Environmental Conservation **29** (3): 331–349 © 2002 Foundation for Environmental Conservation DOI:10.1017/S0376892902000231

Present state and future of the world's mangrove forests

DANIEL M. ALONGI*
Australian Institute of Marine Science, PMB 3, Townsville MC, Queensland, Australia 4810
Date submitted: 28 September 2001 Date accepted: 10 April 2002

SUMMARY

Mangroves, the only woody halophytes living at the confluence of land and sea, have been heavily used traditionally for food, timber, fuel and medicine, and presently occupy about 181 000 km^2 of tropical and subtropical coastline. Over the past 50 years, approximately one-third of the world's mangrove forests have been lost, but most data show very variable loss rates and there is considerable margin of error in most estimates. Mangroves are a valuable ecological and economic resource, being important nursery grounds and breeding sites for birds, fish, crustaceans, shellfish, reptiles and mammals; a renewable source of wood; accumulation sites for sediment, contaminants, carbon and nutrients; and offer protection against coastal erosion. The destruction of mangroves is usually positively related to human population density. Major reasons for destruction are urban development, aquaculture, mining and overexploitation for timber, fish, crustaceans and shellfish. Over the next 25 years, unrestricted clear felling, aquaculture, and overexploitation of fisheries will be the greatest threats, with lesser problems being alteration of hydrology, pollution and global warming. Loss of biodiversity is, and will continue to be, a severe problem as even pristine mangroves are species-poor compared with other tropical ecosystems. The future is not entirely bleak. The number of rehabilitation and restoration projects is increasing worldwide with some countries showing increases in mangrove area. The intensity of coastal aquaculture appears to have levelled off in some parts of the world. Some commercial projects and economic models indicate that mangroves can be used as a sustainable resource, especially for wood. The brightest note is that the rate of population growth is projected to slow during the next 50 years, with a gradual decline thereafter to the end of the century. Mangrove forests will continue to be exploited at current rates to 2025, unless they are seen as a valuable resource to be managed on a sustainable basis. After 2025, the future of mangroves will depend on technological and ecological advances in multi-species silviculture, genetics, and forestry modelling, but the greatest hope for their future is for a reduction in human population growth.

Keywords: mangrove forest, conservation, exploitation, coastal resources, management, current state, projection

INTRODUCTION

Mangroves are the only forests situated at the confluence of land and sea in the world's subtropics and tropics. Mangroves are trees or shrubs that develop best where low wave energy and shelter foster deposition of fine particles enabling these woody plants to establish roots and grow. Mangrove forests are architecturally simple compared to rainforests, often lacking an understorey of ferns and scrubs, and are ordinarily less species-rich than other tropical forests.

The global distribution of mangroves indicates a tropical dominance with major latitudinal limits relating best to major ocean currents and the 20°C seawater isotherm in winter (Fig.1). The latter point underscores the paramount importance of warm temperatures for the existence of mangroves. There are 9 orders, 20 families, 27 genera and roughly 70 species of mangroves occupying a total estimated area of 181 000 km^2 (Spalding *et al.* 1997). The most diverse biogeographical regions are in the Indo-West Pacific (Fig. 1). Indonesia, Australia, Brazil and Nigeria have roughly 43% of the world's mangrove forests.

The standing crop of mangrove forests is, on average, greater than any other aquatic ecosystem, with a decline in above-ground biomass with increasing latitude (Fig. 2). Mangrove forests around the equator can be immense, rivalling the biomass of many tropical rainforests. The biomass of mangrove forests is even greater than in Figure 2 if the biomass of living roots beneath the forest floor is included; below-ground biomass can equal the standing crop rising above-ground (Clough 1992).

Mangroves possess characteristics that, in total, make them structurally and functionally unique. Morphological and ecophysiological characteristics and adaptations of mangrove trees include aerial roots, viviparous embryos, tidal dispersal of propagules, rapid rates of canopy production, frequent absence of an understorey, absence of growth rings, wood with narrow, densely distributed vessels, highly efficient nutrient retention mechanisms, and the ability to cope with salt and to maintain water and carbon balance.

* Correspondence: Dr Daniel M. Alongi Tel: +61 7 47534211 Fax: +61 7 47725852 e-mail: d.alongi@aims.gov.au

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

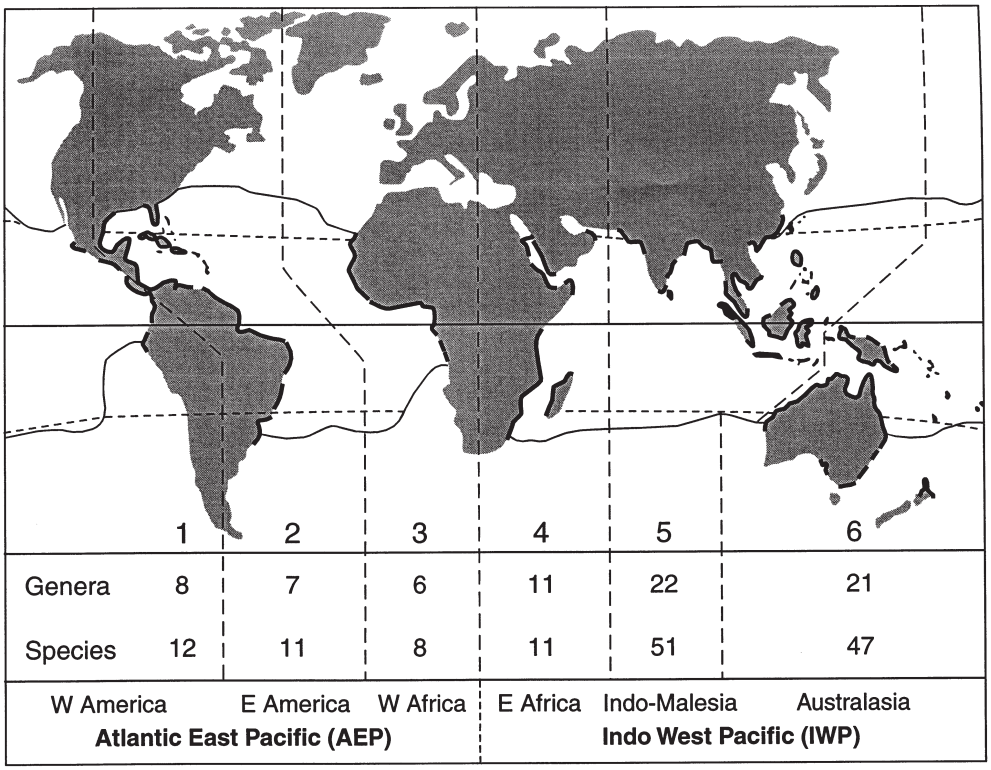


Figure 1 Distribution and biogeographical provinces of the world's mangrove forests. Forests are designated as heavy lines. The numbers of genera and species within each of the six provinces are noted below the map. Modified from Spalding *et al.* (1997) and Duke *et al.* (1998).

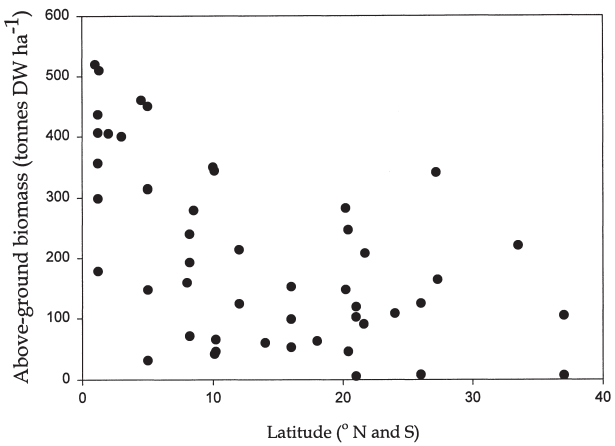


Figure 2 Latitudinal trends in mangrove forest biomass (tonnes dry weight ha^{-1}). Modified and updated from Alongi (1998) and Fromard *et al.* (1998).

Ecosystem characteristics include comparatively simple food webs containing a mixture of marine and terrestrial species; nursery grounds and breeding sites for birds, reptiles and mammals; and accumulation sites for sediment, some contaminants, carbon and nutrients. The biology and ecology of mangroves have been recently reviewed (Hogarth 1999; Ellison & Farnsworth 2000; Kathiresan & Bingham 2001).

The objective of this review is to critically examine the present status of the world's mangrove forests and to offer a best estimate of their future to the year 2025. Such a review is necessary and timely, considering disparate threats to their existence from increasing population growth, global warming, aquaculture, and industrial and urban development. To develop a reasonable prognosis, I first consider trends and salient characteristics of mangrove ecosystems that offer best clues as to how mangroves may respond to threats in future, followed by an assessment of present threats and impacts that are most likely to continue or intensify into the future. Finally, I conclude with some advice for managers, including an analysis of important gaps in knowledge and practical actions that managers can take for the conservation of mangroves.

ENVIRONMENTAL FORCING FACTORS

Natural influences

Factors influencing the structure and function of mangrove forests vary in relation to global, regional and local scales over different time scales (Duke *et al.* 1998). At the global scale, mangroves are ultimately limited by temperature, but at the regional scale the area and biomass of mangrove forests vary in relation to rainfall, tides, waves and rivers. Various schemes have been developed to classify mangroves on local scales. However, in reality, most forests represent a continuum of geomorphological types based on their location within broader settings classified as river-dominated, tide-dominated, wave-dominated, composite wave- and river-dominated, drowned bedrock valley and carbonate

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

(Woodroffe 1992). Waves, tides, rivers and rainfall affect water circulation by generating turbulence, advective and longitudinal mixing and trapping coastal water, influencing the rate of erosion and deposition of sediments on which mangroves grow. Many physical and ecological variations are often expressed within a single estuary (Duke *et al.* 1998).

Mangroves are typically distributed from mean sea level to highest spring tide, and perhaps the most conspicuous feature on first glance is the sequential change of tree species parallel to shore. Many factors have been suggested to account for the apparent zonation of trees and other associated organisms across the intertidal seascape. These include salinity, soil type and chemistry, nutrient content, physiological tolerances, predation and competition (Smith 1992). Some of these factors, such as competition, remain essentially unstudied; the results of recent studies are conflicting, prohibiting generalizations about the mechanisms governing zonation. It is more likely that a few of these factors in combination come into play over different temporal and spatial scales to control mangrove distribution (Bunt 1996; Ball 1998). For an individual tree, several factors operate in tandem to regulate plant growth, including temperature, nutrients, solar radiation, oxygen and water (Clough 1992). For a mangrove ecosystem, natural changes occur on the scale of minutes to hours for microbial and physiological processes, of months to years for tree growth and replacement, and of decades to centuries for regional forest changes (Twilley *et al*. 1996).

Determination of possible impacts in future must be considered against a background of natural disturbance. Mangrove forests are often naturally disturbed by cyclones and other storms, lightning, tsunami and floods, and often take decades to recover (Smith *et al.* 1994). Cyclones are common, for instance, in the Caribbean and the Bay of Bengal regularly destroying millions of trees. Other natural events, such as disease, may be sublethal, causing stunted growth or gradual death or replacement of species. For instance, in the Sunderbans of Bangladesh, nearly 20% of *Heritiera fomes* trees have been severely affected by 'top dying', a disease that slowly kills the trees by moving from leaves, branches and twigs to the main stem (Spalding *et al.* 1997). Mangroves become more susceptible to diseases and pests when stressed by changes in salinity, tidal inundation, sedimentation and soil physicochemistry, the introduction of pollutants such as oils, herbicides, metals, sewage and acids, and damage from storms and cyclones.

Pests can have a severe impact on mangrove forests. Epidemics of bacteria, viruses, fungi, spiders and boring insects and invertebrates that destroy leaves and wood can significantly reduce forest viability. For example, caterpillars parasitize and inhibit germination of fruits of *Rhizophora* trees in northern Australia (Robertson *et al*. 1992). Various organisms such as sesarmid crabs normally chew and consume a small proportion of mangrove vegetation, especially propagules and seedlings, inhibiting replenishment of older stands (Smith 1992). General explanations of such natural phenomena are complicated by the fact that one forest can be severely disturbed by pests or predators, but an adjacent stand may not be affected at all.

The dynamics of natural gaps in mangrove forests is poorly understood, but represents a cycle of natural mortality and regeneration that must be considered when impacts are assessed, especially over the long-term (Smith 1992). Various approaches have been used to assess mangrove forest dynamics, such as traditional measurement of tree species abundance and structure over time (Clough 1992) and more recent modelling methods of simulating competition, spacing and ageing of trees (Berger & Hildenbrandt 2000). Most studies indicate that the temporal and spatial variations within mangrove forests are commonly regulated by intra- and inter-specific competition for light, space and soil nutrients that are also patchy within stands (Lugo 1997). As in other forests, these factors give rise to the so-called self-thinning line, a pattern of tree distribution with a progressive decline in density of growing trees (Clough 1992).

Terrestrial forests and mangrove forests share many of the same basic physical and ecological attributes, but other attributes of mangroves appear to be unique (see Introduction), challenging concepts such as the old-growth or late-successional forest (Lugo 1997). The apparent paradox that mangroves appear to be in steady-state despite exhibiting characteristics of establishment, thinning and transitional stage forests, can be explained by the periodic nature of disturbances (Lugo 1997). For instance, a variety of ecosystem states can develop as a result of mangrove growth and development being altered by changes in sea level, lightning, cyclones and other disturbances, resulting in a forest exhibiting a mosaic of successional characteristics. The difficulty in matching many attributes identified with terrestrial old-growth forests highlights the problem of distinguishing natural from anthropogenic-induced change in mangrove forests.

Existing human impacts and threats

Mangroves are heavily used traditionally and commercially worldwide. Local communities have always used mangroves as a source of wood for cooking and heating, and for building houses, huts, fences, matting and scaffolds (Table 1). Timber is also widely used to produce charcoal, tannins and resins for dying and leather making, furniture, bridges, poles for fish cages and traps, medicines, alcohol, boats and many other products (Kathiresan & Bingham 2001). Mangrove stands and associated waterways are important sites for gathering and small-scale cultivation of shellfish, finfish and crustaceans. Local communities are often faced with the problem of over-exploited fisheries.

Commercial practices are being increasingly adopted in developing nations due to strong pressure to increase wealth and living standards of people living in coastal areas. Commercial exploitation is commonly forced from outside the local community, and is nearly always on a scale much larger than the local forests can sustain. Examples of

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

commercial exploitation include felling for wood products, housing and commercial developments, and modification of natural waterways for bridges and levees (Table 1).

Felling of forests is one of the oldest forms of commercial exploitation. While much felling is unsustainable, evidence from a number of commercial operations suggests that mangrove forests can be sustainably exploited for wood. For example, production of wood from the Matang Mangrove Forest Reserve in Perak, Malaysia has been sustained since 1906 (Gan 1995). The reserve consists of roughly 40 151 ha of pure and mixed stands of *Rhizophora* and *Bruguiera*, of which only 250 ha has been lost to settlement expansion; nearly 1500 ha have been gained by natural accretion of sediment and mangrove colonization. Roughly 1050 ha of forests are clear felled annually over a 30 year rotation cycle, with an average yield of 17.4 t ha^{-1} yr^{-1} (Gan 1995). Management plans for Matang are complex and frequently revised, undoubtedly contributing to the success of the commercial operation.

The loss of mangroves for pond aquaculture is currently one of the largest threats to mangrove forests worldwide. The list of direct and indirect problems caused by pond aquaculture is long and includes:

- immediate loss of mangroves to construct ponds;
- blockage of tidal creeks;
- alteration of natural tidal flows;
- alteration of the groundwater table;
- increase in sedimentation rates and turbidity in natural waters;
- release of toxic wastes;
- overexploitation of wild seed stocks;
- development of acid sulphate soils;
- reduced water quality;
- introduction of excess nutrients; and
- alteration of natural food chains.

Other forms of aquaculture may or may not be less destructive. Cultivation of grouper and sea bass in floating cages offers an inherently less destructive form of fisheries exploitation, but the extent of impact depends upon proper planning and management, including appropriate siting of cage farms, limitations on density of cages, and methods of feeding of cage stock. The same is true for exploitation of shellfish, such as the blood cockle, on mudflats adjacent to mangrove forests (Gan 1995). Limited operations do not appear to have demonstrable impacts on other mangrove resources, but management models to predict sustainable limits are generally lacking for mangrove ecosystems.

Other abuses of mangroves are often subtle, indirect and sublethal. For instance, the encroachment and growth of human populations in coastal areas usually results in increased wastes that are often dumped into mangroves and adjacent coastal waterways. Mangrove waters can assimilate some excess nutrients, but the assimilative capacity for most waterways are unknown and likely to vary depending on the form, type and frequency of effluent discharge, tidal range, waterway dimensions, climate, and plankton productivity and abundance (Trott & Alongi 2000). Mangrove plants and their associated microbes exhibit reduced growth when exposed to dissolved heavy metals particularly at concentrations at least five times greater than those in pristine mangrove soils (Yim & Tam 1999). The effect of some contaminants can be cumulative. Studies of oil spills in the Caribbean have shown that mangroves exhibit increased mutation rates and long (approximately 20 years) recovery times after repeated exposure (Burns *et al.* 1993; Klekowski *et al.* 1994). Physical smothering can often have as great an impact as chemical impairment of physiological performance.

Short-term climatic events may also be important environmental forcing factors. In the only known study of the impact of the El Niño–Southern Oscillation (ENSO) on mangroves, Drexler and Ewel (2001) found that in Micronesia the 1997–1998 ENSO-related drought resulted in greater soil and groundwater salinity. The most dramatic impact was a reversal of groundwater flow that sent groundwater from the mangroves upstream towards freshwater wetlands. The ecological impact of the drought was not examined, but the potential disruption to ecological processes is clear (Drexler & Ewel 2001).

Table 1 Current human impacts on the world's mangrove forests.

Potentially sustainable	*Unsustainable*
Food	Eutrophication
Tannins and resins	Habitat modification/ destruction/alteration for coastal development (including pond aquaculture)
Medicines and other bioproducts	
Furniture, fencing, poles (timber)	
Artisanal and commercial fishing	
Charcoal	Disruption of hydrological cycles (damming)
Cage aquaculture	
Ecotourism	Release of toxins and pathogens
Recreation	Introduction of exotic species
Education	Fouling by litter
	Build-up of chlorinated and petroleum hydrocarbons
	Shoreline erosion/siltation accelerated by deforestation, desertification and other poor land-use practices
	Uncontrolled resource exploitation
	Global climate change
	Noise pollution
	Mine tailings
	Herbicides and defoliants

IDENTIFIED LONG-TERM TRENDS

The ability to differentiate between natural and human-induced disturbance is especially challenging given the lack of long-term data for mangroves. Nevertheless, some data from a few forests can be used to identify natural changes that likely happen over time.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Natural changes in forest structure

Detection of human impacts on the structure of mangrove forests must be considered against a background of natural change in stand succession and canopy structure. Like other forests, mangrove stands follow a natural series of phases over time, from an initial pioneering stage through to rapid early growth and development, to later maturity, senescence and death (Jimenez *et al.* 1985). This natural progression is supported by data from French Guiana where Fromard *et al.* (1998) measured the structure, biomass and stand dynamics of several mangrove species. The data indicate a natural development of mangrove stands with a correlation between stem density and estimated forest age (Fig. 3).

Many stands of mangroves in the Mekong Delta were rehabilitated after the large-scale defoliation and destruction during the Vietnam War. The age of replanting and managed cutting is known, offering a rare opportunity to determine how stand structure changes with increasing age of mangrove forests (Clough *et al.* 1999). A structural analysis of various stands of *Rhizophora apiculata* indicates that tree densities decline with forest age (Fig. 4*a*), in agreement with the model of Jimenez *et al.* (1985). As in other forests, the stands become less dense due to self-thinning, as evidenced by an increase in tree girth or diameter-at-breast-height (Fig. 4*b*). Less dense but larger mature trees lead to an increase in total above-ground biomass per hectare with increasing age (Fig. 4*c*). Embedded within the long-term trend are temporal and spatial variations in individual tree growth, photosynthetic production, respiration and litterfall. In natural forests, changes in species composition occur, especially in light gaps, and with increasing distance upland.

Community structure, abundance and biodiversity

Within forest communities

Trees and bacteria dominate the biomass and productivity of mangrove forests (Fig. 5), but the structure of mangrove food webs is unique, having both marine and terrestrial components. Data on temporal trends in mangrove food webs usually are seasonal rather than inter-annual. Abundance and biomass of organisms living in the canopy, on or beneath the forest floor and in associated waterways often vary seasonally in relation to rainfall, and spatially in response to a variety of factors that are often the same as those regulating the trees (Kathiresan & Bingham 2001).

The structure and function of mangrove food webs is ultimately driven by the production of carbon fixed mostly by the trees and by the flow of dissolved and particulate organic

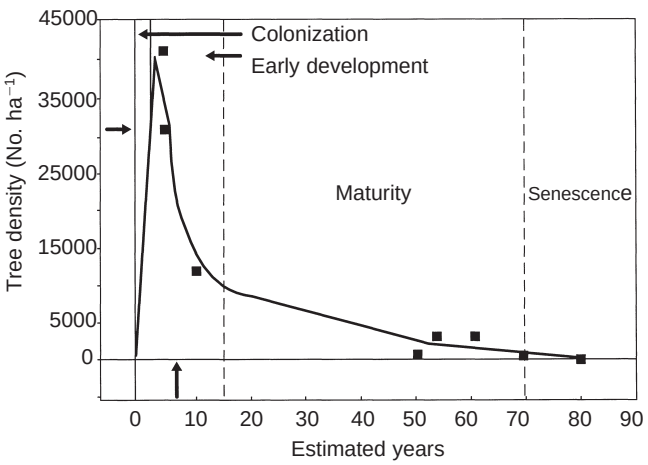


Figure 3 Colonization and development of mangrove forests over time. Data from Fromard *et al.* (1998) based on model of Jimenez *et al.* (1985).

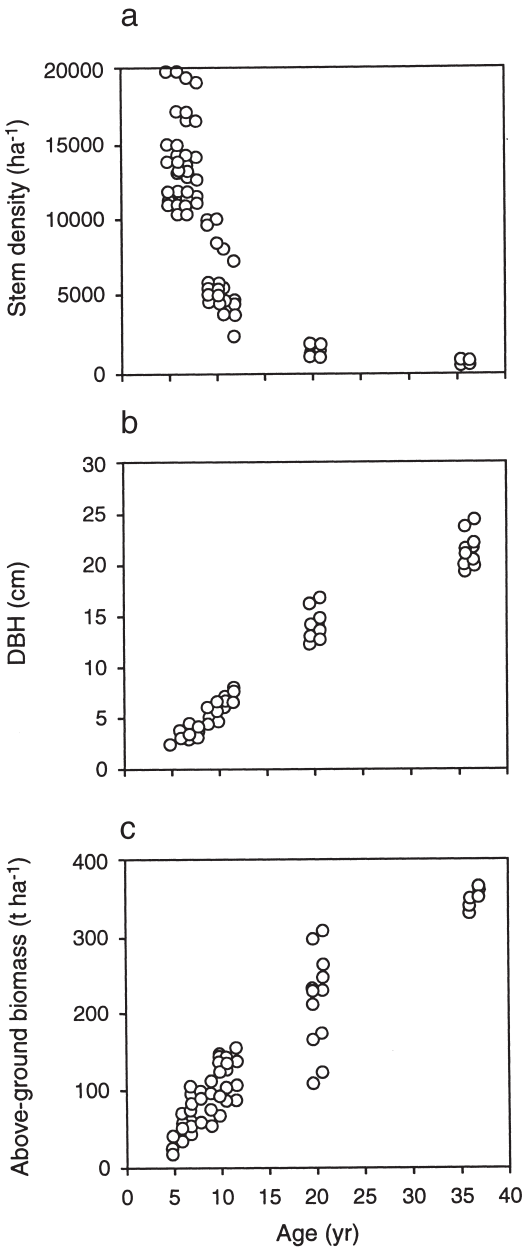


Figure 4 Relationship of (*a*) stem density, (*b*) diameter at breast-height (DBH) and (*c*) above-ground biomass (tonnes dry weight ha^{-1}) to age of *Rhizophora apiculata* forests in the Mekong delta, Vietnam. Modified from Clough *et al.* (1999).

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

matter within the forest and adjacent tidal waters. Within the forests, a suite of decomposer organisms directly or indirectly consumes a variable proportion of forest litter. Sesarmid, portunid, and ocypodid crabs are keystone organisms in many (but not all) forests. These crabs retain litter and recycle nutrients within forest soils, bioturbate the forest floor to stimulate microbial decomposition and, especially in the case of grapsid crabs, prey on propagules to influence the distribution, abundance and succession of tree species (Smith *et al.* 1991). It is simple to predict that losses of crabs as a result of pollution, for example, would negatively affect the growth and natural succession of mangrove forests.

The abundance and species diversity of infauna are generally low compared with other benthic habitats (Alongi & Sasekumar 1992). Low species richness may be the result of negative effects of polyphenolic acids derived from trees, low densities of surface microalgae, and the harsh physical conditions induced by tidal cycles of exposure and inundation.

The abundance and biomass of epifauna and tree-dwelling assemblages can often exceed those of the infauna. Gastropods and crustaceans are the major epifaunal groups, and exhibit clear distribution patterns related to frequency of tidal inundation, changes in sediment granulometry, water content, temperature, food sources, wave energy, salinity, anoxia, competition and predation. On the trunks, prop roots and branches of trees, most animals feed on organic debris and algae; lower on the trunks, an encrusting fauna may in turn provide a rich and mobile cryptofauna with safe refuge. These conspicuous assemblages can form a mosaic of vertically zoned organisms that are often the first residents to be harmed by pollution and other anthropogenic inputs (Alongi & Sasekumar 1992).

No attempts have been made to examine decadal trends in faunal abundance and species composition, but a few studies have examined faunal changes in relation to development and age of forests (Suzuki *et al.* 1997; Sasekumar & Chong 1998). In managed forests at different stages of the harvest cycle in Malaysia, epifaunal density and diversity was greater in a 60 year-old *R. apiculata* forest than in a recently cleared stand. The infauna showed a different pattern with greatest density and biomass in the cleared forest (Sasekumar & Chong 1998); this anomaly was attributed to greater abundance of surface algae with increasing light after canopy removal. In Thailand, an increase in benthic faunal abundance was observed in mangroves replanted in abandoned shrimp ponds (Suzuki *et al.* 1997). The sparse data indicate some impact of forest development and maturity on benthic faunal richness and diversity with a tendency toward more diverse assemblages in undisturbed and mature forests, but no forecast of long-term trends is possible.

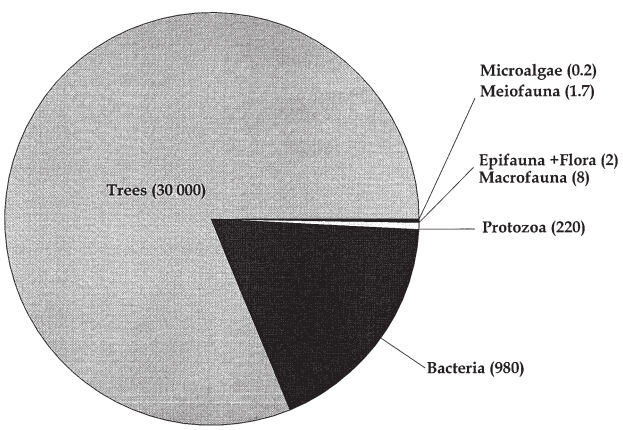


Figure 5 The distribution of living biomass (g dry weight m^{-2} to a sediment depth of 1 m) in a mature mixed *Rhizophora* forest in northern Australia. Based on data in Alongi and Sasekumar (1992) and Alongi (1998).

Higher in the canopy, various species of mammals, insects and birds permanently or temporarily reside in some forests, often in dense assemblages (Kathiresan & Bingham 2001). Bird communities can be spatially and trophically complex with up to eight feeding guilds, namely granivores, frugivores, piscivores, aerial hawkers, and hovering, gleaning, flycatching and bark-foraging insectivores. A few species are nearly confined to mangroves, including several species of yellow warblers, mangrove vireo, and mangrove cuckoo. Noteworthy mammals include monkeys and flying fox, and within tidal waters, dolphins and otters. These animals are also among the first residents to flee or be harmed by human alteration of mangroves.

Pelagic communities

Pelagic food webs in mangrove waterways are usually more responsive than benthic organisms, being ordinarily affected by longitudinal and lateral mixing and trapping of water by currents, tides and waves. Plankton communities in mangrove waters do respond quickly to nutrient enrichment from aquaculture or run-off from agricultural lands, most often exhibiting an increase in growth rate and standing crop (Ayukai & Alongi 2000).

Like benthic animals, diversity and abundance of plankton is usually low and highly variable (Robertson & Blaber 1992). There is a conspicuous lack of information on the ecology of mangrove-associated microbes. The sparse data indicate abundance of bacteria and protozoa within the range of other coastal waters (Robertson & Blaber 1992), but their trophic role is more often presumed, based on relationships in other tropical coastal waters, than based on empirical data.

The ecology of zooplankton in mangrove waterways is somewhat better understood (Robertson & Blaber 1992). Species composition is influenced by seasonal variations in salinity and degree of freshwater input. Decadal studies of plankton dynamics in mangrove waters do not exist, but several annual studies indicate density peaks during summer as a result of temperature control of reproduction (McKinnon & Klumpp 1998).

Studies of nekton, especially prawns and fish, are more common and indicate the importance of mangroves as

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

nursery grounds and refuges (Robertson & Blaber 1992). Many coastal species spend critical early stages of their lives in mangrove waters. The number of microhabitats is a major factor influencing community composition of fish. The number of microhabitats is however ultimately dependent upon environmental factors such as tidal amplitude, water quality and salinity (Robertson & Blaber 1992).

There are several patterns of species richness in fish communities:

- more species are usually found in large (range: 104–197 species) than in small (range: 8–128 species) estuaries;
- mangrove fish communities in the Indo-West Pacific are species-rich compared with those in some Atlantic estuaries;
- subtropical estuaries house fewer species than tropical estuaries;
- connectivity between mangroves and adjacent ecosystems (e.g. coral reefs, seagrass beds) influences community composition; and
- the nature of the offshore environment is critical in determining movements of larvae and juveniles, underscoring the fact that mangroves are not functionally divorced from adjacent coastal habitats.

Densities of juvenile fish in mangrove estuaries are high compared with other estuarine habitats. Robertson and Blaber (1992) suggest that mangroves are sources of various types of food, and provide shelter and protection.

Hypoxia, chemicals, diversion or alteration of natural tidal cycles, damming and other forms of pollution usually lower the abundance of fish and other pelagic (and benthic) organisms. Fish ordinarily escape rather than tolerate lowered water quality, but nonetheless, do not readily return to the scene of impact; the same is true for crocodiles, alligators, snakes, turtles, and lizards (Kathiresan & Bingham 2001). Recovery depends on the nature, areal extent, duration and intensity of disturbance. Recovery from a small-scale disturbance is often rapid, but there may be permanent loss from a catastrophe such as a massive oil spill (Burns *et al.* 1993). Habitat loss results in a lowering of population densities and loss of diversity of most mangrove-associated organisms.

Ecosystem function

Importance of mangrove forest production

Decadal trends in rates of mangrove primary production are unknown, as canopy production remains difficult to quantify and is often measured by indirect methods. The most reliable estimates of net primary production come from incremental measurements of biomass accumulation, but such measurements are time-consuming and laborious. The study by Day *et al.* (1996) in Mexico constitutes the longest temporal record (7 years) of mangrove net primary production. In both basin and scrub forests, Day *et al.* (1996) attributed most inter-annual variability in above-ground production and litterfall to soil salinity, minimum air temperature, and minimum rainfall, highlighting the importance of climate.

Most published estimates of primary production are derived from rapid survey measurement of light attenuation under the canopy. Estimates of net primary production using this technique range from 18–34 kg C ha^{-2} d^{-1}, but these rates are underestimates, insufficient to account for observed accumulation of biomass above-ground. A more recent method based on measurement of light transmission and measurement of net photosynthesis of leaves, indicates net daytime photosynthetic rates nearly 10 times greater than previous production estimates (Clough *et al.* 1997). If accurate, net primary production of mangroves in many regions is likely to be significantly greater than previously thought.

In a comparison of this new method and the older technique in a 22 year-old *R. apiculata* forest in Malaysia, Clough *et al.* (1997) calculated net photosynthetic rates of 155 and 13 kg C ha^{-1} d^{-1} using the new and old methods, respectively. A preliminary carbon balance for these trees (Table 2) indicates that only a small proportion of this production is allocated to above-ground biomass or lost as litterfall; most is probably lost via respiration and allocated to root production. Litterfall is often used as a proxy measure of mangrove production, but this newer data casts doubt on its appropriateness for this purpose. Litterfall is useful to examine annual reproductive patterns and the amount of organic matter potentially available for decomposition and export. Like biomass, litterfall decreases globally with distance from the equator (Saenger & Snedaker 1993).

A plot of net canopy production of different aged *Rhizophora apiculata* forests in south-east Asia (Clough *et al.* 1999), shows a general trend of increase in production until 25–30 years, with the older forests maintaining rapid carbon fixation rates (Fig. 6). The high productivity of older forests shows how important mature forests are in accumulating and storing of carbon over the long-term. This characteristic of mangrove forests is likely to acquire greater relevance with the forecasted increases in atmospheric greenhouse gases this century.

Consumption, export and storage of mangrove carbon

Mangroves are among the most productive plants in the ocean (Duarte & Cebrian 1996), the recent advances in estimating photosynthetic production indicating that, on an areal basis, mangroves are usually more productive than saltmarshes, seagrasses, macroalgae, coral reef algae, microphytobenthos, and phytoplankton. Most mangroves fix carbon well in excess of ecosystem requirements, with the excess carbon representing 40% of net primary production (Duarte & Cebrian 1996). Of the mangrove carbon produced, 9% is consumed by herbivores, 30% is exported, 10% is stored in sediments, and 40% is decomposed and recycled within the system (Duarte & Cebrian 1996). Recent measurements of mangrove photosynthesis (Clough *et al.* 1997) imply that either more carbon is stored in wood and eventually decomposed within the system or more carbon is stored in sediments or exported to the adjacent coastal zone, than estimated by Duarte and Cebrian (1996).

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Table 2 Carbon balance for 22-year-old *Rhizophora apiculata* trees in Malaysia (modified from Clough *et al.* 1997).

Component	*Flux* ($t\ C\ ha^{-1}\ yr^{-1}$)
Net daytime canopy photosynthetic production	56
Carbon allocation	
Above-ground biomass accumulation	6.5
Below-ground biomass accumulation	0.6
Litter fall	4.4
Below-ground root turnover	?
Night time foliar respiration	13
Below-ground root respiration	?
Stem, branch & prop root respiration	?

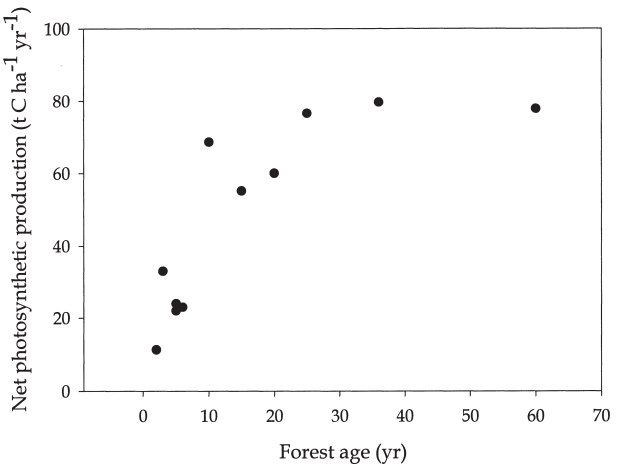


Figure 6 The relationship between forest age and photosynthetic production in *Rhizophora apiculata* forests in South-east Asia (Thailand, Malaysia and Vietnam). Data compiled from Clough *et al.* (1999), Alongi and Dixon (2000) and D.M. Alongi (unpublished data from Malaysia 1999).

Levels of herbivory are known (Ellison & Farnsworth 2000), as is the proportion of organic material exported from mangroves (Robertson *et al.* 1992). There are few data on carbon storage in mangrove wood or sediments but the sparse data suggests that some forests can accumulate carbon (Twilley *et al.* 1992; Alongi *et al.* 2000, 2001). Recent information from tropical rainforests indicates that mature forests have a long-term capacity to store carbon in wood (Chambers *et al.* 2001); such may be the case for some mangrove forests, especially mature stands.

Because mangroves fix and store significant amounts of carbon, their loss may have a significant impact on global carbon budgets. In a recent analysis of the fate of fixed carbon in marine ecosystems, Cebrian (2002) estimated that a loss of about 35% of the world's mangroves has resulted in a net loss of 3.8×10^{14} gC stored as mangrove biomass. This figure is an underestimate because below-ground biomass and the more recent net canopy production estimates were not included in his calculations.

Carbon and nitrogen budgets for mangrove ecosystems: do they reflect human impacts?

Only a few studies have constructed nutrient mass balances for entire mangrove ecosystems to offer insights into what is energetically important to mangrove functioning. A comparison between a relatively young, physically dynamic mangrove ecosystem disturbed by various human activities (Sawi Bay, Thailand) and a mature, more physically quiescent, pristine ecosystem (Hinchinbrook Channel, Australia) illustrates how physical characteristics and the level of human disturbance affect rates and pathways of nutrient and energy flow (Table 3). First, both ecosystems are net autotrophic, producing more fixed carbon than they consume. This is despite the fact that the ratio of mangrove area to total ecosystem area is nearly double in Hinchinbrook Channel. The Sawi Bay mangroves are younger, smaller, but more productive, resulting in slightly more total net production than the Australian mangroves (Table 3). On an areal basis, rates of respiration, phytoplankton production and carbon burial are greater in Sawi Bay than in Hinchinbrook Channel reflecting additional inputs of carbon from the heavily used catchments bordering the bay. Tidal inputs and outwelling are greater in Hinchinbrook Channel, reflecting stronger tides and river run-off from many small rivers on the Australian mainland. A smaller proportion of carbon is buried in Sawi Bay sediments, but proportionally more carbon is lost via respiration. Carbon losses per km^2 are greater in Sawi Bay, which loses more total carbon (78%) than Hinchinbrook Channel (60%). This probably reflects greater anthropogenic inputs and lower efficiency of carbon processing, as well as greater openness of Sawi Bay to shelf waters, than semi-enclosed Hinchinbrook Channel.

The excess carbon produced by both ecosystems is fated differently, reflecting not only human influences but also differences in ecosystem maturity. Most excess carbon accumulates in tree wood and sediments in young forests lining Sawi Bay. In Hinchinbrook Channel, most carbon in excess of respiration and burial is exported (Table 3). In Sawi Bay, most of the carbon accumulating in sediments appears to be derived from land and from imported phytoplankton stimulated by inputs of inorganic nutrients from various industries within the catchment (Ayukai & Alongi 2000; Alongi *et al.* 2001).

A nitrogen budget for the Missionary Bay mangroves at the northern end of Hinchinbrook Island, Australia (Table 4) illustrates how a mature mangrove ecosystem acquires and retains nitrogen. Nitrogen enters the Missionary Bay ecosystem by nitrogen fixation, with little contribution from precipitation and groundwater (Table 4). Tidal inputs are nearly five times greater than biological fixation. Unlike most other coastal ecosystems, denitrification is a small loss compared to tidal outputs. Unlike saltmarshes, the largest inputs are in the form of dissolved organic nitrogen and net input of particulate nitrogen is negligible. This pattern reflects the import of nitrogen in dissolved form to help fuel forest production and the export to refractory nitrogen in the form of old leaf litter, pieces of branch and bark.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Mangroves have evolved efficient mechanisms to conserve nitrogen. In Missionary Bay, where water and sediment nitrogen concentrations are low, nutrients links between trees and microbes are close. The large mass of living trees and dead wood lying on the forest floor, litter processing by crabs, lower rates of denitrification than nitrogen fixation (Table 4), flushing of material in advanced stages of decomposition, all serve to retain and conserve limiting nutrients (Alongi *et al.* 1992). Inputs slightly exceed outputs, but the ecosystem is roughly in balance given the magnitude of error in extrapolating measurements to a large area. Of greater importance is how this budget demonstrates the delicate balance between the import and export of nitrogen in a mature, pristine ecosystem. This implies that such a fine balance can be easily displaced by human interference.

Nitrogen budgets on this scale for polluted mangroves do not exist, but some small-scale studies suggest that mangroves can in most cases tolerate high levels of nitrogen and phosphorus from sources such as sewage and aquaculture effluent (Boto 1992; Robertson & Phillips 1995; Trott & Alongi 2000). The level of tolerance depends on the form of nutrient and, like other types of disturbance, depends on the intensity, duration and areal extent of impact, as well as position along the tidal gradient. Several recent studies (Feller *et al.* 1999; Bouillon *et al.* 2002) suggest that mangroves, even dwarf species, can use high nitrogen and phosphorus inputs to fuel tree production as well as production of other primary producers. Further, there may be a trophic shift from assimilation of mostly mangrove-derived organic matter in pristine mangroves, to use of nutrients derived from blooms of phytoplankton and macroalgae in mangrove systems receiving excess nutrients (Bouillon *et al.* 2002).

Table 3 Comparison of the differences in mean rates of ecosystem-level processes between Sawi Bay and Hinchinbrook Channel (modified from Alongi *et al.* 2000).

	Sawi Bay	*Hinchinbrook Channel*
Ratio mangrove : total ecosystem area	1:5	1:2.8
Mangrove net production (mol C ha^{-1} yr^{-1})	2.8×10^6	2.3×10^6
Phytoplankton production (mmol C m^{-2} d^{-1})	43.9	22.1
Pelagic respiration (mmol C m^{-2} d^{-1})	61.0	10.0
Sediment respiration (mmol C m^{-2} d^{-1})	59.5	41.5
Sediment burial (mmol C m^{-2} d^{-1})	54.1	39.7
Percentage TOC input buried	4%	14%
Percentage TOC input respired	46% (74% including tree respiration)	20% (46% including tree respiration)
Total C inputs per km^2 (mol C km^{-2})	9.4×10^7	4.7×10^7
Total C outputs per km^2 (mol C km^{-2})	7.6×10^7	1.6×10^7
Excess C per km^2 (mol C km^{-2})	1.8×10^7	3.0×10^7
Ecosystem P/R	1.4	2.0

Table 4 Nitrogen budget of an entire mangrove ecosystem, Missionary Bay, Hinchinbrook Island, Australia (modified from Alongi 1998).

	Flux (kg N yr^{-1})
Inputs	
Precipitation	30
Groundwater	30
Nitrogen fixation	36 830
Tidal exchange	168 600
Total	205 490
Outputs	
Tidal exchange	192 430
Denitrification	2900
Sedimentation	?
Total	195 330
Net exchange	+10 160

Fisheries yield

The biological importance of mangroves in terms of wood and fisheries yield is normally not reflected in ecosystem-level budgets and mass balance estimates. Mangroves are important nursery grounds despite statistical arguments to the contrary (Baran 1999). The slope of the relationship of fish and prawn landings to mangrove data differs between regions owing to differences in catch methods, structure and productivity of forests and the fisheries species in question (Chong & Sasekumar 1994).

What is unquestioned is the impact of human perturbations on fisheries' yields in mangrove-dominated regions. In south-east Asia, the growth of the trawl fishing industry has led to overfishing in many areas both as a result of, and causing, habitat destruction and environmental stress (Mohsin & Ambak 1996; Hinrichsen 1998). For instance, the long-term trend of fishing in coastal waters in Malaysia (Fig. 7) shows an unrelenting increase in catch effort. There was an increase in total landings of coastal fish in Malaysia from the late 1950s up to the mid-1980s when landings levelled off by 1986, indicating that total landings were starting to exceed estimates of maximum sustainable yield. However, there was a steep rise in total landings and catch effort into the 1990s caused by the expansion of Malaysia's fishing grounds from 160 740 km^2 to 547 200 km^2 with the establishment of the Exclusive Economic Zone (Mohsin & Ambak 1996). The probability of these coastal waters being overfished again is high given the increase in fishing effort, and will no doubt be exacerbated by any decline in the area and health of mangrove forests (Mohsin & Ambak 1996). It is often difficult to even identify such problems in mangrove-dominated waters owing to the lack of long-term data, especially from commercial operators who for a variety of reasons either do

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

not keep adequate records or do not accurately report their totals to government bodies.

POTENTIAL STATES IN 2025

Predicting the future of mangrove forests is problematic, given the lack of long-term data. Nevertheless, some basic prognoses can be made based on reasonable extrapolations from the salient trends and characteristics of mangroves reviewed here, likely advances in genetics and restoration ecology, and the spread of current sustainable-management practices.

Future threats

Most current uses and abuses of mangroves are unlikely to abate until after 2025. Aquaculture, mining, housing and industrial encroachment and overexploitation of resources will continue and some impacts will probably increase with concomitant growth and development of coastal settlements. Many past and current abuses are now irreversible.

Global production of farmed fish and shellfish in the coastal zone has more than doubled in the past 15 years (Naylor *et al.* 2000). Despite many unsustainable methods and a levelling off of total production, aquaculture will still result in the loss of mangrove resources; they may at best slow in some countries, but they will be maintained or even accelerated in others. As long as human populations grow in size, present impacts will not subside.

There are various threats to the future of mangrove ecosystems (Table 5), nominally divided into high-, medium- and low-level threats, based on the level of past and current impacts. Deforestation remains the single greatest threat to the survival of mangroves. Although reforestation programmes will continue and are likely to increase in future, the loss of biodiversity, especially from old-growth forests, is unlikely to be regained until at least several decades, and perhaps permanently lost if species become locally extinct due to excessive fragmentation of habitats.

Aquaculture is another major threat, being interlinked with both deforestation and overexploitation of fisheries resources. Conversion of mangrove forests and waterways for pond aquaculture will continue in some countries as depletion of natural stocks drives the need to increase dependence on farmed seafood. The upper limits of sustainability are unknown for various resources within mangrove forests, but it is likely that they will be seriously tested in future.

Technological advances are likely to result in less acute pollution such as the emission rate of thermal effluent and oil spills, but the increase in coastal development presages increased threats of low-level, chronic pollution from agriculture and industry. Contaminants seeping into groundwater may, for example, find their way into mangrove forests and adjacent waters (Field 2000). Of more immediate impact in future will be eutrophication, assuming increased boat traffic and other uses of coastal waterways. These threats will in turn increase pressure for development and alteration of waterways.

The combustion of fossil fuels combined with deforestation and other forms of land clearing are leading to an inevitable rise in atmospheric CO_2 concentrations and temperatures, giving rise in turn to an increase in sea level as polar ice melts (IPCC [Intergovernmental Panel on Climate Change] 2001). Conflicting scenarios presently being offered to predict the impact of global warming on Earth's ecosystems reflect ignorance of ecosystem functioning as well as the scale of the problem; synergistic and antagonistic effects are likely to occur as a result of natural feedbacks, complicating modelling predictions. These problems are especially critical for tropical ecosystems where there are fewer empirical data than for temperate ecosystems. Tropical terrestrial forests have recently been shown to play a greater role in determining atmospheric CO_2 concentrations than thought previously (Mahli & Grace 2000); estimates of the mangrove contribution to atmospheric carbon flux is hampered by a critical lack of information.

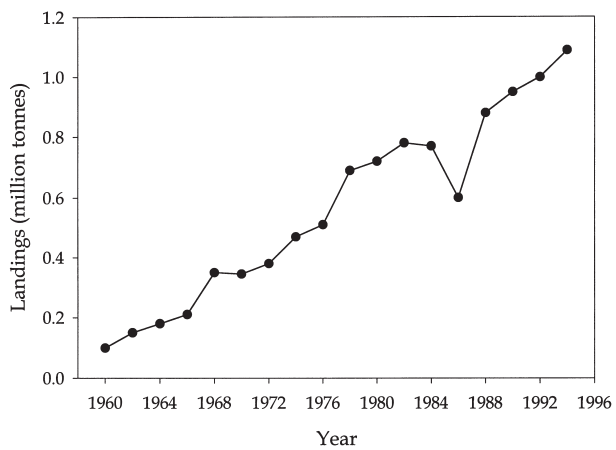


Figure 7 Total annual landings of coastal fish in Malaysia, 1960–1994. Modified from Mohsin and Ambak (1996).

Global warming

By 2025, the atmospheric concentration of CO_2 is expected to rise by approximately 40 ppm, temperatures may rise by 0.5–0.9°C, and sea level may rise by 3–12 cm (IPCC 2001). What impact will these changes have on mangroves?

Over the next 25 years, average atmospheric CO_2 concentrations may increase from the 2000 average of 370 ppm to 410 ppm (IPCC 2001). Experimental evidence indicates that

Table 5 Future threats to the world's mangrove forests.

High-level threats	*Intermediate threats*	*Low-level threats*
Deforestation	Alteration of hydrology	Oil pollution
Pond aquaculture	Global warming	Thermal pollution
Overexploitation of fish and shellfish	Eutrophication	Tourism
		Noise pollution

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

species responses will vary; there may not be a significant overall increase in canopy photosynthesis, growth and litterfall despite decreases in stomatal conductance and transpiration (UNEP [United Nations Environment Programme] 1994). The experiments of Ball and others (e.g. Ball *et al.* 1997) point to complex responses to elevated CO_2 concentrations. Growing *Rhizophora apiculata* and *R. stylosa* in a multifactorial combination of salinity, humidity and atmospheric CO_2, elevated CO_2 had little effect on plant growth when limited by salinity, but growth was stimulated when limited by humidity (Ball *et al.* 1997). Both species had more rapid growth under elevated CO_2 conditions at low salinity. Elevated CO_2 could alter competitive abilities along salinity–humidity gradients (Ball *et al.* 1997).

The expected rise in temperature by as much as 0.9°C (IPCC 2001) may result in expanded latitudinal limits for some species, alteration of community composition, and marginal increases in photosynthesis, respiration, litterfall, microbial decomposition, floral and faunal diversity, growth and reproduction, but reduced rates of sediment accretion (UNEP 1994). However, temperature changes in the tropics may not be as great as at higher latitudes (IPCC 2001), and there may be less seasonality due to forecasted changes in precipitation (UNEP 1994). Such changes are likely to vary greatly on local and regional scales. Nevertheless, they may induce changes in soil water content and salinity, changes in community composition of plants and animals as a result of the salinity changes, and a change in primary production if the precipitation to evaporation ratio is altered (UNEP 1994).

The presumed rise in sea level by as much as 12 cm (IPCC 2001) is difficult to evaluate owing to past and recent variations in local relative sea level (Rull *et al.* 1999). Nevertheless, mangroves may progress landwards at a rate determined by the rate of sea level rise, the rate of vertical accretion, and slope and space at the landward edge. Zonal patterns of plants and animals will be altered slightly and erosion at the seaward front will increase (UNEP 1994). The ability of mangroves to accommodate future sea-level rise will likely depend on other factors such as tidal range, sediment supply and tree species composition. These factors are likely to be magnified on islands of both low- and high-relief and in the arid tropics where rates of sediment supply, available upland space and mangrove growth rates are usually low (Ellison & Stoddart 1991; Parkinson *et al.* 1994; Semeniuk 1994).

Empirical data to test the impact of sea-level rise is limited to one greenhouse study of *Rhizophora mangle* (Ellison & Farnsworth 1997). Growing seedlings in tanks simulating current conditions (control), and a 16 cm increase and a 16 cm decrease in sea level, Ellison and Farnsworth (1997) observed that plants in the increased water level treatment initially grew faster than plants in the other treatments, but slowed rapidly at the sapling stage. By the end of the 2.5-year experiment, control plants were 10–20% larger than the sea-level treatment plants. The reduced growth of *R. mangle* with changes in sea level may offset the possible stimulatory effects of increases in atmospheric CO_2 concentration.

Overall, impacts of climate change on mangrove use and exploitation are predicted to result in increased risks of flooding and erosion in low lying coasts, intrusion of salt wedge and storm surges and collateral damage (UNEP 1994). The severity of these impacts will vary in relation to regional differences in climate change (IPCC 2001).

Global losses

To make realistic prognostications of the future of mangroves, an assessment of the accuracy of the present data of losses and gains in forest area is necessary. While it is clear that large tracts of mangroves have been either severely degraded or destroyed worldwide, most data is apocryphal, reflecting inaccurate surveys, unsubstantiated claims or old estimates not based on empirical measurements (Farnsworth & Ellison 1997; Burke *et al.* 2001). For example, in Fiji total mangrove area has been reported as between 19 700 and 49 777 ha (Spalding *et al.* 1997).

Long-term changes in mangrove area (Fig. 8) show that most countries have lost mangroves, especially Vietnam, Mexico, Singapore, the Philippines and Thailand. In Singapore, the losses were incurred over nearly a century, mainly as a result of urbanization (Spalding *et al.* 1997). In other countries, losses have been sustained mostly over the past 20–30 years as a result of clearing for aquaculture, urbanization and timber products. Vietnam's losses were sustained chiefly as a result of defoliation in the 1960s and early 1970s (Hong & San 1993). Some countries, such as Papua New Guinea, Australia and Belize show no substantial change and a few countries (e.g. Cuba) have regained mangrove forests due to restoration projects (Field 2000).

Summing the empirical estimates of change in mangrove area (Spalding *et al.* 1997) and some regional estimates (Clough 1993; Diop 1993; Lacerda 1993), I calculated that approximately one-third of mangrove forests have been lost over the past 50 years. I used the above documents produced by the International Society for Mangrove Ecosystems because they appear to be the most reliable, based on empirical data in government forestry surveys, remotely sensed images, aerial photos and ground-truth maps. Recent publications have cited a global loss figure of 50% (Burke *et al.* 2001; GESAMP [The Joint Group of Experts on the Scientific Aspects of Marine Environmental Protection] 2001), citing reports (Kelleher *et al.* 1995) that have cited older literature containing neither empirical data nor a description of how the loss estimates were derived. Also, Spalding *et al.* (1997) found numerous inaccuracies in previous works because of what some people and organizations considered mangrove forest. For example, the estimates for Venezuela were consistently gross overestimates because many surveys included non-mangrove species and adjacent swamp forest, saltmarsh or mudflat. Conversely, for Mexico, a previous estimate indicated a total mangrove area of 5315 km^2 when in fact recent high-resolution satellite images show a total mangrove area of 9328 km^2 (Spalding *et al.* 1997).

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

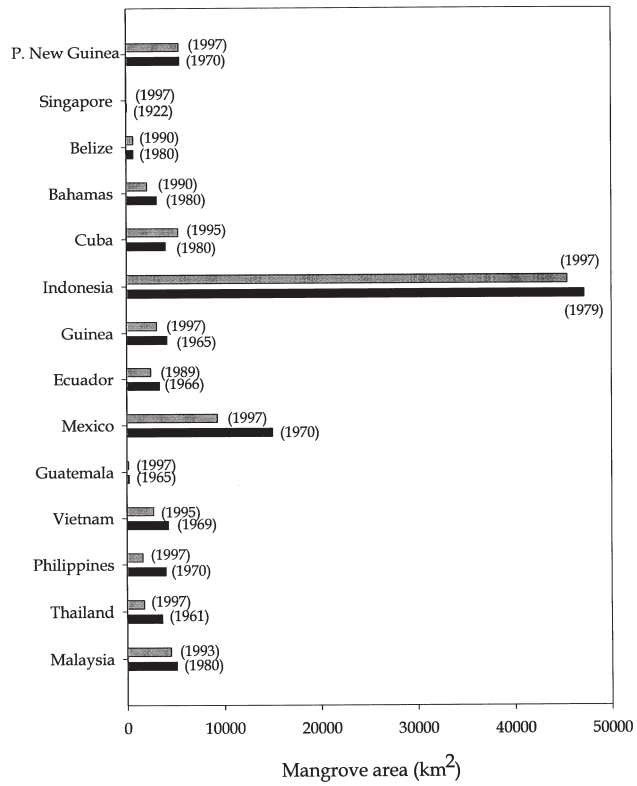


Figure 8 Long-term changes in mangrove forest areas worldwide. Compiled from data in Clough (1993); Diop (1993); Lacerda (1993); and Spalding *et al.* (1997).

Loss rates vary greatly among nations, ranging from 1 to 20% of total forest area per year (Clough 1993; Diop 1993; Lacerda 1993), making it difficult to predict global changes in forest area in future. There are enormous variations within individual countries. For instance, in Thailand losses of mangroves from 1961 to 1989 varied from 0 to 9% in central and lower Gulf of Thailand provinces to as much as 79% along the Andaman Sea coastline (Clough 1993). Similarly, Malaysia experienced an overall reduction in mangroves of approximately 12% since 1980, with greatest losses in Johor, Selangor, Negeri Sembilan and Teerengganu, but some provinces such as Malacca have increased forest area owing to restoration and sustainable management of reserves (Clough 1993). Such is true for several African and Latin American nations (Diop 1993; Lacerda 1993). In those nations that have replanted forests for a net gain, loss of biodiversity of trees and associated organisms appears to be permanent. Most restorations involve monocultures of rapidly growing species (Field 1998). Rare, slow-growing tree species are ordinarily not replaced (see below).

The future of mangroves is intimately linked to changes in forest use, which is directly tied to changes in human population growth and development. Predictions of human population change indicate most rapid growth in tropical developing nations, where the bulk of mangrove forests lie. Assuming that human populations will grow along tropical coasts, so will anthropogenic impacts. In fact, some mangrove areas are already overfished. For example, in the Mekong delta, fish catch per unit effort has declined from the late 1970s (Fig. 9), and continues to decline, as the coastal population grows and mangroves continue to be destroyed for shrimp farming which has increased 35-fold (de Graaf & Xuan 1998). At present one hectare of mangrove supports approximately 0.45 tonnes of marine fish catch per year in the region. Increasing human pressures bring a concomitant rise in the incidence of viral and other diseases, directly impacting seed stock (de Graaf & Xuan 1998), and increasing coastal erosion and saltwater intrusion into groundwater (Hong & San 1993).

The highest-level threats to mangroves in future (Table 5) are likely to be deforestation, aquaculture and overexploitation of wood and fisheries resources. Aquaculture will remain a great threat, although aquaculture production of fish, crustaceans and molluscs in countries with mangroves appears to have levelled off (Fig. 10). This plateau indicates that a sustainable level of coastal aquaculture has been reached and that mangrove clearing for aquaculture operations has also peaked.

Assuming that the rate of deforestation does not change substantially over the next two decades, the felling of mangrove forests to construct new ponds and the discharge of wastes will continue. There have been advances in reducing waste discharge from aquaculture, but this reduction is unlikely to compensate for continued need for more space as aquaculture production per unit area is declining or remaining stable at best (Naylor *et al.* 2000; FAO [Food and Agricultural Organization of the United Nations] 2001).

It has been proposed that mangroves can be used as sinks to filter aquaculture effluent (e.g. Robertson & Phillips 1995), based on the presumption that mangroves have high capacity to tolerate and use dissolved nutrients because of their high rates of primary production. This idea has considerable merit, but maintaining a steady-state condition would be difficult. It is likely that a sustainable operation would be site-

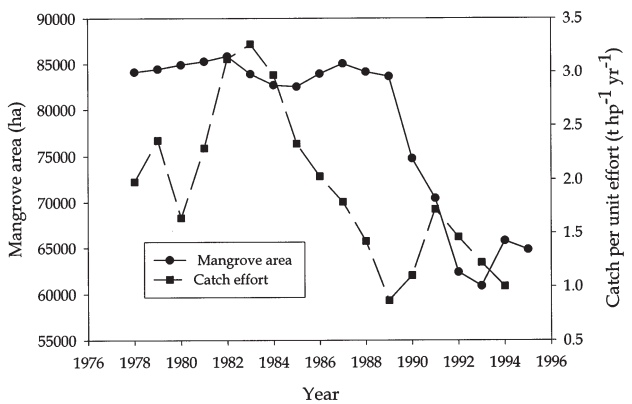


Figure 9 Changes in mangrove forest area (ha) and fisheries catch per unit effort (t hp^{-1} yr^{-1}), Minh Hai Province, Mekong Delta, Vietnam, 1977–1995. Data from deGraaf and Xuan (1998). hp = total engine capacity in horsepower.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

specific, depending on the quantity and quality of waste, the proportion of particulate to dissolved waste, how and when the waste was applied to the forests, the extent of tidal flushing, and forest productivity and age (Trott & Alongi 2000). In short, no universal formula for success is forthcoming, given the lack of long-term data on the impact of aquaculture effluent discharge on mangrove forests and associated waterways. Further, an impact may be cumulative rather than immediate and overt, and may not be discernible for several years. Cage aquaculture is less destructive than ponds, but even sustaining a particular number of cages in a given area would greatly depend on hydrodynamics and coastal geomorphology, as well as the level of cultivation intensity. For both mangroves and commercial operations to be sustained, they must be properly managed and guided by national development plans.

Rehabilitation and sustainable management

Environmental degradation in many parts of the world, especially in Asia and Latin America, has led to attempts to rehabilitate and restore mangroves. Most rehabilitation and restoration projects have had mixed results, with the main reasons for failure being lack of adequate site selection and proper use of soil preparation and planting techniques (Ellison 2000). In many cases, futile attempts have been made to rehabilitate a site that is beyond restoration. In such cases, the sites are often highly saline with acid sulphate soils and with both tidal water and soils extremely low in oxygen and nutrient content; sites of shrimp faming, mining and timber harvesting are frequently in this category.

Critical to the success of a rehabilitation project is proper selection of species to be planted, and whether or not they are to regenerate naturally or artificially. Natural replenishment requires that sufficient undisturbed forests reside nearby to serve as sources of seed stock. Artificial replanting success depends on funding, time and the level of expertise available to use appropriate methods.

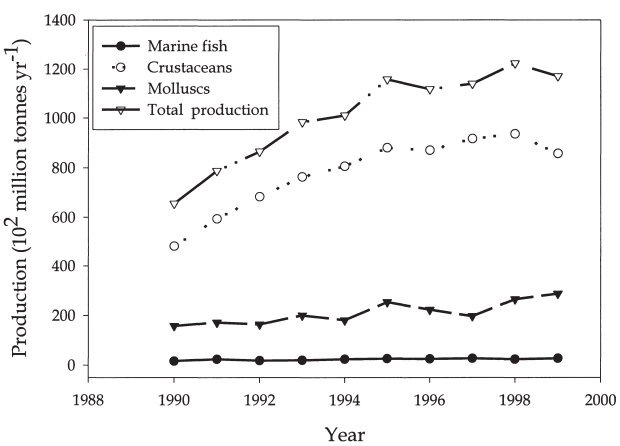


Figure 10 Changes in aquaculture production in all countries inhabited by mangroves, 1990–1999. Data from FAO (2001).

The technology exists to regrow trees but restoring fauna and ecosystem function is exceedingly difficult. The fact remains that most rehabilitated sites are mono-cultures or low diversity poly-cultures having little, if any, resemblance to the original habitat. Only a few species are commonly used, namely *Rhizophora apiculata*, *Rhizophora mucronata*, *Rhizophora mangle*, *Avicennia marina* and *Sonneratia apetala*. Mangrove forests can often be rehabilitated but not restored.

Mangroves are in a sense among the easiest systems to reconstruct, but the emphasis has been, and continues to be, on reintroduction of trees. It is presumed that over time animals such as crabs, fish, meiofauna and algae will recolonize replanted sites and that ecosystem linkages will be restored. The primary objectives of mangrove rehabilitation projects, in descending order of frequency, are silviculture, mitigation, coastal stabilization, ecosystem function and fisheries.

Restoration of mangrove ecosystems can theoretically be achieved, given that mangroves have been cultivated for several centuries. Mangroves can grow and thrive if hydrological and geomorphological conditions are optimal, and there is some evidence that replanted forests can approach the biomass, stand structure and productivity of undisturbed forests within 20–25 years (e.g. McKee & Faulkner 2000). However, restoration requires time, which is most often contrary to political, cultural and economic priorities. To date, extensive replanting of mangroves has been achieved only in Pakistan, Cuba and Bangladesh (Spalding *et al.* 1997).

The Bangladesh scenario is arguably the most impressive attempt to reforest mangroves along a large portion of tropical coastline (Saenger & Siddiqi 1993). Severe cyclone damage led the Bangladesh Forest Department in 1966 to initiate an afforestation programme to increase coastal protection afforded by expansion of mangrove forest. Up until 1993, nearly 120 000 ha were planted on accreting banks formed from sediment delivered to the eastern Sundarbans from the Ganges and Brahmaputra Rivers; two species, *Sonneratia apetala* and *Avicennia officinalis* were the dominant trees planted. There were some difficulties encountered with sediment stability, but the benefits have been substantial. The greatest lessons learned were: (1) to have more adaptable replanting schemes as soil salinities change over time; and (2) monospecific cultures are not a universal remedy, as they can generate problems all their own that are costly and difficult to rectify.

Most restoration projects continue to emphasize silviculture to generate production of timber, wood chips, charcoal and fuelwood (Ellison 2000). Given economic imperatives in most coastal communities in developing countries, most immediate value and emphasis is naturally placed on wood production. This trend is likely to continue to at least 2025. Indeed, the greatest success in sustainable management of mangroves has been achieved in silviculture.

Guidelines for sustainable management of mangroves have been developed by a number of organizations and agencies, and all express several commonalities:

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

- within a national boundary, mangroves should be assigned to one or other of the following categories: conservation reserve, forest reserve, fisheries reserve and alienable mangrove land;
- mangroves on alienable land should be maintained;
- specific management goals and practices should be clearly identified and implemented;
- appropriate laws and regulations should be enacted and enforced;
- the best available technical expertise should be used;
- there should be a buffer zone between mangroves and adjacent industry, housing and tourist development;
- pond aquaculture should not be permitted within mangrove reserves;
- within permissible areas, ponds should not be closer than 200 m to mangroves;
- an environmental impact assessment and feasibility study should be required for all development projects; and
- strict pollution controls should be established.

If these guidelines were adhered to, loss of mangroves worldwide could be minimized in future, certainly to a level not greater than an annual global loss rate of about 1% (current estimate of Kaly & Jones 1998). Fragmentation and loss of diversity, given the lack of consensus on estimating the minimum expanse of mangroves required to sustain all key processes, is still a danger (Kaly & Jones 1998).

Technological improvements, such as genetic and microbial advances, may ameliorate problems in conserving and maximizing mangrove ecosystem structure and function in rehabilitated environments. It is likely that protocols will be established for *in vitro* propagation of several key mangrove species, as can be done with *Excoecaria agallocha*, an extract of which is currently used for relief of rheumatism and treatment of ulcers (Rao *et al.* 1998). Microbes stimulate seedling growth, so culture success might be improved by inoculating seedlings with bacteria, such as nitrogen fixers, that promote plant growth (Holguin *et al.* 2001). Also, less destructive mud crab cultivation is being successfully trialled in many regions (Keenan & Blackshaw 1999), and may offer a reasonable alternative to destructive pond cultivation.

Ecological economics: towards a pragmatic solution?

If mangrove resources are to be conserved, sustainable management realistically must operate on the basis of economics (Turner *et al.* 1993). It is human nature to protect and conserve a resource that is a source of income. Economic self-interest must play a role in management if mangroves are to persist and thrive in the face of human encroachment. A few case studies indicate that the idea of conserving mangroves as economic investment is realistic (Ronnback 1999).

The mean monetary value of mangroves has recently been estimated at US$ 9990 ha^{-1} yr^{-1}, second only to the value of estuaries and seagrass beds, and greater than the economic value of coral reefs, continental shelves and the open sea (Costanza *et al.* 1998). The commercial value of mangrove resources has been recognized since early last century. Mangrove-related fisheries resources generally are valued more highly than natural and agricultural goods, such as wood, with the value of fisheries ranging from US$ 120–3000 ha^{-1} yr^{-1} and timber from US$ 60–800 ha^{-1} yr^{-1} (Clough 1993; Diop 1993; Lacerda 1993). These figures are only indicative of their fair value; some products are worth more than others, and the same product is often worth more in one region than in another for various reasons such as quality and local market demand.

The competing demands of coastal industries and mangroves are manageable if relevant ecological information is collected and used properly to design management plans that reflect how mangrove ecosystems support fisheries. For example, until the mid-1980s, mangroves were heavily exploited in Colombia for artisanal and commercial fishing, wood extraction for poles, charcoal, paper and housing materials, with no clear national or regional plans for sustainable development (Lacerda 1993). As a result of these unsustainable losses, the National Institute for Renewable Resources and Environment started a National Mangrove Committee with the aim to formulate policies for the conservation and sustainable management of mangroves in Colombia. As a result of these policies, mangrove protective areas have been enlarged and the coastline divided into areas for protection, public interest, forestry and fisheries reserve, special management and special protection (Lacerda 1993).

On the Caribbean coast of Colombia where semi-intensive shrimp aquaculture is practised, proper environmental management plans have been drawn up as a result of an urgent need for ecologically sustainable development. The study of Larsson *et al.* (1994) is a prime example of the type of critical economic and ecological analysis necessary for sustainable management as legislated in Colombia. In their model, Larsson *et al.* (1994) first estimated the ecosystem area that is required to produce the food, clean water and nursery areas to support the shrimp farms and to assimilate their wastes. Their results show that a semi-intensive farm needs an area of mangroves 35–190 times larger than the area of the farm; for each joule of edible shrimp protein produced, approximately 295 J of ecosystem work is required. In 1990, an area equivalent to about 20–30% of Colombia's entire mangroves was required to supply the industry's entire needs for post-larval shrimp. In comparing the energetic requirements of Colombia's aquaculture industry to other food production systems, Larsson *et al.* (1994) concluded that coastal aquaculture is one of the most resource-intensive industries, and characterized it as ecologically unsustainable. To maximize use and to minimize impact, Colombia's aquaculture operations should retain natural tidal flows, locate new farms to marginal saltpans, maximize distance between farms, use vegetable instead of animal feeds, use filter feeders to naturally clarify pond waters, and improve artificial rearing methods (Larsson *et al.* 1994). It is likely that aquaculture industries in other nations would do well to take up some or all of these suggestions, where applicable.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Similar efforts to establish a clear ecological and economic link between mangroves and the value of fisheries have been difficult. Cost-benefit and multi-criteria analyses, while valuable in some circumstances, have their limitations and are often impossible to apply. In the Philippines, felling of mangroves for aquaculture has been banned since 1981, but the current decline in fish catch per unit effort has increased pressure to re-examine the protective legislation. Consequently, Janssen and Padilla (1999) compared the costs and benefits of mangrove conservation with those generated by various alternative plans of aquaculture and forestry. A comparison of net annual benefits of goods and services provided by mangroves indicates that aquaculture generates the greatest value at US$ 6793 ha^{-1} yr^{-1}, followed by forestry (US$ 150 ha^{-1} yr^{-1}) and fisheries (US$ 60 ha^{-1} yr^{-1}). Based on the trade-offs of efficiency and equity, commercial forestry delivers the most equity and semi-intensive aquaculture the most efficient alternatives; intensive aquaculture was the worst alternative. Given the limitations of not being able to value mangrove biodiversity, shore protection and flood mitigation, Janssen and Padilla (1999) concluded that semi-intensive aquaculture was the policy alternative with the highest economic value. However, they questioned whether it was possible to adequately value the impact of losses of species and ecosystems on the way of life of the indigenous people.

Several studies modelling the trade-off between mangroves and resource use argue for minimal destruction or use of forests and associated waterways, especially against the backdrop of overfishing. Using an open-access fishery model, Barbier and Strand (1998) estimated the impact of change in mangrove area on nearshore shrimp production in Campeche, Mexico. Simulating a marginal decline in mangrove forest area, their model indicated a concomitant decline in shrimp harvest and an increase in price per kg harvest and cost per vessel. Their model, however, suggested that the fishery might be sensitive to the level of mangrove exploitation; a modest decline in mangrove area may lead to a disproportionate decline in shrimp harvest and revenue if the ecosystem is deforested beyond the current levels of 2 km^2 yr^{-1} (Barbier & Strand 1998). Moreover, while mangrove deforestation contributed to a decline in the fishery so did the pervasive problem of overexploitation. It is likely that the shrimp fishery has been operating at or slightly above sustainable limits. Better management and involvement of the community in controlling overfishing is just as critical as limiting the destruction of mangrove nursery grounds.

Optimizing the trade-off between mangrove preservation and human exploitation has been modelled successfully, and these models have indicated the importance of some basic ecological variables. Employing both dynamic optimization and simulation models of the economic link between fishery production and mangrove use in Brazil, Grasso (1998) found that the optimisation model suggested how best to employ forestry and fishery workers. The worst scenario would be over-exploitation of mangrove stocks if there were no equilibrium established between forestry and fishery efforts. The best management option in the long-term, however, was to have more workers in fisheries than forestry. Grasso (1998) suggested that clear felling of mangroves should be reduced to a minimum to avoid ecosystem collapse. The most important variable in the simulation model was the rate of forest growth, underscoring the importance of the relationship between forest age, growth and the extent of forest resource use (Grasso 1998).

The ecological ties between mangroves and adjacent environments can serve as a key for sustainable management. Resource-use models encompassing the strength of linkages between ecosystem compartments show that severe restrictions on mangrove clearing can optimize economic output. In the Bintuni Bay area of Indonesia where mangroves are heavily exploited for woodchips, and artisanal and commercial fisheries, strong economic arguments exist for limited clearing (Ruitenbeek 1994). Cost-benefit analysis of forest management options incorporating links among fishery production, mangrove use and clearance rates, erosion control and biodiversity (Ruitenbeek 1994) indicate that clear-felling of mangroves is a viable management option only when all the linkages are ignored. Assuming that clear linkages exist between mangroves and environmental functions and fisheries, a ban on cutting is optimal; if the linkages incorporate time lags on the order of years, selective cutting of 25% of total harvestable mangroves is the optimal strategy (Ruitenbeek 1994). In any case, conservative cutting appears to be a good strategy because a wrong management decision based on total ignorance would likely have severe economic and ecological consequences for several decades.

CONCLUSIONS AND MANAGEMENT

Mangroves are the only woody halophyte-dominated ecosystems situated at the confluence of land and sea. Most mangrove forests are highly productive and net autotrophic, helping to support coastal food chains, including commercially valuable fish, crustaceans and molluscs. The world's mangrove forests are economically very valuable, worth an estimated US$ 180 895 923 000 based on the valuation of Costanza *et al.* (1998).

Mangroves have traditionally been heavily used for timber, poles, food, medicines and a wide variety of other items. Most nations have lost mangroves; a few countries have gained single-species forests as a result of reforestation projects. Claims that 50% of the world's mangrove forests have disappeared over the past century (GESAMP 2001) may be exaggerated due to lack of empirical data. An analysis of current estimates (Clough 1993; Diop 1993; Lacerda 1993; Spalding *et al.* 1997) based on more reliable information suggests that cumulative losses over the past 50 years are closer to one-third. The exact losses will never be known, and even today, a precise estimate of global extent of mangrove forests is not easy (Spalding *et al.* 1997). Some countries such as Liberia, the Ivory Coast and Guinea have experienced

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

heavy losses, but most countries with expansive mangroves, such as Brazil and Australia, have experienced comparatively little deforestation (Spalding *et al.* 1997).

Most losses have been the direct result of felling for shrimp ponds, housing and industrial developments (Alongi 1998), but severe losses have occurred in some regions due to shoreline erosion/siltation accelerated by terrestrial deforestation, desertification and other poor land-use practices. Herbicides and defoliants, pollution, alteration of natural tidal cycles and water flow, and uncontrolled resource exploitation, also degrade and destroy mangrove ecosystems. In future, the greatest threats to the continued existence of mangroves are deforestation, pond aquaculture and a pervasive overexploitation of fisheries resources. Global warming and chronic eutrophication will have a lesser impact on the health of mangrove ecosystems over the next 25 years. Mangrove losses are positively related to human population density and growth; the fewer people who live at or near a forest, the less destruction and exploitation there will be.

The future is not necessarily bleak for mangroves. Lutz *et al.* (2001) estimate that the rate of world population growth is already declining, with an 85% chance that the global population will stop growing before the end of the century. The projections for sub-Sahara Africa, south Asia, Latin America, and the Asia Pacific regions show that population size will plateau by about 2050 (Lutz *et al.* 2001). Given the apparent link between the exploitation of mangroves and human population density, this implies that overexploitation will continue until 2050, but decline thereafter. Coupled with technological improvements in aquaculture, restoration ecology and genetics, hopefully the worst direct exploitation will be over by 2025. The biggest problem in future is the loss of biodiversity. Most rehabilitation projects replant fewer species than were originally lost. Loss of biodiversity is a critical issue given that mangrove forests are less diverse than most other tropical ecosystems.

The major problem in predicting mangrove responses to human impacts is the lack of long-term data, and the ability to distinguish natural from anthropogenic change. There is a lack of knowledge of:

- gross and net canopy production;
- below-ground root production;
- tree and below-ground root respiration;
- natural successional states over time;
- whole-ecosystem mass balances for carbon, nitrogen and phosphorus;
- physiological information (water and carbon balance);
- factors regulating colonization (propagule dispersal, seedling establishment);
- secondary production;
- plant-soil-microbial relations;
- species diversity of flora and fauna;
- forestry models to determine maximum sustainable yield;
- silviculture of rare species;
- experimental effects of greenhouse gas and sea level change; and
- experimental effects of excess nutrients on mangrove growth and survival.

Actions can be taken to improve conservation of mangroves. The Charter for Mangroves put forward by the International Society for Mangrove Ecosystems (Field 1995) would be a logical first step. The charter was adopted in 1991 to complement the World Charter for Nature proclaimed by the General Assembly of the United Nations in 1982. The mangrove charter affirms that mangroves will be respected and not compromised in terms of their genetic viability, that they will be conserved where ever possible, and managed on a sustainable basis. The major stumbling block to practical implementation of the charter remains commitment from local and national governments to provide adequate resources to implement management plans. The best example of sustained management of a mangrove ecosystem is the Matang Mangrove Forest Reserve in peninsular Malaysia. The success of this enterprise can be directly attributed to government commitment and a good relationship between government, business and the local community.

It is essential for governments and people to understand that mangroves are a valuable social and economic resource. It is a fact of human nature that we tend to preserve and protect resources that are of economic importance; aesthetics is historically not high on the list of reasons why we conserve resources. If mangrove forests are not seen as a fundamental economic and ecological resource to be treasured, they will continue to be exploited at current rates until at least 2025. The greatest hope in reducing the rate of mangrove losses is the projection that human population growth will decline, and possibly stop, later in the century.

ACKNOWLEDGEMENTS

I am grateful to many colleagues for their comments on an earlier draft of the manuscript, Nick Polunin for his help, and to the AIMS librarians for chasing many references. Contribution No. 1101 from the Australian Institute of Marine Science

References

Alongi, D.M. (1998) *Coastal Ecosystem Processes*. New York, USA: CRC Press: 419 pp.

Alongi, D.M. & Dixon, P. (2000) Mangrove primary production and above- and below-ground biomass in Sawi Bay, southern Thailand. *Phuket Marine Biological Center Special Publication* **22:** 31–38.

Alongi, D.M. & Sasekumar, A. (1992) Benthic communities. In: *Tropical Mangrove Ecosystems*, ed. A.I. Robertson & D.M. Alongi, pp. 137–172. Washington DC, USA: American Geophysical Union.

Alongi, D.M., Boto, K.G. & Robertson, A.I. (1992) Nitrogen and phosphorus cycles In: *Tropical Mangrove Ecosystems,* ed. A.I. Robertson & D.M. Alongi, pp. 225–249. Washington DC, USA: American Geophysical Union.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Alongi, D.M., Wattayakorn, G., Ayukai, T., Clough, B.F., Wolanski, E. & G.J. Brunskill (2000) An organic carbon budget for mangrove-fringed Sawi Bay, southern Thailand. *Phuket Marine Biological Center Special Publication* **22:** 79–85.

Alongi, D.M., Wattayakorn, G., Pfitzner, J., Tirendi, F., Zagorskis, I., Brunskill, G.J., Davidson, A. & Clough, B.F. (2001) Organic carbon accumulation and metabolic pathways in sediments of mangrove forests in southern Thailand. *Marine Geology* **179:** 85–103.

Ayukai, T. & Alongi, D.M. (2000) Pelagic carbon fixation and heterotrophy in shallow coastal waters of Sawi Bay, southern Thailand. *Phuket Marine Biological Center Special Publication* **22:** 39–50.

Ball, M.C. (1998) Mangrove species richness in relation to salinity and waterlogging: A case study along the Adelaide River floodplain, northern Australia. *Global Ecology and Biogeography Letters* **7:** 73–82.

Ball, M.C., Cochrane, M.J. & Rawson, H.M. (1997) Growth and water use of the mangroves *Rhizophora apiculata* and *R. stylosa* in response to salinity and humidity under ambient and elevated concentrations of atmospheric CO_2. *Plant, Cell and Environment* **20:** 1158–1166.

Baran, E. (1999) A review of quantified relationships between mangroves and coastal resources. *Phuket Marine Biological Center Research Bulletin* **62:** 57–64.

Barbier, E.B. & Strand, I. (1998) Valuing mangrove-fishery linkages: a case study of Campeche, Mexico. *Environmental and Resource Economics* **12:** 151–166.

Berger, U. & Hildenbrandt, H. (2000) A new approach to spatially explicit modelling of forest dynamics: spacing, aging and neighbourhood competition of mangrove trees. *Ecological Modelling* **132:** 287–302.

Boto, K.G. (1992) Nutrients and mangroves. In: *Pollution in Tropical Aquatic Systems*, ed. D.W. Connell and D.W. Hawker, pp. 129–145. Boca Raton, USA: CRC Press, Inc.

Bouillon, S., Koedam, N., Raman, A.V. & Dehairs, F. (2002) Primary producers sustaining macro-invertebrate communities in intertidal mangrove forests. *Oecologia* **130:** 441–448.

Bunt, J.S. (1996) Mangrove zonation: An examination of data from 17 riverine estuaries in tropical Australia. *Annals of Botany* **78:** 333–341.

Burke, L., Kura, Y., Kassem, K., Revenga, C., Spalding, M. & McAllister, D. (2001) *Pilot Analysis of Global Ecosystems: Coastal Ecosystems.* Washington, DC, USA: World Resources Institute:77 pp.

Burns, K. A., Garrity, S.D. & Levings, S.C. (1993) How many years until mangrove ecosystems recover from catastrophic oil spills? *Marine Pollution Bulletin* **26:** 239–248.

Cebrian, J. (2002) Variability and control of carbon consumption, export, and accumulation in marine communities. *Limnology and Oceanography* **47:** 11–22.

Chambers, J.Q., Higuchi, N., Tribuzy, E.S. & Trumbore, S.E. (2001) Carbon sink for a century: intact rainforests have a long-term storage capacity. *Nature* **410:** 429.

Chong, V.C. & Sasekumar, A. (1994) Status of mangrove fisheries in the ASEAN region. In: *Living Coastal Resources of Southeast Asia: Status and Management,* ed. C.R. Wilkinson, pp. 56–61. Townsville, Australia: Australian Institute of Marine Science.

Clough, B.F. (1992) Primary productivity and growth of mangrove forests. In: *Tropical Mangrove Ecosystems,* ed. A.I. Robertson & D.M. Alongi, pp. 225–249. Washington DC, USA: American Geophysical Union.

Clough, B.F. (1993) *Conservation and Sustainable Utilization of Mangrove Forests and Their Present State of Conservation in the South-east Asia/Pacific Region*, *Mangrove Ecosystems Technical Reports, Vol. 1.* Okinawa, Japan: International Society for Mangrove Ecosystems: 202 pp.

Clough, B.F., Ong, J.E. & Gong, W.K. (1997) Estimating leaf area index and photosynthetic production in canopies of the mangrove *Rhizophora apiculata*. *Marine Ecology Progress Series* **159:** 285–292.

Clough, B.F., Tan, D.T., Buu, D.C. & Phuong, D.X. (1999) Mangrove forest structure and growth. In: *Mixed Shrimp Farming-Mangrove Forestry Models in the Mekong Delta, Termination Report, Part B: Technical Appendices*, ed. B. Clough, pp.235–251. Canberra, ACT, Australia: Australian Centre for International Agricultural Research.

Costanza, R.R., d'Arge, R., deGroot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K, Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. & van den Belt, M. (1998) The value of the world's ecosystem services and natural capital. *Ecological Economics* **25:** 3–15.

Day Jr, J.W., Coronado-Molina, C., Vera-Herrera, F.R., Twilley, R., Rivera-Monroy, V.H., Alvarez-Guillen, H., Day, R. & Conner, W. (1996) A 7 year record of above-ground net primary production in a southeastern Mexican mangrove forest. *Aquatic Botany* **55:** 39–60.

deGraaf, G.J. & Xuan, T.T. (1998) Extensive shrimp farming, mangrove clearance and marine fisheries in the southern provinces of Vietnam. *Mangroves and Salt Marshes* **2:** 159–166.

Diop, E.S. (1993) *Conservation and Sustainable Utilization of Mangrove Forests and Their Present State of Conservation in Latin America and Africa Regions*, *Part II-Africa, Mangrove Ecosystems Technical Reports, Volume 3.* Okinawa, Japan: International Society for Mangrove Ecosystems: 262 pp.

Drexler, J.Z. & Ewel, K.C. (2001) Effect of the 1997–1998 ENSO-related drought on hydrology and salinity in a Micronesian wetland complex. *Estuaries* **24:** 347–356.

Duarte, C.M. & Cebrian, J. (1996) The fate of marine autotrophic production. *Limnology and Oceanography* **41:** 1758–1766.

Duke, N.C., Ball, M.C. & Ellison, J.C. (1998) Factors influencing the biodiversity and distributional gradients in mangroves. *Global Ecology and Biogeography Letters* **7:** 27–47.

Ellison, A.M. (2000) Mangrove restoration: do we know enough? *Restoration Ecology* **8:** 219–229.

Ellison, A.M. & Farnsworth, E.J. (1997) Simulated sea level change alters anatomy, physiology, growth, and reproduction of red mangrove (*Rhizophora mangle* L.). *Oecologia* **112:** 435–446.

Ellison, A.M. & Farnsworth, E.J. (2000) Mangrove communities. In: *Marine Community Ecology,* ed. M.D. Bertness, S.D. Gaines & M.E. Hay, pp. 423–442. New York, USA: Sinauer Associates.

Ellison, J.C. & Stoddart, D.R. (1991) Mangrove ecosystem collapse during predicted sea-level rise: Holocene analogues and implications. *Journal of Coastal Research* **7:** 151–165.

FAO (2001) *Fishery Statistics 1999 Yearbook, Aquaculture Production, Volume 88/2.* FAO Fisheries Series No. 58. Rome, Italy: Food and Agriculture Organization of the United Nations.

Farnsworth, E.J. & Ellison, A.M. (1997) The global conservation status of mangroves. *Ambio* **26:** 328–334.

Feller, I.C., Whigham, D.F. O'Neill, J.P. & McKee, K.L. (1999) Effects of nutrient enrichment on within-stand cycling in a mangrove forest. *Ecology* **80:** 2193–2205.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Field, C.D. (1995) *Journey amongst Mangroves.* Okinawa, Japan: International Society for Mangrove Ecosystems: 140 pp.

Field, C.D. (1998) Rehabilitation of mangrove ecosystems: an overview. *Marine Pollution Bulletin* **37:** 383–392.

Field, C.D. (2000) Mangroves. In: *Seas at The Millenium: An Environmental Evaluation. Volume III Global Issues and Processes,* ed. C. R. C. Sheppard, pp. 17–31. Amsterdam, The Netherlands: Pergamon Press.

Fromard, F., Puig, H., Mougin, E., Marty, G., Betoulle, J.L. & Cadamuro, L. (1998) Structure, above-ground biomass and dynamics of mangrove ecosystems: new data from French Guiana. *Oecologia* **115:** 39–53.

Gan, B.K. (1995) *A Working Plan for the Matang Mangrove Forest Reserve Perak*. Perak, Malaysia: State Government of Perak Darul Ridzuan: 214 pp.

GESAMP (2001) A sea of troubles. Reports and Studies GESAMP No. 70: 35 pp.

Grasso, M. (1998) Ecological-economic model for optimal mangrove trade off between forestry and fishery production: comparing a dynamic optimization and a simulation model. *Ecological Modelling* **112:** 131–150.

Hinrichsen, D. (1998) *Coastal Waters of the World: Trends, Threats, and Strategies.* Washington, DC,USA: Island Press: 275 pp.

Hogarth, P.J. (1999) *The Biology of Mangroves.* Oxford, UK: Oxford University Press: 228 pp.

Holguin, G., Vazquez, P. & Bashan, Y. (2001) The role of sediment microorganisms in the productivity, conservation, and rehabilitation of mangrove ecosystems: an overview. *Biology and Fertility of Soils* **33**: 265–278.

Hong, P.N. & San, H.T. (1993) *Mangroves of Vietnam*. Bangkok, Thailand: IUCN: 173 pp.

IPCC (2001) *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge, UK: Cambridge University Press: 881 pp.

Janssen, R. & Padilla, J.E. (1999) Preservation or conversion? Valuation and evaluation of a mangrove forest in the Philippines. *Environmental and Resource Economics* **14:** 297–331.

Jimenez, J.A., Lugo, A.E. & Contron, G. (1985) Tree mortality in mangrove forests. *Biotropica* **17:** 177–185.

Kaly, U. & Jones, G.P. (1998) Mangrove restoration: a potential tool for coastal management in tropical developing countries. *Ambio* **27:** 656–661.

Kathiresan, K. & Bingham, B.L. (2001) Biology of mangroves and mangrove ecosystems. *Advances in Marine Biology* **40:** 81–251.

Keenan, C.P. & Blackshaw, A. (1999) *Mud Crab Aquaculture and Biology. Proceedings of an International Scientific Forum held in Darwin, Australia, 21–24 April 1997.* ACIAR Proceedings No. 78. Canberra, Australia: Australian Centre for International and Agricultural Research: 216 pp.

Kelleher, G., Bleakley, C. & Wells, S. (1995) *A Global Representative System of Marine Protected Areas, Volume 1.* Washington, DC, USA: World Bank: 219 pp.

Klekowski Jr, E.J., Corredor, J.E., Morrell, J.M. & Delcastillo, C.A. (1994) Petroleum pollution and mutation in mangroves. *Marine Pollution Bulletin* **28:** 166–169.

Lacerda, L.D. (1993) *Conservation and Sustainable Utilization of Mangrove Forests and Their Present State of Conservation in Latin America and Africa Regions*, *Part I-Latin America, Mangrove Ecosystems Technical Reports, Volume 2.* Okinawa, Japan: International Society for Mangrove Ecosystems: 272 pp.

Larsson, J., Folke, C. & Kautsky, N. (1994) Ecological limitations and appropriation of ecosystem support by shrimp farming in Colombia. *Environmental Management* **18:** 663–676.

Lugo, A.E. (1997) Old-growth mangrove forests in the United States. *Conservation Biology* **11:** 11–20.

Lutz, W., Sanderson, W. & Scherbov, S. (2001) The end of world population growth. *Nature* **412:** 543–545.

Mahli, Y. & Grace, J. (2000) Tropical forests and atmospheric carbon dioxide. *Trends in Ecology and Evolution* **15:** 332–337.

McKee, K.L. & Faulkner, P.L. (2000) Biogeochemical functioning of restored and natural mangrove forests in southwest Florida, USA. *Restoration Ecology* **8:** 247–259.

McKinnon, A.D. & Klumpp, D.K. (1998) Mangrove zooplankton of North Queensland, Australia. II. Copepod egg production and diet. *Hydrobiologia* **362:** 145–160.

Mohsin, A.K.M. & Ambak, M.A. (1996) *Marine Fishes and Fisheries of Malaysia and Neighbouring Countries.* Serdang, Malaysia: Universiti Pertanian Malaysia Press: 744 pp.

Naylor, R.L., Goldburg, R.J., Primavera J.H., Kautsky, N., Beveridge, M.C.M., Clay, J., Folke C., Lubchenco, J., Mooney, H. & Troell, M. (2000) Effect of aquaculture on world fish supplies. *Nature* **405:** 1017–1024.

Parkinson, R.W., DeLaune, R.D. & White, J.R. (1994) Holocene sea-level rise and the fate of mangrove forests within the wider Caribbean region. *Journal of Coastal Research* **10:** 1077–1086.

Rao, C.S., Eganathan, P., Anand, A., Balakrishna, P. & Reddy, T.P. (1998) Protocol for *in vitro* propagation of *Excoecaria agallocha* L., a medicinally important mangrove species. *Plant Cell Reports* **17:** 861–865.

Robertson, A.I. & Blaber, S.J.M. (1992) Plankton, epibenthos and fish communities. In: *Tropical Mangrove Ecosystems*, ed. A.I. Robertson & D.M. Alongi, pp. 173–224. Washington DC, USA: American Geophysical Union.

Robertson, A.I. & Phillips, M.J. (1995) Mangroves as filters of shrimp pond effluent: predictions and biogeochemical research needs. *Hydrobiologia* **295:** 311–321.

Robertson, A.I., Alongi, D.M. & Boto, K.G. (1992) Food chains and carbon fluxes. In: *Tropical Mangrove Ecosystems*, ed. A.I. Robertson & D.M. Alongi, pp. 293–326. Washington DC, USA: American Geophysical Union.

Ronnback, P. (1999) The ecological basis for economic value of seafood production supported by mangrove ecosystems. *Ecological Economics* **29:** 235–252.

Rull, V., Vegas-Vilarrubia, T. & de Pernia, N.E. (1999) Palynological record of an early-mid Holocene mangrove in eastern Venezuela. Implications for sea-level rise and disturbance history. *Journal of Coastal Research* **15:** 496–504.

Ruitenbeek, H.J. (1994) Modelling economy-ecology linkages in mangroves: economic evidence for promoting conservation in Bintuni Bay, Indonesia. *Ecological Economics* **10:** 233–247.

Saenger, P. & Siddiqi, N.A. (1993) Land from the sea: the mangrove afforestation program of Bangladesh. *Ocean and Coastal Management* **20:** 23–39.

Saenger, P. & Snedaker, S.C. (1993) Pantropical trends in mangrove above-ground biomass and annual litterfall. *Oecologia* **96:** 293–299.

Sasekumar, A. & Chong, V.C. (1998) Faunal diversity in Malaysian mangroves. *Global Ecology and Biogeography Letters* **7:** 57–60.

Semeniuk, V. (1994) Predicting the effect of sea-level rise on mangroves in northwestern Australia. *Journal of Coastal Research* **10:** 1050–1076.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press

Smith, T.J., III (1992) Forest structure. In: *Tropical Mangrove Ecosystems,* ed. A.I. Robertson & D.M. Alongi, pp. 101–136. Washington DC, USA: American Geophysical Union.

Smith, T.J., III, Boto, K.G., Frusher, S.D. & Giddens, R.L. (1991) Keystone species and mangrove forest dynamics: the influence of burrowing by crabs on soil nutrient status and forest productivity. *Estuarine, Coastal and Shelf Science* **33:** 419–432.

Smith, T.J., III, Robblee, M.B., Wanless, H.R. & Doyle, T.W. (1994) Mangroves, hurricanes, and lightning strikes. *Bioscience* **44:** 256–262.

Spalding, M., Blasco, F. & Field, C. (1997) *World Mangrove Atlas.* Okinawa, Japan: The International Society for Mangrove Ecosystems: 178 pp.

Suzuki, T., Nishihira, M., Paphavasit, N., Shikano, S., Nakasone, Y., Piumsomboon, A. & Aumnuch, E. (1997). Ecological distribution and community structure of benthic animals in Samut Songkhram mangrove swamp, Thailand. In: *Benthic Communities and Biodiversity in Thai Mangrove Swamps*, ed. M. Nishihira, pp. 41–78. Sendai, Japan: Biological Institute, Tohoku University.

Trott, L.A. & Alongi, D.M. (2000) The impact of shrimp pond effluent on water quality and phytoplankton biomass in a tropical mangrove estuary. *Marine Pollution Bulletin* **40:** 947–951.

Turner, R.K., Pearce, D. & Bateman, I. (1993) *Environmental Economics: An Elementary Introduction.* Baltimore, USA: Johns Hopkins University Press: 328 pp.

Twilley, R.R., Chen, R.H. & Hargis, T. (1992) Carbon sinks in mangroves and their implications to carbon budget of tropical coastal ecosystems. *Water, Air, and Soil Pollution* **64:** 265–288.

Twilley, R.R., Snedaker, S.C., Yanez-Arancibia, A. & Medina, E. (1996) Biodiversity and ecosystem processes in tropical estuaries: perspectives of mangrove ecosystems. In: *Functional Roles of Biodiversity: A Global Perspective,* ed. H.A. Mooney, J.H. Cushman, E. Medina, O.E. Sala & E.-D. Schulze, pp. 327–370. Chichester, UK: John Wiley & Sons.

UNEP (1994) Assessment and monitoring of climatic change impacts on mangrove ecosystems. UNEP Regional Seas Reports and Studies No. 154. Nairobi, Kenya: United Nations Environment Programme: 62 pp.

Woodroffe, C. (1992) Mangrove sediments and geomorphology. In: *Tropical Mangrove Ecosystems,* ed. A.I. Robertson & D.M. Alongi, pp. 7–41. Washington DC, USA: American Geophysical Union.

Yim, M.W. & Tam, N.F. Y. (1999) Effects of wastewater-borne heavy metals on mangrove plants and soil microbial activities. *Marine Pollution Bulletin* **39:** 179–186.

https://doi.org/10.1017/S0376892902000231 Published online by Cambridge University Press