Coral Reefs of the Indian Ocean

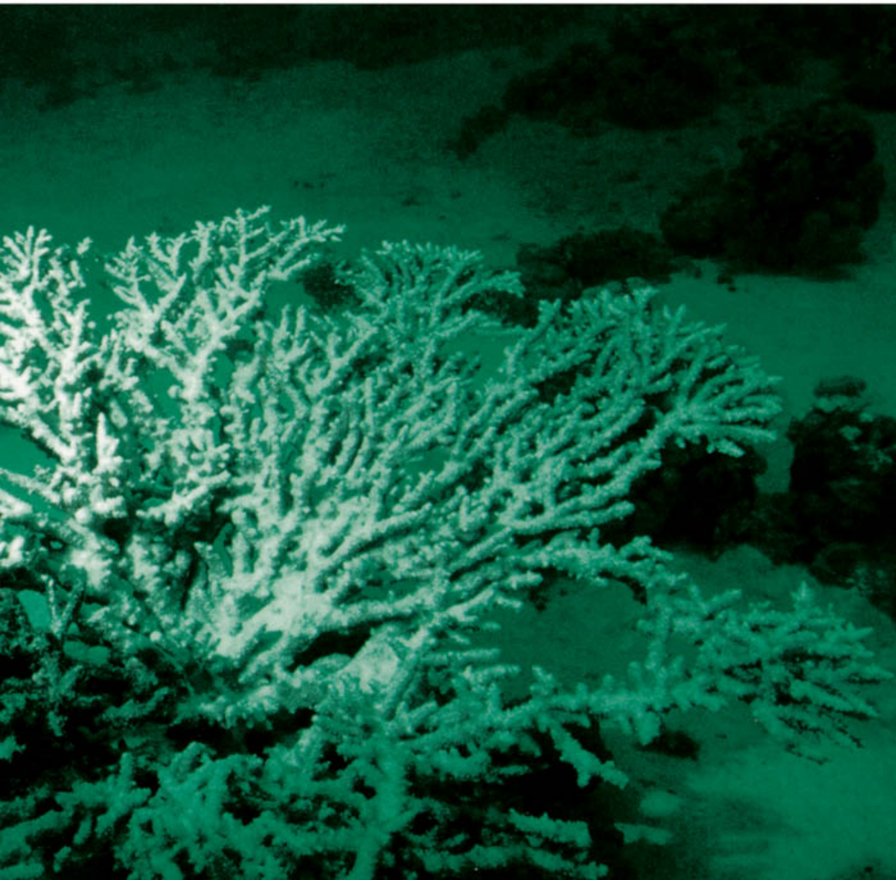
THEIR ECOLOGY AND CONSERVATION

EDITED BY

Tim R. McClanahan

Charles R. C. Sheppard

David O. Obura



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Introduction

This book was written for students, teachers, naturalists, ecotourists, researchers and managers learning or working in the marine environment who would like a recent review of the status of coral reefs and reef science and conservation in the Indian Ocean. It is focused on the western Indian Ocean as this represents a distinct biogeographic unit (see Chapter 1) that shares many of the same species and has many common processes and responses to environmental or human disturbances. The scientific literature from this region is scattered and much of it is not published in the standard journals or difficult to access. This book will therefore make it easy for the reader to become current with existing information as well as with current thinking and foci of reef investigations.

This book was developed from a workshop organized by The Wildlife Conservation Society's Coral Reef Conservation Project as part of the 1997 International Year of the Reef (IYOR) activities. One of the primary focuses of IYOR was to assess the status of coral reefs worldwide and the workshop and book represent part of this continuing effort. The authors of the following chapters focus on introducing the reader to the coral reefs of the region through past surveys, scientific research and conservation work. Environmental descriptions are not, however, restricted to the physicochemical and biological environment but also incorporate the human environment including the use of resources, the structures and mandates of national government and nongovernment organizations and their successes and failures in conserving marine resources.

Each chapter discusses the physical environment, the distribution of coral reefs, factors which are important for ecological processes and species diversity, and discuss how these ecological factors can be affected by present and projected human influences. Human influences over different time and spatial scales are considered and include harvesting, aquaculture, dynamite blasting, coral mining, pollution and poisons, global warming and species losses. The causes of ecological changes are discussed as well as the way reefs could be used in a sustainable way. The book also contains a number of case studies both in the text and in boxes which describe important concepts, problems or reef sites, such as the status of coral-eating starfish, coral disesases or the effects of aquaculture on reef resources. Authors have made an effort to keep the reviews and language simple and easy to understand. Readers may want to read the first two introductory chapters and then move to subsequent chapters as their interest dictates. Consequently, we have kept some redundancy among chapters.

The workshop and book were also an attempt to coordinate methods and activities of coral reef investigators and investigations in this region which is known to have poor scientific societal organization. Consequently, we held the workshop adjacent to the recently created Mombasa Marine National Park so that participants could undertake comparative field studies on the coral-reef parks and reserves of Kenya during the meeting. This workshop, the presentations of regional organizations, and the book's chapters suggest that the level of information and human capacity to collect and disseminate this information has increased greatly in the last decade. The presentations also demonstrate, however, that reefs are threatened by a number of environmental problems that are only moderately documented and understood. Nonetheless, these chapters do reveal the underlying causes of reef degradation and suggest ways to prevent it. Finding successful conservation, restoration or mitigation methods may increase the rate at which the elusive goal of sustainable resource use in this region can be reached. We hope this book helps to make the next step in assessing and ultimately managing this precious and biologically diverse tropical ecosystem.

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Chapter 1

Coral Reefs of the Western Indian Ocean: An Overview

Charles R.C. Sheppard

Coral reefs of the Indian Ocean exist in a very wide range of environments. Good examples exist of classic, oceanic atolls in clear water, and also of extensive fringing and patch reefs which grow in conditions of high environmental stress, where corals mix with other major benthic groups. Reefs develop best where sea surface temperatures remain above about 22°C, and classically, the reef province has previously been defined as that where temperatures rarely fall below about 18°C (40,47). The relationship between reef distribution and sea surface temperature has, however, turned out to be much too simplistic. Many reef species tolerate much lower water temperatures, and thriving coral communities may occur in conditions which are too cool, or perhaps too rich in nutrients, for reef construction to occur. The Indian Ocean is particularly rich in these examples, which will be discussed later.

As well as containing many clearly defined reef areas, the periphery of the ocean also contains extended mosaics of a wide range of benthic habitats. In these areas, reefs are but one integrated component of the shallow oceanic system. Research which has focused, not only on the reefs but on their links with adjacent habitats, has led to greater understanding of crucial processes that drive the Indian Ocean system. Knowledge of the energy, productivity, and mineral linkages between the different ecosystems may also be used to help manage and reduce the continuing damage that is being done to reefs in this region.

The Western Indian Ocean

The western ndian Ocean forms a coherent subdivision of the world's largest biogeographic province - the tropical Indo-Pacific (54). Yet, at first site it does not seem to be a particularly well-defined biogeographical area. The Indian Ocean as a whole is a more understandable sub-region, being bounded by great continental land masses, but even this is illusory as on its eastern side tropical water flows continuously through to the Pacific Ocean. Indeed, many shallow-water species of the Indian Ocean occur continuously along an equatorial band which stretches around nearly three quarters of the Earth's circumference. Within this realm, however, several sub-divisions are identifiable by groupings or associations of species. These groupings may be well defined and contained within boundaries, clearly marked by land masses, or they may be constrained by currents or by oceanic expanses which lack suitable shallow habitat.

The western Indian Ocean grouping may be determined in part by its distance from the high diversity locus in south-eastern Asia. The origin and maintenance of this high-diversity locus is not well understood but is central to much of the biogeographical debate about sub-regional areas within the Indo-Pacific. In the case of corals, diversity contour lines have been drawn since as early as 1971 using genera (65), and the early 1980s using species (53). Diversity is highest in the Indonesian region, falling in a regular way eastwards across the Pacific. However, diversity does not fall in a regular way, or at all, westwards across the Indian Ocean. Instead, species richness stays high along the equatorial belt across the whole width of the ocean. Species identity does tend to change from east to west, along with a decline in Asian species, but this species loss is made up for by Indian Ocean endemics. As a consequence, contours of coral species richness, when drawn for the Indian Ocean, tend to remain similarly high roughly between the Tropics of Capricorn and Cancer, then collapse over very short latitudinal distances to the north and south. The Indian Ocean as a whole is, thus, unlike the Pacific, and there are no simple diversity clines expanding outwards neatly from the highest diversity center around Indonesia.

Nevertheless, there is a drop in coral diversity immediately west of Indonesia. This is because there is a lack of land and shallow water suitable for reef development for a considerable distance. Islands which do exist are tiny and, for reasons connected with small size, support a greatly reduced biotic diversity. Shallow continental substrate around the Bay of Bengal and along eastern India is too muddy for reef growth, and with only rare and small exceptions, is devoid of any corals (1). Substantial quantities of substrate suitable for reefs do not occur westwards until the Lakshadweep - Chagos chain of atolls.

The distribution of substrate in the western part of this ocean which is capable of supporting reefs is shown in Figure 1.1. Suitability is determined, partly by depth, but is also affected greatly by a range of other controls which preclude reef development. Westwards from the Lakshadweep - Chagos ridge lie the numerous islands and shallow platforms of the Seychelles territories, the Mascarene group and their outliers. Also, and probably most importantly, there is the vast range of shoals and shallow waters which stretch discontinuously between the Seychelles and Mascarenes; these include the Nazareth Bank, Saya de Malha Bank and Cargados Carajos Shoals. The potential reef substrate on this mainly submerged limestone chain is at least as great as that of all other islanded and inhabited groups, and is greater than that along the continental rim of the ocean. Yet, apart from limited and tantalizing anecdotes suggesting that this platform supports reefs with enormous algal ridges (63), it is still largely unknown territory. All shallow areas combined in the western Indian Ocean contain almost as much potentially reefal area as does the oceanic Pacific, and several times more than that which exists in the Atlantic province.

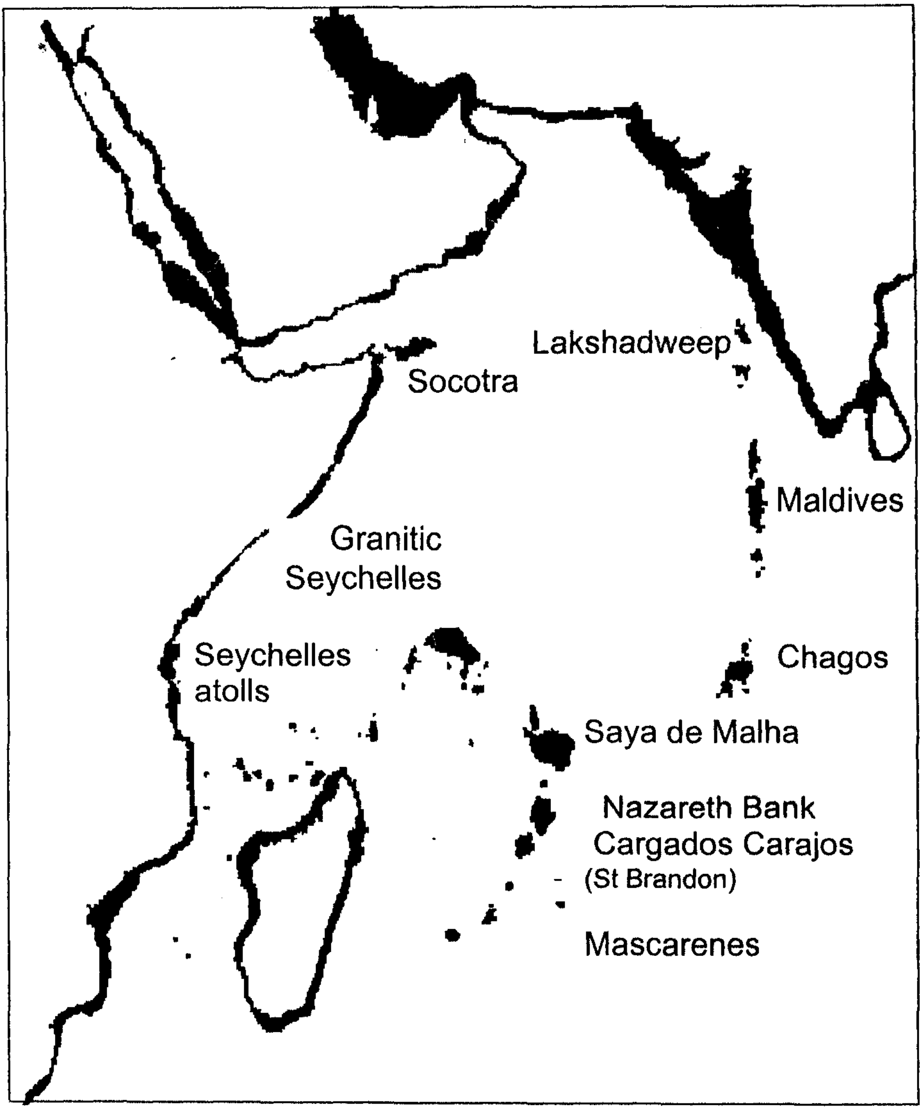

Figure 1.1. Potential reef substrate in the western Indian Ocean. Shaded areas are those where water is shallow enough for reef development. Based on GEBCO Digital Map of the Oceans, from 200 m contours with modifications. Not all shaded areas actually support reefs for reasons described in the text.

Reefal areas of the western Indian Ocean are thus separated by substantial distances of deep ocean or muddy shallow water from the richer areas to the east. Although boundaries defined by an absence of anything, like lack of suitable substrate, may be vague, they are nonetheless important, and geographically there is a marked contiguity about the western side of the Ocean and a validity to its definition as a 'region'. This is amplified in more detail later from the viewpoint of the reef-building corals themselves.

Present Knowledge of Western Indian Ocean Reefs

Thirty years ago researchers noted that the Indian Ocean was the least known and understood of the tropical oceans (3,74). Since then, considerable work has clarified our understanding of its biological systems and processes, but much less than for other tropical oceans, leaving this still very much the least known of the tropical oceans. For example, it is surprising that the Seychelles, which is spread out over such a large fraction of the Indian Ocean, is the source of so few marine science publications. There are very few established research institutions located in the area, unlike the case in the other tropical oceans, so that although notable work has come from some local research stations, most of our knowledge has come from occasional expeditions originating outside the region.

Scarce knowledge does not mean that human influences on the coastal and marine habitats are equally limited, however. Human pressure on marine habitats is increasing to the point, in some cases, where serious concerns exist as to their continued integrity. These concerns are not limited to the immediate proximity to areas of dense human populations since it is becoming clear, for example, that wide-ranging fishing fleets have caused fish stocks on some of the unstudied areas to become depleted in similar manner to reefs closer to home.

Our understanding of marine systems is often couched in terms of three broad features: biodiversity, productivity and system integrity (57), all of which require priority attention when habitats are under pressure. The first two of these, diversity and productivity may, in some cases, exhibit a reciprocal relationship. In the tropical Indian Ocean, biodiversity patterns are now becoming slightly better known, while productivity of the marine systems is similarly becoming better known from an increasing number of studies scattered across the region, from the Arabian peninsula to the Mascarenes. The third feature, system integrity, is an emergent one, derived in part from the first two The need to determine the system integrity of Indian Ocean habitats remains a priority, as does the need to maintain it.

The main function of this chapter is to place coral reefs of the Indian Ocean into a wider ecological context. Many of the main controls which act on reefs of the region, such as currents, tides and other oceanographic conditions, are described for each area of the Indian Ocean in the relevant chapters of this volume. Box 1.1 provides an overview of salient features of marine climate which connect, separate or otherwise interact with the major marine habitats on an oceanic scale. This chapter also presents a large-scale perspective of all Indian Ocean shallow habitats, including those areas where corals and reefs are not necessarily at their most abundant or profuse. Such areas are generally much less studied than are 'good' reef areas, and by understanding the environment in which they live, marginal areas tell us a great deal about the limits which reefs can tolerate before being extinguished.

Box 1.1. Marine Climate: Ocean-Scale Effects

The main climatic control on the northern Indian Ocean's reefs is the monsoon cycle. In January the Intertropical Convergence Zone (ITCZ) lies south of the equator where the southeast trades winds blow, while in the north the northeast monsoon is fully developed. In the second quarter, the ITCZ moves north reaching southern India in late April. From then, the southeast trades occupy the whole of the southern ocean, while in the north, rainfall become frequent and a few systems develop into cyclones. In the third quarter the southwest monsoon holds sway over the north where mean wind speeds and rainfall reach their maximum, and in the southern ocean, the southeast trades reach a mean speed of 9 m/sec - the world's most vigorous trade winds. Finally, in the fourth quarter, the southwest monsoon diminishes, winds change to north-easterly, and the ITCZ migrates south again (2,4). The currents driven by this create one of the world's five major upwelling systems, whose nutrient enriching properties have profound effect in the north-west, generating most of the pelagic productivity of the Indian Ocean (3). The Arabian upwelling (see Fig. 1.10), which has varied in intensity through the Holocene (5), offers a significant, selective barrier to the migration of species (6).

Storms and cyclones are equally important to some reefal areas. They generally track northwest and southwest from the equatorial belt between 5°N and 5°S. The southwest Indian Ocean experiences the most, peaking in January, but affected land is relatively sparse. The northern Indian Ocean has fewer cyclones than the south, but many more reach populous areas, especially in May and November. Generally, soft substrate habitats are affected more than reefs. Arabian areas experience cyclone strength winds only rarely, but strong thermally generated winds are very common, causing desiccation of shallow habitats in summer and chilling in winter.

Currents close to shore are well mapped, but those in mid ocean are sometimes only vaguely sketched and sometimes even contradictory. Most major currents are seasonal and follow the monsoons, but the west-flowing South Equatorial current in the southern Indian Ocean exists all year. These have significant larval mixing consequences on an ocean-wide scale, and some major currents are shown in Figure 1.11 in connection with productivity patterns. Deep currents are also important. From principal water sources in the Antarctic region, at least two northerly streams flow up both sides of the Indian Ocean and are deflected back towards the central Indian Ocean near or north of the equator. The western stream is deflected off Arabia where nutrient rich upwelling occurs. Another important deep current arises from evaporation and increased salinity in the Red Sea and Arabian Gulf; dense water flows into the Arabian Sea and Indian Ocean where it is detectable as far east as India.

Sea surface temperature is the one limiting factor for reefs and corals. In the extreme north of the Bay of Bengal and Arabian Sea, as well as in the semi-enclosed Red Sea and Gulf, temperatures rarely have extreme values or greater seasonal ranges than can be tolerated by most corals, but in many cases other factors combine to restrict reefs, such as turbidity, unsuitable substrate, and high nutrients. Off many of the oceanic islands in particular, thermoclines may exist shallower than 50 m, below which temperatures may drop 2 to 4°C, but in these areas surface temperatures have low seasonal variation. In the region of present interest, coral distribution is restricted by low temperatures only on the southern African coast. High temperatures may restrict corals in local areas throughout the region, particularly the north-west.

Oceanic surface salinity shows a clear gradient from greatest in the west and Arabian Sea (36 to 37 ppt) to lowest in the east and Bay of Bengal (<33 ppt). Except in embayments, extreme levels seldom impact any of the coastal marine habitats. In the Red Sea and Arabian Gulf, salinity rises gradually to over 41 ppt apparently without affecting corals or other habitats which appear to be well adjusted to these elevations, until levels exceeding 45 or even 48 ppt are reached.

Throughout the ocean where reefs occur, tidal ranges are usually 2 m or less, though in the far north, tidal ranges increase gradually to 5 m. In the northerly coral bearing Gulf of Kutch, tides reach 6 m and generate sediment laden currents of 2.5 m/s (1).

Charles R. C. Sheppard

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Western Indian Ocean Tropical Marine Habitats

The tropical Indian Ocean, like other tropical oceans, is only 'tropical' in its uppermost 50 or 100 meters of water (56). Below this depth, rapidly falling temperatures provide conditions which are similar to temperate and Arctic seas. Tropical benthic habitats occur only where this relatively thin film of warm water spills over continental shelves. Tropical habitats are disrupted where this thin film is displaced by permanent, seasonal or even apparently random episodes of cool currents, extreme salinity or nutrient enrichment. Such factors are important for controlling the distribution of the habitats themselves, and for determining levels and origins of productivity. There are very few areas of the Indian Ocean where the cold-water layer is much deeper than the limits of the photic zone, one unusual example where this is the case is the Red Sea. It is as common for the vertical extent of so-called tropical communities to be controlled by temperature drop as much as by loss of illumination. Horizontal mixing of water is 100 to a 1000 times greater than vertical mixing (32) for physical reasons connected with properties of water and the Earth's rotation. Productivity is greatest where vertical and horizontal mixing are both greatest.

Indian Ocean Reefs and Corals

Work on Indian Ocean reefs increased during a period which saw the start of analytical rather than descriptive work (50,63,67,68). Coral reef structure, profile and zonation has been described more than adequately (40) and is not repeated here. Indeed, there may have been a preoccupation with describing reefs which has led to too simplistic a view that there are only a few discrete kinds or shapes of reefs, including those initially described by Darwin, and this has sometimes concealed the vast array of reef shapes and 'types' that actually exists. A continuum exists not only between reef 'types' themselves but, as importantly, between reef habitats of all forms and non-reefal habitats, especially in marginal areas in the Indian Ocean.

Coral reefs fringe less than one half of the continental shorelines of the tropical Indian Ocean. Reefs are limited in the north by the lack of firm substrate, massive fresh water and sedimentary inputs from the Indus, Ganges and other smaller rivers (Fig. 1.2). Therefore, Pakistan and much of India and Bangladesh have no significant reefs. In the northwest, Oman, South Yemen and Somalia have very restricted reef development due to cold-water upwelling, and reefs there exist mostly in conjunction with macro-algal communities. The Red Sea has extensive fringing and barrier reefs in the north and central regions but has much less reef development in the south. Reefs fringe only a relatively small part of Indian and about half of the Sri Lankan coastlines, partly due to turbid conditions, and partly due to seasonal monsoon changes which drive massive quantities of sand causing severe scouring. In East Africa, substantial fringing reefs are found discontinuously between 5° North and 20° South, along with numerous forms of 'shelf' or 'patch' reefs arising from the continental shelf.

Atolls are abundant on the Lakshadweep - Chagos ridge, in several Seychelles groups and on other limestone plateaux in mid ocean. High islands may have good reef development (Rodrigues, Andamans, Nicobars), but many of the tropical high islands have relatively poor reefs or even no reefs at all (Reunion, Mahé). Notable features include the Mayotte double barrier reef and numerous exceptionally large algal ridges, notably those on the Cargados Carajos shoals and Chagos. The range of atoll size is also striking. Some are enormous (Great Chagos Bank) or have a nearly continuous island rim (Diego Garcia). Several atolls of the Seychelles have extremely shallow lagoons (Farquhar), while many have very deep lagoons or wholly drowned rims as well. The relationship of lagoon depth with atoll size is tenuous at best (66) though past sea level is known to be an important controlling factor on many aspects of reef structure (see Box 1.2).

Coral Biogeography of the Western Indian Ocean. Strong underpinning for the concept of a western Indian Ocean region comes from the biogeographic pattern of corals. A new database of Indian Ocean corals has been compiled and reanalyzed (58), building on work done 15 years earlier

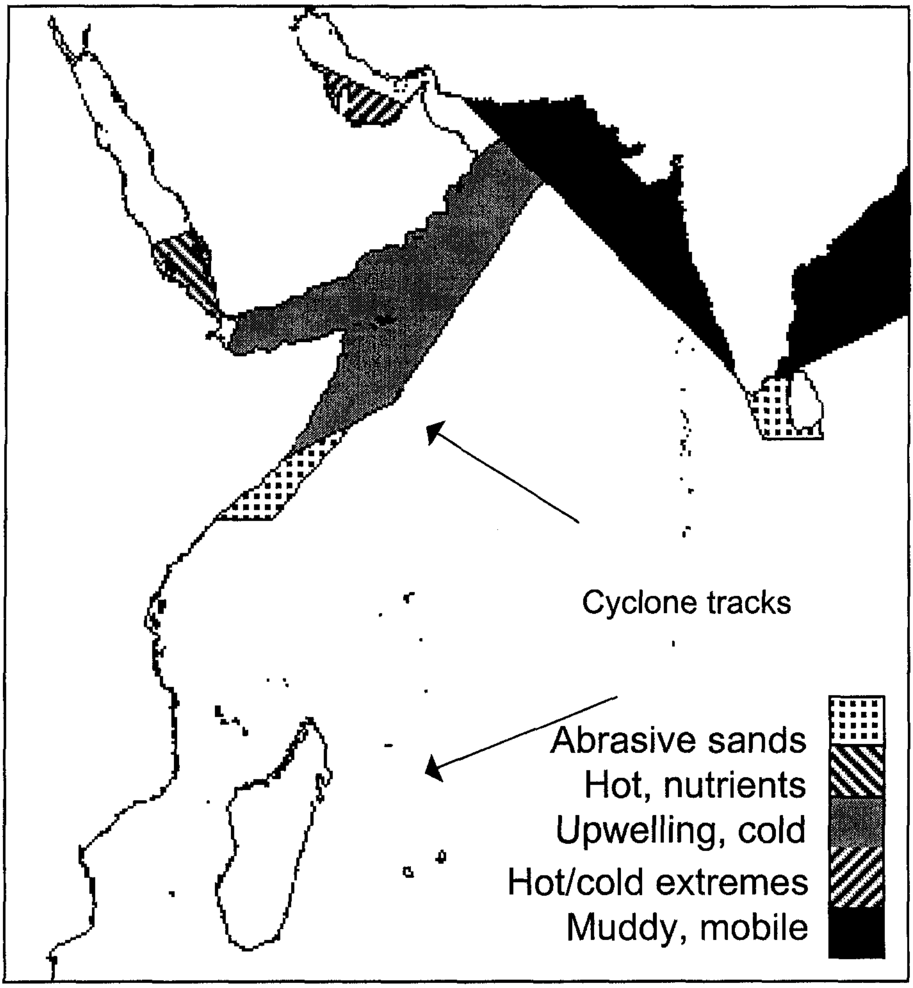

Figure 1.2. Generalized distribution of conditions which are hostile to the establishment of reefs. The annual mean 20°C contour which conventionally defines the limits to reef growth is not drawn though it roughly coincides with the bottom of the map. There is no equivalent temperature contour in the north of the ocean. Arrows show cyclone tracks in the ocean.

(54). Table 1.1 summarizes generic and species data from sites across the whole Indian Ocean. In the data matrix of 26 sites and 491 coral species, about 5000 of the cells, or 40%, are 'filled', nearly double that recorded in the compilation of 15 years ago. Cluster analysis has confirmed that, from the viewpoint of corals, there is a clear biogeographic separation of the region west of the Sri Lanka to Chagos line (Fig. 1.3). A sub-regional structure is also evident. Reinforcing the validity of the cluster analyses is the fact that tests for the effects of error in the taxonomic database show that considerably more error can be contained in the species lists before these patterns disappear. The

Box 1.2. Reefs and Sea Level Changes

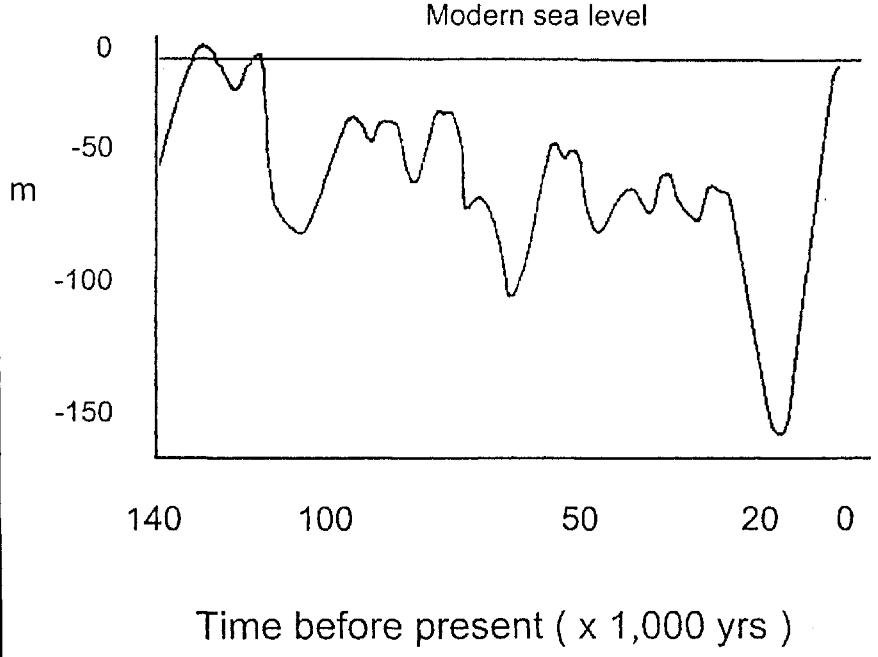

Figure. Sea level changes, based mainly from reef studies using a combination of dating and the relative locations of micro-atolls.

At the start of the Holocene, sea level was approximately 130 m or more below present (5) following a long period of major fluctuations (Fig. 1.1). Then sea level rose rapidly to near its present day level during the last 7000 years.

For the Red Sea, minimum water level lay close to the depth of the sill at its entrance. Complete "drying out" of the Red Sea was unlikely, but outward flows of highly saline water could not be supported, and salinity increased to >50 ppt and even 70 ppt (7,8) enough to kill most biota (3,4), though episodes of new inflows of Indian Ocean water occurred (1). Elsewhere, shallow, coastal areas including the Arabian Gulf dried out, and the limits of drying approximately match the shaded area in Figure 1.1. Recruitment of macroscopic marine life into all such areas commenced anew about 6000 years B.P.

Because the lagoons of most atolls are shallower than 130 m, sea level changes had profound effects on the amount of land and shallow reef flat that was exposed. Apart from islands about 2 to 3 meters above high tide, a typical atoll top is a vast reef flat near low water level. Seaward of atolls, reef slopes are generally steep, plunging in steps or continuously to depths of hundreds of meters. Within atoll rims, lagoons are most commonly 10 to 200 m deep, depth bearing only a loose relationship to atoll diameter (9). Thus even modest falls in sea level will expose reef flats and some lagoon floors as well, greatly increasing the dry land area. At lower still stands, new 'benchmarks' developed, evidenced by shelves, relict spurs and erosion caves seen in many reefs 20 to 60 m below present sea level.

Sea level fall is likely to have had little effect on the quantity of steep seaward reef slope habitat; the sea level merely sliding up and down seaward slopes at rates sufficiently slow to permit more than adequate time for coral and other species to 'relocate' vertically. A great reduction of lagoonal habitat may have occurred, where existing lagoons emerged. Current ideas of lagoon formation suggest, however, that exposed limestone subjected to rain erodes into dish-shaped lagoons cut by channels whose depth equals the deepest part of the lagoon floor, a condition actually observed in most atolls. In this manner, rain tends to erode atolls back down to sea level, maintaining an atoll shape. Conversely, sea level rises are generally thought to be balanced by upward reef growth, whose rate is usually, but not always, capable of keeping up with sea level rise (6).

On continental shelves, sea level change has complex effects caused by extensive lateral movement of the waterline, the slopes being very gradual in comparison to atoll slopes. In several continental areas, tectonic rise or fall of the shore also modifies the pattern greatly - elevated fringing reefs line much of the Red Sea and African shores, for example. Many patch reefs located mid way on shelves probably owe their origins to patches of ground which lay in water much shallower than today, their growth matching subsequent sea level rise. Chains of present-day patch reefs are located on top of old reefs which used to line palaeo shores; excellent examples being seen in Somalia (2) and in the 'Little Barrier Reef' off Saudi Arabia (8).

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general pattern is, therefore, robust, although further sampling in several sites may influence details.

Several of the most distinct clusters are the subject of separate chapters in this volume. The Red Sea is a relatively homogeneous basin in terms of species presence, though it contains marked environmental gradients along its length (59). The Arabian Gulf, Gulf of Oman, and Arabian Sea is out on a limb, like the Red Sea only more so, as is reflected by its lower diversity. Due to the different kinds of environmental extremes in this area (Fig. 1.2 and see later Table 1.5) the Arabian Gulf is rather dissimilar to that of the Red Sea despite being geographically closest. Its ecological constraints have been more severe since the start of the Holocene (60).

The oceanic island groups of the central and western Indian Ocean similarly reveal a diversity and species substructure which has important consequences. Firstly, it shows that the Indian Ocean is not a thoroughly well-mixed basin. Distances are great, which undoubtedly is important, but sub-regional differences in the environment almost certainly are important as well. Of all the coral species in the Indian Ocean, about one third are very widespread and one third are restricted to less than three or four sites, almost always geographically adjacent ones.

In support of the view that the western Indian Ocean is a sub-province, at generic level eight genera appear only to the west of the central line. This has long been recognized (46), but is strengthened with subsequent records (Table 1.2). All these genera are monospecific and may be described as western Indian Ocean genera. Also shown in Table 1.2 are genera which occur in the eastern but not western Indian Ocean. These too are monospecific genera. There are of course, several other genera of the Indo-Pacific realm which do not occur in any part of the Indian Ocean at all.

A total of about 400 different species have been recorded for the western Indian Ocean, 80% of the number for the whole ocean. Figure 1.4 shows the patterns of species and generic diversity with both latitude and longitude in the 21 western Indian Ocean sites for which adequate data are available. R^2 values and lines of fit are added for the species distributions. These are not very strong, and those for genera are very weak. Scatter is considerable, but there is a tendency for a decline with increasing latitude both north and south, and there is a richer fauna in the extreme east and west. Using these data it is safest to assume that there is no developed diversity trend in any direction, and certainly not a very significant gradient. Decline in diversity with high latitude is abrupt when it occurs.

Distributions and Environmental Constraints. The coral diversity pattern noted is only very loosely correlated with the abundance or even with the existence of reefs over this oceanic scale. Areas with high coral diversity may contain well developed reefs, marginal and weakly developed reefs, or even no true reefs at all but which instead support rich coral

Table 1.1. Summary of number of species and genera in 26 relatively well-sampled sites in the Indian Ocean region. Sites from the eastern Indian Ocean are included since these are pertinent to determination of a western Indian Ocean province. Sources are exactly those discussed extensively in (58) and used in the cluster analyses described in the text. Newer work, for example (31) and Veron (unpublished data for East Africa), as well as new personal observations for East Africa are not included to remain consistent with the figures.

Site	Latitude at center	Longitude at center	No Species	No Genera
All sites			491	87
Gulf of Aqaba, Gulf of Suez	27	34	138	54
Central Red Sea (Yanbu)	23	37	150	50
South Red Sea Jeddah-Jizan, Sudan	16	41	115	49
Arabian Gulf	26	51	62	27
Gulf of Oman	24	59	77	34
South Oman, Gulf of Aden, Socotra	14	53	101	43
Gulf of Kutch	23	69	37	20
Somalia	5	49	52	22
Kenya / Tanzania	-5	40	112	50
Mozambique	-20	35	110	44
Tulear Madagascar	-24	43	112	57
South Africa	-28	32	89	39
Aldabra, Cosmoledo, Farquhar	-9	46	95	40
Granitic Seychelles, Amirantes	-4	55	174	55
SE India, Sri Lanka	8	79	182	55
Lakshadweep	11	73	95	34
Maldives	5	73	187	57
Chagos	-7	72	220	58
Reunion	-21	56	124	43
Mauritius	-20	58	133	47
Rodriguez	-20	64	84	36
Cocos Keeling	-12	97	94	29
Nicobars, Andamans	10	92	131	50
Thailand, Mergui Archipelago	10	98	214	64
Northwest Australia	-18	116	311	71
Southwest Australia	-30	115	192	47

communities on non-reefal substrates. Conversely, areas with relatively low diversity may contain well-developed reefs. There is no strong relationship between coral diversity and degree of reef development. Many areas contain moderate coral diversity but do not form reefs, the corals growing on a wide variety of non-limestone substrates and old limestone platforms which currently do not accrete (60).

For example, in the Arabian Gulf as a whole, diversity is fairly low, probably more because of barriers to recruitment provided by upwelling and muddy substrate (Fig. 1.2, and see Fig. 1.10 later) rather than to conditions in most of the Gulf, yet substantial coral reefs exist there. Conversely, the Oman and Somalia coasts which are subjected to seasonal upwelling, have more than double the number of coral species, but contain very poor reef development. The identity of the species are similar, though there are more of them, but over wide expanses they do not develop into reefs. Commonly they exist mixed with macroalgae. Similar accounts can be drawn for several areas, from the Mascarenes where reef development is poor in several parts (39), to Sri Lanka (61). Table 1.3 shows that the considerable influence of adverse conditions in the north-western part of the Indian Ocean extends to several other

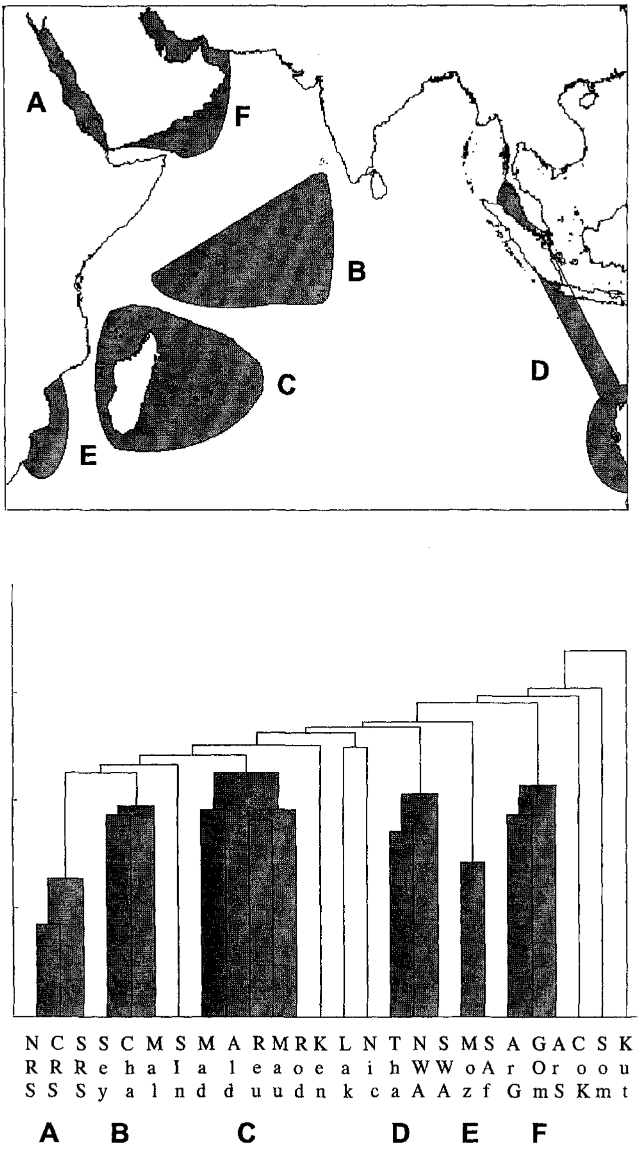


Figure 1.3. Cluster analysis of coral species records. The Jaccard similarity coefficient was used, with weighted clustering. Clusters are shaded, both on the map and dendrogram: the clusters marked A to E on the dendrogram correspond to the same letters on the map. Site codes on dendrogram: NRS= Northern Red Sea, CRS= Central Red Sea, SRS= South Red Sea , ArG= Arabian Gulf, Gom= Gulf of Oman, ArS= Arabian Sea, Kut= Gulf of Kutch, Som= Somalia, Ken= Kenya + Tanzania, Moz= Mozambique, Mad= Tulear Madagascar, SAf= South Africa, Ald= Aldabra + Cosmoledo + Faarquhar, Sey= Granitic Seychelles + Amirantes, Sin= SE India + Sri Lanka, Lak= Lakshadweep, Mal= Maldives, Cha= Chagos, Reu= Reunion, Mau= Mauritius, Rod= Rodriguez, CoK= Cocos Keeling, Nic= Nicobars + Andamans, Tha= Thailand + Mergui Archipelago, NWA= Northwest Australia, SWA= Southwest Australia.

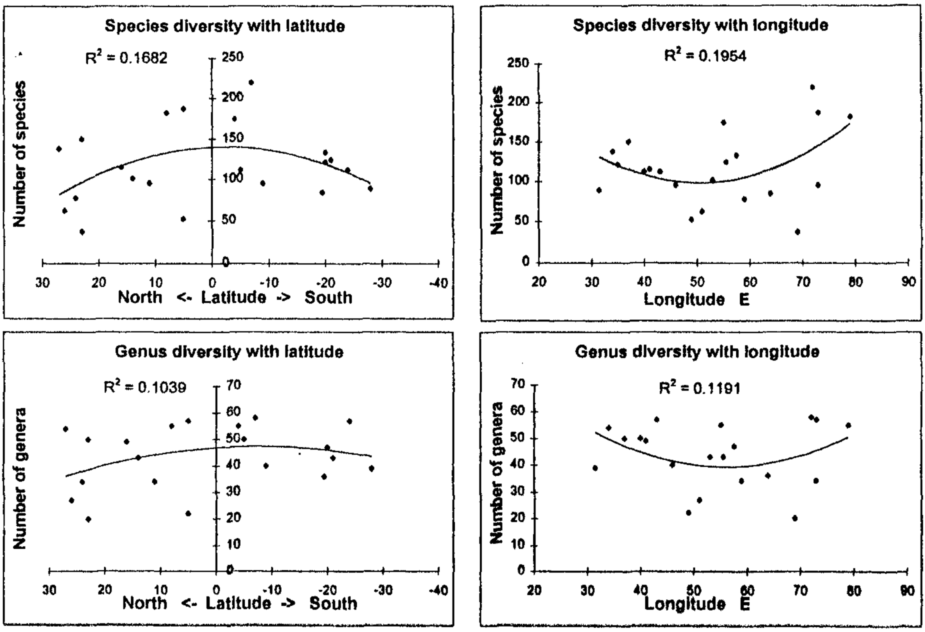


Figure 1.4. Plots of species (top) and genera (bottom) against latitude (left) and longitude (right) in the 21 western Indian Ocean sites.

major biotic groups as well. All fall in diversity from east to west in these sites. The Red Sea is a special case. Characteristics such as higher than oceanic rates of speciation, forcing by currents which makes the Red Sea act like a large catchment, and a reasonably equitable environment, all mean that diversity in the Red Sea, for many groups, rises again to levels higher than in many other parts of the Indian Ocean.

Questions have sometimes been raised about the validity of phrases like 'stressful environment' or 'increasing stress' (or 'equitable environment' used above) since stress for one group may be inconsequential or even desirable to another. From the viewpoint of the corals and reefs, however, the use is clear: increasing stress refers to an environmental gradient along which, at some point, corals can no longer live. Examples include elevated salinity, low or high water temperature, and elevated nutrients and sediments.

There is of course no doubt that environmental conditions of increasing severity do eventually kill off both reef development and coral diversity. Figure 1.5 shows a decline in diversity with increasing salinity in the northwest of this region, while Table 1.4 presents data showing the rate at which diversity is lost with increasing seasonal temperature fluctuation rather than just with high or low temperature.

It is clear that the demise of reef growth may take place at quite different points along an environmental gradient than the demise of corals. The reasons for this have been discussed, but are still not explained (60). While it is now understood that reefs do not simply develop because corals grow on top of other corals, other so far undetermined causes of reef construction require explaining possibly incorporating microbial or micro-chemical processes (60). The 'corals-

Table 1.2. Zooxanthellate coral genera restricted to the western and central Indian Ocean, and those found in the eastern Indian Ocean which do not occur in the western region. Several additional genera of the South East Asian region do not occur in any part of the Indian Ocean.

Genus	Family	Where recorded
Western Indian Ocean		
Anomastrea	Siderastreidae	Arabia, Africa, Seychelles
Astraeosmilia	Faviidae	Africa, Chagos
Craterastrea	Siderastreidae	Arabia, Chagos
Ctenella	Meandrinidae	Chagos
Erythrastrea	Faviidae	Arabia
Gyrosmilia	Caryophylliidae	Arabia, Africa, Aldabra, Mascarenes
Horastrea	Siderastreidae	Africa, Madagascar, Mascarenes
Parasimplastrea	Faviidae	Arabia
Eastern Indian Ocean		
Palauastrea	Pocilloporiidae	
Lithophyllon	Fungiidae	
Moseleya	Faviidae	
Acrhelia	Oculinidae	
Scapophyllia	Merulinidae	
Physophyllia	Pectinidae	
Montigyra	Caryophylliidae	
Duncanopsammia	Dendrophylliidae	

Table 1.3. Gradients in the number of species in six groups in three broad locations of the Indian Ocean. Western and 'central' Indian Ocean refers to the main body of the Ocean excluding peripheral seas.

Taxonomic group	Arabian Gulf	Arabian Sea	Western and 'central' Indian Ocean
Dinoflagellates	~50	130	452
Corals	~50	~80	300+
Non-reef fishes	300	300-500	600+
Reef fishes	190	200-300	1,400
Mangroves	1	3-10	50+
Seagrasses	3	11	~20

Table 1.4. Temperature extremes recorded in reef areas in embayments in peripheral parts of the Indian Ocean (60), and numbers of coral species.

Location	Latitude (°N)	Min (°C)	Max (°C)	Range	Coral diversity
Saudi Gulf	27	11.4	36.2	24.8	60
Qatar Gulf	24	14.1	36.0	21.9	40-60
Abu Dhabi Gulf	25	16.0	36.0	20.0	40-60
Kuwait	29	13.2	31.5	18.3	40
Gulf of Suez	29.5	17.5	30.0	12.5	100
Gulf of Aqaba	29	20.0	28.0	8.0	150+

on-corals' scenario for reef development does exist, but it is not particularly common. Examples include the huge *Porites* clusters which develop in many sheltered embayments throughout the Indian Ocean. Few other corals can form reefs in this way. Equally dense cover of *Acropora*, *Pocillopora* or even *Montipora* exist, but these do not necessarily consolidate into anything more than a tangle of friable limestone branches. The test of reef durability will come only when their survival is seen following a cyclone, or with a glacial-

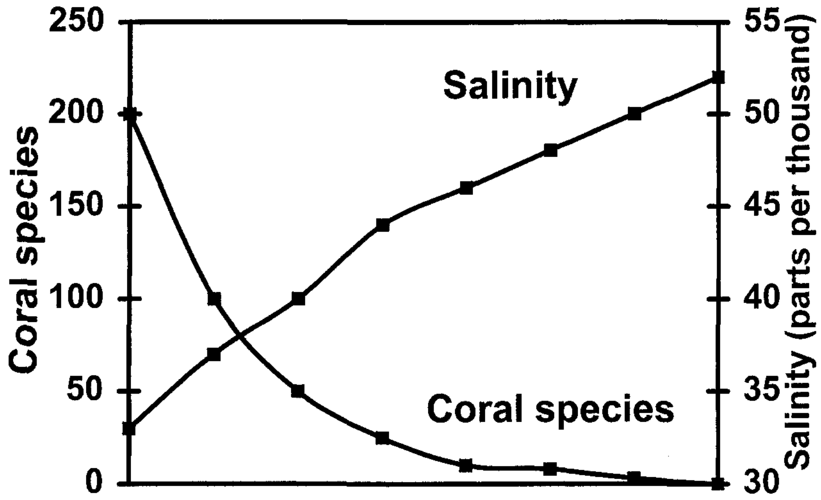


Figure 1.5. Decline of coral diversity with increasing salinity in the Indian Ocean. The decreasing line is coral diversity (left axis), increasing line is salinity (right axis). Sampled sites are all from the Arabian region where sufficient measurements exist. In many sites with oceanic conditions (about 33 ppt salinity) diversity exceeds 200 species of corals.

scale fall in sea level. Observation of pre-Holocene structures suggests that only those with a substantial cementing matrix, in addition to coral skeletons, survive (20).

In the Indian Ocean there is an abundance of habitats which, for any of several reasons, is marginal for both reefs and corals. These may be found over two scales. Firstly there is a 'macro-scale' as has just been mentioned, of hundreds or a few thousand kilometers, over which increasing stress gradually eliminates the ability of reefs to develop, causing the sequence: corals and accreting reefs > corals without reef formation, commonly with macro-algae > algal communities on non-coral reef substrates. An example, apart from the Arabian Sea already noted, is the Red Sea which shows this sequence in a southerly direction (59). Secondly, there is a 'meso-scale' at which reefs and corals habitat disappears over a distance of tens of meters to a few kilometers at most, as they grade into adjacent habitats dominated by, for example, seagrasses or mangroves.

Together, both conditions account for substantial expanses of gradually grading or mosaic habitats. The area is certainly substantial but it cannot at present be estimated with any degree of certainty, perhaps a reflection in part of the species-group approach of most marine ecologists to date. Table 1.5 summarizes physical characteristics in several such areas. There is very little indication to suggest that any one variable is present consistently or is essential in driving a coral-based system towards an algal based one, though elevated nutrients is a likely common characteristic. For any one species of coral there are clear inhibiting variables, as shown by the fact that corals drop out in a fairly consistent sequence along the transects shown earlier in Figure 1.5 and Table 1.4. At the level of the coral community, however, any consistency has yet to be discovered.

Table 1.5. Physical characteristics of reef and other hard substrate areas where corals live but where reefs do not develop and where fleshy macroalgae dominate some or all of the shallow substrate. This excludes coralline algal ridges and reef crests made mainly from encrusting reds.

Reef/Algal Characteristics	Salinity	Temperature			Sedim.	Nutr.	Areas
		Summer		Winter			
	High	High	Low	Low	High	High	
Red algal patch reefs covered with *Sargassum*, very low coral cover	No	Yes	No	No	Yes	Yes	Southern Red Sea
High to moderate coral cover, *Sargassum* dominated reef crest but coral domination on reef slope	slight, 36 to 40 ppt	Yes	No	No	No	Yes	Central, Southern Red Sea
Limestone domes, mainly devoid of corals, in 1 to 5 m deep	Yes, > 40 ppt	Yes	No	Yes	Yes	No	Central and eastern Arabian Gulf
Reef flats at 0 to 1 m below low water springs, high energy areas, abundant algae on reef flats, but high coral diversity deeper	No	No	No	No	Yes some areas	Yes some areas	for example Western Sri Lanka
Upwelling areas, mainly dominated by Fucales but including *Ecklonia*	No	No	Yes	No	No	Yes	Oman to Somalia, *Ecklonia* in southern Oman, possibly also Yemen.
Simplest 'corals-on-corals' mode of reef development	No	No	No	No	Yes	Yes some areas	Embayments, these are notably formed by *Porites*

Productivity The overall high production that occurs on reef slopes with good coral and turf algal cover is well established and has been reviewed more than once (29,40). It should be recognized, however, that the many different components of reefs, such as reef flats, shallow slopes and lagoon floors, have widely different productivity. The variation in 'average reef' values, some established long ago, arises partly because of the different ways of extrapolating from the experimental glass jar on a patch of reef to the whole reef. The inclusion of sandy patches, 'bare' patches, and the different estimates of planar surface area or the inclusion of a three-dimensional aspect, all affect calculations greatly and probably none, by themselves, are either 'right' or 'wrong'. Listing 'typical values' should only be done with recognition of these limitations. Table 1.6 lists a selection of values of comparative levels of production for coral reefs and their components. It also includes comparative values for all non-reef groups discussed later in this chapter. Other than the difficulties already noted, the real differences in production, seen in different parts of reefs, are partly a consequence of the different light, sediment, and exposure regimes. Productivity, in turn, is probably important in driving differences in diversity and consumer biomass in each zone. It remains reasonable to state that the reefs of the Indian Ocean are highly productive. Also, as we see later, their productivity is of a very similar order to most other benthic habitats with which they might be compared.

Seagrasses of the Western Indian Ocean

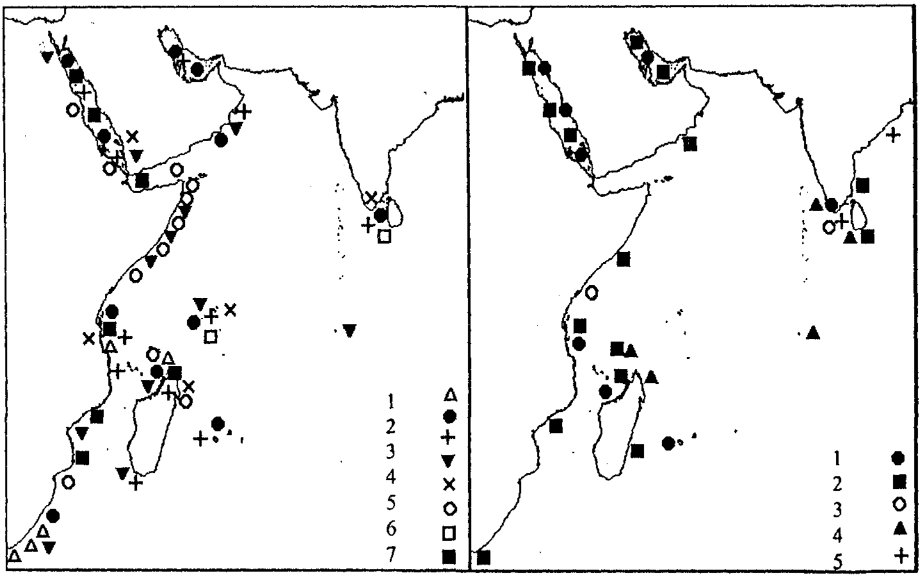
Seagrasses are widespread in the Indian Ocean where they are commonly associated with coral reefs, although areas such as bays where they develop their largest stands generally contain only weakly developed reefs or scattered corals. Seagrasses are supported on continental reefs flats, but more rarely on those of oceanic atolls. World wide there are about 50 species of twelve genera, of which about half are tropical. The western Indian Ocean contains 13 species of nine genera (38). Currently known geographical distributions of these are mapped in Figure 1.6. It is apparent that several seagrasses are likely to be found in areas where they are not yet formally recorded, and it is also the case that their diversity has no correlation with their cover. For example, the Arabian Gulf has only three species which form vast, unbroken expanses in shallow water, while less enclosed sites may have more species which grow in smaller, ecologically less important quantities. Biogeographical patterns of seagrasses show several similarities in distribution to those of corals. The Arabian Sea region (25) is similar to the Arabian Gulf but dissimilar to the Red Sea. The central atolls are insufficiently studied, but appear to be relatively poor in both abundance and diversity.

Stands of several species may be monospecific, though mixing of several species is common, in which case zonation from low intertidal to about 10 m deep may be seen (25). Dense stands are generally found in shallow, sheltered water, including bays and reef flats, and although seagrasses may occur in deep water they generally are sparse below about 10 to 20 meters, unlike the case for the Caribbean, or Mediterranean for example, where dense beds extend to over 30 m depth. Most stands are fairly dynamic, their position being determined by frequency of exposure, sediment grain size and sediment movement.. Curiously, the scattered seagrasses on reef flats which are sheltered by the reef crest may persist more readily than do dense beds in deeper water further offshore which are not protected.

In the Red Sea, seagrasses show a marked and significant increase in abundance southwards, at least along the northern shore, which is the reciprocal of the diversity and abundance of coral reefs (60). Overlap of reefs and seagrass communities extends over hundreds of kilometers. In the north, dense beds of seagrasses are limited to sheltered shallow sites and to scattered patches on reef flats. As shallow shelf conditions increase towards the south, reef development declines and seagrasses (with macroalgae) increase. Sites along the coast of Africa, India and Sri Lanka similarly have mixtures of both corals and seagrasses (38). Commonly an abrupt transition in dominant species takes place which can be ascribed to a sudden deepening of the substrate on a reef flat, for example.

In particularly dense seagrass beds, such as in sheltered, saline areas in the Arabian Gulf, seagrasses are mixed with algae. While it is commonly held that seagrasses occur in soft substrates and algae are attached to hard substrates, in very sheltered sites mixtures of both groups occur together over many hundreds of km^2. Substrates may be coarse and shelly, to muddy, but if the shelter is sufficient, both seagrasses and algae up to 30 cm tall occur profusely.

Productivity. Seagrass areas are extremely productive (Table 1.6). Their roots add to the stability of otherwise dynamic substrates, encouraging algal



1. *Zostera capiensis*
2. *Halodule uninervis*
3. *Syringodium isoetifolium*
4. *Enhalus acoroides*
5. *Thalassia hemprichii*
6. *Cymodocea serrulata*
7. *C. rotundata + serrulata*

1. *Halophila stipulacea*
2. *Halophila ovalis*
3. *Halophila minor*
4. *Halophila decipiens*
5. *Halophila beccarii*

Figure 1.6. Seagrass distribution in the western Indian Ocean. Based on Phillips and Menez (38) with later additions for East Africa and atoll groups in central Indian Ocean.

settlement in sheltered areas. Seagrass blades are generally covered with epibiota, and it has been suggested that the high productivity of seagrasses is partly because each 1 m^2 of seagrass bed provides up to 12 m^2 of attachment substratum. Average leaf turnover or renewal time is about 35 days. Epiphytes are dominated by nitrogen-fixing cyanophytes and diatoms, and the amount of nutrient transfer between epiphytes and host plants suggests that these attachments might be symbiotic rather than merely mechanical. Fauna associated with seagrass beds is commonly extremely abundant, with organism densities of 2000 and even 52 000 per m^2 of seagrass being recorded (6,72), in the latter case these being mainly gastropods, bivalves and polychaetes (nematodes which might be expected to occur in still greater number were not, apparently, recorded). Seagrasses are also important food for several vertebrates, including rabbitfish and parrotfish (33), as well as for turtles and dugong.

Migratory and other animals provide a major link between seagrasses and other ecosystems, for example, shrimp between seagrasses and algae, snappers and turtles between seagrasses and reefs. 'Halos' around outcrops of hard substrate projecting above seagrass beds also reflect the intensity of foraging

Table 1.6. Values for productivity of Indian Ocean systems, from numerous sources (40,56,60). Some of the generalized data are from outside the Indian Ocean, for which much less data exists than for the Pacific and Caribbean. Values are g C /m^2 /d unless otherwise stated.

System	Common or average values (g C /m^2/ d)	Extreme records (g C /m^2 /d)	P/R ratio
Reefs			
Whole reef systems	3.2-4.0	2.3-6.0	Usually ~ 1
Outer slopes	2.0-7.1		0.7-1.1
"High activity areas"	9.0-14.0	8.0-23.0	0.6-1.7
Reef flats, lagoons	3.0-7.0	2.9-19	0.7-2.5
Corals with zooxanthellae	2.63		
Sandy reef areas	0.9-1.5	0.6-2.7	0.6-1.1
Mangroves			
Global averages	6.0-15.0		1.2
"Dwarf" in Red Sea	<6.0		
Seagrasses			
Global averages	6.0-15.0		1.2
Thalassia, Syringodium, Lakshadweep	5.8		
Northwest Indian Ocean	3.0		
Algae			
Turfs and pavement	2.0-7.0	1.0-14.0	0.5-13.7
Coralline algae	0.8-1.0	7.0	1.3-1.4
Sargassum belts	60	(dry organic wt)	
Tropical kelp (Oman)	4.0	(dry organic wt)	
Halimeda beds	0.2-6.0		
"Mixed algae" Lakshadweep	1.9		
Cyanophytes	0.62-1.39		
Endolithic algae (*Ostrobium*)	0.4-0.6		
Benthic diatoms (sand, 5m)	0.41		
Bacterial			
pelagic	0.007-.11		
in sediments	1.2		
on coral rubble	0.01-0.1		
Planktonic			
Open ocean	0.04-0.06	.003-.4	0.3-1.4
Arabian upwelling southwest monsoon	1.16		
Arabian upwelling northeast monsoon	0.23		
Arabian Sea, central	0.12-0.76		
East Africa, aouthwest monsoon	0.83		
East Africa, northeast monsoon	0.42		
Bay of Bengal	0.21		
Atoll Lagoons	0.10-0.42		
near shore or reefs	0.2-0.9	0.1-1.0	
North Red Sea	0.21-0.50		
Central Red Sea	0.39		
Southern Red Sea	1.60		

and grazing in such boundary areas. The net effect is transfer of nutrients and biomass between the habitats. Seagrass detritus itself becomes widely scattered throughout the continental shelf area.

Productivity of dense seagrass beds is as high as that recorded for reefs (Table 1.6) but difficulties arise when scattered seagrasses or sparse beds are included in the records. Areas suffering disturbance may always contain seagrass beds whose densities are very sub-optimal, a consequence of the dynamic substrate on which they occur. Many inlets and indeed 'inlets' the

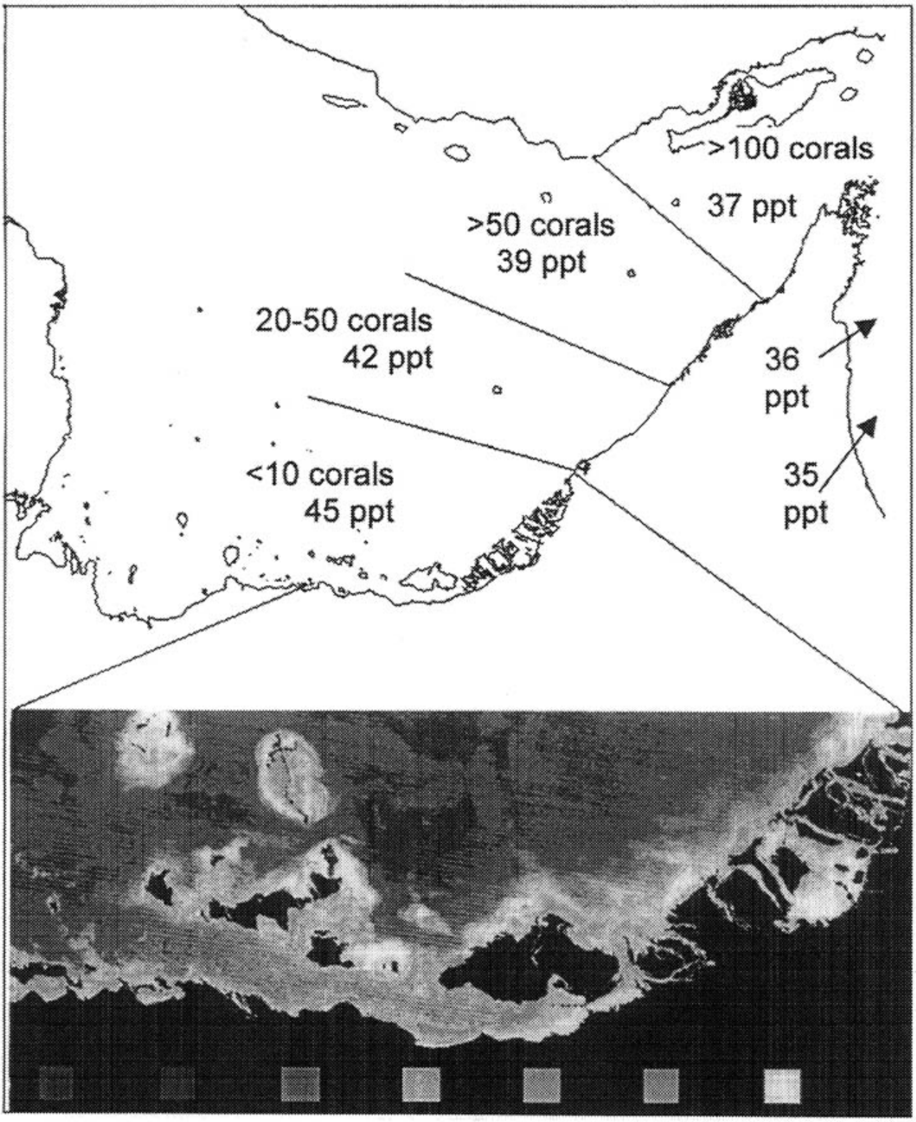


Figure 1.7. Section of coast with extensive seagrass and mixed seagrass and algal beds (Abu Dhabi). Remote sensed scene is Landsat TM, brightest areas being 100% cover of substrate, mid range grays being 40 to 60% cover, darkest shades being 0 to 10% benthic plant cover. Land is black. Numbers and contours show mean salinity and coral diversity.

size of the entire Arabian Gulf show high productivity. One such area (Fig. 1.7) from the Arabian Gulf is typical of many examples found throughout the Indian Ocean's continental shelf. Seagrasses are thoroughly mixed with algae, so that separation of algal production from that of seagrass is virtually impossible. The highest production comes from substrate completely and densely packed with a mixture of seagrasses and algae (Sheppard, C. personal observations). From literature values, production is in the order of >10g C/m^2/d. The lowest shading in Figure 1.7, representing areas with <10% vegetative cover, is likely to have production values of closer to 1g C /m^2/d.

Mangroves of the Western Indian Ocean

Mangroves form important ecological transition zones between terrestrial and marine habitats, and form effective sediment traps between land and reefs, the latter becoming increasingly important in view of wide scale-soil erosion in many countries. Partly because they, too, are threatened and declining habitats they have been extensively studied in the past decade (22). Additionally, a new atlas of mangrove distribution shows the current extent in the Indian Ocean in some detail (64). These details are not repeated here; instead, the association and interactions of mangal communities with coral reefs are examined.

Mangrove stands are greatest in shallow estuaries and bays of the continental rim of the Indian Ocean. In such areas, corals generally do not exist at all. Unlike seagrasses which can exist abundantly in conjunction with corals, the environmental demands made by developed mangrove stands, preclude all but occasional hardy corals. Mangroves trap mud efficiently and, unless human destruction occurs, this process extends the muddy habitat seaward at rates of many meters each year, which prevents coral reefs from developing. However, sparse mangroves or the edges of developed mangrove stands may happily coexist with corals over distances of a few hundred meters or less. Such areas are widespread. More widespread still are regions where mangroves occupy a shoreline area of shallow embayments, and well developed reefs extend seawards of them.

Over 40 species of mangrove tree exist on the northern continental rim of the Indian Ocean, reducing to ten or less in the eastern and north-eastern sides, to one or two in the peripheral Red Sea and Arabian Gulf (Table 1.3). *Avicennia marina* is the most widespread and hardy species. All species are restricted to warm waters of salinity ranging from brackish to slightly elevated. Rising salinity probably keeps diversity low in the Red Sea, but the final extinction in the north-west corner of the Indian Ocean is due to cold winter temperatures rather than either high salinity or hot summer temperatures. Possibly the broadest stands in the world today are the Bangladesh Sundabans (34), though stands in parts of north-western India may have been substantial until this century. In many parts of the Indian and Sri Lankan shore, for example, a recent sudden surge in mangrove destruction has taken place due to development of shrimp farms, which themselves tend to last only a few years until diseases or chemical changes in the soils render them unworkable, requiring more new mangrove conversion (34,61).

Of particular interest in the present context of reefs are the 'hard substrate' or 'reef' mangals (41) which are common in many parts, notably in the Red Sea but also as far east as Sri Lanka. These trees, mostly the species *Avicennia marina*, have shallow, spreading root systems and develop dense stands of many hectares at landward sides of reef flats (Fig. 1.8). Their substrate is extremely thin, may be sandy rather than muddy, and the stands may be independent of any larger, adjacent muddy mangrove stands. Indeed in the more arid regions of the north of the western Indian Ocean they might often be the only trees for

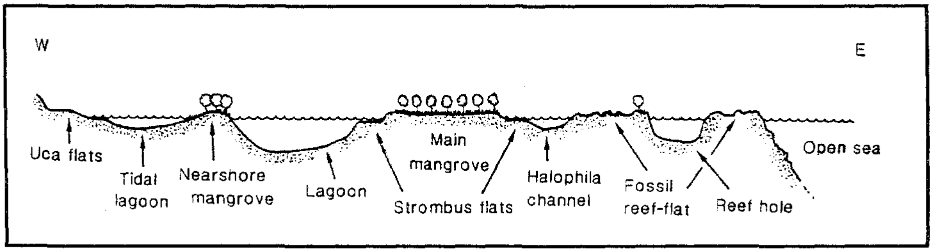


Figure 1.8. Cross section through a typical 'hard substrate mangrove stand. Evident in this illustration are depressions containing substrate suitable for seagrasses. The open sea at the right of the illustration is typically a steep reef slope. These hard substrate mangrove profiles are common in the western Indian Ocean from the Red Sea to Sri Lanka, though much less common than the typical mangrove-filled muddy embayments.

hundreds of kilometers. The fauna associated with them is similar to that of soft substrates (60) though being on reef flats, there is a much greater abundance of typical reef species, including corals, sponges and echinoderms, groups not usually associated with mangroves. The corals may even grow attached to mangrove roots in these areas.

Productivity. Table 1.6 provides typical examples of mangrove production. The main marine biota associated with mangroves is generally similar in species composition to that found over adjacent soft substrates not colonized by mangroves (41,56) though relative abundance of the component species may differ. For most species, the benefit of the mangroves are physical attachment and shelter, as much as the organically rich muds trapped by the tree roots. Densities of small invertebrates may be enormous, exceeding 5000/m^2 in the case of polychaetes and small gastropods. Of the total production of a typical mangrove stand in the northern Red Sea, 86% may come from the mangrove trees themselves, with 12% from benthic macroalgae, leaving less than 1% coming from microalgae and phytoplankton (9). This is in undisturbed conditions. Disturbance, such as occurred in an adjacent site covering many hectares where chlorinated water from a power station discharged through the mangroves, benthic grazers were killed and algae formed a thick mat within a few weeks, eventually causing the demise of some of the trees themselves (52), demonstrating the dynamic nature of these systems.

Cyanophyte Flats and Salt Marshes

Almost as much shoreline in the Indian Ocean is dominated by mud or saline flats as by any other habitat, though being much less commonly studied, there is a relatively poor literature on these habitats. Generally, but not always, corals are seldom found in such areas, though reefs and mud flats commonly form mosaics in which reefal areas provide the protection behind which muddy areas can develop. In the Indian Ocean, mud flats remain bare of larger plants to a degree rarely seen in higher latitudes, or even in tropical parts of the Atlantic. These apparently bare flats extend from the high intertidal regions and above, down to the lowest tidal areas where seagrasses generally colonize. High salinity resulting from high evaporative rates, as well as high temperatures, are usually associated with flats devoid of macro-biota. Surface water temperatures of well over 40°C and salinity exceeding 80 ppt often arise in tidal water, especially in the northern parts of the Indian Ocean, in embayments in Arabia, northern India, Pakistan and Sri Lanka. In ponded areas salinity of double this value are common (60).

Mud flats which are inundated at least daily and which have salinity of below about 70 ppt support abundant invertebrates, and commonly spectacular bird life. As salinity rises, very high productivity is maintained by the development of 'algal mats', based on a micro-flora, including diatoms, filamentous algae, and most importantly, 'blue-green algae' (also termed cyanophytes or cyanobacteria). The most salt-resistant diatoms ever recorded are from the Sinai, which tolerate up to 180 ppt, but cyanophytes can grow in water with up to 300 ppt salinity, and halophilic bacteria may thrive in salinity up to 400 ppt in hypersaline lakes in Somalia (11,14). As salinity increases, the amount of dissolved oxygen falls to less than a quarter that of the open sea at the same temperature. Consequently, primary producing biota in high salinity regions often are those which use hydrogen sulfide anaerobically as a hydrogen donor rather than water, resulting in the release of sulfur instead of oxygen. These mats are commonly called 'sabkha', a word from the Arabian region where this community occupies tens of thousands of square kilometers, and where single continuous sabkha may cover areas 32 by 300 kilometers in size (26,27).

The upper surface of the sabkha community is a mixture, possibly symbiotic or commensal in part, of cyanophytes and a varying composition of algae, the latter depending on exact conditions. The mats which develop have a vertical thickness of 1 to 3 cm, and vertical stratification of the community is pronounced. The lower side has a clear sulfur odor, is anoxic, and composed mainly of bacteria (Fig. 1.9). In times of desiccation, the whole community cracks into easily recognizable polygons and may sparkle from large surface crystals of gypsum as well as common salt. When hydrated sufficiently the mats form a continuous slippery sheet. Cyanophytes' ability to withstand severe desiccation comes not only from physiological adaptation, which is extremely developed and which includes secretion of mucilaginous jackets, but also from wicking and capillary action of water, assisted by hygroscopic salts which can attract water from relative humidities as low as 10%.

Sabkha systems may expand seaward and have a role in dissolving and re-precipitating aragonite, the form of limestone also deposited by corals (26,27). The exact composition of the mats depends partly on the precise elevation, allowing some use to be made of the community as palaeographic markers (42,43). Over sufficient time, the shoreline may be considerably modified by seaward extension. One important feature of the mats is the ability of the cyanophyte component to fix nitrogen. Most areas experience at least seasonal tidal flushing, and fertilization of surrounding areas is one possible, little researched, consequence of these communities.

Coastal Marshes. In past centuries, salt marshes growing in extensive stands of over seven meters tall formed a much more significant component of the northern Indian Ocean coastal environment than is the case today. Possibly no tropical coastal habitat has been as severely affected by man. Once

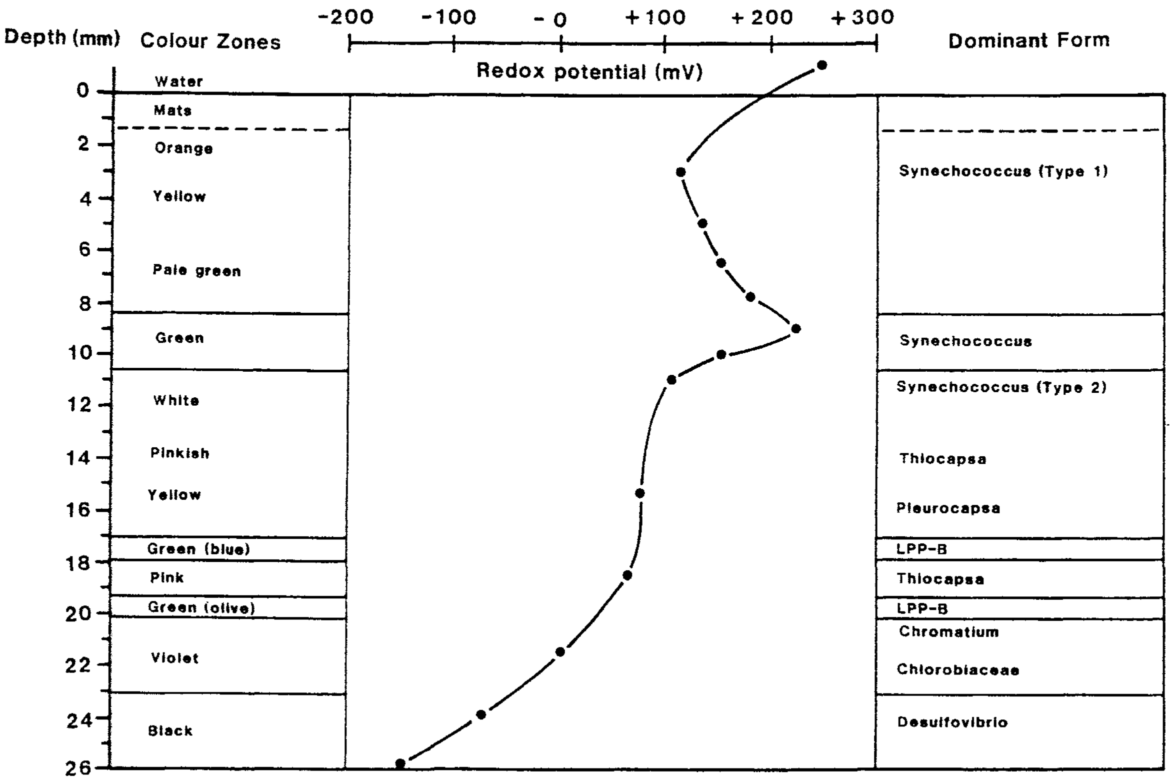


Figure 1.9. Cyanophyte algal mats. Chemical and physical details through a typical algal mat on a Sabkha (composite) (14). Thickness of mat (mm) is shown on left, with color of the various 'sub-layers'. Redox potential shows anoxic conditions below about 2 cm deep. Main microorganism groups at each depth point are indicated on right.

widespread, it is clear that impressive areas grew in the Arabian Gulf, Gulf of Suez, probably southern Red Sea and many other arid parts of the north-western Indian Ocean region; indeed in 1792 Niebuhr suggested that one contender for the name Red Sea is *Jam Suf* meaning Reed Sea (35), though there is no remnant left now of the vast marshes and fens reported by Strabo in 5 B.C. Ironically, today, there is a possibility of a recovery of reed beds in some areas in the vicinity of cities where sewage has led to enrichment of coastal waters (60). In Bahrain in the Arabian Gulf, and Jeddah in the Red Sea, salt marshes now show up on remote sensed images more strongly than mangrove stands.

Phragmites and *Typha* dominate reed swamp vegetation in many *wadis* on the African side of the southern Red Sea (37) where up to twenty community types of salt marsh vegetation can be classified, identified by their dominant species. Apart from the above, most of these community types are those of *Halocnemum, Limonium, Nitraria* and allied forms, which appear to form some of the most productive zones in these regions. These areas are not well studied, beyond description of the bird communities and general plant zonation patterns. While the term salt marsh is appropriate, they may more simply be termed eutrophic and mesotrophic zones.

Where conditions are appropriate, notably near a tropical river estuary, true marshes and reed beds develop. These occur nowhere more extensively than in the Shatt al Arab waterway, a large deltaic plain of the Euphrates, Tigris and Karun rivers covering an area of about 18 500 km^2 in the late 1980s (18). Eleven halophytic community types occur in northern Kuwait, the most important being dominated by *Juncus* and *Phragmites*, which reach 1.3 and 2.5 m tall respectively. The latter especially covers thousands of km^2. The woody stems float, and are extensively used by the 'Marsh Arabs' for rafts from which they fish and on which many live. However, because the local population opposes the Iraqi government, in the past five years this area has been systematically drained to allow access for military vehicles (imposition of a 'no-fly' zone in the region precluded aerial attack). By 1996, in the first three years of the drainage program, 50% of this vast, last remaining marsh of the Indian Ocean province had already been destroyed (36).

Along the African coast detailed descriptions of marsh plants show some extensive patches (21), though here also, the utility of the plants have led to their extensive over-exploitation. No data is available for marshlands along the Indian coast, though conditions would seem to be similarly favorable as in Africa. The islands of the Indian Ocean contain little or no habitat suitable for such communities.

Macroalgae Communities

Raised levels of nutrients encourage increased growth of macroalgae. In areas where nutrients are raised above oceanic levels, corals decline in diversity, even though some species may remain abundant and provide high coral cover. This is a common feature of 'marginal' reef conditions, a term commonly taken to mean conditions found in high latitude locations, although in several parts of the Indian Ocean marginal conditions increase towards the equator rather than away from it due to the Arabian upwelling. The condition of high latitude is not essential, neither are those of large temperature fluctuations or elevated salinity, though all these factors are commonly associated with algal dominance. Elevated nutrients is essential in most cases (Table 1.5) though the complete reason for strong development of algal communities is likely to be more complex and involve several variables. Where coral dominated communities grade into algal dominated ones, there is debate over whether the gradual change from coral domination to algal domination is a simple consequence of conditions being favorable to algal growth and unfavorable to corals, or whether competition between the two groups plays a major role (4,5,60). Probably both factors are important. Such areas are common throughout the Indian Ocean, and also on the eastern side of the ocean along Australia.

The most important macroalgal group is the Fucales which includes *Sargassum, Sargassopsis, Cystoseira,* and *Hormophysa.* In the Red Sea an increase in *Sargassum* dominance on the seaward edges of reef flats leads to the formation of nearly impenetrable barriers up to 40 to 50 m wide. These develop from the center of the Red Sea southwards, to a point at which fringing coral reefs literally disappear, grading into reefs composed entirely of red coralline algae covered in *Sargassum. Halimeda* may be locally abundant also, as is the case in numerous patches throughout the Indian Ocean. In areas with seasonal stress and high nutrients, low cover of corals correlates with raised algal cover (55), and areas suffering substantial abrasion affected by the southwest monsoon likewise have Fucales domination.

Kelp communities of southern Oman are notable for their curiosity value as much as for extended abundance. These may extend into Yemen also. The genus concerned, *Ecklonia,* is otherwise restricted to the southern hemisphere (2) where it grows in southern Africa, Australia and New Zealand. This kelp co-occurs with *Sargassopsis,* and unlike the *Sargassum* communities more common on reefs, has a marked seasonal cycle. The flora beneath the canopy has a particularly high diversity of at least 90 other algal species. Remarkably, corals of modest diversity (about 100 species) may be found scattered among the algae and beneath the canopy, though these rarely develop true coral reefs (49,62).

Other notable algal genera which are associated with reefs include *Turbinaria,* sometimes quantitatively important and an easily recognizable genus particularly in shallow water and reef flats (although it is confusing that this genus name is shared with a coral, beside which the alga commonly grows, especially on reef flats). A most important algal genus is *Halimeda* which is important for its production of copious quantities of calcareous disks. Although, to date, no huge bioherms of the genus appear to have been found in the Indian Ocean as they have in the Caribbean and eastern Australia, the density of coverage by members of the genus in sheltered areas such as central oceanic lagoons is such that it provides much of the sediment in such places.

Plankton

The plankton of the Indian Ocean have been divided into eight geographical regions, determined by the relative ratios of diatoms, dinoflagellates and cyanophytes, itself influenced by whether there is annual stability or strong seasonality induced by upwelling (30). These regions are not necessarily continuous: for example the Arabian Sea is grouped with upwelling areas off Australia and Indonesia. All regions may be viewed as components of a 'basic

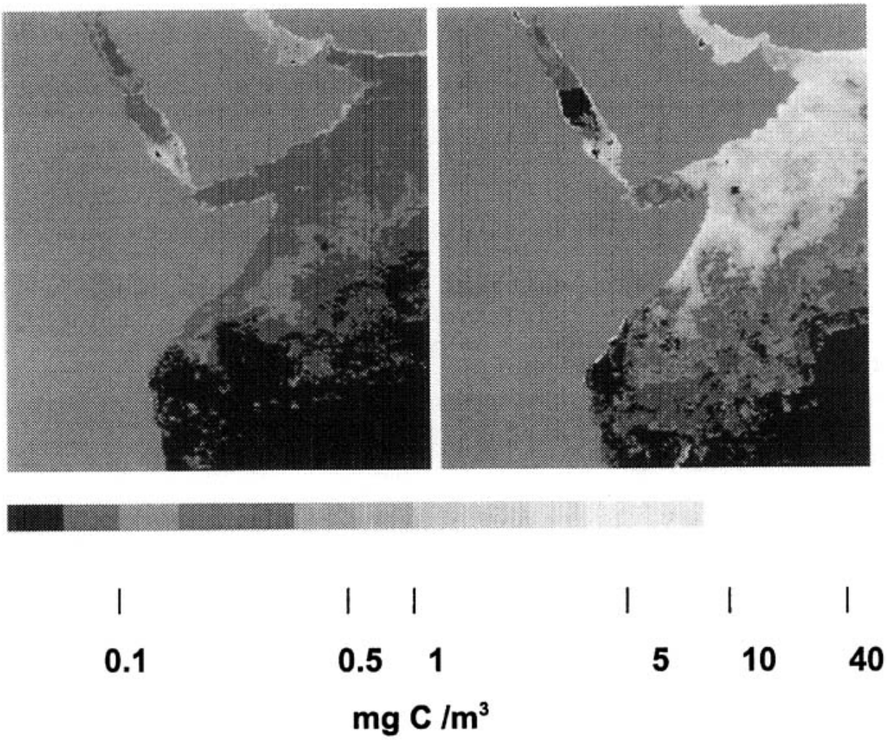


Figure 1.10. Arabian Sea upwelling. Images derived from Coastal Zone Color Scanner of the Arabian region showing (left) northern winter and (right) northern summer upwelling values of chlorophyll in surface waters. Data from several overpasses were used to form monthly average composites (in 1979) on a grid of nominal size 20 x 20 km. Top scale on color bar is a linear mapping interval, lower scale is chlorophyll in C mg /m^3, on log10 scale. (Images adapted from UNESCO TredMar remote sensing lessons series with permission from the author.)

Indo-oceanic complex' in which several dinoflagellates and diatoms are an outstanding feature of the whole Indian Ocean (28). In terms of diversity there is a general and marked decline from east to west. For example, of 452 known Indian Ocean dinoflagellates, only 130 are recorded from the Arabian Sea and only 88 and about 50 recorded from the western enclaves of the Red Sea and Gulf respectively (see Table 1.3).

Diversity, of course, commonly has no simple correlation with productivity. In fact the two variables may act in opposition, something demonstrated in terrestrial systems (24) but not so far in the sea (57). The most productive parts of the Indian Ocean in large scale terms is the Arabian upwelling (Fig. 1.10). This Coastal Zone Color Scanner image (CZCS) shows January (non-upwelling) and July (upwelling) conditions in the Arabian Sea, the upwelling causing increased pelagic production by a factor of 10 to 20. This upwelling is fundamental to the fishery of several adjacent countries (16). Also regionally important is the continuously raised pelagic productivity in the southern Red Sea. This is caused by wind driven forcing. Although the plankton entering the Red Sea do not survive, the quantities are sufficient to drive the general system