

STATE OF KNOWLEDGE
OF CORAL REEFS AS ECOSYSTEMS

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INTRODUCTION

The following brief review of current knowledge about coral reefs as ecosystems was written early in 1972, mostly from material furnished by the CITRE working groups. It attempts to describe the status of reef ecology papers which are particularly relevant to the modeling approach. No information on the systematics of reef biota is included in this summary, although inventories are obviously fundamental to any bio-ecological work. This review has become out-of-date in certain respects and should, ideally, be thoroughly revised. Time for this is not available, and only a certain amount of updating has been done. The bibliography has been gone over very carefully, corrected and very much enlarged. I acknowledge with thanks the work of Dr. Bryce Decker in this matter, and the help of former CITRE participants, especially those working in the Smithsonian.

In its present form, and with apologies for its shortcomings, I believe this review may still be of value, especially to readers not thoroughly familiar with the coral reef field, or those familiar with other aspects of coral reef research, e.g. systematics.

Since the November 1971 workshop, and the January 1972 completion of the CITRE proposal, the results of a number of Symposia and Seminars have been published, as well as several special issues of journals, devoted largely to coral reef research. They demonstrate how active and varied such research is, and should be consulted for topics outside the scope of this review, for details of studies only briefly mentioned here, and for more recent developments not covered here. Among such volumes can be cited the Proceedings of the 1969 "Mandapam Symposium" issued in 1972 (Mukundan and Pillai, eds.), those of the 1972 International Helgoland Symposium, "Man in the sea," assembled in a whole volume (24:1973) of *Helgoländer wissenschaftliche Meeresuntersuchungen*, the March and June 1973 issues of the *Bulletin of Marine Science*, containing 17 papers "In Memory of Dr. Thomas F. Goreau," and a recent issue of *Atoll Research Bulletin* (166-170) devoted to five papers on Acanthaster infestations.

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The results of an Acanthaster symposium at the Second Inter-Congress meeting in Guam, May 1973, have just been published in *Micronesica* (Dec. 1973). Also just received is the first volume of the long awaited treatise on Biology and geology of coral reefs (Jones and Endean, 1973). Several other symposia and review volumes are still in press, including the results of the "Floating Symposium" (2nd International Symposium on Coral Reefs, Great Barrier Reef), June 1973. Hot off the press at the time of the Glover's Reef workshop and the preparation of the CITRE proposal were *Regional Variation in Indian Ocean Coral Reefs* (Stoddart and Yonge, 1971) and the *Supplement to Island Bibliographies* (Sachet and Fosberg, 1971).

BACKGROUND

Following Charles Darwin's description and theory of atoll origin (1842, 1962), a growing controversy over the "coral reef problem" (i.e. origin of atolls and reefs) led to vigorous debates based mainly on information collected from published bathymetric charts and insufficient field data (e.g. Daly, 1910, 1915; Vaughan, 1916a, 1916b; Davis, 1928). An exception was the results of the Funafuti expeditions of the Royal Society (1904) and of the Australian Museum (Hedley, 1896-1900). Over the past 20 years, the "coral reef problem" controversy has abated, particularly since drilling techniques have made it possible to establish that atoll formation is indeed associated with subsidence--notably in studies by Ladd and co-investigators (Ladd et al., 1953; Ladd and Schlanger, 1960; Ladd et al., 1967).

The enormous volume of work carried out on reefs and atolls in the earlier periods and in recent years is summarized in literature reviews such as those of Stoddart (1969a), Ladd (in press) and Glynn (in press). Major topics discussed in previous reports include reef formation (Ladd and Tracey, 1949), geology of reefs (Ladd, 1961; Fairbridge, 1950; Newell, 1959), biological zonation of reefs (Wells, 1954, 1957a, Goreau 1959), and coral physiology (Yonge, 1940, 1963, 1968) to list but a few. In addition, several bibliographies of coral-reef studies have been compiled recently (Pugh, 1950; Sachet and Fosberg, 1955, 1971; Wells, 1957b; Ranson, 1958; Milliman, 1965).

As in the early expeditions, most of the work on specific atolls in the last 20 years has consisted of detailed descriptions and inventories (Ladd, ed. 1954-date; Sachet 1962b; Direction des Centres d'Expérimentations nucléaires, 1969). A qualitative description of the coral atoll ecosystem was prepared in 1957 by Fosberg (1961, 1963b). These descriptions furnish an excellent baseline for comparative studies and a starting point for the quantitative observations needed for model construction. It can be safely stated that neither the qualitative constitution nor the role of a single functional component has been completely elucidated in any one reef environment. Ecological processes on tropical reefs have been estimated on occasion by projecting data from long-term or detailed studies of temperate marine communities (Paine and Vadas, 1970; Newman, 1970). An aspect of reef ecology which has hardly been developed as yet

is any work permitting an estimation of carrying capacity for exploitation by human populations.

GENERAL REEF SURVEYS

Since Darwin's reef studies, there have been many important general investigations of the nature of these structures from various viewpoints. Some of these were one-man enterprises, such as those of Alexander Agassiz at the end of the 19th century aboard the ALBATROSS, in all the major reef areas of the world, those of J. Stanley Gardiner in the Indian and Pacific Oceans in the first part of the twentieth century, that of Wood-Jones on Cocos-Keeling, results published in 1909 and 1910, and that of Gibson-Hill, also on Cocos-Keeling just before World War II. David Stoddart made three detailed geomorphological studies of the British Honduras reefs and cays between 1959 and 1965.

Notable were a substantial number of cooperative investigations involving people with different interests and backgrounds. Among these have been the Royal Society's and the Australian Museum's expeditions to Funafuti, Ellice Islands, reported on by David and Sweet in a volume published by the Royal Society of London in 1904 and in papers edited by Hedley (1896-1900); the Great Barrier Reef Expedition in 1928-1929, under the leadership of C.M. Yonge (1930a, 1930b, 1931); the Carnegie Institution of Washington's Coral Reef Program, with work especially at the Dry Tortugas Laboratory and in American Samoa and Tahiti in the first third of this century. Involved in this were especially Alfred G. Mayor (Mayer), W.A. Setchell, and T. Wayland Vaughan; some of their publications are listed in the references.

After World War II came a comprehensive program of work on Bikini and Eniwetok Atolls in connection with the atomic weapons tests there (Ladd, 1973). This work is published as an enormous series of papers collectively known as USGS Professional Paper 260, parts of which are still appearing. The USGS-Army Map Service Far East survey of the Northern Marshall Islands in 1951-1952 led to many papers, especially the Military Geography of the Northern Marshall Islands and Atoll Research Bulletin 113 (Fosberg et al., 1956, Fosberg and Carroll, 1965), and a review by MacNeil (1972).

During the 1950's the Pacific Science Board's Coral Atoll Program sent multi-disciplinary expeditions to Arno Atoll, Onotoa Atoll, Raroia Atoll, Kapingamarangi Atoll, and Ifaluk. In 1958 and 1960, under this same program were two expeditions to Jaluit Atoll to study the effects of Typhoon Ophelia. Reports were published in the Atoll Research Bulletin. ORSTOM, the French overseas research organization, sponsors a multidisciplinary study of coral reefs around Nosy-Bé, Malagasy. From 1967 to the present time the Royal Society has sponsored continuing work on Aldabra Atoll and other southwest Indian Ocean coral islands and reefs. A small research station is now maintained on Aldabra to continue this work. Preliminary results are presented in Philosophical Transactions of the Royal Society of London vol. B, 260, 1971. A comprehensive discussion of the geology of Aldabra has been published recently (Braithwaite et al.

1973). The Fondation Singer-Polignac during the 1960's sponsored a number of expeditions to New Caledonia and French Polynesia, and maintained a research vessel in the area for this purpose. Results are published in Cahiers du Pacifique and in a series of beautifully illustrated Mémoires. In connection with the nuclear tests on Mururoa, Tuamotus, the French government sponsored an extensive series of investigations in the Tuamotus, especially Mururoa, and in Clipperton Island. Reports are published in Cahiers du Pacifique and in a series of duplicated papers on Clipperton Island. In 1971, a small research station ("Antenne de Tahiti") of the Muséum National d'Histoire Naturelle, Paris, was created in Moorea, near Tahiti, to continue such research, and an impressive list of papers is already available, several of which are cited below (Chevalier, Denizot, Salvat, etc.) The marine station of Endoume-Marseille has for some years sponsored coral reef investigations at the marine station at Tulear, Malagasy, comprehensive reports have been published in special issues of the Recueil des Travaux series and later of Téthys. A general description of the reefs of Madagascar was presented by Pichon (1972).

The University of Hawaii recently acquired a station on Fanning Island in the Line Islands and during 1969 staged a broad-scale NSF-sponsored investigation of the Fanning Islands reefs. The results have been published in Pacific Science (April 1971) and in a special report issued by the Hawaii Institute of Geophysics (Chave, ed., 1970); this is a continuing program, and further results can be expected. Since 1968, a University of Hawaii Sea Grant project to study various quantitative aspects of reefs and reef biota in Kaneohe Bay, Oahu, has been underway. The first results of that program have been published (S.V. Smith et. al., 1973).

The work of several other surveys is mentioned throughout the following sections though the present discussion is by no means exhaustive.

PHYSICAL ENVIRONMENT

Much of the oceanographic work carried out in the tropical seas in the past, and especially in the last 25 years, is a source of environmental data on coral reefs. One example is work on surface currents, of significance in the distribution of reef and island biota. Specific research on atolls and reefs, however, has been pursued only by a small number of investigators and with a limited scope. Work at Bikini Atoll (von Arx, 1954; Munk and Sargent 1954) has delineated the circulation pattern within the lagoon that is established in response to prevailing winds and influenced by tides, waves, and local ocean currents. The Bikini study, as well as the research at Fanning Island (Gallagher et.al., 1971), provides volumetric estimates of exchanges of water between lagoon and ocean. Fanning Island investigations also produced measurements of salt and heat fluxes. The waters of the Great Barrier Reef have been studied by Brandon (1973). These studies and others devoted to specific physical parameters on reefs can contribute guidelines for an ecosystem model, but the majority of oceanographic projects on reefs have not included coordinated studies of interactions of the physical environment

with the biological reef communities; see for instance the work of Van Dorn, and Vastano and Reid, on Wake Island.

Atoll meteorology was mostly limited, prior to World War II, to sporadic weather records (see for instance those used by Sachet, 1957), observations on storms and hurricanes, and the like. With World War II action, and the atomic tests in the Pacific, as well as the increase in geophysical research generally, much more information in meteorology and climatology has become available. Weather data are more complete and collected from more stations. Summaries such as those of R. C. Taylor (1973) and Zipser and Taylor (1968), and volumes of data such as those prepared for U.S. Joint Task Force Seven, are a few examples among many, which supply important data in the study of atoll ecosystems. See also studies by Montgomery (1973) and Quinn and Burt (1970), and the very detailed work of Blumenstock and Rex (1960) on Eniwetok. Even more closely related to the ecosystem approach are papers describing hurricanes, typhoons and other storms, and their effects on reefs and islands. The work of Blumenstock and others (1958, 1961) on Jaluit, that of Stoddart on the British Honduras reefs (1963, 1969d), and the Solomon Is. (1973), of Sachet relative to Clipperton (1962b) are a few examples.

More general work on hurricanes and other meteorological phenomena is included in the work of Ramage and others, in the U.S. Navy Atlases (1956-68) and many other useful sources.

Atolls have also been used as "observation platforms" (Lavoie, 1963) in atmospheric and other studies, notably by the Hawaii Institute of Geophysics and the U.S. Joint Task Force Seven (e.g. McCreary 1959).

GEOLOGY

The geological record of fossil reefs has been the subject of exhaustive studies, especially by petroleum geologists, and some of the reviews and bibliographies cited above are concerned with fossil reef studies, including paleoecology. Those references will not be detailed here (but cf. Ladd, 1957; Laporte 1974). Suffice it to say that a vast amount of knowledge of fossil reefs has accumulated, from which studies of modern reefs can derive data as well as ideas (Hedgepeth, 1957). To a certain extent, of course, the fossil and modern reefs cannot be separated. The modern sections of the reef are considered here to be material deposited in relation to present sea levels, approximately during the last 5,000 years.

Since the late 19th century, modern coral reefs have been studied by geologists primarily to provide information on pre-existing environmental conditions documented in the lithological record of the geological column. With few exceptions these studies have concentrated on descriptions of reef components rather than on the processes responsible for component formation. However, much attention has been paid to the influence of sea level changes on the nature of present-day reefs (Fairbridge 1958; cf. Stoddart 1971).

Studies of reef morphology (reviewed by Stoddart, 1969a) generally have included mapping bottom topography at intermediate scales (1:50,000) and describing topographical zonation and size of features in such terms as mean reef width, knoll dimensions, etc. (e.g. Emery et al. 1954). There have been few quantitative studies of reef features, apart from the work in Kaneohe Bay, Oahu, by Roy (1970a), at Fanning Island by Roy and Smith (1971), and in the Maldives and elsewhere by Stoddart (unpublished).

Many studies concern the mineralogy, composition, and texture of reef and near-reef sediments with a view to understanding sequences in the geological record (e.g. Ginsburg, 1956; Neumann, 1965, Macintyre, 1970). Recent trends have been to examine CaCO_3 budgets in areas of carbonate sedimentation (Stockman et al., 1967; Neumann and Land, 1969; Land, 1970; S.V. Smith et al., 1970, 1971; S.V. Smith 1971a, 1973; Chave et al., 1971). Such studies have only considered some (or even only one) of the components in the budget; or they have integrated the components of the budget across a very restricted environment; some have not even dealt with tropical reef systems. What is needed now is the generation of a total carbonate budget through time, in order to describe the relationships among reef development, sediment generation, sediment transport, and subsequent deposition.

Little information is available on former zonations in various stages of reef development, yet work on specific problems associated with coral reefs has indicated that significant data may result from exposing internal reef structures: Shinn (1963) investigated the origin of spurs in reefs off Florida and subsequently (Ginsburg et al., 1967) studied marine cementation and internal sedimentation within reefs off Bermuda. To date, rather little coring has been attempted (Mayor, 1924; Cary, 1931; Ladd and Schlanger, 1960; Stoddart 1971) on modern coral reefs, with the result that the internal structures and limestone facies of these reefs are largely unknown. Most of this work has involved only one or a few core holes per reef. More detailed drilling with a submersible drill that can penetrate 2 meters into the reef is underway on reefs of Jamaica (L. Land, personal communication, 1970).

It has been suggested that living coral reefs consist of a thin veneer of modern reef growth over older foundations which generally dictate their present-day morphology (Newell, 1962; Stoddart, 1969a, 1973). However, modern reef construction has been shown to form massive wave-resistant frameworks, notably in Jamaica (Goreau, 1961b, Goreau and Land, 1974) and in British Honduras (Purdy, 1974).

Numerous workers have investigated growth rates (e.g. Vaughan, 1915; Mayor, 1924; Shinn, 1966) or calcium carbonate deposition rates (e.g., Kawaguti and Sakumoto, 1948; Goreau 1959; Goreau and Goreau, 1959; Goreau, 1961a) or general reef CaCO_3 production rates (e.g. Chave et al. 1971; S.V. Smith et al., 1971, S.V. Smith, 1973, Glynn et al. 1971), as well as skeletal framework destruction by mechanical (Stoddart, 1963; Glynn et al., 1965; Ball et al., 1967; Perkins and Enos, 1968) and biological means (Duerden, 1902; Otter, 1937; Yonge, 1963; Goreau and

Hartman, 1963; Bakus 1964, 1967; Neumann, 1966). However, concurrent investigations of most of these processes have not been carried out at a single reef site in order to determine the relative importance of the various parameters controlling the net accumulation of modern reef framework.

The success of framework construction depends largely on the growth rate of reef organisms. Other factors affecting construction include predation, competition between corals and other organisms, variation in distribution of coral and other species, biological erosion of skeletal framework and of frame-cementing agents, mechanical erosion, and the rate of sea level change. Cement infilling and lithification of internal sediment in various cavities tend to negate the destructive action of coral borers. For example, some coral heads collected from submerged reefs in the eastern Caribbean have been almost completely altered--through repeated boring, infilling, and lithification--to a dense micritic limestone (Macintyre, 1972).

Biota have long been thought to be the major frame-cementing agents, but in recent years extensive Mg-calcite cementation of reef framework and inner framework has been recognized (summarized in Bricker, 1971). The relation, if any, of biological agents to this cementation is not altogether clear. The origin of magnesian calcite cement remains unexplained, but chemical analysis of reef interstitial waters may offer some clues to the processes responsible for its precipitation.

Within the reef ecosystem, interactions between waters and solid CaCO_3 appear to be largely the result of biological calcification processes, or interactions between biogenic rock, detritus, and waters separated from open ocean waters--e.g., the waters within the interstices of skeletal fragments or the reef frame itself.

Direct chemical precipitation and solution reactions of CaCO_3 in seawater appear to be inhibited or prevented by interactions of dissolved organic compounds in sea water with CaCO_3 mineral surfaces (Chave, 1965; Chave and Suess, 1967, 1970; Suess, 1970). Chemical reactions between seawater and carbonate minerals may occur, for example, in the formation of ooliths, grapestone, whittings, and beachrock; but these reactions are, at best, minor in a coral-reef ecosystem, if they are inorganic at all.

Two interactions between reef waters and biogenic carbonates appear to be important when considering the flow of carbon in a reef ecosystem. First, recent reports indicate that chemical or biochemical precipitation of CaCO_3 within the reef is as important, or even more important, than biogenic calcification with respect to binding the components to form a rigid, wave-resistant framework (see Bricker, 1971). The second interaction between reef waters and biogenic carbonates is the removal of dissolved carbonate from interstitial waters of sediments and deposition of CaCO_3 within the sediment components (see Bricker, 1971). The importance of this interaction is not only that it represents a flow of carbon from seawater into the reef ecosystem but that the result of this flow directly affects the character and hydraulic properties of the sediment.

In order to understand fully the processes responsible for the precipitation of CaCO_3 , both in the framework and within sediment grains, it is necessary to investigate the whole reef CaCO_3 system--namely both water and rock chemistry. By studying the whole chemical system, it should be possible to determine whether the cementation process involves only an internal cycling of CaCO_3 , or whether significant amounts of CaCO_3 are derived from external sources.

The CO_2 system in seawater provides a unique link between geochemical and biological processes. The link is particularly important in coral reefs, where both calcification and organic carbon production-consumption greatly affect the system. The organic carbon transfer should be mentioned; it is sufficient for this paper to point out that (as discussed in some detail by Park, 1969) measurement of two parameters in the marine CO_2 system is sufficient to partition the system changes into inorganic CaCO_3 precipitation-solution and organic C production-respiration.

Separating changes in deep ocean CO_2 into solution and oxidation has been undertaken by several authors (e.g. Park, 1968; S.V. Smith, 1971a). Both S.V. Smith (1973) and Kinsey (unpub. data and personal comm.) have studied diel variability in the CO_2 system in coral reefs. S.V. Smith (1973) has related this variability² to organic carbon production and utilization and to calcification.

The present major limitation of these short-term studies is the small amount of change in the marine CO_2 system caused by inorganic chemical processes and organic metabolic activities of the reef communities. Kinsey's studies were performed on water which "aged" over several hours and consequently experienced easily measurable changes in the CO_2 system. Smith's studies dealt with water "aged" less than one hour therefore showing barely measurable perturbations in the CO_2 system.

BIOTIC ENVIRONMENT

The biotic components of the surrounding sea should not be ignored. Perhaps most important is the plankton, which is a significant food supply of the corals and many other reef animals. This has been studied with relation to reef animals by A.R. Emory (1968).

Small pelagic fish and fry are also food for reef-dwelling carnivorous fish, as well as for sea-birds. Predaceous pelagic fish visit the reefs and prey upon the reef fishes. The same is true of porpoises, other small cetaceans and pinnipeds.

Detritus of organic origin brought to the reefs by water movement is also an important input into the reef system (N. Marshall 1965). All these biotic components are discussed in more detail below.

TERRESTRIAL ECOSYSTEM

To the best of our knowledge, the only attempt at a generalization

of the functioning of the terrestrial coral atoll ecosystem is the description written in 1957 by Fosberg (1961, 1963b). That description attempts to conceptualize the system in abstract, non-quantitative, non-mathematical terms, and to indicate functional groups of entities in the system which can be studied in terms of their relationships to the whole. This work was not followed up except for extending it to high islands. It resulted logically from the general program for atoll studies proposed at two coral atoll research symposia sponsored in 1951 by the Pacific Science Board (cf. papers in *Atoll Research Bulletins* 1, 2, 1951, Fosberg ed.). Five expeditions planned to provide comparable descriptive and inventory data on atolls of different types were carried out (to Arno, Onotoa, Raroia, Kapingamarangi and Ifaluk). Their results, as well as those of many other studies of land (and marine) aspects of atolls were published over the next 20 years in the *Atoll Research Bulletin* and elsewhere. An attempt at bringing together this great mass of data was made by Wiens (1962), but it was not entirely successful in representing the world atolls as an ecosystem. Other qualitative descriptions of the island ecosystem are included in Numata (1967) especially those papers by Jackson, and Sachet. See also Stoddart, 1969c. An idea of the enormous amount of basic information available on the terrestrial aspects of coral atolls may be gained by perusing the 261 pages devoted to this subject in *Island Bibliographies* and 236 in its supplement (Sachet and Fosberg 1955, 1971).

From this wealth of data, and citing only a few specific references, we can derive a fair idea of components and processes involved in the terrestrial or cay ecosystem and influences on the adjacent submerged reef ecosystems. Some components and processes, such as nutrient content of ground water, salt spray, rain water, animal and plant bodies, and sediments, have never been quantified but can be measured by standard analytical procedures. Standing crops of the macroscopic organisms present no problem, but again, there are no quantitative data for coral islands. Estimates can be reasonably made by simple sampling, counting, and weighing procedures. Imports of organic matter (fish, squid, etc.) by seabirds and shore and wading birds into the terrestrial atoll ecosystem have never been estimated.

Some observations have been made on the ground water of atolls, beginning with Charles Darwin (1839), but mostly within the last few years (Fosberg, 1959; Cox, 1951; Arnou, 1954, 1955; Tracey *et al.*, 1961). The general nature of the atoll ground water lens has been established, but detailed studies of its behavior under varying conditions of geological structure and rainfall amounts and regimes, as well as of tidal ranges and regimes, are still required.

The terrestrial geology of certain atolls has been studied by a number of expeditions and individuals (e.g. Royal Society, 1904; Wentworth, 1931; Fosberg *et al.*, 1956, Newell, 1956; Fosberg, 1957a; McKee, 1958, 1959; Fosberg and Carroll, 1965; Sachet 1962b; Stoddart, 1962, 1969b). Very few quantitative measurements of sediments are available.

Fairly detailed soil studies are available for a few Pacific atolls (Stone, 1951; Fosberg, 1954; Fosberg *et al.*, 1956; Fosberg and Carroll,

1965; Tercinier 1956, 1969) as well as a general discussion of atoll soils (Stone, 1953). Most of the atoll soil types are very widespread and the patterns rather simple. There has been no systematic investigation to determine if Caribbean atoll soil types correspond to those in the Pacific.

The occurrence and origin of atoll phosphate rock in the central Pacific atolls were elucidated by Fosberg (1957b); and further observations have been reported by Stone (1953), Fosberg *et al.* (1956), Niering (1961, 1963), and Roy (1970b). Similar rock was described for the Indian Ocean atolls by Piggott (1968) and recently was found on Glover's Reef, British Honduras by Fosberg. Hutchinson (1950) deals in great detail with background information on phosphate accumulation.

Substantial information is available on atoll floras and vegetation (Fosberg 1949; Hatheway, 1953, 1955; Fosberg, 1953; Fosberg *et al.* 1956; Fosberg, 1957; Sachet 1962a; Stoddart, 1962; etc.) Pure stands of certain trees and shrubs are frequently found, an unusual occurrence in the tropics.

The land animals of coral islands are reasonably well known, but information, except for that on birds, is mostly scattered in monographs and papers on the groups concerned. A few papers specifically on atoll faunas are found in the Atoll Research Bulletin series and in the reports of the British Indian Ocean expeditions (Percy Sladen, etc.) of the early twentieth century. There is an extensive literature on atoll birds (listed and annotated by Sachet and Fosberg 1955, 1971). The atoll bird data have never been reviewed as a whole, but the Smithsonian field guides (Watson *et al.* 1963; King, 1967) and a number of regional papers (Amerson, 1959; Baker, 1951; Pelzl, ms.) are steps in this direction.

Atoll insects, as well as the insects of high islands, are discussed in the Pacific Insects and Insects of Micronesia series (Gressitt, ed.). Papers that deal with the interactions of atoll faunas are available for Arno atoll (Marshall, 1951) and the Tokelaus (Hinckley, 1969). Data on the consequences to the rest of the atoll ecosystem of the presence of large numbers of seabirds are brought together by Hutchinson (1950).

No work has been done on either terrestrial primary productivity or nitrogen fixation on atolls, nor is there much information on terrestrial food chains, predation or decomposition of organic matter under atoll conditions. Extrapolations may be made from other ecosystems, but it would be important to know just how well these extrapolations correspond to actual atoll patterns.

HUMAN INFLUENCES

The complex of human influences on and interactions with the cay ecosystem and the total reef ecosystem is quite apparent but difficult to characterize and summarize satisfactorily (Johannes 1970-71). The pesticide or, better, biocide, component is of general importance and is very probably pervasive in all parts of the system. This particular problem is dealt with specifically below. The nature of changes brought

about by human activity varies from obvious (Stoddart 1968a) and easily measured to very obscure and hard to estimate, but the importance of these changes to the system may not necessarily be proportional to their obviousness. Pollution in terms of addition of human wastes (sewage, etc.) can be estimated from standard figures and tables. The amounts and effects of solid-waste pollution are probably in proportion to amount of human activity on the cays and within the lagoon, with a substantial addition from drift materials washed in from the open ocean. An FAO conference on Marine Pollution (Ruivo, ed., 1972) included several accounts of pollution of reefs, atolls and lagoon (see especially Johannes, Chan, Bagnis). Increased sedimentation is another frequent result of man's activities, as exemplified by Kaneohe Bay, Oahu (Roy, 1970a). This latter problem is likely to be more severe on high islands than on atolls.

One of the most significant effects of human activity is the destruction and/or alteration of habitats of other organisms (Sachet, 1963; Jackson, 1967). The replacement of natural forest by coconut plantation is a good example (cf. Stoddart, 1968). Except for simple measurement of area, we know of no way to measure such changes or their effects, or, in many cases, even to assign specific effects to particular causes. This does not in any way minimize their importance. A volume edited by Fosberg (1963a), deals with islands including atolls, with special reference to man's role in their ecology.

The presence of a marine laboratory in Kaneohe Bay, Oahu, Hawaii, has led to a large number of studies concerning various aspects of human effects on the barrier and fringing reef complex there. Among the papers dealing with that bay are Bathen (1968); Roy (1970a); Smith *et al.* (1970, 1973); Smith (1971b); Caperon *et al.* (1971); Clutter (1972); and Johannes (1970, 1972). These papers have dealt primarily with the high nutrient level and rapid deposition rate in the bay.

Pollution of the biosphere by man-made chemical compounds has reached a level such that all faunal elements of the earth are contaminated (Risebrough *et al.*, 1970). These compounds are of two types: 1) biocides (primarily chlorinated hydrocarbons) manufactured and distributed specifically to eradicate or control "pest" organisms; and 2) chemicals manufactured for and used in industrial processes which "escape" from their intended area of use (primarily polychlorinated biphenyls and heavy metals). The accumulated literature on the distribution of these compounds is extensive but only recently have their physiological effects on metabolic processes begun to be elucidated. New information on induction or inhibition of various enzyme systems and chemical reactions by man-made chemicals becomes available with each edition of the pertinent journals. These physiological effects are especially relevant to marine organisms, since accumulation and biological concentration occur most readily in aquatic systems.

While biocides have been detected by all studies thus far designed to investigate their presence or absence, few such studies have been carried out on coral atolls; and little investigation has been made of

biocide accumulation in any level of the food web of a coral atoll. To our knowledge, the only non-marine data available for a tropical island are in unpublished information on Sooty Tern eggs from the Dry Tortugas, Florida, in which DDE and PCBs were present in all samples (W.B. Robertson, Jr. pers. comm.).

By an accident of geography, atolls have been the most numerous sites of atomic and nuclear atmospheric bomb-tests and, inevitably, the sites of pollution by radionuclides. Between 1946 and 1958, more than 59 tests took place at Eniwetok and Bikini atolls (Welander, 1969). Later Christmas and Johnston Islands were involved, and more recently, Mururoa and Fangataufa Atolls in the Tuamotus.

In the Marshall Islands, a survey of the ecosystem had been carried out prior to any tests (Ladd, 1973), and periodic resurveys followed. They gave rise to an enormous literature much of it in classified or hard-to-get AEC reports. Only after many years did papers appear in scientific journals of more general distribution, as well as in proceedings of conferences and symposia (see for instance papers by Beasley, Beasley and others, Held, Held and others, Nelson and Evans, Templeton *et al.*, and many others). Such information has not yet been integrated as a whole picture of radionuclide pollution on coral reefs and atolls, but much data continues to be accumulated. There is much less easily available information on Johnston Island, Christmas Island (Palumbo *et al.*, 1966) or the Tuamotus.

In the Marshalls, as the result of a catastrophic incident (Operation Castle, 1954) the effects of exposure to radiation on atoll human population became available for study. Detailed medical surveys of the exposed islanders have been carried out and repeated at regular intervals. See for example papers by Conard *et al.*, Robbins *et al.* and Lisco and Conard. The sociological effects of the Castle disaster, as well as those of the displacement of the Eniwetok and Bikini populations are other aspects of human interference with the coral island ecosystem (Stoddart 1968a). Many others, the impact of war on atolls, of organized migration, of changes in economic patterns, could be mentioned, but cannot be detailed here. This type of information is beyond the scope of this review, but it is obvious that anthropology and history can furnish evidence relevant to the total picture of coral island ecosystems.

MARINE BIOTA: BENTHIC PLANTS

Benthic marine algae make major contributions to primary productivity, nitrogen fixation, community structure, organism distribution, carbonate production, and reef consolidation and destruction. Setchell (1926, 1928) was probably the first biologist to recognize fully the variety and importance of these roles of algae in coral reefs, and much work has followed his pioneer effort.

Setchell (1928) described zonation of algae across the reef, as have Kanda (1944), Doty and Morrison (1954), Gilmartin (1960), Doty

(1967, 1970) and Tsuda (1970). Seasonal occurrence has been described by Bernatowicz (1952) and Denizot (1969), and measured on Guam by Tsuda (1972), and Dahl (1972) has analyzed community structure of Samoan algae. Dahl (1971) has also demonstrated that certain benthic algae are useful as ecological indicators and can even provide a continuous record of environmental conditions.

Studies on temperate and subtropical algae have demonstrated their importance in ecological investigations and have developed techniques for surveying field populations. Line transects can provide a useful basis for describing community structure and measuring seasonal variations, as in the work by Neushul (1967) on subtidal vegetation in western Washington, and the recent survey of subtidal ecology off southern California (Neushul *et al.*, 1967; Clarke and Neushul, 1967). Experimental techniques can add considerably to the field data on community composition and ecology (Neushul and Dahl, 1967).

Crustose coralline algae (Melobesioidea) may be at least as important as corals in the development of reef structures (Setchell, 1926; J.H. Johnson, 1961; Gross *et al.*, 1969). These algae have been especially noted in the Pacific, where they have given their name to the "Lithothamnion ridge," a striking but misnamed topographic feature of Pacific atolls; however, the importance of coralline algae to reef construction in general is probably greater than the extant reef literature would indicate (Denizot, 1972). In many areas of the Pacific (e.g. Ladd *et al.*, 1970; J.H. Johnson 1961) as well as in the Tethys Seaway (e.g. Lemoine, 1939; J.H. Johnson, 1965) and even in the Atlantic (Iams, 1969) encrusting coralline algae have been important or even the primary contributors to sedimentary formations. Considering the widespread occurrence of encrusting coralline algae, their importance in determining the nature of the substratum-water interface, and their presence in the Fossil record, they have been rather neglected. They are considered to be a difficult group (see for example W.R. Taylor 1960; Adey 1970) and have often been treated as part of the "dead" substrate. Adey has underway a detailed study of the role of coralline algae in the reef ecosystem.

Calcareous green algae (mostly *Halimeda* spp.) contribute greatly to loose sediments in certain areas of the reef, especially certain zones of lagoons (Chapman, 1901; Emery *et al.*, 1954; Hoskin, 1963). Stockman *et al.* (1967) and Neumann and Land (1969) have also shown the importance of the genus *Penicillus* in the formation of lime muds in Florida and the Bahamas. Land (1971) has studied the importance of sediment production by *Melobesia*, a red alga which commonly encrusts sea grasses.

The roles of boring algae and microbenthic algae have yet to be delineated in respect to calcium carbonate breakdown though Nestéroff (1956) and others ascribe to them a major responsibility for intertidal erosion.

Some attempts at including crustose coralline algae in regional studies of calcium carbonate budgets (S.V. Smith et al., 1970, 1972a) and in investigations of primary productivity (Marsh, 1970; Littler, 1971) have been undertaken. The results are preliminary, however, as there is likely a variation by several orders of magnitude in growth and metabolic rates, as a function of light, temperature, species, and even part of an individual plant considered (Adey and McKibbin, 1970). Some preliminary productivity measurements have also been made on reef algae by Doty (1971) and Soegiarto (1972). Recent studies have indeed shown that the alga-covered reef flat, a visually unimpressive and often ignored component of the reef community (Dahl, 1972), was in fact, twice as productive as areas of rich coral cover and supported large roving populations of herbivorous fishes (Johannes et al., 1972).

Symbiosis, or the occurrence of zooxanthellae within living coral tissues has long been known, but only recently has their role as nutrient acceptors been demonstrated (Goreau and Goreau, 1960; Muscatine and Hand, 1958). The zooxanthellae also play a significant role in the calcification of some corals (Goreau, 1961a, Goreau and Goreau, 1960). There is still considerable debate over the interaction between plant and animal components. Recent work has only begun to explore the variety of marine symbiotic relationships (see for example, D.L. Taylor 1969a, 1969b, 1971).

Information on grazing of algae by reef herbivores includes general observations on predation upon algae via studies of gut contents and results from caging; herbivore densities have not been reported beyond presence or absence, nor have the plant communities in which the experiments were carried out been rigorously defined (Randall, 1961, 1965; Mathiesen et al., 1972; Earle 1972). The slate-pencil urchin, Heterocentrotus mammillatus, has been observed to feed heavily on Porolithon sp. on the algal ridge of Bikar Atoll in the Marshall Islands, and to have a significant influence in the erosion of the reef edge (Fosberg, pers. comm.).

"Sea grasses" are locally important in tropical nearshore environments. In his monograph, den Hartog (1970) summarizes under each species what is known of its biology, its role as food for herbivores (e.g. Randall, 1965), and its function as a substratum stabilizer. Recently, the echinoid Diadema has been shown to graze heavily on Thalassia in certain situations in the Caribbean (Ogden et al., 1973). There have been rather few quantitative studies on the productivity of turtle grass (Thalassia testudinum), one of the more abundant and the best known species. Early studies were made by Pomeroy (1960), Odum (1957), and Jones (1968) on productivity measured by the O_2 method. However, closer inspection by Zieman (1968) has shown that this method is suspect for Thalassia productivity, as the leaves have the capacity to expand and store gasses in interstitial lacunae. This phenomenon has also been demonstrated by Hartman and Brown (1967) for the fresh-water species Elodea canadensis and Ceratophyllum dimersum.

INVERTEBRATES

It is impossible here to discuss the individual roles of the numerous groups of invertebrates in the reef ecosystem, or the enormous amount of available work basic to an integrated study of the system. Many pertinent papers on invertebrates have appeared in Cahiers du Pacifique, which also include bibliographies of certain groups, and in recent Symposium volumes cited pp. 1-2. This review will only touch on a few highlights of recent research on invertebrates in their functions in the system. Since coral reefs are almost entirely the result of biological activity, an analysis of reef development may be approached by examining structural activities (construction, maintenance, and destruction) and the contribution of the various biota involved (calcification by hermatypes, binding and baffling properties of some soft-bodied species, and biodegradation by a variety of invertebrates).

Work on growth rates or calcium carbonate deposition rates has been mentioned in previous sections. The minimal energy requirements of corals were investigated by Coles (1969), who concluded that three common reef species are capable of capturing and ingesting sufficient zooplankton to account for daily maintenance under laboratory conditions. Yet it was determined from a field study in Bermuda that the energy needs of corals were of an order of magnitude greater than could be met by the supply of drifting net zooplankton (Johannes et al., 1970). Obviously these metabolic studies are not conclusive

Further studies of coral metabolism should include examination of coral feeding and digestive mechanisms and the relation of these mechanisms to coral morphology and food type.

Hartman and Goreau (1970) have called attention to the sclerospores as an important constructional element besides scleractinian framebuilders in the sub-reef and deeper reef framework. It is also clear that many benthic reef invertebrates play an important role in maintenance processes. An example is that of the sponge Mycale laevis, which protects the lower surfaces of some massive corals from the destructive effects of boring sponges (Goreau and Hartman, 1966).

Although corals are commonly the principal animal contributors of skeletal materials to the framework and loose sediments that make up the reef, several other invertebrate groups can make substantial additions (especially mollusks, echinoderms, and Foraminifera). The latter, in addition to their commonly recognized role as stratigraphic markers, are frequently a prominent component of loose sediments. Some entire atoll beaches in the central Pacific are made up of the worn tests of Calcarina and Baculogypsina, two genera that inhabit windward reef flats. Homotrema forms conspicuous dark red crusts on the coral fragments seen on Glover's Reef and other atolls.

Skeletal framework destruction by biological means has been discussed above. Some processes are direct and obvious, such as the feeding of fishes, crabs, worms, snails, etc. on living corals. Notable also is the recent population explosion of Acanthaster planci which feeds upon and locally devastates reefs in Pacific areas (Antonius 1971a, Chesher, 1969; Newman 1970; Randall 1972; Atoll Res. Bull. 166-170, 1973; Micronesica, 9(2), Dec. 1973; and numerous other recent papers). Feeding of fishes on invertebrates, e.g. corals and sponges, was studied by Randall (1967), Randall and Hartman (1968), and Bakus (1967). Many endolithic boring and burrowing forms are also known (e.g. sponges: Goreau and Hartman 1963, and Ruetzler, 1971; sipunculids: Rice, 1969; mollusks: R. Robertson, 1970, and rates of destruction have been calculated for some of them (Neumann, 1966; Glynn et al. 1971).

Interactions involving invertebrates have been summarized for Western Atlantic reefs by Glynn (in press). Lang (1970, 1971) obtained information on the interspecific aggressive behavior of hermatypic corals, representing a feedback loop within a single functional component.

Research on the role of small interstitial animals in the coral reef ecosystem has lagged behind other areas of study. Preliminary sampling has indicated, for example, that groups such as Turbellaria, Nematoda, Polychaeta, and Crustacea are abundant in reef sediments, raising the possibility that they may provide a significant food resource for deposit feeders and possibly grazers and browsers (Renaud-Mornant, et al., 1971; Thomassin 1972; papers presented at the "Floating Symposium" (see p.2) by Thomassin, J.F. Grassle and other participants).

FISH (AND OTHER VERTEBRATES)

The place of fishes in the budget of the reef ecosystem seems to have been elucidated perhaps in more detail than that of most other vertebrate groups. Except for the green turtle, the biology of which is being studied in various parts of the tropics (e.g. Frazier ms.; Ehrenfeld 1974), little consideration has been given to such other vertebrates as seals or sea-snakes, which are only locally significant. Sea birds have already been mentioned with respect to the terrestrial part of the ecosystem.

Estimates of fish biomass have been made by Odum and Odum, 1955 (425 kg/hect.); Bardach, 1959 (450 kg/hect.); Randall, 1963b (1590 kg/hect.) Brock, 1954 (1850 kg/hect.); and Goldman and Talbot, in press (200-2100 kg/hect. from different reef areas). These widely different estimates may be due in part to different sampling techniques and in part to the variation that is now known to occur between different parts of a single reef. As yet, there is no good information on differences between widely separated reefs, particularly from ocean to ocean. Some of the factors in fish biology which affect biomass may be detailed as follows:

Habitat selectivity is marked in reef fishes. Distribution is obviously affected by depth, shelter, food availability and competitive interactions. Various areas of the reef have different specificity in many zones. Up to 25 per cent of species may be restricted to single areas of the reef (Talbot, unpublished information).

From the work done on the movements of fishes on coral reefs (Springer and McErlean, 1962; Randall, 1961, 1962, 1963a; Bardach, 1958; C.L. Smith and Tyler, 1972; Moe, 1969; Winn and Bardach, 1960; Reese, 1964) it seems that the majority of reef fishes are restricted to a reef or even individual patch reefs, at least for long periods. Many species are territorial. Some few pelagic species such as some scombrids, carangids, and sharks, apparently move between reefs (Tester and Wass, personal communication). These species feed mostly on reef fishes.

Within their territories, many fishes have different feeding and resting areas and may move up to a mile or even more on daily feeding migrations (Winn and Bardach, 1960; Randall and Randall, 1963; Randall, 1963; Bardach and Menzel, 1957). Some fishes may have daily breeding migrations. Others may rest in caves down the deep reef front and feed on the reef flat or rest on patch reefs by day and feed over Thalassia beds at night. Some diel changes in distribution have been documented by Hobson (1965, 1968, 1972), Starck and Davis (1966), and Collette and Talbot (1972).

The food habits of West Indian and Pacific coral fishes have been studied by a number of workers, and this information forms a solid qualitative basis for further study (Hiatt and Strasburg, 1960, Suyehiro, 1962, Randall, 1967; Plessis 1972; Starck, Emery, personal communications). Few data on feeding efficiency and conversion are available for coral reef fishes, but a fair amount is known about metabolic rates in temperate freshwater and marine fishes. It appears that conversion factors could be used to calculate the metabolism of coral reef fishes. Some further work is needed, however, on selected species of different sizes, activity patterns, and feeding habits for accurate ecosystem modeling.

Most investigators who have worked on the problem of age and growth rates have found that conventional techniques are not always applicable to tropical fishes. Recent work (Moe, 1969) has shown, however, that otoliths can be used for some species, and size-frequency techniques as well as aging population dynamics may yield data for representative species (Gulland, 1970).

Relatively little is known of the reproductive biology of coral reef fishes (Breder and Rosen, 1966). Fishes exhibit a wide variety of reproductive mechanisms, from extreme parental care (e.g. mouth breeding) to random scattering of eggs. A few species have been shown to undergo daily or annual breeding migrations (Randall and Randall, 1963; Reinboth, 1973; C.L. Smith and Tyler 1972). Sex ratios are greatly variable, and several types of hermaphroditism are common

Fecundity, recruitment, and egg and larvae losses are perhaps most poorly known.

Reef fishes can also play a role in reef destruction. Bardach (1961) has documented the role of destruction by fishes on Bermudian reefs, while Glynn *et al.* (1971) have done likewise for fishes on the Pacific reefs of Panama. Grazing by parrot-fishes and some other reef fishes is commonly observed on reefs in all areas.

PLANKTON

At present, the quantitative contribution of phyto- and zooplankton to the reef ecosystem is unknown. Estimations of the standing crop of zooplankton around coral atolls and in the lagoon areas can be found in M.W. Johnson (1949, 1954), Gilmartin (1958), Mahnken (1966), Barnett (ms.), O.A. Mathisen (1964), Odum and Odum (1955), and A.R. Emery (1968). Most investigators have found that the biomass of zooplankton in the vicinities of reefs and atolls and inside coral reef lagoons is higher than the biomass in the open ocean at the same latitudes, yet the reef zooplankton biomass has probably been underestimated due to the inadequate sampling of epibenthic (hovering above the water-bottom interface or within the coral heads) and neustonic (near surface) forms. Present estimates of zooplankton biomass, however, are orders of magnitude (Odum and Odum, 1955) smaller than estimates of benthic organism and fish biomass.

The standing stock of phytoplankton has been expressed by chlorophyll-A values (N. Marshall), but conversion of these values into carbon is unrealistic without further analysis.

The literature does contain information on such necessary inputs to tropical phytoplankton as light, nutrients, and trace metals (Strickland, 1960; Jeffrey, 1968). One common component of the coral reef water column, *Trichodesmium*, has been studied extensively (Prabhu *et al.*, 1966; Calef and Grice, 1966; Goering *et al.*, 1966; Ramamurthy and Seshadri, 1966a, 1966b; Ramamurthy and Krishnamurthy, 1967).

It is obvious that many reef organisms feed on zooplankton. Quantity of plankton utilized by one reef assemblage in Puerto Rico was determined by Glynn (ms). Glynn (in press and ms.) has also given quantitative data on feeding activity of fishes and invertebrates on zooplankton as well as data on zooplankton recruitment (Glynn, in press).

NUTRIENTS AND DETRITUS

Studies of total community metabolism on atoll reef flats situated in largely unidirectional currents were initially developed by Sargeant and Austin (1949, 1954). Their method has been applied in a number of later studies (e.g. Odum and Odum, 1955; Kohn and Helfrich, 1957; Gordon and Kelly, 1962; Milliman and Mahnken, 1961; Qasim and Sankaranarayanan, 1970; Odum *et al.*, 1959). The method was first used in a comprehensive

manner at Eniwetok in 1971 during Project Symbios (Johannes *et al.*, 1972). That project proved without doubt the efficacy of this approach; for instance, the symbios studies explained why reef communities are so productive biologically though bathed in waters very low in plant nutrients. Nitrogen fixation and unusually efficient recycling of phosphorus within the community are apparently responsible. These two phenomena, therefore, should now be focused upon at the subcommunity and species levels. Random searching, species by species, would probably not have revealed the great quantitative significance of these processes.

Net reef photosynthesis and total nighttime respiration can be determined by measuring the increase in the oxygen concentration in the water as it crosses the reef during the day, and its decrease at night. Another method which can help monitor community productivity and respiration uses changes in the CO₂ system (S.V. Smith, 1972). The system was analyzed according to some of the calculations outlined by Park (1969). This approach has a number of advantages (cf. S.V. Smith, 1973; Smith and Marsh, 1973; Kanwisher, 1963).

Still another approach to community metabolism consists of measurements made in fenced enclosures with the water surface open to the atmosphere; it has been successfully used to a depth of 1 m on the Great Barrier Reef by Kinsey (1972, and unpublished observations).

The reef imports organic matter from upstream in the form of zooplankton and exports it downstream in the form of mucus aggregates and algal detritus (N. Marshall, 1965; Johannes, 1967, Johannes *et al.*, 1972). This transfer is likely to be of great significance in lagoon ecology and potential aquaculture.

A curious result of recent studies at Eniwetok (Pilson and Betzer, 1973) has been to demonstrate that levels of dissolved phosphorus change remarkably little across the reef. The mechanism by which this constancy is maintained is by no means clear as yet. It may be that organisms paving the reef constitute a significant phosphorus sink and that exchange between this sink and the overlying water constitutes a mechanism for buffering phosphorus levels in the water. Such a mechanism has been demonstrated between sediments and the overlying water in salt marshes by Pomeroy *et al.* (1965, 1967, 1971).

ECOSYSTEM ANALYSIS

Interest in a mathematical representation of ecological phenomena developed early in connection with the dynamics of populations and epidemics. Names such as Malthus, Pearl, Merhulst, Lotka, and Volterra will always be cited in any history of mathematical ecology. At the present time, much active research centers on extensions and elaborations of the original Lotka-Volterra competition equations. This approach is particularly popular in population ecology.

In community and ecosystem ecology, the dominant models currently

used are compartment models. They deal with storages and flows of energy and materials in systems and have been usefully complementary to chemical and radiobiological techniques developed and utilized in ecology during the last twenty years. They will continue to be important, despite suggestions that ecologists expand their mathematical horizons (e.g. Clymer, 1972) precisely because of this compatibility with current and prospective experimental methodology. The current status of systems modeling in ecology is summarized by Patten (1971, 1972). A model from a geological view point is presented by Macintyre et al., 1974.

The International Biological Program (IBP) has been instrumental in accelerating the pace of development of total ecosystem modeling (in particular with the Analysis of Ecosystems Project of the U.S. IBP). All the Biome Programs (Grassland, Deciduous Forest, Desert, Tundra, Coniferous Forest, etc.) are committed to some form of mathematical ecosystem analysis. Progress to date has been variable, and the degree of emphasis also differs from program to program. The Grassland Biome Program is explicitly engaged in total ecosystem modeling (cf. Bledsoe et al., 1971). Others (e.g. Deciduous Forest, Desert) are emphasizing process models as potential modules for eventual total ecosystem models.

The general philosophy and methodology of the ecosystem analysis approach as developed for reefs at the Glover's Reef workshop are described elsewhere in this issue by Dahl et al.

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