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THE IMPACT OF SEA LEVEL RISE ON THE DUTCH COASTAL ECOSYSTEMS

J.J.W.M. Brouns

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1 Introduction.

The rising concentration of "Greenhouse" gasses, notably carbon dioxide and methane, will alter the radiative properties of the atmosphere and is expected to produce a warmer climate in the future. The warming of the earth is envisaged to result in a warming, hence thermal expansion, of the ocean, and a melt down of continental glaciers. The possible impact of a rise in sea level on the functioning of ecosystems in the Waddensea is assessed from the literature. This report is restricted to those ecosystems which are reached by sea water, but projections about beach erosion are omitted. Dunes also are excluded as they are mainly glycophytic in character.

1.1 Global observations.

Eustatic sea level rise is attributed to global warming through melting of the ice masses on the continents, especially wasting of the mid-latitude glaciers (Meier, 1984), and thermal expansion of the oceanic watermasses (Gornitz et al., 1982). Changes in the mass balance of Antarctic ice will be of little importance in the next few centuries (Bolin et al., 1987). A possible increase of precipitation in the Antarctic (Oerlemans, 1982), taking water out of the sea, might even reduce the rate of sea level rise, an expectation which was confirmed recently (Polar Research Board, 1985). The rate of change of mass of the ocean cannot be distinguished from zero. Melting of arctic (sea) ice does not affect sea level. The gains (in the central area) and the losses (at the margins) of the Greenland ice sheet are about equal.

The estimates for the global sea-level rise in the past century range from 10 - 15 cm (Gornitz et al., 1982, Polar Research Board, 1985, Titus, 1987). The values, corrected for glacio-isostatic rebound, show considerable spatial variations (0.8 - 3 mm yr^{-1}) implying that other poorly defined tectonic or oceanographic effects are important (Polar

Research Board, 1985). The regional differences in observed sea-level changes are illustrated in Fig. 1. Apparently the most pronounced changes are experienced at the Atlantic coast of North America. Here tectonic processes contribute significantly. Recent estimates of wetlands loss for the entire US amount already to approximately 0.5% yr^{-1} (Gosselink & Baumann, 1980).

Barnett (1984) calculated a almost double rate of sea level rise (23 cm/century) for the period 1920-1980. For the whole period, including the early 1900's, he estimated a rise of 14.3 cm/century, which is close to the value presented by Gornitz et al.(1982). However different methods of analysis can cause 50% variations in the estimates of the trend in the existing data set (Barnett, 1984).

1.2 Prognosis of future sea levels.

Estimations of future sea-levels can not be more than crude estimates as part of the observed present-day rate is inadequately explained by physical processes. The steric effect of a 0.4 °C global warming would cause a rise in sea-level at a rate of 0.6 mm y-1 until a new equilibrium is reached (Gornitz et al., 1982), approximately 50% of the observed present-day rate (Peltier, 1987). Thermal expansion, provided the calculated rise of global temperature of Gornitz et al. (1982) and Hansen et al. (1984) are true, accounts for less than 50% of the observed rise (Fig. 2). This global warming, by some estimated as 0.4 °C during the last few decades, however is not yet ascertained.

High and low assumptions for the various atmospheric variables give estimates of 345 and 56 cm respectively by 2100 AD (Fig. 3). An extreme case of a high level of atmospheric retention of CO_2 and very high levels of trace gasses coinciding with an increase in solar luminosity by 0.5% would produce a rise of 429 cm (Titus, 1987). The figures for sea level rise given above are obtained by multiplying the thermal expansion figure by two or tree because of the observed 10-15 cm rise during the last 100 years. Only 4-5 cm can be explained by thermal expansion, a major weakness of the calculations (Shennan, 1987). The now most widely accepted analysis of all data and results of models is presented by de Q Robin (1987), who reached the conclusion that sea level would rise 80 cm due to CO_2 doubling. However the possible range was 20-165 cm.

2 Local observations of sea level rise.

2.1 Holocene.

The Holocene period has been characterized by a worldwide transgression produced by the melting of the late Pleistocene ice sheets, Laurentide (Wisconsinian) and Fennoscandian (Weichselian)) and the thermal expansion of the ocean volume as the temperature rose. A rapid rise occurred in prehistoric times. About 18,000 years ago, at the end of the last glacial cold period (Weichselian), sea level stood about 140 m lower than it does now. Global warming has produced a rapid sea level rise since, the Flandrian Transgression (in West-European geological scales) (Fig.4, Fig.5).

Indications for a relatively short period of a very high rate in rise around 7000 BP is presented by Smith et al., (1985), although their interpretation of a sedimentary record accepts extreme storm surges also. The relative high water levels for the North Sea were estimated at -24 m around 7800 BP, -1.3 m at about 1500 BP and the same as today in 550 BP (Hanisch, 1980). The relative rates of MSL rise have been estimated as 1 m $century^{-1}$ between 7000 and 6500 BP, followed by a decrease to 0.37 m $century^{-1}$ between 6500 and 5000 BP, 0.2 m $century^{-1}$ between 5000 and 4500 BP and between 4500 and 2000 BP it was only 0.1 m $century^{-1}$ (Van der Plassche, 1982). Tectonic processes are of little importance for the Netherlands as it is just outside the zone of influence of the isostatic rebound (Fig.6).

The barriers of the coasts of the Netherlands are of late-Atlantic and sub-Boreal age. They were formed in a period of 2000 years. The historical profiles and topography for this area during the Holocene are shown in Fig.7 (Zagwijn, 1986).

2.2 North Sea coasts.

Local and short-term disturbances (i.e. meteorological) are also a part of the observed sea-level. These are generally large compared to the trend in sea level rise. This can be illustrated by some values that are valid for most parts of Denmark. While sea level is rising at a rate of 1 mm yr-1, the interannual variation in mean sea level amounts to 130 mm, the monthly variations to 550 mm while diurnal variations during storm surges can be more than 5000 mm (Christiansen et al., 1985). The sea acts also as a reverse barometer. A 1 mb pressurefall causes a 1 cm rise in sea level.

The influence of wind direction and wind speed on the observed water level, as compared to the astronomically predicted water level (tide tables), is illustrated by the observations into this effect at Wilhelmshaven (Fig.8). The displacement of cyclonic tracks towards higher latitudes has been related to the warmer climate in the 20th century. This caused extreme wind velocities to be less frequent and also caused changes in the wind directions. Danish wind statistics for the periods 1876-1925 and 1931-1960 show that the frequency of NW-winds decreased and winds from W and SW are becoming more frequent. Apparently, the frequency of NW-winds and the the number of storms are increasing again. This will affect deposition and erosion patterns (Christiansen *et al.*, 1985).

The mean tidal ranges observed on monitoring stations at the Dutch coast are summarized in Fig.9. The middle part (Hoek van Holland to Den Helder) represents stations on the North Sea coast proper. To the left the tidal range at the main station (Vlissingen = Flushing) in the South-West estuary of the rivers Rhine, Meuse and Scheldt is shown, while to the right the tidal range as observed in the Wadden Sea is presented (Van Malde, 1986). The rates observed in the countries bordering the North Sea, illustrating the differences that are observed in this small area which is under the influence of isostatic processes and changes in the hydrology, are presented for the Dutch (Fig.10, Fig.11, Van Malde, 1984), German (Fig.12, Führboter, 1986) and Danish (Fig.13, Christiansen _et_ _al_., 1985) stations. The average rate of sea level rise on the Dutch coast amounted to 18 cm century^{-1}, as calculated from tidal observations during the period 1934-1984 (Van Malde, 1986). The data obtained at stations bordering the Wadden Sea show also a quite recent regional effect as the increase in MHW is larger than the increase in MSL.

2.3 The Wadden Sea

The preserved geological record of migrating barriers and deposition of marine sediments, on the Pleistocene sand, is shown in a schematic cross-section through the Wadden Sea (Fig.14).

The Wadden Sea and the barrier islands to the North and West are, from a geological viewpoint, recent developments (van Straaten, 1965). In the last 15000 years sea level has risen approximately 110 m. The transgressing North Sea caused sediments to move inland and to higher elevations. The rate of sea level rise was too high until 6500 yr BP for peat formation. The extensive peat deposits in the Wadden Sea sediment originated during periods with a relatively low rate of sea level rise, but all after 6500 yr BP. The absence of peat in the sediments deposited after 1800 BP is as yet unexplained (Streif, 1986).

The sea level rise during the holocene caused the shore-line to move 200-300 km in a south-easterly direction. At 4000 yr BP the Wadden Sea was in some places at least 40 km wider than it is now. Large parts of the present day provinces of Groningen and Friesland were flooded. This part of the basin has been filled since.

The highest rate of sea level rise (0.7 m century^{-1}) in recent times has occurred between 1000 and 1225 yr AD (Streif, 1986). The deposition patterns in the last 3 centuries indicate an average rate of 0.25 m century^{-1} rise (Hamisch,1980). Apparently the present day topography of the Wadden Sea is the result of deposition during a sea level rise at half the expected rate for the next century, while the regression of the sea in respect to the northern shores has continued. The total area to be elevated, in order to preserve the distribution of land and sea while sea level rises, is distinctly smaller than it was during the last centuries. Hence, the amount of sediment required is less.

3 Coast line regression.

The coast line changes that will develop are not only depending on the changes in ASL (apparent sea level) but will also be affected by changes in amplitude of the tides, the profile and the erodability of the substrate.

3.1 Bruun's rule.

The Bruun rule states that a beach that has attained equilibrium with coastal processes (Profile 1) will respond to a rise in sea level by loosing sand from the upper part of the profile and gaining it in the nearshore area until a new equilibrium (Profile 2) is established (Fig.15), basically to provide sediments to the shore bottom so that it can be elevated in proportion to the rise in water level. The coastline will thus retreat from A to B as the direct result of the sea level rise, and from B to C as a result of the transference of sand seaward (Bruun, 1962). An assumption for Bruun's rule is that (1) the coast has a fully developed equilibrium profile and (2) there is sufficient loose sediment both on the beach and near-shore. These assumptions are normally fullfilled on coasts with small to moderate gradients (Christiansen et al., 1985). However, the key prerequisite, and keyword, for the application of this rule is: equilibrium. Therefore, it is possible to have regression (retreat of the sea) even with rising sea-levels if the sediment budget can more than compensate (Fig.16). For instance, the coast in the Wadden Sea between Blavand and Sylt, where sealevel is rising 1.17 mm yr^{-1}, is prograding (Christiansen et al., 1985). The adjustments of the beach profile are not instantaneous. Sea level rise sets the stage. Storms will cause the sudden adjustment because of the disequilibrium.

Bird (1986) listed the factors that favour initiation or acceleration of beach erosion. The factors that possibly may be of importance in The Netherlands are extracted (Table I).

Table I. Factors favouring coastal erosion (Bird, 1986)

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1. Reduction in sand supply from eroding sand outcrops (e.g. because of the building of sea walls to halt recession).
2. Reduction of sand supply to the shore where dunes that had been moving from inland are stabilised, either by natural vegetation colonisation or by conservation works, or where the sand supply from this source has run out. This is of little importance in the Netherlands, because of the prevailing wind direction in respect to coastal orientation.
3. Reduction in sand supply from alongshore sources as the result of interception, e.g. by a constructed breakwater.
4. Increased losses of sand from the beach to the backshore and hinterland areas by landward drifting of dunes, notably where backshore dunes have lost their retaining vegetation cover and drifted inland, lowering the terrain immediately behind the beach and thus reducing the volume of sand to be removed to achieve coastal recession.
5. Losses of sand from intensively used recreational beaches.
6. Increased wave attack resulting from the deepening of nearshore water (e.g. where a shoal has drifted away, where seagrass vegetation has disappeared, or where dredging has taken place).
7. Submergence and increased wave attack as the result of a rise of sea level relative to the land.
8. Increased wave attack due to climatic change yielding a higher frequency, duration, or severity of storms in coastal waters.
9. Dimunition in the volume of beach material as the result of weathering, solution or attrition, leading to a lowering of the beach face and a consequent increase of wave attack on the backshore.
10. Increased beach erosion resulting from a rise in the water table, rendering the beach sand wet and more readily eroded.

3.2 Barrier Islands.

The Wadden Sea is separated from the North Sea by a chain of barrier islands. These islands are mobile features that move about in the absence of "protective" measures. They grow or shrink in response to storms and to fluctuations in sea level, currents, and sediment supply. Barrier islands are separated from each other by inlets, which are relatively narrow channels of water, providing for exchange of sea water. Major alterations in the shape and location of barrier islands are often the results of the formation or migration of inlets. The addition of new sand gives the island volume and elevation and the sea level rise causes the shoreline to migrate or retreat landwards (Clark, 1977).

The fate of barrier islands, lacking artificial protection, during periods of sea level rise appears to be uncertain as there are two lines of thought concerning the behaviour (Fig.17).

a. Inplace drowning, stepwise retreat.

This hypothesis states that as sea level rises, the barrier may remain in place while the water body on its landward side deepens and widens. Eventually, the breaker zone reaches the level of the top of the barrier ridge, the sea drowns the barrier, and the breaker zone oversteps landward to form a new barrier shoreline along the landward edge of the former lagoon. When the barriers are drowned in place, the surf zone does not pass continuously across the area submerged but it moves across the area in successive leaps (Rampino & Sanders, 1980).

b. Shoreface retreat.

This is the most widely supported hypothesis and is applicable to the Wadden Sea. This view states that as sea level rises, the barriers migrate continuously landward and the breaker zone traverses the entire area submerged. This continuous movement of the shoreline would lead to complete or almost complete destruction of the backbarrier sediments exposed to wave reworking on the shoreface. In the Mississippi Deltaic Plain, an area subsiding typically 2 mm y^{-1}, but locally with rates up to 12 mm y^{-1}, the barrier islands decreased in size by 44% between 1955 and 1978 and migrated landward in the mean time (Gagliano et al., 1981).

The two theories are apparently conciliable by introduction of sand supply and rate of sea level rise as determinants, but a consensus has not yet been reached (Leatherman, 1983).

3.3 Effects of submergence.

Bird (1986) has summarized the possible effects of submergence on coasts. Not all are of importance in the Netherlands since some coastal features do not exist here. The effects will depend on the topography and the change in ASL. On cliffed coasts submergence is likely to accelerate coastline recession, except on outcrops of hard rock formations (dikes), where the high and low tide lines will move up the cliff face. Existing shore platforms and abrasion ramps will disappear.

The shores of deltas and coastal plains will retreat, except where they are maintained by coastal sedimentation. Beaches will be narrowed, and beach erosion will become much more extensive and severe than it is now.

Inlets, embayments, and estuaries will be enlarged and deepened, and increasing salinity penetration will cause a regression of brackish ecosystems: where possible salt marsh communities will move back into terrain presently occupied by brackish or freshwater vegetation. The salinity increase might be beneficial to animal abundance. The formation of peat will generally be impaired.

Coastal lagoons will also become larger and deeper, but the enclosing barriers may transgress landward on to them. If the barriers are submerged, or destroyed by erosion, the lagoons will become coastal inlets or embayments.

Erosion, structural damage, and marine flooding caused by storm surges will intensify because of the greater heights of waves arriving through deepening coastal waters. Water tables will rise in coastal regions, and soil and water salinity will be augmented.

The response of marshes to rapid sea level rise would be by inundation, upward shift in vegetation zones, and creation of new intertidal habitats, rather than alteration of the substrate topography (Kana, 1984), provided sediment supply would be insufficient. Marsh vegetation is very rapidly established and will always occupy the niche between MHWN and spring high tide in sheltered habitats.

4 Salt marshes in relation to submergence.

4.1 Introduction.

The salt marshes have been formed in sheltered places by waterborne sediments collected by those halophytes which can populate the intertidal zone. Of these Spartina, Salicornia and Puccinellia are the principal genera. The marshes, as we know them today, have developed during a period of rising sea level, and in some marshes peat deposits are preserved. The interaction of tidal flow, the resulting sedimentation, and the physiology of the halophytes has produced a unique land form (Redfield, 1974).

Salt marshes are a main feature of the landscape bordering the Wadden Sea (Fig.18) and the estuaries of the rivers Rhine, Meuse and Scheldt in the southwest of The Netherlands (Fig.19). However, as much of the research on salt marsh ecology has been performed on the Atlantic seaboard of the USA, many examples will be drawn from papers dealing with the marshes from that area. The marshes in the USA are different from the European marshes. Processes, however, might be comparable.

Sources of sediments for estuarine systems include rivers and offshore waters, shoreline erosion and resuspended materials from subtidal and intertidal sediments. Sediment surface stability of the intertidal flats, the initial stages of an eventually developing salt marsh, is influenced by a complex of factors that include: sediment grain size, porosity and packing, the presence of macroheterotrophs, the presence or absence of algal mats, diatom and bacterial films (Welsh, 1980) and physical factors such as temperature, waves,ice and rain (Kraeuter & Wetzel, 1986). Any factor influencing sediment surface stability affects sediment erodability. The entrapment and stabilization of suspended inorganic sediment on the marsh surface by vegetation is an important process in helping to maintain elevation with respect to sealevel. The incoming sediment also supplies nutrients for plants which in turn enhance further sediment entrapment and stabilization. The increased primary production contributes to the organic pool of the marsh. Maintenance of a viable marsh is thus affected through aggradational processes of plant growth, organic detritus accumulation and inorganic deposition (Beeftink, 1976, DeLaune et al., 1978).

4.2 The algal component.

Apart from the phanerogams, maritime salt marshes also carry an extensive algal vegetation which may, in places, be as important as the phanerogames. As may be expected, Cyanophyceae (blue-green algae or cyanobacteria) are abundant. There are also characteristic members of the Rhodophyceae (red algae), especially Catenella and Bostrychia, which are to be found at the base of the plants at the higher levels (den Hartog, 1959). Many of the Cyanophyceae associated with marsh soils are known to fix nitrogen (Latcovic, 1965, Stewart, 1967)

The algal communities of the salt-marshes are separated into 10 formations, grouped according to similarity in structure, mode of growth and reproductive cycle of the dominant species. The 3 dominant algal communities are listed below (Table II). A finer subdivision, in 47 consocions, can be found in Polderman (1979).

Table II. Algal formations of salt-marshes (after Polderman, 1979).

Vaucheria	Dark green velvet patches. Lower to upper salt-marsh and beach plains. *Vaucheria* spp.
Rhizoclonium	Felt-like and curly patches. All saline habitats. *Enteromorpha*, *Ulothrix*, *Cladophora*, *Rhizoclonium* spp.
Oscillatoriaceae	Black-green leathery crusts. All saline habitats. *Oscillatoria*, *Microcoleus*, *Symploca* spp.

The first three formations determine the algal component of most saline habitats in the Wadden Sea. The pattern is generally a mosaic and a zonation is related to the vascular plants and the type of substrate is critical in determining the species composition.

Production values for the algal component of the marshes are unknown, but typical biomass values of from 110 to 360 g ADW m^{-2} below and in between the phanerogamic vegetation, in the salt marshes of the USA, imply a high contribution by the algal vegetation to the production of the community. The importance of the algae in the primary production of the ecosystem is stressed by the general agreement that only the above-ground vegetation is available for uptake in the food chain and possibly exported (Teal, 1962, Odum & de la Cruz, 1967, Smith et al., 1979).

The snails *Hydrobia ulvae* and *Ovatella myosotis* insect larvae, amphipods and collembolans are important invertebrate consumers of micro-algae in salt marshes. Selective grazing on algal mats, especially on tidal flats, is recorded for the mullet *Liza ramada* (Polderman, 1974), but a number of indiscrimate grazers take algae as well (e.g. *Branta bernicla*, *Tadorna tadorna*) (Nienhuis, 1975).

4.3 The zonation pattern.

Tidal periods are due to tide-producing forces which are given. Only their phases and amplitudes depend on local conditions. The resulting tidal curves can be calculated and predicted. These predicted tide levels are usually presented in tide tables, but tide predictions alone are not sufficient to explain the observed zonation patterns in salt marshes along shallow seas.

Table III Tide levels and definitions (van der Plassche, 1985).

Supratidal zone			
HAT	Highest astronomical tide		(strand-line deposits)

MHWS	Mean high water spring	----	
LHWS	Lowest high water spring	----	(wet at least once every monthly cycle)
MHHW	Mean higher high water	----	
MHW	Mean high water	----	(lower boundary **supralittoral**)
MHWN	Mean high water neap	----	
LHWN	Lowest high water neap		(wet every tide of the year)
MSL	Mean sea level (approximately NAP and NN)		
MTL	Mean tide level		
HLWN	Highest low water neap		(exposed every tide of the year)
MLWN	Mean low water neap		
MLW	Mean low water		(upper boundary **sublittoral**)
MLLW	Mean lower low water		
HLWS	Highest low water spring		(exposed at least once every monthly cycle)
MLWS	Mean low water spring		
LLWS	Lowest low water spring		
Subtidal zone			

---- = amplitude of maritime salt marshes in Europe (between MHWN and MHWS/HAT).
NAP = Nieuw Amsterdams Peil (Dutch ordnance datum)
NN = Normal Null (German ordnance datum)

The tidal characteristics and the terminology used are summarized in Table III (Van der Plassche, 1985). Particularly frequent and sometimes very strong disturbances of the water level are caused by the wind-induced setup of water which may result in storm surges. The superimposed wind-induced setup on the tides is for the largest part attributable to the wind pile-up in the Wadden Sea and Delta estuaries but is, for a minor part, also affected by the events on the North Sea. The profound influence of wind-induced setup can be illustrated by the observation that the level of MHWS (predicted 50-60 times a year) is actually flooded 210 times. The zonation of salt marshes is therefore influenced by the local topography and climate, exposition in relation to the prevailing wind-directions and location relative to the main water bodies. If a disfavourable change in any of these aspects occurs, the zonation will change accordingly and a shift will eventually follow. If the number of floodings per year is taken as the determinant for the zonation of a salt-marsh, than it can be argued that eventual changes in the local weather, depending on climatic changes, have a much more severe potential impact on the distribution of species than the periodic but gradual rise of the sea level.

Coastal salt marshes have evolved under the controlling influence of the sea. Tidal amplitude in relation to the slope and the elevation of the shore define the area for the development and the maintenance of the salt marsh. A distinct zonation of plant populations as monotypic stands or mixed vegetational types characterize temperate salt marshes, especially those strongly influenced by the sea (Beeftink, 1966, Eleuterius & Eleuterius, 1979). However, tidal phenomena _per se_ can not be shown to account for salt marsh zonation. The relationship of plants to tide levels is complex and entails other environmental, especially edaphic, factors as well as biotic interactions.

4.3.1 Pioneer zone (Spartinion, Thero-Salicornion).

Communities of mud flats and low salt marshes. Ss in Table IV.

-Thero-Salicornion. (Thero=summer).
Pioneer communities of succulent annuals (_Salicornia_ spp.) from 40 cm below MHW, on tidal mud flats of euhaline and polyhaline areas in the eulittoral and in well drained depressions of the salt marsh. Optimal

growth in saline media. Distribution restricted to saline and wet habitats, but plants do not tolerate prolonged inundation, especially during the period of reproduction. Germination of *Salicornia* in coastal marshes is restricted to neap tide periods.

Predominantly on firm sandy and well drained soils (Dijkema, 1983) but according to Beeftink (1977) the soil is only superficially aerated (0.5-1 cm) or totally reduced. The community is poor in species. Drift algae may be abundant and on sites enriched by nutrients *Suaeda maritima* can be an accompanying species. The perennial alga *Fucus vesiculosus* is common in this habitat (Nienhuis, 1975). *Salicornia* stimulates sedimentation in the summer (annuals) and the sediment is stabilized by the algal mat (mainly Cyanophyceae) on the surface (Den Hartog, 1958). *Salicornia* can stimulate the seaward spread of *Puccinellia maritima* if entangled fragments of this species root successfully (Kamps, 1962).

-Spartinion.

Spartina spp., grasses typical of waterlogged and anaerobic soils of coastal marshes. The genus consists of a group of species, each being dominant in certain parts of the world. Hybrids can be formed (e.g. *Spartina townsendii* H. et J. Groves). Propagation in *Spartina* is vegetatively, from rhizomes, as well as from seeds. Germination of some seeds (e.g. *S. anglica*) is inhibited by light. Long submersion under muddy seawater may thus be of stimulatory value for germination by reducing light levels. However, burial in too frequently flooded flats causes seed rot (van Eerdt, 1985).

The characteristics and history of this community on the coasts in the southern part of the North Sea will be elaborated on. Not only because the sometimes dominant species in this community is important, but also because it will serve to illustrate the rapid changes that can occur, the plasticity of a species in its response to changes, the wide range of tolerances and the impact of evolutionary pathways. Furthermore, *Spartina* is the only salt marsh species from this area in which it is ascertained that CO_2 uptake is through the C_4 pathway. Hence, the functioning of this species will be affected in a different way, compared to all other species, by the primary cause of sea level rise; the increase of atmospheric carbon dioxide. The importance of this species is also derived from the fact that this species reaches its northern limit in the Wadden Sea. A change in temperature as is envisaged from the greenhouse effect will influence the distribution of this species to a large extent.

S. anglica, colonizing the tidal mud at the lower end of the saltmarsh association is entering the niches which were formerly occupied by various annual Salicornia spp., Spartina maritima and Puccinellia. Spartina anglica is a most successful competitor as it spreads vegetatively with great vigour from tussocks established from seeds and vegetative fragments. Its perennial habit enables rapid invasion of the Salicornia zone and subsequent entry into other parts of the marsh.

Spartina anglica wins the competition with Salicornia on less drained, more waterlogged soils under conditions of accretion. The Spartinion forms a belt mainly below MHW level bordering preferentially mesohaline to oligohaline tidal water bodies. Spartina anglica has now virtually outcompeted S. maritima in the marshes of south-west Netherlands, which occupied this niche before the introduction of S. anglica. The vegetation is more resistant against erosion than the other pioneer communities of the mud flats but the susceptibility to frost can cause sudden erosive processes (Beeftink, 1977). Isolated tussocks are more sensitive than dense well developed meadows (Dijkema, 1983). The original fertile hybrid reached its northern limit in the Danish Wadden area, but new, frost resistant, strains have developed in the last decades. The success of the species, on the Frisian islands, is still restricted by the too high sand content of the substrate while too much drainage prevents rapid colonization on the mainland coasts of the Wadden area (Dijkema, 1983).

The establishment of S. anglica at its lowest level may be affected by mechanical action of waves. The seaward spread of *Spartina* is, in sheltered areas, limited by the amount of light reaching the plants in November, when the buds which will produce the shoots of the following year develop. A lower limit of 2.3 h per day of exposure was determined (Hubbard, 1969). This seaward spread of existing vegetation can be limited by wave action also (Morley, 1973). Characteristically *Spartina* shows dwarfing at the lower limit of the marsh. In the dwarf plant zone a very low rate of rhizome development occurred and the annual accretion of sediment in this zone was low, indicating wave-beating.

Spartina plants grow best on muddy soils and have only low competitive ability with other species on sandy substrates (Waisel, 1972). Soft mud is usually considered to be the best habitat for *Spartina*, but closed monotypic *Spartina* vegetations occur also on cohesionless sand (van Eerdt, 1985). Deposition of *Spartina* seeds in the lowest regions occurs only at neap tides. The establishment of *Spartina* at its lowest level is facilitated by fine substrates. The seedlings develop into clumps, which increase the diameter at a rate of 30-180 cm y^{-1}, depending on the texture of the substrate and the initial circumference of the clump (Chater & Jones, 1957). The circular patches fuse and create a closed vegetation. After colonization of the lowest zone, especially by means of vegetative seaward spread, *Spartina* reaches there the highest density. Nutrient supply and mechanical fragmentation are presented as possible causes (Hubbard, 1969). The gradual shift upland, due to sea level rise, of the zone undergoing a typical degree of wave action, will facilitate the upward migration of *Spartina*, provided sedimentation rates are insufficient to maintain the meadow at the site.

4.3.2 Succession

Of particular interest is the community development following colonization by *Spartina*. In its usual habitat where there is deep, soft mud, *Spartina* grows so vigourously and forms so dense a cover that scarcely anything can exist among it (Chater & Jones, 1957). The species stabilizes formerly shifting mudflats and has turned erosion of many foreshores into accretion (Beeftink, 1975). In the south-west Netherlands the species successfully competed with *Salicornia stricta*, *Spartina maritima* and *Puccinellia maritima* in the lower reaches of the marshes. However, *Spartina townsendii* (the infertile "original" hybrid of *S. alterniflora* and *S. maritima*) appears to be unsuccessful in the succession series. The species lost vigour and the population declined, reversing the sites to the original mudflats following a period of increased erosion and cliff formation (Hubbard, 1965). This sequence appears to occur predominantly under euhaline and polyhaline conditions. Apparently *Spartina* modifies the substrate in such a way that this is henceforth also unsuitable for those species which occur naturally in this niche (Beeftink, 1975).

On more sandy substrate, the lower stature and more open growth of the *Spartina* allows colonization of other species (e.g. *Puccinellia maritima*, *Armeria maritima*, *Aster tripolium*, *Trichlochin maritima* and *Agrostis stolonifera)* after the substrate level has reached the appropriate height (Chater & Jones, 1957). Clumps of *Spartina* typically become invaded first in the center, predominantly by *Puccinellia maritima*, due to the rising level of the substrate and the general tendency for a loss of vigour there. The two species can become co-dominant at those sites (Fig.20).

A common feature of the *Puccinellia* and *Festuca* zones is the occurrence of *Spartina* along the margins of channels and in depressions. From there *Spartina* is capable to invade the vegetation by means of underground stolons, the apices eventually reaching the surface to form new shoots . The rate of invasion of *Spartina* is highest in the neighbourhood of water and reaches 15 cm y^{-1}, much lower than the rate of colonization of bare substrates (Chater & Jones, 1957). *Festuca rubra* replaces *Puccinellia maritima* with further accretion of the high marsh and is in a later stage of development accompanied by *Agrostis stolonifera* and/or *Juncus gerardii*.

Table IV. Distribution of major vegetation types of the Wadden Sea islands and Dutch mainland coastal areas, in ha, calculated from "Landscape and vegetation map of the Wadden Sea islands and mainland coastal areas, K.S. Dijkema, 1983.

	SS	ST	SP	SF	TU	TO	TI	TOTAL
Mainland								
Friesland	780	-	980	360	52	-	1320	3492
Groningen	1185	80	1550	280	-	-	66	3507
North-Holland	-	-	-	31	-	-	-	31
West Frisian Islands								
Texel	20	-	150	60	-	150	-	380
Vlieland	6	-	27	16	-	-	12	61
Terschelling	260	-	740	270	-	220	41	1531
Ameland	56	-	65	270	21	34	15	461
Schiermonnikoog	190	-	160	260	97	270	-	977
Rottum	91	-	44	-	-	22	-	157
Griend	-	-	7	-	-	-	-	7
TOTAL	2588	80	3723	1807	170	696	1540	10604

SS = Halophytic pioneer communities with *Spartina anglica* and *Salicornea europaea* within daily tidal range and on beach plains.
ST = Halophytic pioneer community with *Aster tripolium* on mud flats.
SP = Halophytic grasslands and dwarf shrub vegetation with *Puccinellia maritima*, *Limonium vulgare* and *Halimione portulacoides* on low salt marshes and beach plains.
SF = Halophytic grasslands with *Festuca rubra*, *Juncus gerardii* and *Agrostis stolonifera* on high salt marshes, brackish marshes and beach plains.
TU = Open communities with *Spergularia marina*, *Glaux maritima*, *Agrostis stolonifera* and *Juncus anceps* on beach plains and in young dune slacks.
TO = Closed grasslands with *Ononis spinosa*, *Lotus corniculatus*, *Agrostis stolonifera*, *Carex distans*, *Juncus maritimus* and *Scirpus rufus* on transitions between salt marshes or beach plains and young dune slacks or dunes.
TI = Brackish pastures with *Lolium perenne*, *Trifolium repens* and *Elymus repens* on the highest (grazed) salt marshes, often protected by low summer-dike.
Source: Dijkema & Wolff, 1983.

4.3.3 The low marsh

Puccinellion.

These grassland and shrub communities are characterized by Puccinellia maritima, Limonium vulgare and Halimione portulacoides. This zone is inundated during mean spring tides. Depending on soil characteristics and drainage Spartina anglica may persist. The species composition is also dependent on the amount of grazing, either by the natural grazers or by cattle. Undrained and ungrazed areas stimulate Limonium. Improved drainage stimulates Halimione as is shown by the dominance of this species on creek walls and in artificially drained foreland salt marshes. Halimione is possibly a C_4 species and therefore would be stimulated by increasing temperatures. Furthermore, this species reaches its northern limit in the Danish Wadden Sea (Beeftink, 1959; Gehu & Rivas-Martinez, 1984). Apparently this species has increased from the 1930's onwards (Fig.21) and continues to do so (Ketner, personal communication). This is attributed to the stimulatory effect of the temperature rise which has been observed in the last decades. This response and the susceptibility to impoverished drainage will be conflicting in the view of climatic change and sea level rise. The species has locally disappeared during a few years because of severe frost damage. In most cases it could be shown that Halimione will become re-established again within a few years (Beeftink, 1987).

4.3.4 The high marsh

Armerion

These grassland communities, situated above mean spring tide, are characterized by Festuca rubra, Juncus gerardii and Agrostis stolonifera. On many grazed salt marshes at this level a closed Juncus vegetation develops in which Armeria maritima is an accompanying character species. Locally Limonium has retained its importance in a community in which Puccinellia is replaced by Juncus.

All communities and the variants are extensively described in numerous papers (e.g. Beeftink, Kettner, Dijkema, Westhoff, for which the reader is referred to the reference list). The ecotones are summarized in Fig.22, shown in some more detail from vegetation studies on the island of Ameland (Fig.23), and are listed in Table V (Dijkema, 1983).

4.4 Vertical amplitude of species and communities.

At the seaward side of some of the barrages in the delta of the south-west Netherlands, the tidal amplitude increased abruptly after closure of these barrages. However, the maximum increase in the high tide level was not reached immediately after closure. Apparently the capacity of the tidal channels was insufficient to allow entry to the full tidal wedge. In later years the channels were eroded shock-wise. The increase in tidal hight was dependent on the locality (distance from the inlet). The suddenness of these man-induced changes make the response of the species and communities less useful in their predictive value for the occurrences that will follow the expected sea level rise, as this will happen gradually. Salt marsh biota particularly are considered characterized by the influence of continuously changing disturbances. The species are adapted and cope. Furthermore, the species modify, directly or indirectly, their habitat, initiating and sustaining succession, for pioneers ultimately the cause of their decline in a given small area. The following case stories are according to Beeftink (1986, 1987). The barrier was closed in 1969, causing the most substantial in high tide level. In 1973-1974 and 1978-1979 high tide levels rose again, although to a lesser extent.

Spartinetum anglicae

(Effective rise 27 cm; substrate level 1966 1.62 m $^{+}$MSL).

The community experienced sudden increases in MHW levels (24, 11 and 7 cm). These rises caused temporal decreases in the Spartina canopy. The gaps were filled by Aster tripolium and Puccinellia maritima. The community as a whole was not affected by a rise of 36 cm MHW.

Table V. Outline of communities occurring on the Danish, German and Dutch Wadden Sea (from Dijkema, 1983).

	code synoptic Tables 19-22	legend units 1:100,000 map
Communities of tidal mud- and sand flats		
Alliance Spartinion Conard 1952		
Spartinetum townsendii Corillion 1953	S	Ss
Alliance Thero-Salicornion Br.-Bl. 1933 em. R.Tx. 1950		
Salicornietum strictae Christiansen 1955	Q	
Communities of low salt marshes		
Alliance Puccinellion maritimae Christiansen 1927 *em.* R.Tx. 1937		
Puccinellietum maritimae typicum Westhoff 1947		
- initial phase with Spartina anglica nom. nov.	Ps	Sp
- initial phase with Puccinellia maritima Westhoff 1947	P	
- variant with Halimione portulacoides Beeftink 1962 pro phase	Ph	
- variant with Limonium vulgare Beeftink 1962	Pl	
- variant with Aster tripolium Beeftink 1965	Pas	
- *facies of Puccinellia maritima Beeftink 1962*	Pp	
Halimonetum portulacoides Kuhnholtz-Lordat 1927	H	
- terminal phase with Artemisia maritima Beeftink 1959	Hf	
Communities of high salt marshes		
Alliance Armerion maritimae Br.-Bl. et De Leeuw 1936		
Artemisietum maritimae typicum Beeftink 1962	F	Sf
- facies of Artemisia maritima Beeftink 1965 pro phase	Ft	
- facies of Agropyron pungens Feekes 1950	Fe	
Artemisietum maritimae armerietosum Beeftink 1962	Fa	
Juncetum gerardii inops nom. nov.		
- variant with Juncus gerardii Beeftink 1962	Jj	
- variant with Agrostis stolonifera and Festuca rubra nom. nov.	Jg	
Juncetum gerardii armerietosum nom. nov.		
- variant with Juncus gerardii Beeftink 1962	Aj	
- variant with Agrostis stolonifera and Festuca rubra nom. nov.	Ag	
Juncetum gerardii variant with Limonium vulgare and Plantago maritma Beeftink 1962	Al	
Junco-Caricetum extensae Br.-Bl. et De Leeuw 1936	-	
Communities of highest salt marshes and summer-polders		
Alliance Agropyro-Rumicion crispi Nordh. 1940 em. R.Tx. 1950		
Agropyretum repentis maritimum Nordh. 1940	Re	Tl
Poo-Lolietum D.M. de Vries et Westhoff n.n. apud A. Bakker 1965	Ru	
Potentillo-Festucetum arundinaceae Nordh. 1940	Rr	
Communities of salt marsh and beach plain to sand dune transitions		
Alliance Agropyro-Rumicion crispi Nordh. 1940 em. R.Tx. 1950		
Ononido-Caricetum distantis R.Tx. 1955 n.n.	Ro	To
Community of Agrostis stolonifera subvar. salina and Trifolium fragiferum Westhoff 1947	-	
Alliance Armerion maritimae Br.-Bl. et De Leeuw 1936		
Juncus maritmus-Oenanthe lachenalii association R.Tx. 1937	Bm	
Scirpetum rufi (G.E. et G. Du Rietz 1925) Gillner 1960	-	
Communities of brackish habitats		
Order Glauco-Puccinellietalia Beeftink et Westhoff 1962		
Aster tripolium-sociation Beeftink 1965	Bas	St
Halo-Scirpetum maritmi (Van Langendonck 1931) Dahl et Hadac 1941	Bi	Wp
Phragmites australis-consociation Beeftink 1962	B	
Agrostis stolonifera salina-sociation Beeftink 1962	Bg	Sf
Communities of habitats instable in salt- and water content		
Glaux maritima-sociation	-	Tu
Alliance Puccinellion maritimae Christiansen 1927 em. R.Tx. 1937		
Puccinellietum maritimae pharapholietosum Westhoff 1947	-	
Alliance Puccinellio-Spergularion salinae Beeftink 1965		
Puccinellietum distantis Feekes (1934) 1943	-	
Puccinellietum retroflexae (Almquist 1929) Beeftink 1965	-	
Alliance Saginion maritimae Westhoff, Van Leeuwen et Adriani 1962		
Sagino maritmae-Cochlearietum danicae (R.Tx. 1937) R.Tx. et Gillner 1957	-	
Alliance Nanocyperion flavescentis W. Koch 1926		
Cicendietum filiformis Allorge 1922	-	
Centaurio-Saginetum moniliformis Diemont, Siss. et Westhoff 1940	-	
Communities of tide marks		
Suaedetum maritimae (Conard 1935) Pignatti 1953	-	
Atriplicetum littoralis (Warming 1906) Westhoff et Beeftink 1950	-	

Puccinellietum maritimae

(Effective rise 38 cm; substrate level 1966 1.9 $^+$MSL).

Decrease of cover percentages after a shock-wise flood increase, but the species recovered. Triglochin maritima increases after a flood increase, but declines when Puccinellia maritima recovers. Limonium vulgare reached maximum cover following the second rise. The area is gradually invaded by Spartina anglica. The vegetation appears to change into a Spartinetum.

Puccinellietum maritimae

(no MHW rise; substrate level 1966 2.29 m $^+$MSL).

Large interannual fluctuations in cover of the two dominant species Puccinellia maritima and Triglochin maritima due to changes in flooding frequency and summer drought. No permanent alterations in the community occurred. The changes reflect the natural interannual variability of a salt marsh vegetation.

Plantagini-Limonietum

(MHW rise 48 cm yr; substrate level 1966 1.78 m $^+$MSL).

Plantago maritima appeared to cope with a MHW rise of 35 cm during several years. However, the species did not recover after a decline caused by another stress (drought in this case). Triglochin maritima increased significantly after the decline of Plantago. The cover percentages of the other species (Puccinellia maritima, Limonium vulgare) remained more or less constant. Because of the decline of Plantago, the community gradually changed into a Puccinellietum, rich in Triglochin.

Plantagini-Limonietum

(MHW rise 5 cm; substrate level 1966 2.38 m $^+$MSL).

Because the species characteristic of the Armerion maritimae (upper salt marsh) (Plantago and Armeria) declined and the species characteristic of the middle marsh (Triglochin and Limonium) increased, the community changed from a Plantagini-Limonietum into a Puccinellietum maritimae.

Halimionetum portulacoides

(MHW rise 29 cm; substrate level 1966 1.84 m $^{+}$MSL).

The pattern is heavily disturbed by two years with frost damage from which *Halimione portulacoides* in spite of the MHW rise appears to recover. *Aster tripolium* and *Suaeda maritima* temporaly filled up the gaps. The invasion of *Puccinellia maritima* was permanent and the community appears to change into a Puccinellietum maritimae.

Halimionetum portulacoides

(no MHW rise; substrate level 1966 2.39 m $^{+}$MSL).

Highly influenced by the amount of deposited plant litter which particularly affects *Halimione* negatively. This in contrast to *Elymus*, which species thrives and is responsible for an additional source of detritus. In this community *Puccinellia* and *Festuca rubra* disappeared as a result of enhanced growth of *Elymus* in combination with litter deposition, masking any effect of flood level rise.

Artemisietum maritimae

(MHW rise 44 cm; substrate level 1966 1.90 m $^{+}$MSL).

The first flood rise (24 cm) stimulated *Artemisia*, but the species disappeared when the flood level had risen 42 cm. *Festuca* declined from a cover of 100% to a cover of 10% after the first rise, hence appears to withstand such a rise (at least a few years). Following the next rise (11 cm) the cover of this species was reduced from 10% to 2%, but again, this cover percentage was maintained several years. The addition of the final rise (7 cm) halved the cover once more (to 1%). Apparently *Festuca* has a range (from 100% to 1% cover) of at least 44 cm downward on this tidal gradient. *Festuca* is replaced by *Halimione* which in turn is replaced by *Puccinellia*. *Aster* fills the gaps during transient periods. At this site *Spartina* invaded following the last rise. The community changed into a Halimionetum portulacoides and showed the first steps of a change into a Puccinellietum maritimae.

Artemisietum maritimae
(MHW rise 4 cm; substrate level 1966 2.49 m $^{+}$MSL).
This community (with Festuca and Artemisia) is also susceptible to choking by large amounts of detritus. Elymus might be promoted, but very high levels of deposition will eventually kill this species after which annual Atriplex spp. will take over.

The sensitivity of the communities can be summarised as follows; (after Beeftink, 1986).

Table VI. Sensitivity of saltmarsh communities to rapid sea level rise.

Maximum sustainable rise	Community
3 cm	Armerion maritimae (high marsh)
10-15 cm	Puccinellion maritimae (middle marsh)
30-40 cm	Spartinion (low marsh)

All the above described phenomena should be considered regression patterns, but for a situation where sea level rises gradually little can be deduced from it, because of the magnitude of the stepwise increased MHW levels. Only the final effect has some predictive value.

The response of plants to more gradual changes in sea level is dependent on the flexibility, the ecological amplitude and the response to flooding of the species. Most flexible are, of course, the annuals (e.g. Salicornia, Suaeda), and a short-lived perennial (e.g. Aster) is more responsive than long-lived perennials (e.g. Halimione). Spartina, Triglochin and Limonium reacted favourably, by means of stimulated vegetative reproduction, to the increase of flooding frequency. This in contrast to Glaux, Festuca, Artemisia and Elymus. In general, the flooding frequency governs the species distribution. In a zone of the middle marsh species from the lower reaches will increase while species of the higher marsh will decrease with more frequent flooding. In this aspect not the numerical increase of the flooding frequency is important but, the relative change. A few additional days of submergence will be insignificant in the low marshes but not in the higher reaches where they might cause a doubling of the flooding frequency. Changes of this magnitude will have effect there. However, sea level rise will have similar, relative, effects on the flooding frequency, irrespective of the level in the marsh, a consequence of the exponential relation between elevation and flooding frequency. In the Wadden Sea every 20 cm MHW rise will cause a doubling of the flooding frequency. Species with a large ecological amplitude (e.g. Aster) will move along the gradient, and will often occupy gaps temporarily, as will annuals.

4.5 Tolerance to flooding/inundation.

Salt-marsh communities are subjected to a number of gradients in which the zonation is apparently reflected. However, the environmental conditions vary temporaly and localy in such a magnitude that the vegetation and communities should be described as a mozaic of small and large patches. The vegetation reflects tolerances more than preferences. The opinion on the relative importance of the various physicochemical factors differs considerably among the researchers.

Aeration, salinity, redox-potential and temperature are some of the more influential abiotic characteristics that will change when the frequency and/or the duration of flooding increase. The tolerance of plants to waterlogging and salinity differs in a way which is correlated with their position on the salt marsh ecotone.

Species composition is related to aeration during the summer. Aeration is influenced strongly by tidal inundation. Armstrong et al. (1985)

distinguished three main soil-aeration patterns.
a. Reducing conditions throughout the soil profile and indifferent to periods of exposure, characteristic of Spartina anglica sites. Phases of oxidation occur only near the surface and during neap tides.
b. Puccinellia maritima sites; creek-banks dominated by Halimione portulacoides and Elymus pycanthus sites showed lowered redox potentials only during spring high tides.
c. In the high marsh only the very high spring tides influenced aeration.

Elytrigia pungens (2.2 m +NAP Stroodorpepolder, high marsh) is able to withstand inundation for periods up to 8 days in the natural environment, however decreased the production in an artificial environment (Groenendijk, 1984).

Pucinellia maritima showed a preference for waterlogged soils (Cooper, 1982), but prolonged inundation (up to 8 days) reduced growth (Groenendijk, 1984).

Agrostis stolonifera is regarded as a species which can tolerate transient soil waterlogging whilst Festuca rubra is regarded as a species sensitive to flooding (Rozema and Blom, 1977, Cooper, 1982, Davies and Singh, 1983). In this species a considerable degree of genotypic variation occurs between the populations of the marshes proper and those of more inland localities. The reduction in shoot yield by waterlogging was generally least in those populations from the salt marshes. A. stolonifera yield approximately doubled under waterlogged conditions and the intraspecific variation between populations was, in this aspect, not significant (Davies and Singh, 1983). These two species of the high marsh (Juncetum gerardii association) occupy the higher zones of the high marshes (0.45-0.75 m^{+}MHW in the Wadden Sea)

4.6 Propagation and sedimentation.

Successful propagation by seeds in Spartina anglica is dependent on substrate stability. Because the upper layer of unvegetated intertidal flats is subject to frequent disturbances, a net accretionary balance of at least 5 mm during the period of germination and settlement is necessary. This condition is not met on the mud flats in The Netherlands and if the seeds remain buried, seed rot as result of waterlogging will prevent germination. The natural generative spreading of S. anglica is restricted to the zone where an open vegetation already occurs (van Eerdt, 1985).

Marsh vegetation would shift from high marsh to low marsh position with sea level rise and would produce a wide, shallow platform that would attenuate wave energy in much the same way as existing shorelines. There is an upward and landward shift of environments as opposed to a one-dimensional shore retreat.

4.7 Changes in the microenvironment of saltmarshes.

Gray and Bunce (1972) consider the edaphic (soil related) factors as important as the submergence frequency in determining the type of vegetation. There is a general agreement that edaphic rather than biotic factors are principal in limiting species to any particular zone in a salt marsh and the spatial heterogeneity is influenced by the rate of exchange between tidal and interstitial water. Changes in waterlogging and inundation will affect marsh vegetation by a number of mechanisms and the resultant appearance of the vegetation is frequently ecophenic and not genetic (Howes et al, 1981). However, there is a considerable divergence of opinion as to the relative importance of the various physicochemical parameters involved (Cooper, 1982). Linthurst (1980) lists 8 possible causes of die-back in Spartina alterniflora, some of which are likely to occur as a result of sea level rise. (1) excess salinity, (2) waterlogging, (3) lack of available iron, (4) hydrogen sulphide toxicity, (5) oxygen deficiency in roots, (6) change in tidal regime, (7) trash wrack coverage by death plant material, (8) pollution. Many of these are interrelated, but anaerobiosis and waterlogging appear to be the dominant factors.

4.7.1 Salinity tolerance

Generally, species capable of tolerating 0.5% (66 me/kg) or more NaCl are regarded as halophytes. Some evidence has been published to indicate that some species are obligate halophytes and reach their optimum growth at moderate to high salinities. Only a relativily small number of plant species are capable of tolerating the degrees of salinity that occur. As a result, there are broad geographical areas in which there is a substantial uniformity in the vegetation (Chapman, 1974). All halophytes respond positively to NaCl. The optimal NaCl concentration for the growth of halophytes ranges from 20-500 mM NaCl (oceanic water 479 mM NaCl, 559 mM Cl^-, Head, 1985) and growth rates can be 10-fold in optimal salinity as compared to fresh water (e.g. in Salicornia europaea, Flowers et al., 1977). Nevertheless, there is no evidence for an obligate requirement for high electrolyte concentrations among higher plants. All halophytes will survive non-saline conditions although growth rates will generally be reduced to 40-80% of the rate in optimum saline conditions. Humidity of the air appears to be especially important as is shown for Atriplex halimus from Australia (Gale et al., 1970). The optimum salinity decreased with increased relative humidity (RH) and relative growth rates (as compared to non-saline conditions) increased an order of magnitude when the halophyte was exposed to dry air (27% relative humidity). The responses can be explained from the changes in water potential in the compartments of the microenvironment in which the plant lives. The water potential of "dry" air (50 % RH) amounts to -933 bar while this reduces to -300 bar for humid (80% RH) air (Larcher, 1975). On the other hand an increase of the ionic strength of the soil water reduces the water potential also. The difference between the two water potentials, the driving force for uptake processes, connected by the plant, becomes smaller and the capability for water and solutes uptake diminishes.

Halophytes take up ions and therefore decrease their water potential to an average -20 to -50 bars (Flowers et al., 1977). A plant withdraws water from the soil only as long as the water potential of its fine roots is more negative than that of the soil solution. The increase in ion content facilitates uptake of water and results in increased turgor (internal pressure). Turgor is a major control of growth in plants. Too low turgor values cause wilting. Prolonged wilting causes death.

Soil water potential is not only dependent on the ionic strenght of interstitial water but also on the composition of the sediments. The crucial component in this aspect is the matrix potential, the force with which water is held by capillary action and adsorption to colloids. This potential is particularly large in soils having small pores and a large colloid content (loamy and clay soils) (Fig.24).

Climate change and the concomitant sea level rise will influence many, if not all, of these aspects in salt marsh functioning. Also, the direction and the magnitude of the effect will depend on species composition and substrate characteristics in small areas.

4.7.2 Waterlogging and inundation.

Changes in the water level, as caused by sea-level rise, will have direct effects on perennial plants only. Annuals will be affected indirectly as die-back phenomena might create gaps in the vegetation cover, an advantageous development or, migration of species of the lower marsh into higher reaches might reduce available free substrate, detrimental to the annuals. However, the sensitivity to salt spray is far higher of flowers than that of the vegetative organs. Perennial plants may thus survive under conditions which prevent generative reproduction. The direction of changes will depend on too many variables to allow a generalized prediction.

The annuals of the genus Salicornia from the lowest zones of the marine salt marshes thrive when submerged once daily (as in regions with semi-diurnal tides) and hence on saline soils (Cooper, 1982) compared to conditions of no or twice daily submergence (Langlois & Ungar, 1976).

In some S. alterniflora marshes the growth is inversely related to the salinity of the interstitial water (Nestler, 1977) but, because a comparable variability in growth forms is found in marshes where the salinity of interstitial water is homogeneous throughout a vegetation zone, other factors (e.g. iron, sulphur, redox-potential, oxygen) are certainly involved. Increasing the subsurface drainage in a stand of intermediate-height Spartina alterniflora (in the USA) caused significant increases in the shoot height and in above-ground production, indicating that soil water movement is a determinant of productivity in a salt marsh (Wiegert et al., 1983). However, in a more elaborate series of experiments, in another marsh but with the same species, Linthurst & Seneca (1980) obtained very different results. A number of parameters are extracted from their paper and represented in Table VII and shown in Fig.25. The plants of which the substrate level was artificially lowered 20 or 30 cm had died in September of the first year. Redox potentials, free sulphide, and salinity, all substrate characteristics, may act as the dominant response regulating variables.

The data of Linthurst & Seneca (1980) are indicative for the sensitivity of even these plants from the lower reaches of the salt marsh to changes in flooding frequency.

The response is dependent on the species, particularly on the characters that govern the natural distribution. Species of the lower marshes are less susceptible than species of the high marsh (Rozema et al., 1985). The most important factor for the distribution of the species in Dutch coastal marshes appeared to be salinity where inundation can be regarded as an additional influence (Groenendijk et al., 1985, Rozema et al., 1985).

Table VII. Changes in a number of characteristics caused by artificial waterlogging

	Elevation (deviation from marsh surface), cm.				
	-30	-20	-10	0	+10
Variable					
Biological (m^{-2})					
Density	0	0	28	1144	802
Living aerial (g)	0	0	6	141	117
Death aerial (g)	220	309	237	231	338
Physical & Chemical					
pH top	6.9	6.8	6.0	6.0	4.9
pH -15 cm	6.9	6.9	6.1	5.7	4.8
Oxygen (ppm)	0.2	0.3	1.8	n.a	n.a
E_{h7} soil (mv)	-195	-200	-180	+ 12	+105
Free sulphide (M)	$10^{-2.1}$	$10^{-1.2}$	$10^{-9.3}$	$10^{-13.1}$	$10^{-16.1}$
Salinity o/oo	18.4	20.1	18.6	12.9	9.6

Waterlogging was the major factor affecting the distribution of Salicornia europaea and Puccinellia maritima and drainage produced a different response in both species, with P. maritima showing a preference for less well aerated soils (Brereton, 1971), the species is well suited to its role as a pioneer species of the lower zones of the salt marsh. Both species have a characteristic high shoot/root ratio, a functional advantage on waterlogged soils, but also a disadvantage in higher reaches of the marsh where severe water stress can occur. However, Groenendijk (1987) argues that the phenology of P. maritima (an evergreen) is reflected in the comparatively high shoot/root ratio as compared to the other species of this zone, many of which allocate relatively much to the below-ground parts as a reserve for the production of new shoots (from buds) in early spring.

Shoot/root ratios increase as a result of saline flooding (and associated processes) (Cooper, 1982, Groenendijk, 1987). Tillering is the main mechanism for settlement and colonization in Puccinellia. As increased CO_2 stimulates tillering (Tissue & Oechel, 1987) this will offset the disadvantage of this species in respect to waterlogging.

Elevated CO_2 levels promote the growth of roots in agricultural crops and reduce the shoot/root ratio (Goudriaan & Ketner, 1985). If P. maritima responds in such a way, the species may be capable to expand its range into higher regions of the marsh. In this and other species the changes in the microenvironment might counteract. Increased shoot/root ratios because of flooding, and conversely decreased shoot/root ratios due to the stimulation of root growth by elevated levels of atmospheric CO_2.

Clumping of Salicornia and Puccinellia on salt marshes is controlled by the interaction of salinity and the degree of waterlogging (Brereton, 1971). Experimental work with Puccinellia maritima has shown that maximal growth occurs under glycophytic conditions and relatively little growth takes place if the water is more than 1/3 the concentration of open sea water. The species produces long creeping stolons at daylength of 16 hrs and caespitose tufts at daylength of 12 hrs. Optimal growth occurred between 17-23 ^{0}C with flooding twice a day and with a salt content of 1/4 sea water (Weihe & Dreyling, 1970).

Waterlogging and reduced yields were associated with an increase in shoot iron and manganese concentrations (Cooper, 1982) but a toxic effect of iron was not apparent in Spartina alterniflora (Haines & Dunn, 1976). On the contrary, according to Adams (1963) this species is limited in its distribution to the low marsh because only there its high iron requirements are met. The respective roles of anoxia, waterlogging, iron and mangenese are not yet separated nor understood in their ecological significance for marsh vegetation (Rozema & Blom, 1977).

P. maritima was also at a competitive advantage over Festuca rubra when subjected to both waterlogged and saline treatments (Gray & Scott, 1977). Of the other salt marsh species, Juncus gerardii and Armeria maritima were also not tolerant of neither waterlogging nor salinity when compared with Plantago maritima, Aster tripolium, Triglochin maritima, S. europaea and P. maritima (Cooper, 1982). Responses in agreement with the position of the species in the salt marsh zonation.

In Agrostis stolonifera, a flooding-tolerant form of the high marshes, production was stimulated by flooding with fresh water but under saline conditions (50% seawater) plant growth was reduced (Rozema & Blom, 1977, Davies & Singh, 1983). This in contrast to Juncus gerardii, a species from a lower zone of the high marsh, which reduced growth under waterlogged conditions, but was not affected by salinity, and is at least partly flooding tolerant (Beeftink, 1965). Waterlogging stimulated iron and manganese uptake in both species. The latter species occupies a lower range in the salt marsh ecotone, hence it might be concluded that sea level rise will influence these two species in different ways but with comparable results. Increased waterlogging will reduce growth of J. gerardii in the lower reaches of its range, while increased salinity, due to increased flooding, will affect A. stolonifera. Both species will migrate upland and J. gerardii will invade and eventually occupy the zone in which the vitality of A. stolonifera diminishes. The other flood-tolerant Juncus species (e.g. J. maritimus, J. effusus), having long erect leaves, remain in contact with atmospheric oxygen and anaerobiosis of the shoot is less likely to occur (Rozema & Blom, 1977).

Therefore, no predictions can be made and only some possibilities are presented.

-increased salt damage to inflorescences, counteracted by increased allocation to reproductive structures as result of higher CO_2 concentrations.

-increased salinity in the higher marsh causing lowering of the water potential of the soil, impairing water uptake, counteracted by increased water-use efficiency in a higher CO_2 environment.

-changed sediment deposition patterns, beneficial to water uptake if the structure becomes coarser and in this aspect disfavourable if the clay content becomes higher. Counteracted by possible changes in nutrient supply. The effect of changed percolation rates might work both ways. -decreased salinity with heightened flooding frequency during dry periods, facilitating water uptake but possibly offset by the impact of waterlogging.

4.7.3 Aeration and soil oxygen.

Only the upper few centimeters of the soil in a maritime marsh contained any oxygen and, in general, reduction intensity was high except in well drained areas (Teal and Kanwisher, 1961). This suggests that in certain areas the low oxygen concentration of the soil atmosphere may be a limiting factor in the invasion by some species (e.g. of the *Spartina alterniflora* zone and the *Aster* marshes). *Spartina alterniflora* is a major oxygen consumer and in deeper roots the amount of oxygen present in air lacunae may be as low as 3%, presumably because of its absence in the soil atmosphere. In Great Britain, 'die-back' in *Spartina townsendii*, in which centres of clumps die out, has been related to a toxic reduced inorganic ion -possibly sulphide- in the soil (Goodman and Williams, 1961). These soil sulphides may be indirectly responsible by lowering the oxygen content of the soil. Silvanesan & Mannus (1972) pointed out that bacteria in the muds may aggravate the reducing conditions, especially those associated with sulphate reducers, and hence the production of the sulphides. This problem is mainly associated with low marshes because as marshes become higher and exposure periods longer oxidation processes progessivily set in (Brummer *et. al*., 1971). Sea level rise has a reversed effect, and consequently reducing conditions will recur gradually in the marshes and may accelerate the die-back of *Spartina*.

S. alterniflora oxidizes the sediments in which it grows through both passive oxygen release and active metabolic processes. Consequently, the Eh (redox-potential) is highest in the root zone. The sediment redox condition and the production of *S. alterniflora* are related through a positive feedback loop. Lowered Eh inhibits above-ground production, but, conversely, more productive plants have a greater capacity for sediment oxidation (Howes et al., 1981). S. alterniflora shoot height was inversely proportional to rate and extent of oxygen decline during submergence (Gleason & Zieman, 1981). When tidal water covers the plant, diffusion of oxygen from the atmosphere to the shoot is curtailed and attenuation of available light may reduce photosynthetic production of oxygen (Armstrong & Gaynard, 1976). Because tall plants undergo less complete submergence than short plants, the sensitivity to flooding will be most pronounced in seedlings. The timing of tidal submergence relative to the diurnal light cycle has a clear influence, but in this aspect nothing will change.

Waterlogged sediments inhibit plant growth by decreasing passive oxygen release. Oxygen deprivation during periods of submergence, particularly in darkness, inhibits the growth of below-ground organs. Especially the apical meristems, the growth initiating tissue, is susceptible to damage by anoxia. Root anaerobiosis acts as a barrier to seaward extension of Spartina. Increased ASL will therefore curtail rejuvenation of the lower part of the vegetation and therefore initiate the retreat to higher zones. This process will proceed slowly and gradually.

Reduced oxygenation of marsh soils influences plant growth in more than one way, some of which may act synergistically, but the relative effect of the changes separately is not fully understood. High concentrations of dissolved inorganic nitrogen (DIN) are common in marsh sediments (Mendelssohn, 1979, Teal et al., 1979) but DIN uptake is maximal in oxic sediments and nutrient uptake rate is positively related to the oxygen concentration (Howes et al, 1981). The oxygen content of the sediment is severely reduced by the continuous high demand for oxygen by decay processes. The large amounts of H_2S, a respiratory inhibitor, which are released in these processes, impair nutrient uptake and hence growth. Oxygen efflux from roots to rhizosphere protects the plant by oxidizing potential soil toxins. When oxygen supply falls, roots become exposed to poisoning by Mn^{2+}, Fe^{2+} and H_2S (Armstrong, 1975).

4.7.4 Redox-potential.

Redox-potential is an index of soil aeration. From a series of continuous observations it became clear that reducing conditions occur throughout the largest part of the salt marsh zonation and that frequency and duration are dependent on tidal cycles.

```
increased                increased
plant ------------>      metabolic
growth                   oxidation
   f                         f
   f                         f
increased                 increased             increased           decreased
nutrient  <--------       root zone <------     O2 release <-----   sediment
uptake                    oxidation             oxidation           saturation
```

Armstrong et al. (1985) related species composition to aeration during the summer and distinguished three main soil aeration patterns.

a. Reducing conditions, persisting throughout much of the soil profile, indifferent to periods of exposure and, only during neap tides and in the top layer phases of oxidizing conditions. Characteristic vegetation *Spartina anglica*.

b. Redox potentials lowered monthly by high spring tides but at creek banks and sites of *Elymus pycnanthus* rarely falling below 200 mV, during high and very high spring tides. Drainage, in between spring tide periods, enabled highly oxidizing conditions to develop. *Puccinellia maritima* and *Halimione portulacoides* are typical dominant species.

c. In the general salt marsh zone only the very high spring tide levels influenced soil redox-potential. Long stable periods of constant oxidizing conditions are typical. *Festuca rubra* is a characteristic species. The changes in the most important soil chacteristics, as induced by a prolonged waterlogging, are shown in Fig.26.

4.7.5 Microbial processes.

Salt marshes are the base of several food webs. A food web important to many marsh/estuarine species is based on microbial processes which process or reprocess photosynthate and are therefore influenced by changes in community structure or functioning due to sea level rise and increased rates of photosynthesis.

Microbial processes utilize all major components of photosynthate allocation (e.g. excreted dissolved organic matter (DOM), leachates from dead plants, decomposed cellulosic material). Approximately 5% of the daily photosynthate is excreted as DOM in Spartina alterniflora (Fallon & Pfaender, 1976). This DOM is rapidly taken up by bacteria and fungi, the latter having the slowest uptake rate. The bacteria mineralize the material more rapidly whereas the fungi incorporate relatively more in particulate matter. Initially fermentation of DOM is of little importance due to the repression of cellulolytic enzyme synthesis by leachate (glucose, cellobiose) (Reed, 1980). Bacteria are responsible for the major part (+ 60%) of the heterotrophic metabolism in salt marshes. However, the rate of mineralization is highest in a system which contains also the next step in the food chain (e.g. protozoans and microcrustaceans), the grazers on the microbial biomass (especially on bacteria) which accelerate the turn over rate. The high rate of mineralization in this part of the system has as a consequence the low efficiency in converting metabolites into new biomass, hence soil and interstitial CO_2 concentrations are high. The CO_2 might be lost to the atmosphere. The lower efficiency of biomass production and higher rate of mineralization has significant implications for nutrient cycling, increasing the amount of nutrients available, contributing to species richness and abundance.

Mineralization rates of leachates of salt marsh grasses are much lower and range from 0.23-0.63 % day^{-1} (Gosselink & Kirby, 1974, Fallon & Pfaender, 1976). The lowest rate is also the rate observed for the aerobic breakdown of the nonsoluble, cellulosic, plant material.

The possibility exists, as it was the outcome of a modeling experiment (Wiegert, 1986), that increased aerobic microbial production has a negative impact on the production of benthic algae. The response of the algae to the increase in the aerobic microbes is an indirect effect of changes in the algal consumers, specifically seasonal switching by omnivorous consumers between algae and the aerobic microbes.

4.7.6 Sulphide toxicity.

Sulphide is produced in those anaerobic environments where there is a supply of sulphate ions and organic matter adequate for the sulphate reducing bacteria of the genus Desulphovibrio. These organisms utilize sulphate as a terminal electron acceptor for oxidative phosphorylation. These bacteria can respire large amounts of the primary production of a marsh. Howarth (1978) determined the respiration of these bacteria at 1800 g of carbon during a year. In the anaerobic sediments which characterize the seaward parts of the marshes, microbial activity leads to the production of sulphide, reduced iron (Fe^{2+}), manganese (Mn^{2+}) and various hydrocarbons. In the process the redox potential is lowered (sulphate reduction requires a Eh of -150 mV, Ponnamperuma, 1972). The process depends on the release of suitable substrates during decomposition processes, as only a limited range of compounds (short-chained carbohydrates, aminoacids) are accepted as energy sources by SO_4 reducing bacteria (Sorensen, 1984). Microbial activity will be enhanced by the expected increase in mean temperature and through the stimulated allocation of photosynthates to the roots as a response to raised atmospheric CO_2 concentrations.

The product, sulphide, is released into the soil where much of it might be taken up by ions of transition metals, such as iron, copper, and manganese, resulting in the formation of insoluble inorganic sulphides. Sulphide in soils exists in an equilibrium, partly determined by the pH (Ingold & Havill, 1984).

inorganic sulphide		acid sulphide		hydrogen sulphide
S^{2-}	====================	HS^-	================	H_2S
(solids)		(soluble)		(soluble gas)

Hydrogen sulphide is gradually lost to the atmosphere, hence the presence of HS^- will depend on continued microbial sulphide production. The distribution of sulphide in marsh soils appears to be variable. Ingold & Havill (1984) found the highest concentrations (range 0.005-0.4 mM) within 1-2 cm of the soil surface, associated with discrete black horizons, 2-3 mm thick in marshes of the Thames estuary. Sometimes these horizons recurred several times within the top 5 cm. In contrast, the sulphide concentration increased with depth down to 10 cm in the higher reaches of a *Spartina alterniflora* marsh, associated with a low iron concentration, on the Atlantic seaboard of the USA (King et al., 1982).

The shoots of the salt marsh species *Puccinellia maritima*, and *Festuca rubra* were chlorotic and the root system was stunted if the plants were grown in a culture solution containing 0.1 mM sulphide. However, the colonizer *Salicornia europaea* was not affected. In the marsh *S. europaea* appears to be associated, but not restricted to, sulphide rich soils. The cover of this species was positively correlated with sulphide concentrations. By contrast, the cover of *P. maritima* showed a significant negative correlation, reaching the greatest cover on those sites where sulphide was absent throughout the summer. Where sulphide was detectable throughout the summer *P. maritima* was either absent or sparse and *Salicornia* was dominant (Ingold & Havill, 1984). Release of sulphide, stimulated by waterlogging, will initiate the retreat of *P. maritima* and the vacated sites will then be occupied by the annuals of the genus *Salicornia*.

4.7.7 Nutrient gradients.

The grass standing crop in marshes is determined by nutrient supply, and in particular, nitrogen. The standing crop in swards undergoing phosphate enrichments resembled unfertilized, control, standing crops. This response pattern held for total above-ground vegetation and for individual standing crops of *Spartina alterniflora*, *S. patens*, and *Distichlis spicata*, the dominant grasses in a Massachusetts maritime marsh. The with nitrogen fertilized plots resembled swards found at lower elevations in the marsh, suggesting that the great variations in standing crop are related to nitrogen supply. Since nutrients are brought into the salt marsh largely by tidal water, it seems that marsh sediments and microflora are able to remove substantial amounts of dissolved nutrients from tidal water columns. Marshlands are of importance as removers of dissolved nutrients, particularly nitrogen, from estuarine waters (Valiela and Teal, 1974, Dankers *et al.*, 1984). However, the nitrogen flux in an estuary appears to be dependent on the N-species under consideration and the time of the year. Oxidized forms (nitrate and nitrite) are frequently imported while reduced N (ammonia and dissolved organic) is exported (Whiting *et al.*, 1987). If the marsh exports oxidized N this will occur predominantly in fall and winter, after the mineralization of the standing crop commences and uptake is slowed down or has stopped.

Species characteristic of the low marsh and drainage channels (*Aster tripolium*, *Halimione portulacoides* and *Suaeda maritima*) show small but significant increases in frequency after addition of inorganic nitrogen as compared to controls (Jefferies & Perkins, 1977). However, the natural, year to year, variation within the vegetation is much larger than the variation caused by addition of fertilizers. The decrease of *Armeria maritima* in fertilized sites is the result of growth enhancement of the accompanying species and not of a negative response to increased nutrient availability. The species composition does not change and exhibits a strong degree of constancy towards nutritional perturbations. The primary production of the system is therefore not limited by nutrient shortage but by the negative response to high salinities and summer drought. At sites where tidal immersion is frequent, net primary production may be limited by lack of available nitrogen, especially in superficially rooting annuals and perennials with high relative growth rates (e.g. *Spartina alterniflora*). Species with high relative growth rates (e.g. *Suaeda maritima*, *Aster tripolium*, *Halimione portulacoides* and *Salicornia* spp.) are species of the low marsh, where water and nitrogen usually are not limiting. In general, conflicting opinions exist regarding which nutrients, if any, limit growth and production in salt marshes. Nitrogen limitation was found in a number of salt marshes (Ranwell, 1964, Valiela & Teal, 1974, Patrick and DeLaune, 1976). Practically all of the inorganic nitrogen in a reduced soil is found in the ammonium form. Nitrogen fertilization stimulates both growth and the nitrogen content (lower C/N ratio) of the plants (DeLaune & Patrick, 1980).

One of the effects of waterlogging on soils is to increase the availability of phosphorus (Jones, 1975) but fertilization with phosphorus had no effect on plant growth in species of the low marsh in the USA (Patrick and DeLaune, 1976) and phosphorus uptake declined even in waterlogged conditions in *Agrostis stolonifera* and *Festuca rubra*. This might be due to immobilization of phosphorus in roots by iron due to the high uptake of the latter in waterlogged sand (Jones, 1975). On the other hand, Mendelssohn and Seneca (1980) and Linthurst and Seneca (1980) attributed the reduction in growth, under flooded conditions, to reduced availability of nutrients, while Groenendijk (1987) reports an indifference or an increase in the concentrations of nutrients in marshes from the south-west Netherlands. Many aspects of the interaction of sea water and plants are not yet elucidated and responses might vary between species and between sites or locations.

Addition of phosphorus had no effect in the species listed above (Patrick and DeLaune, 1976), but *Agrostis stolonifera* strongly increased growth (Jones, 1975). The availability of phosphates to the plant is, apart from soil concentrations, strongly influenced by the calcium content of the soil, especially in periods of water shortage.

Although some consistent trends have been indicated in the role of nutrients in salt marshes, there is still considerable variability among the various marshes with respect of magnitude and direction of nutrient fluxes. Much of this variability is to be attributed to morphology, location, species composition, hydrology and even size of the marsh (Whiting et al., 1987). A concentration gradient for nutrients exists from the creek banks to the areas away from creeks.

A significant response to additional nutrients is the increased allocation into generative reproduction, but as with shoot frequencies, year to year variation in the number of inflorescences is large (Jefferies & Perkins, 1977)

5 Sedimentation and erosion of saltmarshes and tidal flats.

5.1 Deposition and characterization of sediments.

The culms of mudflat vegetation can facilitate sedimentation by acting as a baffle to current energy so that sediments become trapped and settle out of the water column. For fine-grained material, principally in the clay size range, plant stems and leaves provide an increased opportunity of collision. Therefore, deposition of sticky clays is greatly facilitated by the presence in the water column of vegetation, inasmuch as their settling times for deposition greatly exceed the tidal period (Orson et al., 1985).

Given a rapid rise in sea level, a marsh may be able to compensate and expand laterally if sediment input is sufficient. This is particularly applicable for marshes located near river deltas. Land clearing practices and the resulting erosion may be responsible, by means of increased fluviatile loads, for increased sedimentation rates. It is possible that a previous land-use pattern has masked the effect of sea level rise. A change in this pattern and especially in the prevention of erosion may accentuate the loss of wetlands (Orson et al., 1985).

5.2 Erosion and vegetation.

The transition zone of the tidal flat to salt marsh in The Netherlands generally varies between gently sloping gradual profiles, in accretion environments, to small cliffs (up to 120 cm high) when erosion predominates. Vegetation retards erosion and facilitates sedimentation processes (Chapman, 1977, Orson et al., 1985, Bouwsema et al., 1986). The beneficial influence of the vegetation is caused through the reduction of current speed, in that the above-ground plant parts act as baffles, and through the strengthening of the substrate-root layer by the presence of roots and rhizomes (van Eerdt, 1985). After cliffs have been initiated, the resistance of the cliff to erosion is determined by the strenght of the soil material in combination with the binding effect of the roots and rhizomes. Perennial and especially rhizomatous species are therefore more effective. The contribution of roots to the stability of the cliff is proportional to the number of roots intersecting the potential failure plane which is essentially vertical (van Eerdt, 1985).

The pattern becomes more complicated by the influence of substrate characteristics on the development of below-ground plant parts. The vertical distribution of roots is strongly dependent on soil composition. Density is always on its maximum in the surface layers but decreases sharply at the sandy loam/sand contact plane. And also, loose sand stimulates rhizome growth (e.g. in Spartina anglica). Surprisingly, the combined effect of substrate and root/rhizome growth makes the cohesionless sandy cliffs the most resistant to erosion. The reduced density of roots in the layers containing clay facilitates erosion, undercutting the cliff profile, causing a collaps eventually (Fig.27) (van Eerdt, 1985).

5.3 Sedimentation rates.

In an easterly direction along the mainland coast of the Wadden Sea the sedimentation rates generally increase. The rates, as recorded in, and averaged from 25 years (1960-1985) of observations in the intertidal above MSL, on the coast of the provinces of Groningen and Friesland, are presented in Fig.28. The sedimentation pattern can be described appropriately as (part) of 2 sinusoids for the substrate level from MSL to 140 cm +MSL (part of the mud- and sandflats up to the lower boundary of the high saltmarsh). The combined curves are different in period and amplitude for the two provinces, but the main characteristics are comparable. The lowest sedimentation rate, and in Friesland even a slight erosion, was at the 60 cm +MSL level. Maximum sedimentation rates in both provinces occurred at 100 cm +MSL (the Salicornietum) (Bouwsema et al., 1986).

5.4 Adaptations to sea-level rise.

Salt marshes are often (not always) sites of sediment accumulation where the vertical accretion equals or surpasses the apparent sea-level rise (ASL; eustatic sea-level changes and land subsidence). If the accretion rate is greater than the sea-level rise, a lateral component is added to the development of the salt marsh. Two processes are generally offered in explanation of marsh development; silt deposition from the water column and organic below-ground productivity. This concept incorporates the upward growth of the grasses and herbs to maintain their position during a gradual shift of the sea-level, the actual driving force (McCaffrey & Thomson, 1980). The hypothesis implies that the vertical growth of a salt marsh has kept pace with sea-level rise and that salt marsh species are able to track long-term changes in relative sea-level, even in the presence of relatively high-amplitude, short period tidal fluctuations. However, accretion rates differ between zones, as is shown on the mainland coast of the Wadden Sea where the pioneer zone accumulates too little sediment. Some factor, related to sea level, is controlling accretion so that the marsh maintains its elevational gradient. The rates of accretion vary as do the rates of apparent sea-level changes.

Accretion rates, based on isotope analysis (Lead-210; Cesium-137) of marshes in the USA have been reviewed (Stevenson et al., 1986). The rate of accretion for most marshes was in a narrow range (4.3-5.5 mm yr^{-1}), but higher rates were measured near marshes that are now actually subsiding. Redistribution of sediments was presented as a possible explanation. From the accretion and the changes in ASL an accretionary balance (vertical accretion rate minus local ASL rise) was calculated for marshes of the USA. The full range (low to high) of sedimentary inputs was represented in the analysis. When the accretionary balance was plotted agains mean tidal range for each marsh, a moderate correlation was obtained (r=0.86; n=13; slope=2.4 mm yr^{-1} m^{-1}). This suggests the amount of tidal energy is important under high and low sediment inputs in determining rates of marsh accretion. Similarly a correlation between tidal volume and accumulation of sediment, determined from ^{210}Pb deposits is also proposed for the Wadden Sea (Bartholdy & Pheiffer Madsen, 1985).

The observed accretion rate of the marshes on the islands of the Wadden Sea (0.5 cm yr^{-1} ; Roozen & Westhoff, 1985) and the present local mean sea-level rise (0.2 cm yr^{-1}) are in a similar relationship as the marshes of the northern USA (Fig.29). The same is true for the correlation between the accretionary balance and the mean tidal amplitude (Fig.30). The mean tidal range and the average accretion balance, determined in the Danish Wadden Sea, fit the regression as calculated by Stevenson et al (1985) also quite well. Furthermore, the relationship as calculated by Bartholdy and Pheiffer Madsen (1985) is, according to the authors, in the same order of magnitude in other vegetated areas of the Wadden Sea. Hence, they propose that their relation between tidal volume and sedimentation rate is to be a characteristic parameter of the sedimentation in tidal areas. This than would implicate that the high rates that are found in some parts of the intertidal on the mainland coast are attributable to artificial drainage practices or the different exposure of these sites to the prevailing wind direction. The silt-concentration mechanism (Postma, 1961), operating in the Wadden Sea, enables large amounts of silt to reach the mainland coast.

If these relations are factual, than it becomes possible to determine the critical rate of sea level rise for any natural marsh from the mean tidal range (not the tidal amplitude) by interpolation of Fig.30. However, some caution is due. The sedimentation rate on the island of Terschelling (Roozen & Westhoff, 1985), was determined by means of near-surface marker horizons. Marshes on a "subsiding" coast can cope with an accelerated rise of MSL by means of increased entrapment of sediment or deposition of the primary production of the vegetation. If the analysis of Stevenson et al. (1986) is correct and applicable to the Wadden Sea marshes than these require 2-4 kg m^{-2} yr^{-1} organic deposits, a considerable or the entire part of the production (Table VIII) and the below-ground biomass (Table IX). However, sediments contribute 10-15 kg m^{-2} yr^{-1} and at an average organic content of 10%, only 1-1.5 kg m^{-2} yr^{-1} organic material is deposited of which part of will be imported (Dankers et al., 1984). Most American marshes postdate the mid-Holocene (5000-8000 y BP) indicating the inability of marshes to accrete sufficient material to counteract rapid ASL rise (Rampino & Sanders, 1981). Large expanses of present day tidal coastal marshes in the USA generally formed no earlier than 4000 y BP, coincident with a substantial reduction in rates of relative sea level rise (from 2.5 mm yr^{-1} to 1 mm yr^{-1}) (Orson et al., 1985) The back-barrier marsh systems of the USA are even younger (1000-1500 y BP). As barrier islands move landward during periods of rising sea-level, the marshes behind them are displaced or possibly buried (Shideler et al. 1984). The marshes surrounding the Wadden Sea generally are no older than 500 years, also due to the embankment of the older ones.

Table VIII. Biomass values of some saltmarsh communities and species.

BIOMASS (g DW m^{-2}).	depth core				
Plantagini-Limonietum		A	680	max	Ketner, 1972
	(0-13)	B	3900	max	Ketner, 1972
Junco-Caricetum		A	520	max	Ketner, 1972
Puccinellietum maritimae		A	470	max	Ketner, 1972
S. anglica	(0-60)	B	12600	max	Vink-Lievaart, 1983
J. maritimus		A	770	max	ref. Joenje & Wolff, 1979
Halimione portulacoides	(0-60)	B	17700	max	Vink-Lievaart, 1983
		A	1360	max	Jensen, 1980
Triglochin maritima	(0-60)	B	16000	max	Vink-Lievaart, 1983
Elytrigia pungens		A	580	max	ref. Joenje & Wolff, 1979
	(0-60)	B	9700	max	Vink-Lievaart, 1983
Festuca rubra		A	380	max	ref. Joenje & Wolff, 1979
Artemisia maritima		A	860	max	ref. Joenje & Wolff, 1979

A = aboveground; B = belowground; R = roots; T = total

6 Expected developments.

6.1 Tidal flats.

Stabilization of the surface of tidal flats occurs predominantly by a film of microphytobenthos (diatoms).

The present day Wadden Sea is rather small compared to the extension during some periods in the Holocene and recent history. Whether the gain in hight of the tidal flats will keep up with sea level rise is the most important question from an ecological point of view, and will depend on;

-the amount of available sediment,

-the nature and grain size distribution of the available sediment and

-the interaction of waves, especially during storms.

Table IX. Production values of some saltmarsh communities and species in the Netherlands.

PRODUCTION (g DW m^{-2} yr^{-1})

Association or species				Source
<u>S. anglica</u>	B	ann.	6000 - 6300	Vink-Lievaart, 1983
<u>S. townsendii</u>	A	ann.	720	Wolff et al., 1979
<u>Halimione portulacoides</u>	B	ann.	8000 -12500	Vink-Lievaart, 1983
<u>Triglochin maritima</u>	A	ann.	180	Wolff et al., 1979
	B	ann.	3500 - 4800	Vink-Lievaart, 1983
<u>Elytrigia pungens</u>	A	ann.	1010	Wolff et al., 1979
	B	ann.	4400 - 7600	Vink-Lievaart, 1983
<u>Limonium vulgare</u>	A	ann.	230	Wolff et al., 1979
<u>Puccinellia maritima</u>	A	ann.	300 - 430	Wolff et al., 1979
Puccinellietum maritimae	A	ann.	410 - 500	Ketner, 1972
	A	ann.	1030	Joenje & Wolff, 1979
Salicornietum	A	ann.	200 - 400	Joenje, 1974
Plantagini-Limonietum	A	ann.	390 - 600	Ketner, 1972
	B	max.	1515	Ketner, 1972
Junco-Caricetum	A	ann.	290 - 460	Ketner, 1972
Salt marshes Wadden Sea	A	ann.	400 - 500	Alberda, 1974

A = aboveground; B = belowground; ann.= annual mean; max.= maximum value.

Sediment (sand and silt) as such is available in sufficiently large amounts to keep pace with the projected rates of sea level rise if the sediment would be able to settle permanently. However, the most important factor will be the availability of sand.

A sand deficit in conjunction with wave action would hamper the vertical growth of tidal flats.

Data on the import of sand into the Wadden Sea are scarce and the reliability of the estimates is questionable. The main drawback in the data is the small number of observations, scattered throughout the area. A second drawback is caused by large scale anthropogenic interference.

During the history of the Wadden Sea, up to recent times, tidal embayments have been closed off. As a result the tidal volume, the deposition patterns and the topography of the affected area change because the equilibrium is disturbed. For instance; after closure of the former Zuiderzee in 1932 the originally deep areas silted up rapidly. The increased rate of sedimentation (in average 7.1 cm yr^{-1}) ended between 1971 and 1975 when a new equilibrium was reached (Berger _et al._, 1987).

Virtually all sand originates from the shallower areas of the North Sea and the coast specifically (van Straaten, 1975). The amount of sand deposited in the Wadden Sea is largely determined by the rise in sea level, and a mechanism to maintain the equilibrium is strongly indicated (van Bendegom, 1950). The topography of the Wadden Sea has remained unchanged during the last 2000 years.

The concentration of sand in the water column diminishes from the tidal inlets towards the inner areas of the Wadden Sea. In the Western Wadden Sea, (in this case west of the water divide below the island of Ameland) an area of 1870 km^2, the total amount of sedimentation is estimated at $15.5\ 10^6$ - $18.5\ 10^6\ m^3\ yr^{-1}$, inclusive of the $3.5\ 10^6\ m^3\ yr^{-1}$ dredged sand. That amount of sand would suffice to compensate for a sea level rise of 91 cm $century^{-1}$. But, the range in the data ranges from $3\ 10^6\ m^3\ yr^{-1}$ to $33.5\ 10^6\ m^3\ yr^{-1}$ (Eysink, 1979). Nevertheless from a comparison of depth soundings it is concluded that in this area the tidal flats continue to increase in height while the channels become deeper. The annual amount dredged is the equivalent of a sea level rise of 16 cm $century^{-1}$, close to the observed rate in sea level rise at this moment. Because of the obvious equilibrium in the deposition and erosion patterns of the Wadden Sea, determined by the rate of sea level rise, a prediction of the near future can not be more than an educated guess. Similar data for the eastern part of the Wadden Sea are not available.

Approximately one thirtieth of the amount of silt entering the tidal inlet near Ameland would be sufficient to compensate for a sea level rise of 20 cm century^{-1} (Postma, 1961). During calm weather part of it is deposited while storms will cause resuspention. Therefore the present-day topography of the Wadden Sea reflects an equilibrium between sedimentation and resuspension. As sea level rises, the equilibrium will be temporarily lost but after a lag phase this will be reached again. The importance of storms to maintain the topography is demonstrated by the observation that the amount of substrate,deposited as pseudofaeces by mussels would amount to 4 m century^{-1} if the sediment would not be redistributed during autumn and winter (Dankers, pers. comm.).

Approximately 3 million tons of fine-grained suspended matter (<63 um) per year is deposited in the Wadden Sea (Eisma, 1981). However, the database is as yet insufficient for a reliable budget of sediment accumulation in the Wadden Sea (Postma, 1981) and according to Bartholdy and Pheiffer Madsen (1985) the accumulation can have a value beteen 3.10^6 and 8.10^6 tons yr^{-1}. The sedimentation pattern in the salt marshes is presented elsewhere in this paper. Large scale changes in the area and extent of the intertidal and subtidal sand- and mudflats are not likely to occur if some flexible time limit is allowed. The flats have kept up with a rate of sea level rise of up to 0.25 m century^{-1} during the Holocene. The hydrology of the area might be affected during relatively short time periods, but the restoration of the equilibrium conditions is expected to follow within a few years, until a new disequilibrium originates. Sea, will not change in such a way that deposition patterns will alter permanently.

The Wadden Sea is expected to continue its existence in the familiar way, because excess deposition rates, as compared to the present day situation, are feasible. Winter storms will continue to redistribute and remove the surplus, deposited during the summer. However, the required sand will, for a significant part, have to originate from the Nort Sea coasts of the mainland and the barrier islands. That supply can be and probably will be tampered with. Nevertheless, the Wadden Sea ecosystem has a fair chance to adapt to the estimated rate in sea level rise.

6.2 Wadden Sea Islands.

As has been indicated, an accretionary deficit might develop rather quickly on the marshes at the lee side of the Wadden Islands, if the rate of sea level rise continues to increase (chapter 6.4). The deficit might be lessened if dune sand is permitted to be blown in, because the marshes are at the lee side of the barrier islands, as would occur in a natural situation where islands migrate landward. This would be against the common practise to trap the sand on the dunes. On the other hand, the marshes apparently cope with the present day rate of increase in MHW (0.44 cm yr^{-1}). This high rate is not explained by any global phenomenon, hence is regional, and is probably caused by changes in the hydrology of the area. If the latter is true than it might be possible that a new equilibrium in currents and sedimentation has not yet been reached. Thus, if MSL rise will not surpass 50 cm $century^{-1}$, the most likely scenario for the next 100 years, and the rise in MHW will not be additionally stimulated, than the salt marshes could keep up with the rising sea, but would stop to expand. However, a higher rate of rise or a continuation of the different rates of increase between MSL and MHW, in the same proportions as now, would lead to drowning of the marshes. Then the vegetations of the high marshes will disappear relatively quickly, as they are most susceptible to waterlogging. Consequently, the colonization by the less vulnerable species, those of the low marsh, will increase the area occupied by these species initially. Encroachment of the sea onto the land will probably only be possible in nature reserves. Large areas bordering the Wadden Sea are protected by dikes or well maintained dunes. There the economic value might prevail, hence a small zone of low marshes, separated by a cliff from the mudflats, will remain. And, unless land is abandoned or dunes are permitted to migrate landward, a final stage where the sea laps against dikes, will develop.

The beaches at the exposed sides of the islands show increased rates of erosion. The implications of this aspect is outside the scope of this, in principal ecological, study.

6.3 The mainland coast.

The physiognomy of the salt marshes on the mainland coasts of the provinces of Groningen and Friesland are rather similar presently. The zonation is vertical but because of insufficient deposition of sediments in the pioneer zone, cliffed coast develop. The different rates of sedimentation in these areas have had little influence on the vegetation pattern as the supply was sufficient. An accretionary deficit for the marshes as a whole will not develop. However, a too low rate of sedimentation will develop in some zones. Because the zone where this shortage occurs is dependent on the local sedimentation rate and the rate of sea level rise, different types of vegetation will be sustained in the distinguished areas. To the vertical component a horizontal component in the zonation will be added. The high marsh in Groningen will be more susceptible than the high marsh in Friesland. In the first province the high marsh will, in most sea level rise scenarios, give way to the vegetation of the low marsh. Total disappearence of these vegetation zones (low and high marsh) is not envisaged, although the impact of stimulated formation of cliffed shorelines is unclear. The site of erosion on these exposed coast is dependent on the height of MSL. The zone of maximum erosion will gradually move upward when MSL increases. The eroded soil will be deposited on the higher reaches, but sediment will also be deposited below the site of origin (to restore equilibrium). The development of a terraced coast (mudflats; low marshes; middle or high marshes) could be the first response. Undercutting of the higher reaches of the marsh and deposition of that sediment on top of the remaining high marsh, could cause a steeper shoreline and consequently narrower zones of a vegetation type. A reduction of the lateral extent of the intertidal zone would require a very high rate (more than 1 cm yr^{-1}) of sea level rise. This rate is not expected to develop in the next century.

The marshes in this area have been subject to some profound changes in the tidal regime caused by the closure of an embayment (Fig.32) in the early

1930's. The marshes have adapted to this increase in MHW as no reference could be found indicating that the present day situation is out of the pattern.

The coasts of the Delta in South-West Netherlands are omitted from this study as large scale protective measures, closing off embayments or reducing the tidal wedge to a large extent, have been completed recently. Sedimentation rates will alter but the impact of the artificial structures is as yet unknown. The coastal ecosystems are in the process to adapt to the major changes. The equilibrium has not been yet reached.

6.4 Changes in vegetation.

It is assumed that the sedimentation rate decreases linearly to zero in the high marsh for the purpose of modelling the consequences of a continuous accumulation of sediment, at the observed rates, during the next century, in relation to several sea level rise scenarios. In a model the annually accumulated or eroded sediment is added to or subtracted from an initially straight coastal profile. The new substrate level is corrected for the effect of sea level rise. In the model where MHW rises faster than MSL the necessary corrections are applied to the sinusoids by reduction of the amplitude and extension of the period. In this model the total amount of sediment as represented by the area under the curves, remained constant. However, the effect of developing steep slopes has not been corrected for. The new profiles calculated after 10 consecutive runs, representing 10 years are shown. The sequence is repeated 10 times, the equivalent of 100 years sedimentation and sea level rise. The results, as obtained with different sea level rise scenarios, are shown in Fig.33 a-l and summarized in Table X. The two patterns obtained in the model where no sea level change was applied, resemble the patterns as shown in Fig.34 for the Danish Wadden Sea. Fig.34a resembles Friesland; Fig.34b-d shows some similarity with the pattern as calculated for Groningen.
The horizontal component (from east to west) that will originate from the different sedimentation rates on the mainland coast is illustrated in

Fig.35. To this purpose the vegetation is presented in relation to the logarithm of the flooding frequency. For practical purposes, and describing the relation well, the flooding frequency is taken as an exponential function of the level above MSL. In a previous figure (Fig.23) the zonation is finely divided in respect to the flooding frequency. If this fine division represents a general pattern than the possible shifts in vegetation can be obtained from comparison of these two figures.

A serious negative effect of sea level rise on the tidal wetlands of the area appears to be unavoidable only if any other than the most optimistic scenario proves to be true. The most optimistic scenario suggests a MSL rise in the order of magnitude of the MHW rise as is experienced now.

Table X. Changes in surface area of saltmarsh zones after 100 years.

	Groningen				Friesland			
Rise MSL cm yr^{-1}	M	P	L	H	M	P	L	H
0	=	=	=	++	=	-	-	++
0.20	++	-	++	=	=	-	-	++
0.40	+	--	++	-	-	--	--	++
0.60	+	--	++	--	-	--	--	++
0.80	=	--	++	--	=	--	--	+
1.00	-	--	++	--	-	--	+	-

-- considerable decrease of the zone.
- minor decrease of the zone.
= zone remains approximately unchanged.
+ minor increase of the zone.
++ large increase of the zone.

M = mud- and sandflats in front of the marshes.
P = pioneer zone.
L = low salt marsh.
H = high salt marsh.

6.5 Effects on fauna

The mud- and sandflats of the intertidal are ecologically important areas as they are the main feeding grounds for most animal species. The effect of sea level rise on this ecosytem will be dealt with in this chapter.

Extended periods of submersion had virtually no effect on condition and mortality of intertidal benthic animals (gastropods, bivalves, polychaetes and anemones) (Hummel et al., 1986). If an effect of the anticipated climatic changes will occur it will have to be attributed to temperature changes or a reduction in areas suitable for a species.

The observed biomass of the intertidal macrozoobenthos (mainly molluscs and polychaetes) in the Wadden Sea is for the largest part determined by the composition of the substrate. Tidal flats characterized by coarse sand and a low silt content, as well as extremely silty flats support little secondary production and hence biomass. Intermediate tidal levels are richest (Fig.36). Highest biomass values, on the other hand, are to be found on banks of the two dominant and commercially harvested bivalves of the area (Mytilus edulis and Cerastoderma edule). The mean value of animal benthic biomass is 28 g ADW m^{-2} for the total Wadden Sea, Table XI (Beukema, 1981).

If the lower values of sand deposit estimates are true, than some areas in the inner part of the Wadden Sea will become more silty. As 83% of the tidal flats have a silt content of less than 5% it can be argued that an increase of the silt content will stimulate secondary production, notably of the macrobenthos. Areas where the zoobenthic biomass is high are also the areas where the density of juvenile fish is highest. Hence, as yet no reason to expect significant negative effects for demersal and benthic animals is envisaged.

The interannual variation in biomass of the macrobenthos is relatively small, except for those species (notably Cerastoderma edule) which are susceptible to severe cold. The largest interannual variation in biomass is observed in this species, either because of fishing or of frost. The short period required to restore to normal densities and biomass, following such an event, illustrates the resilience of species from intertidal habitats (Fig. 37).

Table XI. Biomass and production values of intertidal invertebrates in the Dutch Wadden Sea (after Beukema, 1976).

SPECIES Macrobentos	BIOMASS g ADW m^{-2}	PRODUCTION g ADW m^{-2} yr^{-1}
Mytilus edulis	6.2	7.2
Arenicola marina	5.0	3.6
Cerastoderma edule	4.3	5.0
Macoma balthica	2.2	1.5
Nereis diversicolor	1.4	2.8
Lanice conchilega	0.7	1.4
Scolopos armiger	0.4	0.8
Nephtys hombergii	0.3	0.6
Heteromastus filiformis	0.3	0.6
Corophium volutator	0.3	1.2
Hydrobia ulvae	0.2	0.6
Carcinus maenas	0.2	0.4
Crangon crangon	0.4	1.0
Other species	0.4	1.0
Meiobenthos & Microbenthos	1.0	10.0
All species	27.6	39.6

The area subjected to tidal influences, in the Dutch Wadden Sea inclusive of the Dollard is 3050 km^2 (Fig.38, de Ronde, pers. comm.). Approximately 43% of this area is dry at a tidal level of 1 m -MSL while at a tidal level of 1 m +MSL only 6% remains dry. The curve becomes less steep with increase of the substrate level in respect to MSL (NAP). A change in water level represents 22 km^2 area per cm change at 50 cm $^-$MSL (NAP), but only 7.5 km^2 at 50 cm +MSL (NAP) (Fig.39). Consequently, an increase in ASL, followed by the adaptation in the animal zonation, effectively reduces the size of the most productive zones if insufficient sedimentation takes place.

The turnover rate of macrobenthos is high and annual production surpasses the annual mean biomass (P/B ratio > 1.). As sea level rise causes a stimulated influx of suspended matter (the tidal volume increases temporarely) from the North Sea, it is expected that secondary production of suspension and deposit feeders will increase concurrently. The production will also be stimulated by the expected rise in temperature, which results in lengthening of the growing season, provided the initial biomass at the end of the winter is of comparable magnitude. This will probably compensate fully for the small reduction in the size of the most productive zones. However, the effect of changes in species composition due to the warming of the sea or the possible negative effect of a lowering of the pH, in the far future, are not taken into account.

Sea level rise as such will have no effect on fish but climatic changes can have a profound effect. In temperate waters some fish spawn at fixed seasons. Although the period of spawning may last as long as three months, the peak date of spawning has a standard deviation of about a week or less. The production cycle of food for fish larvae can occur at different times from year to year, and it can shift by weeks and even by a month between years. The peaks in the two biological events (hatching of fish larvae and production of phyto- and zooplankton) can therefore match or show some degree of mismatch (Cushing and Dickson, 1976). The latter can have a severe impact on recruitment. The two are studied extensively. Changes in wind strenght and pattern (nutrient flux) and sea water temperature are the major governing factors, much more important than possible changes in primary production. The reader is therefore referred to the study into the assessment of the impact of temperature changes.

The impact of sealevel rise on the predators (birds, fish and seals) of the area will, as a consequence of the foregoing be minor, and because the carrying capacity of the area might be enlarged due to stimulated primary and benthic production some benefit might be gained. The preferred sites for the resting grounds of seals will not be reduced in total area. Major changes will only occur in the marshes. Bird diversity is relatively low in most types of marsh vegetation. Only the high level salt marshes support populations of breeding birds. The slow rate in changes of the sea level, relative to interannual variations during the breeding season and possible stormsurges, provides sufficient leeway to the birds to find alternative sites, unless the high marshes as such disappear.

The interpretation of the effects of sea level rise on an ecosystem appears to be dependent on the compartment of the system under consideration. Most genera are found outside the intertidal, which is a harsh environment and only a few representatives of some genera migrate with the tides (Fig.40). The rate of phytomass production is best, but still insufficiently, known. All other interactions are barely touched and certainly not yet understood. As is said before, for most questions the answer will generally have to be structured as:

If...., than....., and possibly also....., but...... The more so because sea level rise and increasing atmospheric carbon dioxide levels might sometimes counteract and sometimes act synergistically.

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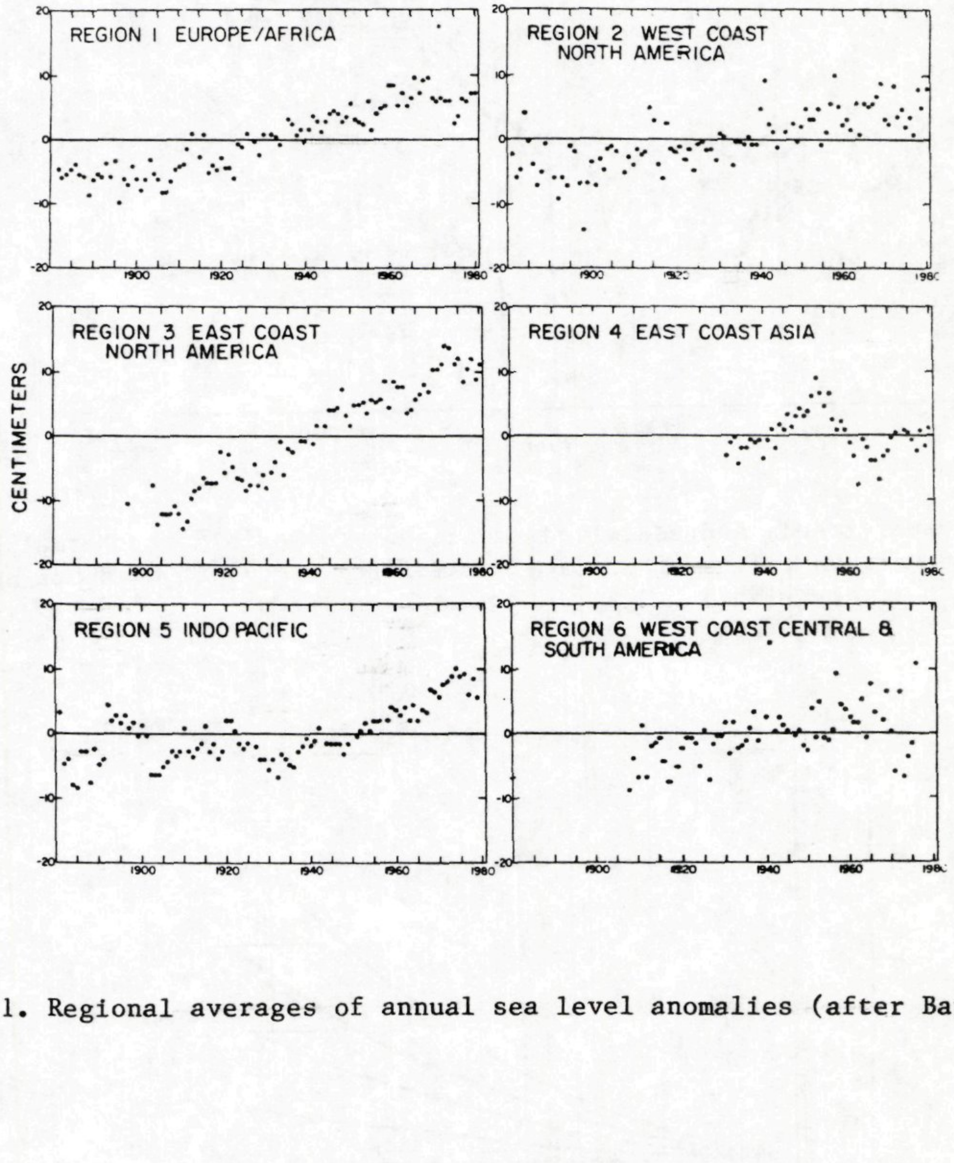


Fig. 1. Regional averages of annual sea level anomalies (after Barnett, 1984)

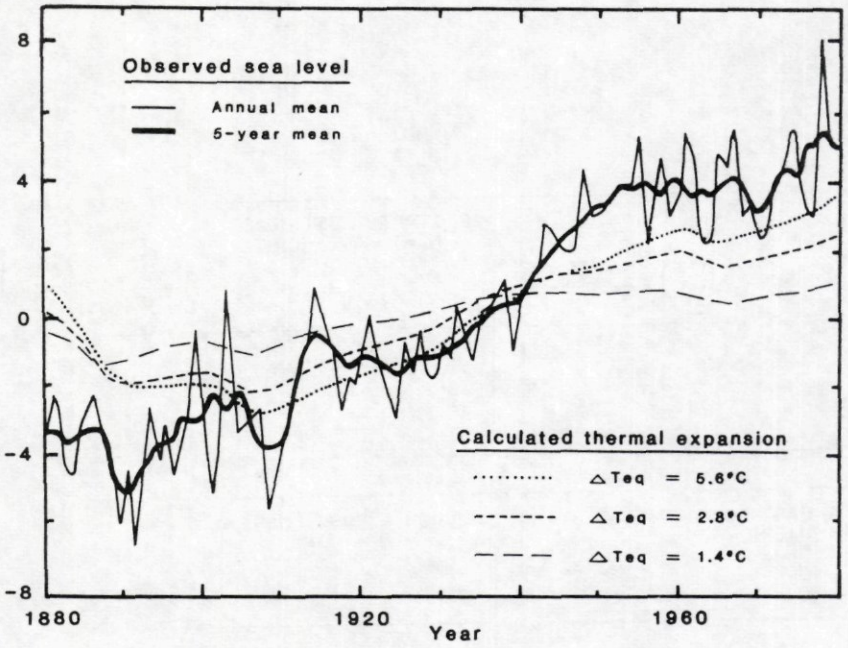


Fig. 2. Sea level trends and estimated trends due (1) solely to thermal expansion for various values of climate sensitivity to (2) a CO_2 doubling (after Gornitz et al., 1982).

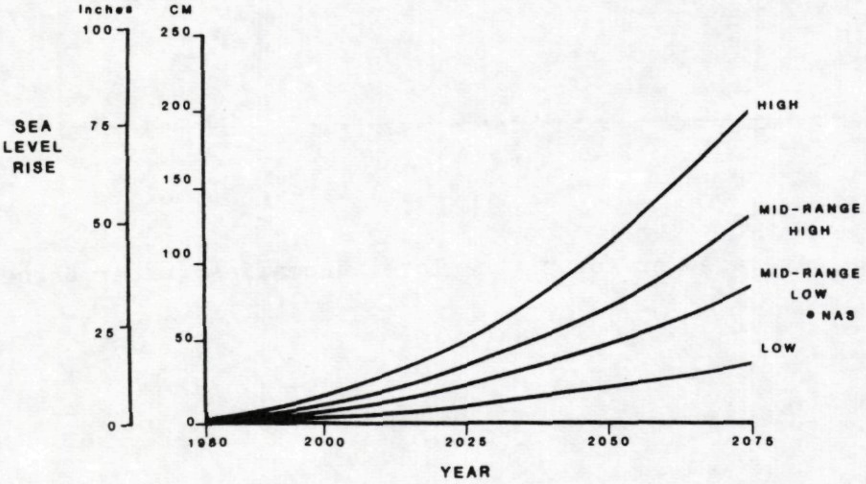


Fig. 3. Global sea level rise scenarios: low, mid-range low, mid-range high and high (after Hoffman et al., 1983).

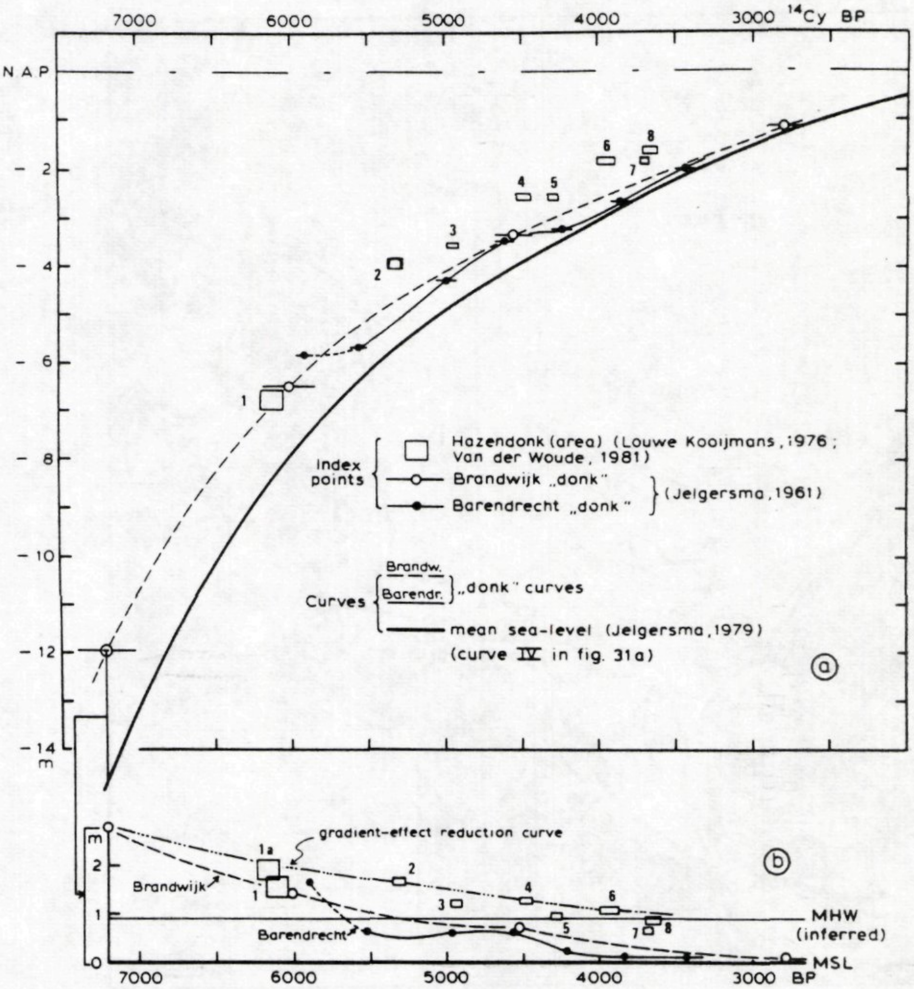


Fig. 4. Time depth diagram showing several published sea level graphs for the Netherlands (after Van der Plassche, 1982).

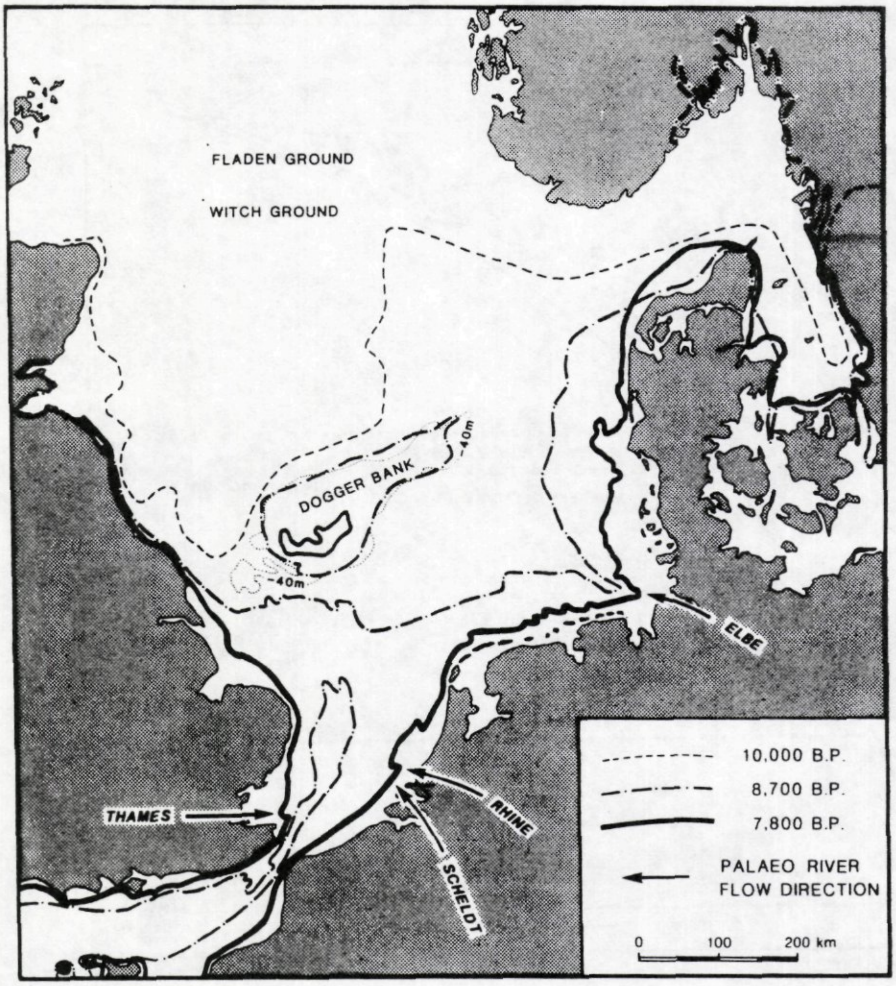


Fig. 5. Holocene shoreline changes in the North Sea Region, showing approximate (hypothetical) shoreline positions for (1) 10,000-10,300 BP, (2) 8,700 BP and (3) 7,800 BP with sea level at 65, 36 and 20 m respectively below present mean sea level (after Jelgersma, 1979; from Devoy, 1987).

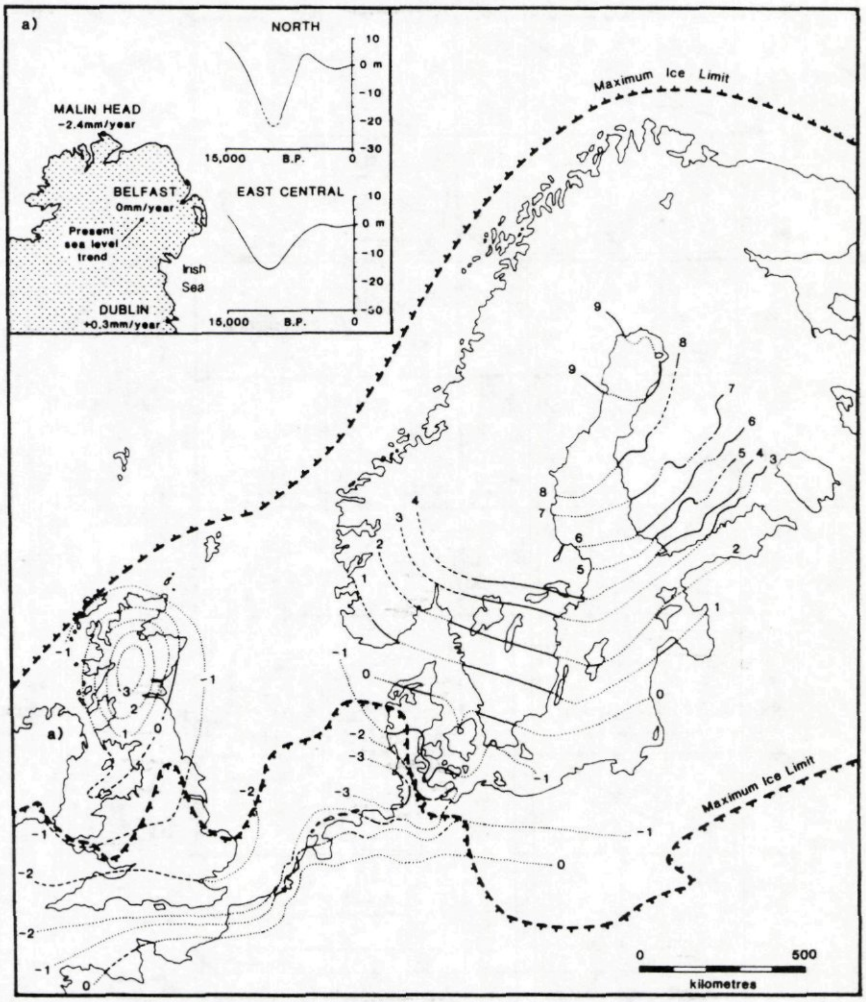


Fig. 6. Present pattern of land uplift and subsidence in Northwest Europe based upon tide gauge data. The isobases show the rate of change (+ or -) in mm yr^{-1} (after Devoy, 1987).

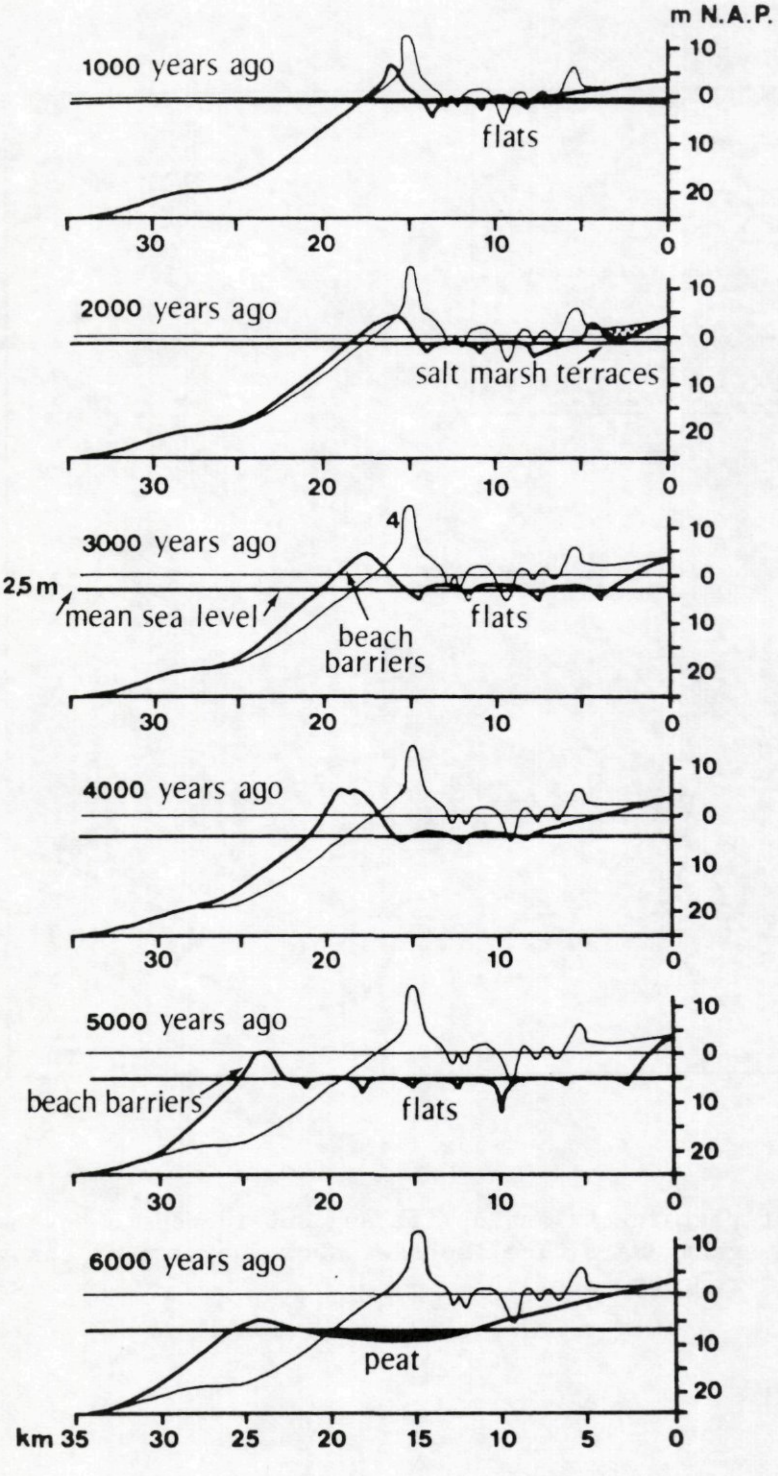


Fig. 7. Evolution of the Wadden Sea between 1000 and 6000 years ago. NAP= Dutch Ordnance Level= MSL (after Veenstra, 1983)

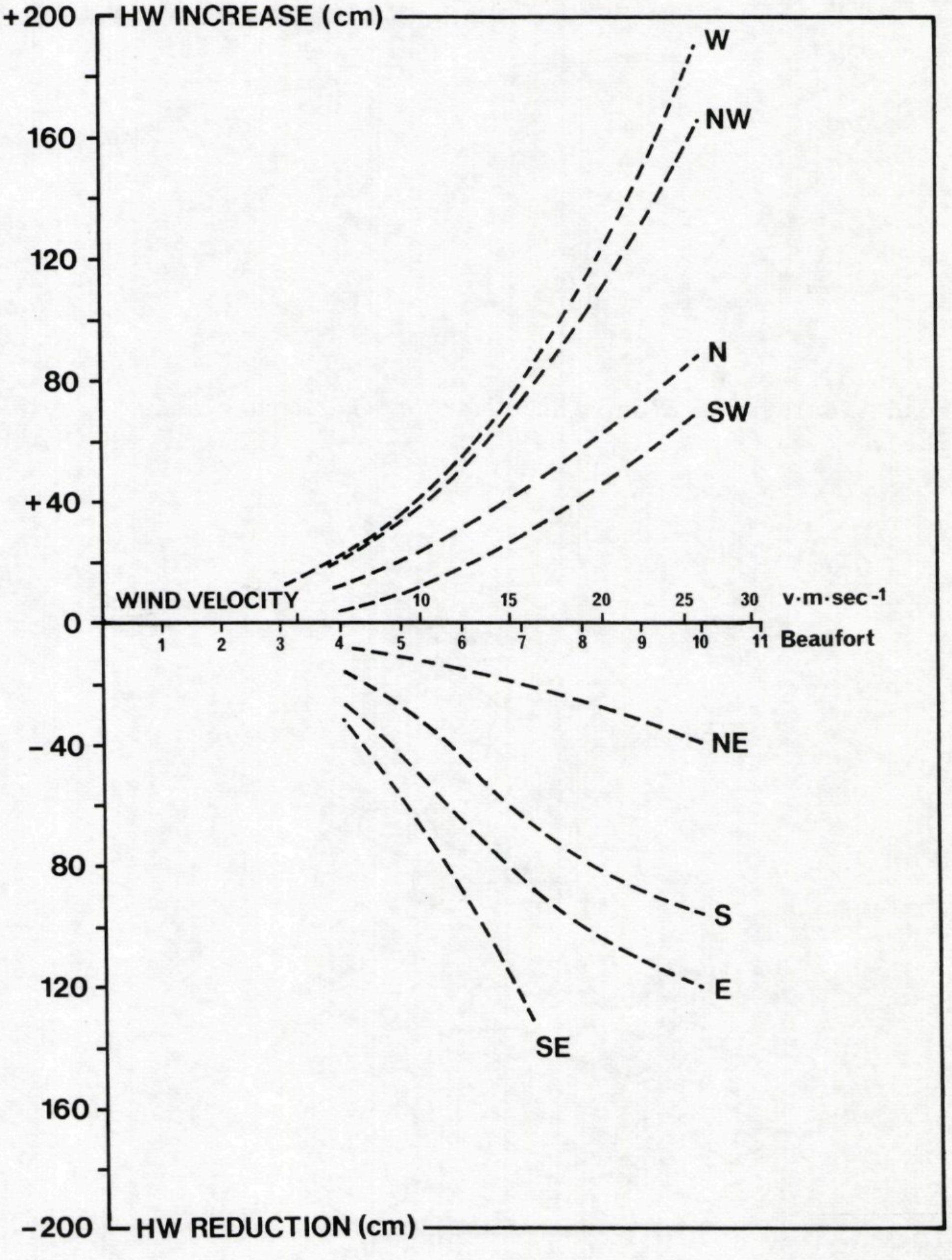


Fig. 8. The effect of variations in wind speed and wind direction on the high tide level at Wilhelmshaven in cm above or below the astronomical tidelevel.

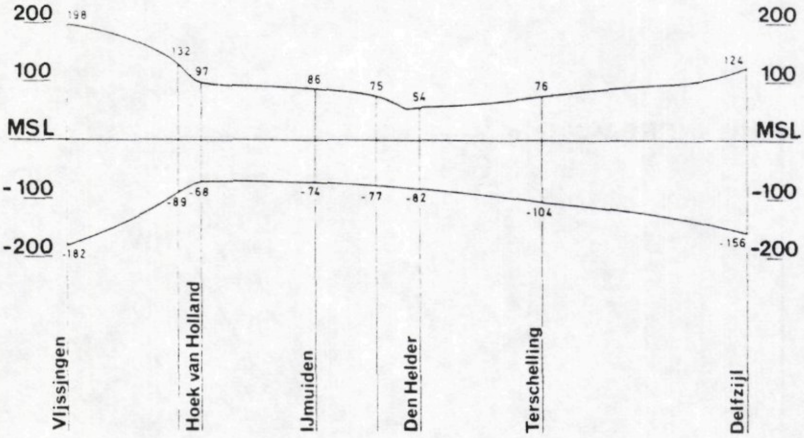


Fig. 9. Mean tidal range along the coast of The Netherlands (after Van Malde, 1986).

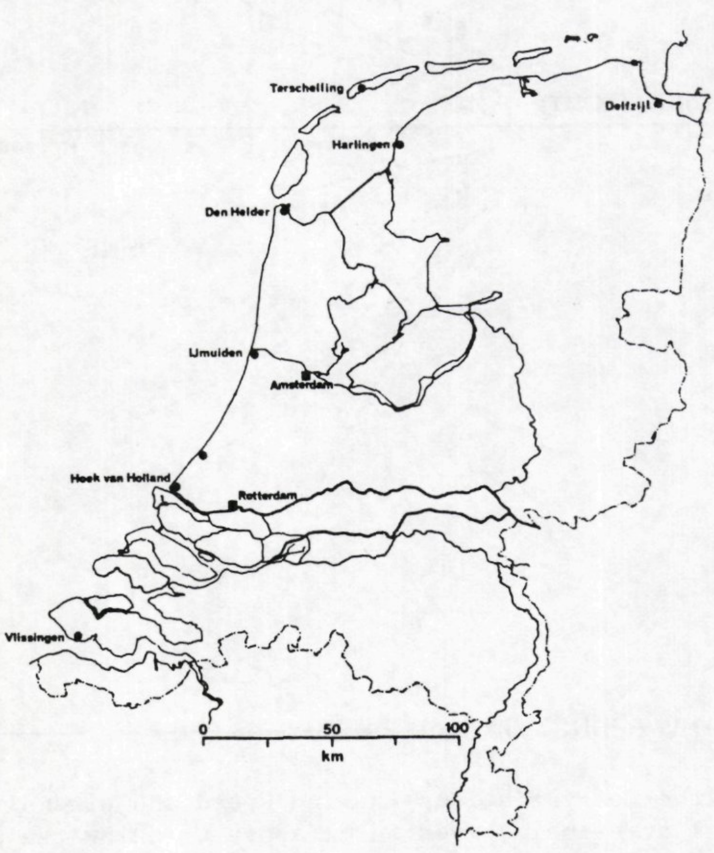


Fig. 10. Geographical distribution of tidal monitoring stations along the Dutch coast (after Van Malde, 1984)

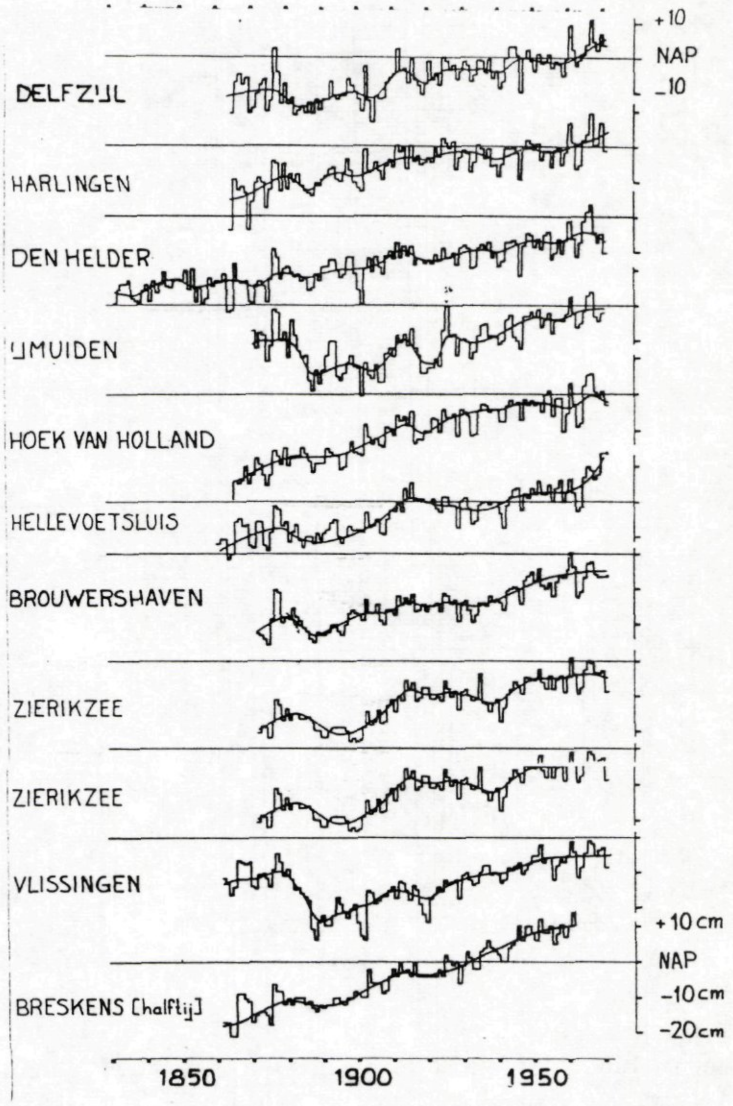


Fig. 11. Changes in MSL along the Dutch coast during the last century (after Van Malde, 1984).

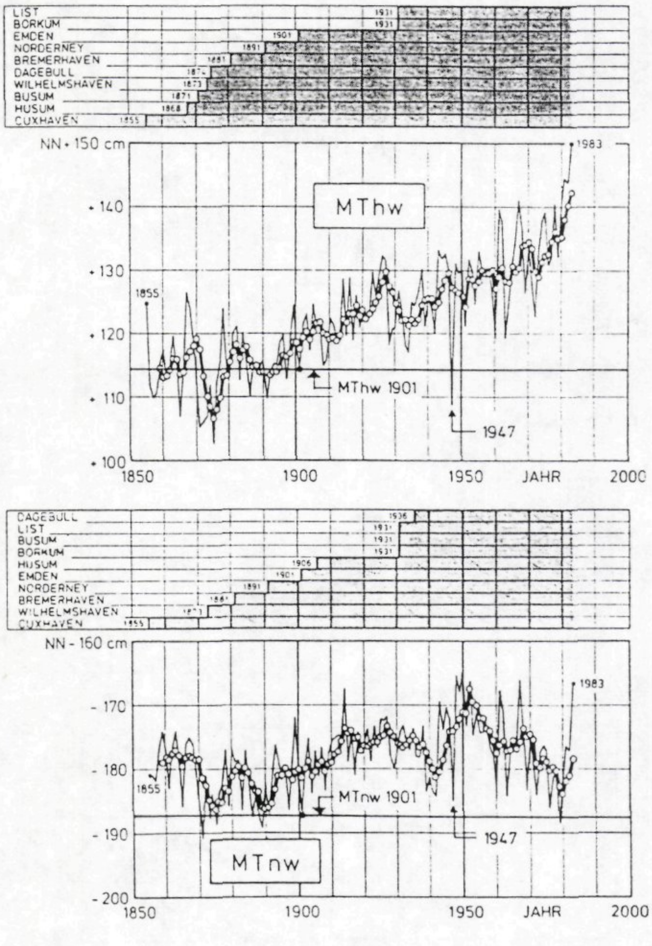


Fig. 12. Changes in MHW (top) and MLW (low) along the German North Sea coast, averaged from 10 tidal monitoring stations. The stations and record length are indicated (after Führboter, 1986).

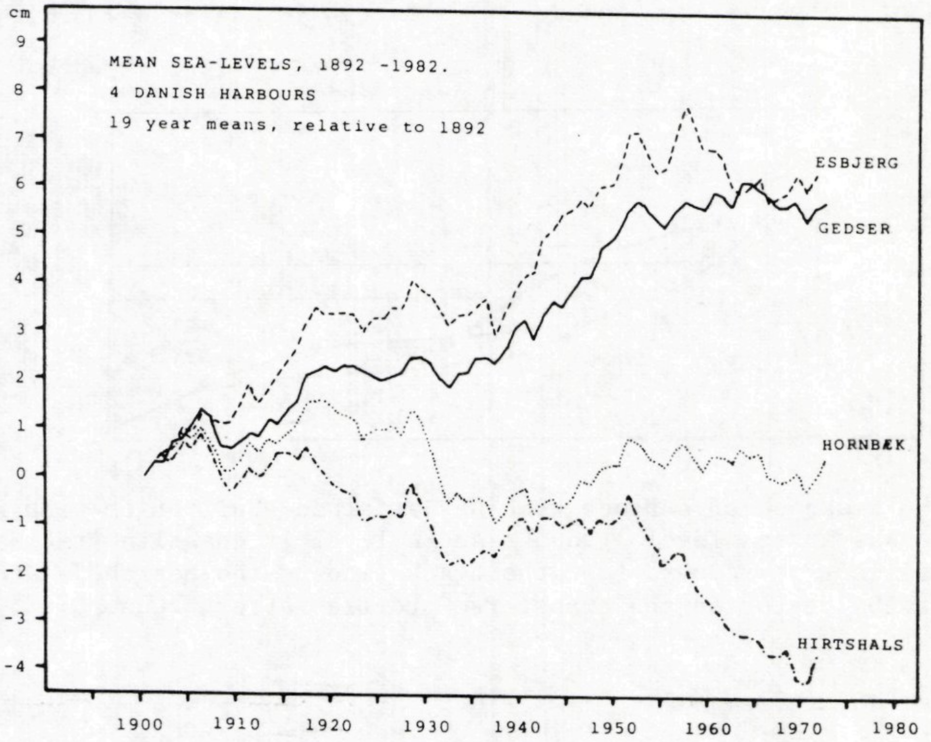


Fig. 13. Changes in mean sea level since 1892 in 4 Danish harbours. Esbjerg (SW on the North Sea coast), Gedser (SE), Hornbaek (middle) and Hirsthals (N on the North Sea coast) showing the effect of isostatic uplift. Note the falling trend in Esbjerg (after Christiansen et al., 1985).

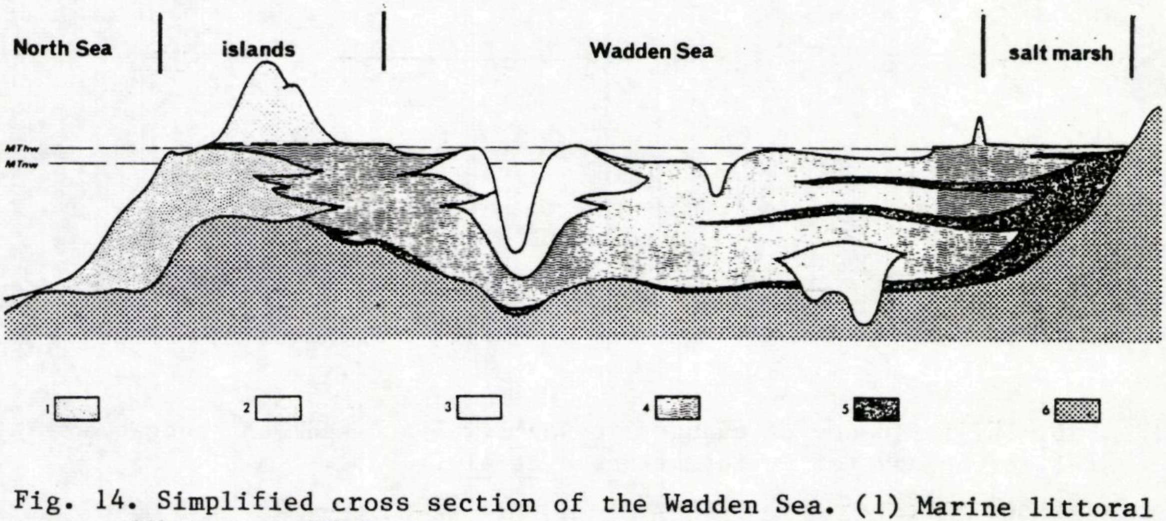


Fig. 14. Simplified cross section of the Wadden Sea. (1) Marine littoral sands. (2) Dunes. (3) Deposits on shores of creeks and channels. (4) Not-stratified sediments. (5) Peat. (6) Pleistocene deposits. (after Streif, 1986).

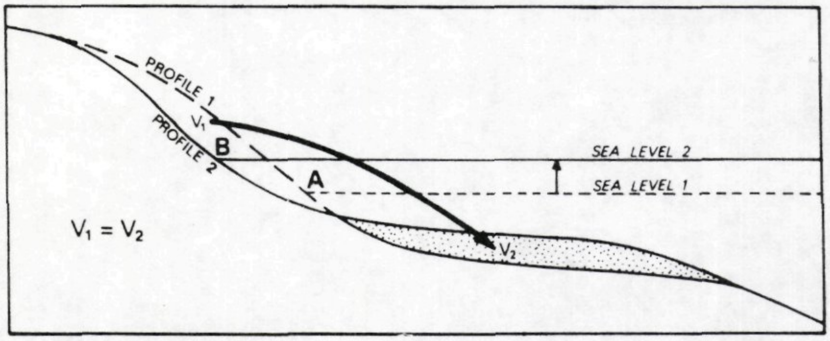


Fig. 15. The response of a beach wich has attained equilibrium with near shore processes at sea level 1 to a rise in level is coastline retreat (A to B) as sediment is removed from the beach face to the nearshore area (V_1 to V_2), thereby restoring the transverse profile (after Bruun, 1962; from Bird, 1985).

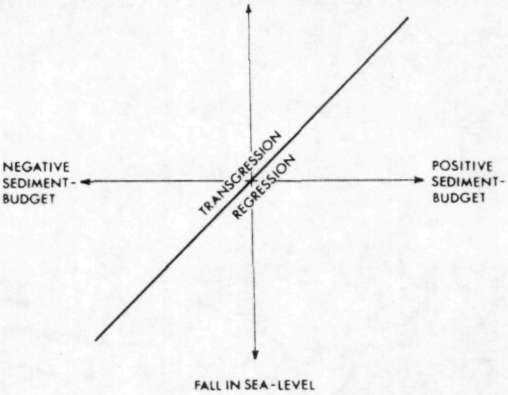


Fig. 16. The influence of changes in sea-level and sediment budget on coastal morphology (after Christiansen _et_ _al_., 1985).

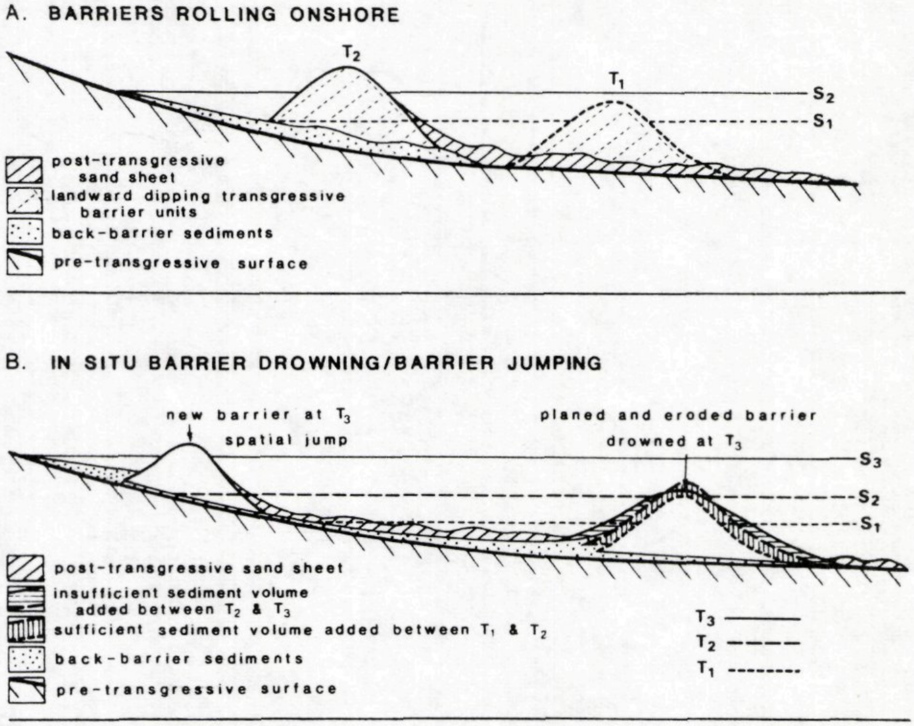


Fig. 17. Models of barrier migration under sea level rise, applied to eastern USA Holocene stratigraphies. A. Continuous spatial migration of a barrier rolling onshore under a rising sea level. B. Discontinuous spatial migration of a barrier due to barrier drowning as a consequence of sea level rise outstripping sediment supply (after Dillon, 1970, from Oxford, 1987).

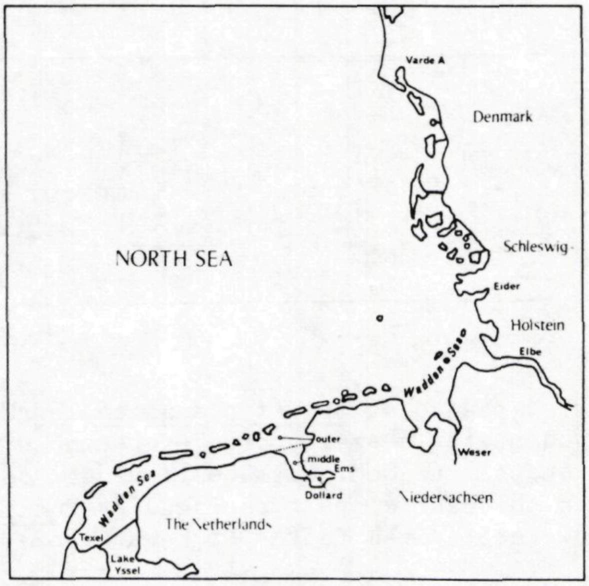


Fig. 18. The North Sea and the adjacent Wadden Sea, possessing the largest expanses of salt marshes.

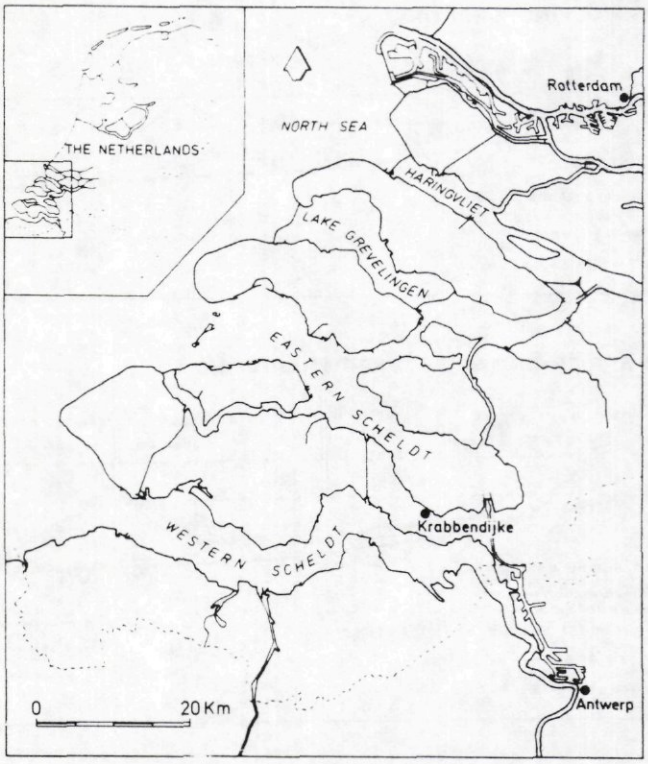


Fig. 19. The estuaries of the rivers Rhine, Meuse and Scheldt in the southwest of The Netherlands.

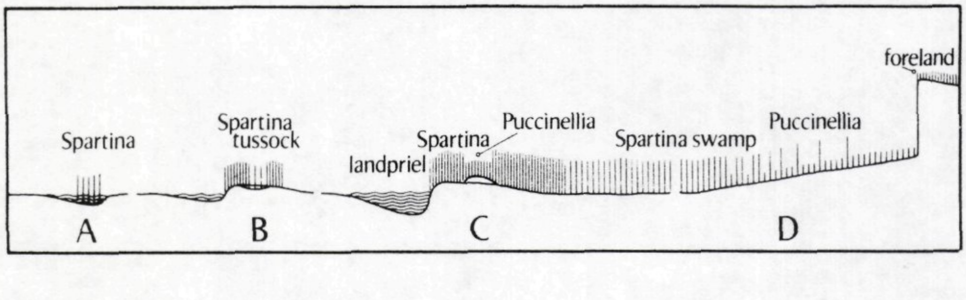


Fig. 20. The different phases of Spartina anglica in the Danish Wadden Sea. A. a puddle wadden with a small open vegetation of Spartina anglica. B. a circular ring shaped tussock. C. a small ridge, densely covered with Spartina anglica. In the central part replaced by Puccinellia maritima. D. an erosionslope, now recolonized (after Dijkema, 1983).

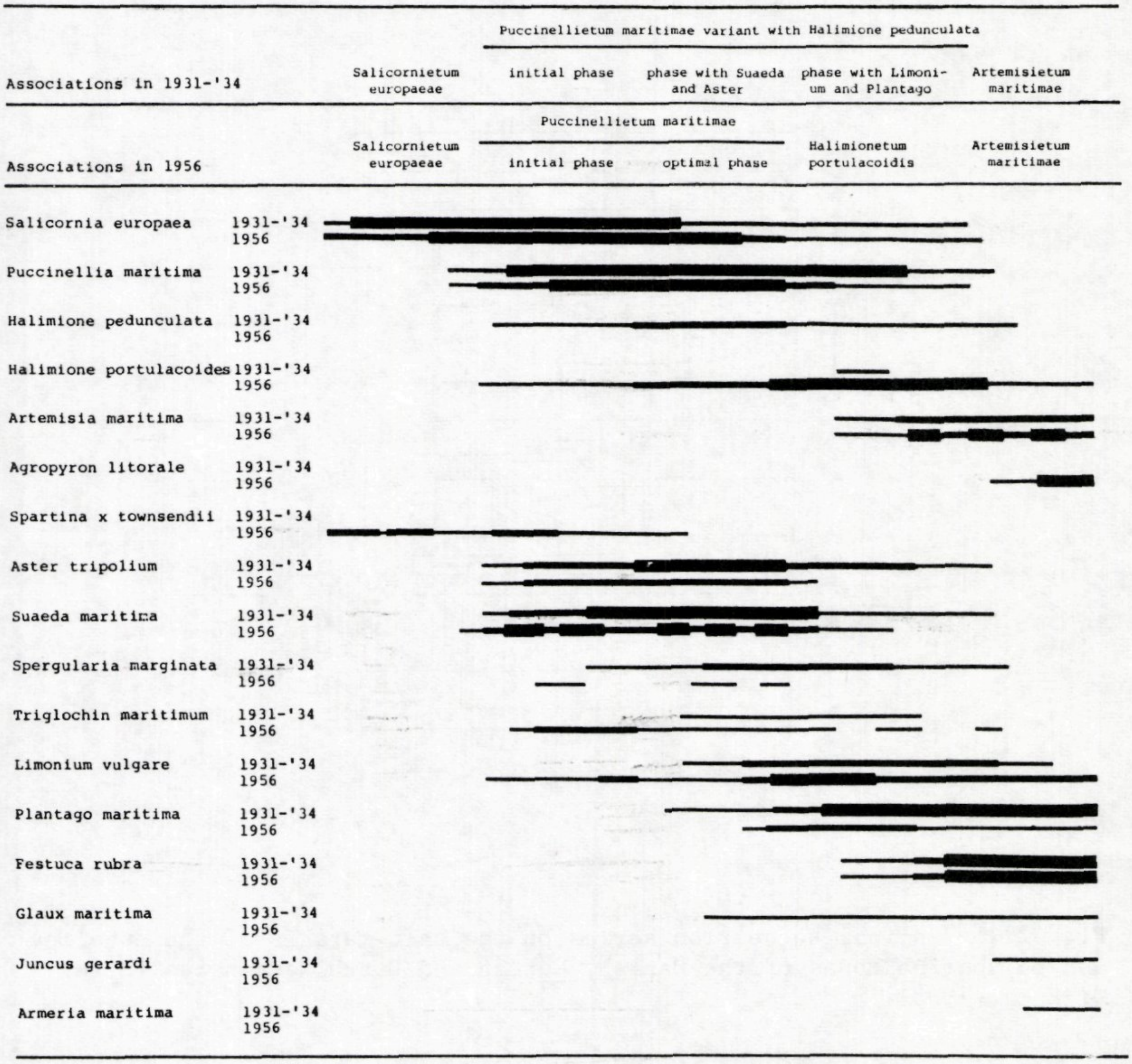


Fig. 21. Changes in cover of the dominant salt marsh species in Wadden Sea marshes, illustrating the rapid increase of Halimione portulacoides during that period, 1934-1956 (after Beeftink, 1966).

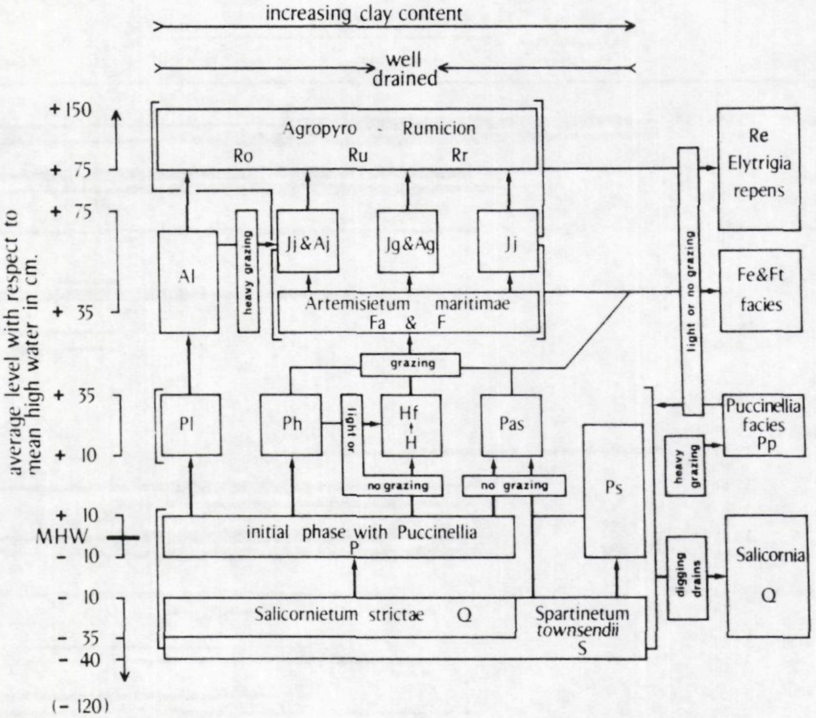


Fig. 22. Principal succession series on the salt marshes of the euhaline and polyhaline zones of the Danish, German and Dutch Wadden Sea (after Dijkema, 1983).

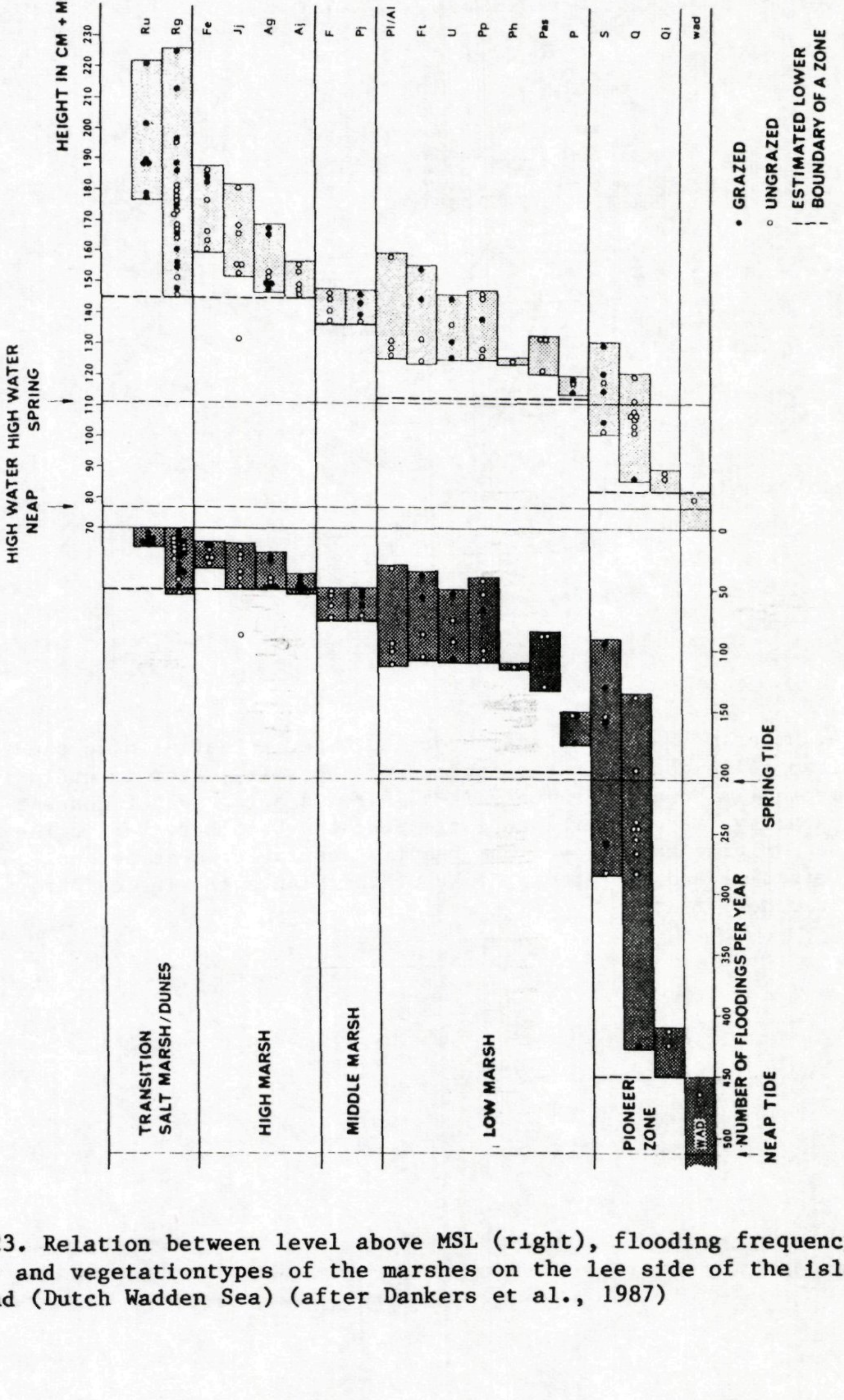


Fig. 23. Relation between level above MSL (right), flooding frequency (left) and vegetationtypes of the marshes on the lee side of the island of Ameland (Dutch Wadden Sea) (after Dankers et al., 1987)

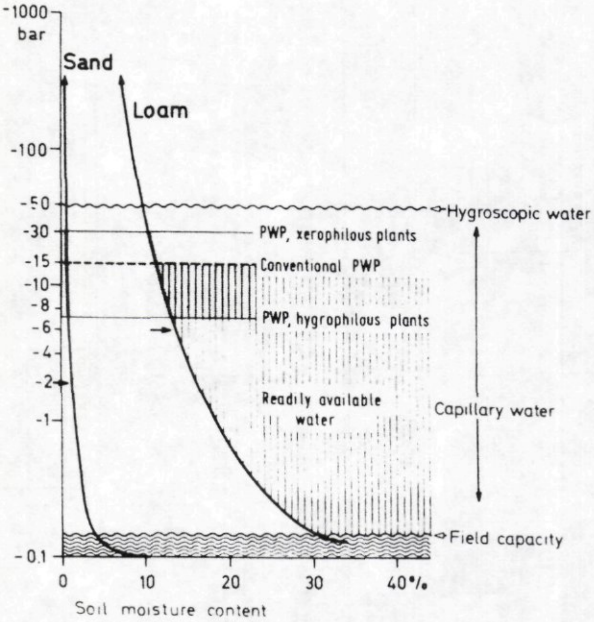


Fig. 24. Diagram of the dependence of the water potential of a sandy soil and a loam soil upon the water content of the soil. Water is exclusively hygroscopically bound at values of -50 bar and below. Water content at field capacity is considered to correspond to -0.15 bar. PWP is the permanent wilting percentage. The readily available water depends on soil characteristics and the specific PWP of the plants growing on this soil (after Larcher, 1975).

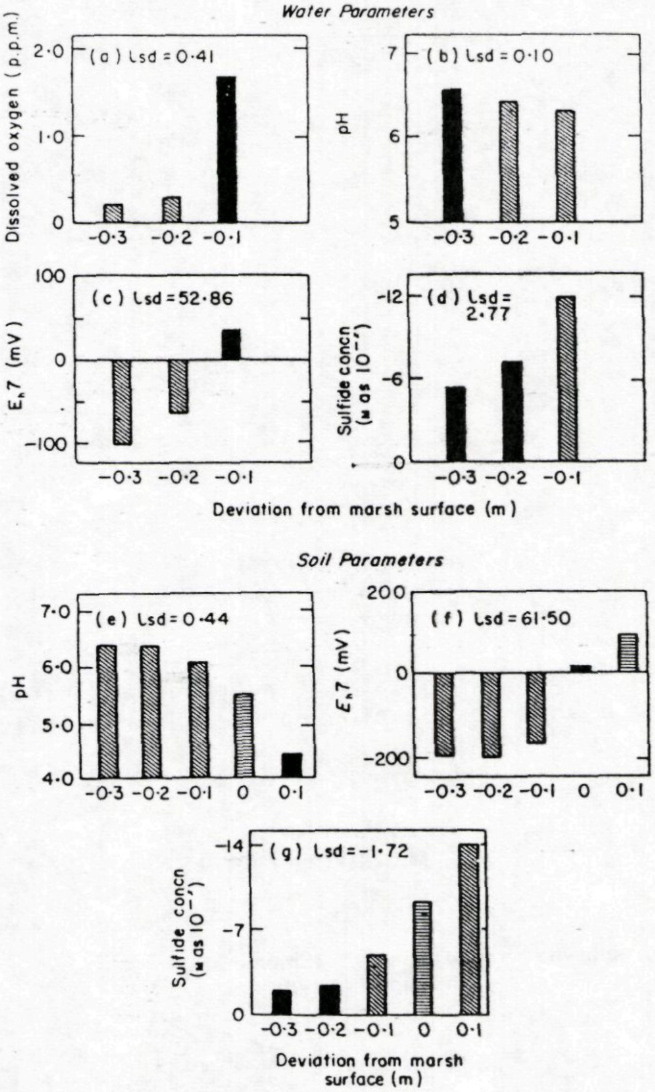


Fig. 25. Physiochemical data for water and soil parameters associated with various changes in elevation of marsh vegetation, indicating the profound changes that will occur after an instanteneous change in inundation duration (after Linthurst & Seneca, 1980).

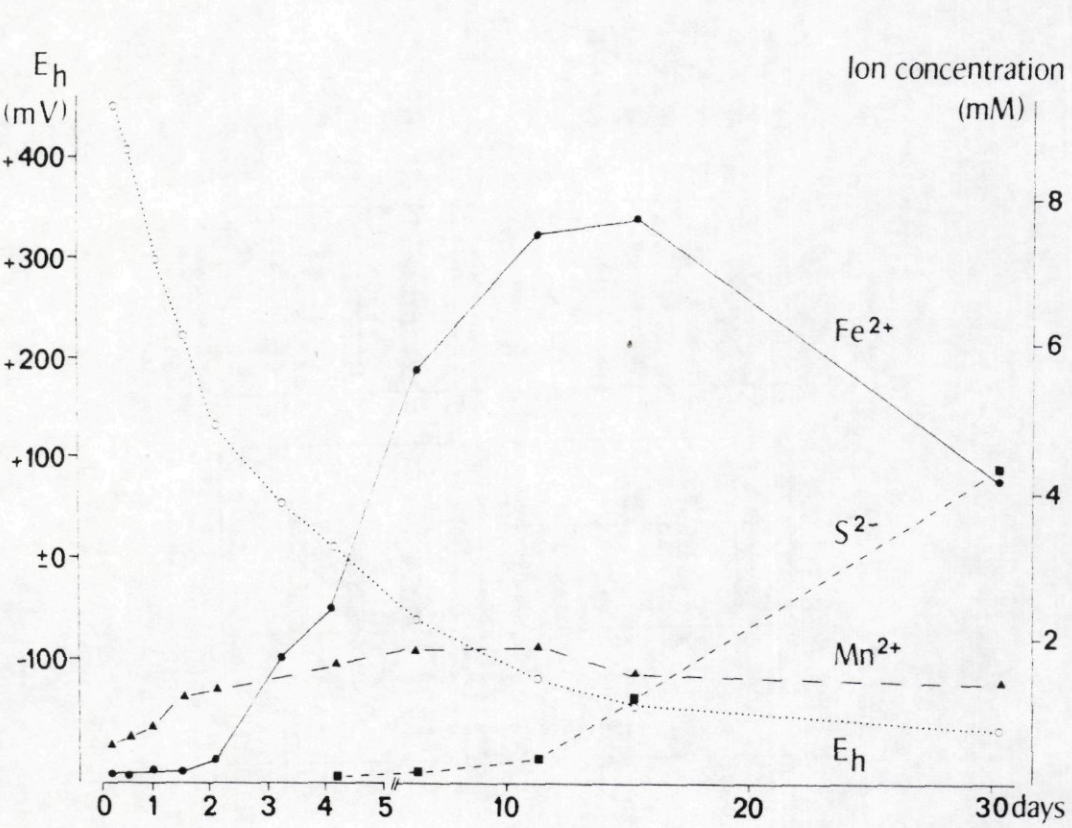


Fig. 26. Redox potential and contents of sulphide and of water soluble and exchangable ions of a soil in relation to the saturation time with seawater.

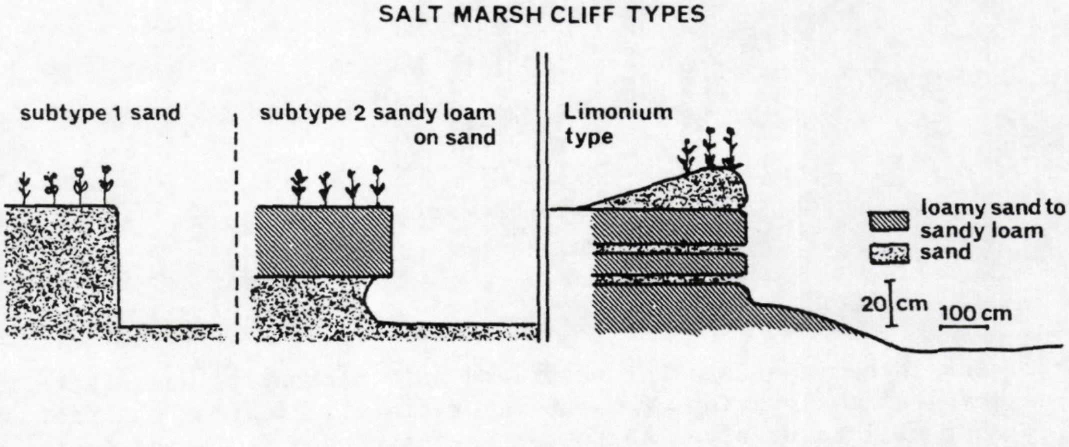


Fig. 27. Soil composition and morphology of three cliff types (after van Eerdt, 1985).

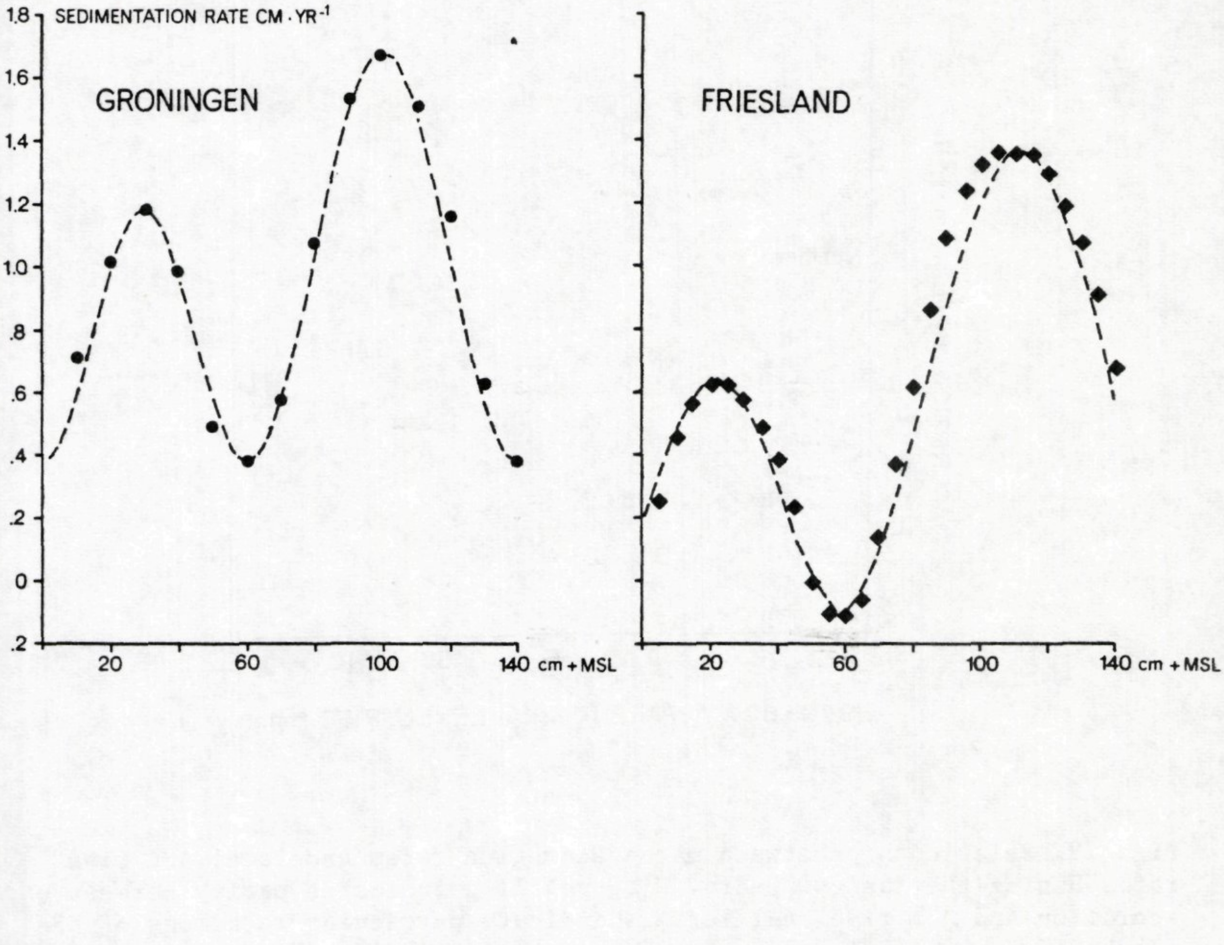


Fig. 28. The rate of sedimentation (in cm yr^{-1}) as observed during the last decades on the salt marshes of the provinces of Groningen (a) and Friesland (b), on the Dutch mainland coast, in relation to the elevation of the substrate above MSL. The data points (+) are averaged from a number of observations by Bouwsema et al (1986). The drawn curve represents parts of the two sinus curves used for the calculations as shown in Figure 33.

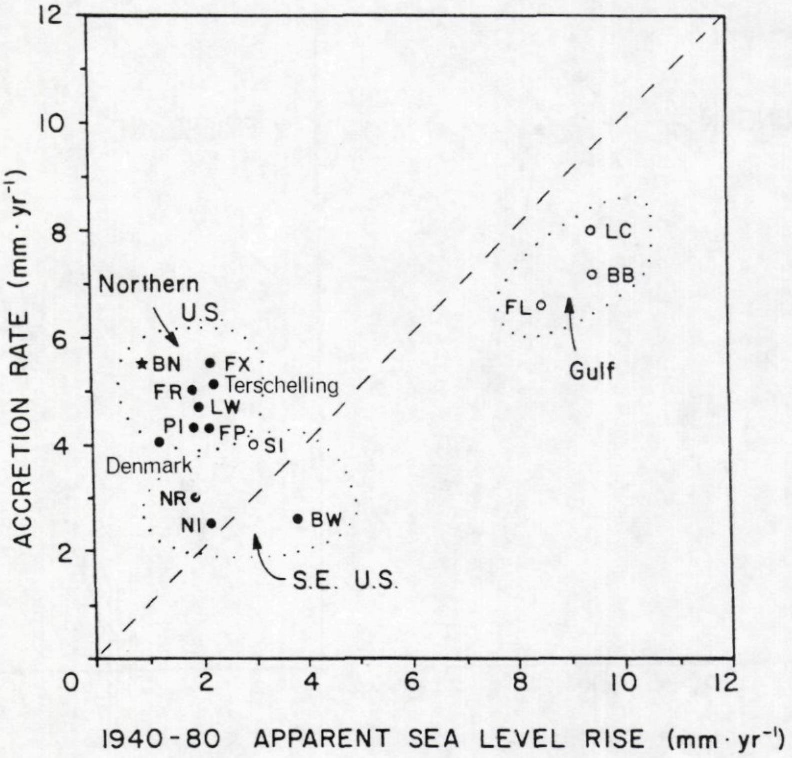


Fig. 29. Relationship between marsh accretion rates and local ASL rise rates during the last 40 years. Diagonal line indicates parity between accretion and ASL rise. All letters indicate particular locations of USA marshes (see original paper, Stevenson et al., 1986). The data points representing the marshes of Terschelling and Danmark are added.

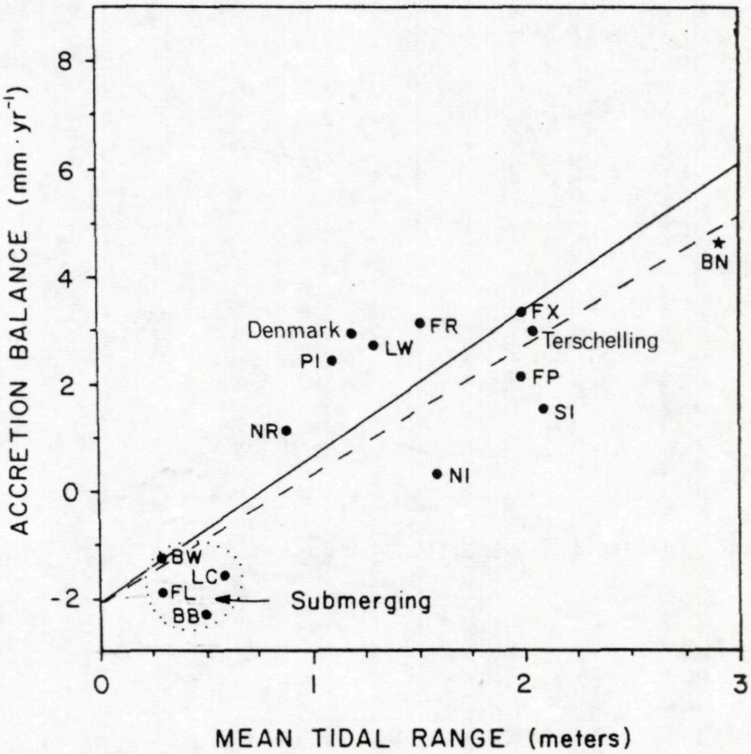


Fig. 30. Relationship between accretionary deficit (vertical accretion rate minus local ASL rise) and mean tidal range of marshes. All letters indicate particular locations of USA marshes (see original paper, Stevenson et al., 1986). The data points representing the marshes of Terschelling and Denmark are added.

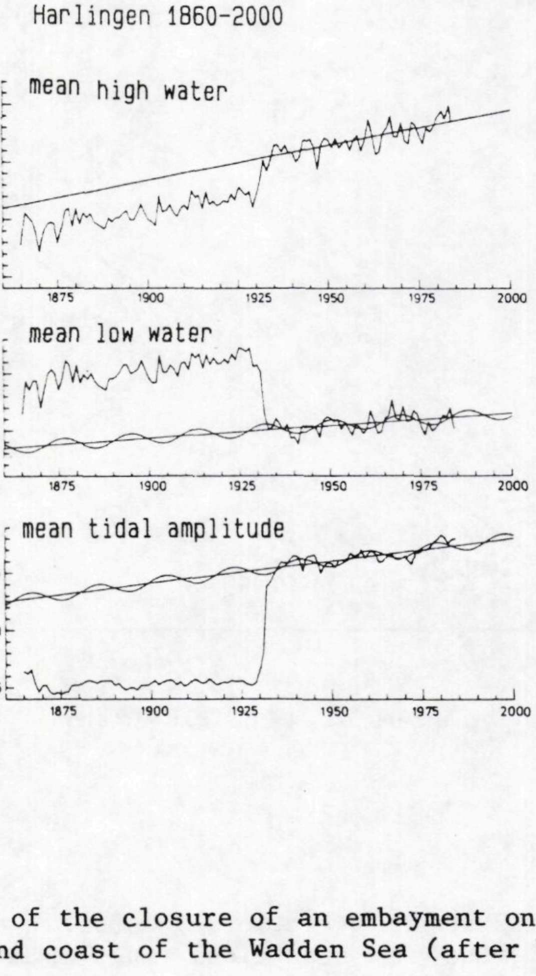


Fig. 32. The effect of the closure of an embayment on the tidal regime of parts of the mainland coast of the Wadden Sea (after Van Malde, 1984).

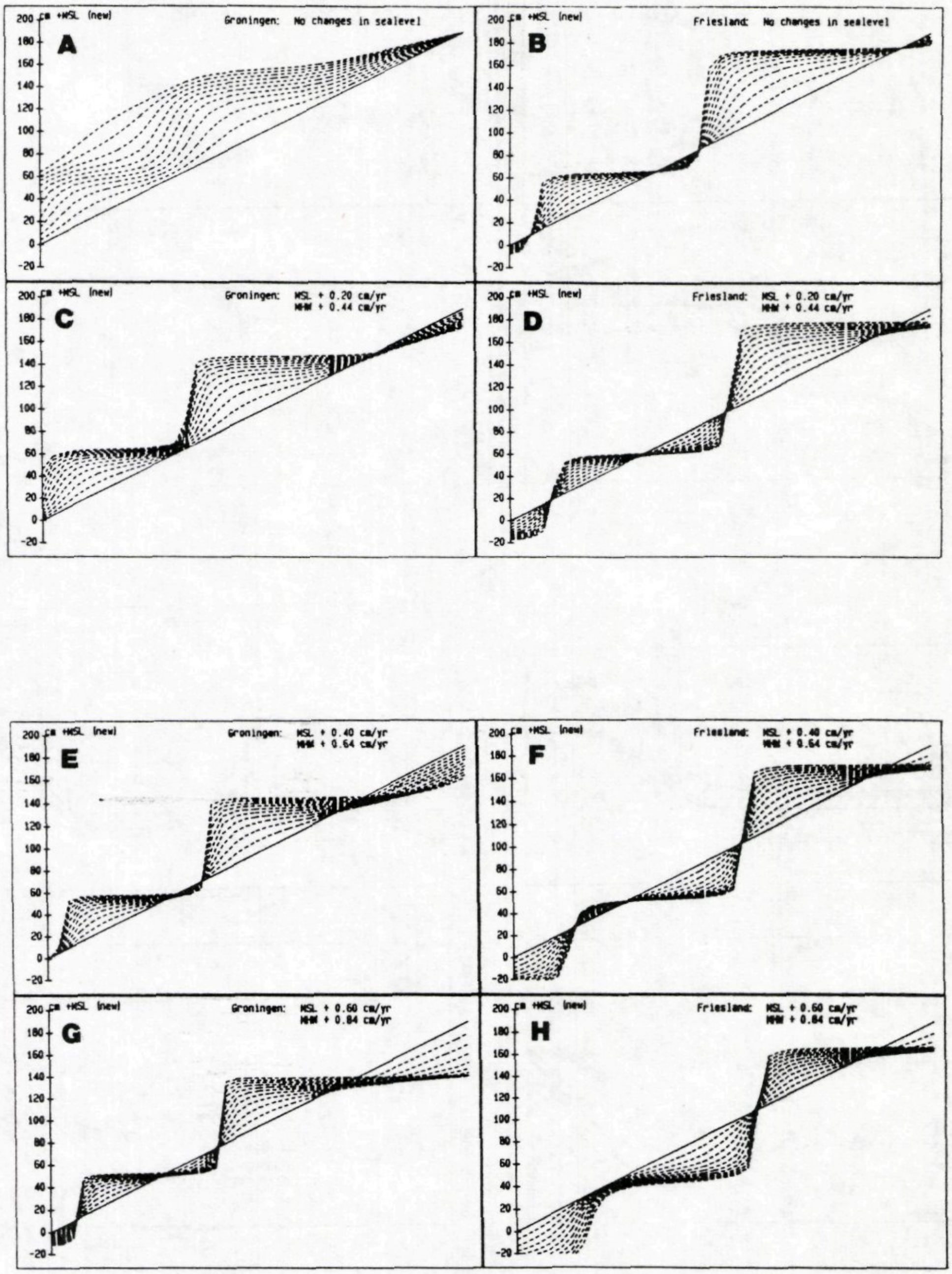
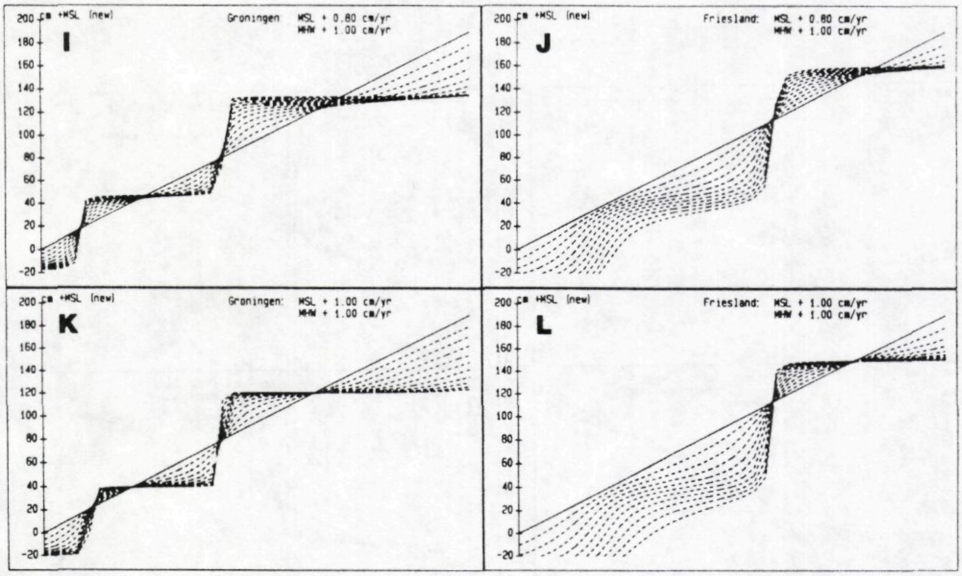


Fig. 33. The calculated new coastal profiles in the provinces of Groningen (left) and Friesland (right) in 10 10 year intervals and during different sea level rise scenarios. For explanation see text.



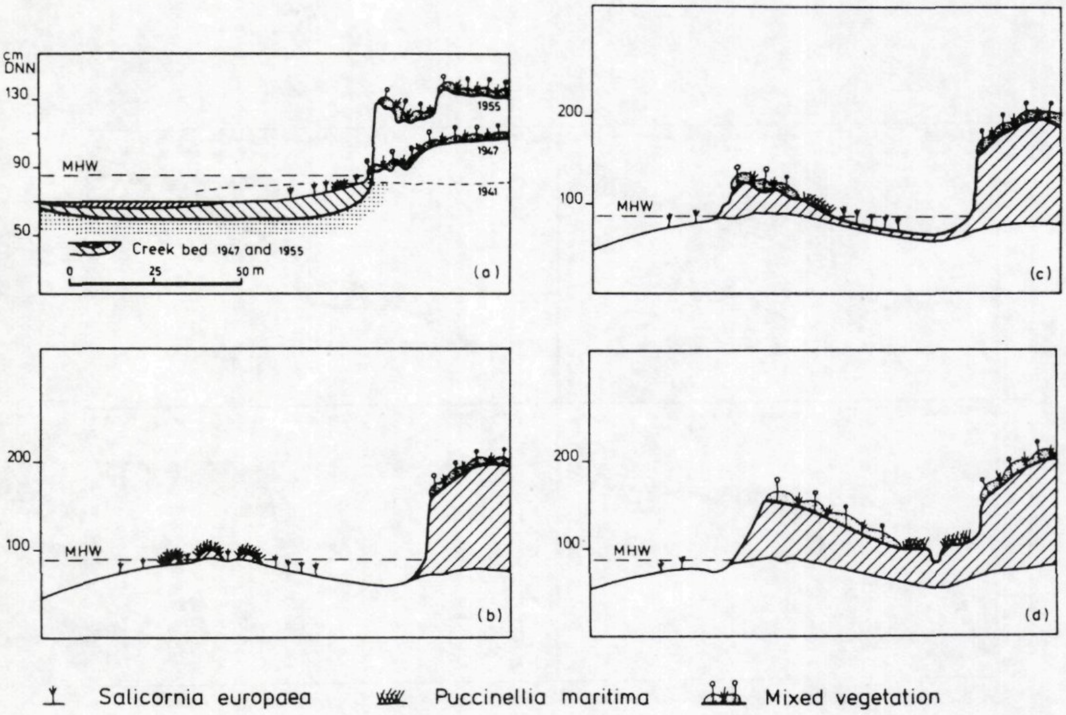


Fig. 34. Formation of a terraced salt marsh. (a) Formation of an offshore channel at the windward side of a new salt marsh in the Danish Wadden area; (b) Initial salt marsh formation on a high-lying tidal flat off the channel; (c) and (d) Continuing formation of a new terrace, the channel filling with mud (after Jakobsen, 1954, 1964; from Beeftink, 1966).

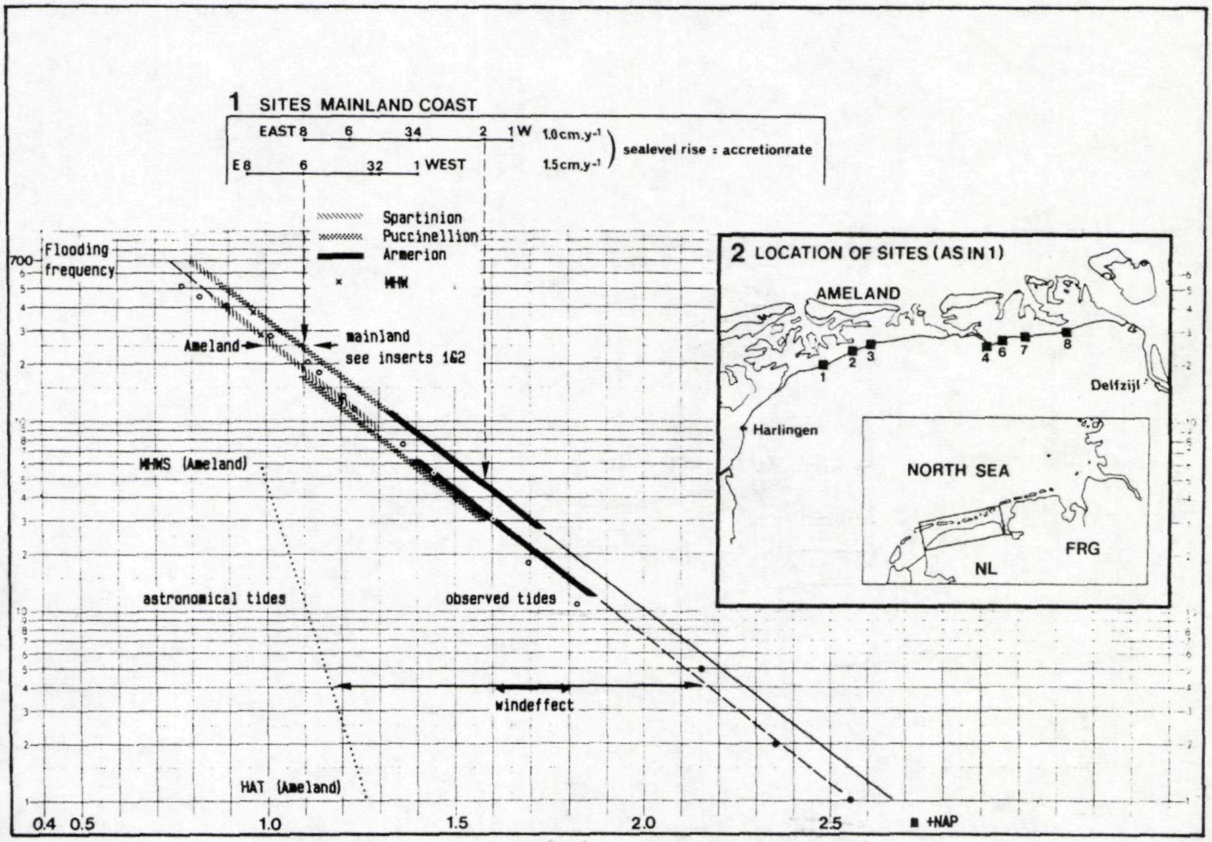


Fig. 35. Correlation between flooding frequency, elevation in respect to MSL, vegetation types and sedimentation rate. The wind effect is also shown. In insert I the level where sedimentation and assumed sea level rise are identical are indicated. A line perpendicular to line B intercepts the vegetation type above which sedimentation is insufficient to maintain that type. For instance: Site 6 has a sedimentation rate of 1.5 cm yr^{-1} at a level of 1.1 m $^{+}$MSL (the low marsh). This type of vegetation can be supported. The higher marshes will revert to low marshes. As can be seen in insert 1 this sedimentation rate occurs on increasingly higher levels going from east to west. The high marsh will receive sufficient sediment only at site 1 in order to be preserved. At a rate of 1.0 cm yr^{-1} in sea level rise, the high marshes at sites 1-4 might remain.

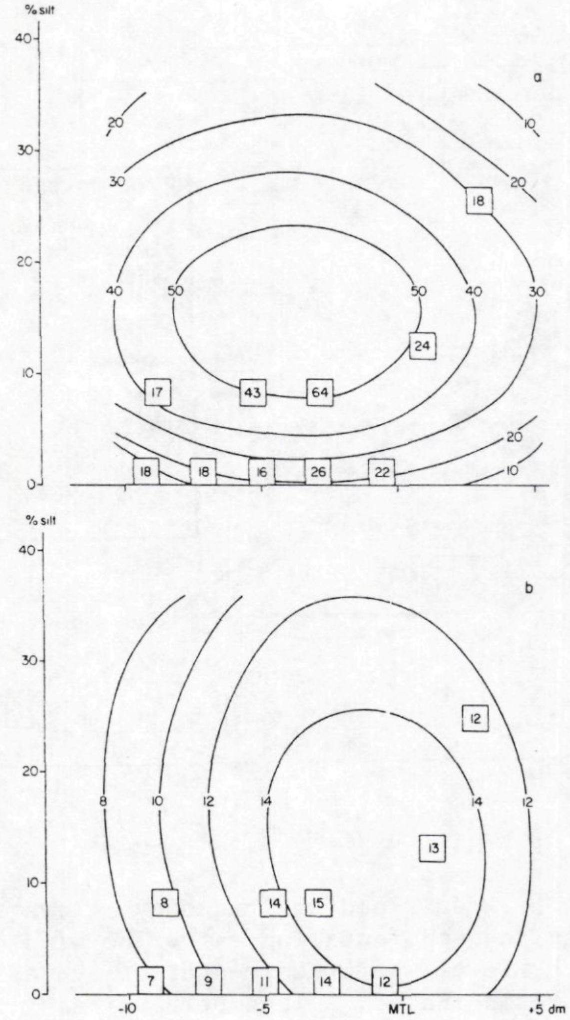


Fig. 36. Mean values of biomass in g m^{-2} ADW (a) and species number per 0.45 m^2 (b) at various combinations of level in the intertidal zone and silt content in 99 transects. Boxed figures are averages of data from 8 to 13 grouped transects (after Beukema, 1976)

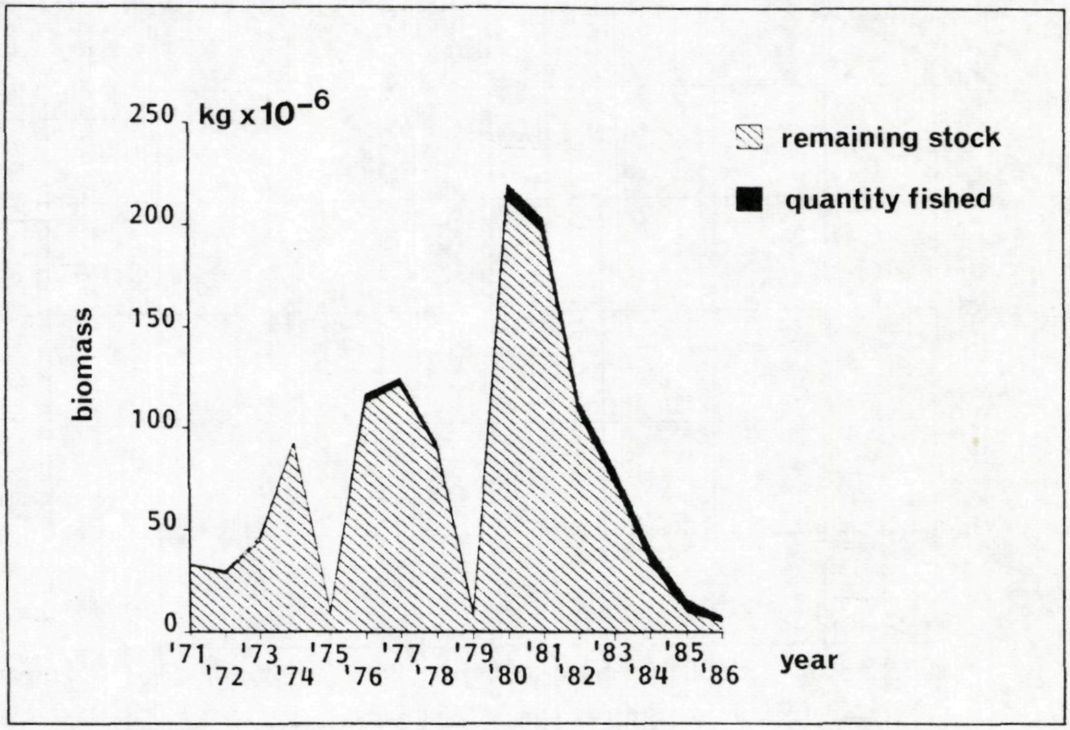


Fig. 37. The interannual fluctuation in the biomass of Cerastoderma edule in the Wadden Sea, showing the large fluctuations and the short recovery time required (after de Vlas, 1982)

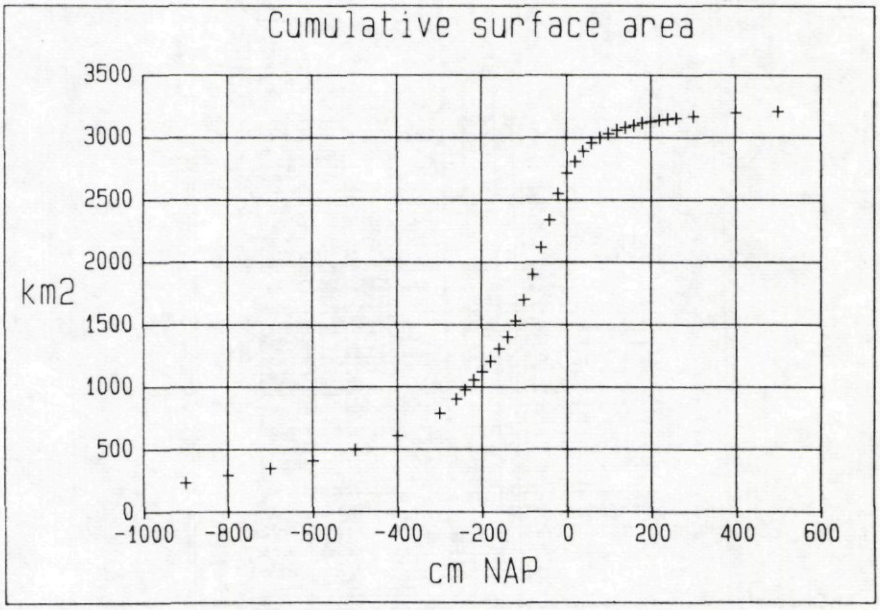


Fig. 38. The cumulative surface area below a given depth in the Dutch part of the Wadden Sea.

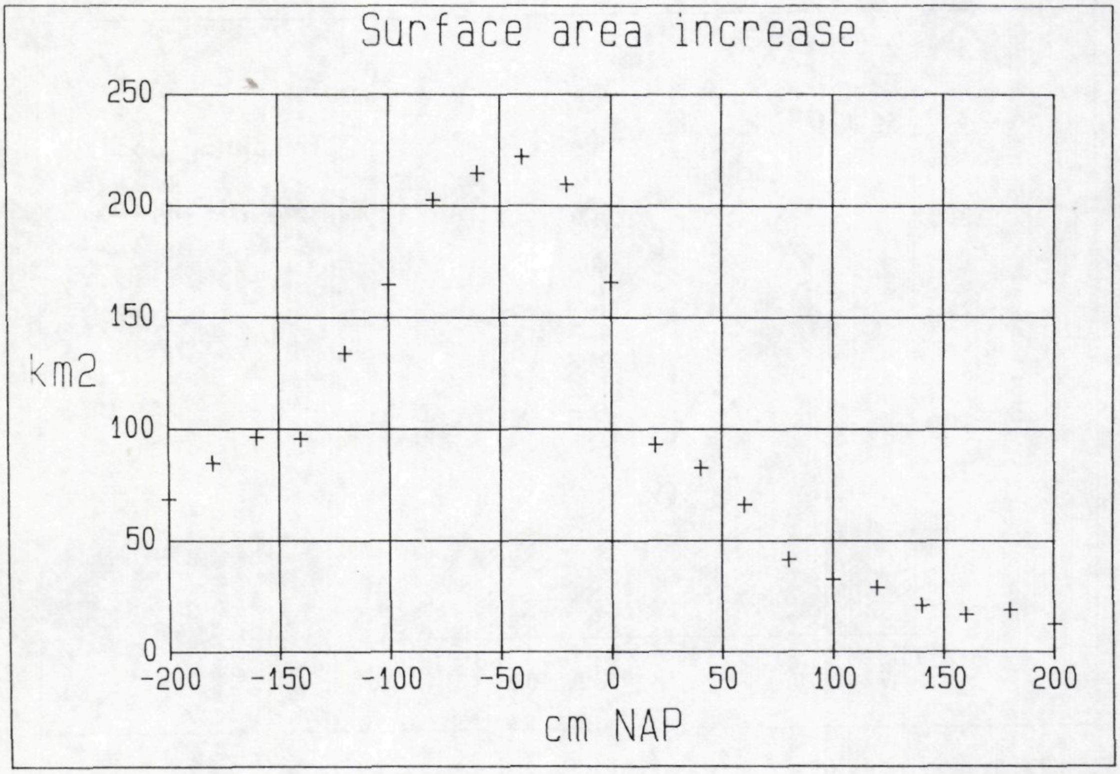


Fig. 39. The increase in surface area in 20 cm intervals in relation to MSL (NAP).

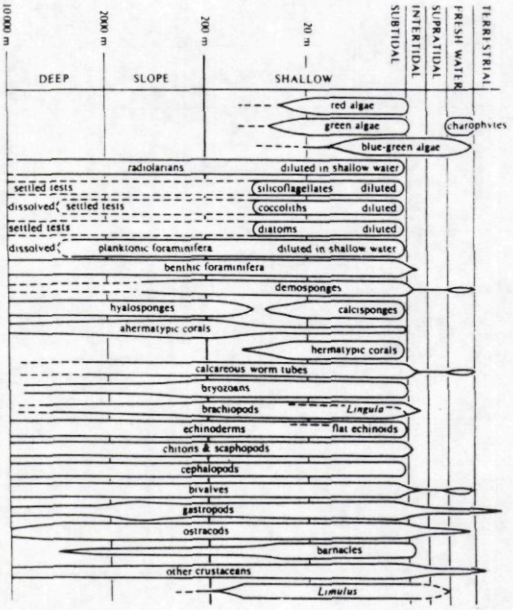


Fig. 40. The distribution of the major genera in the oceans and the intertidal.

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