REGIONAL SEAS

UNITED NATIONS ENVIRONMENT PROGRAMME

Ecological interactions

between tropical coastal ecosystems

UNEP Regional Seas Reports and Studies No. 73

Prepared in co-operation with

ESCAP

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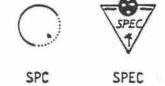# REGIONAL SEAS

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PREFACE

Thirteen years ago the United Nations Conference on the Human Environment (Stockholm 5-16 June 1972) adopted the Action Plan for the Human Environment, including the General Principles for Assessment and Control of Marine Pollution. In the light of the results of the Stockholm Conference, the United Nations General Assembly decided to establish the United Nations Environment Programme (UNEP) to "serve as a focal point for environmental action and co-ordination within the United Nations system" (General Assembly resolution 2997(XXVII) of 15 December 1972). The organizations of the United Nations system were invited "to adopt the measures that may be required to undertake concerted and co-ordinated programmes with regard to international environmental problems", and the "intergovernmental and non-governmental organizations that have an interest in the field of the environment" were also invited "to lend their full support and collaboration to the United Nations with a view to achieving the largest possible degree of co-operation and co-ordination". Subsequently, the Governing Council of UNEP chose "Oceans" as one of the priority areas in which it would focus efforts to fulfil its catalytic and co-ordinating role.

The Regional Seas Programme was initiated by UNEP in 1974. Since then the Governing Council of UNEP has repeatedly endorsed a regional approach to the control of marine pollution and the management of marine and coastal resources and has requested the development of regional action plans.

The Regional Seas Programme at present includes eleven regions [1] and has over 120 coastal States participating in it. It is conceived as an action-oriented programme having concern not only for the consequences but also for the causes of environmental degradation and encompassing a comprehensive approach to combating environmental problems through the management of marine and coastal areas. Each regional action plan is formulated according to the needs of the region as perceived by the Governments concerned. It is designed to link assessment of the quality of the marine environment and the causes of its deterioration with activities for the management and development of the marine and coastal environment. The action plans promote the parallel development of regional legal agreements and of action-oriented programme activities [2].

The idea for a regional South Pacific Environment Management Programme came from the South Pacific Commission (SPC) in 1974. Consultations between SPC and UNEP led, in 1975, to the suggestion of organizing a South Pacific Conference on the Human Environment. The South Pacific Bureau for Economic Co-operation (SPEC) and the Economic and Social Commission for Asia and the Pacific (ESCAP) soon joined SPC's initiative and UNEP supported the development of what became known as the South Pacific Regional Environment Programme (SPREP) as part of its Regional Seas Programme.

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[1] Mediterranean, Kuwait Action Plan Region, West and Central Africa, Wider Caribbean, East Asian Seas, South-East Pacific, South Pacific, Red Sea and Gulf of Aden, Eastern Africa, South-West Atlantic and South Asian Seas.

[2] UNEP: Achievements and planned development of UNEP's Regional Seas Programme and comparable programmes sponsored by other bodies. UNEP Regional Seas Reports and Studies No. 1. UNEP, 1982.

An Action Plan for the South Pacific Regional Environment Programme (SPREP) was adopted at the Conference on Human Environment in the South Pacific at Rarotonga, 8-11 March 1982, and was endorsed seven months later at the South Pacific Conference and South Pacific Forum[3].

This document has been prepared by Mr. Charles Birkeland and Ms. Deborah Grosenbaugh of the University of Guam Marine Laboratory as a contribution to the South Pacific Regional Environment Programme. The sponsors of the study would like to express their gratitude to both of the authors and their institutions.

The objective of this report is to summarize information from the literature on ecological interactions between tropical coastal ecosystems and to review management issues and legislation regarding integrated tropical marine island ecosystems and, on the basis of this review, make recommendations for future directions in research and management. The reviews of scientific research and legislation are organized into separate sections because alternating between these two frames of reference would be confusing to the reader and certain subjects would be more difficult to find if scientific and legislative materials were intermingled.

The review of ecological interactions between coastal ecosystems includes references from around the world and is not limited to the South Pacific. This is because studies concerning mangroves and seagrasses from the South Pacific region include mostly biogeographical, physiological, morphological, and descriptive community studies, but include relatively few studies of interactions between coastal ecosystems. Resource assessment and estimates of rates of productivity, growth, litter production, and nutrient cycling by themselves are static estimates of rate parameters. In order to obtain an understanding of the operations of coastal ecosystems that could contribute towards the design of effective management policies, we must learn of and study the interactions between the components of coastal ecosystems.

A large portion of the existing studies on how rates of processes vary in the interactions between coastal systems have been done in the tropical Atlantic. Therefore, this review cannot be effective if it concentrates solely on the literature from regional studies of the South Pacific. This is why the review of existing information is from a global perspective while the recommendations for the priorities for further research and management practices are based on a regional approach.
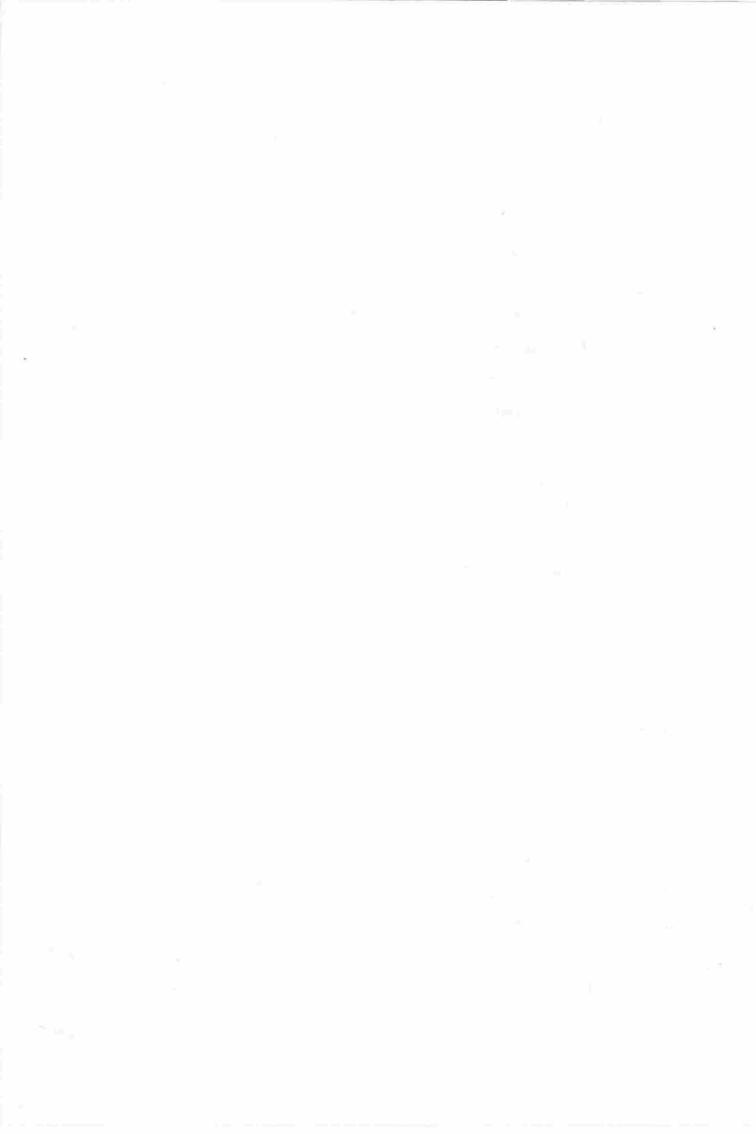
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[3] SPC/SPEC/ESCAP/UNEP: Action Plan for managing the natural resources and environment in the South Pacific Region. UNEP Regional Seas Reports and Studies No. 29. UNEP, 1983.

Contents

ECOLOGICAL INTERACTIONS BETWEEN MANGROVES, SEAGRASS BEDS, AND CORAL REEFS

Charles Birkeland

Introduction

Coastal ecosystems have been of particular importance to tropical Pacific islanders because islanders have always depended upon coastal marine resources for at least 90% of their animal protein (Johannes 1977). The rational management of tropical coastal ecosystems should be of worldwide interest because mangroves, seagrass beds, and coral reefs are among the most productive ecosystems, marine or terrestrial (Table 1). In a literature review by Lewis (1977: Table 2), seagrass beds and coral reefs ranked higher in gross primary productivity per m² per year than other ecosystems, including sugar cane fields in Java and the nutrient-enriched Peru current. Mangrove ecosystems supplied with allochthonous nutrient input produce comparable levels of gross primary productivity (Lugo and Snedaker 1974: Table 2). These three coastal ecosystems are also of interest because of their geographic prevalence in the Pacific islands. These ecosystems provide or influence the important natural resources for Pacific islanders.

According to Adams et al. (1973), it is generally accepted that 75-90% of marine commercial and sport fish species depend on estuarine habitats during at least part of their life cycle. Even if the availability of estuarine habitats is critical for only one period in the life of an organism, the availability of the habitat is important for the success of the population. Estuarine habitats can be important for fishes and invertebrates either as nurseries for juveniles, as a source of food for adults, or both. Most of the productivity of estuarine habitats is a result of the production of marine vascular plants: mangroves, seagrasses or marsh grasses (Golley et al. 1962; Teal 1962; E.P. Odum 1961, 1971; Lugo et al. 1973a,b; and especially Heald 1971 and W.E. Odum 1971 which were cited in Snedaker and Lugo 1973). Since many commercial and sport fishes are dependent on estuarine habitats and since the major portion of the production of estuarine habitats is from marine vascular plants, one might expect that the primary production of marine vascular plants should be important for fisheries. However, this doesn't necessarily follow. The favorable influence of marine vascular plants on fisheries might not be a direct result of their large primary productivity but instead might be a result of their influences towards stabilizing the physical environment, providing habitat and refuge, contributing to the detrital food chain through bacteria and other microbes, or functioning in a role as substrata for epiphytic algae or bacteria. If this is the case, then the primary productivity possibly could be utilized more efficiently by Pacific islands and this is a major topic that will be addressed in this report.

Whether nearshore fisheries are mainly influenced by marine vascular plants through primary productivity or by some other factor, the effect is there. Skud and Wilson (1960); Darnell (1958, 1961, 1967); Sykes and Finucane (1966); Smith et al. (1966); Odum and de la Cruz (1967); Wood et al. (1969); Heald and Odum (1970); Cronin and Mansueti (1971); Odum and Heald (1972); Carr and Adams (1973); Snedaker and Lugo (1973); and Heald (1971) and W.E. Odum (1971), both cited in Snedaker and Lugo (1973),

Table 1. Average gross primary productivity (g C m^{-2} yr^{-1}) in terrestrial and marine habitats (from Lugo and Snedaker 1974; Crisp 1975; Lewis 1977).

Mangrove forest[1]	2300–5074
Tropical seagrass beds	4650
Coral reef	4200
Tropical algal communities	3836
Peru current	3650
Sugar cane fields	3450
Sewage treatment ponds	1800
Kelp bed	1750
Spartina marsh	1600
Estuarine benthos	1320
Temperate algal communities	920
Coniferous woodland	800
Deciduous woodland	785
Mangrove forest[2]	511
Field grass	500
Long Island Sound plankton	470
Eutrophic lakes plankton	75–250
English Channel plankton	135
Sargasso Sea plankton	134
North Sea plankton	100
Open ocean near coral reefs	
Barbados	50
Rongelap	28
Hawaii	21–37
Oligotrophic lakes plankton	7–25

[1] Receives wet season terrestrial nutrient runoff
[2] Lacking obvious external nutrient sources

documented the dependency of commercial and sport fisheries on estuarine systems in which the marine vascular plants were the major primary producers. Because of this, the estimates of the monetary value of marine vascular plant habitats are very high. For example, on the west coast of Florida alone, where the commercial fish production is dependent upon the productivity and organic export from mangroves, the wholesale value of commercial fish catches was worth $10.4 million in 1971 (Adams et al. 1973). The estimated value of fisheries is several times greater when secondary economic benefits are taken into account. The mangroves which support the fisheries would therefore be found to have a large economic value if monetary estimates were made. If estimates were made for the potential monetary value of marine vascular plant communities to Pacific island economies, the value would be high in relation to the total economies.

The potential yield by artisanal fisheries of coral reefs and lagoons is of about the same magnitude as is the offshore tuna harvest, at least for Micronesia (Johannes 1977). For example, the potential harvest of reef fish in Palau by artisanal fishermen is between 2,000 and 11,000 tons per year while the commercial skipjack tuna fisheries of Palau harvested between 2,000 and 9,000 tons annually between 1965 and 1974 (Mitchell 1975; Johannes 1977).

There is a tremendous amount of literature on mangroves, seagrass beds, and coral reefs, but there is very little literature on interactions between these three coastal ecosystems. Bibliographies pertaining to mangroves (Thurgood 1968; van Tine and Snedaker 1974; Rollet 1981) include over 6000 references. Kent W. Bridges (Department of Botany, University of Hawaii) has a bibliography for seagrasses with over 2000 references. A comparable bibliography for coral reefs would be much larger. Despite this overwhelming mass of literature on these three ecosystems, nearly all the papers deal with particular ecosystems or with interactions between the particular ecosystem and terrestrial or offshore environments.

Because of the importance of these ecosystems to the peoples of the South Pacific islands as sources of protein and other resources as well as for logistic reasons, human settlement and urban development on islands has generally concentrated in coastal regions, especially in harbors where they exist, and along rivers which drain into coastal areas nearby. So while coastal resources are traditionally the resources most heavily utilized, they are also the areas which most directly and immediately feel the impact of man's developmental activities such as land-clearing and pollution. An understanding of how the 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.

McNae (1968) suggests that individual plants or species should be referred to as "mangrove" and the community as a whole should be referred to as the "mangal". This has acquired fairly wide acceptance among plant biogeographers (Mann 1982), but we still do not see it commonly in the

ecological literature (Snedaker and Lugo 1973; Lugo and Snedaker 1974) so we chose not to use this extra term in this report.

Nutrient transfer by movements of animals

The interactions between coral reefs and seagrass beds have been reviewed by Ogden and Zieman (1977) and Ogden and Gladfelter (1982). Nutrient transfer from seagrass beds to coral reefs occurs as a result of the foraging of fishes and invertebrates out onto the seagrass beds for food and the subsequent excretion or defecation on the coral reef by the fishes after returning for shelter. This input of nutrients to the coral reef ecosystem from nearby seagrass beds has been indicated by increased biomass of fish communities at reef margins bordering on seagrass beds and has been demonstrated by increased growth rates of corals in the immediate vicinity of daytime aggregations of fishes that have returned from nocturnal foraging in seagrass beds.

Randall (1963) and Ogden and Zieman (1977) observed that reefs near seagrass beds supported a larger biomass of reef fishes than did other reefs. They also noted that the increased biomass was made up largely of carnivorous fishes which exploit seagrass beds at night (pomadasyids, haemulids, lutjanids, holocentrids, apogonids, etc.). When Randall (1963) constructed an artificial reef of 800 construction blocks in a seagrass bed, the artificial reef was able to maintain a resident population of reef fishes with eleven times the biomass per unit area in comparison with comparable areas of natural fringing reefs. However, these observations and experimental results are not conclusively supportive of the influence of nutrient transfer because there are alternative explanations. One alternative explanation is "edge effect". The artificial reef may have been a smaller self-contained entity than the natural reefs. The relative abundance, biomass, or diversity of fishes between reefs may be partly a function of the ratio of border length to surface area of each reef. Further, any bordering area between different habitats might have a greater abundance, biomass, or diversity of animals than the average patch of either habitat. The observations at habitat borders and the artificial reef experiment provide interesting indications of the importance of nutrient transfer from seagrass beds to coral reefs, but these studies should be repeated more rigorously with controls for patch size and edge effect.

Of greater importance is to repeat these studies in the Pacific. Studies of interactions between coral reefs and seagrass beds have all been done in the Caribbean. To my knowledge, there is no indication in the literature to date which indicates that reef fishes are more abundant near seagrass beds in the Indo-Pacific as a result of nutrient transfer. In fact, to my knowledge, no documentation has been obtained in the Indo-Pacific of large-scale movements of reef fishes onto seagrass beds to forage for food.

It has been speculated that excretion and defecation on the reef by fishes that feed in seagrass beds may provide a significant input of nutrients into the coral reef ecosystem (Ogden and Zieman, 1977). The first, and so far only, direct correlative evidence for nutrient

transport substantial enough to affect the reef community is provided by
Meyer et al. (1983). They measured the growth rates of corals in areas
where schools of juvenile haemulid fishes ("grunts") rested during the
day, in areas where the haemulids were absent, and in areas in which the
haemulids were present during the first year, then experimentally removed
for the next eight months. During the first year of the study, two coral
heads (Porites furcata) near fish aggregations grew significantly faster
than did a coral head no more than 25 m away. Water samples were taken
within a resting school of haemulids in a coral head and near a head in
an adjacent area without the fish aggregation. A significantly greater
concentration of ammonium was found in fish aggregations. No differences
were found between the two areas in concentrations of molybdate-reactive
phosphorous. Sediment traps were also placed under a coral head with an
aggregation of fishes and under another head without an aggregation of
fishes. A significantly greater quantity of nitrogen and phosphorous in
addition to particles with significantly higher percentages of these
nutrients were collected from sediment traps under schools of fishes.
The results from the first year of the study thus indicated that juvenile
carnivorous fishes excrete enough ammonium and defecate enough particles
with nitrogen and phosphorous from seagrass beds to significantly affect
the coral reef community.

The conclusions of the first year of the study by Meyer et al. (1983)
were based on correlations between the locations of fish aggregations,
nutrient contents of water and sediment, and growth rates of coral. An
alternative explanation for this correlation could be that fishes
aggregated where corals grew faster because the presence of nutrients
from some source other than fishes was beneficial to both fishes and
corals. To test this alternative hypothesis, the fish aggregation of 304
juveniles was removed from one of the corals with a fish aggregation.
Results from this second set of tests did not support their original
hypothesis rigorously. There was no significant difference in growth of
corals with and without fish aggregations ($t_{[17]}$ = 1.36). The authors
said this was probably because of a decreased number of grunts (haemulid
fishes) over the coral with grunts, more squirrelfish over the coral
without grunts, and weather-related factors were obscuring the effect of
aggregations of grunts. Whatever the confounding factors were, the
experiment did not support conclusively the hypothesis of fish
aggregations in influencing the growth of the corals nearby. It would be
worthwhile to repeat the experiment in the Caribbean in order to clarify
the relative importance of the various factors in influencing the growth
of corals.

Assuming that fish which forage over seagrass beds at night and rest over
coral heads by day add a substantial input of nutrients to the reef
community and can significantly influence the growth of certain coral
heads in the Caribbean, we still cannot assume that this same
relationship will be found in the Pacific. Initial impressions of fish
community structure in the Pacific suggest that the interactions between
coral reefs and seagrass beds may be less substantive than in the
Caribbean. The aggregations of resting haemulids during the daytime on
reefs in the Caribbean are spectacular and appear frequently in travel
brochures and photographic books about Caribbean reefs. Although fishes
such as Gnathodentex, Monotaxis, holocentrids and apogonids may forage

out over seagrass beds then return to the reef for shelter, they do not appear to rest in such large aggregations as do haemulids in the Caribbean and so the influence of their nutrient transport might not be measurable. Whether the pattern observed in the Caribbean (Meyer et al. 1983) is also found in the Pacific is an important question. Is there a substantial number of fishes which forage over seagrass beds in the Pacific and return to coral reefs to rest? Does excretion from fishes in aggregations on reefs in the Pacific provide enough nutrients to increase significantly the growth of nearby corals?

Another form of nutrient transfer from seagrass beds to the coral reef might take place over a longer time frame as a result of seagrass beds functioning as nurseries for juvenile reef fishes. Juvenile Diodon, Mulloidichthys, Acanthurus, Halichoeres, holocentrids and lutjanids may settle from the plankton and complete early stages of growth on seagrass beds, eventually migrating to coral reefs as they become larger (Ogden and Zieman 1977).

Biological interactions between habitats

The influence of coral reef animals on the community structure of seagrass beds at the border of the two habitats was first described by Randall (1965) then studied extensively by Ogden (Ogden et al. 1973; Ogden 1976, 1980; Ogden and Zieman 1977; Ogden and Lobel 1978; Ogden and Gladfelter 1982). While nutrient transfer is essentially a one-way flow from seagrass to coral reef as a result of nocturnal foraging of juvenile carnivorous fishes, the majority of the effects of animal activities on community structure are in the opposite direction, from coral reef to seagrass beds, as a result of nocturnal foraging of urchins and diurnal foraging of herbivorous fishes (Ogden and Gladfelter 1982). Herbivorous fishes and urchins create "halos" (bands of bare sand or heavily grazed seagrass) around coral reefs where they border on seagrass beds in the Caribbean (Randall 1965; Ogden et al. 1973).

The biological factors that create halos were first suggested by Randall (1965) when he observed a halo forming around an artificial reef he created with construction blocks. Although the possibility of the halo being caused largely by changes in current patterns or other physical factors brought about by the presence of a large structure such as a natural or artificial reef was not controlled for in his study, Randall's observations of fish behavior and population growth on the artificial reef supported his hypothesis. Randall (1961) also constructed a large (1 x 1 x 1 yd) fish-exclusion cage to study the effects of grazing by fishes on the benthic community. A normal abundance of urchins (16 Diadema antillarum) was in the fish-exclusion cage. The algae within the cage increased greatly and the 16 Diadema rapidly increased in size by a factor of three, suggesting that grazing by fishes was the most influential factor in regulating the abundance of benthic macroflora in the tropics. Urchins apparently ate voraciously and grew rapidly but were unable to restrain the increase in algal abundance within the cage.

Odgen et al. (1973), on the other hand, presented a strong argument that urchins were more important than herbivorous fishes in the creation of

halos around reefs. In an elegant experiment (i.e., without the use of artificial materials such as cages), Ogden et al. (1973) removed over 7000 urchins from one patch reef and observed the rapid growth of benthic algae on formerly bare substrata on the patch reef. However, Ogden et al. (1973) and Ogden (1976) did comment that herbivorous fishes in the area of their studies were under intense fishing pressure and their abundances may be unnaturally low.

Hay (1981) and Hay et al. (1983) found that over 90% of the material grazed from Thalassia near coral reefs was taken by herbivorous fishes. Urchins removed less than 10%. In further work in widely scattered areas of the Caribbean, Hay (1984a, b) found that urchins were relatively influential on benthic plant communities in areas where fishing pressure by man was intensive and fishes were by far the most influential on benthic plant communities in more pristine or "natural" areas less heavily fished by man. Hay (1984a, b) concluded that much of the research on the influence of herbivores on benthic community structure in the Caribbean was done at marine laboratories in areas in which the resident scientists recognized severe over-fishing was occurring. Hay further warned that since much of the research in the literature on the effects of herbivores on shallow tropical marine communities was done in these overfished areas, we may have a misunderstanding of the functioning of these ecosystems because we assume these studies were done in communities in their near-to-natural states. Hay (1984a, b) conjectures that overfishing probably caused a drastic reduction in the abundances of predators of urchins (e.g., balistids) and so urchins increased in abundance in overfished areas by several orders of magnitude. It is interesting to note the comparative scarcity of urchins in Micronesia as compared to the Caribbean (Table 2). Perhaps Micronesia is still in a relatively natural state as compared to the Caribbean. A multitude of alternative hypotheses could be invoked to explain this difference between oceans in urchin abundances, however, e.g., current patterns, phytoplankton densities, etc.

It is possible that as fishing pressure increases further on coral reef fishes in the Pacific, echinoids will be somewhat released from predation pressure and then become more abundant and influential. One of many alternative possibilities is that the abundances of urchins in the Pacific result from sporadic recruitment success (Ebert 1983) rather than predation pressure on adult urchins.

In addition to clearing or drastically reducing the abundance of seagrass blades in halos in the seagrass beds at the boundary of reefs, the size and morphology of seagrass blades within the halo is also altered by the action of herbivores. Within halos, the blades of Thalassia "form a flat curl and tend to lie flat on the bottom" (Ogden and Zieman 1977:379).

Although the influence of herbivores from a coral reef on seagrass communities is well recognized, the influences of the physical factors such as currents and wave action having been altered by the presence of a coral reef are not precluded. Ogden and Gladfelter (in Ogden and Zieman 1977) showed that the physical factors of water currents and wave action were clearly involved in creating a halo 1 m wide around an artificial reef made of construction blocks at a depth of 12 m. However, in

Table 2. Comparison of abundances of regular urchins on overfished reefs in the Caribbean with fringing reefs in Micronesia.

A. Abundances of regular urchins on patch reefs in the Caribbean (from Hay in prep.).

Urchin Density m^{-2}	Genus	Study Site	References
71	Diadema	Discovery Bay	Sammarco 1980
100	"all species"	Discovery Bay	Sammarco 1980
"as high as 73"	Diadema	Discovery Bay	Lawrence and Sammarco 1981
6-13	Diadema	Discovery Bay	Williams 1981
10-16	Echinometra	Discovery Bay	Williams 1981
5-10	Diadema	St. Croix	Ogden et al.1973
"about 10"	Diadema	St. Croix	Sammarco et al. 1974

B. Abundances of regular urchins on fringing reefs of Micronesia.

Urchin Density m^{-2}	Genus	Study Site	Sample Size	References
.01	Diadeam savignyi	Agana Bay (Guam)	3990 m^2	Randall 1978
.001	Echinothrix diadema			
.001	Tripneustes gratilla			
.002	Echinometra mathaei			
.001	Diadema savignyi	Tumon Bay (Guam)	3140 m^2	Randall 1978
.0035	Echinothrix diadema			
.04	Echinometra mathaei			
.053	Diadema savignyi	Arakabesang Island (Belau)		Randall et al. 1978
.005	Echinothrix diadema			
.25	Echinometra mathaei			
0	*	Malakal Island (Belau)	1020 m^2	Birkeland et al. 1976

* No echinoids in quadrats, although 7 species of asteroids, 5 species of holothurians, and 11 species of crinoids were present.

slightly deeper water (15 m), the currents and waves were not effective enough to create a halo; algae and grazed seagrasses grew right up to the base of the reef at 15 m (Ogden and Zieman 1977).

I have not found any direct evidence in the literature for the influence of herbivores in creating halos in seagrass beds in the tropical Pacific. Halos do exist in seagrass beds in the Pacific at the boundaries to patch reefs, but ripples and excavations in the sand in the halo at the base of the reef made the influence of currents and waves appear to be a more attractive explanation for the halo than the influence of herbivores.

Echinoids are generally less common in the Pacific, at least in Micronesia, than in the Caribbean (Table 2). Whether herbivores from coral reefs have a significant effect on the formation of halos, the morphology, size distributions, and abundances of seagrasses and/or the species composition of the associated algal communities in seagrass beds has not been documented to any extent in the Pacific. There may be significant qualitative differences between the Pacific and the Caribbean in the nature of interactions between seagrass beds and coral reefs and any research on this matter would be worthwhile.

While the transfer of nutrients is almost entirely from the seagrass bed to the coral reef (by urchins and carnivorous or omnivorous fishes that forage from the reef to the seagrass bed at night and by herbivorous fishes that forage by day), the effects of interactions on community structure are almost entirely in the opposite direction, from the coral reef to the seagrass bed by herbivorous fishes and urchins (Ogden and Gladfelter 1982). I have found no substantive evidence for interactions of this nature between mangroves and seagrass beds or between mangroves and coral reefs. Interactions between mangroves and the other two ecosystems appear to be mainly through alteration of the physical environment.

Another form of interaction between coastal habitats occurs when one habitat serves as the nursery for a species which resides in another habitat as an adult. Ogden and Zieman (1977) stated that seagrass beds serve as nurseries for juvenile Diodon, Holocentrus, Ocyurus, Acanthurus, Mulloidichthys, and Halichoeres which apparently settle from the plankton into seagrass beds, spend time in seagrass beds growing as juveniles, then later take up residence on coral reefs. Ogden and Zieman (1977) report that Diodon juveniles are observed to arrive between June 15 and July 15 each year (for at least 3 years previous to 1977) as dense schools of thousands that presumably settle from the plankton. Gladfelter (in Ogden and Zieman 1977) says the schools are visible from an airplane as large dark spots.

Snappers (Lutjanidae), grunts (Haemulidae), and the great barracuda (Sphyraena barracuda) initially recruit to seagrass beds and mangroves. Snappers are particularly dependent on mangroves as a nursery. The great barracuda spends its first year in seagrass beds and its second summer among the roots in the mangrove swamp (de Sylva 1963). It is interesting to note that Sphyraena barracuda and the reef squid Sepioteuthis are circumtropical except for the Pacific coast of the Americas. Seagrass beds are essentially nonexistent along the Pacific coast of the tropics

in America. Perhaps the absence of S. barracuda and Sepioteuthis is a result of the lack of a suitable nursery.

Seagrass beds and mangroves have also long been recognized as important nursery areas for commercial, sport, and bait fishes and for commercial shrimp and spiny lobster (Kutkuhn 1966; Clark 1971; Sastrakusumah 1971; Young and Kirkman 1975; Ogden and Gladfelter 1982). Seagrass beds and mangroves are presumed to serve as nurseries largely because of the shelter provided to small fishes and crustaceans by the extensive field of grass blades or by the complex maze of prop roots. Seagrass beds and mangroves are also richly endowed with a supply of organic detrital materials which serve as a food supply for juveniles. As the fishes and crustaceans grow, the refuge in hiding becomes less effective in seagrass beds and among the roots of mangroves and so they tend to school and eventually move into their respective adult habitats. As Ogden and Gladfelter (1982) point out, seagrass meadows and mangrove regions are excellent fishing areas for tarpon, snook, and other large predatory fishes which roam the habitats in search of juvenile fishes to eat.

The role of nurseries in ecosystem interactions does not fit conveniently into the paradigm of our section headings. If one habitat functions as a nursery for another, then there is a slight nutrient transport from one habitat to the other as the organism moves and takes up residence in the new habitat. There is also an interaction which affects community structure in that the adults of certain species might not be as abundant or even present in the habitat in which they are found if the habitat which serves as a nursery were not nearby to facilitate successful recruitment.

Although seagrass beds and mangrove swamps have been observed to serve as nurseries for several species of juvenile reef fishes, we actually have no direct evidence that the coral reef fish community structure would be any different if these nursery areas were not nearby. While Randall (1963) and Ogden and Zieman (1977) observed that the reef near seagrass beds supported a larger biomass of fishes than did areas on similar reefs away from seagrass beds, they attributed this to be a result of nutrient flow from the seagrass bed to the reef rather than a result of facilitation of recruitment to the coral reef fish community by the influence of nearby seagrass beds as nurseries. There still remains the opportunity for someone to obtain survey or experimental information to resolve the question as to whether or not nearby nursery areas actually have a significant effect on the fish community structure of coral reefs. Are coral reefs separated from mangrove swamps and seagrass beds significantly different in fish community structure from those bordering on mangrove swamps or seagrass beds? If these differences exist, are they a result of species interactions or a result of increased nutrient and energy input?

Physical interactions between habitats

Interactions between coastal ecosystems might well be more a result of their respective modifications of the physical environment and their morphological characteristics than of their contributions to primary

production or nutrients or to interactions between their component species. Coral reefs, mangroves, and seagrass beds all form structures that influence water movements in a manner that stabilizes the physical environment. All three ecosystems produce sediment and, as a result of their modification of water movements, all three ecosystems retain sediments. The role of seagrass beds and mangroves as nursery areas may be more a result of the habitat morphology than productivity because the primary production that goes directly into the herbivore food chain may be production from epiphytic algae which use the seagrasses and mangroves as substrata rather than from the production of the seagrasses and mangroves themselves.

Coral reefs form barriers that dissipate wave energy. Lagoons would not exist without coral reefs. Mangroves and tropical seagrass beds are nearly always found in areas with reduced wave energy. Mangrove seeds have been found to attach and take root where they would not have otherwise because of the reduction in wave action brought about by small, stone, fish trap weirs (Saenger and Hopkins 1975). If mangroves have been able to take root where they would not have otherwise because of changes in water movement brought about by an artisanal, stone, fish weir, then it seems quite possible that coral reefs allow some mangroves to exist where they would not have otherwise by forming barriers which dissipate wave energy. By forming lagoons, coral reefs allow the existence of seagrass beds in some areas where they would not otherwise exist. However, mangroves and seagrass beds also exist in areas away from coral reefs, in natural harbors or in the lees of points of land.

Mangrove forests also occlude and absorb terrestrial freshwater runoff and thereby buffer large salinity changes in coastal waters. Both mangrove forests and seagrass beds trap and stabilize sediments, forming rich depositional basins for sediments and reducing the sediment load on coastal areas. Coral reefs produce calcareous sediments which accumulate in the lee of reefs. Mangroves and seagrass beds produce sediments by depositing leaves and blades. Epiphytic organisms on the prop roots and blades and infaunal organisms in the sediments also produce sediments.

All three ecosystems influence each other favorably by stabilizing the physical environment. Coral reefs, mangrove forests, and seagrass beds all stabilize the physical environment by dissipating wave action (mostly by coral reefs), buffering salinity changes (mostly by mangroves), and by stabilizing sediments. All three ecosystems also produce sediments.

Effects of land mass and water movement patterns

The ecological interactions between coral reefs, seagrass beds, and mangroves are complex and academically interesting. At some locations in the Caribbean, the effects of these interactions are measurable as documented in the previous sections. However, coral reefs can develop fully and survive in the absence of nearby seagrass beds or mangroves. Likewise, seagrass beds and mangroves can develop and survive away from coral reefs and away from each other. Therefore, interactions between coral reefs, seagrass beds, and mangroves are not always completely

necessary for the establishment or maintenance of any of the systems. It may be that situations exist in which seagrass or mangroves would not be present without the protection by the coral reef against wave action but this has not been documented in the Pacific.

In general, interactions between coastal ecosystems are of less importance to the development and productivity of these ecosystems than are the influences of the characteristics of coastal terrain, topography, substratum, water current patterns and rivers. These are the factors more important to understand when attempting to make practical decisions for coastal zone management.

Chemical nutrients, especially nitrates and phosphates, are of particular importance in influencing primary productivity in shallow tropical coastal ecosystems. For example, although mangrove forests rank among the most productive of the world's ecosystems (Table 1), this high productivity depends on external sources of nutrient. Productive mangrove forests are found in river basins or floodplains near the coast, on the protected fringes of estuaries, or generally on coasts that are protected from wave action and supplied with nutrient runoff. Mangroves also live on sand bars, low islands (Lugo et al. 1973a), flat coastal fringes with no obvious external sources of nutrients (Lugo and Snedaker 1974), and on the coasts of deserts (Dor et al. 1977). In areas such as these, however, the mangroves were in the form of a scrub forest and productivity was about an order of magnitude lower than in areas with external sources of nutrient input (see Tables 1 and 2 in Lugo and Snedaker 1974). Computer simulations of the functioning of mangrove ecosystems demonstrated the dependency of these ecosystems on terrestrial nutrient runoff (Lugo et al. 1973b). Descriptive surveys by Davis (1940), MacNae (1967), Walsh (1967), and Craighead (1971) all indicated that the most "productive" (large and "vigorous") mangrove forests were always associated with river basins which undoubtedly had considerable nutrient input.

In the analysis of mangrove ecosystems (Lugo et al. 1973b) and in categorizing mangrove stands into distinctive physiognomic patterns beyond considerations of species composition (Lugo and Snedaker 1974), the deterministic factors in the structure and function of mangrove ecosystems were found to be location with respect to the coastline, topographic irregularities and the total area uniformly covered with mangroves, and the nature of water movements in terms of terrestrial runoff and drainage and tidal patterns.

In reviewing human activities that are harmful to seagrass communities in estuarine and coastal ecosystems, Thayer et al. (1975) listed as particularly important those human activities that changed water movement patterns and altered the nature of the shoreline, e.g., dredging and other disturbances of bottom sediments, clearing of lands for agriculture and channelling of streams which increase rates of erosion and inputs of sediments, and stream diversions, dam construction and irrigation projects. Likewise, sedimentation resulting from bad land management has been recognized as the most significant pollution threat to coral reef communities (Johannes 1975). The rapid destruction of coral reef communities and associated reef organisms by sedimentation has been

particularly prevalent in developing areas where land is cleared for agricultural development (Moberly 1963; Fairbridge and Teichert 1948) and for housing and road construction (Fan and Burnett 1969; Van Eepoel and Grigg 1970; Van Eepoel et al. 1971; Maragos 1972; DiSalvo 1972; Wells et al. 1973; Dodge et al. 1974; Johannes 1975).

Coral reefs are the most susceptible of the coastal ecosystems we are comparing to damaging effects of siltation and terrestrial runoff of nutrients. Seagrasses have a greater tolerance of these factors and at low levels may even benefit from a slight increase. The mangrove ecosystem is the most tolerant and generally benefits from terrestrial runoff. It is clear that to make wise and rational decisions in the management of coastal ecosystems and resources, we should pay particular attention to understanding the influences of land masses, terrestrial input of materials and patterns of water movement on the nearshore coastal ecosystems.

The reason that chemical nutrients are generally sparse in tropical ocean waters is because phytoplankton and benthic algae take up and generally deplete the nutrients in the photic zone and the reservoir of nutrients in the water column below the photic zone is not generally available because the tropical seas are thermally stratified throughout the year. Despite these restrictions on nutrient availability, shallow tropical benthic communities are very productive (Table 1). The productivity of ocean waters is substantially increased near land masses (Doty and Oguri 1956; Jones 1962; Sorokin 1973; Gilmartin and Revelante 1974). This "island mass effect" must result ultimately from either an input or a prolonged retention of nutrients. There are at least nine mechanisms by which the presence of a land mass could produce an increase in input or retention of nutrients: terrestrial runoff, groundwater seepage, nitrogen fixation by benthic organisms, benthic nutrient regeneration, secondary productivity, internal waves, upwelling, eddying, and increased residence time of water. There may be additional ways in which the nature of the nearshore landmass can effect the productivity of nearshore habitats. How these factors interact with coral reef, seagrass, and mangrove ecosystems is of primary importance in understanding and managing the ecosystems.

Evidence for the importance of terrestrial runoff for nearshore fisheries can be found in Chidambaram and Menon (1945), Murty and Edleman (1966), Aleem (1972), Sutcliffe (1972, 1973). The effects of terrestrial runoff of nutrients on aspects of coral reef communities is discussed in Marsh (1977) and Birkeland (1982). An example of the influence of groundwater is presented in FitzGerald (1978). While influential groundwater seepage and terrestrial nutrient runoff may occur only at high islands, nitrogen fixation by blue-green algae is operational at both high islands and atolls. The importance of benthic nutrient regeneration and the magnitude of secondary productivity are presented in Johannes (1967), Johannes and Gerber (1974), Gerber and Marshall (1974 a,b), Sournia and Ricard (1976b), Sournia (1977), Scott and Jitts (1977), Lewis (1982), and Kropp and Birkeland (1982).

Internal waves, eddying, upwelling, and increased residence time of water are all influences on productivity that are brought about by alterations

of patterns of water movement which result from land masses obstructing uniform current flow. These alterations are caused by both high islands and atolls. Finn Sander (1973, 1981) showed that at Barbados, internal waves were far more influential to phytoplankton productivity than were terrestrial runoff or benthic-pelagic coupling of nutrient regeneration. Eddies that form in the wake of land masses or in the lees of points of land can aggregate plankton into concentrations 40 times greater than in adjacent water (Alldredge and Hamner 1980), can facilitate local recruitment of littoral animals with long pelagic larval stages (Boden 1952; Emery 1972), and can maintain offshore populations of coastal planktonic organisms (Emery 1972). This concentration of larval organisms may be particularly influential in attracting pelagic billfishes and tunas to land masses, a process which increases the pelagic fisheries production in the vicinity of land masses.

Upwelling is generally brought about by currents turning offshore or by winds blowing offshore of continental land masses or by currents being shifted upward over a sill. These happenings do not usually occur at oceanic high islands or atolls and so upwelling is not as prevalent a phenomenon at mid-Pacific islands as internal waves might be.

The final mechanism by which land masses enhance the productivity of a region is by enclosing water or causing water to eddy and thereby increasing the cohesion and the residence time of the planktonic community. The incubator effect of cohesion of water masses or relatively long residence time of water may explain some otherwise confusing anomalies in tropical marine systems. For example, an upwelling of nutrients occurs off southeast Taiwan in the Kuroshio current, yet the fisheries are rich off Okinawa to the north. This may be because although the productivity of phytoplankton is high off southeast Taiwan, the standing crop of phytoplankton is still too low to support a fisheries. The water mass remains fairly cohesive as the Kuroshio Current flows north. By the time the water mass reaches Okinawa, the phytoplankton cells have divided enough times to build up a large enough standing crop to support a fisheries.

The Acanthaster outbreaks on Guam originated at the northern ends of both Tumon and Agana bays in both 1968 and 1979, but not at other bays. At the northern ends of these two bays, the water has a relatively long residence time, but the sediment plume is apparently carried out of the other bays and dispersed into the open sea.

This same process may explain why Acanthaster planci outbreaks have been a chronic problem on Ponape but have apparently not occurred on Kosrae. While Kosrae and Ponape are the two high islands which have the greatest potential for phytoplankton blooms of all the Carolines (Cowan and Clayshulte 1980), the waters around Ponape are contained in a lagoon surrounded by a barrier reef while the waters around Kosrae, which is surrounded by a fringing reef, are carried away and dispersed by longshore currents. At Ponape, the lagoon may act as an incubator with water in the lagoon having a long enough residence time to allow phytoplankton to build up a standing crop large enough to support larvae of A. planci. Although the waters off Kosrae contain enough nutrients to allow phytoplankton blooms, the waters move away from the island before

the phytoplankton have undergone enough cell divisions to build up a standing crop sufficient enough to support larvae of A. planci. The dispersion of water could also thin out the concentration of A. planci larvae as well as the food supply of the larvae. Studies of fish larvae indicate that upwelling of nutrient-rich water leads to phytoplankton blooms, but the movement of the upwelling waters disperse food organisms so that the food particles are too low in concentration to support larval anchovy growth (Smith and Lasker 1978).

LAGOONS

By enclosing water in a lagoon, the productivity of an otherwise oligotrophic body of water might be enhanced because of the increased residence time or cohesiveness of the water mass. A particularly striking example of biomass being supported under extremely oligotrophic conditions can be observed in the enclosed lagoons of the Tuamotus. Takapoto is a raised atoll with an enclosed lagoon that is approximately 16 km long, 4.5 km wide and averages 23 m deep. This $1.6 \times 10^9 m^3$ (roughly) of water is connected to the sea by a couple of hoas that a person can easily wade across. Therefore the lagoon must be one of the most self-contained of coral reef systems with waters of particularly long residence time. Sournia and Ricard (1975) found the oceanic waters surrounding Takapoto to have low nutrient (0.36 μ at g ℓ^{-1} NO_3-N; 0.26 μ at g ℓ^{-1} PO_4-P) and chlorophyll a(0.14 μg ℓ^{-1}) contents. They also found that the waters within the enclosed lagoon have even lower nutrients (0.22 μ at g ℓ^{-1} NO_3-N; 0.12 μ at g ℓ^{-1} PO_4-P) but much higher chlorophyll a (0.46 μg ℓ^{-1}) contents. Yet the main industry of Takapoto involves the production of pearls by filter-feeding bivalves. Tons of bivalves (Pinctada, Arca, Tridacna) live in the lagoon despite the water being very sparse in nutrients. It may be that the enclosed lagoonal system is so self-contained that the nutrients are quickly recycled and contained in the biomass of the bivalves and fishes. The main effect of an atoll comes from its configuration which generally increases the residence time of water.

The way in which a lagoon functions leads us to a conclusion concerning a rational method of resource management in lagoons. Like the tropical rainforests, coral reef ecosystems may be able to withstand pruning and recycling but not harvesting and exporting because most of the nutrients are recycled and not imported. The removal of living materials from a coral reef community on a large scale might cause depletion at a rate at which the system would be unable to replenish and maintain itself. At Takapoto, the oysters are harvested but only the pearls are exported, the meat is eventually recycled into the lagoon. If we scrape a temperate shoreline of barnacles, we would expect the barnacles to return in a year or so; barnacles feed on imported suspended material. If we dredge or dynamite a reef, we might expect recovery to take a very great time because the nutrients have been lost and a substantial time may be required for the necessary processes to build up another stockpile.

ESTUARIES

Like lagoons, estuaries are not actually the entities that are productive in the sense that coral reefs, seagrass beds, and mangrove forests are primary producers, but they are situations with topographic or morphological features that bring about interactions of a particular nature. Estuaries are defined as partially enclosed bodies of water which have free connection with the ocean and within which the seawater is measurably diluted with freshwater from terrestrial runoff (Pritchard 1967). This dilution with fresh water, usually from a river, brings about increased productivity by two mechanisms: by input of terrestrial nutrients and by river waters driving upwelling of benthic nutrients by pushing surface waters away from shore, which in turn require a replacement of surface waters by an upwelling of nutrient-rich deeper waters. River runoff is a major stimulant to primary production by phytoplankton (Mann 1982).

In a manner similar to lagoons, estuaries act as nutrient traps. Because of their semiclosed nature, estuaries also allow the accumulation of very fine silt from river discharge and terrestrial runoff. Salt-marshes (in temperate regions) can develop intertidally in estuaries and seagrasses can develop both intertidally and subtidally in estuaries. Mangrove forests do best in estuarine conditions because estuaries are characterized by both shelter from wave action and by nutrient input from river outflow and terrestrial runoff. The optimal conditions facilitate maximum production from mangroves, seagrasses, and salt-marsh vegetation. The litter from these vascular plants often accumulates in the sheltered waters of the estuary and decays slowly but constantly. At the same time, the river outflow stimulates high levels of productivity of phytoplankton. This high rate of primary productivity of phytoplankton, massive production and accumulation of detrital materials by vascular plants, shelter in the form of three-dimensional refuge among seagrass blades, mangrove roots, or salt-marsh grasses, and protection from wave action combine to make estuaries an effective nursery area for fishes and crustaceans.

Stabilizing effects of coastal ecosystems

As discussed above, the physical structure of coastal ecosystems has a stabilizing effect on the physical environment. Coral reefs dissipate the impact of waves on coastal areas and create lagoons and protected waters which are favorable for the growth of seagrasses and mangroves. Mangroves also modify the effects of typhoons on coastal areas. Seagrass beds and mangrove forests trap and bind sediments and thereby reduce the sediment load in the water column. Mangroves occlude freshwater runoff from the land mass which stabilizes the salinity of coastal areas.

With the production of slowly decomposing detrital materials, marine vascular plants have a stabilizing effect on the detrital food chain. As pointed out by Harrison and Mann (1975), seagrass leaves decompose so slowly that they accumulate in a large reservoir of decomposing organic matter. When there was an extensive mortality of seagrass (Zostera marina) in the North Atlantic in the 1930s, the direct consumers of

seagrass virtually disappeared (e.g., the black brant, cf. Cottam 1934). However, the fishes and invertebrates generally did not decrease in abundance during the die-off of Zostera. Harrison and Mann (1975) suggested that this was because the accumulated detrital reserve of seagrasses decomposes so slowly that the foods and nutrients enter the food chain by decomposition at a fairly constant rate, relatively unaffected by any large year-to-year variations in productivity. In this way vascular plants of coastal ecosystems stabilize some food chains as well as some aspects of the physical environment.

Assimilation of vascular plant material by marine invertebrates and fishes

Detrital material from mangroves and seagrasses are often found in the stomachs of marine invertebrates and fishes (Gunter 1945; Darnell 1958, 1961; Springer and Woodburn 1960; Hansen 1969; Odum and Heald 1972; Carr and Adams 1973). These observations are used as documentation of the importance of mangroves and seagrasses for commercial and sport fisheries (Skud and Wilson 1960; Darnell 1967; Sykes and Finucane 1966; Smith et al. 1966; Odum and de la Cruz 1967; Wood et al. 1969; Cronin and Mansueti 1971). While mangroves and seagrasses are probably important to fisheries as providers of structural shelter and refuges for juveniles from predators, as substrata for epiphytic algae and bacteria which in turn contribute substantially to the food web, and as sediment stabilizers, there is evidence that calls to question whether much of the calories and nutrients in vascular plant material in the guts of invertebrates and fishes is actually being assimilated. Although mangrove forests and seagrass beds are among the most productive ecosystems in the world in terms of gross primary productivity (Ryther 1963; McRoy and McMillian 1977; cf. Table 1), it appears that over 90% of the net productivity is going into the detrital food web (Harrison and Mann 1975; Kirkman and Reid 1979) and less than 10% into direct herbivory, although a notable amount passes through the guts of marine invertebrates and fishes.

Even decomposers apparently process vascular plant material more slowly than they process algal or animal material. In temperate Atlantic waters, the kelp Laminaria longicruris decays rapidly and makes a quick substantial contribution to the detrital food web (Mann 1972a, b) while the eelgrass Zostera marina decays slowly, with only 35% loss of dry weight after 100 days at 20¼C in the laboratory in the presence of abundant microorganisms and nutrients (Harrison and Mann 1975). Of this 35%, 82% was from leaching and occurred even under sterile conditions. Coastal sediments in eelgrass beds have accumulations of slowly decomposing eelgrass fragments as a reserve of organic matter which slowly becomes available for benthic consumers. In estuarine creeks of Georgia, over 90% of the detritus is from the marsh grass Spartina (Odum and de la Cruz, 1967). However, leaves of Spartina may enter the detritus slowly as they may die on the stalk and remain attached upright for long periods of time (Lopez et al. 1977). Similarly, the distal portions of tropical seagrasses such as Thalassia remain attached upright long after they become senescent. The great amount of Thalassia blades

lying in the deep (3,000 - 5,000 m) sea floor 500 to 1,000 km from the source Thalassia beds (Zieman et al. 1979) is an indication of a slow process of decomposition.

Cundell et al. (1979) found that microbial populations would not begin to build up on senescent mangrove leaves until the tannins leached out into the water. Therefore it was about 14 to 28 days before decomposition really began. After 70 days (an additional 42 to 56 days after the tannins leech out), the carbon content of decomposing leaves decreased from 46.2 to 36.2%. Smayda (1970) and Kutner (1975) found that the tannins released into the water column from mangrove leaves inhibited the growth of planktonic diatoms in or near mangrove swamps.

Since mangrove, seagrass, and Spartina leaves appear relatively refractory to decomposition, a question yet unanswered is how much material from these sources of primary production actually enters the detrital food web. In order to assess the degree to which materials are consumed and enter the food web, a method has recently been developed to allow examination of the flow of carbon in natural ecosystems. The method involves the determination of stable carbon isotope $^{13}C:^{12}C$ ratios in natural materials such as plant and animal tissues (Parker 1964; Smith and Epstein 1971; Land et al. 1975; Haines 1976; Fry et al. 1978; Thayer et al. 1978; McConnaughey and McRoy 1979 a, b; Hackney and Haines 1980). Plant species differ in their $^{13}C:^{12}C$ ratios in a manner which depends upon which pathway of photosynthetic fixation of CO_2 is used (Park and Epstein 1960; Christeller et al. 1976). Plants using the C_4 photosynthesis pathway tend to incorporate a greater proportion of ^{13}C isotope and plants using the C_3 pathway incorporate a greater proportion of ^{12}C isotope. Animals appear to have about the same carbon isotope ratio in their body tissues as in their diets. This has been shown in the laboratory by raising various species of animals on foods of various $^{13}C:^{12}C$ ratios (Fry 1977). The milk and hair from cows grazing in meadows of C_3 or C_4 plants have carbon isotope ratios that correspond to these dietary difference (Minson et al. 1975).

This method has also proven successful in field studies, both marine and terrestrial. Haines (1976) studied the carbon isotope ratios in tissues of the fiddler crab Uca pugnax and the plant communities in 9 areas of a salt marsh on the Georgia coast. Although U. pugnax is detritivore, the carbon isotope ratios of the fiddler crabs were linearly related to those of the plant communities in the same areas. Fry et al. (1978) examined the carbon isotope ratios in the tissues of 25 species of grasshoppers and 61 species of plants in a west Texas study site and found that the carbon isotope ratios in the tissues of grasshoppers was essentially the same as that in their diets (slope was 0.97 [near 1] and the correlation coefficient was 0.96). Land et al. (1975) examined the variation with depth of proportions of zooxanthellae products and zooplankton in the diets of corals by comparing carbon isotope ratios of coral tissues with those of zooxanthellae and plankton.

Although this carbon isotope ratio method gives only general rather than specific sources of fixed carbon, the method has the advantages of giving a time-integrated indication of which source provided the carbon which

was actually assimilated by the animals and also of giving the actual initial source of carbon regardless of the pathways through the food web.

Rodelli et al. (1984) analyzed the stable carbon isotope ratios for over 600 animals from Malaysian mangrove swamps, coastal inlets, and offshore areas. They found that carbon from mangrove trees was about equally important as carbon from algal sources in the diets of organisms from mangrove swamps. However, animals from collections made offshore showed almost no carbon from mangrove trees to be assimilated into their tissues although mangrove carbon was abundant as detritus at these site. Rodelli et al. (1984) concluded that fragments remaining intact offshore were apparently quite refractory to metabolism.

Mangrove and seagrass leaves also appeared to be generally resistant to digestion by marine invertebrates even within the habitats (Rodelli et al. 1984). The stable carbon isotope ratio demonstrated that suspension-feeders (9 species of barnacles and bivalves) living on the prop-roots or low on the trunks of mangrove trees filtered water that contained a substantial amount of mangrove materials while the tissues of the suspension-feeders were generated mostly from algal sources. The tissues of snails that preyed upon barnacles and mussels (Thais and Murex) also was derived ultimately from algal sources two trophic levels below. Alpheus sp. and Upogebia sp. lived in the mud around the roots of mangrove trees, but the carbon isotope ratios indicated that they were either selectively feeding or selectively assimilating algal materials from the sediment (Rodelli et al. 1984).

In mangrove swamps, shrimps, crabs, and fishes generally assimilated approximately equal proportions of foods from mangrove and algal sources while offshore populations only assimilated algal derived carbon (Rodelli et al. 1984). Note that we are discussing what is being assimilated into the tissues, not what is being consumed. Much of the detrital material available in the sediments and water column both offshore and in the mangrove swamp was derived from mangrove sources. It is most likely that much of the sediment consumed by crabs and shrimp living on mud around roots of mangrove trees and of the water filtered by suspension- feeders attached to roots of mangrove trees contains a substantial amount of material of mangrove origin. Apparently material of mangrove origin is usually resistant to the metabolic processes of marine invertebrates and marine fishes so these animals more easily assimilate material of algal origin. Since proportionately less of the available material of mangrove origin is assimilated by offshore populations of shrimp, crabs, or fishes, Rodelli et al. (1984) were led to speculate that mangrove materials become even more resistant with time during the offshore drift or transport. Studies by Golley et al. (1962) and Wiebe and Pomeroy (1972) also suggest that mangrove and Spartina material was metabolically refractory. Haines (1979) and Haines and Montague (1979) also used the stable carbon isotope method to trace the ultimate source of photosynthetic production in Spartina marshes. They found that Spartina was less important and planktonic and benthic algae were far more important than was previously thought. While insects (note that they had evolved in terrestrial habitats) and marsh snails had ^{13}C values similar to vascular plants, mud-snails, bivalves, and crabs had $^{13}C/^{12}C$ ratios similar to planktonic and benthic algae.

Fry and Parker (1979), Fry et al. (1982), and Fry et al. (1983) also measured stable carbon isotope ratios in 340, 140, and 250 samples to determine the relative importance of planktonic and benthic plants to the materials being assimilated by the animals. They showed that in nearshore habitats, benthic plants are more important in the diet than plankton, but they were not able to distinguish between the contributions of vascular plants and algae. However, Thayer et al. (1978) found that organisms commonly found on seagrass blades actually fed mainly on the epibiota growing on the blades while the rest of the animals in the area appeared linked mainly to the plankton-based food web.

Fenchel (1970) found that the detritus-consuming amphipod Parhyella whelpleyi fed on detritus particles and on its own fecal material but actually assimilated only the microorganisms on the surface of the detrital material; the dead vascular plant (Thalassia testudinum) material passed on through the amphipod undigested.

Randall (1967) found that seagrasses comprised 81% by volume of the stomach contents of the halfbeak Hemiramphus brasiliensis. Similarly, Bell et al. (1978) found that three species of monacanthid fishes in seagrass beds consumed considerable amounts of seagrasses. The stomach contents of Meuschenia freycineti was 65% seagrass. However, Bell et al. (1978) found only the epiphytic algae and the encrusting animals were actually being digested.

While it is apparent that the majority of decomposers and herbivorous invertebrates or fishes do not easily digest or assimilate vascular plant material, there are exceptions. The gastropods Ellobium sp. and Cassidula sp. were exceptional invertebrates in that carbon isotope ratios in their tissues indicated that a substantial portion of their diets consisted of mangrove materials (Rodelli et al. 1984). This observation is corroborated in the review of mangrove biology by MacNae (1968) in which he describes the grazing of mangrove leaf litter by Ellobium and Crassidula as responsible for part of the breakdown of fallen leaves to humus.

The mysid shrimp Mysis stenolepis, is an abundant detritivore in seagrass beds and it has been indicated by ^{14}C studies that M. stenolepis can assimilate structural cellulose from seagrass with 40% efficiency (Foulds and Mann 1978). When the mysids were treated with antibiotics, they lost the ability to digest cellulose. They regained the ability after being fed fresh mysid guts. This implied that M. stenolepis carries a microflora in its gut which is capable of digesting cellulose (Mann 1982). However, Frieson (1981, cited in Mann 1982) failed to find a microflora in the gut which suggests that M. stenolepis may itself produce the cellulase enzyme.

Tannins inhibit the assimilation of mangrove material

The slow rate by which detrital materials from vascular plants enter the marine food web is probably partially a result of the tough structural

chemicals such as cellulose in vascular plants. The leaves of mangroves may be particularly difficult to decompose or digest because of tannins. Tannins are prevalent in mangrove leaves and are the basis of the economic value of mangroves to the leather industry (Swain 1965; Haslam 1979). Tannins are known to form complexes with protein and to inhibit the action of enzymes (Pridham 1963; Goldstein and Swain 1965). By this mechanism, tannins are known to inhibit the ability of microbes to break down leaves (Handley 1961). Tannins inhibit the growth of fungi (Williams 1963) and the transmission of viruses (Bawden and Kleczkowski 1945; Cadman 1960). The colonization and microbial degradation of mangrove leaves in seawater is delayed by the presence of tannins in the leaves and begins after the tannins are leached out (Benoit and Starkey 1968; Cundell et al. 1979).

The tannins released from decaying leaves and dissolved in the water can inhibit the growth of diatoms and presumably other phytoplankters and thereby reduce the phytoplankton productivity in waters in or near mangrove swamps (Smayda 1970; Kutner 1975).

Tannin-containing plants are also repellant to herbivores such as snails (Haberlandt 1914), locusts (Shpan-Gabrielith 1965), and sheep (Wilkins et al 1953), and are actually toxic to cattle, goats, sheep, rabbits, rats and chickens (Dollahite et al. 1962; Kingsbury 1964; Glick and Joslyn 1966; Vohra, Kratzer, and Joslyn 1966). This toxic effect of tannins to herbivores is probably largely a result of formation of tannin-protein complexes in the gastrointestinal tract which results in a reduction of nitrogen assimilation. The proportion of dietary nitrogen that was egested increased by a factor of six compared to controls when 8% tannic acid was incorporated into the diet of rats (Glick and Joslyn 1966).

The inhibition of growth of moth larvae by tannins was also suggested to be the result of the formation of relatively indigestible complexes of tannin with available protein, thus reducing dietary nitrogen assimilation (Feeny 1969). Casein, when complexed with oak leaf tannin, is completely protected from hydrolysis by trypsin at pH 7.6 (Feeny 1970). As little as 1% fresh weight of tannin in the diet of moth larvae causes a significant reduction in larval growth rate and pupal weight (Feeny 1968). The degree of complex formation depends on the ratio of protein to tannin concentrations and on the time of contact between protein and tannin (Feeny 1969). In oak leaves late in the season, for example, the ratio of tannin to protein is about 1:3 and a caterpillar would have to ingest about 4 times the amount of leaf material that it would have had to if there were no tannins in order to obtain adequate nitrogen (Feeny 1970).

Plants store their tannins in vacuoles, separated from the rest of the plant cell by a membrane (Nierenstein 1934). If the membrane of the vacuole is punctured, the tannins can be released and bring about precipitation of protoplasmic proteins in the plant cell (Doby 1965). The synthesis of tannins is achieved through a complex pathway that requires a large quantity of sugars for both energy and structure (Haslam 1966; Feeny 1970; Zucker 1983). The effects of tannins in reducing metabolic efficiency of animals, fungi, and bacteria result from the general formation of hydrogen bonds, and perhaps covalent bonds, with

proteins (Haslam 1966). Because of the generalized nature of this interaction between tannins and proteins, it is improbable for insects to evolve specific detoxification mechanisms for tannins in the manner in which they have successfully adapted to other chemicals of plant defense such as alkaloids (Hodgson et al. 1965; Feeny 1976). Although many insects can eat oak leaves, they are generally not able to cope with the tannins chemically but instead avoid tannins by burrowing beneath the tannin storage in the outer cell layers of the leaf, by feeding early in the season while the leaves are growing rapidly and tannins have not been produced in abundance, or by feeding on fresh tender leaves growing from the stump of a recently fallen tree (Feeny 1970). While Feeny (1970, 1976) and Rhoades and Cates (1976) expause this theory that tannins have generalized nonspecific interactions with proteins, Zucker (1983) has recently produced an extensive review which concludes that tannins are diverse in structure and can be highly specific in their interactions with proteins. At least, he argues, hydrolyzable tannins protect the plant against herbivores (Animalia) while condensed tannins are primarily defensive against microbes and pathogens (Monera and Fungia).

When leaves are shed from mangrove trees and fall into the litter or detritus, they may be physically damaged. If the leaf is damaged, some of the plant cells might be damaged and the vacuoles within the cells might be ruptured and exposed to oxygen. It is almost certain that the tannins would also be oxidized and their inhibitory interaction with proteins would increase (Byrde, Fielding, and Williams 1960), thereby further inhibiting the decomposition processes.

By forming loose complexes with protein molecules by hydrogen bonds (and perhaps some covalent bonds), tannins inhibit the decomposition of mangrove leaves by microbes and fungi, inhibit the digestion of mangrove leaves by both invertebrates and vertebrate herbivores, and might even inhibit the productivity of phytoplankton in the waters in a mangrove swamp. Although the gross primary productivity of mangroves is very high, the tannins greatly delay and inhibit its direct consumption.

Assimilation of vascular plant material by marine reptiles, birds, and mammals

Marine invertebrates and marine fishes have a long history of evolution in the ocean along with the algae on which they feed. They generally do not appear to have metabolically adapted to higher plants such as mangroves, seagrasses, or marsh grasses that have relatively recently invaded the shallow coastal marine environments. Most plant material assimilated by herbivorous invertebrates or fishes in seagrass beds, estuaries with Spartina, and mangrove swamps is probably not fragments of leaves of higher plants but microflora growing on dead plant fragments.

While herbivorous marine invertebrates and fishes feed mainly on algae, herbivorous reptiles (e.g., Chelonias mydas, the green sea turtle), birds (e.g., the black brant, the Canada goose, the pintail and scaup ducks), and mammals (the West Indian manatee and the Western Pacific dugong) all feed extensively on seagrasses. Twenty species of waterfowl feed on seagrasses in the Chesapeake Bay region (Steward 1962). About 80% of the

winter food of the black brant is eelgrass (Cottam 1934) and black brant and Canada geese consume about 17% of the summer standing crop of eelgrass in Alaska (McRoy 1966). When an eelgrass disease killed extensive areas of Zostera marina on the east coast of the United States in the 1930s, the black brant virtually disappeared (Cottam 1934).

Whereas gastropods, urchins, and fishes preferentially feed on the outer senescent portions of blades of seagrasses which are overgrown with epiphytic algae or microbes, green sea turtles (Chelonia mydas) selectively graze at the bases of Thalassia plants where they obtain the youngest, least overgrown portions (Bjorndal 1980, 1982; Mortimer 1981, 1982). After grazing an area, Chelonia mydas will return and recrop the same area, leaving adjacent areas of tall plants ungrazed (Bjorndal 1980). Regenerating blades have higher protein levels than untouched blades (Dawes et al. 1979; Dawes and Lawrence 1979) and by increasing turnover, grazing by green sea turtles might increase the productivity of the area. Thayer et al. (1982) presented evidence that green sea turtles speed up the process of decomposition of seagrasses. Although nutrients are absorbed from the seagrass material during the passage through the digestive tract of the sea turtle, the seagrass material is fragmented further and there is a two-fold increase in amino-acid content which facilitates rapid decomposition of the fecal material.

Unlike herbivorous invertebrates and fishes, green sea turtles avoid blades encrusted with epiphytic algae. However, Chelonia mydas will accept algae in areas where seagrasses are scarce (Mortimer 1981).

Dugongs (Dugong dugon) feed almost exclusively on seagrasses (Heinsohn and Birch 1972; Heinsohn et al. 1977). When seagrasses become scarce, dugongs will feed on algae (Heinsohn and Spain 1974), even consuming quantities of Sargassum (Spain and Heinsohn 1973). The West Indian manatee (Trichechus manatus) ranges more frequently between saltwater and freshwater and so its diet is more catholic (Campbell and Irvine 1977). In salt water, its main food is probably seagrasses (Bertram and Bertram 1968) but in freshwater they will eat water hyacinth, woody emergent reeds and cattails, and even terrestrial vegetation within one foot of the water (Anonymous 1976; Campbell and Irvine 1977). Unlike sea turtles which bite off seagrass above the substratum, dugongs root and dig up the entire plant, including the rhizomes. While feeding, dugongs leave trails 19-25 cm wide, 3-5 cm deep, and 1-5 m long (Heinsohn et al. 1977).

Clearly, marine vertebrates that reinvaded the sea from terrestrial origins evolved from a past association with terrestrial plants and have the metabolic pathways that allow the digestion of seagrasses while marine invertebrates and fishes generally find seagrasses difficult to process metabolically. Invertebrates and fishes generally do not feed on a major portion of the standing stocks of seagrasses and seagrasses do not decay as rapidly as algae. Despite the great primary productivity of seagrass beds (Table 1), much of this production is lost during the slow process of entering the detrital food web. If populations of green sea turtles and dugongs were allowed to recover from overexploitation, they might serve as a mechanism to exploit the production of seagrass beds directly through herbivory rather than indirectly through the detrital food web of invertebrates and fishes.

The generally unexploited primary production of seagrass beds is great under present conditions (Table 1). If populations of green sea turtles and dugongs were allowed to develop, the increased grazing pressure on seagrass beds might increase the turnover and rate of production of seagrasses. Even the detrital food web should benefit by the processing of seagrasses through the guts of sea turtles and dugongs (Thayer et al. 1982). Populations of native fisherman in some areas of the Torres Strait Islands still rely on green sea turtles and dugong as major sources of protein (Johannes 1983). It is fortunate that human populations in the Torres Strait Islands have remained stable for at least 150 years because, as a consequence of this, marine resources are still superabundant in the area (Johannes 1983). If green sea turtles and dugongs are still common in the Torres Strait Islands, then the seagrass beds may have a smaller standing stock but may be more productive because of a greater rate of turnover and because a greater portion of the production goes directly to herbivorous vertebrates.

With direct herbivory on seagrass, an increased population of sea turtles and dugongs would not seem likely to be in competition with other herbivores which feed mainly on algae. Passage through the detrital food web would be accelerated, not cut off. However, this proposal should be studied carefully because unforeseen complications are likely in nature. For example, dugongs dig up seagrass beds quite thoroughly. Seagrass beds serve as nurseries by functioning as three-dimensional refuges and shelter for juvenile fishes and crustaceans from predatory fishes. The seagrass also serves as substrata for productive epiphytic algae. Dugongs could reduce the effectiveness of seagrass beds as nurseries for commercial fishes and curstaceans and reduce the total production of detrital materials although accelerating the production that remains. This must be weighed against the consideration that as direct herbivores, sea turtles and dugongs should be more efficient in converting seagrass to meat than would carnivorous fishes. Herbivorous fishes would be relatively efficient when feeding on algae, but not on seagrasses.

In contrast to dugongs, green sea turtles eat only the seagrass blades and leave rhizomes intact. Some seagrasses regenerate efficiently and so the potential problems with increased abundances of dugongs might not be of concern for increased abundances of sea turtles. We should study these matters because if no serious deleterious side effects exist, then we might have methods by which we could increase the protein production of shallow tropical coastal ecosystems in SPREP regions.

However, C. Limpus (pers. comm.) advised that it will probably not be possible to harvest sea turtles economically because of other aspects of their biology, e.g., the long period of time it takes for sea turtles to reach sexual maturity (decades). He called attention to the fact that there is no evidence of sea turtles being truly abundant before modern times or in remote places away from human exploitation. He believes that, at least in the Pacific, sea turtles would never become abundant enough to make a significant impact on seagrass beds because of a variety of factors, in addition to human exploitation, which limit the abundances of sea turtles.

T. Fritts (pers. comm.) pointed out that while data on growth rates to sexual maturity in the natural environment are not solid, it appears that Chelonia mydas on the Great Barrier Reef and elsewhere in the Pacific generally show slower growth rates than do those around Florida. He suggested that perhaps a greater portion of the diet of C. mydas is algae in populations of slower growing individuals and is seagrass in populations of faster growing individuals. He commented that occasional mangrove shoots may be especially important in C. mydas diets in the Galapagos where they do not obtain other vascular plants. It would be most interesting to test the hypothesis that, on the average, Chelonia mydas grow significantly slower and have a significantly greater proportion of algae in their diets in the Pacific in comparison with populations in the Caribbean.

Summary and conclusions

Coastal marine ecosystems are particularly important to Pacific islanders because most of the animal protein of islands has traditionally come from coastal resources and because human settlements have tended to be in coastal regions for logistic reasons. An understanding of the functioning of coastal marine ecosystems is important both because the resources need more careful management as the human populations grow and because human activities will have the greatest effects on coastal environments where populations are concentrated.

Fishes and invertebrates forage out from coral reefs onto seagrass beds and return for shelter. In the Caribbean, field studies have indicated a flow of nutrients from the seagrass beds to coral reefs such that a greater biomass of fishes is found on reefs near seagrass beds. Also, coral colonies grow faster near the fish-aggregation sites on reefs (for fishes that forage in seagrass beds) than do coral colonies away from fish-aggregation sites. Seagrass beds and mangrove swamps serve as nursery areas for several species of reef fishes. While nutrients move from seagrass beds to coral reefs, the effects of species interactions on community structure are in the other direction. Coral reef herbivores influence the structure of plant communities in the seagrass beds near reefs. Pacific reefs may differ from Caribbean reefs in this regard. Echinoids are far less common in Micronesia than in the Caribbean.

The main effects of coastal habitats on each other are in stabilizing the physical environment by dissipating wave action (especially by coral reefs, which form lagoons), in buffering salinity changes (mainly by mangroves) and in stabilizing sediments (by seagrasses, mangroves, or corals). All three ecosystems also produce sediments and provide substrata for bacteria, epiphytic algae and animals. Seagrasses may provide a stabilizing effect on the detrital food web because the slow rates of decomposition provide a regular flow of nutrients during periods of fluctuation in primary productivity.

Although the ecological interactions between coral reefs, seagrass beds, and mangrove swamps are complex and academically interesting, the evidence in the literature indicates that these interactions are of negligible importance in comparison to the influence of the

characteristics of coastal terrain, topography, substratum, and water current patterns. The latter are the factors more important to understand when attempting to make practical decisions for coastal resource management. Mangroves are an order of magnitude more productive in areas with input from terrestrial runoff than in areas lacking external nutrient sources. Fully developed coral reefs, seagrass beds, and mangrove swamps can exist in isolation from each other. The main effect of lagoons is in increasing the residence time of water which provides an incubator effect on the food web. Estuaries facilitate high rates of production because they are sediment traps, sites of concentration of terrestrial nutrient runoff, sites of upwelling driven by river runoff or tidal action, semiprotected from wave action, and because they generally provide favorable physical environments for mangroves and seagrasses.

Despite the great rates of gross primary production, the predominant portion (90%) of energy and fixed carbon from primary production in mangrove swamps, seagrass beds, and estuaries is not consumed directly by herbivores but enters the food web as organic detritus. Mangrove and seagrass leaves are relatively refractory to decomposition in the marine environment and to digestion and assimilation by marine invertebrates and fishes which have a long history of evolution in the marine environment. The tannins in mangrove leaves inhibit decomposition by microbes, digestion by herbivores, and growth of phytoplankton in the surrounding waters.

Mangroves and seagrasses have evolved from terrestrial plants that reinvaded the sea. The herbivorous vertebrates that have evolved from terrestrial vertebrates that reinvaded the seas (e.g., green sea turtles and dugongs) feed extensively on seagrass. We suggest that if we prevent continued overexploitation of green sea turtles and dugongs, allowing their populations to expand, then harvest them in a rational manner, we will be able to obtain more protein from tropical seagrass beds because of a greater proportion of the primary productivity being directly assimilated by herbivores. Concomitant with greater production of protein by direct utilization of the primary productivity, the primary productivity itself might be increased under greater grazing pressure by increased turnover rates.

Dugongs, however, root up seagrasses entirely and therefore may have damaging effects on the nurseries of fishes and crustaceans. Studies should be made of the interactions between seagrass beds and herbivorous marine vertebrates at Pacific islands because natural systems are usually more complex than they first appear. Seagrass beds are among the most productive ecosystems in the world, yet little of this production goes directly into the herbivore food web, so it is worthwhile to investigate the potential outcomes of these interactions for the resident islanders.

MANAGEMENT ISSUES REGARDING INTEGRATED TROPICAL MARINE ISLAND ECOSYSTEMS

Deborah Grosenbaugh

Introduction

The management of marine resources traditionally has been an integral part of tropical Pacific island cultures. However, as growing populations approach the limited carrying capacity of island ecosystems and Western cultural influence places new strains on traditional management practices, choices often will have to be made between competing needs for economic development and resource protection. Although local perceptions concerning how to best allocate the available resources among competing uses may differ, user groups are equally constrained by the vulnerability of these resources to human exploitation. In many cases, the expansion of the local economy takes precedence over the observance of these limits, causing irreversible damage even before a problem is perceived. Unfortunately, for a variety of reasons, the lessons learned in one area are rarely applied elsewhere. It is this lack of understanding regarding the cause-and-effect that results in a limitation of future options, and the lack of information exchange relative to shared experiences that is addressed herein.

In devising regional management options, it must be taken into consideration that, while the Pacific Ocean unites the islands into a single environmenal entity, great distances have promoted the evolution of a variety of political, cultural and economic factors that will require localized approaches to management problems.

In developing criteria, it must be realized that in an integrated approach to the management of coastal marine ecosystems, the object is not to manage the environment itself but to manage the use and development of that environment within limits that ensure maintenance and integrity of critical ecosystems. Unfortunately, tropical island ecosystems have been shown to have narrower limits than their continental counterparts, making them less tolerant of environmental perturbation and thus more sensitive to human activities. Management schemes that may have been successfully devised for temperate, continental systems cannot be directly applied to the islands of the tropical Pacific without first undertaking regional sensitive environmental assessment and monitoring programs. The kind of assessment and monitoring that would be required to arrive at quantitative criteria on which to base management decisions, however, is a luxury that can exceed the resources of developing island economies. In fact, the scope of such a project probably would far exceed the resources of the entire region. It is therefore necessary to develop flexible parametric guidelines based on the best available information and to monitor their effectiveness within reasonable limits. For example, Johannes (1980) notes that to determine maximum or optimum sustainable yield in a multispecies reef and lagoon fishery is an unrealistic goal. He suggests that a better approach would be to strive for a moderately stable increase in the yields of overexploited fisheries. This approach is the one we have tried to keep in mind in making our recommendations based on our assessment of current efforts to manage tropical coastal ecosytems.

In attempting to assess the status of management efforts relative to these ecosystems, we have sought to catalog government management practices of the region and any legislation that could possibly affect the interactions of the mangrove, seagrass, coral reef, and lagoon-estuarine systems throughout the tropical Pacific region, taking the nature of the associated land masses into account. We have then tried to make some determination as to where management practices are inadequate. In analyzing any management scheme for deficiencies, we have considered not only biological parameters, but political, cultural and economic aspects as well. The following criteria were kept in mind; however, where detailed information was unavailable, generalizations do, by necessity, occur:

1. Do management plans exist that consider coastal marine ecosystems as an integrated extention of the terrestrial environment?

2. Do traditional practices adequately protect the ecosystem and its resources?

3. If traditional values have eroded, does legislation and/or the establishment of reserves provide adequate protection?

4. Are the mechanisms to administer and enforce policy and legal authorities adequate?

Recommendations for the improvement of coastal marine ecosystem management are then presented.

Throughout the study, the authors have attempted to do as comprehensive a review as possible. However, given the size of the study area and the difficulty of obtaining information from a diversity of sources, omissions are likely to occur. We would appreciate being informed of any additional information that should have been considered. We are grateful for the advice and comments provided by Kelvin K. Y. Char, National Marine Sanctuaries Program, NOAA, who read and commented on this report.

Review of management practices and legislation

Information regarding management schemes and conservation legislation was obtained from a variety of sources, principally from the SPREP Country Reports (1980-82), Dahl (1982), Guam Division of Aquatic and Wildlife Resources correspondence regarding regional fish and game laws, and our own inquiries to responsible government agencies and knowledgeable individuals. Table 3 indicates areas where environmental or conservation legislation has been enacted relative to coastal marine systems. Included also in this review is legislation relative to the protection of terrestrial ecosystems from the effects of indiscriminate land clearing and mining operations, siltation being a major cause of degredation to mangrove stands, seagrass beds, and coral reef assemblages. A complete list of all legal authorities that could be determined for each country is contained in Table 4. Table 5 delineates the extent to which sanctuaries and reserves have been established in the region. Whereas

Table 3. Summary of existing marine resource conservation and management legislation in the tropical Pacific region (see appendix).

	Comprehensive Environmental Legislation	Water Quality	Legislation Specific to Coastal Eco-Systems	Enabling Legislation for Reserves & Sanctuaries	Fisheries & Species-Specific Legislation	Outside Terrestrial Activities (Forestry & Mining)	Outside Marine Activities (Oil/Dumping)	EIA Provisions
American Samoa		x		x				x
The Northern Mariana Is.	x	x		x	x			x
Cook Is.	x			x	x			
Fiji		x	x	x	x		x	x
French Polynesia						x	x	
Guam		x	x	x	x	x	x	x
Kiribati				x		x	x	x
Nauru			x					
New Caledonia		x		x		x	x	
Niue		x			x			
Papua New Guinea	x	x		x	x	x	x	x
Pitcairn					x			
Solomon Is.		x		x	x	x		
Tokelau								
Tonga				x	x	x		
Trust Territory of the Pacific		x		x	x	x	x	x
Tuvalu				x	x		x	
Vanuatu					x			
Wallis & Futuna					x			
Western Samoa		x		x	x	x		

Table 4.   Existing legislation relative to the management of tropical Pacific
          marine ecosystems.

American Samoa

   1. Applicable U.S. Federal Legislation

          Coastal Zone Management Act
          Endangered Species Act
          Water Pollution Control Act
          Clean Water Act

   2. Water Pollution Control Act

Commonwealth of the Northern Mariana Islands

   1. Applicable U.S. Federal Legislation (see American Samoa #1)

   2. P.L. 3-47; Coastal Resources Management Act, 1983. Sets forth
       policies and the administrative mechanism for the management of
       coastal resources.

   3. P.L. 2-51; Fish, Game and Endangered Species Act, 1981. Gives the
       authority to regulate the taking of fish and game to the Director of
       Natural Resources.

   4. Emergency Regulations Protecting Fish and Wildlife, 1983.
       Establishes a license requirement and regulations for the taking of
       Trochus, hermatypic corals, green sea turtles and lobster;
       establishes an endangered species list; prohibits the use of
       explosives, poisons, electrical devices; designates Sariguan and Maug
       as sanctuaries. (Note: There is no authority under P.L. 2-51 to
       establish sanctuaries.)

   5. Water Quality Standards and Regulations. Contains provisions for the
       control of erosion and siltation.

Cook Islands

   1. Conservation Act, 1975. Establishes a Director of Conservation,
       responsible for the preservation of the environment and natural
       resources. Includes enabling legislation for the establishment of
       reserves and sanctuaries.

   2. Local Government Act, 1966. Establishes Island Councils which are
       empowered to make by-laws concerning the regulation of reserves
       within their respective jurisdictions.

   3. Harbour Control Act, 1971. Regulates the discharge of pollutants
       into harbors.

Table 4 (cont.)

4. Trochus Act, 1975. Establishes reserves at Aitutake, Parmerston and Manuae.

5. Territorial Sea and Exclusive Economic Zone Act, 1979. Provides for regulations for the protection of the marine environment and fisheries resources.

Fiji

1. Land Conservation and Improvement Act, 1953. Establishes the Land Conservation Board which is responsible for the supervision of water resources, stimulation of public interest regarding natural resources, and recommendations for conservation legislation.

2. National Trust of Fiji Ordinance, 1970. Provides for the development of parks and reserves.

3. Fisheries Act, 1942. Prohibits fishing in native customary fishing grounds without a license.

4. Fisheries Regulations, 1965-1972. Controls the use of fish fences, nets, poisons, and protects turtles and porpoise.

5. Provisions controlling the pollution of coastal waters are included in:
          Native Land Regulations
          Mining Regulations

6. Harbor Act, 1974. Prohibits the pollution of harbors and coastal waters.

7. Mangrove Regulations. A license is required for the exploitation or reclamation of mangrove stands.

French Polynesia

1. Fisheries Legislation. Provides for the protection and management of marine and coastal resources.

2. Forestry Regulations. Controls deforestation by clearing and bush fires.

3. Marine oil pollution is prohibited by law.

Guam

1. Applicable U.S. Federal Legislation. (See American Samoa, #1).

Table 4 (cont.)

2. Government Code of Guam Relative to the Taking of Fish and Game and Regulations Promulgated Under Its Authority. Regulates the taking of fish, Trochus, tridacnid clams, lobsters and coral. Prohibits the taking of hermatypic corals at depths less than 10 meters.

3. Guam Water Quality Standards. Regulates the discharge of pollutants into coastal waters.

4. Territorial Seashore Protection Act. Establishes a "Seashore Reserve" from the mean high water mark inland 10 meters wherein a permit is required for any development.

5. Wetland Rules and Regulations, 1978. Includes performance standards and procedural guidelines for any development in a designated wetland area.

Kiribati

1. Wildlife Conservation Ordinance, 1971 and Wildlife Protection Ordinance, 1975. Provides for the establishment of wildlife sanctuaries (none existing) and protects turtles on land.

2. Closed Districts Ordinance, 1957. Provides for the declaration of prohibited areas.

3. Local Government Ordinance, 1966. Provides for Island Councils that are empowered to regulate such matters as fishing and erosion of land.

4. Fisheries Ordinance, 1957. Provides for the promulgation of fisheries regulations and protects ancient and customary fishing grounds.

5. Harbours Ordinance, 1957. Prohibits the discharge of pollutants into the harbor without permission.

Nauru

1. Marine Resources Act, 1978. Provides that fishing within the Territorial water is permitted only under license with the exception of Nauru residents using small craft.

New Caledonia

1. Resolution No. 108, 1980 (as amended). Provides for the establishment of sanctuaries and reserves.

2. Resolution No. 105, 1968. Controls the discharge of pollutants into coastal waters.

Table 4 (cont.)

    3. Law No. 64-1331, 1964. Prohibits seawater pollution by hydrocarbons.

    4. Decree No. 405, 1910 (as amended). Prohibits deforestation of certain hill slopes and river banks.

    5. Decree 54-1110, 195. Authorizes the Mining Pollution Control Commission to determine pollution control measures.

Niue

    1. Fish Protection Ordinance

    2. Environmental Protection Ordinance

Papua New Guinea

    1. National Constitution (Fourth Goal). Declares national policy to be the conservation of natural resources for the collective benefit of all and of future generations.

    2. Conservation Areas Act, 1978. Provides for the establishment of conservation areas and the criteria therefor.

    3. National Parks Act, 1966 (as amended). Places the adminstration of parks under the supervision of a National Parks Board.

    4. Fauna Protection and Control Act, 1966 (as amended). Allows for the establishment of sanctuaries and protected areas for particular species.

    5. Environmental Contaminants Act, 1978. Requires a license for the discharge of pollutants into coastal waters.

    6. Environmental Planning Act, 1978. Invokes planning procedures when inadequate consideration has been given to environmental effects of development.

    7. Timber Extraction Permits require the institution of reafforestation programs.

    8. Merchant Shipping Act. Contains provision for marine oil pollution of coastal waters.

    9. Coral Harvesting Law. Controls the taking of coral.

Pitcairn Island

    1. Fisheries Zone Ordinance. Empowering legislation for the management of fisheries resource.

Table 4 (cont.)

Solomon Islands

1. National Parks Act, 1954. Enabling legislation for the declaration of National Parks.

2. Public Health Ordinance, 1970. Prohibits the pollution of any watercourse, stream or lake.

3. Mining Act, 1968/69. Prohibits the discharge of pollutants from mining operations into any watercourse.

4. Forest and Timber Act, 1969/77. Provides for the declaration of "controlled forests" wherein clearing for agricultural purposes is prohibited.

5. Fisheries Act, 1972/77.

Tonga

1. Parks and Reserves Act, 1976. Provides for protection of marine natural reserves (five reserves have been so designated).

2. Bird and Fish Preservation Act. Lists sea turtles as protected and provides for reserve areas.

3. Forest Act. Provides for reserves.

4. Fisheries Regulations. Prohibits the use of damaging fishing methods.

Trust Territory of the Pacific Islands (TTPI)

1. Applicable U.S. Federal Legislation. (Note: U.S. legislation will apply until the dissolution of the TTPI, however enforcement is not active at this time.)

   Endangered Species Act
   Fish and Wildlife Coordination Act
   Water Pollution Control Act
   Clean Water Act

2. Applicable TTPI Legislation and Regulations

   Trust Territory Environmental Quality Protection Act
   Trust Territory Endangered Species Act
   Earthmoving and Sedimentation Control Regulations
   Marine and Fresh Water Quality Standards Regulations
   Fishing Law. Specifically prohibits the use of explosives, poisons and chemicals.

Table 4 (cont.)

    3. Specific Legislation and Regulations

       Code of the Federated States of Micronesia (FSM), 1982.
         Establishes regulations for the taking of sea turtles,
         black-lip mother-of-pearl oyster shell, Trochus; prohibits the
         use of explosives and poisons; lists endangered species;
         creates the authority for the management of marine resources.

       Ponape State (FSM). The Marine Resources Conservation Act of 1981
         empowers the Director of the Department of Resources and
         Development to regulate the taking of Trochus, black coral,
         parrotfish, grouper and mangrove crab.

       The Republic of Belau regulates the taking of fish (size limits),
         tridacnid clams, mangrove crab, lobster, and sea turtles. The
         taking of dugongs is prohibited.

Tuvalu

    1. Wildlife Conservation Ordinance, 1975. Enabling legislation for the
       designation of wildlife sanctuaries.

    2. Fisheries Ordinance, 1977. Forbids the use of explosives for
       fishing.

    3. Prohibited Areas Ordinance. Provides for the declaration of
       "prohibited areas".

    4. Harbours Ordinance. Prohibits the discharge of sewage or oil into
       harbours without permission.

Vanuatu

    1. Constitution. Declares that it is the moral duty of every person to
       protect and safeguard national wealth and environment.

    2. Fisheries Act. Contains provisions for the establishment of marine
       reserves.

    3. Joint Regulation No. 17, 1968. Protects crayfish in coastal waters.

    4. Joint Regulation No. 7, 1973. Prohibits night underwater fishing on
       the coast of the island of Efate.

    5. Joint Forestry Regulation No. 30, 1964. Prohibits deforestation in
       declared forest areas except under permit.

Table 4 (cont.)

Wallis and Futuna

    1. Fisheries Regulation: Order No. 83, 1965. Prohibits the use of explosives and poisons for fishing.

Western Samoa

    1. National Parks and Reserves Act, 1974. Provides for the establishment of National parks and reserves.

    2. Water Act, 1965. Controls the discharge of pollutants into coastal waters.

    3. Fish Protection Act, 1972. Prohibits the use of explosives for fishing.

    4. Agriculture, Forests and Fisheries Ordinance, 1959; and Forests Act, 1967. Establishes the Agriculture Department and provides for the maintenance and establishment of areas of forest adequate to protect the climate, soil, and water resources.

Table 5. Provisions for the establishment of marine ecosystem sanctuaries throughout the tropical Pacific region.

	Enabling Legislation	Proposed Marine Sanctuaries or Reserves	Established Marine Sanctuaries or Reserves
American Samoa	X		X
Commonwealth of the Northern Marianas	X	X	X
Cook Islands	X	X	X
Fiji	X	X	X
French Polynesia	X		X
Guam	X	X	
Kiribati	X	X	
Nauru			
New Caledonia	X		X
Niue			
Papua New Guinea	X	X	X
Pitcairn			
Solomon Islands	X	X	X
Tokelau			
Tonga	X	X	X
Trust Territory	X	X	X
Tuvalu	X		
Vanuatu			
Wallis & Futuma			
Western Samoa	X	X	X

management issues can be dealt with in some instances on a species-specific basis, it is generally the case that an integrated approach to ecosystem management must be devised. In this situation, the same cultural and economic problems involved in species management are further complicated by biological interactions that are, at present, not well understood.

Most of the tropical island states have declared as national policy that preservation and responsible exploitation of the marine environment are of high priority. However, comprehensive legal authority to support such policy is not common. As indicated above, most legislation responds only to specific problems. As far as we have been able to determine, only three jurisdictions have enacted specific legislation relative to comprehensive resource management. These are the Cook Islands (Conservation Act of 1975), Papua New Guinea (Conservation Areas Act of 1978), and the Commonwealth of the Northern Mariana Islands (Coastal Resources Management Act of 1982). Even so, most other nations have the legal authority to manage their coastal resources implied in various other legislative efforts, such as water quality laws which regulate discharge into coastal waters and fish and game laws that regulate the taking of certain species.

Thus, a major problem is not the lack of legislation, but coordination among authorities in administering these laws. Complicating these matters are the problems associated with enforcement of existing laws which seem to pervade the entire region.

The first step in devising any management scheme is to evaluate the existing resources. Each island entity should be mapped in respect to its coastal ecosystems and their respective uses. Local governments can best accomplish this task. Where technical resources are a problem, outside help can be provided, but local knowledge is required to determine existing use. Not only designated conservation areas should be included in such a map, but traditional tenured areas as well. A set of regional standards should then be applied to these areas to determine environmental status.

Once this is accomplished, a set of mutually agreed upon objectives for the region should be devised and regional standards and guidelines for their implementation set forth within a framework management scheme. It would then be the responsibility of each participating nation to devise local plans that respond to the regional standards and devise ways to achieve these standards within the regional framework. It is recognized that the technical expertise for such a task is lacking in many areas. Thus, we recommend that a regional advisory board be created to assist in the preparation of local plans.

Island management plans should consider various progressive alternatives starting with simply maintenance of the status quo with regard to traditional conservation measures. In lieu of this, any remaining traditional conservation ethical standards should be institutionalized. Where this has been eroded it will be necessary to enact legislation and designate sanctuaries. However, even appropriate legislation and sanctuary

designation will require local acceptance through either vestigial traditional mores or conservation education:

1) Status Quo

The first task involved in considering management alternatives is to determine if the formulation, implementation and enforcement of a plan are cost-effective. In many cases, an analysis of traditional management measures will show that they provide the protection necessary to maintain designated environmental parameters within tolerable limits. Recognition and legal institutionalization of traditional laws such as reef tenure systems may be all that is required at this point in time. An example of a system that seems to ensure that environmental standards are met is the reef tenure system that remains in force in Yap Lagoon.

In a case such as this, where it can be shown that the traditional conservation system still protects the integrity of the lagoonal ecosystem, it should be left intact and simply monitored for serious departures from locally established criteria.

In some instances, though, reliance on existing traditional authority is not enough. Where Western economics and technology have made inroads, but have not seriously affected customary patterns of marine resource use, legislation legitimatizing traditional uses may be the answer.

2) Institutionalize traditional systems

Should it be determined that the most practical approach to resource management is legislation recognizing traditional exploitation practices, the success of such a program will depend on close coordination with the local users. Additionally, as Johannes (1982) points out, any legal authorities must be flexible and responsive to change, such that customs are not "locked in", preventing the natural evolution of the system.

This approach has been applied with apparent success in Papua New Guinea in relation to the management of certain wildlife species, most notably the dugong (Dugong dugon) (Hudson, 1980).

In most circumstances this type of species-specific management technique will not be cost-effective in dealing with tropical systems (Johannes, 1980). Because of characteristically high species diversity in the tropics, no one or two species dominates catches, even if effort is restricted to certain gear types. For this reason it is generally necessary to devise policies that anticipate environmental perturbations not only within, but outside, the entire coastal ecosystem, rather than the piecemeal, curative approach that dominates island managment schemes.

It should be noted, however, that there are some particularly valuable species that may be responsive to a species approach. Where this is the case, traditional appreciation for the species and its need for management can possibly be used to engender a willingness to accept certain

restrictions relative not only to that particular species, but to its habitat as well.

Papua New Guinea devised an apparently successful approach through the establishment of Wildlife Management Areas. Within these reserves, locally-administered, traditional hunting is permitted in conjunction with a program of biological monitoring and public education, which serves to protect the dugong populations from over-exploitations and their habitat from degredation. Unfortunately, there has been an almost total cessation of field management since 1982. However, the management schemes worked well during the program and should serve as a model for future efforts (Hudson, pers. comm.).

Declining in numbers, if not threatened throughout their range (Anderson and Heinson, 1978; Brownell et al., 1981), dugongs convert seagrass biomass to high-quality protein that supplements usually monotonous traditional island diets. Perhaps more importantly, the actual acquisition of the animals is an important factor in maintaining the cultural integrity of the various peoples of the Pacific. The organized hunt revolves around a complex system of social responsibility and environmental lore that is essential to man's perception of his place in nature and his society. Such awareness is especially critical in facilitating successful adaptation to cultural changes resulting from increased Western contact. For these reasons, overly restrictive management plans, even in the face of overhunting, can do more to expedite a given species' demise and subsequent degredation of its environment than the status quo. Therefore, responsible management measures for critical species must be carefully devised with input from the affected parties.

The maintenance of dugong populations throughout the Indo-Pacific region presents unique management problems, since tourism is not a significant factor. Fortunately, dugong populations, though reduced, do not appear to be in immediate danger of extinction. Limited migration is believed to occur between the breeding populations of Melanesia, the Solomon Islands, New Hebrides and New Caledonia. The total population for this area has been estimated to be 17,000 (Nishiwaki et al., 1979). Because of limited migration, the need for dugong management can be assessed on a local basis.

In instances where traditional values no longer serve to protect a species or its environment, more drastic protective measures are necessary. For example the dugong population of Palau, Western Caroline Islands, though biologically identical to those of the Indo-Pacific region, presents management problems totally different from more western counterparts. Legally protected, the dugong, once an important cultural aspect of Palauan life, is now so rare (ca. 50 individuals), (Brownell et al. 1981), that traditional hunting is no longer possible. Recruitment is believed to be at a maximum and the seagrass beds in Palauan waters are capable of supporting a much larger population. However, the problems associated with the maintenance of small, isolated populations combined with an estimated poaching rate that exceeds the probable recruitment rate will, in all likelihood, cause the extermination of the population by the end of the century. Since, under ideal conditions, this particular population will not be able to sustain any hunting

pressure in the near future, rationalization of conservation and management options will require a different approach than that of a population that is capable of sustaining limited hunting pressure. One such approach could be to engender an appreciation for the beasts and the associated ecosystems as a tourist attraction for the growing number of divers that visit Palau.

Whereas species with limited migration patterns respond to local management schemes, a regional approach will be required for the conservation and management of another important marine herbivore, the green sea turtle (Chelonia mydas) throughout its range. Extensive migration of this species precludes a local approach to management issues. Table 6 illustrates the diversity of protective measures throughout the study area. A regional plan will have to be devised that considers a system of breeding, nesting and feeding sanctuaries combined with regional guidelines for the taking of turtles. Local plans that are responsive to traditional, subsistence taking could then be developed within these guidelines. Balazs (in press) suggests conservation measures for Tokelau that are reasonable for areas where it can be shown that turtle hunting is traditional and necessary.

Where traditional systems have completely broken down, such as generally is the case in the Mariana Islands, a different approach is required. A favorite food fish of the indigenous populations of the Marianas is the rabbitfish (Siganus spp.). These fish are harvested during all stages of their life cycle, including those times at which they are most vulnerable to exploitation: during recruitment when they come over the reef in dense aggregations (Kami and Ikehara, 1976) and during spawning when they again aggregate in a stupor-like state.

In the past, island populations were limited, and no more was taken than could be immediately consumed or preserved by traditional means. But given improved gear technology (monofilament, small-mesh nets) and better methods of preservation and storage, these fish appear to be exploited over the maximum sustainable yield as indicated by apparent population declines in recent years. The fact that these fish are also harvested during spawning gives credence to fishermen's observations that the number of adults on the reef is much lower than in the past.

Guam Fish and Game laws permit the use of small mesh nets for the "traditional harvesting of juveniles". This creates additional problems in that incidental catch of other species is unregulated and seasons are not established. Consequently, in practice, it is legal to use monofilament, small-mesh nets under any circumstances. In a case such as this, regulations should be enacted to permit the harvest of the juveniles only at designated locations and the use of small-mesh nets only be allowed during seasonal runs. It is interesting to note that attempts on the part of Guam's Division of Aquatic and Wildlife Resources to regulate juvenile fish harvest have met with resistance from those claiming the "traditional rights" to do so. Johannes (1982) has observed that villagers, even in remote areas, will invent "traditional rights" if it is advantageous.

Table 6.   Legal authorities for the regulation of the taking of marine turtles
           throughout the tropical Pacific region.

Country	Applicable Legislation or Regulations
American Samoa	U.S. Federal Endangered Species Act of 1973 applies -no taking
Commonwealth of the Northern Mariana Islands	U.S. Federal Endangered Species Act of 1973 applies -no taking except as provided for by "subsistence" exemption for the taking of green sea turtles Emergency Regulation Protecting Fish & Wildlife, 1983 -no taking 1 December to 31 January -carapace length must be greater than 34" (86cm) -no taking on land -no commercial taking -no taking of eggs
Fiji	Fisheries Regulations, 1971 -no taking 1 November to 28 February, carapace length must be greater than 18" (46cm) -no export of shells -no taking of eggs
French Polynesia	Resolution No. 71-209, 1971 -no taking at sea 1 June to 31 January -no taking on land 1 November to 31 January -carapace length must be greater than 65 cm -no taking of eggs
Guam	U.S. Federal Endangered Species Act of 1973 Applies -no taking
New Caledonia	Fisheries Resolution -no taking 1 November to 31 March -no commercial taking -no taking of eggs
Papua New Guinea	Fauna Protection and Control Act, 1966 (as amended) -hunting restricted to PNG natives -no commercial export (member CITES)
Solomon Islands	Fisheries Resolution -no taking of leatherback turtles -no commercial taking of turtles with shells less than 75 cm in length -no taking of eggs
Tonga	Bird and Fish Preservation Act -no taking 1 November to 31 January -no taking of leatherbacks carapace length must be greater than 35" (89 cm)

Table 6 (cont.)

Tonga cont.	-no sale or export of shells less than 35" (89 cm) in length -no taking of eggs
Trust Territory of the Pacific Islands	Endangered Species Act of 1973 applies with subsistence provisions for green sea turtles; however it is not being strenously enforced pending political status negotiations. Local regulations apply: Code of the Federated States of Micronesia, 1982 Republic of Belau Fish and Game Regulation, 1982 -no taking 1 June to 31 August, and 1 December to 31 January -no taking on land carapace length must be greater than 34" (86 cm) for green sea turtles and 27" (67 cm) for hawksbills -no taking of eggs

Effective resource management need not impinge upon traditional rights. Seasonal spawning aggregations of the grouper, <u>Plectropomus</u> <u>leopardus</u>, are being successfully protected in Palau through seasonal closures.

3) <u>Protective legislation</u>

Where traditional systems have deteriorated to the point that traditional authority cannot be relied upon to support institutionalization of mechanisms already in force, it will be necessary to enact legislation designed to protect vital resources and establish sanctuaries to the extent that the provisions can be enforced.

As illustrated in the example above, legislation is usually enacted in response to the depletion of a particular resource. All-encompassing conservation legislation is rare, and where it exists, ambiguous and difficult to enforce. One potentially successful attempt at the regulation of the use of entire ecological units is in the case of Guam's recently enacted (1978) Wetland Rules and Regulations. They include performance standards and procedural guidelines for any development in 14 designated wetland areas, including mangrove systems. To the extent that they can be enforced and not become subject to political pressure, they adequately provide for the protection of wetland resources. However, there has yet to be a permit issued under under these regulations. Should such a system prove successful, similar guidelines should be devised for the entire integrated lagoonal systems, including contiguous land formations for each island system and incorporated into their country management plan.

Even where protective legislation has been enacted, it is often difficult to enforce and obtain the necessary convictions. The use of explosives and hypochlorite bleach has become a problem, especially in areas where there has been an erosion of traditional values. All of these areas have legislation in force prohibiting such practices; however, lack of enforcement and subsequent prosecution do not provide adequate protection. Problems relative to enforcement pervade tropical island systems where pressure by friends and relative is exerted at all levels from field enforcement to high political offices.

The establishment of reserves and sanctuaries concurrent with the above conservation measures will be an integral part of any regional management system. In areas where tenure systems are intact, the most successful approach will be one that utilized existing traditional authority. This has apparently been successfully accomplished in Papua New Guinea with the establishment of Wildlife Management Areas that are locally administered by traditional authority.

Attempts to establish sanctuaries without indigenous support will meet with little if any success. Johannes (1982) suggests that in areas where reef tenure cannot be extended to conservation management areas, reserves be established in untenured waters near population centers. This approach also, has its problems. An attempt was made on Guam to establish Luminao Barrier Reef as a marine preserve. By virtue of existing legislation in force prior to the establishment of Luminao as a

preserve, coral harvesting was prohibited. When an attempt was made to close the area to net fishing, several fisherman put pressure on their senators to repeal the law on grounds that it was discriminatory. Thereupon, a prohibition on all taking of marine life was enacted by public law for a trial period of one year. During the course of that year, enforcement proved to be so difficult that a continuation of sanctuary status was not pursued.

The acceptance of the concept of sanctuaries by the local users is of paramount importance in predicting the success of any regulatory attempt. Governments must be able to demonstrate some discernible benefits of establishing reserves. The speculation that they will serve as seed areas for desirable species and maintain genetic diversity of the whole integrated ecosystem does not translate into higher fisheries yields and improved standards of living. Benefits must be concrete: legal recognition of local village authority, lease payments, protection from outside encroachment, tourist dollars, etc. Only then can the system function.

Conclusions and general recommendations

Devising a regional approach to the management of tropical coastal ecosystems presents some unique problems. All of the islands of the tropical Pacific share a common dependence on marine resources. However, the existence of a diversity of political, cultural and economic factors makes the development of a universally applicable management strategy impractical. Add to this the biological implications inherent in the association of these ecosystems with different island types, and the task of making recommendations that are relevent to the entire region is further complicated. Therefore, the recommended approach is to devise a set of meaningful regional management objectives with which to guide the development of local plans.

Prerequisite for any management program is a set of well-defined objectives that can be clearly understood. In the absence of such objectives, decisions tend to be ad hoc, disorganized and contradictory. Even when management objectives are defined, as is the case in some of the jurisdictions studied, an effective administrative mechanism must be in place and have the support of those affected by the proposed management scheme. It must also be remembered that approaches to management may vary significantly according to differences in the nature of the ecosystem's association with the land mass, traditional patterns of resource exploitation and local perceptions regarding the continued availability of these resources. Little cooperation with respect to quotas, for instance, can be expected in an area where a resource is not perceived to be on the decline. It should also be noted that for any set of management objectives that can be proposed, some may be in direct conflict with others. This situation results from the disparity in interests between various levels of a developing economy. It is under these circumstances that local users, given the alternatives and their consequences, will initially have to set development priorities.

Because of the limited capacity of island ecosystems to absorb the consequences of environmental perturbation and because of multispecific exploitation patterns, the management of tropical coastal ecosystems requires a unique and sophisticated approach that is beyond the technical resources of most developing countries. Many of the tropical island entities have seen the value of developing such holistic schemes as evidenced by government policy statements or the adoption of coastal and marine resource management plans. However, the actual authority for implementing these plans and policies is often unclear, raising questions regarding how the administrative mechanism actually operates in carrying out relative responsibilities. Where enabling legislation exists, it is generally curative, rather than preventative, often ad hoc and usually species-specific, without regard for an organism's intimate association with its environment. Another difficulty is simply that, in practice, resource conservation and environmental management are luxuries to developing island economies and must be integrated with economic and cultural realities such as tourist dollars, outside funding, preservation of traditional practices.

Finally, it is difficult to consider an integrated approach to tropical ecosystem management without also taking into account the biological and ecological nature of the associated land mass. The entire integrated system most likely would be more significantly affected by impacts associated with degredation of contiguous terrestrial ecosystems than from minor changes affecting its ecological integrity. Thus, local management schemes should also consider solutions to problems associated with impacts experienced by land-based activities.

RECOMMENDATIONS

Recommendations for further research on interactions between coastal
ecosystems

Projects of most basic and immediate importance in forming a foundation
on which to base decisions on management of coastal resources are listed
below.

    1. Coastal habitats as nurseries for fauna of other marine habitats

        a. Adams et al. (1973) claim that 75-90% of marine commercial
           and sport fish species in Florida depend on estuarine
           habitats for at least part of their life cycle. Is this
           approximately applicable to commercial and sport fishes of
           tropical Pacific islands? This is an important piece of
           information for coastal management policies or decisions.
           An estimate of the dollar value of estuarine and other
           coastal habitats in terms of fisheries and second order
           economic benefits would be a useful figure to obtain. The
           first part of this question must be answered before it will
           be possible to answer the second part. This study should
           apply to crustaceans and molluscs as well as to fishes.

        b. Are seagrass beds or mangrove swamps necessary as nursery
           areas for any coral reef fishes? A study should be made to
           determine if any coral reef fishes in the Pacific require
           other coastal habitats as a nursery. Does the coral reef
           fish community structure near seagrass beds differ from
           coral reef fish community structure far from seagrass beds
           as a result of recruitment? Alternative factors such as
           food for adults should be controlled or accounted for.

    2. Effects of land mass and water current patterns.

        a. The effects of terrestrial runoff, groundwater seepage,
           internal waves, water current patterns, and water residence
           time on coastal nearshore communities are the most important
           factors to study if we desire an understanding of the island
           ecosystem that would allow us to make rational decisions in
           matters of coastal zone management. While it has been shown
           that mangroves display a tenfold greater rate of production
           where influenced by terrestrial nutrient runoff, the
           influences of location in terms of the nature of the nearby
           land mass, current patterns, and allochthonous nutrient
           supply has not been so well documented for seagrass
           communities. A direction for future studies to take should
           include assessing the standing stock and the rates of
           productivity of seagrass beds at various sites and relating
           these measures to availability of allochthonous nutrients,
           to water movement patterns, and to the substratum and
           topographic characteristics of the nearby land mass.

        b. Comparative studies between relatively pristine coastal
           areas and coastal areas affected by human activities nearby
           (such as reclaimed wetlands or forests cleared for

agriculture or urban development and areas where reef organisms are removed in increasingly large numbers) should be undertaken for seagrass, mangrove and coral reef ecosystems.

c. The degree to which fisheries are affected by human activities mentioned above should be assessed.

3. Ecology of seagrass consumers.

a. Stable carbon isotope ratio studies of invertebrates and fishes have shown that vascular plants are often in their guts but are not assimilated. More studies are needed to firmly settle the question as to whether seagrass leaves and mangrove detritus serves as nutrition or merely serves as a substratum for edible algae and bacteria.

b. It is commonly stated that a greater proportion of fishes (scarids), molluscs (strombids), and echinoids in the Caribbean than in the Pacific are found to consume seagrasses. I cannot find convincing evidence for this in the literature. It would be of interest to do dietary studies in or near seagrass beds in the Pacific with the same methods used in Caribbean studies so that valid comparisons could be made and differences between Pacific and Caribbean seagrass systems could be documented.

c. Are seagrass beds grazed by sea turtles or dugong more productive as a result of increased turnover, or less productive because of less standing crop, than seagrass beds in the usual condition at present in which sea turtles are overexploited and dugongs are absent? Dugongs are still relatively common in the Torres Straits and in local areas of northern Queensland; comparative studies of seagrass beds in regions with and without dugongs could be made. The effects of grazing of green sea turtles could be assessed by experimentally clipping seagrass blades in some areas in the manner of sea turtles while leaving other areas unclipped for controls.

d. Does herbivory by dugongs and sea turtles also speed up processes in the detrital food web?

e. When seagrass beds are grazed by sea turtles, and especially heavily grazed by dugongs, the effectiveness of the seagrass bed as a nursery for fishes and crustaceans may be reduced. This possibility should be assessed and documented before any actual attempts are made to introduce or increase populations of dugongs or green sea turtles in Oceania.

f. Practical and efficient fisheries management plans should be developed for the green sea turtle and the dugong.

g. Traditional methods of resource management should be documented and assessed.

h. The various traditional and present uses and materials obtained from each ecosystem, including the contributions of each ecosystem to fisheries as nurseries or nutrient supply, should be evaluated in terms of an economic unit of measure. This information is often needed to document coastal zone management plans and proposals.

4. Nutrient transfer by foraging animals

a. In the Caribbean, juvenile haemulid fishes ("grunts") feed on invertebrates and small fishes in seagrass beds by night and return to rest on the reef by day. Although some species in the Indo-Pacific may sometimes follow this pattern as individuals or small groups (e.g., perhaps Gnathodentex, Monotaxis, Macolor, apogonids, holocentrids), are there any fishes that forage at night in seagrass beds then aggregate on the reef in groups of hundreds during the day, repeatedly at particular sites? The patterns of movements of fishes between coral reefs and seagrass beds has yet to be documented in the Pacific.

b. If daytime aggregations of fishes which feed in seagrass beds at night are found on coral reefs, do excretions and defecations of these fishes have a measurable affect on the reef community? Are there greater concentrations of ammonium in the water and nitrogen and phosphorus in the sediments and do corals grow faster at sites of these fish aggregations? This is apparently the case in the Caribbean (Meyer et al. 1983), although the evidence available to date for this process is not conclusive. Furthermore, there is no evidence available to date to indicate that this process is of any significance on Indo-Pacific reefs.

c. Do areas of coral reef bordering on seagrass beds or mangroves support a larger biomass of reef fishes than comparable areas of reef margin bordering on other areas? If so, is the increase in biomass mainly accounted for with species of fishes that forage from coral reefs into the mangroves or seagrass beds? Edge effect, patch size, and habitat border effect per se should be controlled in the design of this study. These questions could also be asked about lobsters and other organisms.

5. Biological interactions between habitats

a. In the Caribbean, juvenile haemulids feed on seagrass beds by night and return to rest, defecate and excrete on coral reefs by day. Are there any fishes that follow this pattern of behavior on Pacific reefs (perhaps Gnathodentex, Monotaxis, Macolor)?

b. Are halos in seagrass beds around patch reefs caused by herbivores (fishes or urchins) or by currents and other forms of water movement? At this time, the literature seems to indicate qualitative differences between the Pacific and the Caribbean interactions between coral reefs and seagrass beds; the halos in the Caribbean are often large and are apparently formed by feeding activities of herbivores; the halos at the edges of the Pacific seagrass beds are small and apparently formed by water movement or other physical factors.

c. Are echinoids less abundant in the Pacific than in the Caribbean? If so, is this because the predators of echinoids (e.g., balistids, Diodon) are more abundant in the Pacific?

d. Is the abundance of echinoids or predatory fishes correlated with the fishing activities of man? Is the magnitude of influence of fishing activities by man on abundances of echinoids or fishes negatively correlated with strength of regulation by traditional rules?

e. Is the abundance of echinoids apparently controlled by sporadic recruitment which is correlated with larval food supply and current patterns? Is recruitment of echinoids and other benthic organisms more regular in the Caribbean or in the Indo-West Pacific?

f. Do the echinoids or do the herbivorous fishes have the greater influence on algal communities in the Caribbean?, in the Indo-West Pacific?, on continental shores?, at high islands?, at atolls?

6. Satellite imagery of chlorophyll, temperature and currents

A major problem with sampling such large scale events as those involved with comparative studies of high islands and atolls in relation to current patterns and rainfall (e.g., plumes following the first rains in the rainy season) is that conditions change during the time it takes to move from one site to another and so samples are not as comparable as might be desired. Our perception also may be limited when we are on the surface, viewing each site closely. We should examine the capabilities of satellite imagery in detecting such patterns as chlorophyll content of water in relation to eddies and current patterns and the relations of all these factors in relation to the size and shape of atolls and high islands.

Recommendations for management action

1. Institutionalize any traditional reef tenure systems or management practices that are effective, where they exist.

2. Develop a "framework" regional plan based on regional standards that are flexible enough to account for cultural and environmental differences. A regional plan should include management objectives giving performance standards and guidelines by which they can be attained, criteria for the development of fragile ecosystems, provisions for environmental impact assessments, and regional standards for such parameters as water quality, relative species diversity and biomass based on baseline data.

3. Each jurisdiction should then develop a local plan within the guidelines of the regional plan which should include administrative mechanisms and legal authorities necessary to achieve regional management objectives.

4. Establish a system of marine reserves, especially in areas readily accessible to academic institutions.

5. Create a regional advisory board consisting of a cadre of those familiar with tropical ecosystems to aid in local decision-making by administrators and resource users.

6. In jurisdictions where traditional hunting is an important cultural activity, link valuable species to environmental management through conservation education.

7. Map ecosystems throughout the region determining regional environmental standards relative to environmental status and the current uses.

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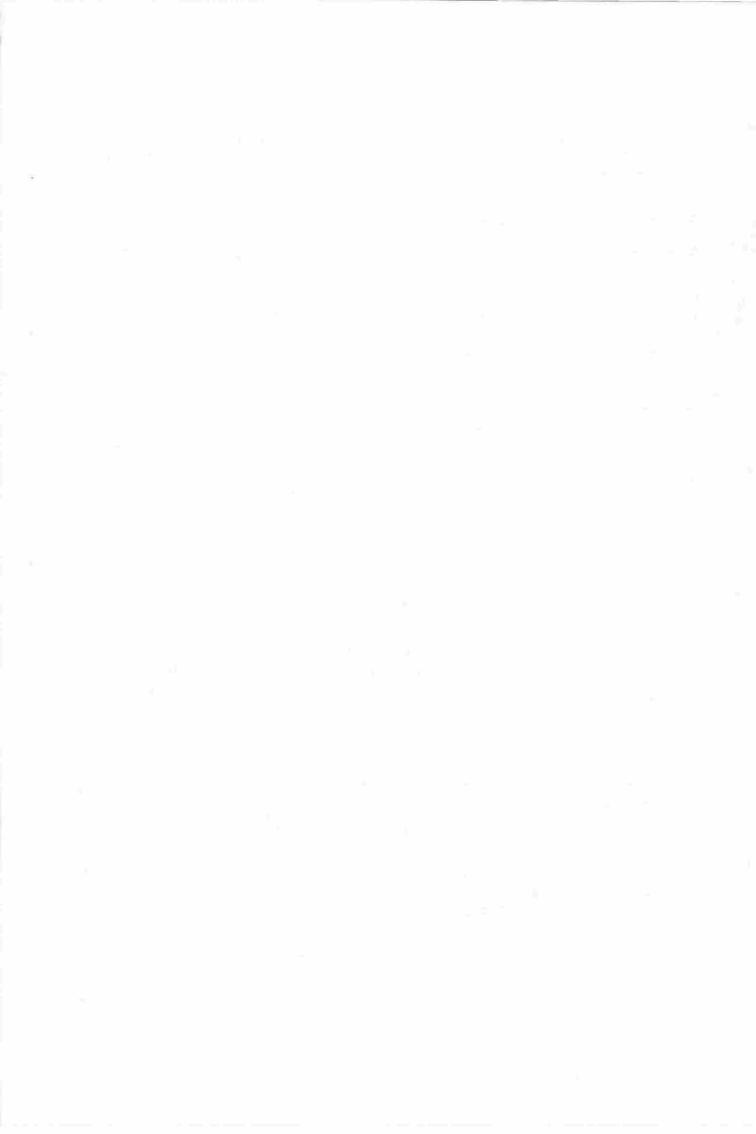Pridham, J.B. 1963. Enzyme chemistry of phenolic compounds. Pergamon Press, N.Y. 142 p.

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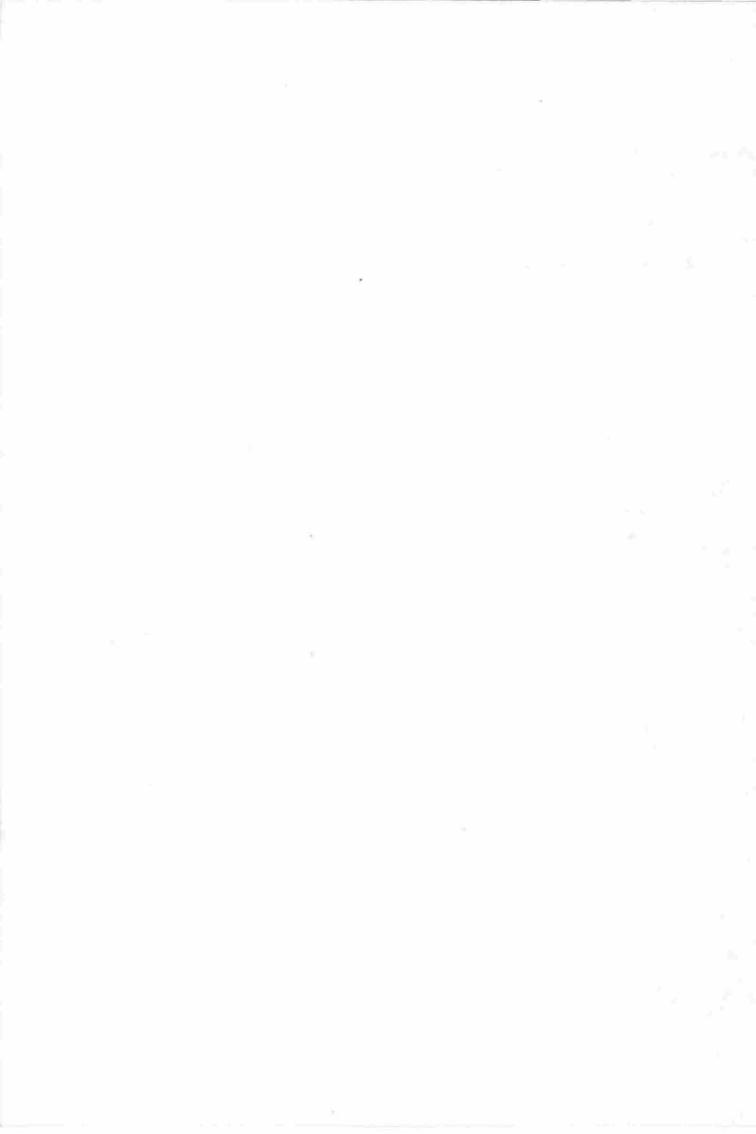No. 53   UNEP: UNEP Regional Seas Programme: the Eastern African Experience.   (1984)

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