ATOLL RESEARCH BULLETIN

No. 81

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by

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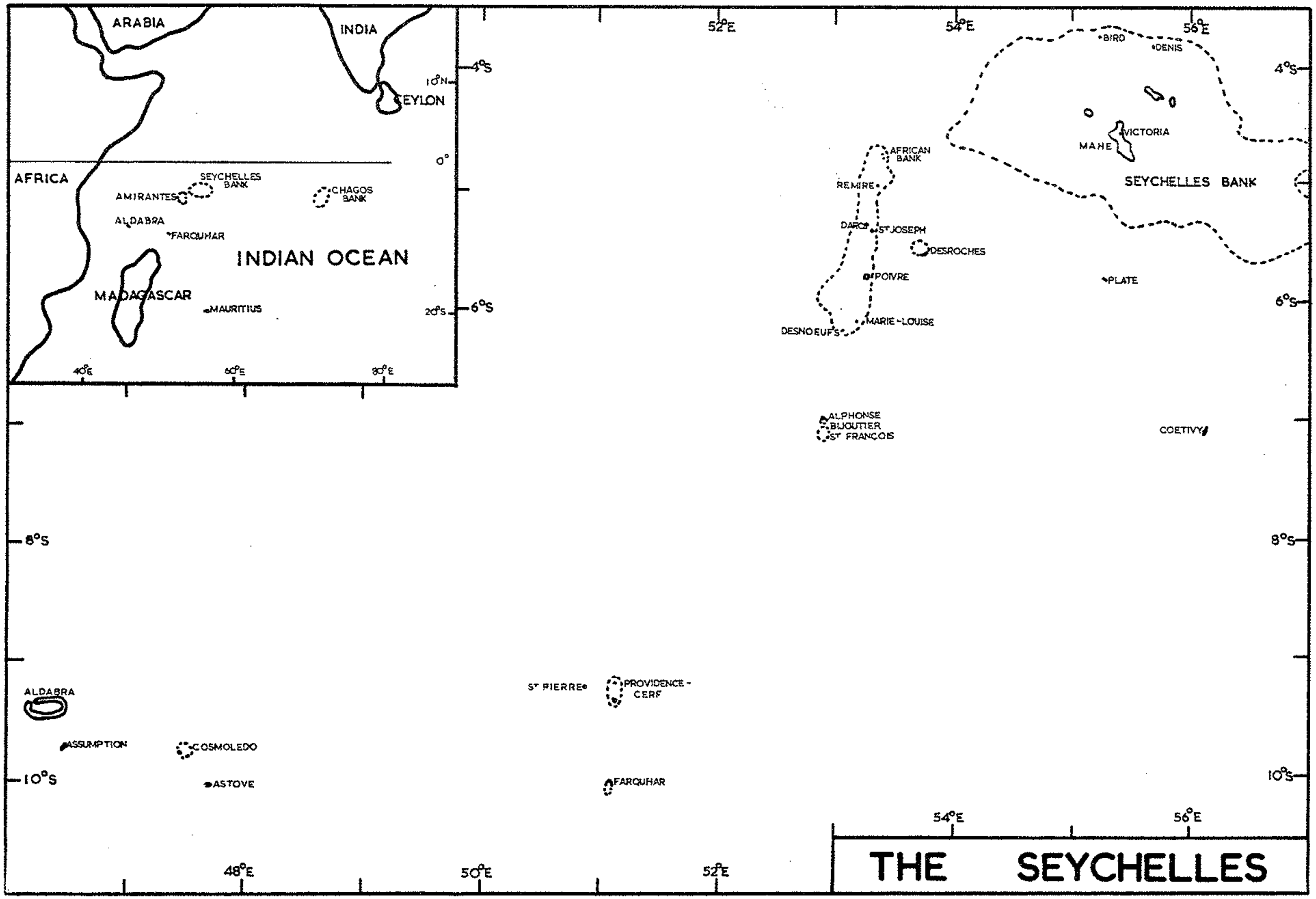
Issued by

THE PACIFIC SCIENCE BOARD

National Academy of Sciences--National Research Council

Washington, D. C.

December 31, 1961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Qualitative Description of the Coral Atoll Ecosystem*

by F. R. Fosberg

A coral atoll may be described, in the briefest terms, as a cap of limestone of organic origin on a mountain on the floor of the ocean, rising to or only slightly above sea level. Some lie on shallow banks or continental shelves. The cap is commonly bowl-shaped on top with a ring-like ridge or reef surrounding a body of water termed a lagoon. Some parts of this reef may emerge above high tide level as islets. These may either be remnants of former higher reef levels or detrital accumulations. Much or all of the reef surface below mean low-tide level and down to depths where sun-light penetration is very attenuated is composed of communities of living plants and animals. In bulk, at least, these are mostly organisms that secrete limy skeletons. Accumulations of these skeletons make up, almost exclusively, the reefs and upper parts of the mountain down to the volcanic (or other) basement rock on which the reefs originally started to grow. The depth of this limestone is known for only a few atolls and may vary from at least 1400 meters to, probably, very much less.

The concept of the ecosystem, first proposed by Tansley (1935), is that of an interacting system composed of an environment and all of the organisms involved with it. It is normally an open system because there is a continuous, though variable, influx and loss of energy and material. Such a system is, of course, an abstraction constructed to facilitate understanding of the complex processes involved in a segment or class of segments of the biosphere. As such its extent is limited only by selection and definition of the segment or segments under study. Thus it may be varied, in different examples, from the smallest observable unit of environment in which organisms live to the entire world's biosphere as a whole with its total environment (Evans, 1956). As the ecosystem is only limited by the extent of the effective environment the maximum could be, theoretically, the entire universe. Practically, however, the definition will not ordinarily extend to the ultimate sources of energy, or even of material. It will be restricted to such extent as will best facilitate observation and understanding of the portion of nature under immediate study. This concept, of obvious and increasing utility but not too easy to handle, and never, apparently, used by its creator, has been, in recent years, adopted by a number of ecologists (e.g. Pitelka, 1955; Billings and Bliss, 1955; Oosting, 1956; Evans, 1956; Cain, 1956; Dansereau, 1957). No two have defined or formulated their ecosystems in exactly similar terms, nor is there any critical need, at this stage, to do so.

In this paper the coral atoll ecosystem will be described in terms of processes involving transfer or transformation of energy and material, with only incidental reference to the actual organisms involved in the system or to the physical structures found in the environment. It is

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* Presented as a part of a symposium on Algal Ecology, with Special Reference to Coral Reefs and Atolls, at the 9th Pacific Science Congress, Bangkok, Nov. 21, 1957.

recognized that in a complete account of such a system these aspects, also, would be described fully. For present purposes it may suffice to say that the biotic component of the system is composed of phytoplankton and zooplankton; free-living but bottom-dwelling animals and other heterotrophic organisms of many sorts; an enormous aggregation of sessile or fixed organisms representing most classes of algae, a few seed plants, and practically all phyla of invertebrate animals; and a diverse assortment of land animals and plants. Many of the marine organisms secrete skeletons of $CaCO_3$ which are added to the material of the substratum. This process forms a lattice-work of limestone in which free skeletons or loose fragments lodge. By several processes these may become bonded in such a way as to form a rather hard and resistant rock. This is built up in the form of a ridge or reef usually enclosing a shallow body of water or lagoon and rising variously to somewhat below, near, or just above high-tide level. This reef is ordinarily rather flat-topped, of varying width, with irregularities or islets extending above high-tide level. Waves commonly break on the outer margin and water flows from the sea to the lagoon and back to the sea over the flat or gently sloping reef surface or through gaps in it. The flow may be in and out with the tides, or in over the windward and out over the leeward sides. The islets are commonly composed in part or wholly of loose porous limestone debris and are mostly covered by vegetation that includes representatives of all major groups of land plants. The land faunas are made up of a large number of species of insects and other arthropods, worms, land molluscs, a few reptiles, some birds, and a few mammals, including rats and man. Larger islets may contain within their porous structures a body of fresh ground water floating on the underlying salt water and retarded by friction from free diffusion with it.

These atoll structures are found in most regions of the tropical and, more rarely, subtropical seas. Temperatures range generally between 75° and 85° F. or in full sun on land, higher, decreasing of course with increasing depth in the sea. General climates range from relatively dry, perhaps 600 mm. precipitation, to wet, 5000 mm. or more. The atolls are in trade wind, doldrum, and monsoon belts. Insolation is generally high, cloudiness low to moderate.

Most atolls are inhabited by human beings, some by relatively large populations. These exert a generally appreciable, often profound, influence on the functioning of the ecosystem. Of specific importance in this connection are the economic activities of planting coconuts, harvesting, drying, and exporting coconut meat, and importing in exchange various foods and other materials.

With this description of the general physical and biological situation, we may proceed to describe in more formal terms, the abstraction called the coral atoll ecosystem. This may be outlined as follows in 12 sections, lettered A to L.

A. Media.

B. Nourishment or inflow.

C. Production.

D. Transformation.

E. Decomposition.

F. Excretion.

G. Accumulation.

H. Turnover.

I. Miscellaneous other effects and processes.

J. Losses.

K. Balance.

L. Trends.

A. Media: The media in which the system exists are two--a layer of sea water and a superimposed layer of air. These, by the nature of the earth-system itself, are constantly changed by sea and air circulation. Through them, or by means of them, all exchange, gain and loss, of matter and energy takes place. These two media are the most universal and pervasive components of the ecosystem and at the same time its environment, influencing in some measure everything in the system.

B. Nourishment or inflow: Since the atoll is an open system there is a continuous addition of matter and energy in many forms. Fundamental, of course, is the daily increment of solar energy without which the system, in anything like its present form, could not exist. Its functioning is in almost every respect dependent on either photosynthetic or thermodynamic processes, which are dependent on constant addition of energy from the sun. The nourishment of organisms and the circulation of both air and water are important examples.

The energy of wind, mostly indirectly a form of solar energy, also exerts its force in various ways in the system. Most of this energy is received elsewhere and transported to the atoll.

The gravitational energy of both sun and moon contributes importantly to sea-water circulation in the form of tides. The movement of ground water in atoll islets also is influenced by tidal fluctuation.

Essential components of the media, such as O_2, N_2, H_2O, CO_2, as well as dissolved salts and suspended organic matter, and even living propagules and disseminules of organisms are continually renewed or carried into the system by air and ocean currents. Relative concentrations of the various components of the media are maintained at a rather constant level in this manner. The replenishment of the ground-water bodies in islets is dependent on incoming fresh water, mostly evaporated elsewhere and deposited as rain on the islets from wind-borne clouds. Surface currents, upwellings, trade-winds, monsoons and cyclonic storms are important aspects of the circulation patterns involved. The introduction into the system of phosphorus, on which organic activity is completely dependent, is believed to be controlled to a considerable extent by upwellings of deep-sea water. One important route of transport of phosphorus from areas of upwelling to the atolls is by means of fish-eating birds and their young which deposit phosphates in their excreta within the area of the system. Essential mineral elements, nitrogen, and organic carbon are also brought in by the birds at the same time. Organic matter, in the form of drifting plankton, driftwood, and dead organisms, is brought to the atolls by currents. Currents also bring small amounts of mineral elements in the form of pumice as well as in solution. Volcanic ash arrives by way of winds, especially high altitude winds.

Finally, with changing patterns of human activity on atolls, increasing amounts of imported foods and other materials as well as alien organisms are introduced into the system. These introductions are effecting various rather profound changes in the equilibria and altering greatly the physical appearance of the atolls.

C. Production: The elaboration by plants of basic organic materials from elements and simple inorganic compounds is termed production, in an ecological sense. Such elaboration provides the fuel and building materials for all other life processes. The effective capacity of a system for production is called its productivity.

(1) The most obvious productive process is photosynthesis, by which carbohydrates are elaborated. Algae and green plants utilize CO_2, H_2O, and energy from sunlight for this purpose. Such algae occur as components of plankton, within the cells of corals and other coelenterates, fixed on the reef surfaces, terrestrially on soil and rocks, and epiphytically on tree trunks. Mosses are found in many terrestrial situations on the islets, as well as on tree trunks, especially where they are shaded. Ferns and psilopsids are common growing on land and epiphytic on trees. Seed plants grow principally on land, but some are epiphytic and a few are marine, growing in shallow lagoon situations on sandy bottoms. All of these groups, together, account for the origin of most of the carbohydrates used in the system.

(2) The other essential type of production is the fixation of atmospheric nitrogen--its oxidation and elaboration into simple compounds. It is well known that this fixation is accomplished by bacteria in the soil and in nodules on the roots of certain leguminous plants. Less well known, but possibly more important in the atoll system, is fixation of nitrogen by blue-green algae. This occurs on the soil surface and possibly in fresh and salt water. Much of the nitrogen available to atoll organisms is probably fixed within the system, but important quantities enter the system by way of birds, rain, and ocean currents.

D. Transformation: The alteration of primary and fabrication of secondary organic compounds: This function may be viewed as a succession of processes, mostly involving a break-down of organic compounds and their re-elaboration into more complex ones. Some of these are of an enormous order of complexity (e.g. nucleo-proteins).

(1) Autotrophic plants, in the nourishment of their own protoplasm and elaboration of stored material, cellulose, lignin and other materials,

carry out the first major step in a series of turnovers of the products of photosynthesis. Of course, additional inorganic materials are incorporated by this process and many of the elaborated compounds are infinitely more complex than the original carbohydrates produced by photosynthesis.

(2) Heterotrophic (parasitic and saprophytic) plants carry this process a step farther in utilizing already elaborated complex substances, as well as simpler materials derived from their hosts and organic substrata. Here may be mentioned the utilization of dissolved organic matter in the media by facultatively heterotrophic planktonic algae as discussed by Saunders (1957).

(3) Animals, feeding on plants in various ways, convert plant organic matter into animal organic matter. The principal classes of processes by which this is accomplished are as follows:

a. Eating of phytoplankton by zooplankton.

b. Utilization of material produced by zooxanthellae, by their coelenterate hosts.

c. Reef grazing and boring.

d. Eating of land plants by animals.

e. Eating of dead plant parts by animals.

f. Parasitism of plants by animals.

(4) Secondary conversion of animal matter to animal matter is accomplished as a result of three well-known classes of processes, namely:

a. Predation.

b. Parasitism.

c. Scavenging.

These are carried on in a great number of different ways by a large number of animals. Reef grazing and boring are important here, too.

(5) Reconversion of animal matter to plant matter is not as conspicuous a process, but is important nevertheless. There seem to be no insectivorous plants on atolls, so this reconversion is principally accomplished by bacteria and fungi living mostly on dead, and occasionally on living organic matter. It is an interesting question whether zooxanthellae utilize in any way the materials of their hosts' tissues.

E. Decomposition (usually but unfortunately termed "reduction"): The destruction of the elaborated organic compounds and reconversion back to simple inorganic compounds and relatively inert organic residues: Two main categories of processes are involved here.

(1) Physiological oxidation (inappropriately termed respiration by many plant physiologists), which is the oxidation of carbohydrate materials within living cells releasing the energy required for other life processes. This process goes on constantly in all living things.

(2) Non-biological oxidation, both by burning and by the slow oxidation of dead materials that normally takes place on exposure to atmospheric oxygen, aided or not by hydrolytic and catalytic action.

The principal products of both sorts of processes are CO_2 and H_2O, with, of course, inorganic and inert organic residues. Chemical energy is released and converted into other forms.

F. Excretion (within the system): The release of waste products and residues by organisms into the media:

(1) In water CO_2 and O_2 are released, as well as excreta and soluble metabolic wastes. Calcareous and siliceous skeletons and oily material remain after disintegration of organisms.

(2) On land, likewise, CO_2, H_2O, O_2, and metabolic wastes are released in solution in air or water. Guano and other excreta, as well as dead bodies and deciduous, caducous, or severed plant parts are deposited on the surface of the ground to decompose.

G. Accumulation: Storage of materials in unchanging or very slowly changing form, i.e. temporary withdrawal of material (and energy) from free circulation in the system.

(1) In bulk the limestone from calcareous skeletons of plants and animals represents the greatest and most important accumulation, the principal component of the atoll itself.

(2) Phosphatic residues, mainly calcium phosphates, are present as phosphate rock, components of soils, guano, and at least in some atolls (e.g. Washington Island) as a phosphatic mud or sludge on the lagoon bottom.

(3) Humus, both as raw humus in *Pisonia* forests, and as more stable humic residues in A_1 horizons of soils, plays an important part in the functioning of the system. The acid raw humus contributes to the formation of phosphate rock, and the soil humus helps to maintain the soil in condition to support growth of larger plants and micro-organisms. Humus, though relatively inert, is continually undergoing a slow oxidation.

(4) Slight accumulations of charcoal, metal oxides, silica and silicates occur where human activity is significant. Silica from sponge, radiolarian, and diatom skeletons also occurs in minute amounts as well as small quantities of silicates from floating pumice.

(5) Finally, fresh water, in the ground-water lens, as well as in the several states of soil water, may be regarded as a temporary accumulation.

The organic matter and other substances in living organisms represent a large total quantity but, as they are in a constant state of turnover, should probably not be classed as an accumulation.

These accumulations, along with the materials in solution in the media, may be regarded as the reservoirs of materials on which the other components may draw for nourishment.

H. Turnover of materials and energy: Categories D, E, and F, above are to be classed as turnover. In addition several more processes may be so regarded.

(1) Re-use of CO_2 released by oxidation.

(2) Re-use of O_2 released by photosynthesis.

(3) Re-use of H_2O released by metabolic and external chemical processes.

(4) Re-use of fixed nitrogen, both from metabolic wastes and from primary biological oxidation.

(5) Re-use of mineral nutrients released by excretion and breakdown of organic materials.

(6) Withdrawal from and return of various materials to media.

(7) Withdrawal from and return to accumulations.

I. Miscellaneous other effects and processes taking place within the system.

(1) Inhibition by salt (NaCl). The organic activity in terrestrial situations seems subject to a considerable inhibition by the salinity of the sea-water medium. This inhibition results from difference in osmotic pressure, the chemical effects of absorption of excess sodium and chlorine ions and consequent inhibition of absorption of others. The number of land organisms completely adapted to the normal salt concentration of the sea is limited. Hence establishment of immigrant organisms is severely limited, and many of those that become established function at below their optimum levels. Salt water enters the land environment as wind-borne spray, as storm waves, and by diffusion through the ground. The conspicuous nature of the limiting effects of salinity may be a reflection either of the small extent of the land habitat and consequently great exposure to salt or of its probable geologically recent origin that has allowed little time as yet for evolution of a special atoll biota.

(2) Effects of sea-air interface: Category 1 is really only one of the consequences of the fact that the land portion of this ecosystem is a thin lens inserted in the general sea-air interface. The distribution of many organisms, marine as well as land, is influenced by the character of this interface. Aeration, principal release of energy from insolation, frequently an abrupt break in temperature gradient, local high salt concentrations resulting from evaporation, solution and other forms of

erosion of limestone, and the shaping of the contours of vegetation and control of its composition are all consequences of the nature of this interface. Many more could be enumerated.

(3) Shelter effects. One of the reasons for the diversity of animal life in such an apparently simple environmental complex may be the variety of habitats resulting from the surface irregularity of the several substrata. The vegetation, the deeply pitted rock, the porous soil, and the intricate nature of the reef lattice provide shelter of various types for a large number of species of animals (and plants, too) that have widely differing requirements.

(4) Burrowing and turning over of soil by crabs is an important factor in the process of incorporating organic matter into the soil. Crab burrows are very common on many atolls, and fresh mineral soil is often piled or scattered around their entrances. The mechanical tilling of the soil in this manner has been compared to that accomplished by earthworms in other habitats. It doubtless is a process of great importance, though no careful assessment of its extent or effects has been made.

J. Losses (or excretion from the system):

a. Of the principal substances lost from the system the first three listed below are present in such constant proportions in the media outside the ecosystem that the losses may be considered as balanced almost exactly by inflow. The others are fluctuating quantities and there is no exact relation between inflow and loss.

(1) CO_2 carried away by winds and currents.

(2) O_2, carried away by winds and currents.

(3) N_2, carried away by winds and currents.

(4) Fresh water dispersed into media and carried away by winds and currents.

(5) Nitrates and organic N, carried away by currents.

(6) Phosphates, carried away by currents in solution and suspension.

(7) Other dissolved mineral substances, carried away by currents.

(8) $CaCO_3$ carried away by currents in solution and suspension.

(9) Plankton carried away by currents.

(10) Dead animals and plants and detached living fixed organisms carried away by currents and storms.

(11) Birds and other organisms which migrate.

(12) Export of copra.

(13) Export of pearl shell, etc.

b. Energy losses:

(1) Light, by reflection.

(2) Heat, by radiation and convection and carried by winds and currents.

(3) Chemical energy lost with elaborated materials.

K. Balance: The resultant of all of the factors at work on the segment of the universe (or of nature) occupied by the atoll ecosystem is the atoll itself. It may be thought of as a system in a state of dynamic equilibrium with a positive offset represented by the physical mass of the atoll with its associated biota, the total accumulation of organic and mineral matter over and above that of the normal media--air and seawater--that otherwise would occupy the space. All the characteristics described serve to set the system off from the surrounding undifferentiated media.

L. Trends: With such complexity it is hard to estimate trends, though it may be easy to discern them. Over very long periods the trend is obviously toward greater accumulation of material and probably toward increasing complexity. This trend usually seems directly related to slow subsidence of substratum on which the atoll is built, and may be expected to continue. On a shorter time scale it is possible to suggest that during periods of general or eustatic rise in sea level mass will increase, by addition of calcareous material in layers. Biotic complexity may at the same time decrease somewhat with tendency toward loss of land habitats. With fall in sea level the trends may be the opposite--loss of mass by erosion and gain in biota with appearance of land habitats, increased activity of sea birds, and especially the results of occupation by man. Presumably for about the last 3500 years the latter trend has been generally maintained. Whether or not the last few decades have witnessed a change in this trend is uncertain.

It seems clear that these major trends and fluctuations are controlled by factors external to the system. The ultimate control of sea level is as yet by no means clear. The variation in CO_2 content of the air has been suggested (Plass, 1956) as a factor that determines, or at least influences, world temperatures, evaporation of sea water, accumulation of ice, and consequent effects on sea level. It has been suggested that the recent apparent reversal of the fall of sea level may be due to the vastly accelerated industrial activity which pours great quantities of CO_2 into the atmosphere. If this is a valid assumption it seems reasonable to think that the present rise will continue, probably at an increasing rate. Thus a prediction might be made that the presently observed loss of land above water by erosion may be accelerated by a rise in sea level and consequent submergence of much or all of the land area of atolls. Such predictions, however, rest on very insecure bases at present.

On a still shorter time scale are the effects produced by the occupancy of the atolls by man, and especially modern man. These effects tend to be drastic as far as the land portions of the ecosystem are concerned but trends are as yet hard to isolate. Certainly the replacement of the native vegetation by coconut plantations and the rise of the export of copra are notable and probably involve a complex of related or dependent effects. This change will probably continue but certainly at a decelerated rate, as land for expansion of plantations is becoming scarce. Augmentation of the land biota will probably continue as man's effect on the land environment continues. Pollution of lagoons will undoubtedly increase, with resulting encouragement to some organisms and ill effects on others. Fishing activities have tended to decrease with contact with civilization but this trend may probably be reversed and with use of such effective methods as dynamiting and poisoning the marine biotas may undergo considerable change. There has as yet been little attempt to measure the results of such factors so that here, as in other aspects of the system, estimation of trends is highly speculative. If such prediction is of interest, attention should be directed toward critical study of the details of the working of the system outlined above, to clarify it and fill in the parts that are at present inferential. It seems possible that if a firm understanding of this ecosystem is achieved it may be used as a model in terms of which to study other ecosystems.

Summary

The general physical and "physiological" framework of the coral atoll ecosystem has been outlined in terms of the media in which the system exists, nine categories of processes taking place within the system, the balance or dynamic equilibrium in the resultant structure brought about by these processes, and suggested trends in the state of this equilibrium. This highly generalized picture rests on a vast accumulation of facts and upon inferences drawn from them and from pertinent facts derived from study of related or analogous situations in other systems. It is hoped that this description may serve, until a better conception is devised, as a framework around which an understanding of this segment of nature may be built and as a guide for future research designed to clarify our knowledge and appreciation of coral atolls.

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