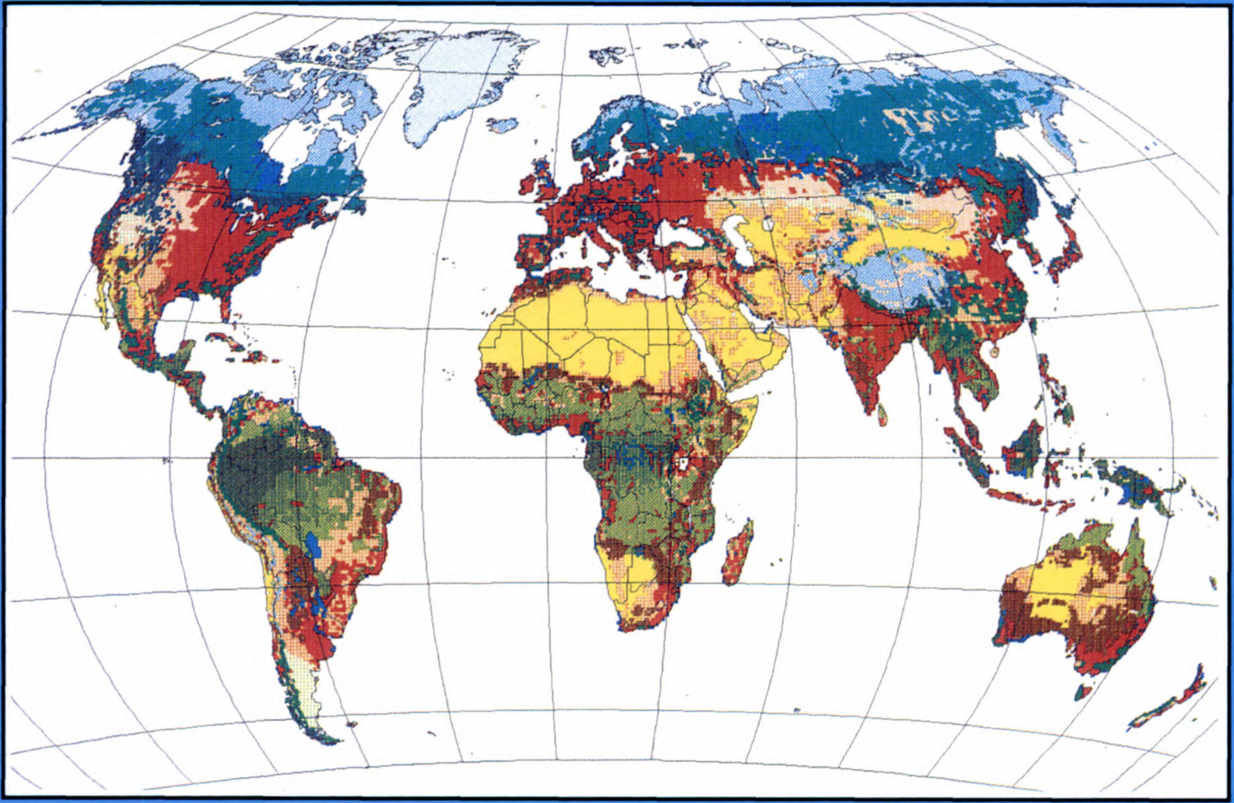
Impacts of Climate Change on Ecosystems and Species: Marine and Coastal Ecosystems



A Marine Conservation and Development Report

IUCN
The World Conservation Union

Impacts of Climate Change on Ecosystems and Species: Marine and Coastal Ecosystems

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The National Institute of Public Health and Environmental Protection (RIVM) is the key reference institute of the Netherlands Ministry of Housing, Physical Planning and Environment in the area of climate change and other global environmental problems. One of the core activities of the RIVM is to describe the state of the environment and the future environmental quality at the national, European and global levels under various scenarios.

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Impacts of Climate Change on Ecosystems and Species: Marine and Coastal Ecosystems

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Foreword

The Amersfoort Symposium on Impact of Climate Change on Ecosystems and Species was well-structured to compare and contrast both ecosystem responses to global change and the approaches of various disciplines to those responses. The climate scenarios and the charges to both authors and working groups provided by the organisers focused attention onto issues that were highly productive, although not always in the ways expected. Discussions of the ways in which coastal systems differ from terrestrial ecosystems with respect to controlling features and processes were particularly enlightening, and produced important distinctions concerning ecosystem vulnerability to climate change and other, non-climatic, stresses.

All of the environments and ecosystems considered in the "coastal" category are strongly influenced by terrestrial and/or atmospheric factors as well as the conditions of the marine environment. Aspects of the resulting complexity identified as important to some or all of the systems discussed included:

1. fluxes of materials (for example, sediment, fresh water, and carbon dioxide) and energy (especially wave energy) into and through the system;

2. long-range connections (for example, the importance to the coastal ecosystem of large-scale ocean current and storm patterns, or of precipitation over large watersheds); and

3. the importance of interactions between climate change and other anthropogenic environmental alterations (such as land use, water management, contamination, etc.).

A recent review has shown that coastal ecosystems play a significant (and previously underestimated) role in the global carbon budget and other geochemical fluxes (Smith & Hollibaugh, 1993). In addition to their large-scale relevance to global climatic processes, their multiple roles and functions make coastal ecosystems both important and vulnerable to human society in more immediate ways. For example, dunes, reefs, and mangroves all serve to develop and provide physical protection for shorelines and coastal geomorphology. Mangroves, estuaries, and lagoons are not only productive ecosystems but are also often important breeding grounds or nurseries for pelagic species, and thus play a role in global biodiversity greater than might be indicated by the permanent components of the communities. Their roles in shaping the physical and biotic interfaces between land and sea give them both ecological and economic importance out of proportion to their biomass or geographic extent.

The complexity of the systems under consideration was emphasised by van der Meulen *et al.*, who provided a thorough review of the multiple physical, chemical, and biological factors that control evolution of dune systems. These systems are the most terrestrial of the environments considered in the marine section and hence the most amenable to landscape-ecological analysis, but they share with the more marine coastal systems the characteristics of discontinuous, quasione-dimensional distributions, association with a wide range of terrestrial ecosystems and climatic regions, and sensitivity to characteristics of the marine "climate" such as sea level and the patterns of currents, waves, and storms.

Kjerve *et al.*, Ellison, and Jelgersma all stressed the importance of sediment budgets to the maintenance of ecosystems in or near the intertidal zone. Ellison summarised research results indicating that the survival of present-day mangrove ecosystems under conditions of rising sea level depends critically on the supply of sediment as well as on coastal topography, and that even the modest additional rates of sea level rise predicted to result from greenhouse warming would exceed the sediment-accumulation capability of low-island mangrove systems. Jelgersma and Kjerve *et al.* stressed the role of human developments such as dams, flood-control, and upstream consumptive water use in robbing many deltas and coastlines of previously "normal" input of terrestrial sediments. This has resulted in net subsidence and erosion in the recent past, processes that seem virtually certain to intensify as the rate of sea level rise accelerates. Kjerve *et al.* also pointed out the complicating effects of human coastal development that prevents the natural landward migration of intertidal and low supratidal ecosystems such as saltmarshes and dune or beach communities in response to coastal inundation or erosion.

Other perspectives were provided by consideration of strictly marine (i.e., subtidal) communities such as coral reefs and seagrass beds. Buddemeier and Smith noted that gradual sea level rise should probably be considered a net positive factor for the many coral reef communities that are limited by present sea level, and that the sediment-related threat to coral reefs is not sediment starvation, such as affects coastlines in developed countries, but excessive sedimentation associated with deforestation and agricultural runoff in developing countries. Chemical effects associated with rising CO_2 concentrations also seem likely to have their greatest impact in this environment. Buddemeier and Smith pointed out that the levels of supersaturation of surface water with respect to the calcium carbonate minerals deposited by corals and coralline algae will decrease; although conclusive data are not available, there is reason for concern that this could reduce the net calcification potential of some organisms and communities. Broun summarised results indicating that the lowered pH and increase in free CO_2 may be expected to have a significant fertilising effect on marine plants that can photosynthesise free CO_2 much more readily than they can the more abundant bicarbonate ion. Equilibration of the surface ocean with increased atmospheric CO_2 concentration may therefore shift competitive balances by enhancing marine plant growth and possibly inhibiting calcification - a climate-related development that would reinforce tendencies already ascribed to anthropogenic nutrient loading of coastal oceans.

Discussions of ecosystem vulnerability assessment by the coastal ecosystems working group turned first to island ecosystems, which were recognised as representing unusual vulnerability with respect to their terrestrial ecosystems because of their high levels of endemism and isolation from potential refugia. These concerns are not generally relevant to the marine ecosystems under consideration, and participants divided into three working groups to develop approaches to vulnerability assessments for coral reefs, mangrove ecosystems, and a broad class of environments including estuaries, deltas, dunes, and lagoons. Each subgroup endeavored to address the objectives specified by the organising committee: to identify the key factors and processes governing responses to climate change; to identify the possible directions and main features of ecosystem and species responses; and to determine the maximum rates of change which different ecosystems can withstand.

Both in general discussion and in the working groups, attention was focused on the degree to which questions and criteria derived from terrestrial landscape ecology could be applied to marine and coastal systems. Among the problems identified were the very different rates and mechanisms of dispersal and migration in the two environments, the dynamic and disturbance-adapted nature of most shallow marine and coastal ecosystems (which means that concepts of equilibrium, gradual succession, and climax communities are either less useful or necessarily very different compared to terrestrial situations), and profound differences in spatial scale (the marine/coastal ecosystems have discontinuous distributions and dimensions that may be small even compared to terrestrial ecotones). These distinctions were particularly important with respect to the problem of determining maximum rates of change an ecosystem could withstand, and the coastal working group decided that the issue of tolerable rate of change could not be addressed on a global or generic basis for the ecosystems under consideration.

The working group strongly emphasised that climate change responses could not be considered separately from the effects of non-climate anthropogenic stresses, both at a global scale (e.g., increased UV exposure and the chemical effects of CO_2 increases) and of a local or regional nature (e.g., land or water use, nutrient loading or contamination, and direct exploitation). The subgroups therefore evaluated probable global-scale ecosystem responses to various climate- and global-change factors, using the IPCC business-as-usual scenario for the year 2100 under both pristine-world (only climate change effects) and dirty-world (with added anthropogenic stresses) conditions.

All of the subgroups identified physical factors such as relative sea level, currents, winds/waves, and storm frequency and intensity as important factors, although the nature of their effects will vary both between and within types of ecosystems. Changes in these factors not only influence sediment dynamics, salt distributions (in the terrestrial coastal environment), and habitat characteristics, but they also interact strongly with other climatic and local anthropogenic factors. For similar reasons, changes in regional precipitation and local freshwater budgets were considered important to most of the coastal ecosystems (excluding oceanic coral reefs and some seagrass environments).

Increased temperature was considered a matter of slight to moderate concern in coastal ecosystems. Most of the marine and coastal ecosystems discussed occupy a wide latitudinal range: high latitude or ice-dependent communities were not among those considered, and predictions for changes in water temperature are less extreme and less well developed than those for land-mass air temperatures. Both coral and mangrove communities would be adversely affected by sustained tropical seawater temperatures in the vicinity of 35° C, and a pronounced increase in high-temperature events would be a concern for coral bleaching and mortality. Although increased high temperature excursions are possible, sustained water temperature elevations are an unlikely prospect in the near future, and latitudinal expansion of tropical and subtropical conditions could benefit both ecosystems.

Non-climatic regional and global changes were also among the factors considered significant. Increased UV exposure is a matter of concern, but data on both predicted changes and probable responses are so scanty that serious evalution is nearly impossible. Increased CO_2 levels may be deleterious to coral reefs, but are likely to result in changes to community structure or productivity rather than systematic stress to the other ecosystems considered. Nutrient loading and anthropogenic changes to regional and local sediment dynamics were considered important forces for change, likely to have negative effects on many existing ecosystems.

The working group strongly supported the view that although climate change is a matter of real concern, most of the ecosystems considered are at least as threatened in the short term by non-climate anthropogenic effects, and in the long term by combined effects of climate change and other anthropogenic stresses. A systematic effort to understand the nature of combined stresses and ecosystem responses was recommended as critical to improving both predictions and conservation or mitigation efforts, and the subgroups urged: 1) research into organism and ecosystem responses; and 2) an expanded program of monitoring and assessment to establish baselines against which to evaluate the causes and effects of future changes. Programmes of conservation and management, as exemplified by integrated coastal zone management programmes, were seen as important ways to enhance ecosystem resilience in responding to climate change by reducing other concurrent stresses.

The reports of the coral reef and mangrove subgroups were subsequently refined and expanded at a meeting of experts in Monaco, the results of which were reported by the Intergovernmental Oceanographic Commission (UNEP-IOC-WMO-IUCN Meeting of Experts on a Long-Term Global Monitoring System of Coastal and Near-Shore Phenomena Related to Climate Change, Pilot Projects on Mangroves and Coral Reefs, Monaco 9-13 December 1991. UNEP-IOC-WMO-IUCN/GCNSMS-II/3. IOC, Paris, 1992).

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1993

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Coral reef responses to climate change: issues and uncertainties

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Summary

Coral reefs as a class of communities have survived major climatic changes over geologic time, but individual reefs are often perceived as particularly sensitive to environmental change because they are restricted to a limited range of environments. Reefs and organisms respond to local environmental influences without regard to their ultimate cause. Because of substantial evidence that non-climate anthropogenic stresses are an important near-term threat to reef ecosystems and will interact with climatic effects, it is not realistic to attempt to assess climate change impacts in isolation.

Climatic effects are likely to be experienced primarily as a change in the frequency and magnitude of extreme events, while non-climate stresses are more likely to be chronic and act to modify reef recovery from acute stress. Climate factors of general importance are: sea level, with the predicted rise representing a moderately positive effect on global reef welfare; and temperature, an increase in which would increase the frequency of high temperature stress and mortality, but could also expand the geographic range of reefs. Other factors such as storm frequency and oceanic current changes will be important but locally variable, and are not at present predictable.

Changes in carbonate saturation state and ultraviolet radiation exposure are not climatic in a narrow sense, but are closely tied to aspects of the greenhouse effect; both may represent significant threats to reef ecosystems on a global scale, and the effects of both are poorly understood. Non-climate factors of importance are contamination (waste disposal), nutrient loading, resource exploitation, and land use (largely through changes in runoff and sedimentation).

Reefs in enclosed basins or in proximity to land masses are likely to be more vulnerable to environmental changes of all types, while oceanic reefs will be primarily responsive to climatic factors. Effective understanding and prediction of the climatic component of reef response to environmental change will require monitoring, assessment, and research across a wide range of time and space scales.

Introduction

Much of the material for this paper has been drawn from a more extensive review of the subject (Smith & Buddemeier, 1992). Information not otherwise attributed is based on that publication.

Because they are restricted to shallow waters and often occur in near-shore coastal environments, coral reefs can experience the effects of climatic or environmental change acting through the atmosphere or the marine or terrestrial environments. For this reason, many have considered the reef ecosystem particularly vulnerable to climate change. However, geological and palaeontological evidence suggests that reefs as a global phenomenon may be relatively resilient in the face of a greenhouse-induced climate change. Coral reef fauna of the western Indo-Pacific appear to have come through the Plio-Pleistocene period of sea-level and climate oscillations with only background rates of extinction; even in the more vulnerable western tropical Atlantic, a late Pliocene extinction pulse was followed by background extinction rates throughout the Pleistocene climate cycles (Paulay, 1991). Further, long-term studies indicate that marine faunal extinctions tend to be associated with episodes of refrigeration (Stanley, 1984), while warm periods of high sea level correspond to survival and radiation of species. Raup and Boyajian (1988) and Sheehan (1985) have demonstrated that reef fauna have been no more vulnerable to past extinction events than other marine communities. These observations are consistent with the work of contemporary ecologists who find that reef communities are tolerant of many types of disturbance (Grigg and Dollar, 1990; Brown and Howard, 1985), and may even be disturbance-adapted in the sense that episodic local destruction and renewal can act to maintain habitat diversity and biodiversity within the larger reef community system.

Although these observations are fundamental components of an assessment of probable reef response to global change, they do not provide a basis for assumptions that present and anticipated environmental changes offer no threats to coral reef systems. In fact, several conceptual and practical issues raise significant concerns. We will address these issues after first discussing the issues of climate and environmental change and the stresses these will impose on coral reef ecosystems. Throughout the discussion that follows we rely on the Intergovernmental Panel on Climate Change (IPCC) Business-as-usual scenario (Houghton *et al.*, 1990) for information on probable future climate change.

Environmental change and coral reef stress

Coral reefs and their constituent organisms respond to local environmental conditions without regard to their ultimate cause; because of this, and because climate change interacts with the physical and biotic environment to produce a variety of effects, we consider it artificial and potentially misleading to discuss narrowly defined climatic factors outside of the broader context of environmental change. Table 1 presents a list of the factors known to influence or control aspects of coral reef development or function, subdivided according to whether environmental changes over the next few decades are more likely to result from changing climate or from other anthropogenic environmental alterations.

Table 1. Dominant sources of near-term coral reef effects

Climate	Other
Sea level rise**	Ultraviolet light**
CO_2 changes**	Nutrients (*?)
Temperature change*	(Fresh water)
Current/storm change	Resource use
Visible light	Sedimentation
(Fresh water)	Toxics
	Turbidity

** global, trends monotonic
* trends in global mean monotonic, local behavior variable

The factors in Table 1 are arranged subjectively in very approximate order of their estimated near-term significance. Fresh water occurs in both columns because of the effects of anthropogenic land use in drainage basins as well possible climatic effects on the hydrologic cycle. "CO_2 changes" refers primarily to the reduction in carbonate mineral saturation states in the surface ocean that is expected to result from equilibration with elevated atmospheric CO_2 concentrations. Having identified these factors, we will briefly discuss some of the key issues involved in attempting to assess probable climate change effects before proceeding to a summary of expected impacts.

Issues in climate impact assessment

Interactions with non-climate environmental change - Population growth and economic development have resulted in local and regional environmental changes that have had direct and obvious detrimental effects on coral reefs (Wells, 1988). Changes caused by waste disposal, construction, deforestation, overfishing, and so on typically occur at rates at least an order of magnitude more rapidly than prompt greenhouse climate changes, and so can be readily identified over the time scale of direct reef observations by humans. There is a growing consensus in the coral reef research community that such changes, either alone or in combination with the climatic and truly global non-climatic changes (e.g., changes in ultraviolet light (UV) and carbonate saturation states), represent greater and more immediate threats to many reefs than do the actual or potential impacts of climate change (D'Elia *et al.*, 1991). These potential interactions greatly complicate the problem of predicting and monitoring climate effects. Climate and non-climate stresses may be indistinguishable in terms of effects, may mask one another, and may interact synergistically. Reefs in proximity to land masses and human population will be most sensitive to non-climate perturbations, and are likely to be the most valued and the most readily studied. On the other hand, proximity to land masses may also correlate with sensitivity to climate change effects because of the amplifying effects of the terrestrial system on changes in the hydrologic cycle and because of the effects of hydrographic changes (currents, wave energy) on coastal geomorphology, and sediment transport (Andrews & Pickard, 1990).

Problems of scale and baseline data - Coral reefs exhibit time constants of decades to centuries, and major developmental changes are largely responses to extreme events, as is true of many other ecosystems. These events may represent the natural variability of present climate and/or biological interactions, an altered climatic variability associated with the greenhouse effect, or the non-climatic impacts of human activities. Unfortunately, detailed human records of reef observation extend back scarcely more than 30 years in time, which does not provide us with an adequate statistical basis for assessing either "normal" frequencies of extreme events or "normal" responses to them. Similar problems exist with respect to spatial scale; although reefs have many similarities in terms of both structure (Huston, 1985) and metabolic function (Kinsey, 1985), their detailed characteristics are heterogeneous on a variety of spatial scales. This greatly complicates the problems of generalising from local observations and disaggregating the predicted effects of global change.

In assessing or predicting climatic effects we must be concerned not only with the nature, frequency, and magnitude of the extreme events, but also with the more subtle - and frequently non-climatic - factors controlling community response and recovery. It is well established, for example, that recovery from damage by storms, fresh water, or temperature stress may be profoundly influenced not only by the extent of the damage but also by such less readily observable factors as nutrient loading (Kinsey, 1988), and predator populations.

Specific versus generic reef survival - Global climate change concerns are often expressed in terms of biodiversity and extinctions at the global level, while conservation, assessment, and monitoring efforts focus on local reefs or regional assemblages of reefs. Although related, the two concerns are not equivalent. Large-scale ecological and geological discussions necessarily treat reef communities as a statistical phenomenon, and the observation that reefs have survived past climate changes applies to reefs as a class of community and to their constitutent organisms in terms of global genetic inventory. Practical human concerns, however, inevitably focus on contemporary reef distributions and characteristics, not on an abstract statistical ensemble. The fact that individual reefs are geologically transient and cannot be indefinitely preserved does not make change more palatable to humans, nor does it eliminate the real and legitimate concern that climate or other anthropogenic environmental change may result in the unnecessary or premature destruction or undesirable alteration of specific, valued reef communities.

Inequivalence of past and future climate change - It is generally considered that greenhouse-induced global temperature change will occur at rates one to two orders of magnitude faster than that caused by natural climate cycles (Houghton *et al.*, 1990); sea level rise, on the other hand, is unlikely to approach the peak rates sustained during the Holocene transgression (Fairbanks, 1988). Although we cannot absolutely prove that there has never been such rapid change in recent evolutionary history (MacCracken *et al.*, 1990), it is prudent to assume that the rates of change expected may place unprecedented stresses on reef communities. The generation times of many corals are on the order of decades to centuries (Potts & Garthwaite, 1991); community responses to change on the time scale of a single generation may be quite different from responses to similar changes spread over many generations.

There is less agreement on the relationship between past and future spatial climate distributions. A matter of particular concern is the future of sea-surface temperature (SST) in the tropics, because of the recognised sensitivity of many corals to temperatures only moderately above ambient. Paleoclimate studies indicate that at the time of the last interglacial (Eemian, 125 Ka BP), sea level was several meters higher than at present and the northern hemisphere was about 2°C warmer than at present (MacCracken *et al.*, 1990), but tropical SST values were comparable (± 1.5°C) to present values (Ruddiman, 1985). Climate models tend to produce predictions of tropical temperature increases in the range of 0-3°C for doubled CO_2, but both calibrations and agreements between models are poor in the marine tropics and there is uncertainty about our understanding of potential feedback and temperature limitation mechanisms (Ramanathan & Collins, 1991; Heymsfield & Miloshevich, 1991). The range of uncertainty is critical, since even a modest increase in SST could result in a substantial increase in the frequency of reef-damaging heat-stress events (Jokiel & Coles, 1990).

Climate, environmental change, and reef responses

In view of the foregoing, of the acknowledged uncertainty in regional climate change predictions, and of high reef biodiversity and community differences between reefs that are equivalent in gross structure and function, there are a limited number of useful generalisations that can be made about probable responses of coral reefs to climate change and their interactions with local conditions. It is important to note that much more specific assessments of vulnerability (and in some cases, actual predictions) can be made by detailed consideration of climate change predictions and reef or environmental characteristics on the local and regional scales. The points identified in this review and related papers (D'Elia *et al.*, 1991; Smith & Buddemeier, 1992) are in large part intended to guide and inform approaches to the essential local and regional assessments. Among the statements that can be made without reference to specific local conditions are:

1. The IPCC sea level rise (SLR) scenario predicts rates of change well within the range of reef accretion rates (Buddemeier & Smith, 1988) and considerably less than maximum Holocene transgression rates (Fairbanks, 1989). At these rates of increase, rising sea levels are likely to have a net positive effect by increasing coral recruitment and community calcification in both reef and non-reef environments where reef communities are limited by sea level (intertidal flats; Kinsey & Hopley, 1991; Hopley & Kinsey, 1988) or circulation (enclosed reef lagoons: Paulay, 1991; Smith & Jokiel, 1978). More rapid SLR, or a combination of the predicted rates with other environmental factors that inhibited reef growth or accretion, could result in gradual inundation (Buddemeier & Smith, 1988).

2. Temperature increases may have dual effects; latitudinal expansion of optimal ranges for coral communities will be a benefit, but temperature extremes are also the primary lethal limit of concern; increases of sea surface temperature (SST) or marine climate variability that result in more episodes of unusually high temperatures on reefs may be expected to increase the frequency of the type of coral bleaching and mortality events described by

Glynn (1989) as resulting from El Niño. It should be noted that the temperature sensitivity of corals appears to be relative to local conditions, that the absolute upper limit of adapted tolerance is not known , and that temperature adaptation clearly occurs, although rates are relatively slow and mechanisms are unknown (Jokiel & Coles, 1990). It is also noteworthy that bleaching (loss of symbiotic algae) is a generalised stress response and not uniquely diagnostic of high temperature.

3. Two potentially important factors are not strictly climatic in a narrow sense, but are probably best included in the broad approach to climate change because of their global scope and atmospheric origin. One of these is the decrease in carbonate saturation state caused by increased atmospheric and oceanic CO_2 concentrations, which may reduce the calcification potential of corals and coralline algae (Mackenzie & Agegian, 1989; Smith & Buddemeier, 1992). The other is the increase in UV exposure caused by stratospheric ozone depletion (Jokiel & York, 1984; Siebeck, 1988). Both have the potential for inhibition of reef development, but virtually nothing is known in a quantitative sense about their effects, individually or in combination with other stresses.

4. There is at present no basis for predicting changes in reproduction other than through the medium of organism morbidity or mortality; dispersal may be affected as a result of shifts in oceanic current patterns, which are not at present predictable (Andrews & Pickard, 1990). Increases in UV exposure may increase larval mortality, but data are insufficient to predict the probability or magnitude of the effect.

5. Our ability to identify and predict climate effects on reefs will improve as we integrate the results of monitoring both reefs and the physical and chemical environments over appropriate time and space scales with the improved climate model predictions now being developed.

Other factors, in particular the patterns and intensities of storms, precipitation, cloudiness, and ocean currents, are expected to be altered by climate change, but there is at present no reliable basis for the identification of net global effects. Additional points that are not climate-specific but are important considerations in terms of monitoring and the assessment of vulnerability and effects include:

6. Small-scale community structure and succession on reefs is notoriously variable and influenced by factors other than climate change (Connell, 1978; Grassle, 1973). However, major or sustained community shifts toward dominance by non-calcifying benthos or by bio eroders is of concern regardless of cause, and will ultimately impair the reef system's ability to keep up with rising sea level.

7. Reef community metabolism has been well characterised, particularly in terms of calcification within reef zones and relationships between gross and net production (Kinsey, 1991). Major metabolic changes, particularly toward lower calcification or increased net organic production, are indicative of shifts away from normal reef function.

Discussion and Conclusions

In the near term, the suggestion is strong that local and regional effects of population growth, land use, and so on will have more effect on reefs than the more widely distributed and gradual climatic changes. Reefs in proximity to land masses or in relatively shallow or enclosed basins will be particularly sensitive (or vulnerable) to the effects of environmental change, but will have a low specificity for climatic variables. Oceanic reefs are probably more sensitive to the truly climatic component of environmental change and could serve as control sites for studies in the more complex nearshore environment (D'Elia *et al.*, 1991).

The effect of climate change on reefs in general, or on specific reefs, is a small (at present) and noisy signal superimposed on a background of natural variability and the effects of local and regional non-climatic anthropogenic change. The climate signal will increase as time goes on, but background "noise" will almost certainly change as well. Detection of specifically climatic effects will require careful control for competing effects, observations over time and space scales larger than many are accustomed to, and consideration of the nature of climate and of coral reefs on a fundamental level (Buddemeier & Hopley, 1988). Specific environmental stress responses can be readily observed on a local and/or regional basis, but problems of scale, variability, and causation will continue to complicate interpretation and prediction.

There is no substitute for careful local and regional assessment of both climate change issues and other anthropogenic stresses, and this must be done on a continuing basis as our experience and understanding continue to increase.

The reef research and monitoring community must address the dilemma of apportioning resources between those reefs that are the most vulnerable and dynamic, but potentially incomprehensible because of environmental complexity, and those "cleaner" systems that can provide information on climate change responses but may be relatively trivial in terms of the dominant threats to coral reef systems at present. In the short term it seems clear that conservation efforts should be primarily focused on reefs threatened by local and regional anthropogenic stresses, but with the recognition that the balance of concern may shift as we learn more about the actual nature of climate change.

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Climate change and sea level rise impacts on mangrove ecosystems

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Abstract

Mangrove forests occur on low energy, sedimentary shorelines of the tropics and occupy an area of about 20 million hectares worldwide. Mangrove trees have special physiological and morphological adaptations to the environmental stresses of their intertidal habitat, of high salinity, low oxygen, poor nutrient availability and substrate mobility. The main impacts of climate change that can be expected to affect mangrove ecosystems are sea level rise and changes in precipitation, primarily through altered sediment budgets; as well as temperature rise and the direct effects of higher levels of atmospheric carbon dioxide changing productivity and ranges of species. These changes may alter the important functions of mangroves as sediment traps promoting vertical accretion and seaward progradation to maintain the quality of coastal waters; natural breakwaters protecting coastlines from erosion during storms; a natural resource base for silviculture and a large range of economic products; habitats for rare fauna; and nurseries for commercially valuable fish and crustacean species.

It is indicated from past analogues that their close relationship with sea level position renders mangrove swamps particularly vulnerable to disruption by future sea level rise consequent upon the enhanced greenhouse effect. Stratigraphy indicates that few large mangrove systems existed in the earlier Holocene, when rates of sea level rise were rapid, from 25 to 100 cm/ 100 years. Mangroves would have survived this period as disorganised, patchy individuals with dominant flushing of organic material away from their roots, as seen today on more exposed shorelines. As sea level stabilised in the mid-Holocene, large mangrove systems established in sheltered locations. These are indicated by peat and mud stratigraphy, large ecosystems trapping organic and allochthonous debris to build up substrate, allowing mangroves to keep up with slower sea level rise, generally less than 25 cm/ 100 years.

Stratigraphic records indicate that the rate of accretion of mangrove substrate is a function of geomorphic location. Mangroves of continental margins and high islands have higher rates of accretion and so can keep up with higher rates of sea level rise, owing to fluvial allochthonous sediment input. But low island mangroves with low accretion rates can only keep up with a sea level rise of up to 10 cm/100 years. Mangroves of low islands are shown to be already under stress where the rate of sea level rise exceeds the rate of accretion.

With respect to climate change, there is a correlation between mangrove distributions and areas where mean monthly water temperature of the warmest month exceeds 24°C, excepting locations too distant to be colonised by mangrove propagules. While most GCMs predict less warming around the equator relative to high latitudes, the predicted sea surface temperature increase of 1.5°C by 2025 can be expected to affect sub-tropical mangroves, resulting in increased diversity of higher latitude marginal mangroves, and some expansion of the latitudinal limits of mangroves into saltmarsh environments. Thermal stress affecting root structures and seedling establishment has been shown to occur in water temperatures above 35°C. Photosynthesis typically reaches an optimum in air temperatures below 35°C; above this rates sharply decline.

As well as affecting climate, increased CO_2 directly affects plant growth and development. Mangroves have a C_3 pathway of carbon fixation in photosynthesis, in which metabolic response to increased atmospheric CO_2 has been shown to be increased productivity, and more efficient water use due to reduced stomatal conductance. It is possible that reduced transpiration will cause changes in salt regulation, particularly in salt secreting species.

Furthermore, changes in frequency or intensity of hurricanes with climate change may have devastating local effects on mangroves. As a consequence of the impacts resulting from factors such as sea level rise, and changes in ecophysiology and community composition relative to climate change, mangroves may be prone to damage in lesser magnitude storms than previously. This scenario may extend to all natural and anthropogenic stresses: mangroves will become far more fragile as ecosystems, hence justifying stronger conservation measures and increased research and management activity.

1. Introduction

The findings of the WMO /UNEP Inter Governmental Panel on Climate Change (IPCC) concerning future climate changes are used as the basis for this review. The mechanisms involved in climate change and sea level rise, and the reasons for the wide range in predictions are not reviewed here. Summarising the IPCC findings (Bolin, 1991), there is presently a "greenhouse effect" of about 50% above pre-industrial levels, resulting from anthropogenic emissions of carbon dioxide (CO_2) and other trace gases. This is believed to have caused an estimated increase in mean equilibrium temperature of the earth's surface of 0.5-1.2°C, and additional warming of 0.8-2.0°C delayed owing to inertia of the climate system. As emissions continue, an equivalent of CO_2 doubling will be reached in about 40 years, by which time a mean equilibrium surface temperature increase of 1.5-4.5°C will have taken place. In the last 100 years there has been a rise of about 10 cm in eustatic sea level; the IPCC working group predicted a future sea level rise of 0.3-0.5 m by 2050, and 1 m by 2100 (IPCC, 1990). This would lead to mean rates of rise of between 50-90 cm/ 100 years over the next century.

The term "mangrove" is used to describe a taxonomically diverse group of woody angiosperms that grow in the intertidal zone of sheltered shores in the tropics. The extent of their cover has been estimated to be 240,000 km^2, fringing 75% of low lying tropical coastlines (Snedaker &

Getter, 1985). Adaptations to their saline wetland environment such as aerial roots, halophytic strategies and vivipary, distinguish mangrove trees as a specialised minority within their families (Hadac, 1976). Of the nine true mangrove families and 34 species described by Tomlinson (1986), each has a distribution centred on one of two areas, Indo-Malaya or Central America. The Indo-Malayan mangrove centre of diversity includes species that extend in their ranges westwards to East Africa and eastwards to the central Pacific. This species assemblage is considerably more diverse than that of the Central American assemblage, 26 species compared to eight (Tomlinson, 1986), this 3:1 disparity combined with fossil records suggesting a centre of origin of the mangrove habit in the S.E. Asia/ S.W. Pacific region, and subsequent spread to the Neotropics (Van Steenis, 1962; Chapman, 1975; Ellison, 1991).

Mangrove species show preference to particular elevations within the tidal range, as this generally controls salinity, groundwater availability, frequency of inundation and strength of wave action. This commonly results in zonation of species. Within their general requirement for sheltered sedimentary coastlines, mangroves occupy a variety of physiographic settings of deltas, estuaries and coastal lagoons (Thom, 1982), with heterogeneous conditions of river discharge, tidal and wave energy regimes and coastal morphology. A separate case are the mangroves of low islands. With no sources of sediment from fluvial or along-shore sources, they accumulate autochthonous sediment on top of reef flats (Woodroffe, 1987).

The importance of mangrove ecosystems is well established, as sediment traps to clear coastal waters of suspended sediment and promote vertical accretion and seaward progradation of the mangrove margin. In addition these provide a natural breakwater to protect coastlines from erosion during storms; a natural resource base for silviculture and a large range of economic products; habitats for rare fauna, and nurseries for commercially valuable fish and crustacean species. These are described in detail by Chapman (1976), Christensen (1983), Salm and Clark (1984), Hamilton and Snedaker (1984) and Tomlinson (1986).

The main impacts of climate change that can be expected to affect mangrove ecosystems and species are sea level rise, temperature rise, changes in precipitation, and changes in frequency or intensity of hurricanes, as well as changes in productivity caused by higher levels of atmospheric carbon dioxide. To date, there has been very little research that directly addresses these issues. These changes will occur in combination with each other as well as with stresses on mangrove communities consequent from sharing the tropical coastal zone with the majority of the world's human population. As stated by IUCN (1989), mangroves are today one of the most threatened of the world's natural communities, as they share lowland coastal areas with large, high density human populations.

Research techniques for investigating these issues fall into three areas. First, impacts of alteration of a climatic parameter on a particular species or physiological system can be studied in isolation from other environmental parameters under controlled conditions. This gives useful data, but problems occur in combining changes to indicate system response. Second, climate change effects on an ecosystem can be reconstructed from the past, provided the evidence is available from proxy indicators. This technique has the advantage of indicating complex system response, though detail of responses to individual components of change can usually only be speculated. Third, climate change effects in combination with other variables can be modelled, based on data obtained from the above techniques. As with all environmental research, it is best to operate all techniques to obtain a broadly based consensus. This review of the present state of knowledge is not exhaustive, but indicates the paucity of knowledge despite the obvious impacts on mangroves of changes in environmental variables.

The possible impacts of climate change on mangroves are reviewed on the basis of the findings of relevant research primarily concerned with the investigation of individual environmental parameters. Since mangrove species are limited to specific ranges within the tidal spectrum, the impacts of sea level rise can be expected to be the most important of all sources of climatic change. The impacts of sea level rise on mangroves have been investigated by reconstruction of mangrove response to past sea level change, and monitoring of present system response.

2. Climate change

At the global scale, mangrove distribution is controlled by temperature; the dispersal abilities of propagules; and ocean currents. At the regional scale, rainfall conditions control the type and diversity of zonation.

2.1 Climate warming

Mangrove ecosystem development occurs only when the average air temperature of the coldest month is higher than 20°C, and where the seasonal range does not exceed 10°C (Walsh, 1974; Chapman, 1975, 1977). There is a reasonable correlation between mangrove limits, the 16°C isotherm for air temperature of the coldest month, and the margins of incidence of ground frost. With respect to water temperature, Barth (1982) has shown a correlation between mangrove distributions and areas where water temperature of the warmest month exceeds exceeds 24°C, with limits where temperatures never exceed 24°C. There are exceptions where warm currents extend from the tropics into the subtropics bringing both warmer water and a supply of colonising mangrove propagules.

Simple comparison of the ranges of mangrove species (Chapman, 1976) relative to annual sea surface temperature (Levitus, 1982) indicates variability between and within mangrove species limits. In America, the *Rhizophora mangle* limit corresponds with the 24°C isotherm in north Florida but the 27°C isotherm on the east coast of S. America. The limit of *Rhizophora racemosa* is at 27°C in the north but 24°C in the south. The limit of *Avicennia germinans* is at the 24°C isotherm in Florida but at 20°C in S. America and California. In Asia, to the north and south the limit of *Rhizophora apiculata* is at the 27.5°C isotherm, *R. mucronata* at the 26°C isotherm and *R. stylosa* is at the 26°C isotherm. The limit of *Avicennia marina* is at 16°C in New Zealand and Australia but at 22°C in S.E. Africa and China. The limit of *Avicennia alba* is at 26°C in Australia and SE Asia but at 28°C in India. The limit of *Sonneratia alba* is at 26°C in SE Africa and Australia, 27°C in the N. Indian Ocean and 28°C in SE Africa. These differences indicate that various factors act in combination to limit mangrove species, such as sea surface temperature, air temperature, incidence of ground frost and aridity.

In the Caribbean, Hanson and Maul (1989) in their assessment of climate change impacts utilised an expected sea surface temperature increase of 1.5°C by 2025. In the Caribbean and other regions this can be expected to cause increased diversity of higher latitude marginal mangroves, expansion of *Rhizophora* species into mangrove margins only occupied by *Avicennia* species, and expansion of the ranges of mangroves into saltmarsh environments. However, the heterogeneity of regional sea surface temperature limits of mangrove species ranges would indicate regional differences in mangrove response. Variable gradients of sea surface isotherms mean that, for example, the expansion of range in south eastern USA will be less than that in SE Australia or SE Africa.

Table 1 compiles data available on mangrove litter production from different locations, indicating a range between 5 and 10 t^{1} ha^{-1} yr^{-1}, with variation due to latitude, species of mangrove, and topographic situation: fringe, basin, delta, etc. If a warmer climate combined with higher ambient CO_2 levels (discussed in section 3.0.) increases mangrove productivity, then increased growth and litter production can be expected to occur at all locations.

While coral reefs exhibit an upper thermal limit through coral bleaching (Williams & Bunkley-Williams, 1990), mangroves are unlikely to reach such a limit with the predicted increase in temperature. Responses of mangroves to thermal stress have been shown from areas of waste heat pollution (Banus, 1983), where water temperatures in excess of 35°C affected roots of *Rhizophora mangle*, with many rotted off at high tide level, and others become more slender and more numerous. Diversity of invertebrate root communities was much reduced, and seedling establishment prevented. Laboratory experiments showed seedling survival in temperatures of up to 35°C, and seedling death over 38°C. The upper thermal limits of mangrove associates have been shown by Kolehmainen *et al.* (1973) as being 37°C for blue green algae and barnacles; 36.5°C for tree oysters; 36°C for sponges; and 34.5°C for tunicates, bryozoans, polychaetes, mangrove oysters, and green, brown and red algae. Lugo and Snedaker (1974) and Canoy (1975) showed that in temperature stressed conditions, *Rhizophora mangle* produced more numerous but smaller leaves. Macmillan (1971) showed inhibition of rooting of *Avicennia germinans* propagules at 37°C, with 48 hour exposure to 39-40°C causing death of rooted but stemless seedlings, but not of rooted seedlings with stems.

With respect to air temperatures, mangrove photosynthesis has an optimum below 35°C (Clough *et al.*, 1982). Moore *et al.* (1972, 1973) showed for *Rhizophora mangle* in Florida that optimal temperatures for photosynthesis were below 35°C, with little or no photosynthesis occurring above 40°C. Hence, there is possibly a thermal limit for mangroves at 38°C (100°F), above which carbon assimilation through photosynthesis is limited. Such conditions may be reached in drier localities where humidity does not moderate temperatures. Moore *et al.* (1973) show sizeable seasonal shifts in the photosynthetic and transpirational behaviour of *Rhizophora mangle* in south Florida, with less marked changes in *Avicennia germinans* and *Laguncularia racemosa*. This indicates that *Rhizophora* may be more susceptible to temperature changes than the other two species.

Temperature affects photosynthetic rates, but also water balance through stomatal opening and transpiration, and salt uptake and loss. Hence climate change effects should be considered in combination with precipitation changes, and the direct effects of raising of ambient CO_2 concentrations.

Table 1.
Mangrove litter production v. latitude

Source	**Location**	**Species**	**Litter (t^{-1} ha^{-1} yr^{-1})**
Woodroffe & Moss, 1984	7°S, Tuvalu	*Rhizophora stylosa*	7.8
Christensen, 1978	8°N; Phuket Is. Thailand	*Rhizophora apiculata*	6.7
Leach & Burgin, 1985	9°S, PNG	*Rhizophora stylosa*	14.3
Woodroffe *et al.*, 1988	12°S, NT, Australia	*Avicennia marina*	14.0
		Ceriops/Bruguiera	7.5
		Ceriops tagal (tall)	6.9
		Ceriops tagal (low)	3.0
Day *et al.*, 1987	18°40'N, Mexico	*Rhizophora mangle*	8.3
		Avicennia germinans	12.5
Lee, 1989	18°N, Hong Kong	*Kandelia candel*	11.1
Duke, Bunt & Williams, 1981	18°S, Queensland, Australia	*Rhizophora apiculata*	10.9
		Bruguiera parviflora	10.0
		Rhizophora stylosa	9.3
		Rhizophora lamarkii	8.7
		Avicennia sp.	8.0
		Bruguiera gymnorhiza	8.0
		Sonneratia alba	7.9
		Ceriops tagal	7.2
Flores-Verdugo *et al.*, 1987	23°N, Mexico	*Laguncularia racemosa*	11.0
Odum & Heald 1975	25°N, S. Florida	*Rhizophora mangle*	7.3
Twilley *et al.*, 1986	25°N, S. Florida	*Rhizophora mangle*	7.5
		Avicennia germinans	
		Laguncularia racemosa	
		Avicennia germinans	4.7-5.4
	26°N, S. Florida	*Rhizophora mangle*	8.7
		Avicennia germinans	
		Laguncularia racemosa	
		Avicennia germinans	3.5
Pool, Lugo & Snedaker, 1975	25°N, S. Florida	*Rhizophora mangle*	7.7
Teas, 1979	26°N, S. Florida	*Rhizophora mangle*	1.3-10.7
		Laguncularia racemosa	
		Avicennia germinans	2.9
Lugo & Snedaker, 1974	26°N, S. Florida	*Avicennia germinans*	6.5
Love, 1981	33°51'S, Sydney	*Avicennia marina*	6.8
	34°S, Sydney	*Avicennia marina*	7.0
Goulter & Allaway, 1979	34°S, NSW	*Avicennia marina*	5.8
Woodroffe, 1982	36°48'S, Tuff Crater NZ	*Avicennia marina* (tall)	8.1
		Avicennia marina (low)	3.7
Clough & Attiwill, 1982	38°S, Victoria	*Avicennia marina*	1.6

2.2 Precipitation changes

The combined effects of precipitation regime and temperature on mangrove distributions has been analysed by Blasco (1984), utilising the ratio of mean annual rainfall (P) to potential evapotranspiration (Etp) after Penman. It was found that:

1). Over 90% of the world's mangroves are found in warm humid regions, where P/Etp>0.75, the temperature of the coldest month (tm) exceeds 10°C, and the average of the warmest month exceeds 20°C. The conditions occur from south Mexico to Colombia, in the Caribbean, north Brazil, and from SE Asia to north Queensland (Australia).

2). Mangroves are occasionally found in sub-humid climates, where 0.5<P/Etp<0.75, such as East Africa, India, south Queensland (Australia), Mexico and Venezuela.

3). Mangroves are rarely found in semi-arid conditions, where 0.2<P/Etp<0.5, and then usually only close to major river mouths, such as the Indus Delta (Pakistan), Gujarat (India), the Western and Northern Territory provinces of Australia, and Ecuador.

4). Mangroves are practically unknown in arid climates, where 0.03<P/Etp<0.2, except where there are winter rains, such as the Ethiopian and Egyptian coastlines of the Red Sea, the Persian Gulf and the Gulf of California.

In equatorial and tropical summer rainfall regions (1) mangroves are tall, dense and floristically diverse. In subtropical dry regions (3) mangroves are low, scattered and sporadic. Areas of higher coastal rainfall and high riverine inputs of freshwater tend to support more diverse communities of mangroves than areas of low coastal rainfall and limited runoff. This is shown in Australia, where at 20°S there are four species on the drier west coast and 20 species on the wetter east coast (Tomlinson, 1986). On the Queensland coast, tallest forests of mangroves with complete cover and five distinct zones occur where mean annual rainfall is over 1500 mm and distributed throughout the year. Where rainfall is less than 1500 mm and seasonal, mangroves are shorter, with gaps, landward zones can be taken over by halophytic herbs and naked salt flats and the seaward zones are narrower (Macnae, 1966).

The various General Circulation Models (GCMs) for increased CO_2 all predict substantial changes in precipitation with global warming. Some GCM models suggest that precipitation may be enhanced by 5-20% in low latitude areas where rainfall is already heavy, but may be reduced in today's semi-arid regions. However, models are presently unable to simulate such regional effects of changing water balance (Commonwealth Group of Experts, 1989). Decreased rainfall and increased evaporation can be expected to reduce the extent of mangrove areas, particularly with loss of the landward zone to unvegetated hypersaline flats. The number of mangrove zones and the diversity of these can be expected to decrease, and growth rates decline. In conditions of increased rainfall the extent of mangrove areas can be expected to increase, with colonisation of previously unvegetated areas of the landward fringe. The diversity of mangrove zones and growth rates should increase.

The reasons for these patterns relate to salt stress. Under humid conditions, mangrove soils are almost continuously leached by heavy rains, and fresh water is available from river discharge and groundwater outflow, which provides nutrients. Under arid conditions, evaporation from the intertidal mangroves at low tide leads to high concentrations of salt, and can result in unvegetated hypersaline flats around high tide level. Increase in salinity in mangroves leading to salt stress can result from sea level rise, groundwater depletion owing to reduced hydraulic gradient and groundwater extraction, as well as reduced rainfall. The nature and effects of salinity stress are discussed more fully in Section 4.3.

2.3 Storms

Modelling studies suggest an increase in the intensity of tropical hurricanes by 40-60% (Emanuel, 1987), and increased frequency (Shapiro, 1988), as a result of increasing sea-surface temperatures. The effects of storms on mangroves can be roughly classified as minor (some defoliation), severe (partial destruction of the mangrove ecosystem) and destructive (almost all mangrove trees killed) (Blasco, 1984). Studies have been largely observational.

Storm destruction of mangroves has been recorded in Florida by Davis (1940) in the hurricanes of 1926, 1929 and 1935. Craighead (1971) reviewed the devastating effects of hurricanes on the Florida mangroves in 1935, 1960 and 1965, when large areas were destroyed. Severe hurricanes have been affecting Florida throughout the Holocene (Davis *et al.*, 1989), and the Everglades could have become a hurricane dependant ecosystem, relying on storms for the maintenance of diversity and fresh water input by rainfall and runoff (Vogl, 1980). Venkatesan (1966) described the effects of the November 1952 cyclone on the mangroves of the Cauvery in south India, where a surge caused the Muthupet and Chattram forests to be submerged by 2 m for a fortnight. As a result of this, *Avicennia* was killed over large areas. In February 1990 Cyclone Ofa in Tutuila, American Samoa killed four acres of 16 m tall *Bruguiera gymnorrhiza* at Aoa on the east shore, and some 10 acres at Masefau on the north shore. Trees remained standing but were defoliated and the above ground pneumatophores were buried in sediment.

Mangroves may be prone to damage in lesser magnitude storms than previously owing to their action in combination with sea level rise and changes in ecophysiology and community composition with climate change.

3.0 Increased CO_2

As well as its climate effects, CO_2 directly affects plant growth and development. Most work on the possible impacts of enhanced CO_2 levels has been done on agricultural plants, less on natural vegetation, and very little on mangroves. Mangroves have a C3 pathway of carbon fixation in photosynthesis (Clough *et al.*, 1982), where metabolic responses to increased atmospheric CO_2 have been shown to be increased productivity and more efficient water use due to reduced stomatal conductance (Warrick *et al.*, 1987). Clough *et al.*, (1982) reported experimental results of the effects of CO_2 partial pressure on assimilation in *Avicennia* and *Rhizophora apiculata*, where a CO_2 compensation point was reached at around 60 ppm at 25°C, and proportional increase in assimilation occurred with internal CO_2 partial pressure until well above the atmospheric rate. This indicates that increasing levels of ambient CO_2 can be expected to increase the productivity of mangroves.

Shugart *et al.* (1986) discuss the different scales of response, and the cumulative effects of increased CO_2 levels on forests. Fast responses occur in the leaf environment involving exchanges of water, heat and CO_2 during photosynthesis, respiration and transpiration. Cumulative effects affecting the growth rate of the tree as the product of photosynthetic production involve intermediate responses such as altered width of a tree ring. This can be affected by competition, pests and herbivores. Cumulative stress at this scale leads to long-term responses such as changes in geographical extent as a product of senescence in unsuitable conditions and successful germination in suitable conditions. It should be noted that with increasing unsuitability of conditions, death events can appear to be sudden, when a small change acts as "the final straw" for the disadvantaged ecosystem.

Reekie and Bazzaz (1989) studied effects of elevated CO_2 on five Mexican rainforest species, finding that the greatest effect was on species competition, in that changes in growth patterns changed the competition for light. In predicting the effects of increased CO_2 levels on mangrove ecosystems, one is faced with a huge problem from lack of data, as is the case for all other ecosystems (Shugart *et al.*, 1986). Data available is from short-term, small scale experiments on leaves and individual plants, leading to problems scaling up to ecosystem response over decades. Clearly, more experimental and modelling work is needed.

4.0 Sea level rise

Growing in the upper half of the tidal range, their close relationship with sea level renders mangrove swamps particularly vulnerable to disruption by sea level rise (Ellison & Stoddart, 1991). Mangrove species have different preferences of elevation, salinity and frequency of inundation, resulting in species zones. Substrate elevation can be increased under mangroves, by accumulation of vegetative detritus to form a mangrove peat, or by mud containing allochthonous matter brought in by the tides and by rivers.

4.1 Past analogues

The accumulation of peat or mud under mangroves gives the mangrove substrate some ability to keep up with rising sea level. Indications of rates of accretion are available from studies that have used mangrove peat or mud as a former sea level indicator. Peat extracted from different depths in coastal sediment cores is dated using isotopic techniques. Detailed work on mangrove stratigraphy of low, limestone islands has been carried out on Bermuda, Grand Cayman, Cayman Islands, and Tongatapu, Tonga. Studies of mangrove and deltaic stratigraphy of high Pacific islands have been carried out on Viti Levu (Fiji), Western Samoa and on Pohnpei and Kosrae (Caroline Islands). The results of these studies are summarised in Table 2, and detailed analysis of all sites except Bermuda is given in Ellison and Stoddart (1991). Mangrove stratigraphy on continental margins has been investigated in Florida and northern Australia.

Table 2.
Rates of mangrove peat accretion (from Ellison and Stoddart, 1991)

Location (source)	**Rate of accretion (cm/100 years)**	**Location (source)**	**Rate of accretion (cm/100 years)**
High islands		Low islands	
Fiji		Tongatapu	
(Southern, 1986)	11.7	(Ellison, 1989)	7.7
(Matsushima, *et al.*, 1984)	7.6		
(Latham, 1979)	13.1	Grand Cayman	
		(Woodroffe, 1981)	8.8-9.0
Caroline Islands			
(Ward, 1988)	13.4-14.0	Bermuda	
(Matsumoto, *et al.*, 1986)	13.7	(Ellison, 1993)	8.5-10.6
(Bloom, 1970)	3.0		
Samoa			
(Matsushima, *et al.*, 1984)	9.9-10.5		
(Bloom, 1980)	18.8		
(Ellison, unpublished)	15.2-40.0		

Stratigraphy indicates that few large mangrove systems existed in the earlier Holocene when rates of sea level rise were rapid, from 25 to 100 cm/100 years. Mangroves would have survived this period as disorganised, patchy individuals with dominant flushing of organic material away from their roots, as seen today on more exposed shorelines. As sea level stabilised in the mid-Holocene, large mangrove systems became established in sheltered locations. These are indicated by mangrove peat and mud deposits, large ecosystems trap organic and allochthonous debris to build up substrate, allowing mangroves to keep up with slower sea level rise, generally less than 25 cm/100 years.

Data on Holocene mangrove stratigraphy exists from three low island locations. In Grand Cayman, Woodroffe (1981) found an accretion rate of 8.8 cm/100 years over the last 3,000 years, and in Bermuda, Ellison (1993) found an accretion rate of 8.5-10.6 cm/100 years over the same period. In Tongatapu, Ellison (1989) found an accretion rate of a 7.7 cm/100 years through a mid-Holocene mangrove peat. Each of these developed during conditions of slowly rising sea level, of less than 12 cm/100 years. These types of mangrove systems have limited allochthonous sediment input since low islands lack rivers, and peat buildup is from organic production of the mangrove trees. The data from these three sites indicates that the rate at which this peat accumulation can occur is remarkably constant, in the range of 8-11 cm/ 100 years.

On high islands such as Viti Levu and Lakeba, Fiji, and Kosrae, Caroline Islands sediment supply has been accelerated by anthropogenically enhanced rates of soil erosion inland. This gives the rapid sediment accumulation rates recorded in Table 2. These cases indicate that the dominant process affecting mangroves of high islands and continental coasts may be input of terrestrial sediment such that the effects of sea level rise are lessened. Because of the allochthonous component in these sediments, mangrove substrates are accreting at a faster rate than the peats of low limestone islands, up to 25 cm/100 years.

These stratigraphic records indicate that the rate of accretion of mangrove substrate is a function of geomorphic location. Mangroves of continental margins and high islands have higher rates of accretion and so can keep up with higher rates of sea level rise, owing to fluvial allochthonous sediment input. But low island mangroves with low accretion rates can only keep up with a sea level rise of up to 11 cm/100 years. Mangroves of low islands can be considered to be already under stress from sea level rise as mean global rates this century are 10-12 cm/100 years (Gornitz *et al.*, 1982). It is clear that low islands are the most vulnerable to loss of mangrove ecosystems during sea level rise, but all mangroves will be severely threatened by the rates of sea level rise projected for the future.

The reasons for this apparent inability of mangroves to keep up with higher rates of sea level rise is not apparent from these past analogues. Some problems are demonstrated by mangrove dieback in Bermuda, a low island with a long tide gauge record of relatively rapid sea level rise (Ellison, 1993).

4.2 Erosion

Bermuda is a low limestone island without rivers, and the most northerly location for mangroves. Tide gauge records since 1932 show sea level rise at a rate of 28±18 cm/100 years (Pirazzoli, 1986). The largest mangrove area (6.26 acres) at Hungry Bay has for the last 2000 years been building peat at a rate of 8.5 to 10.6 cm/100 years (Ellison, 1993). The rate of sea level rise has exceeded the rate of sediment accretion, leading to retreat of the seaward margin accompanied by erosion. The substrate elevation of the seaward margin of mangroves is below mean sea level, the normal lower limit for mangroves. Retreat of the seaward edge has caused loss of 2.24 acres of mangroves, commencing in the last few hundred years, with a second dieback between 1900 and 1947, and a third dieback in the last decade. Stratigraphy shows that before 4000 BP sea level rose at a rate of 25 cm/100 years, from 4000 to 1000 BP the rate of sea level rise declined to 6 cm/100 years during which time mangroves established, and in the last 1,000 years there was an increase to 14.3 cm/100 years, during which time the mangroves died back.

It is shown from Bermuda that mangrove sediment is subject to erosion with rising sea level, with removal of mangrove substrate (above MSL) and with some deposition subtidally offshore of the mangroves (Ellison, 1993). This corresponds with the Bruun Rule of beach erosion with sea level rise (Bruun, 1962; Schwartz, 1967). Sheet erosion occurs at the peat surface, indicated by a 20 to 25 cm difference between the peat level above a small cliff, and the former peat surface as indicated by exposed horizontal roots of *Avicennia*. Then, as trees recede and loosen the sediment, more rapid erosion occurs to form a 40-50 cm small cliff. Such erosion enhances the existing problem, for as the mangrove substrate surface is lowered and creeks widen, the problem of the differential between elevation and MSL increases.

Similar erosion patterns have been described by Semeniuk (1980) in NW Australia, identifying reversed succession as elevation declines. The effect of sheet erosion on mangrove zonation was migration of pioneer/ seaward mangroves into more landward zones. The effect of cliffing on mangrove zonation was loss of the seaward zone, leading to truncated zonation and narrow fringes. The effect of tidal creek erosion was slumping of banks and loss of trees.

There is evidence of cliff erosion at the seaward edge of mangroves from the N. Caribbean, Woodroffe (1981) describes from Little Sound, Grand Cayman shelly mud depositing over mangrove peat in water depths of 10-200 cm, and the adjacent mangrove fringe fronted by a scarp of peat 30-200 cm high. The regional pattern is of sea level rise in excess of 20 cm/100 years (Pirazzoli, 1989), but the local tide gauge has too short a record to confirm this interpretation.

Erosion of mangrove substrate would seem to be a major problem under conditions of sea level rise. It is indicated that the Bruun Rule of beach erosion with sea level rise is also appropriate for mangrove swamps, and may occur earlier owing to the finer texture of the sediment.

4.3 Increased salinity

Increase in salinity in mangroves leading to salt stress can result from a number of factors: sea level rise, groundwater depletion owing to reduced freshwater flux, groundwater extraction, and reduced rainfall. Two major physiological adaptations enable mangrove survival in saline ocean water (Scholander *et al.*, 1962): salt exclusion in species of *Rhizophora* and *Laguncularia*, and salt excretion in species of *Aegialitis* and *Aegiceras*. Salt excluders not only operate ultrafiltration, but also cease or diminish transpiration and photosynthesis when exposed to saline water. Salt secretors can continue photosynthesis utilising ocean water in transpiration, owing to salt glands in the leaves.

Stern and Voight (1959) grew 200 seedlings of *Rhizophora mangle* under different salinities, and found that seedling survival and growth as measured by increase in dry weight and seedling height were all inversely related to salt concentrations of the growing solutions. Ball and Farquhar (1984a) studied gas exchange characteristics in *Aegiceras corniculatum* and *Avicennia marina* under different salinity and humidity conditions. They showed decreased photosynthetic capacity with increase of salinity, with *Aegiceras* being the more sensitive. Ball and Farquhar (1984b) studied the gas exchange characteristics of *Avicennia marina* with increasing salinity, finding that CO_2 assimilation rate, stomatal conductance, intercellular CO_2 concentration and evaporation rate all decreased. Increased salinity has the effect of decreasing net primary productivity to result in reduced growth, with a differential effect on species, indicating stress and changing competition between mangrove species during the climate change consequences of reduced precipitation and sea level rise.

The shallow water table of southern Florida is susceptible to saline intrusion from sea level rise and groundwater extraction owing to low topography and porous rock. Alexander (1974) and Alexander and Crook (1974) described landward encroachment of mangroves into grasslands and cypress swamps from evidence of pine stumps in a salt water mangrove area of Key Largo. Sternberg and Swart (1987) used isotopic measurements of plant stem water to determine relative ocean water and fresh water utilisation in plants, and showed that mangroves can range from utilisation of fresh to ocean water, indicating plasticity in the salt-tolerant physiological system. This would indicate that mangroves gain a competitive edge over faster growing glycophylic plants in conditions of increasing salinity.

4.4 Inundation

Impoundment of mangroves for mosquito control provides an analogy to the effects of increased inundation. Harrington and Harrington (1982) recorded extensive death of *Avicennia germinans* and *Rhizophora mangle* at India River, eastern Florida following four months of 30-45 cm depth of flooding of an impoundment. Flooding was sudden inundation, then sustained over the period. The natural tidal range in this area is 10-20 cm (Lahmann, 1988).

Naidoo (1983) found that prolonged flooding resulted in lower leaf water potentials; an increase in stomatal closing; and degeneration of chloroplasts in *Bruguiera gymnorrhiza*, leading to reduced rates of photosynthesis. When lenticels of aerial roots become inundated, oxygen concentrations in the plant fall dramatically (Scholander, 1955). If inundation is sustained, anoxic conditions and mortalities follow. This is thought to have been the cause of widespread mortality of *Avicennia germinans* stands in Puerto Rico recorded by Jimenez *et al.* (1985), following permanent flooding as a consequence of adjacent dredging.

Lahmann (1988) found that rates of litterfall in an impounded mangrove forest in Florida were reduced relative to natural fringe forest during flooded months. This indicates that the above ground net productivity of *Rhizophora mangle* is reduced by flooding, though phenology was not changed. Survival of *Avicennia germinans* and *Laguncularia racemosa* seedlings was prevented over several years of flooding, and *Rhizophora mangle* became more common, despite its poor seedling establishment during flooded periods. The depth of flooding was not indicated.

5.0 Human responses, policy and monitoring

Monitoring activities in mangrove ecosystems are suggested that will greatly assist in the identification of problems resulting from climate change and sea level rise as they start to occur, and will help decision making concerned with active management strategies.

5.1 Tide gauges

The understanding and prediction of global sea level trends is only possible through a coordinated system of tide gauges, such as the Global Sea Level Observing System (GLOSS) of the Intergovernmental Oceanographic Commission, or the National Oceanic and Atmospheric Administration (NOAA) network. The establishment of such tide gauges in areas with mangroves should be supported, as this will allow trends in local sea level that may cause problems to mangrove ecosystems to be identified.

5.2 Mapping and compiling information

Mangrove areas should be mapped and remapped periodically to show the location of different mangrove zones and the seaward and landward extent of the mangrove area. Older records from the mangrove area should be compiled into a database. Large scale colour air photographs should be taken. Information on the history of sites should be compiled from climate records, previous studies and records of logging or other activities. This enables climate change impacts to be distinguished from other changes underway.

5.3 Elevations

It is critical to determine elevation of the mangrove substrate with respect to absolute datum to allow surveys to be related to records of the nearest tide gauge. Such topographic surveys will indicate the preferred elevations of different mangrove species, which will be of use should replanting become necessary with sea level rise. Such surveys could also be used to identify areas low in the tidal spectrum which may already be experiencing erosion problems. A permanent benchmark should be established close to each mangrove area, to which different surveys can be related for comparison.

5.4 Litter fall and sedimentation rates

Sedimentation rates within the mangrove ecosystem should be monitored, as sediment accumulation is the natural process by which mangrove substrates can keep pace with sea level rise. Litter fall should be quantified (see Brown, 1984) as is being established in the Caribbean by CARICOMP (1991) in a programme using low technology standard techniques to monitor productivity. Substrate sedimentation can be most easily monitored by use of inserted pegs (see Spenceley, 1982), though a standard methodology for this needs to be established.

5.5 Genetic resource centres

Owing to the destruction of habitats by man, extinctions of species have caused erosion of the genetic diversity of natural forests. Nature reserves have been established to preserve a fragment of the natural vegetation. One of the principal concerns of ecologists regarding the effects of climate change is that these designated reserves may no longer have the appropriate climate. This will necessitate planned replanting as forests cannot migrate naturally between these effective habitat islands, and may result in further extinctions of species (Schneider, 1989).

This is not a major problem for mangrove forests as, owing to their coastal habitat and water dispersed propagules, they can colonise at a rate faster than the 25-2000 m yr^1 for temperate dry forest species (Huntley & Birks, 1983). It is possible however that mangrove species may face threat of extinction from loss of habitat in conditions of rapid sea level rise. At a workshop in Madras in January 1991 a project was formulated to establish a global network of mangrove genetic resource centres in response to the threat of mangrove loss from sea level rise. This is to be centred at the M. S. Swaminathan Centre for Research on Sustainable Agricultural and Rural Development in Madras (Deshmukh & Mahalingham, 1991). Four more sites have been selected in 1992, three in Asia and Oceania and one in West Africa. This initiative is sponsored by the International Tropical Timber Organisation with financial support from the Japanese Government.

5.6 Research and communication

Sea level position is central to the functional ecology of a mangrove swamp. Rise in sea level will perturb every aspect of the ecosystem and, combined with effects of climate change, stresses from storms and human disturbances, the world's mangroves are likely to face severe disruption in the next few decades. Effective understanding and management of these problems requires an applied direction among the different mangrove scientists, and communication between scientists and with those responsible for the conservation and sustainable utilisation of mangrove forests. Effects of climate change and rise in sea level will also vary between mangroves in different parts of the world and in different physiographic locations, owing to such factors as productivity, species composition and sediment supply. Here also, communication between management personnel of different countries will allow separation and analysis of problems of local and regional scale.

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Impacts of climate change in estuary and delta environments

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Summary

Coastal ecosystems stand to be drastically impacted as a result of global climate warming. Increasing carbon dioxide concentration in the atmosphere will probably result in elevated temperatures, global sea level rise, alteration of local and regional hydrologic regimes, and increased frequency and magnitude tropical storms. Anthropogenic impacts associated with coastal development will have an important synergistic effect by amplifying relative sea level rise and possibly intensifying coastal erosion. Predictions of coastal responses to global warming remain very speculative. However, case studies provide some indications as to how global climate change will be manifested in coastal areas. For example, two temperate coastal sites in South Carolina, USA, an estuarine complex (North Inlet) and a deltaic complex (Santee River) have experienced impacts as the result of natural (hurricane) and anthropogenic (river diversion) disturbances, respectively. We contend that these two sites can serve as models for probable impacts of a warmer climate. Both sites are undergoing relative sea level rise at a rate of 0.3 m/century, and have experienced striking ecological change as a result of the disturbances. The coastal environments are migrating landward and bringing about shifts in marginal vegetation and fauna. In each instance, the coastal ecosystem changes are made more pronounced because of local development along the landward margins, which hinders the natural inland migration of the ecosystem and results in enhanced stress and local impact. Thus, humans foreclose on the options of natural coastal change and response. Systematic monitoring, comparative analyses and interpretation, and modelling need to be implemented worldwide in order to understand how impacts in coastal areas are linked to global climate change and to provide more accurate predictions of future change.

Global warming manifestations

Coastal ecosystems exist as a thin rim around the continents of the globe with widths in the order of kilometers. They constitute the borders between continental and marine systems, and like other boundary systems, they exhibit great variability in environmental parameters. To extract the effects or trends of a changing global climate in a noisy system with multiple highly variable signals is by no means an easy task. Unfortunately, Global Climate Models (GCMs) are generally far too crude in space and time to resolve and predict accurately climatic change and its impact on coastal systems. GCMs lack detailed agreement and differ in the handling of cloud cover and type. In addition, dynamic bi-directional feedbacks between ocean and atmosphere are still not an integral component of existing GCMs. Change scenarios in coastal systems and expected impacts related to global climate change remain speculative, since pertinent long-term time series of data are unavailable and existing data sets frequently contain so many signals of variable magnitude and frequency that global climate-related trends are statistically insignificant. The global population has in the past century increased from less than two to almost six billion people. Future population increases are forecast to continue to be concentrated in coastal areas. On the local scale, it is usually quite difficult to distinguish between climate-related change and the responses due to direct or local anthropogenic impact.

The main reason for predicting climatic warming is that re-radiated energy from the earth's surface will be trapped more efficiently by the increased concentration of greenhouse gases in the earth's atmosphere. These gases include carbon dioxide, methane, nitrous oxides, and chloro-fluorocarbons. Atmospheric carbon dioxide has been studied most intensively, and its concentration is known to have increased from 280 ppm in 1880 to 350 ppm in 1990, primarily in response to anthropogenic burning of fossil fuels. According to most estimates, the efficiency of the greenhouse gases to trap re-radiated energy will double within the next 50-100 years and in all likelihood bring about an average global temperature increase of 1.5-3.0°C.

Although global warming seems to be an unequivocal fact during the next century, many uncertainties remain regarding the magnitudes and effects of climatic change. Whereas average climatic warming appears likely to result in increases of 1.5-3.0°C during the next century, local temperatures could either be significantly higher or lower by several degrees, as indicated by numerical GCM simulations (Houghton *et al*., 1990). Large spatial differences in temperature exist from model region to model region, illustrating the danger in appraising climatic change on the basis of an average global temperature increase. During the past century, the average global surface temperature, including the oceans, has apparently increased 0.5°C. The reasons for the increase could, however, be explained equally well by a temperature rebound following the end of the Little Ice Age (1400-1880) or a temperature rise resulting from the anthropogenic burning of fossil fuels (Stewart *et al.*, 1990).

As with other coastal systems, identifying the impacts of climatic warming on estuaries, deltas, and marine wetlands, is largely speculative. Climatic change will manifest itself in coastal and estuarine areas in several ways in addition to increases in atmospheric CO_2 concentration and global temperature. Of the potential changes, the rise in eustatic sea level has received the most attention. However, the rate of relative sea level change is highly variable. Impacts often are more closely related to anthropogenic use of the coastal zone subsequent to pumping of groundwater, damming of rivers, and coastal construction. In addition to sea level change, local and regional hydrologic regimes, including rainfall, runoff, evapotranspiration, net radiation, and water and soil salinities, are likely to change in coastal areas and adjacent watersheds. Cloudiness will increase with climate warming but predictability of cloud cover, type of clouds, and precipitation patterns is not tractable at the moment. Further, predicting even the tendency of local change is difficult since it is likely to vary significantly on a regional basis.

Climatic warming does not mean that sea level will rise everywhere. Although a rise in sea level will result from the melting of small and large glaciers, significant melting of the ice sheets is not expected to occur. During the past century, global sea level rose approximately 0.15 m (Stewart *et al.*, 1990). Although predictions of global sea level rise as high as 4.5 m have been published (EPA), the best estimates of global sea level rise in the next 100 years range from 0.6 to 1.0 m. However, large variations will occur locally because of variability in rates of tectonic uplift or subsidence in addition to eustatic and local changes in sea level.

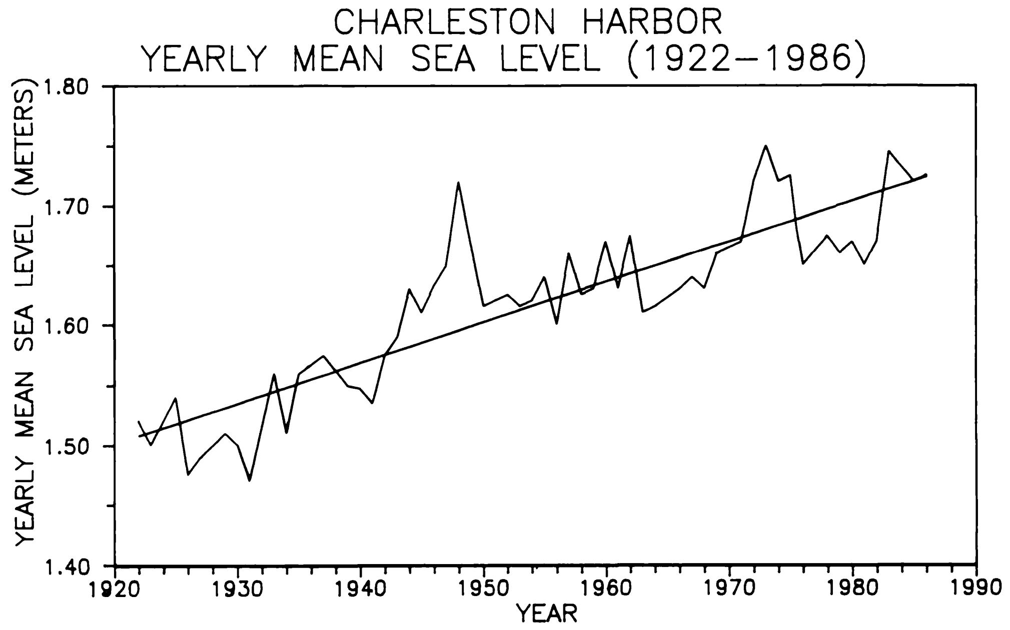
Reasons for relative sea level change

The combined effect of vertical land and sea level variations locally is referred to as *relative sea level change*. The relative sea level rise in Charleston, South Carolina, is shown in Figure 1. The vertical change in water level locally is related to climatic warming effects through (a) melting of small glaciers and ice sheets; (b) steric change in ocean water volume due to an increase in the temperature of the upper ocean; (c) water level changes induced by changes in ocean wind and pressure fields; (d) water level changes induced by changes in the oceanic circulation; and (e) changes in regional hydrologic processes. Although effects (a) and (b) are largely eustatic, effects (c), (d), and (e) are highly variable from coast to coast. The variations in land level are due to (a) isostatic rebound; (b) warping of continental margins; (c) slight deepening of the ocean basins; (d) extraction of ground water or hydrocarbons; and (e) changes in sedimentation patterns (Stewart *et al.*, 1990; Kjerfve, 1991).

Anthropogenic effects result from the pumping of ground water and hydrocarbons as well as changes in sedimentation patterns due to dam construction, coastal development and related activities. Most anthropogenic activities on the coast result in a decrease in land elevation and thus accelerate relative sea level rise. Many forms of coastal construction result in establishment of fixed boundaries in the form of roads, walls, houses, dikes, ditches and so on at short distances from the shore. As local sea level continues to rise, erosion and other local impacts will be aggravated as the width of the coastal zone decreases. Coastal development restricts the natural evolution of coastal buffer systems, and as a result, long-term impacts could be locally severe.

In addition to these water-land effects, the center of gravity of the earth is likely to shift slightly as high latitude ice is transformed into a water mass which spreads towards lower latitudes. As a result the geopotential surfaces, which represent the plane of absolute vertical reference, will be readjusted with unforeseen consequences for tides and oceanic circulation patterns.

Figure 1.
Relative sea level change in Charleston, South Carolina, 1922-1986, showing the variability in sea level from year to year. The average local rate of sea level rise of 34 cm/century is more than twice the rate of eustatic sea level rise.



Whereas the eustatic change in sea level measures 0.15 m over the past 100 years, and is expected to reach 0.60-1.00 m in the next 100 years, the relative local sea level change may be significantly greater. For example, Bangkok, a major city with a population of 8 million, situated in the delta of the Chao Phrya River is experiencing a dramatic rise in sea level of 4.5 m/100 years (since 1960), largely as a result of groundwater pumping and deltaic subsidence. At the other end of the spectrum, most of Scandinavia is experiencing continued isostatic rebound and the relative sea level is falling at a rate of 1.5 m/100 years.

In addition to groundwater removal and changes in sedimentation rates and patterns, another interesting example of anthropogenic sea level change effect relates to the construction of river dams and reservoirs. These, in effect, represent a removal of water from the oceans. According to Chao (1991), there were 10,000 reservoirs with a total volume of 5,000 km^3 in 1972. By 1991, the storage volume had increased to 10,000 km^3. The net change translates into a decrease in sea level of 0.07 m/100 years or an annual equivalent offset of half of the eustatic sea level rise (Chao, 1991). As the reservoirs fill with sediment at least half of the water stored in them will spill into the oceans, thereby adding to the rate of eustatic sea level rise.

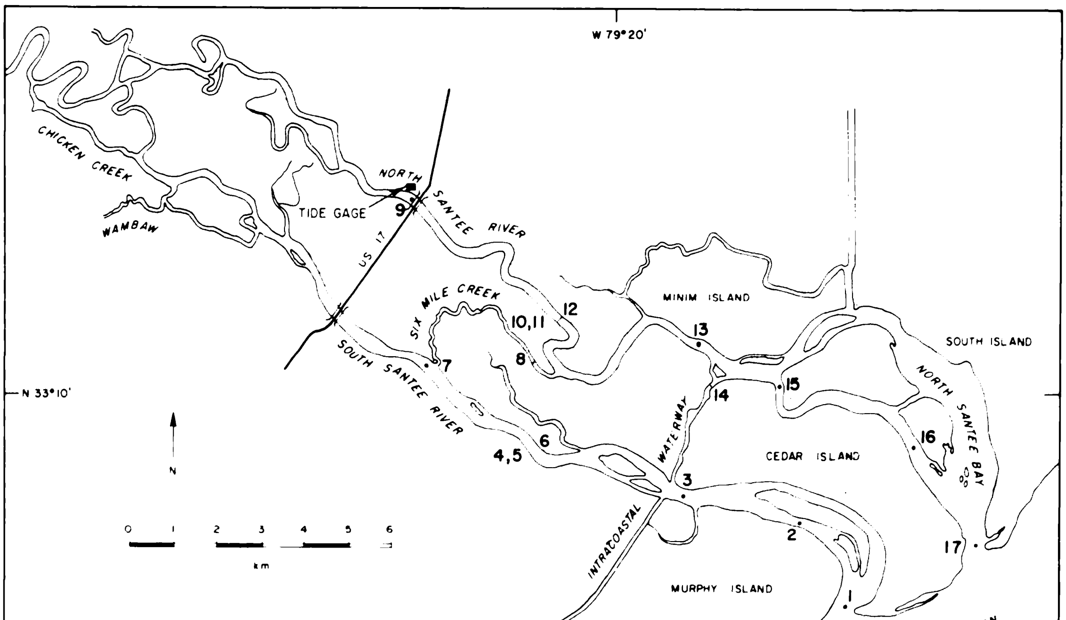
Clearly, while eustatic sea level change is expected to increase with climatic warming, it is not going to be easy to focus exclusively on this global signal in view of the often much larger signals associated with local sea, land, and anthropogenic effects.

Flow diversions in the Santee River delta

The probable impacts resulting from rising sea level can effectively be studied in coastal systems subjected to large water diversion projects. Significant lowering of freshwater discharge in a river system is approximately equivalent to a higher sea level stand during times of warmer climate. One such example is the delta of the Santee River, South Carolina, USA (Figure 2) (cf. Kjerfve, 1976). The Santee River systems drains a 41,000 km^2 basin and had until 1941 the fourth largest freshwater discharge on the US east coast with an average annual discharge of 560 m^3 s^{-1}. However, as a part of public projects in the 1930s, a decision was made to dam the Santee River (17 dams actually exist today) and divert the freshwater flow into Charleston Harbor, SC. In addition to providing jobs, the reason for the diversion was to take advantage of the physiography of the terrain to generate hydro-power. As a result, the Santee discharge averaged only 60 m^3 s^{-1} from 1942 to 1985, when a new water project restored the Santee discharge to approximately 400 m^3 s^{-1}.

Figure 2.

Map of the lower Santee River, South Carolina, between North Inlet and Charleston.
The entire wetland inland of the ocean barriers were covered with freshwater cypress stands and marshes prior to the 1942 diversion. *Spartina* and other salt-tolerant grasses now dominate the vegetation as far inland as the US 17 bridge. Since rediversion was completed in 1985, the Santee River is again receiving more freshwater discharge and vegetation changes can be expected to occur. The numers indicate hydrographic sampling locations in the Santee.



Conditions and changes in the delta during the years with below average low flow resemble in many respects the effects that may occur in the delta during times of rising sea level. The effects included substantial coastal erosion of marginal delta barriers and a significant retreat of the marginal delta flanks. The increased salinity within the delta caused a shift in vegetation. Extensive cypress forests started to die as the soil salinity increased, and the freshwater dominated vegetation was overtaken by the saltmarsh cord grass *Spartina alterniflora*. As the water salinity increased within the delta environments, productive oyster populations (*Crassostrea virginica*) in the adjacent delta waterways started dying off. However, experimental introduction of hard clams (*Mercenaria*) within the lower delta met with success, and are yielding commercial production.

Hurricane impact in the North Inlet Estuary - saltmarsh system

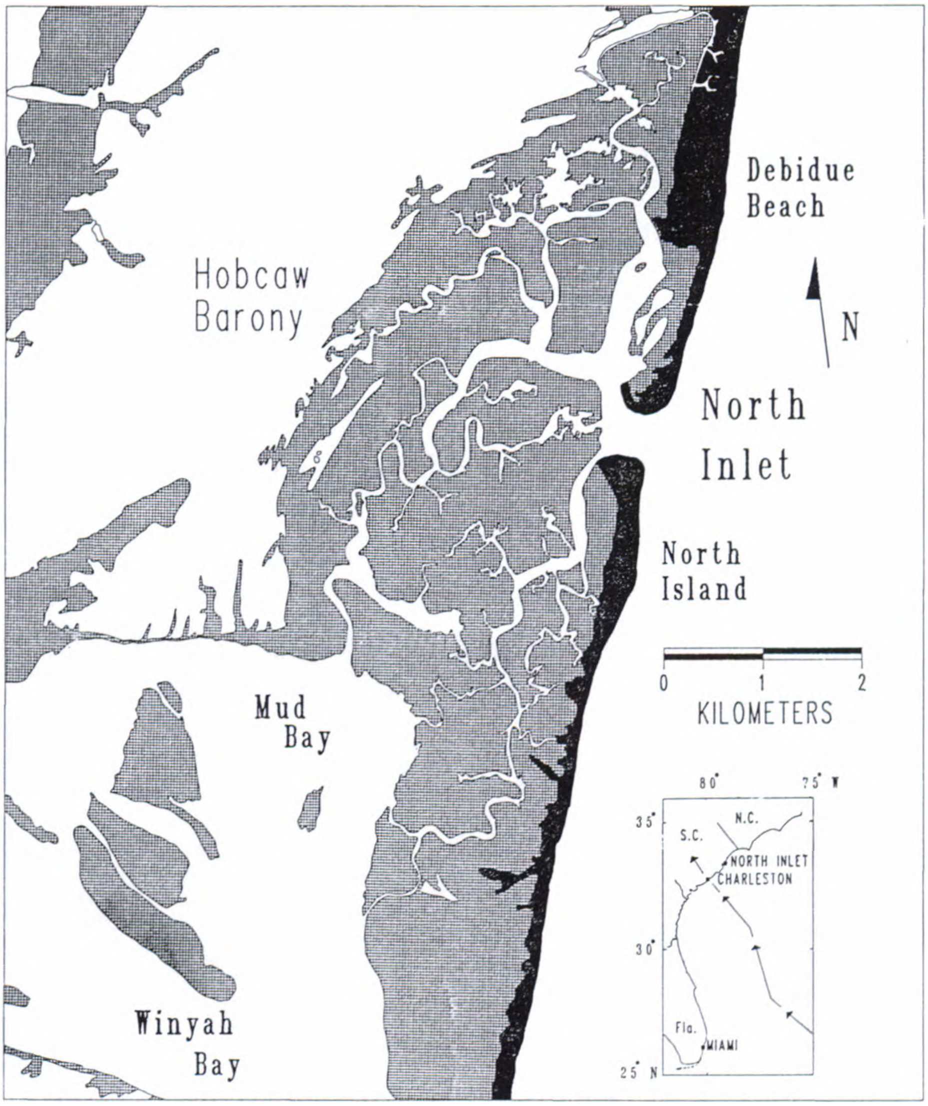
The Long-Term Ecological Research (LTER) program in the USA, sponsored by the National Science Foundation since 1979, links 18 ecological research sites in a network of research activities. The research focuses on ecosystems and regional and global-scale processes and is designed to identify and explain long-term variability and trends. Two coastal sites, the North Inlet estuarine saltmarsh system in South Carolina and the Virginia barrier island-lagoon complex, are designated as LTER sites.

The coastal landscape at the North Inlet (Figure 3) site represents a dynamic environment that has evolved during a regime of slowly rising sea level and recurrent natural disturbances (drought, tropical storms, forest fires) (Gardner & Bohn, 1980). Although, relatively pristine, man has nevertheless altered the natural coastal landscape through forestry management practices, development of barrier islands, and urbanisation of saltmarshes and estuaries. Furthermore, the landward migration of the coastal landscape under a regime of rising sea level has been restricted by the building of bulkheads, dikes, channels and roads.

Hurricane Hugo (Figure 4) made landfall near Charleston, SC, 70 km southwest of the North Inlet LTER site (33°N, 79°W) in September 1989. Hurricane Hugo provided a unique opportunity to observe and test hypotheses about how a coastal landscape responds to a major system-wide perturbation. The resulting impact on the barrier island-saltmarsh-maritime forest ecosystem can effectively be likened to impacts which may occur as the global climate warms, and the frequency and intensity of tropical storms increase. We assume that the North Inlet estuarine complex can serve as a representative model for soft-bottom, temperate coastal environments in a warmer climatic state.

Hurricane Hugo was a category 4 storm, as was Hurricane Hazel in 1959, and one of 25 hurricanes and tropical storms that have made landfall in South Carolina during this century (Gardner *et al.*, 1991; in press). Hugo was the most costly storm in US history in terms of physical damage, having caused damages totalling $6 billion mostly in property, agricultural, and forest losses (Sparks, 1991). Unlike other recent storms, Hurricane Hugo made landfall at high tide, causing extensive marine flooding along the coast but was accompanied by only limited rainfall.

Figure 3.
Map of the North Inlet, South Carolina, LTER site relative to the track of Hurricane Hugo. The barrier island fronting the ocean is shown in black and indicates the location of numerous storm-induced current and past washover fans extending into the *Spartina* saltmarsh (dark grey).

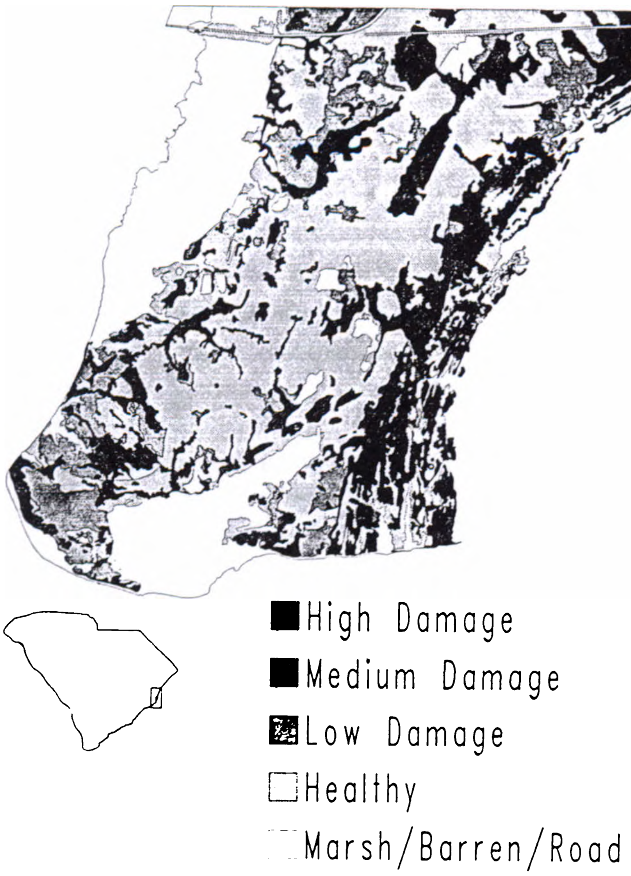


Generally, the saltmarsh ecosystem demonstrated its resilience to the storm disturbance, and primary and secondary production patterns observed prior to Hugo remained unchanged or were quickly reestablished after Hugo. However, the physical structure of the larger coastal landscape including the maritime forest was significantly altered. Whereas Hurricane Hugo did only minor damage to the barrier beach and saltmarsh environments (Gardner *et al.*, 1991), the damage to the adjacent maritime forest (Figure 5) constituted a major impact due both to the initial damage by winds, and also the slower destruction of vegetation associated with increased soil salinities (Gardner *et al.*, in press). Heavy damage occurred in areas ranging in size from a few trees to 500,000 m^2. Based on aerial photo and satellite image analyses, it was shown that 45% of the North Inlet maritime forest was severely damaged by Hugo, of which 8% was directly attributable to the storm surge and subsequent die-off due to salt stress (Michener *et al.*, 1991). Above normal salt concentrations were found in shallow groundwater samples from sites up to 3 m above mean sea level. At the time of the storm surge, water table elevations in swales were high and most of the saltwater infiltrated ridge soils. Subsequent rainfall events led to downslope movement of saline water and corresponding increases in sodium concentrations observed in swale groundwater. Within one year of Hugo, the sodium concentration had decreased by one order of magnitude but the chronic stress on the vegetation and die-off of trees continues.

Large numbers of birds were killed at North Inlet during Hurricane Hugo, and important colonial waterbird and shorebird nesting islands were heavily eroded (Marsh & Wilkerson, 1991). The most dramatic effect was the significant decline in white ibises nesting on Pumpkinseed Island (Shepard *et al.*, in press), related to the alteration of critical habitat for this species. Freshwater impoundments along the coast were either breached or inundated with saltwater. These habitats serve as the primary source of crawfish, which are essential components of juvenile white ibis diets.

Figure 4.
NOAA satellite image of Hurricane Hugo making landfall just north of Charleston, South Carolina, on 22 September 1989.

Figure 5.
Distribution of extent and magnitude of forest damage by Hurricane Hugo (September 1989) on the coastal landscape at the North Inlet LTER site in South Carolina.
The map is based on change detection in low-altitude color infrared photographs in February 1990 compared to 1989, and processed and displayed using Arc/Info geographical information system (GIS).



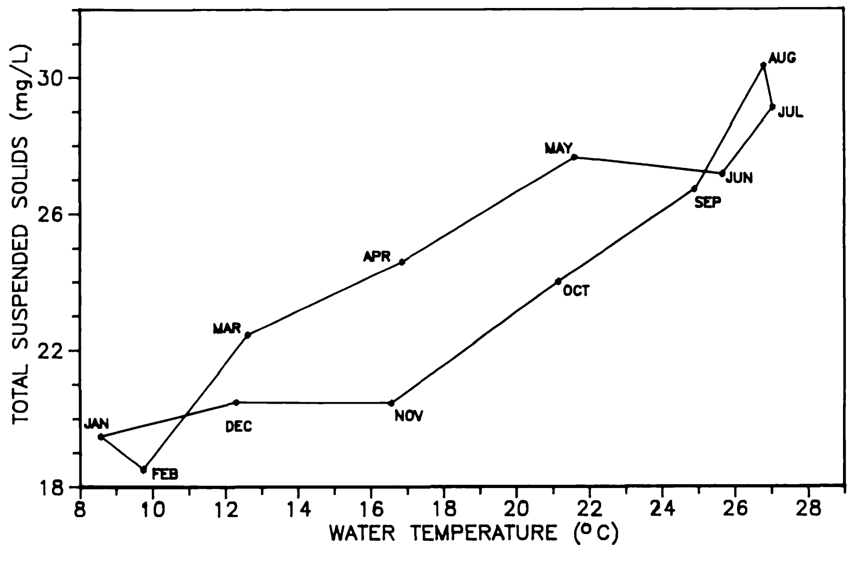
Some ecological responses to climate warming

Coastal productivity is a key integrating factor in assessing the local impact of climate change on estuarine and delta systems. Rising relative sea level is likely to result in increases in both primary and secondary production (Morris *et al.*, 1990; Bradley *et al.*, 1990) at least on time-scales of coastal ecosystem adjustment. This scenario is likely, because *Spartina* production during the past decade as well as shrimp and menhaden landings along the South Carolina coast, 1920-1985, are positively correlated to sea level anomalies (i.e. the relative sea level change minus the long-term trend), which explain as much as 20% of the variability (Morris *et al.*, 1990). At present, the North Inlet marsh is inundated 14% of the time but when the relative sea level has risen 20 cm, the inundation time of the marsh will be doubled. However, at some point a critical threshold is reached and systems with primary production dominated by macrophytes are likely to become dominated by phytoplankton as the ratio of open water to marsh increases. This change from macrophyte to phytoplankton-dominated production may be accelerated in areas where bulkheading, diking, and development has restricted the extent to which saltmarshes and mangroves can migrate inland and upslope.

The direct impact of temperature increase may not appear important, but when coupled with changes in the hydrologic cycle, can bring about drastic changes. The combined effect of temperature and hydrology produces drought years or wet years. In the Southeastern USA, 20-25% of all months during the past 100 years have been drought periods, typically lasting from 1.5 to 7 years (Michener *et al.*, 1990). For example, 1986 was a particular severe drought year in South Carolina with 83 days having maximum temperatures in excess of 32.2°C as compared to an average 49 days during non-drought years. State river flows measured only 50% of the long-term average discharges, resulting in much higher salinities and inland extension of the estuarine zone. In response to the increased temperature and salinity, oyster spat settlement in the North Inlet saltmarsh was impaired, resulting in high mortality and low larval recruitment (Michener *et al.*, 1990).

Temperature can also affect water turbidity. The turbidity in North Inlet varies significantly with the seasons, exhibiting high total suspended solids concentrations of 30-40 mgl^{-1} in the summer and winter lows around 5 mgl^{-1} (Figure 6). With a warming climate, the turbidity can be expected to increase in all seasons, as the North Inlet turbidity is largely due to bioturbation in the estuary and adjacent marsh (Gardner *et al.,* 1989). As water temperature increases in response to climatic warming, the season of intense bioturbation will expand, thus raising the annual average turbidity in North Inlet. Any early spring increase, in particular, could affect the benthic algal and phytoplankton production by lowering the estuarine light intensity and penetration and thus decreasing primary production.

Figure 6.
Monthly distribution of total suspended sediment concentration data 1981-1986 as a function of water temperature at the North Inlet LTER water sampling site near the entrance to the estuary. Higher temperature implies more bioturbation and higher suspended sediment concentrations.



Tropical storm and disturbance impacts

As the sea surface temperature (SST) increases, a much larger area in the tropics and subtropics, will experience temperatures above 26°C. Twenty-six degrees Celsius is a prerequisite for tropical storm formation. Thus, as the global climate warms, conditions for tropical storm and hurricane-typhoon formation become favourable over a much expanded area of the globe. We are likely to experience:

* increased frequency of tropical storms;
* increased storm intensity;
* increased duration of the annual storm season; and
* expanded domain where tropical storms form and propagate.

It could well be that areas that presently do not experience tropical storms and hurricanes, such as tropical South Atlantic, would become storm prone. Although the changes related to tropical storms are rather speculative, they are likely to be one source of major impact resulting from global climate change.

When the increased threat of tropical storms is coupled with an increase in relative sea level and a larger coastal population, the synergism among the various effects is likely to result in major impacts. Climate change in coastal areas in general, including estuaries and deltas, is most likely to be manifested in a series of catastrophic events or episodic perturbations during storm or flooding events. As an example, the April 1991 catastrophic cyclone which made landfall near Chitagong, Bangladesh, caused dikes to collapse and lowlands to flood, and resulted in a human death toll of at least 150,000 but maybe as many as 300,000 persons. It may well be that the recent category 5 "killer storms" in the tropical north Atlantic, Hurricane Allen in 1980 and Hurricane Gilbert in 1988, signify the increased frequency and occurrence of "monster storms". Certainly, the detailed study of impacts associated with tropical storms on coastal areas can give a realistic view of impacts to be expected. We need to ask not just what coastal change will be in response to climate change , but also how it will occur. The "how" may be the important question as it probably will determine the magnitude of the impact.

One of the most striking features of natural ecosystems is their ability to recover from catastrophic disturbances. Man has, however, by creating roads, bulkheads, dikes, ditches, and by land use practices, altered the coastal landscape, restricting the extent to which disturbances can propagate through marine wetlands and deltas. The abiotic and biotic environment, which serves as the template and source of materials necessary for ecosystem recovery, have been significantly modified and impacted by man's activities via eutrophication of inland and coastal waters, dredging and filling of waterways and wetlands, extraction of ground water, sediment starvation through construction of dams, introduction of exotic species, and so on. The extent to which man has altered the disturbance regime and the coastal landscape's ability to recover from disturbances remains unresolved.

Conclusions and recommendations for priority research needs

Impacts on estuaries and deltas as a result of global climate change will vary greatly on a regional basis. Climate change signals in coastal environments are characterised by low-frequency, small amplitude variability against a backdrop of high-frequency, large amplitude environmental variability. Increases in frequency and magnitude of tropical storms will be associated with global climate change and are likely to have significant impacts on coastal ecosystems.

The synergistic effect between global climate change and direct anthropogenic impacts could cause a much greater overall change than the sum of the individual effects. There is a need to pose better hypotheses related to synergistic coupling between climatic and anthropogenic processes and how they will impact coastal ecosystems. For example, demographic shifts to coastal areas and continued coastal development will have a tremendous future impact by causing increased rates of relative sea level rise in many localities, inducing eutrophication events, speeding coastal erosion, and bringing about general coastal degradation. Distinguishing the impacts directly related to global climate change is not an easy task.

Some of the priority needs for investigations in coastal areas to assess the effects and impacts of global climate change on coastal ecosystems include:

* comparison of regional-scale patterns of relative sea level change and rates of sedimentation and erosion;

* applying appropriate coastal ocean-atmosphere-land models to assist in understanding processes and forecasting impacts associated with global climate warming;

* assessment of changes in regional hydrology in coastal areas and adjacent watersheds related to climate warming through monitoring, analysis, and modelling;

* analysis of how climate change is manifested as well as the rate of climate-related change (e.g. catastrophic impacts by tropical storms, eutrophication events, etc.);

* development of focused and coordinated regional comparative studies to collect, analyse, and synthesise existing data to identify regional and global trends.

Acknowledgements

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Examples of the geological past: evolution of coastal sedimentation sequences during Holocene sea level rise

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Abstract

Future sea level rise caused by the greenhouse effect may have an important impact on the coastal wetlands of the world. A much discussed subject is the the expected changes in the ecology of these wetlands. During the recent geological past, the Holocene, the types of sediment deposited under various rates of relative sea level rise are known through investigations of buried deposits in various coastal basins. These studies of the past may contribute to a better understanding of the changes of the shoreline, the backswamp and its ecology which may occur under future rapid sea level rise as predicted by the greenhouse effect.

In this contribution four examples of coastal basin developing under various rates of past relative sea level changes and sediment input are discussed. The main conclusion is that intertidal conditions can only develop when relative sea level rise and sediment input are in balance.

Introduction

An increasing body of evidence suggests that in the coming decades global warming due to the greenhouse effect may lead to a substantial rise in sea level. There is a controversy about the extent of future sea level rise that can be expected in the coming century. Hofman *et al.* (1983) give an estimate between 56 and 358 cm, Robin (1986) calculated the future rise in sea level as being between 20 and 140 cm and Warrick and Oerlemans (1990) suggested a rise of between 31 and 110 cm with a best estimate of 66 cm. The last mentioned estimate is that in the report of Working Group I of the Intergovernmental Panel on Climate Change (Houghton *et al.*, 1990).

These differences in the various estimates are due to the uncertainties concerning the input to the models. Robin (1986) expressed this problem as follows: "*With our lack of knowledge of the hydrological cycle and the dynamics of the oceans and the polar ice sheets, forecasting global changes of sea level involves considerable extrapolation and speculation.*"

The future rise in sea level would have its most severe effects in low lying coastal regions, deltas, estuaries and riverplains. About half of the worlds' population live in these coastal lowlands, and they are zones of intense economic and agriculture activity. Future sea level rise will have serious impacts on the socio economics of these areas and on the remaining natural wetlands.

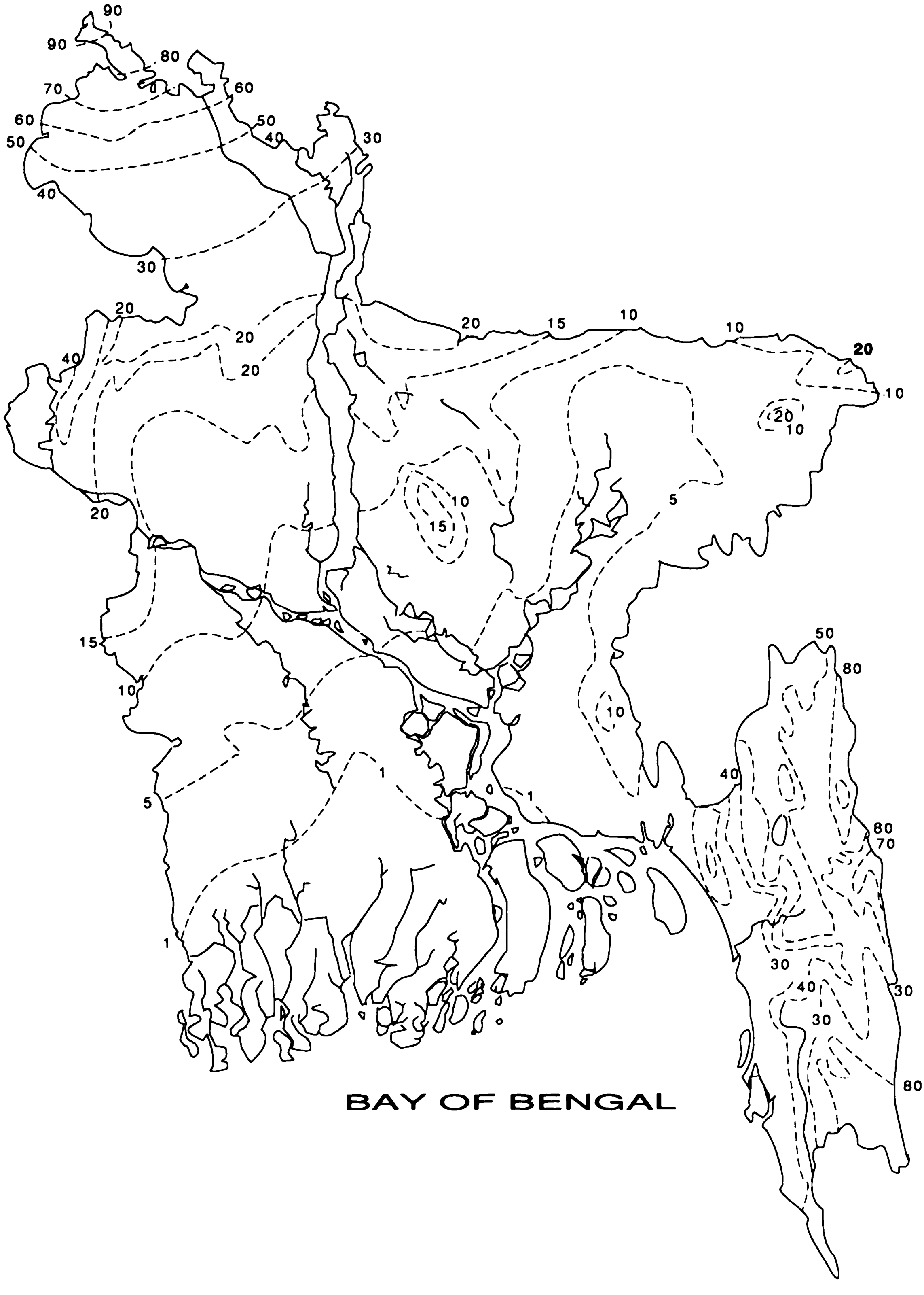
Even without a future sea level rise most coastal wetlands are already endangered habitats owing to human interference. Pollution, land reclamation and human alterations in shoreline processes all pose serious threats to existing wetlands. Even more serious is the decrease in supply of sediments to wetlands caused by the construction of dams and reservoirs for hydropower and irrigation. The best known example is the Nile Delta. After the construction of the High Aswan dam the sediment supply to the delta was reduced to zero. Most deltas in the world are eroding, mainly due to serious sediment reduction caused by the construction of dams and reservoirs. The economic benefit of these constructions for irrigated agriculture, water resource management, electricity generation and flood control are important but the coastal wetlands are being lost.

There is a lively discussion among ecologists about the changes in morphology in coastal wetlands which may result from future sea level rise. The intertidal flats, the humid tropical mangroves and, at higher latitudes, the saltmarshes are of great importance as fish nurseries and for resident and migratory bird populations. The important question is: can the vertical sedimentation on those intertidal flats keep up with sea level rise? If this is not the case a change to subtidal flats will occur resulting in open water. Another question is whether and how sea level rise will move the various salt and brackish water environments landwards. It should be stated that these future changes in the coastal morphology are highly dependent on the rate of sedimentation which is governed by the input of sediments; by catchment area; by the action of the sea; and by the magnitude of the tidal range which redistribute sediments and; the trapping of sediments such as occurs in the mangrove root system. It is evident that these changes are locally and regional highly variable.

Some investigations which attempt to forecast future shoreline position following sea level rise ignore the fact that vertical sedimentation actually takes place during sea level rise. This approach indicates areas to be lost by a rise of sea level of one, two or three meters (Milliman *et al.*, 1989) as demonstrated in figure 1. The same method has been used in the case studies presented by the Coastal Zone Management Subgroup of the Intergovernmental Panel on Climate Change (1992). This "bath-tub" approach to future sea level rise ignores the rules of sedimentary processes and gives a doomsday picture to people in the areas concerned.

Another approach to forecasting changes in morphology and shoreline position is to study the effects of post glacial sea level rise in coastal lowlands. The deposits related to this important period of sea level rise are present in the shallow subsurface layers of the coastal plains. The types of sediment under various rates of relative sea level rise can be studied by geological investigations in these coastal plains. The recognition of these sedimentary environments in the geological past is the physical, chemical and biological conditions at the site of sediment accumulation. This means that their lithology, sedimentary structure, fossil assemblages (pollen, diatoms and shells) and chemical content are analysed.

Figure 1.
Topographic contours (in meters) of Bangladesh



The various deposits can be dated by radio carbon techniques and their relation to former sea level fixed. Such studies of the past can contribute to a better understanding of future changes of the shoreline and its ecology caused by a future rapid sea level rise resulting from the greenhouse effect. In undertaking analysis we have to realise that human interference in the coastal zone and in river areas represent new and very important inputs that were not present in the geological past. Accordingly care has to be taken in translating the "key to the past as a key to the present. These problems were recognised and formulated during the European Workshop on Interrelated and Bioclimatic Land Use Changes, Noordwijkerhout, The Netherlands, Oct. 1987 (Tooley & Jelgersma, 1992).

Four examples of coastal plains developing under various rates of past sea level changes and sediment input are evaluated in this paper in the light of the following short outline of Holocene sea level changes.

Sea level changes during the last 18,000 years

During the last glaciation, the Weichsel or Wisconsin cold period, the build up of ice caps on land caused a drop in sea level of more than 100 m. The lowest position of sea level was reached during the maximal extension of the icecaps; about 18,000 years ago. Shortly afterwards these enormous ice caps started to melt down resulting in a rise in sea level.

Post glacial sea level changes can be subdivided into three time periods: from 18000 - 6000 BP; from 6000 BP to recent times; and over the last 100 years. During the time period 18000 - 6000 BP the restoration of ocean level was dominated by the melting of the continental ice sheets which can be inferred from the geological mapping of retreating ice margins and from the marine oxygen isotope record. The rate of sea level rise during this period was very high: > 1 m/century levelling off to ca. 60 cm/century at end of this period. (Fairbanks, 1989).

After 6000 BP sea level changes are dominated by movements of the earth's crust since the continental ice caps had disappeared. Nakade *et al.* (1988) however mention the possibility that during the last 6,000 years three metres of sea level rise may have resulted from glacier melting in Antartica. The tectonic component seems to have been the most important factor influencing sea level curves over the last 6,000 years which consequently show great regional variation.

Sea level curves of SE Asia and Australia indicate a higher sea level about 6000 BP levelling off to the present level (Figure 2) other curves from the east coast of the USA and The Netherlands show a slow continous rise of sea level after 6000 BP (Figure 3).

During the last 100 years, tide gauge readings have given indications of sea level changes but more precisely of movement of land relative to the sea. These measurements provide evidence of land surface uplift in former glaciated areas due to isostatic rebound. In areas of plate tectonics abrupt shifts in the earth crust in horizontal or vertical directions have been observed. In other areas, especially deltas, slow subsidence of the land relative to the sea is measured. Tide gauge readings have been used to detect eustatic sea level rise by scientific analyses of trends and patterns. After carefully filtering the data, a mean global figure of 1.2 mm/year sea level rise over the first half of the 20th century was obtained by Gornitz *et al.*, 1987. Warrick and Oerlemans (1990) suggest an average rise of mean sea level of 1.0 - 2.0 mm/year due to thermal expansion of the ocean and increased melting of mountain glaciers caused by global warming of the greeenhouse effect. Other scientists (Pirazolli, 1989) have noted that tectonic subsidence and compaction may be included in this global sea level rise figure. Consequently it is questionable if the observed sea level rise is indeed a real signal of the greenhouse effect.

Case histories

Holocene sedimentation sequences from four different areas are discussed below: The Netherlands, the three Guianas, N. Australia, Papua New Guinea and SW Florida, USA. In all investigated areas rapid rise of sea level occured in the period before 5000 BP. The climatic circumstances show important differences between wet tropical and temperate, between areas of macro or micro tidal range and important differences in sediment input either from the rivers or from the sea.

Figure 2.
Sea level changes over the last 10,000 years in the Western Paciifc

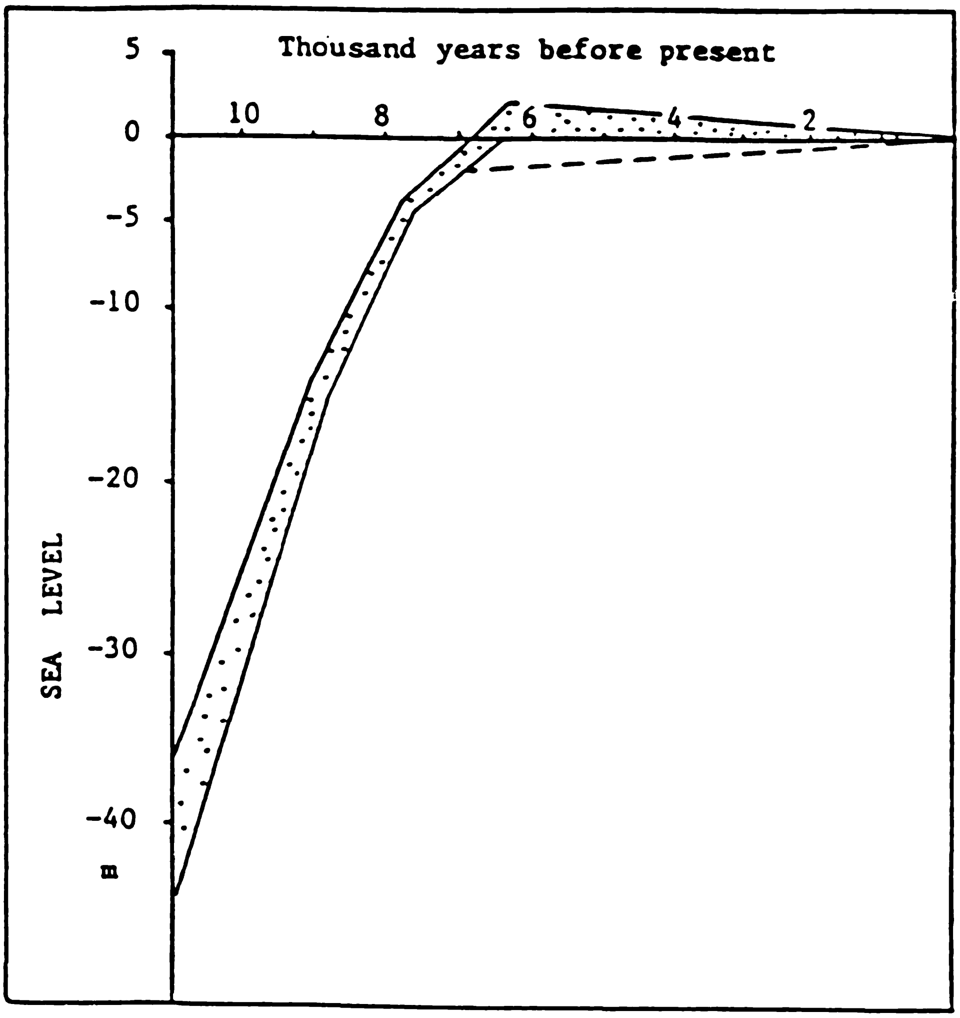
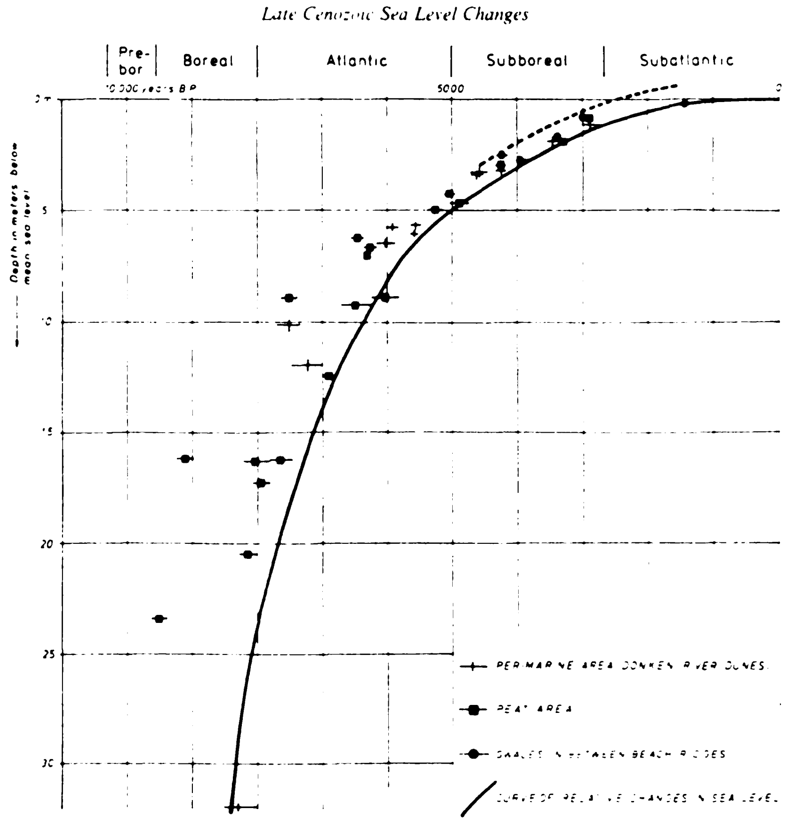


Figure 3.
Sea level curve for the coastal area of the Netherlands (after Jelgersma, 1966)



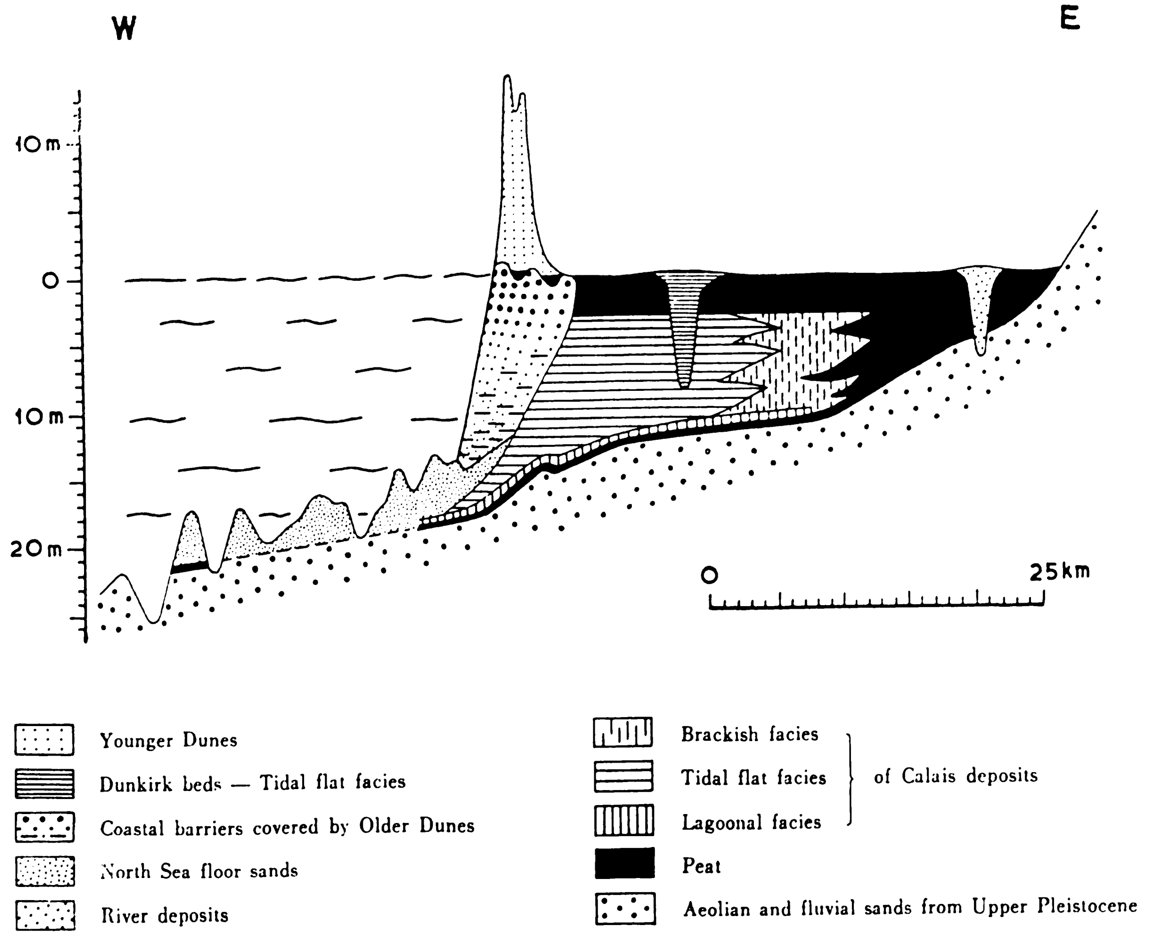
Owing to these variables, the sedimentation rate and the sedimentary environment show great differences in the different case study areas. In all the coastal lowlands, post glacial sea level rise has resulted in a wedge of soft sediments situated on top of the pre-Holocene deposits. The type of sediment in this wedge in the case study areas is discussed below.

The Netherlands

The coastal area of The Netherlands can be classified as a meso to micro tidal, wind dominated, clastic shoreline. At the present time the rivers Rhine - Meuse deliver mud to the North Sea which was calculated to be 1.5 x 10^9 kg/year in 1985. Due to engineering work this has been reduced to 0.5 x 10^3 kg/year at the present time (Visser *et al.*, 1991). The low lying part of The Netherlands has been formed by the sedimentation caused by the post glacial sea level rise.

A cross-section through the coastal plain of The Netherlands (Figure 4) provides evidence of the various sedimentary environments during the Holocene. The decreasing rates of sea level rise during this period are given in Figure 3. The Holocene transgression penetrated through the low lying parts of the pre Holocene surface and gave rise to several tidal basins. The sedimentation in one of these tidal basins, in the NW part of The Netherlands under decreasing rates of sea level rise, has been subject to careful subsurface investigations (van der Spek & Beets, 1992).

Figure 4.
Section across the Holocene deposits of the W. Netherlands (after Van Straaten, 1961)



The recognition of the sedimentary environments encountered in the Holocene has been by cored bore analysis and the studies of lithology, sedimentary structures and the fossil content (pollen, diatoms and shells). The absolute age determinations have been done by the radio carbon method. These investigations have given rise to the recognition of three different stages of sedimentation and sea level rise.

During the first stage, prior to 7000 BP when the relative rise of sea level was more than 75 cm/century, intertidal sediments were restricted to the vicinity of the tidal inlets and channels. Landward lagoons were present, bordered by fresh water swamps. No salt marshes have been encountered in the sedimentary structures and the fossil content. It may be concluded that during this stage the relative sea level rise was greater than the available sediment input in the tidal basin accordingly extensive intertidal flats and saltmarshes could not develop.

During the second stage between 7000 and 5500 BP, relative sea level rise was levelling off to 30 cm/century the sediment supply started to balance the storage capacity created by sea level rise. Intertidal flats increased in size, but saltmarshes were still rare. During the third stage between 5500 and 3500 BP when the rate of sea level rise slowed down to 15 cm/century, the sediment supply was sufficient to fill the basin. Accordingly the lagoons changed into intertidal flats and after 4000 BP saltmarshes became common features.

It may be concluded that during the third period sediment supply was in balance with the relative sea level rise. Van der Spek and Beets (1992) have used the data from the past to forecast the impact of a future sea level rise, more than 60 cm/century, on the Wadden Sea situated in the Northern part of The Netherlands.

The present rate of sedimentation in this important intertidal area is thought to be in balance with the observed relative sea level rise of the last 100 years (15 cm/century). If the sediment supply to the Wadden Sea remains the same in future it seems likely that with a future sea level rise of more than 60 cm/century much of the intertidal flats will become subtidal. The saltmarshes will disappear as the sedimentation rate will be less than the rate of sea level rise, and accordingly much more open water will be present in the Wadden Sea.

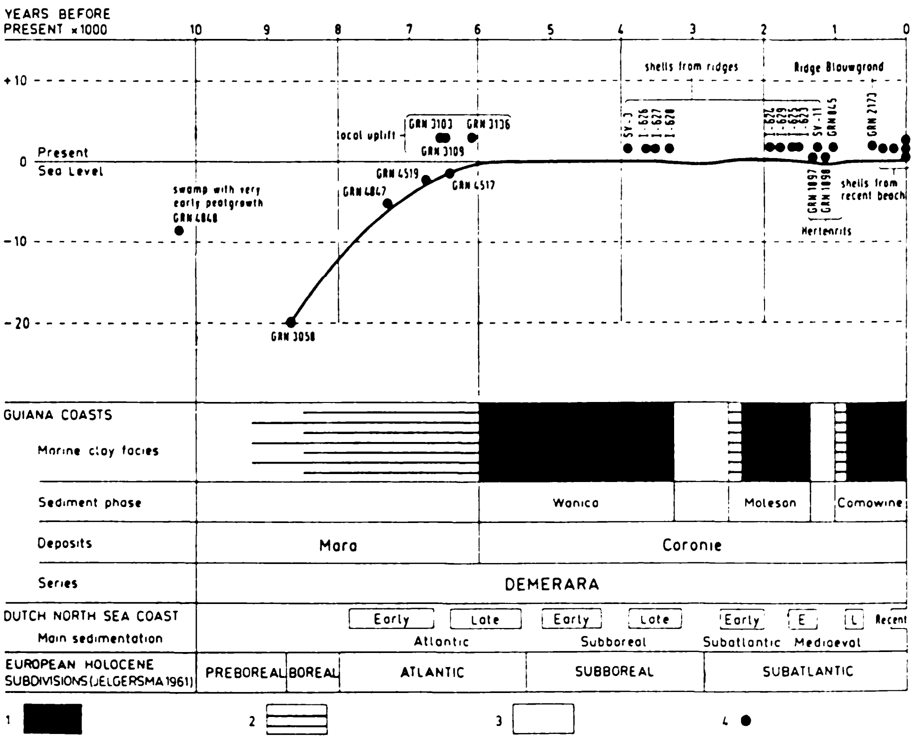
The three Guyanas

Extensive pedogeomorphological and geological mapping has been carried out in the coastal plain of the three Guyanas, northern South America (Brinkman *et al.*, 1968). The coastal landforms of the Guyanas are the product of the post glacial sea level rise and the enormous quantities of silt discharged by the Amazon River and transported by waves and currents. The sediments from the Amazon River form migrating mudflats with associated subtidal mudflats. There is a net transport to the west with a considerable deposit of material in this direction, Wells and Coleman (1977) mention that the near shore waters of the Guyanas are among the muddiest in the world (maximum of 26 - 37 /100 mg/l in near shore muddy coastal waters). The tides are mesotidal, the longshore transport is trade monsoon influenced and shows a westerly drift. The climate is tropical with wet and dry seasons and a high relative humidity.

Palynological studies together with C^{14} age determinations have given indications of the past vegetation, the age of the coastal deposits and sea level changes (van der Hammen, 1963; Roeleveld,1969), together with the work of Brinkman *et al.* (1968) provide the following picture of Holocene coastal development:

In the coastal plain two typical facies of clay sedimentation have been encountered; one at a stable level (Coronie deposits), the other associated with a rapidly rising sea level (Mara deposits, Figure 5). The sediments deposited under stable sea level, dated after 6000 - 5500 BP, are characterised by rapid successive lateral sedimentation of clays low in organic matter and pyrite, colonised by mainly *Avicennia* mangroves succeded by freshwater swamp vegetation as the distance to the sea increased. The sediments formed under a rising sea level, before 6000 BP, accumulated vertically under an actively growing vegetation of almost pure *Rhizophora* extending many kilometers inland from the coast. They contain large proportions of organic matter from the abundant fine *Rhizophora* roots and of pyrite, formed by reduction of sulphates from the brackish water and iron oxide from the sediment. The vertical accretion must have kept pace with a sea level rise of about 0.6 m/century for centuries, with the sediment supply maintained by the long shore current from the Amazon mouths. A thickness of this clay deposit of some 5 m is quite common, *Rhizophora* clays have been found in depressions of up to 40 m in some localities (Van der Hammen, 1963).

Figure 5.
Holocene sea level curve of the Guiana coast near Paramaribo (after Brinkman & Pons, 1968)



LEGEND
1. Deposition of "normal" sea clays at constant sea level
2. Deposition of pyrite clays at rising sea level
3. Erosion
4. C^{14} age determinations

Northern Australia, Papua New Guinea and some remarks on the Mekong, Ganges-Brahmaputra and Choa Phraya Delta

Chappell (1990) describes the sedimentation during rapid sea level rise in two tropical riverine lowlands. In both areas a steep sea level rise is observed until 6000 BP but the sediment input from the land and the magnitude of the tidal range are different. The floodplain of the South Alligator River in North Australia include fresh water wetlands due to the tropical monsoon climate. The sediment input from the land is low, the tidal range is high.

Investigations by mean of boring in the shallow subsurface of the riverine plain give the following data about the environment of sedimentation and the relative sea level movements. The sea level curve, figure 2, indicates a steeply rising sea level until 6000 BP with a level higher than at present, levelling off after that time to the present level. Underneath the recent river deposits in the South Alligator plain, an extensive mangrove clay is present.

The mangrove muds, up to 10-14 m thick, are deposited during a steep rise of sea level of about 12 m between 8000 and 6000 BP. It may be concluded that the mangrove clay sedimentation throughout the valley kept pace with the sea level rise during this period. A vertical sedimentation rate of 0.6 m/century seems likely.

As the sediment input of the land is rather low the source of the mud in the plain is thought to be marine muds. The strong sea level rise caused these muds to penetrate in the valley and the strong tidal current redistributed the sediment.

The flood plains of the Sepik and Ramu Rivers in Papua New Guinea are characterised by a high river water and sediment input and a low tidal range. Accordingly tidal currents are insignificant. As the continental shelf is very narrow much of the river sediments disappears to the deep ocean floor.

Geological investigations of the shallow subsurface deposits of the river plain have given the following data about the sedimentary environment during the steep sea level rise before 6000 BP. During this period an island sea developed in this area bordered by mangrove intertidal flats. The maximum extension of this inland sea was mapped and dated at about 6000 years BP. After that time, during stabilisation of sea level, the inland sea was gradually filled up with sediments from the catchment area. This investigation provides evidence that the sedimentation during the steep sea level rise did not keep pace with this sea level rise. Radiocarbon data indicate a sedimentation rate of 30 cm/century, if future sea level rise exceeds this the river plain will be tranformed into an inland sea.

In the Ganges-Brahmaputra, the Mekong Delta and the Chao-Phraya Delta the same Holocene sea level movements are present as in Northern Australia. Extensive subsurface mapping of those deltas is not available but C14 data of *Rhizophora* clays encountered beneath recent fluvial deposits are present.

These *Rhizophora* clays are dated about 5500 BP and are present as far as 100 km inland from the present coastline. (Brinkman & Pons, 1968; Brinkman,1984, 1987; Somboon *et al.*, 1990). Unfortunately insufficient subsurface data are available to indicate the rate of sedimentation in these deltas and to establish the balance between vertical sedimentation and sea level rise.

Mangrove ecosystems on carbonate platforms, SW Florida

Ellison and Stoddart (1991) give an excellent review of the work of Scholl (1964), Scholl *et al.* (1969), Bloom (1970), Ellison (1989) and others, on sea level changes derived from submerged mangrove peats. In this specific area of carbonate platforms like SW Florida mangroves exists in a more or less narrow belt. It is evident (Scholl *et al.*, 1969) that the sediment sources in SW Florida are limited to biological sources; molluscs, algae and rooted vegetation. In the fresh water, calcite mud formation, sedimentation rate is found to have been 1.6 cm/century during the last 4000 years, in the coastal area the sedimentation has kept pace with the sea level rise of 3.5 cm/century during this time. The investigation in S.W. Florida of Scholl (1964) indicates that after sea level slowed down to less than 9 cm/century mangrove systems could develop.

Ellison and Stoddart's (1991) conclusion, based on the geological record of the past, is that the mangrove ecosystem that only derive autochthonous organic accumulation will collapse if future sea level rise is more than 10 cm/century.

Conclusions

These parallels from the past show four important facts:

1. If sufficient sediment is available, vertical accretion can keep pace even with a rapid sea level rise. This means that under favourable conditions of sediment supply the intertidal conditions of our present wetland can be maintained.

2. The magnitude of the tidal current is an important agent in redistributing sediment. Accordingly it influences the rate of sedimentation.

3. A rapid sea level rise can change the inland fresh water environment of a deltaic plain in the humid tropics into an extensive zone of brackish *Rhizophora* clays if enough sediments are available. A lack of sediment can give rise to inland seas.

4. The simple "bath-tub" approach of some authors (Milliman *et al.*, 1989) estimating land loss by comparison of topographic elevations and future sea level heights, exaggerates loss and is inadequate since it neglects the remodelling of the coastal and deltaic plain and the supply and redistribution of sediment.

It must be stressed that construction of dams and barrages has drastically curtailed the sediment supply to many shorelines and deltas, and accordingly the impact of a future sea level rise will not be comparable to the geological data of the past.

In some coastal plains however the shorelines are expanding seawards owing to an increased sediment supply caused by human induced erosion of the hinterland (e.g. N. Java, Madagascar). In these areas the lessons of the geological past are similarly less comparable with a future impact of sea level rise.

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Seagrasses and climate change

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Abstract

Seagrasses are marine flowering plants (angiosperms) with rhizomes and roots that complete their lifecycle while submerged. Climatic change will influence seagrass ecosystems through sea level rise, through the uptake of CO_2 by the oceans, and because of the increase in seawater temperature. A seagrass meadow is a sedimentation habitat and an additional source of sediment is of biotic origin. Compensation for sea level rise, at the predicted rates, by increased sedimentation will not affect seagrasses negatively. A doubling of the atmospheric CO_2 concentration causes a slight (0.3 pH-units) acidification of seawater. Hence more CO_2, the preferred carbon-species, will be available for photosynthesis and seagrass production will increase because of the additional CO_2. However, the production and biomass of the epiphytic algae on the seagrass leaves will increase also, causing more shading. The reduction of apical dominance in a high CO_2 environment will facilitate vegetative propagation. The production of the seagrass community as a whole is expected to increase 20% after doubling of the atmospheric CO_2 concentration. An increase in global temperature will permit the expansion of the perennial growth form into more northern latitudes. Seagrasses and seagrass ecosystems will in general benefit from the expected climatic change. Negative effects which undoubtedly will occur locally will be of little global importance.

Introduction

Seagrasses, an ecological group represented by 12 genera, are marine monocotyledonous angiosperms, that are unique amongst flowering plants as they live and complete their lifecycle, pollination included, while submerged in seawater. As compared to propagation by means of seeds, vegetative propagation is of greater importance in tropical and temperate species. Most species are perennial but in some species such as *Zostera* in the northern hemisphere, annual as well as perennial forms exist. Seagrasses grow worldwide in suitable shallow marine and brackish waters. Only in the high Arctic and on the Antarctic continent are seagrasses absent (Den Hartog, 1970). Substrate requirements are diverse; seagrasses grow in sediments ranging from almost liquid mud to coarse coral rubble and, for some (e.g. *Phyllospadix* spp.), crevices in otherwise bare rock suffice. The upper limit is imposed by desiccation during low tide for the species that extend into the intertidal. Light attenuation underwater limits the depth distribution; some species are recorded from depths down to 80 m (Duarte, 1991). However, most species are limited to shallow coastal areas where the maximum standing crop of almost all species is found. Seagrasses occur in shallow marine environments ranging from permanently tranquil protected embayments to wave-washed shores.

Until a decade ago, seagrasses were considered to be comparable to terrestrial crops in primary productivity (McRoy & McMillan, 1977; Zieman & Wetzel, 1980).This view has been adjusted to more realistic values (Hillman *et al.*, 1989 and references therein). The gross productivity of a well developed seagrass meadow, inclusive of the production of below-ground parts and epiphytes is generally in the order of 500-1,000 g C m^{-2} yr^{-1} for the larger species, which is still among the highest recorded for marine ecosystems. However, the net production of a seagrass ecosystem, and therefore the possible input in the foodweb and contribution to adjacent ecosystems, is significantly lower if community respiration is taken into account (Lindeboom & Sandee, 1989).

Trophodynamic relationships in seagrass ecosystems are complex and differ regionally. The pathways of energy flow are far from clear. Primary production enters the food web through three major routes; grazing of seagrasses, of algae, either epiphytic or otherwise associated with the seagrass community, and via detritus. Some large invertebrates and vertebrates utilise the seagrasses directly. In temperate ecosystems seagrasses are an important food source for resident and/or wintering waterfowl. In tropical ecosystems, the dugong *Dugong dugon* and green turtle *Chelonia mydas* are important grazers from a conservation point of view (both are on the 'IUCN Red List of Threatened Animals'), and some fish species ingest large quantities of seagrasses. It is unclear whether the seagrass leaves or the periphyton on the leaves are most important for these herbivorous fish. In general terms the epiphytes are considered to be the most valuable nutrient source. Epiphytes and detritus support a foodchain in which invertebrate grazers and invertebrate primary predators form the base and predatory fish are at the top. For a review and discussion of the literature see Klumpp *et al.* (1989). Ecosystems dominated by seagrasses have been shown to be important in providing shelter and food for many species. A high economic value is derived from their function as nursery grounds for juveniles of many species of commercially important fish and invertebrates and their stabilizing effect on coastlines.

Carbon dioxide and the sea

Total inorganic carbon concentration (C_T) in the ocean is approximately 2.3 mM. In the equilibria of dissolved aqueous carbonate species six components are interdependent: CO_2, H_2CO_3, HCO_3^-, CO_3^{2-}, H^+ and OH^-. The increase in atmospheric CO_2 caused by the emission of fossil CO_2 will be only partially transferred to the ocean. This buffer effect (Revelle factor) which relates CO_2 partial pressure to C_T at constant alkalinity, temperature and salinity is about 10, i.e. an increase of the atmospheric CO_2 partial pressure of x% from the present partial pressure will raise C_T by x/10% (Kratz, 1985). The uptake is rapid and the equilibrium between atmosphere and the surface layer of the ocean is maintained. The rate of pCO_2 increase in surface ocean water is nearly equal to that in the atmosphere (Takahashi, 1979). The buffer factor increases with increasing pCO_2. A doubling of the present CO_2 content in the atmosphere would increase C_T by about 5 to 6%.

Doubling of the atmospheric pCO_2 will result in a lowering of the surface sea water pH. Baes (1982) estimated the decrease of seawater pH at 0.2 pH units. Stumm and Morgan (1981) calculated a lowering of 0.279 pH units under equilibrium conditions (Figure 1), while a decrease of 0.5 pH was determined by Holm-Hansen (1982). The general agreement is now on 0.3 pH units lower (Sibley and Strickland, 1985), provided alkalinity does not change (Brewer, 1983). Alkalinity is not affected by the uptake of atmospheric CO_2.

Lowering of the pH by 0.3 pH units from pH 8.2 to pH 7.9 will approximately double the amount of free CO_2 in the water from 10 M to 20 M (Figure 2). Free CO_2 is the carbon source used preferentially by many aquatic macrophytes. A doubling in the supply of this frequently limiting nutrient will have an effect on aquatic communities of macrophytes, some of which can be judged beneficial to the ecosystem. There remains the philosophical or ethical question of whether a man-induced change in ecosystem structure or functioning can ever be considered as being positive.

Figure 1.
Change of the pH of seawater in response to increased atmospheric carbon dioxide concentration. The decrease caused by a doubling of the CO_2 concentration is indicated.
(after Stumm and Morgan, 1981)

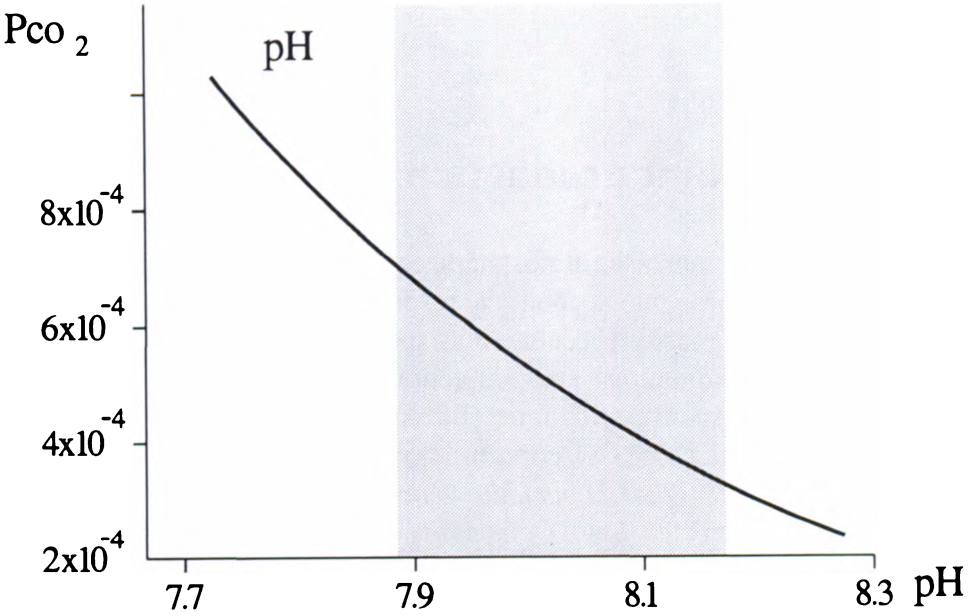
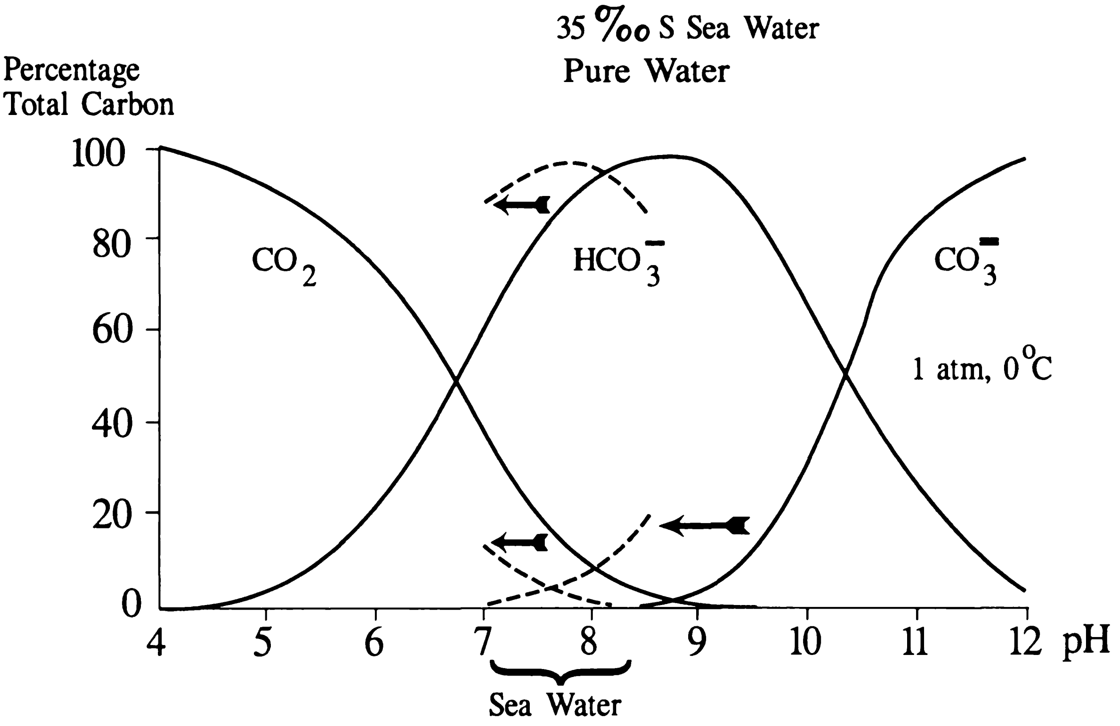


Figure 2.
Relative distribution of carbon species in relation to pH (after Larkum *et al.*, 1989).



Carbon dioxide and plant production

Evidence is accumulating that increased atmospheric carbon dioxide could stimulate yields in agriculture and forestry, but predictions about the response of terrestrial ecosystems that are much more complicated, are mostly speculative as species-specific responses, competitive interactions, environmental limitations and adaptation to a higher CO_2 environment will influence and modify the response with time (Bazzaz *et al.*, 1985). Nevertheless, when summarizing the effects of increasing CO_2 concentrations on plant communities the following statements have been made: "*Total community biomass will increase in essentially all communities (uncertainty: extremely low); Community composition will change (uncertainty: low for the general principle, high for exactly what changes will occur) and; Vegetation growth enhancement will result in reproductive enhancement (uncertainty: low)*" (Bazzaz *et al.*, 1985). Increased photosynthesis and improved water use efficiency are considered the most important processes in terrestrial plants in a higher CO_2 environment. Obviously improved water use efficiency is not an issue in seagrasses. Seagrasses neither possess nor need stomata and therefore only the effect of increased dissolved CO_2 has to be considered.

Seagrasses

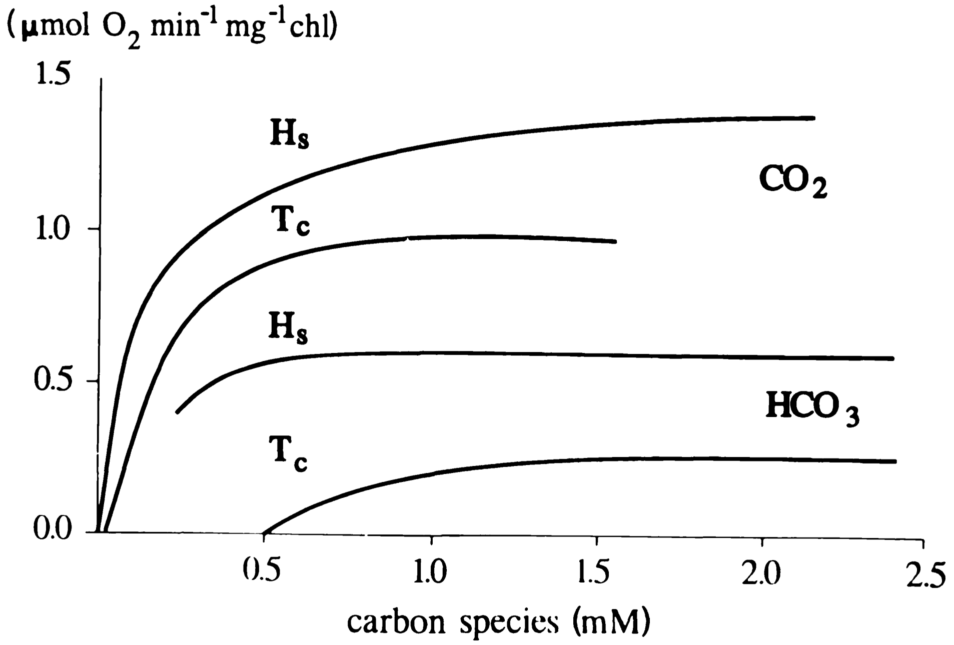
Standing crop (above-sediment biomass) of seagrasses is highly variable. The highest value (8,100 g DW m^{-2}) is recorded for subtropical meadows of *Thalassia testudinum* in Florida (Bauersfield *et al.*, 1969) while the next highest (1,840 g DW m^{-2}) is reported for *Zostera marina* in Alaska (McRoy, 1970). Surprisingly no standing crops even approaching these values have been reported since 1970. Studies performed in the last two decades rarely report standing crop values higher than 500 g DW m^{-2}. There is too little information on the conditions prevailing at the sample sites to explain the differences between early and more recent studies. It is not my intention to suggest that a seagrass decline is taking place on a more than regional scale. Nevertheless, a seagrass meadow with a standing crop of 500 g DW m^{-2} is considered well developed. Annual above ground productivity is generally between 100 and 500 g C m^{-2} yr^{-1}. For a recent overview see Hillman *et al.* (1989). In-sediment parts constitute 50-90% of the total seagrass biomass in most species, but values as low as 5% are reported for amphibolids. The reasons for differences within species are largely unknown (Hillman *et al.*, 1989).

In contrast to terrestrial plants which only have gaseous CO_2 available for photosynthesis, three sources of inorganic carbon are available to the plants in the marine environment; dissolved CO_2, bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}). The role of CO_3^{2-} in plant metabolism is only important in calcification processes in calcareous algae and will not be considered here. The bulk (89%) of the inorganic carbon is in the form of HCO_3^- and the increase in the concentration of this ion, in response to the uptake of atmospheric CO_2 by the oceans, will be relatively small. Only the concentration of CO_2 (0.5%) will change significantly (double), hence the effect of CO_2 on marine aquatic vegetation has to be the primary consideration.

A change in the availability of CO_2 can only be of consequence to a plant if this ion is preferentially assimilated and if the paucity of this ion limits plant productivity. HCO_3^-, available in virtually unlimited quantities, has been suggested as the primary source of inorganic carbon in marine photosynthesis (Benedict & Scott, 1976). If this is true, the effect of more atmospheric carbon dioxide would be minor and in most species negligible. This view is based on the ratio of the stable carbon isotopes ^{12}C and ^{13}C in plant tissue. The ratio of ^{12}C and ^{13}C in the atmosphere is relatively constant but $^{13}CO_2$ hydrates more readily, hence dissolved HCO_3^- contains proportionally more ^{13}C than the atmosphere and so do seagrasses. In photosynthesis two pathways exist for the initial fixation of inorganic carbon; RUBISCO (ribulose 1.5. biphosphate carboxylase/oxygenase) and phosphoenolpyruvate (PEP)carboxylase. The first pathway, present in all plants, uses CO_2 as the substrate and has a higher affinity to the lighter isotope. The second pathway, additional in some plants (C4 plants), uses HCO_3^- as substrate and has no higher affinity to either of the isotopes. The view that the comparable isotopic composition of HCO_3^- and seagrasses can be fully explained as the result of direct utilisation of HCO_3^- in photosynthesis by seagrasses has been largely abandoned. The phenomenon is now attributed to boundary layer effects, (bio)chemical processes at the leaf surface and internal pools of inorganic carbon (Abel & Drew, 1989). Detailed analysis of the labelling patterns of photosynthesis in seagrasses shows RUBISCO to be the carboxylating enzyme that fixes inorganic carbon. However, several species show relatively high concentrations of C4 acids, the role in carbon assimilation of which is not understood (Abel & Drew, 1989). Abel (1984) reaches the conclusion that the carbon fixation mechanism in seagrasses of the genus *Thalassia* is unable to access seawater HCO_3^- directly, but Larkum *et al.* (1989) warn that such a conclusion should at present be treated with caution, in view of the high rates of primary production.

A distinction has to be made between the effects of lowering the pH by 0.3 pH units and of the effect of doubling the free CO_2 in marine waters which can also be reached by a higher total inorganic carbon concentration (Figure 3). The study of carbon fixation, productivity and effects of pH and CO_2 concentration are performed predominantly on leaf cuttings and less frequently on whole shoots. The observed photosynthesis at pH values higher than pH 8.2 are cited as proof of the ability of seagrasses to incorporate HCO_3^- in *Halophila stipulacea, Thalassodendron ciliatum, Halodule uninervis, Syringodium isoetifolium* (Beer *et al.*, 1977) *Cymodocea nodosa, Halophila ovalis* (Beer & Waisel, 1979), *Zostera marina* (Sand-Jensen & Gordon, 1984) and *Zostera muelleri* (Millhouse & Strother, 1986). I will not repeat the discussions here and have limited this paper to observations made in the narrow pH range between pH 8.2 and pH 7.9, under conditions of present and expected pH of seawater and in solutions that have a comparable inorganic carbon content to seawater.

Figure 3.
Rates of photosynthesis as a function of CO_2 or HCO_3^- concentration in the seagrasses *Halophila stipulacea* and *Thalassodendron ciliatum* (redrawn after Beer *et al.*, 1977).



Thalassia hemprichii shows an exponentially increasing rate of photosynthesis with decreasing pH in the range pH 9 to pH 6 (Abel, 1984). In *Cymodocea nodosa, Syringodium isoetifolium* and *Halophila ovalis* the increase in rates of photosynthesis in the range pH 8.2 to pH 7.9 is probably not significant. An increase in rate commences near pH 7.9 and than roughly doubles in the range from pH 8 to pH 7 (Beer *et al.*, 1977; Beer & Waisel, 1979). In *Thalassodendron ciliatum, Halophila stipulacea* and *Halodule uninervis* stimulation of photosynthesis starts at pH 8.1 and a lowering of the pH by one unit increases the rate of photosynthesis by a factor of approximately three (Beer *et al.*, 1977) (Figure 4). In *Zostera muelleri* comparable observations are made, but the authors mention the inhibition of photosynthesis at pH levels less than 7.8 - 8.0. However the consequences with respect to the presented rates of photosynthesis are not clear (Millhouse & Strother, 1986).

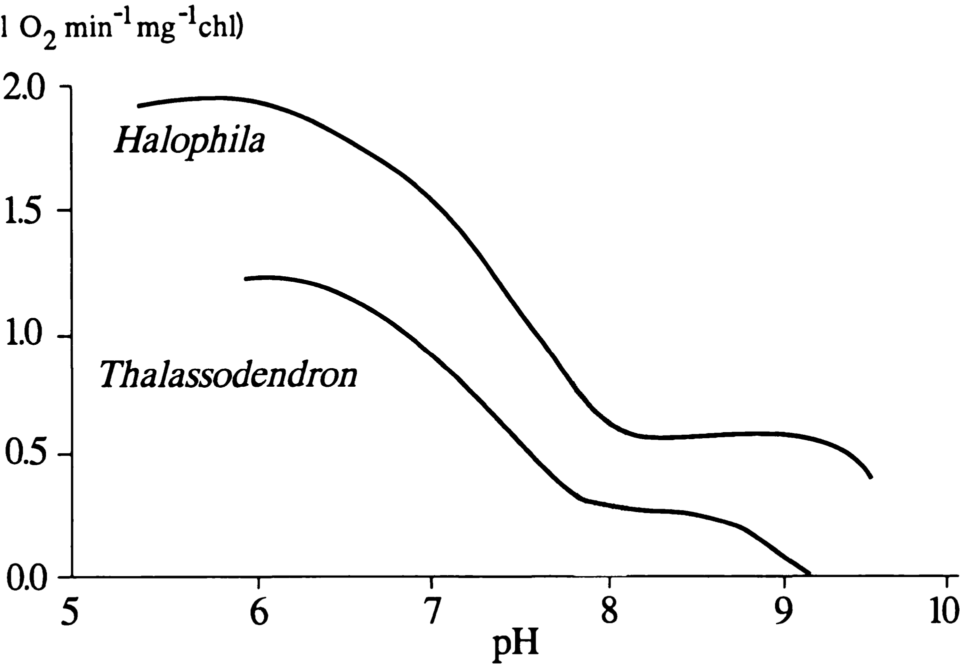
In summary, Madsen and Sand-Jensen (1991) state: "*marine angiosperms show a relatively higher correspondence between realized and maximum rates of photosynthesis than do freshwater macrophytes. The excess capacity for carbon assimilation is not realized and this indicates the importance of usable inorganic carbon as a potential limiting factor for photosynthesis and growth*". The potential realisation of excess capacity will partially follow the change in atmospheric carbon dioxide. The laboratory studies are all in agreement that doubling of available CO_2 will have no detrimental effects and in most species will stimulate productivity. These results are obtained under favourable conditions (stirring, light, nutrients). In complex ecosystems and under field conditions the effect will be lower in magnitude.

Increased plant production generally results in increased vegetative and sexual reproduction (Harper, 1977) and if a limited supply of CO_2 to the plant acts as a stress factor, than relaxation of this stress will result in suppression of apical dominance and more branches of the rhizome might appear. Almost sixfold increases in tillering rates have been observed in a terrestrial species (the sedge *Eriophorum vaginatum*) after doubling of the CO_2 concentration in ambient air (Tissue & Oechel, 1987). However, whether this also applies to annuals and other species, remains unknown. Paez *et al.* (1980) showed that the release from apical dominance by an increased level of CO_2 resulted in the development of more branches, flower buds, flowers and fruits but that the effect was insignificant on maturity of the annual plant, *Pisum sativum.* Annual forms of seagrasses occur predominantly in temperate waters and only in these is the effect of stimulated generative propagation of consequence. Most seagrasses from other areas are perennial and very long lived, as continuous rejuvenation takes place through branching of the rhizomes (Tomlinson, 1974; Brouns, 1987). In these seagrasses stimulated branching will be of considerable importance. Changes in biomass and productivity of above and below sediment plant parts could be of significance, but as meristem development is highly variable between species, species composition and patterns of dominance might be altered.

Algae

Next to the seagrasses themselves, microphytic and macrophytic algae are dominant components in seagrass ecosystems (Brouns & Heijs, 1991). In estimating the impact of increased CO_2 supply to the vegetation, the role of the algae has to be taken into account since they may modify the magnitude of the seagrasses response because they will also benefit from the increased CO_2 concentation.

Figure 4.
Rates of photosynthesis as a function of pH for the seagrasses *Halophila stipulacea* and *Thalassodendron ciliatum*. (redrawn after Beer *et al.*, 1977)



Macrophytic algae occur throughout a seagrass meadow and compete for the available nutrients and space. The biomass of the macroalgae associated with seagrasses is highly variable, and mostly well below the standing crop of the seagrasses themselves (Heijs, 1987), although values of 15,000 g DW m^{-2} have been reported (Virnstein & Carbonara, 1985). The availability of hard substrate suitable for settlement is frequently the most important limiting factor. Photosynthesis in coralline red algae responds positively to additional CO_2, and lowering of the pH (Smith & Roth, 1979; Borowitzka, 1981). Stimulation of photosynthesis is also reported for coralline green algae (Borowitzka *et al.*, 1976). Carbon limitation in non-coralline algae has been demonstrated in a number of species (Wetzel & Grace, 1983)

The epiphytic component of a seagrass ecosystem resembles, in structure and individual species'growth form, the fast growing and highly productive coral reef turf assemblages in which Hackney and Sze (1988) document that productivity declined when pH rose, probably because of declining supply of CO_2 and HCO_3^-. Algae will also profit from more CO_2. Since most invertebrate grazers prefer the epiphyte-periphyton complex as a food source, secondary production is expected to show an increase too.

Interaction of algae and seagrasses

Compared to terrestrial plants, aquatic macrophytes experience a diffusion barrier (leaf boundary layer) which considerably slows the transport of nutrients and CO_2. For submerged plants gas diffusion is 10^4 times slower than in air. Boundary layer resistance to CO_2 transport from the water column to the plant tissue is an important limiting factor in aquatic plant productivity (Barko *et al.*, 1986; Larkum *et al.*, 1989). The mass-transport of CO_2 through this unstirred boundary layer is solely by molecular diffusion.

Provided all other conditions remain unchanged, the thickness of the boundary layer depends on the roughness of the surface and the speed of the water flow. The diffusion boundary layer is reduced in thickness when the flow changes from laminar to turbulent. Increased roughness of the surface lowers the speed of flow required for this change to take place. Increased CO_2 will exert an influence in two opposing directions. A denser canopy will reduce the flow, increase the thickness of the boundary layer and hence counteract the beneficial effect of more available CO_2. However, stimulated growth of epiphytes will improve the roughness of the surface and lower the required speed to reach turbulence, but a thicker layer of epiphytes in itself increases the thickness of the diffusive boundary layer. The overall impact of these stimuli and negative feedbacks remains to be elucidated.

Seagrass leaves function as a hard substrate and are suitable for settlement of algal spores and juvenile individuals of species which are essentially macroalgae are also found as epiphytes. The epiphytic component can intercept a considerable amount of CO_2 (Penhale, 1977) and the reduction of light reaching the leaves can be also be reduced significantly. Epiphytes will cause drag and this together with the brittleness caused by calcareous deposits can cause earlier fragmentation of the leaves (Borowitzka & Lethbridge, 1989). More CO_2 delays senescence of the leaves and this potential beneficial effect would than be counteracted by earlier fragmentation. Epiphytes are considered a liability to seagrasses.

Depth range

At limiting light levels, growth of plants will be stimulated relatively more by an increase in the ambient CO_2 concentration than in high light conditions owing to increased quantum yield of photosynthesis (Ehleringer & Björkman, 1977). In seagrasses light is reduced by either self-shading, growth of epiphytes on the leaf surfaces, or attenuation of the light in the water column. Hence, it is probable that the depth that can successfully be colonised by seagrasses will be increased, provided the light regime does not change. Furthermore, photosynthesis and the number of meristems are expected to increase in plants growing in the present depth range. Rhizomes growing towards greater depths are observed in all species at the lower limit of their occurrence. Die-back occurs and is expected to be a recurring, perhaps annual, phenomenon.

Light attenuation in the water column is partially caused by phytoplankton. Since at least in some phytoplankton species the division rate and the productivity are enhanced by additional CO_2 (Laing & Helm, 1981) the light attenuation in coastal waters might increase. The impact will be small as plankton productivity is limited by additional factors. In oceanic waters iron is frequently limiting (Ritschard, 1992), but it is unknown if this is also true for coastal waters. Nevertheless, the effect of an increased quantum yield which might enable seagrasses to grow at greater depth might well be countered by the reduction in available light at depth through stimulated growth of plankton. In addition, climate change is expected to cause increased storminess and hence turbidity by resuspension of sediments.

It has been documented that three species of intertidal seagrasses are able to maintain a high rate of photosynthesis while exposed to air during low tide, and to use atmospheric CO_2 during this period (Clough & Attiwill, 1980; Leuchner & Rees, 1993). Increased atmospheric CO_2 could thus benefit the seagrasses directly, and could facilitate colonisation the higher reaches of the intertidal in response to sea level rise through mitigating the stresses of intense light and desiccation, although this is unlikely to be be very important.

Wetzel and Grace (1983) have summarised the possible effect of doubling the CO_2 concentration on aquatic plant communities and reached the conclusion that potential photosynthetic responses of marine angiosperms may rise by a factor of two compared to the present rates. However the response of the total community is estimated as an increase of 1.2 times the present level.

Sea level rise

Climate change will have an effect on seagrasses indirectly because of the anticipated sea level rise. Under the "business as usual" scenarios predictions of expected sea level rise converge on 0.6 cm yr^{-1}. Seagrass ecosystems are expected to be able to cope with this rate of sea level rise without any difficulty as seagrasses modify their own environment by trapping large amounts of sediment. The strap-like leaves of the canopy slow the current speed sufficiently to enable suspended sediments to settle. This is illustrated convincingly by the way blow-outs deeper than 10 m are recolonised and become indistinguishable from the surrounding meadow in the course of a few years to a decade. Furthermore, seagrass ecosystems themselves generate a large amount of calcareous sediment. The main sources are the calcareous remnants of animals and algae that occupied the surface of the leaf blades. After senescence the leaf fragments and most of the material is retained in the system. Deposition rates of 1 cm yr^{-1} are possible in areas rich in foraminiferans and tube dwelling polychaetes.

Seagrasses propagate predominantly vegetatively and the rhizomes are most important in this aspect. The actively growing rhizomes adjust to the depth of the sediment layer covering them. This mechanism ensures a sometimes periodic but otherwise continuous rejuvenation of the meadow and also compensates for sedimentation. In response to increased sedimentation they will grow upward and maintain their relative position. Especially in the mixed meadows of the tropics the maintenance of the diversity and structure largely depends on the ability of species to invade the same area over and over again. More frequent branching, and the effect of reduced apical dominance, will facilitate this process.

Coastline changes that will undoubtedly occur will be influenced by the profile and the erodability of the substrate. The Bruun rule states that a beach that has attained equilibrium with coastal processes will respond to a rise in sea level by losing sand from the upper part of the profile and gaining it in the near-shore area until a new equilibrium is established. Basically this provides sediments to the shore bottom such that it is elevated in proportion to the rise in water level. The coastline will thus retreat as a direct result of sea level rise and retreat additionally as a result of the transference of sand seaward (Bruun, 1962). Assumptions underlying Bruun's (1962) rule are that the coast has a fully developed equilibrium profile and that there is sufficient loose sediment both on the beach and near-shore. The assumptions are normally fulfilled on coasts with small to moderate gradients (Christiansen *et al.*, 1985). A problem arises because of the human occupation of near-shore areas. Human settlements and agricultural land have exploited the coastal areas as far seaward as possible. Frequently dykes and other man-made structures protect the land from incursions of the sea. Then the Bruun rule does not apply.

Temperature

Some seagrass species have spatially separated annual and perennial populations. The annual growth form, which depends on seeds for propagation and establishment each year, is considered the dominant form in areas that are sub-optimal. Low winter temperatures are one of the limiting environmental factors important in this regard. In these populations the life cycle is completed within a few months, and biomass during winter is negligible. In the perennial growth form production continues all year round, though with lower values during the winter. The population is independent of the production of seeds. An increase of global temperature will enable the expansion of the perennial growth form towards northern latitudes.

Summary and conclusions

Seagrass density and biomass will be stimulated by the increase in atmospheric carbon dioxide. Vegetative and generative propagation will both be stimulated, particularly the former. It is not known whether species composition and dominance patterns will change in mixed meadows. The depth range of the plants will be expanded to deeper water in response to more efficient use of available light at depth. Provided natural sedimentation and erosion processes can proceed, seagrass communities will respond easily to sea level rise.

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Impact of climate change on coastal dune ecosystems

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Abstract

This review paper deals with the possible impact of climate change on the coastal dune ecosystem. Coastal dunes (marine sand sedimentary systems) are found in various climate regions all over the world. They are dynamic systems with high nature conservation values. Because of their situation on the border of land and sea they also provide important economic functions for society. Coastal dunes protect many of the world's lowland areas with a high population density. Climate change will affect these systems in two ways: first, the functioning of ecosystems themselves will be affected; second, entire ecosystems may disappear altogether as a result of accelerated sea level rise and coastline retreat. Changes and even loss of coastal resources will have enormous impacts on society.

The coastal dune is defined as the foreshore-beach-dune interaction system. Distinctive landscape ecological processes of this system are reviewed at various scales (coastline processes, dune morphology, groundwater hydrology, soil maturation, vegetation succession).

The impact of climate change (changes in temperature and precipitation as well as accelerated relative sea level rise) is discussed in two ways:

1) On a local/regional scale. For this purpose, examples are given from the Dutch coast. We discuss predictions of coastline changes and impacts in terms of loss of land and changes in groundwater level (with help of a geographic information system (GIS) and a vegetation-hydrology interaction model), changes in soil parameters and in vegetation succession.
2) On a European scale. Regionalised monthly climate scenarios are used to portray the changes in temperature and precipitation. In Europe, dunes are found in contrasting climate regions from the Baltic to the Mediterranean. The impact of climate change on principal soil-forming processes in these regions (decalcification, podzolisation, accumulation of organic matter) is discussed. This may result in shifts of ecosystems or species and may change the character of dunes from mobile to stable or the opposite.

When applicable, specific ecosystems or species are mentioned to illustrate changes. The Raunkiaer lifeform system is suggested for monitoring species response.

Introduction

Climate change is related to many other environmental problems, which occur at different scales, from local to global, and cannot be considered independently. They develop due to the pressure on the natural environment; caused by the amount and intensity of human activities, which increases continously.

Two factors are clearly important: the massive conversion of fossil fuels into carbon dioxide, and the global destruction of forests, which results in the conversion of carbon stored in plants and in soils to carbon dioxide. Other greenhouse gases reinforce and accelerate the impact due to carbon dioxide alone.

As a result of greenhouse gases, it is now believed that in the first half of the next century a rise of global mean temperature could occur which is greater than any in man's history. The accelerated increase in concentrations of greenhouse gases in the atmosphere, if continued, will probably result in a mean surface temperature increase of the earth of 1.5 - 4.5°C before the middle of the next century.

Marked variations in the extent of warming are expected. For example, in the coastal areas of western Europe the mean values of temperature are expected to increase 1-5°C under a doubling of CO_2 concentration depending on latitude. In northern latitudes the warming may be twice of the southern average (RIVM, 1991). Consequently, the amount of precipitation will change. Due to all kinds of feedback mechanisms, however, there is no clear relationship between changes in temperature and amount of precipitation, so that different scenarios result in significantly different prediction of precipitation changes (Wetherald & Manabe, 1986; Schlesinger & Zhao, 1989).

Global warming will also accelerate the present relative sea level rise. This will probably be in the order of 30 cm but could possibly be as much as 150 cm by the middle of the next century (Titus, 1986; Oerlemans, 1989). A 100 cm rise would seriously threaten low-lying coastal areas; would flood productive land, contaminate fresh water supplies and change coastlines (Houghton *et al.*, 1990). All of these impacts can be exacerbated if droughts and storms become more severe. Rapid sea level rise would change coastal ecology and threaten many plant and animal species.

A rise in sea level causes marine sedimentation, which has given rise to the existence of many lowlands (and coastal dunes) of the world. However, under natural conditions sedimentation is able to keep up with a sea level rise of 10 to 15 cm/100 years, provided there is enough sediment available on the foreshore (Jelgersma, 1987). The supply of sediments to the coast has greatly decreased in the last few decades through the damming of rivers. Coastal lowlands belong to the world's most densily populated and industrialised areas. Over 50 million people could be forced to move with a sea level rise of 150 cm (IPCC, 1990). Coastal ecology will change drastically.

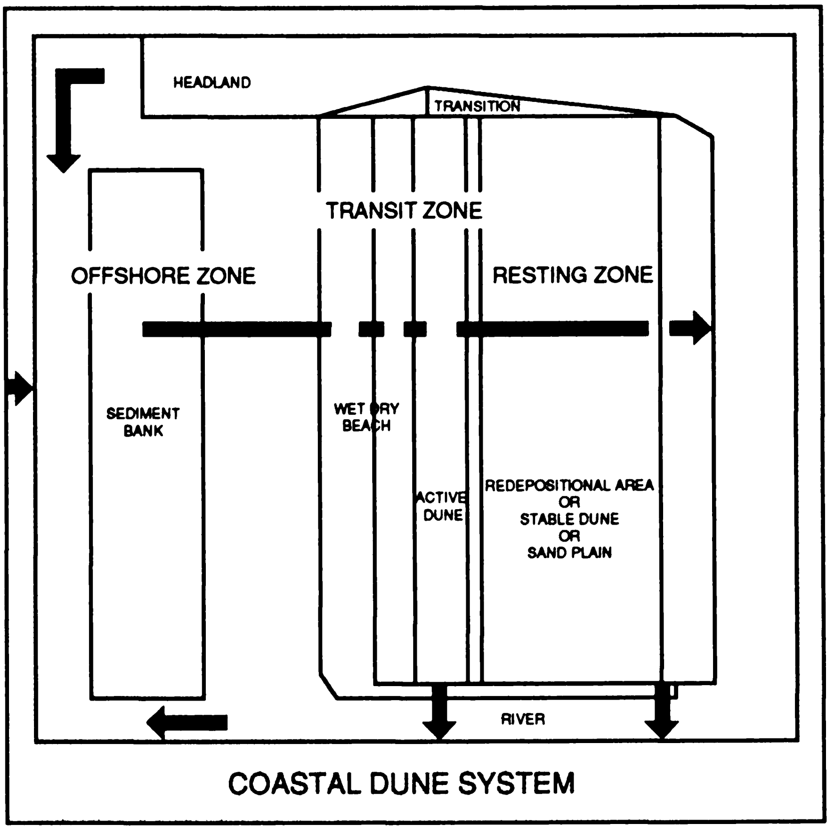
In this paper we examine the possible impacts on coastal dune ecology and review the recently published literature on this subject.

The coastal dune ecosystem

Because of their location on the border between land and sea, coastal dunes are used for many purposes. Coastal defence, recreation and tourism, drinking water production and nature conservation are the main types of use. Changes in climate will not only affect the ecology of the coast as such but also the functions for society. This paper concentrates on ecological impacts.

The coastal dune system is defined as the sand sedimentary system along sea coasts. Sand is supplied from an offshore sediment bank either by the deeper seabottom and/or by rivers discharging their sediments into the sea (Figure1). The dunes form the residual part of the sand system. They consist of a mobile transit zone (beach and active foredune) and a resting zone (inner dune). In coastal morphology, the foreshore up to -20m below ASL is usually included in the coastal zone. For our purposes this is not necessary. But it should be realised that the foreshore forms part of the dynamic sediment store which enables the system to adapt to sea level rise.

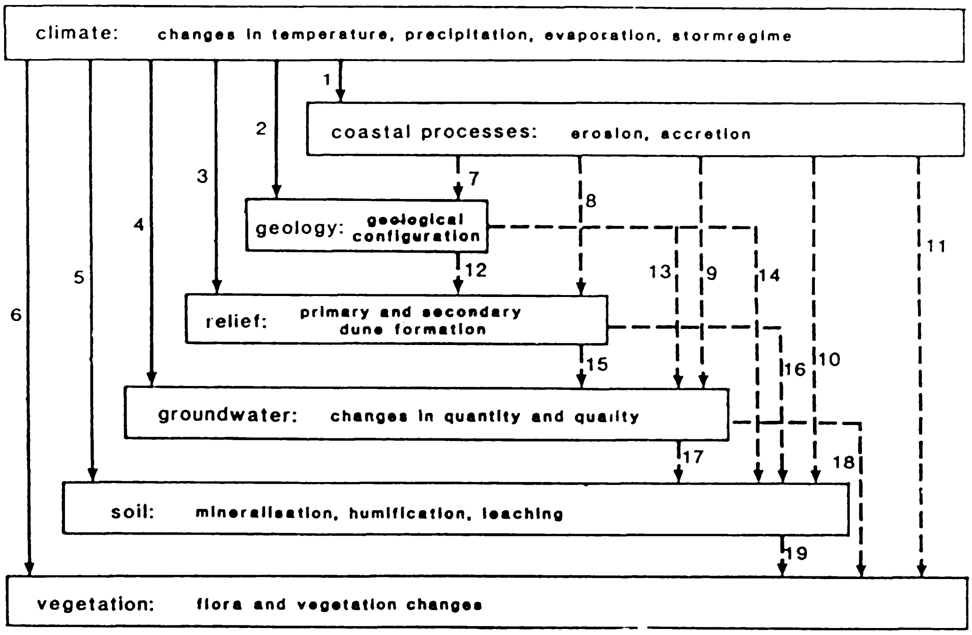
Figure 1.
The coastal dune system



To examine the possible impacts on coastal dune ecosystems we concentrate on the main processes which operate in them. A useful way to present these processes is the hierarchical scheme presented in figure 2. It shows the main relations between landscape components starting with climate. Processes affected by climate change and discussed in this paper are the following:

Landscape component	**Process**
coastline	erosion/accretion/offshore sand budget
geology/relief	primary and secondary dune formation
groundwater	inundation/desiccation, (salt-fresh)
soil	mineralisation, humification, decalcification, podzolisation, leaching
vegetation	C-economy, succession, species composition change

Figure 2.
Main relations between landscape components starting with climate. Feedback relations not shown **(Meulen 1990 after Bakker *et al.*,1981)**



——> / - - - - > = direct / indirect relation;
1 = temperature, relative sealevel rise, change in storm regime;
2, 7 = speed of sealevel rise, erosion or accretion;
3, 8 = storm regime, phases of dune formation;
4 = change in amount and/or distribution of yearly evaporation;
5 = change in effective precipitation, temperature, sunshine, air humidity, soil formation;
6 = change in all climate factors;
9 = change in width of dunes causing change in groundwater level and influence of sea-spray;
10, 11 = drift-sand activity / wind erosion, change in seaspray;
12, 14 = lime content, mineral composition of sand, grain size;
13 = hydrogeology;
15 = microtopography groundwater table;
16, 17 = changes in groundwater regime, soil and vegetation;
18 = inundation or desiccation of valleys;
19 = succession, (de-)eutrophication, decalcification and acidification.

Impact of climate change on coastal dune ecosystems

The expected effects of climate change on coastal ecology result from climate change as such and from accelerated sea level rise (cf. Meulen 1990; Noest *et al.,* 1992). Thus one can distinguish between:

- loss of land and all its coastal ecosystems due to enhanced erosion and/or inundation
- change in character of the more inward dunes now facing the sea due to the influence of the sea (water)
- change in character of the remaining dunes due to climate change.

The first two impacts chiefly concern foredunes, the latter the entire dune zone.

Impacts on a local/regional scale with examples from the Dutch coast

1. Coastline processes, erosion and accretion, sandbudgets

Sand budgets. Sand budgets for the Dutch coast were calculated by Rijkswaterstaat (1990). The active zone taken into account is located between the crest of the first dune ridgre and the 8m depth contour. One of the obvious conclusions is that the coast of the North Sea and the Wadden Islands in the north looses sand to the benefit of the Wadden Sea, a large tidal marsh area between the mainland and the Wadden islands in the north. Furthermore it became clear that the profile of the coast becomes steeper because sand from the deeper parts of the profile is transported to the shallower parts. Erosion of the Wadden Islands is probably increased by the "sand hunger" of the Wadden Sea. To get an insight in what processes are responsible for the sand budget changes at the coast of Schouwen, Vessem & Stolk (1990) distinguished a supratidal zone (mainly influenced by storm surges and eolian processes), an intertidal zone (influenced by eolian processes and wave action) and a subtidal zone (influenced by wave, wind and tide-related processes).

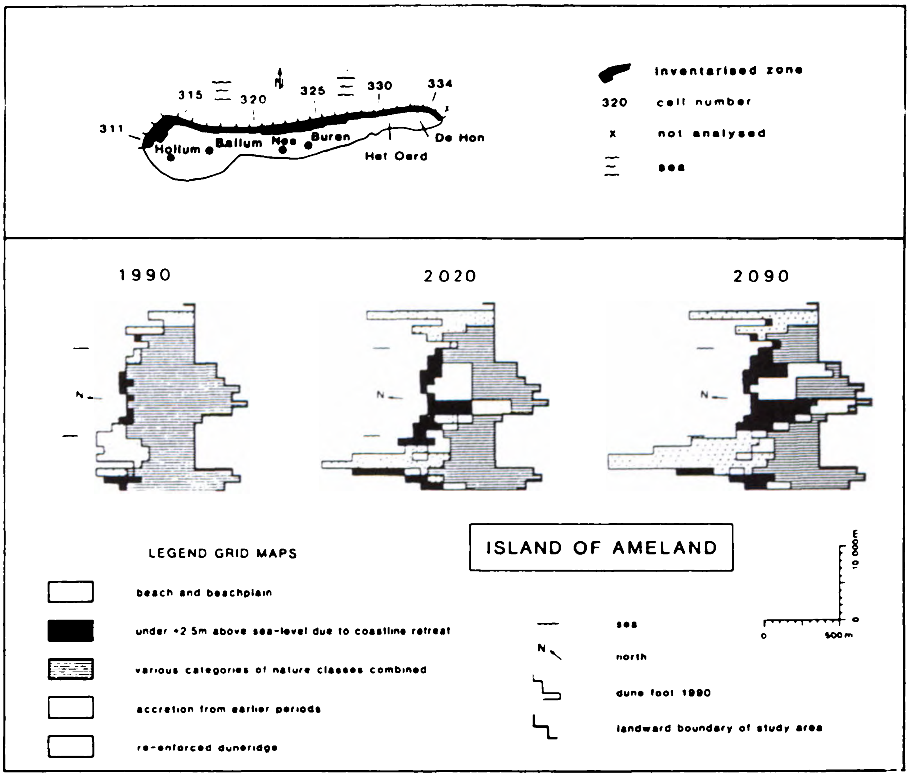
Erosion and accretion. To study the impact of accelerated sea level rise on the coqastal dunes, the Dutch Rijkswaterstaat carried out a large interdisciplinary study (Rijkswaterstaat, 1990). The study predicted coastline changes between 1990-2090. These predictions were based on trend analyses of long-term monitoring of transect profiles along the Dutch coast. Three possible scenarios of sea level rise were considered: 0.20 m/century (a projection of the present trend), 0.60 m/century (the expected trend) and 0.85 m/century (a pessimistic scenario which takes into account expected changes in wind and wave climate).

The effect of sea level rise on coastal foredunes largely depends on the amount of sediment available on the foreshore. If enough sand is available a rising sea level will cause dune formation. At present the majority of European coasts face a negative sediment budget (Meulen *et al.*,1991). This causes erosion and coastline retreat. Besides sediment budget, wave height and wave inclination are important aspects but these are still difficult to predict (see for example Booij & Holthuijsen, 1991).

The influence of coastline retreat on nature was studied with the help of a GIS (Meulen *et al.*,1991). Expected coastline changes for the period 1990-2090 (present trend scenario) are shown in figure 3 for the Wadden Island of Ameland. The loss of natural areas is also indicated. On Ameland both erosion (middle section) and accretion (end sections) will occur (though on the Dutch Wadden Islands as a whole erosion will prevail).

Erosion and a loss of land affects foredune ecosystems. On the Wadden Islands these often include primary dunes (dry and wet). They contain respectively pioneer communities of the xerosere (*Ammophilion borealis*; syntaxa after Westhoff, 1979), and the hygrosere (*Littorellion uniflorae*, Nanocyperion (eg. *Centaurio-Saginetum moniliformis*), *Caricion davallianae* and *Caricion curto-nigrae* (eg. *Caricetum trinervi-nigrae*). These vegetation types are very critical with regard to groundwater fluctuations. Characteristic plant species include *Centaurium littorale*, *Blackstonia perfoliata* ssp. *serotina*, *Sagina nodosa* var. *moniliformis*, *Parnassia palustris*, *Schoenus nigricans* and various species of Orchidaceae, *Juncus* and *Carex*. The loss of hygrosere habitats is serious because their vegetation is of high nature conservation value. A loss of secondary dune vegetations is not considered of immediate importance because these also occur in more inland dunes (eg. *Violion caninae*, *Ericion tetralicis, Calluno-Genistion pilosae*, all poor in lime).

Figure 3.
Coastline development and loss of nature between 1990-2090 on the island of Ameland as shown on grid maps in a GIS (Meulen *et al.*, 1991)



In the event of accretion, beach plains with embryo dunes and possibly also new primary dunes may develop. Beach plains and embryo dunes will support pioneer communities of the xerosere and halosere like the *Atriplicion littoralis, Salsolo-Honkenyon* and *Agropyro-Honkenyon.* Green beaches may develop at places where the sand is mixed with some silt or clay. Halosere communities like *Saginion maritimae*, *Armerion maritimae* and *Puccinellion maritimae* may develop here.

On the other hand a sea level rise may also drown plant communities of the halosere in the tidal marshes, especially the low lying communities of the tidal range.

The precise effects of sea level rise can hardly be predicted. They will depend on the sediment balance, not only of the coastal sand in the foreshore-beach-foredune system but also of the clay/ sand deposits at the intertidal zones.

It can be questioned whether sea level rise and consequent inundation by salt or fresh water (see next section) always results in loss of natural habitats. Accompanying the loss of dry coastal ecosystems would be a gain of wet coastal ecosystems, such as new wetlands and saltmarshes.

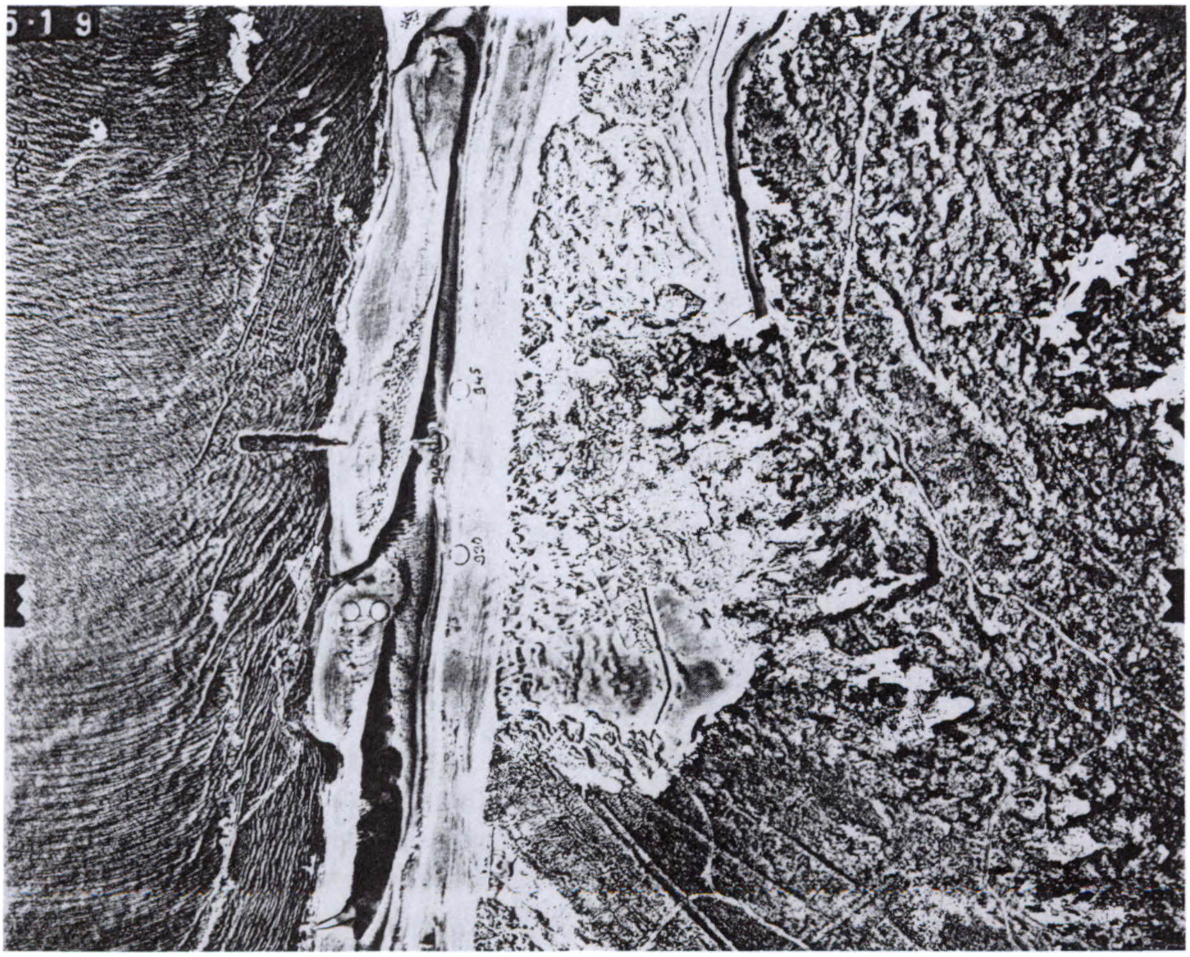
Coastal ecosystems will have a better chance of adjusting to increased sea levels when the systems can be kept in a certain dynamic equilibrium (IPCC, 1990). For purposes of coastal defence, soft options (sand nourishments) are preferred to hard structures (dikes, groins, floodwalls, seawalls). For nature conservation, soft options are also preferable to hard ones (cf. Louisse & Meulen, 1991).

There are two other effects of erosion of the foredunes. The first is a further inland influence of salt spray; the second is that the new "foredunes" will be overblown by fresh sand altering the morphology and the vegetation (see Figure 4). Apart from this the effects on the dry dune system may be minor. Salt spray may increase, due to the smaller distance to the sea. However, a loss in foredunes of 100 m width will hardly affect the amount of salts deposited in the inland dune system. Salt spray reaches background values at 1 km distance from the sea, but salt levels decrease rapidly (exponentially) over the first few hundred metres (Veelenturf, 1982). Thus, the majority of salt particles stays at the beach and a small increase in the inner dunes will not seriously change the vegetation.

2. Groundwater processes, inundation and desiccation

The rise and fall of the water table in dunes is one of the main controls of dune development. The response of the groundwater table to long-term coastal erosion is shown in figure 5 (Carter, 1991). It can be seen that a rising sea level, shoreline erosion and a narrowing of the dunebody may at first cause the phreatic level to decline and wet dune valleys to dry out. But at the onset of sea level rise, the phreatic level may rise and dune valleys may be inundated, either by fresh or salt water.

Figure 4.
Air photo of a part of the Island of Texel showing stable vegetation overblown with sand from eroding foredunes. Photo courtesy of Topographic Survey, The Netherlands



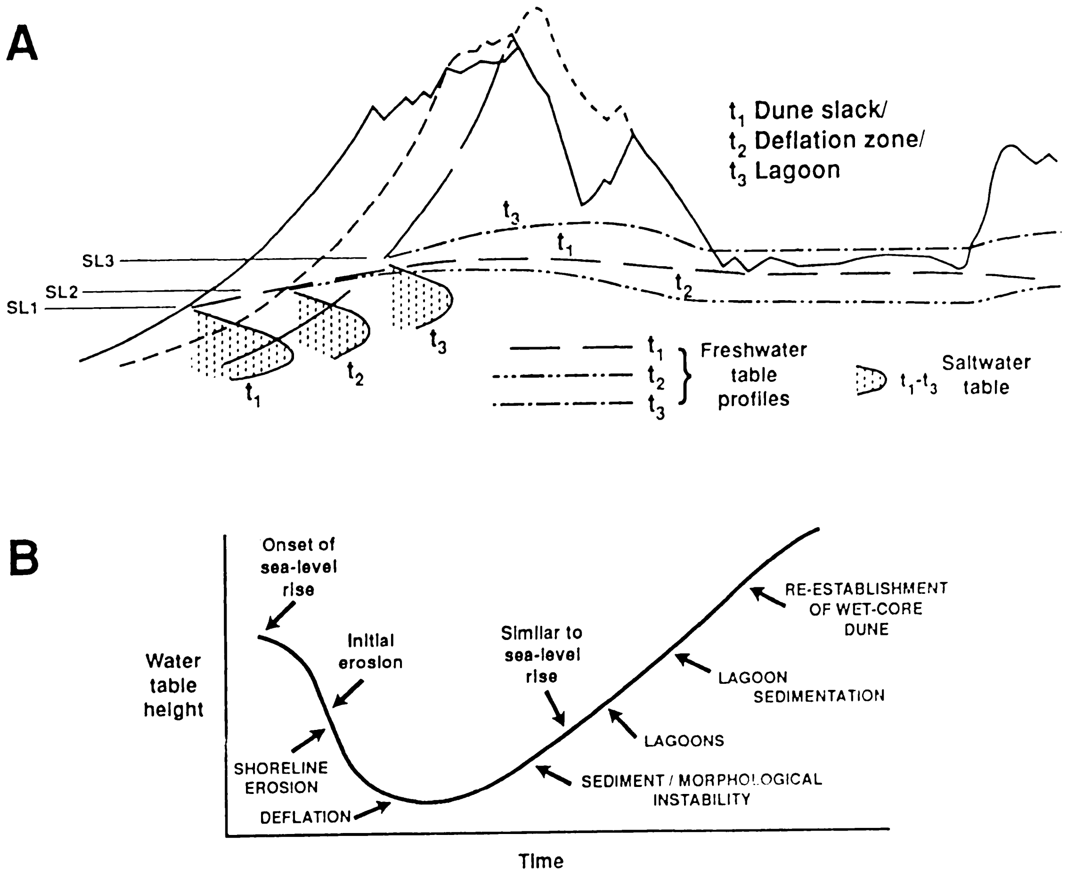
Noest (1991) simulated the impact of sea level rise on the phreatic level and the vegetation of dune slacks. With help of a interaction model "hydrology-vegetation" effects of coastline retreat on groundwater level and species composition of vegetation are predicted. The effect of sea level rise on the groundwater level in slacks appeared to be dependent on conditions like coastline retreat, original dune width, predicted sea level rise and the distance of the slack to the foredunes (Figure 6). Slacks with vegetation quadrat numbers 3,22 and 23 become wetter (shift towards top left) because the impact of sea level rise exceeds that of coastline retreat; slacks with all other nrumbers also become wetter first but then drier (shift towards bottom right) because the impact of coastline retreat exceeds that of sea level rise. The slacks furthest from the foredunes (top right numberrs) seem to react less spectacular than those closest to it (bottom left numbers).

Noest correctly points out that the vegetation of an old dune slack with a well-developed, humose soil will not be replaced by a pioneer slack vegetation by a mere rise of the groundwater level. Additional management activities such as removal of the top soil are needed to realise this.

Figure 5.

A) The response of groundwater to long-term shoreline erosion in a dune system.

B) Graphic representation of water table height over time through a phase of sea level change (Carter, 1991)



A map of the CO_2-induced change of precipitation (RIVM, 1991) for the June-August period indicates that, in summer soil becomes drier over very extensive coastal regions of middle and southern Europe in response to the doubling of atmospheric carbon dioxide. The summer decrease of soil wetness does not continue through winter, when precipitation increases (RIVM, 1991). Besides, the summer dryness will be enhanced due to the increased sunshine reaching the ground as reduced evaporation from drier continental surface causes a decrease in cloudiness (Titus, 1986). However, one should keep in mind that only these very broad scale features of the precipitation changes are significant.

A rise in sea level increases the level of soil salinity by altering the balance between freshwater and saltwater forces. Sea level rise in combination with a decrease in precipitation would result in a significant change of the fresh water dome of the inner dunes. The dynamic geohydrological balance in the dunes between fresh and salt water causes the ratio of h/H= 1/20 (h=height of phreatic level; H=depth of salt/fresh water boundary) (Bakker *et al.*,1979). For example,when the phreatic level decreases by 1m, the salt/fresh water boundary in the lower dune body will rise about 20m (Figure 7).

Figure 6.

Top: Position of species and main environmental variables (arrows) from a Canonical Correspondence Analysis. Species names from data of slack vegetations at Voorne, Netherlands. Wet slacks at top left (INUN), dry slacks at bottom right (DRY); slacks distant from foredunes at top right (DIST)

Bottom: Simulated shifts of slack-vegetations for the period 1989-2050 or 1989-2090 respectively under a limited coastline retreat of 25-50m (option 1) and an advanced coastline retreat of 50-100m (option 2) (Noest, 1991)

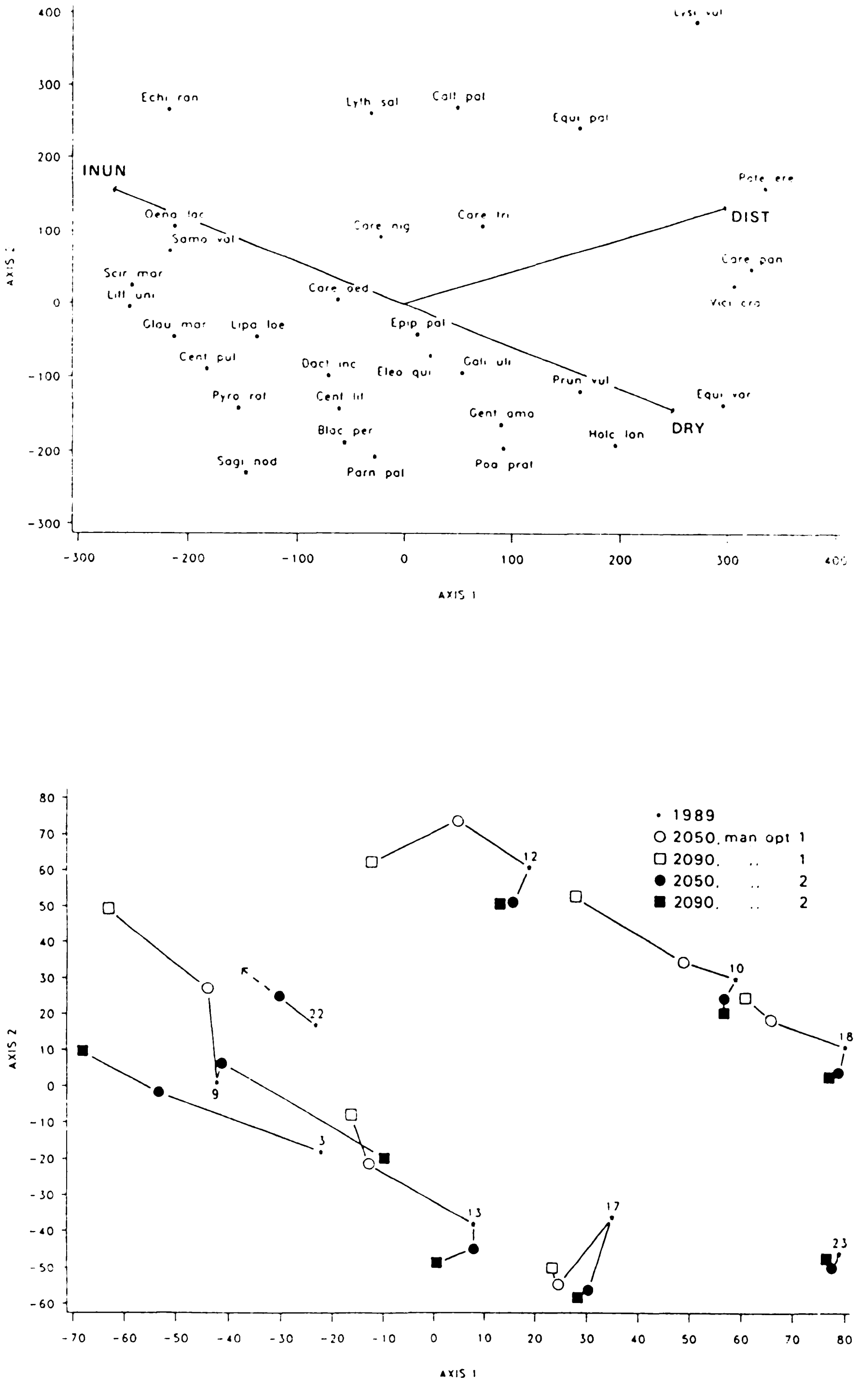
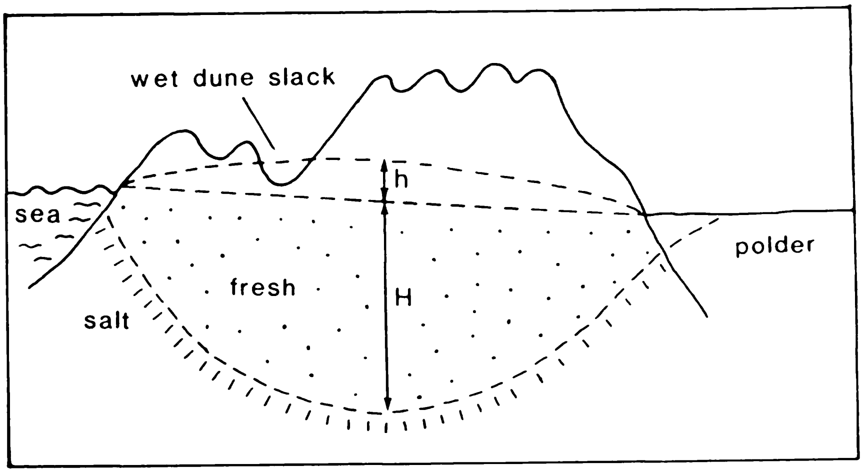


Figure 7.
Height and depth of the freshwater body in a coastal dune between sea and polder (after Bakker *et al.*, 1979)

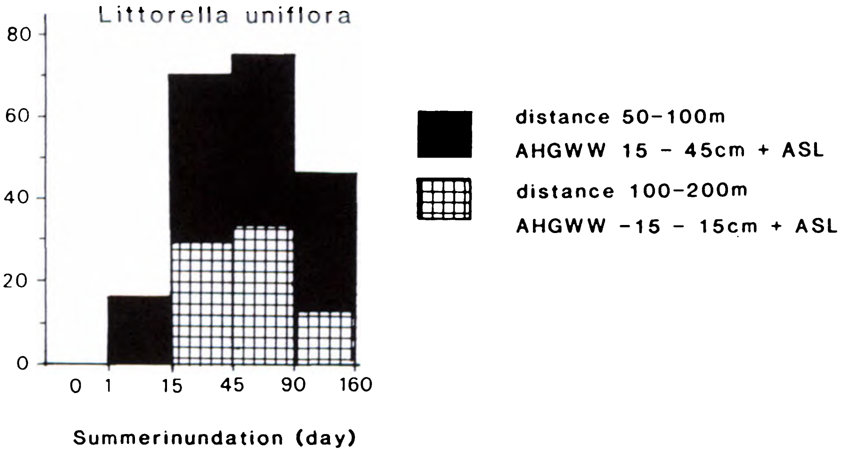


The micro-climate of dunes is usually very diverse due to the variable morphology, consequently site-to-site differences in irridation intensity and in shelter (Boerboom, 1964; Ranwell 1972; Boorman, 1977; Hundt, 1985), and the diurnal fluctuations in such parameters as temperature and relative humidity close to the dune surface may exceed the daily macro-climatic fluctuations during the growing season (Vestergaard, 1990).

A distinction should be made between the high-lying and low-lying parts of the coastal areas. The higher parts normally have a relatively low water table and changes of the water dome will hardly affect these parts. Here, the soils are freely drained, and temperature is the prevailing influence on the micro climatical conditions, which can be rather extreme in summer under the current climate (Ten Harkel *et al.*,1991). Besides by difference in age, the site-to-site variation in the vegetation of the higher parts of the dunes mostly seems determined by differences in micro-climate.

In the lower parts, the wet dune slacks, decrease of the summer precipitation and thus lowering of the freshwater table would induce a significant change of growth conditions for the vegetation. Obviously, on a local scale a change of vegetation belts from the drier to the wetter parts would occur. For example, Noest (1990) developed an interaction model on hydrology and vegetation of wet dune slacks, which is based on a dataset of c. 30 years. The results showed that there is a significant relation between amount of precipitation and the groundwater table and as a consequence changes of precipitation have a significant impact on the species composition of this type of ecosystems. She concludes that the period of inundation during the growing season (April - August) and the total yearly fluctuation of the water table in combination with the distance from the dune ridge are the most important variables for the plant species composition (Figure 8).

Figure 8.
***Littorella uniflora* uit Noest, 1990**



A negative development accompanying a sea level rise is the expected fall of the groundwater level in the dunes. This lowering is caused by narrowing of the dune strip due to erosion. This effect has been calculated by Arens *et al.* (1989) for the the Dutch coast using the formula of Bakker *et al.* (1979)

$$x_c = \frac{+2kD\Delta G}{P\Delta K}_{max}$$

Where:

ΔG = lowering of the ground water table at location x
P = net precipitation
ΔK = displacement of coast line
k = penetrability of the soil
D = depth of first waterproof soil layer
x_c = distance of location x from the polder

Arens *et al.* (1989) showed that this effect can be serious. For example, a coastline regression of 100 m at a place where the dunes are 3 km wide will cause a lowering of water table in excess of 40 cm in these dunes. The geographical impact on dune slack vegetation of a fall in groundwater level was studied by Arens *et al.* (1989) with help of a GIS.

3. Change of soil parameters

The three major consequences of "global warming": sea level rise, the increase in temperature and changes in the precipitation, resulting in a lower rain water surplus, have an impact on soil processes.

At the beach and the developing dune system, desalinisation plays a major role. The process of desalinisation is regulated by the amount of surplus precipitation, due to the rapid dissociation of NaCl in water (Klijn, 1981). In soils at the beach, desalinisation will be counteracted by increased frequency and duration of flooding with salt water. Desalinisation in pioneer dunes will slow down, due to a shift in the balance between precipitation and evaporation.

In the fore dune system, decalcification may be affected by changes in the precipitation surplus. The dissolution of $CaCO_3$ is dependent on the amount and the pH of percolating water (Klijn, 1981). The decrease in precipitation surplus will negatively affect the rate of decalcification. In addition, in the drier fore dune system plant growth, production of organic material and decomposition processes may be retarded because of water stress. In dry grasslands, soil respiration is primarily regulated by soil moisture (Hunt, 1977; Orchard & Cook, 1983). Decomposition and mineralisation processes are stimulated by an increase in temperature, but may be more sensitive to the low availability of water (van Beckhoven & Ernst, 1990). This results in a slowing down of soil development and a further decrease in decalcification because of a decrease in the internal production of acid components (de Vries & Breeuwsma, 1986). The slowing down of soil development may also result in an increased sensitivity to wind erosion (Jungerius & Meulen, 1985) and desertification.

In salt marshes, the increase in flooding regime will have an impact on several soil processes. The rate of desalinisation will decrease, also due to a decrease in the surplus of rain water. The development of soils may locally be affected by an increased deposition of sediment, while other parts disappear, depending on the balance between sedimentation and subsidence (Baumann *et al*.,1984). Furthermore, flooding may result in anaerobic soil conditions (Patrick & Delaune, 1977), affecting the formation of soil toxins, such as sulfide and Fe^{2+} (Mendelssohn *et al.*, 1982, King *et al.*, 1982). The rise in temperature influences soil processes such as decomposition and mineralisation. In the salt marsh, where water deficits do not occur for long periods, the cycling of nutrients may be accelerated. Also depending on the negative effects of anaerobic conditions on the availability of N (Patrick & Delaune, 1977) and a positive effect on P through the dissociation of $Fe^{3+}PO_4$ (van Dijk, 1985), this may lead to a higher trophic status of the system.

In inland (dry) dunes, soil processes may be slowed down. Rates of decalcification decrease, due to changes in water regime. Decomposition and mineralisation probably slow down, because of prolonged periods with water deficits. Acidification of the soil may occur at a lower rate, due to a decrease in decalcification, internal production of acids and a (small) increase in salt spray (Veelenturf 1982). The latter has a positive impact on the base status of the soil exchange complex, which forms the major buffer capacity in decalcified soils (Vertegaal *et al.*, 1991). In more advanced stages of soil development and vegetation succession, podzolisation and the formation of organic eluvial horizons, will become an important soil process. Podzolisation is stimulated by a high amount of percolating water, a low pH, the presence of slowly decomposable organic matter and a low temperature, slowing down decomposition processes (Scheffer & Schachtschabel, 1982). These factors are all affected by"global warming", with the result that the overall changes are negative for the process of podzolisation.

In wet dune valleys, the impact of "global warming" depends on the balance between the positive effects of sea level rise and the negative effects of loss of the fore dunes and a decrease in precipitation surplus on the groundwater level (see also section 2). In case of a rise of the groundwater level, the non-adapted existing vegetation may die. This results in a flux of organic material and, in combination with the wetter conditions, in an increase of decomposition and mineralisation (Louman & Slings, 1990; van Beckhoven & Ernst, 1990) and a decrease of the amount of organic matter (Beijersbergen, 1990). The nutrient availability may further increase by the anaerobic conditions affecting the dissolution of $Fe^{3+}PO_4$ (van Dijk, 1985). In dune valleys with a lowering water table, drier conditions may result in the death of the vegetation and a temporary flux of organic material. Increased rates of decomposition may increase the availability of nutrients. After this temporary eutrophication, leaching and acidification may occur (Louman & Slings, 1990).

4. Change of vegetation parameters

The growth-stimulating effect of elevated CO_2 concentration has been reported by many authors (eg. Carlson & Bazzaz, 1980; Kramer, 1981; Cure & Acock, 1986). A change in respiration of 5 to 45 % has been reported, which would affect growth and at the same time more CO_2 is re-emitted (Gifford *et al.*, 1985). A comprehensive review of agricultural crops by Kimball (1983) indicates that for all of the many species which have been studied in this regard, the mean increase in crop yield produced by a doubling of the air's CO_2 content is approximately 33%. Generally speaking, plants with a potentially high relative growth rate accelerate their growth at the expense of other plant species, and as a consequence the plant species composition would change.
Temperature increase affects the physiology of plants, e.g. the rates of photosynthesis, respiration and transpiration change under changed temperature regimes. A relatively small increase in temperature of 1 or 2°C would cause a significant change in net photosynthesis of all plant species (Larcher, 1980). Similar to CO_2 enrichment, temperature increase may cause particular plant species to grow more vigorously than other plant species, and as a consequence the species composition of the dune ecosystems would be affected.

Generally, vegetation in coastal dune systems is distributed along a primary gradient according to sand stability and a secondary gradient along the slope of dunes according to a seasonality of fresh and salt groundwater.

In dry dune habitats which ecologically are characterised by low availability of water, due to low field capacity of the substrate, an increase in aridity generally will further favour xerophytes in competition with non-xerophytes. Xerophytes are plants growing in xeric or dry habitats and are able to tolerate drought for at least part of their lives (Woodell, 1973). The response of the species will, however, depend on their water interception strategy (Boorman, 1977). Deep rooting geophytes, such as *Ammophila arenaria*, and species with deep tap roots, such as *Hypochaeris radicata* and *Artemisia campestris*, exploiting deeper, more moist sand layers, may be less influenced by increased aridity than species with more superficial rooting systems, such as *Sedum acre* and *Carex arenaria* (Vestergaard, 1990).

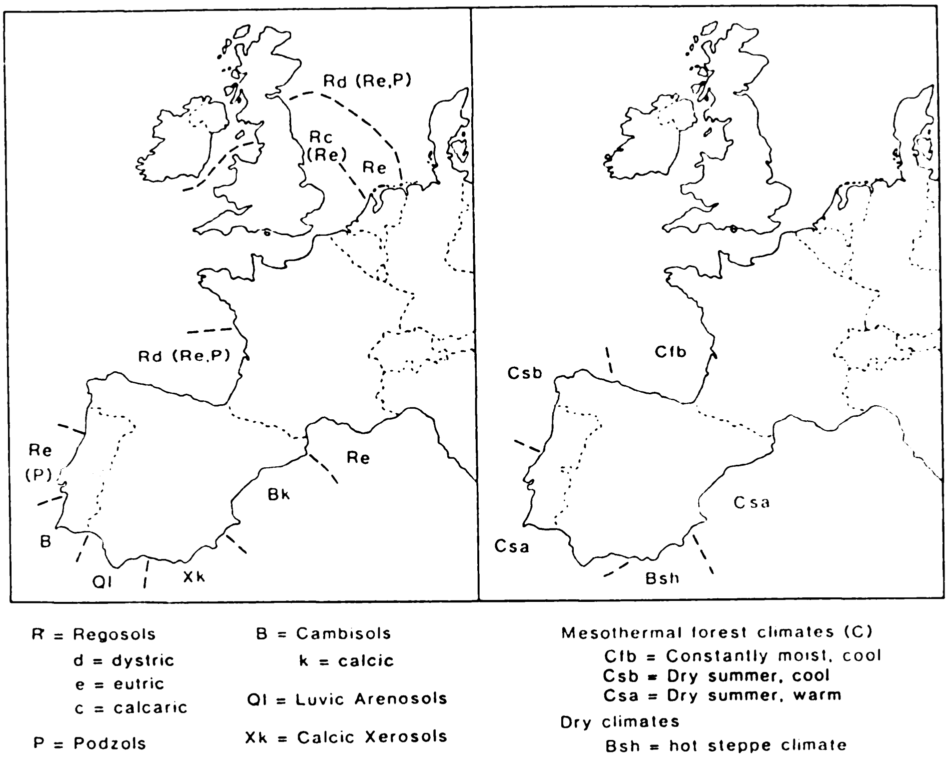
Increase in aridity may cause invasion of southern species and an extended distribution of continental xerophytes, already present, such as *Silene viscosa* in Denmark (Vestergaard, 1990), in a northward direction. Species with a more oceanic or northern distribution may be suppressed along their southern limit of distribution.

In the wet dune habitats a more local shift of species composition would appear, viz. when a change of the ground water table occurs, plant species of moist parts, such as *Littorella uniflora* and *Leontodon nudicaulis*, would shift to the more wet parts of a slack, and similarly plant species characteristic of wetter parts, such as *Thalictrum flavum* and *Potamogeton gramineus*, would shift to even wetter parts. Accurate predictions of the overall change in plant communities will require a detailed knowledge of the life strategies of individual species and the way they react with each other. The HYVEG model of Noest (1991) is an example of how this can be carried out. However, this model requires many input variables. It may be feasible to consider a small number of species which have vulnerable stages in their life cycles.

A changing European scene: soil and vegetation

To discuss the impact of climate change on a wider scale, we consider the European coasts. Europe has a long coastline with a great variety of dunes, in many cases also exemplary to the situation in other parts of the world (Gehu, 1985; Olson & Maarel, 1989). The Baltic, Atlantic and Mediterranean coasts have their own contrasting climates (see Figure 9, after Sevink, 1991).

Figure 9.
Left: Major soils in the coastal dunes, classified according to the FOA/UNESCO Soil Map of the World and based on the soil map of the European Communities 1985
Right: Climates according to the classification of Köppen



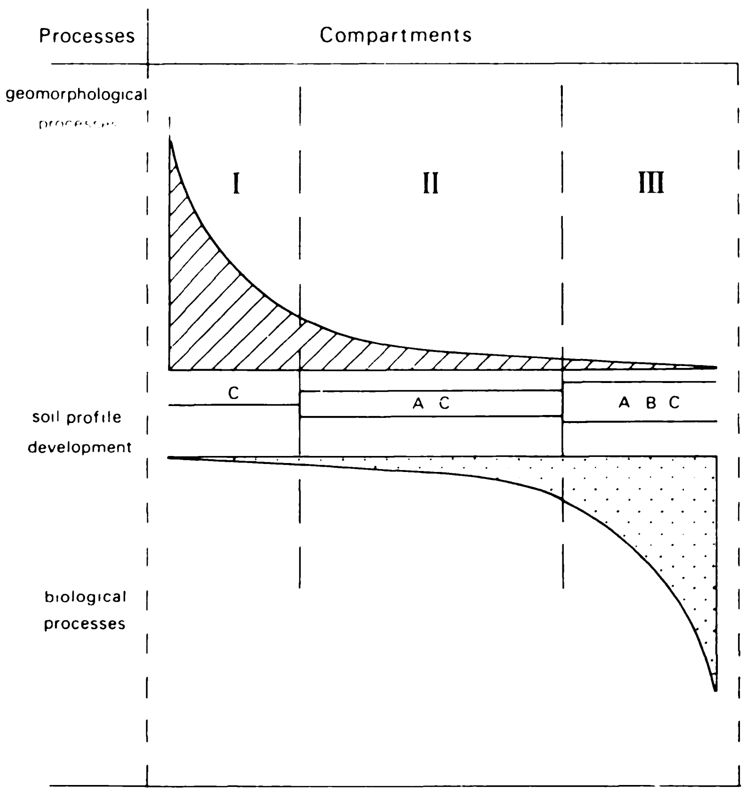
To discuss impacts of climate change on European dunes we select the soil as key factor in the ecosystem. The soil profile reflects the balance between geomorphological and biological processes (Figure10, after Jungerius & Meulen, 1988). Dunes of the European coasts range from recent, active dunes with sparse vegetation to old dunes which have been stable for many centuries and carry a well developed vegetation. Young, incipient soils {C or (A)C profiles} reflect a dominance of geomorphological processes and active dunes with scarce, low vegetation. Mature soils {AhC, A(B)C or ABC profiles} reflect a dominance of tall vegetation successional on stable dunes. In European dunes three divisions can be distinguished:

division I:	active dunes with minimal soil formation and initial vegetation succession
division II:	intermediate between I and III
division III:	stable dunes with optimal soil formation and final vegetation succession, starting with grasses and shrubs but finally developing into a forest

The divisions run more or less parallel to the shore. Division I corresponds to the white and yellow dunes of traditional literature; division III to the grey and black dunes.

A change in climate which favours vegetation growth will cause the situation of compartment III to predominate while the reverse will cause active dunes to prevail.

Figure 10.
Schematic presentation of interaction of main processes of dune ecosystems (coastline morphology and groundwater not included) (Jungerius & Meulen, 1988)



In European literature on coastal dune soils little or no attention is paid to soil development in relation to climate. Recently, a useful paper appeared by Sevink (1991). He argues that the available studies are too limited in number and to varied with respect to mineralogy and lithology of the sand, vegetation and age of the deposits, to allow detailed description of the effects of climate. However, general trends can be mentioned. Sevink (1991) distinguishes two major soil forming processes in dunes (their effects being different in freely drained and poorly drained soils):

1) accumulation of organic matter, and
2) leaching and related processes, eventually leading to podzolisation.

Accumulation of organic matter

This process is:

a) well developed in boreal (northern Europe) and humid temperate climates (north-western Europe)(mor humus types),
b) lesser developed in less humid temperate climates (south western Europe)(moder) and
c) slightly developed in Mediterranean climates (southern Europe) (moder-mull) (Figure 11).

For poorly drained soils trends will differ. Litter decomposition will vary in relation to soil temperature. It will increase with increasing temperature and this will decrease the accumulation of organic matter.

Figure 11.
Main European coastal climates and soil forming processes

	BOREAL	TEMP.OCEANIC		MEDITERRANEAN
		humid	dry	
leaching	+ +	+	+ −	−
organic matter accumulation	+ +	+ +	+ −	−
humus type	mor	mor	moder	mull

+ + = very pronounced, + = pronounced, + − = slightly pronounced, − = not pronounced

Leaching and related processes

Dune soils have low water storage capacity and high permeability and therefore are susceptible to rapid leaching. The leaching depends on the initial carbonate content because the remaining quartz fraction of the dune sands has a very low acid-buffering capacity. Leaching is:

a) high in boreal and perhumid oceanic climates with a precipitation surplus,
b) lower in temperate oceanic climates where podzolisation only occurs in very old dune soils, and
c) lowest in mediteranean climates where podzolisation is negligable (Figure 10).

Generally, a higher precipitation surplus and lower temperatures are associated with lower rates of organic matter decomposition and concurrent acidification.

Studies from Portugal indicate that the southern limit for podzols in Holocene dunes more or less coincides with the 600mm isohyete.
A precipitation deficit will prevent decalcification while a surplus will lead to decalcification, acidification and finally podzolisation. Higher temperatures and higher precipitation deficit will lead to lesser leaching and lower acidification.

The effect of climate changes is expected to be most evident in areas which already have low precipitation surplus. In areas with larger surplusses effects will be less prominent because the important processes of acidification and podzolisation will be little affected.

Climate changes

Regionalised climate maps (RIVM, 1991) indicate changes in climate for Europe. We have used maps depicting current climate and GFDL scenario (which showed most pronounced changes). The maps give temperatures and precipitation for the winter (December-February) and the summer (June-August). It should be realised that the maps indicate general changes over the entire European continent. The special character of the coastal areas is not taken into account. Furthermore only average values are given; extreme events, often triggering changes, are not known. Also the diverse influence of man on the coastal systems is not accounted for.

The expected climate change and its possible effect on soils and vegetation of Europe's dunes is summarised in Figure 12.

Precipitation
All the regions of Europe (southern Baltic, northwest Europe, southwest Europe, Mediterranean) show a decrease in summer precipitation of about one class (25mm in three months). In the Mediterranean, the decrease may be more than one class. This is also the case in Atlantic France and Spain and in parts of Portugal. In winter there is no distinct change.

Temperature
All regions show an increase in summer and winter temperatures of one class (5°C).

Figure 12.
Summary of expected climate change and impact on soil and vegetation of European coasts

	BALTIC	NORTHWEST	ATLANTIC-SOUTHWEST	MEDITERRANEAN
summer precipitation	—	—	— —	— —
temperature (summer and winter)	+	+	+	+
impact on soils	more organic matter decomposition less podzolisation		southern limit of podzolisation shift northward	less decalcification more salinisation
impact on vegetation	increased growth shift from needle to deciduous trees stable surface	favour xerophytes		mediterranean species move northwards unstable surface

Effects on soils and vegetation

For the Meditteranean areas a higher precipitation deficit is expected caused by less rainfall and higher temperatures. This will result in lower decalcification and acidification rates. In poorly drained soils salinisation may become imminent. In general, vegetation growth and cover is impeded and active dunes become more common. This could be especially in the western Mediterranean. A higher evapotranspiration, particularly in Mediterranean *Pinus*, will lead to lowering of the level of the water table and further water deficiency in soils.

For Portugal, Atlantic Spain and Atlantic France the southern limit of podzolisation may shift northward. Also the southern limit of coastal maquis may shift northward. A change in species composition is also possible for this area because Mediterranean plants appear to have a higher tolerance for water stress than oceanic species (Merino, 1986).

For northern Europe (Atlantic and Baltic) no important changes are to be inferred from the maps. A somewhat warmer and slightly drier climate might favour the decomposition of organic material and impede podzolisation in Baltic regions. Moder-mull type humus could become more common. Consequently, a better vegetation development could lead to more stable dunes. Famous mobile dune systems like Slowinsky (Poland) may change this way. In northern regions which are warmer (Atlantic/North Sea), slightly less rainfall and higher temperatures may favour xeric situations and influence the competition between mesophytes and xerophytes accordingly.

Conclusions

To monitor the effects of climate change various processes can be considered as discussed in this paper. Shoreline processes can be monitored, or changes in relief and concurrent vegetation cover, changes in groundwater level, changes in soil processes (such as decalcification, podzolisation or accumulation of organic matter) and changes in species or vegetation. Of those, biological processes usually react most quickly. Impacts of climate change on ecosystems or species might be revealed at an early stage.

When monitoring ecosystems or species, it is important to realise that coastal dunes do not represent systems on their own. For example there is a ecological relationship in Europe between grasslands of calcareous dunes (*Galio-Koelerion* Ass.) and chalk grasslands (*Mesobromion* All.) of England, Netherlands and Germany (a species showing such a relationship is *Carlina vulgaris*). Monitoring species or communities which have a wider distribution over Europe will make climate change predictions more widely applicable.

A useful plant life form strategy system for monitoring purposes is that of Raunkiaer (1934). He distinguished functional life form strategies on the basis of the way in which plants survive the unfavourable season (i.e. winter frost or drought) with their buds, i.e. the height of the buds above ground in the unfavourable season. It appears that the hemicryptophytes are a useful category. Hemicryptophytes are plants with periodic shoot reduction to a remnant shoot system that lies on or near the ground surface (others have shoot systems remaining more than 50cm above ground or reduce the shoot system to storage organs below ground). Future temperature changes will be most apparent immediately at or near the soil surface and hemicryptophytes might therefore be sensitive indicators to such changes.

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The impacts of climate change and sea level rise on the ecosystems and biological communities of oceanic islands: examples from the tropical Pacific

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Abstract

This review considers the potential impacts of climate change and sea level rise on the species and ecosystems, both marine and terrestrial, of oceanic islands. It is suggested that the consequences of predicted changes for the native fauna and flora of islands may be considerable given the limited land areas, isolation, unusual guilds of species, high rates of endemicity, and low species diversity characteristic of the terrestrial biological communities of small islands. For shallow water marine and coastal communities the impacts may be locally severe although the losses in terms of species extinctions may be less important from a global perspective given the generally wider geographic distribution of such species.

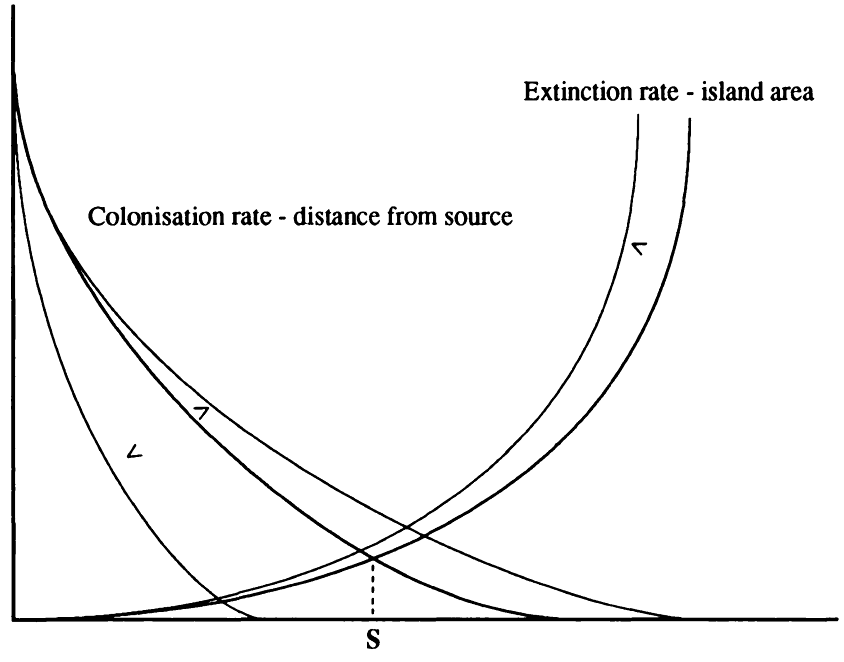
Introduction

Climate change and island biogeography

The "distant" view of the biological communities of islands, as seen from the perspective of the MacArthur Wilson models of island biogeography (MacArthur & Wilson, 1967) suggests that the structure and diversity of the biological communities found on islands is a reflection of the dynamic interaction between island size - which affects species extinction rates - and the distance from the nearest source of propagules which alters colonisation rates. The number of species present thus represents a dynamic equilibrium between these two opposing processes (Figure 1).

Under scenarios of global climate change and sea level rise both of these parameters will change. Island size or area is likely to diminish, both as a consequence of inundation of low-lying coastal areas and of enhanced erosion rates. Decreased land area will increase extinction rates in proportion to the area of land lost.

Figure 1.
Equilibrium curves under present circumstances resulting in equilibrium number of species S. < and > indicate possible shifts as a consequence of global climate change. Decreased island areas will result in enhanced extiction rates while changes to wind and ocean current speed may change colonisation rates positively or negatively.



Under future climatic conditions, distance from a mainland source of propagules may be effectively altered by changes in ocean current patterns, or wind strength and direction.

Depending upon the location of the island in relation to sources of colonising individuals; the future pattern of such environmental variables; and, the modes of dispersal of the species concerned, changes may be either positive or negative, reducing or enhancing colonisation rates (Figure 1).

The "near" view of biological communities on islands such as that of Lack, (Lack, 1969; Pernetta & Watling, 1979) suggests that the MacArthur Wilson models only provide a global explanation for island diversity. The "near" view suggests that other abiotic features of individual islands such as topography, climate and edaphic factors also play a significant role in determining the species composition of an island community. Geology and pedology affect the species composition of vegetation with volcanic islands, for example, generally having a more diverse plant community than raised limestone and atoll islands in the tropical Pacific. Of the 1,371 plants of New Caledonia for which data on preferred soil types are available, 30.8% are limited in distribution to areas of ultrabasic rock (Morat *et al.*, 1984).

Biotic factors may also influence the species composition on particular islands. The existence of guilds of birds (Diamond & May, 1976) may result in environmentally similar islands supporting quite different avian communities depending upon the sequence of colonisation and establishment of the individual species forming such a guild. In addition it is well recognised that specialist birds such as obligate frugivores and top predators are dependent on the existence of large enough populations of their food species in order to maintain viable populations on isolated islands.

Much of the biogeographic literature concerned with island communities and ecosystems has considered only the terrestrial fauna and flora for which the ocean forms a barrier to dispersal. Indeed the biogeographic models themselves were developed on the basis of empirical data from such terrestrial faunas and floras. The same assumptions used in developing such models are however, equally applicable to a consideration of the composition and diversity of the shallow water marine communities on oceanic islands, where the open ocean separating individual islands or archipelagos functions as a filter or barrier to dispersal. In the case of shallow water benthic organisms, dispersal normally occurs during the planktonic phase of the life cycle. The length of the planktonic stage of the life history determines in part the width of the open ocean barriers which can be crossed. The significance of floating materials such as pumice in assisting dispersal of benthic organisms including corals over long distance should not be ignored. Floating debris serves as a temporary base for attachment of metamorphosing larvae, effectively increasing the length of the dispersal phase.

For shallow water benthic organisms the effectiveness of the oceanic barrier reflects both the physical distance separating suitable oceanic island habitats; the direction, speed and continuity of currents; and the length of the planktonic stage of the life cycle. A major change in the pattern of oceanic currents such as occurs during El Nino Southern Oscillation (ENSO) events in the Pacific can effectively alter the rate of dispersal and successful colonisation. The implications of such changes for future dispersal and colonisation of shallow water marine organisms is difficult to predict with any certainty in the absence of regional and sub-regional models of future ocean current regimes. Despite this unpredictability, it is possible to state with some confidence that changes in colonisation rates are likely to be more important to the fate of the shallow water marine species and communities than changes to extinction rates. Since reduction in the physical extent of the shallow water habitats of oceanic islands is likely to be small, at least for the foreseeable future, extinction rates will be relatively unaffected by climatic changes and sea level rise.

The biogeographic patterns of present distribution among pan-tropical and sub-tropical shallow water marine organisms reflect temporal patterns which are generally "older" in a geological sense than patterns of distribution displayed by the terrestrial biota of oceanic islands. This reflects in part the greater rates of insular and archipelagic speciation amongst terrestrial organisms, and in part the original contiguity between shallow water marine communities which existed at a time when the Tethys sea provided continuous connection between the major ocean basins. Geologically old affinities are found in some terrestrial plant genera such as *Nothofagus*, *Auracaria* and *Agathis* for example but, many elements of the terrestrial fauna of Pacific islands display affinity with the oriental region rather than with more ancient Gondwanaland stocks.

Terrestrial insular communities: some examples from the Pacific

Diversity and endemicity

Although insular communities tend to have a low species diversity compared with an equivalent area of continental mainland, they are characterised by high rates of endemicity, as the following examples illustrate. The Fijian fauna includes only 59 species of land birds, (compared with the 670 species found on the much larger island of New Guinea). Of these however, 21 species are endemic to Fiji and most of those have distributions restricted to only part of the Fijian Archipelago (Pernetta & Watling, 1979). The Juan Fernandes Islands, 600 Km off the coast of Chile have a flora of only 147 indigenous angiosperms of which, 69% of the species and 19% of the genera are endemic (Skottsberg, 1956; Stuerssy *et al.*, 1984).

Such high rates of endemicity are displayed by particular genera or colonising stocks which have undergone archipelagic speciation, amongst which the honey creepers (Drepanididae) of Hawaii; the finches (Geospizinae) of the Galapagos and the moas (Dinornithidae) of New Zealand are well known examples. Less spectacular radiations are found in other groups such as the fruit doves of the genus *Ptilinopus*, five species of which occur in Fiji, Samoa and Tonga. Three of these species have restricted distributions centred around a single major island within the Fijian archipelago (Watling, 1982).

Not only are such patterns of speciation found in all terrestrial avifaunas throughout the Pacific and Indian Ocean archipelagos but they are also paralleled amongst less well studied vertebrate groups such as the reptiles. The pantropical gecko genus, *Lepidodactylus* is represented throughout the Pacific including Fiji, by the ubiquitous, hermaphroditic species *Lepidodactylus lugubris*. In Fiji an endemic species *Lepidodactylus manni* is also present. The skink genus *Emoia* has radiated widely, with allopatrically distributed endemic species occurring on islands throughout Melanesia and Central Polynesia. New Caledonia is home to two endemic gecko genera.

Similar patterns of endemicity are observed amongst invertebrate groups such as the picture winged *Drosophila* of Hawaii (Carson, 1984). In this case careful genetic analysis provides a reconstruction of the sequence of evolutionary events which have lead to the present species diversity within this group of closely related flies. This analysis provides insights into the long-term (geological time scales) response of genetic stocks, isolated on islands subject to submergence and changes in shape and size occurring over periods of thousands and millions of years.

The end product of a critical examination of the biogeographic and species distribution patterns displayed by the faunas of Pacific Islands leads to a conclusion that conservation issues in terms of maintaining species are perhaps more pressing in the tropical insular Pacific than elsewhere. Dahl (1984) has calculated for example that there is in the insular Pacific, one endangered species of bird for every 90,000 inhabitants, a high figure compared with Australia which has one endangered species for every 840,000 people. This figure was calculated as a measure of response capability but from the perspective of conservation needs the situation is better exemplified in terms of the numbers of endemic species per unit of land area which Hay (1985) suggests is higher in the Pacific than any where else in the world.

Community structure

Within the tropical Pacific, island ecosystems are dominated by forest formations with dense closed canopy rainforests typical of the high and wetter islands of Melanesia and Polynesia and less dense more open vegetation in drier areas such as the western side of Viti Levu, Fiji. Smaller islands tend to display open canopy forest, dominated by species such as *Pisonia grandis*, while atoll islands have far fewer woody species and a generally depauperate floral community. The flora of the Marshall, Gilbert and Ellice islands for example contains only 63 genera of plants; that of the Line islands, Phoenix and Tokelaus, 36 genera. The flora of these islands is dominated by associations of tropical shore plants such as *Barringtonia, Casuarina* and *Ipomea* (Van Balgooy, 1960). In terms of the biogeographical affinities of such floras most species are widespread opportunistic species with a high tolerance for calcareous, nutrient poor soils and maritime conditions.

Atoll islands - In general terms the land areas and elevations of atoll islands are such that this category of island may be considered as being the most susceptible to climate change impacts. A ranking of physical vulnerability to rising sea level (Pernetta, 1990) suggests that of the twenty four island groups of the Pacific Basin the most vulnerable to climate change are the atoll archipelagos of the Tokelaus, the Marshalls, Tuvalu, Line islands and Kiribati. For most of these islands the bulk of the land area, up to 85% in some instances, is at or below one metre above sea level and maximum elevations may be as low as eight metres. From the perspective of the conservation of botanical diversity however their vulnerability may be considered unimportant since few species are endemic to these island groups. In addition most are "r" adapted species which might be expected to adapt most rapidly to changing environmental conditions, including erosion and shifts in location of the islands upon which their populations are presently found.

High islands - In contrast, the floras of high islands in Melanesia and the central Pacific include a greater number of species of conservation interest. The Bismark archipelago contains some 514 genera including one endemic genus *Clymenia* and 42 genera for which the Bismarks represent the eastern limit of their distribution. Passing eastward the flora of the Solomons contains 431 genera, that of Vanuatu 371, 449 in Fiji and 302 in Tonga (Van Balgooy, 1960). There are 12 endemic genera in Fiji including the monotypic, primitive *Degeneria* which forms a separate family. Most of the endemic species and genera in the flora of Melanesia and the central Pacific are "k" adapted species found in closed canopy forest formations.

In their detailed analysis of the floristic relationships of New Caledonian rain forest phanerogams Morat *et al.* (1984) show that the proportion of endemic species is higher among the rainforest species than in the total flora. Ninety percent of rainforest species (1,358 out of 1,511) are endemic compared with 76% for the total flora (2,474 out of 3,256). Similar patterns of endemicity are found in the flora of other Pacific islands and are in turn reflected in the patterns of habitat distribution amongst the native vertebrates. Pernetta and Watling (1979) showed that for the native vertebrates of Fiji 66% of the mammals; 87% percent of the birds; 59% of the reptiles and both amphibian species are found predominantly in forest habitats. Among the 59 native land bird species 18 are confined to rainforest and only 23 species (43%) can be observed in agricultural areas, while 15 species (28%) are found in suburban areas. Seven of the 17 native reptiles are also confined to forest habitats.

In the majority of cases however, the native forest vertebrates of Fiji may be found in both montane and lowland wooded habitats suggesting a lack of habitat and ecological specialisation among the Fijian vertebrates which is characteristic of mainland vertebrate faunas (Lack, 1969). For the fauna of island archipelagos such as Fiji, allopatric distribution of congeneric pairs of species appears to be the most important form of avoiding competition. One congeneric pair of bats and five congeneric pairs of birds occur sympatrically in Fiji and in all but one case, one of the species is restricted to forest habitats while the other is a more generalised species with wide habitat tolerance. All other congeneric pairs are allopatrically distributed on different islands.

Climate change impacts on native habitats and species

The coastal and low lying habitats of tropical high islands are generally dominated by the same widely distributed species of plants and animals that are characteristic of the floras and faunas of lower lying atoll islands. Such species and communities, although they are likely to be immediately and directly affected by climate change and sea level rise contain few species of conservation concern. The "r" adapted species characteristic of such floral formations have high dispersal capabilities such that individuals may be expected to recolonise rapidly following local extinction. The overall impacts of climatic change and sea level rise on global biodiversity through total extinction of such species is therefore unlikely to occur within the foreseeable future, even under scenarios of extremely rapid sea level rise.

From a local perspective losses of biodiversity may in some instance be significant. If for example, mangrove habitats on low islands are lost or significantly reduced in extent as suggested by Ellison (this volume) then the consequences for dependent species of vertebrates and invertebrates may be significant, with potential environmental and economic consequences for human populations. Mangroves and seagrass communities on small islands in the Pacific although important in a local context are not generally important from a global perspective, representing as they do attentuated sub-sets of species derived from the more species rich areas in western Melanesia and the Oriental region.

In contrast the native forest formations of high islands contain a large number of plant and animal species of conservation interest. Such communities and ecosystems may be considered to be most vulnerable to any changes in rainfall and to a lesser extent changes in temperature rather than physical changes resulting from sea level rise and enhanced erosion rates.

The altitudinal distribution of plant and dependent animal communities will change under warmer climates since the altitudinal limits of natural vegetation will extend upwards by around 320 metres for a two degree rise in temperature. The upper limit of the lower montane forest which presently extends to between 1,500 and 2,000 metres in New Guinea (Johns, 1977) would rise to between 1,800 and 2,300 m. The upper limit of the mid-montane forest would gradually rise from 2,700-3,000 to 3,000-3,300 metres. The upper montane forest which presently extends over a relatively narrow altitudinal band to 3,200 metres would seriously encroach on the sub-alpine and alpine grasslands and shrublands which would disappear from most of Papua New Guinea remaining only around the summits of Mt Wilhelm and Mt Giluwe (Hughes & Sullivan, 1990). Hughes and Sullivan also argue that the increased productivity and altitudinal range within which subsistence agriculture can be practiced would result in further reductions in the extent of natural vegetation in the heavily populated highlands regions of the country.

The consequences of such changes may be severe for restricted montane ecosystems in eastern Melanesia which will be dramatically reduced in extent and further fragmented into smaller habitat islands leading to greatly increased extinction rates. Similar changes can be expected to the altitudinal distribution of montane forest types in all high islands including such species rich communities as those of New Caledonia and Fiji. Again the consequences may be less important from a conservation perspective than might appear at first sight, since the alpine flora of New Guinea is a mixture of "young" species from Malaysian, Australian and New Zealand sources with little generic endemism (Diamond, 1984).

Of wider concern from the perspective of forest cover on Pacific islands are possible changes in rainfall which might significantly reduce the suitability of areas with seasonal periods of drought stress for forest cover. It has been suggested (Parham, 1956) that originally the whole of Viti Levu in Fiji was covered by primary forests, which are now restricted in their distribution to the inland and wetter eastern sides of the main islands. This present distribution follows forest clearance by both the pre-colonial Fijian populations and the post-European introduction of large scale plantation agriculture. Such changes to the distribution of forest vegetation parallel those changes which might be expected to occur without human interference but under conditions of declining annual and seasonal rainfall. The absence of regional and sub-regional models or scenarios of future rainfall patterns make the prediction of such changes to insular vegetation formations difficult at the present time.

The picture is further confused by the introduction of exotic species which have changed the process of succession in many insular communities and ecosystems. The grassland and scrub formations of the drier eastern side of islands such as Viti Levu for example are now dominated by introduced species such as the mission grass *Pennisetum polystachyon* and the wire grass *Sporobolus indicus,* species which have replaced the native reed grass *Miscanthus floridulus* in most areas (Parham, 1956). Several introduced, invasive, scrubby weeds such as *Piper aduncum, Psidium guajava,* and *Leucaena leucophala* now dominate the intermediate vegetation between the grasslands and rainforest.

In addition, many native plant communities on islands are under threat from anthropogenic pressures which include logging, forest clearance for agriculture, mining and the introduction of domestic animals such as sheep, goats and cattle. Steussy *et al.* (1984) quantified the levels of disappearance of plant species at seven locations in the Juan Fernandes Islands over a sixty year period as between 9% and 76% and concluded that the main cause was destruction by domesticated and feral animals including goats, cattle, coatimundis, rabbits and horses. In New Caledonia nearly all exploited timber species are endemic and the 13 endemic species of *Auracaria* have restricted distributions, mostly in mining areas (Dahl, 1980)

Marine and coastal communities

From a marine perspective, oceanic islands represent "hot spots" of diversity in the watery equivalent of deserts. Their high productivity reflects a complex community structure which ensures recycling and conservation of essential nutrients within the shallow water ecosystems. Any changes to the ecological balance of such communities could, if it reduced this efficiency, result in collapse or major perturbation of the entire system.

Patterns of species distribution

Unlike the terrestrial communities of many Pacific islands, coastal ecosystems contain a large number of widely distributed species. Even in such communities however, biogeographic provinces can be distinguished which represent the dynamic temporal end point of interactions over time and space. The Indo-Pacific marine biogeographical Province covers one fourth of the globe, from around 30°N to 30°S, stretching from East Africa across the Indian Ocean and into the Pacific as far east as the Hawaiian, Society and Marquesas islands. According to Ekman (1935, 1953) the centre of diversity was the Indo-Malayan region, from which the other areas were presumed to have derived their fauna.

This classic view has however been subject to recent revision by Kay (1984) who suggests that rather than representing a diverse centre from which species have spread outwards, the Indo-Malayan region may represent an area in which species have aggregated from the Pacific and Indian Oceans. Unlike the terrestrial flora and fauna the shallow water marine organisms of this Province contain no families endemic to any one of the three areas (Indian Ocean, Indo-west Pacific, and Pacific plate). At a generic level three quarters of all the genera examined by Kay (1984) were widespread, 17% were restricted to the western Pacific and 5% and 2% were endemic to the Indian and Pacific Oceans respectively. At the species level 18% and 16% were found to be endemic to the Indian and Pacific Oceans respectively. In the Pacific Basin, around 40% of the species in the groups of crustaceans, molluscs, echinoderms and fishes analysed by Kay were found to be endemic, of which around half are widely distributed throughout the Pacific plate area the remainder being centred on either the Hawaiian Islands or southeastern Polynesia.

It would appear that this present pattern of distribution reflects in part the cosmopolitan nature of past tropical marine faunas reflecting the past connection between the Pacific and Caribbean during the Cretaceous. This connection was severed during the Palaeocene and Eocene at a time of rapid extinction among the cosmopolitan marine faunal groups. The Indo-west Pacific fauna of the Eocene and Miocene was markedly different from the present fauna and this Tethyan fauna was subsequently split, allowing independent radiation in the now isolated ocean areas of the Caribbean, Mediterranean and Indo-west Pacific. The Pacific plate then functioned as a centre for speciation from which species spread westward to accumulate in the western Pacific alongside others which arose in the Indian Ocean and those which evolved in the Indo-west Pacific itself.

In contrast, the Caribbean contains an impoverished sub-set of the tropical coastal flora and fauna, reflecting the size of the area and the length of time it has been separated from the Pacific. The Atlantico-east Pacific province contains only four genera and seven species of obligate mangroves for example, compared with the thirteen genera and at least 30 species, characteristic of the Indo-west Pacific. *Nautilus*, Tridacnid clams, cowries and cones now display truncated distributions in comparison with their former distributions which included the Mediterranean region. In examining the possible responses of shallow water marine communities on oceanic islands to the impacts of potential climate change and sea level rise it is important therefore to bear in mind the nature of regional floral and faunal differences which may influence or modify the response of the community as a whole.

Species and community responses to climatic change impacts

Non-linear responses - It is clear that the present populations of hermatypic corals growing in a number of widely dispersed localities are currently growing at or near their limits of temperature tolerance. Some evidence does exist that coral communities growing in different areas may respond quite differently to thermal stress depending upon the normal conditions of temperature. Mortality in Pocilloporid corals reached over 90% in the Galapagos and Pearl Islands during the 1982-83 El Nino whereas in the normally warmer waters of the Contreras and Secas Islands mortalities only reached between 50 and 70% (Glynn *et al.*, 1988).

Increased sea surface temperatures can be expected to generally increase the frequency and/or severity of bleaching events and mass mortality. It has been argued (Buddemeier & Smith, this volume) that the bleaching response of corals to temperature is aggravated by other sources of anthropogenic stress, an argument which may be more widely applicable (see below). Regardless of whether or not this is the case, any source of mass mortality amongst the structural components of reef communities is likely to have dramatic impacts on other components of the reef ecosystem.

Changes in community processes - Although our present understanding of the complexity of community and ecosystem interactions in coral reefs can be described in some respects as rudimentary, it is known that the same species may behave quite differently in different areas depending upon the other species present. Thus for example, *Eucidaris thouarsi* feeds on algae, seagrasses and sponges in reef systems off Panama and Colombia but feeds on live *Pocillopora* corals in the Galapagos islands, apparently as a consequence of lower fish predation (Glynn & Wellington, 1983). The predation of *Eucidaris* on corals apparently results in reduced reef growth rates. Changes to only one component of such linked chains may result in unforeseen consequences for the community or ecosystem as a whole.

The overall level of community diversity is likely to influence the nature of the systems response. Communities with low species diversity are more likely to display abrupt changes to processes and rates than are highly diverse communities where the consequences of changes to a single species may be balanced by compensatory changes to other species within the system. On this basis it could be argued that the response of impoverished Caribbean communities to the stresses imposed by global climate change is likely to differ significantly from that of the more complex and species rich communities of South East Asia. Theoretically it could be argued that the more diverse communities of the Indo-west Pacific are likely to prove more adaptable to climatic change, containing as they do a greater reservoir of species and hence potentially being capable of reaching a greater number of points of dynamic stability in terms of community structure.

Such a conclusion is however debatable and should not be used as the basis for policy decisions relating to the conservation of marine and island communities. The response of any coastal ecological community to global climate change is unlikely to be gradual since the present community structure itself reflects the balance of interactions between species, and their co-evolutionary adaptations not merely the potential individual responses of its component species.

Changes in patterns of distribution - As the largest global transition zone the coastal zone represents the dynamic interface between terrestrial and marine systems. The species diversity and composition of coastal ecosystems reflects this transitional nature. Species on the seaward side show greater adaptation to marine conditions, species on the landward, displaying less maritime and more terrestrial or freshwater characteristics. The clear zonation of coastal communities reflects this and it would appear obvious that a change in sea level will automatically be reflected by landward shifts in the distribution of coastal species. What is less obvious but nevertheless true, is that individual ecotones will not respond equally to changes in sea level. Such unequal shifts of distinct vegetation formations have been demonstrated in the case of wetland plant communities in Louisiana and may be expected in other, longer lived coastal plant communities such as mangroves.

Influence of land-based changes - Coastal habitats and ecosystems are affected by events at considerable distance away, both on land and in the open ocean. Changes to rainfall and run-off, with consequent changes in sediment load, nutrients and the salinity of coastal waters will all have major impacts on coastal organisms in addition to the changes which will result from increased sea level and higher water temperature (Pernetta & Elder, 1992). Non-linear, abrupt changes in coastal communities may be expected to characterise the response of such ecosystems to changes resulting from land based impacts of global climate changes. Increased sedimentation in coastal areas resulting from either increased rainfall and hence erosion or from changes in land use practices can alter the suitability of coastal areas for reef establishment and maintenance and could result in switches such that the local distribution of reef ecosystems changes. Similarly it appears likely that mangrove and seagrass ecosystems may be dependent upon sources of terrigenous sediments if they are to keep pace with rising sea level. Once a critical rate of sea level rise has been exceeded the response of such ecosystems may be non-linear collapse. The probability of such collapse is more likely in the case of small and low islands where terrigenous inputs into coastal environments are already at a low level.

Regrettably until regional and sub-regional scenarios of future climates are available to enable prediction of changes to land-based inputs to the marine environment, the likelihood of ecosystem collapse cannot be estimated.

Influence of population size and isolation - Owing to their isolation and small size, many individual species populations may not encompass sufficient genetic variability within their genomes to respond rapidly to environmental change. It might be similarly argued that the coastal and shallow water marine communities of oceanic islands generally lack sufficient diversity at the species level to adapt to environmental change as rapidly as more complex, diverse communities on mainland coasts or in dense archipelagic areas. In such areas the opportunities for successful recolonisation from neighbouring coastal communities is higher following local extinction, and the rate of gene flow between populations is also higher thus effectively enlarging the pool of genetic variability available at any one location.

Episodic events - The susceptibility of marine organisms to local extinction following over-exploitation is well demonstrated, while the impacts of episodic events such as disease outbreaks, hurricanes, storm induced pulses of sediments and El Nino are known to alter community structure and species composition in coastal ecosystems. For oceanic islands re-colonisation rates following local extinction may be insufficient to maintain existing diversity at a local level. It should be noted however that no such local extinction following the single occurrence of an episodic event is documented to date. Hence increases in frequency of episodic events and synergistic interactions between different sources of stress may be more critical than changes to the severity of single events.

Predictions that tropical hurricanes may increase in frequency and intensity, and that the areas of their occurrence may shift under the influence of global climate changes is a cause for some concern. Increased frequency and intensity could possibly result in local extinction of sensitive species. Physical damage to sensitive shallow water communities such as coral reefs may be extensive and such communities may take decades to recover. The impacts of hurricanes on islands not normally subject to such episodic events may be far more extensive than in areas such as Guam which have adapted to a high frequency of storm damage. Whilst it is obvious that such changes would have impacts on the nature and functioning of shallow water marine communities, the extent and detail of such impacts cannot be predicted at the present time.

Discussion and Conclusions

The fate of the biological communities of oceanic islands in the face of changes predicted to occur as a consequence of global warming has not been considered in detail to date and this paper attempts to provide an initial overview of some of the potential impacts on such ecosystems and communities.

In the case of terrestrial communities of plants and animals, the impacts may be both more extensive and more important from a conservation perspective than in shallow water marine communities. The high endemicity, and low species diversity in terrestrial insular environments may make such communities less resilient than marine communities to the changes predicted to occur as a consequence of global climate change and sea level rise. The long distances separating insular communities mean than colonisation rates are low, operating on time scales of hundreds and thousands of years, which is slow in comparison with the rapid rates of environmental change predicted to occur over the next century. Potential natural recolonisation following local extinction will not keep pace with the anticipated rate of loss of native species even in those instances where surviving populations exist elsewhere. In the case of insular endemics the evolutionary rates which have resulted in present levels of diversity are also on quite different time scales from predicted rates of global change.

Most endemic terrestrial species in the Pacific are adapted to, or components of forest habitats, hence any changes which impact forest vegetation will have the greatest overall impact on the species of oceanic islands. The key factor likely to impact the lowland forest vegetation of tropical oceanic islands is a change in rainfall, particularly any reductions in either total annual rainfall or changes in seasonal patterns which increase the length or severity of seasonal drought stress. Both are significant limiting factors to the distribution of forest habitats in some island groups at the present time.

Higher altitude forest formations, alpine and sub-alpine, and grasslands and scrub vegetation are likely to be placed under increasing stress as a consequence of increasing temperature restricting suitable areas to fewer and smaller habitat islands. Such changes are likely to greatly increase the rate at which species are lost through extinction as a consequence of decreases in the size of populations of individual species. In the case of alpine and sub-alpine grass and scrub this is not of major conservation concern.

It is concluded however, that the potential loss of terrestrial island endemics may seriously deplete the global pool of species diversity. Such global species losses are less likely to occur among coastal marine species. Nevertheless the coastal communities and ecosystems of individual oceanic islands may become less diverse than at present owing to enhanced extinction rates and the difficulties of recolonisation over extended oceanic distances.

The biological communities of oceanic islands may display non-linear response to climate change. The potential impacts of climate change on island populations and ecosystems could be both more extensive and more abrupt than is the case for comparable communities in mainland areas.

The differentiation of vegetation patterns with the dominance of forest formations on tropical islands has resulted in adaptation and survival of animal species dependent upon such plant communities. Insular communities of animals are generally characterised by a high proportion of generalist species. Niche separation in many bird communities is not based to the same extent on feeding strategy and feeding station as in the case of mainland bird communities. Despite this, most species are generally obligate forest dwellers. Changes to the vegetation consequent upon changes in rainfall, temperature and water balance may have far reaching effects on the dependent animal community particularly if the climax vegetation changes from closed canopy to more open savannah woodland or scrub.

Recent evidence of the susceptibility of insular animal communities to human intervention through forest clearance and the introduction of alien species, both competitors and predators, demonstrates the susceptibility of native communities to external interference. Human interventions in both the terrestrial and marine communities, resulting from human population growth and aggregation, changes to land use and freshwater management, and waste disposal are already reducing the population size and geographic extent of many native insular communities of plants and animals.

The potential losses of species as a direct consequence of climatic changes must therefore be considered against the present background of other sources of anthropogenic change in island environments. Increasing human populations resulting in increased demand for agricultural production combined with economic development of national assets such as forests and mineral deposits are already threatening many native plant and animal communities. Increased densities of people and their increasing aggregation around centres of services are also resulting in serious pollution of both the land and near-shore marine environments and overexploitation of marine resources. These existing stresses are seriously reducing the capacity of natural ecosystems and communities to withstand the added pressures which are likely to occur in a rapidly changing environment.

A failure to manage existing environmental problems will therefore place the goal of maintaining ecosystem diversity, upon which sustainable development ultimately depends, beyond the reach of many insular societies. The global consequences of such a failure may well be the loss of a significant number of unique animals and plants.

The rates of anthropogenic change are at present high, compared with the rate of change predicted to occur as a consequence of global climate change. Nevertheless the added stress of climate change impacts may result in significant losses of global biodiversity as measured in terms of the numbers of species. The ability of insular populations and communities to withstand environmental change is, in part, a function of population and community size, hence the added stress of climatic change and sea level rise may result in the extinction of vulnerable species and communities. Predicted changes are likely to favour "r" adapted rather than "k" adapted species at least in the short term. Many of the latter are island endemics and hence of conservation interest.

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