis	H	*	*	12
Acropora valida	H	*	*	12
Cyphastrea ocellina	x	B	yr	13
Dendrophyllia manni	x	B	sr-f	1
Fungia scutaria	G	S	sr	15
Montipora verrucosa	H	S	sr	10
Pocillopora damicornis	H	B	yr	16,17
Porites lutea	G	S	sr	10
Tubastrea aurea	x	B	sr-f	1,10
	2G:5H:3?	4B:3S		

Central Pacific

Acrhelia horrescens	x	B	yr	20
Acropora bruggemanni	x	B	x	18
Acropora corymbosa	x	B	sr	13
Acropora humilis	x	B	sr	13
Acropora palawensis	x	B	x	19
Acropora striata	x	B	w	13
Euphyllia glabrescens	x	B	x	20
Fungia actiniformis	H?	B	yr	21
Galaxea aspera	x	B	yr	23
Goniastrea aspera	x	B	f	21
Goniopora queenslandiae	G	B	sr	1
Pocillopora damicornis	H	B	yr	13,17
Pocillopora elegans	x	B	sr	13
Pocillopora verrucosa	x	B	yr	13
Seriatopora hystrix	x	B	yr	13
Stylophora pistillata	x	B	yr	13,22
		16B:0S		

eastern Pacific - work in progress

Pocillopora damicornis -after 2 years, only immature ovaries observed (spring). No complete gametogenesis, spawning or planulation observed. (Richmond 1985).

Pocillopora elegans -spermaries and ovaries observed near maturity during summer (A. Yedid, pers. comm.).

Tubastrea aurea -planulated June through November during both 1984 and 1985 (Richmond, unpublished).

Species under study by Glynn and Richmond

Porites lobata	(larval recruits observed)
Porites panamensis	(larval recruits observed)
Psammocora stellata	(larval recruits observed)
Pocillopora capitata	
Pavona varians	(larval recruits observed)
Pavona clavus	
Pavona gigantea	
Gardineroseris planulata	(larval recruits observed)

Great Barrier Reef

Acropora aspera	H(s)	S	seasonal	4
Acropora cuneata	H(s)	B	x	4
Acropora digitifera	H(s)	S	sp-sr	4
Acropora formosa	H	S	sp-sr	5
Acropora humilis	H(s)	S	sp-sr	4
Acropora hyacinthus	H(s)	S	sp-sr	4
Acropora millepora	H(s)	S	sp-sr	4
Acropora palifera	H(s)	B	x	4
Acropora pulchra	H(s)	S	sp-sr	4
Acropora robusta	H(s)	S	sp-sr	4
Acropora variablis	H(s)	S	sp-sr	4
Favia abdita	H(s)	S	sp-sr	3
Favia favus	H(s)	S	sr	5
Favia pallida	H(s)	S	sp-sr	1
Goniastrea aspera	H(pg)	S	x	9,11
Goniastrea australensis	H(pa)	S	sp-sr	2,9
Leptoria phrygia	H(s)	S	sp-sr	3
Lobophyllia corymbosa	H(s)	S	sr	1,5
Montipora ramosa	H	S	x	5
Pavona cactus	G	S	x	25
Platygyra sinensis	x	S	x	9
Pocillopora damicornis	H	B	yr	1,25
Porites andrewsi	G	S	sp-sr	24
Porites australiensis	G	S	sp-sr-f	5
Porites haddoni	x	B	sr-f	25
Porites lobata	G	S	sp-sr	24
Porites lutea	G	S	sp-sr	5,24
Porites murrayensis	G	B	sp-sr-f	24
Seriatopora hystrix	x	B	sp-sr	26
Symphyllia recta	H	S	sp-sr	25
	6G:21H:3?	6B:24S		

a total of 133 species out of 356 have been observed to mass spawn during the week following the full moon in October (see Willis et al., 1985 for details).

Red Sea

Acropora eurystoma	H(pg)	S	sp	27
Acropora hemprichii	H	x	x	28
Acropora humilis	H(pg)	S	sp	27
Acropora hyacinthus	H(pg)	S	sr	27
Acropora scandens	H(pg)	S	sr	27
Alveopora daedalea	H(pg)	B	f-w	27
Astreopora myriophthalma	H(pg)	S	sr	27
Favia favus	H(pg)	S	sr	27
Galaxea fascicularis	H(pg)	S	sr	27
Goniastrea retiformis	H(pg)	S	sr	27
Platygyra lamellina	H(pg)	S	sr	27,28
Pocillopora verrucosa	H(pg)	S	sr	27
Seriatopora caliendrum	H(pg)	B	sp-sr-f	27,28
Stylophora pistillata	H(pg)	B	w-sp-sr	27,28
	0G:14H	3B:10S:1?		

Sources: 1. Fadlallah 1983; 2. Kojis & Quinn 1981; 3. Kojis & Quinn 1982b; 4. Bothwell 1982; 5. Harriot 1983; 6. Szmant-Froelich 1984; 7. Wyers 1985; 8. Van Moorsel 1983; 9. Babcock 1984; 10. Richmond pers. obs.; 11. Babcock 1985; 12. Grigg et al. 1981; 13. Stimson 1978; 14. Heyward in press; 15. Krupp 1983; 16. Harrigan 1972; 17. Richmond & Jokiel 1984; 18. Atoda 1951a; 19. Kawaguti 1940; 20. Kawaguti 1941; 21. Abe 1937; 22. Atoda 1947; 23. Atoda 1951b; 24. Kojis & Quinn 1982a; 25. Marshall & Stephenson 1933; 26. Sammarco 1982; 27. Shlesinger & Loya 1985; 28. Rinkevich & Loya 1979; 29. Szmant 1986.

Symbols: Sex: H = hermaphroditic; G = gonochoric; pg = protogynous; pa = protandrous; s = simultaneous; x = unknown. Mode: S = spawner; B = brooder; * = possibly sterile. Season: w = winter; sp = spring; sr = summer; f = fall; yr = year-round; x = unknown.

Table 2. Global comparisons of reproductive characterisitics

	Caribbean	Hawaii	Central Pacific	GBR	Red Sea	
Gonochoric	6	2	1	6	0	(15)
Hermaphroditic	9	5	2	21	14	(51)
Unknown	41	50	353	329		(356)
Brood	11	4	16	6	3	(40)
Spawn	7	3	0	133	10	(153)

that brooders enjoy the greatest recruitment success in the Caribbean, while spawners (particularly acroporids and poritids), are the successful recruiters in the Pacific.

Comments: Spawning is associated with higher fecundity, while brooding produces larvae which appear to have greater dispersal potential (Fadlallah 1983; Richmond 1985; Richmond 1987).

C. Timing, Seasonality, Synchrony, and Periodicity

Sexual reproduction in corals may occur monthly, seasonally, yearly, or not at all (Stimson 1978; Bothwell 1982; Richmond and Jokiel 1984; Richmond 1985; Willis et al. 1985). Temperature, photoperiod, and nocturnal illumination all appear to be important in providing temporal cues (Jokiel et al. 1985; Willis et al. 1985). A major tread in yearly multispecies synchronous spawning has been observed for 133 species on the Great Barrier Reef (Harrison et al. 1984; Willis, et al. 1985). Shlesinger and Loya (1985) have reported a noticeable asynchrony between species in the Red Sea, but that 12 of 13 species sampled exhibited lunar periodicty in their reproductive activity. Lunar periodicity of planulation was found to differ between populations of Pocillopora damicornis at Enewetak and Hawaii (Richmond and Jokiel 1984). While populations at both localities are believed to cue in on night-time illumination (Jokiel et al. 1985), differences in local conditions are believed to be responsible for the asynchrony.

Differences in reproductive seasonality can occur within a species, over its distributional range. For widely distributed species, variations can be detected within as well as between the regions chosen in this paper. Data are summarized in Table 1.

Trends: A definate pattern of multispecies synchronous spawning has emerged for the Great Barrier Reef, while asynchrony between species was found for Red Sea corals (Shlesinger and Loya 1985). Otherwise, regional trends are hard to discern, as seasonal variability within sites can be of sufficient magnitude to cause differences in reproductive timing.

Comments: Multispecies synchronous spawning is believed to be an adaptation to reduce loss to predators, as they can only eat so much at one sitting. Synchronous maturation of gametes within a species is necessary for successful sexual reproduction.

D. Asexual Reproduction in Corals

Due to their relatively simple level of development, corals are capable of asexual reproduction. Asexual reproductive processes include formation of "polyp-balls" (Rosen and Taylor 1969), polyp bail-out (Sammarco 1982; Richmond 1985), asexual production of planulae (Stoddart 1983), and fragmentation (Highsmith 1982).

Asexual reproduction via fragmentation appears to be important for several coral species, and especially for populations at the edge of their physiological limits, as well as in areas of intense predation. Grigg et al. (1981), reported lack of mature gonads in populations of 3 species of Acropora from the Leeward Islands of Hawaii. Reproduction via fragmentation appeared to be the major means of population growth. Likewise, Pocillopora damicornis populations in the eastern Pacific had not produced mature gonads nor planulae during a two year study, yet were the dominant reef species off the coast of Panama (Richmond 1985). Eastern Pacific P. damicornis exhibit higher colony growth rates than Central Pacific populations, which enhances population growth via fragmentation (Richmond 1985). High predation rates on corals in the eastern Pacific make fragmentation important for massive species such as Porites lobata as well (Highsmith 1982).

Trends: Asexual reproduction of corals is found in all regions covered in this report, but appears to dominate in areas which are marginal for coral growth, including the eastern Pacific, the Leeward Hawaiian Islands, southern Australia, and possibly Bermuda. Within regions with optimal conditions for coral growth, asexual processes may dominate specific habitats including high energy zones, and areas of soft substrata.

Comments: Enhanced colony growth rate and subsequent fragmentation may result from allocation of energy away from production of sexual products, notably in environments where sexual processes are physiologically constrained. The occurance of sterile population distributions has been described for other invertebrates (Mileikovsky 1971). Asexual reproduction has the advantage of not requiring a partner, plus asexually derived fragments usually have a refuge-in-size from predation and burial by sediments.

PLANULA LARVAE

Coral planulae can result from internal fertilization and be brooded until developed or they can result from the external fertilization of spawned gametes, and subsequently develop outside the parent colony (Harrigan 1972; Kojis and Quinn 1982b). Stoddart (1983) found that planulae may also be produced asexually.

The brooded planulae of Pocillopora damicornis contain symbiotic zooxanthellae upon release from the parent, as well as a large quantity of lipid. With the additional ability to feed while planktonic, these planulae remain competent for over 100 days, a period of time to allow dispersal over large distances (Richmond 1982; Richmond 1987). Planulae resulting from spawned gametes may lack zooxanthellae upon fertilization, eventually acquiring the algal cells from the environment. No competency data are available for externally fertilized planulae at present, but it appears that brooded larvae have advantages that would enable enhanced dispersal potential. Larval competency (the ability for larvae to successfully settle and metamorphose) may be a character which determines the species composition of certain reefs, particularly those in the eastern Pacific. It has been proposed that the present coral fauna of the eastern Pacific is the result of long-distance dispersal of planulae from Central Pacific stock (Dana 1975; Richmond 1987). Endemism may be the result of abbreviated larval competency periods.

RECRUITMENT

Reproductive success can best be measured by subsequent recruitment. Recruitment is mediated by both biotic factors, such as predation and competition, and by abiotic factors such as environmental variability and disturbance. Regional differences in these factors will cause regional differences in both reproduction and recruitment.

The pan-Pacific coral Pocillopora damicornis provides a good example of how life history characterisitics may vary with respect to local conditions. Enewetak Atoll and Hawaii are characterized as having low rates of predation on P. damicornis, relatively low seasonal variability, yet a relatively high frequency of mortality causing disturbances (hurricanes and typhoons). P. damicornis colonies planulate monthly, throughout the year, at these sites and the oldest colonies observed are estimated to be less than 10 years old. The eastern Pacific of Panama is characterized as having high rates of predation on P. damicornis, high levels of seasonal variability, low frequencies of mortality-causing events. In this area, P. damicornis has never been found to release planulae, has a higher colony growth rate, is the dominant coral in terms of competitive interactions with other corals, with colonies estimated to be at least 70 years old. Theories on the evolution of life history characteristics have been proposed which suggest under conditions of environmental instability, where lethal disturbances occur at a relatively high rate, formation of large numbers of motile propagules should be preferred, while under stable conditions, clonal (asexual) growth should be selected for (Williams 1975; Maynard-Smith 1978). Likewise, under conditions of low juvenile versus high adult mortality, and relatively low competitive ability versus competitive dominance, the sexual mode should be selected for rather than the asexual mode (Abrahamson 1980; Douglas 1981). P. damicornis fits these predicted patterns over its distributional range.

PRACTICAL APPLICATIONS

As coral reefs throughout the world are showing signs of degradation, management of reef resources is becoming a growing concern. Corals can be considered as fishery resources, and management can be approached the same way. Areas of reef which have been destroyed may be re-seeded, and the most efficient means will depend on local conditions. In areas where sedimentation is high, corallivores are present in large numbers, and/or disturbance rate is low, cementing larger numbers of smaller fragments is suggested. In areas where environmental conditions support sexual reproduction of corals, juvenile mortality is expected to be relatively low, and suitable substrata is available, transplanting gravid heads into an area is suggested.

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APPENDIX I

LIST OF PARTICIPANTS

1. Dr. J.R.E. Harger
UNESCO/ROSTSEA
Jl. Thamrin 14, Tromolpos 273/JKT
Jakarta, INDONESIA

2. Dr. Charles Birkeland
Marine Laboratory
University of Guam
UOG Station
Mangilao, Guam 96923

3. Dr. Jon E. Brodie
School of Pure and Applied Sciences
University of the South Pacific
P.O. Box 1168
Suva, FIJI

4. Dr. Hansa Chansang
Phuket Marine Biological Center
Department of Fisheries
P.O. Box 60
Phuket, THAILAND 83000

5. Miss Milika Naqasima
School of Pure and Applied Sciences
University of the South Pacific
P.O. Box 1168
Suva, FIJI

6. Dr. James D. Parrish
Hawaii Cooperative Fishery Research Unit
2538 The Mall
University of Hawaii at Manoa
Honolulu, Hawaii 96822

7. Dr. Robert H. Richmond
Marine Laboratory
University of Guam
UOG Station
Mangilao, Guam 96923

8. Dr. Paul W. Sammarco
Australian Institute of Marine Sciences
P.M.B. No. 3
Townsville, M.C., QLD 4810
AUSTRALIA

9. Dr. Ronald E. Thresher
CSIRO Marine Laboratory
G.P.O. Box 1538
Hobart, Tasmania 7001
AUSTRALIA

10. Dr. Geerat J. Vermeij
Department of Zoology
University of Maryland
College Park, Maryland 20742

11. Dr. William Wiebe
814 Bio Science Building
University of Georgia
Athens, Georgia 30602

12. Dr. Clive R. Wilkinson
Australian Institute of Marine Sciences
P.M.B. No. 3
Townsville M.C., QLD 4810
AUSTRALIA

APPENDIX II

Opening address to the UNESCO/COMAR Workshop on Differences Between Atlantic and Pacific Tropical Seas in Terms of Community Structure, Ecological Processes and Productivity of Coastal Ecosystems

Dr. J.R.E. Harger
Programme Specialist in Marine Sciences
UNESCO/ROSTSEA
Jl. Thamrin 14
Jakarta, INDONESIA

First of all please allow me to welcome all of you to this meeting, coming as you do from such widely separated parts of the globe, and to thank you for so kindly making your time available to be here.

This seminar is the first of its kind since UNESCO has not previously organized a similar exercise to compare marine ecologies of two separate geographical areas having such obvious differences and parallels in community structure. It is therefore to be hoped that something of lasting value will emerge from this activity.

There has already been considerable speculation as to the difference in coastal ecologies of the Caribbean and the Pacific but little has been presented in the way of systematic data relating to the two areas. I have no doubt that a number of interesting comparisons will be made in the course of your deliberations. Although the conclusions drawn from such comparisons will undoubtedly be valid within the context of the arguments presented, I should none the less like to suggest that it is now time to put aside the concept of separate research items and to start to develop data-base fragments covering the important aspects of marine ecosystems.

Such data-base fragments can be easily carried about and exchanged on floppy disks using convenient data-base management systems such as DB-III, and the resulting sets can be readily integrated at the microcomputer level and then analyzed and reanalyzed by anyone having access to commercial programmes such as STATPRO, SPSS-PC and ENERGRAPHICS, to name a few only.

To date the Australian Institute of Marine Science has made a start on this approach using their life-forms survey methodology on the Australian Great Barrier Reef. The Australian Government is also working with the 5 ASEAN nations to construct a coastal marine data base started at resource management using similar techniques.

In March 1985, a preliminary survey of the Jakarta Bay, Pulau Seribu area, was carried out by the Indonesian Institute of Oceanography (LON-LIPI) and UNESCO. This survey showed that coral reefs in the Jakarta Bay area were degraded and the information gathered was then used to plan the sampling stations used in a subsequent workshop entitled "UNESCO/COMAR Research Workshop and Advanced Training on Human-Induced Damage to Coral Reefs", which was held in Indonesia from 21-22 May 1985. During the latter activity a total of twenty-five participants spent thirteen days in the Pulau Seribu area gathering data for the purpose of assessing the effects of environmental trends and associated human-induced impact on coral reefs of the area.

The workshop gathered approximately 550 man-days of data concerning coral reef structure in the Pulau Seribu region to establish a comprehensive coral reef data base. This information can be used to provide preliminary insight into the ecological structure of coral reefs in the Pulau Seribu region.

At the present time the data base consists of records of coral reef structure obtained at two depths (roughly 1 meter and 3 meters below the mean tidal level) from the north face of approximately 28 islands. Additionally, measurements were made of physical environmental factors such as: Secchi disk extinction depth, surface and 3-meter salinity and temperature. Estimates of the concentration of drift-line debris were also made for most of the islands and additional items of information such as population density, island circumference, distance from the mainland, distance from Jakarta, etc., were recorded.

In the case of the biological indicators of population structure, two basic methods of investigation were applied to sessile communities and two slightly different procedures were used for the assessment of fish populations. For sessile communities, two groups of participants gathered data utilizing three 60-m line-intercept transects, parallel to the shoreline at each of the two depths mentioned previously (1 m and 3 m). One group of investigators utilized the method proposed by the Australian Institute of Marine Sciences (AIMS) which consists of subdividing coral assemblages according to categories, characterized by some categories such as coral-massive, coral-branching, turf algae, etc. The second group of investigators utilized 60-m replicated line-intercept transects, but identified each hard coral to the species level and recorded colony sizes together with measurements on the additional flora and fauna encountered. Part of the rational of the exercise was to test under field conditions the capability of the resulting data sets in order to be guided in making choices for a regional standard in data acquisition relating to coral-reef community structure. The resulting data base consists of approximately 19,000 records in 117 fields in addition to an array of colony-size data for the individual corals identified to the species level.

The major portion of this data set is currently available as two DB-III files on a standard 5 1/4" floppy disk formatted to run on an IBM-PC. The files can also be written to a number of other formats and can be obtained by sending a blank diskette and a written request to UNESCO/ROSTSEA, Jakarta.

In summary then I should like to ask this meeting to give some consideration to the basic elements of marine coastal ecological structure and function in the tropics that should be incorporated into such data bases, particularly by referring to the items identified as being critically different (or important) as far as Caribbean and Pacific systems are concerned.

I should also like to ask you to identify what you consider to be the most important problem areas relating to marine coastal resource analysis in the Pacific and Caribbean for future attention by UNESCO through international research workshops, etc. Finally, since we are meeting in the Pacific, I should like to ask you to pay particular emphasis to the question of future marine science activities and programmes that UNESCO might implement in this region.

Thank you.

APPENDIX III

SEVUSEVU CEREMONY

Miss Milika Naqasima
School of Pure and Applied Science
University of the South Pacific
Suva, FIJI

Following a tradition that dates back hundreds of years, a necessary formality had to be carried out upon reaching Dravuni Island. This was the presentation of yaqona which is the root of the plant Piper mysticum. This ceremony is called the sevusevu which is accorded to the chief and other village elders.

The sevusevu is carried out when visiting a village or any other traditional settlement, relatives and friends, for the first time. The yaqona is presented by the visitors which on this trip was done by the Fijian caretaker of the USP field station, on behalf of the group.

After placing the sack containing the roots before the elders, he went on to explain the reason for the visit and asked if the group could be permitted to dive on the reefs surrounding the island and to carry out the scientific investigations that they had planned. The chief, who does not receive the gift personally, has a spokesman who does it on his behalf. This designated elder said how honored they were by having the visitors and thanked them for the gift which they had brought. He then went on to say that the village and surrounding sea were open to the visitors and that they were welcome to stay and carry out whatever work they had planned to do. Not only was permission granted but he expressed the blessings of the elders and their wish that everything would go well with the guests.

There was the traditional chanting and clapping to acknowledge the presentation and to thank the visitors for it. The visitors were also instructed to clap their hands as a gesture of thanks and of respect. With the ceremony over, the visitors were briefly introduced to the elders who then shook hands with each person.

The sevusevu, which is an important ceremony in the Fijian culture, lasted a mere twenty minutes; nevertheless it was essential for the visit.

No matter which village or traditional settlement one visits in Fiji, particularly if one is to do work in the area, a sevusevu has to be presented to the chief or any other appointed representative of his. Not to present one would be considered as gross disrespect for the inhabitants.

This has always been the tradition of our forefathers to ensure that no person can enter another's territory and use its resources without first obtaining permission. It is thus a form of traditional management of resources, and one that should be maintained as it has proved to be an effective method of conserving natural resources.

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No.		Year
40	Human induced damage to coral reefs Results of a regional Unesco (COMAR) workshop with advanced training Diponegoro University, Jepara and National Institute of Oceanology Jakarta, Indonesia May 1985 English only	1986
41	Caribbean coastal marine productivity Results of a Planning Workshop at Discovery Bay Marine Laboratory, University of the West Indies Jamaica, November, 1985 English only	1986
42	The application of digital remote sensing techniques in coral reef, oceanographic and estuarine studies. Report on a regional Unesco/COMAR/GBRMPA Workshop Townsville, Australia August 1985 English only	1986
43	Quaternary coastal geology of West Africa and South America. Papers prepared for the INQUA-ASEQUA Symposium in Dakar, April 1986 Available in English and French	1987
44	Physical oceanography of the Eastern Mediterranean (POEM): Initial Results Unesco/IOC First POEM Scientific Workshop Erdemli, Turkey 16-20 June 1986 English only	1987
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Title of numbers which are out of stock

No.		Year
3	Benthic ecology and sedimentation of the south Atlantic continental platform Report of the seminar organized by Unesco in Montevideo, Uruguay, 9-12 May 1978	1979
7	Coastal ecosystems of the Southern Mediterranean; lagoons, deltas and salt marshes, Report of a meeting of experts, Tunis, 25-27 September 1978	1979
11	Programa de Plancton para el Pacífico Oriental Informe final del Seminario-Taller realizado en el Instituto del Mar del Perú, El Callao, Perú, 8-11 de septiembre de 1980	1981
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13	Seminario Latinoamericano sobre Enseñanza de la Oceanografía Informe final del Seminario organizado por la Unesco en São Paulo, Brasil, 17-20 de noviembre de 1978	1981
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