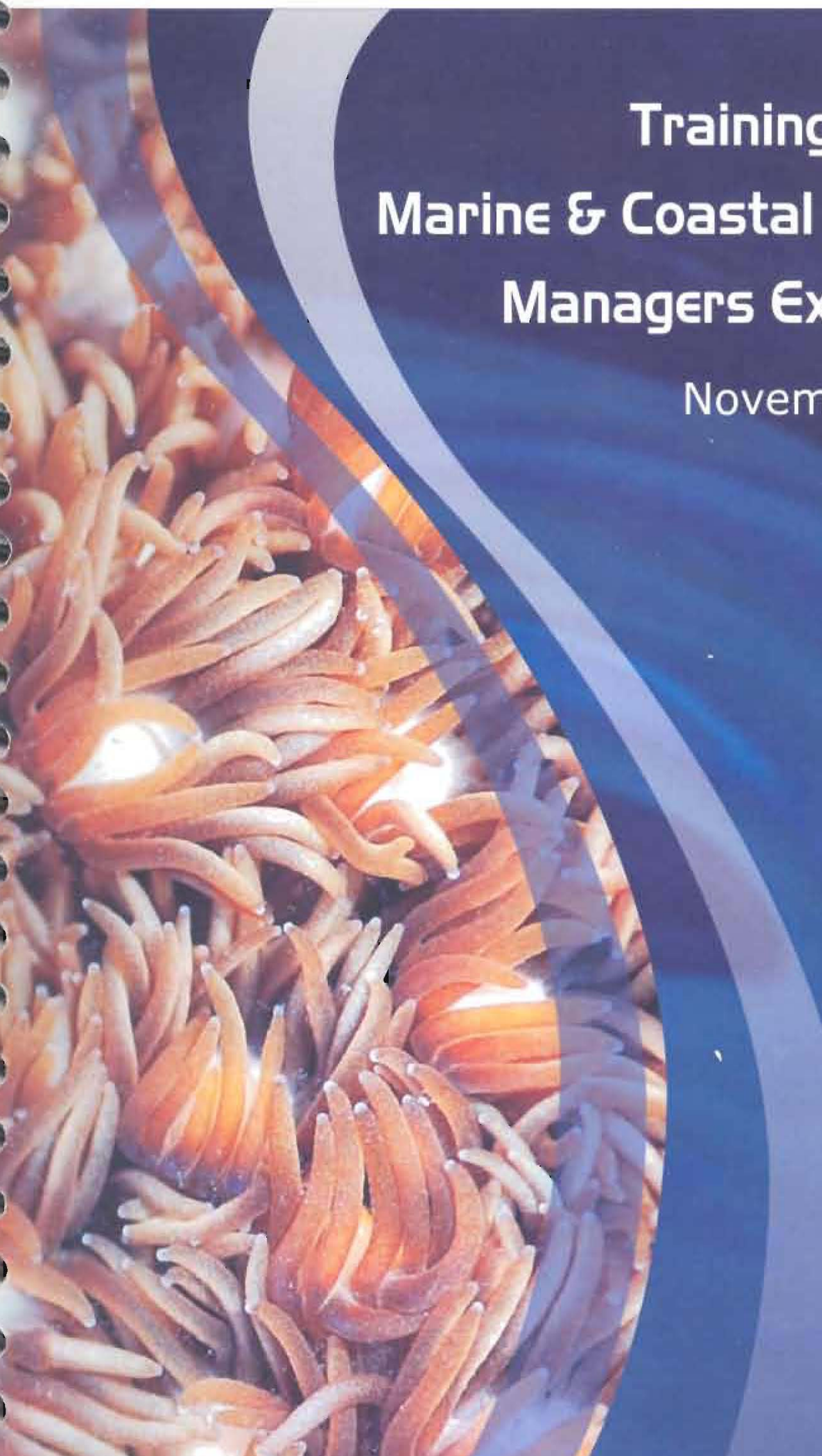


Training Workshop on Marine & Coastal Protected Areas (MCPA) Managers Exchange Programme

November 5-8, 2008

Reference Articles

Sponsored by

South Asia Co-operative Environment Programme
Sri Lanka

Ministry of Environment & Forests
Government of India, New Delhi

Organised by

Gujarat Ecological Education & Research Foundation
Gandhinagar, Gujarat

Foreword

The tropical coastline of the world is endowed with one of the most wonderful and magnificent creations of nature in the form of corals and coral reefs. Nature is at its best here, proving its undisputed superiority over everything human. The tiny creatures, which evolved millions of years ago, have, at places, built the reefs that are the biggest structures built by any living organism on earth till date. It is these structures, popularly known as coral reefs, that are home to a myriad of marine biodiversity forming an ecosystem that matches the tropical rain forests in terms of the richness of life forms that it supports. But, unfortunately in the last few decades they are under stress due to various anthropogenic pressures. The life forms that the nature took millions of years to create are under threat of getting lost in a relatively very short span of time.

Coral reefs are aragonite structures created by living organisms known as corals that are colonial cnidarians that secret an exoskeleton of calcium carbonate. The accumulation of skeletal material produces massive calcareous formations supporting a variety of live corals as well as other living organisms. Though, corals are found in temperate and tropical waters, they have a major presence in the tropical and subtropical coastal waters in a zone between the latitudes of 30^0 North and 30^0 South.

The South Asian countries significantly contribute to coral diversity and the extent of coral reef areas in the world. However, looking to the present stress experienced on this highly fragile ecosystem, there is an urgent need to have effective conservation action plan for corals. The first step towards effective conservation is to have proper understanding and networking among various Marine Protected Area managers so that sharing of experiences may lead to solution finding to different issues. South Asia Cooperative Environment Programme (SACEP), a group of inter-governmental heads in South Asia has taken an important step forward by forming South Asia Coral Reef Task Force (SACRTF). The present workshop, supported by SACEP and the Ministry of Environment & Forests, Government of India, of coral reef managers is expected to facilitate the process of mutual learning and the exchange of experiences among coral reef managers of maritime countries of South Asia- namely Bangladesh, India, Maldives, Pakistan and Sri Lanka. It is hoped that this 4 day training workshop- MCPA Managers Exchange Programme- would lead to better understanding and conservation of corals and coral reefs which would go a long way to improve the future management strategies.

The present compendium is a collection of reading material about the subject of the workshop which, I am sure, the delegates would find very useful.

With best wishes,

C N Pandey
Director,
GEER Foundation, Gandhinagar

CONTENTS

MARINE ECOSYSTEMS

J. Frederick Grassle
Institute of Marine and Coastal Sciences, Rutgers University

GLOSSARY

benthic Pertaining to the bottom of the sea or other aquatic environment.

benthos Organisms living on, in, or near the seabed or at the bottom of some other aquatic environment.

coastal Estuaries, semi-enclosed seas, and shallower regions of the ocean, including areas influenced by rivers and runoff from land.

community A group of species co-occurring in an area and interacting through trophic and spatial relationships.

coral reef Benthic environments characterized by reef-building corals with symbiotic dinoflagellates.

deep sea Volumes of water or areas of ocean bottom at depths greater than 200 m.

ecosystem A community of organisms and their physical environment interacting as an ecological unit.

habitat The locality or three-dimensional space occupied by an organism.

mangrove Environments characterized by mangrove trees.

nekton Actively swimming pelagic organisms.

pelagic Pertaining to the water column in aquatic environments.

plankton Organisms that float freely in the water column and do not maintain their position independent of water movements. Phytoplankton (literally plant plankton) is plankton with photosynthetic pigments and zooplankton is animals of the plankton.

MARINE ECOSYSTEMS may be defined as major units of ecological function in the marine environment. Ecosystems are communities of organisms and their physical, chemical, and geological environment—distinct assemblages of species coevolved with a particular environment over long periods of evolutionary history. As units of function, ecosystems have measurable imports and exports of material and energy. In comparison to ecosystems on land, ocean ecosystems have less clearly defined boundaries, a greater variety of major taxonomic divisions of organisms, and a long evolutionary history that preceded colonization of land. As the diversity of life in the oceans is explored, the importance of previously unrecognized aspects of ocean circulation, flux of energy and materials, and bottom characteristics to marine ecosystems are becoming better understood.

I. MARINE ECOSYSTEMS

A. Ecosystem Units

On land, ecosystems are separated into two-dimensional biomes, land areas defined by characteristic primary producing plants such as trees, grasses, and shrubs. Most shallow lakes and streams are similarly two-dimensional; however a few freshwater deep, ancient lakes, such as Lake Baikal in Siberia, and large rivers such as the Amazon have spatial complexity comparable to many coastal marine ecosystems. The ocean biosphere has an average depth of 4 km and comprises 99.5% of the biosphere. The dense seawater medium allows at least part of the life cycle of almost all marine organisms to be transported and dispersed by ocean currents. One ocean phylum is entirely pelagic, and about a third of the ocean phyla have representatives that spend their entire life cycle in near-surface waters as plankton. The boundaries that define ocean habitats and communities may involve a variety of overlapping criteria such as depth, distance from land, separation by landmasses, ocean currents, water masses of characteristic salinity and temperature, depth, and sea bottom characteristics such as sediment texture, composition, and surface topography. In addition, interactions with land and rivers and patterns of ocean circulation, light, nutrients, hydrology, and physical energy of water movements can strongly influence the distribution of species.

Descriptions of species boundaries are few and biogeographical classification depends heavily on the groups of organisms considered and how well they have been sampled. The ocean generally lacks the obvious barriers to dispersal characteristic of terrestrial environments. There may be multiple criteria for defining biogeographical provinces or marine ecosystems.

Major estuaries, where fresh water from rivers mixes with ocean water, are among the smallest individual ecosystem units in area. The largest units are regions defined by major boundary currents features such as the Gulf Stream, Kiroshio, and Brazil currents, and the north and south subtropical ocean gyres (the Sargasso Sea and South Atlantic Gyre in the Atlantic and the North Pacific Subtropical and South Pacific Subtropical Gyres in the Pacific). In the far north, the Arctic Ocean ecosystem is a distinct ocean basin covered by ice and the southern ocean around Antarctica is separated from the circulation of the Atlantic, Indian, and Pacific Oceans by the cyclonic circulation of the Antarctic Circumpolar Current.

As with terrestrial environments, marine ecosystems may be classified by their characteristic primary producers (i.e., single-celled phytoplankton that float in the surface layers of the ocean, marsh grasses, sea grasses, mangrove trees, seaweeds such as those forming kelp beds, the single-celled plants called zooxanthellae that live symbiotically with corals, and the chemosynthetic bacteria living in water, sediments, or symbiotically with other organisms at hydrothermal vents or other seep environments rich in chemically reduced compounds such as sulfide or methane).

Using combinations of coastline, coastal bathymetry, ocean current systems, surface winds, and biota, the near-surface pelagic layer of the ocean where primary productivity occurs has been classified into 51 provinces (Fig. 1) by Longhurst (1998). Similar criteria have been used to classify coastal areas (Briggs, 1974). Marine sediments cover almost the entire surface of the ocean floor, yet a consistent global biogeographic classification of these benthic ecosystems has yet to be developed (Snelgrove *et al.*, 1997).

B. Comparison of Marine Environments with Land

The ocean occupies 71% of the surface area of the globe and the deep sea at depths below 200 m occupies 63.5% of the earth's surface. Seawater is 830 times more dense than air and supports most of the biomass in the ocean. The volume of seawater in the ocean provides 99.5% of the livable volume of the earth (Cohen, 1994).

Concentrations of near-surface chlorophyll in the ocean are measured according to wavelengths of light reflected from the surface of the ocean, which are sensed by earth-orbiting satellites. Extensive studies of the relationship between near-surface chlorophyll and primary production allow satellite-derived information on chlorophyll to be converted to maps of primary productivity. Until very recently, overall primary production was thought to be approximately half that on land. Using distribution of chlorophyll in satellite photographs and models, primary productivity of the oceans has been shown to be about the same as that on land (~45–50 Pg C per annum in the ocean and ~55 Pg C per annum on land; Falkowski *et al.*, 1998). For regions without ice cover, average net primary productivity (NPP) per area in the ocean is a third of that on land (ocean: 140 g C m^{-2} $year^{-1}$, and land: 426 g C m^{-2} $year^{-1}$). Only about 1.7% of the ocean surface area has NPP greater than 500 g C m^{-2} $year^{-1}$ compared to 25% for land. Most productivity in the marine environment is from phytoplankton. Attached, multicellular algae contribute only about 2%. The highest productivity occurs in estu-

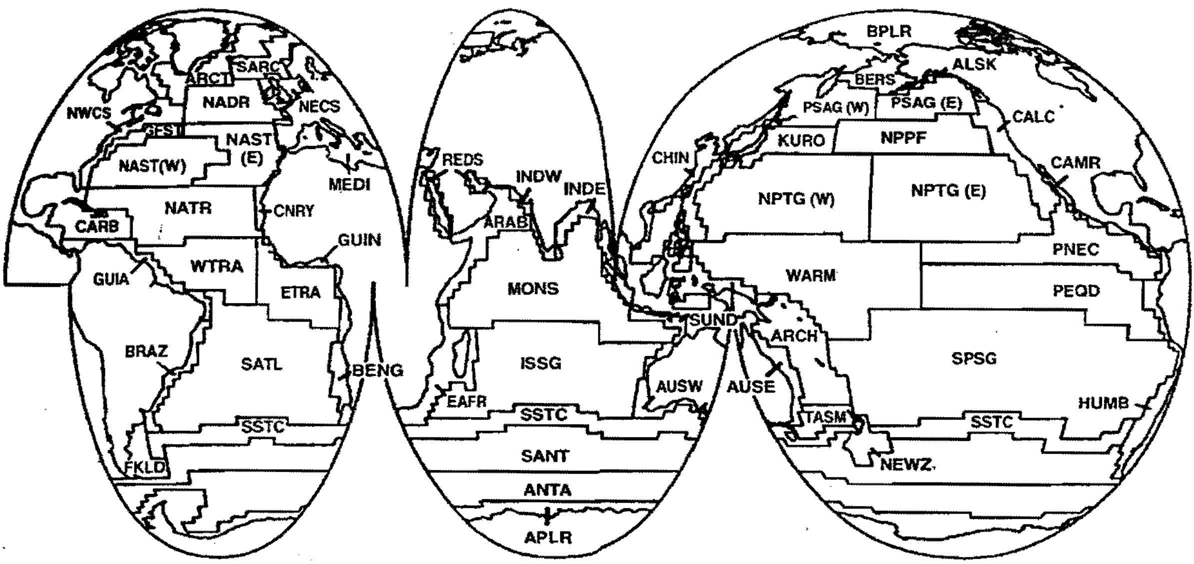


FIGURE 1 Pelagic biomes (Longhurst, 1998).

aries and upwelling areas—these highly productive areas contribute approximately 18% to net ocean primary productivity. In the open ocean, the greatest primary productivity is near the equator and at midtemperate latitudes in the Northern Hemisphere where there are regional maxima in terrestrial productivity. A smaller peak in productivity occurs in the Southern Subtropical Convergence where physical processes supply high concentrations of nutrients to surface waters (Falkowski *et al.*, 1998; Field *et al.*, 1998).

Marine primary producers are small and mobile whereas terrestrial primary producers are mostly large and rooted in the ground—trees account for approximately 80% of the primary production in terrestrial systems. By contrast, in central ocean gyres, photoautotrophic bacteria less than 2 μ in diameter and short generation times account for most of the primary production. Oceanic biomass is extremely dilute and filtering of organic particles is an important mode of feeding in marine environments.

Oceanic food webs have an average food chain length of nearly six trophic links as opposed to four trophic links in terrestrial systems (Cohen, 1994). The number of species of smallest marine organisms, such as the various groups of one-celled marine organisms, are extremely poorly known. The relationship between the spectrum of individual body size and the spectrum of rates of population growth differs in marine and terrestrial systems (Fig. 2). In open ocean food webs, the hierarchy of size is not apparent at the lower trophic levels because of the broad overlap in size of consumers and primary producers (Fig. 3, Karl, 1999).

The pattern of temporal variability of the physical environment differs between oceans and land. Marine ecosystems are characterized by about the same environmental variation over weeks and years as over days—variability is constant at frequencies ranging from days to decades. In terrestrial environments the variance of environmental parameters (e.g., temperature) increases steadily from frequencies of hours to millennia. Beyond 50 years the variance increases with increasing frequency as it does over the entire time spectrum on land (Steele, 1985).

On land, individual organisms have a high probability of surviving the relatively predicable patterns of environmental variation that occur over time periods up to decades. For example, individual trees and many vertebrate animals resist adverse effects of variation at all frequencies up to several decades because of their large size and long generation time. In the open ocean, time series measurements at a single station show that primary production varies significantly on periods from days to decades (Karl, 1999). Both seasonal and daily differences in cloud cover may result in three-fold variation in light at the surface. Vertical displacements of phytoplankton by internal waves further increase the amount of light absorbed by seawater before it reaches the photosynthetic organisms, creating a further source of variability. Small bacterial and flagellate primary producers have reduced the adverse effect of this variation

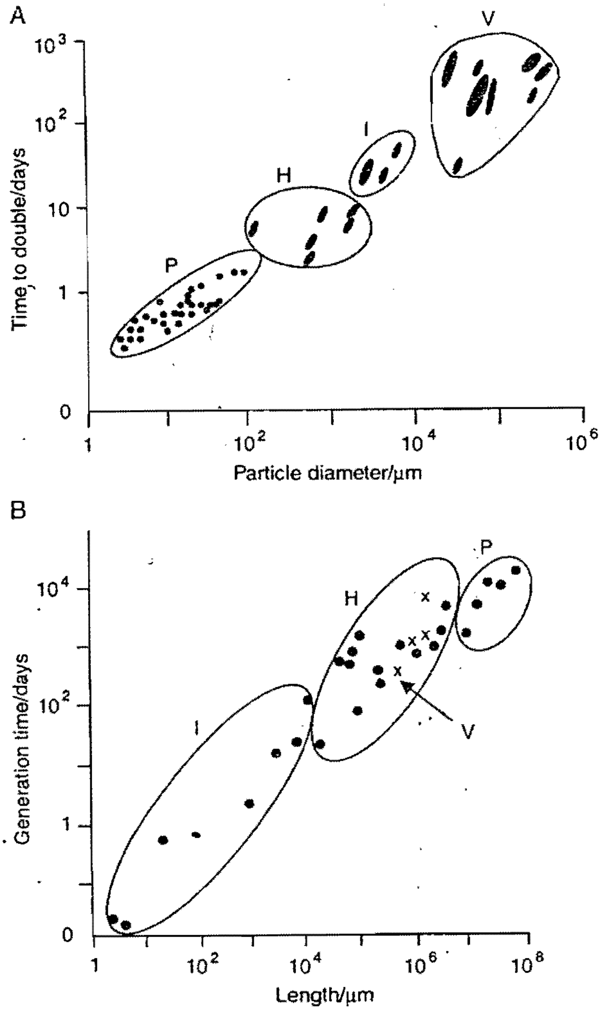


FIGURE 2 Relation of size to growth for plants (P), herbivores (H), other invertebrates (I), and vertebrates (V). (a) From Sheldon *et al.* (1972) for pelagic marine ecosystems. (b) From Bonner (1965, reprinted by permission of Princeton University Press) using only the terrestrial species. Derived from Cohen (1994, p. 60).

in light by supplementing their diet from the pool of dissolved organic matter excreted by other organisms.

Other distinctive features of marine populations are outlined by Cohen (1994) and in a U.S. National Academy of Sciences book on marine biological diversity (National Academy of Sciences, 1995). Plant and animal populations in marine ecosystems generally spend part of their life cycle as floating or swimming stages in the plankton. Unlike most terrestrial systems, the connections between benthic and planktonic life-history stages assume great significance and there is an unusually broad range of dispersal abilities, reproductive rates, and generation times. Almost all species have the ability to disperse in the water column as larval stages produced by some form of sexual reproduction. As a consequence, marine ecosystems are largely open and distant marine habitats can be linked by dispersing larvae. Terrestrial systems are more localized functionally and localized extinction of species occurs more frequently. Invertebrate predators and grazers generally have very high reproductive output, which makes population fluctuations more likely. Fluctuations at the highest trophic levels affect interactions among species at successively lower trophic levels. This cascading effect often has unpredictable consequences, and even the lowest trophic level of primary producers may be controlled from the top down. Bottom-up control of food webs is exerted through the effects of nutrients and physical processes on primary productivity.

II. BIODIVERSITY OF MARINE ECOSYSTEMS

A. Higher Taxa

The three main biological lineages are the Bacteria, Archaea, and Eukarya (includes plants, fungi, protists, and animals). Recent advances in molecular-biological techniques permit the first measurements of highly diverse oceanic assemblages of bacteria and archaea that cannot presently be cultured in the laboratory. Bacteria are more abundant in the photic zone and archaea are more abundant in deeper water.

The Eukarya (all taxa except the Bacteria and Archaea) are divided into 71 well-defined monophyletic groups with no apparent taxonomic affinity with one another on the basis of cell organization (Patterson, 1999). Each of these groups includes taxa formerly assigned to the protists. By this classification animals and their relatives the choanoflagellates, and fungi and their relatives the chytrids, are defined as a single group. Plants are in another group altogether with 11 categories (~7000 species) of green algae.

Important groups of primary producers have affinities with several other monophyletic groups. The red algae are a distinct group with about 4000 known species; the ~1000 species of dinoflagellates are related to the ciliates. The ~10,000 species of diatoms are in a highly diverse lineage that includes kelps and other brown algae. The conspicuous red, green, and brown seaweeds of rocky shores are divided among three separate lineages. The two most important primary producers in the open ocean were formerly called blue-green

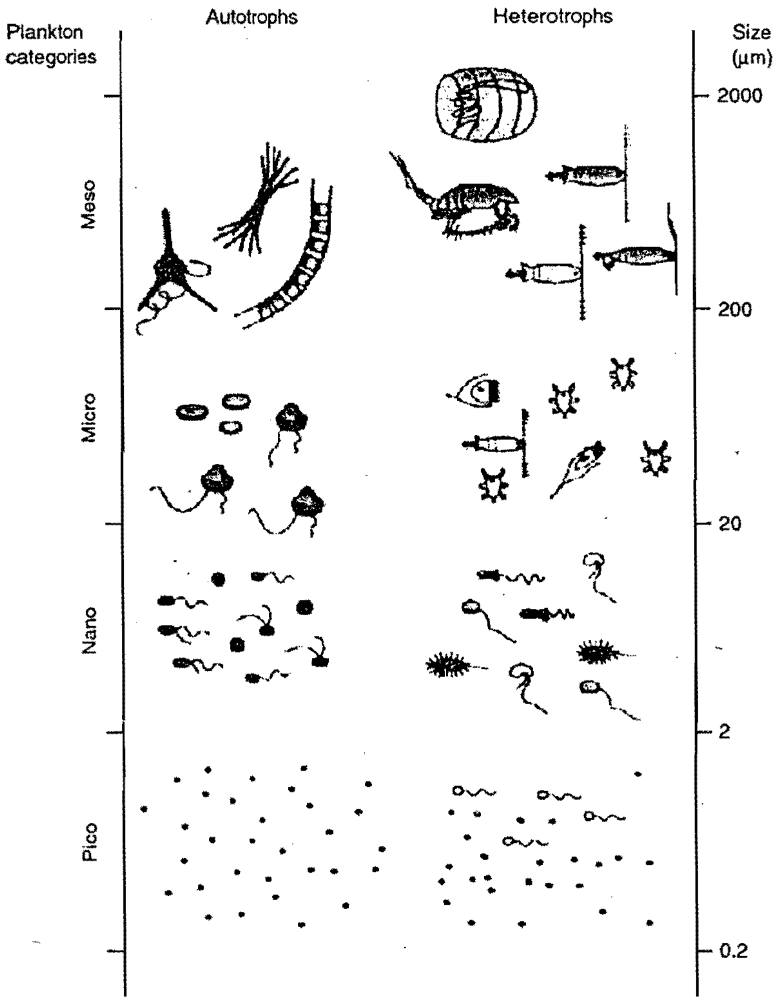


FIGURE 3 Representative classification of planktonic organisms by size showing the diversity of various autotrophic and heterotrophic groups. Size, per se, cannot be used to separate autotrophs from heterotrophs in NPSG plankton assemblages. Courtesy of Albert Calbet in Karl (1999).

algae. They are actually prokaryotic bacteria in two groups: the Synechococcus with three lineages, and the Prochlorococcus group with two lineages. These organisms account for most of the phototrophic standing stock and primary production in the open ocean (Andersen *et al.*, 1996).

Among the many nonphotosynthetic unicellular marine organisms, the ubiquitous Foraminifera are common both on the bottom at all depths and as pelagic organisms. Two abundant, poorly described benthic groups, the Komokiacea and the Xenophyophora (~40,000 known species), are big enough to be seen on the surface of deep-sea sediments. A leaflike form of Xenophyophora may be as large as 25 cm in diameter. These groups are separate lineages with no obvious relatives.

In the classification of marine, free-living, multicellular animals there are 29 phyla. Figure 4 (modified from May, 1994) compares the described diversity and abundance among marine benthic, marine pelagic, freshwater, and terrestrial environments. Of the 29 known Phyla, all are known to have lived in the ocean and 14, or about half, are known only from the ocean. Living representatives of the Phylum Onychophora are presently found only on land in the Southern Hemisphere, but are also known from fossil organisms that

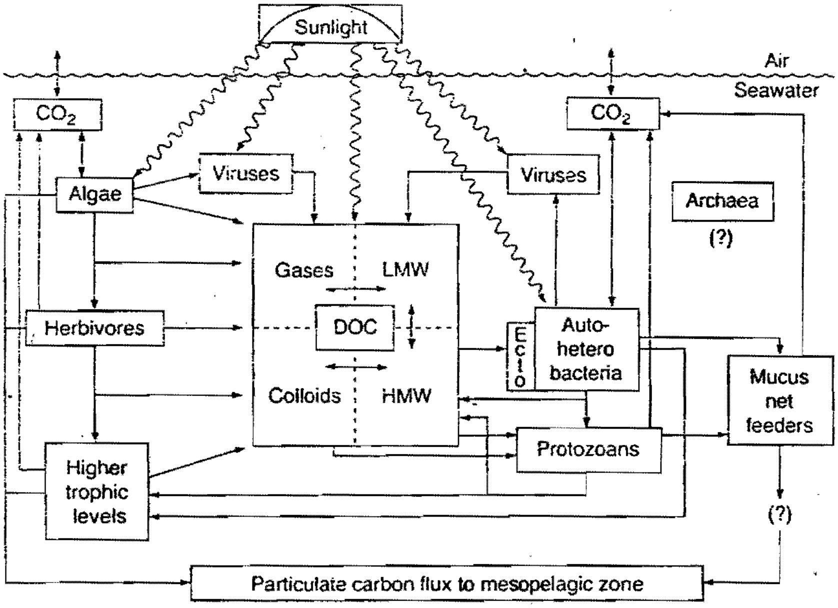


FIGURE 4 Schematic representation of the oceanic food web showing. On left, the classic pathway of carbon and energy flow through the photosynthetic eukarya to herbivores and on to higher trophic levels. Depicted on the right is the microbial food web, which uses energy stored in the nonliving, detrital carbon pool to produce microbial biomass that can reenter the classic pathway of carbon and energy flow. Cell-associated ectoenzymes (ECTO) enable bacteria to use high molecular weight (HMW) DOC in addition to the more traditional low molecular weight (LMW) and gaseous carbon substrates. Also shown in the microbial food web are viral particles and *archaea*. At the present time, there is only rudimentary knowledge of the role of archaea in the oceanic food web. Shown at the bottom of this diagram is the downward flux of particulate carbon (and energy), which is now thought to fuel most subeuphotic zone processes. The classic algae-herbivore grazer pathway is most important in this regard. From Karl (1999).

lived in the ocean more than 300 million years ago. Species diversity on land is dominated by insects and trees, groups that play a significant role only at the margins of the marine environment. Only about 15% of described species are found in the marine environment, but this may reflect the much greater cumulative effort devoted to species descriptions on land, rather than an actual difference in the number of species (May, 1994).

B. Species

Species are the basic units of evolution and represent the biological variability for future generations of life. For whole collections, species diversity is measured as the number of species and their relative abundances within and between habitats, regions, or other ecological or geographical units. Species richness is measured by collecting enough samples to represent very large numbers of individuals over very large areas. Ideally, communities should be sampled until the rate at which new species are found declines, and a plot of species versus area approaches a constant number of species. This level of sampling effort is achieved for groups with few rare species (e.g., larger animals including most vertebrates, planktonic organisms, and macrophytic plants). For species-rich taxa of bottom-dwelling invertebrates from coral-reef or deep-sea habitats, this level of sampling has not been attained. Where habitats are patchy and the vast majority of species are rare, it is seldom possible to collect and process enough samples to estimate species richness accurately.

For individual samples, indices based on the absolute number of species and the relative abundance of species are used to study species diversity. The most commonly used index is the Shannon-Wiener information function, H′, which equals the frequency of each species, $p_i = s_i/\Sigma s_i$ multiplied by $\log_2 p_i$ summed over the number of species (n) collected (e.g., $\Sigma p_i \log_2 p_i$). Another measure, Hurlburt rarefaction, calculates a species versus individuals curve for each sample based on the expected number of species in successively smaller subsamples drawn from an actual sample. These species diversity curves are especially useful in comparing samples of unequal size.

There are approximately 200,000 described species of animals in the marine environment (Table I). The most species-rich and least well known areas are coral reefs and the sediments of the deep-sea floor. There are no precise estimates for these environments but estimates for coral reefs alone exceed 600,000 species (Reaka-Kudla, 1997). Based on quantitative analysis of 233 box core samples from the Atlantic Ocean continental slope and rise off the east coast of North America, Grassle and Maciolek (1992) estimated 1 to 10 million macrofaunal species in the deep sea (Gage and Tyler, 1991). May (1994) estimated 0.5 million based on the portion of species previously undescribed in the Grassle and Maciolek study. Poore and Wilson (1993) analyzed samples from the Southern Pacific Ocean off Australia and, on the same basis, estimated that there are 5 million species in deep-sea sediments. Multicellular animals small enough to pass through a 1 mm sieve (meiofauna), such as nematode worms, are even less well known and Lambshead has argued that there may be 100 million species if nematodes are included (Lambshead 1993). Reasons for high diversity of species in the ocean include the long evolutionary history of the ocean, the vast area of deep-sea floor (3×10^8 km^2) with relatively few barriers to dispersal, and the episodic nature of patch formation within and between habitats on a variety of spatial and temporal scales.

TABLE I

Free-Living Animal Phyla and Their Relative Numbers of Described Species (4 = $>10^4$, 3 = $>10^3$, 2 = $>10^2$, 1 = present)

	Marine			
Phylum	Benthic	Pelagic	Freshwater	Terrestrial
Annelida	4	1	2	3
Arthropoda	4	3	3	5
Brachiopoda	2	0	0	0
Bryozoa	3	0	1	0
Chaetognatha	1	1	0	0
Chordata	3	3	3	3
Cnidaria	3	2	1	0
Ctenophora	0	1	0	0
Dicyemida	0	0	0	0
Echinodermata	3	1	0	0
Echiura	2	0	0	0
Gastrotricha	2	0	2	0
Gnathostomulida	2	0	0	0
Hemichorodata	1	0	0	0
Kamptozoa	1	0	1	0
Kinorhyncha	2	0	0	0
Loricifera	1	0	0	0
Mollusca	4	2	3	4
Nematoda	3	0	3	3
Nematomorpha	0	0	0	0
Nemertea	2	1	1	1
Onychophora	0	0	0	1
Phoronida	1	0	0	0
Placozoa	1	0	0	0
Plathyhelminthes	3	1	3	2
Pogonophora	2	0	0	0
Porifera	3	0	1	0
Priapula	1	0	0	0
Rotifera	1	1	2	1
Sipuncula	2	0	0	0
Tardigrada	1	0	2	1
Total (30)	27	11	14	10
endemic	13		0	1

C. Genes

Genetic diversity is the heritable variation among individuals measured as allelic diversity at a broad sampling of genetic loci or as genetic sequence information at the molecular level within populations. Genetic variation occurs among subpopulations as well as within populations. Differentiation among subpopulations results from natural selection for genetic variants adapted to local patterns of environmental variation or random loss of genetic variants in small isolated subpopulations. Species with relatively high rates of dispersal are less likely to form subpopulations and species with very poor dispersal ability are more likely to diverge from parent populations as a result of random processes. In coastal areas, genetic divergence is related to the length of life of dispersal stages and barriers to current flow from one place to another along a coastline. For some shallow-water species, genetic isolation of island populations is related to distances among islands. The archipelagos in the central Indopacific in the vicinity of Indonesia and Papua New Guinea have a high richness of species, which then declines eastward to relatively isolated peripheral island archipelogos (Planes and Galzin, 1997; Stehli, 1965). In the same region, in a study of population differentiation in four species of sea urchins, Palumbi (1997) found high genetic diversity (mitochondrial DNA sequence diversity) in the central area (1.6% variation among individuals) and much lower genetic diversity (0.5% variation among individuals) in peripheral island localities to the east. For these species, genetic diversity and species diversity covary across gradients suggesting a similarity in the processes maintaining gradients in diversity despite different mechanisms for the origin of the variation. Fluctuations in population size in relatively isolated populations could result in both loss of genetic variants and reductions in number of species (Palumbi, 1997).

In the deep ocean, hydrothermal vents are analogous to islands in the sense that these fluid flows support widely separated biological communities, linearly aligned along the Mid-Ocean Ridge. The patterns of deep-sea ocean currents that transport dispersal stages of species restricted to hydrothermal vents are poorly understood, but it is possible to make estimates of gene flow from the extent of genetic differentiation among populations of individual species. The flow of hydrothermal fluids, containing energy-rich reduced compounds such as hydrogen sulfide, supports chemosynthetic primary productivity. At East Pacific Rise vents, the flow of hydrothermal fluid may last only a decade or two at any one site and all populations are maintained by dispersal over considerable distances. Species can be divided into three categories: those that show no geographic pattern of genetic differentiation, those that are isolated by distance, and species without a free-living larval dispersal stage, which apparently have good dispersal to sites along a single ridge segment but poor dispersal between separated ridge segments (Vrijenhoek, 1997). The latest methods for measuring genetic diversity have been applied to very few marine species and rapid advances in this area of research can be expected.

III. ECOSYSTEM FUNCTION

It is useful to classify members of species assemblages according to their feeding relationships with other species in the ecosystem. A trophic unit includes all species that eat the same kinds of foods or are consumed by the same kinds of consumers. Within a food chain, there is a hierarchy of consumers from primary producers to primary consumers followed by a further sequence of consumers. Each step in a food chain results in a reduction in biomass, and simple food chains are often described as a pyramid with plants at the base and apex predators at the top. In the water column, unicelular phytoplankton form the first trophic level of marine food chains. The second level is formed by herbivores and detritivores and subsequent levels are formed by successive levels of predators. Species at the highest trophic levels can affect the food web relationships among species at lower levels. For example, removal of a top predator can have cascading effects on herbivores and ultimately on primary producers.

Because of the dilute seawater medium, a great many marine species have developed both active and passive means for filtering or trapping food particles from the dilute seawater medium. Copepods, the most common animals in the water column, have filtering appendages and gelatinous zooplankton cast mucous nets to feed on phytoplankton. Baleen whales filter zooplankton (krill) from the water column. On the sea bottom, clams and sea cucumbers pump water past internal filters and many animals in sediments pump water through burrows in order to feed. Other bottom animals have appendages protruding above the sediments that trap or filter food particles. In many marine organisms, the distinction between producers and consumers is blurred. Reef-building corals use their tentacles to trap zooplankton yet may take most of their sustenance from photosynthetic dinoflagellates living symbiotically in their tissues. Other animal-plant relationships of this sort are found in tropical clams and one-celled radiolarians and foraminifera.

Some marine species play another important functional role by providing habitat for other species, either on a large spatial scale—as with coral or coralline algae reefs, polychaete worm reefs, seagrasses, kelps, marsh grasses, and mangrove trees. On a smaller scale, biogenic sediment structures (tubes, burrows, mounds, fecal aggregations) and more persistent structures made by tube builders, sponges, or shell-bearing animals may serve as habitat for other species.

Some species significantly affect the ecosystem by regenerating nutrients that limit primary production. Burrowing animals release nitrogen into the water column and stimulate phytoplankton growth. In chemically reduced sediments, animals pump water into sediments for respiration or feeding and supply oxygen to chemosynthetic primary producers living in the burrow. The role of single species is often not obvious, and several different criteria may be used to assign species to functional groups within an ecosystem. In general, redundancy of ecosystem function within a functional group has the potential to stabilize ecosystem processes despite fluctuations in the environment. Loss of functional groups implies drastic changes in ecosystem function.

IV. ECOSYSTEM DIVERSITY

A. The Edge of the Ocean

1. Intertidal Beaches

Beaches can be classified according to topography, organic content of sediments, and wave action. Reflective beaches are dominated by low wave energy, low organic content, and coarse sand. Reflective beaches have waves 1 m high or less and are generally found on open coasts with deep embayments, tropical coasts, and coasts of polar seas. Surging wave action filters and drains large volumes of water through the interstices of the sediments, resulting in well-flushed and highly oxygenated coarse sand deposits (Alongi, 1998). Dissipative beaches, at the other extreme of a continuum, are produced by a combination of high waves (>2.5 m) and fine sand deposits with higher amounts of organic matter. These are common on the west coasts of Australia and Southern Africa and seasonally on the west coast of North America where high wave swells and fine sands are abundant. Intertidal sand and mudflats are common on dissipative beaches.

Many beaches have adjacent seagrass beds, kelp beds, or other sources of macrodetritus, which are deposited as thick layers of wrack on the beach. These accumulations support communities that include both marine and terrestrial invertebrates (e.g., beach hoppers, beetles, and kelp-fly larvae). Other beaches are more dependent on growth of diatoms in the sediments and input of small, filterable organic particles. Many animals live in the sediments, and in some high energy situations animals such as mole crabs and small bivalves move up and down the beach with the tides filtering particles from the waves. Large areas of sand flats, such as the Wadden Sea in the Netherlands, may be especially productive and support high standing stocks of grazing invertebrates.

2. Kelp Beds

Kelps attach to the bottom and form a surface canopy at depths up to ~20 m. Under the most favorable conditions these large marine plants form subtidal forests and attain rates of primary production in excess of 1000 g C m^{-2} d^{-1}. These forests provide protection and food for a rich community of fish and invertebrates. The biomass and abundance of kelps may be regulated by sea urchin consumers. Sea otters play an important role in maintaining kelp forests by controlling the abundance of sea urchins. In the absence of sea otters, kelp forests are reduced by urchins to a pavement of encrusting algae and sea urchins. Kelp forests are important nursery areas for many species of fish and their detrital production enhances the abundance of benthic populations (United Nations Environmental Programme, 1995). Kelp populations are influenced over large scales by oceanographic climate. Nutrient-rich conditions during La Nina years result in increased growth and reproduction of the competitively dominant, canopy kelp species, *Macrocystis pyrifera*. Interdecadal-scale shifts in community composition result from fluctuations in kelp density (Dayton *et al.*, 1999).

3. Rocky Shores

Rocky coasts exposed to the open ocean are characterized by wave action resulting in communities of attached seaweeds and filter-feeding bivalve mollusks, such as mussels that provide physical structure for other species. Wave energy enhances the productivity of these ecosystems by continually renewing nutrients and food. The shore face and the organisms that reside on the shore can be divided into zones according to tidal height and length of exposure to air and the interactions of the dominant species with herbivores such as snails (gastropod mollusks) and predators (particularly snails, starfish, and birds). The large-scale pattern of rocky-shore communities depends on the distribution of rocky outcrops and sporadic changes in climate resulting in unusually heavy waves, ice cover, or sedimentation from rivers. The interaction of physical change and biological relationships among species at a variety of spatial scales (from local to regional) and temporal scales (from annual storm events to interdecadal climatic change) are most clearly worked out for rocky intertidal ecosystems.

4. Coral Reefs

Coral reef ecosystems occur where conditions are favorable for growth of reef-forming corals with dinoflagellate primary producers living symbiotically in their tissues. Growth of corals over many generations in geologic time results in major limestone structures such as coral atolls or the Great Barrier Reef off Australia. Dense growths of coral can sometimes occur in the deep sea, but these species lack photosynthetic symbionts, grow relatively slowly, and do not form major reef structures.

Reefs grow in strong light and clear water at temperatures from 18°C to 30°C at latitudes between 30°N and 30°S. Coral reefs are adversely affected by high nutrient concentrations, runoff of sediments from land, direct removal, and overfishing. The midrange of primary production of corals in combination with their symbiotic dinoflagellates is about 25 g C m^{-2} d^{-1} and varies greatly from species to species. Over large areas, net primary productivity of the most actively growing reef crests and slopes ranges from 1 to 5 g C m^{-2} d^{-1}.

Reefs support an enormous species richness and complexity of interactions among species. Conspicuous large animals include enormous coral heads and large fish such as groupers, stingrays, and manta rays. Many of the colorful reef fish do not move far and develop complex behavioral relationships both within and between species. Some live symbiotically with other species, for example, individual anemone fish live in close association with patches of anemones. Cleaner fish set up cleaning stations where they feed on the ectoparasites attached to the gills of other fish. Some species mimic the cleaner fish and take bites out of the fish expecting to be cleaned of parasites.

B. Continental Shelves

Continental shelf coastal areas, on the order of 10,000 km^2 or more, have been called "large marine ecosystems" (Sherman, 1993). These are separated from other areas of the ocean by continental shelf depth and ocean currents, and the shapes of coastlines form major seas, bays, or gulfs. Examples include the Baltic, North, Mediterranean, Black, Caspian, Red, Arabian, Barents, Bering, Okhotsk, Japan, Yellow, East China, Sulu, Celebes, and Caribbean Seas; Bay of Bengal and Walvis Bay; and Gulfs of Alaska, California, and Mexico. Primary productivity in these systems ranges from below 35 g C m^{-2} yr^{-1} in the low latitude, warm waters of the Red Sea and high latitude, cold waters of the Beaufort Sea (10–20 g C m^{-2} yr^{-1}) to the very high primary productivity of Eastern Boundary Current upwelling areas in the Southern Hemisphere (1000–2000 g C m^{-2} yr^{-1}) of the Peru Current and Walvis Bay (Walsh, 1988). Most of the world's major fisheries are on continental shelves in midlatitudes.

C. The Open Ocean and Deep Sea

1. Pelagic

The largest ecosystems in the ocean are the central gyres of the Atlantic, Pacific, and Indian Oceans. Ecosystem processes in the North Pacific Subtropical Gyre (NPSG) have been summarized by Karl (1999). This ecosystem is the largest circulation feature on the planet (2×10^7 km^2) and one of the most persistent, its boundaries having remained approximately the same for the past 10^7 years. The NPSG has a clockwise circulation of less than 4 cm s^{-1} and forms a circumscribed, stable, and relatively homogenous habitat. The surface mixed layer varies from 40 m to 100 m depth and is characterized by surface temperatures are 24°C or higher low nitrate concentrations but relatively high dissolved organic nitrogen, and low standing stocks of organisms. The zone of primary productivity can be divided into two layers: an upper layer where chlorophyll increases in the winter and decreases in the summer and lower layer (100–175 m) where chlorophyll increases in the spring and declines in the fall. Recharge of nutrients is from deeper water below as a result of vertical eddy diffusion and episodic mixing events leading to considerable spatial variability in mixing processes and nutrient concentrations varying by as much as three orders of magnitude. Phytoplankton primary production was once thought to be mostly by Eukaryotes (diatoms and flagellates), but is now known to be more than 90% from the small bacterial taxa Synechococcus and Prochlorococcus. The standing stock of these autotrophic bacteria groups comprise 80% of chlorophyll a and feed a microbial loop that internally regenerates nutrients and maintains a pool of dissolved organic matter, which supports them (Fig. 4). The abundance of these auto-heterotrophs is controlled by light, nutrients, and predation by bacteria and a mixed assemblage of protists. Viral infection may also be an important source of mortality for these organisms. Archaea are abundant but it is not clear whether these are significant chemosynthetic primary producers because little is presently known about these organisms.

Very little organic matter escapes remineralization and the microbial loop provides negligible subsidy to the rest of the food web. The classic food chain pathway of eucaryote phytoplankton to copepod herbivores and on to higher trophic-level fish is ephemeral and occurs more frequently in surface waters during the summer. Organic matter produced by the eucaryotic phytoplankton food chain produces most of the exportable carbon during aperiodic, pulsed events.

Falkowski *et al.* (1998) provide a summary of biogeochemical processes controlling primary production in the open ocean. The central ocean gyres in the Atlantic, Pacific, and Indian Oceans have been considered analogous to deserts on land with low primary productivity and contain only ~0.2 mg m^{-3} of chlorophyll. Coastal upwelling regions, seasonally mixed regions of temperate and boreal seas, divergent subpolar gyres, and mesoscale features with eddy-induced pumping have sufficient vertical flux of nutrients to support 5 mg m^{-3} of chlorophyll. Throughout most of the coastal and open ocean, primary production is limited by the availability of inorganic fixed nitrogen. In some instances, the cyanobacteria that fix nitrogen in the open ocean are limited by iron and an important source of iron to the ocean is dust carried from land by winds. Limitation of primary production by lack of iron is especially notable in the South Pacific (Falkowski *et al.*, 1998).

2. Benthic

The deep-sea floor is divided into major ocean basins by continents and the Mid-Ocean Ridge. Communities within ocean basins may be further divided according to depth, sediment type, and level of energy of deep-sea currents. The deep ocean floor is the least-known part of the planet but, through use of manned and unmanned submersibles, distinct ecosystem processes at hydrothermal vents, continental margin seeps, seamounts, ocean trenches, and areas of strong bottom currents are being explored and described.

The largest ocean basins and deep ocean trenches each have some species that live only in that basin and nowhere else. Hydrothermal processes along the Mid-Ocean Ridge mix seawater through porous rock at high temperatures yielding an energy-rich fluid containing reduced compounds. These compounds support chemosynthetic microorganisms that provide primary production for a discrete ecosystem clustered around each hydrothermal vent. Flow of subsurface fluid seeps out of sediments deposited along some ocean margins providing similarly energy-rich fluid to chemosynthetic organisms.

The food supply for the deep sea comes from the productivity of surface waters. When diatoms bloom, or gelatinous animals such as salps multiply rapidly, they die and sink, so that organic material accumulates in low areas of the uneven surface of the sea floor and in burrows and depressions left by the larger inhabitants. Even in the central ocean gyres where export production is low, the dead remains of fish, marine mammals, or terrestrial plant material carried seaward sink and form widely separated organic patches on the sea floor. Species respond to these patches at different rates and the probability that two species reach the same patch at the same time is low. This reduces the likelihood of species competing and of one species eliminating another. Most deep-sea species are small and many species, including most fish species, are relatively slow growing, long lived, and late in maturation. Attempts to sustain deep-water fisheries have proven unsuccessful because low rates of population growth cannot keep up with rates of removal.

Species that grow relatively fast characteristically respond to patchy but concentrated sources of food from the ocean surface, such as wood from rivers, or the bodies of pelagic animals that settle to the bottom. For example, wood-boring bivalves rapidly colonize pieces of wood, grow to maturity in a few months feeding on their wood habitat, and produce thousands of eggs and larvae to colonize the next piece of wood that settles to the sea floor. Other species of bivalves grow very slowly in relatively homogeneous sediments, take several decades to reach maturity, and may produce only one egg at a time—in contrast to the rapid maturation and production of millions of eggs produced by most shallow-water bivalves.

Submarine canyons form conduits for sediment from continental shelves into the deep ocean. Unpredictable events of sediment erosion or scouring by intense currents result in relatively few species in the soft sediments at the bottom and sides of canyons. Seamounts are undersea mountains formed by the same processes at the hot spots on the ocean floor that form volcanic islands. Seamounts often support large populations of fish, and more than 70 species of commercially important fish have been reported. Interactions of currents with the steep topography of seamounts results in areas of enhanced primary productivity and concentrations of zooplankton that provide food for fish and dense concentrations of bottom animals (Rogers, 1994).

D. Mid-Ocean Ridges and Hydrothermal Vents

The 40,000 nautical mile Mid-Ocean Ridge system is the largest feature on the deep-sea floor. In 1977 a unique ecosystem was discovered at sites where a plume of high-temperature fluid rich in reduced compounds pours out into the water column. It is now known that sulfur oxidizers are among the most numerous bacteria and form a major base of the food chain. Other energy sources include reduced iron, manganese, and hydrogen. In the Pacific, large, red-plumed worms up to 2 m long and large clams and mussels dominate the vents. These animals feed on organic compounds produced by symbiotic sulfur bacteria living in their tissues. Vents in the Atlantic have some of the same kinds of animals, but the most conspicuous are shrimp, which swarm over the surface of vent chimneys. Vents usually have a restricted distribution on any given ridge segment and persist for about 10 to 20 years, until there is local extinction of the vent community. Animals colonize new vents rapidly, grow fast, and produce enough offspring to colonize the next vent. In comparison with the rest of the deep sea, few species have adapted to the extreme thermal (4°C up to temperatures in excess of 150°C), chemical (high concentrations of cadmium, lead, cobalt, and arsenic) conditions at hydrothermal vents (Grassle, 1986). Most species found at hydrothermal vents live exclusively in this environment. Of the 443 species found at hydrothermal vents, 15 have been found in other sulfide-rich environments and only 30 species are known from elsewhere in the deep sea (Tunnicliffe *et al.*, 1998).

V. POTENTIAL CONSEQUENCES OF ANTHROPOGENIC CHANGE

A. Eutrophication

Eutrophication is the increase in the rate of supply of organic matter to an ecosystem. Increases in global inputs of nitrogenous fertilizers and the mining of phosphate rock have generated increased concern about the effects of eutrophication on enclosed marine ecosystems (Nixon, 1995). Eutrophic ecosystems have algal production in excess of 300 g C m^{-2} y^{-1}, which results in areas of anoxia and loss of habitat for fish and other organisms. Relatively high rates of denitrification on continental shelves remove excess nitrogen originating from land sources and, in concert with dilution, help prevent adverse eutrophication effects in open coastal areas.

B. Overfishing

Globally, about 30% of commercial fish stocks are overfished and another 44% are being fished at or near the maximum potential long-term catch rate. Atlantic halibut, cod, orange roughy, and many species of salmon are now severely depleted. Significant changes in community structure as a result of overfishing have occurred in ecosystem structure in the Bering, Barents, and Baltic Seas (National Academy of Sciences, Committee on Ecosystem Management for Sustainable Marine Fisheries, 1999). Bottom-fishing has been shown to result in physical destruction of some bottom habitats. Fishing gear, when dragged over the bottom, levels structures such as worm tubes, burrows, and shell hash necessary for the survival of many species.

Overfishing has resulted in major changes in coral reef ecosystems. Normally, herbivorous fish heavily graze the attached algae, ensuring enough open reef surface for corals to settle and grow. This is especially true following major storms when wave action reduces coral coverage and circumstances are favorable for rapid algal growth. In the Caribbean, under normal circumstances, sea urchin grazing may compensate for reductions in fish grazing. A combination of overfishing and the decimation of sea urchin grazers by disease favored algal growth following a hurricane, which has resulted in reefs dominated by algae (National Academy of Sciences, 1995).

C. Invasive Species

Unwanted, exotic species are sometimes introduced to new geographic regions both deliberately to start new fisheries and accidentally through release from aquaria or ballast water carried by ships, sometimes with disastrous consequences. The Asian clam became established in the San Francisco Bay in 1986 and quickly displaced other species from large areas of the seabed and altered the water chemistry of the bay (National Academy of Sciences, 1995). The introduction of predatory green crabs to coastal environments on the east coast resulted in major reductions in shellfish beds. In short, invasive species have become a significant problem in many marine coastal environments and considerable effort is needed to curb this severe problem.

In summary, the oceans encompass a broad array of habitats that differ in their diversity, function, and vulnerability. Much of the vast area of the oceans is poorly described, but we have some understanding of a variety of globally essential ecosystem processes, and species loss may threaten not only the organisms themselves but also the many ecological processes that serve the rest of the planet and its human populations.

See Also the Following Articles

COASTAL BEACH ECOSYSTEMS • ENDANGERED MARINE INVERTEBRATES • ESTUARINE ECOSYSTEMS • INTERTIDAL ECOSYSTEMS • INVERTEBRATES, MARINE, OVERVIEW • MANGROVE ECOSYSTEMS • MARINE ECOSYSTEMS, HUMAN IMPACT ON • PELAGIC ECOSYSTEMS • REEF ECOSYSTEMS • VENTS

Bibliography

Alongi, D. M. (1998). *Coastal Ecosystem Process*. CRC Press, Boca Raton.

Briggs, J. C. (1974). *Marine Zoogeography*. McGraw Hill, New York.

Cohen, J. E. (1994). Marine and continental food webs: Three paradoxes? *Phil Trans. R. Soc. Lond. B* 343, 57–69.

Dayton, P. K., Tegner, M. J., Edwards, P. B., and Riser, K. L. (1999). Temporal and spatial scales of kelp demography: The role of oceanographic climate. *Ecol. Monogr.* 69, 219–250.

Falkowski, P. G., Barber, R. T., and Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary production. *Science* 281, 200–206.

Gage, J., and Tyler, P. A. (1991). *Deep-Sea Biology: A Natural History* *of Organisms at the Deep-Sea Floor.* Cambridge University Press, Cambridge.

Grassle, J. F. (1986). The ecology of deep-sea hydrothermal vent communities. *Advances in Marine Biology* 23, 443–452.

Gray, J. S. (1997). Marine biodiversity: Patterns, threats and conservation needs. *Biodiversity and Conservation* 6, 153–175.

Karl, D. M. (1999). A sea of change: Biogeochemical variability in the North Pacific Subtopical Gyre. *Ecosystems* 2, 181–214.

Longhurst, A. (1998). *Ecological Geography of the Sea.* Academic Press, San Diego, CA.

May, R. M. (1994). Biological diversity: Differences between land and sea. *Phil. Trans. R. Soc. Lond. B* 343, 105–111.

National Academy of Sciences, Committee on Biological Diversity in Marine Systems. (1995). *Understanding Marine Biodiversity.* National Academy Press, Washington, D.C.

National Academy of Sciences, Committee on Ecosystem Management for Sustainable Marine Fisheries. (1999). *Sustaining Marine Fisheries.* National Academy Press, Washington, D.C.

Palumbi, S. R. (1997). Molecular biogeography of the Pacific. *Coral Reefs* 16, Suppl.: S47–S52.

Patterson, D. J. (1999). The diversity of Eukaryotes. *American Naturalist* 154, Suppl., S96–S124.

Reaka-Kudla, M. L. (1997). The global biodiversity of coral reefs: a comparison with rain forests. In *Biodiversity II* (M. L. Reaka-Kudla, D. E. Wilson, and E. O. Wilson, Eds.). Joseph Henry Press, Washington, D.C.

Rogers, A. D. (1994). The biology of seamounts. *Advances in Marine Biology* 30, 305–350.

Sheldon, R. W., Prakash, A., and Sutcliffe, W. H., Jr., (1972). The size distribution of particles in the ocean. *Limnol. Oceanogr.* 17, 327–340.

Sherman, K. (1993). Large marine ecosystems as global units for marine resources management—An ecological perspective. In *Large Marine Ecosystems* (K. Sherman, L. M. Alexander, and B. D. Gold, Eds.). AAAS Press, Washington, D.C.

Snelgrove, P. V. R., Blackburn, T. H., Hutchings, P. A., Alongi, D. M., Grassle, J. F., Hummel, H., King, G., Koike, I., Lambshead, P. J. D., Ramsing, N. B., and Solis-Weiss, V. (1997). The importance of marine sediment biodiversity in ecosystem processes. *Ambio* 26, 578–583.

Stehli, F. G. (1965). Taxonomic diversity gradients in pole location: The recent model. In *Evolution and Environment* (E. T. Drake, Ed.). Yale University Press, New Haven, CT.

Tunnicliffe, V., McArthur, A. G., and McHugh, D. (1998). A biogeographical perspective of the deep-sea hydrothermal vent fauna. *Advances in Marine Biology* 34, 353–442.

United Nations Environmental Programme. (1995). In *Global Biodiversity Assessment* (V. H. Heywood, Exec. Ed., R. T. Watson, Chair), pp. 370–399. Cambridge University Press, Cambridge.

Vrijenhoek, R. C. (1997). Gene flow and genetic diversity in naturally fragmented metapopulations of deep-sea hydrothermal vent animals. *Journal of Heredity* 88, 285–293.

MARINE ECOSYSTEMS, HUMAN IMPACTS ON

Juan Carlos Castilla
Pontificia Universidad Católica de Chile

GLOSSARY

alien: introduced, exotic, nonindigenous, nonnative, invasive species A species that has been transported by human activity (i.e., mariculture), intentionally or accidentally, to a site at which it does not naturally occur.

ballast water Water carried by a vessel to improve stability.

benthic organism An organism pertaining to the seabed; bottom-dwelling.

biodiversity The variability among living organisms from all sources and the ecological systems of which they are a part.

disturbance Any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment.

ecosystem A complex nonlinear community of organisms in their physical environment.

ecosystem engineer species Species that directly or indirectly modulate the availability of resources (other than themselves to other species) by causing physical state changes in biotic or abiotic material and in so doing modify, maintain, and/or create habitats.

eutrophication Enrichment of a body of water with nutrients causing excessive growth of phytoplankton, seaweed, or vascular plants and often accompanied by a depletion of oxygen.

food web, trophic web A network of interconnected trophic chains in a community. A network of consumer–resource interactions among a group of organisms, populations, or aggregate trophic units.

guild A group of species having similar functional roles in the community (i.e., herbivores).

keystone species A group of species whose effects on the structure, dynamics, and functioning of the community is disproportionately large relative to its abundance.

pelagic organism A free-swimming (nekton) or floating (plankton) organism that lives exclusively in the water column.

resilience The resistance to a disturbance of a system and the speed of return to an equilibrium point, or the disturbance that can be absorbed before the system changes in structure by the change of variables and processes that control system behavior.

species diversity The number of species in a given community (= species richness) and the way the species' abundances (i.e., number, biomass, and cover) are distributed among species (= species evenness).

trophic level Feeding level in a food chain or pyramid (e.g., carnivores).

Encyclopedia of Biodiversity, Volume 4

MARINE ECOSYSTEMS represent the greater part of the earth's total biological system. At the present time these marine communities are threatened by human effects, both direct and indirect, such as resource extraction (e.g., fishing), introduction of alien species, pollution, and water temperature modification. These effects demonstrate the unique ability of humans to profoundly influence the status of ecosystems.

I. INTRODUCTION

The main threats to marine ecosystems are the human alteration of habitats, the excessive extraction of resources, pollution (Castilla, 1996), invasive species (i.e., introduction through mariculture and ballast water; Cohen and Carlton, 1998), eutrophication, and nonanthropogenic environmental changes [National Research Council (NRC), 1999; Castilla and Camus, 1992]. Furthermore, multiple and compounded perturbations related to physically and biological based disturbances are resulting in communities entering new domains or "ecological surprises" (Paine *et al.*, 1998), with important modifications in their structure (i.e., species composition) and dynamics (i.e., alternative states).

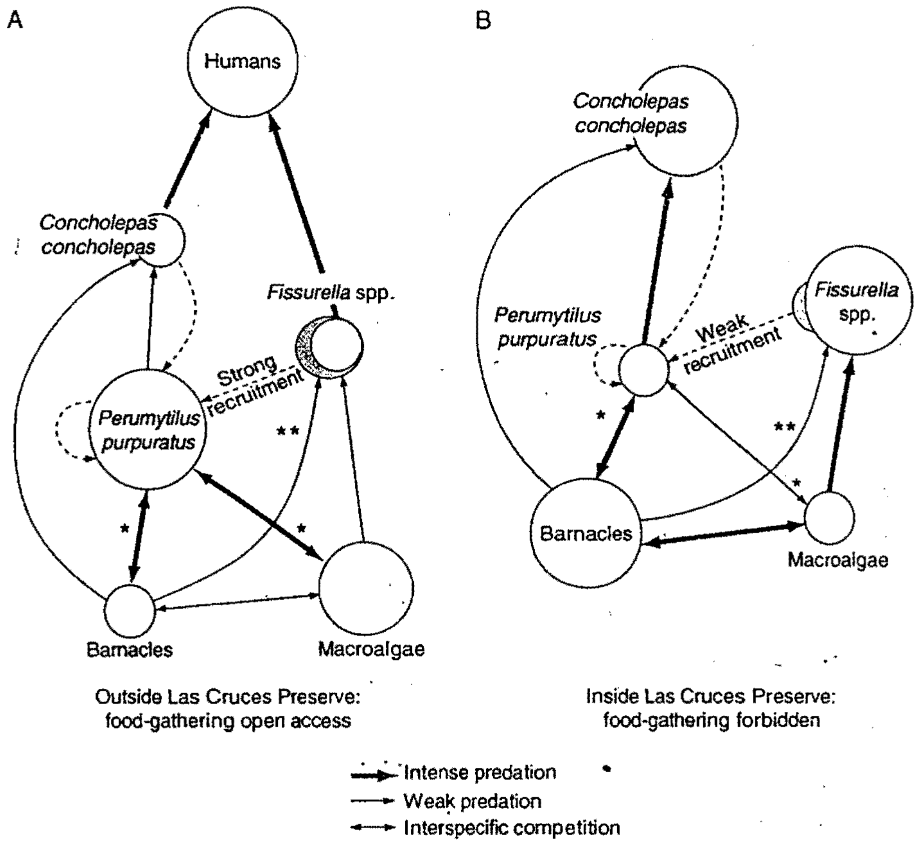
Single, multiple, or compounded impacts on ecosystems may directly or indirectly affect their structure, including species diversity and functioning. Ecosystems are complexly linked nonlinear systems and their dynamics may be sensitive to past conditions and subjected to shifts when exposed to anthropogenic and nonanthropogenic environmental stress (NRC, 1999).

The concept of biological diversity (biodiversity; Heywood, 1995) is defined as: the variability among living organisms from all sources and the ecological system to which they are part. The analysis of biodiversity considers four levels: genetic, species, community, and ecosystems. This article focuses on the species diversity (richness, the number of species in a given community; evenness, species abundance), community resilience, and ecosystem functioning. One of the best avenues to integrate species diversity functioning and community resilience (Holling, 1973) is to study their dynamics through long-term manipulations. The article reviews long-term experiments and impacts on marine communities and ecosystems in which humans are one of the key ecological factors (Castilla, 1999).

II. HUMAN IMPACTS ON MARINE COMMUNITIES AND THE EFFECTS ON SPECIES DIVERSITY AND FUNCTIONING

A. Rocky Intertidal Communities

Castilla (1999), based on a 16-year intertidal huma exclusion experiment in central Chile (Las Cruce fenced Marine Coastal Preserve; ECIM), summarize the ecological roles played by humans as top predato on rocky mid-intertidal marine communities. The functional intertidal food web, without humans (inside th ECIM preserve) and with humans (outside ECIM), differed substantially. On these rocky shores the impac of intertidal food gatherers is significant (Durán *et al* 1986). The collectors target mainly the keystone muricid snail *Concholepas concholepas*, locally known a "loco" (Castilla *et al.*, 1998). The high density of loco inside ECIM, following its closure to collectors in 198 resulted in strong loco predation on the competitiv dominant mussel *Perumytilus purpuratus*, which canno "escape in size" from its predator. Therefore, a fe years after the fencing of ECIM, the original dense mid-intertidal mussel beds inside ECIM were almost completely eliminated by the locos (Castilla, 1999). Th primary space, so liberated, was readily invaded by tw species of barnacles, *Jehlius cirratus* and *Notochthamalu scabrosus*, and several species of algae. Despite the fac that the loco also consumes barnacles, they have persisted for several years since they have a "weed recruitment strategy" (Castilla, 1988): After removal they kee reinvading the shore. This is not the case for *P. purpuratus*, which requires special substratum conditions t reinvade the shore (Navarrete and Castilla, 1990). Following the closure of the rocky shore at ECIM, specie richness and evenness of sessile organisms using primary substrata increased inside ECIM. Outside ECI (control), under reduced loco density due to food gathering, primary space is still dominated almost exclusively by the competitive dominant mussel *P. purpuratus*, and the biological diversity of the sessile primar substrata users is reduced since the mussels are long-term winners and appropriate the rock resource (Fig 1). Castilla (1999) provided a detailed account of direc and indirect human impacts on these communities an discussed differences in their functioning. For instance it was noted that the settlement of keyhole limpets *Fissurella* spp., was indirectly negatively impacted inside ECIM since their recruitment substratum, the bed



Outside Las Cruces Preserve: food-gathering open access

Inside Las Cruces Preserve: food-gathering forbidden

FIGURE 1 Diagrammatic representation of rocky intertidal food webs and human impacts outside (A) and inside (B) the Las Cruces (ECIM) Marine Preserve, central Chile. The size of the circles represents the approximate density of populations. An arrow with a singe asterisk indicates predation. The point of the arrow shows the flow of energy and the width indicates strong (wide) or weak (narrow) interactions. A double-asterisk arrow represents interspecific competition and the point width indicates the long-term competitive dominant (wider) or subordinate (narrower) species (intraspecific interactions are not considered). Settlement is shown by dashed lines and the arrows on these lines show the settler facilitator. One asterisk indicates that barnacles and macroalgae, apart from their ability to settle directly on rock, settle on top of mussel shells. A double asterisk indicates keyhole limpet browsing on young barnacles. *Concholepas concholepas* is a carnivore muricid. *Fissurella* spp. are herbivore gastropods (reprinted from Castilla, Rocky intertidal food webs and human impacts © 1999, p. 281, with permission of Elsevier Science).

of the mussels *P. purpuratus*, were absent due to loco's direct predatory impacts (Fig. 1).

Nevertheless, in the papers previously noted, no mention was made that rocky intertidal species diversity should be viewed in a more comprehensive way so as to include the secondary substrata generated by *P. purpuratus*, an ecosystem engineer species (Jones *et al.*, 1994). Mussel matrices allow for the establishment of a rich macroinvertebrate and algal community composed of dozens of species (Paredes and Tarazona, 1980; Lohse, 1993) which live inside the matrices and on mussel shells. Although in central Chile this effect has not been evaluated, the *P. purpuratus* matrices enhance species richness (for southern Chile, see López and Osorio, 1977) in sites impacted by humans (outside ECIM) compared to those not impacted (inside ECIM, J. Castilla, unpublished results).

Similar ecological direct and indirect humans impacts and drastic modification in rocky intertidal species evenness and intertidal community functioning (Fig. 2) have been reported at Mehuín's southern Chile coastal preserve (Moreno *et al.*, 1984). Lindberg *et al.*

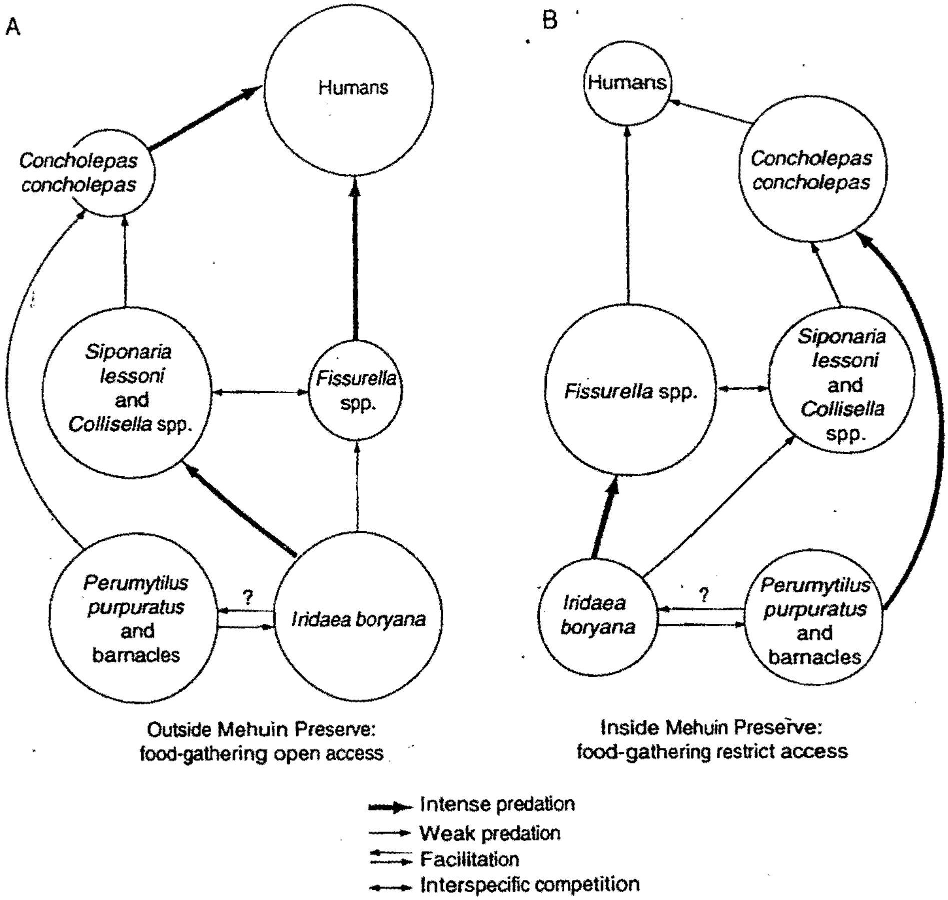


FIGURE 2 Diagrammatic representation of rocky intertidal food webs and human impacts outside (A) and inside (B) the Mehuín's Marine Preserve, southern Chile. Symbols are as described in the legend to Fig. 1 (reproduced with permission from Moreno, 1986).

(1998), through manipulative and "natural" experiments, described a three-trophic-level interaction among the American black oystercatcher (*Haematopus bachmani*), limpets (*Lottia spp.*), and erect fleshy algae in rocky intertidal bench communities of central and southern California. Human disturbances, such as the selective collection of large-size limpets and the reduction of shorebirds (in shores frequented by humans), drive the communities to a state dominated by small limpets and high cover of fleshy algae. Intertidal benches in relatively isolated islands (e.g., San Nicolas in central California) with large densities of oystercatchers and an absence of limpet human collection present communities in a different alternative state, which is characterized by large-size limpet populations and comparatively reduced fleshy algal cover.

B. Rocky Subtidal Communities

The Cape rock lobster *Jasus lalandii*, commercially most important lobster species in South Africa, cau profound direct and indirect effects on subtidal com itive dominant mussel species, such as *Choromyt meridionalis* and *Aulacomya ater* (Griffiths and Seide 1980), severely modifying species diversity and c munity functioning. Barkai and Branch (1988a, b) c pared the nearshore benthic communities of two a cent islands on the west coast of South Africa: Ma and Marcus Islands (33°S, 18'E), which are appr mately 4 km apart. The biotas of both islands have protected from human exploitation since 1929. In 1960s both islands supported populations of rock sters, but later, due to overfishing, a management was established which included a catch quota. Currently, Malgas still supports an unusually dense population of *J. lalandii* (probably partly due to the management plan) with densities of up to 10 individuals per square meter, whereas Marcus has a very reduced adult population of lobster. The benthic communities of both islands have only 34% of species in common. The biota of Malgas is dominated by numerous species of algae, whereas that of Marcus consists of thick beds of the black mussel *C. meridionalis*, an autogenic ecosystem engineer species that has a rich and diverse associated fauna (Barkai and Branch, 1988a). At Malgas, the predatory lobsters have eliminated a large proportion of spatial competitors, including mussels and barnacles, and sea urchins are absent. As a consequence, macroalgae proliferated. At Marcus, due to the absence of lobsters, the competitive dominant *C. meriodionalis* formed dense beds, outcompeting other species of mussels, such as *A. ater* and algae; sea urchins are common (Castilla *et al.*, 1994). Barkai and Branch (1988a, b) discussed this ecological situation and argued for the existence of alternative stable states on the contrasting islands. Figure 3 provides a summary of the main species involved, relative biomass, and direct, indirect, positive, and negative interactions between organisms on both islands.

The ecological impact of the Cape rock lobster at Malgas was experimentally demonstrated by Barkai and McQuaid (1988). The experiments showed that the drastic community differences between the islands were due to the dense population of lobster at Malgas and its absence at Marcus. In fact, the introduction of 1000 lobsters at Marcus ended amazingly: The lobsters were attacked by thousand of snails, *Burnupena* sp., which exist at Marcus in densities of up to 250 per square meter, and the lobsters perished within 30 min. This may explain their absence at Marcus, supporting the existence of an alternative ecological state.

In South African waters, it is unknown to what extent the commercial exploitation of rock lobsters or conservation measures (i.e., coastal closures) have impacted the nearshore rocky subtidal communities or in how

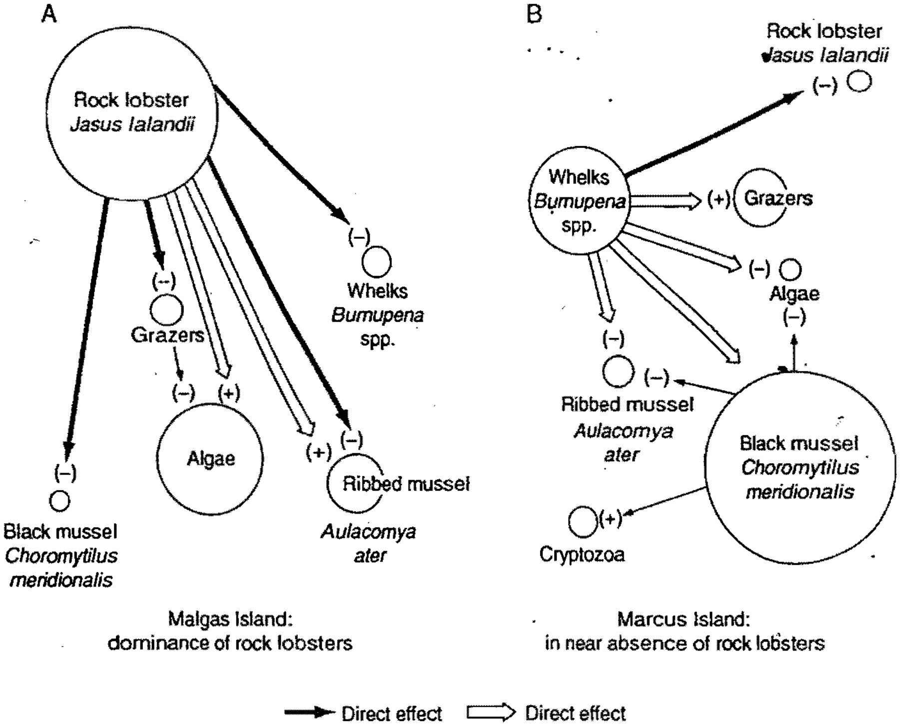


FIGURE 3 Rock lobster direct (+) and indirect (−) effects on mussel, welk, and grazer (sea urchin) preys in two South African islands. (A) Malgas, with a high density of adult lobsters. (B) Marcus, with a virtual absence of lobsters. The circles indicate relative biomasses (reproduced with permission from Rocky Shores: Exploitation in Chile and South Africa. Castilla *et al.*, Exploitation of two critical predators, pp. 101–130, fig. 6.6 1994 © Springer-Verlag).

many cases (other than Marcus and Malgas Islands) alternative stable states have been reached. This is a classical example in which both extreme attitudes—overexploitation and total conservation (no-take areas)—can result in drastically different species diversity and community functioning, mediated by the role of a high-trophic-level predator.

C. Humans and Linkages between Coastal and Oceanic Waters

Enhydra lutris, the northern sea otter, is found in nearshore environments ranging across the Pacific rim from Hokkaido (Japan) to Baja California (Mexico). The exploitation of their pelts led to the near extinction of otter populations in approximately 1911, when unregulated hunting was ended. Since then, the recovery of otter populations has occurred, particularly in the Aleutian Island chain, where by the 1970s the populations reached near maximum densities in some areas, were growing rapidly in others, and remained absent from others. Otters as keystone species (Power *et al.*, 1996) control the local biomass and the abundance of sea urchins, which regulate benthic algae biomass and productivity. Aleutian interisland comparisons (Estes *et al.*, 1998) have shown that kelp deforestation occurred in islands with low sea otter densities due to the increased density of sea urchins, whereas islands with high sea otter densities showed high kelp biomass. Estes *et al.* reported the complete transformation of a subtidal kelp forest in islands of the Aleutian Archipelago from three to four trophic-level systems and the release of sea urchin populations from the limiting influence of their predator, *E. lutris*. In the original circumstances, in the absence of sea otters, sea urchin populations increased rapidly and overgrazed the kelp forest, setting in motion a suite of different ecological impacts which drastically transformed the coastal ecosystems. These transformations had implications in the functioning of the communities and affected species diversity. Humans are highly involved in Estes *et al.*'s findings. In recent years in western Alaska, declines of *E. lutris* populations have been observed. The authors have argued that this is probably due to the recent increased predation on sea otters by killer whales, *Orcinus orca*. *Orcinus* may have initiated predatory influences that cascaded down successively lower trophic levels, first through the reduction of densities of sea otters, which triggered the increase of sea urchin populations, and ultimately the depletion of kelp biomass due to overgrazing. Estes *et al.*'s paper includes documented information on declines of sea otter populations and increases in the density and intensity of grazing of sea urchins on the kelp beds. Sea otters and killer whales have coinhabited the Aleutian Archipelago for millennia and Estes *et al.* attributed the sudden change of behavior of killer whales to a shift in their prey resource base. This has probably resulted from the collapse of pinniped populations, such as the Stellar sea lion and harbor seals, which were among the killer whale's main prey items. It has been suggested that the pinniped populations may have collapsed due to the Northwest Pacific midwater-trawl overfishing of walleye pollock (*Theragra chalcogramma*) (Alverson *et al.*, 1994) and/or increases in the ocean temperature. The authors recognized that some of their arguments contained speculations and that the critical one refers to the direct/indirect impacts of humans on marine ecosystems. In fact, sea otters, pinnipeds, and whales are under national and international protection in the Aleutians through different treaties and agreements signed dozens of years ago, but it also has to be recognized that their food resources have been depleted independently through overfishing. For instance, there is evidence that in the case of the pinnipeds a reduction (population collapses in some cases) has occurred mostly due to overfishing of pinnipeds, or of their fish resources, and also to climate changes. Overfishing is directly linked to human activities, and in Estes *et al.*'s scenario, humans and not killer whales may be considered as the apex predator. Humans have redirected the functioning of oceanic and coastal marine ecosystems in these localities and modified trophic linkages.

These examples indicate that there are at least two aspects of human ecological influences on marine communities that are difficult to evaluate and hence demonstrate an indisputable cause–effect situation. First, in many cases, the functioning of the marine communities is affected indirectly by anthropogenic activities—for example, human overfishing of pinniped's fish resources, collapse of pinniped populations, a shift in the prey item of killer whales, predation on the sea otter, population explosion of sea urchins, and overgrazing of kelp beds. The cascading down to successively lower trophic levels is complex and requires long-term observation and experiments to be understood. Furthermore, nonanthropogenic impacts also need to be considered. Second, limited knowledge exists on the resilience properties of marine communities and ecological conclusions on linkages between marine ecosystems are based on preliminary data.

D. Humans and Ecosystem Engineer and Invasive Species

Ecosystem engineer species are species that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials, and in so doing they modify, maintain, and/or create habitats (Jones *et al.*, 1994). Jones *et al.* distinguished (i) autogenic engineers, when the changes in the environment occurred via their own physical structure, living or dead tissues (e.g., coral reefs), and (ii) allogenic engineers, when they produced changes in the environment through the transformation of living or nonliving materials from one physical state to another via mechanical means (e.g., rabbits and burrows). In marine coastal communities, there are numerous autogenetic engineer species playing roles in the functioning of the community and ecosystem and creating the physical conditions for other species to exist (e.g., mussels; Lohse, 1993). In the Southern Hemisphere, rocky littoral zone tunicates of the genus *Pyura* play such a role (see Fielding *et al.*, 1994, for *P. stolonifera* in S. Africa). These tunicates are also important as species extracted for food and/or bait by recreational fishers, divers, and intertidal food gatherers (for *Pyura praeputialis* in Australia, see Fairweather, 1991; for *P. praeputialis* in Antofagasta, northern Chile, see Castilla, 1998). The tunicates form dense intertidal and subtidal belt monocultures and attain collective cemented beds, creating microhabitats used by several dozen macroinvertebrates and algae. Fielding *et al.* identified 83 taxa of macroinvertebrates in intertidal and subtidal *Pyura stolonifera* beds around Durban, South Africa, whereas more than 100 taxa of macroinvertebrates and algae have been found in intertidal *P. praeputialis* beds in Antofagasta.

The *P. praeputialis* beds in Chile present a very restricted geographical distribution of only 60–70 km around Antofagasta Bay (Clarke *et al.*, 1999). According to a working hypothesis (J. Castilla, work in progress), the species might have been introduced recently to Antofagasta by ships or arrived on floating objects from Australia. In Antofagasta, a contrasting situation concerning species richness is found in sites with *P. praeputialis*, with more than 100 taxa in the *Pyura* beds, as opposed to sites without the tunicate, which have about one-third to one-fourth of the species. It is unknown how much ecological damage, if any, human extraction causes on the dynamics of *Pyura* populations or on species diversity at a local scale. However, preliminary information at Antofagasta indicates that following *Pyura* removals by waves, predators, or humans, the species reinvades intertidal sites (the center of its distribution) within 1 year (J. Castilla, work in progress). A higher rate of anthropogenic or nonanthropogenic removal of engineer species than the rate of recovery may be key to local species diversity.

Invasive species are displacing native species throughout the world. They are altering the physical nature of habitats (e.g., the effects of the Asian clam *Potamocorbula amurensis* in the San Francisco Bay) and causing changes in food webs of economically important species (NRC, 1999). The best reported case is that of the Bay of San Francisco, in which ship activities (i.e., the elimination of ballast waters) have increased drastically the number of exotic species in the bay's benthic communities (Carlton, 1996). At the pelagic level the introduction in the bay of the zooplanktonic mysid *Acanthomysis* sp., which displaced another species of mysid, *Neomysis mercedis*, a major food item of the striped bass *Morone saxitilis*, is partly responsible for a severe decline in the bay's bass population (NRC, 1999). Furthermore, there are recent reports showing that the predator green crab *Carcinus maenas* has invaded the San Francisco Bay and is spreading through the coastal waters of California (Cohen and Carlton, 1998).

E. Mariculture

The intensive and extensive marine farming of fish, shellfish, and algae has a long history and is a controversial issue. For instance, mariculture production expectations have not been achieved (NRC, 1999) and adverse environmental effects, such as contamination of surface waters by fish wastes, eutrophication, spread of diseases, introduction of unwanted species, and deterioration of coastal habitats (e.g., mangroves in connection with shrimp farming in Asia and Latin America), have occurred (Chamberlain, 1997; Anderson, 1997). The introduction of exotic cultured species may be a serious and irreversible event to native ecosystems which merits careful consideration. For instance, oysters have been transported by man from country to country and there are several cases of the concomitant spread of pests (unwanted species) and diseases, even under strict import controls. The introduction of the American oyster *Cassostrea virginica* into English waters (late 1800s and 1939) brought in several exotic species, the worst being the American oyster drill *Urosalpinx cinerea* and the gastropod competitor *Crepidula fornicata* (Edwards, 1990). Critical epizootic disease events in the Gulf of

St. Lawrence that caused serious oyster stock depletions were ascribed to the transplant of oysters in 1914 from New England to Canada (Edwards, 1990). No comprehensive ecological reports on the ecological effects of these species introductions and diseases on local species diversity or community functioning have been published.

The intensive farm-raising of high-value species, such as shrimp and salmon, is far from trouble-free. There are concerns about the increase in the deposition of particulates and accumulation of organic matter under salmon cages in intensive mariculture installations due to unwanted effects, such as anoxic conditions and the production of toxic gases (Beveridge, 1996). Coastal ecosystem destruction, nutrient loading, antibiotics wastes, accidental release of alien or genetically altered organisms, and disease spreading to native species are some of the threats to community and ecosystem functioning.

F. Human Overfishing, Diseases, and Trophic Cascades

Hughes (1994) and Jackson (1997) reported major ecological effects on coral reef communities as a consequence of the overexploitation of herbivorous fishes and a disease killing sea urchins. In Caribbean coral reefs, a chain of effects, starting with the overfishing of herbivorous fishes, appeared following category 5 hurricane Allen in 1980. Allen severely damaged coral reefs in Jamaica, but by 1983 there was evidence of their recuperation. Nevertheless, at that time a disease devastated the herbivorous populations of the sea urchin *Diadema antillarum*. The elimination of the herbivore guild caused dramatic food cascading effects, resulting in reefs overgrown by algae and the detention of their recuperation. Species diversity and community functioning severely changed: The coral cover was reduced from approximately 52% in 1977 to 3% in the early 1990s, and cover of macroalgae increased from approximately 3 to 92% (Hughes, 1994).

G. Pollution and Artificial Reefs

The cases exemplified are among the best known ecological situations in which human impacts and the function of communities or ecosystems, combined with changes in species diversity, have been observed or studied. However, there are additional examples showing anthropogenic negative, as well as positive, impact on marine communities and ecosystems. Among nega tive impacts on marine species diversity and communit functioning, the most conspicuous (not discussed here is pollution (Castilla, 1996). Among positive impact is the building of marine reefs for fishing enhanceme and recreational purposes. Artificial habitats may locall enhance species diversity and resources and drive co munity structure toward alternative states (Buckle 1982).

III. NONANTHROPOGENIC ENVIRONMENTAL CHANGES AND VARIABILITY

Nonanthropogenic environmental changes and impac on marine populations and communities have been we documented. For instance, Soutar and Isaacs (197 reported large fluctuations in the density of scales hake, anchovy, and sardines in sediment cores duri the past 2000 years, well before fishing was a facto Large-scale ocean climate changes, such as El Ni Southern Oscillation (ENSO) events, have dramat negative (Arntz and Fahrbach, 1996) or positive (Ca tilla and Camus, 1992) impacts on fish, shellfish, a algae populations in the Southeastern Pacific. ENS also causes multiple positive and negative oceani freshwater, and terrestrial impacts throughout t world.

Barry *et al.* (1995) reported changes between 19 and 1933 and between 1994 and 1995 in speci richness and evenness of intertidal invertebrates at rocky intertidal transect in the Hopkins Marine St tion, Monterey, California. They reported speci latitudinal range shifting northward, suggesting a co sistency with predictions associated with anthrop genic-linked climate warming (but see alternative e planation by Denny and Paine, 1998). Neverthele it is debatable whether the current global warmi trend, due partly to the build-up of several greenhou gases, is part of a long-term climatic trend. In a case, marine species with different geographical origi would have different responses to water temperatu alterations (Castilla and Camus, 1992). Moreover, the case of the oceans, water temperature modifi tions would be just one of the potential fact affecting the distribution of species. For instan temperature effects on the turbulence of the oce waters, and their association with wind stress, m have major implications for plankton dispersal. Also, the predicted north–south interhemispheric asymmetry, due to the thermal inertia in the south, must be considered before drawing firm conclusions on marine species latitudinal shifts (Bernal, 1994). Furthermore, since the ocean is affected simultaneously by several climate forces (including anthropogenic greenhouse effects), it is difficult to determine the real cause of any observed change, such as that in surface seawater temperature. Shifts in marine populations, community structure, and their functioning represent the integrated response of species assemblages to nonanthropogenic long-term climate changes superimposed on the effects of numerous short-term factors, including anthropogenic forcing.

IV. CONCLUSIONS

This article discussed several marine examples in which direct anthropogenic and nonanthropogenic impacts (or combinations), such as species extraction and oceanic water temperature modifications, caused drastic ecological shifts on marine benthic intertidal, subtidal, and coastal–oceanic communities, and thereby modified species diversity and the functioning of associated communities. Interestingly, extreme conservation measures (e.g., the establishment of no-take areas) to protect species, habitat, community, or ecosystem may also cause drastic modifications in the functioning of marine communities and drive communities into alternative ecological states (Castilla *et al.*, 1994; Estes *et al.*, 1998; Castilla, 1999). This article highlighted that anthropogenic activities (e.g., mariculture) and impacts (e.g., overfishing) on different ecological categories of species (predator, keystone, engineer, invasive, and competitive dominant) translate into differential responses and functioning at the species diversity and community level. The unique ecological role played by humans and their apex keystone position in trophic webs were discussed.

Acknowledgments

I acknowledge financial support received through the Cátedra Presidencial en Ciencias, Chile (awarded in 1997) and the Pew Charitable Fund as a Pew Fellow in Marine Conservation (1997). Minera Escondida Ltd. supported fieldwork in Antofagasta, Chile. Comments and suggestions on a preliminary manuscript made by a referee are acknowledged.

See Also the Following Articles

AQUACULTURE • INTERTIDAL ECOSYSTEMS • MARINE AND AQUATIC COMMUNITIES, STRESS FROM EUTROPHICATION • MARINE ECOSYSTEMS • RESOURCE EXPLOITATION, FISHERIES

Bibliography

Alverson, D. L., Freeberg, M. H., Murawski, S. A., and Pope, J. G. (1994). A global assessment of fisheries bycatch and discards, FAO Fisheries Technical Paper No. 339. Food and Agriculture Organization, Rome.

Anderson, J. L. (1997). The growth of salmon aquaculture and the emerging new world order of the salmon industry. In *Global Trends in Fisheries Management* (E. Pikitch, D. D. Huppert, and M. Sissenwine, Eds.), American Fisheries Society Symposium No. 20, pp. 175–184. American Fisheries Society, Bethesda, MD.

Arntz, W. E., and Fahrbach, E. (1996). *El Niño: Experimento Climático de la Naturaleza.* Fondo de Cultura Económica, México D. F., México.

Barkai, A., and Branch, G. M. (1988a). Contrast between the benthic communities of subtidal hard substrata at Marcus and Malgas Islands: A case of alternative stable states? *S. Afr. J. Mar. Sci.* 7, 117–137.

Barkai, A., and Branch, G. M. (1988b). The influence of predation and substrata complexity on recruitment to settlement plates: A test of the theory of alternative states. *J. Exp. Mar. Biol. Ecol.* 124, 215–237.

Barkai, A., and McQuaid, C. D. (1988). Predator–prey role reversal in a marine benthic ecosystem. *Science* 242, 62–64.

Barry, J. P., Baxter, R. D., Sagarin, R. D., and Gilman, S. E. (1995). Climate-related long-term faunal changes in a California rocky intertidal community. *Science* 267, 672–675.

Bernal, P. A. (1994). Global climate change in the ocean: A review. In *Earth System Response to Global Change: Contrast between North and South America* (H. A. Mooney, E. R. Fuentes, and B. Kronberg, Eds.), pp. 1–15. Academic Press, San Diego.

Beveridge, M. C. M. (1996). *Cage Aquaculture.* Fishing News Book, Oxford.

Buckley, R. M. (1982). Marine habitat enhancement and urban recreational fishing in Washington. *Mar. Fish. Rev.* 44, 28–37.

Carlton, J. T. (1996). Biological invasions and cryptogenic species. *Ecology* 77, 1653–1655.

Castilla, J. C. (1988). Earthquake-caused coastal uplift and its effects on rocky intertidal kelp communities. *Science* 242, 440–443.

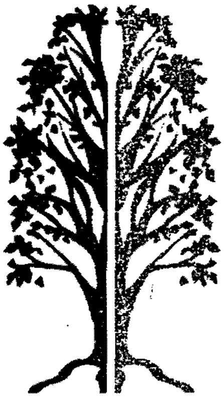
Castilla, J. C. (1996). Copper mine tailing disposal in northern Chile rocky shores: *Enteromorpha compressa* (Chlorophyta) as a sentinel species. *Environ. Monit. Asess.* 40, 171–184.

Castilla, J. C. (1998). Las comunidades intermareales de la Bahía San Jorge: Estudios de Línea Base y el Programa Ambiental de Minera Escondida Ltda. en Punta Coloso. In *Minería del Cobre, Ecología y Ambiente Costero* (D. Arcos, Ed.), pp. 221–224. Editora Aníbal Pinto S. A., Talcahuano, Chile.

Castilla, J. C. (1999). Coastal marine communities: Trends and perspectives from human-exclusion experiments. *TREE* 14, 28–83.

Castilla, J. C., and Camus, P. A. (1992). The Humboldt-El Niño scenario: Coastal benthic resources and anthropogenic influences, with particular reference to the 1982/82 ENSO. *S. Afr. J. Mar. Sci.* 12, 703–712.

Castilla, J. C., Branch, G. M., and Barkai, A. (1994). Exploitation of



ESTUARINE ECOSYSTEMS

G. Carleton Ray
University of Virginia

> The cold remote islands
> And the blue estuaries
> Where what breathes, breathes
> The restless wind of the inlets
> And what drinks, drinks
> The incoming tide.
>
> *LOUISE BOGAN, "NIGHT"*

GLOSSARY

biological diversity (biodiversity) The collection of genomes, species, and ecosystems occurring in a geographically defined region (NRC, 1995).

coastal zone Zone whose terrestrial boundary is defined by (a) the inland extent of astronomical tidal influence or (b) the inland limit of penetration of marine aerosols within the atmospheric boundary layer and including both salts and suspended liquids, whichever is greater; the seaward limit is defined by (a) the outer extent of the continental shelf (approximately 200 m depth) or (b) the limits of territorial waters, whichever is greater (Hayden *et al.*, 1984).

estuary Semi-enclosed coastal body of water that has a free connection with the open sea and within which seawater is measurably diluted with freshwater derived from land drainage (Pritchard, 1967).

functional diversity Variety of different responses to environmental change, especially the diverse time and space scales with which organisms react to each other and to the environment (Steele, 1991).

metapopulation An abstraction of the population to a higher level at which individuals frequently move from one place (population) to another, typically across habitat types that are not suitable for their feeding and breeding activities, and often with substantial risk of failing to locate another suitable habitat patch in which to settle (Hanski and Gilpin, 1991).

ESTUARIES ARE AMONG THE MOST IMPORTANT INTERCONNECTIONS between land and sea. They are situated in the coastal zone, which accounts for a disproportionate amount of global ecological functions. For example, the coastal zone (modified from Pernetta and Milliman, 1995):

- occupies only 18% of the surface of the globe, 8% of the ocean surface, and 0.5% of ocean volume;
- but provides for up to 50% of global denitrification, 80% of global organic matter burial, 90% of global

- sedimentary mineralization, 75–90% of the global sink of suspended river load and its associated elements/pollutants, and in excess of 50% of present-day global carbonate deposition;
- also supplies approximately a quarter of global primary production, around 14% of global ocean production, and 90% of the world fish catch.

It follows that estuaries, as major pathways of aquatic exchange between land and sea, are major influences on a large proportion of these functions.

I. INTRODUCTION

Some of the steepest environmental gradients on planet Earth occur in the coastal zone, where land, sea, and atmosphere uniquely interact to exchange energy and materials. Also, the dynamic linkages among biological, physical, and chemical systems are exceptionally strong in estuaries, and are characterized by cyclic changes that occur at different frequencies—such as for tides, salinity cycles, freshwater inputs, light, and temperature stratification. Estuaries also bear the brunt of extreme events, such as flooding, storms, hurricanes, and seasonal sea ice. All of these are of importance for organisms, which have evolved suites of adaptive mechanisms to cope.

Estuaries have usually been considered as transitional areas between freshwater and saltwater environments. However, relatively few species are totally confined to estuarine conditions, even though various stages of many species' life cycles are estuary-dependent. This raises questions about whether estuaries can be considered as transitional or as more-or-less autonomous ecosystems in their own right. The distribution of biodiversity provides important information toward the resolution of this apparent dichotomy, which needless to say is essential for conservation and management.

Our present knowledge about estuary-dependent biodiversity is sparse. Fundamental questions remain about species distributions in estuaries, in what ways species are adapted to estuaries, and how some species may affect others by means of structural or functional interrelationships. Furthermore, the diversity of estuaries relative to other ecosystems remains to be clarified. These questions require both ultimate, historical-evolutionary explanations and proximate, functional-ecological explanations.

Despite the location of estuaries in the critical portion of Earth called the "coastal zone," the *Global Biodiversity Assessment* (Heywood and Watson, 1995) contains no sections specifically devoted to them; the term "estuary" does not even appear in the index! Nevertheless, this volume does characterize biodiversity as comprising three disciplines, which also apply to estuaries: (1) taxonomy: provides the reference system and depicts the pattern or tree of diversity for all organisms; (2) genetics: gives a direct knowledge of the gene variations found within and between species; and (3) ecology: provides knowledge of the varied ecological systems in which taxonomic and genetic diversity are located, and it also provides the functional components. Evolutionary biology brings these together, as it "provides explanations of how biodiversity arose, and the processes, such as speciation and extinction, by which it continues to change."

The third aspect of biodiversity, namely, the functional-ecological aspect, is the focus of this article. In this respect, it is worthwhile to note that, even today, estuarine science continues to be organized along disciplinary lines. Although the study of land–seascape ecology of estuaries remains in its infancy, there are extensive publications on geomorphology, land–sea interactions, coastal zone management, and other disciplines from which to gain an integrated understanding of estuaries. Nevertheless, a comprehensive understanding of the functional biodiversity of estuaries remains a future goal.

Estuaries became topics of intensive concern and research only in the mid-twentieth century. This is ironic, as humans have lived in close proximity to estuaries and have been dependent on them and their biological resources for millennia. Reasons for human proximity to and dependence on estuarine environments are both social and ecological, for estuaries are ecologically diverse and productive, making possible the sustainment of large and sophisticated human societies. Indeed, it is more than coincidental that among the first known city-states were those of the lower reaches of the Tigris and Euphrates Rivers of Mesopotamia.

The distribution of estuaries corresponds to regional and coastal characteristics; that is, they tend to be extensive, large, and numerous where coastal plains are wide and flat, but are relatively small where coastal plains are steep and narrow. Particularly in the former, estuaries and associated lagoons constitute a much higher percentage of the coasts than is generally recognized. In fact, many of the world's largest cities (London, New York, Karachi, Amsterdam, Alexandria, Tokyo, etc.) have been built on or near drained marshes or filled land adjacent to estuaries. In the United States, 80–90% of the Atlantic and Gulf Coasts and 10–20% of the

Pacific Coast consist of estuaries and lagoons (Emery, 1967).

Estuaries are best understood in the context of the coastal zone, definitions of which vary. Ketchum (1972) was among the first to take a functional perspective, that the coastal zone "is the broad interface between land and water where production, consumption, and exchange processes occur at high rates of intensity." NERC (1992), on the other hand, defined the coastal zone as: "An indefinite zone of land and sea that straddles the shoreline; includes all land that is the product of, and/or at risk from (Holocene) marine processes, and extends seaward from the shoreline to water depths of about 30 m." The key element is "marine processes" and, from that point of view, it seems best to adopt Ketchum's broader view. Accordingly, Hayden *et al.* (1984) adopted Ketchum's definition (see Glossary), which makes sense of such interactions as the existence of coastal vegetation under the influence of aerosols, sedimentation induced by freshwater flows and atmosphere–ocean processes, and the coastal distribution of aquatic biota worldwide. With respect to the latter, Nelson (1984) estimated that of about 21,700 described species of fishes, about 8400 (39%) occur in freshwater and 2700 (12%) are oceanic. Nearly half of these fishes (10,600 species, or 49%) are coastal, that is, occur from estuaries to the outer extent of the continental shelf. This proliferation of fish diversity is powerful evidence of the functional importance and the extent of the coastal zone.

Within this coastal zone context, Pritchard's (1967) definition of "estuary" also makes sense (see Glossary). However, other definitions must be acknowledged. For example, Mann (1982) defined an estuary as "a region where river water mixes with, and measurably dilutes, sea-water." Yet this definition could include semi-enclosed seas (e.g., the Baltic), plumes of large rivers, and diluted water off open coasts, making difficult any geographic analysis of estuarine biodiversity or function. Additionally, Pritchard's definition takes account of Pleistocene rises and falls in sea level, as well as of terrestrial processes, such as sedimentation, which clearly affect the distributions of aquatic biota.

Thus, estuaries are best defined functionally in a land–sea context and as important portions of the coastal zone. In this context, estuaries are subject to rapid environmental, structural-functional change, which has major consequences for biodiversity. Hydrological, biological, and sedimentary processes and events may substantially alter or destroy estuaries at many spatial and temporal scales. The estuaries that we now see are the result of the latest major episodes of sea level fall and rise and, in fact, the age of the present estuaries is only about 1% of the age of the continental shelf (Emery, 1967). It is reasonable to assume that the communities of estuarine biota that exist today are as young and equally subject to change.

Many estuaries around the world have been studied in some detail. The North American bias in this article reflects the considerable body of research that has been conducted on North American estuaries during the past few decades, motivated unfortunately by the depleted, over-enriched, polluted, and over-populated states of many of them, some aspects of which will be examined in the Chesapeake Bay case study in Section V.

II. ESTUARINE CLASSIFICATION

Classification is essential as a comparative reference system, for otherwise data and information cannot be made comparable among estuaries. Various classifications, or typologies, of estuaries have been attempted, but these are mostly physical; no typology is directed specifically to biodiversity, even though the distributions of estuarine species have resulted in various classification schemes.

To my knowledge, the first classification was the so-called "Venice system" (Anonymous, 1959), in which estuaries were divided into salinity zones. This was modified later by Bulger *et al.* (1993) on the basis of species' salinity tolerances. These two schemes align rather closely and may be compared as follows (Anonymous, 1959 = V; Bulger *et al.*, 1993 = B; ppt = parts per thousand):

Limnetic: freshwater, 0.5 ppt (V); freshwater, 4 ppt (B)
Oligohaline: 0.5–5 ppt (V); 2–14 ppt (B)
Mesohaline: 5–18 ppt (V); 11–18 ppt (B)
Polyhaline: 18–30 ppt (V); 16–27 ppt (B)
Euhaline: 30 ppt–full marine (V); 24-ppt marine (B)

The reason for the differences in salinity ranges between the Venice system and Bulger *et al.* is that the former was derived from salinity, whereas the latter was derived analytically from species' salinity tolerances, in which the zones would be expected to overlap. In both cases, however, the compartments are over-simplistic, as estuaries exhibit many characteristics that influence biotic distribution and the distinction of estuarine zones, variably identified as "upper reaches," "upper-middle reaches," "lower reaches," and so forth. Nor do salinity-derived systems distinguish zones according to variations in bottom type, water movement, volume of flow, and other attributes important to the biota.

Another classification concerns basin geomorphology, which is of obvious importance for circulation patterns. Classification on this basis appears in many texts and may be summarized as:

- coastal plain estuary (drowned river valley): Usually confined to areas with a wide coastal plain where seawater has invaded existing rivers because of sea level rise since the Pleistocene Ice Age. Generally the up-estuary limit is where chlorinity is about 0.06% (salinity about 0.1%); above this point there may be a portion of tidal freshwater.
- fjord: Generally U-shaped in cross section, in which the sides are steep and have been glaciated. May be fed by a river, have a deep basin, and a shallow sill may be present near the mouth.
- bar-built: Occurs in flat, low-lying areas, where sand tends to be deposited in bars lying parallel to the coast. Usually shallow and wind-mixed. Can be a composite of drowned river valleys and embayments, and occurs when offshore sand barriers are built between headlands into a chain to enclose the body of water. May be fed by multiple rivers, but the total drainage area is usually not large.
- tectonic: A miscellaneous category including estuaries formed from faults or folding of Earth's crust. Often have an excess of freshwater flow.

The interchange of freshwater and seawater provides yet another classification. The inlet (mouth) must be of sufficient dimension to allow mixing of seawater and freshwater, and the dilution of seawater provides the density gradients that drive characteristic circulation patterns. In terms of this interchange, the general classification is:

- salt wedge: Wherein a layer of relatively fresh water flows out at the surface.
- partially mixed (moderately stratified): Wherein tidal flow, turbulence, and mixing are increased, tending to erase the salt wedge.
- vertically homogeneous: Wherein tidal flow is strong, river runoff is weak, and all stratification is broken down.

Combinations of these typologies are possible; that is, it may be possible to find a stratified or a mixed bar-built estuary, or a fjord with a salt wedge or not. Furthermore, the extents of salinity zones can vary considerably for all categories. Such combinations of structure and hydrologic process result in highly varied conditions in the distributions of, for example, sediment, phytoplankton, submerged aquatic vegetation, and fishes and invertebrates. Additionally, variations in freshwater inputs, circulation, turbulence, and mixing can modify the typology.

A final classification concerns estuarine evolution, such as that of Roy (1984) for estuaries of New South Wales, Australia. There, estuaries are of three successional types: drowned river valleys, barrier estuaries, and saline coastal lakes. All are characterized by infilling during relatively short time spans. This affects their size, configuration, the invasion of mangroves and other aquatic vegetation, and fish communities. Biodiversity maxima are reached in the intermediate stages, because faunal population densities and species diversity increase with ecological complexity. However, as infilling becomes more advanced, the estuary becomes simplified and biological diversity declines. Therefore, estuarine geology, hydrology, and biology form a hierarchical succession.

III. ESTUARINE BIODIVERSITY

From the foregoing discussion, the impression may be gained that estuaries are simply transitional and, therefore, not biologically diverse. Indeed, Sanders (1968) found that estuaries are relatively non-diverse biologically, but also noted: "What is significant is that each environment seems to have its own characteristic rate of species increment." This is to say that salinity, for example, is an important determinant of the distribution of the biota, but also that estuaries exhibit high habitat and land–seascape diversity, a consequence of which is high variability among the biota and a high degree of biotic interaction. Thus, estuarine biotic communities would be expected to be especially varied and complex, contrary to earlier impressions of estuarine biological and ecological simplicity. Additionally, their biota have evolved resiliency to disturbance, both natural and human-caused. This is expressed at species, community, and ecosystem levels, leading to the impression that estuarine species are facultative with respect to estuaries as preferred environments. These characteristics have resulted in a tendency to describe any species that enters estuaries, or those that tolerate brackish waters, as "estuarine," which can be misleading. Nevertheless, some species seem to be restricted to estuarine and near-shore environments, at least at some life-history stage. A notable example concerns temperate oysters, which build extensive reefs in estuaries and lagoons and nowhere else. These reefs provide habitat for dozens of species, representative of almost every animal phylum.

Carriker (1967) noted that estuarine biota have adapted in different ways to estuarine conditions; for example, oligohaline organisms disappear at the head of the estuary; euryhaline species constitute the majority of the estuarine biota, as they can tolerate salinities as low as 5 ppt, as well as full salt water; and stenohaline species do not tolerate salinities of <25 ppt and are found only at the mouths of estuaries or on open seashores. This leaves "true estuarine organisms"—those relatively few species that are restricted to estuaries and that are best represented in the upper and middle reaches. Carriker concentrated mainly on benthic invertebrates, but concluded that an "estuarine biocenose" may be justified as a discrete functional aggregation of interdependent, regularly recurring, dominant, benthic populations that are strongly represented numerically. He acknowledged that much needs to be learned of ecology and life histories to justify this, but that the estuarine biotope appears to be more than "just a simple overlapping of factors (an ecotone) extending from the sea and the land, but is characterized by a unique set of its own factors arising from within the estuary from the materials and forces contributed by its bounding environments" (Carriker, 1967).

Some of the dominant, or "true," macroscopic biota of estuaries that he named are the plants—*Spartina alterniflora, Zostera marina, Ruppia maritima, Cymodocea mamatorium, Rhizophora mangle*, and *Avicennia nitida*, and the invertebrates—*Nereis diversicolor, Balanus improvisus*, xanthid mud crabs, *Uca pugnax, Callinectes sapidus, Mya arenaria, Mytilus edulis, Modiolus demissus*, and *Crassostrea virginica*. Additionally, he noted that characteristic estuarine habitats include tidal marshes, mangrove swamps, seagrasses, oyster reefs, soft clam–clam worm flats, and others. Finally, Carriker stated that: "Little is known of the sum of these effects on community structure, but they do emphasize the need to consider benthic organisms in the context of the total ecosystem rather than as an independent benthic biocenose." This statement, made a third of a century ago, has yet to be fully realized.

Fishes are the best known of aquatic groups in a general sense, mostly due to their commercial value. Therefore, insights into "estuarine dependency" may be best revealed through their study. One reason for this is their mobility in which various life-history stages inhabit quite different environments. Winemiller (1995) reviewed fish ecology and made the following points. First, fishes are by far the most diverse vertebrates, and they inhabit an incredibly wide range of aquatic habitats from pole to pole. Second, fishes are ecologically diverse, with a wide variety of food habits, behaviors, reproductive habits, physiologies, and morphologies. Third, fishes exhibit a range of life-history strategies that result from trade-offs among various attributes, including clutch and egg size; these strategies can be classified as opportunistic, periodic, and equilibrium, but a range of intermediate strategies also exist. Finally, fishes and their diversity in ecosystems can be used as "indicators" of environmental conditions.

Recently, much attention has been directed toward the early life histories of fishes, as this is closely related to recruitment and, therefore, of much interest to fish ecologists and to fisheries. Houde (1997) provided a review of the selection factors that are of special importance in this regard. Able and Fahay (1998) extended studies on juvenile stages of fishes to "estuarine dependence" and determined that the numbers of permanent estuarine residents is relatively low, at least in part because estuaries exhibit extremes in environmental conditions. Also, the fish diversity of estuaries is augmented by transients, such as freshwater species that occasionally occur in estuaries and marine species that spawn at sea but whose young use estuaries as nurseries. Therefore, the estuarine fish fauna includes both residents and transients and a wide range of sizes, ages, and adaptations. In addition, those species that have successfully invaded estuaries usually inhabit only a small number of broad niches, implying that larger estuaries have larger numbers of species owing to increased habitat and niche complexity.

Able and Fahay found that, of the species for which good information is available, 60% are transients, 28% are residents (uncannily close to the "educated guess" of C. R. Robins and myself that 27% are "obligate" on estuaries; see Section V), 6% are infrequent, and 6% are unclassified. Furthermore, they have suggested the following adaptive groups for juveniles:

Group I. Facultative estuarine breeders: species whose nurseries are either in estuaries or on the inner shelf (e.g., *Centroptristis striata, Brevoortia tyrannus*).

Group II. Seasonal residents: species whose adults migrate into estuaries to spawn in spring or summer (e.g., *Menidia menidia, Mustelus canis*).

Group III. Anadromous species: species whose adults migrate through estuaries in order to spawn in freshwaters (e.g., *Morone saxatilus, Alosa* spp.).

Groups IV–VI. Early users, delayed users, and distant spawners: species that spawn exclusively in the ocean, but the location, timing, and manner of use of estuaries by young-of-the-year juveniles vary (e.g., *Pollachius virens, Prionotus carolinus, Mugil cephalus*).

Group VII. Expatriates: species whose estuarine larvae come from distant spawning (e.g., *Chaetodon ocellatus, Monacanthus hispidus*).

Group VIII. Summer spawners: the largest group, represented by shallow-water spawners whose larvae develop in the immediate vicinity of spawning sites (e.g., *Cyprinodon variegatus, Fundulus heteroclitus*).

Group IX. Winter–spring spawners: a few species that spawn in the winter or spring (e.g., *Pseudopleuronectes americanus*).

Group X. Migrating spawners: species that undergo spawning migrations within the estuary (e.g., *Morone americana*).

Group XI. Species difficult to classify: species for which some populations appear to be estuarine and other populations do not (e.g., *Tautogolabrus adspersus*).

Able and Fahay (1998) caution that, for fishes at least, "estuarine dependence" depends on the resolution of three areas of research: (1) the need to sample well-defined areas thoroughly for habitat evaluation; (2) assessment of the effects of habitat loss; and (3) more detail on temporal and spatial use of habitats where early stages are collected. In short, a coherent understanding of the life-history factors that control the early life histories of fishes remains to be accomplished. The same no doubt holds for invertebrates. For macroscopic plants, the situation is perhaps less uncertain, as their life histories are simpler and assessments are more easily accomplished.

In sum, most truly estuarine species are typically resistant to environmental variations due to the extreme conditions of estuaries, and/or take advantage of favorable situations; consequently, they do not appear to have strong habitat associations. This makes difficult the strict establishment of a definition of "estuarine dependency." Also, the seaward boundary of an "estuary" is often blurred, so that the definition of "dependency" is hampered by lack of comparative, quantitative data from offshore habitats. The easiest distinctions are for those species for which at least one stage is shown to be physiologically or behaviorally obligate, but good natural history and experimental data are required for this. Therefore, the question "What is an estuarine species?" remains elusive. In addition, the oft-made contention that estuaries with similar habitats may support similar species assemblages seems reasonable, but may be misleading if assumptions of estuarine dependency are based on occurrence rather than in an adaptive-evolutionary sense.

IV. ECOLOGICAL FUNCTION OF BIODIVERSITY

In addition to genome, species, and ecosystem aspects of biodiversity, a fourth category must be considered, namely, "functional diversity" (Steele, 1991; see Glossary), which concerns ecological functions with respect to environmental maintenance and change. Ecological functions within the coastal zone and its estuaries are complex and variable, and they must be understood before we can interpret the composition and patterns of biodiversity. Holligan and Reiners (1992) listed a number of factors that underlie the biological diversity of the coastal zone and its estuaries, first for natural processes:

Exchanges of Materials Riverine and atmospheric export and import, groundwater exchange, and ocean–land material transport operate at various levels, but are presently poorly understood. [Recent information on anadromous fishes is shedding light on organic-matter transport; e.g., Hesslein *et al.* (1991); Bilby *et al.* (1996); Garman and Macko (1998).]

Physico-chemical Properties The coastal zone is a region of high energy exchange due to interactive oceanic and atmospheric forcing associated with topographical discontinuities, density gradients caused by freshwater inflows, and seasonal heat exchanges. Deltas, estuaries, and lagoons are the major sites for transformation and accumulation of organic matter and sediment, and all are highly variable spatially and temporally, so that their average conditions are not good indicators of net fluxes. Estuaries, in particular, are "sites of complex interactions, related to salinity gradients, phase transformation involving particle–water reactions, and to biological processes that cause biogeochemical transformations" (Holligan and Reiners, 1992).

Biological Properties Favorable conditions of light and nutrients in the coastal zone maintain high rates of primary productivity that are several times greater than for the open ocean, and even greater than for certain coastal upwelling areas; some coastal systems, such as salt marshes, mangrove swamps, mudflats, beds of aquatic vegetation, and coral reefs, exhibit even higher productivity. Some areas act as sources, others as sinks, and the nature of the coupling of primary productivity to the bottom or to open waters may determine community structure and function.

Biogeochemical Processes Organic matter is readily reoxidized in coastal waters, but some poorly drained areas may become anaerobic. This is especially apparent in the bottom water of estuaries in summer, when temperatures are high.

Many present-day human activities influence both ecological functions and biological diversity:

Altered Delivery of Freshwater Freshwater impoundment by damming has decreased total discharge into estuaries and coastal seas by about 15% since the 1950s, an amount equivalent to a change in sea level of −0.7 mm/yr. Seasonal flows have also been altered; alteration in the residence time of water in estuaries may have far-reaching effects on chemical processes.

Changes in the Transport and Fate of Suspended Matter Coastal subsidence, sediment starvation and consolidation, and nutrient levels have all been altered by human interventions. Land clearing especially on steep slopes, has increased sedimentation.

Chemical Modification Nutrients, eutrophy, and blooms have become widespread and their frequency seems to be increasing. Contaminants that are of most concern include heavy metals, synthetic organic compounds, radionuclides, and hydrocarbons.

Ecosystem Modification This takes many forms, from physical change, to habitat loss, to depletion of resources. The worst-affected areas are those with high human population densities, such as Southeast Asia, and along temperate coasts that have significant sources of pollutants, such as the Baltic Sea.

Longer-term processes that influence biodiversity are the effects of climate change, especially in response to global warming, should that continue to occur:

Natural Variations in Climate Many climate-change studies describe possible variations in the altered distributions of biota. However, rather subtle changes in climatic conditions can induce large ecological changes that reflect the sensitive nature of marine food chains to climate and to climate-dependent factors such as nutrient levels and salinity. The direct effects of climate are difficult to distinguish from those incurred by humans.

Temperature The largest climate changes are expected in the higher latitudes. Thus, the poleward extension of climate-sensitive species is to be expected in case of global warming. Temperature changes can also affect behavior and physiology (e.g., reproduction, feeding and food availability, predation, migration), so that predictions are destined to be speculative.

Wind Wind strongly influences upwelling and stratification, thus affecting productivity through nutrient and light availability. According to most climate change scenarios, wind intensity is expected to increase.

Extreme Events Short time-scale events are also expected to increase with climate warming, and these may induce dramatic, long-term changes. A single storm lasting <5 days can result in sand transport equivalent to two-thirds of the total for an average year. Tsunamis have had the greatest effects recorded to date.

Changes in Sea Level Presently, sea level is rising faster than the rate during the late Holocene due to a combination of thermal expansion of seawater and melting of ice as the climate warms. Severe impacts of sea level rise on deltas and estuaries are already apparent, partly because they are low-lying, strongly perturbed by humans, and exhibit enhanced erosion and subsidence. Natural communities of plants and animals play a crucial role in determining the response of the coastal zone to changes in sea level.

This array of effects requires the development of research programs to address hypotheses that are relevant to the ecological function of estuarine biodiversity. Among many possibilities, the following seem essential (slightly modified from Solbrig, 1991):

- For species: no aspect of life history has any influence on extinction probability.
- For communities: keystone species are essential for maintaining species richness in communities under all environmental conditions.
- For ecosystems: removal or addition of functional or structural groups that produce changes in temporal or spatial configuration of landscape elements will have no significant effect on ecosystem properties over a range of time and space scales.

These hypotheses can be clarified by means of a case-by-case examination (see the Chesapeake Bay case study). For example, some species seem very alike in their life histories. However, redundancy in species function may mean that diversity and function are somewhat independent of one another. Many species of benthic infauna and epifauna are extremely abundant and ecologically important in estuaries. Many feed on sediments, and those with complete alimentary canals can consolidate organic residues into often long-lived, sculptured pellets. The question is: Many species have similar ecological requirements and, therefore, are species replaceable?

With respect to physical structure, Roy (1984) stated that the ecology of an estuary depends on the geological stage it has reached in its evolutionary progression, and that the rate and direction of natural change provide a yardstick to assess impacts induced by humans. However, as Roy emphasized, factors influencing estuary development include (1) inherited factors, mainly of a geological nature, that control the size and shape of the basin and the nature of the sediment supply, and (2) contemporary factors of a process nature (such as tides, river discharge, waves, etc.) that influence modes of sedimentation, hydrodynamics, and the biota. This prompts the question: To what extent are structure and biodiversity related?

Mann (1982) observed that, in general, estuaries are more productive than adjacent shelf systems, bringing up the question of nutrient flushing. That is, estuaries tend to act as nutrient traps. Many are enriched by pollution; the Hudson is a spectacular example of enrichment of a large shelf area well beyond its mouth. Within 600 km^2 of sea at the apex of the New York Bight, phytoplankton production amounted to about 370 g C/m^2/day, compared with only 100 g C/m^2/yr at the edge of the shelf. Mann and Lazier (1991) also noted that the dynamics of coastal waters, including estuaries, are made complex by: (1) shallowness, resulting in relatively mixed water that may extend to the bottom, and dead biological material that may accumulate to release nutrients that are carried rapidly to surface waters; (2) tidal currents that create turbulent mixing, which has especially marked effects on food particles, fertilization of planktonic eggs, and larval dispersal; and (3) barriers to convection imposed by coastlines, meaning that wind drives surface water away from the coast, and upwelling is the only way for it to be replaced, bringing nutrients to the surface. The question here is: To what extent are enrichment and/or pollution and circulation related to biodiversity?

Turning to larval transport, a variety of organisms have adapted to the seaward flow of low-salinity water and a compensatory landward flow of bottom water in estuaries. Organisms can make vertical migrations to maintain themselves in the estuary, or to enter or leave it seasonally. For example, estuarine larval transport and retention mechanisms are evident on two scales: circulation patterns on a large, regional scale and small-scale, local water motion. There is evidence that oyster larvae (*Crassostrea virginicus*) rise into the water column to be carried upstream, and that this is cued by increasing salinity associated with increasing upstream flow; larvae of the blue crab (*Callinectes sapidus*), on the other hand, occur in maximum numbers in surface waters at the mouth of Chesapeake Bay at night as the salinity falls on the ebb tide (Boicourt, 1982). From this and other evidence, it has been concluded that the crab larvae develop offshore, then reinvade as megalopa larvae or juveniles. Fishes have also been shown to vary their depths, some rising into surface waters during flood to remain in the estuary, and others doing the opposite to be taken out to sea: Thus, many invertebrates and fishes utilize the two-layered estuarine structure for dispersal, and this may not be entirely passive, as has often been assumed. Despite some improved knowledge, Boicourt's conclusion is still pertinent, that the larval transport and retention problem "stands at the state of the art in both physical and biological fields." The question is: Does recruitment depend on return or retention (in the strict sense) as the operative process, and to what extent do larvae determine their own fates?

As another example of the importance of functional diversity, juveniles of the five species of Pacific salmons (*Onchorhynchus* spp.) vary in time spent in estuaries, but for all of them a high proportion of their prey tends to be detritus feeders (Healey, 1982). This means that the configuration of the estuary and the efficiency of entrapment of detrital matter are important for juvenile salmon habitat. Retention of detritus is enhanced by restricted exchange with the ocean and low bed-load transport. Marshes and submerged aquatic vegetation are efficient detritus traps, and these habitats also shelter salmon from predation. Thus, it may be hypothesized that the complex of intertidal marshes, tidal creeks and secondary river channels, lower intertidal and subtidal weed beds, and basin morphology all contribute to the carrying capacity of the estuary for young salmon, and that the appropriate configurations must be conserved if salmon production is to be maintained. The question here concerns how the complexity of the land–seascape enhances biodiversity, and how this may operate differently for closely related species.

From these examples, it is apparent that, insofar as ecosystem functioning is concerned, the addition or deletion of species, structural groups, or essential processes can have profound effects on the capacity of an estuary to maintain its biodiversity. This is especially true for "keystone" species, which have influences out of proportion to their density or biomass. Likewise, the fragmentation and/or simplification of habitats and of land–seascapes may have profound effects on estuaries, since these impacts shift ecological complexity and community structure and function. Furthermore, it is likely that the functional autonomy of estuaries depends on their size and the time intervals of various processes. That is, the degree to which an ecological system may be autonomous depends on the extent to which it is independent of the ecological dynamics outside its domain. Of course, no ecosystem can be completely independent owing to the climatic, ecological, and geological connections among all portions of Earth. However, the larger the domain, the more it may tend to be autonomous during the time spans of investigation. Consideration of autonomy requires one to consider to what extent estuaries are forced functionally by the dynamics of the contributing watershed and adjacent shelf (e.g., tides, currents, flushing, river inputs, storms). Obviously, the elucidation of autonomy for a domain of a given size is not a simple endeavor. However, the simple fact is that under many management regimes, autonomy may be incorrectly assumed.

V. A CASE STUDY: THE CHESAPEAKE BAY

Chesapeake Bay is one of Earth's largest estuaries. Its origin is that of a drowned river valley. This is the case for many estuaries associated with coastal plains, wherein the dominant processes are sedimentary and erosional and whereby the bottom is largely soft sand and mud. Chesapeake Bay's one major hard feature is that of the oyster reef, formed by the eastern Oyster, *Crassostrea virginicus*.

Many scientists have observed the drastic decline of oysters and of oyster reefs during the past hundred years and more, and the associated ecosystem effects. From a structural point of view, oyster reefs represent a unique and dominant biogenic structure of the Bay. Their distribution and ecological importance during the mid-1800s were analyzed by McCormick-Ray (1998). Their loss would be expected to have extensive repercussions on biological, hydrological, erosional, and sedimentary patterns and processes, all of which can have major influences on biological diversity. Indeed, history has borne out this conclusion. For example, a review by Rothschild *et al.* (1994) stated that "considerable concern is voiced regarding Chesapeake Bay water quality and the effects of disease on oysters" and that "the effects of a diminished oyster population abundance certainly must have changed the 'ecology' of Chesapeake Bay, and these effects must have become evident at the time of maximum stock decline (1884 to 1910)."

To understand the ecosystem effects of the oyster and oyster reefs better, one must begin at the regional scale, wherein the coastal zone is conceived as a nested hierarchical system (Ray *et al.*, 1997). The regional scale is that of biogeographic and physiographic provinces. The mesoscale is represented by major regional subdivisions, such as watersheds, estuaries, coastal islands, lagoons, and coastal–ocean fronts that separate major marine regimes. The smallest scale is that of the interacting mosaics of land–seascapes, for example, wetlands, hard and soft bottoms, and water masses that are distinguished by salinity, temperature, and density. The oyster reef represents this latter scale.

This hierarchy is illustrated in Fig. 1, which indicates top-down "controls" and bottom-up "feedbacks" and which places estuaries in a central role. First, the biogeographic province (and/or "region") is an area whose limits are defined by the relative homogeneity of the biota. For example, the traditionally accepted boundaries for the Virginian Province are Cape Cod, Massachusetts, to Cape Hatteras, North Carolina. These capes are significant points of deflection for major ocean currents, principally the warm, north-flowing Gulf Stream and the cold, south-flowing Labrador Current. At these capes, dramatic changes in coastal characteristics, such as water temperatures and circulation patterns, occur and these physical features play major roles in determining the ranges of the biota. One major feature of the Virginian Province is the presence of very large estuaries, such as the Chesapeake and Delaware Bays.

Species' ranges respond to these large-scale attributes, as well as to species' physiological and behavioral adaptations. Fishes are a case in point. Of the almost 1100 East Coast fish species, 556 species presently occur in the Virginian–Carolinian region (Ray, 1997; Ray *et al.*, 1997). Estuary-dependent species are drawn from this species pool. As discussed earlier, "estuary-dependent" has usually been interpreted very broadly. C. R. Robins and I re-examined this matter and concluded that occurrence and even abundance of fishes in estuaries do not necessarily infer "dependence." Rather, we determined that a species must be truly "obligate" in an evolutionary, adaptive sense for this definition to apply; that is, if estuaries were removed.

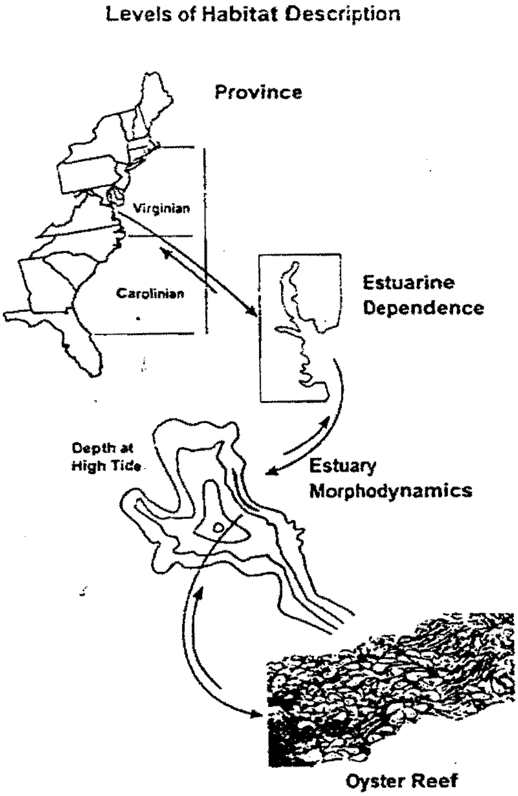


FIGURE 1 A hierarchical model of coastal zone relationships, showing top-down "controls" and bottom-up "feedbacks" of coastal zone interactions, involving levels from biogeographic provinces, to estuaries, to the oyster reef. The biogeographic province provides the species pool from which estuaries may draw "estuary-dependent" representatives. This biota is influenced by the morphometrics of individual estuaries, leading to different species communities among the estuaries in a biogeographic region. The oyster is a "keystone" species both biologically and ecologically, as the reefs it builds influence the morphometrics of the estuaries in which it occurs. Overharvesting of oysters in the Chesapeake Bay, and elsewhere, has had major effects on estuarine function, structure, and probably biodiversity as well. (From Ray *et al.*, 1997.)

"dependent" species would be at risk of significant depletion, even to the point of local or regional extirpation. According to this definition, we determined that 151 species (27% of 556 species) qualify as "estuary dependent," less than has been assumed in the past, but still a significant part of the total. This figure is remarkably consistent with the results of Able and Fahay (1998: see Section III). A principal components analysis of the ranges of these species resulted in four assemblages. Figure 2 shows these assemblages and demonstrates that so-called "faunal breaks" between provinces must be viewed as gradients, and not as "boundaries" in a rigid sense.

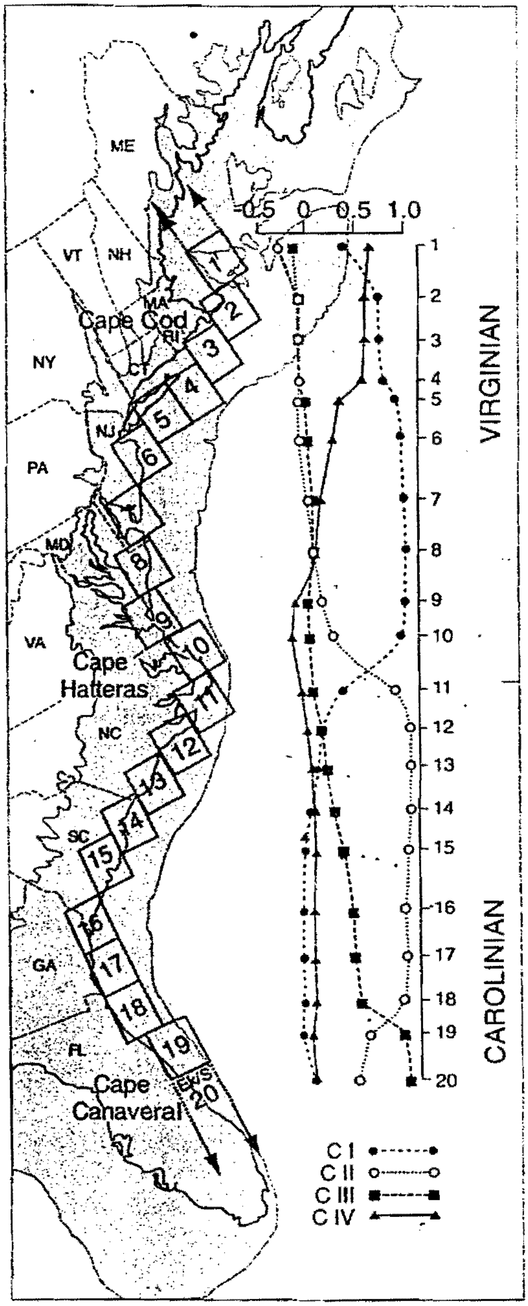


FIGURE 2 A principal components analysis of the ranges of 151 Carolinian and Virginian estuary-dependent species revealed the following assemblages: Component I = Virginian; Component II = Carolinian; Component III = tropical; and Component IV = boreal. These four assemblages overlap, as would be expected. (From Ray *et al.*, 1997.)

This finding brings up the following question: How might changes in estuaries, human-caused or not, influence the composition of these fish assemblages? For insight into an answer, we must examine the dynamics of estuaries themselves. Many factors interact to characterize an estuary. Among these are drainage area, tides and mixing, estuary area, depth, dimension, water column stratification, floods, habitat types, and many others. A principal components analysis (Ray *et al.*, 1997) revealed five components that may influence biological diversity: estuarine dimensions, dominance of marine processes, co-dominance of marine and freshwater processes, fjord-like attributes, and surface area. The interplay of these factors may be used to classify estuaries into the following types: (1) those that are long and wide with extensive catchment areas; (2) large, embayed, well-stratified estuaries with extensive seawater zones; (3) marine-dominated, deep, and well-stratified estuaries; (4) long and narrow, fjord-like estuaries, with large tidal prisms; and (5) estuaries with large surface areas. Chesapeake Bay falls somewhere between the first and second categories.

It seems reasonable, from what we know of the natural histories of the biota, that these estuarine types would be expected to host different communities of species, and further that different disturbance regimes would be expected to affect these estuarine types and their species' communities differently. The conclusion seems obvious that biotic communities will differ among estuaries and that seasonal or weather-related changes in salinity and other factors will be reflected in the variability of biotic patterns. Furthermore, because the great majority of estuarine fishes, in particular, also occur over the continental shelf, fluctuations of estuarine fish communities would also be reflected, up-scale, by shelf-fish communities.

This approach offers a series of environmental top-down "controls" over biodiversity and ecosystem function. But this can not totally explain what might be the consequence of bottom-up environmental alterations. That is, the prediction of biodiversity and faunal dynamics requires that the response of the organism to the environment at different scales and the modifications the organism may make to the environment both be made explicit. For example, Fig. 1 indicates that the decline or removal of a species or a local structure, in this case oyster reefs, will influence the total biological diversity of the system by influencing environmental conditions through environmental feedbacks.

For the Chesapeake Bay, and many other Virginian–Carolinian estuaries, oysters are especially critical because they form reefs, which influence biodiversity at many levels (McCormick-Ray, 1998). The location of these reefs is not accidental. Their formation depends on the geometry of the estuarine basin, tidal stream channels and meanders, and other factors. Furthermore, oyster reefs influence estuarine development, sedimentation, and water clarity, and thus the formation of habitats (e.g., submerged aquatic vegetation, marshes, soft bottoms, and hard bottoms) for a host of organisms. In sum, the eastern oyster appears to be a classic example of a "keystone" species at the level of the ecosystem. Structurally and functionally, individual oysters and the reefs they build strongly influence species diversity and productivity. Additionally, the distribution of oyster reefs may be of fundamental importance to development of the estuarine land–seascape.

Another type of feedback concerns the fact that most species exist as a number of separate populations that mix together as one or more "metapopulations." For example, an estuary-dependent species, such as menhaden (*Brevoortia tyrannus*), forms populations in individual estuaries, and these populations assemble over the shelf to form one or more metapopulations. Furthermore, these metapopulations join those of other species and become part of the shelf "metacommunity," as illustrated in Figure 3. It follows that fluctuations of any one metapopulation within any one estuary will affect the total "metacommunity" to a greater or lesser extent (Ray, 1997). This form of biodiversity concerns community composition, not necessarily the presence or absence of individual species, and is strongly affected by functional alterations of estuaries. The conclusion is that at the scale of the large, regional ecosystem, each estuary may be conceived in terms of the sum total of estuaries and is responsible, to a greater or lesser degree, for the overall large-scale dynamics of the biogeographic region. This approach fuses concepts of landscape ecology with metapopulation theory.

The concepts presented in the case of the Chesapeake Bay suggest controls and feedbacks among organisms and the environment at several scales, in which one fundamental factor seems clear. East Coast estuaries have been perturbed in many ways, but one of the most dramatic for the Chesapeake Bay has been the depletion of oyster reefs and the practical eradication of their functional ecosystem role. Although data are lacking that would explain beyond doubt what changes have been perpetrated by the oyster's decline in Chesapeake Bay, it seems apparent that, at the very least, the oyster reef's demise has had a marked effect on the distributions of estuarine species, not necessarily because the

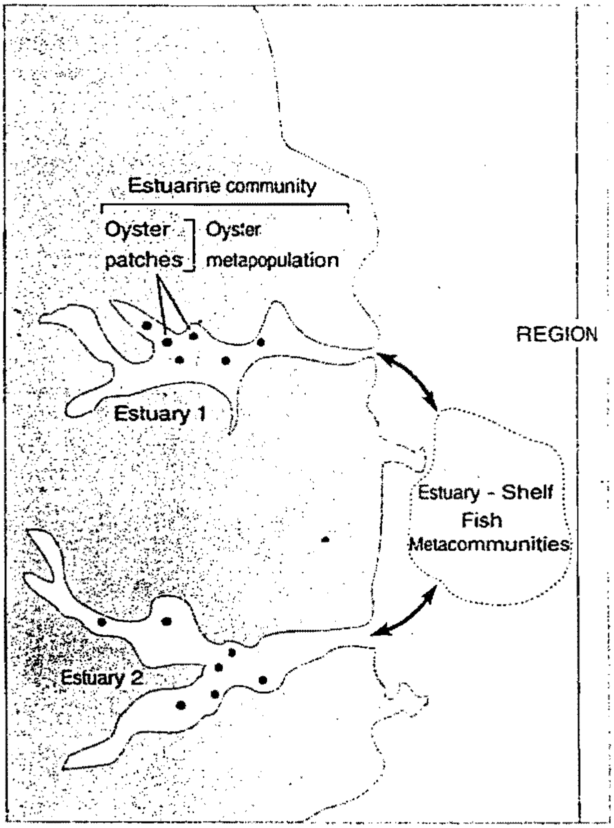


FIGURE 3 The concept of estuarine metapopulations and shelf metacommunities. Oyster reef metapopulations influence estuarine morphometrics and biodiversity. Consequently, the fish biota of various estuaries influence the fish metacommunity of the shelf.

reef is required habitat, but because of its functional importance to the Bay as a whole. It is possible that these effects may have cascaded up-scale to the adjacent continental shelf.

VI. FUTURE CHALLENGES

I make three points in conclusion. The first concerns the need for greatly increased attention to the natural histories of estuarine and shelf species. The natural histories of these organisms underlie both theory and management practice. The minimal requirements for informed conservation and management are descriptions of species' life histories in the context of their environmental relationships.

Second, many estuarine organisms range widely and form metapopulations over the shelf, as components of estuary–shelf communities. Thus, the minimal scale for sustainability of biodiversity becomes that of the biogeographic region. Quantitative, landscape-level descriptions of the regional coastal zone, including estuarine habitats, are a necessary prerequisite for conservation and management.

Third, it has become a truism in ecology that no one scale adequately describes ecosystem phenomena. Rather, the interaction among phenomena on different scales must become the centerpiece of research and management. This strongly suggests that explanations for fluctuations in biodiversity, including those within biotic communities and at regional scales, will continue to be obscure until multiscale ecosystem functions are better understood. Ecosystem management is the logical outcome of interdisciplinary, multiscale knowledge. This recognizes that understanding the ecology and diversity of coastal zone biota depends in large part on understanding land–sea and estuarine interactions, and also on the joint application of metapopulation and land–seascape theory and methods.

The National Research Council (NRC, 1995) stated that a major future research objective is "to understand the patterns, processes and consequences of changing marine biological diversity by focusing on critical environmental issues and their threshold effects, and to address these effects at spatial scales from local to regional." This objective cannot be met absent a specific consideration of estuaries as major, scale-dependent pathways of biotic and abiotic interchanges. Estuarine biodiversity, structure, and function have been severely modified by humans around the globe. Nevertheless, many estuaries remain either good candidates for restoration or relatively rich, productive, and resilient. Documentation of impacts is severely hampered by lack of long-term baseline information, inadequate assessment of biodiversity, lack of trained taxonomists, and difficulty in sampling.

Nevertheless, an extensive estuarine literature is now available, and it illustrates that control of pollution, development, excessive natural resource extractions, and changes in ecosystem function urgently need to be addressed. Problems may not be eliminated, only ameliorated, but increased understanding is essential for the future sustainability of estuaries. Carriker (1967) put the matter boldly three decades ago: "There is consequently an urgency to study estuaries before unenlightened defacement obliterates them and before it becomes expedient to investigate them primarily as outdoor pollution laboratories."

See Also the Following Articles

COASTAL BEACH ECOSYSTEMS • FRESHWATER ECOSYSTEMS • INTERTIDAL ECOSYSTEMS • LAKE AND POND ECOSYSTEMS • MARINE ECOSYSTEMS • RIVER ECOSYSTEMS • WETLANDS ECOSYSTEMS

Bibliography

Able, K. W., and Fahay M. P. (1998). The *First Year in the Life of Fishes in the Middle Atlantic Bight.* Rutgers University Press, New Brunswick, New Jersey.

Anonymous. (1959). Symposium on the classification of brackish waters. April 8–14, 1958, Venice, Italy. *Archivo di Oceanografia e Limnologia,* Vol. 11, supplemento.

Bilby, R. E., Fransen, B. R., and Bisson P. A. (1996). Incorporation of nitrogen and carbon from spawning coho salmon into the trophic system of small streams: Evidence from stable isotopes. *Canad. J. Fisheries Aquatic Sci.* 53, 164–173.

Boicourt, W. C. (1982). Estuarine larval retention mechanisms on two scales. In *Estuarine Comparisons* (V. S. Kennedy, ed.), pp. 445–457. Academic Press, New York.

Bulger, A. J., Hayden, B. P., Monaco, M. E., Nelson, D. M., and McCormick-Ray, M. G. (1993). Biology-based estuarine salinity zones derived from a multivariate analysis. *Estuaries* 16(2), 311–322.

Carriker, M. R. (1967). Ecology of estuarine benthic invertebrates: A perspective. In *Estuaries* (G. H. Lauff, ed.), AAAS Sci. Publ. No. 83, pp. 442–487. American Association for the Advancement of Science, Washington, D.C.

Emery, K. O. (1967). Estuaries and lagoons in relation to continental shelves. In *Estuaries* (G. H. Lauff, ed.), AAAS Sci. Publ. No. 83, pp. 9–11. American Association for the Advancement of Science, Washington, D.C.

Garman, G. C., and Macko, S. A. (1998). Contribution of marine-derived organic matter to an Atlantic coast, freshwater, tidal stream by anadromous clupeid fishes. *J. North Amer. Benthol. Soc.* 17(3), 277–285.

Hanski, I., and Gilpin, M. (1991). Metapopulation dynamics: Brief history and conceptual domain. *Biol. J. Linnaean Soc.* 42, 3–16.

Hayden, B. P., Ray, G. C., and Dolan, R. (1984). Classification of coastal and marine environments. *Environ. Conservation* 2(3), 199–207.

Healey, M. C. (1982). Juvenile salmon in estuaries: The life support system. In *Estuarine Comparisons* (V. S. Kennedy, ed.), pp. 315–341. Academic Press, New York.

Hesslein, R. H., Capel, M. J., Fox, D. E., and Hallard, K. A. (1991). Stable isotopes of sulfur, carbon and nitrogen as indicators of trophic level and fish migration in the lower Mackensie River basin, Canada. *Canad. J. Fisheries Aquatic Sci.* 48, 2258–2265.

Heywood, V. H., and Watson, R. T. (eds.). (1995). *Global Biodiversity Assessment.* Published for the United Nations Environment Programme by Cambridge University Press, Cambridge, United Kingdom.

Holligan, P. M., and Reiners, W. A. (1992). Predicting the responses of the coastal zone to global change. *Adv. Ecol. Res.* 22, 211–255.

Houde, E. W. (1997). Patterns and consequences of selective processes in teleost early life histories. In *Early Life History and Recruitment in Fish Populations* (R. C. Chambers and E. A. Trippel, eds.), pp. 173–196. Chapman and Hall, London.

Ketchum, B. H. (ed.). (1972). *The Water's Edge: Critical Problems of the Coastal Zone.* Massachusetts Institute of Technology Press, Cambridge, Massachusetts.

Mann, K. H. (1982). *Ecology of Coastal Waters: A Systems Approach.* University of California Press, Berkeley.

Mann, K. H., and Lazier, J. R. N. (1991). *Dynamics of Marine Systems: Biological–Physical Interactions in the Oceans.* Blackwell Scientific Publications, Boston.

McCormick-Ray, M. G. (1998). Oyster reefs in 1878 seascape pattern—Winslow revisited. *Estuaries* 21(4B), 784–800.

Nelson, J. S. (1984). *Fishes of the World,* 2nd ed. Wiley–Interscience, New York.

National Research Council (NRC). (1995). *Understanding Marine Biodiversity.* National Research Council, Washington, D.C.

Natural Environment Research Council (NERC). (1992). *Land–Ocean Interaction Study (LOIS): Science Plan for a Community Research Project.* Natural Environment Research Council, Swindon, Wiltshire, United Kingdom.

Pernetta, J. C., and Milliman, J. D. (eds.). (1995) *Land–Ocean Interactions in the Coastal Zone: Implementation Plan.* Global Change Report No. 33. International Geosphere–Biosphere Programme of the International Council of Scientific Unions (ICSU), Stockholm.

Pritchard, D. W. (1967). What is an estuary: Physical viewpoint. In *Estuaries* (G. H. Lauff, ed.), AAAS Sci. Publ. No. 83, pp. 3–5. American Association for the Advancement of Science, Washington, D.C.

Ray, G. C. (1997). Do the metapopulation dynamics of estuarine fishes influence the stability of shelf systems? *Bull. Mar. Sci.* 60(3), 1040–1049.

Ray, G. C., Hayden, B. P., McCormick-Ray, M. G., and Smith, T. M. (1997). Land–seascape diversity of the U.S. east coast coastal zone with particular reference to estuaries. In *Marine Biodiversity: Causes and Consequences* (R. F. G. Ormond, J. D. Gage, and M. V. Angel, eds.), pp. 337–371. Cambridge University Press, Cambridge, United Kingdom.

Rothschild, B. J., Ault, J. S., Goulletquer, P., and Heral, M. (1994). Decline of the Chesapeake Bay oyster population: A century of habitat destruction and overfishing. *Mar. Ecol. Progress Ser.* 111, 29–39.

Roy, P. S. (1984). New South Wales estuaries: Their origin and evolution. In *Coastal Geomorphology in Australia* (B. G. Thom, ed.), pp. 99–121. Academic Press, Orlando, Florida.

Sanders, H. L. (1968). Marine benthic diversity: A comparative study. *Amer. Naturalist* 102, 243–282.

Solbrig, O. T. (1991). *From Genes to Ecosystems: A Research Agenda for Biodiversity.* Report of a IUBS–UNESCO Workshop, June 1991, Harvard Forest, Massachusetts. International Union of Biological Sciences, Paris.

Steele, J. H. (1991). Marine functional diversity. *BioScience* 41(7), 470–474.

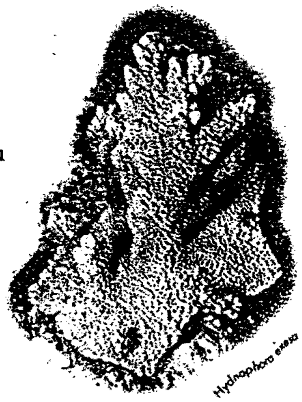
Winemiller, K. O. (1995). Fish ecology. In *Encyclopedia of Environmental Biology,* Vol. 2, pp. 49–65. Academic Press, Orlando, Florida.

Geological History

Earliest 'reefs' – Palaeozoic reefs – Family Tree of Scleractinia – history of Mesozoic reefs – extinction events – Cenozoic reefs – origins of modern corals

Nowhere do the sciences of biology and geology come closer together than in the study of coral reefs, for reefs are geological structures yet are made by living organisms.

Reef-like structures of one form or another have existed on earth for at least 2,000 million years. At this time, life consisted only of simple organisms including bacteria and algae. The first reef-like limestone accumulations, found in Proterozoic rocks the world over, were simple structures formed by stromatolites. These were hemispherical mounds of what were probably blue-green algae that entrapped fine sediment, much as stromatolites do today (illustrated next page). The predominance of plant life, unchecked by animals, was responsible for the first atmospheric oxygen and it was the combination of oxygen and food-providing plants that set the stage for the evolution of the first animals, including the first reef-like structures of animal origin. These animals were sponge-like archaeocyaths of the Cambrian and they formed calcareous thickets in very shallow water (illustrated below).

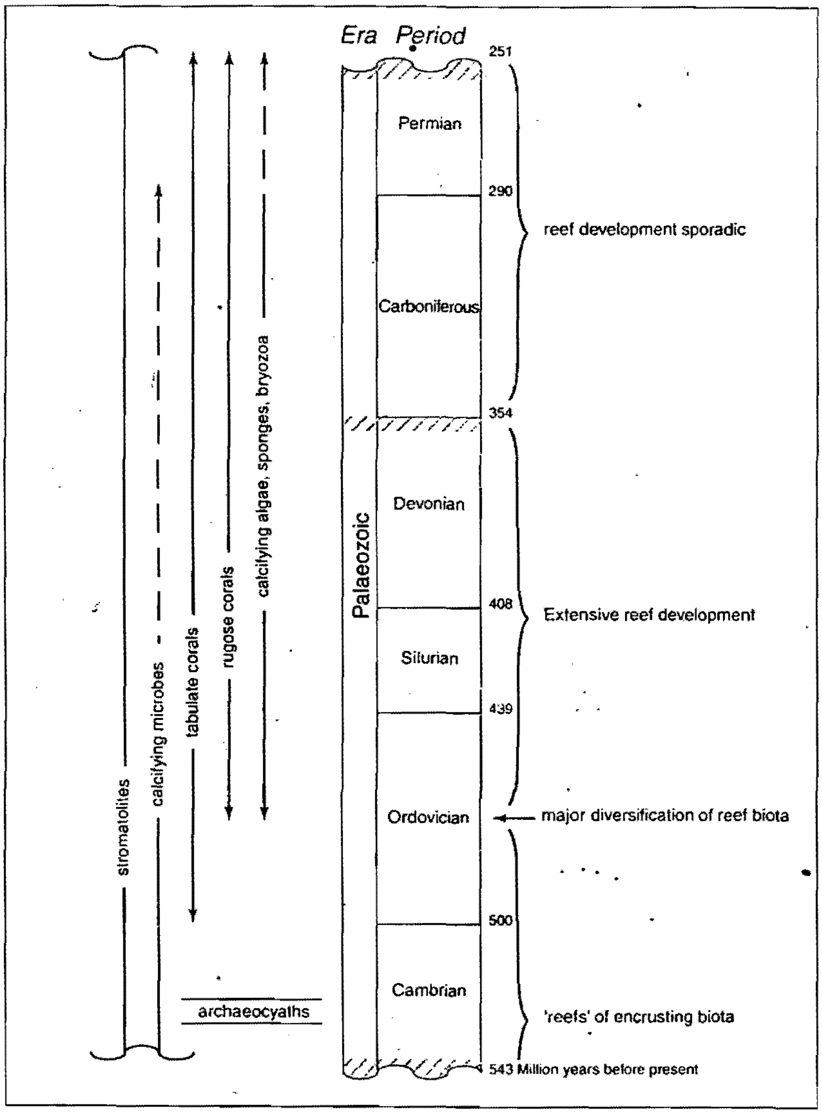


By the Middle Ordovician, complex algae and invertebrate reef communities had become widespread and reef biota had diversified. Archaeocyaths had long been extinct and stromatolites were mostly replaced by a combination of red coralline algae, stromatoporoid sponges, stony bryozoans and tabulate and rugose reef corals (illustrated pp34-5). These are the oldest known reef coral communities, possibly the outcome of endo-symbiotic animal/algal associations. For at least 150 million years, different combinations of these algae, sponges and corals built reefs around the tropical world. Reef development reached a peak in the Devonian Period and even after all this time, what remains today of these reefs are sometimes of awesome size (illustrated opposite).

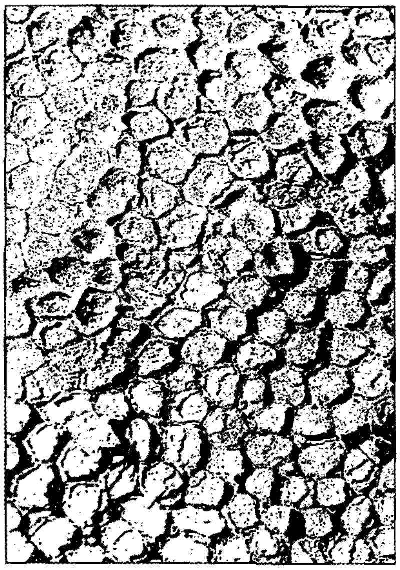
Previous page: Large coral reefs can be awesome sights from the air. MARSHALL ISLANDS *Photograph: Jim Maragos*

Opposite: Scleractinia were not the original builders of coral reefs. Far from it: Devonian reefs, built by other types of corals and other calcifying organisms, are still found in many countries. Although this reef, built by calcifying sponges and algae together with rugose and tabulate corals, is 375 million years old, its eroded remains suggest an original size comparable to any scleractinian reef. NORTH-WESTERN AUSTRALIA *Photograph: author*

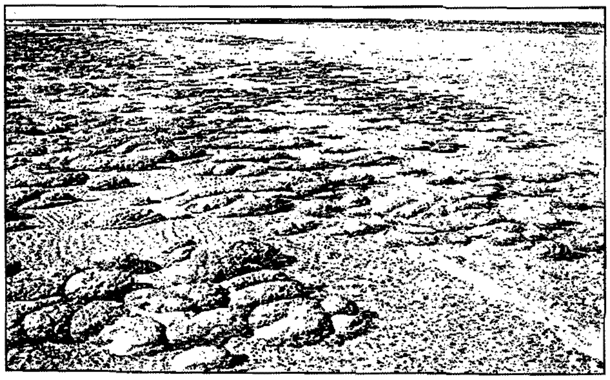
1 The Early Cambrian remains of an archaeocyath 'reef'. LABRADOR, CANADA *Photograph: Paul Copper*



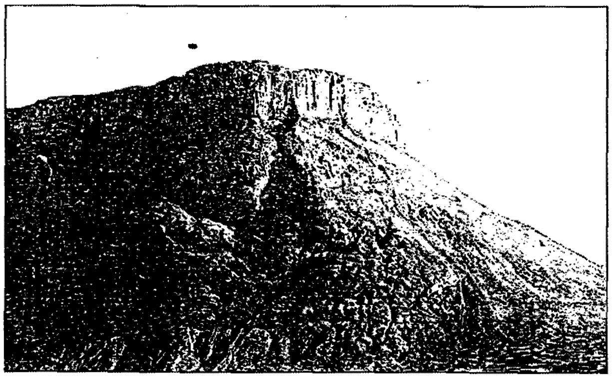
The Palaeozoic Era. Summary of reef development before the evolution of the Scleractinia. Time is in millions of years before present. Colours of the column indicate major cycles of global warming (red) and cooling (blue). Major mass extinctions are indicated by red cross-hatches. The geological longevity of principal groups of reef-building organisms are indicated on the left. Principal geological events in reef building are summarised on the right. The latter does not include a multitude of finer scale extinction and reef building geological intervals.



1



2



3

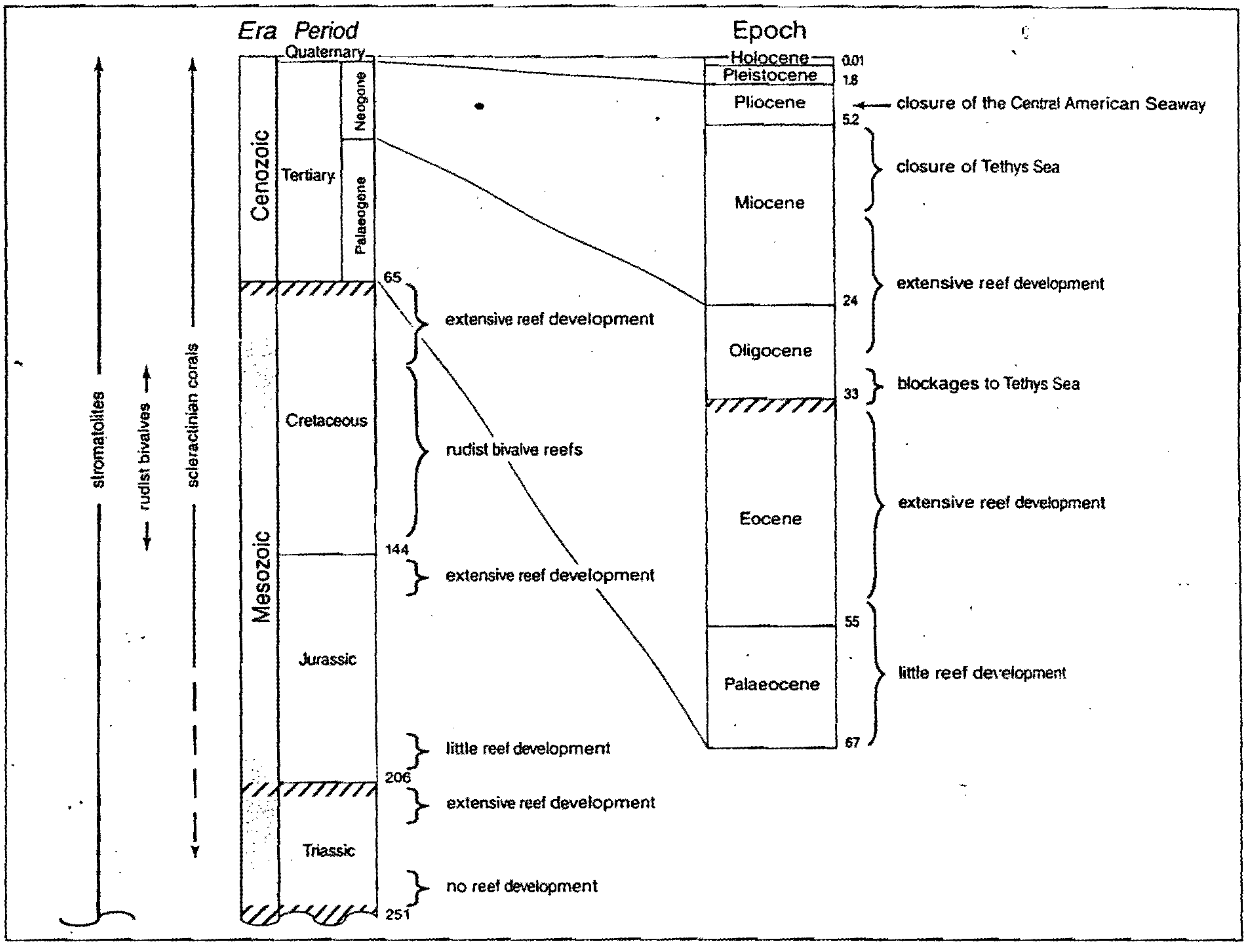
1 Tabulate corals abounded with rugose corals during the Palaeozoic Era. In gross structure they were not unlike the extant organ pipe coral (*Tubipora musica*). Like the Rugosa, they did not survive the end-Palaeozoic extinctions. *Photograph: author*

2 Living stromatolites in shallow muddy water. SHARK BAY, WESTERN AUSTRALIA *Photograph: Paul Copper*

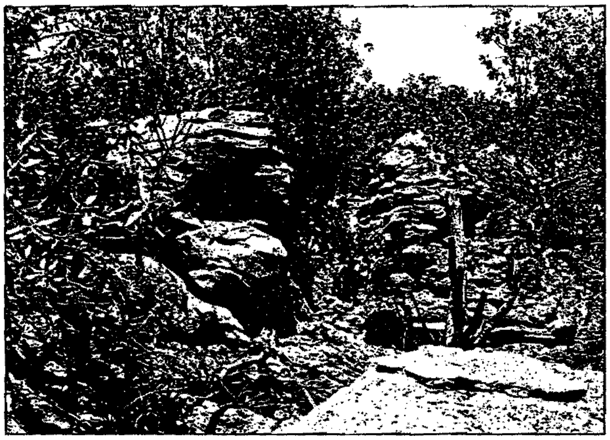
3 Silurian reefs were abundant and diverse. Some, as these remains show, reached impressive sizes. GREENLAND *Photograph: Paul Copper*

4 Stromatoporoids were massive sponge-like organisms, the remains of which often dominate Devonian reefs. NORTH-EAST AUSTRALIA *Photograph: Clive Wilkinson*

5 Rugose corals such as this abounded during much of the Palaeozoic Era. The Rugosa were major builders of big Palaeozoic reefs, but are unlikely to be the ancestors of the Scleractinia. The Rugosa had a serial rather than radial system of septa and had skeletons made of calcite rather than the aragonite of Scleractinia. Rugose corals did not survive the end-Palaeozoic extinctions. *Photograph: author*

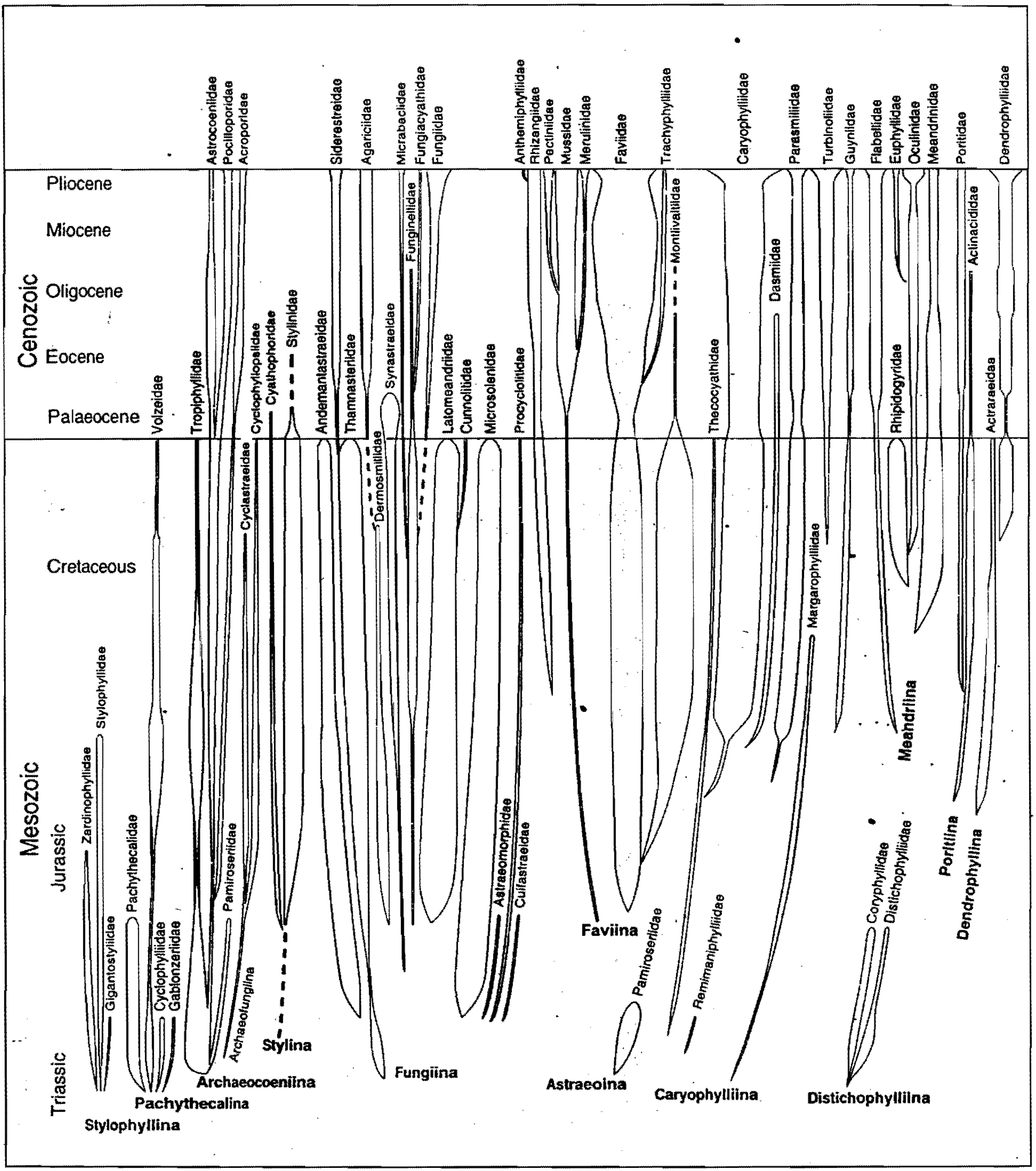


Mesozoic to present day. Summary of the geological history of scleractinian reefs. Time is in millions of years before present. Colours of the column indicate major cycles of global warming (red) and cooling (blue). Major mass extinctions are indicated by red cross-hatches. The geological longevity of the principal groups of reef-building organisms are indicated on the left. Principal geological events in reef-building are summarised on the right.


4


5

Corals were seldom the dominant organisms of Devonian reefs although rugose corals are often abundant in them and have a wide variety of growth-forms. Tabulate corals, which were a less varied group, mostly occupied protected or inter-reef environments. Unlike the Scleractinia, both these groups of corals make excellent fossils because their skeletons were made of calcite, a far more stable form of calcium carbonate than the aragonite skeletons of Scleractinia. Curiously, neither of these diverse and abundant groups of corals survived the mass extinction at the end of the Palaeozoic Era, the only major groups of

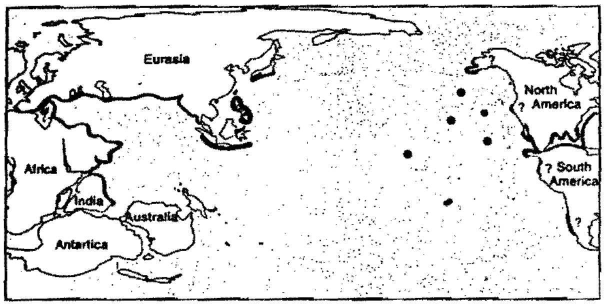


The Family Tree of Scleractinia. This tree consists of 13 suborders (of which 6 are extant), 61 families (of which 25 are extant) and 1,216 genera (of which 246 are extant). The widths of branches indicate the number of genera in each family for each geological interval. This immense fauna varies greatly with geological time: the gaps that are left in the fossil record have been filled in for the sake of clarity. There may also be many families that are not included in this tree because their fossil remains are not sufficiently well preserved for adequate study.

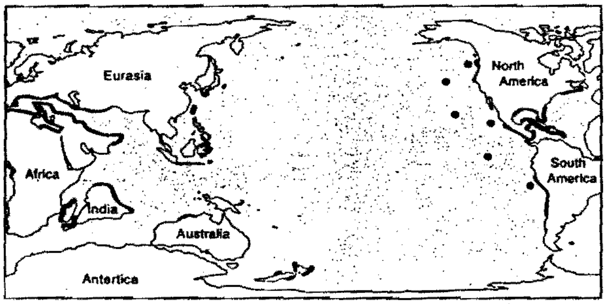
marine organisms known not to have done so. For many millions of years after the end-Palaeozoic extinctions, there appear to have been no reef-building organisms of any kind.

The Scleractinia have left a long and complex fossil record dating at least as far back as the Early Triassic. The reconstruction of the evolutionary sequences of Scleractinia is a complicated process for it must encompass the fossil record over very great intervals of time, the taxonomic relationships of extant corals, as well as studies of coral systematics using molecular techniques. The outcome of this blending of information is the Family Tree (above). The top of the tree

The Late Triassic world showing the distribution maximum of coral reefs and/or reef corals. The reefs that now occur along the eastern Panthalassa rim (indicated with a ?) may have originated in the western Panthalassa and moved eastwards through sea floor spreading and subduction. The broken lines indicate principal coral provinces.



The Late Jurassic world showing the distribution maximum of coral reefs and/or reef corals. The broken lines indicate principal coral provinces. An Asiatic Province extended along the northern margin of the Tethys, with sub-provinces along the east Asian coast. There was also a distinct province along the southern coast of the Tethys.



The Late Cretaceous world showing the distribution maximum of coral reefs and/or reef corals. At the Cretaceous maximum sea level, the area of land was much less than indicated here.

(the families of extant corals) is well established. We also know about the main branches through the Cenozoic Era, for most of these have extant representatives. However, we know very little about the Mesozoic ancestors of corals, for most do not have extant representatives and the majority of families are extinct.

The first organisms that we are tempted to call scleractinians are known from a few Palaeozoic fossils from China and Scotland. They were probably anemone-like organisms that had skeletal structures. The earliest proliferation of organisms that were clearly ancestral Scleractinia are Middle Triassic and consisted of at least seven, but possibly nine, suborders. These corals did not build reefs; they were small solitary or phaceloid organisms of the shallow Tethys Sea of what is now southern Europe and Indo-China.

During the Middle and Late Triassic Period, corals became widespread throughout the Tethys region and their fossils are now found around much of the equatorial Panthalassa Ocean rim (illustrated next page). Curiously, there was a time interval of 20-25 million years between the earliest corals of the Triassic and the earliest widespread coral reefs. This may well have been a time when corals had no algal symbiosis and thus did not have the capacity to build reefs: corals existed as anemone-like creatures that had skeletons.

Importantly for the ancestry of modern corals, both the fossil record and DNA studies agree that two of the most major families today, the Acroporidae and the Pocilloporidae, have their origins with the Astrocoeniidae as far back as the Triassic and have remained separate from other corals ever since. The ancestors of the Siderastreidae may also have a Triassic origin as the extinct Family Thamnasteriidae.

The end of the Triassic was marked with a mass extinction that was not the equal of the extinctions that marked the end of the Palaeozoic Era 45 million years earlier, but it may have rivalled the extinctions at the end of the Mesozoic. The inheritance of the Jurassic was a remnant of these extinctions – a depauperate although diverse suite of genera. Early Jurassic reefs are rare everywhere in the world and all Triassic genera were extinct by the end of the Early Jurassic.

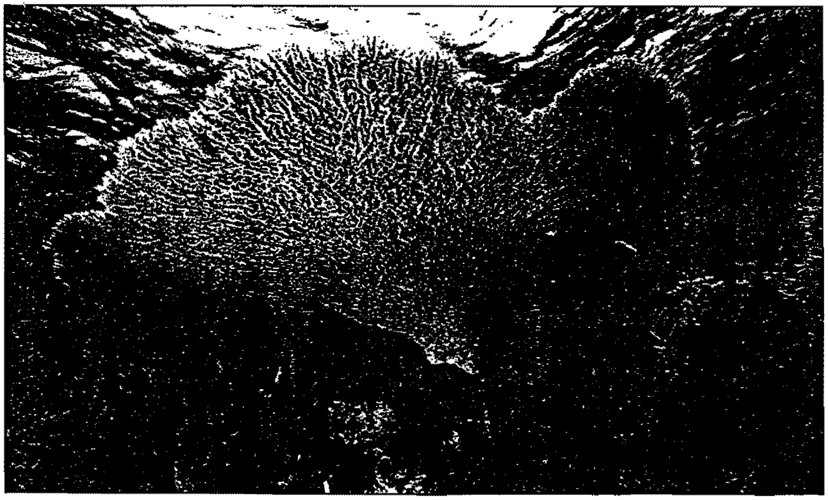
Many theories have been offered to explain the great proliferation of corals in the Jurassic. The opening of the Protoatlantic Ocean (the beginning of the Atlantic of today) probably had much to do with it. By the Middle Jurassic, reef development proliferated in the Tethys Sea of present day Europe and the Mediterranean, but remained poorly developed in the Panthalassa. It may have remained thus throughout the whole Jurassic. It was in the Late Jurassic that the probable all time global maximum of Mesozoic coral diversity occurred, with at least 150 genera recorded in the European Tethys and 51 genera in the Panthalassa. Palaeobiogeographic provinces can be recognised at this time, which reflect continental plate movements, especially the increasing width of the Protoatlantic. By the Late Jurassic the palaeobiogeographic pattern that had developed was the precursor to the pattern that persisted into the Cenozoic Era. It was dominated by massive reef development throughout the Tethys, the Atlantic and the eastern Pacific. The vast empty expanse of the eastern Panthalassa was probably a barrier to dispersion, just as the empty far eastern Pacific is today.

Clearly, a high proportion of the families of corals of today have their origins in the ancient seas of the Middle to Late Jurassic. For most of these families the fossil record is anything but clear and this is why there are so few links between the main branches of the Family Tree (p36). The Jurassic was the time of the origin of two of the most major groups of corals, the Fungiina and the Faviina. The Fungiina dominated much of the Jurassic as well as the Cretaceous. As a group it was greatly diminished by the mass extinctions at the end of the Cretaceous and the families attributed to it today have uncertain affinities. The Faviina, on the other hand, are a well defined group and the Faviidae have remained a major family for 150 million years.

Interesting though the Jurassic was from the point of view of diversity, it was the Cretaceous, when marine faunas came under intervals of acute environmental pressure, that is the most informative from an evolutionary point of view. Continental positions affected the Cretaceous world (illustrated p37) just as they did in other geological intervals, but they were probably secondary to the traumatic impacts of repeated environmental upheavals. The Late Cretaceous was a time of extreme sea level change, periodically flooding nearly 40% of the continents and leaving only 18% of the earth's surface as land (compared with 29% today). Significantly for corals, this created a 'Super-Tethys' Ocean, which covered much of present day Europe. The consequences for reefs are unknown because the rate of sea level change is unknown, but the continually decreasing sea levels of the Late Cretaceous may have had a greater impact on coral communities than did the fluctuating sea levels of the Pleistocene.

Much of the Middle Cretaceous was characterised by extensive vulcanism around the continental plate margins and this, together with the accumulation of organic matter associated with sea level changes, may have increased the acidity of much of the ocean surface. Ocean and atmospheric temperatures were much higher (perhaps 10 to 15°C) than they are now, over a range of latitude from the equator to the poles. This would have varied greatly over time, but subtropical conditions may have periodically extended to 45°N and possibly 70°S, and there were no polar ice caps. These conditions would have resulted in weaker ocean currents than we have today. Corals would have been far more widely dispersed and there would have been a much greater development of distinctive regional provinces. By the close of the Mesozoic, the flooding of the continents had ceased and the warm climates that had dominated the Cretaceous had begun a long and irregular decline towards a glacial mode.

The beginning of the Cretaceous was not marked by any mass extinction event, but there was, nevertheless, a drastic change in coral communities. Rudist bivalves, a previously obscure group of molluscs, displaced corals as the dominant reef biota, and thus it remained for 30 million years. During this time, zooxanthellate corals coexisted with rudists, but largely in separate habitats (probably at greater depths). The reefs of that time probably resembled inshore fringing reefs of today: mostly banks of entrapped sediment, with no algal cementation, and repeatedly destroyed by changing sea levels. The rudist bivalves were probably zooxanthellate and, as they had a lesser amount of



1

1 The evolutionary history of corals has been a saga of change, not improvement. The appearance of plate-forming *Acropora* in the Middle Cenozoic was an exception. With their array of highly integrated architectures, *Acropora* were able exploit a wide range of environments because they could maximise growth rate, substrate coverage, exposure to sunlight and the ability to capture plankton. At the same time, they could minimise the quantity of skeletal material required. There are about 800,000 individuals in this colony. GREAT BARRIER REEF, AUSTRALIA
Photograph: Valerie Taylor

aragonite in their shells than corals, they probably survived acidic conditions better than the corals.

Corals returned to their position of dominance during the Late Cretaceous, followed by total extinction of the rudists. By the close of the Cretaceous, reefs probably again occurred worldwide, but there are few remains of them today. Most genera of the time are likely to have had a worldwide distribution, largely due to the endurance of the Tethys.

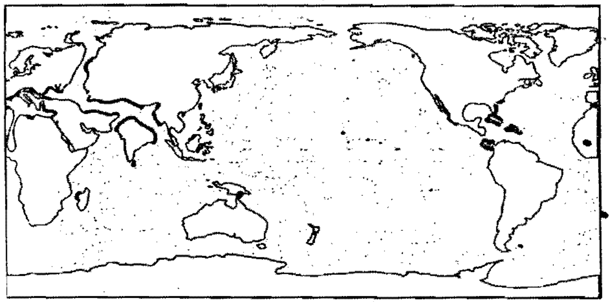
Recurring mass extinction events and the evolution of algal symbiosis are the two great evolutionary dimensions that have shaped the evolution of modern zooxanthellate corals. Two extinctions at least – the end-Triassic and the end-Cretaceous – were so drastic that the very existence of the Scleractinia appears, from the fossil record, to have hung on the survival of only a tiny fraction of the diversity we have today. More to the point, it did so for millions of years. The extinctions at the end of the Cretaceous may have been due to a meteorite bombardment that created a dust layer in the upper atmosphere causing light depletion and surface temperatures to plummet. Whatever the cause, it left no longterm mark: the boundary is a biological one, not geological. It caused the extinction of most marine reptiles, both orders of dinosaurs, all ammonites, a high percentage of bivalves, gastropods and echinoids and a high proportion of planktonic foraminifera and radiolaria. Many of these groups became extinct within an apparently brief period, others took longer and some plant and animal groups appear to have been little affected.

The statistics from the fossil record are impressive, as can be seen in the Family Tree (p36). One-third of all families and over 70% of all genera became completely extinct. The Faviidae is the only family that was a major component of Mesozoic reefs and survived to be a dominant in the Cenozoic. Approximately 6 out of 16 faviid genera survived; all other families survived with one or two genera. Surprisingly, the endurance of azooxanthellate genera was comparable: the Caryophylliidae survived with 13 genera (out of approximately 27), the Rhizangiidae survived with 3 genera, the remainder by one or two. There is no adequate basis for evaluating the survival of 'species' as there is no recognisable species level continuity between the Mesozoic and Cenozoic.

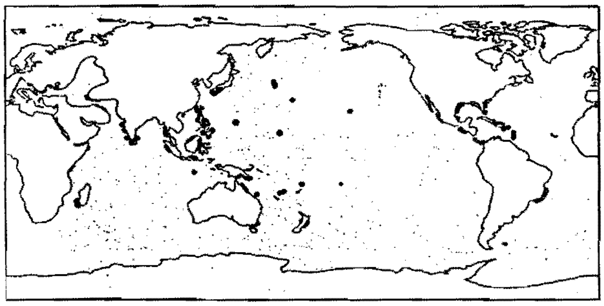
The evolutionary history of modern corals is divisible into three geological intervals: the Palaeogene (67 to 24 million years ago), when the few survivors of the end-Cretaceous extinctions proliferated into a diverse cosmopolitan fauna, the Miocene (24 to 5.2 million years ago) when this fauna became subdivided into the broad biogeographic provinces we have today and most extant 'species' evolved, and the Plio-Pleistocene to present, when the world went into full glacial mode and modern distribution patterns emerged.

For 12 million years after the end-Cretaceous extinctions only thirteen new genera of corals have been recorded. Probably only three of these were zooxanthellate; *Stylophora* is the only one now living. It was thus a radiation of new zooxanthellate genera that populated the seas of the Eocene (illustrated below). Seventeen Eocene genera are extant, but as Eocene reefs are sparse in most parts of the world, the fossil record is unreliable. Of the extant genera, 6 are known only from the Tethys, 12 (4 doubtfully) only from the Caribbean and 10 from both the Tethys and Caribbean.

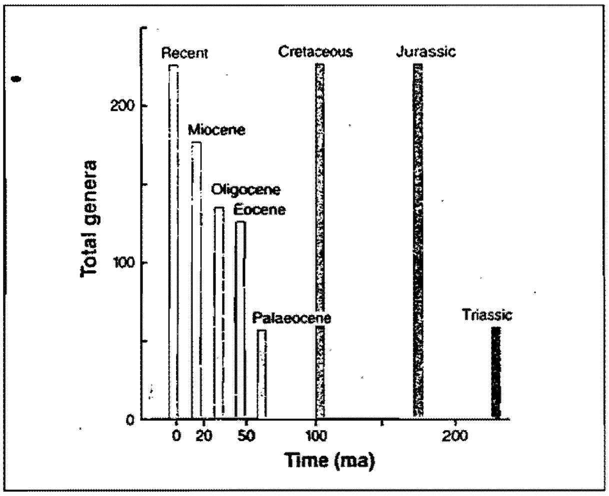
It was in the Late Oligocene that reef development became worldwide and diversity reached an all time high for the Tethys and Caribbean. Of the extant



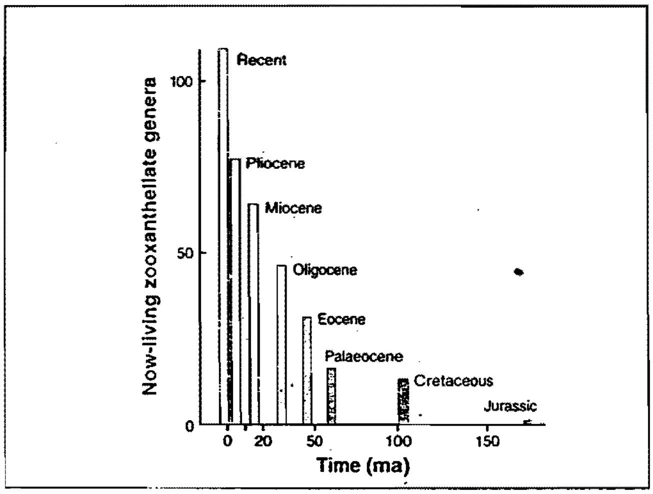
The Eocene world showing the distribution maximum of coral reefs and/or reef corals. The development of a circum-Antarctic circulation (through the opening of the Australian-Antarctic seaway, development of the Kerguelen Plateau and the opening of Drake Passage) is the key to Palaeogene climates. The most important feature of the tropical world remains the tropical circum-global ocean circulation through the Tethys Sea and the Central American Seaway. The slow blockage of this circulation underpins all Cenozoic tropical palaeobiogeography.



The Miocene world showing the distribution maximum of coral reefs and/or reef corals. The continents are close to their present positions. The Tethys Sea is reduced to a narrow band connecting the Indian Ocean with the proto-Mediterranean. Reef development globally is at a maximum for the Cenozoic.



Total numbers of scleractinian genera. Showing the total number of Scleractinian genera (both zooxanthellate and azooxanthellate) recorded in each of the geological intervals indicated. Note that these numbers are rough estimates only, as not all Jurassic and Cretaceous genera would have existed concurrently and others have presumably left no fossil record.



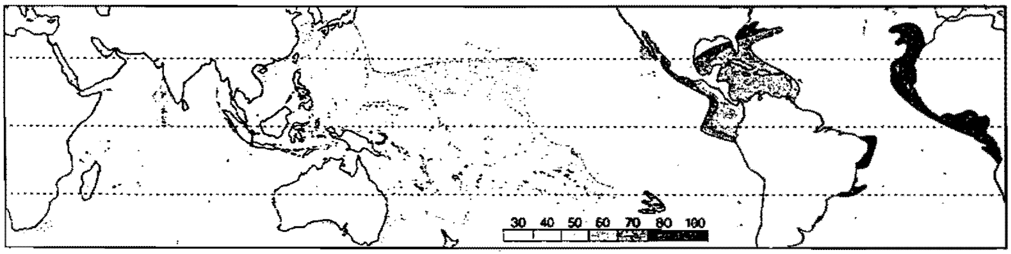
Extant zooxanthellate genera in time. Showing numbers of extant zooxanthellate scleractinian genera (ie. genera covered in this book) in the fossil record. Note that nearly half have existed as far back as the Oligocene (over 24 million years) and that nearly one quarter have existed as far back as the Eocene (over 33 million years).

genera, 9 are known only from the Tethys, 4 only from the Caribbean and 25 from both the Tethys and Caribbean.

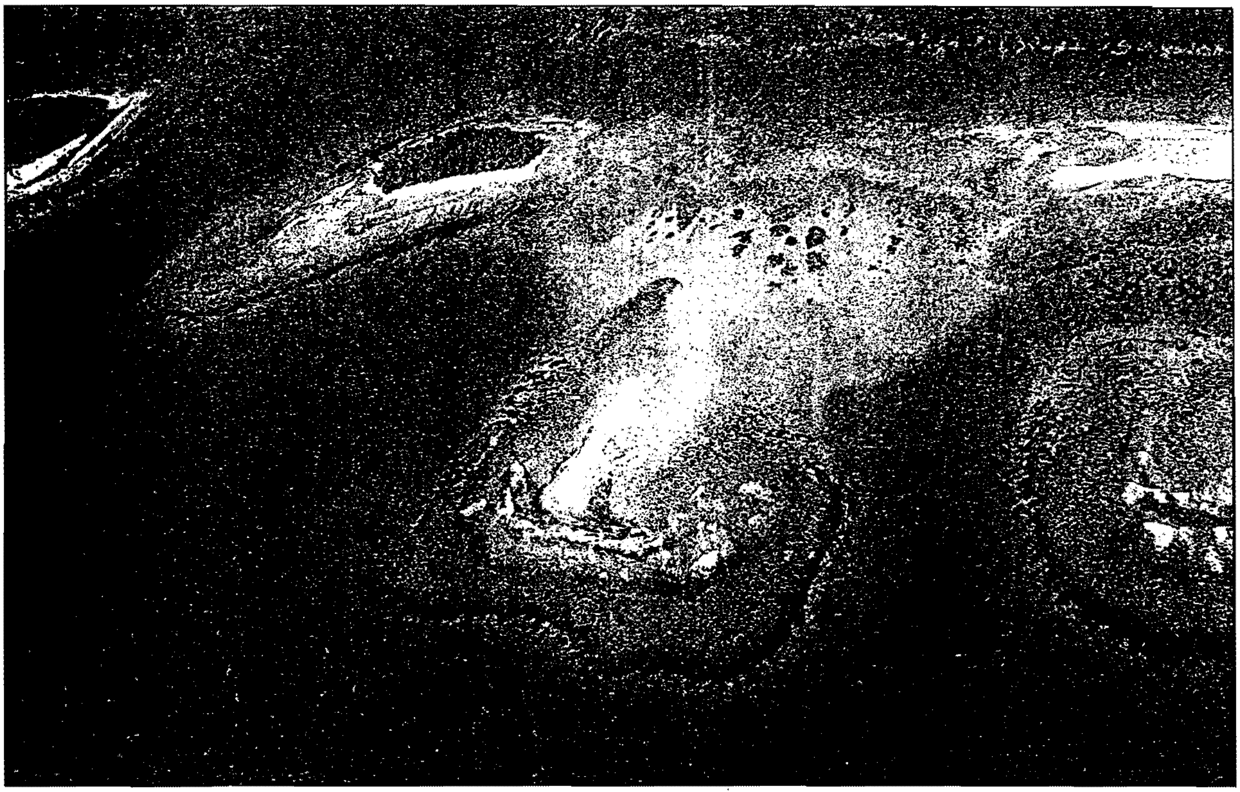
The Miocene is the Epoch of greatest interest in the evolution of extant corals. It is probably the time of origin of all non-Oligocene extant genera and the immediate ancestors (at least) of extant species. It is also the time of obliteration of the Tethys Sea, the extinction of zooxanthellate corals from the Mediterranean (assuming the 4 zooxanthellate species now found re-developed algal symbiosis), and the start of the separate evolutionary histories of Atlantic and Indo-Pacific species. Of Tethys-Atlantic extant genera, 16 are known only from the Tethys, 14 only from the Caribbean and 24 from both the Tethys and Caribbean. *Porites* was the dominant genus in the final stages of the Tethys and may have been the last genus to go extinct there.

The two diagrams (left) summarise the main changes that have taken place in Cenozoic coral genera. Compared with most other major groups of animals, coral genera are long lived in geological time and have low extinction rates.

The history of corals subsequent to the Miocene becomes decreasingly visible in the fossil record and increasingly visible in the taxonomy and distribution of living corals. The Plio-Pleistocene fossil record of the Caribbean is much better than in the Indo-Pacific and it is in the Caribbean that the impacts of the Ice Ages were greatest. The corals most affected by extinctions were the Pocilloporidae (*Stylophora* and *Pocillopora*) the Agariciidae (*Pavona* and *Gardineroseris*) and free-living faviids and meandrinids. Some genera that became extinct in the Caribbean are now extinct worldwide, however most are now found in the Indo-Pacific. The last genus to go extinct in the Caribbean was *Pocillopora*.



Average age of extant zooxanthellate genera (millions of years). The central Indo-Pacific centre of diversity has an average generic age of 30 million years, about half that of the Caribbean. The likely reason for this is that Caribbean genera of Tethyan origin are older than Pacific genera, not that evolution has been faster in the Indo-Pacific. The average age of genera in peripheral regions of both the Atlantic and Indo-Pacific is the outcome of a small number of highly dispersed species, it is not created by older genera having more species nor is it created by displacement of species as has been suggested. The peripheral pattern is therefore created by dispersion, not evolution.



1 Coral reefs like this might be considered the natural habitat for corals. Not so. The reefs of today are the outcome of an unusually long period of stable sea levels. For most of their geological history, the corals that formed this reef would have existed in pockets around the margins of emergent limestone platforms or high islands. Or they would have been submerged to varying depths where they would have been exposed to varying amounts of wave action. MARSHALL ISLANDS *Photograph: Anne Orcutt*

The progressive closure of the Central American Seaway was one of the most important events in the history of modern corals. Long before the closure there may have been no distinction between the corals of the far eastern Pacific and those of the Caribbean. Little is known about what corals were actually on the Pacific side of the developing Isthmus of Panama although it is known that *Dichocoenia*, *Diploria*, *Eusmilia*, *Solenastrea*, and *Isophyllia*, all now restricted to the Caribbean region, formerly occupied the Gulf of California. After the closure just over 3 million years ago, the corals of the Pacific side of the Isthmus were extinguished, or nearly so. Today, there are no Indo-Pacific species in the Caribbean. Most far-eastern Pacific species also occur in the central Indo-Pacific and have migrated to the east in relatively recent times. Such migrations are probably not uncommon, especially as some species, notably of pocilloporids, are frequently found attached to floating objects such as pumice, and others have larvae that remain competent to metamorphose after floating on the sea surface for months.

This account of the history of corals is continued in the concluding chapters of Volume 3. In these chapters, biogeographic and taxonomic observations of living corals are used to explain the mechanisms evolutionary change. The emphasis moves away from the big changes that are seen in the fossil record to the relatively small changes that occur in space as well as in time.

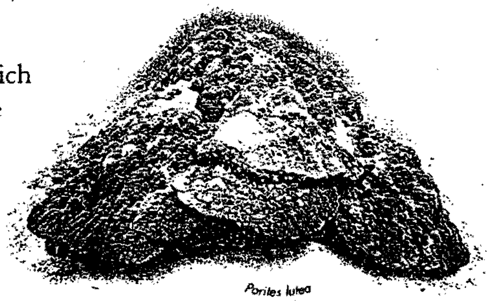
Further reading: This account is based on the authors' (1995) book *Corals in Space and Time*. This book gives the multitude of sources of original information and references for further reading. For further details of Mesozoic corals see also Turnšek (1997) and for details of ancient reefs see Wood (1999).

* * *

Structure

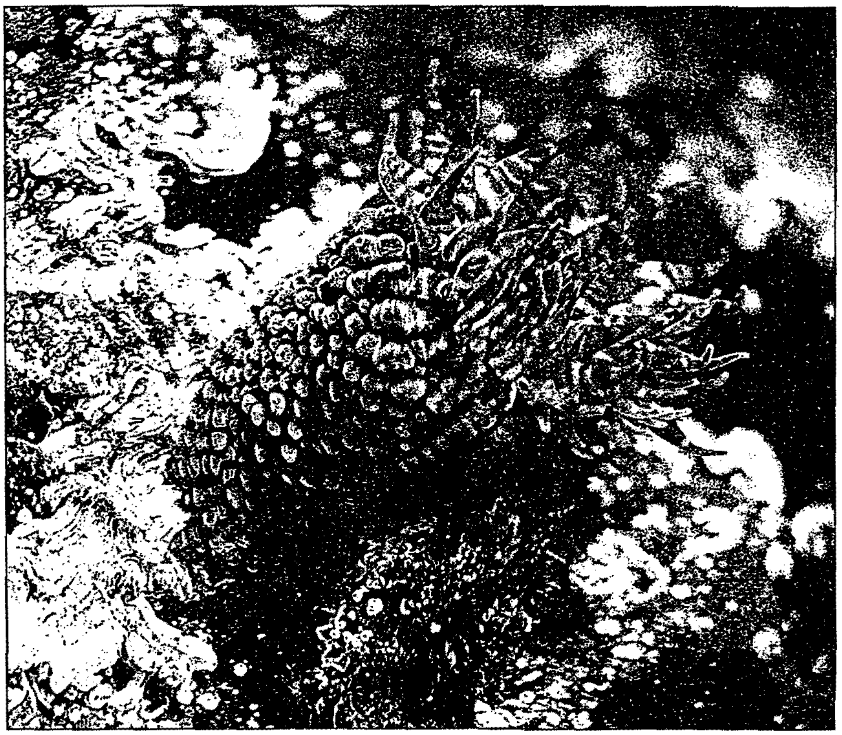
Skeletal structures – polyp tissues – colony formation – growth-forms

The Scleractinia are one of approximately 25 orders of animals belonging to Phylum Coelenterata. This phylum includes corals, soft corals, hydroids, jellyfish and sea anemones, all of which have the same general body plan. They are all symmetrical about a central axis (that is, they are radially symmetrical) and have a sac-like body cavity with only one opening, which serves as both mouth and anus. This opening is surrounded by tentacles which have stinging cells. The body wall, unlike that of any other group of animals except comb-jellies, consists of two cell layers, the ectodermis and gastrodermis, separated by a jelly-like layer, the mesoglea. Two forms of this plan occur within the phylum, a polyp form which is usually sedentary and a medusa form which is usually free swimming. The one is the upside-down equivalent of the other.



Corals are basically anemone-like animals that secrete a skeleton. Some corals are solitary and look just like simple anemones when their tentacles are extended. Others, including most that are seen on coral reefs, are colonial. Although corals are primitive organisms, their skeletons, like those of many other primitive organisms, are often complex. Fortunately it is not

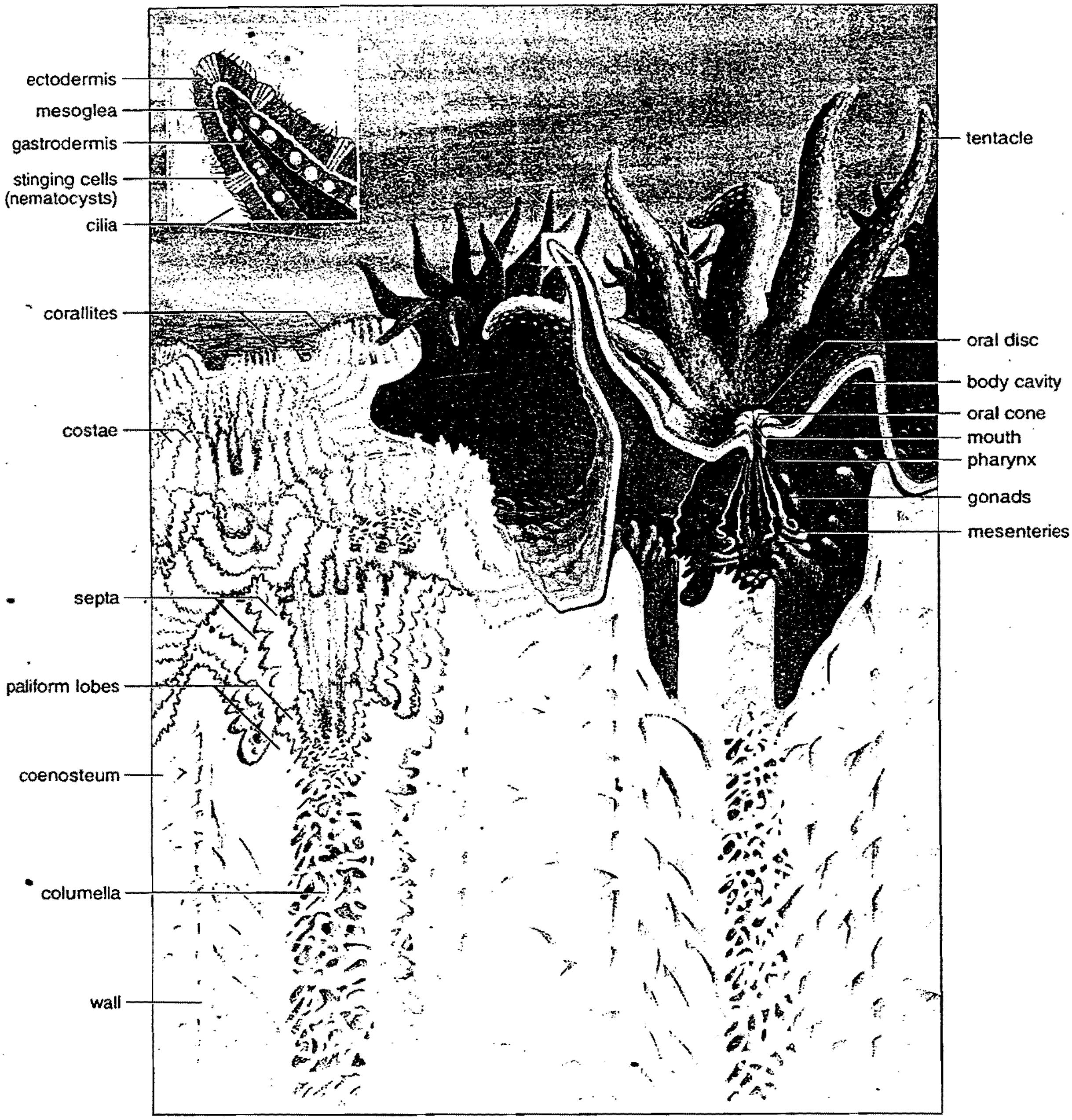
1



Previous page: A colourful *Tubastrea*. Azooxanthellate corals like this do not form complex skeletal frameworks like their zooxanthellate relatives. MALDIVES *Photograph: Neville Coleman*

Opposite: A columnar colony of *Meandrina meandrites*. BAHAMAS *Photograph: Pat Colin*

1 A solitary anemone. Corals are basically anemones with skeletons. *Photograph: David Ayre*



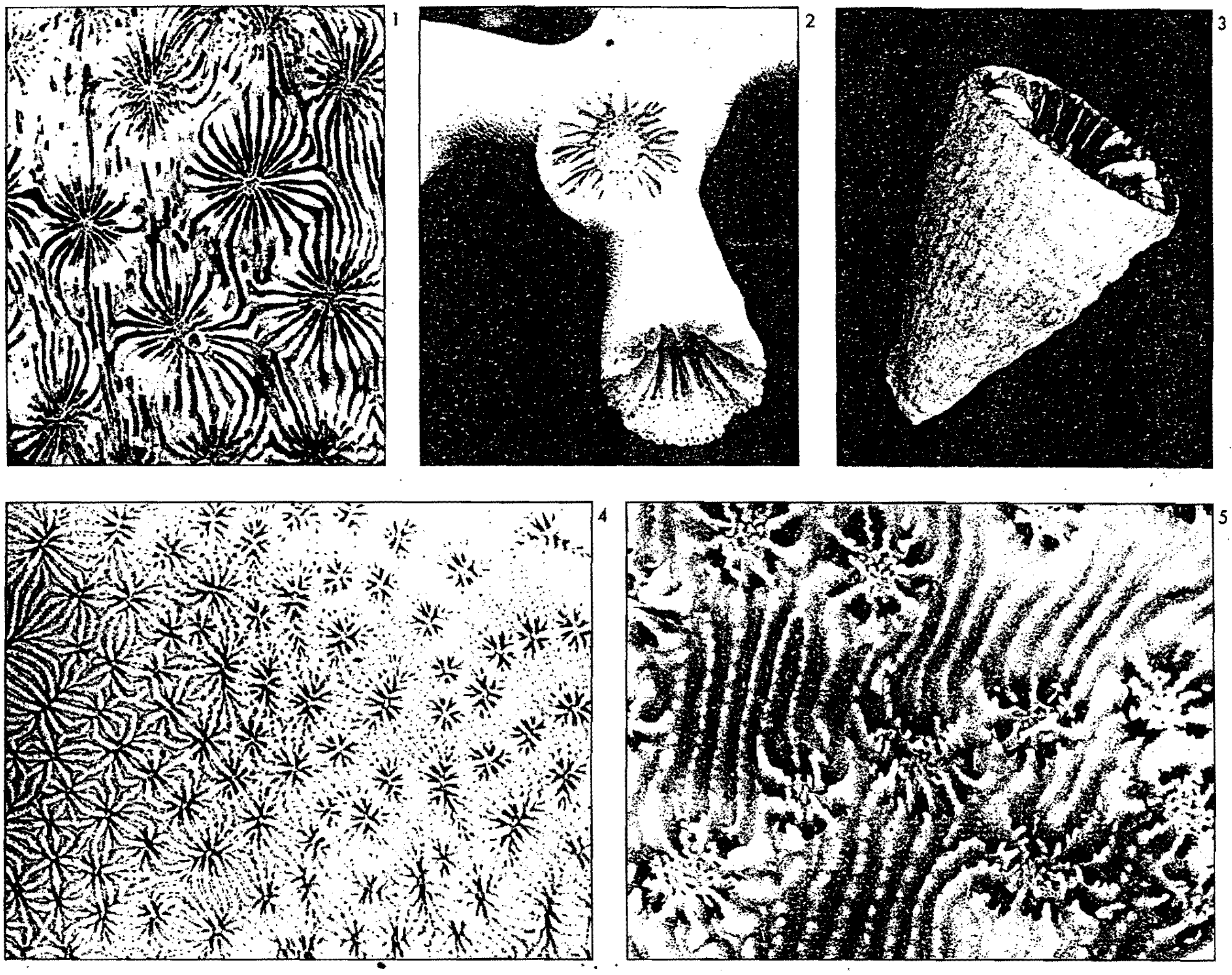
Coral structure. The general structure of the polyp and underlying skeleton. *Painting: Geoff Kelley*

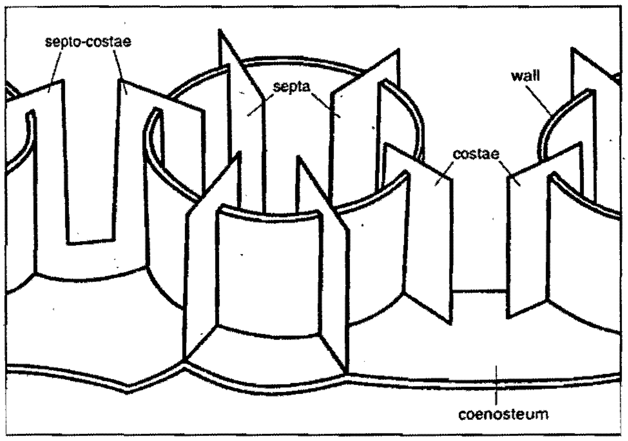
necessary to understand much about this complexity in order to identify corals.

The polyp skeleton. The skeleton of an individual polyp, called the corallite, is a tube that contains vertical plates radiating from the centre. The tube itself is the corallite wall and the plates are the septo-costae. The tubes are joined together by horizontal plates and other structures, collectively called the coenosteum. Some polyps have an additional thin film of skeleton around the wall called the epitheca.

The wall is formed by five skeletal elements which vary in proportion in different coral families and/or genera. These elements are (a) septo-costae (which become thickened within the wall), (b) coenosteum (which forms a sponge-like structure), (c) synapticulae (which are horizontal rods forming a lattice between the septo-costae), (d) sterome (which form a non-porous layer within the wall) and (e) epitheca (which forms a thin non-porous layer on the outside of the wall). The wall is very prominent in some corals, but is inconspicuous in others where individual polyps are indistinct.

The septo-costae are the radial elements of the corallite and are divided (by the wall) into two components: the septa, which are inside the wall and the costae, which are outside the wall. Where the wall is indistinct (as in the Siderastreidae, Agariciidae and

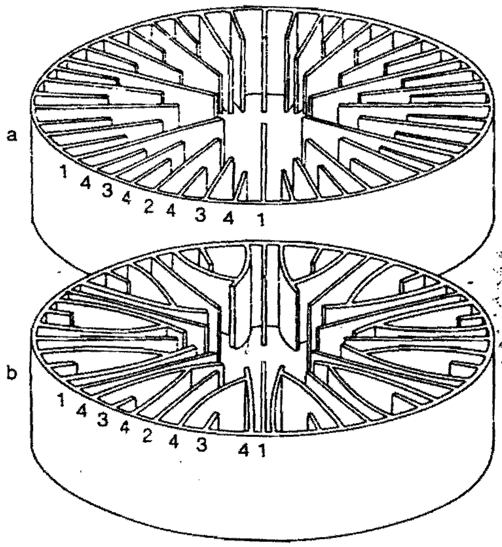




Skeletal elements. Diagrammatic representation of the basic skeletal elements of a coral.

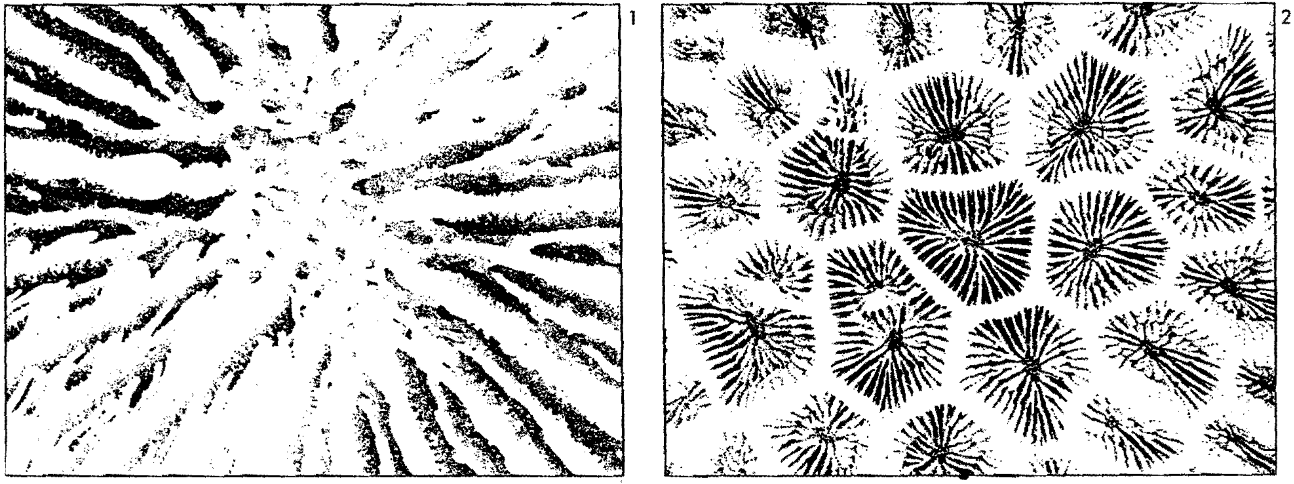
1-5 Basic wall components. (1) The wall of this *Acanthastrea* is primarily composed of thickened septo-costae. This is best seen in families Faviidae and Mussidae, and also some Caryophylliidae. (2) The wall of this *Duncanopsammia* is primarily composed of sponge-like coenosteum. This is best seen in families Dendrophylliidae and Poritidae (except *Alveopora*). (3) The wall of this *Conotrochus* is partly composed of epitheca. This mostly occurs in azooxanthellate corals including the Flabellidae and some Caryophylliidae. (4) The wall of this *Pavona* is primarily composed of horizontal rods of synapticulae. This is best seen in families Siderastreidae, Agariciidae and Fungiidae. (5) The wall of this *Echinophyllia* is primarily composed of sterome. This is best seen in the Euphyllidae, Oculinidae, Meandrinidae and Pectiniidae. Other major families may have two equally dominant wall components: the Pocilloporidae and Acroporidae have walls of mixtures of thickened septo-costae and coenosteum; most Caryophylliidae have walls of mixtures of thickened septo-costae and epitheca.

colonial fungiids) the septo-costae are single uniform elements. In solitary fungiids the wall is horizontally compressed, with the septa above it and the costae below it. In most corals, the septa are of different lengths and have a cyclical symmetry. They may be in cycles (with 6 septa in the 1st cycle, 6 in the 2nd cycle, 12 in the 3rd, 24 in the 4th and so on if present) or orders (where there is an indeterminate number of septa of each length). In practice, this cyclical arrangement is often unclear. In many corals, but especially in Dendrophylliidae, the cyclical arrangement of septa is embellished into a pattern of fusion called pourtàles plan, where septa of the 4th cycle curve in front of those of the 3rd cycle and fuse. This appears to be a primitive characteristic of the Scleractinia as it sporadically occurs in several families



Septa. (a) Normal cycles of septa, (b) pourtàles plan. Numbers indicate cycles.

Pali. A vertical section of a corallite divided into horizontal layers to show the origin of pali. The single palus (arrowed) is part of two fused 4th cycle septa at the bottom of the diagram, but appears to be part of a single 3rd cycle septum at the top.
Drawing: Marty Eden

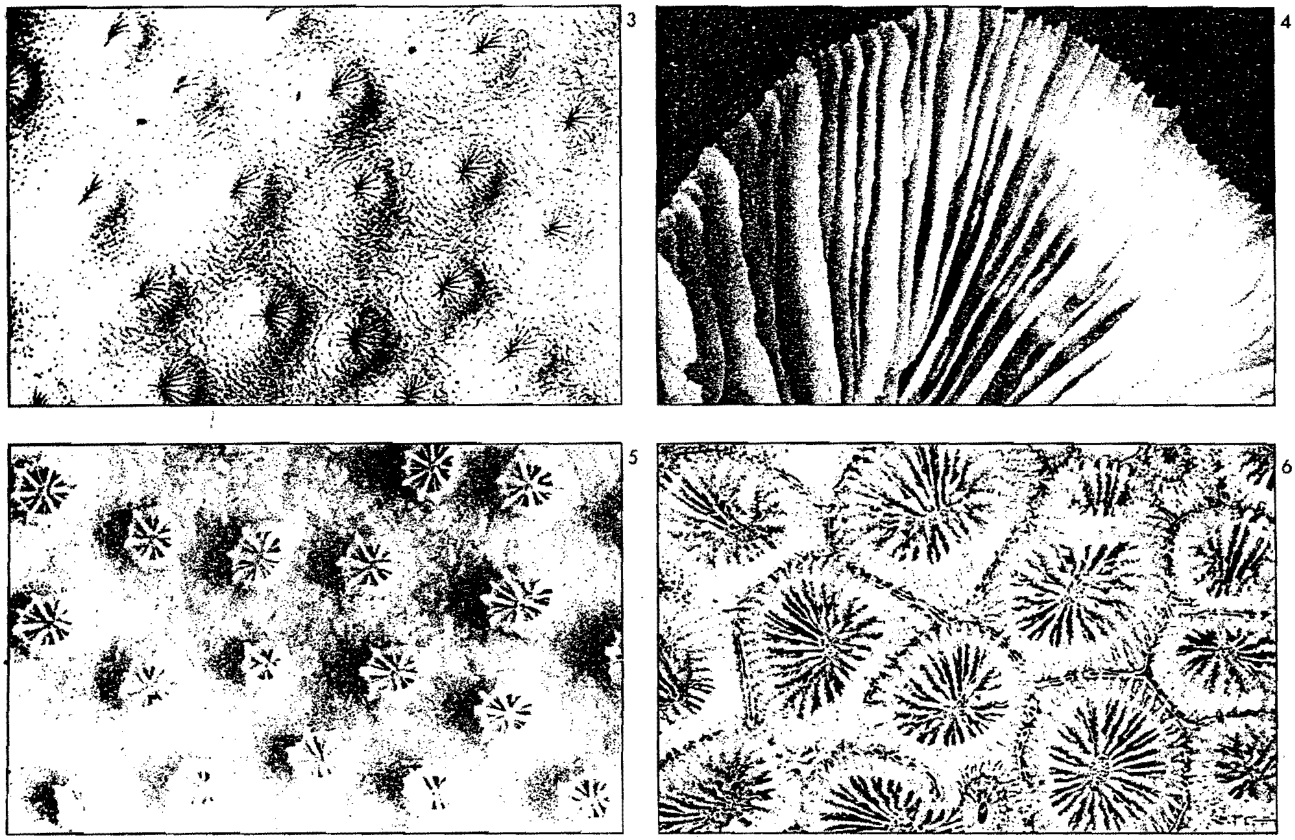


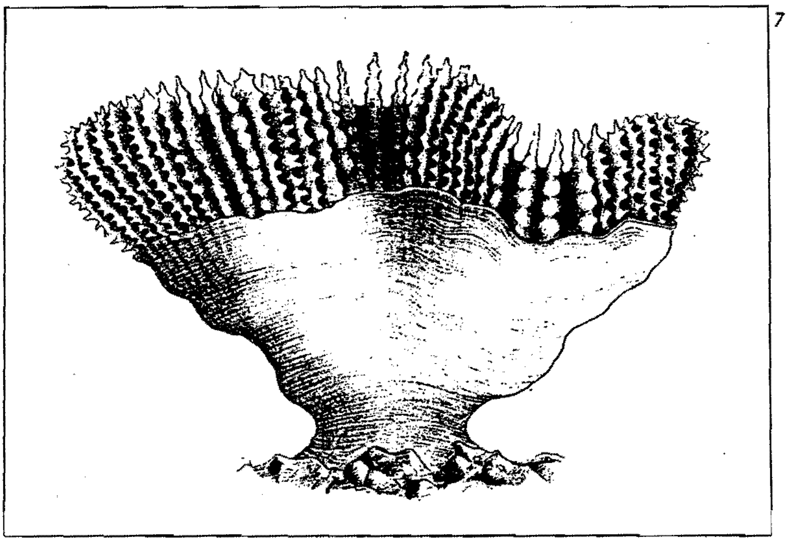
1, 2 Skeletal structures. The appearance of the columella and paliform lobes. (1) A *Scolymia* showing the typical appearance of a columella composed of a tangle of spines from the inner margins of septa. (2) A *Goniastrea* with paliform lobes forming a neat crown.

and can also be seen in the earliest fossils. The genus *Porites* has a unique septal plan which, as shown in the treatment of the genus in this book, is used extensively in taxonomy.

Septa seldom join at the centre of the corallite (except in the Astrocoeniidae and Pocilloporidae). Instead, their inner margins usually have fine inward projecting teeth which, in most corals, become intertwined forming a tangle called the columella. In some families, especially the Astrocoeniidae and Pocilloporidae, the columella is pillar- or dome-shaped. In others, especially the Acroporidae, it is usually absent. Many corals have pillar-like projections on the inner margin of some or all of their septa called paliform lobes and these often form a neat circle around the columella called a paliform crown. Some groups of corals have pali instead of paliform lobes. These are the result of the pourtàles plan pattern of septal fusion although the pattern may not be visible in mature corallites.

There are four other parts of the skeleton which are used in general descriptions of corals (apart from being components of corallite walls as noted above): coenosteum, sterome, dissepiments and epitheca. The coenosteum is a general term for porous (not solid) skeletal material situated between the costae of corallites or between one corallite and the next. This is best seen in the Dendrophylliidae where the corallite

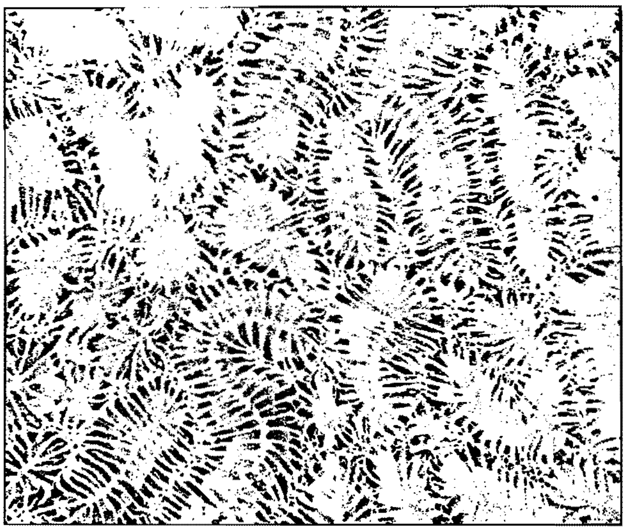




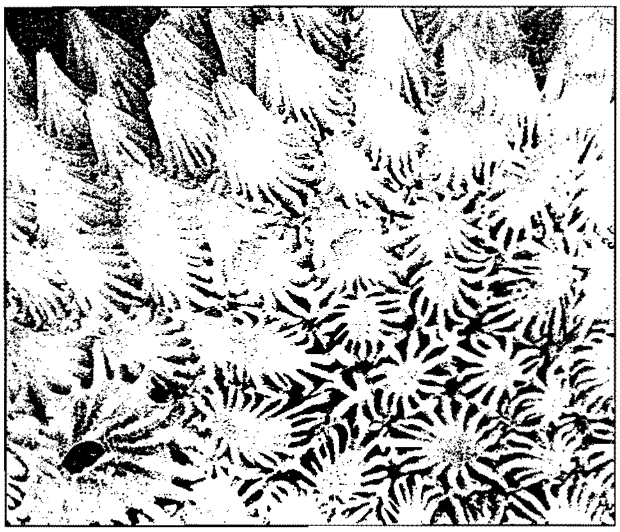
3-7 Skeletal structures. (3) Corallite walls and the skeleton between the corallites of this *Turbinaria* skeleton consist of a sponge-like matrix, the coenosteum. (4) The smooth skeleton between the septa of this *Catalophyllia* skeleton is the sterome. (5) The fine blisters of skeletal material between the corallites of this *Galaxea* are the dissepiments. (6) Fine skeletal structures between the corallites of this *Montastrea* are called 'groove-and-tubercle' structures and are composed of epitheca. (7) The skeletal layer covering the outside of this *Trachyphyllia* is the epitheca. *Drawing: Geoff Kelley*

wall and the skeleton between the corallites consist of a sponge-like matrix of coenosteum. The sterome is a solid sheet which forms the inner lining of (or all of) the corallite wall. This is best seen in families Euphyllidae, Oculinidae and Meandrinidae and gives the skeleton a porcelain-like finish. The dissepiments are thin, blister-like layers of skeleton which form between the corallites and are structurally similar to the sterome. The epitheca is a delicate translucent skeletal layer. It initially occurs as the basal plate deposited by the planula larva on settlement, and thereafter may continue growing to envelop individual corallites. The epitheca is always a distinct skeletal entity which is not covered by living tissue; in some faviids its growth is controlled by tiny polychaete worms to form 'groove-and-tubercle' structures. These structures are all illustrated above.

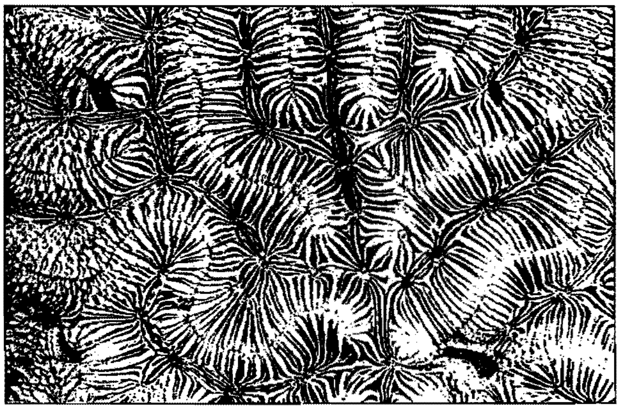
Some skeletal structures are found only in some corals. *Montipora* and *Porites* in particular, have additional skeletal structures which are useful in identification and are explained in the introduction to these genera. Monticules (illustrated overleaf) are primarily found in *Hydnophora*, but may occur in other genera. Ambulacral grooves (illustrated overleaf) are seen in a scattering of unrelated species.



1



2



3

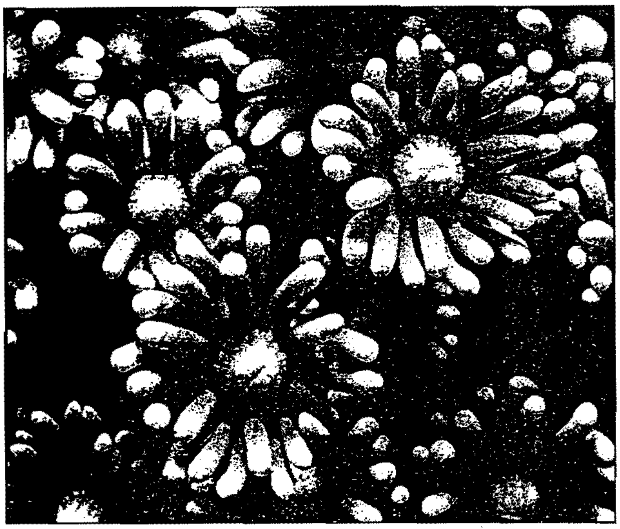
The polyp tissues. The sac-like body cavity of the coral polyp is the coelenteron (p48), which has a single opening to the outside. The coelenteron of one polyp is linked to those of adjacent polyps by tubes through which water circulates and nutrients are transported. The coelenteron serves many functions including digestion and the circulation of fluids for respiration and nutrition. The mouth leads to a short tube, the pharynx, which opens into the body cavity. In most corals it is short, in others (notably *Goniopora* and *Alveopora*) it is extraordinarily extendable, allowing the mouth and tentacles to protrude far beyond the skeleton to aid food capture. The coelenteron is a complex structure, made so by the skeletal structures, all of which lie outside it, but which are enveloped by it. The coelenteron is partitioned by vertical mesenteries, arranged in a radial fashion according to the position of the septa. These mesenteries give the gastrodermis a large surface area for digestion, photosynthesis and respiration, and also contain the reproductive organs. A series of coiled filaments, the mesenteric filaments, are packed along the inner margins of the mesenteries. These further extend the surface area of the mesenteries and are extruded through the mouth in response to stress.

As with all coelenterates, the body wall is primarily composed of two cell layers, the ectodermis on the outside and the gastrodermis on the inside. These layers are separated by the mesoglea, which is initially non-cellular but which may contain a wide range of cells after initial growth. In corals with small corallites the mesoglea is microscopically thin while in others, notably the big mussids, it may be several millimetres thick and is of tough construction.

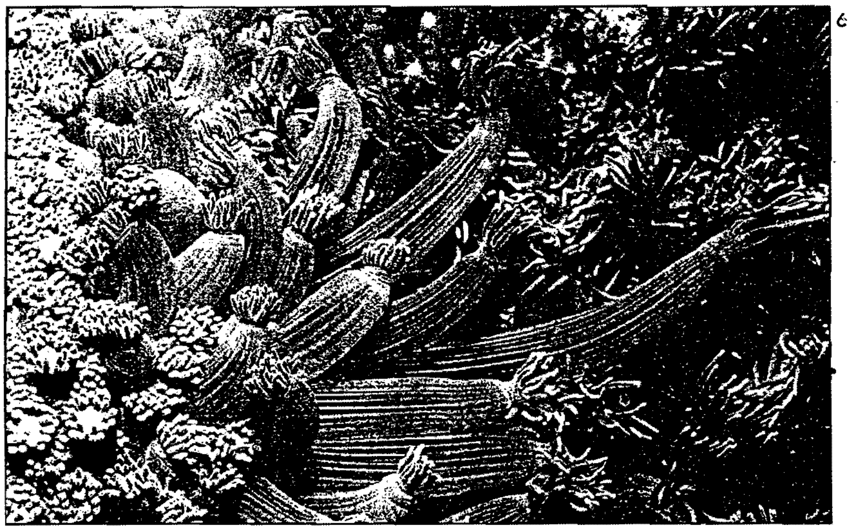
Extended polyps have an anemone-like appearance. The mouth is usually slit-like and may be surrounded by an oral cone. The tissue between the mouth and tentacles is the oral disc.

Tentacles are tubular and have the same two tissue layers as the rest of the polyp so that the cavity inside them is part of the coelenteron. Tentacles are smooth in corals that feed on detritus but most have stinging cells for defence or food capture. These cells, the nematocysts, are microscopic in size, but in most corals are grouped into wart-like nematocyst batteries, which are clearly visible underwater. Nematocysts also occur on vesicles of *Physogyra* and *Plerogyra*, which are sac-like structures composed of body wall that are inflated with water when tentacles are retracted during the day. Other cells of the ectodermis secrete slimy mucous which coats the polyp and which is moved around by microscopic cilia. The mucous is used to remove sediment from the polyp surface and is also used by detritus feeders to capture food.

Coelenterates are the simplest organisms to have discrete nervous, muscular and reproductive systems and in corals all these are well developed. A simple nerve net, composed of both ectodermal and gastrodermal cells permeates the body wall, with connections to a variety of specialised cells responsible for sensing mechanical and chemical stimuli as well as light. A muscular system, consisting of specialised cells of both ectodermal and gastrodermal origin, allows polyps to extend and retract in response to signals


4


5


6


7

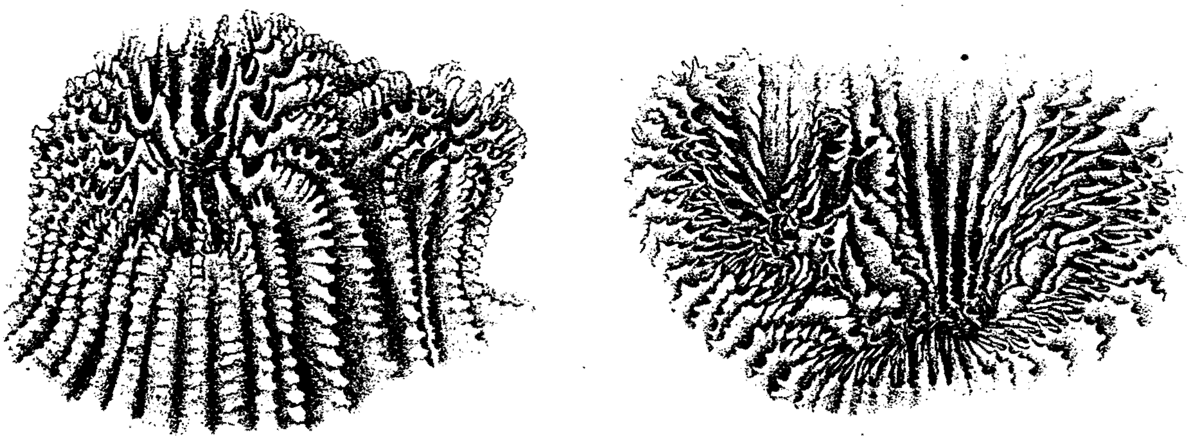
1-3 Skeletal structures. (1, 2) The formation of monticules. *Hydnophora* colonies with sections of wall of variable length (left) intergrade with other colonies with walls as short as they are wide (right). The star-like structures that result are the monticules. The ribs down the sides of the monticules are costae. (3) The grooves running along the tops of the walls are ambulacral grooves. They represent a tendency toward flabello-meandroid structure in meandroid colonies.

4-7 Soft tissues. (4) Polyps of *Goniopora* showing slit-like mouths and well defined oral cones. (5) Nematocyst batteries on the tentacles of a large *Cynarina* polyp. (6) Polyps of a *Goniopora* retracting in sequence after the left side of the colony was mechanically stimulated. (7) Microscopic zooxanthellae as seen when a tentacle is squashed onto a microscope slide. **4** ESSINGTON PENINSULA, NORTHERN AUSTRALIA **5** GREAT BARRIER REEF, AUSTRALIA **6** NORFOLK ISLAND, WESTERN PACIFIC *Photographs: 4-6 author 7 Ove Hoegh-Guldberg*

from the nerve net. These signals are transmitted from polyp to polyp, as seen in the progressive retraction of polyps when part of a colony is mechanically disturbed.

Reproductive organs develop within the mesoglea of the mesenteries. This happens on an annual cycle in most species, after which the organs disappear, to re-form the following year. Some corals, notably *Fungia* and *Porites*, have separate male and female sexes, but most are hermaphroditic. In either case, the gonads are arranged around the base of the pharynx in radial symmetry. Some hermaphrodite corals have male and female gonads on different mesenteries, in others the testes are above the ovaries on the same mesenteries and in others the testes and ovaries grow together.

The gastrodermis has an array of specialised cells for digestion, part of which occurs in the body cavity, and part inside the digestive cells themselves. Nutrients are readily moved among polyps so that neighbouring polyps have a similar rate of growth and thus do not compete for space. The gastrodermis also contains the zooxanthellae, the unicellular symbiotic algae which are essential to the growth and survival of most zooxanthellate corals. These algae are minute, approximately 0.008-0.012 millimetres diameter, and occur in enormous numbers except in the growing tips of *Acropora* and other fast growing corals.



Types of corallite budding. Extratentacular budding (left) and intratentacular budding (right) in faviid colonies. *Drawings: Geoff Kelley*

Colony formation. In most corals, the overall appearance of a colony is not a direct outcome of the way its corallites multiply. However, in the Family Faviidae, the type of budding may determine the type of colony that results. In this family, the terms used to describe both budding (the formation of corallites) and growth-form are usually the same. (For example, the term 'meandroid' may be used to describe both the type of budding and the type of colony.)

In most corals, there is a clear distinction between what is an individual and what is a colony. This is not always so, as seen in the Family Fungiidae, where there is a continual gradation between solitary individuals (with a single mouth) and colonies (with many mouths), as exemplified by the sequence *Cycloseris* — *Fungia* — *Ctenactis* — *Herpolitha* — *Polyphyllia*. In this sequence, *Cycloseris* and (usually) *Fungia* exist only as solitary individuals with a single mouth while *Polyphyllia* forms colonies with many mouths. A single specimen of *Ctenactis* or *Herpolitha* could be considered a solitary individual with many mouths or a colony of individuals, each with a single mouth. Likewise, in some corals there may not be a clear distinction between what is an individual and what is a row of individuals. This is best seen in Families Faviidae and Mussidae, where there is a continual gradation between colonies composed of distinct polyps (corallites) to colonies where individuals are recognisable only by the existence of mouths and/or columella centres, to colonies where there is no sign of individuality.

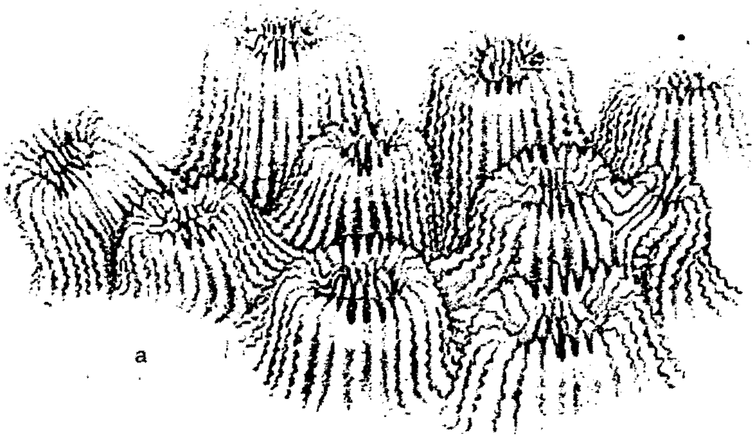
All corals that form colonies do so by a process of budding, where the parent polyp divides itself into two or more daughter polyps (intratentacular budding), or daughter polyps form on the side of the parent polyp (extratentacular budding), or polyps lose their identity, as seen in colonies with valleys. Some colonies have both intra- and extratentacular buds.

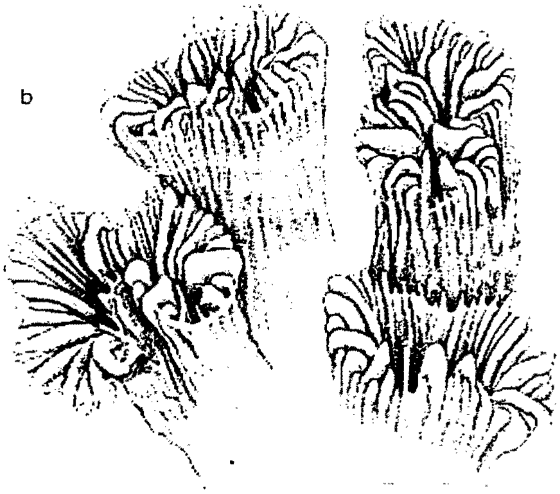
If the corallites of a colony all have their own walls they are called plocoid or phaceloid, depending on how elongate they are. If they share common walls they are called meandroid or cerioid, depending on whether or not they form valleys. If they are meandroid and have their own walls they are termed flabello-meandroid (see opposite).

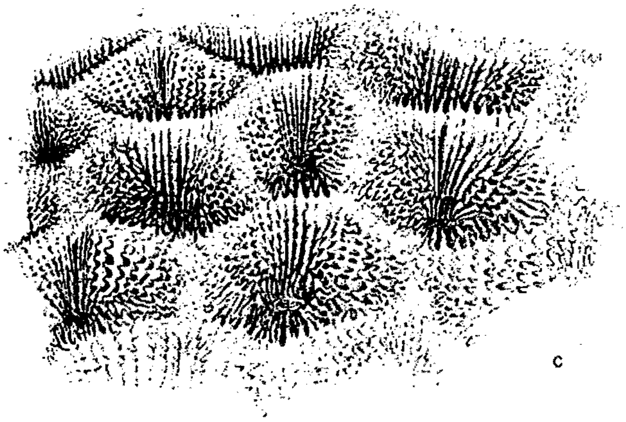
These growth-forms confer several constraints on corallite replication and growth. Plocoid and phaceloid colonies can have both intratentacular and extratentacular budding, while cerioid colonies can only have intratentacular budding. Plocoid, cerioid and meandroid colonies have integrated corallites or valleys, while adjacent corallites or valleys of phaceloid and flabello-meandroid colonies may have little or no connecting tissue. The latter may compete for space and other resources, with the result that some parts of colonies overgrow other parts.

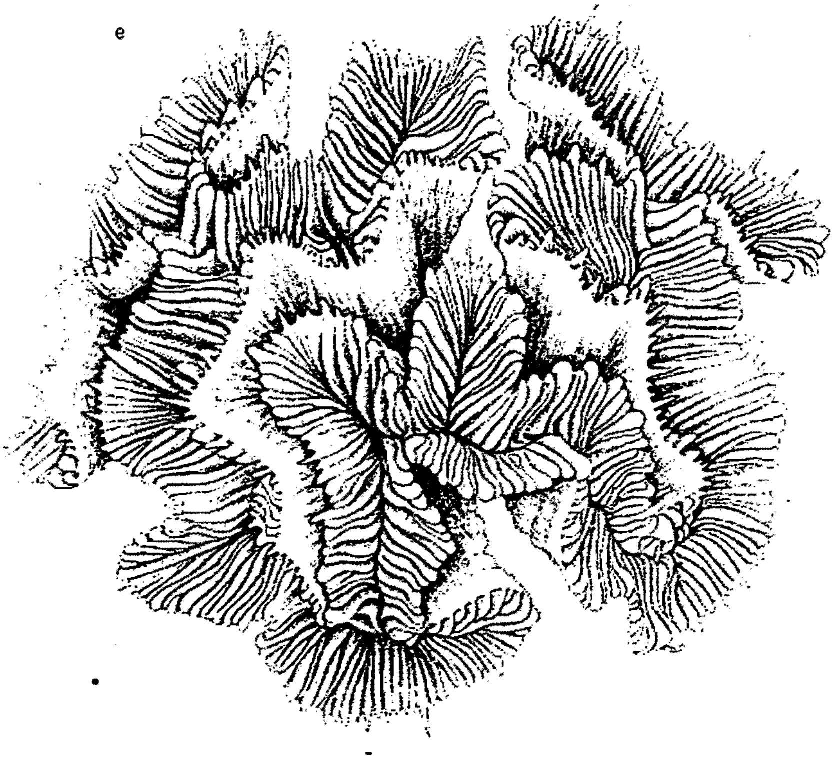
Some colonies combine two growth-forms. *Euphyllia* and *Lobophyllia* colonies may be phaceloid toward the colony centre (where lack of space constrains valley formation) and be flabello-meandroid at the periphery (where there are no such constraints). Similarly, *Symphyllia* colonies may have both meandroid and flabello-meandroid areas; *Favia* colonies may have both plocoid and meandroid areas; *Favites* and *Goniastrea* colonies may be both plocoid and cerioid. There are also many intermediate forms between plocoid and fully phaceloid and (very commonly) between cerioid and fully meandroid colonies.

A variety of other types of colony formation are found in corals, but these are uncommon.

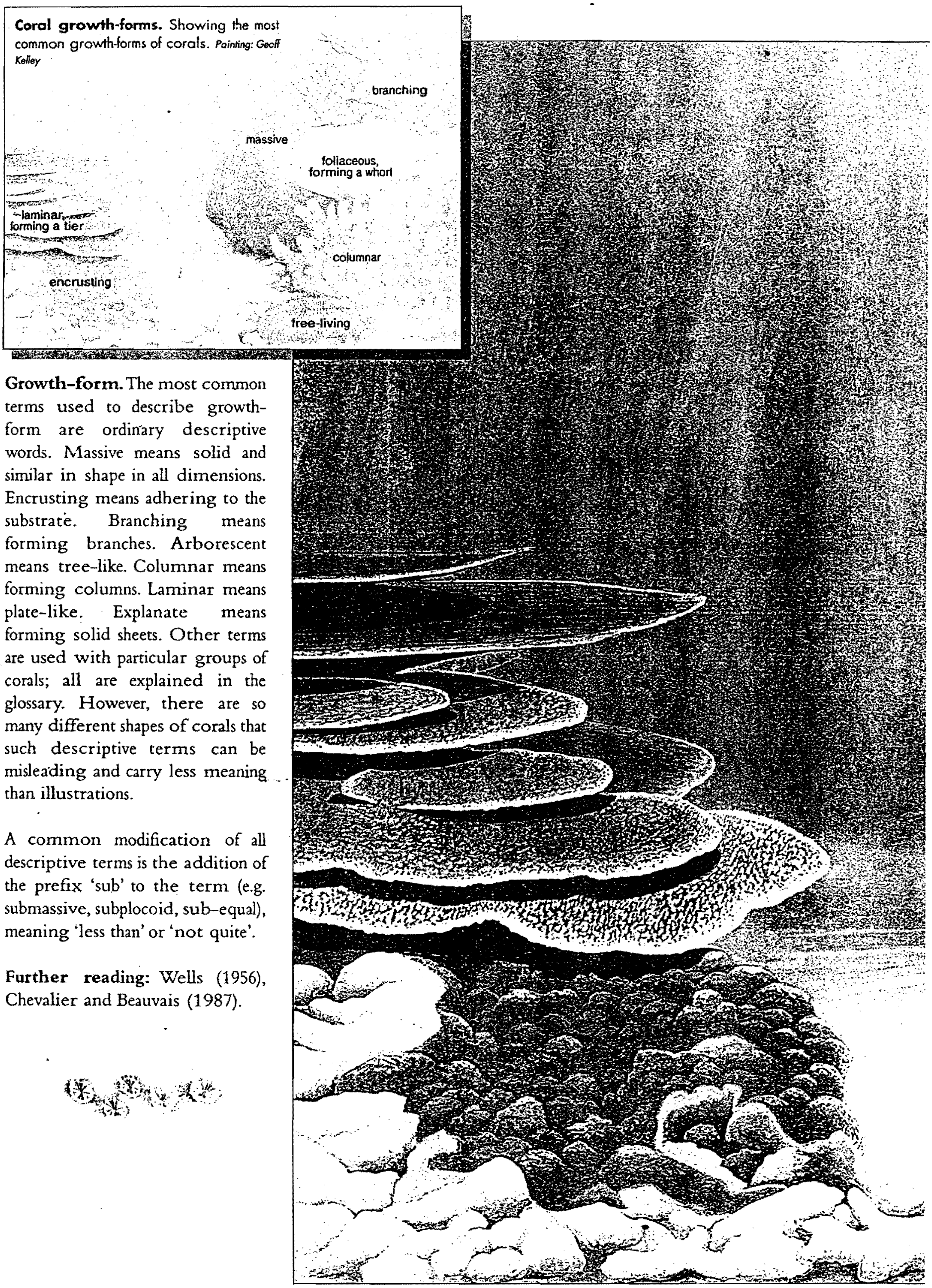








Corallite formation. (a) Plocoid colonies have corallites with their own walls; (b) phaceloid colonies also have corallites with their own walls, but these are long and tubular; (c) cerioid colonies have polyps which have common walls; (d) meandroid colonies have valleys rather than polyps; (e) flabello-meandroid colonies also have valleys, but do not have common walls.
Drawings: Geoff Kelley

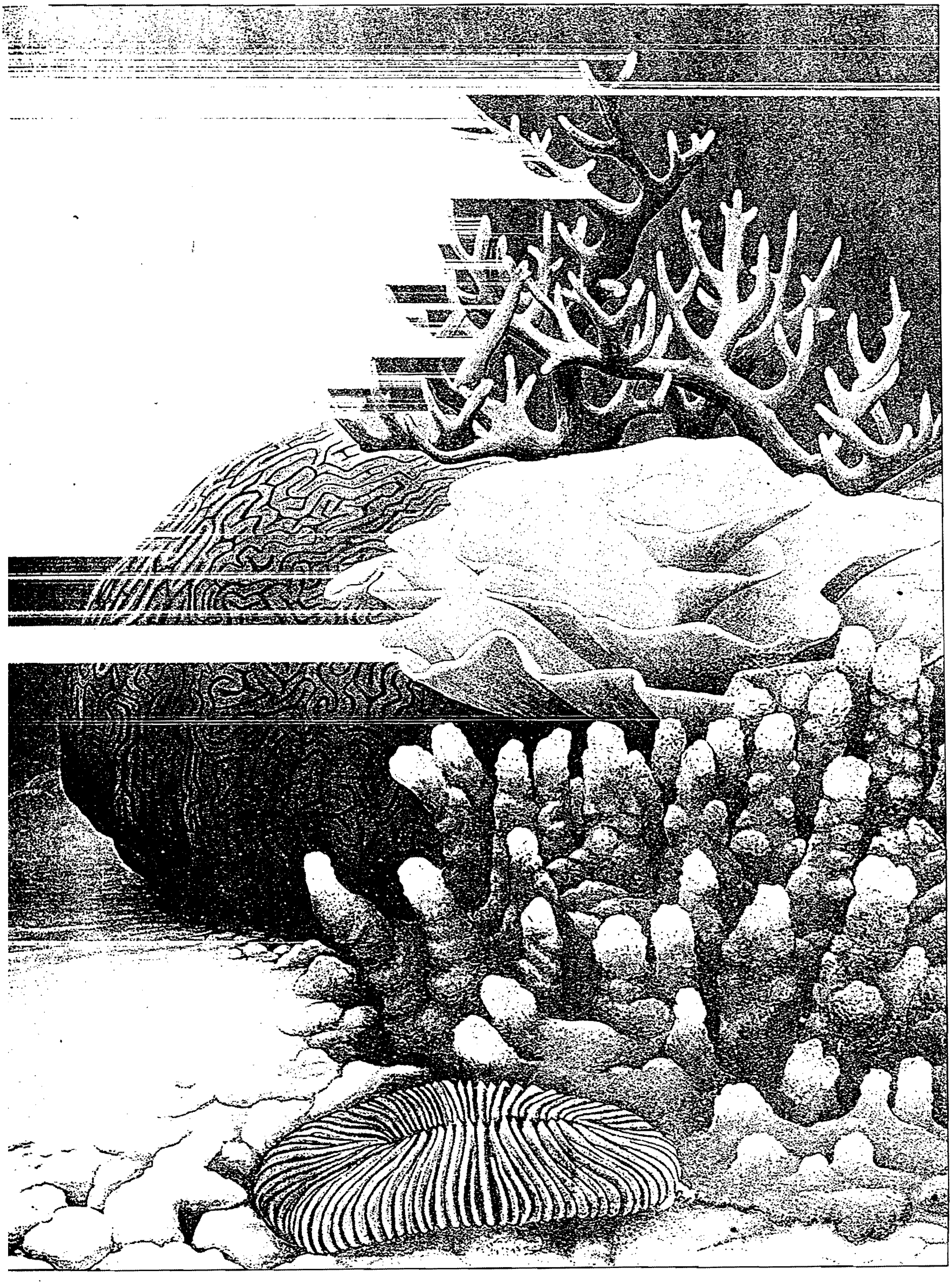


Coral growth-forms. Showing the most common growth-forms of corals. *Painting: Geoff Kelley*

Growth-form. The most common terms used to describe growth-form are ordinary descriptive words. Massive means solid and similar in shape in all dimensions. Encrusting means adhering to the substrate. Branching means forming branches. Arborescent means tree-like. Columnar means forming columns. Laminar means plate-like. Explanate means forming solid sheets. Other terms are used with particular groups of corals; all are explained in the glossary. However, there are so many different shapes of corals that such descriptive terms can be misleading and carry less meaning than illustrations.

A common modification of all descriptive terms is the addition of the prefix 'sub' to the term (e.g. submassive, subplocoid, sub-equal), meaning 'less than' or 'not quite'.

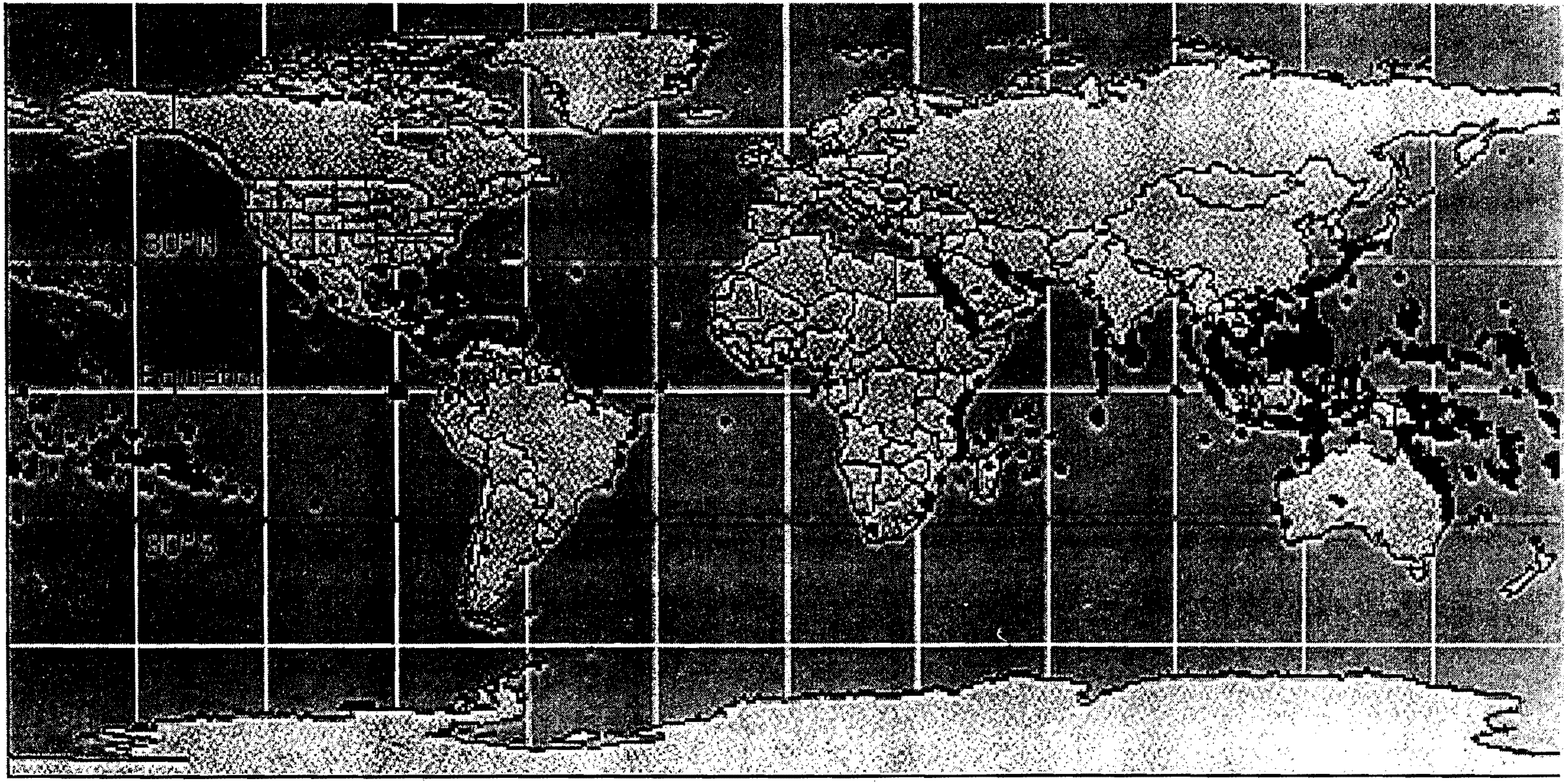
Further reading: Wells (1956), Chevalier and Beauvais (1987).

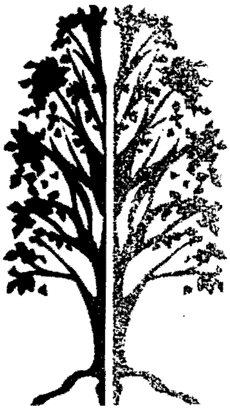


Ranking of top 21 Countries of the world that have more than 1% coral reef area of the world.

Country	Coral Area km^2	World total %
1. Indonesia	51020	17.95
2. Australia	48960	17.22
3. Philippines	25060	8.81
4. France	14280	5.02
5. Papua New Guinea	13840	4.87
6. Fiji	10020	3.52
7. Maldives	8920	3.14
8. Saudi Arabia	6660	2.34
9. Marshall Islands	6110	2.15
10. India	5790	2.04
11. Solomon Islands	5750	2.02
12. United Kingdom	5510	1.94
13. Micronesia	4340	1.53
14. Vanuatu	4110	1.45
15. Egypt	3800	1.34
16. USA	3770	1.33
17. Malaysia	3600	1.27
18. Tanzania	3580	1.26
19. Eritrea	3260	1.15
20. Bahamas	3150	1.11
21. Cuba	3020	1.06

CORAL REEF AREAS OF THE WORLD





REEF ECOSYSTEMS: THREATS TO THEIR BIODIVERSITY

James W. Porter and Jennifer I. Tougas
University of Georgia

I. Coral Reef Biodiversity
II. Coral Biology
III. Anthropogenic Causes of Coral Decline
IV. Coral Disease
V. Coral Reefs and Global Climate Change

GLOSSARY

biodiversity Refers to the diversity of life, including genetic biodiversity (diversity within a species), species biodiversity (diversity among species), and ecosystem biodiversity (diversity among ecosystems).

bleaching The loss of symbiotic zooxanthellae from corals. Bleaching is usually caused by elevated sea surface temperatures, but it can also be caused by sedimentation, salinity variation, or bacterial infection.

calcification The deposition of calcium carbonate skeletons by aquatic plants or animals. In reef-building corals, calcium is deposited in its aragonitic mineral form.

Cnidaria The marine invertebrate phylum containing the reef-building corals.

disease Any impairment of the normal physiological functions of an organism. While disease normally refers to infection by bacterial, fungal, protozoan, or viral pathogens, technically bleaching could also be classified as a disease based on its physiological effect.

epizootic Disease outbreaks among animal populations (as distinguished from an epidemic in human populations).

eutrophication Nutrient enrichment, typically in the form of nitrates or phosphates, most often from human sources such as agriculture, sewage, or urban runoff from land.

extinction Extinction is said to occur when a species is not definitely located in the wild during the past 50 years.

global climate change Refers to a suite of changes in the Earth's climate, including phenomena such as global warming, severe storm frequency and intensity, and glacial melting. Increasingly, scientists believe that global climate change is being accelerated by anthropogenic inputs of CO_2.

gonochoric A mode of reproduction in which individuals of the species are either male or female and produce either eggs or sperm within a single colony.

hermaphroditic A mode of reproduction in which individuals of the species produce both eggs and sperm within a single colony, sometimes within the same polyp.

hermatypic Reef-building; more recently, this term has been replaced by the term zooxanthellate to refer to those coral species with symbiotic algae.

nematocysts Harpoon-like stinging cells found in the tentacles of all cnidarians. They are used to pierce, immobilize, and capture zooplankton food.

oligotrophic Low in nutrients and low in primary production. Coral reefs grow in oligotrophic water.

planula A coral larva. This ciliated planktonic stage

Encyclopedia of Biodiversity, Volume 5

rarely lasts for more than 1 or 2 weeks prior to settlement.

P/R The ratio between photosynthetic and respiratory rates of the combined coral host and zooxanthellate symbiont. A ratio greater than 1 ($P/R > 1$) indicates a net gain of energy that is then available for growth and reproduction.

Scleractinia The taxonomic order of cnidarians that includes the reef-building corals.

sedimentation Particulate material falling out of the water column onto the seafloor.

trophic efficiency The percentage of material or energy that moves, without loss, from one trophic level to the next. Most food chains have trophic efficiencies around 10%. Through tight internal recycling, corals routinely achieve trophic efficiencies in excess of 90%.

trophic level Position within the food chain, e.g., primary producer, herbivore, and carnivore. Corals, however, with their symbiotic algae and their ability to feed on zooplankton, exist at all three trophic levels simultaneously.

turbidity Particulate material suspended in the water column that reduces water clarity, light penetration, and hence photosynthesis.

zooxanthellae Symbiotic dinoflagellate algae in corals and other tropical marine invertebrates.

‰ The oceanographic symbol for salinity, or the salt content of seawater in parts per thousand.

CORAL REEFS ARE the oldest and most diverse communities on Earth. With 32 of the 34 presently known animal phyla, reef ecosystems are vastly more diverse than tropical rain forests, which support only 9 free-living phyla. There are many close analogies between coral reefs and tropical rain forests. Both exhibit high species diversity, both have high topographic complexity (trees in the rain forest, corals on the reef), and both have a high proportion of their organic material resident in the living biota rather than in organic-rich soils or sediments. However, it is probable that no other ecosystem on Earth has, or ever had, as many higher level taxa as are present on modern-day coral reefs.

To a certain extent, coral reefs are an enigma: on the one hand, they are the most luxuriant ecosystems on Earth, supporting high diversity and high biomass, and yet on the other, they achieve this status in the least fertile waters on Earth. Corals solve this problem by tight recycling and high efficiency. The flesh of corals is a symbiotic association between algae, called zooxanthellae, and cnidarians (10% plant, 90% animal). Corals are primary producers, herbivores, and carnivores all at the same time. This tightly knit symbiosis produces trophic efficiencies as high as 90%. Furthermore, filter-feeding invertebrates, which create and cover the topographically complex three-dimensional structure of the reef, capture and retain a high proportion of the material that moves over them.

From a geological perspective, reefs may be defined as masses of carbonate limestone, built up from the seafloor by the accumulation of the skeletal material of many coral reef plants and animals. For every gram of carbon dioxide fixed into organic (living) material by coral photosynthesis, an equal amount of carbon dioxide is deposited into inorganic material (limestone) by calcification. Reef growth has shaped the face of the Earth by creating limestone structures over 1.3 km thick (Enewetak Atoll) to over 2000 km long (Great Barrier Reef). Depending on their proximity to land, coral reefs are classified as either fringing reefs (paralleling the coast line at a distance of <1 km from shore), barrier reefs (paralleling the coast line >5 km from shore), or atoll reefs (midoceanic reefs without any relationship to continental or island land masses). Reefs can be further subdivided into back-reef, patch-reef, or off-shore-reef habitats.

Coral reefs flourish on stable substrates within a very narrow range of physical parameters. These requirements include shallow depths (0–50 m), normal oceanic salinities (32–38 parts per thousand), warm sea surface temperatures (mean annual values of 22–26°C), high ambient light levels (100–2000 $\mu E\ m^{-2}\ s^{-1}$ at solar noon), high water clarity (transmittance values above 90%), high oxygen concentrations (near 90% full saturation), and extremely low nutrient concentrations ($<1.0\ \mu M$ dissolved inorganic nitrogen; $<0.1\ \mu M$ soluble reactive phosphorus). Although some coral reefs can exist under conditions slightly suboptimal to these, such reefs are never the richest, fastest growing, or most diverse. As a result of these requirements, coral reefs are restricted to the tropics, generally between 25° north and south latitude, and predominantly on the western boundaries of the world's oceans in the Caribbean and the Indo-Pacific. Tropical coastal zones cover $9.8 \times 10^6\ km^2$, or 1.9% of the Earth's surface; coral reefs are thought to occupy only $0.6 \times 10^6\ km^2$, or slightly less than 0.1% of the planet. Humans have a special responsibility and a special challenge to preserve these environments as they house the fullest expression of the evolution of life on Earth.

I. CORAL REEF BIODIVERSITY

A. Phyletic Diversity

Coral reefs harbor extraordinary biodiversity. At the phyletic level, a level that more accurately tallies the diversity of evolved life forms in an ecosystem, 32 of the 34 described phyla are found on coral reefs. In contrast, only 9 are found free-living in the tropical rain forest (Table I). Even if freshwater and parasitic forms are included in the count, the rain forest total rises to 17 phyla, approximately half of the phyletic diversity of coral reefs.

This observation raises important concerns in the conservation of biodiversity. Whereas most biologists focus on issues pertaining to species loss, geologists frequently examine extinction patters in higher level taxa (Veron, 1995). Ninety percent of the 83 described animal classes are marine. Almost all of these are found on coral reefs, and some, such as the class Sclerospongiae, are exclusively tropical. If coral reef habitats worldwide become significantly degraded, then it might be reasonable for ecologists (as well as geologists) to contemplate the loss, over the next century, of some of the Earth's higher taxa.

TABLE I

The Phyletic Diversity of Coral Reefs Vastly Exceeds That of Any Other Habitat on Earth[a]

Phylum	Tropical coral reef	Tropical freshwater	Tropical rain forest
Placozoa	X		
Porifera	X	X	
Cnidaria	X	X	
Ctenophora	X		
Mesozoa	X		
Platyhelminthes	X	X	X
Nemertina	X	X	X
Gnathostomulida	X		
Gastrotricha	X	X	
Rotifera	X	X	
Kinorhyncha	X		
Loricifera	X		
Acanthocephala	X	X[b]	
Entoprocta	X		
Cycliophora	X		
Nematoda	X	X	X
Nematomorpha	X	X[b]	
Ectoprocta	X	X	
Phoronida	X		
Brachiopoda	X		
Mollusca	X	X	X
Priapulida	X		
Sipuncula	X		
Echiura	X		
Annelida	X	X	X
Tardigrada	X	X	X
Pentastoma	X	X[b]	
Onychophora			X
Arthropoda	X	X	X
Pogonophora			
Echinodermata	X		
Chaetognatha	X		
Hemichordata	X		
Chordata	X	X	X
Total	32	16	9

[a] Of the 34 animal phyla, 32 are found on coral reefs. Only the phylum Onychophora is found exclusively in moist forests; all other rain forest phyla are also found on coral reefs. The deep-sea phylum Pogonophora is the only phylum found neither on coral reefs nor in tropical rain forests.

[b] Found in terrestrial organisms as internal parasites only.

B. Species Diversity

The species diversity of coral reefs greatly exceeds that of any other marine environment. Of the roughly 1.86 million plant and animal species described, 274,000 are thought to be marine and more than half of these are tropical (Table II). At present, there are thought to be 93,000 described species of coral reef plants and animals. Almost 66,000 of these are macroscopic invertebrates. Specific examples of this extraordinary diversity exist in the disparate coral reef literature; a few of these remarkable numbers are listed in Table III. At present, no fully comprehensive all-taxa biodiversity inventory has ever been conducted on a coral reef (Ormond *et al.*, 1997), but it is obvious that were this to be done, the total biodiversity would be extremely high.

As in the rain forest, estimates of coral reef species diversity based on the number of described species are considered to be a gross underestimate of the actual number of species there. Also, as in the rain forest, the tiniest members of the community (insects in the rain forest and microinvertebrates on the coral reef) are thought to be the most diverse, and least well described, component of the fauna. Reaka-Kudla (1997) has pointed out that most of the diversity and most of the biomass of coral reefs reside within the cryptofauna,

TABLE II

Biodiversity Patterns Suggest That, as with Terrestrial Organisms, Species Diversity among Marine Organisms Is Higher in the Tropics Than in the Temperate or Arctic Zones[a]

Group	Number of described species (to nearest 1,000)	Percentage of total described species (1.87 million)
Observed species diversity		
Total described global biodiversity	1,868,000	—
Total marine species, all taxa	274,000	14.7
Total macroscopic marine species	200,000	10.7
Total animals	193,000	10.3
Macroinvertebrates	180,000	9.6
Total algae	4,000–8,000	0.2–0.4
Total described tropical coastal species	195,000	10.4
Total described coral reef species	93,000	5.0
Total macroscopic coral reef species	*68,000*	3.6
Animals	66,000	3.5
Algae	2,000–3,000	0.1–0.2
Expected species diversity		
Total expected coral reef species		
Most conservative estimate	618,000	34.3
Intermediate estimate	948,000	—
Least conservative estimate	9,477,000	—

[a] Despite the paucity of data on marine biodiversity, it also appears (1) that most of the biodiversity of coral reefs has not been described and (2) that many species may already have gone extinct. The data are summarized from Reaka-Kudla (1997).

not the large spectacular corals and fishes that sit on or swim over the reef. This generality is reflected in the proportion of undescribed species observed in samples taken in a systematic fashion from some of the world's richest coral reef habitats (Table IV). In general, this table reveals that the smaller the body size of the organisms, the greater the proportion of undescribed species in the sample. Since most of the species on a coral reef are small and cryptic, it follows that most are also undescribed.

Reaka-Kudla (1997) has attempted to estimate the actual number of species on a coral reef based on the comparative species richness of coral reefs versus tropical rain forests and their relative surface areas. Depending on which assumptions are accepted, her formulae result in a low estimate of 618,000 species and a high estimate of 9,477,000. The most reasonable intermediate estimate puts the biodiversity estimate at slightly less than 1 million species (Table II). Briggs (1999) has argued against such extrapolations, pointing out that statistical errors are compounded unrealistically when small sample sizes are increased by several orders of magnitude, e.g., from 93,000 observed species to 9,477,000 expected species (Table II). After an exhaustive review of the literature and advice from marine systematists, Poore and Wilson (1993) argue that only 1 in 20 marine species have been described, producing a conservative estimate for tropical marine biodiversity of 1,870,000 species. This 1.87 million estimate suggests that the number of species to be found on a coral reef equals all of the currently described life forms on our planet (Table II).

If we accept as fact that tropical marine biota is almost certainly more poorly described than temperate biota, that is, that the ratio of undescribed to described species is greater than 20 to 1, then there appear to be somewhere between 1.86 and 9.47 million species on coral reefs. Regardless of the estimating technique used,

TABLE III

Examples of the Extraordinary Biodiversity of Coral Reefs

Group	Number of species	Sampling unit	Location	Source[a]
Organisms > 0.2 mm (all groups)	309	Colonies of the coral *Oculina arbuscula*	Florida	McCloskey, 1970
Infaunal invertebrates	800	10 m^2	Australia	Poore and Wilson, 1993
	350	10 m^2	Aldabra Atoll	Hughes and Gamble, 1977
Polycheates	158	6 liters of sediment	Oahu, HI	Butman and Carlton, 1993
	103	One colony of living coral	Heron Island, Australia	Grassle, 1973
Motile cryptofauna	776	One reef flat	Moorea	Peyrot-Clausade, 1983
Mollusks	637	Milne Bay, Papua	New Guinea	Werner and Allen, 1998
Boring cryptofauna	220	Dead coral	Solomon Islands	Gibbs, 1971
Cheilostome bryozoans	46	Hard substrates	Jamaica	Jackson, 1984
Hermatypic corals	362	Milne Bay, Papua	New Guinea	Werner and Allen, 1998
	350	Great Barrier Reef	Australia	Veron, 1985
	242	Ishigaki Island	Indo-Pacific	Veron, 1985
	53	Discovery Bay	Jamaica	Wells, 1973
Fishes (all groups)	1500	Great Barrier Reef	Australia	Sale, 1977
	1039	Milne Bay, Papua	New Guinea	Werner and Allen, 1998
	496	Bahamas	Caribbean	Bohlke and Chapin, 1968
	442	Dry Tortugas	Florida	Longley and Hildegrand, 1941
	517	Alligator Reef	Florida	Starck, 1968
	23	Single coral head, Big Pine Key	Florida	Bohnsack, 1979

[a] Bohlke, J., and Chapin, C. (1968). *Fishes of the Bahamas and Adjacent Tropical Waters*. Livingston, Wynnewood, PA. Bohnsack, J. A. (1979). "The Ecology of Reef Fishes on Isolated Coral Heads: An Experimental Approach with an Emphasis on Island Biogeographic Theory," Ph.D. Dissertation, University of Miami, Coral Gables, FL. Butman, C. A., and Carlton, J. T. (1993). *Biological Diversity in Marine Systems*. National Science Foundation, Washington, D.C. Gibbs, P. E. (1971). *Bull. Br. Mus. (Nat. Hist.) Zool.* 21, 99–211. Grassle, J. F. (1973). In *Biology and Geology of Coral Reefs* (O. A. Jones and R. Endean, Eds.), pp. 247–270. Academic Press, New York. Hughes, R., and Gamble, J. (1977). *Philos. Trans. R. Soc. London, B* 279, 324–355. Jackson, J. B. C. (1984). *J. Exp. Mar. Biol. Ecol.* 75, 37–57. Longley, W., and Hildegrand, S. (1941). *Pap. Tortugas Lab.* 34, 1–331. McCloskey, L. (1970). *Int. Rev. Ges. Hydrobiol.* 55, 13–81. Peyrot-Clausade, M. (1983). *Thalassgraphica* 6, 27–48. Poore, G. B. C., and Wilson, G. D. F. (1993). *Nature* 361, 597–598. Sale, P. F. (1977). *Am. Nat.* 111, 337–359. Starck, W. (1968). *Undersea Biol.* 1, 1–40. Veron, J. (1985). *Proc. Fifth Int. Coral Reef Cong.* 4, 83–88. Wells, J. (1973). *Bull. Mar. Sci.* 23, 16–58. Werner, T., and Allen, G. (Eds.) (1998). *A Rapid Biodiversity Assessment of the Coral Reefs of Milne Bay Province, Papua New Guinea*. Conservation International, Washington, D.C.

and regardless of how fully we accept Brigg's caveat, the gathering impression is that, with the exception of species in a few showy classes and orders, the vast majority of coral reef species are as yet undescribed.

C. Control of Scleractinian Coral Biodiversity

Geography, age, and temperature appear to control biodiversity patterns in reef-building corals. The Indo-Pacific region, with its vastly greater age and geographic extent is richer by far than the Caribbean (Veron, 1995). For instance, whereas 362 species of coral are found on the eastern end of Papua New Guinea, only 53 are found in Jamaica (Table III). The Indo-Pacific has a "species-generating" topography: tens of thousands of isolated islands scattered across vast spaces. Despite the recent discovery of sibling species of corals even within the relatively well known Caribbean genus *Montastrea* (Knowlton *et al.*, 1992), the numerical disparity between the two regions will persist as the list of described species from both oceans lengthens.

Figure 1 shows the widespread distribution of coral genera throughout the Caribbean. The dense packing of generic diversity isopleths along the eastern coast of

TABLE IV

Examples of Undescribed Biodiversity among Several Tropical Marine Invertebrate Faunae from Familiar and Easily Accessible Marine Habitats (Merrell, 1995)[a]

Site	Taxon	Number of undescribed species out of the total collected in the taxon	Source[b]
New Guinea	Corals	14 of 362	Werner and Allen, 1998
New Guinea	Fish	3 of 1039	Werner and Allen, 1998
New Guinea	Snails, sea slugs	310 of 564	Gosliner, 1993
Phillipines (one island, multiple sites)	Snails, sea slugs	135 of 320	Gosliner, 1993
Hawaii (one island, 6 liters of coral reef sediment)	Marine polycheate worms	112 of 158	Dutch, 1988
Great Barrier Reef (two islands)	Marine flatworms (Polyclads)	123 of 134	Newman and Cannon, 1994
Gulf of Mexico	Copepods (Harpacticoids)	19–27 out of 29	Merrell, 1995

[a] This table has been arranged from larger to smaller body size and suggests that, as with fauna everywhere, especially in the tropics, the smaller the body size, the higher the percentage of undescribed species in the sample.

[b] Sampling effort and number of samples varied among studies. Dutch, M. (1988). "A Characterization of Polycheate Assemblages on a Hawaiian Fringing Reef" Master's Thesis, Zoology Department. University of Hawaii, Honolulu, HI. Gosliner, T. M. (1993). *Proc. Seventh Int. Coral Reef Symp.* 2, 702–709. Merrell, W. J. (1995). *Understanding Marine Biodiversity: A Research Agenda for the Nation.* National Academy Press, Washington, D.C. Newman, L. J., and Cannon, L. R. G. (1994). *Mem. Queensl. Mus.* 36, 159–163. Werner, T., and Allen, G. (Eds.) (1998). *A Rapid Biodiversity Assessment of the Coral Reefs of Milne Bay Province, Papua New Guinea.* Conservation International, Washington, D.C.

Florida correlates with the frequency and intensity of cold water disturbances (Birkeland, 1996). Cold temperature limits the distribution of coral reefs northward in the Northern Hemisphere and southward in the Southern Hemisphere.

From a biodiversity perspective, Bermuda (with 14 hermatypic scleractinian coral genera) may have more in common with the coral reefs of the Florida Middle Grounds (12 genera) and the Flower Garden Banks (13 genera) than with coral reefs of the Florida Keys (24 genera; Fig. 1). The absence of the family Acroporidae from all three of these northern localities is probably more a function of winter cold kills than of limits to dispersal due to geographic isolation. These three reef localities demonstrate that temperature tolerances of individual Caribbean species are probably more important than distance in determining which species are present at a given location.

Local environmental conditions can also influence coral diversity. The loss of coral diversity along the northern and eastern coast of South America is probably due to sedimentation, not temperature. The presence of extensive terrigenous beaches and sediments transported from tropical rivers, such as the Orinoco and the Amazon, diminishes coral reef survival in these locations. It would be interesting to see if the species and genera waning as one travels south along the coast of South America (where low temperature is not a factor) are the same as those disappearing as one travels north along the coast of Florida (where low temperature is the controlling factor).

D. Species Loss

Both IUCN (International Union for Conservation of Nature and Natural Resources) and CITES (Convention on the International Trade in Endangered Species) define extinction as occurring when a species is not definitely located in the wild during the past 50 years. With this strict definition, and in the complete absence of monitoring efforts at the appropriate temporal and spatial scales, extinctions in the marine environment in general, and on coral reefs in particular, are almost impossible to prove. An example of this kind of difficulty can be seen in the announcement of the extinction of an eastern Pacific coral species due to severe El Niño conditions, and an almost immediate retraction when it was subsequently rediscovered alive (Glynn and Feingold, 1992). Nevertheless, Carlton (1993), in his review of modern marine invertebrate extinctions, includes one tropical species in his list, the Indo-Pacific mangrove periwinkle, *Littoraria flammea*, which was last seen in the mid-1800s.

There are several methodological reasons why marine extinctions might be especially difficult to detect. As pointed out by Ray (1988), "The last fallen mahogany

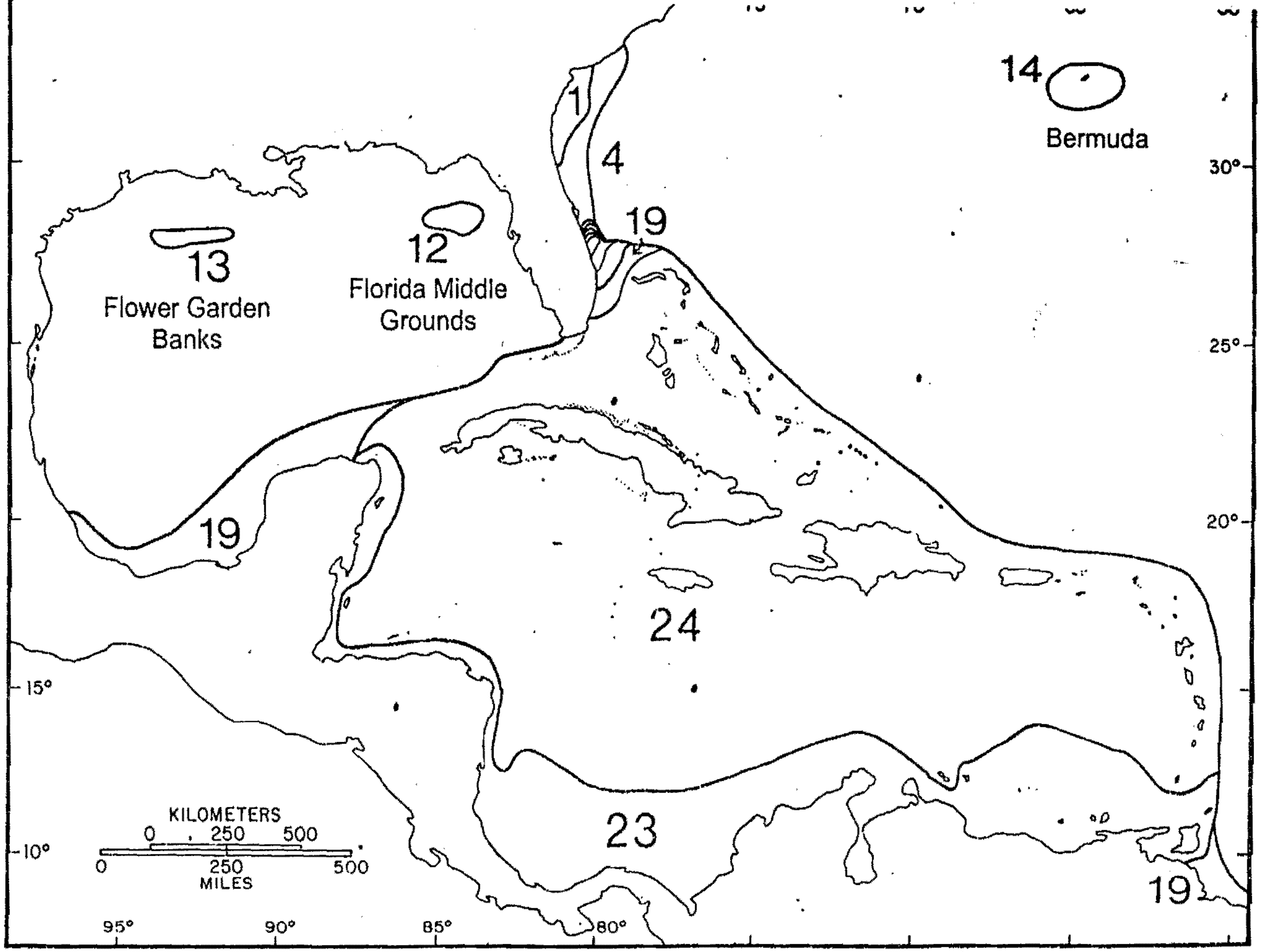


FIGURE 1 Patterns of generic scleractinian coral diversity in the Caribbean reveal no endemism within the region, but rather broad-scale distribution followed by rapid faunal diminution north and south. Coral loss northward along the coast of Florida is due to cold temperature limitations; faunal loss southward along the coast of South America is probably due to the influence of river sediments pouring into the coastal zone. While the northward distribution of corals in the Caribbean is due to historical patterns of global temperature regimes, the sediment load of costal environments in South America is increasingly influenced by anthropogenic upland management practices in the coastal zone.

would lie perceptibly on the landscape, and the last black rhino would be obvious in its loneliness, but a marine species may disappear beneath the waves unobserved, and the sea would seem to roll on the same as always." In addition, there is the perception that marine species are somehow less susceptible to extinctions. Lamark, in his 1809 *Philosophie Zoologique*, states that "Animals living in the waters, especially the sea waters . . . are protected from the destruction of their species by man. Their multiplication is so rapid and their means of evading pursuit or traps are so great, that there is no likelihood of his being able to destroy the entire species of any of these animals."

While this argument may carry some validity, Reaka-Kudla (1997) points out that most species on coral reefs are small and that these smaller species also have much smaller geographic ranges. This leads to the conclusion that most species on coral reefs may be much more vulnerable to extinction than has been widely assumed. The few clear examples of marine extinctions have in common a vulnerable, extinguishable habitat. Coral reefs, especially those located near population centers, fall into this category. The most interesting perspective on the complex, worrisome, but poorly researched topic of marine extinctions may belong to Carlton (1993), "At the end of the 20th Century, one of the major crises in global marine invertebrate conservation is not so much that invertebrates are becoming extinct at a rapid rate (although they may be)—the crisis is that we do not know."

II. CORAL BIOLOGY

A. Anatomy

Corals are benthic marine invertebrates belonging to the phylum Cnidaria, which is characterized by two distinct tissue layers, the inner endoderm and outer ectoderm, separated by an amorphous collection of cells called the mesoglea. A single coral polyp has a central mouth cavity surrounded by tentacles armed with stinging cells called nematocysts. Corals can be solitary, consisting of a single large polyp, or colonial, consisting of thousands of interconnected polyps. Colonies form through budding—one polyp produces a daughter polyp that is genetically identical to the original.

B. Reproduction and Recruitment

Corals can reproduce asexually through fragmentation or self-generation of brooded larvae. This form of reproduction restricts genetic diversity of coral populations. In contrast, sexual reproduction through fertilization of gametes originating from genetically distinct colonies increases the genetic diversity of coral populations.

Sexual reproduction in corals occurs in one of two ways: either through mass spawning, in which thousand of gametes (eggs and sperm) are released simultaneously into the water column where fertilization takes place, or by brooding, in which sperm are released into the water column and are taken inside the maternal coral polyp to fertilize the eggs stored there. Depending on the species, a given colony may be hermaphroditic, producing both eggs and sperm, or gonochoric, producing either eggs or sperm. In both instances, ciliated planulae larvae are produced (Birkeland, 1996).

The coral larvae spend between 3 days and 3 weeks in the water column, during which time they disperse. They may travel only a few meters away on the same reef or to entirely different reefs kilometers away. Dispersion maintains gene flow in coral populations. After dispersion, larvae settle onto relatively clean, hard surfaces on the reefs, metamorphose into polyps, and begin to form new colonies through asexual budding (Birkeland, 1996).

Coral recruitment is favored by nutrient-poor conditions with high light availability, low sedimentation rates (Rogers, 1990), limited competition for space by algae, and decreased predation by fish, sea urchins, and starfish. The patterns of settlement, survival, and growth of coral recruits directly influence the structure and function of coral communities and associated reefs.

C. Calcification

Common to all scleractinian (stony) corals is the ability to secrete calcium carbonate. The shape of the resulting skeleton is species specific at the polyp level, but the overall shape of the colony is influenced, within limits, by environmental conditions. Colony morphologies aid in the removal of trapped sediments (Rogers, 1990) and the capture of food and influence both zooxanthellate and host physiology (Sebens, 1994).

As a chemical process, deposition of $CaCO_3$ is influenced by the ambient concentration of CO_2, which is directly related to temperature, pressure, and concentrations of other dissolved materials. As a biological process, calcification is driven by photosynthesis and is closely controlled by temperature (Dubinsky, 1990). Under optimal conditions, growth rates of branching corals, such as the Caribbean coral *Acropora cervicornis*, can exceed 10 cm per year. However, local variables such as nutrient concentrations and sedimentation rates reduce realized growth rates (Birkeland, 1996).

Calcification by thousands of colonies over hundreds of thousands of years produces the complex, three-dimensional structure of modern reefs essential to the maintenance of reef biodiversity. For example, topographical features are important for the distribution, survival, and resulting abundance of many reef fishes and invertebrates (Sebens, 1994).

D. Photosynthesis

While corals can capture prey with their tentacles, many sclerectinian corals rely on endosymbiotic algae for nourishment. Known as zooxanthellae, the algae are located within the ectoderm of the coral. Depending on the species, corals may host a variety of zooxanthellae within a colony through space and time (Rowan *et al.*, 1997). Photosynthesis by the zooxanthellae provides nutrients required by the coral for growth and reproduction and drives calcification and subsequent reef formation. As a result, the bathymetric distribution of reef-building corals is largely restricted to high light environments, typically less than 50-m depth, which can sustain this symbiotic relationship (Dubinsky, 1990).

Depending on the clarity of the water, ultraviolet light penetrates the ocean to about 5 m. Ultraviolet radiation inhibits photosynthesis and is damaging to many organisms, including corals and zooxanthellae. However, some coral species have developed protective pigments that allow the transmission of visible light while blocking ultraviolet radiation (Dubinsky, 1990). As not all corals have this ability, the distribution of corals is also influenced by the presence of ultraviolet radiation.

If the relationship between the coral and its symbiotic zooxanthellae is disturbed through increased temperatures or exposure to elevated UV light, bleaching may occur. The term "bleaching" describes the condition in which the zooxanthellae exit, or are expelled from, the coral, thus showing the stark white skeleton beneath the coral tissue. Without the symbiotic algae, corals lose their vital source of nutrition, slow their growth rates, stop reproducing, and sometimes die (Birkeland, 1996). When environmental conditions return to normal, zooxanthellae repopulate the coral. Susceptibility to bleaching is influenced by the species of coral in question and the species of zooxanthellae it hosts (Rowan *et al.*, 1997). Consequently, two colonies of the same species may have dramatically different bleaching responses to the same stresses.

E. Physiological Limitations

While availability of light limits the depth distribution of corals, temperature limits the latitudinal and longitudinal distribution and is one of the best predictors of coral diversity (Veron, 1995). Optimal temperature for coral growth and reproduction ranges from 22 to 26°C, depending on geographic location and species in question. Corals generally do not grow in waters in which minimum temperatures drop below 18°C, and such a thermal barrier also limits dispersal of larvae. A few corals survive in temperatures above 30°C, such as those found in some locations in the Middle East. To some extent, corals are able to adapt to ambient conditions; consequently, upper lethal temperatures for a species in the tropical zone will be higher than those of the same species in a subtropical zone (Dubinsky, 1990).

Salinities can also influence the distribution of corals. Corals grow well in water that has a constant salinity of 32–36‰. Low salinity (<20‰), due to increased freshwater flow from localized flooding or exposure to heavy rainfall during low tides, limits coral distribution and reduces diversity. High salinities (>38‰) can also inhibit coral growth, particularly in the Persian Gulf (Dubinsky, 1990).

III. ANTHROPOGENIC CAUSES OF CORAL DECLINE

A. Benefits from Coral Reefs

Humans benefit from both the resources and recreation that coral reefs provide. Coral is used for building materials in areas where there is no viable alternative. In fact, many inhabited tropical islands around the world were, at one point, coral reefs themselves. In addition, coral reefs reduce coastal erosion by protecting coastlines from severe storms (Hoegh-Guldberg, 1999). This is particularly important in tropical waters where hurricanes and tropical storms occur frequently (Richmond, 1993). Indeed, entire islands have been washed into the sea when their surrounding living coral reefs were removed.

Coral reefs are important for the development of local economies (Birkeland, 1996). The reefs support valuable fisheries for local consumption and for the aquarium trade. Throughout the Caribbean and Indo-Pacific, local diets derive nearly 60% of their intake of protein from these reefs. The life cycles of many commercially important fish and shellfish are dependent on the presence of healthy mangrove swamps, coral reefs, sea grass beds, and coastal lagoons.

A multibillion dollar tourism industry is supported by tropical coral reefs (Hoegh-Guldberg, 1999), and is a critical source of income, particularly for small island nations with few alternative resources to exploit. For the 1992–1993 fiscal year, attendance at the Coral Reef State Park on Key Largo, Florida, had the highest visitation of any state park in Florida that year (Fig. 2). Tourism can only be a viable option for economic development if reefs are healthy.

Finally, pharmaceutical companies have discovered naturally occurring bioactive compounds among the organisms found on coral reefs (Birkeland, 1996): antitumor compounds have been found in the mucus of corals, anti-inflammatory agents have been isolated from soft corals, and coral has successfully been used as a bone substitute in reconstructive surgeries.

B. Coastal Urbanization

Despite their importance, coral reefs around the world have been declining at an alarming rate. At the core of this decline are human activities (Fig. 3), spurred by population growth (Table V). Nearly 15% of the human population lives within 100 km of coral reefs (Hoegh-Guldberg, 1999). The geographical locations of highest coral diversity also coincide with large human populations. More than 100 countries have coral reefs within their territorial boundaries (Birkeland, 1996). Most of these are developing nations and have, by far, the fastest growing populations due to advances in medicine, technology, and public health services. Coastal cities are growing rapidly by attracting immigrants from country interiors to these bustling centers of trade and commerce. Influxes of tourists can substantially increase the effective population of an area and place additional demands on potable fresh water, power, and sewage systems. For example, in 1990, the population of the Florida Keys was 80,500, but there were over 2,000,000 visitors per year to this tourist destination.

As populations continue to expand, human pressures on coral reefs will increase. There is a direct correlation between reef degradation and proximity to urban centers. Activities associated with urbanization include waste disposal and power and desalination plant operation. Rapid urbanization has outpaced sewage treatment capacities in several regions and has caused eutrophication in coastal zones as raw sewage is often discharged directly into nearshore waters (Richmond, 1993; Sebens, 1994). The effluents from operating power and desalination plants are up to 5 or 6°C warmer than ambient temperatures.

Industrialization often accompanies urbanization and is encouraged by economic demands for hard currency and international commerce. Effluents from some

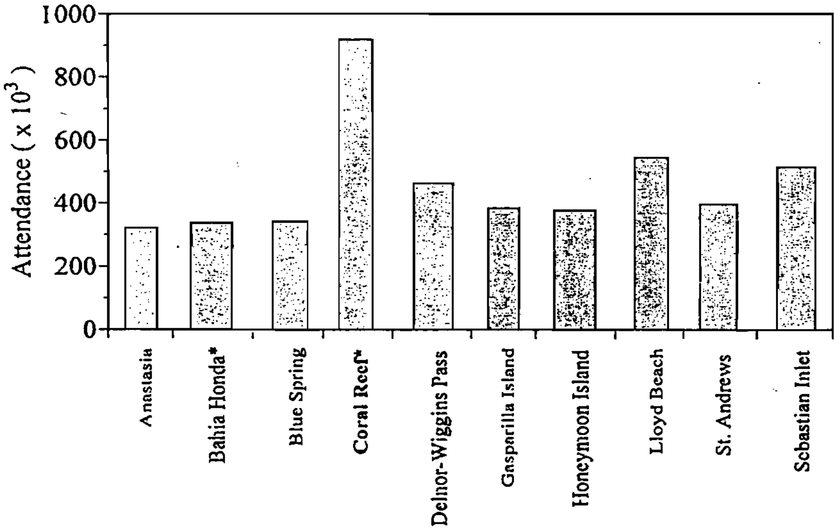


FIGURE 2 Coral reefs are popular tourist destinations. For fiscal year 1992–1993, the most frequently visited state park in Florida was Coral Reef State Park. Attendance at this park was nearly twice that of Lloyd Beach, the second most visited park. Asterisks indicate parks with coral reefs. Tourism provides an important source of economic development for tropical island countries with coral reefs.

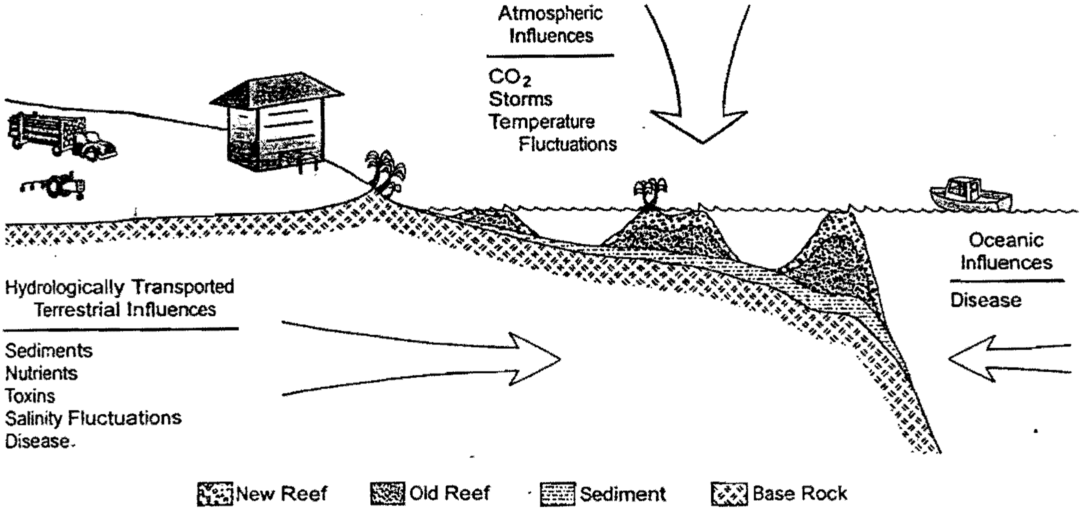


FIGURE 3 Coral reefs are subject to terrestrial, atmospheric, and oceanic influences. Sediments, nutrients, and toxins, released from activities such as deforestation, agriculture, and industry, are hydrologically transported to coral reefs through local rivers. CO_2 buildup in the atmosphere increases CO_2 concentrations in the ocean and alters climate patterns. Finally, diseases are circulated by ocean currents. Reefs located near human population centers are subjected to multiple stresses simultaneously and so suffer losses in diversity and cover [adapted from Wilkinson, C. R., and Buddemeier, R. W. (1994). *Global Climate Change and Coral Reefs: Implications for People and Reefs. Report of the UNEP–IOC–ASPEI–IUCN Global Task Team on the Implications of Climate Change on Coral Reefs.* IUCN, Gland, Switzerland].

industries, such as rum distilleries and fertilizer plants, contribute to coastal eutrophication and heavy metal contamination. Ores are one of the few available resources for economic development in the tropics and mining activities can be a significant source of sediments. Furthermore, heavy metals readily bind to clays and are transported by terrigenous sediments to the reefs. Mining activities throughout the Indo-Pacific and Caribbean deliver thousands of tons of toxin-laden sediments to coral reefs each year.

Another land-based activity that affects coral reefs is deforestation. Nearly 70% of all tropical hardwood products originate from Southeast Asia. In the Philippines, forests have been reduced to 25% of their original cover. Upland areas of French Polynesia are cleared for residential and commercial construction as well as for agriculture and hydroelectricity. Deforestation, particularly of coastal mangroves (Rogers, 1990), increases erosion and the amount of soils transported from the land to the reefs. Erosion can be severe when heavy rains fall on logged areas (Birkeland, 1996).

Agricultural activities often take over land cleared for timber production. Millions of hectares of mangrove forests have been reclaimed for aquaculture and agriculture. In Southeast Asia, farming has become universally dependent on the use of agrochemicals. As a result of agricultural activities, nearshore waters are subjected to increased nutrients, sediments, and agrochemicals (Richmond, 1993). Heavy metals found in corals from Panama and Costa Rica were common components of agricultural pesticides (Guzmán and Jiménez, 1992).

Upland and coastal ecosystems on land are intimately linked with coral reefs in the sea (Porter *et al.*, 1999). At the organismal level, corals subjected to land-based pollution undergo metabolic changes that lead to bleaching, reduced growth and reproduction rates, and, on occasion, death (Richmond, 1993). Coral recovery after natural disturbances is inhibited by pollution. At the ecosystem level, these effects lead to losses in coral diversity, coral cover (Edinger *et al.*, 1998), and shifts in dominant benthic organisms (Lapointe, 1999). The causal agents include sedimentation, eutrophication, altered temperatures, and altered salinities.

C. Sedimentation

Sedimentation influences coral communities through lethal and sublethal mechanisms, depending on the sediment load and the life cycle of the marine organisms. While increased sedimentation causes direct mortality of corals by smothering them, most effects are sublethal. Corals remove sediments by secreting copious amounts of mucous that trap the sediments. These mucous sheets, which are moved off of the coral through ciliary

TABLE V

Disturbances to Reef Ecosystems: Their Sources and Consequences

Disturbance	Effect of disturbance	Source of disturbance	Cause of source
Sedimentation	Lethal effects	Deforestation	Human population growth
	Smothering	Infrastructure construction	Migration to cities
	Reduced coral cover	Road construction	Tourism
	Reduced coral diversity	Logging in the watershed	Economic demands
	Sublethal effects	Clearing for agriculture	
	Decreased water clarity	Clearing mangroves	
	Shift toward shallower community	Industry	Introduction of new technologies
	Decreased photosynthesis	Mining	Economic demands
	Increased respiration		Introduction of new technologies
	Increased mucus production		
	Reduced coral recruitment		
Eutrophication	Lethal effects	Waste management	Human population growth
	Overgrowth by macroalgae		Migration to cities
	Reduced coral cover		Tourism
	Reduced coral diversity	Agriculture	Introduction of new technologies
	Sublethal effects	Fertilizer application	Food needs
	Decreased water clarity	Ranching (raising pigs)	
	Shift toward shallower community	Industry	Introduction of new technologies
	Decreased photosynthesis	Fertilizer plant operation	Economic demands
	Reduced coral reproduction	Rum distillery operation	
	Reduced coral recruitment		
	Increased activity of boring algae		
Toxic contamination	Lethal effects	Agriculture	Economic demands
Heavy metals	Death	Pesticide application	Food needs
Pesticides	Increased bacterial infections	Herbicide application	Introduction of new technologies
Herbicides	Sublethal effects	Industry	Human population growth
	Increased mucus production	Mining	Migration to cities
	Increased respiration rates	Fertilizer plant operation	Economic demands
	Decreased photosynthesis	Power plant operation	Introduction of new technologies
	Decreased growth	Desalination plant operation	
	Decreased reproduction		
	Bleaching		
Altered temperatures	Lethal effects	Industry	Human population growth
Increases	Bleaching, leading to death	Power plant operation	Migration to cities
Decreases	Decreased coral cover	Desalination plant operation	Tourism
	Decreased coral diversity	Altered hydrology	
	Sublethal effects	Global climate change	Fossil fuel consumption
	Bleaching and recovery		Human population growth
	Increased respiration		Introduction of new technologies
	Decreased photosynthesis		Urban development
	Reduced reproduction		

continues

Continued

Disturbance	Effect of disturbance	Source of disturbance	Cause of source
Altered salinity	Lethal effects Bleaching, leading to death Decreased coral cover Decreased coral diversity	High salinities Desalination plant operations Reduction of freshwater input	Human population growth Migration to cities Tourism
	Sublethal effects Bleaching and recovery Increased mucus production Decreased photosynthesis Decreased respiration Reduced fertilization	Low salinities Increased freshwater runoff from deforestation of watersheds	Introduction of new technologies Urban development
Disease	Lethal effects Tissue death Sublethal effects Decreased photosynthesis Decreased growth Decreased reproduction	Largely unidentified pathogens	Increased susceptibility to disease by multiple stressors
Storms Increased frequency Increased intensity	Lethal effects Scouring Fragmentation Sublethal effects Fragmentation Increased sedimentation Increased turbidity Increased nutrients	Global climate change	Fossil fuel consumption Human population growth Introduction of new technologies Urban development

action, constitute a tremendous energy drain for the corals and cause a decrease in the *P/R* by increasing respiration (Rogers, 1990). Despite this removal process, sediments tend to accumulate in depressions on large, massive colonies and cause death to those patches. Consequently, there is a positive correlation between the amount of terrigenous sediments and the amount of coral injury.

Water turbidity, which increases when sediments are suspended in the water column, decreases the amount of light available for photosynthesis. As photosynthetic rates decrease, so do growth and reproduction rates. Because of the reduced availability of light, the maximum depth at which corals can grow decreases and the coral community compresses into shallower environments (Dubinsky, 1990).

Adult corals are more tolerant to sedimentation stresses than juveniles. Coral larvae are not able to settle on loose sediments (Rogers, 1990). Consequently, if a fine layer of sediments covers the reef benthos, then coral settlement patterns shift toward vertical surfaces (Rogers, 1990) and successful recruitment drops dramatically (Richmond, 1993).

D. Eutrophication

The effect of eutrophication varies according to the quantity and quality of the nutrient source, as well as the hydrographic regime in the area, and becomes especially apparent when high nutrients are present for an extended period of time. On naturally oligotrophic reefs, tight nutrient cycling between the coral host and zooxanthellate symbionts affords a competitive advantage to the coral: corals are able to flourish and outcompete many other primary producers on the reef. When nutrients are added to the system, the competitive edge shifts to faster growing macroalgae (Lapointe, 1999; Richmond, 1993) and filter feeders. The algae proceed to overgrow the corals and effectively shade them until the corals die. Coral recruitment is reduced because algae occupy space on the reef and prevent coral larvae from settling (Lapointe, 1999). Finally, the growth of boring organisms is promoted, which weakens the reef structure itself and increases the probability of storm damage (Richmond, 1993).

Eutrophication is also associated with increased turbidity and a concomitant decrease in light availability (Richmond, 1993), largely due to an increase in phytoplankton densities. When photosynthesis decreases, growth rates and reproduction diminish. This leads to decreases in coral diversity and coral cover (Birkeland, 1996). Furthermore, vertical zonation becomes truncated under decreased light availability (Dubinsky, 1990).

E. Heavy Metals and Toxins

Howard and Brown (1984) reviewed the effects heavy metals have on corals. Corals are able to directly absorb soluble metals from seawater. Alternatively, they may ingest metals directly by catching particulate matter in mucous nets or indirectly as a result of feeding on copepods, which accumulate metals in their chitinous skeletons. Some metals may be deposited directly into the skeleton and become immobilized. Others remain in the coral tissues and cause dramatic physiological responses. These include excessive mucous production, increased bacterial infections, bleaching, decreased skeletal deposition, which decreases vertical growth rates, reduced reproduction, and death (Howard and Brown, 1984). Similarly, when corals are exposed to agrochemicals, responses include increased respiration, decreased photosynthesis, increased mucous production, increased planulae release (a common stress response for brooding species), and decreased larval settlement (Birkeland, 1996).

F. Altered Temperatures

Although the warmth of tropical water may seem benign to humans, reef-building corals live much closer to their upper lethal temperature (the temperature that will kill or disable them) than to their lower lethal temperature. In fact, a rise in the water temperature of only 2–3°C above the normal summertime average is much more stressful physiologically than a drop of 2–3°C below this value. There are two ways in which elevated temperatures affect coral: increased respiration and decreased photosynthesis. Under severe thermal stress, bleaching occurs. Anything that acts to increase temperatures has the potential to adversely affect the health and survival of coral reefs.

Coral respiration increases with increasing temperatures (Porter *et al.*, 1999). Bleaching under increased temperature is correlated with increased respiratory rates and a decrease in photosynthesis (Porter *et al.*, 1999). Under both of these conditions, the *P*/*R* ratio decreases for the coral, and growth and reproduction decrease. If exposed for an extended period of time to temperatures above the average maximum temperature they are accustomed to, bleaching can occur and the coral colonies can die (Birkeland, 1996).

Reproductive success decreases with increased temperatures and is far more sensitive to temperature fluctuations than growth rates. Consequently, healthy adult corals could live in environments unsuitable for reproduction. Nonetheless, as temperature-sensitive species die, or fail to reproduce, the composition of coral communities will change (Hoegh-Guldberg, 1999).

G. Altered Salinity

Hyposalinity results from increased discharge or runoff associated with deforestation, particularly of mangrove forests, and from urban development. On the other hand, hypersalinity is associated with power and desalination plant effluents as well as large-scale reductions of freshwater flow from land.

Responses of corals to altered salinities vary according to species and region. In Florida, the coral *Siderastrea siderea* can grow in areas where salinity fluctuations are prevalent. Changes in salinity of up to 10‰ away from the mean produces little response in the coral. Beyond 10‰ above the mean, respiration and photosynthesis decreased and some bleaching was observed. In contrast, *Porites* species have demonstrated a narrower tolerance to salinity fluctuations: an increase of 10‰ causes corals to contract their polyps, shed copious amounts of mucus, and bleach [as cited in Porter *et al.* (1999)].

In Kaneohe Bay, Hawaii, widespread coral death has accompanied increased freshwater runoff. Low salinities also inhibit fertilization and larval survival (Richmond, 1993). Fertilization of mass-spawning species takes place at the water surface, where eggs and sperm mix. Once the eggs have been fertilized, the resultant larvae float near the water surface for several days. Freshwater also floats on seawater. Therefore, the gametes and larvae could be exposed to lowered salinities if mass spawning occurs during heavy rainfall. In one study, fertilization rates and larval survivorship dropped by more than 50% when the salinity dropped to 28‰. These results demonstrated that terrestrial runoff can have a major influence on reproductive success (Richmond, 1993).

Water from Florida Bay naturally flows through channels between the keys and out over the reef tract. Extensive channelization of water for use in Miami and agricultural areas and for flood control has decreased the amount of freshwater entering the bay. Consequently, salinities in Florida Bay rose dramatically in the 1980s, particularly during drought years. Because Florida Bay is shallow, temperatures fluctuate with the seasons. Warm, hypersaline waters originating from Florida Bay have been recorded at depth on reefs along the Florida Keys (Porter *et al.*, 1999). In a study of six sites along the Florida Keys reef tract, between 1984 and 1991, all six sites lost coral diversity, and five out of six sites lost coral cover. Looe Reef, the southernmost and hardest hit reef, lost 43.9% of its coral cover (Porter *et al.*, 1999). Porter *et al.* (1999) suggested that the reef degradation observed could result from the influence of poor water quality originating from Florida Bay. Another potential source of stress from Florida Bay water is eutrophication (Lapointe, 1999).

IV. CORAL DISEASE

A. Identification of Diseases

Coral reefs are no exception to the truism that, even in healthy ecosystems, disease is part of the natural environment. Diseases in the ocean, however, are poorly understood because of the conceptual and methodological challenges in studying ephemeral phenomena in an alien environment. This explains why most coral reef pathogens are unidentified (Table VI). For instance, of the twelve scleractinian coral diseases easily recognized by their symptoms, only two have been positively identified (Table VI). Nonetheless, an increase in either the frequency or severity of disease epidemics, called epizootics in animal populations, can be cause for legitimate concern.

While there is a perception that the incidence of coral disease has increased (Harvell *et al.*, 1999), it is easy to dismiss these accounts as either biased by heightened environmental concern or unfounded in the

TABLE VI

Coral Disease Conditions Commonly Observed in the Florida Keys

General disease category[a]	Common name	Pathogen	Reference[b]
Black line disease	Black band	*Phormidium corallyticum*	Rutzler and Santavy, 1983
White line diseases	White pox	Unknown	Porter *et al.*, in press Holden, 1996
	White band, Type I	Unknown	Williams and Bunkley-Williams, 1990
	White band, Type II	Unknown	Ritchie and Smith, 1998
	White plague, Type I	*Sphingomonas* sp. nov.	Richardson *et al.*, 1998b
	White plague, Type II	Unknown	Richardson *et al.*, 1998a
Other diseases	Yellow blotch	Unknown	Santavy *et al.*, 1999
	Dark spot	Unknown	Goreau *et al.*, 1998
	Ridge mortality	Unknown	Goreau *et al.*, 1998
	Red band	*Oscillatoria?*	Goreau *et al.*, 1998
	Rapid wasting	Fungal/predation	Cervino *et al.*, 1998
	Neoplasia	Cancer?	Goreau *et al.*, 1998

[a] Criteria for disease designation: Active tissue mortality, tissue necrosis, bared skeleton, mucus production, bisected or partial polyps.

[b] Cervino, J., Goreau, T., Hayes, R., Kaufman, L., Nagelkerken, I., Patterson, K., Porter, J., Smith, G., and Quirolo, C. (1998). *Science* 199, 1302–1310. Goreau, T., Cervino, J., Goreau, M., Hayes, R., Richardson, L., Smith, G., DeMeyer, K., Nagelkerken, I., Garzon-Ferra, J., Gil, D., Garrison, G., Williams, E., Bunkley-Williams, L., Quirolo, C., Patterson, K., Porter, J., and Porter, K. (1998). *Rev. Biol. Trop.* 46 (Suppl. 5), 157–172. Holden, C. (1996). *Science* 274, 2017. Porter, J., Patterson, K., Porter, K., Peters, E., Mueller, E., Santavy, D., and Quirolo, C. *Coral Reefs* (in press). Richardson, L., Goldberg, W., Carlton, R., and Halas, J. (1998a). *Rev. Biol. Trop.* 46 (Suppl. 5), 117–198. Richardson, L., Goldberg, W. M., Kuta, K. G., Aronson, R. B., Smith, G. W., Ritchie, K. B., Halas, J. C., Feingold, J. S., and Miller, S. L. (1998b). *Nature* 392, 557–558. Ritchie, K., and Smith, W. (1998). *Rev. Biol. Trop.* 46 (Suppl. 5), 199–203. Rutzler, K., and Santavy, D. (1983). *Mar. Ecol* 4, 301–319. Santavy, D., Peters, E., Quiolor, C., Porter, J., and Bianchi, N. (1999). *Coral Reefs* 18, 97. Williams, E., and Bunkley-Williams, L. (1990). *Atoll Res. Bull.* 335, 1–71.

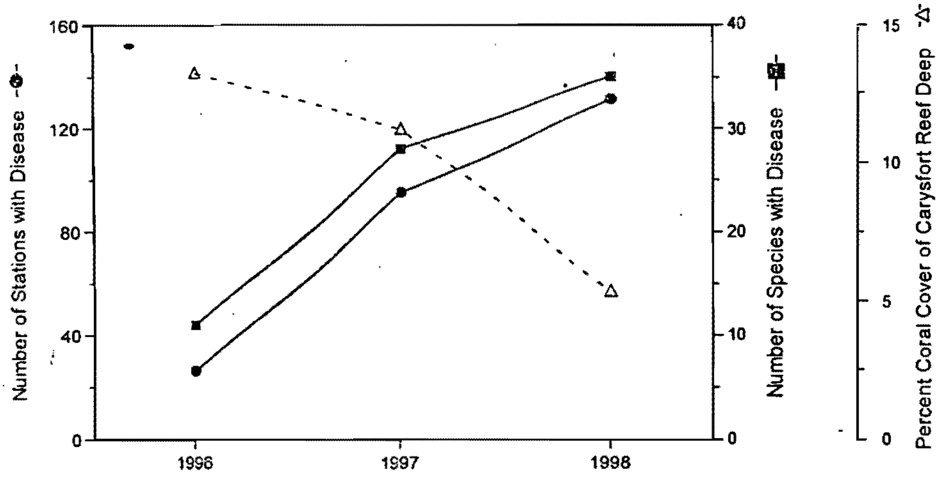


FIGURE 4 Coral disease and coral mortality in the Florida Keys, 1996–1998. The number of stations exhibiting disease (out of a possible total of 160 stations) and number of coral species exhibiting disease (out of a total of 41 species in the survey) are plotted against percent coral cover data from one of the hardest hit reef sites (out of a total of 40 reef sites in the survey), Carysfort Reef Deep. The data show that between 1996 and 1998, coral disease became more widespread in the Keys, affected more species, and had a devastating effect on the live coral cover of at least one reef in the Florida Keys (Porter *et al.*, in press).

absence of baseline data. However, evidence to the contrary is mounting. White band disease in the Caribbean inflicted heavy losses in both St. Croix and Belize (Aronson and Precht, 1997). Paleontological evidence has demonstrated that disease outbreaks in Belize have no historical precedence over the past 5000 years (Aronson and Precht, 1997), lending credence to the idea that disease outbreaks on the present scale are a recent phenomenon.

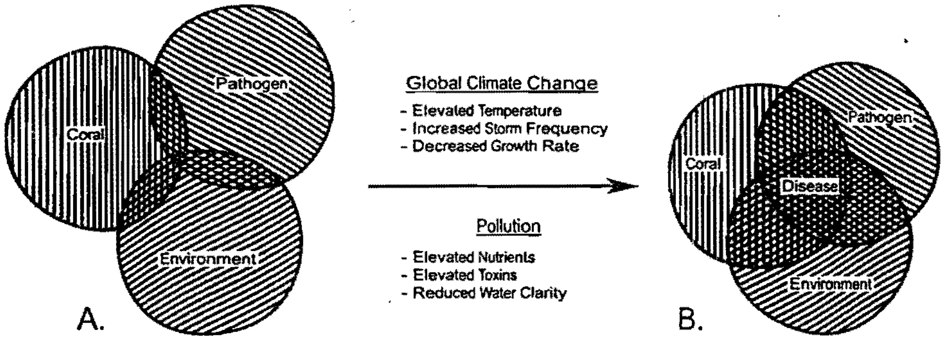
To date, most of the well-documented epizootics are from the Caribbean, but it is not clear if this represents a real difference between the Caribbean and the Indo-Pacific or merely a difference in observational coverage. The need to know more is urgent. Only multidisciplinary teams will be able to provide the ecological information necessary to devise appropriate management strategies.

B. Effects of Diseases on Diversity

Coral reef scientists are coming late to the realization that disease may exert a major control on diversity. In his review of factors explaining the biological diversity of coral reefs, Connell (1978) does not mention disease. The Environmental Protection Agency's Coral Reef Monitoring Project in the Florida Keys has been collecting information on coral disease since 1996 (Fig. 4). Because these data have been collected systematically, they allow one to resolve whether coral diseases are more widespread now than in the past. For the 3-year period covered by the survey, these data show significant increases in all disease parameters measured, including the number of stations and the number of species with diseases present. Of the 160 stations surveyed from Key Largo (in the Upper Florida Keys) to Key West (in the Lower Keys), the number of stations with diseased corals rose from 26 in 1996 to 131 in 1998, an increase of 404%. Over the same period, the number of species affected by disease rose from 11 to 35, an increase of 218%. Many of the rarest corals disappeared from the study sites due to disease.

C. Ecosystem Effects of Disease

When diseases dramatically affect populations of a single species, the effects can influence whole ecosystems. The first documented coral reef epizootic occurred between 1982 and 1983 when almost all of the black-spined sea urchins, *Diadema antillarum*, in the Caribbean died from an unknown pathogen. From its point of origin near the Atlantic terminus of the Panama Canal, this disease spread throughout the Caribbean as a waterborne agent moving at the same speed and in the same direction as well-mapped Caribbean oceanic currents (Lessios *et al.*, 1984). *Diadema* is a major herbivore on Caribbean coral reefs, and its loss led to an increase in algal abundance, especially on reefs with reduced herbivorous fish populations due to overfishing



A. Low Incidence of Disease		B. High Incidence of Disease
Naturally Fluctuating Environment	⇨ ⇨ ⇨	Anthropogenically Altered Environment
Healthy Corals	⇨ ⇨ ⇨	Immuno-Compromised Corals
Low Number of Pathogens	⇨ ⇨ ⇨	High Number of Pathogens
Low Pathogen Virulence	⇨ ⇨ ⇨	High Pathogen Virulence
Few Susceptible Species	⇨ ⇨ ⇨	Many Susceptible Species
Few Locations with Disease	⇨ ⇨ ⇨	Many Locations with Disease
Low Coral Mortality Rates	⇨ ⇨ ⇨	High Coral Mortality Rates

FIGURE 5 Coral disease stress model. While natural background levels of disease are expected even in healthy ecosystems, a variety of stresses could lead to the suppression of the immune and disease defense systems in coral. The consequence of reduced health would be an increase in the number of pathogenic organisms, susceptible species, locations, and mortality rates. All of these results have been observed in the Florida Keys, and while they do not prove the accuracy of this model, this hypothesis is at present the only one that explains all of the observations.

(Hughes and Connell, 1999) or on reefs with elevated nutrient levels from coastal eutrophication (Lapointe, 1999).

Corals themselves have experienced mass mortalities due to epizootics. A new disease, white pox, has inflicted high mortality among *Acropora palmata* stands on some Key West coral reefs (Table VI). For some white pox and white-band outbreaks, coral mortality rates were as high as coral losses during the worst crown-of-thorns starfish "plagues" in the Indo-Pacific (Birkeland, 1996). In the Florida Keys, the most dramatic change linked to coral disease can be seen in the loss of living coral exhibited at the deep site (18 m) on Carysfort Reef in the Upper Keys (Fig. 4). Sixty percent of the living coral there died in 2 years, mostly due to disease. Clearly, Floridian coral reefs cannot survive if these mortality rates continue.

Because corals grow slowly and live for decades or centuries, epizootics will have far-reaching impact on coral reefs on geological time scales. When deadly diseases decimate coral populations to this extent, geological rates of carbonate deposition in the Caribbean may actually be affected (Aronson and Precht, 1997). It is clear that disease epidemics can have a real impact on coral reefs.

D. The Coral Disease Model

We propose a coral reef disease model (Fig. 5) that depicts how changes in environmental conditions alter the interactions between hosts and pathogens and subsequently enable disease outbreaks. Stress factors (Porter *et al.*, 1999) are considered relevant, even for corals whose immune systems are not well known, because the ability to resist infection is a function of the host's overall health. Compromised immune systems result in increased susceptibility to disease. One of the most striking aspects of the disease patterns seen in the Florida Keys is the simultaneous increase in all disease parameters measured (Fig. 4). Only a hypothesis that addresses environmental quality will explain the simultaneous increase in the number of diseases, the number of species affected, and the rates of coral mortality throughout such a large geographic area. If this model is correct, then the incidence of disease would be expected to be higher near polluted population centers,

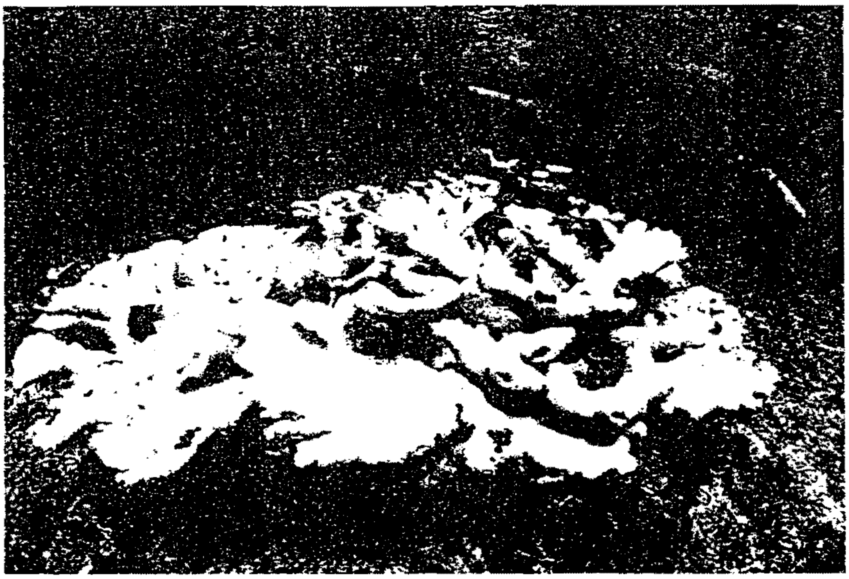


FIGURE 6 In 1997 and 1998, severe coral bleaching episodes were caused by dramatically elevated sea surface temperatures worldwide (see also Fig. 8). A vast majority of elk horn corals (*Acropora palmata*) on Looe Key, in the Florida Keys, bleached stark white. It is not known whether these colonies would have recovered because on August 27, 1998, Hurricane Georges removed nearly all branching corals from this reef, including the bleached colonies shown here (photograph by James W. Porter).

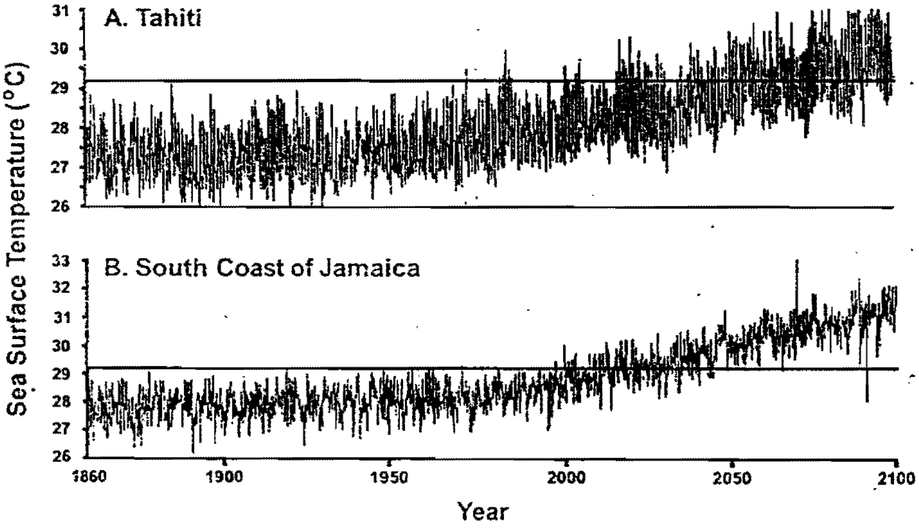


FIGURE 7 A model of sea surface temperatures based on greenhouse gas concentrations and El Niño Southern Oscillation events predicts temperatures will exceed normal thresholds for many reefs in the very near future. The horizontal lines indicate the temperature thresholds at which corals begin to bleach. As the twenty-first century proceeds, a higher percentage of time is spent above this line [Hoegh-Guldberg, O. (1999). *Mar. Freshwater Res.* 50, 839–866].

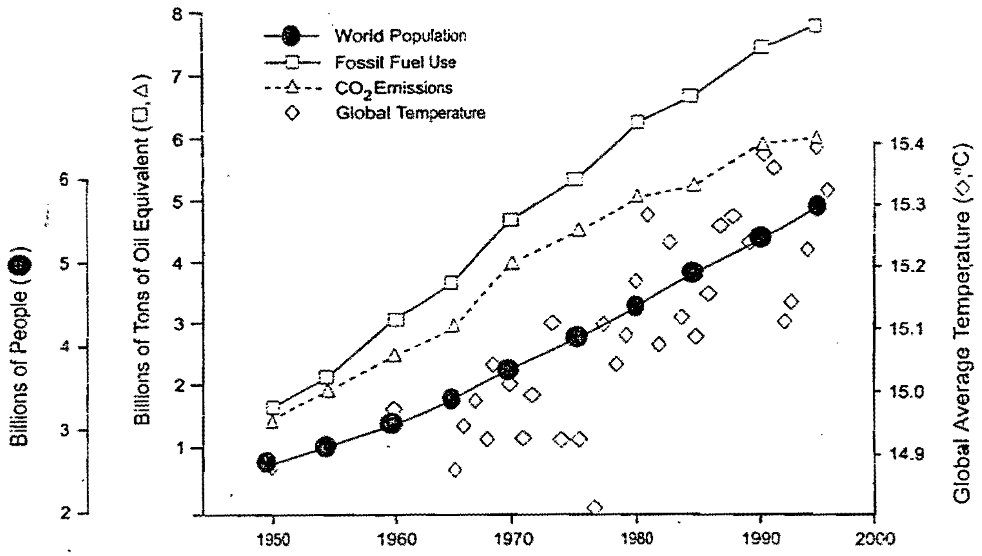


FIGURE 8 The burning of fossil fuels (coal, oil, and natural gas) and the destruction of a majority of the Earth's forests by an increasing human population have caused an increase in atmospheric CO$_2$ concentrations over the past half century. It is highly likely that these elevated atmospheric CO$_2$ concentrations have also caused the incontrovertible increase in the Earth's temperature over the same time period. Even if population growth shows some signs of slowing down as we enter the twenty-first century, energy consumption shows no such sign of declining. An increased reliance on coal, especially toward the latter half of the twenty-first century, could exacerbate rising CO$_2$ levels considerably [Houghton, J. T., Meira Filho, L. G., Callander, B. A., Harris, N., Kattenberg, A., and Maskell, K. (1996). *Climate Change 1995. The Science of Climate Change*. Cambridge Univ. Press, Cambridge, UK]. The low temperature value in 1976 resulted in coral death in the Florida Keys [Porter, J., Battey, J., and Smith, G. (1981). *Proc. Natl. Acad. Sci. USA* 79, 1678–1681].

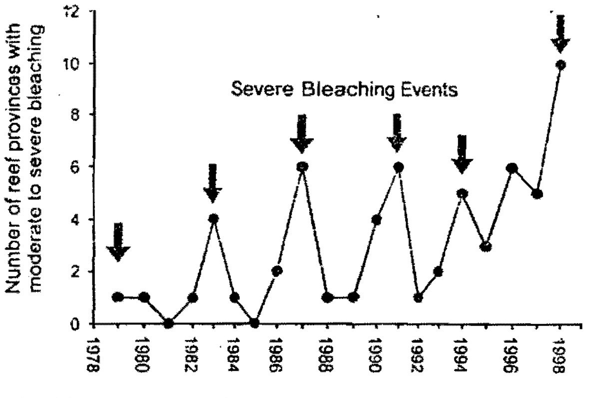


FIGURE 9 Recently, the frequency, intensity, and geographical extent of bleaching episodes have increased. During the strongest bleaching event to date, 1998, bleached corals were recorded for the first time in many provinces [Hoegh-Guldberg, O. (1999). *Mar. Freshwater Res.* 50, 839–866].

for example, or following bleaching events (Fig. 6), both of which might be expected to compromise the coral's immune system.

E. The Human Connection

Oceanic diseases (Harvell *et al.*, 1999), and wildlife diseases in general (McCallum and Dobson, 1995), appear to have increased. It is not premature to ask whether or not these disease outbreaks are caused by, or influenced by, humans. At present, the historical novelty of the outbreaks is a suggestive, but not a definitive, answer to this question (Aronson and Precht, 1997). Recently, however, the disease link to human activities has been strengthened by an examination of a fungal pathogen, *Aspergillus sydowii*, of sea fans (Harvell *et al.*, 1999). These authors have proposed that this marine pathogen is a terrestrial fungus that has secondarily invaded the marine environment via sediment runoff from land.

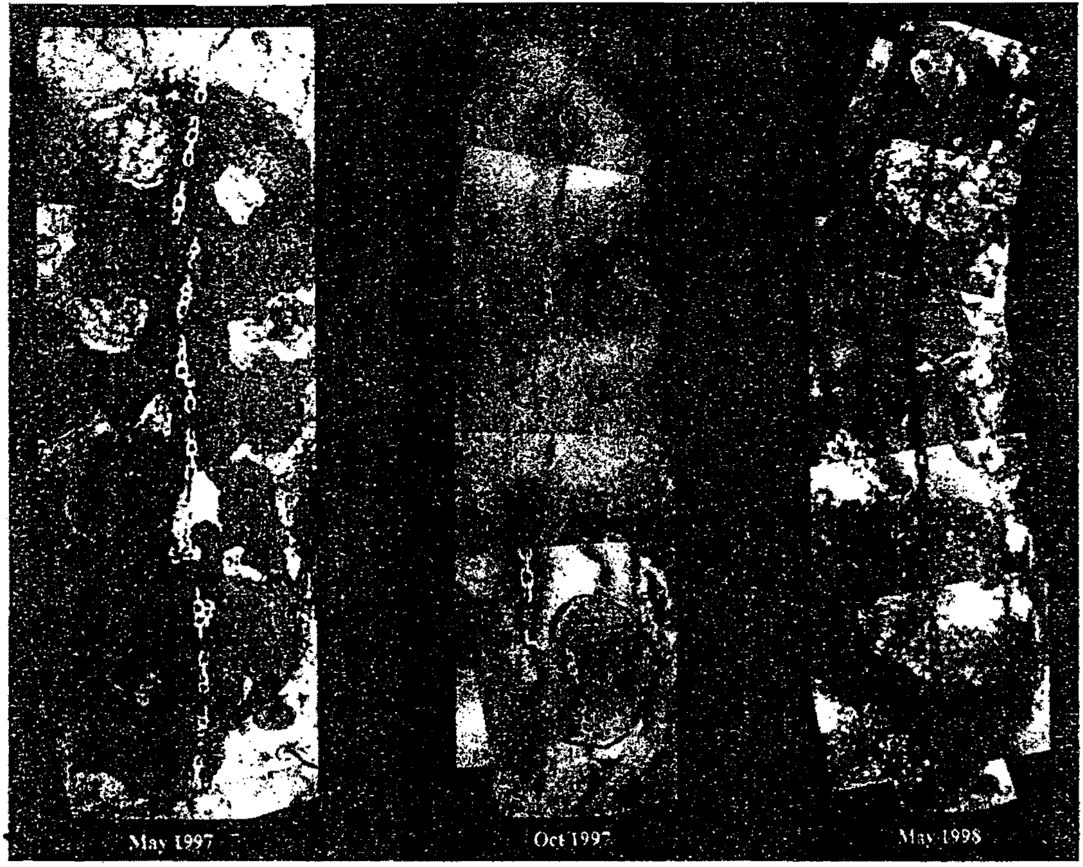


FIGURE 10 The potential interaction between coral bleaching and disease can be seen in this montage of images from 1997 to 1998. Healthy colonies of *Montastrea annularis* [left (May, 1997)] on Looe Key, in the Florida Keys, bleached in late summer due to elevated sea surface temperatures [middle (October, 1997)]. This colony also contracted black band disease (middle, lower part of the image). By May, 1998 (left), most of the colony had recovered, but the black band damaged tissue did not.

V. CORAL REEFS AND GLOBAL CLIMATE CHANGE

A. CO_2, Temperature, and Human Population Growth

The Earth is warming. Data from analyses of tree rings, sea ice extent, and ice cores, as well as direct measures of air and sea surface temperatures in both the Atlantic and the Pacific (Hoegh-Guldberg (1999). Fig. 7) demonstrate that the Earth is warmer now than a half century ago. The temperature rise closely parallels human population growth and the growth of atmospheric CO_2 inputs from the burning of fossil fuels (Fig. 8). CO_2 is one of the greenhouse gases, and the general consensus is that the buildup of this gas in the Earth's atmosphere is causally related to the measured temperature increases.

The frequency and intensity of major storms, such as hurricanes, are expected to increase with increasing temperatures. These storms cause direct physical destruction of corals by increased wave action and scouring (Birkeland, 1996). Indirect effects include increased sedimentation and turbidity and release of nutrients from dying tissues. Some species are more resistant to storm damage than others, so the frequency with which storms strike could influence the diversity of corals present on a reef (Birkeland, 1996). There is an ongoing debate as to whether storms increase coral diversity (Connell, 1978), and there is substantial evidence for both sides of the argument (Sebens, 1994). Ultimately, the effects of storms will depend on the ability of the reef corals to recover from this disturbance.

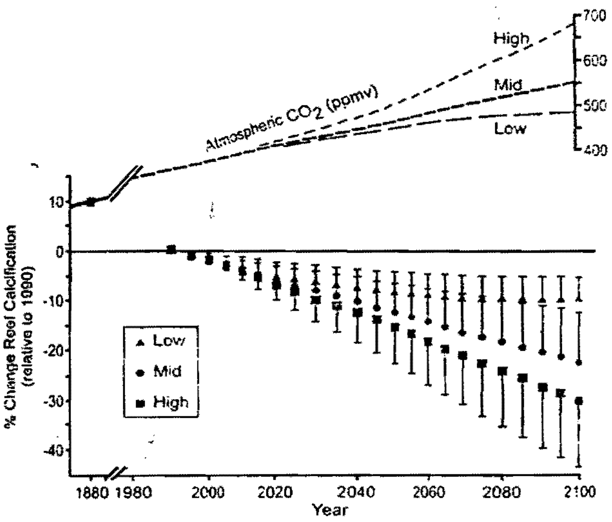


FIGURE 11 The percent change in coral reef calcification through time (1880–2100) is plotted as a function of atmospheric CO_2 concentration [Gattuso, J.-P., Allemand, D., and Frankignoulle, M. (1999). *Am. Zool.* 39, 160–183]. This graph demonstrates the linkage between anthropogenic carbon dioxide production from the burning of fossil fuels and decling coral reef growth rates.

Their recovery ability may be severely compromised in areas subjected to strong anthropogenic influences (Sebens, 1994).

B. Coral Bleaching and Elevated Sea Surface Temperatures

Coral bleaching is the loss of the symbiotic algae and is caused by elevated temperature. All marine organisms harboring zooxanthellae loose their symbiotic algae when exposed to high temperatures. Temperature-induced bleaching occurs in one of two ways, either by brief exposure to moderately increased temperature (1.5–2.0°C above average summertime temperatures for several days) or by prolonged exposure to slightly elevated temperature (only 1.0–1.5°C above normal for 3–4 weeks beyond the end of the typical summer warm season). Bleached corals appear white and lifeless (Fig. 6). The ghostlike appearance is deceptive. The chalky coloration is not due to the coral's death but instead due to the fact that, in the absence of pigmentation conferred by the symbiotic algae, the flesh of the coral is transparent. The white limestone skeleton of the coral is visible underneath its tissue. If very high temperatures persist for a few weeks, or even if moderately high temperatures persist for more than a month, the coral will die.

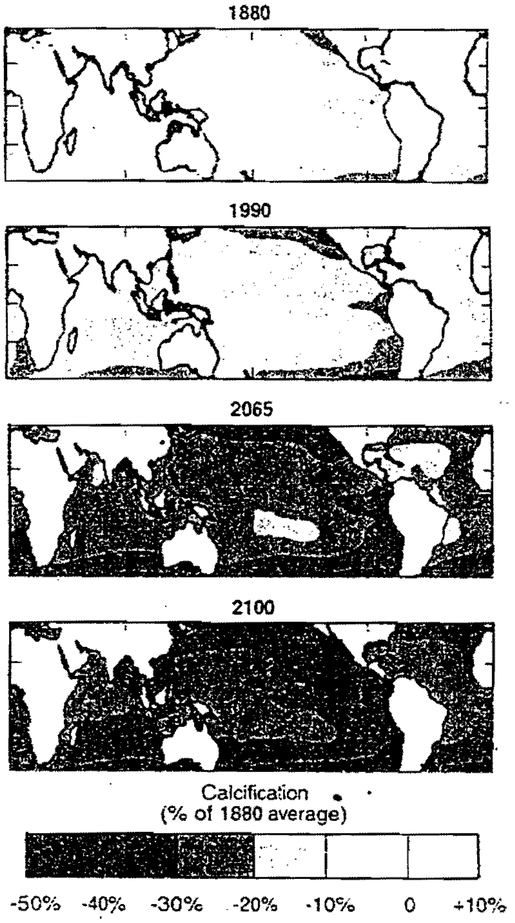


FIGURE 12 Projected changes in reef calcification rates are depicted as a percent of conditions from 1880 [reprinted from Kleypas, J. A., Buddemeier, R. W., Archer, D., Gattuso, J.-P., Langdon, C., and Opdyke, B. N. (1999). *Science* 284, 118–120 © 1999 American Association for the Advancement of Science]. This model suggests that oceanic conditions in the year 2100 will be substantially less optimal for coral growth than in the nineteenth century.

The evidence suggests that coral reefs are at serious risk from high temperatures. Over the past 20 years, there has been a dramatic increase in the number of reef provinces bleaching (Fig. 9) and in the severity of these bleaching episodes. During the 1982–1983 bleaching event, Glynn and Feingold (1992) documented up to 95% loss of corals in the Galapagos Islands. Mass mortalities have also been reported recently for Australia and the Indian Ocean (Hoegh-Guldberg, 1999). Unfortunately, arguments over the cause of high temperatures have clouded the unambiguous connection between rising temperatures and increased coral mortality. As the earth warms, more corals will die. It remains to be seen whether corals can evolve genetic

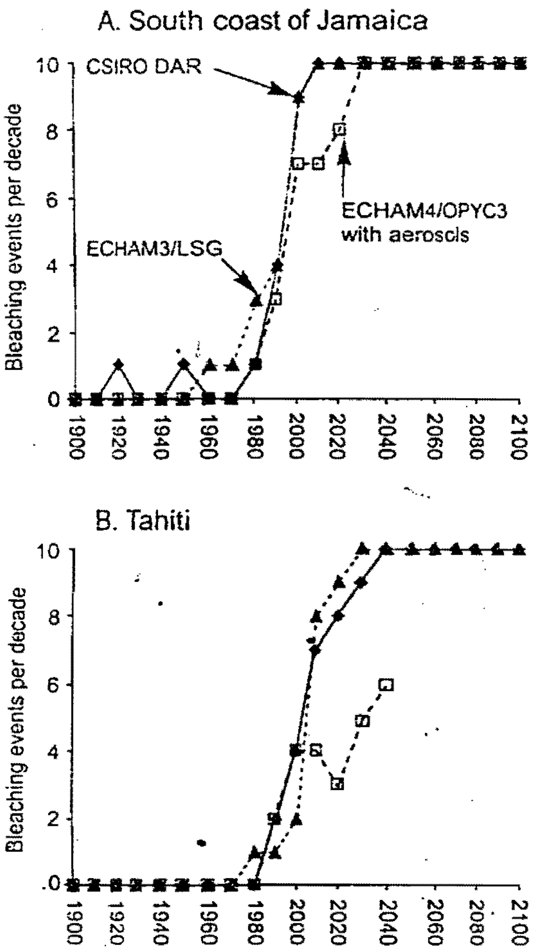


FIGURE 13 Based on predicted increases in sea surface temperatures, models indicate bleaching events per decade will increase [Hoegh-Guldberg, O. (1999). *Mar. Freshwater Res.* 50, 839–866].

resistance fast enough to survive this coming thermal stress, or alternatively, whether human energy policy can evolve fast enough to prevent corals from the necessity of having to do so.

Bleaching represents a life-threatening stress to corals. The disease model presented in Fig. 5 suggests that bleaching should promote increased susceptibility to disease. This hypothesis has not been tested experimentally, but anecdotal observations from the Florida Keys suggest it may be correct (Fig. 10).

C. Coral Calcification and Elevated CO_2

Since the ocean is in equilibrium with the atmosphere, rising CO_2 concentrations will cause an immediate increase in the amount of carbon dioxide dissolved in seawater. While this increase is not expected to modify the highly buffered pH of the ocean, it will alter the ocean's chemistry (Fig. 11). Tropical surface waters are supersaturated with dissolved calcium carbonate. Corals exploit this supersaturation to manufacture their calcium carbonate skeletons at a substantially reduced metabolic cost. Over the next century, grossly elevated atmospheric CO_2 concentrations are expected to reduce this supersaturation and reduce coral growth (Fig. 11). Kleypas *et al.* (1999) argue convincingly that this reduction in coral reef calcification has already begun (Fig. 12). The end point of this global experiment is not known, but it is extremely worrisome.

D. Global Climate Change and Coral Reef Survival

Climate change models predict that tropical sea surface temperatures will continue to rise (Figs. 7 and 13). If these scenarios are correct, then bleaching will be (a) more frequent, (b) more prolonged, and (c) more lethal (Hoegh-Guldberg, 1999). These predictions are not for the distant future, but for the near future, only a few decades away. It is also becoming clear that although coastal zone management practices are critical in protecting the well-being of some coral reefs, especially those near population centers, over the next century, global climate change, and how humans mitigate this anthropogenic stress, will determine the long-term survival of the most diverse environment on Earth.

Acknowledgments

We thank G. P. Schmahl (Sanctuary Program, NOAA) for coral biodiversity information about the Flower Gardens Bank, Kathryn L. Patterson (University of Georgia, Athens), Stephanie Borrett (University of Georgia, Athens), DeeVon and Craig Quirolo (Reef Relief, Key West) for editorial suggestions.

See Also the Following Articles

CRUSTACEANS • EUTROPHICATION AND OLIGOTROPHICATION • GRAZING, EFFECTS OF • INVERTEBRATES, MARINE, OVERVIEW • MARINE ECOSYSTEMS • PLANKTON, STATUS AND ROLE OF

Bibliography

Aronson, R., and Precht, W. (1997). Stasis, biological disturbance and community structure of a Holocene coral reef. *Paleobiology* 23, 326–346.

Birkeland, C. (1996). *Life and Death of Coral Reefs*. Chapman & Hall, New York.

Briggs, J. C. (1999). Marine species diversity. *BioScience* 49, 351.

Carlton, J. T. (1993). Neoextinctions of marine invertebrates. *Am. Zool.* 33, 499–509.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.

Dubinsky, Z. (Ed.) (1990). *Coral Reefs*. Elsevier, Amsterdam.

Edinger, E., Jompa, J., Limmon, G., Widjatmoko, W., and Risk, M. (1998). Reef degradation and coral biodiversity in Indonesia: Effects of land-based pollution, destructive fishing practices and changes over time. *Mar. Pollut. Bull.* 36, 617–630.

Glynn, P. W., and Feingold, J. S. (1992). Hydrocoral species not extinct. *Science* 257, 1845.

Guzmán, H. M., and Jiménez, C. E. (1992). Contamination of coral reefs by heavy metals along the Caribbean coast of Central America (Costa Rica and Panama). *Mar. Pollut. Bull.* 24, 554–561.

Harvell, C. D., Kim, K., Burkholder, J. M., Colwell, R. R., Epstein, P. R., Grimes, J., Hofmann, E. E., Lipp, E., Osterhaus, A. D. M. E., Overstreet, R., Porter, J. W., Smith, G. G. W., and Vasta, G. (1999). Emerging marine diseases—Climate links and anthropogenic factors. *Science* 285, 1505–1510.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshwater Res.* 50, 839–866.

Howard, L. S., and Brown, B. E. (1984). Heavy metals and reef corals. *Oceanogr. Mar. Biol. Annu. Rev.* 22, 195–210.

Hughes, T. P., and Connell, J. H. (1999). Multiple stressors on coral reefs: A long-term perspective. *Limnol. Oceanogr.* 44, 932–940.

Knowlton, N., Weil, W., Weight, A., and Guzman, H. M. (1992). Sibling species in *Montastrea annularis*, coral bleaching and the coral climate record. *Science* 255, 330–333.

Lapointe, B. E. (1999). Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs (reply to the comment by Hughes *et al.*). *Limnol. Oceanogr.* 44, 1586–1592.

Lessios, H. A., Robertson, D. R., and Cubit, J. D. (1984). Spread of *Diadema* mass mortality through the Caribbean. *Science* 226, 335–337.

McCallum, H., and Dobson, A. (1995). Detecting disease and parasite threats to endangered species and ecosystems. *Trends Ecol. Evol.* 10, 190–191.

Ormond, R., Gage, J., and Angel, M. (Eds.) (1997). *Marine Biodiversity: Patterns and Processes*. Cambridge Univ. Press, Cambridge, UK.

Poore, G. B. C., and Wilson, G. D. F. (1993). Marine species richness. *Nature* 361, 597–598.

Porter, J. W., Lewis, S. K., and Porter, K. G. (1999). The effect of multiple stressers on the Florida Keys coral reef ecosystem: A landscape hypothesis and a physiological test. *Limnol. Oceanogr.* 44, 941–949.

Ray, G. C. (1988). Ecological diversity in coastal zones and oceans. In *Biodiversity* (E. O. Wilson and F. M. Peter, Eds.), pp. 36–50. National Academy Press, Washington, D.C.

Reaka-Kudla, M., Wilson, D., and Wilson, E. (Eds.) (1997). *Biodiversity II. Understanding and Protecting Our Biological Resources*. Joseph Henry Press, Washington, D.C.

Richmond, R. H. (1993). Coral reefs: Present problems and future concerns resulting from anthropogenic disturbance. *Am. Zool.* 33, 524–536.

Rogers, C. S. (1990). Responses of coral reefs and reef organisms to sedimentation. *Mar. Ecol. Prog. Ser.* 62, 185–202.

Rowan, R., Knowlton, N., Baker, A., and Jara, J. (1997). Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388, 265–269.

Sebens, K. P. (1994). Biodiversity of coral reefs: What are we losing and why? *Am. Zool.* 34, 115–133.

Veron, J. (1995). *Corals in Space and Time. The Biogeography and Evolution of the Scleractinia.* Comstock–Cornell Press, Ithaca, NY.

CORAL DISTRIBUTION IN THE WORLD

---- compiled by GEER Foundation

Coral reefs of the world cover an estimated area of 600,000 km^2 (Smith, 1978; Kleypas, 1997), or somewhat less than 0.2% of the global ocean area and about 15% of the shallow sea areas within 0-30 m depth (Lalli and Parsons, 1997). Over half of this (54%) lies in the Asiatic Mediterranean and the Indian Ocean. Of the remaining, Pacific reefs account for 25%, Atlantic reefs for 6%, Caribbean reefs for 9%, Red Sea reefs for 4% and Persian Gulf reefs for 2% (Smith, 1978). Majority of the coral reefs are concentrated on the western sides of the three oceans (Scheer, 1985). Coral reefs are distributed in a circum tropical band mostly between 20^0 North latitude and 20^0 South latitude. The western Atlantic and the Indo-Pacific are the two main coral reef regions in the world (Well, 1988). From the biodiversity point of view, the Indo-Pacific is roughly ten times more diverse than the western Atlantic. For example, there are approximately 60 species of hermatypic corals inhabiting the coral reefs of the western Atlantic as against an estimated 500-600 species in the Indo-Pacific (Fig. 1).

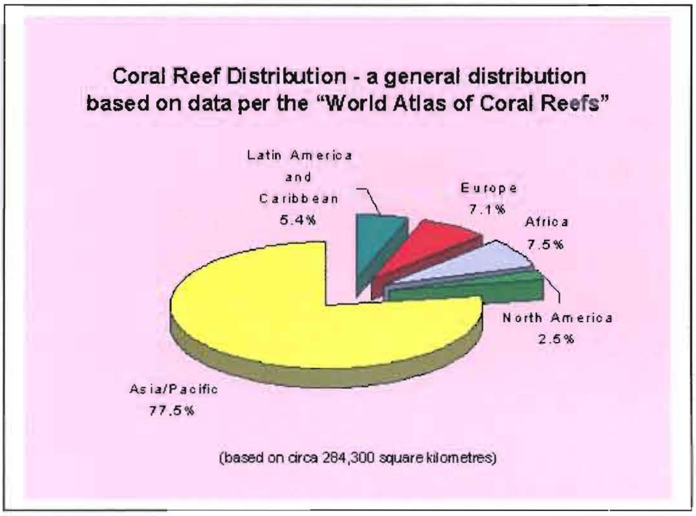


Figure-1 The distribution of coral reefs in the different parts of the world. Functional zones of a coral reef

The main features of a reef as found in the Indo-Pacific area are the reef slope, reef front, algal ridge, reef flat, lagoon, patch reef, and the leeward reef (Fig. 2). The reef front is the zone of most active growth of corals and coralline algae. It is exposed to the maximum wave energy; thus, organisms experience a constant renewal of water that bears nutrients and plankton. In exposed situations the reef front develops an extremely strong structure consisting of spurs or buttresses projecting seaward, alternating with deep grooves. This formation allows the waves to dissipate their energy by surging up the channels between the spurs. As the water washes back, it tends to carry a load of sediment and accentuates the grooves by erosion. The reef front usually drops quite steeply to a depth of 5 to 15m, then gently to 18m. A platform at about 18m is characteristic of numerous localities, these platforms probably were formed in the Pleistocene when sea levels were much lower than at present. Below 18m mark is the reef slope. Some corals grow as deep as 40m in clear water, but for the most part the reef slope consists of fragments of coral and coralline algal debris.

Behind the front is found the windward reef flat, exposed at low tide, although it may be kept moist by water and spray from breaking waves at the front. Many Pacific reefs have an algal ridge on the outer flat, formed from crustose coralline algae. Development of this ridge depends on there being a prevailing wind, constant in direction and never failing, which enables the algae to grow as much as 100cm above low tide level, moistened by the surge and splash of the waves.

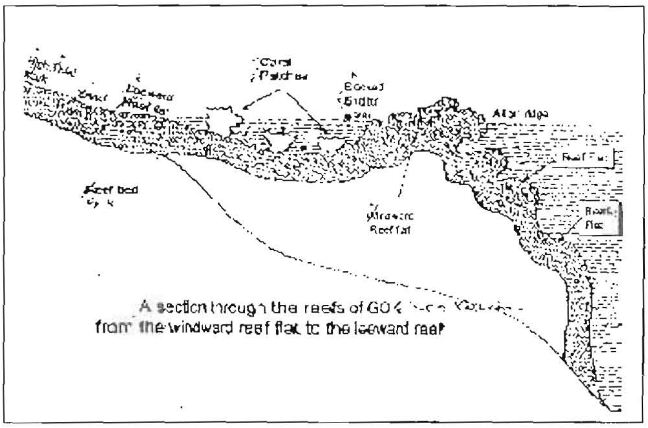


Fig.-2 Typical reef front and reef slopes

On a fringing reef, the reef flat abuts against the land. On a barrier reef and on an atoll, there is a lagoon within the outer reef flat. In the Caribbean the lagoon depth is almost always in the range of 5 to 15m, but in the Indo-Pacific the depth of atoll lagoons is related to the size of the atoll and may be as deep as 70m. The lagoon floor consists mainly of sediment derived from erosion of the reef. Microalgae live on the sediment surface, and seagrass beds often develop. A wide range of invertebrates inhabits the lagoon. Rising from the floor of the lagoon are isolated coral reefs, ranging from low knolls to large patch reefs, often the most diverse zone on the whole reef complex.

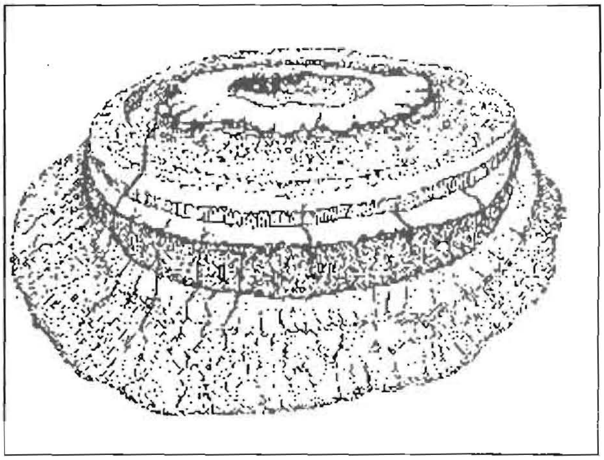


Fig.3 A three dimensional impression of an island in the Gulf of Kachchh showing the functional zones of the reef area.

On the leeward side of an atoll there is a leeward reef. The structure may be similar to that of the windward reef, but in the absence of heavy wave action the coral growth is less rapid and the algal ridge is weak or absent. In places where currents tend to accumulate coral sand, the sand may protrude above high water long enough for land plants to colonize. The whole structure then becomes a trap for sediment, and an island or cay is formed.

A three-dimensional impression of Pirotan Island in the Gulf of Kachchh is shown in Fig.-3. This reef has a particularly large proportion of algae in the reef flat, so that it is called the windward algal flat. The Pleistocence wave-cut platform is clearly shown; below it is sharp drop-off, the Pleistocene cliff. Below that again is the accumulated coral rubble of the reef slope.

Coral reefs in Indian waters

In Indian seas, the reefs are distributed along the east and west coasts at restricted places and all the major reef types are present. Fringing reefs exist in the Gulf of Mannar and Palk Bay. Platform reefs are seen along the Gulf of Kachchh. Patchy reefs are found near Ratnagiri and Malwan coasts in Maharashtra. Atolls can be observed in the Lakshadweep archipelago. Fringing and barrier reef surround the Andaman and Nicobar islands. Recently live corals have been recorded from Mumbai in Colaba area. Coral polyps were also collected in sediment - grab samples at the Bombay High Oilfield of the ONGC. Though both of the later sites are under high anthropogenic pressures, but the

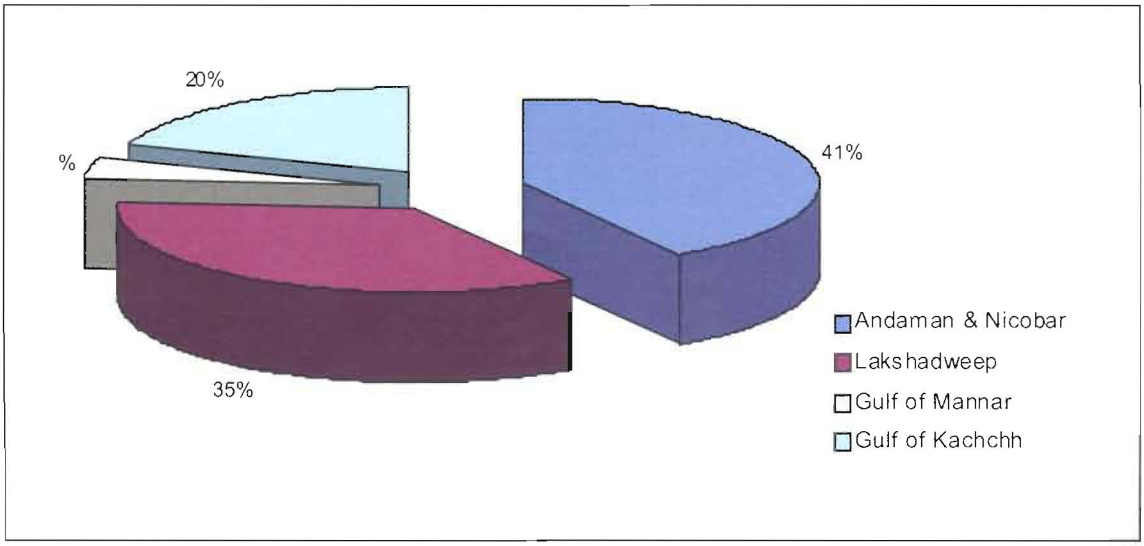


Fig.-4 The coral reef area distribution among the major reef areas in India

possibility of presence of corals cannot be withdrawn. The area wise distribution of major coral reefs of India is shown in Fig. 4.

Due to the highest freshwater flow with considerable sediment load through a large number of rivers draining into the Bay of Bengal, there were no significant coral reef formations on the East Coast of India. Satellite image shows scattered patches of corals in the intertidal areas and occasionally at subtidal depths down to a few meters along the west coast of India, notably at Ratnagiri, Malwan, Redi Port and Vizhingam (Wafar, 1990).

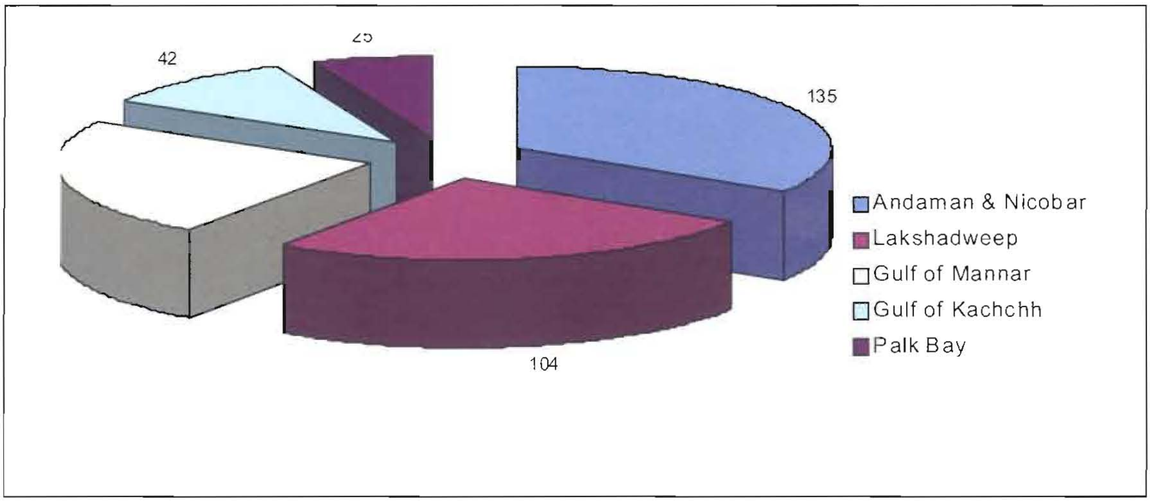


Fig.- 5: The species diversity of hard corals in major reef of India.

Variation in environmental factors in the Indian Ocean regions clearly affect the formation of coral reefs. The seasonal monsoons, equatorial calm, tropical cyclone and trade winds are the major factors regulating the reef distribution. Tidal ranges are important in reef areas because reefs normally grow upto the neap tide level. Exposure to the atmosphere and desiccation limit the growth of corals, algae and other associated organisms in the reef zones (Bakus *et al.*, 1994)

A total of 155 hermatypic coral species belonging to 50 genera and 44 ahermatypic species belonging to 21 genera has been recorded from the Indian coral reef areas (ENVIS, 1998). The species diversity of hard corals of major coral reef areas is shown in Fig.-5.

Increasing human population and anthropogenic pressures have severely affected coral distribution and biodiversity. Natural calamities also cause considerable damage to the coral reefs through direct or indirect means. Further, global warming leads to the increase of volume of seawater due to melting of ice sheets.

CORALS IN INDIA

---- compiled by GEER Foundation

Coral distribution

Corals are distributed in temperate as well as tropical zones, i.e. from the icy waters of the Arctic and Antarctic to the balmy, crystal-clear seas of the tropics. Yet coral reefs, with their majestic walls and enormous limestone skeletons, are found largely in the swath of oceans around the equator. In this tropical bands, biology, chemistry, and climate meet the exacting balance required for the survival of reef-building corals. Reef-building corals thrive in this delicate equilibrium, creating one of the most productive and diverse ecosystems in the world. Southeast Asia is the heart of this incredible diversity, holding more than 77% of the almost 800 reef-building coral species.

India, despite its vast size, has only a few coral reefs off its mainland coast, mostly concentrated around the Gulf of Kutch to the northwest, and the Gulf of Mannar near Sri Lanka in the southeast. Reefs are highly developed in the more remote archipelagos of Lakshadweep and the Andaman and Nicobar islands. The distribution and status of any reefs outside these areas remains largely unknown.

The reefs and coral communities of the Gulf of Kutch are predominantly patchy structures built up on sandstone or other banks or around the small islands on the southern side of the gulf. They have adapted to extreme environmental conditions of high temperatures, fluctuating and high salinities, large tidal ranges and heavy sediment loads. As a result diversity is low, with 51 coral species (41 hard corals and 10 soft corals).

Corals are also reported from the Gaveshani Bank some 100 kilometers off the coast from Mangalore. The best developed mainland reef structures are located in the southeast, with fringing reefs occurring off Palk Bay, and on the coasts and islands of the Gulf of Mannar, including Adams Bridge, a string of reefs stretching across towards Sri Lanka. Diversity is high in this area, with 117 hard coral species recorded, as well as a number of ecosystems including seagrass and mangrove communities. A large proportion of the reefs in both the Gulf of Kutch and the Gulf of Mannar now fall within protected areas, but these suffer from both weak management and virtually no monitoring. There are concerns that the Gulf of Kutch Marine National Park will be rescinded to allow for industrial development.

The Lakshadweep Islands (Laccadives) are located about 300 kilometers west of the southernmost tip of India. They are true atolls and related reef structures, built up over a volcanic base, marking the northernmost and oldest trace of the Réunion hot spot which went on to form the entire Chagos-Laccadives Ridge. There are 12 coral atolls with about 36 islands (with a total land area of 32 square kilometers), about a third of which are inhabited, and also four major submerged reefs and five major submerged banks. Typically the atolls have shallow lagoons, averaging a depth of 3-5 meters, with islands mostly occurring on the eastern rims. The outer slopes of the atolls descend steeply and have prolific coral growth. The local population on these islands numbers some 51 000, and fishing is an important activity, although largely focussed on offshore (non-reef) stocks. There has been sand mining in some lagoons which is likely to have impacted areas of reef. Tourism is a small but growing activity here:

The Andaman and Nicobar group consist of some 500 islands. Many are the high peaks of a submerged mountain range, a continuation of the Arakan mountains of Myanmar. The islands fall into two clear districts: Andaman to the north and Nicobar to the south, separated by the 160 kilometer wide Ten Degree Channel. There are fringing reefs along the coastlines of many of these islands. Their location is far closer to Indonesia and the Southeast Asian center of biodiversity than to India, and species diversity is higher than at any other reefs in India, with some 219 coral species recorded and around 571 species of reef fish. Although only 38 islands are inhabited, the population has been rising rapidly, largely through immigration, especially in the Andaman District. Close to these areas there may now be some human impacts on the reef communities, while sedimentation is expected to increase as further areas are opened up to logging. At the present time, however, many of the reefs are still largely free from human impacts, and pollution generally remains low.

There are 4 major coral reef areas in India: Gulf of Mannar; Andaman and Nicobar Islands (1962km coastline); Lakshadweep Islands (132km coastline); and the Gulf of Kutch (Kachchh). There is also scattered coral growth on submerged banks along the east and west coasts of the mainland. Coral reefs are important economically for the livelihoods and social welfare of coastal communities providing up to 25% of the total fish catch.

Reefs in the **Gulf of Mannar** are found around a string of 21 islands, 8km off the southeast coast of India. The 3 island groups (Mandapam, Keelakari and Tuticorin) form the 'Pamban to Tuticorin barrier reef', which contains fringing, platform, patch and barrier reefs. Narrow fringing reefs surround the islands extending 100m from the shore. Patch reefs are also found and are typically 1-2km long, 50m wide and 2 to 9m deep. Reef flats are extensive on all islands. The total area includes approximately 65kmsup2; of reef flat and 14kmsup2; of algal growth. The major economic activities are fishing, coral mining for construction, harvesting of sacred chanks (*Turbinella pyrum*), sea cucumber, pipefishes, sea horses and seaweeds.

The **Lakshadweep Islands** are true atolls at the northern end of the Laccadive-Chagos ridge, 225-450km west of the Kerala coast. There are 12 coral atolls with 36 islands and 5 submerged banks. Islands vary in size from 0.1km^2 to 4.8km^2 (total area 32km^2) and are surrounded by 4,200km^2 of lagoon, raised reefs and banks. The population on the 10 inhabited islands ranges from 100 on Bitra Island to 10,000 on Kavaratti. Offshore fishing is the most important activity, and reef fisheries are not economically important. Tourism is slowly developing, but provides little income for the local community.

There are 42 islands with fringing reefs in the southern part of the **Gulf of Kutch** along with extensive mangroves in the Indus River Delta. Corals survive through extreme environmental conditions such as high temperature, salinity changes, high-suspended particulate loads and extreme tides, as high as 12m.

Source: Rajasuriya, A., K. Venkataraman, E.V. Muley, H. Zahir and B. Cattermoul , 2002, Status of Coral Reefs in South Asia: Bangladesh, India, Maldives, Sri Lanka.. In: C.R. Wilkinson (ed.), Status of coral reefs of the world:2002. GCRMN Report, Australian Institute of Marine Science, Townsville. Chapter 6, pp 101-121.

NEW INTERNATIONAL INITIATIVES TO CONSERVE CORAL REEFS

- Since the Status 2000 report, many major initiatives have started to have positive effects on coral reef conservation. Some of these are:
- The US Coral Reef Task Force and other government bodies have provided more funds and expertise to manage coral reefs across the globe, particularly in US dependent and associated territories.
- Governments and others partners in ICRI have established the priority needs of coral reefs as recognised priorities in the WSSD and in the work programs of the multilateral environmental agreements including the Conventions on Biological Diversity, Wetlands of International Significance (RAMSAR) and World Heritage.

- The International Coral Reef Action Network (ICRAN), with initial funding from the United Nations Foundation, has started strengthening reef management at key demonstration sites in four of the major coral reef areas of the world.
- WWF (World Wildlife Fund), TNC (The Nature Conservancy) and CI (Conservation International) launched a partnership of initiatives on coral reefs in the centre of coral reef biodiversity in Southeast Asia.
- Private Foundations, especially those in the USA and Australia (Great Barrier Reef Research Foundation) are increasingly targeting coral reefs in the Western Pacific, Southeast Asia and the USA as part of biodiversity conservation programs.
- Other foundation in the USA, Japan, France and Australia are taking a greater interest in coral reefs and assisting ICRAN and the more active NGOs (WWF, The Nature Conservancy, Conservation International, CORAL, World Resources Institute, Marine Aquarium Council, Reef Check) establish large MPAs or link existing MPAs in order to arrest coral reef degradation.
- At the WSSD, USAID and the UN Foundation announced a grant of US$3 million to the ICRAN partnership to tackle coral reef problems along the Caribbean coast of Mesoamerica.

CONSERVATION INITIATIVES IN INDIA

---- *compiled by GEER Foundation*

Realising the importance of coral reefs, the Government of India declared it as ecologically sensitive areas under the Environmental Protection Act in 1986 and further prohibiting its exploitation, development activities and disposal of wastes by Costal Regulation Zone (CRZ) Notification (1991). Ministry of Environment and Forests initiated a plan of scheme on conservation and management of coral reefs in the year 1986-87 and constituted a National Committee to advise the Government on relevant policies and programs. Taking into consideration the importance of coral reefs and the factors responsible for their deterioration, Andaman and Nicobar islands, Lakshadweep islands, Gulf of Mannar and Gulf of Kachchh have been identified for conservation and management. Efforts have been initiated to establish Indian Coral Reef Monitoring Network (ICRMN) to integrate various activities on coral reefs through national and international initiatives.

In India, the human population in coastal districts is over 175 million. The increasing pressure on the coastal zone due to concentration of population, development of industries and ports, discharge of waste effluents and municipal sewage and spurt in recreational activities, has adversely affected the coastal environment. Coastal Regulation Zone (CRZ) Act 1991 was enacted by the Government of India to protect Indian coast from degradation. The area influenced by tidal action up to 500m from High Tide Line (HTL) and the land between the Low Tide Line (LTL) and HTL has been declared as a Coastal Regulation Zone (CRZ). As per the classification of CRZ, coastal zone has been divided into the following four categories CRZ-I, II, III and IV as per the Act for regulating developmental activities and conserving coastal flora and fauna.

Category–I (CRZ-I) : Ecologically sensitive areas like mangroves, coral reefs, wildlife habitat between LTL & HTL.

Category–II (CRZ-II) : Developed areas close to shore mainly urban or built-up area.

Category–III (CRZ-III) : Coastal zone in rural areas, which do not belong to Category – I & II.

Category-IV (CRZ-IV) : Coastal stretches in Andaman and Nicobar, Lakshadweep & other small islands.

Out of these four zones, The CRZ – I zone includes ecologically sensitive areas like mangroves, coral reefs close to breeding grounds of fishes and other marine life, areas of outstanding natural beauty and Marine Protected Areas. This zone qualifies for strict protection. Under a public litigation in the Supreme Court of India, the court has directed all the coastal states to prepare and implement the CRZ plan. Most of the states have prepared their plans for implementation to protect coastal zones from degradation.

To provide protection to ecologically important areas, India initiated action through state governments to create network of MPAs under Wildlife (Protection) Act, 1972. Gradually their number increased to cover critical and important marine ecosystems. Now majority of the coral reefs and mangroves are part of the MPAs in the country.

Recognizing ecological values and their importance for biodiversity conservation, the Government of India has notified three Biosphere Reserved in marine areas under the programme of the Man and Biosphere Reserve. Great Nicobar Biosphere Reserve in Andaman and Nicobar, Gulf of Mannar Biosphere Reserve in Tamil Nadu and Sundarbans Biosphere Reserve in West Bengal were notified in 1989, which also covers some MPAs as core zone.

Department of Ocean Development has launched a program on Integrated Coastal and Marine Area Management (ICMAM) during 1999-2000 to facilitate integration of various land based and sea based activities so as to avoid conflicting use of Coastal and Marine areas with minimal damage to Coastal and Marine Environment. Establishment of National Coral Reef Research Centre at Port Blair in 2001 are other initiative to strengthen the conservation measures.

A. Indian Coral Reef Monitoring Network: The ICRMN is a project coordinated and funded by the Ministry of Environment & Forests, Government of India. The project was initiated early in 1999 with funding approved for a preliminary three year period. The objective of the ICRMN is to provide a framework for monitoring of coral reefs in the four main coral reef areas of India: Andaman & Nicobars, Lakshadweep, Gulf of Mannar and Gulf of Kachchh. As such ICRMN provides a National Level Program in India for participation in the GCRMN. Implication of the ICRMN is through the relevant Environment & Forests Departments in each area. There are four components to the ICRMN:

- Infrastructure development
- Training & Capacity building

- Establishment of database and networking
- Research activities

B. Global Coral Reef Monitoring Network: The GCRMN is a worldwide program jointly promoted by four international agencies: the Intergovernmental Oceanographic Commission of UNESCO (IOC); the United Nations Environment Program (UNEP); the World Conservation Union (IUCN) and the World Bank. The aim of the GCRMN is to provide co-ordination and technical support to coral reef countries throughout the world and to develop national-level coral reef monitoring programs. The purpose of such monitoring is to develop sustainable management of coral reef-resources and to improve livelihoods dependent on coral reef resources. The South Asia regional component of GCRMN (GCRMN South Asia) encompasses India, Sri Lanka & Republic of Maldives and is one of six operational regions worldwide. The others are the Western Indian Ocean, the Middle-east, East Asia, the Pacific and the Carribean.

Phase I of GCRMN South Asia program started from July 1997 to March 1999 and the objectives of this phase program were:

- Regional training in coral reefs survey methods & socio-economic monitoring.
- Implementation of a number of pilot monitoring exercises in the region.
- Production of coral reef monitoring action plans (CRMAPs) for each of the six main coral reef areas in South Asia.

The world agency for GCRMN South Asia in India during implementation of the above program was the Department of Ocean Development (DoD). The Ministry of Environment & Forests (MoEF) has also been closely associated with the implementation of project activities.

C. Coral Reef Degradation in Indian Ocean: CORDIO is a program created to respond to the degradation of coral reefs throughout the Indian Ocean, in particular the mass bleaching and mortality of corals that occurred during 1998. The CORDIO program was launched in the last months of 1998, as a response to the coral mortality throughout the Indian Ocean. The aim of the program is to provide information on the extent and speed of coral reef degradation in the Indian Ocean region. The program supports targeted studies and monitoring in several countries in the region. Ecological as well as socio-economic effects are studied. Investigations also focus on natural recovery processes on different reefs, and methods of mitigation of damage and artificial recovery of reefs. Finally, the program supports alternative livelihood among local human populations affected by the coral mortality. During its initial phase, the CORDIO program is supported by SIDA (Swedish International Development Co-operation Agency), FRN (The Swedish Council for Planning & Co-ordination of Research), MISTRA (Foundation for Strategic Environmental Research), WWF-Sweden, and the Word Bank through Dutch Trust Funds.

A mid-September 2001, United Nations Environment Programme ("UNEP") press release offers a new global estimate for the area currently covered by coral reefs world-wide: of just 284,300 sq km; this per the World Atlas of Coral Reefs, prepared by the United Nations Environment Programme-World Conservation Monitoring Centre ("UNEP-WCMC"). The following chart offers a general view in terms of reef geographical locations:

The Atlas identifies 80 countries and/or geographical regions where coral reefs may be found - the greatest concentration is to be found around Indonesia, closely followed by Australia. India is identified as hosting 5,790 km^2 (representing 2.04% of the overall total).

CORAL REEFS OF THE GULF OF KACHCHH

---- *compiled by GEER Foundation*

The coral formations in the Gulf of Kachchh are found between 22^0 20'N and 22^0 40'N latitudes and 69^0 to 70^0E longitudes along the coast of Jamnagar district - the only site in Gujarat State. The Gulf of Kachchh forms almost the northern limit of coral formations in the Indian Ocean, but for the northern portions of the Red Sea. The coral fauna of the Red Sea is found to have a total of 64 genera of which 56 genera occur in the Gulf of Aqaba (Scheer and Pillai, 1983). The Gulf of Kachchh laying further south is known to have only 24 genera, while the Maldives still south, is reported to have 75 genera of corals (Pillai and Scheer, 1976). This is an indication that the latitudinal difference is not the major factor that restricts the genetic diversity in the Gulf of Kachchh. Geographic isolation is also a factor. The Persian Gulf is mainly due to extreme environmental parameters. The Gulf of Kachchh is one of the most isolated areas as far as coral growth is concerned. The age of these corals as dated from the raised beaches, vary from 5240 years at Salaya to 45,000 ± 105 years before present at Okha (Gupta, 1972). He concluded that the 'inland coral reefs and raised beaches of the Saurashtra Coast are the remnants of a high sea level stands rather than an indication of the recent uplift of the coast'. The uplift of the fossil corals of this area may be due to local tectonic upheavals. Nevertheless, the present day coral growths are observed on wave cut banks covered with loose boulders, sometimes having well developed fringing reefs, though nothing comparable to a lagoon is present (Pillai and Patel, 1988).

Based on the existing classifications, these reefs are classified into fringing reefs (north of Okha, north of Bet Dwarka, fringing the mainland from Dhani to Sikka, Jindra and Chhad, Pirotan, near Valsura), Platform reefs (Paga reefs, Bural Chank reef, Kalubhar, Munde Ka reef, etc.), patch reefs (Goose and Ajad) and several coral pinnacles (Chandri reef) (Bahuguna and Nayak, 1998). The most northerly reefs or coral patches are found at Munde Ka reef and Pirotan island, but solitary corals are found as far as Jakhau in the east and Dwarka on the Saurashtra coast.

Satellite images indicated that the total reef area in the Gulf was 217 Km^2 in 1975, which decreased to 118 Km^2 in 1985 and 123 Km^2 in 1986 with a net loss of 94 Km^2 of coral cover equivalent to 43%. No mud depositions were observed in the 1975 satellite data (Nayak *et al.*, 1989). The satellite pictures show that the reefs that are interpreted as having died out between 1975 and

1985 in fact lie buried under mud, proving conclusively that the important, if not the only, cause for coral damage is the heavy silt load (NIO, 1992).

Satellite image also showed clearly that within the core area of the Marine National Park, coral reef, which covered 116 Km^2 in 1975 was reduced to 83 Km^2 in 1982 and 53 Km^2 in 1985. The remote sensing data supported by ground truth data collection revealed that between 1985 and 1991, a net improvement (from 53 to 85 Km^2), in coral cover within the core area of the Marine National Park has taken place (Bahuguna and Nayak, 1998).

The reefs are generally restricted to areas exposed to the strongest tidal currents and live corals generally confined to the northern and western sides of the islands. The diversity of coral species in the Gulf is the lowest of all Indian reefs. Pillai and Patel (1988) reported 37 species of stony corals belonging to 24 genera. However, Patel (1985) reported a total of 44 species of Scleractinian corals and 12 species of soft corals. The monograph on Biological Diversity of Gujarat (GEC, 1996) has listed 40 species and 23 genera of stony corals, 3 species of soft corals and 4 species of sea fans from the same area. Most of these corals are hermatypes (reef forming) while only a few are ahermatypes from the Gulf. As per a study by GEER Foundation, the species diversity comprise of 51 species (41 species of hard corals and 10 species of soft corals).

The whole stretch of coral reefs and mangroves in the Gulf of Kachchh from Okha to Jodiya, covering an area of 458 Km^2, has been declared a Marine Sanctuary and 163 Km^2 as Marine National Park - the first of its kind in India - in 1982. All activities of exploitation of corals, including personal collections, are expected to be totally prohibited.

As stated earlier coral reefs protect the coast, increase its stability and help create sheltered harbors. Because of the coral reefs (live and dead), the northern coast of Saurashtra is protected from erosion even though storms and high waves periodically visit the area, the most recent being in June 1998. This surely has helped the ongoing industrialisation and harbor construction along the Gulf of Kachchh coast of Saurashtra. On the other hand, there is practically no coral reef along the Kachchh peninsula resulting in regular coastal erosion there. This is perhaps the most important reason to merit the conservation and protection of the coral reef though it is comparatively small in length.

The coral reefs are also rich in biological resources, with associated flora and fauna such as food fishes. In the recent year's species other than food fishes, too have attained interest and importance. These include molluscs, macroalgae and ornamental fishes. The 'Shankh' industry at Dwarka, Bet Dwarka and other tourist places like Somnath is thriving on collection of the molluscs and corals from the Gulf of Kachchh region. A huge biomass of economically important marine algae is being harvested from Okha and nearby areas by the cottage industries every year. Many of the marine algae and some of the corals, particularly soft corals, contain a host of pharmacologically important chemicals.

CORAL REEF MONITORING STUDY BY GEER FOUNDATION IN THE GULF OF KACHCHH

The distribution of corals among the various study localities in MPA is shown in Fig.-1. This pie- diagram shows percentage of occurrence of corals at 72 study localities from MPA. Out of 72 localities studied during present study, 37 were locations from islands and 35 were in the coastal areas of mainland. The areas with corals constituted 19 islands with coral sites, 6 submerged reefs with corals and 5 coastal areas with corals. Altogether, the coral areas occupied 41% of total area in MPA. The area without corals (59%) constituted 12 islands and 30 coastal area of mainland in the MPA.

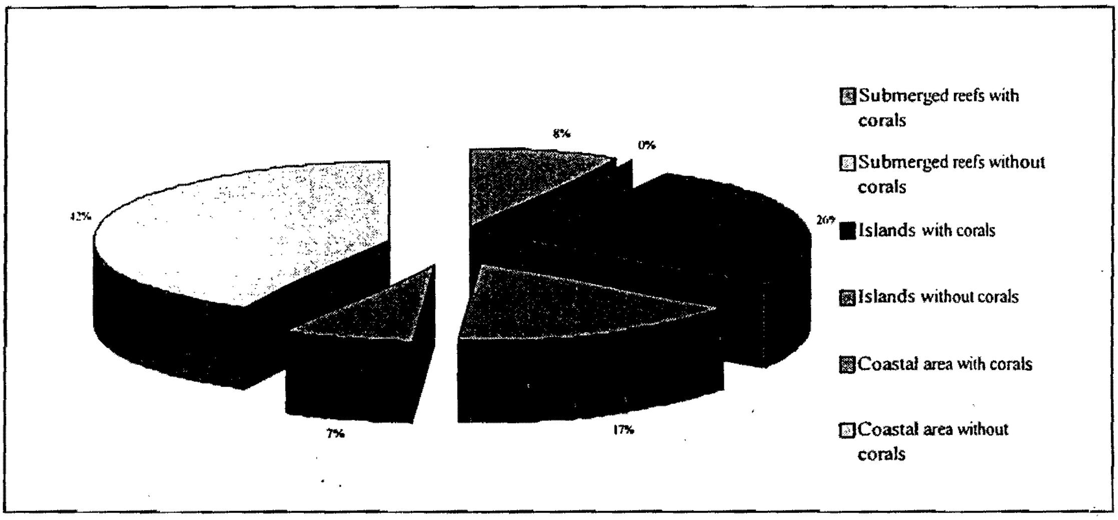


Fig.-1 The pie-chart showing the preference of corals among the study localities in MPA.

The coral species recorded in the recently completed bio-physical monitoring study by GEER Foundation are shown in Table below along with their common names, habitats and status. It shows that *Montipora, Porites, Goniopora, Favia, Favites, Turbinaria* etc. are the common genera of hard corals recorded among the study. Usually all the hard corals prefer reef rock as the substratum for attachment and clean water. Among the soft corals, *Lobophyton, Sinularia, Subergorgia* are the common forms. Soft corals usually observed on the reef slopes in subtidal region where the disturbances were minimum and the habitat was undisturbed. Soft corals usually need hard substratum for the support by attachment. Altogether, a total of 41 species of hard corals was recorded from 9 families and 24 genera. However, a total of 10 species of soft corals was recorded from 4 sub-orders and 9 genera during the study. The list of 41 hard coral species is given below.

Table-1 Hard Coral species recorded by GEER Foundation in Gulf of Kachchh, Gujarat

Sr. No.	Scientific Name
	Family: Acroporidae
1	*Acropora humilis*
2	*Montipora monastriata*
3	*Montipora foliosa*
4	*Montipora turgescens*
5	*Montipora explanata*
6	*Montipora hispida*
7	*Montipora venosa*
	Family: Siderastreidae
8	*Psammocora digitata*
9	*Siderastrea savignyana*
10	*Pseudosiderastrea tayami*
11	*Coscinarea monile*
	Family: Poritidae
12	*Goniopora planulata*
13	*Goniopora minor*
14	*Goniopora nigra*
15	*Porites lutea*
16	*Porites compressa*
17	*Porites solida*
18	*Porites lichen*
	Family: Faviidae
19	*Favia speciosa*
20	*Favia favus*

Sr. No.	Scientific Name
21	*Favia stelligera*
22	*Favites bestae*
23	*Favites complanata*
24	*Goniastrea pectinata*
25	*Platygyra sinensis*
26	*Platygyra lamellina*
27	*Platygyra daedalea*
28	*Plesiastrea versipora*
29	*Leptastrea purpurea*
30	*Cyphastrea seraillia*
	Family: Caryophyllidae
31	*Paracyathus stockesi*
32	*Polycyathus verrilli*
	Family: Merulinidae
33	*Hydnophora exesa*
	Family: Mussidae
34	*Acanthastrea hillae*
35	*symphyllia radians*
36	*Symphyllia recta*
	Family: Pectiniidae
37	*Mycedium elephantotus*
	Family:Dendrophyllidae
38	*Dendrophyllia minuscula*
39	*Tuibastrea aurea*
40	*Turbinaria peltata*
41	*Turbinaria crates*

Out of 9 families, Acroporidae, Poritidae, Faviidae and Dendrophyllidae are commonly found during the study. However, the families Thamnasteriidae, Siderastreidae, Mussidae and Pectiniidae were recorded very sparsely.

Glossary

Volume numbers are in bold.
Terms are explained here as they are used in this book, not necessarily other publications.

acanthocauli: juvenile corals (mostly *Fungia*) attached to the substrate either directly or on stalks.

acolonial corals: solitary corals that do not form colonies.

allopatric speciation: the splitting of a widespread population into two or more isolates by a geological or ecological isolating barrier and subsequent differentiation into new species, or the dispersal of a few propagules across a pre-existing barrier and subsequent differentiation into new species.

ambulacral grooves: grooves along the top of common walls between adjacent corallites, see **1**:52-3.

ampullae: the swollen part of a canal in skeletal Hydrozoa that hold medusae produced by internal fertilisation.

anastomose: descriptive term for branches which re-fuse after having initially divided.

appressed corallites: corallites which are fused (partly or completely) with the coenosteum on one side so that their axis is approximately parallel with the coenosteum, see **1**:179.

aragonite skeletons: skeletons primarily composed of the aragonite form of calcium carbonate. All Scleractinia have aragonitic skeletons (cf. calcite skeletons).

arborescent colonies: colonies with a tree-like growth form, see **1**:56,179.

archaeocyaths: sponge-like metazoans that had skeletons. They were mostly restricted to the Cambrian Era, see **1**:33.

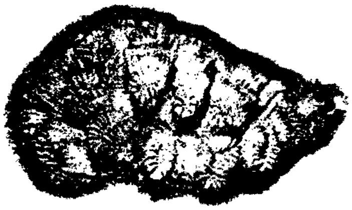
attachment scars: a scar-like patch on the central undersurface of free-living fungiids from where they were attached to the substrate as juveniles.

atolls: reefs and islands that are the remnants of submerged land masses, see **1**:23-6.

autotomy: a means of asexual reproduction by the break up of a parent polyp. Seen commonly in *Diaseris*, see **2**:248.

axial corallite: a corallite which forms the tip of a branch. Most *Acropora* have axial corallites whereas they only occur sporadically in other corals, see **1**:179.

axial furrow: a groove along the axis of the upper surface of some fungiids.


Eusmilia fastigiata

azooxanthellate corals: corals that do not have zooxanthellae. These are commonly found on reefs, but most are restricted to deep water, below the level of light penetration.

barrier reefs: reefs along continental shelf breaks or otherwise well separated from landmasses, see **1**:23-7.

basal plate: the first skeletal element deposited by a planula larva.

bifacial: describes plates which have corallites on both sides.

bifurcate: divide into two equal branches.

biodiversity: a term that has acquired many meanings, but can be considered synonymous with 'systematic diversity'. Biodiversity thus has the same relationship to taxonomic diversity as systematics has to taxonomy. Patterns of taxonomic diversity are indicative of patterns of biodiversity.

biogeography: the study of the distribution of life and the reason for that distribution. In practice, biogeography is divisible into observations of distributions and explanations for those observations.

bioherms: reefs or large reef-like structures built of calcium carbonate of biological origin, see **1**:27.

biological species concept: the concept that biological species, unlike other taxa, are units within which genes are (or can be) freely exchanged, but within which gene flow does not occur, at least under normal circumstances.

bleaching: expulsion of zooxanthellae by corals. Usually occurs as a result of environmental stress and frequently results in the death of the coral.

bottlebrush branching: a descriptive term for a branch with compact radial sub-branches, usually used for some *Acropora* species, see **1**:178.

branching colonies: any growth-form where branches are formed.

brooding: development of larvae within the coelenteron of an adult coral.

Opposite: Columns of *Coscinaraea exesa*. GREAT BARRIER REEF, AUSTRALIA *Photograph: Mary Stafford-Smith*

budding: a form of asexual reproduction where a 'parent' corallite forms one or more 'daughter' corallites, see 1:54.

caespitose: a descriptive term for branches which interlock similarly in three dimensions, usually used for some *Acropora* species, see 1:178.

calcite skeletons: skeletons composed of the calcite form of calcium carbonate. All Rugose corals and molluscs have calcitic skeletons (cf. aragonitic skeletons).

calice: the upper surface of a corallite bounded by the wall.

Cambrian: a geological Period of the Palaeozoic Era, see 1:34.

Cenozoic: a geological Era, see 1:35.

Central American Seaway: a former seaway between north and south America, now closed by the Isthmus of Panama.

central arch: a raised area surrounding the mouth of some solitary fungiids.

cerioid corals: massive corals that have corallites sharing common walls, see 1;54-5.

chimeras: single larvae, polyps or colonies which have developed from more than one original embryo and which have more than one genotype.

chromosomes: thread-like structures in cell nuclei carrying genetic information in a linear sequence.

cilia: microscopic hair-like structures growing on the ectodermis of polyps or planulae and which aid mucous movement or locomotion (respectively).

clade: a phylogeny inferred to be monophyletic; groups of taxa sharing a closer common ancestry with one another than with members of any other clade.

coelenteron: the body cavity of a coelenterate, see 1:47,52.

coenosteum: thin horizontal plates between corallites, see 1:48-51.

coenosteum pit: the point of insertion, or commencement, of septa, mostly found in Pectiniidae and Fungiidae.

coenosteum style: prominent projections from the coenosteum usually associated with a single corallite, see *Stylocoeniella*, 2:4.

collines: skeletal ridges composed of coenosteum which separate corallites.

colonial corals: corals composed of many individuals. There may be no clear distinction between single individuals with many mouths and colonies with individuals with single mouths, see 1:54.

columellae: skeletal structures at the axis of corallites. May be 'spine-like', 'spire-like', a 'tangle' of rods, or 'spongy' (structured like a sponge although not soft), see 1:48,50.

columnar colonies: colonies forming into one or more columns, see 1:56,178.

commensal: a partner in a mutually beneficial relationship between two different types of organisms.

compact branching: where branches of a colony are close together.

continua: where there is no clear discontinuity in morphology, genotype or distribution.

coral: unless the context indicates otherwise (eg. rugose coral, soft coral) the word 'coral' is used in this book to mean 'hard' or 'stony' coral.

coralline algae: algae that form solid calcium carbonate accretions.

corallite: the skeleton of an individual polyp, see 1:48-51.

corymbose: a descriptive term for colonies which have horizontal interlocking branches and have short upright branchlets, usually used for some *Acropora* species, see 1:178.

cosmopolitan: with a worldwide distribution within habitat limits.

costae: radial skeletal elements outside the corallite wall, see 1:48-50.

Cretaceous: a geological Period of the Mesozoic Era, see 1:35.

Crown-of-thorns starfish (*Acanthaster planci*): large starfish which eat coral. Typically they occur in plague-like outbreaks which cause widespread destruction.

cycles of septa/septo-costae: where radial elements occur in a set sequence of size (6 primary, 6 secondary, 12 tertiary and so on), see 1:49-50.

cyclosystem: a system of fine tubes that links the polyps of calcareous hydrozoans.

dactylopores: the external opening in the skeleton through which dactylozooids extend nematocyst spines.

dactylozooids: polyps of Hydrozoa specialised for food capture, which have no mouth but have elongate nematocyst spines.

deltas of septa: fusion of septa into a hexamerous pattern of spongy columella. Common in *Goniopora*.

dendrogram: a tree-like hierarchical classification with a single root and branching representing levels of dissimilarities of objects. In this book, the objects are localities and the dendrograms are measures of dissimilarities in coral species compositions.

depauperate: having a relatively small number of species.

Devonian: a geological Period of the Palaeozoic Era, see 1:34.

digitate: a colony with short branches shaped like the upturned fingers of a hand.

dispersal: the process of movement of propagules resulting in dispersion.

dissepiments: blistery horizontal plates of calcium carbonate adjoining corallites, see 1:51.

distal: remote from the centre, eg. the end of a branch.

diversity: the number of taxa in a group or place, see biodiversity.

ectodermis: the outer cell layer of a polyp, see 1:48,52.

encrusting colonies: thin colonies which adhere closely, and are attached to, the substrate.

endemic: a species restricted to a specific region.

endemism: reflecting the proportion of species restricted to a specific region, see 3:412-3.

endo-symbiotic: symbiosis where individuals of one organism (zooxanthellae in the case of extant corals) live within the cells of another.

entire: without substantial irregularities.

environmental variation: the variety of environmental parameters associated with a particular place.

Eocene: a geological Epoch of the Cenozoic Era, see 1:35.

epitheca: a tissue-like layer of calcium carbonate that grows outside corallite walls. Originally derived from the basal plate, see 1:48-9.

explanate corals: colonies which spread horizontally as branches fuse into a solid or near solid plate.

extant: now living.

extinct: no longer living.

extratentacular budding: where daughter corallites grow from the outside wall of parent corallites, see 1:54.

family: the taxon level representing a group of related genera.

flabello-meandroid corals: corals which have valleys with walls that are separate from the walls of adjacent valleys, see 1:54-5.

flaring corallites: with expanding (trumpet-like) curves to the outer corallite wall.

fossa: a cavity or hole in the skeleton.

Foraminifera: Protozoa of the Order Foraminiferida which are abundant in the plankton and benthos of all oceans.

foveolate corallites: corallites of some species of *Montipora* which are situated at the base of funnel-shaped depressions, see 1:65.

free-living coral: corals that are not attached to the substrate.

fringing reefs: reefs which occur adjacent to a shoreline, see 1:24-5.

fuzzy boundaries: geographic, morphological taxonomic or systematic boundaries that are not clearly defined.

gametes: sex (egg and sperm) cells.

gastrodermis: the inner cell layer which lines the coelenteron, see 1:48,52-3.

gastropores: the external opening in the skeleton of Hydrozoans through which gastrozooids are extended during feeding.

gastrozooids: polyps specialised for feeding in Hydrozoa and other Cnidaria.

genotype: the set of genes possessed by an individual organism.

genus/genera: the taxon level representing a group of related species.

geographic variation: geographic variation in morphology which has a genetic basis.

glabrous: devoid of attached structures.

gonads: testes and ovaries. These are usually developed annually, see 1:48.

granulated: covered with sand-like particles.

groove-and-tubercle structures: fine epithecal structures, the development of which is controlled by polychaete worms, see 1:51.

hermaphrodite: individuals that are both male and female.

hermatypic: literally 'reef building' but commonly used as a descriptor for marine invertebrates that have photosynthetic plants living symbiotically within their tissues. Because the word is a misnomer, several terms including 'reef-building', 'symbiotic' and 'zooxanthellate', are used synonymously. Of these, the first two are ambiguous and the last is, at least theoretically, restricted to extant taxa.

hermatypic corals: zooxanthellate or reef-building corals: the corals included in this book.

holotype: the principal specimen on which a species name is based.

hybrid: an individual with parents of different species.

hybridisation: formation of a hybrid.

hydnophore: an alternative name for monticule, sometimes used with *Hydnophora*.

incipient axial corallites: corallites intermediate in development between radial and axial corallites of *Acropora*.

immersed corallites: corallites which are embedded in the surrounding coenosteum.

intratentacular budding: where daughter corallites grow from the inside wall of parent corallites, usually by division of the parent corallite, see 1:54.

Jurassic: a geological Period of the Mesozoic Era, see 1:35.

lateral pairs of septa: two pairs of septa on each side of *Porites* corallites, see 3:277-8.

latitudinal attenuation: the progressive decrease in diversity along continental coastlines with increasing distance from the equator, see 3:414.

macroalgae: algae that are of conspicuous size.

mass extinction: an extinction that is characterised by loss of many taxa in a geologically brief time period.

mass spawning: spawning events where many taxa spawn simultaneously, see 3:417-9.

massive colonies: colonies which are solid and which are typically hemispherical or otherwise have approximately similar dimensions in all directions, see 1:56.

meandroid colonies: massive colonies that have corallite mouths aligned in valleys such that there are no individual polyps, see 1:54-5.

medusae: free-living sexual reproductive stage of Hydrozoa and jellyfish. Morphologically, these are bell-shaped: the upsidedown equivalent of polyps.

mesoglea: an initially non-cellular layer between the ectodermis and gastrodermis, see 1:48,52.

Mesozoic: a geological Era, see 1:35.

metamorphosis: the transformation of a planula larva into a polyp.

micro-atoll: A colony shaped like an atoll because low tide level permits only lateral growth, illustrated 3:287.

microhabitat: a vague word indicating a particular type of habitat occupied by a coral colony.

migration: large-scale movement of a population. Synonymous with dispersal except implying an activity specific in time or space.

Milankovitch cycles: cycles of variation the earth's orbital motion including oscillation of the earth's axis and eccentricities of the earth's orbit around the sun.

Miocene: a geological Epoch of the Cenozoic Era, see 1:35.

monospecific: describes a genus with one species only, or a coral community with one species only.

monticules: conical sections of common wall between corallites which have a secondary radial symmetry, see 1:51-2.

mucous: gelatinous substance secreted by the ectodermis for protection, to aid the capture of food, or to remove sediment. Mucous is usually moved by cilia.

nariform: a radial corallite, usually of *Acropora*, shaped like an upsidedown 'roman' nose, see 1:178.

nematocysts: microscopic stinging cells occurring individually in the ectodermis or grouped into wart-like clumps on tentacles, see 1:48,52-3.

neo-Darwinian synthesis: a synthesis of Darwin's concept of species and Mendelian genetics. This encapsulates the notion that evolutionary change occurs within species as a result of natural selection acting on variation within populations, variations that ultimately arise from random mutations.

neoplasm: cancerous growths commonly found on corals, see 3:421.

nomenclature, rules of: an international code for the naming of taxa, see 1:11-2.

nominal species: species that exist in name only.

obligate association: an association between two very different types of organisms where one member of the partnership cannot live without the other.

Oligocene: a geological Epoch of the Cenozoic Era, see 1:35.

Ordovician: a geological Period of the Palaeozoic Era, see 1:34.

oral cone: a mound of soft tissue surrounding the mouth, see 1:48,52.

oral disc: the soft tissue between the mouth and the surrounding tentacles, see 1:48,52.

orders of septa/septo-costae: where radial elements occur in different sizes, but not as cycles, see 1:49-50.

palaeobiogeographic patterns: biogeographic patterns as seen in the fossil record.

Palaeocene: a geological Epoch of the Tertiary Period, see **1**:35.

Palaeozoic: a geological Era, see **1**:34.

pali: upright skeletal rods or plates at the inner margin of septa formed by pourtàles plan fusions, see **1**:50.

paliform crown: a circle of paliform lobes surrounding the columella, see **1**:50.

paliform lobes: upright skeletal rods or plates at the inner margin of septa formed by upward growth of the septum, see **1**:48,50.

papillae: projections of coenosteum on the surface of many species of *Montipora* that are less than a corallite in width, see **1**:64.

paradigm: a well defined perspective on a major area of thought or knowledge.

Permian: a geological Period of the Palaeozoic Era, see **1**:34.

petaloid septa: primary septa which have a tapered or curved (tear-drop) shape because they are enclosed by other septa, illustrated **2**:132.

phaceloid corals: corals that have corallites of uniform height and adjoined towards their base, see **1**:54-5.

phylum: the taxon level representing a group of related families.

pinnule: small upright structures, usually columellae, which are cylindrical in shape.

planula larvae/planulae: larvae of coral.

plate tectonics: the drifting of continents over geological time creating major changes in the shape of land masses and oceans.

platform reefs: general term for reefs which are not clearly derived from sea level change or the proximity of land, see **1**:24,27.

Pleistocene: a geological Epoch of the Cenozoic Era, see **1**:35.

Pliocene: a geological Epoch of the Cenozoic Era, see **1**:35.

plocoid colonies: colonies which have conical corallites with their own walls, see **1**:54-5.

polymorphic species: species which have a wide range of morphological variation.

polyp: an individual coral including soft tissues and skeleton, see **1**:48-53.

polyploidy; possessing more than two entire chromosome complements.

pourtàles plan: a cyclical arrangement of septa created by a specific pattern of fusion, see **1**:49-50.

propagule: a sexually or asexually produced reproductive body capable of developing into an adult organism.

prostrate: a descriptive term for a colony which sprawls horizontally over the substrate.

Proterozoic: a geological Era before the Palaeozoic Era.

Protoatlantic Ocean: the precurser of the modern Atlantic Ocean, see **1**:37.

proximal: close to the centre, eg. the base of a branch.

radial corallite: corallites on the sides of branches as opposed to axial corallites on the tips of branches. The term is usually used with *Acropora* and *Anacropora*, see **1**:178.

radii: inconspicuous septal elements connecting septa with the columella. Used in the taxonomy of *Porites*, see **3**:278.

rafting: the transport of biota on floating objects. This is a means of dispersal of some corals.

rasp-like corallites: regularly arranged corallites with sharp edges reminiscent of a wood rasp.

reef-building corals: zooxanthellate or hermatypic corals: the corals included in this book.

reef flat: the flat intertidal parts of reefs that are exposed to wave action.

reef slope: the sloping parts of reefs below the reef flat.

reefs: limestone platforms of shallow tropical seas built by corals, coralline algae and other photosynthetic organisms or symbionts.

reticulate evolution: evolution dominated by sequential division and fusion of clades, see **3**:438-43.

reticulate repackaging: the sequential division and fusion of phylogenies so that the genetic complement of species varies over evolutionary time, see **3**:438-41.

reticulation: interbreeding that creates reticulate patterns within and among species over large geographic areas or in evolutionary time..

rudists: a large group of Mesozoic bivalves that dominated reefs throughout much of the Cretaceous and which became extinct at the close of the Cretaceous.

rugose corals: a major group of non-scleractinian corals that became extinct at the close of the Palaeozoic Era.

satellite colonies: colonies that develop within the tissue of parent colonies and which have their own unattached skeletons. Best seen in *Goniopora stokesi*, see **3**:352.

scale-like corallites: corallites forming a pattern reminiscent of the pattern of fish scales.

scleractinian corals: 'hard' corals which have limestone skeletons and which belong to the order Scleractinia.

sea level change: change in sea level relative to the land, due to global change in ocean height primarily due to the extent of polar glaciation and/or upward or downward movement of land masses.

septa: radial skeletal elements projecting inwards from the corallite wall, see **1**:48-50.

septo-costae: radial skeletal elements crossing the corallite wall, composed of both septa and costae, see **1**:48-9.

septal teeth: sharp tooth-like or lobed structures along the margins of septa.

sibling species: similar species that are assumed to be the product of relatively recent speciation.

Silurian: a geological Period of the Palaeozoic Era, see **1**:34.

similarity, measures of: quantitative measure of the similarity between different faunal regions, see **3**:413.

solitary corals: corals composed of single individuals. There may be no clear distinction between single individuals with many mouths and colonies with individuals which have single mouths, see **1**:54.

spat: pinhead-sized single corallites that form immediately after metamorphosis of planula larvae.

spawning: the release of gametes into the water column.

species: a general term with a wide range of meanings. In this book (and most others), species are morphological units recognised by taxonomists. Within a single region they are morphologically distinguishable from other species and genetically semi-isolated from other species. Over their full geographic range, most vary morphologically and genetically to the extent that they intergrade with other species, see Index.

spinule: a spine of near microscopic size.

staghorn: common name for arborescent *Acropora*.

sterome: skeletal infilling derived from the thickening of septa to provide most of the content of corallite walls in some coral families, see **1**:48-9,51.

striae: a string-like arrangement of skeletal elements or soft tissue.

stolons: horizontal polyp outgrowths from which daughter polyps are budded. Common in *Astrangia.*

stromatolites: mounds of limestone formed by the growth of blue-green algae. Common in the Proterozoic Era and still extant.

stromatoporoids: sponge-like organisms that were major builders of Palaeozoic reefs.

sub-: a prefix meaning 'less than' or 'not quite'.

symbiosis: the close association between two organisms where there is substantial mutual benefit.

sympatric speciation: the formation of a new species in the same geographic region as the parent species.

synapticulae: rods linking septa, either forming a network or, in some coral families, contributing to the content of corallite walls, see 1:48-9.

syngameon: a complex of species that can interbreed. Such a complex may have no well defined morphological characteristics, see Index.

synonymy: a list of names considered by a taxonomist to apply to a given taxon other than the name by which the taxon should be known.

systematics: study of the genetic relationship between taxa.

tabulate corals: a major group of non-scleractinian corals that became extinct at the close of the Palaeozoic Era.

taxon: a taxonomic unit.

taxonomy: study of the morphological relationship between taxa and the naming of taxa.

tentacles: tubular extensions of the polyp. The interior of the tentacles is continuous with the coelenteron, see 1:48,52.

tentacular lobe: a lobe at the beginning (point of insertion) of a septum. Commonly found in *Fungia* where each lobe supports a single tentacle.

tethyan: originating in the Tethys Sea.

Tethys Sea: the ancient tropical sea that once connected the Indian and Atlantic Oceans, see 1:37,40-2.

thicket: a descriptive term for colonies composed of closely compacted upright branches.

Triassic: a geological Period of the Mesozoic Era, see 1:35.

trident: pattern of fusion of the ventral septa of some *Porites* where the septa are linked by a cross-bar.

triplet, of septa: the three ventral septa of *Porites* corallites, see 3:278.

tuberculae: projections of coenosteum on the surface of many species of *Montipora* that are more than a corallite in width, see 1:64.

type locality: the place where a species was originally described from.

type species: the species that a genus is primarily based on.

type specimens: the specimens that a species was originally described from. A single or principle specimen is the holotype.

unifacial: describes plates which have corallites on one side only.

verrucae: mounds of coenosteum on the surface of many species of *Montipora* and *Pocillopora* that are wider than a corallite, see 1:64 and 2:24.

vesicles: large grape-like sacs that are expanded during the day in some Euphylliidae.

vicariance: the process that occurs when a formerly continuous population is divided by a barrier and evolves into two or more species. Also the reverse of this process.

zooxanthellae: photosynthetic algae (dinoflagellates) that can occur symbiotically in animal tissue.

zooxanthellate corals: corals that have zooxanthellae.

MANGROVE ECOSYSTEMS

Peter J. Hogarth
University of York

GLOSSARY

aerenchyma A spongy plant tissue composed largely of air spaces enabling gas exchange to take place by diffusion in underground mangrove roots.

aerial roots In mangrove species such as *Rhizophora*, roots branch out from the stem some distance above the soil surface. Lenticels (pores) in the aerial portion of these roots enable gas exchange to take place, through aerenchyma tissue, with the respiring underground portions of the root.

mangal A term sometimes used to specify the mangrove habitat as a whole as opposed to "mangrove" applying specifically to the trees themselves. For the most part, however, mangrove is considered to apply to both trees and habitat.

pneumatophores In some species of mangrove, such as *Avicennia* and *Sonneratia*, underground roots spread laterally from the main stem. Pneumatophores grow vertically from these, typically standing 10–20 cm above the soil surface, enabling gas exchange to take place with the underground roots.

pseudofecal pellet Fiddler crabs and their relatives collect soil with their mouthparts, separate organic particles from mineral components by a complex flotation process, ingest the former, and discard the latter in the form of compact pellets. These are known as pseudofecal because, although extraction has taken place, the waste material has not passed through the gut.

MANGROVES ARE a group of trees and shrubs, mostly evergreen, which have convergently evolved physiological and morphological adaptations to shallow intertidal environments. These are mostly composed of soft sediment, in which other vascular plants are rare. Mangroves are almost exclusively tropical in distribution and often dominate large areas of coastline or estuary.

I. MANGROVE TREES

Currently, the total mangrove area in the world is estimated at 170,000 km^2. They are the principal source of primary productivity in such areas. By their presence, they also provide shelter for other organisms. Mangroves are therefore the energy base, and physical substrate, of an often complex and diverse ecosystem. Mangrove faunas, to a unique extent, comprise organisms of both marine and terrestrial origin.

Encyclopedia of Biodiversity, Volume 3

A. The Mangrove Habitat

The mangrove environment is a demanding one. Typically, mangroves are regularly inundated by tides and are therefore usually in a permanently waterlogged state. The tidal water is saline, so mangrove trees have the problem of coping with salt and acquiring sufficient water against an osmotic gradient. In hot climates, evaporation may make the salinity even greater than that of seawater. In the Indus Delta (Pakistan), for example, the prevailing salinity may be as much as twice that of seawater. Among the vascular plants, only mangroves flourish in such an inhospitable environment (Fig. 1).

Mangroves are defined physiologically as trees that can survive in the mangrove habitat, or mangal. The term is not a taxonomic one, nor does it indicate phylogenetic divergence from a common mangrove ancestor. The approximately 50 species generally recognized as mangroves belong to 20 genera in 16 families, although 2 families, Avicenniaceae and Rhizophoraceae, dominate in number of species (as they do also in abundance) (Table I). In most cases these genera and families also contain nonmangrove members. Mangrove species have evolved their specialist features as the result of convergent evolution, and mangrove attributes have probably evolved independently at least 15 times.

In addition to true mangrove species, there is also a loosely defined category of mangrove associates. These are species often occurring in mangrove habitats but which also occur elsewhere. Some are found only at the landward margins of the mangal, whereas others, such as creepers and lianes, have their roots above the intertidal zone but invade the mangal by using the mangrove trees purely for support. Other plants associated with mangrove trees are epiphytes, which include ferns and the "ant-house" plants (see Section II.A), and parasitic mangrove mistletoes.

B. Adaptations to the Mangrove Environment

1. Salinity

Three principal mechanisms enable mangrove trees to survive saline environments. Some species exclude salt at the root surface while continuing to take in water. In *Aegiceras* and *Avicennia*, up to 97% of the salt is excluded, apparently by a physical rather than a metabolic mechanism. This has the effect of locally increasing the salinity of the soil around the roots, with implications for other organisms: mangrove trees modify their environment as well as respond to it. In other instances, trees take in salt but sequester it within cells in such a way that sensitive metabolic processes are protected from contact with excessive salt concentrations. Finally, several mangrove species secrete excess salt, at considerable metabolic cost, from specialized salt glands on their leaves. Many mangrove species use a combination of these mechanisms, as shown in Table II.

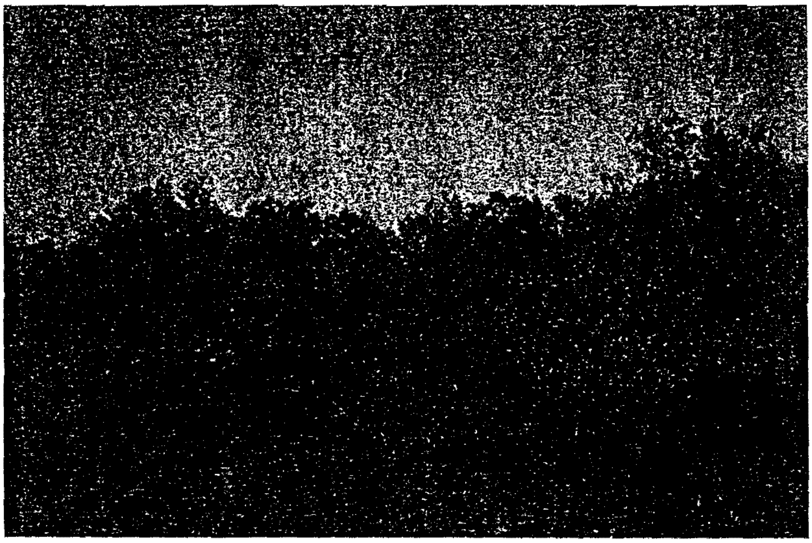


FIGURE 1 Mangroves (*Avicennia* and *Rhizophora*) fringing a tidal creek in the Indus Delta, Pakistan.

TABLE I

Distribution of Mangrove Species by Family and Genus[a]

Family	Genus	Number of mangrove species
Avicenniaceae	*Avicennia*	8
Combretaceae	*Laguncularia*	1
	Lumnitzera	2
Palmae	*Nypa*	1
Rhizophoraceae	*Bruguiera*	6
	Ceriops	2
	Kandelia	1
	Rhizophora	5
Sonneratiaceae	*Sonneratia*	5
Bombacaceae	*Camptostemon*	2
Euphorbiaceae	*Excoecaria*	1
Lythraceae	*Pemphis*	1
Meliaceae	*Xylocarpus*	2
Myrsinaceae	*Aegiceras*	2
Myrtaceae	*Osbornia*	1
Pellicieraceae	*Pelliciera*	1
Plumbaginaceae	*Aegialitis*	2
Pteridaceae	*Acrostichum*	3
Rubiaceae	*Scyphiphora*	1
Sterculaceae	*Heritiera*	3
Total		
16	20	54

[a] This follows the classification of Tomlinson (1986); there are althernative views on the status of certain species as true mangroves or mangrove associate species.

TABLE II

Methods of Salt Tolerance Employed by Mangrove Species

Species	Exclude	Secrete	Accumulate
Acanthus		+	
Aegialitis	+	+	
Aegiceras	+	+	
Avicennia	+	+	+
Bruguiera	+		
Ceriops	+		
Excoecaria	+		
Laguncularia		+	
Osbornia	+		+
Rhizophora	+		+
Sonneratia	+	+	+
Xylocarpus			+

2. Waterlogging

The major problem of waterlogged soils is lack of oxygen. Underground roots, like all tissues, require oxygen for respiration. In a normal soil, gas exchange takes place readily through air-filled spaces between soil particles. In water, the rate of diffusion of oxygen is very low, and in consequence waterlogged soils are generally virtually lacking in free oxygen. One of the most widespread mangrove trees, *Rhizophora*, adapts to such anoxic soils by keeping much of the root mass above the mud surface, surrounded by air. The stretches of these aerial roots (Fig. 2) close to the soil carry numerous gas-exchange pores, or lenticels, whereas the underground portions are honeycombed with air-filled spaces.

This air-filled tissue, or aerenchyma, is also a feature of *Avicennia* and *Sonneratia*, whose roots are horizontal and close to the surface. These species respire by growing numerous pencil-like pneumatophores which protrude above the mud surface and allow gas exchange with the underground tissues (Fig. 3). Pneumatophore growth is facultative: The less waterlogged the soil, the lower the pneumatophore density. In the extreme and atypical case of *Avicennia* growing in sand between the Egyptian Sinai desert and the sea, the soil is so well oxygenated that no pneumatophores develop.

The aerial roots of *Rhizophora* and the intertwined underground horizontal roots of *Avicennia* physically support the trees in what is often a relatively unstable and shifting soil. Aerial roots and pneumatophores provide attachment sites for epibionts and facilitate the accretion of sediment by impeding water movement.

3. Reproduction

Many mangrove species show some form of vivipary. *Rhizophora* is an example. The ovum is fertilized while still on the parent tree and grows by a combination of photosynthesis and acquisition of nutrients from the parent until it may reach a length of 50 cm (Fig. 4). This structure—neither a seed nor a fruit, and hence usually termed a propagule—then falls to the ground. The propagules of some species root almost immediately, but others appear to have an obligatory floating period before they sink and establish themselves. The majority of floating propagules probably settle close to the parent, but long-distance dispersal is also possible. Floating mangrove propagules may remain viable for a month or longer: Depending on current speed and

FIGURE 2 Aerial roots of *Rhizophora* in a Malaysian mangrove forest. See also color insert, Volume 1.

direction, they could travel a considerable distance. It is not uncommon for mangrove seedlings from Mexico, for instance, to be stranded and take root in Texas virtually across the length of the Gulf of Mexico. An even greater dispersal may explain the mangrove species *Rhizophora samoensis*, which is found only in Samoa and adjacent islands, at the opposite extremity of the Pacific from its presumed ancestor, the species *R. mangle* of Central America. The significance of dispersal ability for the geographical distribution of mangrove species is discussed in Section V.B.

II. MANGROVE ANIMALS: FAUNA OF TERRESTRIAL ORIGIN

Although mangrove roots are periodically immersed, the branches and leaves provide an environment little

FIGURE 3 Mangrove pneumatophores in Negombo Lagoon, Sri Lanka.

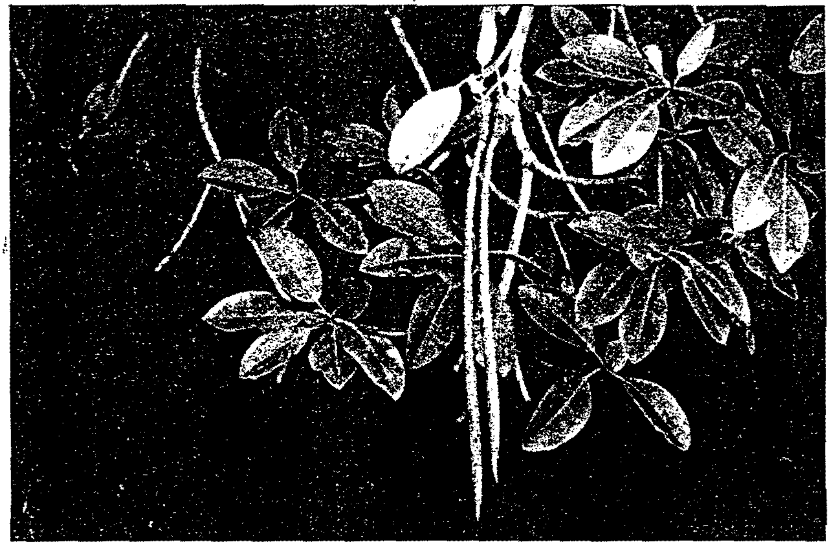


FIGURE 4 Mangrove propagules on a *Rhizophora* tree, Indus Delta, Pakistan. See also color insert, Volume 1.

different from that in adjacent terrestrial forests, with which they consequently share much of their fauna. Mangrove animals of terrestrial, rather than marine, origin include arthropods (particularly insects, but also spiders and myriapods), amphibians, reptiles, birds, and mammals. Virtually none are found exclusively in mangroves.

A. Insects

Anyone who has worked in mangroves can testify to the abundance of biting insects, particularly mosquitoes and "sand flies" or biting midges (Ceratopogonidae). Mosquito larvae develop in rot holes in mangrove trees, in semipermanent brackish pools, or in the water retained in crab burrows. In the latter case, one East African species, *Aëdes pembaensis*, ensures a suitable burrow environment for its larvae by laying its eggs directly onto the claws of the crab *Sesarma meinerti*. Prey of adult mosquitoes includes, apart from humans, a variety of mangrove mammals and birds, and in some cases it extends to fish.

Ants are often abundant in mangroves, including the aggressive nest-building weaver ants (*Oecophylla*) of the Indo-Pacific and leaf-cutter ants (*Atta*) of South America. Particularly complex relationships have evolved between ants, epiphytic "ant-house" plants, and mangrove trees (Fig. 5). Ant-house plants have bulbous stems (which may weigh several kilograms) honeycombed with passages inhabited by ants. One such plant, *Hydnophytum formicarium*, has specialized chambers in which ants deposit the remains of their prey, and from which the plant can absorb nutrients released by fungal action. The situation is further complicated by the presence of butterfly larvae (*Hypochrysops*) which feed on the ant-house plant and which are tended by the ants. The relationship therefore involves interac-

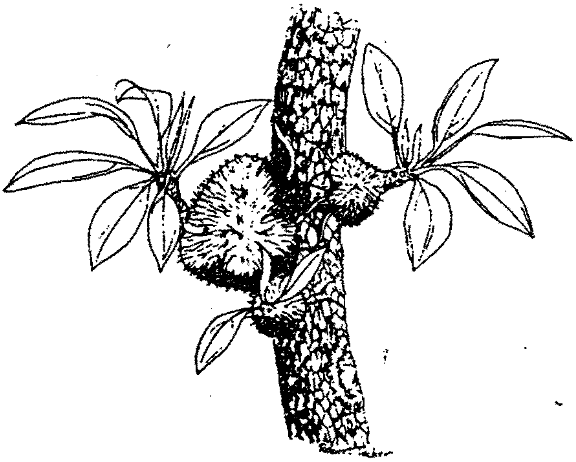


FIGURE 5 The "ant-house plant" *Myrmecodia*, epiphytic on a mangrove branch [reprinted from Saenger, P., Hegerl, E. J., and Davie, J. D. S. (1983). Global status of mangrove ecosystems. *Environmentalist* 3(Suppl. 3), 1–88, 1983, with permission of the International Union for the Conservation of Nature and Natural Resources].

tions between two plant species, two animal species, and one or more fungus.

Most mangrove ants are arboreal and essentially terrestrial animals. In many cases they nest outside the intertidal zone and forage in the mangal only at low tide. One Australian species, *Polyrachis sokolova*, is truly intertidal, retreating at high tide to nests within the mangrove mud. Nothing is actually known of its physiology: like other intertidal insects, it may retain a surface film of air and therefore avoid the need for any special adaptations to immersion or varying salinity.

Probably of greater ecological significance are the various plant-eating insects. Termites play a major role in disposing of dead wood. Some species construct nests of mud on tree trunks several meters above high-tide level, with access galleries snaking down the trunk to the aerial roots and upwards to the canopy.

The most important herbivores are those that eat mangrove leaves and seedlings, particularly the larvae of moths and beetles. Typically, only a small proportion of leaf production falls to herbivory. Sometime, however, it reached epidemic proportions. Individual trees in an otherwise healthy forest may be completely defoliated, and occasionally areas of many hectares are stripped of leaves. Canopy loss may result in the defoliated trees dying and being replaced by other species that are more tolerant of unshaded conditions. Insect herbivory therefore may alter mangrove community structure.

Other mangrove insects include the spectacular synchronously flashing fireflies of Malaysia (*Pteroptyx*), which occupy the mangrove *Sonneratia* for their displays, and numerous species of butterfly and moth. Hawkmoths, bees, and drosophilidid flies are among the species which are probably of importance in pollinating mangrove flowers.

B. Amphibia and Reptiles

Amphibia are rare in brackish or salt water, but one species, the crab-eating frog (*Rana cancrivora*), is common in mangrove habitats of Southeast Asia. Tadpoles survive well in salinity up to 50% that of seawater.

Reptiles are more abundant. Numerous species of snake forage within the mangal at low tide, including terrestrial or arboreal species but also some for which the mangal is their primary habitat. Mangrove snakes eat crabs (sometimes reciprocated), insects, and fish. In Southeast Asia, one of the most formidable mangrove predators is the monitor lizard (*Varanus indicus*), which may reach 1 m in length. Crocodiles, caimans, and alligators also occur in mangroves, although these are now rare in many areas due to human activities.

C. Birds

Birds are highly mobile. Many spend only part of their time in mangroves, migrating seasonally, daily, or tidally. Mangroves provide a feeding area, a nesting site, a refuge from the rising tide, or some combination of these. Waders probe for invertebrates in the mud of the mangal or adjacent mudflats. Kingfishers, egrets, and herons catch fish or invertebrates in the shallow water of mangrove creeks. Larger fish eaters, such as pelicans, ospreys, and cormorants, range further afield and may return to the mangal to roost or breed. In the Caribbean, roosts and nesting colonies of cattle egrets (*Bubulculus ibis*) and scarlet ibis (*Eudocinus ruber*) are so densely packed that the consequent enrichment of the soil with guano leads to significantly enhanced local growth of the mangrove trees.

Mangrove forests typically include numerous passerine species. Nectar feeders such as sunbirds in Malaysia, honeyeaters in Australia, and hummingbirds in South America move seasonally into mangroves and may be important pollinators. Insectivorous passerines specialize in hawking for insects in the canopy or, among low-lying vegetation, in picking insects off leaves or from bark crevices or from different species of tree. Broadly similar guilds of insectivorous birds, comprising different constituent species, seem to occur in different geographical regions.

Few of the species found within the mangal are mangrove specialists, and those which are restricted to mangroves in one part of the world may occupy different habitats elsewhere. One example is the cosmopolitan Great tit (*Parus major*), distributed from western Europe to China: only in Malaysia is it a mangrove species. The lack of mangrove specialists is probably due to the relative simplicity of the mangrove forest structure compared with typical tropical forest, allowing less scope for niche specialization. Another reason is probably the proximity of a pool of competing species in adjacent tropical rain forest. There are proportionally fewer mangrove specialists in New Guinea, where rain forest usually abuts mangrove habitats, than in Australia, where this juxtaposition is less common. Within Australia, there are few specialists in the mangroves of Queensland, which are extensive and contiguous with rain forest, than in northwestern Australia, where this is not the case. Most mangrove birds are probably using the habitat opportunistically.

D. Mammals

As with birds, many mammal species use the mangal opportunistically. These include small rodents, agoutis, wild pigs, antelopes, deer, and rhinoceroses; the Sundarbans of Bengal are the last major redoubt of the Bengal tiger (*Panthera tigris*). Domestic animals, such as camels and buffalo, are often a major element in the mangrove fauna. Otters may also be abundant, feeding on fish and crabs from the mangrove creeks.

Monkeys are common in mangroves. In Southeast Asia these include macaques (*Macaca*) which forage on the mud for crabs and mollusks. They also uproot large numbers of mangrove seedlings: Because these are seldom eaten or even greatly damaged, the purpose is not clear. Herbivorous monkeys are found in the forest canopy, including leaf monkeys (*Presbytis*) and, in the mangrove forests of Sarawak, the striking proboscis monkey (*Nasalis larvatus*). This is found only in mangroves and riverine forests, and it specializes in eating foliage, which is digested in an elaborate multichambered stomach with the aid of resident bacteria.

Bats are often abundant in mangroves. Resource partitioning in insectivorous bats parallels that of insectivorous birds, with species specializing in different zones of the mangrove vegetation and catching their prey with different flight techniques. A single bat may eat up to one-third of its body weight of insects each night: A 30-g bat might therefore consume 5000 insects nightly. The impact on the insect population of foraging bats must be considerable.

The exclusively Old World fruit bats often occur in mangrove forests in vast numbers: Roosts of an estimated 220,000 individuals have been recorded. Most fruit bats feed on nectar and fruit, and it is this which attracts many species into the mangal. In Malaysia, the long-tongued fruit bat *Macroglossus minimus* is an important pollinator of the mangrove *Sonneratia*: the long tongue is specialized for insertion into the *Sonneratia* flower, which carries large projecting stamens to deposit pollen onto the fur of the feeding bat. *Sonneratia* flowers last for only a single night, possibly because of the wear and tear resulting from visits by such a large pollinator. This species of bat is a true mangrove specialist, and in western Malaysia at least, it has not been recorded from other habitats. Mangrove specialization is possible only because the three species of *Sonneratia* in the area have different flowering patterns so that nectar is available throughout the year. Other fruit bats switch seasonally between mangrove and nonmangrove species.

III. FAUNA OF MARINE ORIGIN

One of the principal reasons for the high faunal diversity of mangrove ecosystems is their accessibility to occupation by organisms from both terrestrial and marine habitats. Of these, the marine invaders are the more numerous in terms of numbers and diversity of species. These include more or less sessile organisms settling on aerial roots and pneumatophores as well as more mobile species living on and under the mud. Many animal groups are represented in the mangal, the most conspicuous and ecologically most significant being teleost fish, crustacea, and mollusks. As with the land-derived mangrove fauna, the majority of species occur elsewhere and accumulate in mangroves because of the availability of food, shelter, or suitable substrate.

Considering mangrove communities at a scale of, for example, hectares, the diversity of such animals is often high. At smaller scale, however, the anoxic conditions caused by waterlogging, exacerbated by microbial decomposition of detritus, may greatly reduce both species diversity and abundance.

A. Root Communities

Mangrove roots and pneumatophores provide a hard substrate often covered with a rich and diverse growth of sponges, sea anemones, bryozoans, tunicates, barnacles, tubeworms, and mollusks as well as epiphytic algae. These in turn may attract a more mobile population of browsers or predators. The epibionts are mostly filter feeders, extracting organic particles suspended in the water, or predators of zooplankton, with no direct interaction with their mangrove host. A particularly thick growth, however, can adversely affect the host tree by occluding lenticels and restricting gas exchange with the underground roots. The relationship is sometimes mutually beneficial, as encrusting sponges may transfer nitrogenous nutrients to their host, and encrusting fauna can protect the root from attack by wood borers.

The labyrinthine aerenchyma tissue of the roots is easily penetrated by wood-burrowing organisms. The isopod crustacean *Sphaeroma* is a common root borer and may cause severe damage and even death. *Sphaeroma*-induced damage near the growing tip of a root may induce forking, with a resulting increase in the number of roots entering the soil: This may benefit the tree. The "shipworm" *Teredo* (which is in fact a mollusk) also bores dead roots and trunks extensively and plays a similar role to that of termites in disposing of woody debris. Like termites, *Teredo* relies on symbiotic microorganisms to digest the more intransigent components of wood.

B. Fish

Mangrove creeks and inlets are frequently occupied by abundant and diverse fish populations. In Southeast Asia, for instance, records of more than 100 species are by no means unusual. Many of these species spend only part of their time within the mangal, often moving to other habitats seasonally or at different stages of their life cycle. Mullets (*Liza*) eat significant amounts of mangrove detritus, such as shed leaves: most hunt small crustacea or other invertebrates. Some fish are permanent creek residents, commuting into the forest when it is submerged at high tide and foraging among the mangrove roots.

At low tide, Asian mangroves are occupied by mudskippers, which are relatives of the gobies (Fig. 6). As their name suggests, they skip across the exposed mud surface using their tails and leg-like pectoral fins, sometimes even climbing up aerial roots or pneumatophores. This amphibious life requires appropriate physiological adaptations, particularly in relation to respiration. Mudskippers are largely air-breathing, with gas exchange taking place not just across the gills but also at highly vascularized areas of the skin. Some store air within their burrows to enable aerial respiration even at high tide.

All mudskippers are probably to some extent omnivorous, but some are predominantly deposit feeders and others carnivores. Prey of the latter include crabs, insects, spiders, shrimps, and snails.

C. Crustacea

Mangrove habitats, particularly in the Indo-West Pacific, are dominated by crabs belonging to two families, Grapsidae and Ocypodidae. The former are predominantly herbivores or detritus feeders and the latter deposit feeders, extracting fine organic particles from mangrove mud. Predatory crabs, such as the formidable *Scylla*, may also be important components of the mangrove fauna. Shrimps (Penaeoidea) and mud lobsters (*Thalassina anomala*), and smaller crustacea such as amphipods and isopods, may also be significant as scavengers, in breaking down leaf litter, or as predators of smaller organisms.

1. Grapsid Crabs

Grapsid crabs of the subfamily Sesarminae, particularly of the genus *Sesarma*, are characteristic of mangroves, although a few species of this genus occur in other habitats (Fig. 7). More than 40 species of sesarmine have been reported from the mangroves of Malaysia alone, and many species, here and in other regions, undoubtedly remain to be described.

Sesarma are small (usually less than 3 cm in breadth) and inconspicuously colored. They are amphibious, re-

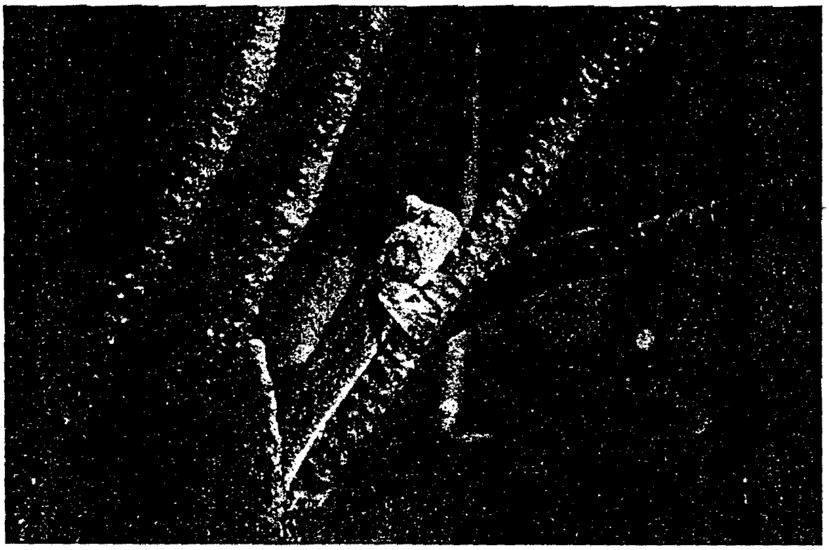


FIGURE 6 Mudskipper on an *Avicennia* pneumatophore (photograph courtesy of HAR).

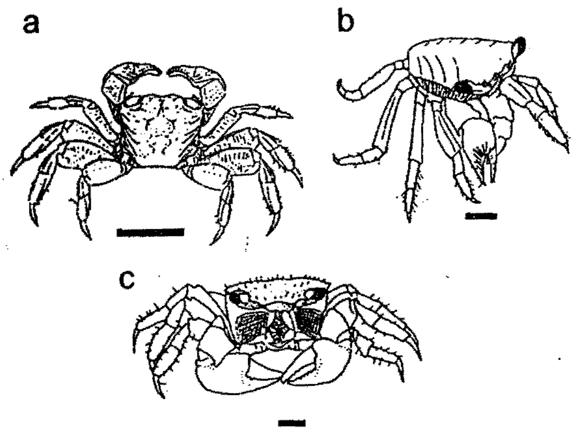


FIGURE 7 Mangrove sesarmine crabs: (a) *Parasesarma plicata*, (b) *Aratus pisonii*, and (c) *Neosarmatium smithi* [reprinted from Jones, D. A. (1984). Crabs of the mangal ecosystem. In *Hydrobiology of the Mangal* (F. D. Por and I. Dor, Eds.), pp. 89–109, with kind permission from Kluwer Academic Publishers and the author].

treating into burrows at high tide and foraging on the exposed mud at low tide. Respiration in air is achieved partly by recirculating water from the gill chambers over the carapace where it can be reoxygenated: evaporative cooling during this process also serves to reduce the dangers of high air temperature. Water loss can be offset by the acquisition of soil water through tufts of root-like hairs. Sesarmines are euryhaline, although differing degrees of salt tolerance probably contribute to the zonation of crab species along estuaries or with shore level.

In some cases, sesarmine crabs climb trees to feed on fresh leaves or buds. In East Africa, *Sesarma leptosoma* undertakes synchronized mass migrations twice daily from refuges among mangrove roots to forage on the tips of the branches of the trees. The virtually indistinguishable Caribbean species *Aratus pisonii* spends most of its time in trees, only rarely descending onto the mud.

Most sesarmines, however, subsist on fallen leaves or propagules. Mangrove leaves are often rich in tannins and other aversive materials, and several crab species have been shown to select leaves from the more palatable species of tree. Many leaves are collected as soon as they fall and cached in crab burrows. As decomposition proceeds, tannin levels decrease and nitrogen content increases through the accumulation of microbial biomass: storage therefore increases leaf palatability.

Much of the leaf material eaten is not assimilated but redeposited onto the mud as feces, available for microbial decomposition. It has been estimated that processing of leaf material by crabs increases the rate of breakdown of leaf litter 75-fold compared with the rate of decomposition under microbial action alone. Therefore, sesarmine crabs collectively play a very important role in facilitating energy flow through the mangrove ecosystem. By eating propagules, they also affect species distribution and community structure of mangrove trees (see Section V.C.1). However, there are geographical differences: in Southeast Asia and Australia, sesarmines are crucial in litter breakdown and selective removal of propagules, whereas in Florida and the Caribbean they are of lesser significance.

2. Ocypodid Crabs

Some crabs of the family Ocypodidae, such as the Central American hairy land crab *Ucides*, consume mangrove detritus. The majority are deposit feeders. Among these, the most conspicuous are the gaudily colored fiddler crabs (*Uca* spp.), widespread throughout the mangroves of the Old and New World (Fig. 8).

The common name derives from the one greatly enlarged claw of male fiddlers, which is used in courtship and in deterring rival males. The smaller claw of males and both claws of females are devoted to feeding. Mud is scraped into the buccal cavity in which, by a complicated process of flotation and manipulation by the mouthparts, fine organic particles are separated from the mineral components. The former is ingested and the latter deposited as a ball of sand, or "pseudofecal pellet." The process of separation may be quite selective. In some species, what is extracted consists almost entirely of microbial cells rather than, for example, fragmented leaf material. Others have subtly different extraction techniques and may specialize in the smaller meiofaunal animals. There may be as many as 60 fiddler crabs per square meter, resulting in 500 g of soil being processed daily. The toll on meiofauna is probably considerable, and the effects on soil texture and composition are profound.

3. Other Mangrove Crustacea

Other crabs found in mangroves are important predators. The most conspicuous is the mud crab *Scylla serrata* of the family of swimming crabs (Portunidae). *Scylla* reaches a carapace width of up to 20 cm, making it the largest invertebrate predator found in mangroves. Equally formidable predators are the mantis shrimps (Stomatopoda), which live in burrows in the mud and lacerate prey by rapidly shooting out their viciously spiked raptorial appendages. Other rarely seen burrowing crustaceans include pistol or snapping shrimps

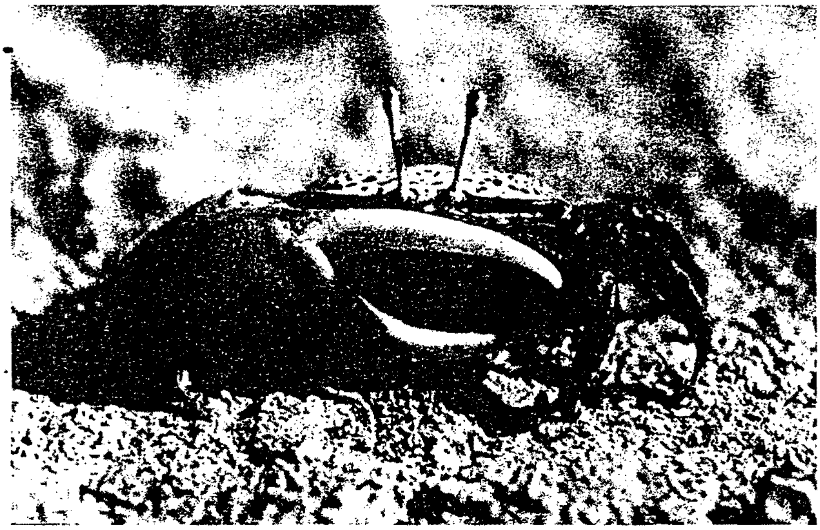


FIGURE 8 Fiddler crab (*Uca*) in a Mozambique mangrove (photograph courtesy of D. Barnes). See also color insert, Volume 1.

(*Alpheus* spp.) and the mud lobster *Thalassina* (see Section III.C.4).

More general mangrove scavengers include hermit crabs, particularly *Clibanarius*, which forage on the mud surface at high tide. Shrimps may also be abundant in mangroves and mangrove creeks. Penaeid shrimps, which in at least some parts of the world depend heavily on mangroves for feeding and breeding, are an important commercial crop. The shrimp *Merguia* apparently lives only in mangroves and has the distinction of being the only semiterrestrial shrimp: it actually climbs trees. Only two species are known. One occurs in the Indo-West Pacific region, from Kenya to Indonesia, and the other occurs in Panama, Brazil, and Nigeria. Indo-West Pacific and Atlantic regions differ in the composition of their mangrove floras, and the separation of the two species of mangrove-associated shrimps may have occurred in parallel with the divergence of the mangroves themselves.

4. Crustacea as Ecosystem Engineers

All species have an impact on their environment, at the very least exchanging materials in the form of food, waste materials, and respiratory gases. Some species have effects beyond these simple transactions and alter the nature of their environment in ways that affect species other than their direct competitors, predators, or prey. Such species are often termed "ecosystem engineers."

In a mangrove ecosystem, the trees are the greatest engineers, influencing sedimentation rates and creating a physical environment. Crustacea also, in important ways, transform their surroundings. The topography of mangrove swamps in Southeast Asia is often visibly modified by mud lobsters (see section III.C.3). While processing mud, *Thalassina* throws up waste material from beneath the surface, forming mounds which may reach 2 m in height. These create patches of dry mud which provide habitats for other species, including the mangrove fern *Acrostichum*, fiddler crabs, and a variety of other burrowing crustacea and mollusks. Between the mounds the mud surface is lower, and more waterlogged, than it would be otherwise. Burrowing crabs also contour their environment, although less dramatically.

Much of the microbial activity of mangrove mud occurs in the surface layer, to a depth limited by the diffusion and exchange of gases with the atmosphere. As fiddler crabs process surface mud, they continually expose fresh material, facilitating microbial activity, while the active surface of the mud is increased in area by crab burrows. Burrowing activity also oxygenates the deeper soil and creates an underground labyrinth of interconnecting passages, through which significant underground water flow occurs. Experimental evidence suggests that crab activities significantly affect nutrient recycling and enhance growth of mangrove trees. Crustacea therefore alter the state of their environment in ways that significantly affect other species.

D. Mollusks

1. Bivalves

The most visible bivalve mollusks of mangroves are the oysters and mussels found attached to roots. Within the mud, however, there is often an abundant population of burrowing species. These, like the oysters and mussels, are largely filter feeders, extracting fine organic particles from suspension. A less typical group of bivalves are the shipworms of the family Teredinidae (see Section III.A), including the giant mangrove shipworm *Dicyathifer*, which may reach 2 m in length.

2. Snails

Gastropod snails are also generally abundant in mangroves. As with the crustacean fauna, these include herbivores, detritus and deposit feeders, and predators. Although a few species are uniquely found in mangroves, the majority of surface-living species also occur on open mudflats.

The principal predatory snails are species of *Thais*, found in mangroves worldwide. These cruise over mud and mangrove roots, feeding on barnacles or smaller gastropods. In the mangroves of Costa Rica, for example, *T. kiosquiformis* densities may reach more than 200 per square meter, and the species plays a major role in maintaining the function of mangroves by removing encrusting fauna from their roots.

Many gastropod species are deposit feeders, ranging in size from tiny and almost invisible species to the massive *Terebralia* and *Telescopium* of the Indo-Pacific region, which may reach a length of 10 cm (Fig. 9). One species, *Terebralia palustris*, feeds on small detritus particles when young, but on reaching a length of approximately 3 cm it switches to a diet of fallen leaves. The teeth on the radula (the ribbon-like tongue) of gastropods metamorphose appropriately to a form suitable for the altered diet. In Florida, snails are important consumers of mangrove seedlings, at some locations destroying nearly three-fourths of the seedling population. This is an interesting geographical contrast with other regions, such as Malaysia and Australia, where crabs fulfil this role (see Section III.C.1).

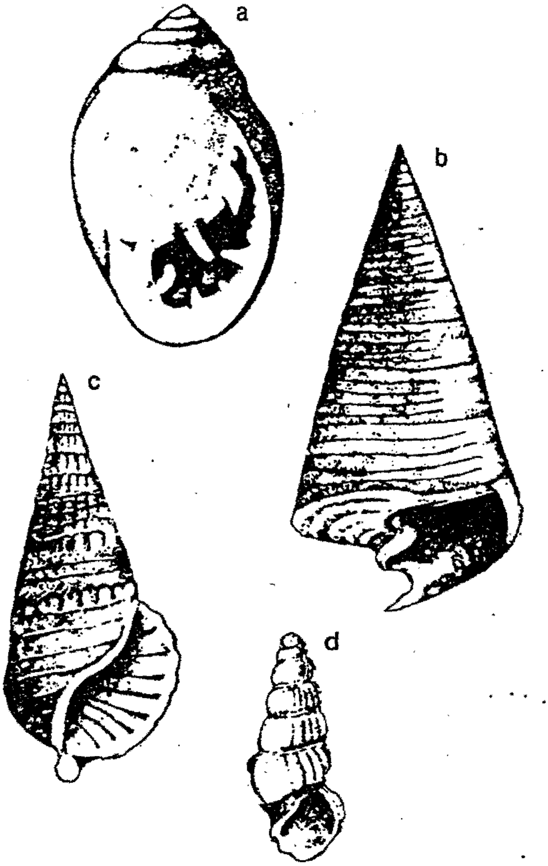


FIGURE 9 Gastropod mollusks typical of Indo-West Pacific mangroves: (A) *Pythia* (2.5 cm), (B) *Telescopium* (10 cm), (C) *Terebralia* (6 cm), and (D) *Cerithidea* (2 cm) (reprinted from *Advances in Marine Biology* 6, W. Macnae, A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific Region, 74–270, 1968, by permission of Academic Press).

The most abundant snails on the mangrove trees are often species of *Littoraria*, close relatives of the periwinkles of temperate rocky shores. In Central America, on both sides of the Isthmus of Panama, the common species is *L. angulifera*. In the Indo-Pacific, this species is replaced by many others, which partition between them the slightly different habitats afforded by a tree. In Papua New Guinea, *L. scabra* prefers the bark of trees on the seaward side of a forest, *L. intermedia* prefers trees next to freshwater creeks, whereas the polymorphic species *L. pallescens* is found solely on leaves.

E. Meiofauna

Within the mangrove mud lies a rich fauna virtually invisible to the naked eye—the meiofauna. Beneath an area of 10 cm^2 of mud there may be many thousands of individuals. Orders of magnitude smaller than the more conspicuous macrofaunal crabs and snails are meiofaunal herbivores, detritivores, and formidable predators, with food chains probably dependent on photosynthetic cyanobacteria ("blue-green algae") and heterotrophic bacteria. Meiofauna colonize fallen leaves, and the stages of leaf breakdown are accompanied by complex interactions and successional shifts in species composition and community structure which parallel, on a microscopic scale, the processes of macroecology.

The numbers of meiofaunal individuals are immense, and their diversity is astonishingly high. Not only are there many species but also the species show a higher level of taxonomic diversity. Among the macrofauna virtually all species belong to just three phyla: arthropods, mollusks, and chordates. The meiofauna from just one mangrove area in Australia, for example, yields turbellarian flatworms, nematodes, copepods, Ciliophora, Foraminifera, bivalve mollusks, oligochaete and polychaete annelids, hydrozoa, archiannelids, kinorhynchs, tardigrades, and gastrotrichs.

Very little is understood about the meiofauna of mangroves, their interactions, their functional significance in the ecosystem as a whole, and the relationship between the meiofaunal and macrofaunal worlds. Their small size belies their great importance.

IV. CONNECTIONS

The salient features of typical mangrove ecosystems are relatively high rates of primary productivity, much of the results of which enter decomposition pathways, either directly or after initial breakdown by leaf-eating crabs or mollusks. This is true of leaves and reproductive structures and, on a more protracted timescale, of the woody components of the trees. Particulate organic matter, either small leaf fragments or bacterial cells, is ingested by molluskan and crustacean deposit and filter feeders, enters meiofaunal food chains, or accumulates in the mud.

The ecosystem can be viewed physically as well as in terms of the flow of energy or matter. Mangrove trees supply hard surfaces on which other organisms settle, and they modify (as well as respond to) the physical environment by stabilizing the soil, facilitating accretion of mud, and retarding erosion. The environment is further modified by the physical activities of burrowing crustacea and other animals.

Mangrove ecosystems cannot be considered in isolation. They interact with adjacent habitats through the trapping of exogenous sediment or export of particulate or soluble organic matter or inorganic nutrients. Animals, by moving between mangroves and other habitats, also contribute to import and export of matter. Commercially important penaeid shrimps use mangroves as nursery areas so that shrimp catches many miles away may depend critically on mangrove productivity. Hard evidence for such connections between mangroves and other ecosystems, however, is sometimes elusive, and the strength of such linkages is almost impossible to quantify.

V. MANGROVE DIVERSITY

Mangrove diversity must be considered at a range of spatial scales, from global patterns of species richness to the pattern of distribution, at a particular location, at a scale of a few meters. In considering mangrove fauna, even smaller spatial scales become relevant. At all scales, diversity is affected by the past history of the area, by physical factors, and by biotic interactions, but the importance of each of these and the timescales over which they operate vary with scale.

A. Global Patterns

1. Latitudinal Range and Species Diversity

Mangroves are almost exclusively tropical or subtropical. This distribution is a reflection of a temperature limitation: The global distribution of mangroves correlates very closely with, for example, the winter position of the 20°C isotherm (Fig. 10). The number of mangrove species declines with increasing latitude, with the most northerly and southerly mangroves being species of *Avicennia*. In temperate regions, mangroves are replaced by salt marsh vegetation: plants which, like mangroves, are adapted to conditions of salinity and waterlogging but which do not carry the additional burden of being a tree or of producing large propagules.

2. Longitudinal Differences

Within their temperature and latitudinal constraints, mangroves show interesting patterns of species distribution. The principal biogeographic division is between the Indo-West Pacific (IWP) and Atlantic–Caribbean–east Pacific (ACEP) regions. These two regions have broadly similar areas of mangrove habitat, but the IWP has four times more genera and six times as many species of mangrove: 17 genera compared to 4, and 40 species compared to 7. It is apparent that none of the mangrove genera are very diverse, possibly because of a general limitation on species diversification in harsh intertidal conditions. Genera occurring in the IWP, however, are slightly more speciose than those of the ACEP: 2.35 compared with 1.75 species per genus.

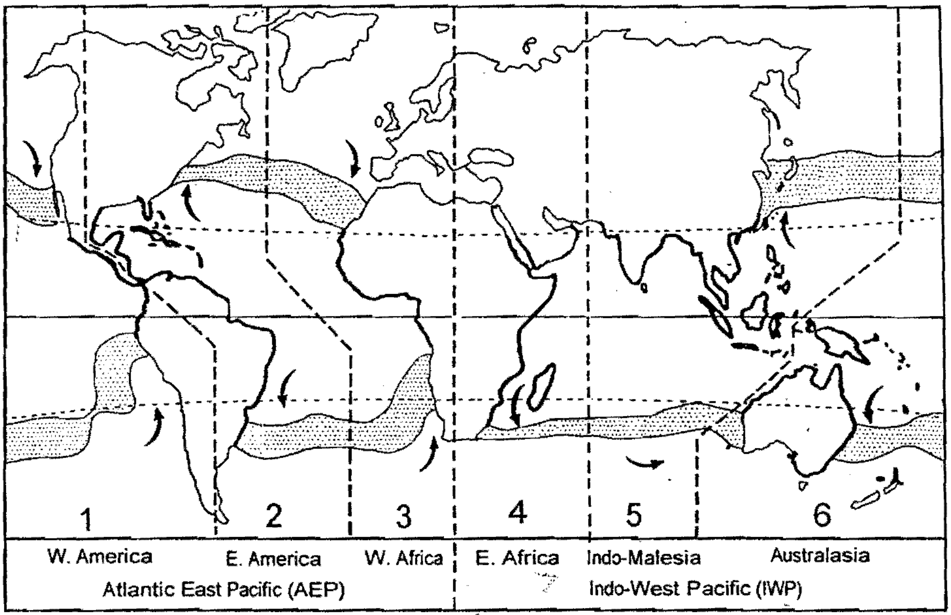


FIGURE 10 World distribution of mangroves in relation to 20°C isotherms [reprinted from Duke, N. C. (1992). Mangrove floristics and biogeography. In *Tropical Ecosystems* (A. I. Robertson and D. M. Alongi, Eds.), pp. 63–100, with permission of the American Geophysical Union and the author].

The differences between the IWP and ACEP regions are maintained by major barriers. The most obvious of these is the African continent (Fig. 10). Less obvious is the barrier represented by the central Pacific. This results principally from dispersal limitations rather than from the absence of suitable habitat. Suitable environments are present on many Pacific islands without natural mangrove populations, as shown by the success of the artificial introduction of mangrove species to Hawaii.

Further dispersal barriers, including the Isthmus of Panama, open ocean, and arid coasts unsuitable for mangrove occupation, divide the major regions into smaller subregions, each with a more or less distinctive mangrove flora (Fig. 11). Only one species occurs in all six subregions: the mangrove fern *Acrostichum aureum*. Two genera, *Avicennia* and *Rhizophora*, are common to both IWP and ACEP regions. All other genera are found exclusively in either the IWP or the ACEP, although the close similarity between *Laguncularia* (ACEP) and *Lumnitzera* (IWP) suggests a recent separation of these two genera.

The traditional explanation of mangrove species distribution is of a center of origin and of diversification in Southeast Asia, followed by dispersal restricted by physical barriers. This clearly makes little sense in relation to the current dispersal barriers. Fossil evidence of mangroves is widespread and reveals a much wider distribution during the Eocene and earlier epochs: Fossil *Nypa*, *Avicennia*, and *Rhizophora* pollen and other remains, for instance, have been identified in Eocene and Miocene deposits that now form part of North and South America, Europe, and North Africa as well as

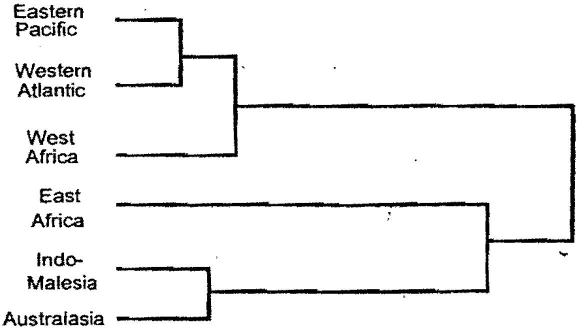


FIGURE 11 Comparison of the mangrove flora in six geographical subregions. Because of the recent closure of the Isthmus of Panama, the eastern Pacific and western Atlantic (including Caribbean) are most similar in species composition. Note also the separation between Atlantic–Caribbean–eastern Pacific (ACEP) and Indo-West Pacific (IWP) regions.

south and east Asia. At the time, these locations were connected by the Tethys Sea, continuous through what is now the Mediterranean and Indian Ocean.

Subsequently, this pantropical distribution was partitioned as a consequence of continental movements. Cosmopolitan genera such as *Avicennia* and *Rhizophora* were separated into regional populations by the approach of Africa to Asia 30–35 million years ago which closed the Tethys Sea, and separation of the sister genera *Laguncularia* and *Lumnitzera* followed the widening of the Atlantic barrier. The emergence of modern species ensued within the isolated subregions. Closure of the Isthmus of Panama was geologically very recent (a mere 2 or 3 million years ago) so that differences between eastern Pacific and Caribbean species are slight. One species (*Pelliciera rhizophorae*) is found on both sides of the Isthmus, presumably reflecting a separation into two populations too recently for allopatric speciation to have occurred.

An originally pantropical mangrove distribution was therefore partitioned into regions and subregions, with subsequent evolutionary divergence. Climatic conditions then eliminated mangrove species from areas such as southern Europe and the Mediterranean fringes. The current distribution pattern results from a combination of large-scale geographical factors and more regional climatic ones.

3. Diversity of Mangrove Fauna

It might be expected that faunal species diversity would follow a similar pattern to that of mangrove tree diversity both because the mangrove fauna has presumably been exposed to the same influences and because of a presumption that faunal diversity should respond to tree diversity.

The IWP region, richer in plant diversity than the ACEP, is also richer in species of mangrove-associated crustacea and mollusks (Table III). The reverse is true of other taxonomic groups, particularly those that form constituents of the root communities, such as sponges, coelenterates, and echinoderms. This may reflect regional differences in tidal range and availability of roots for settlement. For many groups, unfortunately, little comparable data are available and recorded species numbers reflect taxonomic interest and effort rather than the composition of actual species assemblages.

B. Regional Patterns of Diversity

Species diversity varies within regions in response to many different factors. The ACEP region, in addition to having fewer mangrove species in total, shows less differentiation between localities within the region, and all the species available in the geographical vicinity are likely to be represented at most locations.

Various factors may result in local variation in species diversity. Mangroves do not grow on rocky shores or in areas where fresh water is completely lacking (which is in part why all tropical shores are not dominated by mangroves). Stretches of inhospitable coastline therefore act as barriers which affect mangrove dispersal and geographical distribution. The arid shores of Soma-

TABLE III

Number of Species Recorded from Mangroves in Various Localities in the Regions Indicated[a]

	Atlantic–Caribbean–east Pacific	Indo-West Pacific		
Taxonomic group	Caribbean/W. Atlantic	East Africa	Indo-Malesia	Australia
Sponges/bryozoa	36	1	5	7
Coelenterata/ctenophora	42	12	3	6
Nonpolychaete worms	13	3	13	74
Polychaetes	33	72	11	35
Crustacea	87	163	229	128
Mollusks	124	117	211	145
Echinoderms	29	23	1	10
Ascidians	30	13		8
Fish	212	114	283	156
Reptiles	3		22	3
Birds	138		177	244
Mammals	5		36	7

[a] From Saenger *et al.*, 1983.

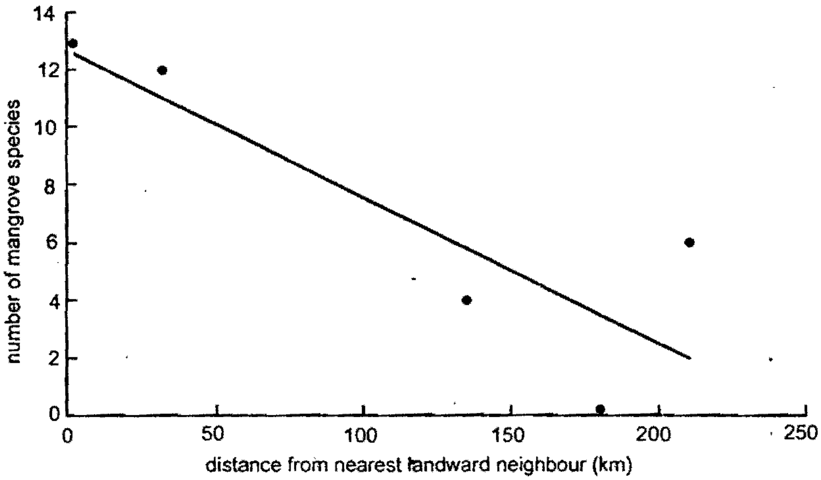


FIGURE 12 The number of species of mangrove occurring on West African islands in relation to their distance from the nearest landward neighbor [reprinted from Saenger, P., and Bellan, M. F. (1995). *The Mangrove Vegetation of the Atlantic Coast of Africa. A Review*, pp. 1–96, with permission of the Laboratoire d'Ecologie Terrestre de Toulouse].

lia, for example, result in the reduction in species number northwards so that *Avicennia marina* is virtually the only mangrove species found in the Red Sea. Separation of mangrove estuaries from each other by arid coastline, and regional-scale variation in physical variables, also affects the species distribution of mangroves around the Australian coasts.

Dispersal ability also affects species distributions within regions. The number of mangrove species on islands of the western Pacific shows clear attenuation with increasing distance from the species-rich areas of Australia and Papua New Guinea. Similarly, among islands off the West African coast there is a clear relationship between the number of mangrove species present and the distance from the nearest landward neighbor (Fig. 12). Species number also correlates with island size, with larger islands containing more species.

C. Local Variation in Species Distribution and Diversity

1. Tree Distribution

At a specific location, the distribution of mangrove species responds to physical variables in the environment. These often vary as gradients: in an estuarine mangal, for instance, salinity and the influence of tidal fluctuations tend to diminish with distance up the river. Sediment composition and nutrient dynamics also alter with distance from the open sea. Mangrove species respond differentially to such upriver/downriver gradients, resulting in zonation of species.

Similarly, in areas dominated by tide rather than river flow, tidal fluctuations establish gradients of physical variables, particularly in salinity and the extent of waterlogging of the soil. Again, mangrove species respond differentially to these physical variables and tend to form distinct zones. Where both river and tidal influences interact, the pattern of species distribution can be extremely complex.

In relation to salinity, species generally grow better at low salinity and differ more in the tolerance range than in their salinity optima. Low salinity, in consequence, tends to be associated with higher species diversity. At higher salinities, tolerance differences result in differing competitive success and translate into zonation of mangrove species along a salinity gradient, with species dominating zones at which they compete best, rather than those corresponding to salinity growth optima.

Although response to physical gradients suggests a gradual transition from one species to another as the determining physical variable gradually alters, this is often not the case. Mangrove species are frequently found in virtually monospecific stands or zones, with a more or less abrupt transition from one dominant species to another. This suggests that interactions between tree species, and mutual exclusion, may play a part in defining zone boundaries. Other physical variables, such as the degree of waterlogging and soil anoxia, nutrient availability, and biotic interactions between species, similarly affect species distribution within the mangal.

Superimposed on the sorting of species under the influence of physical variables are variations resulting from interactions with the mangrove fauna. Of the faunal influences, the most significant is the selective destruction of mangrove propagules by sesarmine crabs (see Section III.C.1). At least in Southeast Asia and Australia, this is a major factor determining mangrove species distribution. Mangrove animals respond to physical gradients of salinity and inundation regime. Sesarmine abundance is often greatest at midshore, and it is therefore here that mangrove propagules are most vulnerable. For reasons related to nutritional value and the levels of aversive tannins, *Avicennia* is generally the preferred food of sesarmines: hence at some locations the distribution of *Avicennia* in the upper and lower shore and their virtual absence from intermediate shore levels.

Random factors can also affect mangrove species distributions. If a gap is created in a mangrove forest because of the death of a tree, it is most rapidly filled by the species that are the best colonizers and best able to flourish in unshaded conditions. In Southeast Asia, the result is often an initial invasion of the mangrove fern *Acrostichum*. This may be succeeded by seedlings of *Bruguiera parviflora*. This species has relatively small and easily dispersed seedlings, whose growth is suppressed by the shade of an intact canopy. These in turn are replaced by slower growing shade-tolerant species such as *B. gymnorrhiza*. *Avicennia marina* is less tolerant of shade but is less likely to occupy a small gap because of propagule destruction by crabs. If, however, the gap is a large one, *Avicennia* is more likely to establish itself, probably because foraging crabs are vulnerable to predation in large open spaces. The distribution of species within a mangrove forest may therefore be patchy and reflect the stochastic nature of tree death and the subsequent successional history. On a larger scale, extensive death of trees by typhoons, by widespread defoliation by insect attack, or even by oil spills can have profound and long-lasting effects on species composition.

The structure of a mangrove forest is therefore in part explainable in terms of "patch dynamics"—of gaps appearing by chance and being filled by a changing assemblage of species differing in composition (at least for a time) from the surrounding forest. Eventually, something similar to the surrounding forest emerges. With a high incidence of gaps, a mangrove forest could be seen as a mosaic of patches of different successional age: if patches appear relatively rarely, the effect would be transient aberrations in an otherwise homogeneous, or consistently zoned, environment.

2. Distribution of Mangrove Animals

The species distribution of the mangrove fauna is less well understood since small, cryptic, and often mobile animal species are less easy to describe and analyze than large and immobile trees. A high level of taxonomic confusion compounds the problem. Nevertheless, it seems likely that the same general considerations apply. The distribution of mangrove crabs, for instance, forms zones related to shore level, salinity, and soil texture, whereas mollusks show zonation patterns in relation to shore level and to vertical position on the roots and trunks of mangrove trees.

The distribution of species of mangrove animals may also be related to patch size and the distance between neighboring patches, on a smaller spatial scale than applies to the distribution of mangrove species themselves, corresponding to the more limited dispersal ability of the species in question. This was demonstrated in the classical experiments of Simberloff on the terrestrial arthropod fauna (principally insects) of mangrove islets in the Caribbean. The species richness on a range of mangrove islets increased with the area of the islets and decreased with increasing distance from potential sources of fresh colonists. When the fauna of islets was completely eliminated with pesticides, recolonization soon established an equilibrium species richness similar to that before the elimination. In terms of the representation of different functional groups the previous situation was largely replicated, but the actual species comprising the new assemblages differed. Finally, artificially reducing the area of mangrove in experimental islets reduced species richness, showing that it was causally related to habitat area rather than to habitat diversity.

At an even smaller scale, individual mangrove roots can be regarded as "islands" of habitat suitable for epibiont settlement, surrounded by areas of unsuitable habitat. Here, too, the composition of root epibiont communities appears relatively stable in terms of functional groups. The actual species present are much more unpredictable and particularly affected by physical variables and by the supply of colonizing larvae. These factors are of different significance at different time and spatial scales.

Meiofaunal diversity has scarcely been investigated, although the same considerations apply as in the macrofaunal world. Variation in physical variables, species interactions, patchiness, dispersal, and the other factors relevant to larger organisms must also affect the meiofauna. To date, limited research interest (and the intrinsic difficulty of studying species interactions or measuring, e.g., nutrient gradients at a scale of millimeters) has restricted our knowledge of mangrove meiofaunal diversity and the factors which determine it.

D. Genetic Diversity of Mangroves

The advent of molecular genetic techniques has made it possible to study diversity at levels lower than the species. To date, few species have been studied, and clear general conclusions cannot be drawn. In some cases, such as the self-pollinating *Rhizophora mangle* of Florida and the Caribbean, populations appear to be genetically homogeneous, with slightly more genetic variation toward the northern extremes of the species' range. The extent of intraspecific genetic variation varies with the breeding structure of the population, with dioecious species showing much greater polymorphism. Genetic variation between populations is naturally greater than that within a population at a particular location, although West African mangroves have greater levels of genetic diversity than the same species in the Florida and Caribbean. This confirms the belief that western Atlantic mangroves derive from African populations rather than the reverse. As research proceeds, no doubt many such insights into the causes and consequences of intraspecific diversity will emerge.

VI. USES AND ABUSES OF MANGROVES

Mangroves are of interest not just to biologists. Their diversity and productivity makes them the source, directly and indirectly, of many products of use (and commercial importance) to humans.

Mangrove trees are exploited for timber for construction and firewood. This ranges from the casual collection of fallen wood to major charcoal industries based on the intensively managed mangroves of, for example, western peninsular Malaysia. Foliage may also be grazed directly or harvested for fodder for domestic animals. On a smaller scale, mangrove products are collected for a host of other purposes, including thatching houses, the manufacture of fish traps, for use in medicine, for tanning leather, and for use in various foods and drinks. Indirectly, mangrove productivity supports fisheries, both within the mangal and offshore. Less tangibly, mangroves can be of considerable importance in consolidating shorelines and limiting coastal erosion.

The significance of mangroves to humans varies greatly from place to place, but attempts have been made to achieve an overall economic valuation of the goods and services supplied. One recent estimate indicates that, on average, the annual value of a hectare of mangroves is approximately $10,000, resulting in a worldwide total contribution of $1,648,000,000.

An asset of this magnitude is worth conserving. Unfortunately, sustainable management of mangrove resources is the exception rather than the rule. In almost all parts of the world, mangroves are under pressure from irrigation schemes which divert rivers and prevent fresh water from reaching mangroves and from pollution, overexploitation, or deliberate clearance for construction or for the planting of alternative crops. One of the most destructive processes in many countries of Southeast Asia and Central America has been the clearance of mangroves for the construction of shrimp ponds—an attempt to increase the production of species dependent on mangroves while simultaneously reducing the primary production on which they depend. Not surprisingly, this has not been a success.

During the past few decades, loss of mangrove area in many countries has been dramatic. In the Philippines, for example, 60% of the mangrove area has disappeared, whereas in other countries such as Malaysia, Thailand, and Pakistan, annual losses are on the order of 1–3%. It may be, however, that the tide is turning. The virtual collapse of the shrimp industry in several countries and a greater awareness of the value of mangroves as a natural resource have focused attention on rational management strategies and on the possibility of reversing some of the damage. Much effort is now being put into replanting mangroves in abandoned shrimp ponds and the rehabilitation of denuded areas for coastal protection or in support of local fisheries as well as into developing suitable mangrove areas for ecotourism. The destruction of mangroves has largely been due to human activities: In the future their survival may also depend on mankind.

See Also the Following Articles

COASTAL BEACH ECOSYSTEMS • INTERTIDAL ECOSYSTEMS

Bibliography

Bandaranayake, W. M. (1998). Traditional and medicinal uses of mangroves. *Mangroves Salt Marshes* 2, 133–148.

Duke, N. C., Ball, M. C., and Ellison, J. C. (1998). Factors influencing biodiversity and distributional gradients in mangroves. *Global Ecol. Biogeogr. Lett.* 7, 27–47.

Field, C. (1995). *Journey amongst Mangroves*. International Society for Mangrove Ecosystems, Okinawa, Japan.

Hogarth, P. J. (1999). *The Biology of Mangroves*. Oxford Univ. Press, Oxford.

Hutchings, P., and Saenger, P. (1987). *Ecology of Mangroves*. Univ. of Queensland Press, Brisbane.

Macnae, W. (1968). A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. *Adv. Mar. Biol.* 6, 73–270.

Por, F. D., and Dor, I. (eds.) (1984). *Hydrobiology of the Mangal. The Ecosystem of the Mangrove Forests*. Junk, The Hague.

Robertson, A. I., and Alongi, D. M. (eds.) (1992). *Tropical Mangrove Ecosystems*, Coastal and Estuarine Studies 41. American Geophysical Union, Washington D.C.

Rützler, K., and Feller, I. C. (1996). Caribbean mangrove swamps. *Sci. Am.* 274(3), 94–99.

Spalding, M., Blasco, F., and Field, C. (eds.) (1997). *World Mangrove Atlas*. International Society for Mangrove Ecosystems, Okinawa, Japan.

Stafford-Deitsch, J. (1996). *Mangrove. The Forgotten Habitat*. Immel, London.

Tomlinson, P. B. (1986). *The Botany of Mangroves*. Cambridge Univ. Press, Cambridge, UK.

Source:
Gopal, B and Krishnamurthy, K (1993): Wetlands of South Asia, in: Handbook of Vegetation Science, Vol. 1 (Wetlands of the World) Ed. D. F. Whigham et al., Kluwer Academic Publishers, Netherlands..

Mangroves

Mangroves are among the best investigated wetlands and have been studied for more than a century. Among the earliest noteworthy reports are those on the Sunderbans (Roxburgh 1814, Schimper 1891, Clarke 1896, Prain 1903), Bombay Presidency (Blatter 1905), and Indus delta (Blatter *et al.* 1927–28). Mangroves were the subject of a national symposium in India in 1957 (Anonymous 1959) and interest in them has grown over the past few years. A number of regional and national reviews, varying in their scope and coverage have appeared (Mathauda 1959, Waheed Khan 1959, Rao and Sastry 1972, 1974, Navalkar 1973, Chapman 1970, 1974, 1975, Blasco 1975, 1977, Krishnamurthy *et al.* 1975, Sen and Raj Purohit 1982, Bhosale *et al.* 1983, Snedaker 1984, Kogo 1985, Pinto 1986, Ansari 1987, A.N. Rao 1987). A state-of-the-art report has been prepared by the Government of India (Anonymous 1987a) and a mangrove bibliography has been compiled (Untwale 1982). UNESCO in cooperation with United Nation's Development Programme launched a long-term programme of research and training in mangroves of Asia and the Pacific. The program has organised many workshops, courses and conferences at which mangrove studies have been reviewed from time to time. Two important recent publications are by Soepadmo *et al.* (1984) and Umali *et al.* (1987).

Distribution and area. Mangroves in south Asia are part of the Indo-Pacific mangrove forests which form the world's most extensive and diverse mangrove system (Macnae 1968, Snedaker 1984). The term "mangal" is often

Table 4. Areal extent (sq. km) of mangroves in south Asia based on Blasco (1977) and field work of Krishnamurthy. Considerably different estimates are given by other authors.

Country and Location	Blasco	Krishnamurthy
1. Bangladesh: Ganges-Brahmaputra delta	6,000	6,000
2. India:		
a. Ganges delta (W. Bengal)	2,000	4,222
b. Mahanadi delta	50	150
c. Godavari and Krishna deltas	100	200
d. Cauvery delta	15	150
e. Saurashtra and Kutch coast	200	260
f. Bombay coast		330
g. Goa	200	200
h. Karnataka coast		60
i. Andaman and Nicobar Islands	1,000	1,190
3. Pakistan: Indus delta		2,495
4. Burma:		
a. Arakan coast		1,002
b. Irrawady delta		2,796
c. Tennasserim coast		1,842
5. Sri Lanka		320–400

used in reference to the living natural communities of organisms on coastal mudflats and waterways. Mangroves can be divided regionally into three zones (Fig. 7). In the Bay of Bengal, rivers such as Irrawaddy, Ganges (known as Padma in Bangladesh), Brahmaputra (Meghna in Bangladesh and Tsangpo in Tibet), Mahanadi, Godavari, Krishna, and Cauvery discharge enormous quantities of silt and freshwater, and form extensive deltas that are dominated by mangroves. The Arabian Sea coast is characterised by typical funnel-shapped estuaries of major rivers (Indus, Narmada, Tapti) or backwaters, creeks, and neritic inlets that are dominated by the estuarine and backwater type mangroves. A third type of mangrove occurs in the Bay of Bengal on islands (Andaman, Nicobar) which are in the "epicentre" of the tropical cyclone storms. On these islands, there are many tidal estuaries, small rivers, neritic islets, and lagoons which support a rich mangrove flora. Mangroves in Sri Lanka are of nearly similar nature.

Estimates of the area covered by mangroves differ widely because there is no agreed definition of the term "mangrove". Some authors include coastal saline areas without any significant vegetation in their estimates (e.g., Sidhu 1963). Blasco (1975, 1977) only considered forested areas. One of us (KK) has estimated that mangroves occupy an area of 21216 km^2 of which 6,760 km^2 are in India alone. The distribution of major mangrove areas is shown in Fig. 7 and the area estimates for different countries are given in Table 4.

Mangroves in the deltas of the Ganges and Brahmaputra in India and Bangladesh and Irrawady delta in Burma, and around the Andaman and

Nicobar Islands in the Bay of Bengal are among the largest in the Indo-Pacific region. Smaller patches of mangroves are associated with the deltas on rivers Mahanadi, Godavari, Krishna, and Cauvery on the eastern coast of India. In the western part of the region, large mangroves occur in the Indus delta of Pakistan, and smaller areas along the Indian coast near Bombay, Goa, and in Kutch (Saurashtra).

Habitat and vegetation. More than one hundred fifty species of angiosperms and ferns, often grouped into major and minor components and mangrove associates (A. N. Rao 1987), occur in the south Asian mangroves. Of these about eighty species are more common (Table 5). Dominant species belong to the genera *Rhizophora*, *Avicennia*, *Bruguiera*, *Kandelia*, *Ceriops*, *Excoecaria*, *Sonneratia*, *Lumnitzera*, *Nypa*, *Aegiceras*, *Heritiera*, *Aegialitis*, and *Xylocarpus*. Associated and usually less abundant species belong to the genera *Sesuvium*, *Suaeda*, *Salicornia*, *Acrostichum*, *Brownlowia*, *Thespesia*, *Clerodendron*, *Hibiscus*, *Derris*, *Salvadora*, *Phoenix*, *Porterasia*, *Aeluropus*, and *Urochondra*. Many species are found only in mangroves of Sri Lanka (Table 5). There are significant differences in species composition among mangroves of the east coast and also in different parts of the same coast depending upon the hydrological, edaphic, and biotic factors. Major vegetational features of different areas listed in Table 4 are therefore described below separately.

1. *Ganges-Brahmaputra delta.* Mangroves of the Ganges-Brahmaputra delta, commonly known as Sunderbans, are contiguous between India and Bangladesh (Fig. 8) and form the largest mangrove complex in the world. The undivided Sunderbans include the major portions of the Bakarganj and Khulna districts of Bangladesh and the 24–Parganas district of West Bengal (India). They occupy an area of more than 10,000 km^2 of which 4,222 km^2 is in India.

These mangroves were the first to receive botanical attention in the region (Clarke 1896, Prain 1903). During the past few years many studies have been made of these mangroves on the Indian side (Banerjee 1964, Blasco 1975, Mukherjee 1975, Mukherjee and Mukherjee 1978, Mukherjee 1984, Naskar and GuhaBakshi 1987) whereas very little is still known about them in Bangladesh (Ahmad 1984, Ismail 1989).

Various distributaries of the Ganges carry large amounts of freshwater which causes a distinct gradient in salinity in the eastern Sunderbans (LaFond 1966). The salinity differences result in three distinct areas: (a) a northeast area that is almost always fresh, (b) an area of moderate salinity east of the Raimangal river, and (c) an area of high salinity west of the Raimangal river. Vegetation and its zonation in the three areas were described by Curtis

Table 5. Distribution of mangrove species of South Asia. Sunderbans (I) of India and Bangladesh are contiguous, and hence placed together. Other mangrove areas are: II. India (a. Andaman and Nicobar Islands, b. Mahanadi delta, c. Godavari and Krishna deltas, d. Cauvery delta, e. Saurashtra and Kutch coast, f. Bombay coast, g. Goa, h. Karnataka coast, i. Kerala Coast), III. Burma, IV. Pakistan, and V. Sri Lanka. Trees are indicated with an * (adapted from Blasco 1975, 1977, A. N. Rao 1987).

Family	Species	Distribution I	II a	b	c	d	e	f	g	h	i	III	IV	V
Acanthaceae	*Acanthus ebracteatus* Vahl.		+											+
	Acanthus ilicifolius Lour.	+	+	+	+	+	+	+	+	+	+			+
	Acanthus volubilis Wall.		+											
Aizoaceae	*Sesuvium portulacastrum* L.		+											+
Apocynaceae	*Cerbera manghas* L. *		+											+
	Cerbera odollam Gaertn. *													+
	Ervatamia pandacagui Pichon.													+
Asclepiadaceae	*Sarcolobus carinatus* Wall.		+											
	Sarcolobus globulus Wall.		+											
	Finlaysonia obovata Wall.													+
Avicenniaceae	*Avicennia officinalis* L. *	+	+	+	+	+	+	+	+	+	+			
	Avicennia alba Blume *	+	+		+	+	+	+		+				+
	Avicennia marina (Forsk.) Vierh. *	+	+	+	+	+	+						+	+
Bignoniaceae	*Dolichandrone spathacea* (L.f.) Schum.													+
Boraginaceae	*Heliotropium curassavicum* L.													
Caesalpiniaceae	*Caesalpinia crista* L.													+
	Cynometra ramiflora Willd. *													+
Chenopodiaceae	*Arthrocnemum indicum* (Willd.) Moq.													+
	Atriplex stocksii Boiss.													
	Salicornia brachiata Roxb.													+
	Suaeda fruticosa Forsk.													
	Suaeda maritima (L.) Dum.													+
	Suaeda monoica Forsk.													+
Combretaceae (= Terminaliaceae)	*Lumnitzera racemosa* Willd. *	+	+	+	+	+		+	+					+
	Lumnitzera littorea (Jack.) Voigt		+			+								+
Convolvulaceae	*Stictocardia tiliaefolia* Hallier f.													
Cyperaceae	*Scirpus littoralis* Schrad.													
Euphorbiaceae	*Excoecaria agallocha* L. *	+	+	+	+	+		+	+	+				+
Lythraceae	*Pemphis acidula* J. R. & G. Fors.													
Malvaceae	*Hibiscus tiliaceus* L. *													+
Meliaceae	*Amoora cucullata* Roxb. *												+	+
	Xylocarpus granatum (L.) Koenig * (= *Xylocarpus obovatus* Grewe) (= *Carapa obovata* (Bl.) Grewe)	+	+	+		+		+						+
	Xylocarpus moluccensis (Lamk) Roem. * (= *Carapa moluccensis* Lamk.)	+		+	+	+								+
	Xylocarpus mekongensis Pierre					+								
	Xylocarpus gangeticus (Prain) Parkinson *													
Myrsinaceae	*Aegiceras corniculatum* (L.) Blume (= *Aegiceras majus* Gaertn).	+	+	+	+	+	+	+	+	+			+	+
	Ardisia littoralis Dryand.													+
	Myrsine umbellata Wall.													+
	Rapanea porteriana Merr.													+
	Rapanea umbellata Elm.													+
Myrtaceae	*Melaleuca leucodendra* L.													+
Palmae	*Nypa fruticans* Wurmb.	+	+											+
	Phoenix paludosa Roxb.	+	+	+										+
	Phoenix pusilla Gaertn.													
Pandanaceae	*Pandanus tectorius* Soland.													
Papilionaceae	*Dalbergia spinosa* Roxb.													
	Derris heterophylla Willd.													
	Derris trifoliata Lour.		+	+	+	+	+		+		+			
	Derris uliginosa Benth.					+								

Table 5. Continued.

Family	Species	Distribution I	II									III	IV	V
			a	b	c	d	e	f	g	h	i			
Plumbaginaceae	*Aegialitis rotundifolia* Roxb.													+
Poaceae	*Aeluropus lagopoides* (L.) Trin.													+
	Myriostachya wightiana Hk. f.													
	Porteresia coarctata (Roxb.) Takeaka													
	Sporobolus virginicus Kunth													
	Urochondra setulosa (Trin.) Hubbard													
Rhizophoraceae	*Bruguiera gymnorhiza* (L.) Lamk. *	+	+	+	+	+	+	+	+		+		+	+
	(= *Bruguiera conjugata* Merr.)													
	Bruguiera cylindrica (L.) Blume *	+		+	+	+		+						+
	(= *Bruguiera caryophylloides* Bl.)													
	(= *Bruguiera caryophylloides* Burm.)													
	Bruguiera parviflora (Roxb.) Wight & Arn.	+	+	+			+	+	+	+				+
	Bruguiera sexangula (Lour.) Poir *	+	+	+	+	+								+
	(= *Rhizophora eriopetala*													
	Ceriops decandra (Griffith) Ding Hou *	+	+	+	+	+		+					+	+
	(= *Ceriops roxburghiana* Arn.)													
	Ceriops tagal (Perr) C. B. Robins *	+	+	+	+	+	+	+	+	+			+	+
	(= *Ceriops candolleana* Arn.)													
	Kandelia candel (L.) Druce *	+		+		+	+	+		+			+	
	(= *Kandelia rheedi* W. & A.)													
	Rhizophora mucronata Lamk. *	+	+	+	+	+	+	+	+	+	+			+
	Rhizophora stylosa Griff. *			+		+								
	Rhizophora apiculata Blume *	+	+	+	+	+	+	+		+	+			+
	(= *Rhizophora conjugata* (non L.) Arn.													
	(= *Rhizophora candelaria* DC.)													
	Rhizophora lamarckii Montrouz *					+								
Rubiaceae	*Guettarda speciosa* L.													+
	Scyphiphora hydrophyllacea Gaertn.													+
Salsolaceae	*Salsola foetida* Delile													
	Salsola kali L.													
Salvadoraceae	*Salvadora persica* L. *													
	Salvadora oleoides Dcne *													
Sonneratiaceae	*Sonneratia apetala* Buch-Ham. *	+	+	+	+	+		+	+		+			+
	Sonneratia alba J. Sm. *		+					+	+					+
	Sonneratia griffithi Kurz. *													
	Sonneratia caseolaris (L.) Engler *		+	+			+	+	+	+			+	+
	(= *Sonneratia acida* (L.) Back.)													
Sterculiaceae	*Heritiera fomes* Buch-Ham. *	+		+										
	(= *Heritiera minor*)													
	Heritiera littoralis Dryand ex. Ait. *	+	+	+			+	+	+					+
	Kleinhovia hospita Linn.													+
Tamaricaceae	*Tamarix gallica* L.													+
Tiliaceae	*Brownlowia lanceolata* Benth.													+
Verbenaceae	*Clerodendron inerme* (L.) Gaertn.													+
Filicopsida (ferns)	*Acrostichum aureum* L.													+
	Acrostichum speciosum Willd.													+
	Stenochlaena palustre (Burm.) Bedd.													

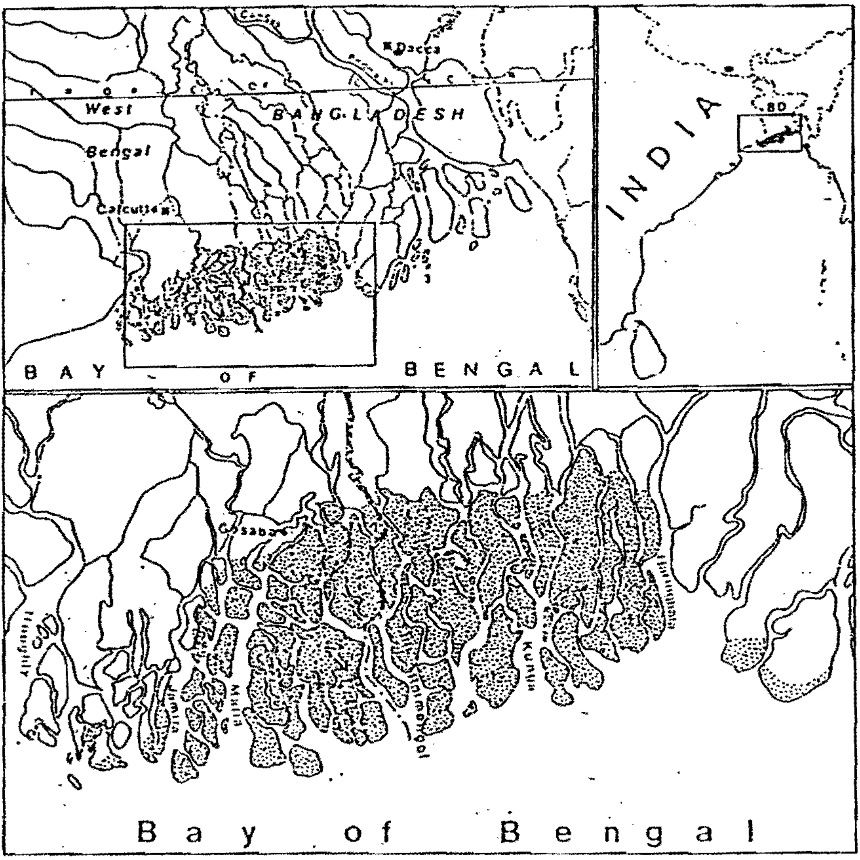


Figure 8. Sunderbans (stippled areas) in Ganges-Brahmaputra delta in India and Bangladesh.

(1933), Champion and Seth (1968), and Blasco (1977). Four or five zones are generally recognised in relation to the salinity gradient.

In the most saline inland areas, a scrub vegetation (referred to as back mangroves) is composed chiefly of *Salicornia brachiata*, *Heliotropium curassavicum*, *Suaeda maritima*, and *Sesuvium portulacastrum*. Occasionally, bushy growth form of *Aegialitis rotundifolia* and *Aegiceras corniculatum* occur on river banks. In areas regularly leached by freshwater, tall and dense forests (dense mangroves) that are dominated by *Heritiera fomes* ("Sunderi" in Bengali from which these forests derive their name), *Excoecaria agallocha*, *Xylocarpus moluccensis*, *Bruguiera cylindrica*, and *Sonneratia apetala*. *Ceriops decandra*, *Avicennia officinalis* and *A. corniculatum* are other important species but *Nypa fruticans* is now rare. In moderately saline water, *Rhizophora* and *A. rotundifolia* are abundant while saltwater areas are dominated by *Avicennia alba*, *A. marina*, *X. granatum*, and *Kandelia candel* (Ahmad 1966). A palm (*Phoenix paludosa*) occurs throughout the mangroves and forms dense stands in tidal zones near the edges of water courses. Other common species in the palm swamps are *E. agallocha* and *S. apetala*.

In the Sunderbans of West Bengal, freshwater contribution through the Ganga river is practically negligible and over the last few centuries major flow of the Ganges has been diverted from Bhagirathi to Padma. Considerable changes have subsequently occurred in the morphology of Ganges delta. This is supposed to have been the result of tectonic and morphogenetic uplift of the western part together with a eastward shift of the river (Gupta 1957, Chowdhury 1966). The lack of freshwater flow has affected the mangrove species such as *H. fomes* and *N. fructicans* which have practically disappeared from Indian part of Sunderbans.

The flow of sufficient freshwater through the Ganges-Brahmaputra riverine system throughout the year is essential for the deltaic mangroves of both India and Bangladesh. It may be pointed out that recent efforts in India to augment this flow (which would help restore the ecological balance, save species from extermination and also reduce siltation in Indian ports) have resulted in intergovernmental disputes.

2. *Mahanadi delta*. The River Mahanadi forms a delta somewhat southwest of the Sunderbans on the east coast. Mangroves here cover a relatively small area and very little is known of them although they are highly disturbed. These mangroves are floristically very similar to the Sunderbans as *H. fomes*, *H. littoralis*, and *P. paludosa* occur here as well. Recent studies show that many species, particularly *Kandelia rheedii* and *Rhizophora conjugata* have disappeared from this region during recent decades (Anonymous 1987a). *Aegialitis rotundifolia*, now restricted to Sunderbans, also occurred earlier in these mangroves (Rao and Sastry 1974). Species like *R. mucronata*, *A. majus*, and *P. paludosa* are now rare. Though earlier studies recognised a deltaic swamp forest zone and a littoral scrub fringe, the vegetation is highly degraded with stunted growth due to soil erosion and increasing salinity. Rao and Mukherjee (1972) recognised seven vegetation zones along Burabalanga estuary (Balasore district) and related them to differences in soil texture, moisture gradient, and soil chemistry. However, detailed information on these mangroves is not available.

3. *Godavari and Krishna deltas*. Southwards on the Andhra coast, the deltas of the Godavari and Krishna Rivers lying adjacent to each other support the second largest mangrove complex in the region. Dense mangrove forests also exist at Yanam on the banks of the Coringa river near Kakinada and in the Gautami-Godavari deltaic system. These mangroves are relatively better known floristically and ecologically.

The region is characterised by large seasonal variations in salinity. During the monsoon, the river Godavari carries large amounts of freshwater and salinity remains very low for at least half a year from July, and especially between October–November when rainfall is high (exceeding 200 mm a day). On the other hand, the development of an off-shore sand bar in the Coringa region has reduced the influence of sea water. However, during the dry season the salinity increases considerably.

Floristically, Godavari delta forms the dividing line between the mangroves of Mahanadi and Sunderbans on one hand and those of the peninsular India on the other. Venkateswarlu (1944) reported some 26 species of mangroves from the mouths of Godavari and Gautami rivers. More detailed studies in the Godavari delta were made by R. S. Rao (1959), Sidhu (1963), Venkatesan (1966), and T. A. Rao *et al.* (1972). The mangroves differ from those elsewhere in India in the dominance of *Avicennia* (represented by all the three species, *A. marina*, *A. alba*, and *A. officinalis*), *S. apetala*, and a grass (*Myriostachya wightiana*) which occurs otherwise only in Sunderbans. Members of the Rhizophoraceae are very rare except near river banks where *Bruguiera gymnorhiza* and *R. mucronata* are common. *Avicennia officinalis* and *Hibiscus tiliaceus* are common along rivers. Among other species, *E. agallocha*, *Dalbergia spinosa*, and *Stictocardia tiliaefolia* are common in somewhat inland areas.

4. *Cauvery delta.* Further south in Tamil Nadu, mangroves occur in the Cauvery delta Fig. 9). The mangrove forests in the region of Pichavaram (Vellar estuary) and Muthupet-Chattram (Cauvery proper) are also among the best studied wetlands (Rajagopalan 1952, Venkatesan 1966, Blasco and Caratini 1973, Caratini *et al.* 1973, Krishnamurthy *et al.* 1981, Krishnamurthy 1983, Lakshmanan *et al.* 1984). These mangroves are rich in species, and exhibit a clear zonation but occupy a very small area.

Near the shores, on constantly wet soils, there is a narrow belt of dense forest (Fig. 9) dominated by *R. apiculata*, *R. mucronata* and other Rhizophoraceae including *B. cylindrica* and *S. apetala.* Other common species are: *Lumnitzera racemosa*, *Aegiceras corniculatum*, *C. decandra*, and *Derris trifoliata.* Behind this belt is a belt of smaller trees of *A. marina* with shrubby undergrowth of *S. maritima* and *E. agallocha*. Further inland only halophytic shrubs and herbs like *S. brachiata*, *Acanthus ilicifolius*, *S. portulacastum*, and *A. indicum* are found on periodically flooded highly saline soils.

Small patches of mangroves occur also on Pamban, Rameshwaram and other islands in the Gulf of Mannar but these have rarely been investigated (T. A. Rao *et al.* 1963 a,b). Common species are: *Rhizophora conjugata, A. alba*, *C. tagal*, *E. agallocha*, and *Arthrocnemum indicum.*

5. *West coast mangroves.* The west coast is characterized by the funnel

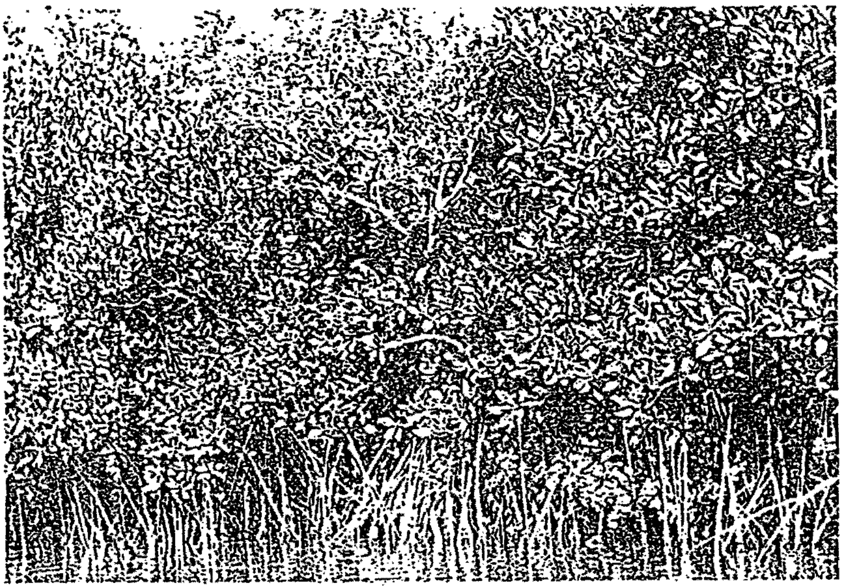


Figure 9. Mangrove forest dominated by *Rhizophora apiculata* and *Rhizophora mucronata* at Pichavaram in Cauvery delta.

shaped estuaries and typical deltas with alluvial deposits are almost totally absent. Thus, the mangroves on the west coast are of estuarine and backwater type as compared to deltaic type on the east coast. They are not extensive and are rapidly disappearing under anthropogenic pressure. Further, these mangroves differ markedly from those of the east coast by the absence of palms, and species of *Heritiera* and *Xylocarpus* (Table 5) whereas some species like *Sonneratia caseolaris* and *Urochondra setulosa* occur only on the west coast. An overview of these mangroves is provided by Untawale (1984).

In Kerala (most southern part of the Peninsula) only small mangrove area are now left near Quilon and Cochin. The mangroves at Veli near Trivandrum disappeared only about two decades ago. An important species still found in Kerala is *Cerbera manghas* (Blasco 1975).

North of Kerala, small areas of fringing mangroves occur on the Karnataka coast (Untawale 1984, Radhakrishnan 1985, Untawale and Wafar 1986). Fourteen species have been recorded with the dominants being *A. marina*, *A. officinalis*, *S. caseolaris*, *R. conjugata*, *R. mucronata*, *A. corniculatum*, *E. agallocha*, *H. littoralis*, *Cynometra numosoides*, and *Acanthus ilicifolius*.

The distribution, zonation, and ecology of mangroves around Goa have been studied in detail by Dwivedi *et al.* (1975), Bhosale (1978), Untawale *et al.* (1973, 1982), and Jagtap (1985, 1986). Most important mangroves occur along the Mandovi and Zuari estuaries. There are about twenty species of which *S. caseolaris*, *K. candel*, *R. mucronata*, *R. apiculata*, *S. alba*, *A. officinalis*, *B. parviflora*, *A. ilicifolis*, and *Derris heterophylla* are important. Untawale *et al.* (1982) described zonation of vegetation in relation to salinity (oligohaline to polyhaline) and sediments. *Sonneratia caseolaris* and *Acrostichum aureum* occur in oligohaline areas with silty substrata whereas polyhaline zones with sandy clay substrate are occupied by *R. mucronata*, *B. parviflora*, *A. marina*, and *S. alba*.

Further north, in the state of Maharashtra, mangroves occur around Bombay (Fig. 7) in small patches along creeks and on small islands. These are among the best studied mangroves in the country and many systematic and eco-physiological studies have been made (Cooke 1901–1908, Blatter 1905, Navalkar 1951, 1956, 1973, Qureshi 1959, Patil 1959, Kumar and Chaphekar 1985). The vegetation is dominated mainly by shrubby *R. apiculata* (Joshi and Bhosale 1982). *Rhizophora mucronata*, *B. cylindrica*, and *C. tagal* occur along the sea shore but inland the vegetation consists mainly of dense growth of *Avicennia* spp. and *E. agallocha*. *Salicornia brachiata* and *Derris scandens* are also found. *Sonneratia apetala*, and *S. alba* occur on some islands (Blasco 1977). Navalkar (1956) reported *K. candel* which is not found here any more. The presence of Salvadoraceae (*Salvadora persica* and *S. oleoides*) in Bombay is of interest as these are considered to represent old mangroves (Qureshi 1959). *Salvadora oleoides* does not occur at latitudes south of Bombay (Blasco 1975).

The halophytic formation in the Saurashtra region (Fig. 7) are often classified as mangroves but do not have characteristic mangrove plants (Rao and Aggarwal 1964, Rao *et al.* 1966, Rao and Shanware 1967). The area has been already described above as the seasonally flooded wetland. Only in the Gulf of Kutch, stunted woody growth of *A. marina* is obtained.

6. *Mangroves of Andaman-Nicobar islands*. The Andaman and Nicobar group of islands (Fig. 7) in the Bay of Bengal (6 to 14° N and 92 to 94° E) have an irregular coastline deeply indented with numerous tidal creeks and sheltered bays which provide excellent habitats for mangroves. These more or less virgin mangroves, due to the remoteness of the islands and low population density, account for about 17% of India's total mangrove area (Table 4). There are number of floristic surveys (Parkinson 1923, Chengapa 1944, Banerji 1958a,b, Sahni 1953, Thothathri 1960a,b, 1962) of this region, and in recent years, Mall *et al.* (1982, 1986) have made ecological studies of these mangroves. Floristically, the mangroves of Andaman-Nicobar islands stand in great contrast with those of the peninsular India (Thothathri 1981). *Nypa fruticans*, absent from peninsular India, is most abundant here. Other dominant species are: *R. mucronata*, *R. stylosa*, *R. apiculata*, *B. gymnorhiza*, *B. parviflora*, *C. tagal*, and *A. corniculatum*. *Xylocarpus granatum* and *Lumnitzera littorea* are also abundant but rare on the coasts of peninsular India.

Other important species found only in the island mangroves are *Guettarda speciosa*, *Hernandia ovigera*, *Brownlowia lanceolata*, and *Scyphiophora hydrophyllacea*. However, *Aeluropus lagopoides*, and *Porterasia coarctata* are absent from these islands. *Sonneratia apetala* reported absent earlier by Blasco (1975) has been recorded recently by Mall *et al.* (1986). Epiphytes like *Hydrophytum formicarum* and *Dischidia major* and the orchid *Papilionanthe teres* are also very common.

The vegetation zones based on the frequency and duration of inundation have been recognised by Mall *et al.* (1986). These are: a. Proximal zone with prolonged and most frequent inundation, b. Middle zone lying inwards and less frequently flooded, and c. Distal zone on the landward fringe with higher salinity. Species of *Rhizophora* dominate the proximal zone whereas species of *Bruguiera*, *C. tagal*, and *L. littorea* occur in the middle zone. *Excoecaria agallocha*, *Nypa fruticans*, and *H. littoralis* commonly occupy the distal zone.

7. *Mangroves of Pakistan*. The mangroves of Pakistan are confined to coastal Sind, particularly in the Indus delta and cover approximately 2,495 km^2 (Khan 1966, Saenger *et al.* 1983). They are nearly similar to those on the West coast of India but are floristically poor, being represented by only eight species (Table 5, Nasir and Ali 1970–85). There are several reports on the distribution and general ecological problems (Champion *et al.* 1965, Khan 1965, 1966, Kogo 1985, Ansari 1987) of these mangroves but detailed ecological studies have not been done.

Avicennia marina is the most dominant species forming dense mangroves along the creeks on recent alluvium. It is often associated with *C. tagal*. In the Indus delta, the normal mangrove vegetation is composed of *R. mucronata*, *R. apiculata*, *B. gymnorhiza*, *A. corniculatum*, and *S. caseolaris*. The associated vegetation in the sheltered areas include many other halophytes.

During recent years, many dams and barrages have been constructed on the river Indus for agriculture. Therefore, freshwater discharge into the coastal areas is small for about 9 months of the year. As a result, mangroves of the Indus delta are becoming decadent and their growth is retarded (Saenger *et al.* 1983, Ansari 1987).

8. *Mangroves of Sri Lanka*. Mangroves in Sri Lanka occur along the sea coast throughout the island (Fig. 10). In Jaffna peninsula (in the region of Gulf of Mannar) mangroves extend to seafront while in other places they are confined to estuaries and lagoons. The northern lagoons are in permanent communication with the sea (Raphael 1977) but those in the south are partially closed by sandbars for most part of the year and hence, experience lesser influence of sea. The tidal amplitude is also small (about one metre) and therefore, variation in inundation levels is not significant. The estimates

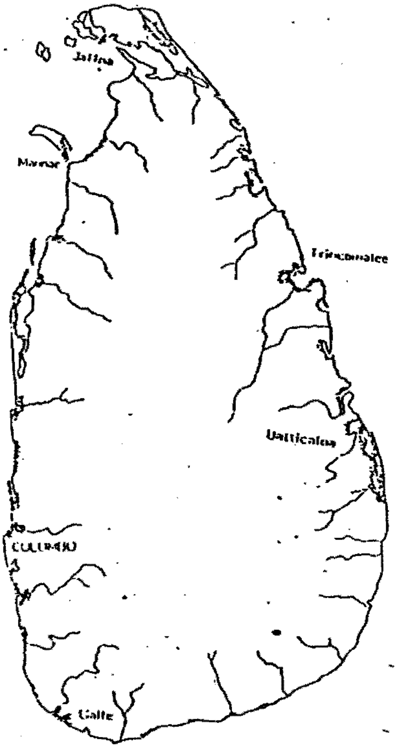


Figure 10. Distribution of mangroves in Sri Lanka (adapted from Jayewardene 1987).

of area under mangroves in Sri Lanka vary considerably: Seneviratne (1978) estimated the cover between 320 and 400 km^2 whereas Arulchelvam (1968) and Saengar *et al.* (1983) put the estimate at only 40 and 36 km^2 respectively. More recent estimates using remote sensing techniques show that about 63 km^2 mangrove area lies in the six coastal districts (Jayewardene 1987). The mangrove definitely occupied in the past a much larger area, most of which has been now reclaimed.

Thirty seven species of mangrove plants, including the associates, occur in Sri Lanka (Jayewardene 1987). *Rhizophora mucronata* or *R. apiculata* dominate near water's edge or on steep shores or river banks. Behind them, *B. gymnorhiza, S. caseolaris, A. officinalis, A. marina, C. tagal, C. decandra, A. corniculatum, Scyphiophora hydrophyllacea,* and *L. racemosa* are abundant. *Nypa fruticans* occurs on the southeastern coast and in some lagoons (Abeywickrama 1966). Though peats are not known from Indian mangroves, Abeywickrama (1966) has reported large peat deposits at Muturajawela in Sri Lanka.

Mangroves of Sri Lanka have been grouped into five types (de Silva 1985) namely: a. riverine mangroves in the estuaries of major rivers on south and southwest coast, b. fringing mangroves along shallow lagoons, c. basin mangroves associated with Vadamarachchi lagoon, d. scrub mangroves with stunted growth along lagoons on the east and west coasts, and e. overwash mangroves on small islands in Puttalam and Negombo lagoons.

9. *Mangroves of Burma.* The mangroves of Burma are distributed between 20 and 10° N Latitude and 94 and 98° E Longitude. They occur in estuarine areas and deltas wherever tidal action provides suitable conditions for growth of mangroves. Many islands along southern coastline have extensive mangrove forests. There are no accurate data on the mangroves of Burma. Wolker (1966) reported an area of about 5,200 km² in the Irrawaddy delta alone, leaving large areas on Arakan and Tennasserim coasts. Recently Than Htay and Saw Han (1984) put the estimate at over 5,700 km² of which 2,750 are in Irrawady delta, 1,863 on the Tenasserim coast, and 1,020 on the Arakan coast.

Moodie (1924–25) and Stamp (1925) referred to mangroves in the Irrawaddy delta and suggested that they are similar to mangroves in the Ganges-Brahmaputra delta. Like eastern Sunderbans, the deltaic mangroves in Burma are also dominated by *H. fomes* in freshwater dominated zones and *R. mucronata* in areas flooded with seawater. Other common taxa are: *B. gymnorhiza*, *A. officianalis*, *X. moluccensis*, *S. apetala*, *S. acida*, *E. agallocha*, *Ceriops roxburghiana*, and *N. fruticans*. The Arakan coastline is also dominated by members of Rhizophoraceae (*R. mucronata*, *B. gymnorrhiza*).

Associated fauna. Mangroves support a large diversity of both vertebrate and invertebrate fauna (A. N. Rao 1987) which are adapted to different salinity and hydrological gradients. In south Asia, the fauna of Indian Sunderbans have been investigated in more detail than of other mangroves (Chaudhuri and Chakrabanti 1973, Choudhury *et al.* 1984, Kurian 1984, Sarkar *et al.* 1984, Chakraborty and Choudhury 1986, Samant 1986, Kasinathan and Shanmugam 1986, Palaniappan and Baskaran 1986, Naskar and Guha Bakshi 1987, Mandal and Nandi 1989). There are also a few reports on the mangrove fauna of Sri Lanka (Pinto 1984, 1986, Jayewardene 1987) and Pakistan (Kogo 1985, Ansari 1987). Estuarine fisheries of India have been described in detail by Jhingaran (1982). Among invertebrates, more than 500 species of insects and Arachnida, 229 species of crustacea, 212 species of molluscs, 50 species of nematodes, and 150 species of planktonic and benthic organisms are known from Indian mangroves (Anonymous 1987a). Vertebrate fauna are represented by 300 species of fish, 177 species of birds, 36 species of mammals and 22 species of reptiles. Many of these are economically exploited.

Whereas some animals are only temporary visitors and move in and out of the mangroves at different times of the year, many are characteristic of these habitats. Important invertebrates include prawns (*Penaeus indicus*, *P. merguiensis*, *P. monodon*, *Macrobrachium rosenbergii*), crabs (*Uca lactea*. *Scylla serrata*, *Thalassina* sp., *Sesarma fascinata*, *Canosesarma minuta*, *Telescopicum telescopicum*, *Cerithidea alata*, *Clibanarius longitarsus*), molluscs, and oysters (*Crassostrea cucullata*, *Mytilus* sp.) and many insects especially honey bee (*Apis dorsata*, *Apis mellifera*), weaver ants (*Oecophylla* sp.), and mosquitoes (*Anopheles sundericus*, *Anopheles indigo*, *Culex fatigans*, *Aedes butleri*, *Aedes niveus*). Common fishes are mudskippers (*Periophthalmus* sp.), carangids, cluepeids, serranids, sciaenids, mullets, hilsa, seabass, and milkfish. Avifauna includes herons, storks, sea eagles, egrets, kingfishers, sandpipers, tits, and whistlers. Flamingoes are abundant in most of the areas (particularly Kutch). Frogs (*Rana hexadactyla*) and toads (*Rhocophorus maculatus*) are also common in Sunderbans. Sunderbans are well known for the Royal Bengal Tiger (*Panthera tigris*). In view of the rapid decline in tiger population, about 200 km^2 area of Indian Sunderbans (in 24–Paragnas district) had been protected as a Tiger Reserve in 1973. Chital deer (*Axis axis*), another mammal found only in Sunderbans, has also been recently protected to save it from extinction. Another important animal in Indian mangroves is crocodile (*Crocodylus porosus*) which occurs only in Mahanadi delta (Orissa) and in Andaman Nicobar islands. Excessive exploitation in the past reduced its populations to small number but the trend has now been reversed by breeding them in crocodile farms in coastal areas. The Pacific Ridley turtle (*Lepiodochelys olivaceae*) also nests on adjacent beaches. Other noteworthy animals are: dolphins (*Platenista gangetica*), mangrove monkey (*Macaca mulatta*), and otter (*Lutra perspicillata*).

Mention must also be made here of wild ass (*Asinus hemionus*) which occurs only in Kutch and feeds on saline scrub and grass. It is also an endangered species and efforts are being made to conserve it.

Important animals in mangroves of Sri Lanka (Pinto 1986) are: Portunid crabs (*Thalamita crenata*, *Portunus pelagicus*, *Scylla serrata*), Fiddler crabs (*Macrophthalmus depressus*, *Uca lactea*, *Uca dussumieri*), Graspid crabs (*Neosermatium malabaricum*, *Metaspograpsus messor*, *Chiromantes indiarum*), mud lobster (*Thalassina anomala*), prawns (*P. indicus*, *Metapenaeus dobsoni*, *M. rosenbergi*), molluscs (*Nerita polita*, *Littorina scabra*, *Gaffrarium tumidum*, *Geloina coaxans*), oysters (*Saccostrea* sp. and *Crassostrea* sp.) and mud skipper (*Periophthalmus sorbinus*).

In Pakistan, mangrove fauna include about 100 species of fish of which perciformes (46 species) and clupeiformes (15 species) are dominant groups (Ansari 1987). Many species of prawns, crabs and other crustaceans are abundant and form a major component of mangrove fauna. Lizards (*Stenodactylus orientalis*, *Acanthodactylus cantoris*, *Ophiomorus tridactylus*), and sea snakes (species of *Hydrophis*, *Microcephalopphis*, *Pelanis*) are also common.

Freshwater wetlands

Freshwater wetlands associated with both lentic and lotic waterbodies are widely distributed throughout the subcontinent from sea level to about 2,000 m in the Himalayan ranges. Because of the distinct seasonality in rainfall and a prolonged dry summer season, there are few permanently flooded natural areas. There are numerous man-made reservoirs that are generally small and shallow and often dry up completely during the summer. The large reservoirs also exhibit such large water level changes that their relatively large shallow littoral zones are subject to periodic drying. Thus, permanently flooded wetlands are rather rare, and most freshwater wetlands are only seasonal. Further, the long dry period is not conducive to the establishment and growth of woody species and most of the wetlands are, therefore, dominated by herbaceous vegetation. Forested or shrub dominated wetlands are confined to areas adjacent to perennial lotic water bodies. The herbaceous wetlands of temporary or permanent and lentic or lotic habitats exhibit only small differences in their floristic composition.

The relationship between the vegetation of different wetlands and their hydrological regimes has received little attention, and therefore a detailed account of wetland types suggested earlier (Table 3) is not possible. For the purpose of this review, freshwater wetlands are simply grouped into forested and herbaceous wetlands.

Forested wetlands

Forested wetlands occur primarily along rivers and are adapted to periodic flooding that is associated with the monsoonal rainy season. Wetland forests are, thus, best designated as floodplain or riparian forests. Forested wetlands of the Indian subcontinent are among the least investigated ecosystems. Besides a few preliminary studies, the only account of these wetlands is that by Champion and Seth (1968) whose classification is shown in Table 2. They emphasized that "ecologically they may be viewed as stages in natural succession or as edaphic preclimaxes". Following their scheme of classification, some important features of forested wetlands are given below.

Freshwater swamp forests. These forests occur on wet alluvium on the floodplains of rivers where soils are waterlogged throughout the year. These are subdivided into two categories.

1. Myristica *swamp forests*. They are distributed only in Travancore (Kerala) along streams (below 300 m altitude) on sandy alluvium rich in humus (Krishnamoorthy 1960). The soils are inundated during the latter half of the year. The dense evergreen, 15–30 m high forests are dominated by *Myristica mag-*

Mangrove Ecosystem: Structure and Function

Introduction

The term "Mangrove" was much used to define the coastal forests and individual plants of coastal forests and sometimes it meant for both as "Mangrove plants" and "Mangrove ecosystem" (Mac Nae, 1968). Chapman (1976) has defined these two terms separately, viz "Mangal": as the forest formation and "Mangrove": as intertidal plants. Therefore, quintessential mangrove ecosystem has, as a key component, trees with aerial roots that are frequently inundated by tides. However, physiognomy varies with local biotic and edaphic factors and physical gradients in which mangroves are found. Besides, a wide spectrum of other flora and fauna form an intrinsic part of mangrove ecosystem.

Origin and Dispersion

The earliest mangrove species originated in the Indo-Malayan region. This may account for the fact that there are far more mangrove species present in this region than anywhere else. Because of their unique floating propagules and seeds, some of these early mangrove species spread westward, borne by ocean currents, to India and East Africa, and eastward to the Americas, arriving in Central and South America during the upper Cretaceous period and lower Miocene epoch, between 66 and 23 million years ago. During that time, mangroves spread throughout the Caribbean Sea across an open seaway which once existed where Panama lies today. Later, sea currents meight have carried mangrove seeds to the western coast of Africa and as far south as New Zealand. This might explain why the mangroves of West Africa and the Americas contain fewer, but similar colonizing species, whereas those of Asia, India, and East Africa contain a much fuller range of mangrove species (Alfredo Quarto 1994).

Global Distribution

Global distribution of mangrove have been divided into two zones 1) Indo-Pacific Region and 2) Western Africa and America (Rao A. N. 1994).The Indo-Pacific Region comprises East Africa, the Red Sea, India, South East Asia, Southern Japan, Philippines, Australia, New Zealand and the South eastern Archipelago as far as Samoa. The West Africa –America Region includes the Atlantic coast of Africa and Americas, the Pacefic coast of Tropical America, and the Galapagoes Island (Rao A. N. 1994).

Mangroves are present in 112 countries and territories (Kathiresan 2005). Further, they are largely restricted to latitudes between 30° north and 30° south.

Northern extensions of this limit occurs in Japan (31°22′N) and Bermuda (32°20′N); southern extensions are in New Zealand (38°03′S), Australia (38°45′S) and on the east coast of South Africa (32°59′S; Spalding, 1997, Yang *et al.*, 1997). Global coverage has been variously estimated at 10 million hectares (Bunt, 1992), 14-15 million hectares (Schwamborn and Saint-Paul, 1996), and 24 million hectares (Twilley *et al.*, 1992). Spalding (1997) gave a recent estimate of over 18 million hectares, with 41.4% in south and southeast Asia and an additional 23.5% in Indonesia. Mangroves are not native to the Hawaiian Islands, but since the early 1900's, at least 6 species have been introduced there.

Mangrove in India

India has a coastline of about 7517 km. bounded by the Indian Ocean predominantly comprising of Indian Sea, Arabian Sea and the Bay of Bengal. The Indian coastline is distributed into nine coastal states and four Union Territories. As per the density classification adopted by Forest survey of India (FSI), the country total 4,445 sq. km of mangrove cover of which 1,147 sq. km. (25.80% of mangrove cover) very dense mangrove cover; 1,629 sq. km. (36.64% of mangrove cover) moderately dense mangrove cover while 1,669 sq. km. (37.54%) open mangrove cover in 2005. Compared to the 2001 assessment, there was a marginal net decrease by 3 sq. km. in the mangrove cover in the country in 2005. Gujarat and West Bengal, however, showed increase whereas a sizable net reduction has been registered in Andaman & Nicobar Islands.

The distribution of mangrove area and total mangrove cover on the East and West Coasts of India are indicated below:

Table 1 Density Classification of Mangrove Cover in Different States (FSI, 2005)

Sr. No.	State/UT	Very Dense Mangrove	Moderately Dense Mangrove	Open Mangrove	Total
1.	Andhra Pradesh	0	15	314	329
2.	Goa	0	14	2	16
3.	Gujarat	0	195	741	936
4.	Karnataka	0	3	0	3
5.	Kerala	0	3	5	8

Sr. No.	State/UT	Very Dense Mangrove	Moderately Dense Mangrove	Open Mangrove	Total
6.	Maharashtra	0	58	100	158
7.	Orissa	0	156	47	203
8.	Tamil Nadu	0	18	17	35
9.	West Bengal	892	895	331	2,118
10	Andaman & Nicobar Islands	255	272	110	637
11	Daman & Diu	0	0	1	1
12	Pondicherry	0	0	1	1
	Total	1,147	1,629	1,669	4,445

Mangrove in Gujarat

Gujarat has the mangrove forest cover of 936 Km^2 (FSI report 2005) covering 195 sq Km dense forests and 741 sq Km sparse mangrove forests. The mangrove forests are predominantly distributed over three mangrove zones and, as we move southwards on the coastline of Gujarat, these zones are Kori creek, Gulf of Kachchh and Gulf of Khambhat. Out of the 26 districts of the state, the state has 15 coastal districts. However, as per the FSI report (2005), the mangrove cover of 936 km2 is spread, rather unevenly, over 10 districts only. About 75.53% (707 km2.) of the total mangrove forest is located in the single district of Kachchh, covering the forests of Kori creek. While 16.02% (150 Km2.) mangrove forests are distributed in Jamnagar district which covers the mangrove forests of Gulf of Kachchh. The remaining 8.4% (79 km2) are distributed in eight districts hosting the mangrove forests of Gulf of Khambhat.

Floristic Diversity of Mangrove

The decisive factors to identify the mangrove species have not been yet recognized globally. The plants mostly growing in the inter-tidal regions and sharing some morphological and physiological features are called mangroves. The mangrove species identified by various scientists for different regions are given in Table -2.

Table-2 No. of mangrove species identified by different Scientists for various regions

Scientist	**No. of Mangrove Species**	**Geographical Regions**
Walsh (1974)	55	Global
Blasco *et al.* (1975)	60	Global
Chapman (1976)	90	Global
Saenger *et al.* (1983)	60	Global
Tomilson (1986)	54-75	Global
Naskar & Guha Bukshi (1987)	35	India
Untawale *et al.* (1987)	33/47	India
Bunerjee, *et al.* (1989)	59	India
Kathiresan (2005)	72	India

Floristic Distribution of Mangrove – Global Aspect

The rich regions in species diversity are Malay Archipelago (44 spp), South East Asia (37 spp), South Asia (35 spp), East Asia (27 spp), and Australia (18 spp). The regions supporting less mangrove diversity are Africa (12 spp), Central South America (9 spp), Southwest Pacific (9 spp), West Pacific (6 spp) South east USA (5 spp) (Anonymous 1986).

Avicennia marina is known to be most wide spread in Indo west Pacific Region. However, it distribution in equatorial latitude, is less as compared to *Avicennia alba*. Further, the members of Rhizophoraceae are commonly seen in mangrove forests. Although the one genus of the member of this family, *Rhizophora,* is exceedingly common around the world, none of the individual species is actually cosmopolitan. However, *R. mangle* (Red mangrove), is the most widespread species among all other species of *Rhizophora*. In Old World (Indo-Pacific Region), *Bruguiera gymnorrhiza* is especially widespread, ranging from East Africa to eastern Australia, Samoa in the Pacific Basin, and the Ryukyu Islands in Asia. There are other exceedingly widespread species of this family in Old World mangal, including the two species of *Ceriops* and *Kandelia candel*.

Avicennia spp, black mangrove, is ubiquitous in mangals. In the Western Hemisphere, *A. germinans* is co-dominant with red mangrove, *R. mangle*, and a variant of this *Avicennia* occurs along the coastline of West Africa. Two other species in the genus may be found in the New World. *Avicennia marina* is the most widespread species of the Old World, extending from East Africa to Fiji in Polynesia and the North Island of New Zealand, and occurring at the coldest localities in New Zealand, subtropical China (26 degrees north latitude), and southeastern Australia (Victoria, at 38.45 degrees south latitude).

Sonneratia alba (family Sonneratiaceae) is characteristic of the tropical mangal of the Old World, generally appearing with *Avicennia, Excoecaria agallocha* (family Euphorbiaceae), *Xylocarpus granatum* (family Meliaceae), *Aegiceras corniculatum* (family Myrsinaceae; a shrubby understory), *Osbornia octodonta* (family Myrtaceae), and *Lumnitzera racemosa* (family Combretaceae).

In mangal of the Americas, diversity of the woody species is much lower. In addition to *Rhizophora mangle* and *Avicennia germinans,* a visitor to a New World mangrove swamp is likely to find *Laguncularia racemosa* (family Combretaceae) and either *Conocarpus erectus* (family Combretaceae) or *Pelliciera rhizophorae* (family Pellicieraceae).

The Nypa palm, *Nypa fruticans,* is a very aggressive colonizer of estuarine banks and lagoons of the Old World tropics. This plant crowds out all potential competitors by forming subterranean rhizomes in the mud, from which arise the pinnately compound leaves. The other monocotyledon of mangal, species of *Pandanus,* most commonly grows in coastal swamps than within the dense thicket of mangal. The only terrestrial ferns of mangal are species of *Acrostichum,* which tend to grow in less saline microhabitats and also can tolerate shade, but are still very tolerant of salinity.

Floristic Diversity of Mangroves in India

There are different reports about the mangrove species diversity in India. Blaso (1975) recorded 60 species and 41 genera belonging to 29 families. Untawale (1985) opined that the mangrove diversity of India comprise of 59 species, 41 genera belonging to 29 families. According to the Botanical Survey of India (Mangroves in India- Identification Mannual 1989) India has 59 species under 41 genera and 41 families which comprise the major and significant part of Indian Mangrove flora. Of these, 34 species are present on the East Coast, 45 species on Andaman and Nicobar Islands and 25 species on West Coast. Kathiresan (2005) has opined that India has 71 species of mangroves and associates belonging to 43 genera and 28 families. Of these 65 species (belonging to 43 genera and 28 families) occur on the East Coast, 45 species (belonging to 28 genera and 20 families) occur on the Andman & Nicobar Islands and 38 species (belonging to 25 genera and 18 families) occur on the West Coast.

Table 3 Mangrove Species Recorded on West Coast of India (Kathiresan 2005)

Sr. No.	Family	Genera	Species
1.	Acanthaceae	*Acanthus*	*ilicifolius*
2.			*ebracteatus*
3.	Apocynaceae	*Cerbera*	*manghas*
4.			*odollam*
5.	Avicenniaceae	*Avicennia*	*alba*
6.			*marina*
7.			*officinalis*
8.	Bignoniaceae	*Dolichandrone*	*spathaceae*
9.	Caesalpiniaceae	*Caesalpinia*	*bonduc*
10.			*crista*
11.	Combretaceae	*Lumnitzera*	*racemosa*
12.	Cyperaceae	*Scirpus*	*littoralis*
13.	Euphorbiaceae	*Excoecaria*	*agallocha*
14.	Flagellariceae	*Flagellaria*	*indica*
15.	Lythraceae	*Pemphis*	*acidula*
16.	Malvaceae	*Hibiscus*	*tiliacceus*
17.		*Thespesia*	*populnea*
18.	Meliaceae	*Xylocarpus*	*granatum*
19.			*mekongensis*
20.			*moluccensis*

21.	Myrsinaceae	*Aegiceras*	*corniculatum*
22.	Papilionaceae	*Derris*	*scandens*
23.			*trifoliata*
24.		*Mucuna*	*gigantea*
25.	Poaceae	*Myriostachya*	*wightiana*
26.		*Porteresia*	*coarctata*
27.		*Urochondra*	*setulosa*
28.	Pteridaceae	*Acrostichum*	*aureum*
29.	Rhizophoraceae	*Ceriops*	*decandra*
30.			*tagal*
31.		*Bruguiera*	*gymnorrhiza*
32.			*cylindrical*
33.			*parviflora*
34.			*sexangula*
35.		*Kandelia*	*candel*
36.		*Rhizophora*	*mucronata*
37.			*apiculata*
38.	Sonneratiaceae	*Sonneratia*	*griffithii*
39.			*caseolaris*
40.			*apetala*
41.	Verbenaceae	*Clerodendrum*	*inerme*

Table 4 Mangrove species found in East and West Coasts (Kathiresan 2005)

Sr. No.	Family	Genus	Species
1.	Acanthaceae	*Acanthus*	*ilicifolius*
2.	Apocynaceae	*Cerbera*	*odollum*
3.	Avicenniaceae	*Avicennia*	*alba*
4.			*marina*
5.			*officinalis*
6.	Bignoniaceae	*Dolichandron*	*spathacea*
7.	Caesalpiniaceae	*Caesalpinia*	*bonduc*
8.			*crista*
9.	Combretaceae	*Lumnitzera*	*racemosa*
10.	Euphorbiaceae	*Exoecaria*	*agallocha*
11.	Flagellariaceae	*Flagellaria*	*indica*
12.	Malvaceae	*Thespesia*	*populneoides*
13.	Myrisinaceae	*Aegiceras*	*corniculatum*
14.	Papilionaceae	*Derris*	*scandens*
15.			*trifoliata*
16.	Pteridaceae	*Acrostichum*	*aureum*
17.	Rhizophoraceae	*Brugiera*	*cylindrica*
18.			*gymnorrhiza*
19.			*parviflora*
20.		*Ceriops*	*tagal*
21.		*Kandelia*	*candle*
22.		*Rhizophora*	*apiculata*
23.			*mucronata*
24.	Sonneratiaceae	*Sonneratia*	*caseolaris*
25.			*alba*
26.	Verbenaceae	*Clerodendron*	*inerme*

Floristic Diversity of Mangrove Forests in Gujarat

The floristic diversity of mangrove forests of Gujarat is less as compared to many other mangrove regions of the country. Gujarat has 22% of country's mangrove cover and about 15% of the total species diversity of the country has been recorded from the state. Further, different mangrove species are not uniformly distributed in the state and the community distribution is highly skewed in favour of only one genus (Avicennia) which is represented by three species. Out of the three species of Avicennia, only one species i.e. A. marina is abundant and other two species are conspicuously rare. Therefore, even at the species level, the mangrove community of Gujarat shows a highly skewed distribution in favour of only one species i.e. A. marina. Therefore, the state has a relatively low species richness of mangroves. Only 13 species belonging to 8 genera and 6 families have been reported from Gujarat. Out of the 13 mangrove species, reported from Gujarat, two species have not been recorded for more than two decades. The 13 mangrove species recorded from the state are as mentioned below:

Family: **Avicennaceae**

1. *Avicennia alba* Blume
2. *Avicennia marina* (Fosrk.) Vierh.,
3. *Avicennia officinalis* L.

Family: **Rhizophoraceae**

1. *Brugiera cylindrica* (L.) BL.
2. *Brugiera gymnorrhiza* (L.) Lamk
3. *Ceriops decandra* (Griff.) Ding Hou
4. *Ceriops tagal* Arnold.
5. *Rhizophora apiculata* BL
6. *Rhizophora mucronata* Lamk

Family: **Sonneratiaceae**

1. *Sonneratia apetala* Buch. –Ham.

Family: **Euphorbiaceae**

1. *Exoecaria agallocha* L.

Family: **Acanthaceae**

1. *Acanthus ilicifolius* L.

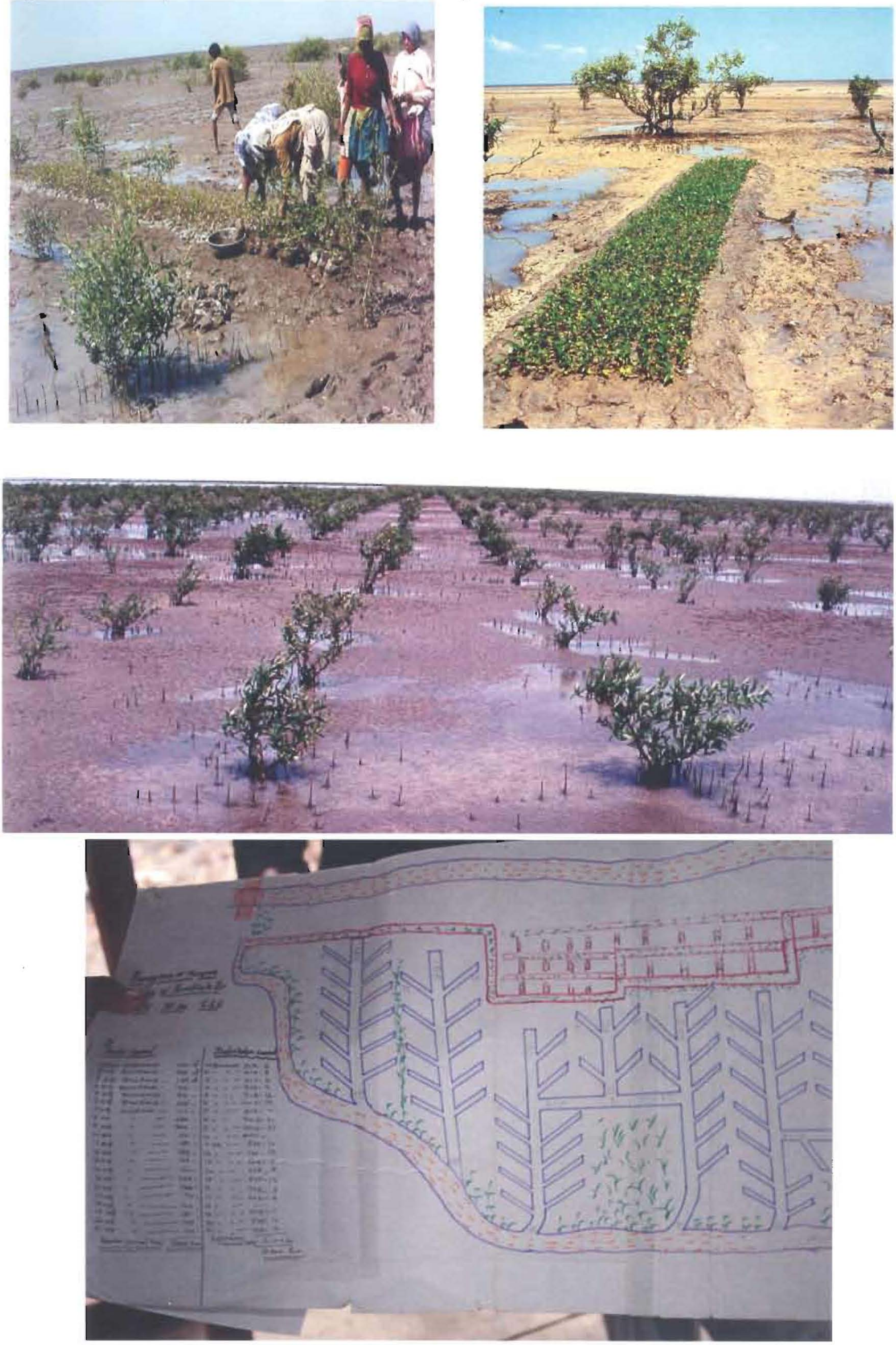
Family: **Myrsinaceae**

1. *Aegiceras corniculatum* (L.) Blanco

Mangrove Afforestation

Three plantation models is being followed for the afforestation of mangrove in the India viz. direct seed sowing, plantation on raised mounts and fishbone design. In the first model, the seeds/propagules are sown directing without any treatment. In the second model the seed/ propagules are sown on the elevated mounts. The mounts are of one meter diameter and 6-8 inch height. The third model, fishbone design, has been developed by Tamil Nadu Forest Department. This model is very found to be successful in the areas with very low tidal amplitude. In this model a wider feeder canal has side distribution canal at 45 degree fanning out to the either side. The structure of the canal is given in Fig. No.1. Since the tidal amplitude is very high in Gujarat, fishbone design model is not required at most of the locations. In Gujarat majority of the Afforestation of mangroves are being carried out by direct seed sowing and by raised mount method. According to the study by Gujarat Ecological education and Research (GEER) Foundation, Gandhinagar 637.15 km^2 area has been identified as potential area for mangrove plantation in the state.

Fig. different plantation models for mangroves in India



Types of mangrove Forests

Lugo & Snedaker (1974) recognize six physiographic types of mangrove stands: fringe mangroves, basin mangroves, riverine mangroves, overwash mangroves, scrub mangroves, and hammocks. Each of these types is influenced by sets of similar energy signatures so that within each forest type, similar levels of structural development are attained. Hogarth (1999) recognizes the following types of mangrove systems.

- **Fringe Mangroves** (tide-dominated): This type of mangrove forest is characterized by a high tidal range over a shallow intertidal zone that is often colonized by mangrove trees. Tidal water is typically full strength sea water, but wave action is diffused quickly by passage over a stepped intertidal zone. Sediment and mangrove soils are likely to be more dynamic as tides deposit and remove sediments from the sea and from inland river estuaries. Receive less runoff of terrestrial nutrients compared to riverine forests.

- **Basin Mangroves:** This type of mangrove forest is located on the landward side of fringing mangroves in estuaries. Sheltered from wave action, and inundated infrequently. Highly variable salinity depending on rainfall, groundwater flow, and local tidal surges. Often exhibit high evaporation rates, which can result in hypersaline soils. Due to low currents and little turbulence, basin mangroves can be sinks for nutrients and sediment.

- **Riverine Mangroves:** Many large expanses of mangroves are located at river deltas where soils and salinity are amenable to mangrove community development (e.g. Amazon delta). Have low tidal ranges, and strong freshwater flow carrying substantial sediment loads, much of which is deposited within the mangrove communities. Characterized by shifting river channels, and typically mangal expanding inland as well as outward in the shifting, sediment-driven river deltas.

- **Scrub Mangroves:** Found in extreme environments where nutrients and freshwater may be limiting.

- **Hammock Mangroves:** Relative isolation from rivers or the sea leads to a domed accumulation of organic peat over depressions, where mangroves take root.

- **Carbonate Setting Mangroves:** On low-energy coasts where carbonate has accumulated from coral reef breakdown, resulting in lime sediment and silt accumulation.

- **Inland Mangroves:** Areas where the mangroves are completely cut-off from the sea, often in sink holes or other depressions.

Mangrove Ecology

Being an open type of ecosystem, any change in mangrove ecosystem influences the other ecosystems or habitats which may or may not be physically connected to it and vise versa. Therefore, any alteration affecting mangrove ecosystem has potential to affect other related ecosystems. Mangrove ecology, as other ecosystems, consist tow factors biotic and abiotic which contribute to structure and function of the ecosystem.

Abiotic Factors

Among abiotic factors, the primary factor of the natural environment that affects mangroves over the long term is sea level and its fluctuations. Other shorter-term factors are air temperature, salinity, ocean currents, protection, shallow shore, and soil substrate (Duke, 1992, De Lange and De Lange, 1994).

- **Air temperature**
  The best mangrove development has been found to occur only when the average air temperature of the coldest month is higher than 20 ^{0}C and where the seasonal range does not exceed ten degrees.

- **Mud substrate**
  Most extensive mangroves are associated with muddy soils along deltaic coasts, in lagoons and along estuarine shorelines as it provide firm substrata and therefore minimum sediment movement which in terns give stability to the recruits and trees.

- **Protection**
  A protected coastline is essential for the survival of mangrove communities as mangroves cannot develop where high levels of wave action prevent the establishment of seedlings.

- **Salt water**
  In terms of salt water, there is increasing evidence that most mangroves have their optimal growth in the presence of some additional sodium chloride.

- **Tidal range**
  The tidal range plays an important role in mangrove development. The greater the tidal range, the greater the vertical range available for the community. Also for a given tidal range, steep shores tend to have narrower mangrove zones than do gently sloping ones.

- **Ocean currents**
  The currents are essential since they disperse the mangrove propagules and distribute them along the coasts.

- **Shallow shores**
  The need for a shallow shore is also a major aspect of mangrove forests. This is because the seedlings cannot get anchored in deep water and the mangrove requires a large proportion of its body to be above the water (Hutchings and Saenger, 1987).

Biotic Factors

The biotic components of mangrove ecosystem comprise of a wide range of floral and faunal diversity. A number of other flowering species flourishing in this ecosystem but do not form a conspicuous part of whole ecosystem, called mangrove associates play significant role in mangrove ecosystem. Besides mangrove associates, algae also plays important part in the mangrove ecosystem. The faunal component of mangrove ecosystem is much diverse than that of floral components. It comprise of invertebrates and vertebrates both. Various microorganisms, of the forest floor, bivalves, crabs, insects, spiders, moth, butterfly, mosquitoes etc. represent invertebrate group. While the vertebrate group is represented by fishes, prawns, snakes, pythons, crocodiles, lizards, birds; jackals, bats, dolphins etc. Therefore, the complex linkages between various biotic and abiotic components of mangrove ecosystem determine the structure and function of mangrove ecosystem.

Mangrove Biology

Mangroves are mostly distributed in estuaries, sheltered coastlines, islands etc. where the tidal currents, salinity and substratum determine the species composition and their distribution. The plants get submerged by the tidal currents which, therefore, inhibit the regular gaseous exchange process of most of the mangrove habitats. Further, the salinity gradient of sea water is higher than the cell sap of the plans; hence the water has to move against the osmotic potential gradient which needs energy expenditure. These environmental conditions of tropical and subtropical coastal and estuarine regions initiated the structural and functional adaptations in the plants through the genetic expressions which resulted into formation of mangrove community.

Canopy Structure and Function

Different foliar arrangements forming various canopy forms determine the structural and functional strength of mangrove plants which can uphold the plant in difficult environmental and stress conditions. The foliar orientation determines the quantity of photosynthetic products; however, the branching architecture decides sustainability of plants in extreme tidal amplitude and wind velocities. Further, reiteration is the usual response to other environmental conditions by most of the mangrove trees which means a partial or complete repetition of the architecture of the tree. Avicennia, Ceriops, Aegiceras and Rhizophora show remarkable flexibility of canopy and the same architectural model can be recorded in any of theses species either tall trees having slender crown or shrubby plants with extensive crown.

Root System: Structure and Function

Most of the mangrove species have aerial root system in addition to the regular root system. The root system of mangroves has significant importance in their physiological processes as well as it gives strength to the plant against tidal current and wind. Apart from mineral and water absorption and anchoring, the root system of mangroves have several other functions such as maintaining the salt balance, mitigating the effect of anaerobic substrata and some time uplifting the plant above the water level (Rhizophora).

Aerial Roots

The term 'aerial root' has been coined by Tomlinson and Gill (1975) to the roots exposed to atmosphere at least part of the day. Various types of aerial root is discussed below.

Stilt-Root

The root arises from the trunk of the plant and lower branches. The circumference of the stilt root area is generally comparable to the circumference of the crown of the tree. The stilt root uplifts the plant above the water level. It initiates from some lower branches. This type of aerial root is found in *Rhizophora sp. Avicennia alba* and *A. officinalis.*

Pneumatophore

This type of root develops as erect appendages from the subterranean first order horizontal root system. The pneumatophore is formed by lateral growth of the horizontal root system. The pneumatophore of *Avicennia* and *Sonneratia* are conical and appears as pencil and mostly unbranched (branching may occur in case of physical damage).

Knee Root

Such type of aerial root is found in *Ceriops, Bruguiera, Xylocarpus* spp. of mangrove plants. Like pneumatophore it also develops from the first order horizontal root system. However, the knee roots are not developed as erect aerial roots like pneumatophores rather the horizontal root system grow upward without any branching and afterwards it bent downwards like the knee assuming a 'V' shape. Such aerial root system attains a height of 10-20 cm.

Gaseous Exchange in root system

The mangrove soils could be sandy, muddy or a combination of both. The availability of soil oxygen varies with the texture and composition of soil. Sandy soil has better oxygen availability as compared to muddy soil. However, the water logged soil of mangrove ecosystem lacks proper gaseous column which makes it anaerobic in nature. Sometimes the oxygen content of the soil goes as low as 1% (Singh and Garge 1993). Therefore, the root system of mangrove plants does not go very deep. Further, the aerial roots have lenticels on their surface for gaseous exchange during the low tide period when it is exposed to the atmosphere. The linkage between the aerial roots and the subterranean roots forms the passage for gaseous movement with the entire root system.

Salinity Balance

High salinity of soil and water hinders water absorption and act as toxicant for the physiological processes. Every mangrove plant eliminates the extra salt in the water or atmosphere through various mechanisms such as filtration, secretion, vaporization, crystallization or simply blowing away. The mangrove plants can be categorized broadly into two groups; secretors and non-secretors. In the first group of mangrove plants the extra salt is secreted through salt glands, cuticular epidermis or it can be accumulated in the vacuoles of the cell sap of leaves which gets detached afterwards. The mangrove species which eliminate the extra salt through secretion are Avicennia, Aegiceras, and *Aegialitis* etc. However, the non secretors filter most of the salt at root itself through ultra-filtration mechanism. The ultra-filtration mechanism is purely physical processes as it does not get interrupted by chemical poisons or high temperature (Scholander 1968). The non secretor group of mangrove consists of *Bruguiera, Rhizophora, Sonneratia and Lumnitzera.*

Mineral Absorption

The water logged soil has very low oxygen diffusion capacity. The degree of anaerobic condition of soil varies with the frequency and duration of tidal inundation. The aerobic bacterial population requires oxygen as electron acceptor for their metabolic process which is lacking in swampy areas of mangrove forests. Therefore, the aerobic population significantly decreases and the facultative anaerobic bacteria develop in the flooded soil of mangrove forests. These bacteria requires alternative source of electron acceptor such as nitrate, $Fe+++$, $Mn++++$ for respiration. Further, the bacterial populations (except chemotrops) require carbon as source of energy which is also very insufficient on mangrove soil. Hence, the metabolic processes of bacterial population slowed down. Consequently, the rate of decomposition of the litter and other organic compounds decrease significantly resulting very slow mineralization. The soil chemistry of mangrove soil differs distinctly from the soil of terrestrial or aquatic system both (Upadhyay 1984).

The redox potential of the soil significantly influences the availability of minerals like Fe, Mn, phosphate and nitrate etc to the mangrove plants. When the redox potential of the soil is positive, the $Fe+++$ converts into $Fe++$ which is readily absorbed by the plant. Similarly $Mn++++$ converts into $Mn++$ which can be easily absorbed by the plants. Further, phosphate ($PO4--$) can be absorbed in the inorganic state. Iron and manganese combine the phosphate and make it available to the plants (Upadhyay 1984).

Nitrogen can be absorbed by the plant in the inorganic form like phosphate. The anaerobic soil of swampy system has a thin aerobic layer (1-5mm). The ammonium ions ($NH4+$) of anaerobic soil diffuse to the aerobic soil and get converted into nitrate ions ($NO3-$) through microbial activity. These nitrate ions then again move down to the anaerobic soil through diffusion which then gets converted into nitrogen gas or nitrous oxide which can't be absorbed by the mangrove plants. Therefore, the soil of mangrove forests has nitrogen deficiency which acts as the limiting factor for growth and development (Upadhyay 1984).

The sulphates ($SO4--$) of seawater get reduced to sulphide ($S--$) in the highly anaerobic soil of mangrove forests. Sulphide ion is very toxic to the plant system and many times damage the physiological processes of the plants. Moreover, most of the metal sulphides are insoluble, therefore, become unavailable to the plants. The sulphide when combined with the pyrite minerals, forms a complex compound calls jarosite which on oxidation form sulfuric acid. The sulfuric acid released makes the soil highly acidic which hinders the plants growth.

Water Absorption

Water is absorbed due to the gradient of osmotic potential. The osmotic potential of pure water is considered as zero and any impurity in water makes its osmotic potential to negative. Further, water always moves from higher to lower osmotic potential. The osmotic potential of cell sap is negative while the osmotic potential of pure water is zero thus the water moves from the soil to plant. However, the osmotic potential of cell sap is more than the sea water, therefore, the water can not be absorbed through osmotic potential. Hence, the water is absorbed against the gradient of osmotic potential by expenditure of energy. Thus most of the energy of mangrove plants gets utilized in absorption of water.

Reproductive Biology

Evolutionary adjustments to varying coastal marine environments have produced some astounding biological characteristics within mangrove plant communities. Certain mangrove species can propagate successfully in a marine environment because of special adaptations. Through "viviparity," embryo germination begins on the tree itself; the tree later drops its developed embryos, called seedlings, which may take root in the soil beneath. Viviparity may have evolved as an adaptive mechanism to prepare the seedlings for long-distance dispersal, and survival and growth within a harsh saline environment. During this viviparous development, the propagules are nourished on the parent tree, thus accumulating the carbohydrates and other compounds required for later autonomous growth. The structural complexity achieved by the seedlings at this early stage of plant development helps acclimate the seedlings to extreme physical conditions which otherwise might preclude normal seed germination.
Another special adaptation is the dispersal of certain mangroves' "propagules" which hang from the branches of mature trees. These fall off and eventually take root in the soil surrounding the parent tree or are carried to distant shorelines. Depending on the species, these propagules may float for extended periods, up to a year, and still remain viable. Viviparity and the long-lived propagules allow these mangrove species to disperse over wide areas.

Physiological adaptation in Fauna of Mangrove Ecosystem

Besides mangrove species, a number of faunal species have also known to develop various physiological and morphological adaptations to survive in the mangrove ecosystem. Some of them are discussed below.

Crab and other Invertebrates

The marine invertebrates comprise a large proportion of the mangrove inhabitants. The most evident marine invertebrates are different types of crabs. These crustaceans are represented by a large numbers of species belonging to several families. Other common invertebrates include bivalves, barnacles and polychaetes. While many of the shrimps and amphipods are restricted to lower levels of the mangrove shore, crabs tend to occur throughout the mangrove zone (Teas, 1983).

Birds

Other examples of adaptations to mangrove habitats come from vertebrates. Endemic bird species show the most adaptations to the mangrove habitat and most of these are concerned with feeding. Longer bills are found in the mangrove robin, white-breasted whistler, mangrove fantail, dusky gerygone, red-headed honeyeater and the mangrove gerygone. Perhaps this is to prevent the clogging of bristles around the mouth and muddying of the face while foraging for food on surface mud. Also the white-breasted whistler has a hooked beak for the cracking of crustacean shells. Another adaptation is the more rounded wing and tail of the mangrove robin as compared to other species of the same genus. This difference is believed to allow for greater maneuverability as the robin flies through the mangrove canopy (Hutchings and Saenger, 1987).

Mudskippers

Another noteworthy example of physiological adaptation to the mangrove habitat is seen in the mudskipper. Mudskippers are fish related to gobies and are characterized by their fused pelvic fins. They are found in tropical mangroves and are well adapted to varying degrees of tidal levels from exposure to air to complete submersion. They have very mobile eyes that compensate for the absence of the neck. The eyes are set in turrets and are protected from drying out by secondary spectacles. Since the eyes are set high on top of the head their field of view is increased. The mudskipper also has accessory respiratory surfaces on its fins and in the nasal sac diverticula. It is not known whether these additional surfaces aid in respiration or if they are associated with salt regulation. Besides normal fishlike swimming the mudskipper has three other forms of locomotion due to its modifications in skeletal structure and musculature. The first is termed "ecrutching" since the pectoral fins are used as crutches. The second is a type of skipping on land that is normally used as an escape reaction. The last type is skimming across the water in a series of bounds where each bound is preceded by a short burst of swimming.

Reptiles

Other adaptations of great importance to mangrove inhabitants are those concerned with the salinity of the environment. Lizards have a nasal gland that secretes brine into the nasal cavity from which it is sneezed. Crocodiles use a number of salt glands located on the tongue and sea turtles have salt glands that are modified into tear glands associated with the eye. Many other salt secreting examples are found among reptiles such as snakes, colubrid snakes and goannas (Hutchings and Saenger, 1987).

Mangrove ecosystem-Ecological Services & Functions

Mangrove forests are vital for healthy coastal ecosystems. It protects the shoreline from natural calamities such as cyclones, Tsunami, etc. It prevents soil erosion. Further, mangrove ecosystem is known to filter many pollutants from the soil and therefore, prevent the other organism being affected by it. It connects the marine and terrestrial ecosystem and forms a buffer zone. The forest detritus, consisting mainly of fallen leaves and branches from the mangroves, provides nutrients for the marine environment and supports immense varieties of sea life in intricate food webs associated directly through detritus or indirectly through the planktonic and epiphytic algal food chains. It provides feeding, breeding and nesting site to many marine creatures.

Protection of shoreline

Mangroves ecosystem protects the shoreline by binding the soil. It reduces the affects of tidal currents and wind and protect the shoreline. Therefore, it plays a very significant role in protection of coastal communities from natural calamities.

Supports Other Ecosystems by Regulating sedimentation

Sea grasses are aquatic flowering plants that make up a large part of the marine food web. Like the mangroves, they are also spawning and nursery grounds for many marine organisms that live in the reef. They too are depended on mangrove ecosystems, being unable to survive in areas of high turbidity and sedimentation. Mangroves help them by slowing down the velocity and forcefulness of the water, thereby preventing fine silt from clouding the water and blocking the sunlight. In this way, the sea grass is able to photosynthesize and flourish under calm, sunny conditions, allowing for perfect nursery grounds for coral reef species. Thus, this process of sea grass protection affects the reefs that depend on the young marine organisms and consequently, the mangrove itself, which depends on the coral reef.

Filtration of Pollutants

In addition to controlling sediment pollution, mangroves also help in controlling other forms of pollution, including excess amounts of nitrogen and phosphorous, petroleum products, and halogenated compounds. Mangroves stop these contaminants from polluting the ocean through a process called rhizofiltration. The lenticels that are present on the mangroves' root systems, allow the area directly around the root to remain aerobic even in anaerobic, saturated soils. Microorganisms that can break down such pollutants thrive in these environments. They use enzymes to break down and make stable the potentially dangerous substances, thus treating the effluent that runs through the mangrove system. This ability to treat effluent is also very important for the local communities. Most of the substances that the mangroves treat are of human origin. Thus, the mangroves are acting as a filter system for the local communities, keeping their ocean waters free of pollution and thus their fish and other food sources free of contaminants.

Form Buffer Zone

Mangrove forests also act as a buffer zone between the open ocean and the land. It connects the terrestrial ecosystem with the aquatic ecosystem, therefore, forming an ecotone. Hence, inhabitants of mangrove ecosystem resemble with the both the ecosystem viz. terrestrial and aquatic yet varies from both of them.

Mangrove Forests: Habitat for creatures of Associated marine ecosystems

Although these ecosystems are not the primary habitat for terrestrial fauna, many terrestrial animals spend time within the confines of mangrove forests. In fact, their intricate root systems provide shelter for many marine and terrestrial animals, protecting them from ocean currents and strong winds. Many endangered species can be found living in mangrove forests. This may be attributed to:

(1) Less predators and/or competitors
(2) Mangroves provide abundant food supply at critical times of the year,
(3) The flora is comprised of species with succulent leaves
(4)The abundant detritus on the forest floor may be important for some insect species (Hutchings and Saenger, 1987).

Invertebrates

Among the terrestrial invertebrates bivalves, crabs, insects and spiders utilize mangrove communities. Termites, mosquitoes and biting midges make up the most highly studied group of insects within mangroves due to their economic and medical importance. Beyond these terrestrial invertebrates others such as butterflies, moths, ants and spiders have been noted to inhabit mangroves (Hutchings and Saenger, 1987).

Fishes

Perhaps the most abundant inhabitants of the mangrove forests are the various fish species. A total of 112,481 fish from 128 species and 43 families have been reported from mangrove ecosystem. The dominant families for these species included Engraulidae, Ambassidae, Leiognathidae, Clupeidae and Atherinidae (Robertson and Duke, 1990).

Reptiles

Within the tropical mangroves reptiles are quite common, but they are rarely seen in temperate forests. Most reptiles use the mangroves as peripheral habitats (Hutchings and Saenger, 1987). The marine fauna proves to be more successful over the freshwater fauna in mangrove forests. One of the most popular reptiles is the saltwater crocodile

Crocodylus porosus. These reptiles come into the mangroves to feed during high tide. They mostly chose sesarmid crabs, prawns and mudskippers and then move on to large mud crabs, birds and mammals as they grow larger. These crocodiles do not nest in mangroves, but instead on the banks where the river comes close to the adjacent floodplain (Hutchings and Saenger, 1987).

Avifauna

Mangroves provide nesting and breeding site to a number of terrestrial, coastal and birds. Besides, mangrove forests are located on the migratory pathways of a number of birds. More than 200 species of birds have been reported from the mangrove forests worldwide. Some of them are herons, sea gulls, pelicans, darter, sand piper, rosy starling, raptors, white eye, purple sun bird, Bee eaters, warblers etc.

Mammals

Most terrestrial vertebrates are not restricted to mangroves, but act as visitors. Varying species of rats including *Xeromys myoides*, water rats, house mice and tree-rats, jackals, bats, etc, represents mammals.

Productivity of mangrove ecosystem

Mangroves are important to many local coastallife forms, both terrestrial and aquatic. For many organisms, mangrove forests serve as the starting place for their food web. Its detritus (fallen leaves and organic material) serves as a nutrient source for plank tonic and epiphytic algal food webs. These microorganisms and macro invertebrates then supply the remaining members of the food web with tremendous amounts of nutrients and energy

The mangrove ecosystem has many unique characteristics associated with it that gives it extreme value. Not only do mangroves provide nesting and breeding sites for many animals, but they also play a large role in maintaining the natural balance of the food chain. Mangroves provide great amounts of nutrients that feed the smallest of organisms, bacteria. Researchers have found ten billion bacteria living in one teaspoon of mangrove mud from a mangrove forests (Hutchings and Saenger, 1987). These bacteria, along with fungi convert relatively indigestible lignin and cellulose from the plant tissue into a protein source that in turn can be digested by higher organisms. This organic matter does not only benefit the immediate higher organisms in a mangrove forest, but is also transported to benefit organisms in surrounding areas.

The leaf litter processing is not accomplished by bacteria and fungi alone, but is first tackled by various invertebrates. The most active leaf-shredders appear to be various species of crabs. A study by Camilleri (1992) looks closely at the leaf processing abilities of invertebrates. He concludes, twelve species of leaf-shredders make particulate organic matter originating from mangroves, available for consumption by at least 38 other species of invertebrates.

Mangrove forests also play an important economic particularly for fishing industry. It has been accepted globally that the mangrove habitat acts as an important feeding and shelter site for juvenile banana prawns. This reliance on mangroves by a variety of fish has also been found to be true in Malaysian mangrove forests (Robertson and Duke, 1990).

Threats

For many years mangrove forests have been abused as wastelands. They have been used as sanitary landfills and converted into oxidation ponds for the tertiary treatment of sewage effluent. The land is also threatened by the charcoal industry, coastal developments and coastal pollution, including oil spills. The latter is extremely damaging to mangroves because of their structure. Since waves and currents on the shoreline transport floating oil, low wave energy ecosystems like mangroves are converted into accumulation sites. Also the inaccessibility of mangroves makes the oil removal extremely difficult. In addition the burrowing activities of crustaceans lead to high levels of oil contamination not only on the surface but also deep into the sediment (Teas, 1975). And although prawn aquaculture is very profitable, it is a major source of destruction to the mangrove forests. The prawn farmers clear large areas of mangrove forest for the construction of large artificial ponds. This clearing of the natural mangrove forests leads to various related problems such as loss of invaluable wildlife habitat, a serious decline in the world's tropical coastal fisheries and coastal destabilization in the form of heavy erosion and siltation resulting in loss of both sea grasses and coral reefs (A. Quarto, 1992).

Ironically, local communities sometimes see mangrove ecosystems as an impediment to their economic practices. As a result, mangrove forests are now among the most threatened habitats in the world. Countries like Vietnam and Ecuador have already lost close to fifty percent of their mangrove forests; others, like Java and Thailand, have lost even more. Sadly, destruction in these countries continues even today.

Developing nations also destruct mangroves through heavy pollution, although they are even more damaging in their direct exploitation. Often, in these countries, mangrove forests are completely destroyed in order to provide places for residential, commercial, and industrial development. Mangroves have been cut down to provide ocean-side land for local housing hotels and structures for shrimp aquaculture industry etc.

References

- Baird, Ian, and Quarto, Alfredo, "The Environmental and Social Costs of Developing Coastal Shrimp Aquaculture in Asia", Earth Island Institute, 1994
- Blasco, F. (1975). Mangroves of India. Inst. Francais, Pondicherry. Trav. Sect. Sci. Tech. 14: 1-175
- Chapman, V.J., "Mangrove Vegetation", J. Cramer, Germany, 1976
- Chapman, V.J., "Mangrove Biogeography", in Hydrobiology of the Mangle, The Ecosystem of the Mangrove Forest, the Hebrew University of Jerusalem, 1984
- Chapman, V. J. 1976. Mangrove biogeography. In: Wet Coastal Ecosystems. Ed. V. J. Chapman. Elsevier Sci. Pub. Co., Amsterdam. Pp. 1-29
- Camillleri, J.C. 1192. Leaf-litter processing by invertebrates in a mangrove forest in Queesland. Marine Biology 114 (1): 139-145
- Duke, N. C. 1992. Mangrove floristics and biogeography. In: A.I. Robertson and D.M. Alongi (Eds.), "Costal and Estuarine studies: Tropical Mangrove Ecosystems". American Geophysical Union, Washington DC., USA, pp. 63-100
- Field, C.D., "Journey Amongst Mangroves", International Society of Mangrove Ecosystems, Okinawa, Japan 1995, 140 pp.
- Hellier, C., "The Mangrove Wastelands", The Ecologist Journal, Vol. 18, No. 2, 1988
- Hong, Phan Nguyen, Hoang Thi San, "Mangroves of Vietnam", IUCN Wetlands Program, 1993
- Hutchings, P. and Saenger, P. 1987.Ecology of mangroves. University of Queensland, Queensland, 388 pp.
- Kathiresan, K. and Qasim S.Z. 2005. Biodiversity of Mangrove Ecosystems. Hindustan Publishing corporation (India) ISBN: 81-7075-079-2 New Delhi.
- Lago, A.E. and Snedaker, S.C. 1974. The ecology of mangroves. Annual Review of Ecology and systematics 5: 39-63.
- Lugo, Ariel E., and S. C. Snedaker,1974 "The ecology of mangroves", Annual Review of Ecology and Systematics: 5:39-64
- MacNae, W. 1968. A general account of the fauna and flora of mangrove swamps and forests in the Indo-West Pacific region. Adv. Mar. Biol. 6:73-270
- Rutzler, Klaus, Feller, Ilka C., "Caribbean Mangrove Swamps", Scientific American, March 1996

- Saenger, P., Hegeri, E.J., and Macintosh, D.J., (eds), "Proceedings of the Asian Symposium on Mangrove Environment, Research and Management", Univ. of Malay, Kuala Lumpur, UNESCO, 1984
- Snedaker, S. C.,1993, "Impact on mangroves", pp. 282-305, In G.A. Maul (ed.) Climatic Change in the Intra-Americas Sea, Edward Arnold, Hodder and Sloughton Publishers, Kent, UK, 389 p.
- Spalding, M. 1997. The global distribution and status of mangrove ecosystems. International News Letter of Coastal Management-Intercost Network, special edition 1: 20-21.
- Scholander, P. F. 1968 How mangroves desalinate water. Physiol. Plant 21:251-61
- Tomlinson, P.B., "The Botany of Mangroves", Cambridge University Press, Cambridge, UK, 1986
- Twilley R.R., Chen, R and Hargis, T. 1992. Carbon sinks in mangroves and their implication to carbon budget of tropical ecosystems. Water, Air and soil Pollution 64: 265-288.
- Untawale, A.G. and Jagtap, T.G. 1985. Marine macrophytes of miniocoy (Lakshadweep) Coral atoll of the Arabian Sea. Aquatic Botany 19: 97-103
- Walsh, G.E. 1974. Mangroves: a review. Pp. 51-174 in Ecology of halophytes. New York: academic Press

Salt Balance in Mangroves [1]

P. F. Scholander, H. T. Hammel [2], E. Hemmingsen, & W. Garey

Scripps Institution of Oceanography, University of California, La Jolla

The tidal zone of tropical seas is frequently lined with great mangrove forests, the dominating species of which belong to such genera as Rhizophora, Bruguiera, Sonneratia, and Avicennia. The outstanding feature of these plants is their adaptation to growing in seawater, and even though all do well in river estuaries they seldom penetrate inland beyond the direct action of ocean tides.

A question which immediately presents itself is "How do these plants handle the salt in the seawater?" Do the roots exclude it from the transpiration stream or do the plants possess special organs for eliminating such salts as may penetrate into the sap? What balance, if any, exists between osmotic potential of seawater, roots, and leaves on one hand and hydrostatic pressure and osmotic potential of the xylem sap on the other? Our aim has been to inquire into these matters.

It has long been realized that various mangroves behave differently with respect to some of these parameters. It is thus easily ascertained that certain species accumulate salt on their leaves. In Aegialitis and Aegiceras salt crystals can be seen covering the leaves and in Avicennia and *Acanthus ilicifolia* one may easily taste the salt. In other species like Sonneratia, Rhizophora, Bruguiera, Ceriops, and Lumnitzera salt can neither be seen nor tasted (5, 17).

Various authors agree that press juices of mangrove leaves have a high osmotic potential, being more or less isotonic with seawater (5, 6, 17). Walter and Steiner, using the same species of Rhizophora, Sonneratia and Avicennia in East Africa as we worked on in Australia, found that the press juices of roots also showed similar values. They determined the transpiration rate of mangrove leaves to be about one-third of that of ordinary plants (20).

Some of the mangroves possess salt glands on the leaves, visible by naked eye as minute dimples in the surface. The histology of the glands has been described in Aegialitis by Ruhland (9) and Avicennia by Walter and Steiner (20), but no experimental studies seem to have been performed on these. However Ruhland (9) determined the amount of salt given off by the isolated leaves of statice (*Limonium latifolium*), and using leaf disks of the same species, Arisz, Camphuis, Heikens, and Van Tooren (2) found that these would secrete salt when floated on a saline solution. The secreted fluid under certain conditions became more concentrated than the medium. This process was stopped by cyanide and other respiratory poisons.

Large mangrove stands are typically rooted in deep muck which is completely anaerobic from decomposing materials. In such habitats the roots are conspicuously swollen by a spongy pneumatic tissue which communicates to the air through a multitude of lenticels located on stilt roots (Rhizophora, Bruguiera) or special pneumatophores (Avicennia, Sonneratia). The ventilatory function of these structures has been studied in detail in Avicennia and Rhizophora (4, 16, 19).

Materials

The main part of the present investigation was performed at Cape York peninsula, North Australia, on the Scripps Institution Expedition to these waters in August to September 1960. The following species were considered.

Rhizophora mucronata Lamk., *Bruguiera* prob. *exaristata* Ding Hou, *Sonneratia alba* J. Sm., *Lumnitzera littorea* (Jack.) Voigt, *Avicennia marina* (Forsk.) Vierh., *Aegiceras corniculatum* (L) Blanco, *Aegialitis annulata* R. Br.

These plants were growing within or next to a small tidal pool within the estuary of the Jardine River at the very tip of Cape York peninsula. The pool was usually inundated by high tide but could run dry at exceptionally low tides, and had a rather fluctuating salinity varying from 2.2% to 3.6%. Young trees or bushes from 1 to 3 meters tall were used for the most part. These species were compared with *Hibiscus tiliaccus* L, growing higher up on the sandy beach, and *Eugenia suborbicularis* Benth., found in the dry scrub forest away from the beach.

Supplementary data to these studies were obtained on *Rhizophora mangle* L, *Avicennia nitida* Jacq., and *Laguncularia racemosa* Gaertn. at Marine Laboratory, University of Miami, and at the Lerner Marine Laboratory, Bimini, Bahamas, in September 1961, and January 1962; also at La Paz, Baja Cal., July 1962.

▶ Salt Secretion From Leaves. The rate of salt excretion from attached leaves was determined by washing them off with distilled water at certain intervals. The wash water was titrated for chloride,

---

[1] Received March 5, 1962.

[2] Address: John B. Pierce Foundation, 290 Congress Avenue, New Haven, Conn.

delivering silver nitrate from a syringe burette (15) and using potassium chromate as indicator. At the end of the series, the leaves were detached from the bush and traced on paper for later area determination.

The species separated into two groups (fig 1): A, the salt-secreting species Aegialitis, Aegiceras, and Avicennia, and B, the non-secreting species which comprised the rest. When the leaves were washed every 3 hours, the secretion had a pronounced diurnal cycle with minimum activity in the night. This was particularly pronounced in Aegialitis (fig 4), less so in Aegiceras (fig 5), but did not show up clearly in Avicennia. When attached leaves of Aegialitis were enclosed in a roomy bag of aluminum foil, together with a desiccant, salt secretion almost ceased, but recovered in light. In a transparent bag there was no slowdown. A possible explanation would be a primary stomata closure in the dark, with consequent reduction of transpiration and source of salts to be excreted.

A more comprehensive study of the salt composition was made on preserved specimens at Scripps and showed that some 90 % of the chloride is matched by sodium and about 4 % by potassium, leaving the ionic ratios about the same as in seawater (table I).

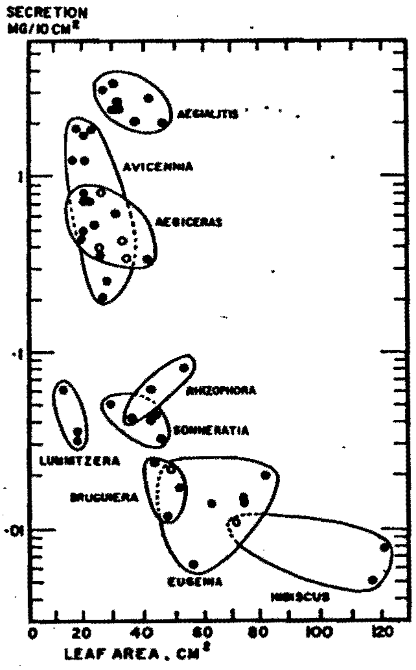
Table I

Ionic Composition of Salts in Sap of Mangroves

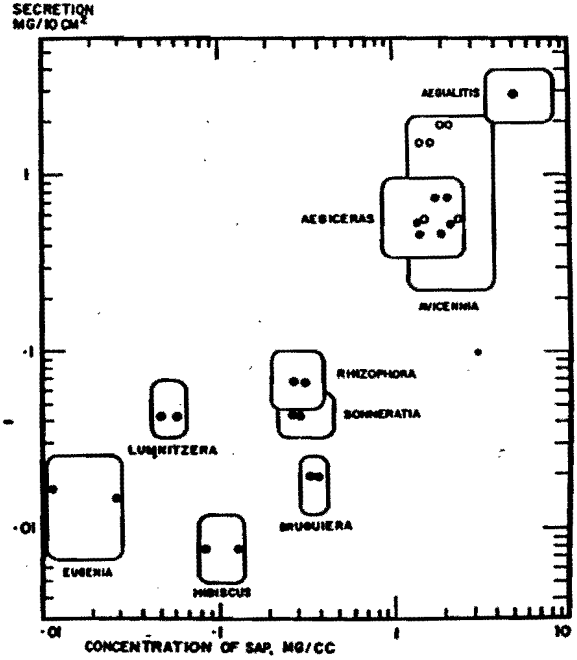
	Na/Cl	K/Cl	Na+K/Cl
Aegialitis	94 %	1.8 %	96 %
Aegiceras	86 %	2.6 %	87 %
Avicennia	87 %	5.8 %	93 %
Seawater	85 %	1.8 %	87 %

Ammonia and total nitrogen were present in minute quantities, less than 0.1 % of the other constituents. Sodium chloride is therefore, by far, the major component of the secretion.

► Salt Glands. By a mere inspection of the leaves of Aegialitis and Aegiceras it was clear that the salt is secreted through little dimples in the leaves, corresponding to the salt glands. When exposed to the sunshine, the secreted liquid rapidly evaporates and one observes dry salt residues rather than liquid drops. However, little drops were observed to form readily under a layer of stopcock grease or oil, and this made it possible to determine the concentration of the secreted fluid. The attached leaf was turned up at the edges and charged with a pool of mineral



1



2

Fig. 1. Secretion of sodium chloride from the leaves of various mangroves and two control trees over 9 daylight hours (0900–1800).

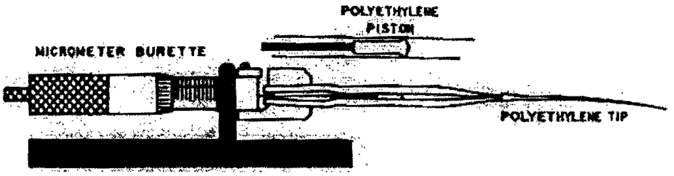
Fig. 2. Secretion of sodium chloride in various mangroves and two control trees over 9 daylight hours as related to the concentration of sodium chloride in the xylem sap. Numerous determinations of the latter were taken, the range of which is given on the width of the rectangles. Only those points are given where secretion data were obtained at the same time.

oil. Through a dissecting microscope the secretion could be observed as tiny drops under the oil (fig 6). These were made to coalesce by means of a hair-fine wire loop so that about one cubic millimeter could be drawn into the fine tip of a micrometer burette behind a bubble of air (fig 3 & 7). The volume was measured, transferred into a few drops of distilled water, and titrated for chlorides with the same burette. Checks revealed no detectable evaporation loss through the oil.

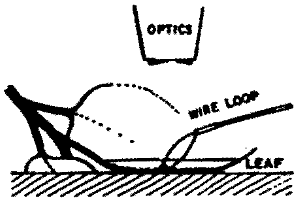
In Aegialitis the concentration of NaCl in the secreted liquid varied from 1.8 to 4.9 %, and when collected every 2 hours it revealed a marked diurnal cycle with highest value in the middle of the day (fig 8). In Aegiceras, and especially so in Avicennia, the glands were more sparse, but collection under oil was still possible. In Aegiceras the concentration averaged 2.9 % throughout the daytime and 0.9 % during the night, and one 18-hour collection from Avicennia gave 4.1 %.

► Concentration of Salts in Xylem Sap. As pointed out by Walter and Steiner (20), one would expect that plants which do not secrete salts through their leaves must carry a transpiration stream virtually void of salts. This assumption was checked by extracting sap from fresh stem sections of various mangroves, following a procedure described by Bennet, Anderssen, and Milad (3): A piece of stem, stripped of bark at the lower end, is fitted airtight into a small vacuum container, which connects to an automobile tire pump with reversed piston valve. When the handle is pulled out and fixed, short pieces are cut off from the upper end of the stem, allowing the sap to descend stepwise.

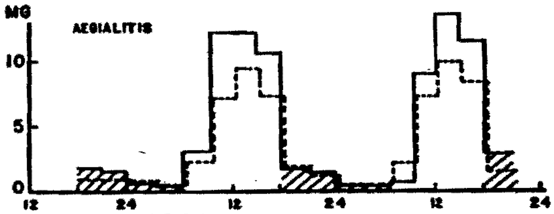
Those species which secrete salt from the leaves are the ones least able to exclude the sea salts (fig 2). But even the non-secreting mangroves may still carry some 10 to 50 times more salt in the sap than Hibiscus and Eugenia, which are in the range of common plants (7).



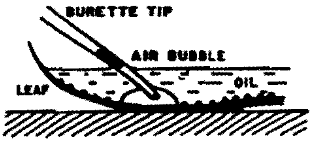
3



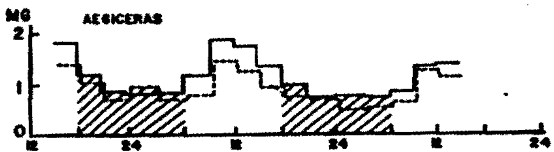
6



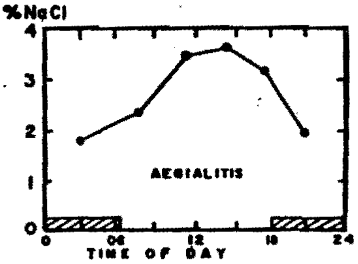
4



7



5



8

Fig. 3. Micrometer burette used for titrating secretion of less than 1 mm^3 volume. The micrometer activates a stainless steel wire furnished with a polyethylene tip which is flared at the end by heat. This flare engages tightly the bore of a precision shrunk glass tubing.

Fig. 4 & 5. Diurnal variation in the NaCl secreted from leaves of two species of mangroves, each represented by determinations in two leaves.

Fig. 6. Aegialitis leaf covered with oil for collecting secretion drops from the salt glands.

Fig. 7. Drops of secretion, brought to confluence by means of a hair-fine wire loop, are drawn into the burette tip behind an air bubble.

Fig. 8. Diurnal variation in the concentration of the secreted fluid collected under oil.

Stem samples of sap from Aegiceras, Avicennia, Sonneratia, and Rhizophora were collected at intervals from the same plant but showed no clear diurnal variation in the salt concentration, and samples taken from base, middle, and upper part of the stem revealed no concentration gradient.

► Osmotic Potential of Xylem Sap. In order to understand the processes involved in producing the near salt-free sap, one must know osmotic potential and hydrostatic pressure of this fluid. Chlorides and freezing points (15) were accordingly determined in sap specimens from a series of Atlantic mangroves, including *Avicennia nitida, Rhizophora mangle,* and *Laguncularia racemosa.* In all species the non-chloride components added at most 1 to 2 atmospheres to the total osmotic potential, which is to say that the seawater exceeds the sap at all times by close to 20 atm.

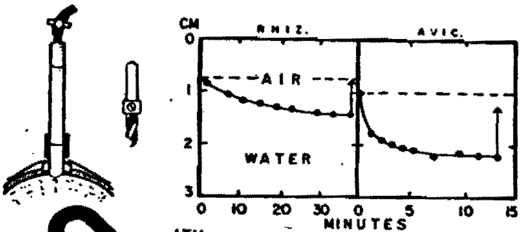
► Rate of Transpiration. In a steady state situation the amount of salt entering the roots equals that excreted by the leaf glands, plus whatever salt may be transferred to tissues. The latter fraction must be very small compared to the salt secretion in species like Aegialitis, Avicennia, and Aegiceras. The salt is transported by the sap flow, and one may, therefore, calculate the transpiration rates from the rate of salt secretion and the concentration of salt in the xylem sap. The average daytime values came out as follows: Aegialitis 5 mg/dm²/minute, Aegiceras 2.5 and Avicennia 6.5. In the non-secreting species the relative salt loss from the sap into tissues may be appreciable and would give too-low transpiration estimates; but this potential error would be counteracted by contamination of the sap with salts from non-conducting severed tissues of the xylem. With these reservations, the figures are: Rhizophora 2.5, Sonneratia 1.5, Lumnitzera 6.5, Hibiscus 6.5, and Eugenia 7.5 mg/dm²/minute. All of these values are low compared to the bulk of data published for other plants, including halophytes, which range from some 10 to 55 mg/dm²/minute (18). The commonly used technique depends upon measuring the weight loss of a freshly detached leaf, with a concomitant disturbance of the normal hydrostatic balance. It would seem that our figures for the transpiration rates in the salt-secreting group of mangroves should be rather reliable.

► Hydrostatic Pressure in Sap of Mangroves. True to classical concepts, one might predict that the hydrostatic sap pressure in mangroves would permanently linger around −20 atm, namely, in order to balance the osmotic potential of similar magnitude in seawater, roots, and leaves. The salt separation would then be explained essentially as an ultrafiltration in the roots, powered by a 20-atm transpiration pull. It would, therefore, be of pivotal interest to be able to measure negative sap pressure, but this, we must painfully admit, is still beyond the wits of man. The cause is not totally lost, however, for there are various ways of detecting strong negative pressures, even when they cannot be accurately measured.

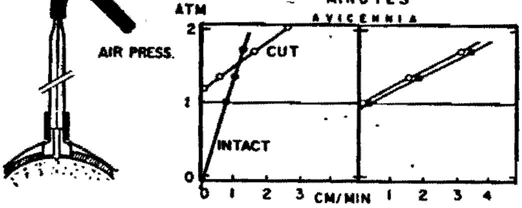
Three different approaches have been used, any one capable of indicating negative pressure, namely, A: the closed burette technique (11, 12), B: the delta pressure technique (14), and C: Renner's potometer technique (8).

► I. With the ***closed burette technique*** (fig 9) one determines the lowest pressure against which the xylem can absorb water; if absorption continues in spite of vacuum, the sap pressure is negative. A disk of bark is carefully removed by means of a cork bore and the exposed surface dried off and lightly greased. A brass button with 5 mm bore and "O" ring passes through a hole in a hose clamp and is strapped tightly onto the xylem. The bore is filled with water, and after test for tightness the xylem is scooped out shallowly with a razor-sharp, specially-

9



10



11

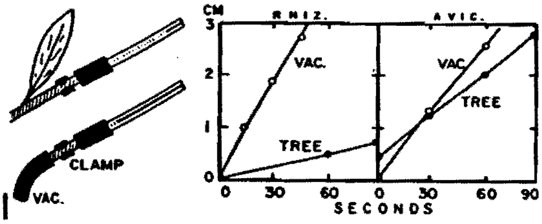


Fig. 9. Closed burette technique for estimating sap pressure. Specially ground drill is shown. Arrows in both panels indicate the shrinking of the gas volume when water was admitted to the burette. The original air volume is between the broken line and the upper frame (vol 0). The curve denotes the position of the meniscus at various times.

Fig. 10. The delta pressure technique for estimating stem pressure. Known air pressures are supplied to the microburette from a pressure tubing. The panels show the effect of added pressure upon the absorption rate in the intact stem (*filled circles*), and in the cut-off stem (*open circles*). Ambient pressure is 1 atm. Each panel shows measurements in one plant. Filtration rates are relative and are given as cm/minute on burette of approximately one millimeter bore.

Fig. 11. Renner's technique for estimating sap pressure. In both cases the vacuum drew liquid through the compressed xylem faster than did the tree.

ground drill which passes through the water. Shavings are flushed out and the burette connected. Air bubbles are dislodged by prolonged and forceful evacuation with a 100 cc syringe; if air leaks in steadily through the xylem another site must be found. The rate of water absorption is determined, whereupon the burette is closed, including a known air volume, and the rate of water absorption is again observed. If it comes to a stop, the gas volume is read before and after admitting water, and the pressure is calculated from the shrinking of the gas. One finally checks that full absorption is resumed when the burette is opened.

A series of measurements, performed on sunny days, gave the following results: 6 *Rhizophora mangle* 0.4 to 0.6 atm, 6 *Avicennia nitida* 0.4 to 0.7 atm, 4 *Laguncularia racemosa* 0.5 to 0.7 atm. In several additional cases practically no water was taken up unless pressure was added, and the sap pressure must hence have been close to ambient (fig 10).

In contrast to these results, one should realize that when this technique is applied to plants with substantial negative pressure, such as may develop in the grape or rattan vine, the picture is very different. One may thus fill the burette completely before stoppering it and the plant will nevertheless absorb the water practically as fast as if the burette were open: in healthy vines the water simply mass-cavitates (boils) and no air, or only traces, leaks from the xylem (11, 12, 13).

► II. With the *delta pressure technique* (fig 10) one determines how sensitive is the absorption rate of water through a xylem cut to changes in the burette pressure. Instrumentation is similar to I, but the cut is kept very small in order to avoid flooding and backpressure in the xylem. Absorption rates are read on a micro burette. Healthy stems frequently yield only traces of gas and one usually gets a linear relation between absorption rate and delta pressure, i.e., like in a simple filtration system. When the rate is plotted on the abscissa and the sap pressure on the ordinate, we assume that the extrapolated intercept reflects the approximate sap pressure. When, as a control, a short section bearing the burette is sawed off, a value close to ambient is obtained (fig 10).

The result will be seen in figures 10 and 12. In most cases the pressure extrapolated to a fraction of one atmosphere, but modest negative pressures were not uncommon. In figure 10 (*right*), we see a strong indication of near ambient pressure in that particular bush. The method appears theoretically sound provided no air spaces are cut open. Cavitation may occur if negative pressure obtains, but stays confined to the severed elements and floods immediately when the cutting edge is withdrawn.

► III. In Renner's *potometer technique* (fig 11) a capillary burette is connected to an attached twig and the water absorption rate is reduced by compressing the xylem with a screw clamp. The twig is detached and one notes how fast a moist vacuum can draw water through the resistance. Assuming simple filtration, the sap pressure can be calculated from the ratio of the flow rates (8).

In Rhizophora water absorption was very slow, and was reduced to one-half by the clamp, but vacuum pulled water through eight times faster than did the tree. In Avicennia the unrestricted flow was very rapid and was slowed down to 1-10 by the clamp; nevertheless, vacuum pulled the water through faster than did the tree. Two samples of each species gave similar results. Also this technique indicated that these plants pulled with a pressure differential of less than one atmosphere.

The main objection which can be raised against these techniques is their vulnerability to a gas phase, and we shall, therefore, briefly discuss this possibility. When a transpiring stem is cut off in air, the sap recedes until stopped by the pit membranes of the first cross-walls. Every active transport element which has been severed thus becomes completely filled with air. Even so, it holds for all common plants that drinking resumes when the stem is promptly put into water. The bypass around this gross embolism takes place through flooded tracheids or other perivascular micro elements which were not severed. If normal flow is restored, it goes at the cost of a considerable pressure drop across the inactivated vessel sections (11, 14).

If, similarly, we make a dry cut into the xylem of our transpiring mangroves, air is drawn into every severed active tracheary compartment. When this cut is inundated and vacuum extracted, as described, air bubbles escape; and when normal pressure is admitted, water enters the xylem, leaving approximately 5 to 10 % of the length of each active

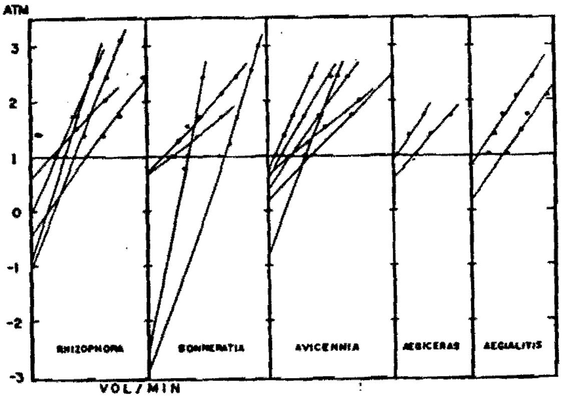


Fig. 12. The delta pressure technique applied to the stems of various mangroves. Ambient pressure is 1 atm. The water absorption rate at various added pressures extrapolates to the stem pressure at the ordinate intercept. Rate units on the abscissa have only relative significance and vary from one experiment to the next, but range from 5 to 20 mm³/minute.

channel occupied by a bubble. Nevertheless, water is always steadily taken in after this treatment, which is to say that also in mangroves there is a ready bypass around an embolism of considerable size[3]. When the cut is properly executed under water no air enters, but the disturbance might conceivably cavitate the sap if high negative pressure obtained. The vapor locks would instantly collapse, however, and whatever bubble might be left would be trifling even at half an atmosphere's pressure; and yet, half an atmosphere stops the flow. Clearly, this is very difficult to reconcile with the idea of negative sap pressure.

A possible source of error would be if gas from a leak would blanket off the cut. Air leaks cannot be derived from active xylem channels if these are to operate at −20 atm, but only from other structures. Xylem leaks are common and vary from a few insignificant micro-bubbles to a steady gush, but it has always been possible to select sites which yield an insignificant amount of gas upon repeated evacuations. With a large and shallow cut and wide bore throughout, most bubbles will rise freely through the vertical burette, and it is easy to prevent gas collection on the cut by steady and sharp tapping of the horizontal stem.

Yet, convincing as these arguments might seem, they must be tempered by other observations that seem conflicting. Thus, when a healthy young stem of *Avicennia nitida* was cut off and the rooted stump was connected with a moist evacuated gallon jug and left overnight, no sap was yielded in spite of a final pressure reading close to vapor tension. Similarly, cut twigs attached to the bushes did not yield sap by vacuum. Possibly the sap pressure was slightly negative in these cases, or perhaps gas was yielded much easier than sap. We did not observe bleeding from an isolated root kept in seawater. Further studies are clearly called for before one may claim a full understanding of the hydrostatic situation in mangroves. But presently it does not seem possible to us that negative pressures of such colossal magnitude as −20 atm could consistently be concealed by three independent techniques.

► Sap Concentration in Relation to Aeration of Roots. In earlier investigations on Atlantic mangroves, it was shown that when high tide covers the lenticels on the stilt roots in Rhizophora or the pneumatophores in Avicennia, the oxygen tension drops in the root system and the gas pressure falls. When the tide recedes, air is aspirated through the lenticels and the oxygen tension rises. If the lenticels are clogged with grease, the oxygen tension falls from some 18 to 12 % down to near zero in a few days (16). It was, therefore, natural to postulate that oxidative processes might assist in the salt separation. In order to test this the pneumatophores of two Sonneratia bushes were cut off and the cut surfaces greased, so as to shut the root system off from air. Similarly, the stilt roots of a Rhizophora were greased. The oxygen tension was determined by drawing gas samples from a hypodermic needle implanted in the roots under the mud. In the Sonneratia plants, which grew on a sandy tide flat, the oxygen tension did not drop below 14 %, but in the Rhizophora growing in deep mud the oxygen fell from 18 % to 4 % in 2 days. In neither case did the salt concentration increase in the stem sap. Possibly, the anoxia was not severe enough to break down the mechanism of salt exclusion.

Discussion

In the present material of mangroves, one may distinguish between two categories, namely, those which excrete salt through the leaves and those which do not. Both groups are rooted in a substrate which is closely isotonic with the seawater. The non-secreting species have a xylem sap which is almost salt-free; and even in the salt-secreting species, the osmotic potential of the sap is mostly below 2 atm. Evidence so far indicates that the hydrostatic pressure of the stem sap under full transpiration, although occasionally a few atmospheres negative, is usually positive but below atmospheric. We may, hence, conclude that it would be premature to treat the steady state separation of freshwater from the sea by the roots in terms of a simple equivalence between hydrostatic pressure and osmotic forces in a semipermeable system, for this would require a permanent sap pressure of at least −20 atm, which is not indicated by present evidence. One is led, therefore, to consider the possibility of active transport. The fact that press juices from roots and leaves are more or less isotonic with seawater gives little help one way or another; but lack of osmotic gradient along the stem shows the rather obvious; namely, that at least here the sap moves by mass flow, rather than by osmosis.

Unbalance between osmotic potential and hydrostatic pressure is commonplace in animals, and certainly occurs in plants. For instance, both marine and freshwater fish have an osmotic potential in the blood of about ten atmospheres, but do not solve their osmotic problem by adjusting the blood pressures to −10 and +10 atmospheres pressure, respectively. The milk pressure in coconuts is another case where such relations do not apply (10), and the salt glands on mangrove leaves, secreting brine under oil, belong here also.

Mangrove roots are well ventilated through pneumatic tissues, and an aerobic energy source is, therefore, readily available for an active transport. One might visualize a system steadily taking in seawater by a moderate transpiration pull. Active transport would eliminate the salts fast enough to satisfy the

---

[3] The perivascular xylem of Avicennia and, in particular, Rhizophora consists of fibers rather than tracheids, but the vessel walls in both species are densely studded with pits, suggesting free water passage into the perivascular tissue. In Avicennia, perivascular fine channels are conspicuous; in Rhizophora not.

transpiration flow, allowing for an inevitable diffusion loss of water at the separation site. The only other system capable of operating on a moderate hydrostatic pressure difference appears to be one involving active secretion of water.

The salt-secreting species all contain a small amount of salt in the xylem sap, which is eliminated by the salt glands on the leaves. The excreta are some 10 to 20 times more concentrated than the sap and may exceed that of the seawater. The secretory process is not driven by the evaporation, for it also takes place under a layer of oil. It also proceeds for some time in detached leaves where the hydrostatic pressure of the sap is kept near ambient.

Interesting questions are: What salinity gradients do these cells operate against? Is the concentration accomplished in one spectacular step from nearly salt-free sap to double seawater? Are the glands situated at the end of a local concentration gradient within the leaves, such as possibly indicated by the high salinity of the crushjuices? Would such a gradient possibly be subtended by a (xylem-phloem) counter-current exchange system such as commonly found in animals, e.g., in the kidneys or swim-bladder where large concentration gradients are maintained? Another facet which invites comparison with animals is the fact that the salt glands regularly become covered by sodium chloride crystals on sunny days. It would appear that the glandular cells are capable of full activity, even though in direct contact with a saturated brine. There is hardly any parallel to this to be found in animal excretory systems. In our sweat glands, for instance, the secreting cells are separated from the drying secreta through a long spiraling duct. In light of the paradoxical situation in the mangroves, one might postulate that the function of these striking ducts in man may be to provide the active cells with a protective diffusion gradient.

Summary

A study has been made of various parameters of the salt balance in several species of mangroves. Some species, like Aegialitis and Avicennia, eliminate large quantities of salts through special glands on the leaves, a property which other species such as Rhizophora and Sonneratia do not possess. The salt concentration in the excreted fluid is often higher than that of seawater and has a marked diurnal cycle in concentration as well as quantity, both with a maximum in the daytime. The xylem sap in the salt-secreting species carries about 0.2 % to 0.5 % sodium chloride, a concentration which exceeds that of non-secreting species by some 10 times, and that of ordinary land plants by about 100 times. The osmotic potential of the sap of the mangroves is at most a few atmospheres. The sap pressure has been studied by three different approaches, which indicate that the pressure is usually below ambient, but that it seldom becomes negative and then only by a few atmospheres. It would, therefore, seem premature to postulate that the separation of fresh water from the seawater is a simple ultrafiltration, for this would demand a permanent sap pressure of −20 atm or less. The root system of mangroves is ventilated by air, and it seems more likely that the separation involves a case of active transport.

Acknowledgments

This investigation was performed on a Scripps Institution of Oceanography expedition, 1960, sponsored by research grant RG-7114 from the U.S. Department of Health, Education, and Welfare, Public Health Service.

We are greatly indebted to Dr. Hugh LeMessurier, Aeromedical Laboratory, University of Adelaide, Australia, for his advice and guidance, and to Mr. C. O'Leary, director of native affairs, Queensland, and his deputy director on Thursday Island, M. P. Kelloran. Dr. Stan Hynd, director of the Commonwealth Scientific and Industrial Research Organization, Division of Fisheries and Oceanography, Thursday Island, gave us the use of every facility of his laboratory. Mr. Vince Vlasoff, master of the expedition ship, the 55-foot "Tropic Seas," and his crew spared no effort in assisting in the program. We also wish to express our appreciation to our native assistant, Mr. Larry McDonald, who managed the chores around our laboratory camp on the Jardine River. During visits to our camp and to Thursday Island we had much help from and many inspired discussions with Dr. Knut Schmidt-Nielson, Duke University, and Dr. Hermann Rahn, University of Buffalo. We also received much help and advice from our plant physiology colleagues on the expedition, Dr. Beatrice Sweeney and Dr. Francis Haxo. We have had the privilege of stimulating discussions with Dr. Katherine Esau and Dr. C. R. Stocking at the Botanical laboratory, University of California, Davis, which kindly prepared xylem sections of our mangroves.

We are greatly indebted to Dr. L. S. Smith and to Dr. S. T. Blake of the Botanic Museum and Herbarium at Brisbane for the identification of our plant material, and wish to acknowledge the use of facilities at the Lerner Marine Laboratory, Bimini, Bahamas, and the Marine Laboratory, University of Miami.

Literature Cited

1. Adriani, M. J. 1956. Der Wasserhaushalt der Halophyten. In: Encyclopedia of Plant Physiology. 3: 902–914. Springer, Berlin.
2. Arisz, W. H., I. J. Camphuis, H. Heikens, & A. J. van Tooren. 1955. The secretion of the salt glands of *Limonium latifolium* Ktze. Acta Botan. Neerl. 4: 322–338.
3. Bennett, J. P., F. G. Anderssen, & Y. Milad. 1927. Methods of obtaining tracheal sap from woody plants. New Phytol. 26: 316–323.
4. Chapman, V. J. 1944. 1939 Cambridge University Expedition to Jamaica. Parts 2 & 3. J. Linnean Soc. London, 52: 448–533.
5. Faber, F. C. von. 1923. Zur Physiologie der Mangroven. Ber. Deutsch. Botan. Ges. 41: 227–234.
6. Harris, J. A. & J. V. Lawrence. 1917. The osmotic concentration of the sap of the leaves of mangrove trees. Biol. Bull. 32: 202–211.
7. Huber, B. 1956. Die Gefässleitung. In: Encyclopedia of Plant Physiology. 3: 541–582. Springer, Berlin.
8. Renner, O. 1911. Experimentelle Beiträge zur Kenntnis der Wasserbewegung. Flora (Ger.) 103: 171–247.

9. Ruhland, W. 1915. Untersuchungen über die Hautdrüsen der Plumbaginaceen. Jahrb. wiss. Botan. 55: 409–498.
10. Scholander, P. F. 1955. Hydrostatic pressure in coconuts. Plant Physiol. 30: 560–561.
11. Scholander, P. F. 1958. The rise of sap in lianas. In: The Physiology of Forest Trees, p. 3–17. The Ronald Press Co., New York.
12. Scholander, P. F., E. Hemmingsen, & W. Garey. 1961. Cohesive lift of sap in the rattan vine. Science 134: 1835–1838.
13. Scholander, P. F., W. E. Love, & J. W. Kanwisher. 1955. The rise of sap in tall grapevines. Plant Physiol. 30: 93–104.
14. Scholander, P. F., Berthe Ruud, & H. Leivestad. 1957. The rise of sap in a tropical liana. Plant Physiol. 32: 1–6.
15. Scholander, P. F., L. van Dam, J. W. Kanwisher, H. T. Hammel, & M. S. Gordon. 1957. Supercooling and osmoregulation in arctic fish. J. Cell. Comp. Physiol. 49: 5–24.
16. Scholander, P. F., L. van Dam, & Susan I. Scholander. 1955. Gas exchange in the roots of mangroves. Am. J. Botany 42: 92–98.
17. Sen-Gupta, J. 1935. Die osmotischen Verhältnisse bei einigen Pflanzen in Bengal (Indien). Ber. Deutsch. Botan. Ges. 53: 783–795.
18. Stocker, O. 1956. Die Abhängigkeit der Transpiration von den Umweltfactoren. In: Encyclopedia. Plant Physiology 3: 436–488. Springer, Berlin.
19. Troll, W. & O. Dragendorff. 1931. Über die Luftwurzeln von Sonneratia L. und ihre biologische Bedeutung. Planta 13: 311–473.
20. Walter, H. & M. Steiner. 1936. Die Ökologie der Ost-Afrikanischen Mangroven. Z. Botan. 30: 65–193.

Glycolic Acid Oxidase Formation in Greening Leaves[1, 2, 3]

M. Kuczmak & N. E. Tolbert

Department of Biochemistry, Michigan State University, East Lansing

The amount of glycolic acid oxidase in green tissue is much greater on a protein nitrogen or weight basis than in tissue without chlorophyll (8, 10, 13, 15). The active enzyme cannot be isolated from roots and tubers (10, 13), but it can be detected in small amounts from etiolated tissues. During greening of the plant tissue in the light the activity of the oxidase increases immensely. Increased enzyme activity has been found in etiolated tissue kept in the dark upon feeding an excess of glycolate to the intact leaves. When glycolate was added to a cell-free extract from etiolated leaves, the enzyme activity increased greatly after 18 hours of incubation at 2 C (15).

An initial explanation for these phenomena was based upon substrate activation of the enzyme and the assumption that glycolate was not present in roots or etiolated tissue (15). For green plants it was known that large amounts of glycolate were produced by photosynthesis (11). However, the presence of some glycolate has since been reported in both roots and etiolated tissue (5, 6, 7). Thus a substrate activation hypothesis seems unsatisfactory unless the possibility of compartmentalization within the cell is invoked. In this paper we have reinvestigated the previous observations on the activation of glycolic acid oxidase. A substantial amount of proenzyme for glycolic acid oxidase has been found in etiolated plants, but in amounts insufficient to account for all the active enzyme in the corresponding green tissue. Since the cofactor for this enzyme is FMN (16), the level of FMN and FAD in etiolated green plants was also measured. Preliminary studies were made on conditions for holoenzyme formation.

Materials & Methods

Etiolated wheat *Triticum vulgare L*, var. Thatcher, was grown in sand with or without nutrient in a totally dark room at about 21 C for 9 to 10 days at which time the plants were about five inches tall. The leaves were ground in a cold mortar immediately

---

[1] Received March 8, 1962.

[2] Published with the approval of the director of the Michigan Agricultural Experiment Station as Journal Article No. 2949. This research was supported by a grant from the National Science Foundation.

[3] The material presented in this paper is taken in part from the thesis of M. Kuczmak which was submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Michigan State University, 1961.

World mangrove resources

The purpose of the 'World Mangrove Atlas' in 1997 was to produce a graphic synthesis of information relating to the distribution and current status of mangrove ecosystems in our increasingly threatened coastal environment (Spalding *et al.*, 1997, Simberloff, 2000).

Inevitably, this atlas contains information or interpretations that not everyone agrees with as well as omissions. As the number of case studies provided in the book was very limited, we have been encouraged to obtain new satellite data, carry out new field surveys and use new analytical methods so that the atlas can be updated in a near future. All the cartographic and statistical outputs are intended to feed into the GLOMIS database.

The present knowledge on the extent of mangroves is summarized in Table 1. The Atlas includes country-by-country analysis and mapping of mangrove coverage. However, the effective monitoring and management of these ecosystems would need a much more accurate inventory for those areas which constitute hotspots for the survival of mangroves, their protection or sustainable use. Let us give three examples selected from coastal areas which are totally distinct from an ecological point of view:

<u>Thailand</u>

-The mangroves of Thailand have been mapped (about 2,700 km^2) and the trends in areal coverage and adverse pressures evaluated (strongly impacted by aquacultural practices). These data do not give any local information. This has to be improved in certain cases. For instance, the mangroves of Phuket, (see Fig. 1) with 780 km^2 of dense, generally well preserved types, are expanding after tin mines were abandoned. They are of special interest in the coastal context of Thailand (Boulbet, 1995).

<u>United Arab Emirates</u>

-The mangroves of the United Arab Emirates were not presented in the Atlas because their total areal extent was unknown and was too small on a worldwide scale. However, these mangroves, which occupy one of the driest habitats in the world, have a very high ecological importance in the Arabian Gulf (Saenger and Blasco, 2000). We know now that the scattered populations of *Avicennia marina* Forsk. Vierh., the only woody species which makes up these ecosystems, covers about 38 km^2 with an estimated standing biomass varying between 70 and 110 t ha^{-1}.

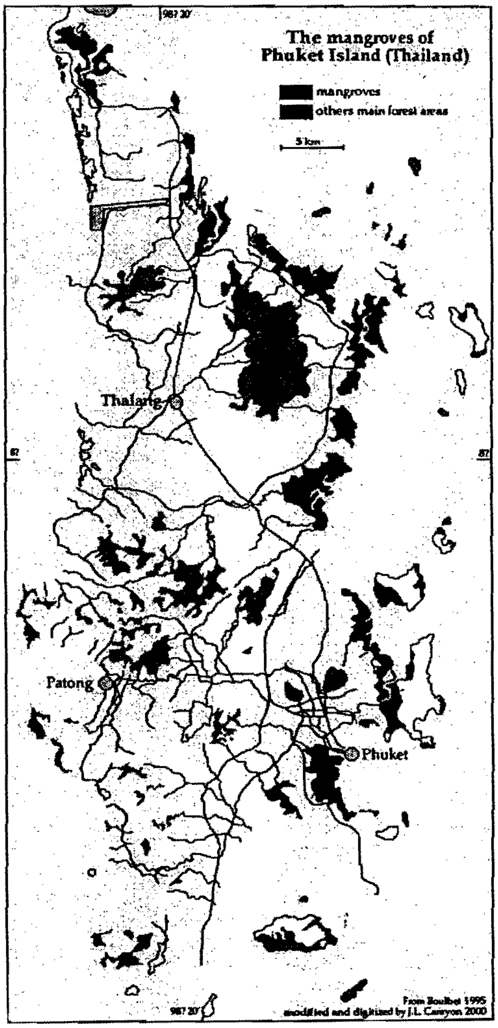


Fig. 1. Mangroves of Phuket island.

Table 1. Various estimates of mangrove areas, together with percentage figures of global totals (km^2)

Region	Mangrove Area Spalding *et al.* (1997)	Mangrove Area Fisher and Spalding (1993)	Mangrove Area IUCN (1983)
South and Southeast Asia	75,173 (41.5%)	76,226 (38.3%)	51,766 (30.7%)
Australasia	18,789 (10.4%)	15,145 (7.6%)	16,980 (10.0%)
The Americas	49,096 (27.1%)	51,286 (25.8%)	67,446 (40.0%)
West Africa	27,995 (15.5%)	49,500 (24.9%)	27,110 (16.0%)
East Africa and the Middle East	10,024 (5.5%)	6,661 (3.4%)	5,508 (3.3%)
Total Area	181,077	198,818	168,810

Indonesia

- The once luxuriant equatorial mangroves of the Mahakam River in Borneo (Indonesia) have lost, during the last 10 years, nearly half of their *Nypa* stands, which were destroyed by uncontrolled and widespread conversion to aquaculture. This striking local case does not appear in the general statistics of the country which has one of the largest mangrove areas in the world (more than 40,000 km^2).

The revised version of the world cartographic mangrove inventory is aimed at serving the needs of the scientific community and those of decision makers, as such, the data provided by satellites are not sufficient (Blasco *et al.*, 1998; Green *et al.*, 1998 and Ramsey *et al.*, 1996). The spectral signature of mangrove components relates almost exclusively to the 'Phytocenose' which is the most visible fraction of the ecosystem. Data on other components ('zoocenose', human interactions, microorganisms, etc.) are generally derived from ancillary sources. This is also the case for the 'geocenose' (habitat peculiarities) which includes hydrological rhythms, geomorphological features, bioclimatic properties, soils and water peculiarities, etc.

For each part of the world, an integration of all these heterogeneous and complex date help understanding of the present status, the ecological equilibrium and the evolutionary trends of each mapped mangrove (Hutchings and Saenger, 1987).

In theory, 70 countries having mangroves, have to be studied and mapped including small islands of the Southern Pacific and the Lesser Antilles. However, the following 18 countries taken together represent about 80% of the mangroves of the world (Table 2).

Hence, the logical statistical hypothesis is that a thorough study of the above 18 countries could be sufficient to provide a faithful illustration of the present status of the mangroves of the world. However, this is incorrect in practice, as already discussed (Phuket island, UAE, and Mahakam delta). Local specific cases and exceptional situations need special attention even in a study carried out at a worldwide scale.

The adopted classification system for the world inventory of the mangroves is based on physiognomic and structural attributes of each ecosystem, primarily because of its applicability to almost all mapping procedures including those using various computerized analysis of high resolution satellite data (Aizpuru *et al.*, 2000).

This current activity can be considered as an essential step towards a monitoring system of the main mangrove ecosystems in the world.

Blasco, F., Carayon, J.L. and Aizpuru, M.
Laboratory for Terrestrial Ecology
13, avenue Colonel Roche – BP 4072
31029 Toulouse Cedex 4 (France)
Tel: +33 5 61 55 85 43
Fax: +33 5 61 55 85 44
e- mail : Francois.Blasco@cict.fr

Table 2. Estimates of mangrove areas from major mangrove holding countries (km^2) (Aizpuru *et al.*, 2000)

America		**Africa**		**SE Asia**		**Oceania**	
Brazil	13,800	Guinea-Bissau	2,500	Vietnam	2,500	Australia	11,700
Colombia	3,700	Nigeria	10,500	Bangladesh	6,300	PNG	4,100
Cuba	5,600	Gabon	2,500	Indonesia	42,500		
Mexico	5,300	Cameroon	2,400	Malaysia	6,400		
Venezuela	2,500	Madagascar	3,200	Myanmar	5,200		
				India	6,700		
Total	30,900	Total	21,100	Total	69,600	Total	15,700

Suggested literatures:

- Aizpuru, M., Achard, F. and Blasco, F., 2000. Global assessment of Cover Change of the Mangrove forest using Satellite imagery at medium to high resolution. In *EEC research project n° 15017-1999-05 FIED ISP FR*, Joint Research Center, Ispra.

Blasco, F., Gauquelin, T., T., Rasolofoharinoro, M., Denis, J., Aizpuru, M. and Calderou, V., 1998. Recent advances in mangrove studies using remote sensing data. *Australian Journal of Marine and Fresh Water Research* 49(4):287-296.

Boulbet, J., 1988. Spot data analysis for Phuket island. AIT Bangkok and Toulouse. 4 maps.

Boulbet, J., 1995. Towards the sense of the Earth: Phuket Prince of Songkla University. Patani, 94000, Thailand, 138pp.

Dodd, R.S., Blasco, F. and Rafii, Z.A., 1999. Mangroves (*Avicennia marina*) and their diversity in cuticular hydrocarbons composition in the arid zones of the United Arab Emirates. *Aquatic Botany* 63:291-304.

Green, E.P., Clark, C.D., Edwards, A.J. and Ellis, A., 1998. Remote sensing techniques for mangrove mapping. *Int. J. Remote Sensing*, 19(5):935-956.

Hutchings, P. and Saenger, P., 1987. Ecology of mangroves. Univ. of Queensland Press. 388pp.

Ramsey, E.W. and Jensen, J.R., 1996. Remote sensing of mangrove wetlands: relating canopy spectra to site specific data. *Photogrammetric Engineering and Remote Sensing* 62(8):939-948.

Saenger, P., Hegerl, E.J., and Davie, J.D.S., 1983. *Global status of mangrove ecosystems*. IUCN, Gland.

Saenger, P. and Snedaker, S.C., 1993. Pantropical trends in mangrove, above-ground biomass and annual litterfall. *Oecologia* 96:293-299.

Saenger, P. and Blasco, F., 2000. The mangrove resources of the UAE with particular emphasis on those of the Abu Dhabi Emirate. 2nd Arab International Conference and Exhibition on Environmental Biotechnology in Abu Dhabi. Coastal Habitats. Abu Dhabi, 8-12 April 2000.

Simberloff, D., 2000. World Mangrove Atlas: Book review. *Biodiversity and Conservation* 9:443-444.

Spalding, M., Blasco, F. and Field, C., 1997. World Mangrove Atlas. ISME Okinawa (Japan). 178pp.