

ASSESSMENT REPORT ON NRP SUBTHEME
"IMPACT OF CLIMATE CHANGE ON THE WADDEN SEA"

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ABSTRACT

This section summarizes studies on the effect of climate change on the estuarine Dutch Wadden Sea. Increased concentration of carbon dioxide is expected to have a rather small effect on saltmarsh vegetation and a negligible effect on the functioning of the Wadden Sea ecosystem. Rates of sealevel rise of 60 and 85 cm per century are not expected to have a major impact on the geomorphology of tidal basins because of increased sedimentation. Also saltmarsh accretion may be able to keep pace with rates of sealevel rise of this magnitude, if erosion at the seaward edge can be controlled. Shorebird population sizes, which appear related to the area of tidal flats in their winter quarters, are not expected to decline because of change in the area of tidal flats in the Wadden Sea. However, because reproduction of several species of bivalve shellfish may be impaired by higher winter temperatures, recruitment of these species may strongly decrease and this may affect shorebird populations. Model calculations do not show a major effect of higher winter temperatures on ecosystem functioning, however.

1. INTRODUCTION

The Wadden Sea is a shallow tidal sea of about 8 000 km² situated along the coasts of The Netherlands, Germany and Denmark. The Dutch part of the Wadden Sea is considered to be the most important nature area of The Netherlands. It has received recognition as such in the Physical Planning Decision (PKB) for the Waddenzee, about 2 000 km² of it are protected under the Nature Conservation Act, together with the Danish and German parts it has been given the status of 'Wetland of international importance' under the Convention of Ramsar, and it is recognized as a Biosphere Reserve by UNESCO.

The Wadden Sea is one of the best studied wetlands of the world. Boekschoten (1973) estimated that, at that time, already 4,150 scientific publications described this area. This number has increased considerably since then. Hence the structure and functioning of the 'normal' Wadden Sea system are well known.

Beukema et al. (1990) arrived at some preliminary conclusions about the possible effects of climate change on the Wadden Sea and other coastal areas. Table 1.1 lists the studies commissioned by the Dutch National Research Programme on Global Air Pollution and Climate Change (NRP I) on the effects of climate change on the Wadden Sea as well as some other relevant studies. In addition research on the effects of climate change has been carried out in the German Wadden Sea.

This report aims at an assessment of the results of studies on the Wadden Sea commissioned by NRP I, taking in account any other relevant study.

Table 1.1

List of projects in the NRP subtheme "impact of climate change on the Wadden Sea"

Title	Project leader	Number
Effects of an increased sealevel rise on geomorphology and ecological functioning of the Wadden Sea	T. Louters	850011
Salt marshes and sealevel rise: plant dynamics in relation to accretion processes and accretion enhancement techniques	J.H.J. Terwindt	850033
Effects of climate change on bird migration strategies	C.J. Smit	850034
Winter temperature and reproductive succes in bivalves living on tidal flats in Western Europe	J.J. Beukema	851053
Integration of effects of climate change on estuarine ecosystem communities	A.G. Brinkman	853127
Non-NRP funding		
Effects of atmospheric CO ₂ enrichment, salinity and flooding on the ecology of C ₃ and C ₄ saltmarsh plants	J. Rozema/ G.M. Lenssen	
Subsidence of a coastal area due to gas extraction as a model for sealevel rise	N. Dankers/ K.S. Dijkema	

2. SHORT DESCRIPTION OF THE WADDEN SEA

The Wadden Sea is a shallow estuarine area situated along the North Sea coasts of Denmark, Germany and The Netherlands. Average tidal ranges vary between 1.4 and 3.4 m. The Wadden Sea occupies about 8,000 km² and about half of this area consists of bare tidal flats. Salt marshes occur only above mean high water mark and cover about 300 km². The Dutch part of the Wadden Sea covers about 2500 km².

The Wadden Sea is considered to be one of the major nature areas of western Europe. Its tidal landscapes where natural processes such as erosion and accretion are visibly active, seem relatively unaffected by humans. The extensive tidal flats contain extremely large numbers of benthic invertebrates and are characterized by high biomasses. Also the subtidal areas are rich in individuals and biomass. On this invertebrate biomass fish and birds feed in very large numbers. Many North Sea fish and crustacean species use the Wadden Sea as a nursery.

The bird population includes both breeding birds, such as gulls, terns, and several species of shorebirds, and non-breeding migratory species. The latter species mainly breed in the Arctic and visit the Wadden Sea as a stopover site during migration or as a wintering site. Non-breeding migratory species include geese, ducks, many species of limicoles, and several other species. It is estimated that altogether about 7 million shorebirds visit the Wadden Sea annually. Wolff (1983) gives an extensive description of the ecology of the Wadden Sea.

The past ecological development of the Wadden Sea has been summarized in two review papers by Wolff (1992a) and Wolff et al. (1994). His conclusions are summarized below.

In a completely natural situation a Wadden Sea landscape would show the following sequence of belts of different landscape types when going from the North Sea to the higher inland areas (Figure 2.1):

- beaches, dunes and salt marshes on barrier islands
- tidal flats and channels
- salt and brackish marshes
- freshwater marshes, swamps, and peat bogs
- high-lying soils with forests and other dry vegetation types.

It may be assumed that these belts have moved shoreward under the influence of the rising sealevel in the geological past (Zagwijn, 1986). An increased rate of sealevel rise due to climate change would in principle have the same effect.

Until about 1000 years ago man hardly interfered with the geomorphological development of the Wadden Sea. At that time, however, the invention of dike-building introduced a major change (Wolff, 1992b). At the end of the 12th century the larger part of the vegetated landscape was separated from the tidal Wadden Sea by a contiguous system of dikes. Thus the connection between the Wadden Sea and the adjacent belt of brackish and fresh wetlands was broken. The result of all embankments and reclamations is a very marked and firm separation between the tidal Wadden Sea on the one hand and the non-tidal land and freshwater areas on the other hand. This hard boundary will prevent further shoreward movement of the coastal ecosystems enumerated above, which leads to the question whether these systems can survive in their present position.

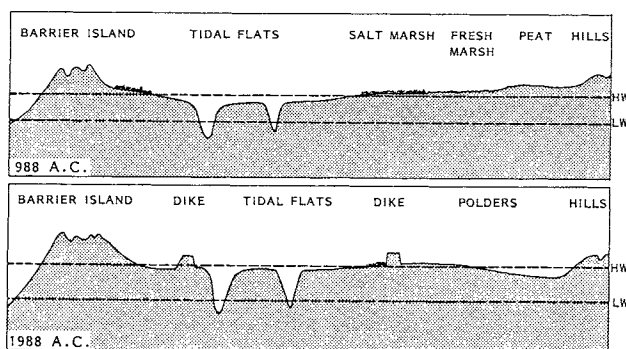


Figure 2.1
Cross-section through the Wadden Sea landscape in the Middle Ages and at present

Many species are known to have been introduced from abroad into the Wadden Sea area by human intervention. Most species were inadvertently introduced; some like the cord grass *Spartina townsendii* and the Japanese oyster *Crassostrea gigas* deliberately for, respectively, stimulation of accretion and oyster farming. Other new species were able to colonize the Wadden Sea because their habitat was introduced there. The best example is the construction of artificial rocky shores in the form of breakwaters, moles, and stone-covered dike slopes. It may be concluded that the Wadden Sea nowadays lodges quite a number of species of algae and invertebrates which did not occur there before. Most of these species have in common that they are relatively small and short-living and that they have short reproduction cycles. They did not change the ecosystems very much. With respect to climate change it may be wondered whether any further immigrations due to an amelioration of the climate will have equally little effect.

On the other hand, human activities have had such a strong impact on the Wadden Sea ecosystem, that several species have become extinct. Wolff (1992a) lists three species of marine mammals, six species of birds, seven species of fish, and three species of molluscs. Climate change might lead to further local extinctions because species cannot cope with the changed conditions.

The following general conclusions may be drawn on the past changes of the Wadden Sea (see also Wolff 1992a; Wolff et al., 1994):

- in a seemingly natural area humans appear to have had a very strong impact on the ecosystems; already in the Middle Ages about half of the ecosystems had been destroyed;
- many large, long-living and slowly reproducing species (K-selected species) have disappeared from the Wadden Sea, whereas many small, short-living and rapidly reproducing species (r-selected species) have colonized the area or increased in numbers.

At present the Wadden Sea is managed as a nature reserve or national park, but at the same time several human activities are still possible. Among these are fisheries for fish, shrimps, and shellfish, mussel culture, extraction of shells, sand, and natural gas, sailing and other forms of water sport, military exercises, and grazing of the salt marshes. Moreover, the Wadden Sea is strongly influenced by land drainage containing nutrients and toxic substances. Especially the influence of the river Rhine is quite important in the Dutch part of the Wadden Sea.

3. EXPECTED EFFECTS OF CLIMATE CHANGE ON THE WADDEN SEA AND CHOICE OF RESEARCH SUBJECTS

In November 1988 a workshop on the expected effects of climate change on marine coastal ecosystems was held at the island of Texel (Beukema et al., 1990). In several contributions the Wadden Sea served as a case study and many of the conclusions of the workshop are applicable to the Wadden Sea.

3.1 Expected effects of an increase of CO₂

In the workshop cited above Long (1990) and Rozema et al. (1990) showed that elevated CO₂-concentrations have a clear impact on saltmarsh plants. This observation has since been studied in the project 'Effects of atmospheric CO₂ enrichment, salinity and flooding on the ecology of C₃ and C₄ salt marsh plants' by

J. Rozema and G.M. Lenssen (Table 1.1). CO₂-effects on the aquatic ecosystems were considered to be less important (Brouns, 1988) and consequently have not been a subject for further study.

3.2 Effects of changes in temperature and other meteorological factors

In the 1988 workshop temperature and related climate factors were clearly identified as a factor which might strongly influence the distribution of plant and animal species (Van den Hoek et al., 1990; Breeman, 1990; De Vooy, 1990; Beukema, 1990; Wilson, 1990; Costa, 1990). Changed meteorological conditions on one hand will lead to the local extinction of species for which the habitat conditions become unsuitable, and on the other hand will enable other species to colonize new areas because the conditions have become suitable for them.

These conclusions have not been followed up by detailed studies since it was reasoned that comparison of the Wadden Sea with estuarine areas more southerly would give enough information on the expected changes of occurrence of plant and animal species (De Vooy, 1990; Costa, 1990).

Less attention was paid to shifts in the abundance of species due to changed conditions. However, one possible shift was singled out because of its possible importance for the Dutch shellfish cultures. This concerns the possibility that a relatively small change of water temperatures might negatively affect the reproduction and subsequent survival of the larvae of a number of shellfish species. This has been studied in greater detail in the project 'Winter temperature and reproductive success in bivalves living on tidal flats in Western Europe' by J.J. Beukema and P.J.C. Honkoop (Table 1.1). However, this study will continue for at least a year after the conclusion of NRP I, so definite conclusions are not yet possible.

3.3 Effects of an increased rate of sealevel rise

In the 1988 workshop an increased rate of sealevel rise was recognized as a factor with potentially great effects on the geomorphology and the ecology of the Wadden Sea and similar areas (Siefert, 1990; Misdorp et al., 1990; Westerhoff and Cleveringa, 1990; Lefeuvre, 1990; Huiskes, 1990; Dijkema et al., 1990; Goss-Custard et al., 1990). Salt marshes and tidal flats could be inundated and this in turn could lead to impacts on the plant and animal species occurring.

Consequently several projects addressed this possible problem (Table 1.1). The potential effects on the geomorphology and benthic fauna of tidal flats were studied in the project 'Effects of an increased sealevel rise on geomorphology and ecological functioning of the Wadden Sea' by J.P.M. Mulder and T. Louters. The possible effects on the geomorphology and vegetation of salt marshes were investigated in the study 'Salt marshes and sealevel rise: plant dynamics in relation to accretion processes and accretion enhancement techniques' by J.H.J. Terwindt, K.S. Dijkema and E.J. Houwing. The consequences of the possible inundation of tidal flats for shorebird populations were the subject of the study 'Effects of climate change on bird migration strategies' by C.J. Smit, B.J. Ens and G. Wintermans. In addition a non-NRP study on 'Subsidence of a coastal area due to gas extraction as a model for sealevel rise' by N. Dankers and K.S. Dijkema could be used as an experimental analogue of an increased rate of sealevel rise.

3.4 Effects of increased UV-B radiation

At the 1988 workshop UV-B was identified as another factor which might have consequences on the Wadden Sea ecosystem (Kramer, 1990; Van de Staay et al., 1990). In the latter study effects on saltmarsh plants were clearly demonstrated. The former study, however, concluded that increased UV-B radiation would have little effect on the biota of the turbid and turbulent Dutch coastal waters. An exception was made, however, for the organisms of tidal flats and shallow pools in the tidal zone during low tide.

In view of this conclusion no further studies were commissioned. However, Peletier et al. (submitted) have shown since that benthic diatoms occurring on the Wadden Sea tidal flats show marked changes of abundance under the influence of increased UV-B.

3.5 Integration of effects

Already in the 1988 workshop it became clear that many biota could become subject to the influence of several aspects of climate change at the same time (e.g. Van de Staay et al., 1990). To address this aspect of the impact of climate change the study 'Integration of effects of climate change on estuarine ecosystem communities' was started by A.G. Brinkman. Based on an already developed simulation model of the ecosystem of the Wadden Sea the various aspects of climate change had to be investigated simultaneously.

4. IMPACT OF INCREASED CO₂ CONCENTRATIONS

4.1 Impact on saltmarsh plants

CO₂ is essential for the growth of terrestrial and some aquatic plants. Other aquatic plant species are dependent on ions derived from dissolved carbon dioxide. In the photosynthetic process CO₂ is chemically reduced to carbohydrates and part of these become plant material. How plants respond to increased CO₂ concentrations depends on the photosynthetic pathway of the plant in question. In so-called C₃ plants the C₃ photosynthetic pathway will result in an increased photosynthetic rate and higher biomass production under higher levels of carbon dioxide. In C₄ plants these effects are small or absent (Strain and Cure, 1985; Rozema et al., 1993).

In Wadden Sea salt marshes both C₃ and C₄ plants occur. Increasing CO₂ concentrations therefore may result in different rates of biomass production and, hence, in changed competitive abilities. This could lead to changes in the composition of saltmarsh vegetation. An effect on the amount of dead plant material exported from the marsh is also possible.

Experimental CO₂ enrichment studies in salt marshes with C₃ and C₄ species in the Chesapeake Bay, USA, analysed the competitive relationships between the two types of plants (Arp, 1991). The CO₂ experiments were done in the field for five continuous years. The C₃ species *Scirpus olneyi* showed increased biomass under elevated atmospheric CO₂, in contrast with the C₄ grass *Spartina patens*. This long-term field research was one of the first experimental studies providing evidence that the competitive balance between C₃ and C₄ plants will shift in favour of the former ones. At the end of the five-year research period the C₃ plants

demonstrated the same increased rates of growth and photosynthesis as at the start. This implies that under field conditions these plant species do not show photosynthetic acclimation, that is a down regulation of the rate of photosynthesis as a result of end product negative feedback.

In The Netherlands Lenssen (1993) investigated the response of three C₃ species (*Aster tripolium*, *Elymus athericus*, *Puccinellia maritima*) and one C₄ species (*Spartina anglica*) to CO₂ enrichment in the project 'Effects of atmospheric CO₂ enrichment, salinity and flooding on the ecology of C₃ and C₄ salt marsh plants' (Table 1.1). In addition he investigated whether the response to CO₂ enrichment was modified by other environmental factors, viz. light, temperature, UV-B radiation, salinity, and flooding.

In his experiments Lenssen (1993) found that at a CO₂ concentration of 720 μmol.mol⁻¹ the C₃ plants showed an increase of plant biomass of 19-33% relative to the ambient CO₂ concentration. The only C₄ plant, however, was not stimulated by an higher concentration. These results confirm the earlier results of Curtis et al. (1990) and Arp (1991) for American salt marshes.

However, the outcome of the experiments appears to be dependent on the other environmental factors studied. Higher temperatures as a result of climate change probably will favour the C₄ species more. Also the other environmental factors influence the effect of increased CO₂, but not in correlation with the C₃ - C₄ separation. It may be concluded that higher atmospheric CO₂ concentrations will result in higher biomass production of the C₃ species and a loss of competitive ability of the C₄ species.

4.2 Evaluation

Changes in competitive ability of saltmarsh plants will probably be reflected in a changed composition of the vegetation on Wadden Sea salt marshes. The higher biomass production probably will have an effect on the exchange of plant organic matter between saltmarsh and adjacent estuary, but in view of the magnitude of this exchange (Dankers et al., 1984) and the relatively small area of Wadden Sea salt marshes (see section 2) the effect on the Wadden Sea system will be negligible. In view of the conclusion drawn in Section 3.1 about the relative unimportance of CO₂-effects below high-tide level, it is concluded here that no further studies on carbon dioxide effects are needed for the Wadden Sea.

5. IMPACT OF SEALEVEL RISE

5.1 Impact of sealevel rise on the morphology of tidal flat environments

A geological evolutionary model of tidal basin development

Van der Spek and Beets (1992) studied the evolution of a Wadden-Sea like tidal basin, the so-called Holland tidal basin, between 7000 BP and 3500 BP. Their results have been used to derive a geological model for tidal basin evolution under the influence of a rise in sealevel. The model emphasizes the balance between the extra storage capacity of the basin created by a sealevel rise, and the amount of sediment available for a geomorphological response. The model shows that if the rate of sealevel rise exceeds the rate of sediment supply, the innermost parts of the basin will not receive sufficient sediment for an intertidal morphology to be

preserved. Eventually, sand will be deposited only in tidal channels and in the flood tidal delta through which the sediment is supplied; mud deposition will occur in the interchannel areas, and salt marshes will disappear.

An empirical model of the morphological behaviour and stability of channels and flats in tidal basins

Departing from the geological model Eysink (1992) has defined an empirical morphological model MORRES (acronym for MORphological RESponse model) which is based on a set of empirical equilibrium relationships between hydrodynamic and geomorphological characteristics of tidal basins. This model is a sediment balance model describing the long-term geomorphological development of the Wadden Sea as a result of increased sealevel rise on the scale of a tidal basin. It covers the geographical units outer delta, inlet and basin. The outer delta is characterized by its sand volume. The inlet is characterized by a cross-sectional area and its length. The tidal basin is characterized by the curve representing the hypsometry. The area and elevation of the tidal flats, defined as the area between mean high water (MHW) and mean low water (MLW), and the depth of the basin are derived from the hypsometric curve. The basin is defined as the surface area at high water. Furthermore, the water motion in the basin is characterized by the tidal prism of the basin. The tidal range in the basin is assumed to remain constant during the morphological adaptation process. The exchange of sediment between the tidal basin and the adjacent sea is based on the principle of a sand trap.

An (accelerated) rise in sealevel will cause a regional rise of the average water level in the Wadden Sea. In other words, the depth of the Wadden Sea will increase somewhat. Hence, the dynamic equilibrium will be slightly disturbed. This slight depth increase will cause a slight deceleration of the average current speeds in the channels and over the flats. Since the capacity for sediment transport is a power function of the current speed, the sediment transport capacity will drop much more as the current speed slows. The flood stream carrying sediment will continue to deposit sediment in the basin. However, the ebb current does not have enough force to lift and remove the total quantity brought in. Thus, over a longer period, this creates a net sand transport towards the tidal basin. This property of deepened tidal basins to demand large quantities of sand is termed sand demand or 'sand hunger'. The total quantity of sand required to restore dynamic equilibrium is directly proportional to the depth increase. Hence, sealevel rise will result in filling in of the tidal basin until a new equilibrium is reached. The sand will be derived from the outer deltas of the inlets and eventually from the coasts of the barrier islands. Other changes in the morphology of a tidal basin, e.g. sand extraction, subsidence of the seafloor due to gas extraction, reduction of the tidal basin due to engineering works or accretion of salt marshes, will cause similar reactions of the tidal basin. To predict the behaviour of the Wadden Sea under conditions of sealevel rise on the basis of the empirical relationships between a number of morphological characteristics, it has been assumed that the system will strive for equilibrium. This assumption can be validated by the observations made after two tidal inlets have been changed drastically by reducing their tidal area through the building of dams (1932: Zuiderzee; 1969: Lauwerszee). In both cases the system shows a development towards a new equilibrium.

The knowledge of the processes governing the morphology of the tidal flats is rather limited. Observations have shown that, generally speaking, the present rate of flat growth can keep up with the current rise in sealevel of about 20 cm per century. The maximum rates of increase of tidal flat level derived from measurements in the period 1925-1987, appear to be around 8-13 mm annually. It seems that the tidal flat system has the capacity to compensate for a wide range of rates of rise in sealevel by raising its level. It remains to be seen whether the flats can keep up this growth rate in an increasingly rough wave climate at an accelerated rise in sealevel. This requires more knowledge of the process.

To make a prediction of the effects of sealevel rise on the Wadden Sea tidal flats, Louters and Gerritsen (1994) used three different rates of sealevel rise: (1) present rate of 20 cm per century, (2) a predicted rate of 60 cm per century, and (3) a worst-case scenario of 85 cm per century. In addition the effects of other human interventions, such as sand and shell extraction, and subsidence due to gas extraction, are taken into account.

Consequences of some likely scenarios of sealevel rise for the tidal flats and channels of the Wadden Sea

The Wadden Sea was created by the rising sealevel. Should this rise slow down or cease in combination with inflow of sediment, the Wadden Sea will silt up. If, on the other hand, the sealevel rises too fast, or too fast in proportion to the inflow of sediment, the tidal flats will become inundated. The future of the Wadden Sea depends on the balance between the supply and the demand of sediment, both of which nowadays are largely under the influence of mankind. On a regional and local scale, the demand for sediment is partly determined by the effects of mineral extraction (gas, sand and shells) and by the size reduction of the basin caused by embankment and reclamation projects.

Table 5.1 shows that under rates of sealevel rise of 60 and 85 cm per century the Wadden Sea system is still able to track sealevel (nearly) without any time lag. Under this assumption the consequences of these rates of sealevel rise for the Dutch Wadden Sea system have been analyzed (Louters and Gerritsen, 1994).

Huge quantities of sediment are transported by the tides between North Sea and Wadden Sea. The flood transports annually about 40-60 million m³ of sand and 100-200 million m³ of silt and clay through the tidal inlets of the Wadden Sea. The ebb carries quantities of the same order of magnitude, but the variance of the data is such that no conclusions can be drawn from the flood and ebb transports about any net transport. It is clear, however, that the quantities transported are much larger than those required to explain sedimentation and/or erosion rates observed in the area.

Table 5.1

Amounts of sediment required annually (in million m³ per year) to compensate for changes in the morphology of the tidal basins of the Dutch Wadden Sea

	Sediment demand (10 ⁶ m ³ per year)		
	1990	2040	2090
- Present rate of sealevel rise (20 cm/100 year)	4-5	4-5	4-5
- Past engineering works	2-3	1-2	1-2
- Extraction of sand and shells	8-9	6	6
- Extraction of natural gas	0.3	1-2	0
- Accretion of salt marshes	0-9	0-9	0-9
- Total sediment requirement at present rate of rise	14-26	12-24	11-22
- Extra required at sealevel rise of 60 cm/100 yrs		4-5	6-7
- Extra required at sealevel rise of 85 cm/100 yrs		6-7	9-10

Louters and Gerritsen (1994) attempt to quantify the amounts of sand needed for the various changes in basin morphology in the Dutch Wadden Sea with use of the empirical model MORRES (Table 5.1).

Effects of engineering works. To restore the disturbed dynamic equilibrium caused by the damming of the Zuiderzee (1932) and Lauwerszee (1969) a long term supply of sand is needed. In the remaining Zuiderzee basin (= the westernmost part of the Wadden Sea) about 100-200 million m³ sediment have been deposited in the past 60 years. Louters and Gerritsen (1994) estimated that the total restoration of the basin morphology will require another 700-900 million m³, of which about 70% will be needed in the first 300 years. Therefore the westernmost part of the Wadden Sea will continue to require 1-2 million m³ annually. The much smaller Lauwerszee basin requires about 50 million m³ of sediment of which about 60% had been deposited up to 1987. It is expected that about 1 million m³ will be deposited annually in the next 30 years. Altogether the compensation required because of past engineering works will demand 2-3 million m³ annually; at a later stage this will become less.

Extraction of sand and shells. Louters and Gerritsen (1994) report that in the period 1960-1990 annually about 8-9 million m³ of sand have been derived from the Wadden Sea. They expect, based on present government policy, that in the future this amount will consist of about 6 million m³ of sand and 0.14 million m³ of shells. About 75% of this will be derived from the Ems estuary by dredging in relation to shipping.

Extraction of gas. Especially in the eastern part of the Dutch Wadden Sea subsidence of the seafloor due to extraction of natural gas will require some 1 million m³ per year for the coming decennia.

Accretion of salt marshes. Natural accretion of salt marshes occurred in the past centuries. Although the exact rates of horizontal accretion are not known, an indication may be derived from the rate of reclamations, since reclamation of salt marshes may be assumed to have kept pace with horizontal accretion of marshes. Hence, in the past the rate of accretion may have been 1.5 km² per year (Dijkema, 1987). This rate will have required a compensatory sand supply to the tidal basin of about 7-9 million m³ annually. Nowadays, however, the salt marshes do not show horizontal accretion any longer; in fact the saltmarsh area has been stable since about 1970. Consequently the sand demand of the Wadden Sea caused by salt marsh accretion may be expected to be much less or even nil nowadays. This situation is dependent on human management of the marshes. For the long term the value of 7-9 million m³ per year may be considered as a ceiling.

Sealevel rise. The present rate of sealevel rise in the Wadden Sea (about 20 cm per century) requires 4-5 million m³ of sand per year for compensation of the depth changes in the tidal basin.

An increased rate of sealevel rise of 60 cm per century will require an additional 6-7 million m³ per year in 2090, and a rate of 85 cm per century will need 9-10 million m³ extra per year.

The rates of sedimentation predicted are much smaller than the amounts of sediment transported. Hence, it is expected that the tidal basins of the Dutch Wadden Sea can keep up with rates of sealevel rise of 60 and 85 cm per century, respectively.

Thus it becomes possible to predict the change in the area of tidal flats in the next 50-100 years. It is concluded that a rate of sealevel rise of 60 cm per century will result in a loss of about 0.5% of the area of tidal flats, provided that the supply of sand remains constant; a rate of 85 cm will result in a loss of about 1%. These insignificant changes are more than compensated by the expected development of new tidal flats in those tidal basins which still are restoring from the effects of engineering works in the past. For the Marsdiep basin a development of new flats of about 30-50 km² is possible (2.5-4% of the Wadden Sea total). However, for the individual tidal basins of the Marsdiep and the Ems-Dollard the total amount of sediment required at rates of sealevel rise of 60 cm and more per century, may come very close to the potential supply.

Evaluation

The study about the effect of accelerated sealevel rise on the flats in tidal basins has a number of aspects which require attention.

In the first place the model MORRES has been based on empirical relationships determined under the present rate of sealevel rise. It can not be verified whether these relationships, such as the assumption of a dynamic equilibrium, will also hold at much higher rates of sealevel rise.

Secondly, the results have been based on the assumption of a sediment supply larger than the sediment demand. Above it was already indicated that this is not necessarily true.

Thirdly, the model operates at the scale of the tidal basin, which makes translation of the result to ecologically meaningful scales difficult.

On the other hand the study provides insight in one of the probably major impacts on the present Wadden Sea system by climate change. Hence, it will be useful to continue the studies on the future development of tidal flat morphology, especially at smaller scales.

5.2 Impact of sealevel rise on erosion, sedimentation and plant dynamics in salt marshes

Salt marshes, saltmarsh works and sealevel rise

Salt marshes are areas covered with terrestrial vegetation under the influence of seawater. In the Wadden Sea these marshes are found at levels above about mean high tide level at neap tides. Originally salt marshes occurred up to the highest level of regular saltwater flooding. This is still the case on parts of the barrier islands, but elsewhere, especially along the mainland coast, salt marshes are bounded by the seawall. Moreover the salt marshes along the larger part of the mainland coast have been created by human intervention through measures stimulating accretion (Figure 5.1). This activity, originally aimed at gaining new land for agriculture, has been abandoned in 1980; nowadays the status quo is maintained for these marshes in order to preserve them as nature reserves.

Hence, the former 'land reclamation works' have been coined now 'saltmarsh works'. The present area of salt marshes, including the saltmarsh works, in the Dutch part of the Wadden Sea is 73 km² (Dijkema et al., 1990).

The vertical growth of the marsh is determined by the rates of minerogenic and organogenic sedimentation, the frequency and period of tidal flooding and the overall compaction of the sediment (Allen, 1990; Craft et al., 1992). The sedimentation rate on the marsh is controlled by the mean tidal amplitude (Stevenson et al., 1986) and is a function of the height of the saltmarsh in relation to mean high water level (Dijkema et al., 1990). For partly or wholly minerogenic marshes the transport of fine sediment to the marsh surface is mainly dominated by the flood tidal currents (Allen, 1990; Postma, 1967). In addition, the sedimentation rate on flats and marshes is high in those areas which are sheltered, frequently overflowed and where the sediment supply is high.

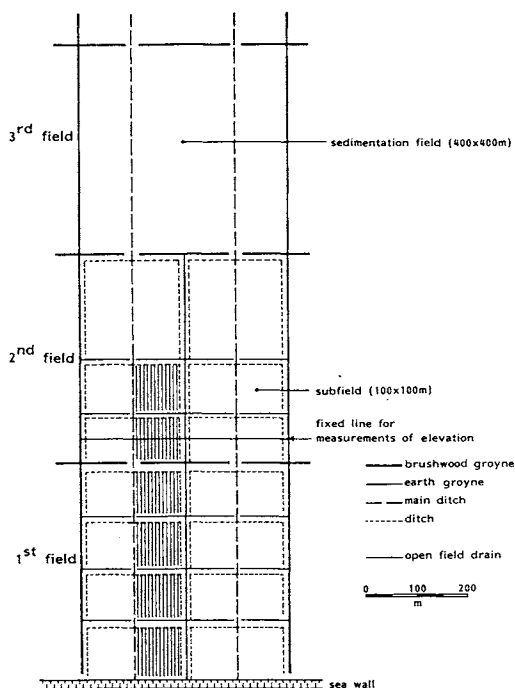


Figure 5.1. Scheme of the saltmarsh works along the mainland coast of the Dutch Wadden Sea. The Wadden Sea is at the top of the figure, the land at the bottom

Wadden Sea salt marshes grow through deposition of sediment which leads to relatively slow (mm's - cm's per year) vertical growth of the marsh and at the same time relatively rapid (dm's - m's per year) horizontal growth at the seaward edge. Wadden Sea salt marshes decrease through erosion, vertically all over the marsh as well as horizontally, often in the form of cliffs, mainly at the seaward side. An horizontally eroding marsh can be growing vertically at the same time. On the marsh the balance between sedimentation and erosion is usually positive. The balance between erosion and accretion at the seaward edge of the marsh, where pioneer vegetation establishes itself during accretion, but where the same vegetation is destroyed during erosion, is much more unstable. This seaward edge or pioneer zone, apparently is the most vulnerable zone of the marsh.

Most salt marshes along the mainland coast have a static boundary at the landward side in the form of a huge seawall; the seaward boundary of many Wadden Sea marshes is fixed by means of the construction of brushwood groynes. Because of the seawall the marshes cannot shift their position landward during an increase in sealevel rise. Their only way to survive is to heighthen up the bed level and so keep pace with the increase in sealevel. It depends on the outcome of the change in processes and sediment transport on and towards the salt marshes, if these marshes eventually will submerge or keep pace with an increase in sealevel rise.

Since the salt marshes in the Netherlands Wadden Sea are a result of the dynamic equilibrium between the sedimentation and the erosion processes, changes in the

hydrodynamic parameters which might be changed by sealevel rise and climate change, like tidal amplitude, mean high water and wave height distribution, are expected to change the sediment transport pattern in the Wadden Sea and the net result of the processes on the salt marshes.

In order to predict the effect of sealevel rise on saltmarsh development, the hydrodynamics and the sedimentation and erosion processes have been studied during NRP I at three locations in the saltmarsh works along the mainland coast. At the same places the adaptation of the vegetation cover to changes in the hydrodynamic parameters has been investigated.

Historical development of Wadden Sea salt marshes

In the mediaeval Wadden Sea large areas of salt marshes occurred. Human impact was negligible and probably consisted mainly of building artificial mounds for building houses and of grazing cattle. Embankment of marshes probably started in the 10th century and by 1300 large areas had been surrounded by dikes. After this time saltmarsh reclamation continued and more or less kept pace with the accretion of new marshes (Dijkema, 1987). On average about 1.5 km² of marsh was reclaimed annually.

From the 17th century onwards man started to build sand dikes on the barrier islands. In the lee of the dune-like constructions new salt marshes developed. Some of these areas have been reclaimed since, but on several areas large areas of saltmarsh still occur.

Along the mainland coast reclamations gradually overtook the natural accretion. One reaction of the coastal population was to stimulate drainage by digging ditches. Thus the marsh area was better drained which enabled the establishment and development of vegetation which again stimulated accretion and growth of the marsh. Subsequently the new marshes could be embanked.

From 1930 onwards, brushwood groynes have been build along the mainland coast of the Dutch Wadden Sea to stimulate accretion even more. The construction of the brushwood groynes significantly increased the rate of sedimentation in the areas in between (Dijkema et al., 1988, 1990). Digging of ditches occurred already before 1930. Through the combination of brushwood groynes and ditches the marsh area expanded seaward with 8.2 m yr⁻¹ for the Friesland coastal area and 4.7 m yr⁻¹ for the Groningen area during the period 1960-1985 (Bakker et al., 1993).

The sedimentation rate and seaward expansion of the saltmarsh was higher during the first years of the construction of the brushwood groynes (1960-1978). Later saltmarsh expansion arrested and erosion occurred from 1978 to present.

In 1980 the Netherlands government decided that the existing salt marshes would not be embanked and instead managed as nature reserves. The saltmarsh works had to be aimed at maintaining the status quo. Since, hardly any further accretion of the marshes has occurred. Partly this can be ascribed to a reduction of the management effort, but other factors have to play a part as well.

Van Malde (1992) found for different gauge stations in the Netherlands part of the Wadden Sea an increase in mean sealevel, according to the trend line computed for the period from 1900 till 1960, of about 0.18 cm yr⁻¹. Recent years have shown an accelerated increase in mean high water level of 0.44 cm yr⁻¹ from 1961 to 1983

(Dijkema et al., 1990). It has been suggested that this recent rapid rise of mean high-tide level could be responsible for the present standstill of the marsh growth thus illustrating the vulnerability of the marsh for increased rates of sealevel rise (Bossinade et al., 1993).

The present management of the man-made marshes or saltmarsh works along the mainland aims in the first place at a reduction of turbulence on and in front of the salt marshes. This is done by the construction of the brushwood groyne. The result is twofold: reduction of the near-bed turbulence leads to less erosion of the bed and it leads to possible increase in sedimentation of mud in and in front of the marsh zone.

Secondly, management of the marsh area aims at protection and improvement of the cover of the vegetation. This results partly from the construction of the groyne: protection of the vegetation against waves and currents, and partly from digging ditches. This ensures a good drainage of the bed which reduces sediment mobility and improves the growth of the vegetation (Reed and Cahoon, 1992).

Transport of sediment and sedimentation

The sediment dynamics on and in front of the salt-marshes are determined by the tidal current and the waves. Waves determine the amount of (re)suspended matter and currents will transport the sediment in suspension. The sedimentation on the salt marshes is dependent on the near-bed turbulence and the grain-size distribution of the transported sediment.

Suspended sediment concentrations have been measured during the NRP I study simultaneously with hydrodynamic measurements. The suspended sediment consists of the mud fraction (<50 μm) only. It is concluded that mud is transported as suspended load throughout the entire water column. Sand, on the contrary, is resuspended by wave action and transported close to the bed as bed load.

The data show a decline in the sediment concentration from flood towards ebb. Thus it seems that suspended sediment is transported into marsh area. However, the amount of transported sediment is a function of the concentration times the current velocity and the net transport is also dependent on the current direction. It is to be expected that the vegetated parts will show less turbulence in the near-bed water column and most sediment will be deposited here.

Advective transport of suspended sediment into the saltmarsh works has been found during moderate weather conditions as well as just before storms and shortly after a storm period. During storm conditions sediment in the saltmarsh works is resuspended by wave action and transported from the marsh by the strong currents. In this case, the brushwood groyne prevent the loss of large quantities of sand out of the sedimentation fields.

These data confirm the earlier results of Dankers et al. (1984) and Asjes et al. (1992) who found a net transport of sediment to Wadden Sea salt marshes on an annual basis. These authors also report that transport towards the marsh occurs during quiet weather, whereas seaward transport may occur during storms.

Net sedimentation rates have been reported by Dijkema et al. (1990). They vary in time and space and range from about - 1 cm per year to + 3 cm per year. Most marshes show positive vertical accretion rates.

Erosion

A recent loss in saltmarsh area in the Wadden Sea might be due to an accelerated increase in mean high water level of 0.44 cm yr⁻¹ from 1961 to 1983 (Dijkema et al., 1990), of which between 1976 and 1983 about 75% is calculated to be due to an increase in average windspeed (Bossinade et al., 1993).

During the NRP I study much attention has been given to erosion processes.

It is concluded from field measurements that the tidal current velocity perpendicular to the shore during moderate (summer) weather conditions never exceeds 10 cm per second inside the brushwood groynes. During storm conditions the waterdepth increases significantly due to wind set up and the current velocity can reach up to 20 cm per second. The ebb current is stronger than the flood current. The alongshore tidal current velocity is extremely low during moderate (summer) conditions. However, wind induced alongshore current velocities can range up to 40 cm per second (as much as 10 times the tidal current component).

Wind waves grow during an increase in windspeed and fetch length. It is concluded that the waterdepth is the limiting factor for wind induced wave growth at the marsh sites. The construction of brushwood groynes, in this situation, does not have any effect on wind wave growth at the measurement location some 200 meter distance from the groynes. This conclusion is confirmed by model calculations showing that the growth of wind waves is completed within 30 meters distance from the groynes (Elfrink and Houwing, in prep).

A new in-situ erosion meter has been developed to measure the in-situ bed-shear strength of cohesive beds. This in-situ erosion flume (ISEF) is a circulating flow system in the vertical plane. The bottom part of the horizontal test-section is open over a length of 0.9 meter. Current velocity and sediment concentration sensors are fixed in the flume. The shear stress, exerted on the bed by the unidirectional current in the ISEF, causes an erosion of the bed. This erosion is measured by the concentration sensor. It is assumed that the current velocity, at initiation of motion of the top layer of the bed, can be used to compute the critical bed-shear stress. This critical shear stress is assumed to be the characteristic parameter which defines the different types of sediment beds.

The results from the ISEF measurements show only small differences in the erosion resistance of the bed within the saltmarsh works. This means that, theoretically, the bed strength does not differ spatially within the fields and erosion of the bed will start, if the shear-stress is high enough, simultaneously at different places. However, visual observations at low tide show that erosion of the bed is very local. It starts at specific locations only, for instance where the structure of the bed is disturbed by bioturbation. These small-scale erosion patterns can generate larger scale erosion forms.

Vegetation and climate change

Sea-level rise could become a threat to coastal marshes by affecting the marsh vegetation through an increase of the frequency of tidal flooding and wave energy. If the accretion of sediment on the marsh is less than the increase in sea-level, the marsh will be flooded more frequently and vegetation deterioration will increase (Reed and Cahoon, 1992). Similarly, erosion of the marsh will also result in a loss of vegetation and subsequently in a loss of saltmarsh area.

Salicornia dolichostachya is the most important pioneer species found in the foreland salt marshes of the Wadden Sea. The first important and perhaps most critical phase in the life cycle of *Salicornia* is the germination and survival of the

seedlings (Ungar, 1978). It determines, in combination with growth, the plant density at the end of the growing season and biomass of the fully grown *Salicornia* population. The second important phase in the life cycle is the seed production. If the amount of seeds remaining in the pioneer zone after the winter is too low, the size of the *Salicornia* population will decline which might have a great influence on the development of the saltmarsh as a whole.

Although *S. dolichostachya* is able to reduce wave energy and thus create suitable circumstances for sediment to settle, this annual species is not able to fix mud and therefore does not seem to be of great value for accretion on salt marshes. However, *Salicornia* fulfils an important role in the spreading and seaward expanding of *Puccinellia maritima*. This very important species for silting up is spread mainly by vegetative parts torn from the parent plant. Part of these tillers get caught behind living, or in winter dead, *Salicornia* plants and can establish themselves especially on the higher parts of the pioneer zone (Kamps, 1962).

Hence, the presence of *Salicornia* in the pioneer zone is very important for the expansion of salt marshes. The size of the glasswort dominated pioneer zone might be an indication of the quality of the saltmarsh. Therefore, more information has been collected about the life cycle and boundary conditions for establishment of this species.

Like Jeffries et al. (1981) no seed bank was found in October before seedfall. Like Beeftink (1985) found for *Salicornia procumbens*, the population of *Salicornia dolichostachya* is thinned especially during the seed phase in winter time (99% of the produced seeds was removed from the pioneer zone) and during the growth from established seedlings to fully grown plants (65 % of the seedlings did not survive). Nevertheless, on both sites the development of the *Salicornia* population does not seem to be limited by a lack of seeds.

In contrast to Joenje (1978), it was found in this study that seeds do not act as in water suspended sediment, but are transported as bed load like sand grains (60-72 μ). Finally, many seeds will end up in creeks bottoms where they cannot germinate because of lack of oxygen and a high salt concentration.

Evaluation

At the time of writing of this assessment report the saltmarsh study was not yet completed. Especially the relationships between the different parts of the study had not yet been sufficiently developed.

Nevertheless the study makes clear that saltmarsh erosion is a complicated process and that further research is required on this subject.

The saltmarsh study under NRP I considered processes at the scale of the m². This makes comparison with the results of the other studies a difficult task. A very detailed in-depth study of some important processes in the saltmarsh, necessarily leads to a lack of overview. On the basis of the results it is not yet possible to make predictions about the impact of sealevel rise on the entire saltmarsh area of the Dutch Wadden Sea.

On the other hand some conclusions on the effectivity of the brushwood groynes in stimulating saltmarsh accretion emerged. These conclusions may be incorporated in the management plans for these areas.

As a preliminary conclusion from the NRP I study emerges that Wadden Sea salt marshes may survive an increased rate of sealevel rise if erosion processes can be

controlled. Sediment supply and accretion rates seem to be sufficient for higher rates of increase of sealevel than at present.

This conclusion is in line with a recent study (Oost and Dijkema, 1993) on the possible effects of soil subsidence due to gas extraction on Wadden Sea salt marshes. They concluded that the salt marshes at the barrier islands could accommodate a soil subsidence (= equivalent to a sealevel rise) of 0.5 cm per year (= 50 cm per century), whereas the mainland marshes could survive a rate of 1.0 cm per year. However, they drew attention to the vulnerability of the pioneer zone of the marshes with respect to erosion processes.

The conclusions reached above might be tested by the large-scale field study of the effects of soil subsidence due to extraction of natural gas (see Table 1.1). This 'experiment' gives information on the behaviour of several km² of salt marshes in a 'simulated' rapid rise of sealevel. Unfortunately the results of this study have not yet been completely analyzed.

5.3 Impact of sealevel rise on benthic animals of tidal flats

Results of a literature study

Louters and Gerritsen (1994) report the results of a literature study on the impact of sealevel rise on benthic animals of tidal flats. They conclude that most of the tidal flat species are characterized by a broad ecological amplitude with regard to salinity, water movements, sediment characteristics, and period of emergence of the tidal flats. Hence, they conclude that sealevel rise as such will not have an important ecological effect on tidal flat organisms as long as the present area of tidal flats does not change very much.

Fragmentation of large tidal flat areas because of sealevel rise might result in a situation with more smaller tidal flats, each with an low-tide edge relatively poor in benthic animals. This might have consequences for the food supply for birds and fish.

Evaluation

This literature study lacks experimental verification, but there is little to indicate that experiments on the effects of higher water levels would result in other conclusions for the individual species. Also the study did not address the impact of sealevel rise on new species which might colonize the Wadden Sea because of higher temperatures.

5.4 Impact of sealevel rise on shorebirds

Defining the problem of sealevel rise for shorebirds

Along coasts many bird species can be seen feeding on the tidal flats. In the Dutch Wadden Sea this includes 15-20 abundant species from different taxonomic groups: geese, ducks, waders, and gulls. The various species breed in an area ranging from N.E. Canada through Greenland, Iceland, Spitsbergen, and Europe to northern Russia and Siberia. After the breeding season these birds migrate to the Wadden Sea either to stay there all winter or to remain there for a shorter period to feed and to moult, after which the birds fly on to wintering areas further South, e.g. in western Africa. Next spring these populations return to the breeding areas, often after another stopover in the Wadden Sea.

During their life cycle these shorebirds are dependent on two very different habitats. They breed in terrestrial environments which differ according to the species concerned. Some species breed in salt marshes or dune areas, other in agricultural landscapes, still others in heathlands or forests, and several species have their breeding habitat in the Arctic tundra. At first sight it seems that many, if not all species occupy huge areas as breeding ranges. Outside the breeding season, however, all these birds concentrate in a rather small number of tidal flat areas where most of them feed on benthic animals such as shellfish and worms, and some graze algae and seagrasses. The total area of tidal flats along the flyway these bird populations use is small, only about 7,000 km² of which about 50% are situated in the Wadden Sea. Hence, it has been suggested that the numbers of these birds are primarily governed by competition for food present in their tidal flat habitat in winter. If so, disappearance of tidal flats due to sealevel rise could have a very large effect on these bird populations. When density-dependent processes operate on both the wintering grounds and the breeding grounds of shorebird populations a reduction of either habitat will lead to a decrease in population size (Fretwell, 1972; Goss-Custard, 1980). This implies that when sealevel rise will cause a change in the area of tidal flats available as feeding grounds, population size of shorebirds may be changing too. Furthermore, many species of shorebirds are concentrated in only a few widely separated estuaries during winter and migration. It is thought that this makes these species especially vulnerable to habitat loss, as this distribution pattern breaks the normal link between the abundance of a species and its immunity to extinction (Myers et al., 1987; Davidson and Piersma, 1992).

Among the bird species dependent on tidal flats limicoles or waders keep a prominent position. Most wader species breed in arctic or subarctic environments and spend the time outside the breeding season on tidal flats south of their breeding areas. There are several indications that competition in the winterquarters does occur. Several species exhibit leapfrog migration, whereby more northerly breeding populations winter south of more southerly breeding populations, which is generally attributed to the avoidance of competition (Greenberg, 1986). There is also direct evidence for both competition for food on the wintering grounds, through interference and prey depletion, and for competition for territorial space on the breeding grounds (Goss-Custard, 1986).

Several studies exist that report on the effects of loss of tidal flats due to human interventions. Evans (1978) reports that following a reclamation of 60 % of the intertidal flats of the Tees estuary in north-east England, the wintering numbers of the majority of wader species decreased by a similar percentage or more in the year following the reclamation. Similar results are reported for reclamation of intertidal areas of the Forth estuary in eastern Scotland (McLusky et al., 1992). The construction of a dam across the entrance of the Grevelingen estuary in The Netherlands ended tidal movements in the estuary and resulted in complete disappearance of the tidal flats. Consequently, nearly all waders disappeared from the area (Wolff et al., 1975); for at least two species it could be proven that numbers in the nearby Oosterschelde estuary had increased at the same time (Van Latesteijn and Lambeck, 1986; Lambeck et al., 1989).

The former studies show that local occurrence of waders is influenced by loss of tidal flats, but they do not show any population effects. Meire (1991), however,

reports that after a 30% decrease of intertidal area in the same Oosterschelde estuary due to the building of a storm-surge barrier and secondary dams about 15 years later, the total number of Oystercatchers in the unaffected parts of the estuary did not increase. Moreover, a temporary reduction of the tidal range in the estuary caused by partly closure of the storm-surge barrier in combination with extensive fisheries for shellfish, led to strongly increased mortality of oystercatchers in winter. In the face of the strong fidelity of adult waders to their wintering grounds (Myers, 1984) it is actually surprising that the wintering numbers so often quickly readjusted to a reduction in feeding area. Thus, the results of the 'field experiments' corroborate the expectations derived from the studies on competition that reduction of tidal flat habitat will lead to reduction of wader population size.

Because bird populations are subject to processes both in the breeding areas and in the winter quarters it is hard to predict the effect of sealevel rise on wader populations. Moreover, the various species and populations normally use several estuaries along their flyway during the non-breeding period and will be influenced by changes in all of these estuaries.

There is no shortage of speculations on the possible consequences of climate change. Although not all possible effects are considered, -apparently nobody seriously suspects an effect of increased levels of UV-B on migratory birds for instance-, the diversity of hypotheses is nonetheless bewildering. Therefore, instead of formulating complex scenarios we must seek to answer a set of interrelated precise questions. At least three questions can be distinguished:

- Which aspects of the climate change or secondary effects will have the greatest impact: global warming, storms, rainfall patterns, sealevel rise?
- At what stage of the life cycle of the birds does the climate change or climate-induced effect operate: breeding season, autumn migration, spring migration, nonbreeding season?
- Which processes must be considered: vagaries during the migratory flight, interspecific competition between resident and non-resident species, intraspecific competition on the breeding grounds, intraspecific competition on the wintering grounds, phenology of the food supply, evolution of the migration schedule?

Second, a formal structure must be devised that will allow us to find an answer to these questions. This formal structure includes mathematical models and a methodology to assess important parameter values.

Hence, it was decided to study the effect of sealevel rise by building mathematical models of the population dynamics and the migratory behaviour of two well-studied species: the Oystercatcher *Haematopus ostralegus* and the Knot *Calidris canutus*. The Oystercatcher serves as a model for a short-distance migrant, whereas the Knot is a clear example of a long-distance migrant. In the short-distance migrant the migratory phase itself is insignificant in time, and attention focusses on how processes on the wintering and breeding grounds affect the population. In contrast, the long-distance migrant spends a significant amount of time preparing for migration and the model specifically focusses on this part of the annual cycle. The next step is to use the models to investigate the consequences of various climate scenarios.

Model development

The basic idea of the model is that both the rate of reproduction in summer and the rate of mortality during winter are dependent on the number of individuals in the population, i.e. the population density.

The primary source of density-dependence in summer is assumed to result from territorial exclusion, i.e. relatively fewer birds breed when the density of potential breeding birds increases. The proportion excluded is expressed as a k -value:

$$k = a_T + b_T \log_{10} N$$

where N is the number of potential breeding birds and the slope b_T measures the compressibility of the territories. When $b_T = 1$, the territories cannot be compressed any further so that, above the numbers set by the intercept a_T , a constant number of pairs breed, irrespective of the numbers attempting to do so. Thus, $b_T = 0$ implies no density dependence and $b_T = 1$ implies perfect 'contest' density dependence. It is not allowed that $b_T < 0$.

The primary source of density dependence in winter is decreased survival chances due to competition for food. At low densities, there is no competition, but only a density-independent proportion (m_w) starving. When bird density increases, eventually a point, c_w , is reached at which mortality begins to increase and so becomes density-dependent. From then on, mortality increases by b_w for every unit increase in bird density.

For the Oystercatcher four sub-populations have been distinguished: Continental coastal, Continental inland, Atlantic coastal, and Atlantic inland. The parameters defined above have been estimated for each sub-population and, where necessary, age class. Furthermore the size is known of each of the four sub-populations. Within the Continental and Atlantic regions, inland-breeding and coastal-breeding sub-populations use the same coastal areas in winter. Finally, the sometimes quite substantial annual fluctuations in the main production and mortality parameters were generally not correlated across sites within a sub-population. This allows the standard deviations of the annual variations in these parameters to be estimated for both sub-populations in each region, so that realistic annual variations could also be included in the model. More details are to be found in Goss-Custard et al. (1994).

During their migratory journeys, birds may cover distances of up to several thousand kilometers in a non-stop flight. The migration of many species, especially waders, consists of a series of such non-stop flights interrupted by stopovers at tidal flat areas during which large quantities of fat are deposited. This fat serves as fuel for the next leg of the journey. It seems likely that waders migrating between their widely separated wintering and breeding grounds can choose among a number of potential stopover sites using different itineraries. However, the factors determining stopover site choice and departure fuel loads from the stopover sites are not well understood.

It has been argued that waders sometimes store more fat than is necessary to fuel the flight to the next site, a phenomenon known as overloading, and that suitable sites are skipped. When only energetic flight costs are considered neither the

skipping of potential sites should occur nor overloads be deposited, because flight costs increase rapidly with increasing body mass. Using the equations of Alerstam and Lindström (1990) and Weber et al. (1994) developed optimality models of departure fat loads and stopover site use with time spent migrating as the currency to be minimised. Under this assumption the only cost is the reduction of marginal rate of gain of flight range with increasing body mass. The models identify conditions under which potential stopover sites are skipped or overloads occur. In these models the conditions leading to a storage of overloads are very restrictive but skipping can occur over a wide range of parameters.

However, several potentially important factors shaping migration schedules and fuel loads cannot be addressed using the aforementioned models. These factors are:

1. At stopover sites or on the wintering grounds birds may face a trade-off between gaining energy for fat deposition and avoiding predation. Predation risk is likely to be influenced by several factors, including flock size, high body mass impairing flight kinematics and consequently the escape response when attacked and the time exposed to predation risk while foraging.
2. Time of arrival in the breeding area and the subsequent timing of the breeding attempt have a strong effect on breeding success. Furthermore, extra body stores at arrival may guard against adverse conditions or pay some of the costs of producing eggs. The rewards associated with time of arrival must not necessarily be always decreasing with later arrival; arriving on the breeding grounds too early could also be disadvantageous, for instance due to snow cover.
3. Foraging at a stopover site and departure decisions are also likely to be influenced by stochasticity of the environment, including the social environment. Stochasticity in food supply and abiotic conditions, like temperature and wind speed and direction affect energy intake and energy expenditure and may therefore lead to unpredictable daily fat deposition rates or even to the risk of starvation. Unpredictable wind conditions during flight may cause uncertainty in expenditure when flying from one stopover site to the next.

The model describes the behavioural decisions of a bird having to migrate from its breeding grounds to its wintering grounds, or vice versa. It is assumed that decisions are made in such a way that fitness upon arrival at the destination is maximised. Fitness expectations upon arrival may depend on both the state of the individual and the time of arrival. Fitness is defined as the life-time contribution of the individual to the next generation.

The environment the bird has to migrate through consists of N sites, i.e. the initial site (e.g. the wintering ground), $N-2$ discrete stopover sites and the final site (e.g. the breeding ground). For simplicity, it is assumed that these sites are arranged linearly, so that the distances between the sites are additive. The complete migration period is divided into T time units; one time unit corresponds to one day. The state of a bird is characterised by its reserve level and its location. Location is referred to as a state variable, because it is affected by the decisions of the bird. The reserve level can take any integer value from 0 up to a maximum reserve level. If the reserves fall to 0 it is assumed that the birds immediately die of starvation.

At the start of each time unit the bird must decide on the best possible course of action, given its location and reserves. It can either decide to stay in the site and feed, or to fly to another site in the direction of the final destination. If it decides to feed, it also has to decide on its foraging intensity u , which can take any value between 0 and 1. When feeding there is also a risk of predation. This risk can be influenced by two variables: the mass of the individual, which is a linear function of reserves, and the foraging intensity u . If the bird decides to depart it must decide on the site where it will land. It is assumed that no mortality occurs during flight, while flight costs are modelled according to the equations of Alerstam and Lindström (1990). Expenditure during flight can be stochastic due to influence of unpredictable wind conditions.

To find the optimal behaviour, the method of dynamic programming (Mangel and Clark 1988) has been applied. For each combination of reserves, site and time, the optimal decision and expected future success is found using backward iteration. Forward iteration then allows to simulate the fate of individual birds, as well as to find population means and standard deviations.

To investigate the effects of habitat change, e.g. because of sealevel rise, a simple situation is considered where the fitness consequences of changes in the environment are determined. These changes could take place at two different time scales: if changes are slow the migrating birds are allowed to adjust their behaviour to the new circumstances, i.e. the birds behave optimally in an environment that deteriorated as compared to an earlier reference situation. Alternatively changes could happen much faster and the birds do not have the chance to adjust their behaviour to the new environment. Birds then use the behaviour which was optimal under better circumstances, i.e. their migratory behaviour is now suboptimal in the new environment. In both scenarios fitness can be affected in several ways: either by changes in mortality en route or by delayed arrival at the breeding site. The birds can also be forced to stay at an intermediate site. Evans et al. (1992) discuss the consequences habitat loss at staging posts can have for migratory waders. Habitat loss is modelled by decreasing the maximum fuel deposition the birds can achieve at a site.

Depending on the situation envisaged habitat change can have different consequences. If the birds can adjust their behaviour to the new conditions habitat destruction at the wintering grounds are most severe. If the birds use a suboptimal policy fitness losses are more pronounced the closer the affected site is to the breeding site. Fitness losses are also more severe when the reward at the breeding site is decreasing over the whole time interval under consideration.

The results show clearly that predation is a potentially important factor shaping migratory strategies. The rates of mass gain are also strongly influenced by predation risk.

Overloads are deposited when the environment is stochastic. Uncertainty in expenditure leads to a level of overloads which are able to deal with the worst possible case of headwinds independent of its probability of occurrence, because if such a situation arises death is certain. The model does not allow to make departure decisions like fuel load and the choice of the target site to depend directly on a particular wind condition; this would make the inclusion of another state variable necessary. Intraspecific differences in site use between years may thus be a consequence of unpredictable meteorological circumstances.

Results of model calculations

Since the final model calculations will be carried out after this assessment report has been finished, only some examples of calculations will be given. Figure 5.2 gives the results of model calculations for the N.W. European population of the Oystercatcher. Four subpopulations are distinguished: coastal breeders of the British Isles and those of the continent, and inland breeders of the British Isles and of the continent. The simulations show that most populations decrease with reduction of their wintering area, but that the size of the reduction is strongly dependent. Especially the density dependence of winter mortality (bW) is a very important parameter.

Fig. 4 gives the results of calculations with the dynamic version of the migration model. Loss of tidal flats has been modelled as decrease of fattening rates. In the top panel it has been assumed that habitat loss is a slow process and that the bird populations can adapt. In the bottom panel habitat loss is rapid and the populations cannot adapt. The simulations show that under the former scenario only changes in the wintering area have an important effect. The latter scenario shows that changes in any site have an effect, although the most severe effect result from changes in the last stopover area before the breeding area is reached. Hence, also for the long-distance migrants habitat loss appears to have negative consequences for population size.

The determination of the area of suitable habitat

The bird study started under the assumption that the area of suitable habitat after a rise of sealevel could be predicted from the present topography of tidal flat areas. The basic idea was that future tidal flat areas could be derived from the height distribution of the present flats, because by higher sealevels lower areas would be drowned. This scenario could be elaborated with the data available.

However, the studies on the morphology of the Wadden Sea (Sections 5.1 and 5.2) have shown that tidal flats and salt marshes are able to accommodate an increased rate of sealevel rise. For the most likely scenarios even no important change in tidal flat area is predicted for the first 100 years. On the other hand the quality of the tidal flats as a feeding area for shorebirds might change with sealevel rise.

Hence, predictions on the area of tidal flats available as feeding areas along the flyways have become very difficult. For the Wadden Sea this is possible, but not for the other areas.

Evaluation

The model of the short-distance migrant, even though it was tied to the Oystercatcher, can easily be applied to other species when relevant parameters are known. Habitat loss due to sealevel rise is predicted to be small (see 5.1), hence effects on wader populations are predicted to be small too, even though the exact magnitude of the effect is hard to predict for such small changes. Other effects are likely to be more important, like shell-fisheries and temperature effects on dynamics of the prey (see Section 6). The current model cannot cope with these effects.

The model of the long-distance migrant, even though the model was constructed with the Knot in mind, is couched in sufficiently general terms, to be applied to other species for which the relevant parameters are known. The model can be incorporated as a migration module for the population dynamics model (i.e. the model for the short-distance migrant), but this was not done, since nothing is

currently known on density-dependent processes on wintering and breeding grounds in the case of Knots. If it is known how habitat loss will affect fattening rates on the stopover sites, the present model can predict the effect on survival rate and reproductive success. The prediction depends on the time scale: if sufficient time has elapsed for adaptation to the new circumstances, habitat loss on the first stopover site on spring migration will have the most serious consequences, otherwise, habitat loss on the last stopover site will have the most serious consequences

During the study it became clear that two basic assumptions were not valid. In a earlier section was already discussed that tidal flat areas do not simply drown during sealevel rise, but that they may be expected to restructure or even to keep pace with moderate levels of sealevel rise. Secondly the developments in the breeding areas cannot be left out of consideration. Especially the Arctic breeding species will face huge changes in their breeding quarters in the case of climate change. These changes should be taken into account if meaningful conclusions are to be drawn about the future of our wader populations.

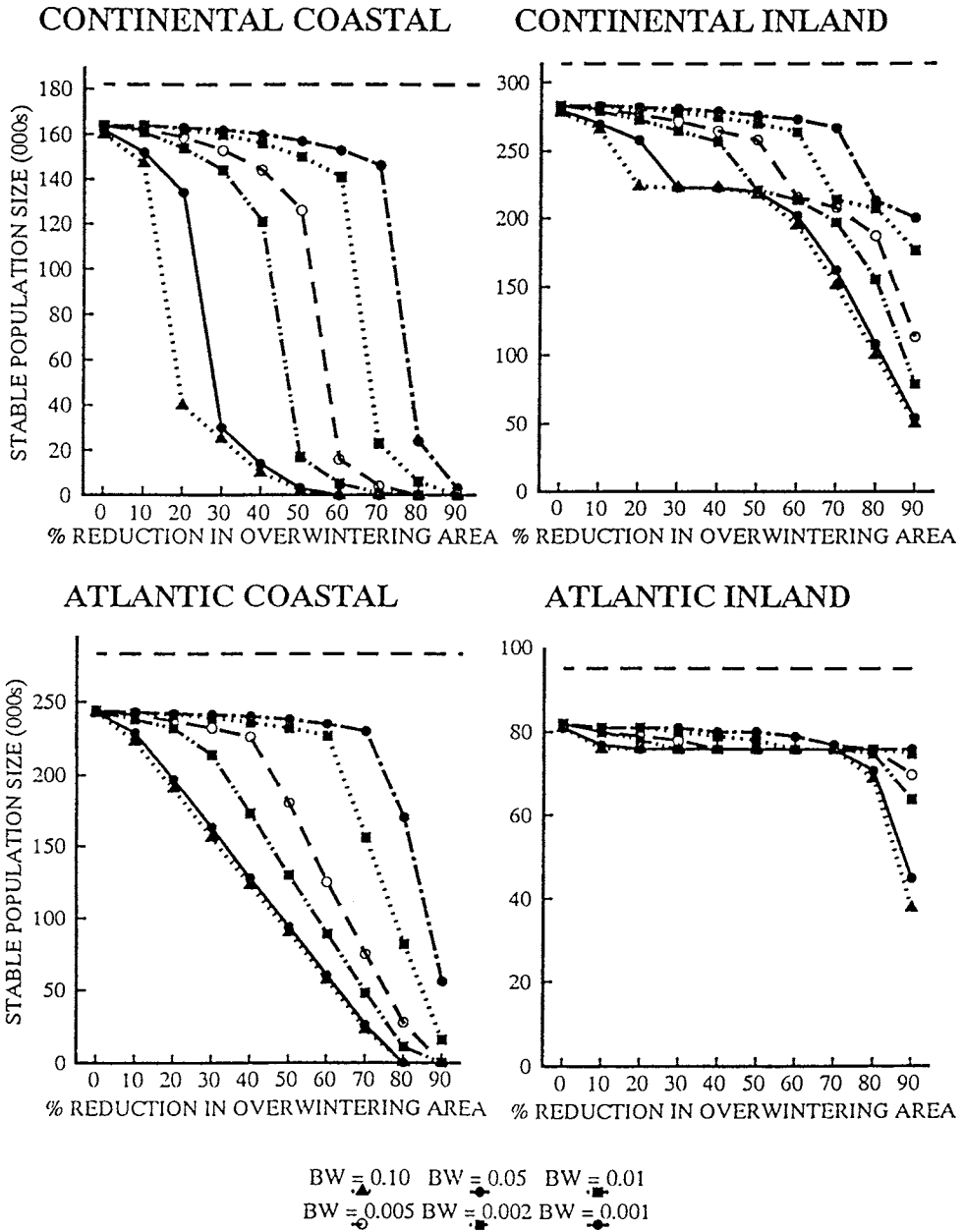


Figure 5.2
 Size of the equilibrium population for four subpopulations of the Oystercatcher as a function of habitat loss at different intensities of density-dependent winter mortality (bW)

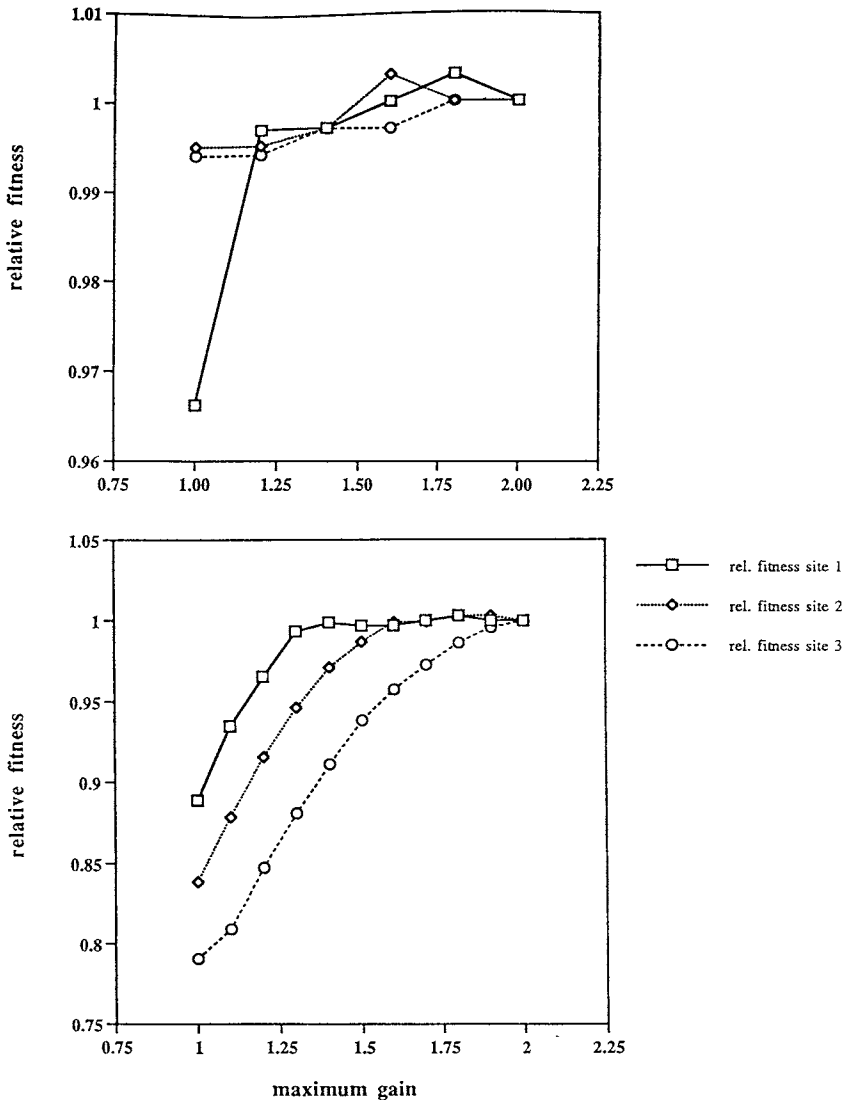


Figure 5.3

The effect of habitat loss (expressed as maximum possible gain of body fat load) on production of young (expressed as relative fitness) by a long-distance migrant. Site 1 is the wintering area, 2 and 3 are stopover sites (3 is the last site before the breeding area is reached). In the simulation one site has been changed whereas the other ones remained the same. In the top panel it has been assumed that changes occurred slowly (e.g. sealevel rise) and that the bird population was able to adapt. In the bottom panel the change occurred quickly (e.g. reclamation) so that the bird population could not adapt

6. IMPACT OF CHANGING WATER TEMPERATURES

6.1 The effects of winter temperature on the reproductive success on some bivalves in the Dutch Wadden Sea

Since 1969 the numbers and biomass of several species of benthic invertebrates are monitored on tidal flats in the westernmost part of the Wadden Sea (Balgzand). The common mussel (*Mytilus edulis*), the Baltic tellin (*Macoma balthica*) and the cockle (*Cerastoderma edule*) are among the most important species. These three species account for a high proportion of the total biomass. Their lifecycle starts with eggs from which planktonic larvae hatch. These larvae spend a period in the water column after which they settle on the tidal flats. The young individuals which thus recruit to the parent population often settle first in a habitat different from that of their parents. At a later stage they move again to settle finally in the habitat of their parents.

Winter temperature appears to be a factor diminishing recruitment. The data series of the Netherlands Institute for Sea Research (NIOZ) show that after mild winters with a mean water temperature in the period January-March of about 6 °C, the recruitment was lower than after cold winters with a mean water temperature of about 1 °C. This results in high recruitment and abundance after cold winters, but relatively low abundance after mild winters, and particularly after a series of mild winters.

Two hypotheses may be formulated to account for this diminished recruitment. The first hypothesis assumes predation of just-settled larvae of these bivalves by brown shrimps (*Crangon crangon*) and shorecrabs (*Carcinus maenas*) resulting in a diminished recruitment. During a cold winter a large proportion of the predators die, whereas they do not in mild winters. This means that after a mild winter the predators arrive early and they are already on the tidal flats at the moment the larvae of the bivalves settle, resulting in heavy mortality of these newly settled larvae. After a cold winter the larvae are ahead of the predators and have grown to a less vulnerable size at the time the predators appear.

The second hypothesis states that the metabolic rate of adult bivalves is on a higher level at higher water temperatures in winter. Since food is scarce in this period, this goes at the expense of stored reserves. As a consequence less energy is available for gametogenesis. As a result the eggs could be smaller, or the number of eggs could be lower, or both.

The first hypothesis is studied by Beukema at NIOZ. This study is dependent on field observations after mild and cold winters and is necessarily long-term. The NRP-I-period has been too short to come up with meaningful results.

The second hypothesis has been studied, mainly experimentally, during NRP I. Four questions have been asked:

1. Are there differences in gonadal development at different winter temperatures?
2. Are eggs after a mild winter smaller than after a cold winter?
3. Is the amount of eggs dependent on the winter temperature?
4. Is the survival of the larvae different at different winter temperatures?

6.2 Experimental tests of the effects of winter temperature on reproductive success of bivalves

So far successful experiments have only been carried out with *Macoma balthica* and *Cerastoderma edule*. Three groups of *Macoma* have been kept in an experimental set-up during the winter months of 1993. One group was kept at ambient temperatures, the second at temperatures about 2 °C higher, and the third group at temperatures 2 °C lower. The first experiment was not completely successful due to the development of an early plankton bloom in the basins, but it nevertheless demonstrated a significant correlation between condition of the animals (expressed as μg ash-free dry weight / (mm shell length)³) and egg size in μm .

A second group of experiments was run in the winter of 1994. Two temperatures were used: cold (3.0 °C) and mild (5.6 °C) in combination with two periods of submergence: continuous (24 h per day) and periodically (16 h per day). The length of the period of submergence determines the possibilities for food consumption in the experimental set-up. Longer submergence should mean more food and a higher condition index.

Indeed, the condition index of the group permanently submerged was higher than that of the group submerged for 16 h a day (Table 6.1). In accordance with the hypothesis formulated the condition index of the cold winter groups was higher than that of the mild winter groups (Table 6.1). Also the number of eggs varied in accordance with the hypothesis (Table 6.1). The same experiment was run for *Cerastoderma edule* with similar results (Table 6.1).

Table 6.1

Condition index (mg ash-free dry weight cm^{-3}), mean egg number, and mean egg size (μ) of *Macoma balthica* and *Cerastoderma edule* after a winter and spring at cold and mild water temperatures. Part of the animals lived permanently submerged (sub), whereas the other group was submerged for 16 h and dry for the remaining 8 h per day (int)

	Condition index	egg number	egg size
<i>Cerastoderma edule</i>			
cold/int	8.7 ± 0.1	214,892	78.2 ± 0.3
cold/sub	11.4 ± 0.2	201,083	79.3 ± 0.2
mild/int	7.8 ± 0.7	65,212	76.7 ± 0.8
mild/sub	10.0 ± 0.1	9,876	75.3 ± 0.1
<i>Macoma balthica</i>			
cold/int	9.5 ± 0.3	29,743	106.9 ± 1.0
cold/sub	13.8 ± 1.3	63,561	104.6 ± 1.0
mild/int	8.1 ± 0.4	19,182	104.1 ± 0.2
mild/sub	9.8 ± 0.4	20,330	106.8 ± 0.8

6.3 Evaluation

As already indicated in Section 3.2 this study is not finished at the end of NRP I, so this evaluation is based on a limited amount of information.

The hypothesis tested so far is confirmed by the data obtained. Whether the same conclusions can be drawn for populations in the field remains to be seen.

In the meantime, nature carried out its own experiment by providing a series of very mild winters on a row. This led to unprecedented low levels of cockles and mussels in the Wadden Sea, thus confirming once more the basic hypothesis that winter temperatures influence the recruitment of bivalve populations (Smit, 1994).

Two conclusions can be drawn from the present data. In the first place the relationship between temperature and ecological function is not a simple one. Through the interaction with food, predators, or competitors the abundance of species can change in unexpected ways. For those species which are abundant in the Wadden Sea nowadays, we can try to investigate in well-planned studies if their numbers might be influenced strongly by some interaction of different factors. However, the reverse is also possible. For rare species, or even species which do not yet occur in the Wadden Sea, it is possible that they become very numerous because of similar interactions. Such cases will be very hard to predict.

The second preliminary conclusion concerns the Wadden Sea shellfish cultures. These might face a bleak future if the conclusions obtained for *Macoma* and *Cerastoderma* hold also for *Mytilus*. On the other hand it is also possible that other ecotypes of these species develop or are introduced from more southern latitudes which might thrive in a warmer Wadden Sea.

7. INTEGRATION

7.1 Integration of effects of climate changes on estuarine ecosystems

All aspects of climate change have a larger or smaller impact on the Wadden Sea at the same time. In this Wadden Sea many different processes interact, as do populations of plants and animals. Other human impacts also play their part.

The studies under NRP I, however, are mostly concerned with only one aspect of climate change and one or a few processes or species. Although the subjects under investigation have been chosen carefully, taking into account the importance of the expected effect and the position of the process or species investigated in the total Wadden Sea system, it will be difficult to generalize the results to the entire system.

For that reason it has been attempted to bring together all studies in the ecosystem model ECOWASP developed by the DLO-Institute for Forestry and Nature Research and the Netherlands Institute for Sea Research. ECOWASP is a formal description of the relations between a number of abiotic factors (light, temperature, nutrients etc.) and a number of species groups (micro-algae, zooplankton, benthic filterfeeders etc.). It covers the western part of the Dutch Wadden Sea; it takes relations with the North Sea and the hinterland into account. Unfortunately the ECOWASP study was commissioned long after the other studies had started and it will continue to March 1995. So there were few opportunities to steer the other studies, and at the moment of this assessment not all results are available. Especially the integration of the various NRP I studies is not yet completed.

7.2 Results of some scenario studies

Scenario studies have been carried out with the original configuration of the ECOWASP model, i.e. a model without salt marshes and birds. Scenarios computed concern addition and reduction of nutrients, changes in turbidity of the water, and increase of the water temperatures. Especially the later scenario is useful for this assessment, but the other ones may serve as interesting comparisons.

The water temperature scenario was computed for both the normal annual course of temperature and for a temperature which was increased 20% (based on degrees Celsius). Remarkable enough, this rather drastic increase of temperature had relatively little effect on the results of the model computations. Only slight changes occurred.

The nutrient scenarios had much stronger effects, suggesting that the effects of climate change for the Wadden Sea might be less important than the effects of direct human interventions. The turbidity scenarios gave contradictory results.

7.3 Evaluation

Evaluation of the integration of the studies by means of the ECOWASP model is hardly possible at this stage.

A general remark is that this kind of simulations of ecosystem behaviour should be verified by experiments with ecosystems. For the Wadden Sea opportunities to do so exist.

8. EVALUATION OF THE WADDEN SEA STUDIES OF NRP I

Did the NRP I studies address the right questions? This question may be answered starting from the different aspects of climate change, but also starting from those aspects of the Wadden Sea considered to be important, either because of their key position in the system, or because of the values society attaches to them.

With the present knowledge it seems that the effects of the increase of CO₂ have been covered sufficiently.

With respect to temperature it seems that more attention to the effects of temperature and other meteorological factors on key species might have been useful. For example, temperature effects on the eider duck, the most important avian predator on the benthic fauna, may be important, because in the Wadden Sea the species is near the southern limit of its distribution. Also the effects on various fish species might be important, both for northern and for southern species. From the viewpoint of sealevel rise the right aspects of the Wadden Sea system seem to have been covered.

Finally, it is believed that UV-B increase should have had more attention, especially with regard to the organisms living on the tidal flats.

From the viewpoint of key elements in the system it may be concluded that tidal flat benthic microalgae and fish have received insufficient attention.

Do the NRP I studies provide a coherent answer to the question of the effects of climate change? The answer is no, chiefly because the studies were conceived as separate research projects by different research groups. Hence, the studies have been carried out using very different spatial scales, respectively of the size of tidal basins, m² 's, entire Wadden Sea, entire flyway population, and again entire

Wadden Sea. Also the temporal scales varied widely from single tide events to centuries. Nevertheless it is possible to integrate them to some extent by using the extensive background information.

Doing this it becomes possible to draw a few preliminary conclusions.

The effects of increase of atmospheric CO₂ are expected to be slight. Some changes may occur in the salt marshes, but on the scale of the Wadden Sea no important effects are expected. Changes in temperature and other meteorological factors are expected to lead to considerable changes in the species composition of the ecosystem with northern species disappearing and (more) southern species colonizing the area. No important changes are expected in ecosystem functioning, unless one or more key species change drastically in abundance. The NRP I study on bivalve molluscs provides an example of this.

It is expected that the most likely scenarios for sealevel rise will not result in disappearance of tidal flats and saltmarshes within the first 100 years. Consequently the plants and animal species depending on tidal flats will not experience large changes. An exception has to be made for the migratory shorebirds which not only will undergo the influence of sealevel rise in their tidal flat habitat in winter, but also the effects of climate change in their arctic and subarctic breeding areas.

UV-B increase may lead to changes in the biota of the tidal flat areas and in the saltmarshes but it is expected that this will mainly affect balances between species.

It has to be stressed that the expectations summarized above are based on assumptions which could not always be verified and on the study of a limited part of a large and complicated ecosystem. In many respects further study is needed to underscore the present conclusions.

The results for the Wadden Sea in general will be applicable to other European estuaries. Only sealevel rise may have very different consequences in some estuaries because of differences in the hydrography and the sedimentology.

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