GLOBAL CHANGE

Dutch National Research Programme on Global Air
Pollution and Climate Change

Modelling the impact of climate change on the Wadden Sea ecosystems

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Nationaal Onderzoek Programma Mondiale Luchtverontreiniging en Klimaatverandering (NOP)

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II Kwetsbaarheid van natuurlijke en maatschappelijke systemen voor klimaatverandering
III Maatschappelijke oorzaken en oplossingen
IV Integratie en assessment

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I Dynamics of the climate system and its component parts
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III Societal causes and solutions
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Responsibilities

For chapters 4, 6 and 7, C.J. Smit (Alterra Texel) was responsible as editor.

ABSTRACT

In the framework of the Dutch National Research Programme on Global Air Pollution and Climate Change, ecological responses of the Wadden Sea ecosystem to changing climate conditions have been studied. A number of characteristic processes, organisms and steering factors have been chosen as themes.

From morphological studies it followed that a future increase in storm surge level and frequency will seriously affect salt marsh development; Friesian salt marshes will develop less fast; salt marshes at the Groninger main land will erode.

Loss of foraging possibilities for migrating birds is the main cause of a decline in bird numbers as a result of sea level rise.

Higher environmental temperatures may cause a lower larvae growth development for the Baltic Tellin *Macoma balthica*. From a comparison of southern and northern populations it followed that southern populations are possibly better adapted to higher temperatures, and they might have a chance to move northwards when situations change.

From the mesocosm studies it followed that for bivalves, the two major climate change aspects had opposite effects: sea level rise stimulated biomass and production, whereas temperature rise depressed bivalve production.

A developed expert system (EcoFuzz) covers time scales that exceed the ones feasible for laboratory research or experiments in model systems or the field. It provides a suitable means for the incorporation of ambiguities and lack of quantitative data into a classification scheme.

The description for benthic filter feeders in the integrating ecosystem model EcoWasp was capable to reproduce and laboratory filtration and respiration measurements, individual mussels growth rates in the field and mussel bed grazing intensities upon algae and particulate matter. Primary production remained underestimated by the model.

Scenario studies showed that the Wadden Sea system is especially sensitive to sea level changes, and temperature changes, especially to whole year temperature changes.

CONTENTS

SUMMARY

In the framework of the Dutch National Research Programme on Global Air Pollution and Climate Change, we investigated the ecological response of the Wadden Sea ecosystem to changing climate conditions.

The project "Modelling the impact of climate change on the Wadden Sea ecosystem" matches the targets mentioned in Theme II of the climate change programme of the Dutch Government "Vulnerability of natural and societal systems to climate change". In this theme II, the study results are expected to show us how natural systems react upon climate change phenomena, and therefore: knowledge of the overall-impact is needed. Furthermore, the consequences for the sustainable use of such coastal areas are mentioned as target of theme II.

We focused on a number of characteristics: morphological phenomena, shell fish processes and birds. We applied three different integrating methods: integration by a model ecosystem study, by the setup of an expert system, and by the further development and application of a dynamic ecosystem model.

We also choose a number of key steering factors to focus on: temperature rise, water level rise and changing tidal volume, increasing strengths of wind and storms, and increasing fresh water inflow as a results of an increasing precipitation in the more central sites of Europe.

The study on morphological processes in the salt marsh area and the tidal flats in front of these areas showed that local wave action determines whether the supplied sediment stays in suspension or is deposited within the sedimentation fields of the salt marshes. The height and maintenance of the brushwood groynes determines the wave action during calm weather condition. During storm surges, when the groynes are submerged, currents are still interrupted but the wave dampening effect is reduced significantly.

A future increase in storm surge level and frequency will seriously affect salt marsh development. Salt marsh areas of the mainland coast of the Dutch Wadden Sea need a two-year period to recover from a year with many storm surges. At the moment, the salt marshes along the

coast of Friesland attain a positive accretion budget, so the effect of an increase in storm surges will lead to a decrease in accretion. The salt marshes along the coast of Groningen show growth stagnation; an increase in storm surges will directly lead to erosion in this area.

The study on bird migration focused on the improvement of bird models. Dynamic models as DEPLETE and LARGEPOP are applicable to investigate climate change effects in a foraging area (DEPLETE) or on a world wide scale (LARFEPOP). Analysis with DEPLETE, and with the habitat suitability model HABITAT both predict a decline of bird numbers in the Wadden Sea as a result of sea level rise. Loss of foraging possibilities is the main cause of such a decline. Because also conditions in breeding areas are affected, an overall view is needed; LARGEPOP predicts a world wide decline of the Brent geese population as a result of sea level rise and changing conditions during the breeding season.

Higher environmental temperatures may cause a lower Body and Gonadal Mass Index, and a lower larvae growth development for the Baltic Tellin *Macoma balthica*. This is demonstrated by the research on shell fish development and reproduction. We compared *M. baltica* from the Gironde, at the southern border of the distribution with populations living further north. Development of larvae from the Gironde are not affected at high temperatures like the Balsfjord (Norway) larvae are. The results indicate that European population(s) of *Macoma balthica* will for sure be affected by higher temperatures. Populations now living further south are possibly better adapted to higher temperatures. Considering the dispersal abilities of *Macoma balthica* these populations might have a chance to move northwards when situations change.

The two aspects of climate change studied in the mesocosms, sea level rise and temperature rise, have an impact on the tidal flat macrobenthos community. In neither of the experiments the numbers of the organisms were affected by the treatment, not by the temperature rise, nor by a sea level rise. It seems that in situations with an increased water level, larvae settlement and growth was more successful. Also, in the high level situation, growth of adults turned out to be better. The length of the inundation period and the biomass production showed a proportional relationship.

With an increased temperature, individual biomass of cockles was lower than in the normal situations. These deviations did not occur during a winter period, but in the April-May period. The model systems were dominated by *Arenicola marina* (especially juveniles), that did not show any relationship with temperature. Therefore, an overall biomass density response to changing temperatures was not found.

For bivalves, the two major climate change aspects had opposite effects: sea level rise stimulated biomass and production, whereas temperature rise depressed bivalve production.

A long term effect cannot be deduced from these experiments, since recruitment did not take place in the basins.

An attempt to integrate climate change related phenomena has been done by the development of an expert system. Such a tool also covers time scales that exceed the ones feasible for laboratory research or experiments in model systems or the field. In this expert system (EcoFuzz), experimental observations, model results and expert knowledge can be integrated and the results can be presented in both a qualitative and a quantitative way. Furthermore, the model offers the user the possibility to define and evaluate cases. In order to develop a model for the whole ecosystem of the Wadden Sea a modular, incremental approach was chosen, as was the application of fuzzy set theory. It provides a suitable means for the incorporation of ambiguities and lack of quantitative data into a classification scheme.

The functionality of EcoFuzz includes the definition of fuzzy membership functions for all relevant aspects, the definition of fuzzy inference rules, and the evaluation of scenarios in a graphical form. The input of this expert system consists of observations from mesocosm experiments, results of model computations, and expert knowledge.

The integrating ecosystem model EcoWasp has been improved considerably during the project, although some of the targets were not realized. Especially the activity description for benthic filter feeders turned out to be capable to describe and laboratory filtration and respiration measurements, individual mussels growth rates in the field and mussel bed grazing intensities upon algae and particulate matter. Thus the model integrated experimental data from completely different time and size scales. The effect of bird predation, however, was not directly implemented in the model, and needed to be part of a general mortality term.

The computations simulated benthic filter feeder biomass quite well; primary production remained lower than figures resulting from extrapolations from field experiments. Until now it has not been possible to compute together a good fit for chlorophyll-a (algae), and for benthic filter feeder biomass and primary production and benthic filter feeder growth and filtration activities. Only primary production remained underestimated by the model.

Effects of climate change have been estimated. The system seems to be sensitive to sea level changes, and temperature changes, especially to whole year temperature changes. With increasing winter temperatures, especially the tidal flat filter feeders lost biomass densities, probably because their individual budget is more under stress than sub-tidal mussels because of the tidal effects.

The main picture resulting from the simulations is that the results are sensitive for timing aspects. Changing periods of development for algae and filter feeders cause large effects; as a result from different conditions for mussel larvae to feed to survive. Changing predation pressure caused by a different behaviour of e.g. crabs and shrimps are still left out of the model; these probably will amplify such timing effects.

SAMENVATTING

In het kader van het Nationaal Onderzoeksprogramma Mondiale Luchtverontreiniging en Klimaatverandering is onderzoek verricht naar de responsie van het Waddenzee ecosysteem op klimatologische veranderingen.
De studie "Modelling the impact of climate change on the Wadden Sea ecosystem" past binnen de doelen die gesteld zijn in Thema II van het van het klimaat-programma van de Nederlandse Overheid "Kwetsbaarheid van natuurlijke en maatschappelijke systemen voor klimaatverandering". Verwacht is dat de resultaten die binnen dit thema II bereikt worden ons zullen leren hoe natuurlijke systemen reageren op verschijnselen die aan klimaat-veranderingen gekoppeld zijn. Geïntegreerde kennis van de gevolgen is een vereiste.
Ook is als doelstelling genoemd van Thema II dat de gevolgen voor het verantwoord gebruik van kustsystemen beter bekend worden.

Binnen ons onderzoek hebben wij ons beperkt tot een aantal karakteristieke processen. Wij hebben aandacht besteed aan enkele morfologische aspecten en aan de gevolgen voor schelpdieren en vogels. Effecten op het systeem als geheel zijn beschreven met een drietal integrerende methoden: een integraal dynamisch ecosysteemmodel, een expert systeem en een studie in een modelecosysteem, waar met metingen een systeemrespons kon worden gevolgd.

Eveneens hebben wij ons op een aantal sleutelfactoren gericht: temperatuurverandering, zeespiegelstijging en een veranderend getijdenvolume, toenemende sterktes van wind en stormen, en een toenemende instroom van zoet water als gevolg van toegenomen neerslag in de meer centraal-Europese gebieden.

De studie naar morfologische processen aan de kwelders en de platen vóór deze gebieden gaf aan dat lokale golfinwerking bepaalt of fijn materiaal in suspensie blijft dan wel sedimenteert in de sedimentatiegebieden van de kwelders. De hoogte en de staat van onderhoud van de rijstdammen bepalen de golfinwerking gedurende kalm weer. Tijdens stormvloeden, als de rijsthouten dammen onder water staan, worden de golven nog wel onderbroken, maar het dempende effect van de dammen is dan aanzienlijk geringer.

Als in de toekomst de hoogte van het water tijdens stormen toeneemt, en de frequentie van overvloedingen eveneens, zal de ontwikkeling van kwelders ernstig negatief beïnvloed worden. De vastelandskwelders in de Nederlandse Waddenzee hebben een periode van twee jaar nodig om te herstellen van een jaar met veel stormvloeden. Momenteel is het sedimentbudget van de kwelders langs de Friese kust nog positief; een toename van stormvloeden zal een verminderde opslibbing te zien geven. De opslibbing op de kwelders langs de Groningse kust is al vrijwel nul; een toename van stormvloeden zal een erosie van de kwelders aldaar inhouden.

De studie naar migratiepatronen van vogels heeft zich geconcentreerd op de verbetering van beschrijvende modellen. Dynamische modellen als DEPLETE en LARGEPOP zijn toepasbaar om effecten in een foerageergebied (DEPLETE) te onderzoeken, of effecten op een wereldwijde schaal te analyseren (LARGEPOP). Een analyse met DEPLETE, alsook die met het habitatgeschiktheidsmodel HABITAT, voorspelt een afname van het aantal vogels in de Waddenzee wanneer de zeespiegel stijgt. Het verlies aan foerageergebied is de hoofdoorzaak van zo'n achteruitgang.

Omdat ook de omstandigheden in de broedgebieden worden beïnvloed is een integrale benadering gewenst. LARGEPOP voorspelt een wereldwijde afname van de populatie brandganzen als gevolg van zeespiegelstijging en gewijzigde condities gedurende het broedseizoen.

Hogere omgevingstemperaturen kunnen de oorzaak zijn dat nonnetjes *Macoma balthica* aan het einde van de winter een lager conditie-index hebben, en een lagere gonadenmassa-index. Hierdoor kan na hogere wintertemperaturen een slechtere reproductie en een slechtere ontwikkeling van larven optreden. Dit is aangetoond na onderzoek naar de ontwikkeling en reproductie van deze schelpdieren. We hebben *M. balthica* uit de Gironde, het meest zuidelijke deel van het verspreidingsgebied van de soort, vergeleken met populaties die noordelijker aangetroffen worden. De ontwikkeling van larven uit de Gironde werd niet beïnvloed door hogere temperaturen, in tegenstelling tot die van larven uit de Balsfjord (Noorwegen). Deze resultaten tonen aan dat Europese populaties zeker beïnvloed zullen worden door hogere temperaturen.

Zuidelijke populaties zijn mogelijk beter aangepast aan hogere temperaturen. Gezien de mogelijkheden tot verspreiding van *M. balthica* hebben deze zuidelijke populaties kansen zich naar noordelijker streken te verplaatsen wanneer de omstandigheden zich wijzigen.

Zowel zeespiegelstijging als temperatuurveranderingen hebben invloed op de macrobenthosgemeenschap van getijdenplaten; beide aspecten zijn onderzocht in middelgrote modelecosystemen: mesocosms. De aantallen organismen werden niet, in geen van beide gevallen, beïnvloed. Vestiging en groei van larven bleek succesvoller te verlopen bij een hoger waterniveau, evenals de groei van grotere exemplaren. De lengte van de inundatieperiode en de biomassaproductie bleken evenredig gerelateerd. Met een stijgende temperatuur bleek de individuele biomassa van kokkels lager te zijn dan in de normale situatie. Dit verschil ontstond niet in de winter periode, maar in de periode maart-april. De modelsystemen werden gedomineerd door *Arenicola marina*, in het bijzonder door juvenielen, die geen verband met de temperatuur vertoonden. Daarom vertoonde de algehele biomassa geen significante respons op temperatuurveranderingen.

Op schelpdieren hadden de twee klimaataspecten tegengestelde effecten: zeespiegelstijging stimuleerde de biomassa en de productie, terwijl een temperatuurverhoging juist de productie van de schelpdieren remde.

Omdat in de bekkens geen reproductie plaats vind, wat een sleutelfactor is bij langere-termijnstudies, kon een effect op lange termijn kon niet uit de experimenten worden afgeleid.

Een poging om verschijnselen die met klimaatverandering van doen hebben te integreren is gerealiseerd door de ontwikkeling van een expertsysteem. Zo'n gereedschap kan ook tijdschalen bevatten die uitstijgen boven wat in het laboratorium, mesocosms of het veld mogelijk is. In dit expertsysteem (EcoFuzz) kunnen experimentele observaties, model resultaten en expertkennis geïntegreerd worden, en zowel kwalitatief als kwantitatief gepresenteerd worden. Verder biedt het model de mogelijkheid 'cases' te definiëren en te evalueren. Om een model voor de hele Waddenzee te ontwerpen werd gekozen voor een modulaire, incrementele benadering, en voor de implementatie van 'fuzzy set'-theorie. Dit biedt een geschikte mogelijkheid om dubbelzinnige aspecten in een classificatieschema onder te brengen; het ontbreken van kwantitatieve gegevens

hoeft eveneens daarbij geen bezwaar te zijn.
De functionaliteit van EcoFuzz omvat ook de definitie van 'fuzzy membership' functies voor alle relevante aspecten, de definitie van 'fuzzy' interferentieregels, en de grafische evaluatie van scenario's. Dit expertsysteem is gevoed met waarnemingen uit de mesocosm experimenten, resultaten van modelberekeningen en expertkennis.

Het integrerende ecosysteemmodel EcoWasp is gedurende het project aanzienlijk verbeterd, alhoewel een deel van de doelen niet gerealiseerd kon worden. In het bijzonder de beschrijving van de activiteit van bentische filtreerders bleek in staat te zijn én laboratorium waarnemingen aan filtratie en respiratie te beschrijven, én individuele groeisnelheden van mosselen in het veld, én begrazing van algen en ander particulair materiaal boven een mosselbank. Het model integreerde aldus experimentele data van totaal verschillende tijd- en grootteschalen. Het effect van predatie door vogels kon echter niet in het model geïmplementeerd worden, en moest nog via een algehele sterfteterm benaderd worden.
De modelberekeningen reproduceerden de biomassa aan bentische filtreerders redelijk goed; de primaire productie bleef lager dan de (literatuur-)waarden voor veldexperimenten. Tot nu toe bleek het niet mogelijk een goede overeenkomst voor zowel chlorofyll-a (algen), als bentische filtreerders, als voor filtratieactiviteiten tegelijk te verkrijgen. In de huidige berekeningen bleef vooral primaire productie achter bij de velddata.
Gevolgen van klimaatveranderingen zijn geschat. Het systeem blijkt gevoelig te zijn voor zeespiegelstijging, en voor temperatuurveranderingen, in het bijzonder wanneer die gedurende het hele jaar optreedt. Stijgt de wintertemperatuur, dan neemt vooral de filtreerderbiomassa op de platen af. Vermoedelijk staat hun individuele budget meer onder druk dan dat van de filtreerders in het subtidal.
Het algehele beeld dat uit de simulaties naar voren komt is dat de resultaten gevoelig zijn voor 'timing' aspecten. Verschuift de periode waarin algen gaan bloeien ten opzichte van het moment waarop filtreerders reproduceren, dan ontstaat een ander systeemgedrag. Andere karakteristieken zoals het voorkomen van krabben en garnalen zijn niet in het model meegenomen; maar deze zullen ongetwijfeld zo'n effect nog eens versterken.

1 PREVIEW

1.1 Framework and considered area

The present study deals with expected or possible climate change phenomena that may influence ecological characteristics or the ecological functioning of the Dutch Wadden Sea. The study matches the targets mentioned in Theme II of the climate change programme of the Dutch Government "Vulnerability of natural and social system to climate change". In this theme II, the study results are expected to learn us how natural systems react on climate change phenomena: knowledge of the overall-impact is needed. Furthermore, the consequences for the sustainable use of such coastal areas is mentioned as target of theme II.

1.2 Expected effects of climate change

There are many different effects related to climate change; some of these will certainly affect the functioning or characteristics of the Wadden Sea ecosystem, and some possibly will not have any effect at all.

The project focusses on quantifying risks from changing temperatures and water levels on the Wadden Sea ecosystem by integrated model computations. Further development and application of an integrated ecosystem model is the core of the project. Model improvement will result from studies on bird migration and food selection processes, on mesoscosm integrated experiments and shell fish processes, on salt marsh accretion and exchange processes, and on morphological processes inside the basin and interrelations with benthic fauna development. All sub-projects involve (further) development of sub-models.

Text box 1.1 Aim of the project as described in the proposal

In our study, we are not looking for primary effects of climate change (like: *what the temperature change might be*), but moreover, we are studying effects of the some relevant phenomena, like: *what will be the effect of a certain temperature change*. What determined our choice, is a result of previous studies (see text box 1.1). For example, we decided not to study effects of UV-radiation, or the effects of increased carbon dioxide contents upon primary production of the system. The choice not to study CO_2-effects is based upon the consideration that carbon dioxide in aquatic systems is provided as dissolved CO_2, and this is assumed to be sufficiently available. Shortages are not expected under present conditions. UV-B radiation effects have been considered as subject, but was not chosen because a) we had to limit our number of themes and b) we realized that UV-B radiation will extinct within a few centimetres, and therefore, will have limited effect upon aquatic processes.

What may be affected as Wadden Sea characteristics is the ebb and flood regime, and its fluctuating morphology. Morphology is influenced by eroding forces due to water flows and waves and by natural deposition of sand and silt in more quiet regions, or by biologically mediated deposition. Temperature effects are expected to be important as well, because the system is shallow, and therefore it will react relatively fast to changing air temperature, solar radiation and changes in long-wave back-radiation. Due to changing precipitation, the inflow of fresh water, as well the nutrient content of this inflowing fresh water, may change and thus alter the nutrient supply of the coastal waters and influence primary and secondary production. Also, on a individual scale, temperature change and sea level rise may effect the functioning of single animals, or may allow other or better survival chances for allochthonous species. Last but not least, changing inundation times, food abundances or food availability may seriously effect populations of birds species migrating along the Eat-Atlantic flyways.

These aspects of climate change effects form the basics of our research project, and they will be paid attention to in this report.

1.3 Setup and organisation of the project

In the first stage of the project, two projects had to be merged. The one was proposed by the former Institute for Forestry and Nature Research (IBN, project leader Prof. Dr. W.J. Wolff), the other was proposed by the National Institute for Coastal Zone Management (RIKZ, project leader Dr. F. Colijn). Also, the financial size of the project had to be reduced substantially. Unfortunately most of the projects goals were reduced much less then the funding, a less favourable situation as the course of the project would show.

Nevertheless, a final product has been achieved, meeting most of the goals mentioned in the project proposal, although some of the targets could not be realised. And, the project result gives us substantial information on Wadden Sea characteristics and their response to climate change phenomena.

During the project, the organisation has (also) been changed. First Dr. L.W.J. Higler took over the principal scientist position from Prof. Dr. W.J. Wolff (1-1-1996), on 1-1-1999 Dr. Ir. A.G. Brinkman became the third project leader in line.

1.4 Partnership

After the merging of both projects, the study group (Fig. 1.1) consisted of

- ALTERRA (before 1-1-2000: Institute for Forestry and Nature Research, IBN), covering three different theme's:
  - ***I-a Ecosystem modelling***: Further model development for the impact of climate change on the Wadden Sea. This project, with project I-b, is assumed to be the integrating project for all the other activities.
  - ***II Bird migration processes and modelling:*** Aims at a further unravelling of the relationship between the foraging needs of migrating birds and the Wadden Sea system. The effects of sea level rise are expected to be the most important thread of the foraging capabilities of the system. Principal scientist Dr. B.J. Ens. Results have to be implemented into the ecosystem model, and as such part of I-a.
  - ***III-a Mesocosms research and modelling:*** Process research on effects of temperature and water level. Principal scientist Dr. K. Kersting. Also: testing of hypotheses, analysis by and calibration of the ecosystem model, and as such part of (I-a)
- Netherlands Institute for Sea Research (NIOZ).
  - ***III-b Mesocosms research and modelling:***. Laboratory and mesocosm research at species level. Principal scientist Dr. J. Beukema; drs. J. Drent did most of the job as PhD-fellow. III-a and III-b worked closely together as far as the subject dealt with mesocosm work. Results are meant to be implemented into I.
- National Institute for Coastal Zone Management (RIKZ).
  - ***I-b Integrating climate change effects by the development and application of a fuzzy***

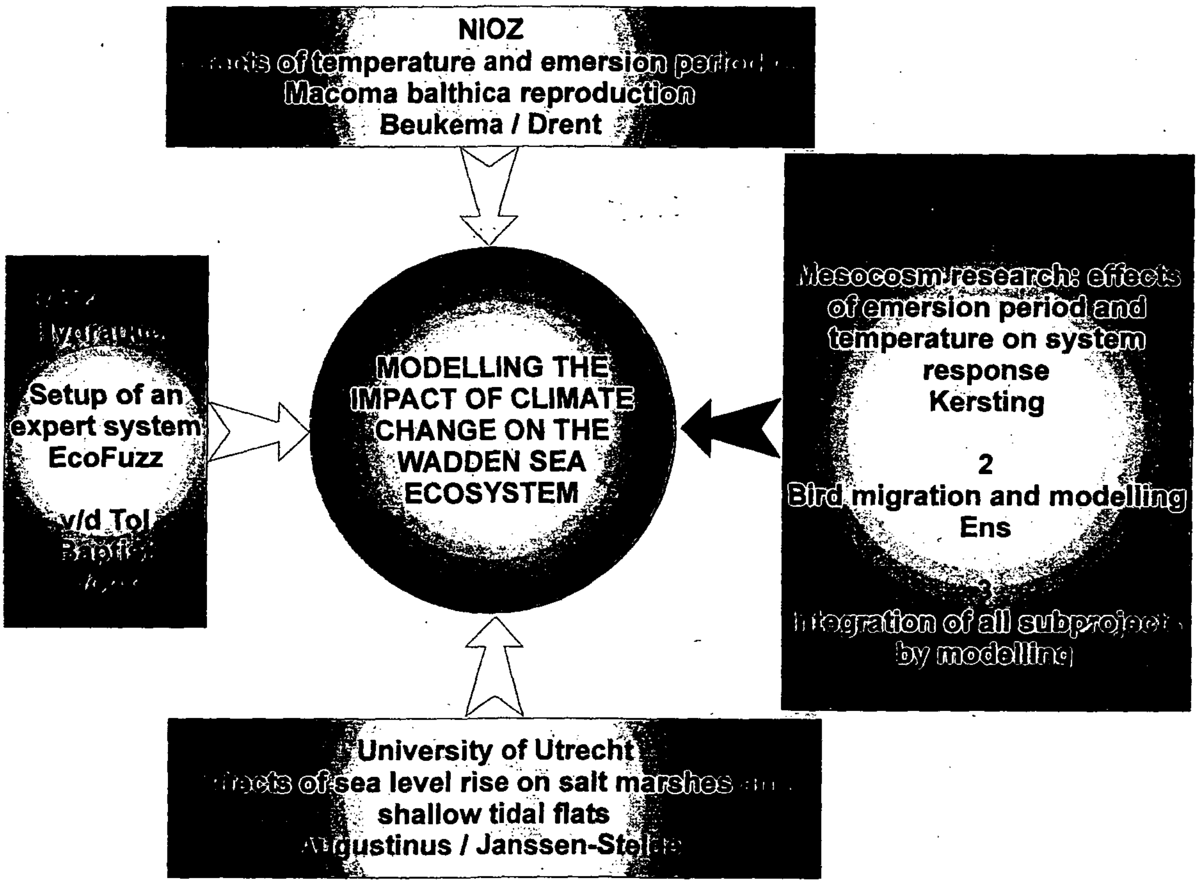


Fig 1.1 The project cooperation

model. Principal scientist Drs. M. van der Tol; Delft Hydraulics, with Ir. M. Baptist and Dr. M. Vonk, performed the job.

- University of Utrecht (RUU), department of Physical Geography

IV Saltmarsh and tidal flat processes, research and modelling. Development and stability of salt marshes and the tidal flats in front of these areas. Principal scientist Dr. P. Augustinus, drs. B.J. Janssen-Stelder did most of the job as PhD-fellow. The aim, to couple results with the ecosystem model (I-a) turned out to be a too optimistic one. This part of the project could not be realized.

Thus, the project knows two integrating projects (I-a and I-b), the first one based upon a dynamical model description, the second aiming at the development of a knowledge-base system, where more qualitative descriptions play a major role.
Twice a year the researchers met during a day, to inform each other on their progress and their setbacks.

To back-up the scientific process as well as the usefulness of the work, an audit group was formed, consisting of:

Ing P. Feddema	Wadden Advies Raad, Leeuwarden
Prof. dr. ir. J. Grasman	Wageningen University, Mathematics Group, Wageningen
Dr. R.H.G. Jongman	Wageningen University, Dept Environmental Sciences, Land Use Planning Group, Wageningen
Ir. J.G. de Ronde	RIKZ (National Institute for Coastal Zone Management), Den Haag

1.5 Application of results to other areas

We restricted our study to the Dutch Wadden Sea area, but the study has been set up in such a way that results may very well be applicable to other comparable tidal areas.

2 OVERVIEW OF CLIMATE CHANGE SCENARIO'S

2.1 Introduction

In the present project, we are dealing with a number of forcing functions, representing expected, or possible effects of global climate change. Most of the effects deal with changes in averages or seasonal variations of temperature, wind speeds, precipitation and sea level. I this chapter 2, a brief outline of relevant scenario's is presented.

2.2 Sources

A huge number institutions deliver results on climate change, based upon expected or assumed forcing functions. These forces concern possible developments of social structures, land and energy uses, and many more. Many of these basic assumptions, as are the results, are distributed by the IPCC, the Intergovernmental Panel on Climate Change, jointly established by the United Nations Environment Programme (UNEP) and the World Meteorological Organisation (WMO). IPCC partly acts as a coordinator and distributor of scenario's on climate change, as well on the cause side, as on the effect-side. Some of the last ones, being important for our study, will be outlined below.

For our study, scenario's provided by the Hadley Centre are most applicable. The NRP-II Programme Office in Bilthoven provided us with these results (Verweij & Viner, 2001). Based on the IPCC-scenarios, the Royal Netherlands Meteorological Institute KNMI (Können et al, 1997) estimated future changes for the local situation in the Netherlands.

2.3 Present developments

As shortly mentioned above, we restrict ourselves to a number of phenomena. Changes in

- temperature
- average sea level
- maximum, minimum levels

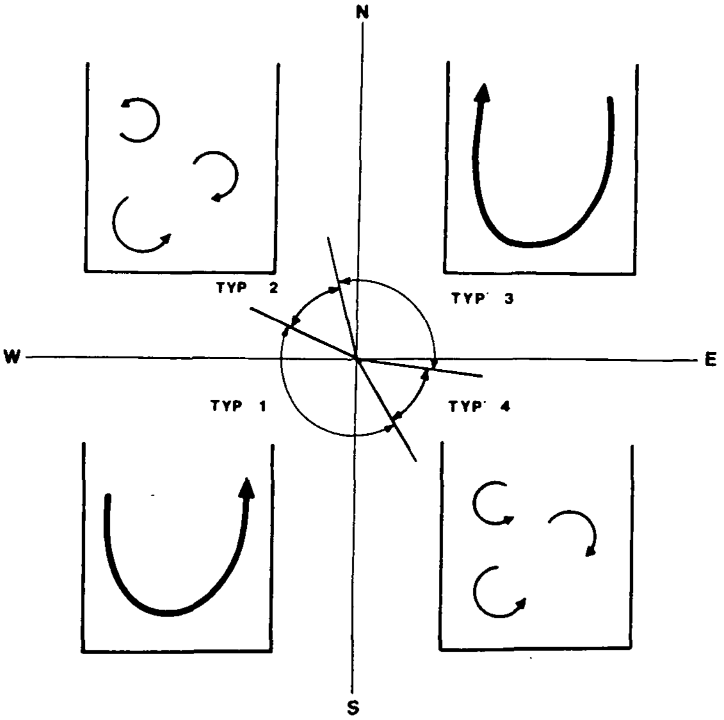


Abb. 1. Schematische Zirkulationsmuster der Nordsee unter Windeinwirkung aus den angegebenen Richtungssektoren; Typ 1: Grundmuster.

Fig. 2.1 Schematic representation of changing water circulation patterns in the North Sea, as affected by a change of the dominant wind directions. From (Backhaus, 1993).

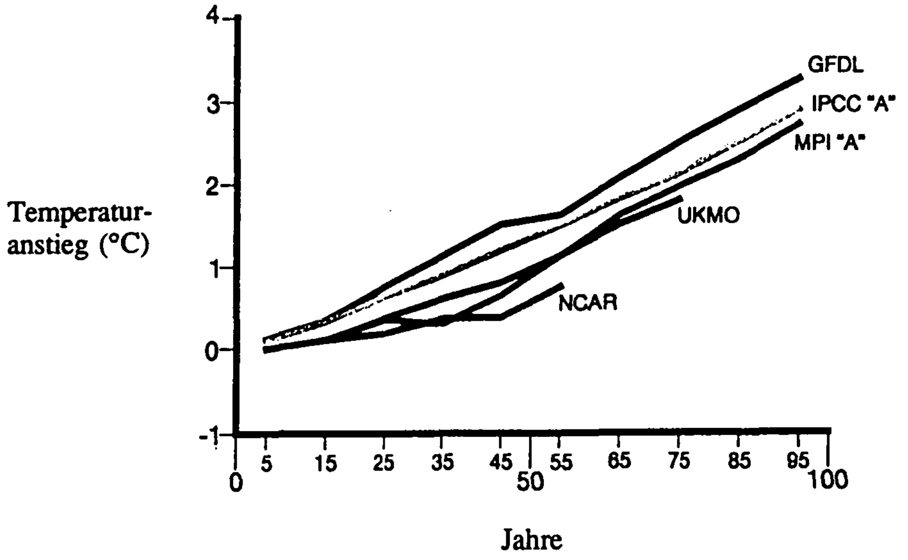


Abb. 1. Berechneter zeitabhängiger mittlerer Temperaturanstieg an der Erdoberfläche nach mehreren gekoppelten Ozean-Atmosphäre-Modellen sowie für maximal zwei Szenarien (A = business as usual, D = drakonische Maßnahmen). GFDL = Geophysical Fluid Dynamics Laboratory, Princeton; NCAR = National Center for Atmospheric Research Boulder; UKMO = United Kingdom Meteorological Office, Bracknell; MPI = Max-Planck-Institut für Meteorologie.

Fig. 2.2 Temperature rise scenarios for the coming century. Taken from Graßl (1993).

- average wind speed
- storm frequency

have been taken into account. Other possibilities like wind direction have not been considered at all, but one. Backhaus (1993) explains that it very well may affect the North Sea circulation pattern (Fig.2.1). If such a change occurs, the situation in the North Sea regions close to the Wadden Sea may change drastically, since the dominant water source will be a one very different from the present situation. Fish distribution and larvae transports will definitely differ completely from the present situation. Because also nutrient sources for the Wadden Sea will change, the eutrophication state for most of the areas will change as well.

2.4 Scenario's

2.4.1 Temperature

As an example, we took Fig. 2.2 from Schnellhuber and Sterr (chapter 2, by H. Grassl). It represents an expected temperature change at the earth' surface, but it does not represent the accompanying changes in water temperature. Also, since we expected that effects of small changes would be hard to measure, we considered a drastic change of 4 degrees Celsius water temperature increase. Based on IPCC scenario's (see eg. IPCC 2000), the KNMI mentions an increase of 1-2 °C in 2050 with a maximum of 4 °C in 2100 for the Dutch situation. Temperature rise in winter is expected to be higher than in summer.

2.4.2 Average sea level

Data for the Dutch coastal area (eg. Bouwmeester, 1993, Fig. 2.3) show an average increase of the mean tidal level of about 18 cm y^{-1}. This value is regarded as the 'present rate' of sea level rise. Increased rates, as forecasted by several studies range from almost 36 cm cm y^{-1} as 'most likely' rates for the local situation, to 60 cm y^{-1} as 'high rates'. A worst case scenario value reads 100 cm y^{-1}.

The Hadley Centre provided us with an average expected rise as presented in Fig 2.4, which has

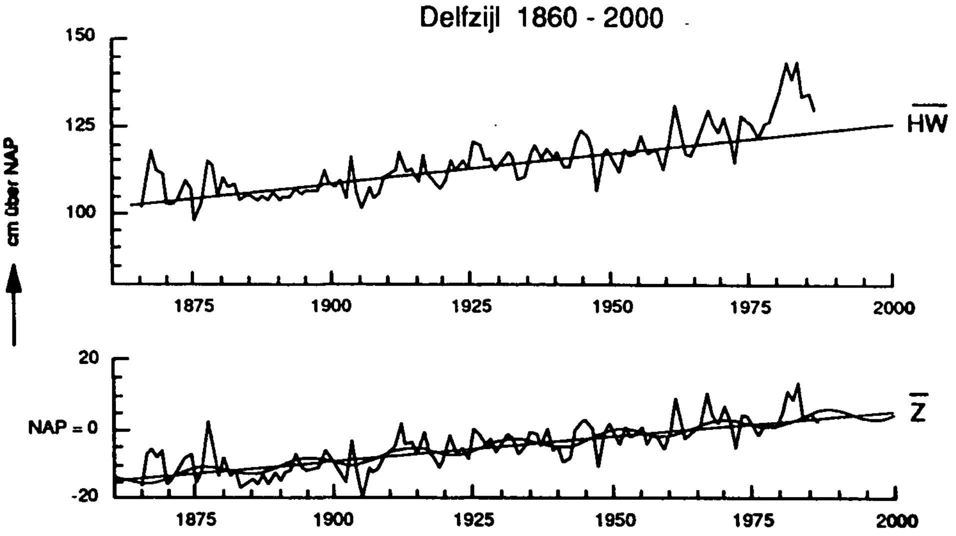


Abb. 4. Mittleres Hochwasser (HW), mittlerer Meeresspiegel (Z), mittleres Niedrigwasser (NW) und mittlerer Tidenhub (TH) bei Delfzijl.

Fig. 2.3. Observed sea water level at the Dutch coast. Taken from Bouwmeester (1993)

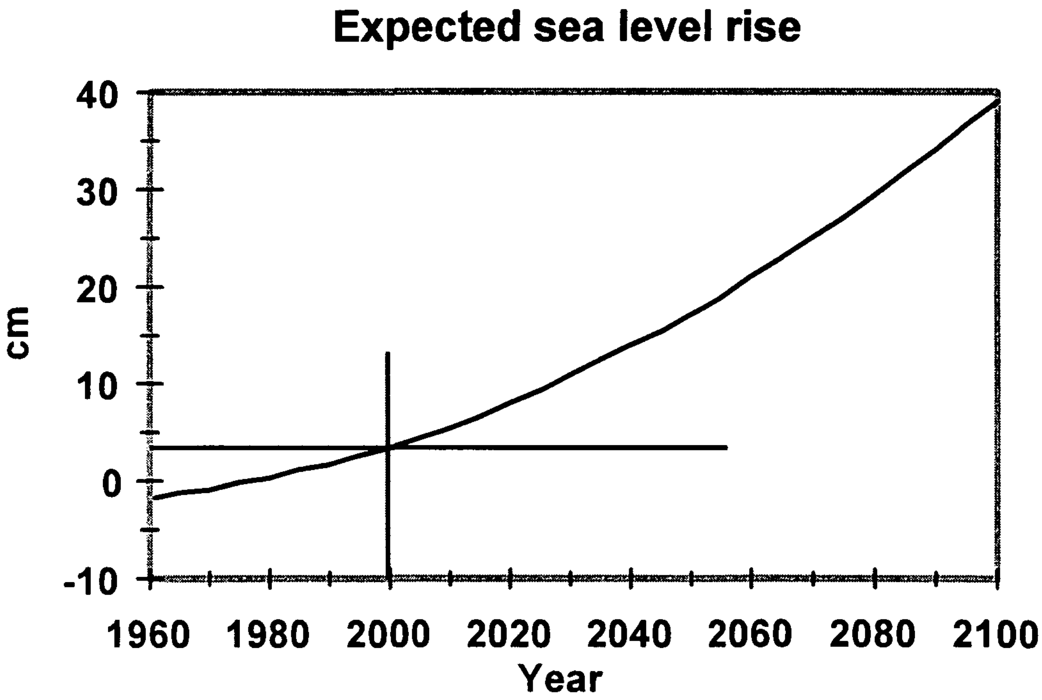


Fig. 2.4. Expected sea level rise, provided by the Hadley Centre

been the basis for our study. According to Bouwmeester, the mean high water level increased somewhat faster than the mean levels during the last century. For the future this would imply that the local tidal amplitude is also expected to increase. As a result, the tidal volume (the amount of water entering and leaving a tidal area each tide) will increase. A 5 cm increase equals about 5% of the present tidal range value. Although the tidal volume is not a linear function of the range, a 5% increase of this tidal volume can be seen as a first estimate of the changes to be expected.

2.4.4 Average wind speed

Data series are available for the period 1970-1999 (the present situation) and 2060-2090 (the expected situation). In Fig.2.5 an example is shown; wind speed is expected to increase somewhat during certain months, but the picture is not very clear.

2.4.5 Storm frequency

One of the expected aspects of climate change is that not only average wind speeds will increase, but also the frequency and intensity of extremes, ie, storms. No clear data are provided by Hadley. Top 10% -wind speeds are about 1.5* as high as average values, as are the maximum values when not daily but 6-hourly values are considered. The shorter the averaging period, the larger the differences. Maximum wind speeds mentioned in reports are usually 10 minute-averages; for storm surges also duration is relevant. Since water bodies need some time to react on changes in wind conditions, 10 minute wind averages are not considered as relevant for the intensity of waves. According to KNMI (Können et al, 1997), there is a chance to have more and heavier storms, but this expectation is highly uncertain.

2.4.6 Solar radiation

Data series are available as averages for the period 2089-2099. For a comparison with present radiation intensities, De Kooij-data from KNMI (KNMI 1976 - 1995) have been used. Data are

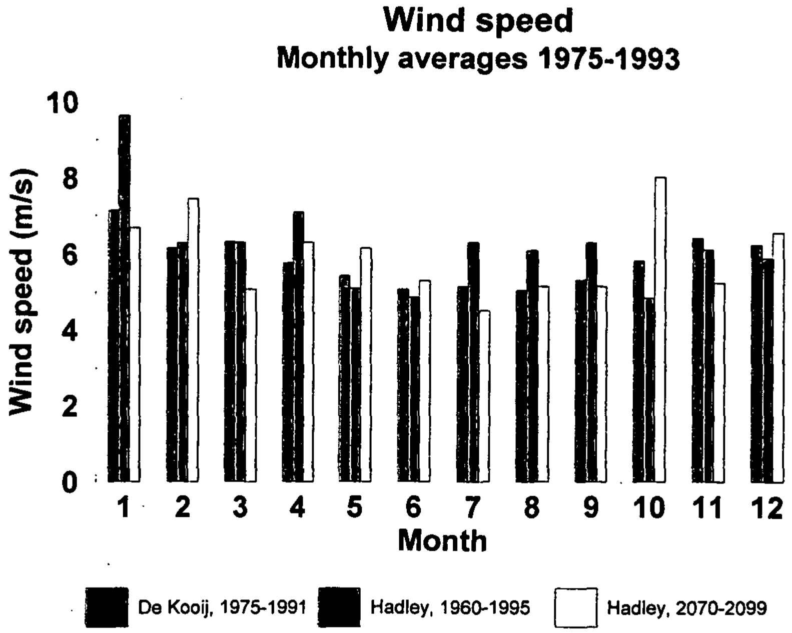


Fig. 2.5 Present and expected future wind speeds for the Wadden Sea region, provided by the Hadley Centre.

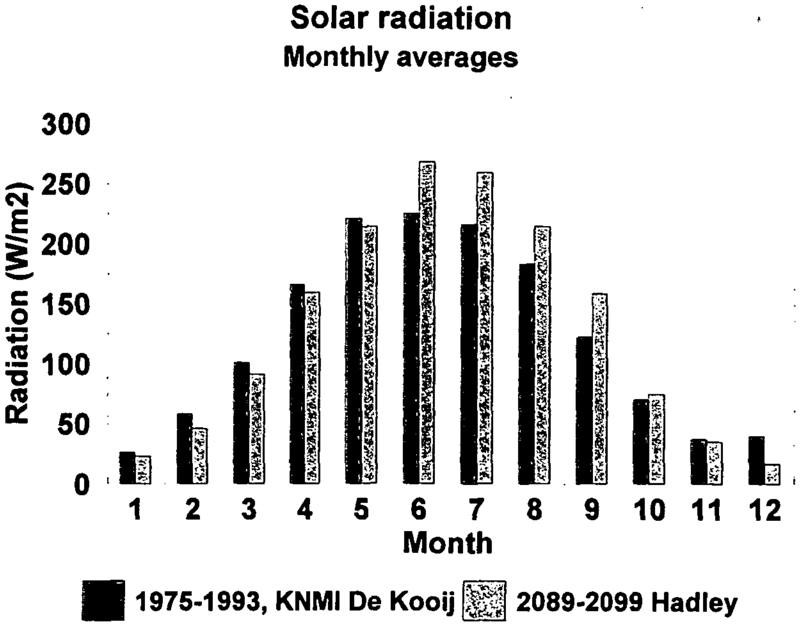


Fig.2.6 Monthly averages for solar radiation. Present values from Station De Kooij Airport (Den Helder), future values from Hadley Centre.

shown in Fig.2.6.

Some differences can be observed, but it is not clear whether this is an effect of the site, or of climate change. Summer values tend to increase, whilst winter values decrease somewhat. For our scenario analyses, these differences have been omitted.

2.4.7 Precipitation

As a consequence of climate change, it is expected that in our regions, precipitation will increase, especially during winter. A typical value reads 6% increase in the winter season; and this values has been taken as basis for a precipitation scenario. It is assumed that the fresh water inflow from Lake IJssel increases during the month October - March. It is also assumed that the nutrient content of the fresh water remains unchanged, although this may lead to a slight overestimation of eutrophication effects. Maximum values (Können et al, 1997) give 25% increase in 2100 during the winter period, while summers show a decrease.

2.4.8 Auxiliary effects

Not only effects that can be considered as more or less direct effects of changing weather conditions, like the ones mentioned above, but also some second order effects may be of importance. Backhaus (1993) mentioned a possible changing North Sea water circulation pattern, resulting from a relatively small change in average wind directions. The present overall circulation pattern is one that causes an southwards flow along the Scottish and English coast, and a northwards flow at the eastern side of the North Sea basin. A change of the average wind direction to more northern winds may influence this pattern thus that a more diverse pattern is created, or even a complete reverse pattern, where the northern water flow is at the western side of the basin. As a result, the boundary conditions for the Wadden Sea may become completely different from the present ones, and consequently, the system characteristics may differ significantly from what they are now.

2.4 Resume

In the above sections, the major steering factors for the Wadden Sea system, affected by climate change, are mentioned. In the following chapters, and the final integration part, the outcome of the several sub- studies are to be coupled with these scenarios.

We choose as major possible changes:

- a temperature increase: 4 °C overall, and some sub-scenarios with only milder winters and same temperatures during summer (chapter 3,6,7,8,9)
- an average water level increase of 20-60 cm (chapter 3,4,5,6,8,9)
- a change in water circulation patter, causing other water quality boundary conditions (chapter 9)
- increase in storm surge intensities. Frequency changes are not considered (chapter 4,9)
- increase in average wind speeds (chapter 4,9)
- changes in solar radiation have not been considered
- changes in precipitation (chapter 9)

Not all effects are taken into account for all the sub-studies, since not every combination is relevant. The number of the chapters are mentioned.

3 STEADY STATE IN A WADDEN SEA SYSTEM: A FIRST ESTIMATION OF CLIMATE CHANGE EFFECTS

3.1 Introduction

Climate change could effect a tidal system like the Dutch Wadden Sea in several ways. A temperature increase and a sea level rise are the two most striking phenomena. Additional effects could be a change in fresh water and/or nutrient inflow, occurrence of species that are known from warmer regions until now, and a change in predation pressure by migrating birds due to different migration patterns or changing predation possibilities.

Based on a steady-state approach for the western Wadden Sea system, a first estimate is given of the effects of changing temperature, nutrient and fresh water inflow. Also the effect of changing bird predation is on a long term steady-state situation in the Wadden Sea. Such a steady-state assumes that boundary conditions, nor the system characteristics change with time. Thus, all the rates (changes of algae content, benthic biomass, etc.) Are assumed to be zero. Or, in other words: all the basic differential equations are set to 0.

Such an approach is used more often in system analysis (..); the results give a first insight in how the dynamic system may response to certain changes in input variables or steering factors. The approach can also be applied in order to get some idea of the importance of model parameters. Finally, dependencies can be investigated: the steady-state method may serve as a tool to find final values for e.g. algae content and benthic biomass limits.

In order to perform such an analysis, the basic equations applied in the dynamic ecosystem model EcoWasp have been rewritten to a steady-state solution; at the same time, they are simplified a lot. In text box 3.1, an overview of the algae and benthic fauna equations is presented, as well as of the steady-state solution.

Average input data are available, as are average data for temperature, solar radiation, etc. Parameter values are partly derived from literature, and tuned by EcoWasp simulations and by comparing results with field data and laboratory experimental data.

3.2 Basic equations

As an outline, basic equations for algae and filter feeder dynamics are given in text box 3.1a. The quasi steady-state solutions are obtained by setting all first derivatives equal to 0.
The result does not give information on a detailed scale (time, space, population), but serves quite well to get rough information on what could be expected on a whole system scale. In text box 3.1b, the steady state solution for such a simplified set of equations is given.
Although not shown, the set of equations also covers a detritus and nutrient steady state, and includes terms for predation upon shell fish by birds, extraction of shell fish by fisheries and extra predation by crabs and star fish.
Input of matter from the North Sea and the fresh water Lake IJssel is implemented.
The light limitation function for algae growth is according to Smith, (see e.g. Brinkman 1993), with Ik as Smith-constant; suspended particles (algae, detritus) contribute to the extinction coefficient of the water column. An average [inorganic solid] is used to cover the effect of silt and sand.

One of the first conclusions one can draw from such a steady-state is that for example the steady-state algae content in the Wadden Sea does not depend on the concentration of algae at the North Sea boundary: Any increase is consumed completely by filter feeders, and vice versa, and thus, it affects filter feeder biomass only. One can also read that algae concentrations in the Wadden Sea certainly does depend on filter feeder characteristics. When the main filter feeders in the Wadden Sea are replaced (for whatever reasons) by other species, with different filtration characteristics, consequently the [algae] will change.

And thus, the primary production does depend on the rate constant for algal growth, and the rate constants for filter feeder removal or mortality.

Roughly, algal dynamics read

$$\frac{dA}{dt} = k_p A - k_d A - k_g A G + \frac{Q}{V}(A_{ext} - A) \qquad (\text{g alg m}^{-3}\ \text{day}^{-1}) \quad \mathbf{(3.1)}$$

with

A = algal content (g DW m^{-3})

A_{ext} = algal content in input water (g DW m^{-3})

G = grazer content (g DW m^{-3})

Q = input or exchange volume (m^3 day^{-1})

V = volume (m^3)

k_p = algal production parameter (day^{-1})

k_d = algal respiration parameter (day^{-1})

k_g = grazing parameter (m^3 gram^{-1} mussel day^{-1})

For mussel growth:

$$\frac{dG}{dt} = \gamma k_g A G - k_r G - k_m G \qquad (\text{g mussel m}^{-3}\ \text{day}^{-1}) \quad (3.2)$$

k_r = mussel respiration parameter (day^{-1})

k_m = mussel mortality parameter (day^{-1})

γ = food efficiency (g mussel g^{-1} algae)

Mussels are computed as biomass per unit volume.

Text box 3.1a Basic equations for algae and filter feeder dynamics

Thus, with

$$y_1 = k_p - k_d - \frac{Q}{V} \tag{3.3}$$

and

$$c = + \frac{Q}{V} A_{ext} \tag{3.4}$$

and

$$y_2 = - k_r - k_m \tag{3.5}$$

it follows that

$$0 = y_1 A - k_g A G + c \tag{3.6}$$

and

$$0 = \gamma k_g A G + y_2 G \tag{3.7}$$

have to be solved. (3.7) directly gives, since G can be removed right away,

$$A = - \frac{y_2}{\gamma k_g} \tag{3.8}$$

Substitution into (3.6) gives

$$G = \frac{y_1}{k_g} + \frac{\gamma c}{y_2} \tag{3.9}$$

Text box 3.1b Steady state solution of the predator-prey equations (2) and (3)

3.3 Considered area

The computations and morphological data all consider the western part of the Dutch Wadden Sea. It was not useful the take the whole Wadden Sea area into account, since it cannot be considered being well mixed and uniform. Therefore, from a modelling point of view, it would be necessary to perform different computations for each of the tidal basins. For the western part we have relatively many data at our disposition, although the number still is quite limited regarding the many variables and processes taken into account.

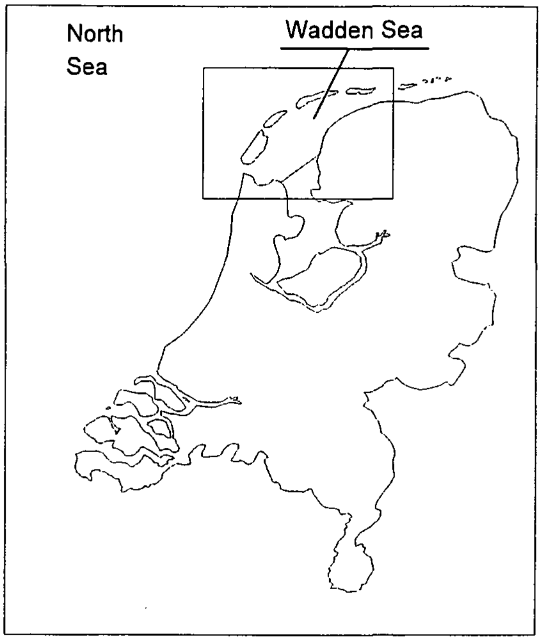


Fig. 3.1 Wadden Sea in the Netherlands

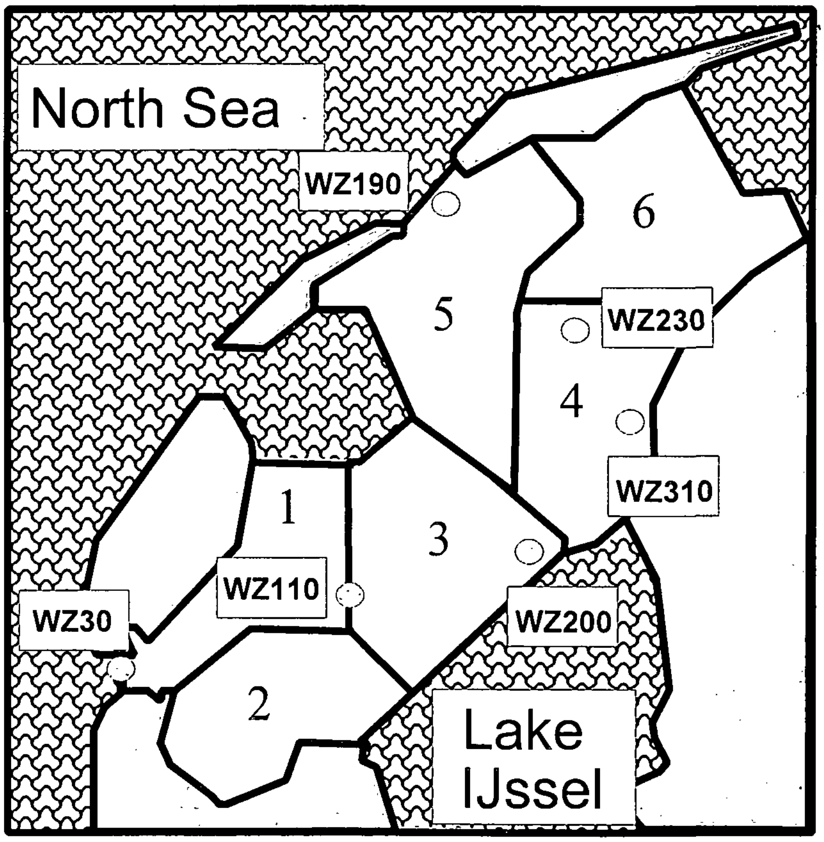


Fig. 3.2 Western part of the Dutch Wadden considered in the computations. Data points show RIKZ monitoring stations. Compartments are not considered in the present exercises, but are used for EcoWasp computations.

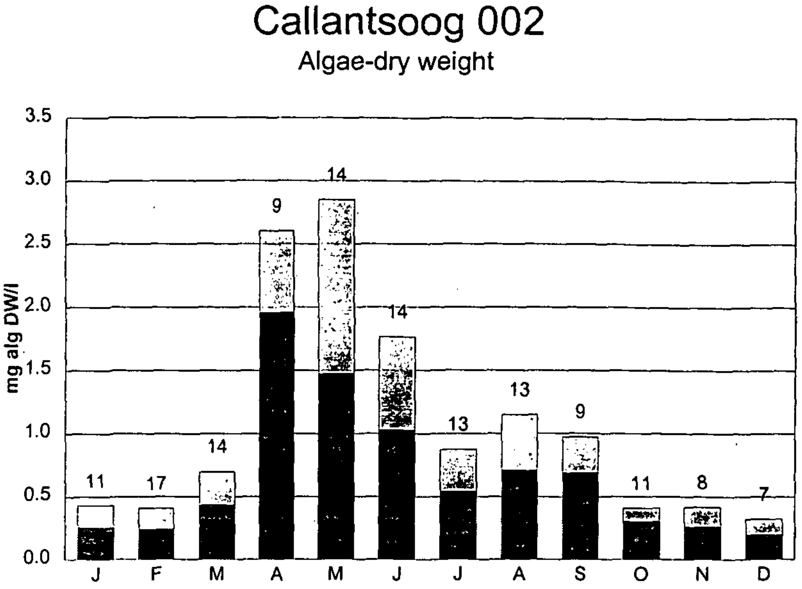


Fig. 3.3 Monthly averages for North Sea algae dry weight. Location Callantsoog, 2 km from coast. Data from Rijkswaterstaat (1976-1996). Dark = average, grey = standard deviation

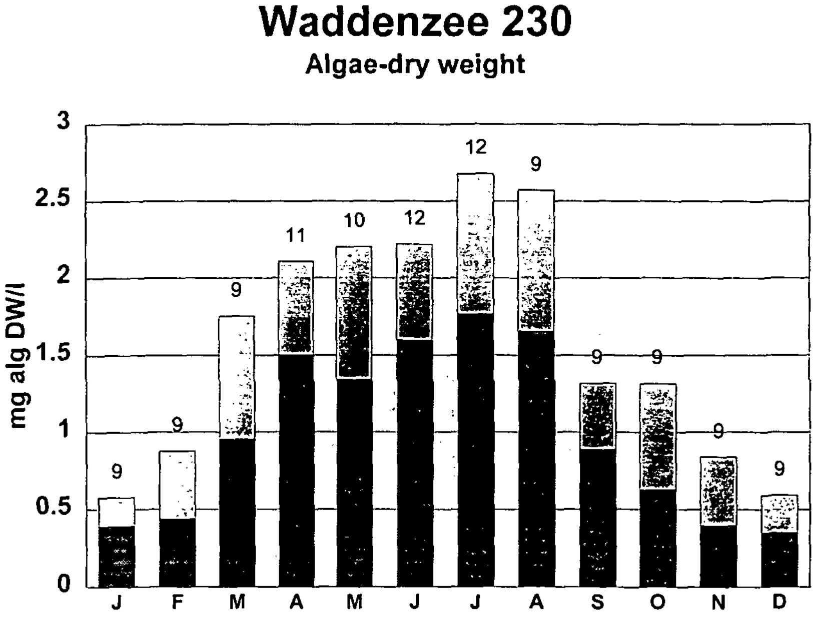


Fig. 3.4 Monthly averages for Wadden Sea algae dry weight. Location WZ230 (see Fig. 3.2). Data from Rijkswaterstaat (1976-1996). Dark = average, grey = standard deviation

3.4 Available data for input and for comparison

3.4.1 Algal concentration in the North Sea, at other boundaries, and in the Wadden Sea

Data for the input from the North Sea, from Lake IJssel, and for the Wadden Sea are available from the Rijkswaterstaat monitoring activities; every month water quality sample are taken at several locations. Algae data, derived from chlorophyll-a analysis, show an average North Sea value of 0.67 ± 0.53 (Fig. 3.3, Location Callantsoog 002). Location Callantsoog 001 (1 km from the coast) gives similar values, location 004 shows lower values (0.43 ± 0.34). This value decreases with increasing distance to the shore.

Algal concentrations are available from the Rijkswaterstaat monitoring activities; every month water quality sample are taken at several locations. Algae data, derived from chlorophyll-a analysis, show an average value between 0.8 and 1.3 g m^{-3} (0.99 ± 0.53) for an inside location (Fig. 3.4) and between 0.7 and 1.0 g m^{-3} (0.82 ± 0.38) for a site more close to the North Sea (site WZ 110). As an average value, 0.90 g m^{-3} seems appropriate.
For both estimates of algae contents, an approximation of the chlorophyll-content of algae of 1.2% (relative to dry-weight) has been used.
There is no input from algae by the fresh water; all fresh water algae are assumed to be detritus.

3.4.2 Detritus concentration

See 3.4.1 for the source. Average data cannot be obtained directly from the monitoring results, but have to be estimated from total organic matter, estimates for algal concentrations, total particulate matter and glowing rests, and data for P- and N-contents (also dissolved, total, total organic) and estimates for P- and N-content of algae and detritus. It is not relevant to explain this procedure, but following such methods, it is possible to derive dissolved and particulate detritus contents of the Wadden Sea and the North Sea. As an extra result, it turned out that most of the detritus (particulate and dissolved) probably is humic-like matter; during the summer period there is an increase in organic dissolved matter, which can be contributed to more reactive components.

For WZ230 the average detritus content is 8.5±2.2 and 9.7±4.1 g m^{-3} , for WZ110 it is 6.6±2.7 and 6.4±2.8 g m^{-3} .

3.4.3 Nutrients

For the computations in this chapter, only phosphorus and nitrate + ammonium (as basic N-sources) have been considered. Average values for Callantsoog 002 are: ortho-P: 1.4 mmol m^{-3} (±0.7), total P: 4.1 mmol m^{-3} (±1). NO_3^-: 28 mmol m^{-3}(±15), NH_4^+: 5.8 mmol m^{-3} (±1.8).
Average Wadden Sea values : ortho-P: 1.7 mmol m^{-3} (±0.4), total P: 5.3 mmol m^{-3} (±0.7). NO_3^-: 33 mmol m^{-3}(±34), NH_4^+: 9.3 mmol m^{-3} (±4.3).

3.4.4 Benthic fauna

Benthic fauna densities are known for recent years from yearly inventories y the RIVO-fishery research institute (eg. Van Stralen, 2000), and before that from extrapolations based upon local investigations. V/d Veer (1989) gives 8.3 g AFDW m^{-2} of mussels alone, and mentions that this is about 38% of total biomass present. For culture plots, he mentions biomass densities of about 250 g AFDW m^{-2} average. Wild mussel beds show densities of about 800 g AFDW m^{-2} when lots of macroalgae are present, and up to 1400 g AFDW m^{-2} when there is little or no vegetation present (Gätje & Reise, 1997).

At the western Wadden Sea culture plots (70 km^2 in the years from 1960, 250 g AFDW m^{-2}), about 17.5 10^6 kg AFDW mussels is present.

RIVO-inventories in the years 1992-2000 (e.g. Van Stralen, 1998; Van Stralen & Kesteloo-Hendriks, 1998) show an average cockle biomass of 8 10^6 kg AFDW in the whole Wadden Sea, which equals 3.2 g AFDW m^{-2}. In 1998 and 1999, this figures is about 2 to 3 times as high as a result of the very good recruitment in 1997. Densities are up to 7-10 g AFDW m^{-2}, but mussel densities were considerably lower.

Combining most data, average biomass densities of 10-20 g AFDW m^{-2} seem to be normal for benthic filter feeders (the latter being the optimistic one); and these values are used as comparison for the computations.

3.4.5 Primary production

There are few data on primary production available. In 1979 and 1986, the NIOZ performed an intensive research in the western Wadden Sea. Primary production data (EON-I, 1988; EON-II, 1988) are given in g m^{-2} y^{-1}, but it is not completely clear how such an extrapolation has been performed from the real measurements. Also, most data come from incubation experiments, where interpretation to field production data is done by the application of an empirical formula:

$$P = 0.5P.E.D \qquad (3.10)$$

with P = mean incubator primary production (g m^{-3} h^{-1}), E= depth of euphotic zone (m), D = daily light period (h d^{-1}). This method contains a lot of possible extrapolation inaccuracies. Values range from 100-340 g C m^{-2} y^{-1}, ie. 250 - 850 g DW m^{-2} y^{-1} as pelagic primary production; the estimates for the 70's read 145 - 200 g C m^{-2} a^{-1}, or 360 - 500 g DW m^{-2} a^{-1}. The lower values are mentioned for the inner part of the Wadden Sea area, the higher ones (about 20-40% higher) for the Marsdiep area (the tidal inlet between the island of Texel and the main land). The data for the 80's are 750 - 1100 g DW m^{-2} a^{-1}; the EMOWAD simulations (EON-II, 1988) show primary productions of 550-1000 g DW m^{-2} a^{-1}, the lower values for the inner compartments. In Table 3.1, some values are summarized.

Table 3.1 Western Wadden Sea pelagic primary production data from literature

	Production (g DW m^{-2} y^{-1})		Reference
Year	Inner side	Outer side	
1963 - 1966	300	425	Postma & Rommets (1970)
	230	375	Cadée & Hegeman (1974b)
1972 - 1937	375 -500		Cadée & Hegeman (1974b)
			Cadée & Hegeman (1979)
1974 - 1975		340 - 360	Cadée & Hegeman (1979)
1981 - 1982		850	Cadée (1986)
1985		650	Cadée (1986)
1986	410	750	Veldhuis et al (1988)

Philippart & Cadée (2000) made an overview, and included estimated production by using regression based formulas, that relate system primary production to nitrogen input. She gave values of 750 g DW m^{-2} y^{-1} in the mid-1970's, 850 g DW m^{-2} y^{-1} in the mid-1980's, and around 800 g DW m^{-2} y^{-1} during the early 1990's. Benthic primary production was estimated at 250, 175 and 225 g DW m^{-2} y^{-1} respectively (these data are less reliable because they are computed as the difference between total and pelagic primary production). According to these figures, these values are too high for the 70's, where, according to Philippart & Cadée, primary production was limited by P and not by N. Macroalgae did not contribute significantly to the primary production in this period.

3.5 Process characteristics

3.5.1 Predation pressure by birds

Mortality caused by birds might be an important factor for the structuring of macro fauna assemblages, or even the limitation of macro benthic biomass. Oystercatchers and Eider Ducks are regarded as the most important benthic shell fish predators in the system (Swennen, 1976; Zwarts, 1996; Ens, 2000). Their body weight is estimated as 550 and 2000 g, respectively (or 110 resp. 400 g DW). Their daily prey consumption is estimated at 0.4 (g g^{-1} day^{-1}). For Oystercatchers, this has been studied intensively, resulting in 2 10^{-3} prey s^{-1} ind^{-1}, with 0.5 g DW prey ind^{-1}. This gives 40-45 g DW $Oystercatcher^{-1}$ day^{-1}, or 200 g flesh weight day^{-1}, and 800 g fresh weight day^{-1} (see e.g. Ens, 2000). For Eider Ducks, a daily average consumption of 600-800 gram flesh per ind^{-1} day^{-1} is assumed, according to Swennen (1976) and Nehls (1995). This also is 0.3-0.4 g g^{-1} day^{-1}.

As a yearly average, 100.000 Oystercatchers and 60.000 Eider Ducks are present in the Dutch Wadden Sea. Maximum numbers are higher: Eider Duck summer numbers are about 30.000 for the nineties, and winter numbers are 100.000 - 160.000 (Camphuysen 1996). Oystercatchers are present with lower numbers of about 20.000-30.000, and maximum numbers of about 250.000 birds. Average value ranges from 100.000-150.000 (Meltofte et al, 1994; Smit & Zegers, 1994).

3.5.2 Predation pressure by starfish and crabs

One aspect that is fairly unknown concerns the effect of starfish (*Asterias rubens*) and crabs (mainly *Carcinus maenas*). Both are capable of eating shellfish, the size depending on the size of the predator. *C. maenas* is rather small, and will restrict itself to really small shells. There is little known about the number of starfish and crabs in the system, nor about their sizes. For an about 10 cm arm length starfish, Saier (2001) found a food demand of about 1 medium sized mussel per 3-5 days; which is about 0.1-0.2 g AFDW per animal per day. She found that only in exceptional cases (high seastar abundances), seastars are capable of structuring sub-tidal mussel beds. Seed (1992) mentioned a structuring effect of starfish feeding on smaller sized mussels in a mussel culture plot. The effect probably was not purely negative; possibly such a predation might create better feeding conditions for the larger, untouched, mussels.

Crabs are capable of consuming the smaller size classes of cockles (<20 mm, Seed, 1992); after Sanchez-Salazar et al (1987), he mentioned that crabs may consume up to 80 cockles m^{-2} $month^{-1}$, in sub-tidal areas.

What lacks in our Wadden Sea situation is that very few data are available on densities of starfish and crabs. They may be numerous, but usually this is a local situation. A whole system overview is not available at this moment. Only after better data on numbers and sizes become available, one could come to better food demand estimates. Until then, only scenarios of an overall food demand can be used here; the coupling to reality remains unclear.

3.5.3 Other mortality

A major mortality cause for filter feeders in the Wadden Sea is related to physical phenomena, like storms and water currents and ice. The effect of both first factors has never been quantified very well; on the mass budget of filter feeders, it is a highly unknown term. Overall winter survival, including all possible factors, has been estimated by Beukema (1985). For cockles, he mentioned a relative winter survival may range from almost 0 to about 70 %. Especially cold winters may cause high mortalities; cockles are relatively susceptible to freezing conditions.

Mussels and Baltic Tellins suffer much less from cold, but mussel beds may be severely damaged by floating ice.

3.5.4 Assimilation efficiency of filter feeders

During preliminary computations with this steady-state description, it turned out that the assimilation efficiency of filter feeders (how efficient can algae be transformed into filter feeder tissue) is a key factor in such a steady state model. The BOEDE-model (Baretta & Ruardij, 1988) uses 0.8 s average value. Begon, Harper &Townsend (1990, following Heal & MacLean, 1975) give for vertebrate herbivores 0.5, for invertebrates 0.4. Invertebrate decomposers reach 0.2. Carnivores come up to 0.8, but for the filter feeder system in the Wadden Sea this is not a relevant value. Kersting (pers com) mentioned also a factor of 0.8 for daphnids; Smaal & Twisk (1997) measured (following Conover's AFDW-method) 0.37 (±0.13) -0.47(±0.06) for mussels Mytilus edulis, depending upon food (Phaeocystis and Phaedactylus, respectively, as food source). Conover (1966) measured for Calanus hyperboreus a value of 0.13-0.17. Thus, an average value of about 0.4 seems to make sense as starting point for the computations with varying single parameter values.

3.5.5 Filtration and respiration rates of filter feeders

Basically, filter feeder filtration and respiration parameters cannot be estimated separately from any steady state-like description, simply because one only deals with the resultant of both processes. However, separate EcoWasp dynamical computations (chapter 9), where growth of individuals is computed, combined with literature data on mussel activities reveal values that also result in a realistic yearly individual growth rate. Also, computed uptake rates of chlorophyll-a fit very well to field measurements, as well do computed and measured exchange rates of ammonium and phosphorus (Asmus & Asmus, 1997). In chapter 9, the process of filtration, respiration and growth has been explained in more detail; here we restrict ourselves to a short overview of applied parameter values (Table 3.2).

3.6 Parameter values

Based on the descriptions given above, basic parameter values are summarized in Table 3.2. Data on the exchange rates between North Sea and Wadden Sea are from Ridderinkhof (1988). Morphological data have been derived from Rijkswaterstaat depth measurements (RIKZ, 1998).

Table 3.2 Basic values for parameters and western Wadden Sea system characteristics

Parameter	Name	Value	Unit
Average depth	Hav	**2.83**	m
Volume	Vol	**3.69E+09**	m3
Inflow from North Sea	Qsea	**6.18E+08**	m3/day
Inflow from Lake IJssel	Qfresh	**4.20E+07**	m3/day
Outflow to North Sea	Qout	**6.60E+08**	m3/day
Uptake rate constant algae	kpa	**2.00E+00**	1/day
Respiration rate constant algae	kda	**2.00E-02**	1/day
Mortality rate constant algae	kma	**2.00E-03**	1/day
Temp-function algae growth	f(F,1)	**1**	(-)
Temp-function algae respir	f(T,2)	**1**	(-)
Temp-function algae mortal	f(T,6)	**1**	(-)
Filtration rate constant filter feeders	kgg	**4.00E-02**	m3/gram/day
Respiration rate constant filter feeders	krg	**1.20E-02**	1/day
Mortality rate constant filter feeders	kmg	**1.20E-02**	1/day
Temp function filter feeder filtration	f(T,3)	**1**	(-)
Temp-function filter feeder respiration	f(T,4)	**1**	(-)
Temp-function filter feeder mortality	f(T,5)	**1**	(-)
Filter feeders eaten per bird	kbb	**4.00E-01**	g/g/day
Filter feeders per Starfish+Crabs	ksf	**4.00E-01**	g/g/day
mineralization rate constant detritus	kmin	**6.00E-04**	1/day
Temp-function detritus decay rate	f(T,7)	**1**	(-)
fraction of algae ending as detritus	beta AD	**1.00E-02**	(-)
fraction of filter feeder ending as detritus	beta GD	**1.00E-03**	(-)
Average residence time of the system	tau	**5.59**	day

Table 3.2 (continued) Basic values for parameters and western Wadden Sea system characteristics

Temp-function filter feeder mortality	f(T,5)	**1**	(-)
Filter feeders eaten per bird	kbb	**4.00E-01**	g/g/day
Filter feeders per Starfish+Crabs	ksf	**4.00E-01**	g/g/day
mineralization rate constant detritus	kmin	**6.00E-04**	1/day
Temp-function detritus decay rate	f(T,7)	**1**	(-)
fraction of algae ending as detritus	beta AD	**1.00E-02**	(-)
fraction of filter feeder ending as detritus	beta GD	**1.00E-03**	(-)
Average residence time of the system	tau	**5.59**	day
Phosphorus content of algae	gamA	**2.3E-04**	mol/g
Phosphorus content of filter feeder	gamG	**2.3E-04**	mol/g
Phosphorus content detritus	gam_D	**8.7E-05**	mol/g
Area Western Wadden Sea	West WS	**1.3E+09**	m2
[Detritus] North Sea water	DetNS	**8.0E+00**	g/m3
[ALG] North Sea water	AlgNS	**6.7E-01**	gram/m3
[Nutrient] North Sea	N_NS	**1.5E-03**	mol/m3
[Nutrient] Lake IJssel	N_IJ	**3.0E-03**	mol/m3
[Detritus] Lake IJssel	DET_IJ	**1.3E+01**	g/m3
basic extinction coefficient water	ext0	**2.0E-01**	m-1
Average [Inorganic Solids] WWS	Sol	**5.2E+01**	g/m3
Fishery ton/year	Fish	**1.4E+08**	g DW/y
Total biomass birds	Birds	**3.5E+07**	g DW / WS-system
Starfish + Crabs	StarFish	**0.0E+00**	g/m3
Monod-constant for algae growth	MONOD	**9.00E-05**	mol/m3
Oystercatchers		**1.00E+05**	Number/system
Eider ducks		**6.00E+04**	Number/system
Fraction dry weigth in shell		**5.00E-02**	g/g
Fraction Light period per day		**1.00**	Day/day
Smith constant algae	SMITH	**1.0E+01**	W/m2
Average solar radiation	I_av	**1.2E+02**	W/m2
Eider duck-weight	AFDW	**400**	gr AFDW/ind
Oystercatcher-weight	AFDW	**110**	gr AFDW/ind

Bird weights are from Glotz et al, AFDW is taken as 20% of total individual mass weight

3.7 Numerical investigations

3.7.1 Computed situations

With the parameter values mentioned above as starting point, a number of computations has been performed. The aim was to examine the effects of

- temperature effects
- the algal concentration at the North Sea boundary
- predation pressure by birds, fisheries and what we called 'Starfish+Crabs', ie all the epibenthic predation upon shellfish, and other mortality reasons
- inflow of fresh water
- average system depth
- algal growth parameter choices
- food efficiency of filter feeders (assimilation efficiency, or the part of ingested food that is taken up by the body, and is not excreted as faeces)
- filter feeder parameter choices (filtration capacity, respiration parameters)

The three latter computations serve two goals. First, they are needed to test the parameter choices and find the most appropriate combination. Second, they will give an idea of what can be expected if other species with other growth and feeding characteristics than the present algae and filter feeders become dominant. Especially the effects of a Japanese Oyster invasion can be sketched. The species has a much larger specific filtration rat than the Blue Mussel or Cockle, and it is capable to out compete mussels partly or even completely. E.g., in the Dutch Delta (Easter Scheldt estuary) the species has become the dominant intertidal filter feeder.

3.7.2 Results

Varying the temperature function value

An increase in temperature function (Fig. 3.5a,b) value results in an increase of the filter feeder biomass, of detritus contents and of primary productivity. The algae content is not very sensitive to changes in temperature, because any change in algae production rates is used completely by filter feeders. Therefore, the end-organisms show most of the effects.

Although the steady state situation is not very affected by T-variations, many characteristics deal with seasonal variations. This analysis is restricted to biomass and production; recruitment and other processes do show a close relationship with temperature variations (chapter 7) and will cause system changes whenever they become reality.

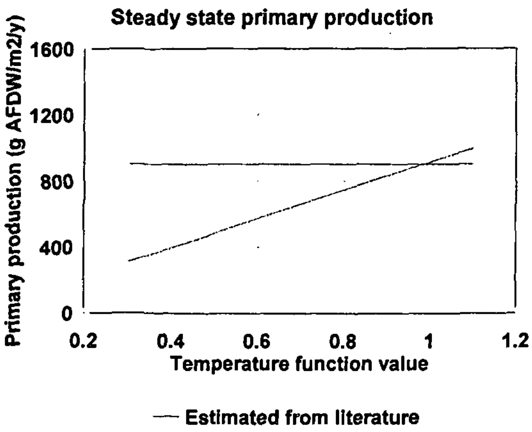
Fig. 3.5a,b also shows that the computed filter feeder biomass density is above the observed range. The reason probably is that in the real world, the maximum value, which is how this steady state value has to be read, will hardly be reached. Or, in other words, on average there will be a large(r) loss factor. This loss may have to do with negatively influenced by a lot of factors, like winter conditions, predation upon larvae by shrimps, and storms flushing away freshly build mussel beds.

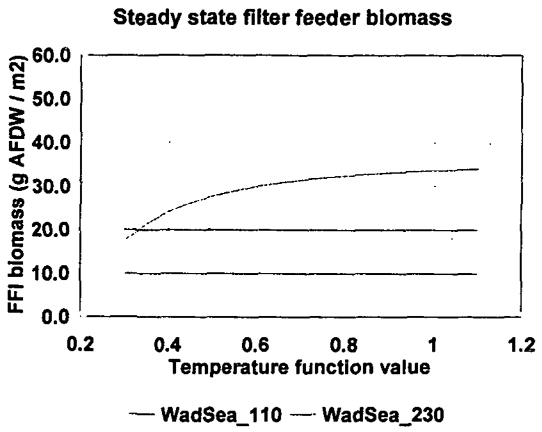
Varying the average system depth

In advance, one would expect that an increase in depth would generally induce an decrease in primary production, and an increase in food availability for filter feeders. But, from the computations it became clear that varying system depth has only very limited over-all meaning for the system's behaviour (Fig. 3.6). Primary production hardly changes, nor does the algae content of the Wadden Sea, and consequently, according to the present computations, there is little effect upon filter feeder total biomass.

Nitrogen as main nutrient instead of phosphorus

The same computations have also been performed with nitrogen ($NO_3^- + NH_4^+$) as nutrients, instead of phosphorus, but this gave only small differences. This indicates that on average, neither P or N can be regarded as *the* main limiting nutrient. In these steady state exercises, there is hardly any effect of nutrient limitation. In reality, where seasonal variations play an important role, nutrient limitations start to be important because maximum growth potential coincides with a minimum of nutrient supply (Chapter 9).


Steady state primary production


Steady state filter feeder biomass

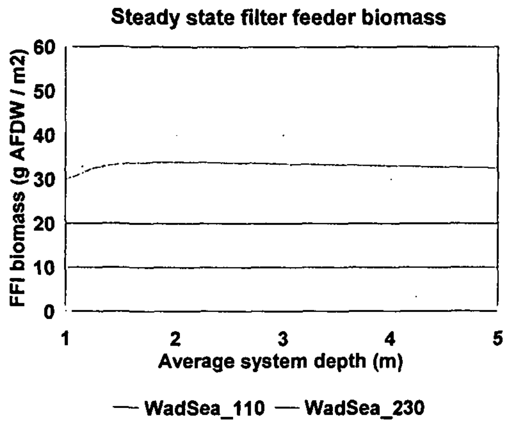
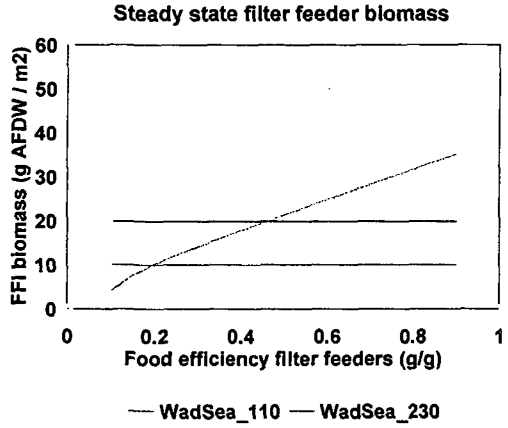

Steady state filter feeder biomass

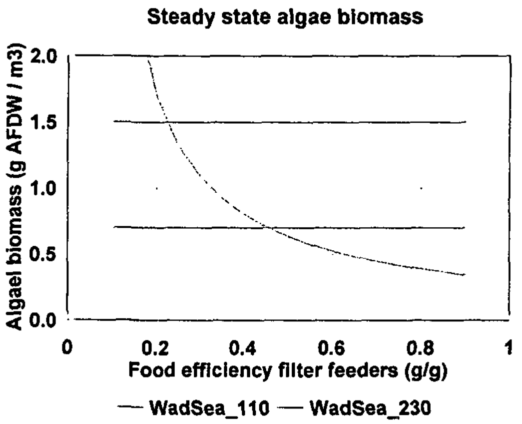
Fig. 3.5a Temperature effects on primary production
Fig. 3.5b Temperature effects on filter feeder biomass

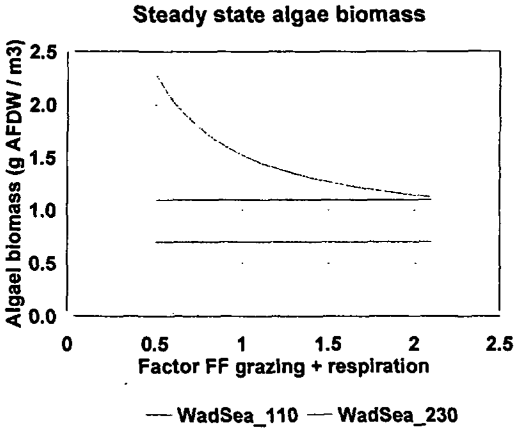
Fig. 3.6 Effect of system depth on filter feeder biomass

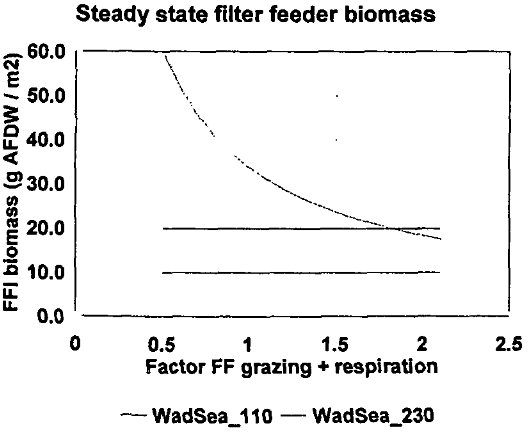
Fig. 3.7a Effect of food assimilation efficiency of filter feeders on steady state biomass density
Fig. 3.7b Effect of food assimilation efficiency of filter feeders on primary production

Fig. 3.8a Effect of filter feeder filtration and respiration rate on primary production
Fig. 3.8b Effect of filter feeder filtration and respiration rate on steady state biomass density


Steady state filter feeder biomass


Steady state algae biomass


Steady state algae biomass


Steady state filter feeder biomass

Varying the algal concentration at the North Sea boundary

Increasing the North Sea boundary algae concentration affects filter feeder biomass directly. Also nutrient concentrations and detritus contents increase, but not algae content ad primary production. Any increase in algae availability is consumed by filter feeders.

Varying the fishery intensity

The result is not very sensitive to slight changes in fishery intensities. Only when the extraction (or read: mortality by whatever causes) is an order of a magnitude higher than 5000 ton flesh year^{-1}, some system characteristics respond. Filter feeder biomass decrease (of course), while steady state nutrient concentrations come close to the average observed values. Primary production and algae biomass increase only slightly, as does the detritus biomass.

Varying the predation pressure by birds

Increasing bird predation pressure is a process similar to increasing fishery extraction, although there are slight differences .

Varying the inflow of fresh water

An increase in fresh water input decreases the filter feeder biomass, because it negatively affects algae availability. Algae contents are not affected; nutrient concentration increases, because of an increased input. Since detritus input increases too, its content in the Wadden Sea increases slightly.

Varying the nutrient concentration in the fresh water inflow

Increasing nutrient concentration in the fresh water input flow only affects the average nutrient concentration self. Reason is that in the steady state computations, there is hardly any effect of nutrient limitation visible: nutrient limitation of plankton growth is only present in a dynamical situation. This is confirmed more or less by the yearly observations: it is also Si that reaches low values first, followed by an abundance change from diatoms towards non-diatoms. Nitrogen and phosphorus both reach low values, and sometimes it seems that N is the relative lower one, and sometimes P. Since fresh water contains much larger amounts of N (compared to P) than North

Sea water does, it is plausible that the inflow quantity of fresh water during the growing season will largely determine whether N or P will limit algae growth.

Varying the assimilation efficiency of filter feeders

The result of the steady-state computations is sensitive to the filter feeder assimilation efficiency (Fig. 3.7a,b). The 'standard' value from table 3.2 results in a slightly too high mean algae concentration, and a nutrient content (based upon phosphorus as main nutrient) that is too low. It is mainly the steady state filter feeder biomass that is high compared to the observed values. This turned out to be the tendency for all computations. Computed primary production is about 700 g DW m^{-2} y^{-1}, which fits the observations satisfactorily.

Varying the filter feeder parameter choices

The steady state result is very sensitive to changing parameters describing filter feeder activities (Fig. 3.8a,b). One effect (assimilation efficiency) has already been mentioned above. An increasing filtration and respiration rate results in lower algae contents; the turnover rate increases, and this acts as a loss factor for algae. Also, both filter feeder biomass and primary production decrease. It is this exercise that is exemplary for the introduction of other species, like the Japanese Oyster, which species does show a higher filtration rate than the Blue Mussel does.

Varying the algal growth parameters

An increasing algae growth rate constant does not influence the [algae] in the Wadden Sea, but only affects [filter feeders], primary production, and to a lesser extend, [detritus].

3.8 Discussion

From the examples given in section 3.6, it is obvious that there are a couple of factors that significantly contribute to whole system characteristics. It is concluded that assimilation efficiency probably should be around 0.4, otherwise most of the results would be out of scope. Also, the filtration and respiration parameter settings turned out to be important, although precise values cannot be estimated accurately enough from steady state model computations. The net individual growth is never part of such computations, and it is this response that is used in dynamic computations that is used to test the adequateness of the chosen parameter values.

Fresh water input nor varying fresh water or North Sea nutrient concentrations induce important changes in the steady-state Wadden Sea ecosystem. North Sea algae content exclusively serves as extra food source for benthic filter feeders, and does not affect algae concentration in the Wadden Sea.

Temperature increase only slightly affects benthic filter feeder densities, as a consequence of increasing primary productivity.

Computed filter feeder densities are a lot higher than observed densities. Reason for this is probably that these results indicate maximum values, while in nature many other factors also contribute to a much higher mortality. Increasing mortality (man-induced, like fisheries, or otherwise, like shrimp predation on larvae, storm losses of mussel beds) gives more realistic densities as well as more realistic nutrient concentrations. Possibly, a far from ideal is something that may really limit filter feeders abundance.

Although solids have not been included in the present computation exercises, solid catchment can be estimated, which will equal maximum solid deposition. This maximum is estimated following dSol/dt=0= -filtration + input - output. Without internal regeneration of suspended solids *and* without explained the computation completely, it follows that the maximum filtration rate is about 2-3 g m^{-3} d^{-1} , or 5-9 g m^{-2} d^{-1}, or, with an average sediment density of 2.5 kg m^{-3}, the maximum biogenic sedimentation is 2-3 mm d^{-1}. In areas with mussel beds, this figure will be much higher; resuspension will reduce the net sedimentation considerably.

4 EFFECTS OF SEA-LEVEL RISE ON SALT MARSHES AND TIDAL FLATS

4.1 Introduction

During the NRP-I project, Houwing et al. (1995) studied the boundary conditions for the development of salt marshes, integrating the hydrodynamics, the morphodynamics and the biologic constraints. In addition, relationships were established between salt marsh extension, sea-level rise and the connected hydro-meteorological conditions. This resulted in a qualitative model for salt marsh development as the result of sea-level rise. This model is verified by some empirical relationships. Using this model it appeared that under sound management conditions the salt marshes along the mainland coast of the Wadden Sea appear to be able to keep pace with rising sea-level through vertical accretion, if the sediment supply is sufficient. However, the reliability of the model is seriously restricted. It is based on empirical data, gained by measurements at a very small site within the sedimentation fields of the Groninger coast. In addition, as a result of sea-level rise, the hydrodynamic conditions, especially the intensity of the tidal currents and the wave action may result in erosion. Furthermore, the estimate of the future sediment supply is uncertain and a lack of sediment could result in erosion and lowering of the salt marsh pioneer zone. Finally, mitigating measures to reduce the negative effects have not been studied in sufficient detail.

During this NRP-II project it has been investigated how the results of the study on the restricted test site of NRP-I can be extended to other salt marsh areas within the sedimentation fields (Fig. 4.1). The study focussed on the pioneer zone of the salt marshes, because this zone attains a very delicate balance between applied shear stress and the bed shear strength. Effects of changes in sea-level rise will firstly be noticed in the pioneer zone of the salt marsh. In addition, during the NRP-II project the test area included the shallow intertidal flats outside the sedimentation fields. When a positive accretion balance is maintained in the areas of the intertidal mudflat and the pioneer zone of the salt marsh there is no problem concerning sea-level rise (Dijkema et al., 1990; Houwing et al., 1995).

In the pioneer zone and on the tidal flats field experiments were conducted to provide data of the hydrodynamics and morphodynamics on sedimentation and erosion. The effects of mitigating measures such as techniques for wave and current reduction were encountered in

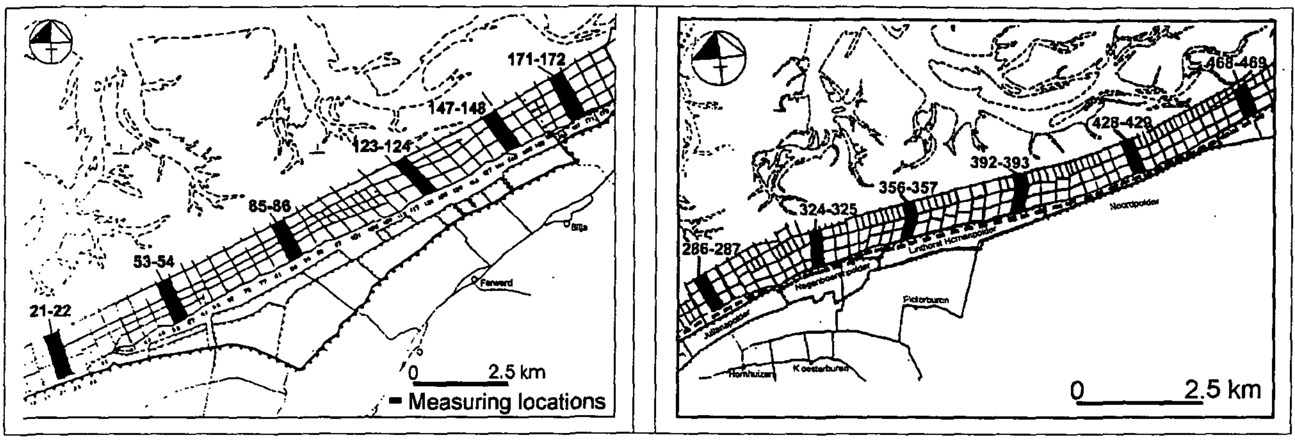


Figure 4.1: Measuring locations along the Dutch salt marsh coast; Friesland (left) and Groningen

Figure 4.2: Leveling instrument.

the study. Besides process knowledge and spatial variations, the role of storm events on salt marsh development was studied to determine the effect of an increase in storm frequency and duration during climatic changes. Another extension of the knowledge on salt marsh development was achieved by studying the effects of long-term changes in wind strength and water levels on salt marsh development. This part of the study was based on long term data of the Ministry of Water Management (Rijkswaterstaat) on height development, wind strength and water levels from 1965 until present.

4.2 Materials and methods

The four-year study period started with a literature study and the writing of a research proposal. For a period of two years field measurements have been executed. The measurements were followed by an extensive analyses period. Furthermore, a model study was done in a GIS (Geographical Information System) using long term Rijkswaterstaat data.

The field measurements in the pioneer zone included measurements of sedimentation and erosion using a leveling instrument (Fig. 4.2). The large scale morphology seaward of the pioneer zone was examined using hydrographic maps of the Wadden Sea. Characteristics of the sedimentation fields were obtained through grain size analyses of bed sediment samples, collected by a core slicer. Current and wave induced shear stress and suspended sediment transport were calculated using continuously collected data of the measuring frames. The instruments that were attached to the frames included pressure sensors, to measure water level fluctuations, electromagnetic flow meters (EMF) and sensors to measure suspended sediment concentrations (SSC-meter) (Fig. 4.3).

The long-term data analyses comprised salt marsh elevation data of the entire salt marsh area along the mainland coast, wind data and water level data. The elevation data, collected since 1965, were processed in a raster based Geographical Information System (GIS) called PCRaster (Van der Meer and Janssen-Stelder, submitted). The yearly collected elevation data were interpolated along the 50 km wide salt marsh coast. The geostatistical method 'universal kriging' was used for this interpolation. The interpolated maps of height, surface, volumes

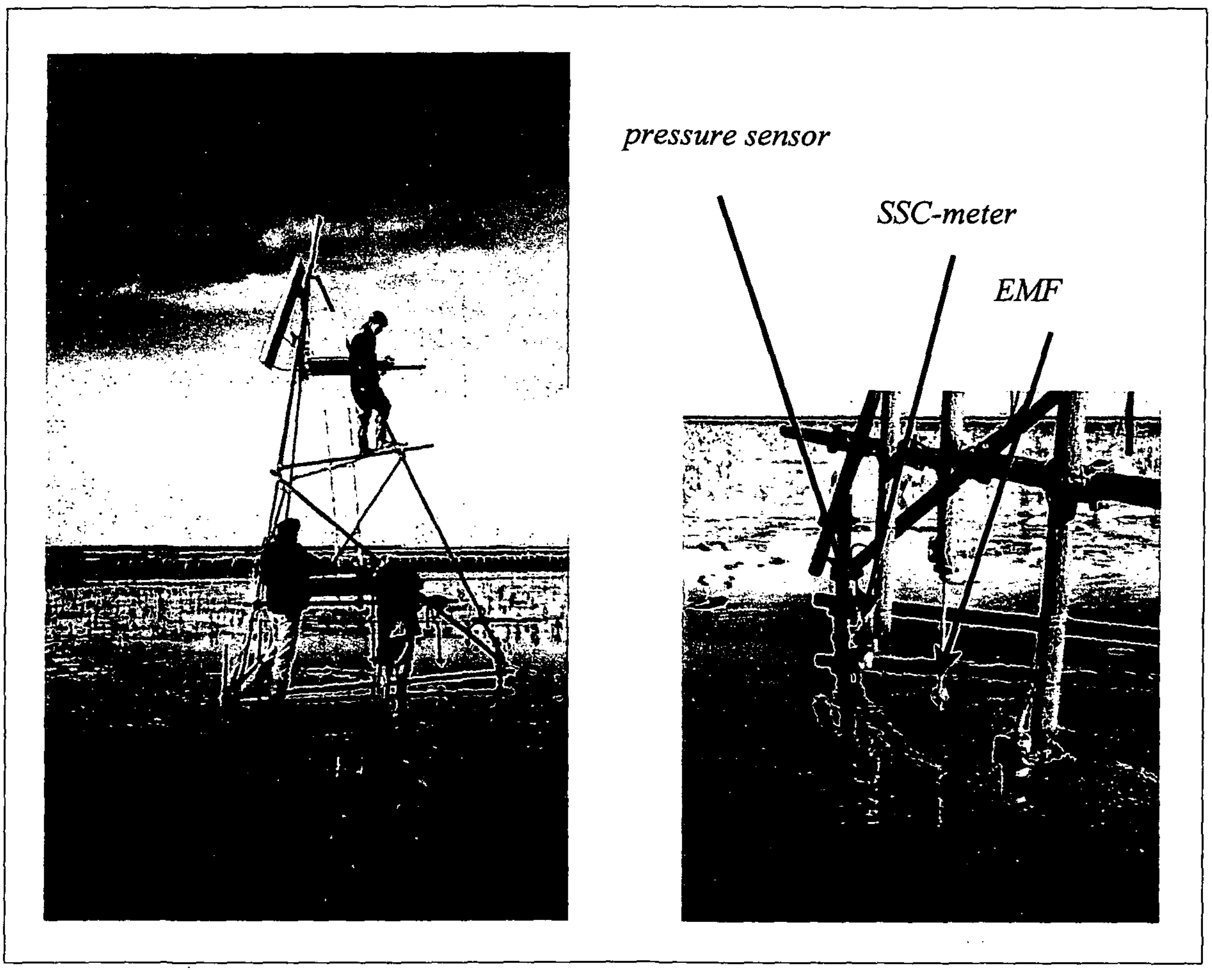


Fig. 4.3: Measuring frame with pressure sensor, electromagnetic flow meter (EMF) and SSC-meter.

Fig. 4.4: Wave reduction by a brushwood groyne.

and seaward extension were created in the GIS model. Wind and water level data was available from a station in Lauwersoog from 1968-1998. From these wind and water level data the average, maximum and top 10% of the values were calculated. The top 10% values were used as a measure for storm frequency and strength. The water levels during the storm events (determined by the wind data) were also calculated.

4.3 Results

4.3.1 Spatial variability in erosion and sedimentation along the coasts of Friesland and Groningen

The interaction between sediment supply and hydrodynamic conditions, especially waves, determines the balance between sedimentation and erosion in the pioneer zone of the salt marshes. Along shore differences in hydrodynamics and sediment supply explain a significant part of the along shore variation in the height development of the studied sedimentation fields. Sediment supply appeared to be an important boundary condition and is strongly related to the morphology of channels and tidal flats seaward of the sedimentation fields (Janssen-Stelder, in press 1). However, whether the sediment is deposited (when the net supply is positive) depends on the wave conditions within the sedimentation fields. The wave heights are greatly influenced by the height and maintenance of the brushwood groynes (Fig. 4.4).

4.3.2 The role of storm events in salt marsh development

During storm events, erosion of the pioneer zone and mudflat is dominated by wave activity. The currents are responsible for transporting the sediment once it is eroded. The correlation between the significant wave height and the net sediment flux is very good for the sites in the pioneer zone of the salt marshes. In case of the mudflat, the correlation is less good but still significant (Janssen-Stelder, in press 2). Storm periods have a similar effect on the pioneer zone at different locations along the salt marsh coast of the Dutch Wadden Sea.

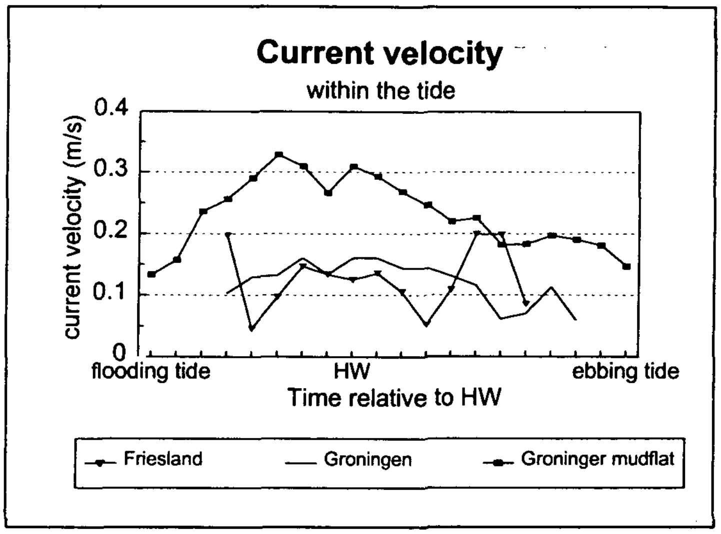


Fig. 4.5: Current velocity within the tide for salt marsh and mudflat locations.

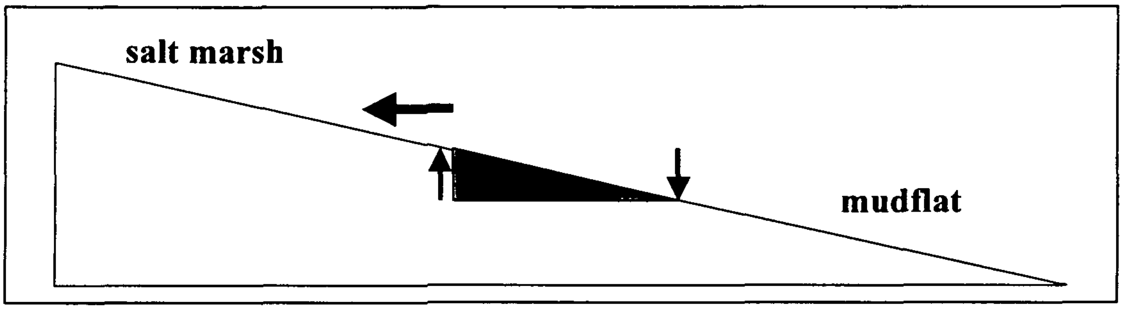


Fig. 4.6: Cliff erosion due to accretion difference on mud flat and salt marsh.

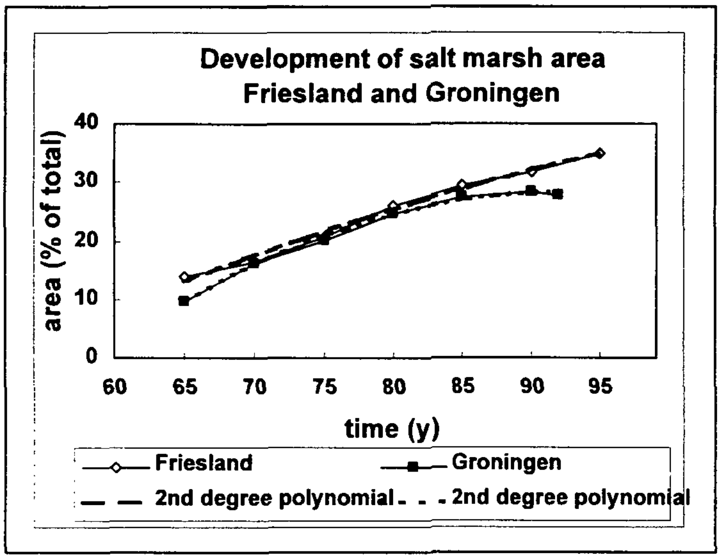


Fig. 4.7: Development of the Friesland and Groningen salt marsh areas between 1965 and 1995.

Wave heights, current velocity and suspended sediment concentrations showed the same values. Therefore the calculated bed shear stresses, sediment fluxes and transport rates agree.

During storm periods more sediment is eroded from the mudflat just seaward of the pioneer zone than in the pioneer zone itself. The main difference between the storm periods in the pioneer zones and the storm period on the mudflat was found in the current velocity, which average value was more than twice as high on the mudflat (Fig. 4.5). Therefore the calculated sediment fluxes and transport rates were larger on the mudflat during events.

The overall conclusion is that severe erosion takes place during storm periods once wave heights exceed 0.20 m. Erosion is greater on the mudflat in front of the pioneer zone of the salt marshes than in the pioneer zone itself. In the pioneer zone the currents are interrupted and slowed down by the brushwood groynes of the sedimentation fields whereas on the mudflat the current is not interrupted and reaches average values that are twice as high as in tethe pioneer zone.

A difference in transport capacity between the mudflat and pioneer zone is caused by this difference in current velocity and induces the difference in erosion between the mudflat and pioneer zone. This results in steepening of the coastal slope. During climatic changes, when wave action increases during increasing storm surges, waves will attack the steeper slope and the salt marsh will suffer from cliff erosion (Fig. 4.6).

4.3.3 Salt marsh development in the Dutch Wadden Sea from 1965 until present

This part of the study is based on long-term elevation data of the entire salt marsh coast of the mainland coast of the Dutch Wadden Sea. The data show that the salt marsh has been accreting since 1965. The accretion is almost linear for the Friesland part of the salt marshes. In the Groningen salt marshes the growth is asymptotic, it has stagnated since 1985 (Fig. 4.7, Janssen-Stelder, submitted).

The effects of wind and water level changes on the development of the total salt marsh area of the Friesland and Groningen coast were examined. The results showed that at a large time scale (decades), the Friesland salt marshes rapidly respond to changes in wind speed and high water levels. The Groningen salt marshes slowly react to changes in wind speed and high water levels. An almost stable accretion balance is attained from 1965 until present in the Friesland salt marshes and therefore this area will better adjust to climatic changes, like increasing storm surge levels, than the Groningen salt marshes.

At a small time scale, the effect of one year with many storm days in combination with high water levels is similar for the Friesland and Groningen salt marshes. At the beginning of the storm year and in the year after the storm year erosion occurs and in the storm year accretion occurs. The salt marsh area is recovered two years after the storm year.

4.4 Discussion

This study has revealed the following issues with respect to climate change. Especially the combinations of sea level rise and an increase in storm frequency and duration effect salt marsh development. High wind speeds from a southwestern to northeastern direction induce a significant set up of the water level in the shallow Wadden Sea. The combination of high wind speeds and high water levels defines a storm surge. During a single storm surge there is a supply of sediment to the sedimentation fields of the salt marshes. On the other hand, erosion occurs on the mudflats located directly seaward of the salt marshes. This difference in accretion results in the development of a height difference between the mudflats and the pioneer zones of the salt marshes. Eventually this will lead to cliff erosion of the salt marsh.

At a larger time scale, an increase in storm surge level has a deteriorating effect on the salt marsh areas along the Friesland and Groningen mainland coast. The results of this study show that the salt marshes need a two-year recovery period after a year with a high storm surge level. When the storm surge frequency increases during climatic changes and high storm surge levels start to occur with an interval period smaller than two years, the salt marsh accretion will not recover from a year with high storm surge levels. The salt marsh accretion will decrease and eventually net erosion will occur. The salt marshes of the Groningen mainland coast attain a very delicate accretion balance at the moment, so these areas will suffer from erosion immediately. A decrease in accretion will occur in the salt marshes of the

Friesland mainland coast. If the sediment supply is sufficient this area may adjust to the climatic changes due to a more stable accretion balance.

The above stated relationships between storm surges and salt marsh development are useful for policy makers. Meteorological and water level data are continuously available for the Wadden Sea area. The salt marsh development can be predicted a few years ahead using these data and the above stated relationships. However, these relationships are only valid when the supply of sediment to the salt marsh areas is sufficient.

4.5 Conclusions and recommendations

Sediment supply and local wave action dominate in salt marsh development along the mainland coast of the Dutch Wadden Sea. During this study, relationships between sediment supply and morphology of the tidal flats and channels directly seaward of the salt marshes were discovered to be plausible. However, the exact relationships could not be proven significantly by the available data. Further research should focus on a holistic approach of the morphological development of the Wadden Sea, including the development of tidal flats, tidal channels and salt marshes.

This study also showed that local wave action determines whether the supplied sediment stays in suspension or is deposited within the sedimentation fields of the salt marshes. The height and maintenance of the brushwood groynes determines the wave action during calm weather condition. During storm surges, when the groynes are submerged, currents are still interrupted but the wave dampening effect reduces significantly. Further research should emphasize on ways to reduce wave action during storm surges in combination with additional supplies of sediment after storm surges.

At a larger time scale, an increase in storm surge level and frequency will seriously affect salt marsh development. This study showed that the salt marsh areas of the mainland coast of the Dutch Wadden Sea need a two-year period to recover from a year with many storm surges. At the moment the salt marshes along the coast of Friesland attain a positive accretion budget so the effect of an increase in storm surges will lead to a decrease in accretion. The salt marshes along the coast of Groningen show growth stagnation so the effect of an increase in storm surges will directly lead to erosion in this area. Further research should focus on the difference between the development of the salt marshes in Friesland and Groningen so maybe a solution to prevent future rapid deterioration of the Groningen salt marshes can be found.

5 BIRD MIGRATION PROCESSES AND MODELLING: IMPROVING THE ECOWASP SHOREBIRD MODULE

5.1 Introduction

How will global climate change affect the many birds that depend on the Wadden Sea for their survival. This report describes the progress that has been made with answering this question during the second phase of the National Research Programme on Global Climate Change (NRP-II). During the first phase (NRP-I) the conceptual foundation of the current investigations and models was laid (Ens *et al.* 1995). During the second phase the models were further developed and scenario calculations could be performed in some cases. An important additional aim was to integrate the models with the ecosystem model of the Wadden Sea (EcoWasp).

The complexity of the problem derives from the fact that we deal with migratory birds. A typical example is the Knot *Calidris canutus*. Fig. 5.1 depicts the arctic breeding areas of the five distinct populations, their migration routes and their wintering areas. Two populations use the Wadden Sea. The *canutus* population passes through the Wadden Sea on migration to the African wintering grounds, while the *islandica* population spends the winter in the Wadden Sea and other estuaries along the coasts of Western Europe. Climate change may affect the birds in the breeding area, on migration and in the wintering area. For the time being, it is not possible to predict the combined effects of climate change in each of these areas. Instead, the annual cycle is broken into different stages and for each stage a model is built, starting from the choices of the individual birds. Next, population models are built that either combine the results of the sub-models, or depend for their justification on the insights generated by the models dealing with the choices of the individuals. Fig. 5.2 shows a simplified scheme and the fancy names given to the models to facilitate discussion.

DYNAMIG deals with the choices the birds have to make during migration (when to be where) and allows us to predict how habitat change will affect fitness components, like survival during migration and reproductive success on the breeding grounds.

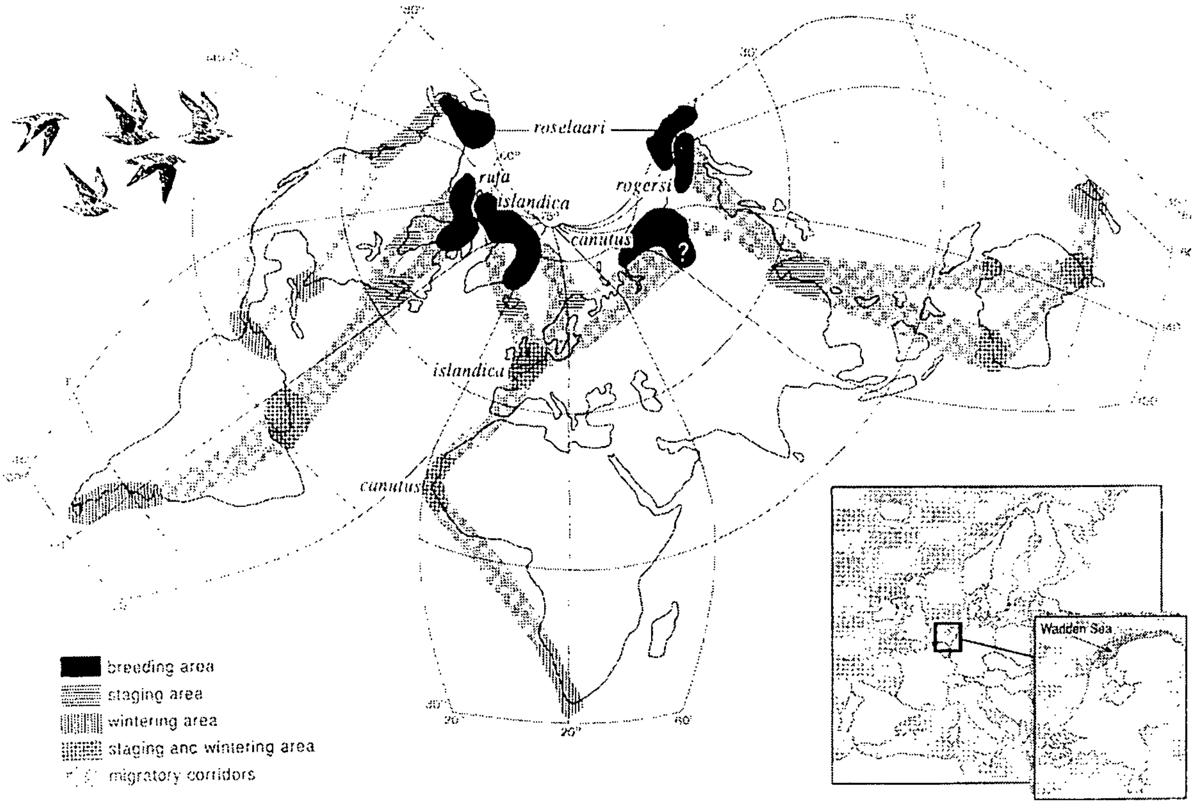


Figure 5.1: The worldwide distribution and the migration routes of the various subspecies of the Knot *Calidris canutus* (courtesy T. Piersma). The inset shows the Wadden Sea, which is important for two subspecies: *canutus* and *islandica*.

DEPLETE deals with the choices of the birds on the wintering grounds (where to feed), including interference during feeding and depletion of the food stock in the course of the winter. When it is known how climate change will affect the food stocks, it can be predicted how many birds will survive the winter under the new conditions.

LARGEPOP does not deal with choices of individuals, but describes the changes in the entire bird population as the result of processes on the wintering ground affecting mortality and processes on the breeding ground affecting reproduction (the migration period is considered to be part of the wintering stage).

HABITAT simply relates the density of birds to characteristics of the breeding, staging or wintering habitat and predicts changes in bird numbers from changes in habitat surface.

In the following we describe each of these models in more detail. Next we investigate for each model how habitat change, as a result of climate change will affect the birds. We end the chapter with a discussion on the most likely effects of climate change on the migratory birds depending on the Wadden Sea.

5.2 Materials and methods

This section describes the mathematical structure of the models in sufficient detail to allow a basic understanding. Detailed descriptions can be found in the various original publications on these models in the scientific literature (DYNAMIG: Weber *et al.* 1998 and Weber *et al.* 1999, DEPLETE: van der Meer & Ens 1997, LARGEPOP: Ebbinge *et al.* submitted, HABITAT: Brinkman & Ens 1998).

5.2.1 DYNAMIG

During migration the bird faces a series of strategic decisions. The ultimate goal is to maximise survival and reproduction. The important point is that the best decision at any one point in time depends on the outcome of previous decisions (Fig. 5.3). A full description of the model is provided by Weber *et al.* (1998), whereas Weber *et al.* (1999) use the model to study the effect of habitat change. The following is a summary of important parts of these two papers.

Basic outline

The environment consists of i = 1,..., N linearly arranged sites, i.e. the wintering ground, N-2 stopover sites and the breeding site N. The distance between site i and i + 1 is denoted as Di. The migration period is divided into t = 0,...,T days. The state of a bird is characterised by its fuel stores x, measured as fuel load divided by lean body mass ($0 < x \leq xmax$) and its location i. If stores fall to 0 the bird dies of starvation. Expected reproductive success depends on date of arrival and fuel load (eq. 5.1a). Reproductive success as a function of date of arrival may take two forms: reproductive success either (i) decreases monotonously, i.e. early arrival is always advantageous, or (ii) increases up to a maximum at an intermediate date and then decreases.

Behavioural options are either to forage with intensity u ($0 \leq u \leq 1$), or to fly to another site. Maximum net fuel gain g per unit time is deterministic. The foraging intensity u describes the fraction of the maximum fuel gain g that will be deposited per unit time. Risk of predation while foraging is only a function of foraging intensity (acquisition costs). Detailed

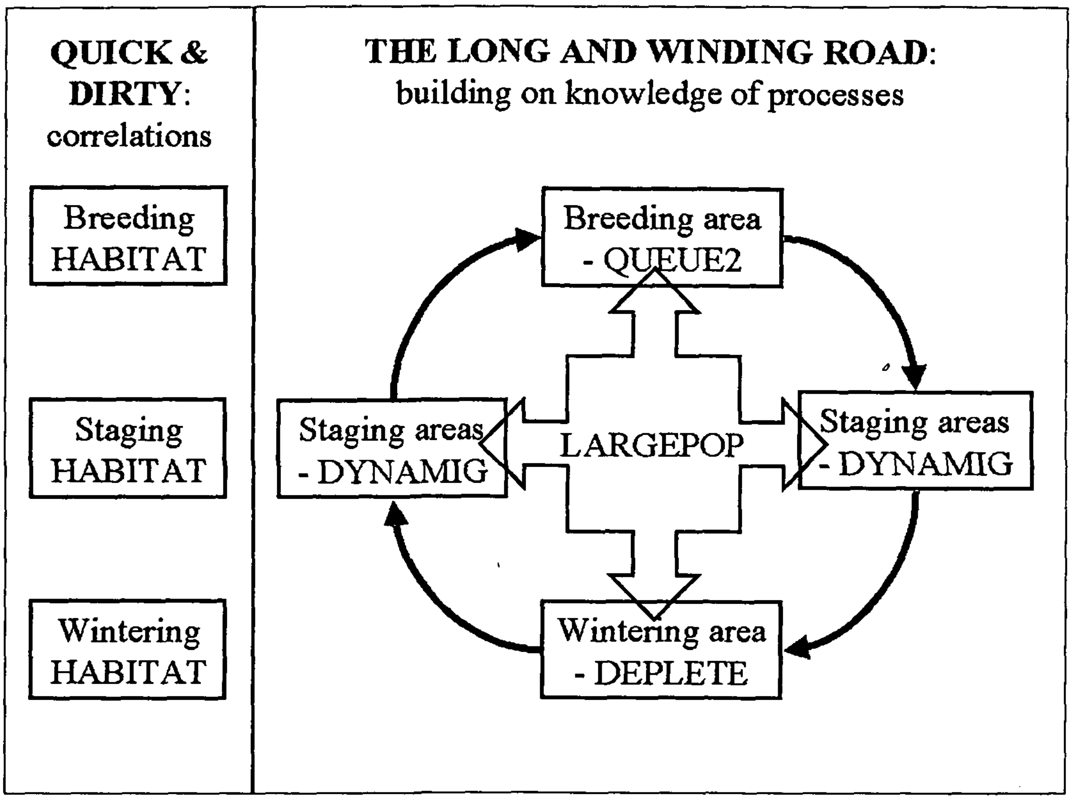


Figure 5.2: Scheme depicting how the various mathematical models relate to the annual cycle and to the modelling approach (correlational or building on knowledge of the underlying processes)

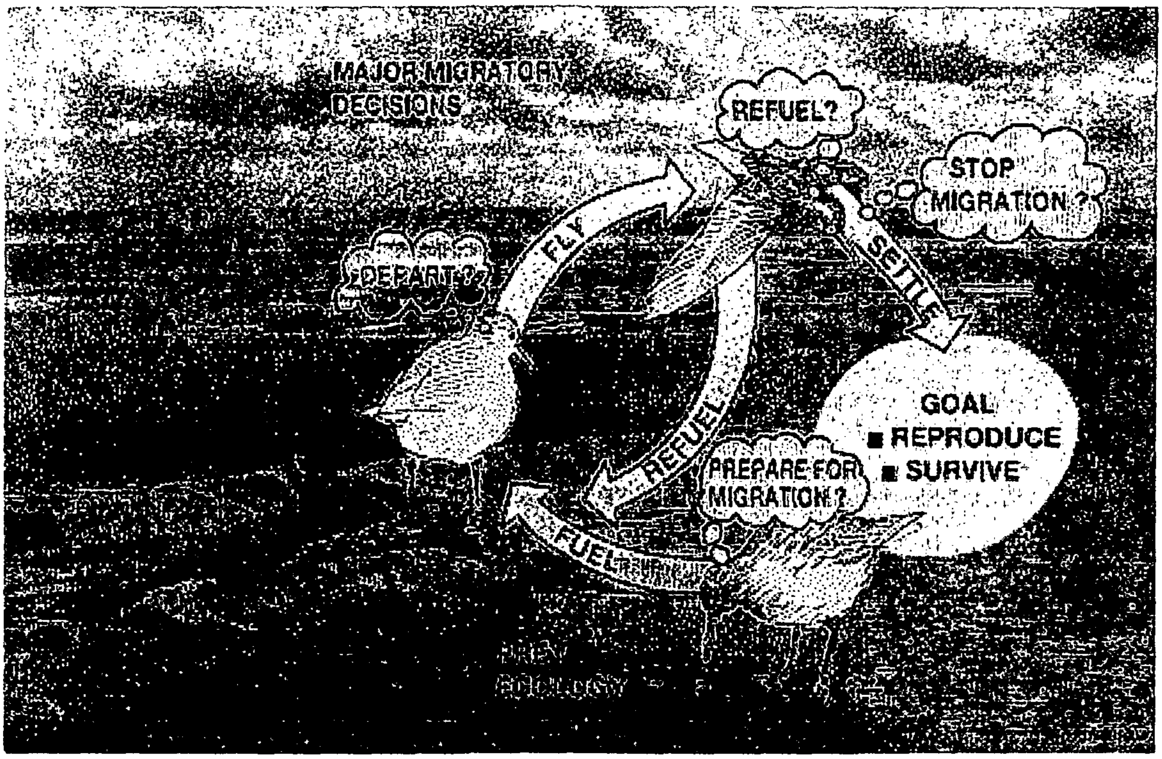


Figure 5.3: Scheme describing the important decisions that birds are facing during migration and the way these decisions are linked to each other (Ens *et al.* 1994).

justifications for the model assumptions and an analysis of other sources of predation risk are given elsewhere (Weber *et al.* 1998). The dynamic programming equations (see below) determine the optimal decision for all combinations of fuel stores, time and site. This decision matrix allows us to follow the fate of individual birds during their migratory journey using a Monte Carlo simulation (Mangel and Clark 1988): starting at site 1 each individual follows the policy defined by the decision matrix, which gives the optimal decision as a function of state and time. If results are derived analytically fuel loads and times are real-valued as opposed to integer-valued.

Parameter values used to study the effects of habitat loss in general

Habitat loss is modelled as a decrease in maximum fuelling rates. To simulate consequences of habitat loss we use two different scenarios: (i) changes occur on a time scale that allows birds to evolve the optimal policy for the new circumstances; (ii) birds use behavioural rules that result in sub-optimal behaviour in altered environments. We distinguish two forms of behavioural rules that lead to sub-optimal behaviour. First, the birds use behaviour that is optimal for a given energetic state, location and time as defined in the decision matrix but is not optimal for the current fuel gain. Second, they use a behaviour that only depends on the initial fuel load at t = 0 and is not at all responsive to the foraging conditions in the altered environment. For most of the cases considered below, this involves using a constant foraging intensity at all sites.

For distances, flight ranges and fuel gains, we have chosen parameter values that roughly conform to medium-sized waders like the Knot *Calidris canutus* and the Sanderling *Calidris alba* migrating along the East-Atlantic flyway to their Arctic breeding grounds. All parameters and their values are summarized in Table 5.1. If forward iterations are used to derive results, they are performed with a cohort of 50000 birds. The initial fuel load at t = 0 is 1 for all birds. The maximum fuel gain at sites i that are unaffected by habitat loss is g(i) = 2 and drops to 0.8 at the sites that are affected.

The dynamic programming equations

The expected future reproductive success of a bird with stores x at time t in location i that behaves optimally is denoted by $F(x,t,i)$. The expected future reproductive success $F(x,t,N)$ upon arrival at the final site N is:

$$F(x,t,N) = R(x)K(t) + B \qquad \text{if } t \le T \text{ and } 0 < x \le x_{max}. \tag{5.1a}$$

Table 5.1: List of model parameters (from Weber *et al.* 1999)

Parameter	Base-line value	Description
N	4	number of sites
D_I	2000 km	distance between site *i* and *i*+1 (*i*<N)
T	100	length of the migration period in days
t_{opt}	76 or 0	optimal arrival date at the breeding ground
B	0	expected future reproductive success
D	1.01 (t_{opt}=76) 0.0025 (t_{opt}=0)	rate of decrease of fitness at the breeding ground
x_{max}	100	maximum fuel load
x_c	1	critical reserve level at the breeding ground required for reproduction
V	60 km/h	flight speed
$m_0(i)$	0	base-line mortality rate (*i*<*N*)
$m_\gamma(i)$	5.10^{-4}	attack rate for intensity-dependent predation risk (*i*<*N*)
B	2	exponent of intensity-dependent predation risk
C	14000 km	determines the flight range for a given fuel load
$g(i)$	2	maximum net fuel gain (*i*<*N*)

The first term on the right-hand side is the expected current reproductive success and *B* is the expected reproductive success from future breeding attempts. Birds that do not reach the breeding grounds in time only receive *B*, i.e. *F(x,T,i)* = *B*, *i* < *N*. The date-dependent function *K(t)* takes the general form

$$K(t) = \begin{cases} \dfrac{t}{t_{opt}} & \text{if } \; t \le t_{opt} \;\; and \;\; t_{opt} > 0 \\ 1 - (t - t_{opt})d & \text{if } \qquad t > t_{opt} \end{cases} \tag{5.1b}$$

with $0 < t \le T$ and $K(t) \ge 0$ for all *t*; t_{opt} is the arrival date where *K(t)* has a maximum and *d* is the rate at which *K(t)* decreases after the optimal time. Either t_{opt} is in the interval $0 < t_{opt} \le T$ such that birds could arrive before t_{opt} or *K(t)* is a strictly monotonously decreasing function, i.e. $t_{opt} = 0$.

R(x) is a unit step function:

$$R(x) = \begin{cases} 1 & \text{if } x \geq x_c \\ 0 & \text{if } x < x_c \end{cases} \qquad (5.1c)$$

$x_c > 0$ is a minimum fuel load necessary for breeding.

Intensity-dependent predation per unit time *(u)* is an accelerating function of foraging intensity u:

$$\gamma(u) = m_\gamma(i) u^b , \qquad i < N \ , \qquad (5.2)$$

where $b > 1$ and m *(i)* is a site specific constant attack rate.

The maximum expected future reproductive success $H_f(x,t,i)$ from foraging with the optimal intensity at any site $i < N$ at time t and gaining $g(i)$ and then following the optimal policy is:

$$H_f(x,t,i) = \max_u \left[(1-\gamma(u))F(x + ug(i), t+1, i)\right]. \qquad (5.3)$$

Starting a flight with fuel load x_0 and flying distance D, the load x_a at arrival is (Weber *et al.* 1998):

$$x_a = \left(\frac{c^2}{\left(c - \left(Y(x_0) - D\right)\right)^2} - 1 \right) 100 \quad , \qquad (5.4)$$

where c is a constant measured in km (Pennycuick 1975); this equation is derived using the flight range equation by Alerstam and Lindström (1990, see also Weber and Houston 1997) Expected maximum future reproductive success when departing from site $i < N$ at time t and then following the optimal policy is:

$$H_d(x,t,i) = \max_j \left\{ F\left(x_a, t + \left(\sum_{l=i}^{j-1} D_l \Big/ 24v \right), j \right) \right\} \quad , \qquad i < j \leq N; \qquad (5.5)$$

v is the flight speed in km per hour.

The optimal decision is the behavioural alternative yielding the highest future expected reproductive success:

$$F(x,t,i) = \max \left\{ H_f(x,t,i), H_d(x,t,i) \right\} \quad . \qquad (5.6)$$

The terminal reward

In all the calculations, for both optimal and sub-optimal behaviour, we have used the terminal reward function that was defined for the unaltered environment. Using a new optimal policy or behaving according to previously optimal rules will, however, affect the reproductive success in subsequent migratory episodes. This may become important if we want to estimate the consequences of habitat loss for population dynamics.

We can analyse the situation by assuming that the terminal reward consists of current and residual lifetime reproductive success. Lifetime reproductive success $V(x,t)$ is given by

$$V(x,t) = B(x,t)(1+n) \quad , \tag{5.7}$$

where $B(x,t)$ is the age-independent reproductive output as a function of state x and date of arrival t on the breeding ground and n is the expected number of future breeding attempts. The expected number of breeding attempts includes the mortality that is incurred during spring migration and is modelled above, but also all the mortality incurred in the rest of the annual cycle for which we provide no explicit model. The terminal reward as defined above is given by

$$\begin{aligned} F(x,t,N) &= V(x,t)/V(x,t_{opt}) \\ &= B(x,t)(1+n)/V(x,t_{opt}) \end{aligned} \quad . \tag{5.8}$$

where t_{opt} is the arrival date where $V(x,t)$ is at its maximum. Behaving according to rules that lead to sub-optimal behaviour results in all cases in a fixed delayed arrival at the breeding ground and an increased mortality. If birds behave optimally both arrival date and mortality can be affected. If the function $B(x,t)$ is not altered after habitat loss, the lifetime reproductive success $V'(x,t)$ in the new environment is

$$V'(x,t) = B(x,t)(1+n') \quad . \tag{5.9}$$

The expected number of breeding attempts n' now includes the increased mortality during the migratory episode and other possible consequences for the rest of the life-cycle. The terminal reward in the new environment is then given by

$$F'(x,t,N) = B(x,t)(1+n')/V(x,t_{opt}) \quad . \tag{5.10}$$

Comparing eqs. (5.8) and (5.10) shows that the terminal reward in the altered environment, $F'(x,t,N)$, is proportional to the terminal reward in the unaltered environment $F(x,t,N)$. Hence all our qualitative conclusions about the ranking of sites will not be affected by the assumption that the terminal reward is changed after the environment is altered.

Parameter values used to study the migration schedule of the Sanderling *(Calidris alba)*

To test if the dynamic migration model could be fitted to the migration schedules of migratory birds in the real world, we organised the international workshop DYNASHOP (Ens 1997, 1998). To this workshop we invited both modelers as well as field workers who had studied the migrations of a particular species in great detail. For each of these species we estimated the parameter values from existing data and we then investigated whether the model could help us understand peculiar aspects of the migration pattern of the species and what would happen when some parameters changed. Nine different species were investigated, but space only permits us to discuss one species, the Sanderling *Calidris alba*, in some detail. Thomas Weber, Gudmundur Gudmundsson and Peter Evans modeled this species.

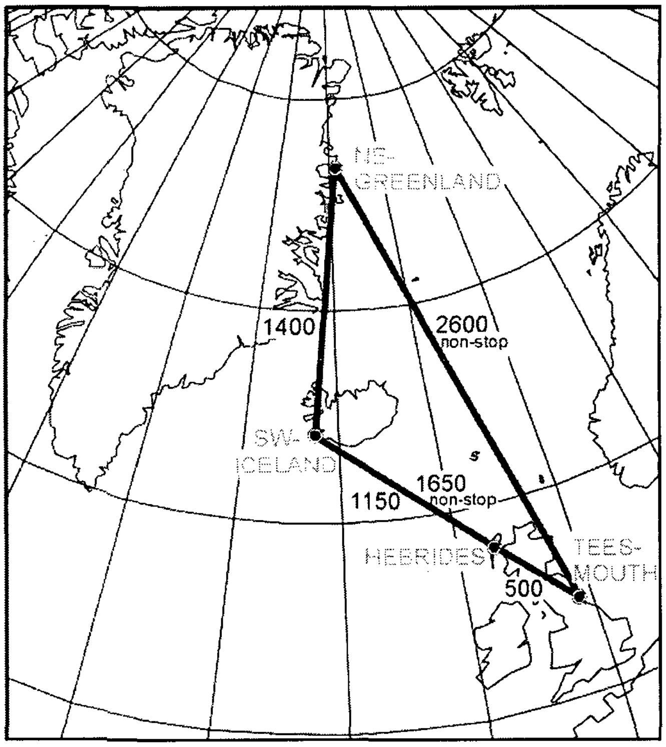


Figure 5.4: Possible migration routes of Sanderlings (*Calidris alba*) spending the winter along the East coast of the United Kingdom (Teesmouth) and breeding in NE Greenland.

The migration patterns of Sanderling passing through Iceland in spring have been reviewed by Gudmundsson *et al.* (1991). They concluded that at least a quarter, but not all, of the northeast Greenland breeding population stop at one or other of two sites in SW Iceland. Some of these birds are known to winter at Teesmouth in N.E. England; others much further south on the eastern Atlantic coasts as far as Ghana. The spring passage through Britain involves stopover sites on both the east coast (including Teesmouth - Pienkowski and Evans 1984) and the west (Ferns 1979). Some birds using the west coast depart with body masses thought to be sufficient for a non-stop flight to Greenland.

The direct line of flight from Teesmouth to NE Greenland would lie to the north and east of Iceland (Fig. 5.4). The direct line of flight from Teesmouth to Iceland would pass over the Western Isles of Scotland (Hebrides), where several thousand Sanderling are known to stage in most springs. None of the 400+ individually colour-ringed Sanderling from the Teesmouth wintering population has been seen in the Hebrides, however, although one has been seen in northwest Scotland.

Using the model of optimal migration strategies, the following quesitons were addressed:
(1) "Should" Sanderlings from Teesmouth stage at the Hebrides on their way to Iceland? If so, under what conditions?
(2) Under what circumstances should Sanderlings fly direct from Britain to NE Greenland, rather than making a dog-leg journey via Iceland and staging there if circumstances necessitate it?

For the first simulation, the parameters from Table 5.2 were used.

5.2.2 DEPLETE

This model deals with birds outside the breeding season, feeding on sessile prey items that do not reproduce during the study period. It describes for instance how a group of oystercatchers gradually deplete the stock of bivalves on which they feed in the course of one winter. It is assumed that the birds are ideal (i.e. they make decisions that maximise fitness and have perfect knowledge) and free (i.e. there are no costs of moving to other patches within the area). Their intake rate of food is positively related to food density and negatively to the density of conspecific competitors. First, we determine how the birds will distribute themselves over a given food supply. Next, we determine how the distribution of both predators and prey will change in the course of one winter. Van der Meer & Ens (1997) give a full description of the model.

Generalized functional response

In the equations that follow, upper-case letters usually denote variables, and lowercase letters parameters. Yet, we make an exception to this rule for those variables that refer to prey densities, predator densities, and patch areas. In those cases lowercase letters refer to a single patch, and upper-case letters to the entire system. For example, p_i (#/m^2) is the predator

Table 5.2: List of parameter values used by Weber, Gudmundsson and Evans to study the migration schedule of the Sanderling during DYNASHOP.

Parameter	name in program	description	values
N	NSites	Number of staging sites	3 (Teesmouth, Hebrides, SW Iceland)
T	FinalTime	number of time steps	70 days, from mid-April to 20 June, by which date most Sanderlings to choose to nest in NE Greenland have laid, or 55 days, resulting from an inability to begin fattening before 1 May, or from an advance in the optimal breeding date in the arctic due to climate warming
x_{max}	Cap		100
	NGains	number of possible gain levels at site	3
	w	determining shape of state dependent fitness function	<10% poor
x_c	xc	determining shape of state dependent fitness function	1
	sigm	0: step fit func at x=1, 1:w & xc determine	0
Di	Y	distance between sites	Teesmouth to Hebrides 500 km Hebrides to Iceland 1150 km SW Iceland to NE Greenland 1450 km Teesmouth to NE Greenland 2600 km
C	c	flight range parameter (km)	11400
V	speed	flight speed (km/day)	1200 km/day
m_0I	b0	predation risks at sites: baseline mortality	2.5 x 10^{-4} per day
$m_\gamma(i)_\beta(i)$	b1	predation risks at sites: coefficient	10^{-7}
A	a	predation risk: mass dependent exponent	2
B	g	predation risk: intensity dependence exponent	0
t_{opt}	topt	optimal arrival time at breeding ground	50-69
D	slopefit	rate of decrease fitness at breeding site	up to day 49: fitness 0 ; day 50-69: fitness1 arrival after day 70: fitness 0
$g_j(i)$	Gains	site 1 gain levels site 2 gain levels site 3 gain levels	Teesmouth 1.0 g/day Hebrides 1.5 g/day Iceland 3.0 g/day
$p_j(i)$	GainsProb	site 1 gain probability site 2 gain probability site 3 gain probability	0 1 0 0 1 0 0 1 0
	ex	expenditure at the sites	0 0 0
	NWind	number of wind classes	5
δ_K	WindAssist	wind assistance	-0.5 –0.25 0 0.25 0.5
q_K	WindProb	probability distribution of wind assistance	during May for Teesmouth to Iceland 0.18 0.40 0.30 0.10 0.02 for Teesmouth - Greenland 0.15 0.30 0.20 0.30 0.15
B	B	expected future reproductive success	0.5

density in patch i, whereas P (#/m^2) is the overall predator density, that is the total number of predators in the system divided by the total area. For the sake of convenience, it is assumed that prey items are of equal size, require equal handling time, and are captured and eaten upon discovery. Unless stated otherwise, predators are always foraging. While foraging, they are either searching, handling, or (in some cases) "fighting". We distinguish searching rate A (m^2/s), which is the area searched per predator per unit searching time, encounter rate E (#/s), which is the number of prey items encountered per predator per unit searching time, and intake rate W (#/s), which is the number of prey items eaten per predator per unit foraging time, i.e. including handling and fighting time.

Generally, the intake rate per unit foraging time per predator in patch i, W_i (#/s) is given by a function of prey density n_i (#/m^2) and predator density p_i (#/m^2)

$$W_i = f(n_i, p_i) \tag{5.11}$$

Usually, the intake rate W increases with increasing prey density n and decreases with increasing predator density. "Ideal" and "free" predators will distribute themselves between patches such that none can improve their intake rate by moving to another patch. Providing that individuals are identical, this means that intake rate is equal across patches. Hence for all patches $i = 1, 2, \cdots, I$ (assuming for the time being that they are all occupied)

$$W_i = f(n_i, p_i) = c \tag{5.12}$$

Below we will for various functions f derive the function g that relates predator density to prey density, the so-called aggregative response:

$$p_i = g(n_i, c) \tag{5.13}$$

for all patches. Given the frequency distribution of habitats in terms of surface area d_i and prey density n_i, the spatial distribution of predators (the "ideal free distribution") is determined by this aggregative response function. The constant c is determined by the constraint

$$\sum_{i=1}^{I} d_i p_i = DP \tag{5.14}$$

where $D = \sum_{i=1}^{I} d_i$ (m^2) is the total surface area of all patches, and DP (#) is the total number of predators in the system. If possible an explicit equation for c will be given. All model parameters are (unless otherwise stated) assumed to be greater than zero.

Deriving the shape of the aggregative response

Two basic approaches exist to estimate the parameters dealing with interference, i.e. the decrease in intake rate due to an increase in the density of conspecifics feeding in the same patch. The mechanistic approach makes assumptions on the mechanism of interaction between the birds and then works out the parameters from these assumptions on the interference process. The phenomenological approach uses empirical studies to estimate the shape of the interference function. Different regression models have been used, leading to different functions. Below, we will only derive results for the models based on the mechanistic approach as these are conceptually more satisfying than the models based on the phenomenological approach. However, at the end of the paragraph we present a table summarizing the main conclusions for all models.

Ruxton *et al.* (1992) made several simple behavioural models of the predation process by using an approach borrowed from chemical reaction kinetics. The predator population is divided in several mutually exclusive states. Given the transition rules between the states, the functional response follows from the steady-state solution of the accompanying differential equations. For example, if a searching and a handling state are distinguished, each transition from handling back to searching is supposed to mean that a prey item is swallowed. Hence the transition rate at the steady-state yields the functional response. It is interesting to note that this simple example leads to Holling's disc equation (Holling 1959), and the intake rate can be written as:

$$W_i = \frac{a n_i}{1 + a h n_i} \tag{5.15}$$

where a is the constant searching rate (m^2/s), and h is the handling time (s). Yet, since interference does not occur (there is no fighting state in which individuals are involved in encounters with conspecifics) and intake rate therefore does not depend on predator density, it is not possible to derive the aggregative response function: all "ideal" and "free" animals will aggregate in the patch with the highest prey density. The relation between intake rate and prey density as given in eq. (5.15) is also known as the type II functional response. Contrary, a type I functional response refers to the situation where the intake rate is proportional to prey density. This can be regarded as a special case of the type II functional response when the handling time h equals zero.

In the more complex models that Ruxton *et al.* (1992) examined, an encounter between predators could mean that a (searching or handling) predator stops its pursuits and enters the "fighting" state. They showed that if a searching predator interacts with both searching and handling individuals, the functional response can be approximated by Beddington's (1975) equation:

$$W_i = \frac{an_i}{1+ahn_i+qp_i} \tag{5.16}$$

where q is a parameter which is actually twice the product of the "rate of predator discovery" (m^2/s) times the "loss of searching time per encounter" (s). As these two parameters always occur together, they can be replaced by the compound parameter q (m^2), which may be called the interference area. If a searching predator may also interact with a predator already involved in an aggressive encounter, the same model arises, but with a slightly different interpretation of the parameter q.

Setting the intake rate equal for all patches i

$$\frac{an_i}{1+ahn_i+qp_i} = c \tag{5.17}$$

leads after some straightforward algebraic manipulation to a linear relationship between predator density p_i and prey density n_i

$$p_i = \frac{1}{q} + \frac{a(1/c-h)}{q} n_i \tag{5.18}$$

For patches with a prey density $n_i < \frac{1}{a(1/c-h)}$ predator densities are set equal to zero, as negative predator densities are nonsense. For the same reason, $1/c$ (which is the average foraging time per prey item consumed and thus includes handling time) must always be larger than the handling time h. This constraint holds for all models that follow.

Now assume that the first $j-1$ patches (the I patches are ordered in increasing prey density) remain unoccupied with predators. Then the value for the constant c can be derived from noticing that the total number of birds in the system, which is known, equals $D^*P^* = \sum_{i=j}^{I} d_i p_i$, where $D^* = \sum_{i=j}^{I} d_i$ is the total surface area (m^2) of all occupied patches, and P^* is the overall predator density (#/m^2) for all occupied patches. Similarly, $D^*N^* = \sum_{i=j}^{I} d_i n_i$, where N^* is the overall prey density (#/m^2) for all occupied patches. Then,

$$P^* = \sum_{i=j}^{I} \frac{d_i}{D^*} p_i = \sum_{i=j}^{I} \frac{d_i\left(a(1/c-h)n_i - 1\right)}{D^* q} \tag{5.19}$$

which results in

$$c = \frac{aN^*}{1 + ahN^* + qP^*} \tag{5.20}$$

The value of j can be derived from noticing that the birds should not visit those patches for which the intake rate without considering interference is smaller than the intake rate (taking interference into account) would be, if only the plots that have a higher prey density are visited. Thus, the patch $j-1$ (recall that patches are ordered in increasing prey density) for which

$$\frac{an_{j-1}}{1 + ahn_{j-1}} < \frac{aN^*}{1 + ahN^* + qP^*} \tag{5.21}$$

holds, remains empty with predators. The same is true for all patches with even lower prey densities. Below we will refer to this model, in which searching predators interact with both searching and handling conspecifics, as the Beddington model.

Ruxton *et al.* (1992) also showed that if a searching predator only interacts with other searching predators, the functional response approximately looks like:

$$W_i = \frac{an_i}{1 + ahn_i + \frac{qp_i}{1 + ahn_i}} \tag{5.22}$$

Proceeding as above,

$$p_i = -\frac{1}{q} + \frac{a(1/c - 2h)}{q} n_i + \frac{a^2 h(1/c - h)}{q} n_i^2 \tag{5.23}$$

and

$$c = \frac{aN^* + a^2 h \frac{\sum_{i=j}^{I} d_i n_i^2}{D^*}}{1 + 2ahN^* + a^2 h^2 \frac{\sum_{i=j}^{I} d_i n_i^2}{D^*} + qP^*} \tag{5.24}$$

In spite of its complexity, the occurrence of the term $\sum d_i n_i^2$ in the latter equation tells us that the intake rate c depends on the variance of the prey densities in the suitable patches $i = j, j+1, \cdots, I$. In contrast, the Beddington model predicted an intake rate (eq. 5.20) that only depends on the overall prey density N^* in the suitable patches. Below we refer to the "search-interaction-only" model as the Ruxton model. In the trivial case when the handling time is zero, the two models are equivalent.

The aggregative responses resulting from the various interference models are compared in Table 5.3.

Table 53: A characterisation of the interference models. The last column shows whether the second derivative of the aggregative response function is positive, zero or negative for all prey densities greater than zero (provided that the searching rate, handling time and interference coefficient are greater than zero). The sign(x) function gives the sign of x, thus if x>0 then sign(x) should be read as +. From van der Meer & Ens (1997).

Model	Effect on	Threshold prey density	Maximum predator density	Second derivative
Beddington	searching and handling	$\frac{1}{a(1/c-h)}$		0
Ruxton	searching	$\frac{1}{a(1/c-h)}$		+
Hassell-Varley	searching rate			$\operatorname{sign}\left(\frac{1}{m}-1\right)$
Doublelog	intake rate		$r\left(\frac{1}{ch}\right)^{1/m}$	–
Semilog	intake rate		$r\exp\left(\frac{1-ch}{m}\right)$	–
Untransformed	intake rate	$\frac{1}{a(1/c-h)}$	$\frac{1-ch}{q}$	–

Prey depletion in the course of one winter

The aggregative responses that we calculated only apply to a single moment in time. However, due to predation prey will be depleted. If there is no concurrent prey renewal, as is the case for waders that feed on benthic invertebrates in winter, this means that the standing stocks of prey in the occupied patches continually decline. Under the ideal free assumption, this may lead to a redistribution of the predators. We are not able to provide analytical solutions for this process of redistribution under depletion, but a look at the shape of the aggregative response points to some generalisations. First, for those aggregative responses that are characterised by a threshold density, it is clear that this threshold prey density will shift downwards as depletion proceeds, i.e. poorer and poorer patches will be occupied. Second, for those models (Hassell-Varley, Ruxton) where predators strongly aggregate in the best patches, these patches will be severely depleted and the predators will subsequently spread out to patches of lower quality, i.e. patches will quickly become more similar in the course of winter. In contrast, if there is a maximum predator density, as in the models that were based on the empirical relationship between intake rate and predator density, it could be

Table 5.4: Parameter values used for various possible descriptions of the generalized functional response.

Model	Parameter	units	value
all models	Maximum search rate	m2/s	0,0007
all models	Handling per prey	s	50
all models	Minimum intake rate	prey/s	0,002
all models	Normal intake rate	prey/s	0,0021
Beddington	Interference area q	m2	1000
Ruxton	Interference area q	m2	1000
Hassell-Varley	Interference factor m	-	0,4
Hassell-Varley	Reference density r	#/m2	0,0001
Doublelog	Interference factor m	-	0,27
Semilog	Reference density r	#/m2	0,0001
Untransformed	Interference area q	m2	20

Table 5.5: Description of the Dutch Wadden Sea. Habitat types are distinguished on the basis of emersion time. The prey density refers to "standardised" shellfish of 0.25 gram AFDM, available to oystercatchers, making up 50% of the total biomass of benthic animals. The table refers to an average year.

habitat type	Surface (km^2) current situation	surface (km^2) after 60 cm sea level rise	height (m)	emersion period (fraction time)	prey density ($\#/m^2$)
1	184	159	0,14	0,06	12
2	197	168	0,45	0,16	36
3	183	156	0,77	0,25	72
4	163	110	1,05	0,34	60
5	162	64	1,33	0,42	48
6	157	48	1,65	0,52	36
7	77	27	1,94	0,64	24
8	123	23	2,38	0,85	6

that a good patch is effectively underused relative to a poor patch so that depletion in terms of the fraction of prey removed will be more intense in the poor patch.

We will examine these suggestions by numerical simulations. We will show the effect of prey depletion in the course of the winter on changes in the aggregative response of the Oystercatcher. In our approach, each day (the winters starts at September 1 and ends at day 215, i.e. March 31) the birds are redistributed over all patches according to the various aggregative response functions. In order to survive, the birds have to balance their energy budget. This requirement implies that they have to gather a more or less fixed amount of food each day. Extra food intake will not increase their fitness, as they can not direct it into growth or reproduction. Thus, the predator-prey system is of a relatively simple structure. Prey decreases at a rate determined by the number of predators in the system times the fixed rate of food intake per predator. Predators either survive or die. They die when their intake rate gets consistently below their energy requirements. Yet in the numerical example presented here this did not occur. Each day prey density n_i in each patch decreases by the bird density p_i times the required intake rate c_0 (#/s) times the day length (s). Model runs are performed for oystercatchers feeding on bivalves of 0.25 g ash-free dry mass. The required intake rate c_0 is based on a power of 8.8 W, which is the estimate for a winter day with a temperature of about 5 °C (Kersten & Piersma 1987). These energy needs correspond to a digestion efficiency of 0.8 (-) times energy content of 22000 (J/g) times a daily averaged ash-free dry mass intake rate of 0.0005 (g/s). This implies a daily food intake of 0.0005 (g/s) times 86400 (s) is 43.2 g/day or 173 #/day. If a day contains 12 hours foraging time the required intake rate while foraging is 0.001 g/s or 0.004 #/s, that is one prey every 250 s. The parameters used for the generalized functional response are given in Table 5.4. The initial prey densities, and the patch areas are given in Table 5.5.

5.2.3 LARGEPOP

Complex simulation models exist to describe the population dynamics of an entire bird population. We had two aims with LARGEPOP. First, to develop a model that was sufficiently simple to be analytically tractable. Two, to develop a model for which the parameters could be estimated from existing data. A paper with a full description has been sent to a scientific journal (Ebbinge *et al.* submitted).

LARGEPOP is a discrete time mathematical model which divides a year into two seasons: a reproductive and a non-reproductive season (akin to models in Fretwell, 1972, and Goss-Custard & Sutherland, 1997). We assume that in the reproductive season there is no mortality. In our model we had to simplify the real world in order to be able to use the existing population data, which are based on annual censuses in mid-January. In the model therefore the population size just after reproduction in August is estimated, by including only those newly born geese that eventually manage to survive till January. Thus, part of the mortality of young-of-the-year is included in the estimated reproduction. Therefore our reproductive season runs from January till August, and the non-reproductive season from August till January. In the model all mortality only occurs during this non-reproductive season. In this way all mortality in the model is concentrated during the period of autumn migration, which realistically coincides with the hunting season. We count years starting just after the breeding season and let k denote the year, $k = 0,1,...$, where 0 corresponds to 1955. We differentiate between two seasons in the same year and we want to express this in the notation. By N_{2k} we denote the population size of Dark-bellied Brent Geese in August of year k, and discount all young that are doomed to die before January. By N_{2k+1} we denote the population size after the autumn migration in January of the next year. So, for example, year 0 has the population sizes N_0 just after the breeding season in 1955 and a population size reduced by mortality N_1 at the start of the wintering season in 1955-56). Likewise N_3 denotes the population size just after the breeding season in year 1 (1956) and N_4 the winter population in 1956-57, etc.

We assume that the number of first-winter birds in year k, is given by

$$N_{2k-1}f(N_{2k-1}) \tag{5.25}$$

where f is a function that describes the possible density dependence in reproductive success (i.e. any density dependence is assumed to arise from the numbers of birds present in the breeding season). Similarly, we assume that the number of birds that do not survive the autumn season in year k is given by

$$N_{2k}h(N_{2k}) \tag{5.26}$$

where $h(N_{2k})$ is the fraction of birds that does not survive the non-reproductive season, which could possibly be density dependent. In the next section we estimate both $Nf(N)$ and $h(N)$ as functions of N from the data.

Our basic model becomes

$$\begin{aligned} N_{2k} &= N_{2k-1}(1+f(N_{2k-1})) \\ N_{2k+1} &= N_{2k}(1-h(N_{2k})). \end{aligned} \tag{5.27}$$

We analyze the following model:

$$\begin{aligned} N_{2k} &= N_{2k-1}(1+(a+bN_{2k-1})e^{-cN_{2k-1}}) \\ N_{2k+1} &= N_{2k}(1-\delta) \end{aligned} \tag{5.28}$$

Since the time-unit of one year has been cut into two half-year seasons, we look for steady state pairs (N, M) such that

$$\begin{aligned} N &= M(1+(a+bM)e^{-cM}) \\ M &= N(1-\delta) \end{aligned} \tag{5.29}$$

(i.e. a steady state is a pair (N, M) such that in each consecutive year there will be N of birds at the start of the summer season and M birds at the start of the winter season). One can immediately see from the second equation that $M = N(1-\delta)$. We can then find N by solving

$$N = N(1-\delta)+(a(1-\delta)N+b(1-\delta)^2N^2)e^{-c(1-\delta)N} \tag{5.30}$$

This leads to $N = 0$, or, for positive N, the possible solution of

$$\frac{\delta}{1-\delta} = (a+b(1-\delta)N)e^{-cN(1-\delta)}. \tag{5.31}$$

We cannot solve the latter equality for N analytically, but we can analyse it graphically by plotting the right-hand side, which we denote by $g(N) = f(N(1-\delta))$, and the left-hand side, a horizontal line, in one graph as functions of N. The behaviour of g as a function of N is straightforward, it is unimodal; at $N = 0$, we have

$$g(0) = a \tag{5.32}$$

and its derivative is given by

$$\frac{d}{dN}g(N) = -c(1-\delta)(a+bN(1-\delta))e^{-cN(1-\delta)} + bN(1-\delta)e^{-cN(1-\delta)}. \tag{5.33}$$

The function g has a maximum at

$$\overline{N} = \frac{b-ca}{cb(1-\delta)}. \tag{5.34}$$

The intersection points N^* correspond to steady state pairs (N^*, $N^*(1 - \delta)$) of our system. We study the various possibilities for intersections of the curves as we vary the only parameter with a clear biological interpretation, i.e. δ, the per capita probability of not surviving the winter season. The other parameters (a, b, c) are set to the values estimated for them from the reproduction data. The bifurcation diagram (Fig. 5.5) is a numerical calculation of the steady

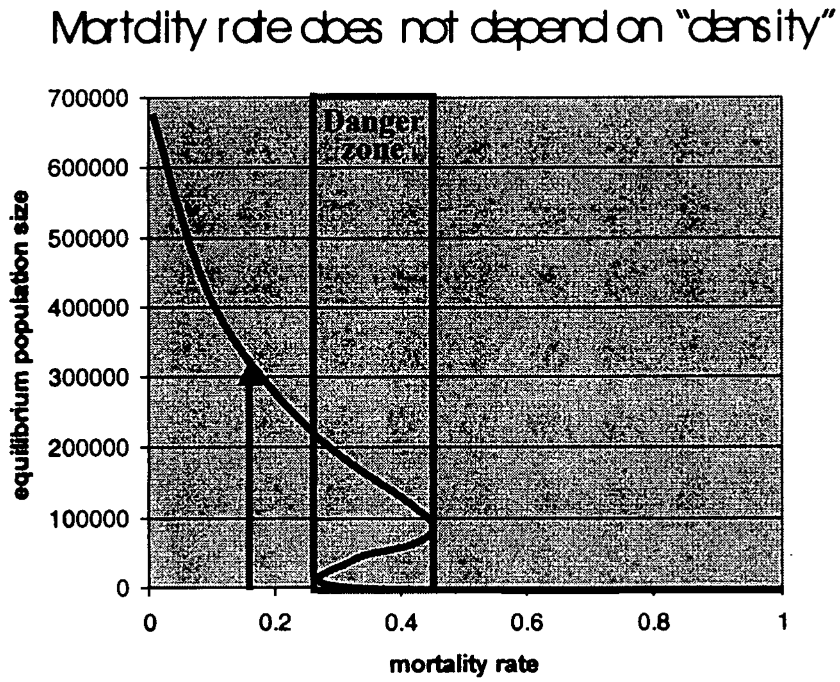


Figure 5.5: Bifurcation diagram where the steady state population size N^*, as calculated from the model, is given as a function of the model parameter δ, the per capita death rate. The graph has two branches. The horizontal branch at $N^*=0$ corresponds to the zero steady state, which exists for all values of δ. This state is unstable to the left of the dot and stable to the right of the dot. The curved branch corresponds to a positive steady state. This state is stable everywhere, except for the backward branching part in between the two dots. From Ebbinge *et al.* (submitted).

state value for N as a function of the parameter δ. We can fully understand the dynamics of the model, and the graph in Fig. 5.5, by the following argument. The unimodal curve $g(N)$ can have no intersection, one intersection or two intersections with the horizontal line $N = \delta/(1-\delta)$. If we increase δ from slightly larger than 0 to slightly less than 1, the horizontal line will shift upward. The unimodal curve will change as well, but will stay unimodal. The different possibilities for the resulting intersections correspond to regions for δ where $N^* = 0$ is the only steady state (and stable), where there is one positive stable steady state, and where there are two positive steady states, one stable and one unstable.

A straightforward calculation allows us to obtain the regions in the interval $0 < \delta < 1$ with the appropriate behaviour. If $\delta/(1-\delta) < a$, there is only one positive intersection, i.e. if $\delta < 0.32$ (approx.). If $\delta/(1-\delta) > a$, there are two positive intersections, until the horizontal line reaches the top of g (where the two intersections merge). This point can be obtained by solving

$$g(\overline{N}) = \frac{\delta}{1-\delta} \qquad (5.35)$$

for δ. This has an explicit unique solution $\delta \approx 0.44$. If δ is increased further we see that the curves no longer intersect and 0 is the only steady state. The steady state 0 is stable for the whole region characterised by $\delta/(1-\delta) > a$.

5.2.4 HABITAT

In stark contrast to the previous models, which seek to derive important relationships from an understanding of the underlying processes, the HABITAT model simply correlates the densities of birds to properties of the habitats in which they live. This can be done for each stage of the annual cycle of the bird. To date we have only developed the model for waders feeding on intertidal mudflats of the Wadden Sea during the non-breeding season, in particular during late summer and early autumn, when numbers are maximal. Brinkman & Ens (1998) provide a full description.

The feeding density of the birds (D in numbers per m^2) is predicted from the median grain size of fractions greater than 16 mu (M in μm) and emersion time (E in hours) as follows:

Table 5.6: Comparison of predicted total number of birds feeding on intertidal mudflats in the Dutch Wadden Sea during July-Sept with the numbers actually counted (N=8) in the period 1979-1990. For each species the following data are listed: the minimum number, the maximum number, the mean number, the standard deviation (SD), the standard deviation as % of the mean (RSD), whether a good habitat model could be fitted, the number predicted and the predicted number as percentage of the mean counted. From Oost *et al.* (1998).

Species	min	max	mean	SD	RSD	fit	pred.	ratio
Curlew Sandpiper	102	1465	795	478	60%	no fit		
Spotted Redshank	914	3130	2006	837	42%		1037	52%
Ringed Plover	888	4752	2114	1199	57%		1287	61%
Turnstone	1225	3870	2257	813	36%	no fit		
Greenshank	1292	4309	2500	1178	47%		1696	68%
Avocet	8308	17554	12790	2895	23%	no fit		
Redshank	12306	31332	18366	6516	35%		43244	235%
Grey Plover	11650	33240	20864	7536	36%		19119	92%
Shelduck	2677	37515	26664	11857	44%	no fit		
Common Gull	18207	43902	29190	9162	31%	no fit		
Bar-tailed Godwit	28152	57655	36687	10530	29%		42278	115%
Knot	29937	52648	42049	8790	21%		5400	13%
Black-headed Gull	43677	98335	72308	20054	28%		340000	470%
Herring Gull	33961	114499	76392	32232	42%		17500	23%
Curlew	44265	138005	91867	26366	29%		65037	71%
Dunlin	119434	375300	187454	81163	43%		19300	10%
Oystercatcher	161485	272818	223671	39181	18%		126268	56%

$$D = \exp(a + bM + cM^2 + dE + eE^2 + fME) \qquad (5.36)$$

where a, b, c, d, e and f are constants. When f=0, this equation yields a Gaussian distribution with contours in the shape of ellipses whose main axes are parallel to the M-axis and the E-axis. When f does not equal 0, the effects of grain size and emersion time are not independent of each other. As a result of this interaction, the two main axes of the contour ellipses will not be parallel to the M-axis and the E-axis.

The constants must be fitted from the data using statistical procedures. We employed a Linear Modelling Technique from the Genstat statistical package, using a least-squares criterion. A problem with the available data set was that we had no observations of sandy flats with a long exposure period. Such areas are known to hold few birds, so we decided to include zero values. Even then it was not always possible to obtain meaningful parameter estimates. When this happened, we have indicated this with *no fit* in Table 5.6. For species where we succeeded in obtaining a meaningful model, we used it to predict the total number of individuals for the entire Dutch Wadden Sea. In some cases there was a large discrepancy between predictions and observations, especially in rare species. However, in a surprising number of species the predicted number was reasonably close to the observed number and for these species we felt confident that we could predict the effects of habitat change.

5.3 Results

Effects of climate change on the Wadden Sea

The various bird models that we discuss in this chapter relate bird numbers or bird behaviour to habitat change. Thus, if we want to predict the effects of climate change, we must first investigate how climate change will affect the habitats on which the birds depend. Precise scenarios are only available for the Wadden Sea, as this was the target area for this NRP project. These scenarios only apply to the effects of sea level rise, i.e. the effects of a rise in temperature are ignored. Both DYNAMIG and LARGEPOP require knowledge on all areas along the migration route. Thus, these Wadden Sea scenarios can only be used for calculations with DEPLETE and HABITAT, which can be applied to the Wadden Sea without knowledge on habitat change elsewhere along the migration route.

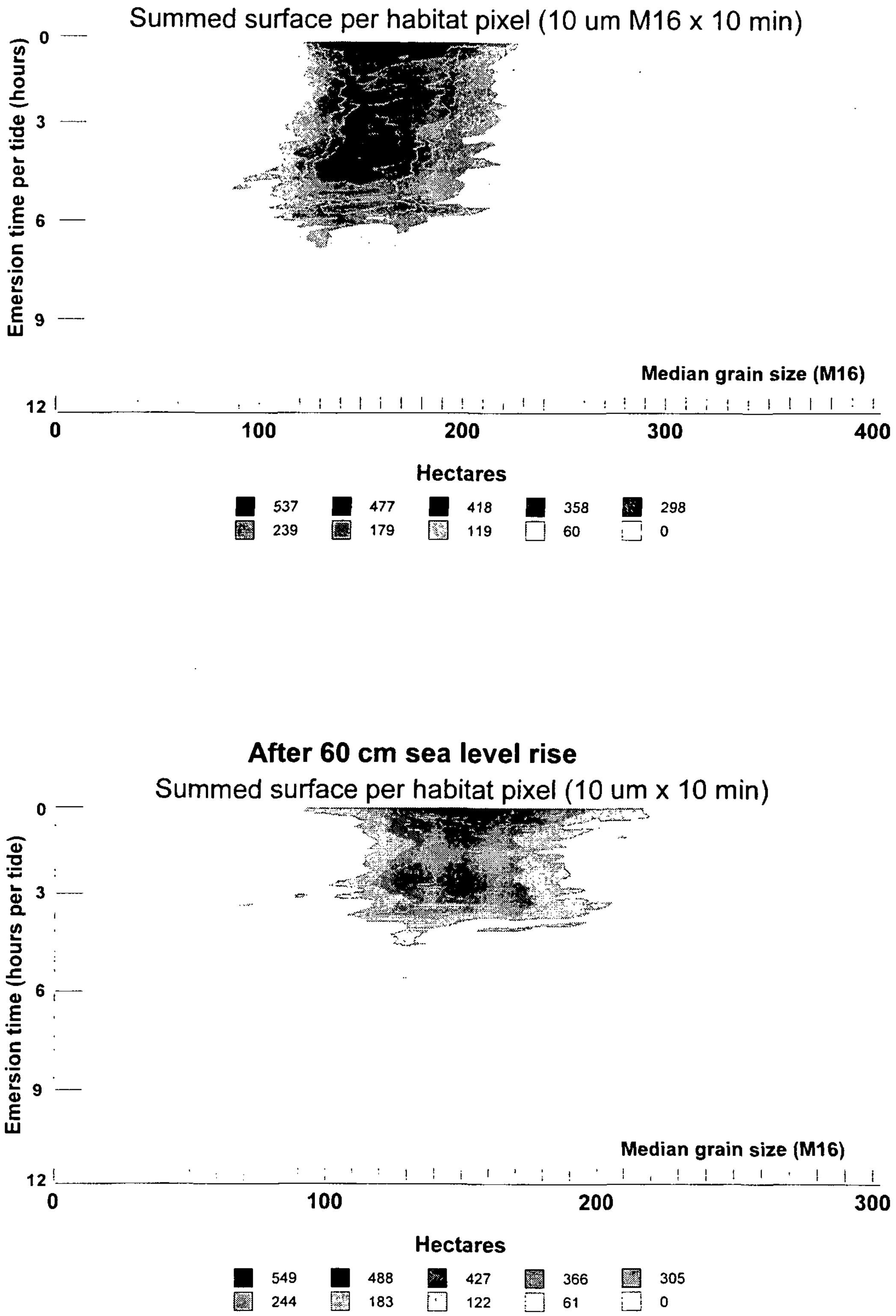


Figure 5.6 a,b: Characterisation of the intertidal habitats in the Dutch Wadden Sea according to emersion time and median grain size for (a) current situation, (b) after 60 cm sea level rise without compensation through sedimentation. From Brinkman & Ens (1998).

For the HABITAT model we need to characterise the Wadden Sea according to emersion time and sediment. It turns out that in the current Wadden Sea there are hardly any flats, which are exposed longer than 6 hours per tidal cycle, while the median grain size (M16) varies between 120 and 200 µm (Fig. 5.6a). On average, areas that are high in the tidal zone are exposed longer and have softer sediments, i.e. with smaller grain size. However, perhaps rather surprisingly, this relationship between emersion time and median grain size is not very strong in the current Wadden Sea. To simulate the effect of sea level rise, an extra amount of water is added and it was calculated how this would affect emersion time in each habitat. We ignored the possibility that the sediment characteristics would be affected as well. Thus, it comes as no surprise that the primary difference between the habitats in the Wadden Sea before and after a 60 cm sea level rise is a strong decrease in the areas with a relatively long emersion time (Fig. 5.6b). The maximum sea level rise that was simulated in this way was 120 cm.

To apply DEPLETE, we need to characterize the Wadden Sea according to the food supply for the birds, i.e. Oystercatchers. This food supply consists of benthic animals living on and in the sediment. For the calculations it was assumed that the food supply was primarily determined by the emersion time, i.e. the effect of grain size was ignored. Table 5.5 shows the density of standardized prey animals weighing 250 gram AFDM for the different habitats. Because of our assumption that prey density is only determined by emersion time, we can indicate the effect of sea level rise in the same table. Especially the surface of habitats with a long emersion time will decrease strongly following a 60 cm increase in sea level that is not compensated by sedimentation.

5.3.1 DYNAMIG

The migration pattern of the Sanderling

As described previously, we chose the Sanderling to exemplify the results of DYNASHOP, the international workshop on dynamic models of migration. Simulation 1 predicted that the birds should use the stopover site in the Hebrides. However, it turned out to be unrealistic as it predicted that all Sanderlings should leave Teesmouth by 1 May and fly to the Hebrides (Fig. 5.7a). Most Sanderling do not leave Teesmouth until at least 2 weeks later. Also it predicts that the departure state from Teesmouth involves fat levels of about 1 % of the lean

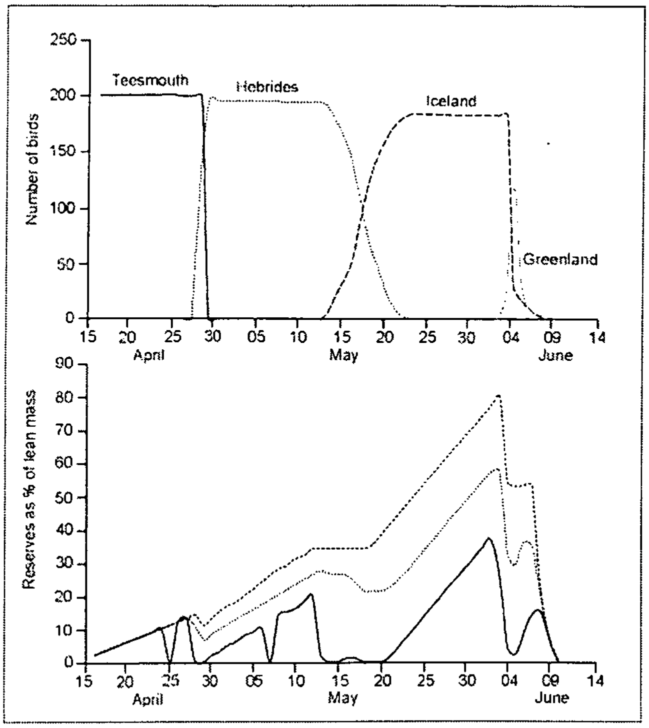


Figure 5.7: Results of simulation 1 by Weber, Gudmundsson and Evans for the Sanderling. (a) Predicted pattern of site use. (b) Predicted pattern of mass gain.

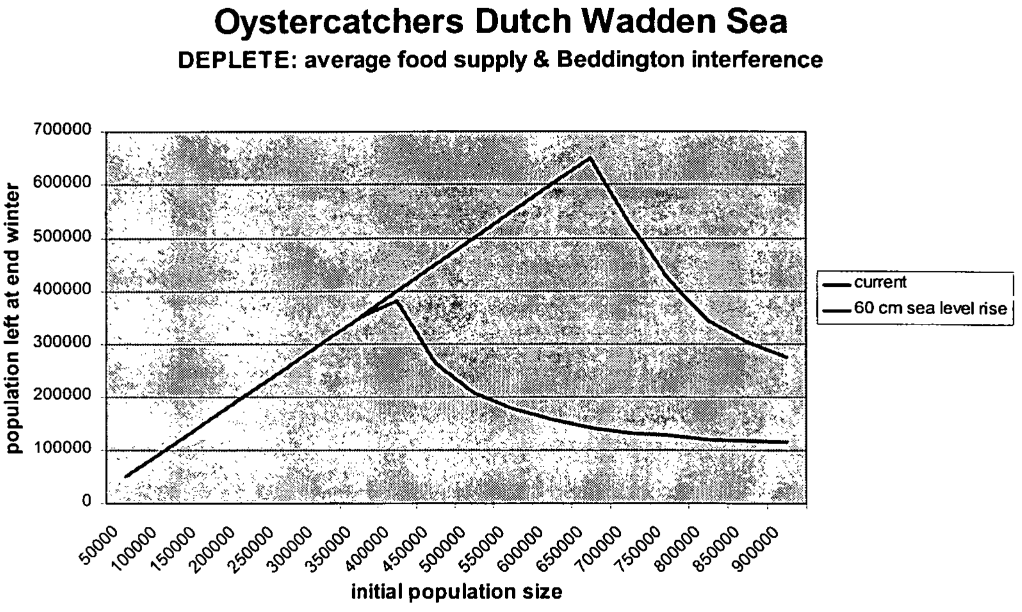


Figure 5.8: Results of simulations with DEPLETE for Oystercatchers using the Dutch Wadden Sea. The population predicted to survive the winter is plotted as a function of the initial population size.for current conditions and when seal level would be 60 cm higher (average food supply and Beddington interference).

mass of 50 g (Fig. 5.7b), i.e. departure total masses of about 56 g, far lower than reality (70-85 g).

The general effects of habitat loss due to climate change

To study the effect of habitat loss due to climate change at migratory stopover sites, we used our dynamic optimization model. Since this is not an analytical model, our results suggest certain rules, but they cannot be taken as a definitive mathematical proof. Weber *et al.* (1999) discuss the results in detail. Here, we can only repeat the summary of their paper.

The model emphasizes costs birds face during stopover (e.g. costs of gaining energy), the timing of site use and the behavioural rules birds might use to implement migratory strategies. Behavioural rules may be flexible enough that birds can still produce optimal behaviour in the changed environment, or the rules may result in sub-optimal behaviour. If birds behave optimally in the altered environment, habitat loss on the wintering ground has the highest impact, because this site, unlike the intermediate stopover sites, cannot be skipped if the quality drops below a threshold. If birds continue to use the old behavioural rules that now result in sub-optimal behaviour, we can distinguish two cases. Birds can continue to use a constant foraging behaviour that was optimal in the unaltered environment under many circumstances. Then the effects of habitat loss are proportional to the length of stay before habitat loss and the departure fuel load from a site. However, the effects of habitat loss do not depend on the location of the site within the network.

In some circumstances birds are expected to forage with intensities that are below maximum. If birds use the foraging behaviour that is appropriate for a given fuel load, time and site but inappropriate for the altered fuel gain, then changes at sites close to the breeding ground have a greater impact than more distant sites. Finally we discuss the importance of sites that are not used before habitat loss. If birds behave optimally these sites may be used in an altered environment and can buffer against habitat loss at other sites.

5.3.2 DEPLETE

There are very few species on which we have sufficient data to calibrate DEPLETE. The Oystercatchers feeding on bivalves on the intertidal mudflats in the Dutch Wadden Sea are a notable exception. In the methods section we describe how we estimated the various parameters. Once the model was fully parametrized for a particular interference function, we varied the initial number of Oystercatchers and calculated the number of individuals that would survive the winter for a given food supply. The particular shape of the interference function had little effect on the general results. In each case the number surviving equalled the initial number until a threshold value was reached, after which the number surviving decreased with increasing initial numbers. The threshold value can be interpreted as the carrying capacity for the particular food conditions of that year. When food conditions are average, slightly less than 700.000 Oystercatchers should be able to survive. This is far above the actual number observed, which varies between 200.000 and 250.000 in mild and normal winters (during cold winters large numbers of Oystercatchers leave the Wadden Sea). When food conditions are lower, the carrying capacity is also lower. This suggests that the number of wintering Oystercatchers is primarily determined during years of poor food supply. This makes sense, because shellfish stocks vary considerably from year to year, whereas Oystercatchers are long-lived birds with a low reproductive rate, so that their numbers vary only slowly. Their numbers will be hit badly during a poor food year and after such a hit numbers will increase only slowly until the next hit by a bad year.

It can now be investigated how sea level rise will affect this curve. When sea level rise is 60 cm and there occurs no compensation due to sedimentation, the maximum number of Oystercatchers is almost halved. This applies not only to years with an average food supply as depicted in Fig. 5.8, but also to years with a poor food supply. On the basis of the previous reasoning it seems therefore likely that the average number of Oystercatcher wintering in the Dutch Wadden Sea would decrease considerably as a result of such a drastic increase in sea level. Clearly, the next step is to link these results of DEPLETE with a model of the breeding season. That would lead to a version of LARGEPOP for Oystercatchers where the parameters have been estimated from individual-based models of competition during the breeding season and during the non-breeding season.

5.3.3 LARGEPOP

We did not find a significant density dependence in the survival of the Brent Geese during the non-reproductive season, i.e. in the statistical analysis the survival counts were found to be directly proportional to the population size. In a log-linear model with only a constant and an offset for *log*(population size), the constant represents the proportionality parameter. Let therefore

$$h(N_{2k}) = \delta \tag{5.37}$$

for all years, with δ the constant fraction of the population that does not survive the non-reproductive season (including death during the migration from Europe to Siberia). The estimate of δ over the 1955-1994 period equals 0.153 with 95% confidence interval (0.134 , 0.174). The years 1961 and 1986 were excluded from the analysis because they had negative death rates. We also tested whether survival differed in the period before and after the hunting ban in 1972. This resulted in the estimates $\delta = 0.182$ for the period 1955-1972 and $\delta = 0.149$ for the period 1973-1994. The two estimates were, however, not significantly different.

Next, we estimated the dependence of the number of first-winter birds on the total winter population size. In terms of the model, this amounted to plotting $Nf(N)$ as a function of N for different functions f. Only years in which the proportion of first-winter birds exceeded 15% were used in this analysis. This threshold value was chosen to exclude the years when successful breeding was impossible for other reasons like high predator levels on the breeding grounds or adverse headwinds during spring migration (Ebbinge 1989). We fitted several non-linear functions through the origin. The following functional form fitted the data best:

$$Nf(N) = (a + bN)Ne^{-cN} \tag{5.38}$$

where a,b,c are estimated as, with standard errors in parentheses: a = 0.479 (0.236), b = 0.00001875 (0.00000850), and c = 0.00001199 (0.00000209).

The model therefore becomes

$$\begin{aligned} N_{2k} &= N_{2k-1}(1 + (a + bN_{2k-1})e^{-cN_{2k-1}}) \\ N_{2k+1} &= N_{2k}(1 - \delta) \end{aligned} \tag{5.39}$$

with a,b,c regression parameters given above, and with the current per capita death rate δ = 0.149. The model allows one or more steady states, depending on the value of δ. In Fig. 5.5 we summarised this behaviour in a bifurcation diagram, which gives the predicted value for the steady state at the start of the winter season (census date) as a function of δ, as δ is varied from 0 to 1. From this graph we can see that the current best estimate for δ would result in a steady state population size of 300.000 birds. The model therefore predicts that the population is likely to stabilise at about 300.000 individuals at the start of the winter season.

From Fig. 5.5 we can also see that the model has a subcritical (i.e. backward) bifurcation as a function of δ. This has the following consequence: if we slowly increase δ from its present value, the steady state number of birds will gradually diminish. At some point, when $\delta = 0.44$ (approximately), the population collapses (even though for $\delta < 0.44$ it was still in the thousands) and the zero steady state is the only stable situation. When that has happened, one sees from Fig. 5.5 that decreasing δ will not have an immediate effect since there exists a steady state in between the stable zero state and the stable upper branch (this intermediate steady state is unstable and delineated by two dots in the graph). We have to decrease δ substantially, i.e. to below 0.32 (approximately) before we can regain a stable steady positive population. Biologically speaking our model therefore suggests that one has to be careful that δ is not increased significantly from its present value (e.g. due to renewed hunting to prevent agricultural damage for instance) because at some point the population might suddenly collapse completely, where after re-establishment is unlikely even if the unfavourable conditions are improved.

With this in mind we can also study the effects of habitat loss for migratory populations as in Fretwell (1972) and Sutherland (1996) based on intersections of curves representing the relation between population density and respectively mortality and reproduction. In the analysis presented in Sutherland (1996) only the steady state population density changes as a result of habitat loss. The reason for this is that the form of the two curves postulated is such that the dynamics of the corresponding system leads to a unique steady state. Of course, from a theoretical point of view, one can immediately state that the dynamics can become more complicated if the curves would behave differently so as to give rise to multiple steady states. What our analysis shows is that these more complicated situations can indeed occur in real systems, when the curves are estimated from data. This has as a consequence that the effects of habitat loss can be more dramatic than a gradual shift in expected steady state densities to adapt to new conditions.

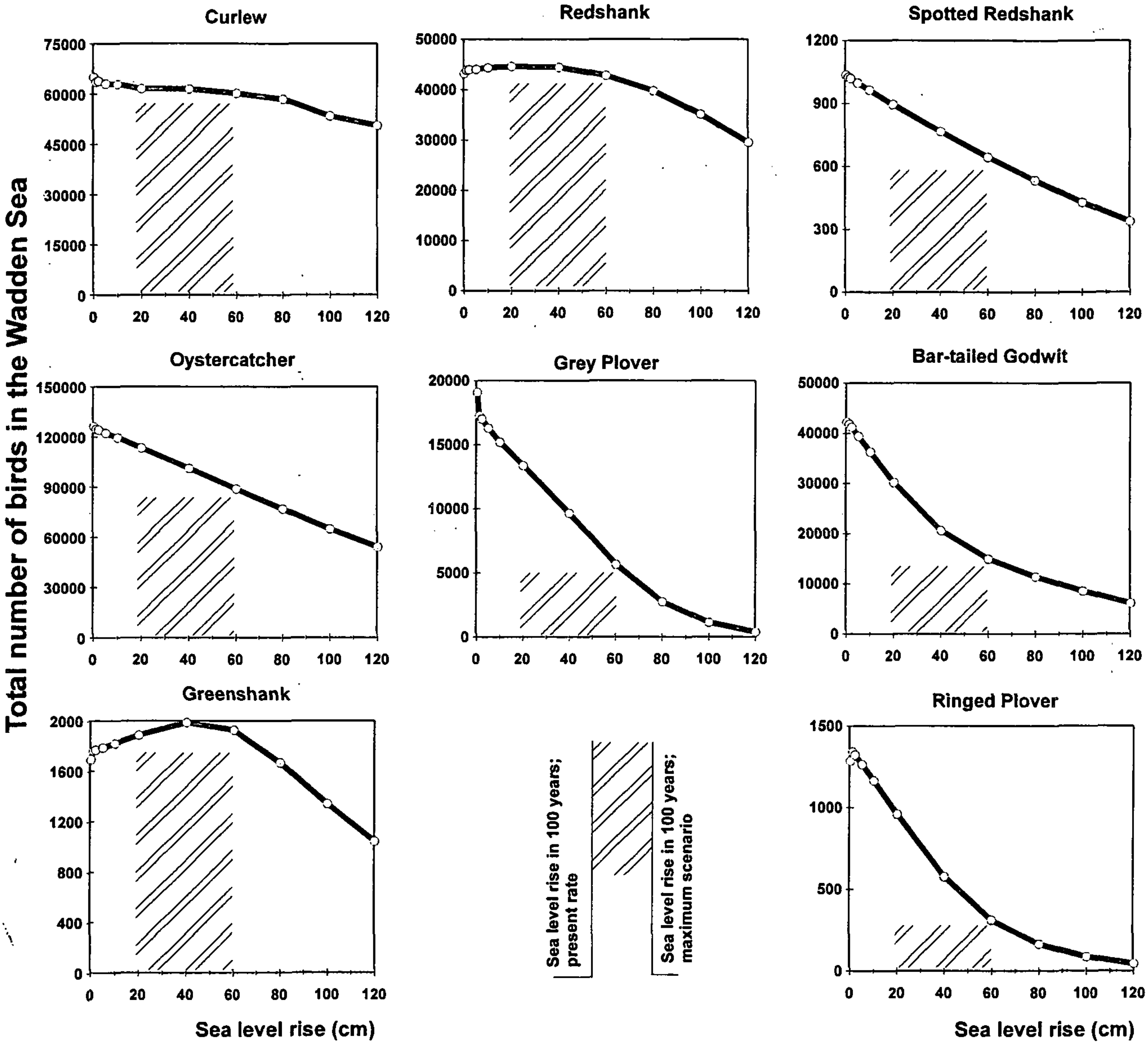


Fig. 5.9. Effect of sea level rise without compensation in the Dutch Wadden Sea on bird populations of selected species using the HABITAT model

5.3.4 HABITAT

When increased sea level rise is not compensated by sedimentation it will have a considerable negative effect on most of the waders feeding on the intertidal flats (Fig. 5.9). Greenshanks may profit at first, but when sea level rise exceeds 40 cm, this species will also start to decline like the other species. Especially grey plover, bar-tailed godwit and ringed plover are predicted to suffer from sea level rise.

5.4 Conclusions

- *A quite sophisticated set of interlocking models dealing with various phases of the annual cycle of migratory birds was developed as part of NRP II. These models can be used to predict the consequences of climate change for the migratory birds, provided that sufficiently precise scenarios are available of how climate change will affect the habitats on which the birds depend for their survival.*
- *Under many scenarios climate change will lead to sea level rise and this may lead to a reduction in the area of intertidal mudflats in the Wadden Sea, especially if the rate of sea level rise accelerates considerably above current levels. Calculations with both DEPLETE, which builds on knowledge of the underlying processes, and HABITAT, which is correlative, leave little doubt that such a reduction in mudflat area will lead to a reduction in the number of waders that can feed on those intertidal mudflats. More precisely, when the rate of sea level rise exceeds 60 cm per century, sedimentation will not keep up with the rising sea and mudflats will be lost.*
- *Excessive sea level rise may lead to a decrease in the area of salt marsh and this may affect the Brent Geese. A decrease in the area of salt marsh could either lead to an increased mortality rate, or to a decrease in the rate at which birds can fatten during spring, which would lead to a decrease in reproduction according to our migration models. In both circumstances LARGEPOP predicts that the world population of Brent Geese will decline.*
- *Climate change may also lead to a change in temperature and this will affect both the population dynamics of the invertebrate prey on which the waders feed and the timing of the growth of the salt marsh vegetation, which is important for the Brent Geese.*

- *During this study we focussed on the Wadden Sea. However, climate change will not affect this area in isolation, but will affect all areas used by the birds spending some part of their annual cycle in the Wadden Sea. The models that were built as part of this project are able to deal with these changes. What is needed as the next step are sufficiently precise scenarios of the combined effects of climate change on the wintering grounds, stopover sites and breeding grounds of well-studied migratory birds.*

6 EFFECTS OF CLIMATIC CHANGE ON BENTHIC FAUNA IN THE WADDEN SEA

6.1 Introduction

The aim of this project was to get insight into the flexibility of the benthic infaunal organisms from the Wadden Sea to changes in the environment due to global change. Only the effect of temperature is further investigated in this project, as it is believed to be by far the most important factor influencing the organisms of interest. As focal organism the common Baltic Tellin, *Macoma balthica* was chosen. *Macoma balthica* is a bivalve which lives buried in the sediment of the intertidal and shallow sub-tidal coastal areas. The European population ranges from the Gironde (France) in the south up to Nova Zembla in the north. This means that the Wadden Sea is a relative southerly habitat for this organism. From the commonly occurring shellfish in the Wadden Sea *Macoma balthica* is the species most adapted to low temperatures. This will be mainly due to its northerly distribution. Temperature changes can easily bring the circumstances close to the thermal limits within which *Macoma balthica* can survive.

The main question asked is "What is the flexibility of *Macoma balthica* to differences in the thermal environment". This question can be divided into several levels. First one can consider the range of temperatures in which an individual *Macoma balthica* from the present local population is able to flourish. This question can be subdivided into several more detailed questions:

- how do the important life history variables growth reproduction and survival depend on temperature
- how well can the individual respond to novel situations.

The second level is the population which is build up by the individuals. They will vary in their ability of coping with higher temperatures. This question can be rephrased as:

- How much of this variation is plasticity of the phenotype and how much is genetic? That information is important to predict the response of the population to the new selective environment.

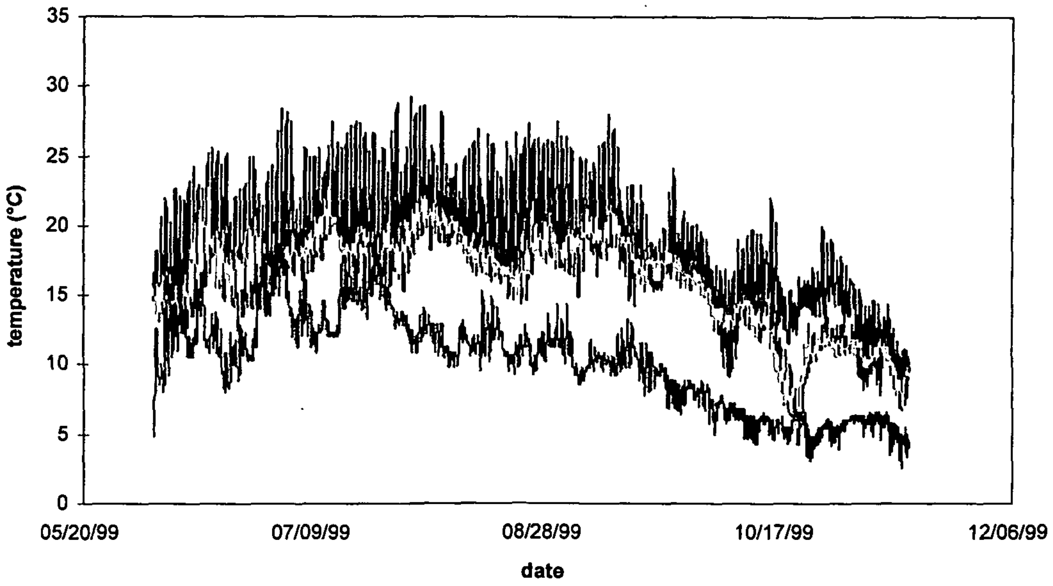


Fig. 6.1 Temperature of the sediment at a depth of 5 cm. The upper red line is from the Gironde. The yellow and green line are from the Mokbaai and Balgzand respectively, both in the Wadden Sea. The lower line blue represents the sediment temperature in Balsfjord.

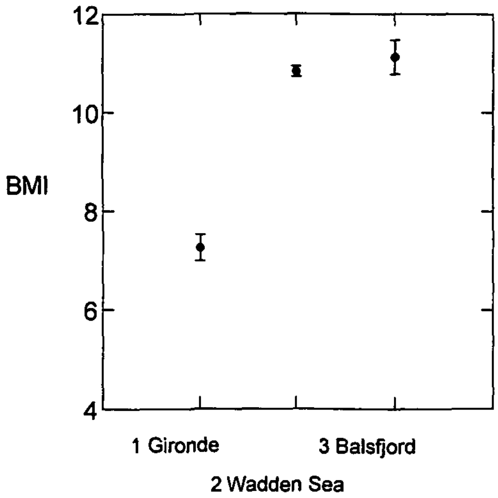


Fig. 6.2 Comparison of the mean body mass index from Gironde, Wadden Sea and Balsfjord.

Thirdly there are questions on the meta-population level. This consists of the total of *Macoma balthica* in Europe. Matter of interest here is the magnitude of structuring.

- Is everything just one gigantic mixing pool of all genetically identical *Macoma balthica* or do the different habitats throughout the distribution range have their own genetically distinct populations adapted to the local circumstances? This can shed light on the question what will be the final result if the local population doesn't make it. Is it possible that populations from elsewhere (from warmer areas further south) replace the present local population?

In order to get answers to the above raised questions, both field- and experimental-studies were carried out.

6.2 Study areas and methods

Two latitudinal different sites were selected to compare *Macoma balthica* populations from the Wadden Sea with populations occurring in naturally different thermal habitats. In the south, the mouth of the Gironde in France at the limit of the distribution of *Macoma balthica* was chosen. In the north the colder Balsfjord in Norway was selected. To quantify the thermal environment the intertidal *Macoma balthica* population experiences, data loggers were buried 5 cm deep in the sediment, recording temperatures at an interval of twenty minutes measures. These measurements have been synchronously collected in the Balsfjord, Wadden Sea and Gironde from June until November 1999 (Fig. 6.1).

Mean body mass indexes were studied by collecting Macoma balthica in the Wadden Sea and the Gironde in 1979. Balsfjord samples were collected in 1999 and 2000. From all collected animals the shell size has been measured, their age has been estimated by counting the growth rings of the shell. The soft parts of the individual shellfish were dissected into somatic tissue and gonadal tissue and dried at 60°C for at least 3 days. The dried samples were weighed and ashed at 560°C and weighed again to determine the ash free dry mass.

The general practical set-up and methods on MOTIF-experiments can be found in Kersting (this volume, Chapter 5). Of each of the four (two warm and two cold) experimental groups 18 specimens were taken from the samples of December 1998 and January 1999. Each animal was fresh dissected in two parts, somatic tissue and gonadal tissue. The samples were dried at 60°C and ashed at 560°C in order to determine ash free dry mass AFDM. Measures, body mass index (BMI) divided in somatic mass index (SMI) and gonad mass index (GMI) are all expressed as mass (mg) per cubic shell length (cm^3) to be able to compare animals with different shell length. Egg-sizes were measured in March, individuals were placed separately in jars and induced to spawn by applying a temperature shock and a solution of PROZAC (Honkoop et al. 1999). Eggs were collected, photographed and diameters measured on slide. In the analyses means of the experimental groups were used. A linear backward stepwise model was used to describe the data of BMI, GMI and SMI.

Settlement experiment of larvae of *Macoma balthica* have been carried out using adults from the Gironde (France) and the Balsfjord (Norway). After being collected they were transported to the laboratory where adults were individually induced to spawn by applying PROZAC and a temperature shock (Honkoop et al. 1999). From each origin four crosses were formed. Each cross was transferred to two litres of filtered sea water with antibiotics added, for three days at 15°C. After three days the larvae from each pair were split into three batches. From each pair the three groups were placed at 10°C, 15°C and 20°C and supplied with *Isochrisis galbana* as food source and antibiotics. After 15 days every two days a sub-sample of the larvae was measured and the development of the foot was scored. The appearance of the foot is an indication that the larvae are ready to settle.

Table 6.1 Sediment temperature at a depth of 5 cm, recorded every 20 minutes. At four sites, Gironde (France), Balgzand & Mokbaai (Wadden Sea) and Balsfjord (Norway). Measurements were taken from June 1999 until October 1999.

	mean	minimum	maximum	range	variance	standard deviation
Gironde	18.6	6.9	29.2	22.3	15.3	3.9
Balgzand	16.6	4.2	24.9	20.7	14.1	3.8
Mokbaai	16.2	5.4	22.8	17.4	12.4	3.5
Balsfjord	10.2	2.5	20.2	17.7	11.6	3.4

6.3 Results

Results have been summarized in Table 6.1. Mean temperatures as well as the maximum and variances are relatively high in the Gironde. The mean temperatures in the Balsfjord are the lowest and least variable. The Wadden Sea has an intermediate position but shows a higher resemblance with the Gironde, with only 2°C lower mean temperatures. The difference with the Balsfjord is about 6°C. The two locations at which temperatures have been recorded in the Wadden Sea show comparable results, indicating that within the geographic locations variation is small as compared to the variation between locations. For *Macoma balthica* in the Gironde not only the mean temperature is highest but also the fluctuations the largest. In the short term temperatures fluctuate with an amplitude of more then 10 °C. For the rates of physiological processes this means that they will change with at least a factor two (Q_{10} of 2). Macrobenthic animals in this area have to cope with a broad spectrum of temperatures.

Mean body mass index (BMI)

An important issue is try to understand which factors are determining the range of occurrence in *Macoma balthica*. Why does it not occur further south? Are the environmental conditions, biological or physical, that far from optimal that the species has trouble to survive and reproduce? In the context of this study especially the effects of the physical environment on the functioning of *Macoma balthica* are of interest. A possible way to get an idea is to quantify some important life history parameters, survival, growth and reproduction at different places in the distribution range.

Mean body mass index (BMI, ash free dry mass per cubic shell length, mg*cm^{-3}) for *Macoma balthica* at the three focal sites are lowest in the Gironde (Fig. 6.2). The Wadden Sea and Balsfjord give similar results. The mean gonadal body mass index (GMI, ash free dry mass of the gonadal tissue per cubic shell length, mg*cm^{-3}) in spring is also lowest at the southern limit of the distribution of *Macoma balthica*, the Gironde. Again Wadden Sea and Balsfjord have similar values (Fig. 6.3). The growth parameters k and lmax, estimated using the Von Bertalanfy growth equation, do not show latitudinal patterns.

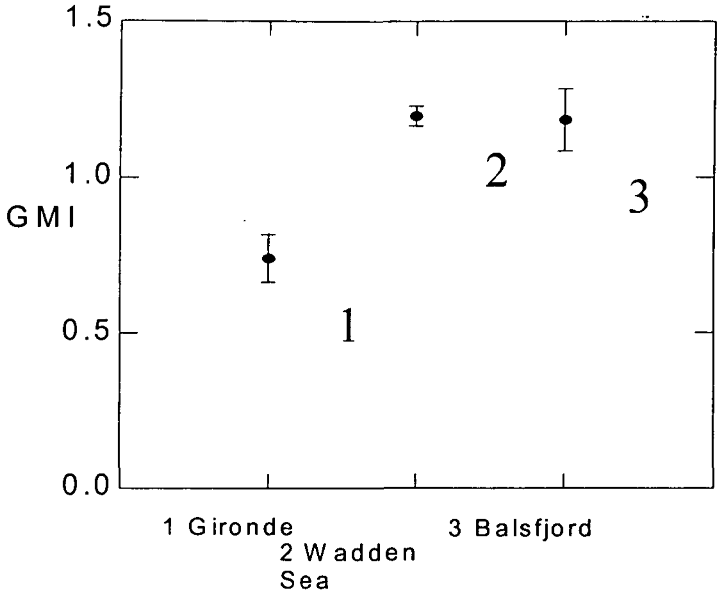


Fig. 6.3 Comparison of the mean gondal mass index (mg*cm^{-3}) from Gironde, Wadden Sea and Balsfjord in spring

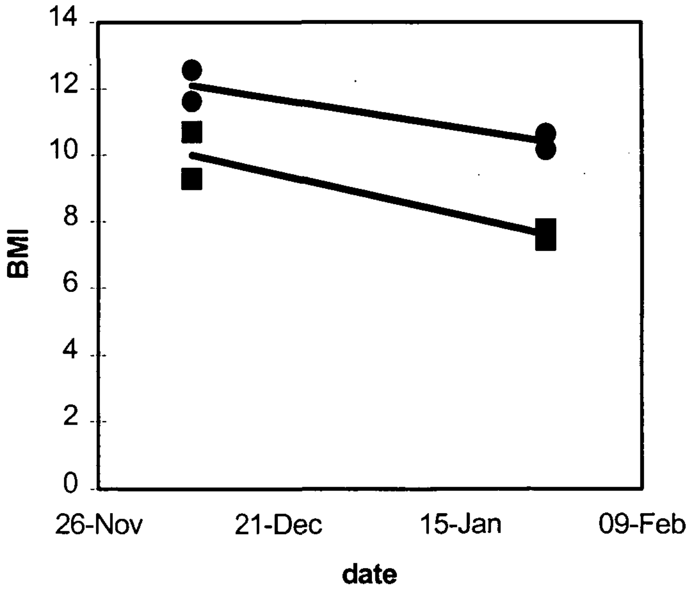


Fig. 6.4 BMI in the motif experiment. The circles and squares represent the cold and warm treatment respectively

The results are consistent with the idea that *Macoma balthica* is more constrained at the border of its distribution. The body condition is lower as well as the reproductive output, quantified by gonadal mass. A second reproductive period in the autumn besides the one in spring mentioned for the Gironde (Bachelet 1980; Bachelet 1986), was not found in this study.

Experiments using MOTIF's

The effect of elevated temperatures on the benthic community was studied in model tidal flat ecosystems, as has been described by Kersting (c.f. Chapter 7). Within this experiment specific attention was paid to the reproduction of *Macoma balthica*. Long term field observations showed that after cold winters recruitment of *Macoma balthica* generally was good after cold winters (Beukema et al. 1998). In a later study winter temperatures have been manipulated, resulting in larger egg numbers produced by the females after cold winters compared to warm winters (Honkoop and Van der Meer 1998). The results were explained by considering the energetics during winter. During winter the food conditions are poor, so for the energetic needs the animal must depend on the reserves build up in the past. The amount of energy needed just for maintaining the body is dependent on temperatures, the higher the temperature the higher the maintenance energy. During warm winters more energy will be consumed for maintenance so less will remain for eggs, resulting in a lower egg production. As a mechanism it was proposed that the actual energy reserves are made up by the eggs. The eggs are synthesised before the winter and partly resorbed during winter to meet the energy demands to survive (Honkoop and Van der Meer 1998).

Egg size is another important parameter in reproduction that also received attention. Experimentally changed winter temperatures did not have an effect on egg size (Honkoop and Van der Meer 1998) although field studies showed marked differences between sites. These differences were correlated with the BMI in August.

Two hypotheses resulting from the study by Hopkoop & Van der Meer have been tested in the MOTIF temperature experiment. The first one is:

- Eggs are synthesised before winter and are being used as energy reserves by resorbing eggs during winter. The second:
- Egg-size is determined by BMI in autumn when the eggs are synthesised.

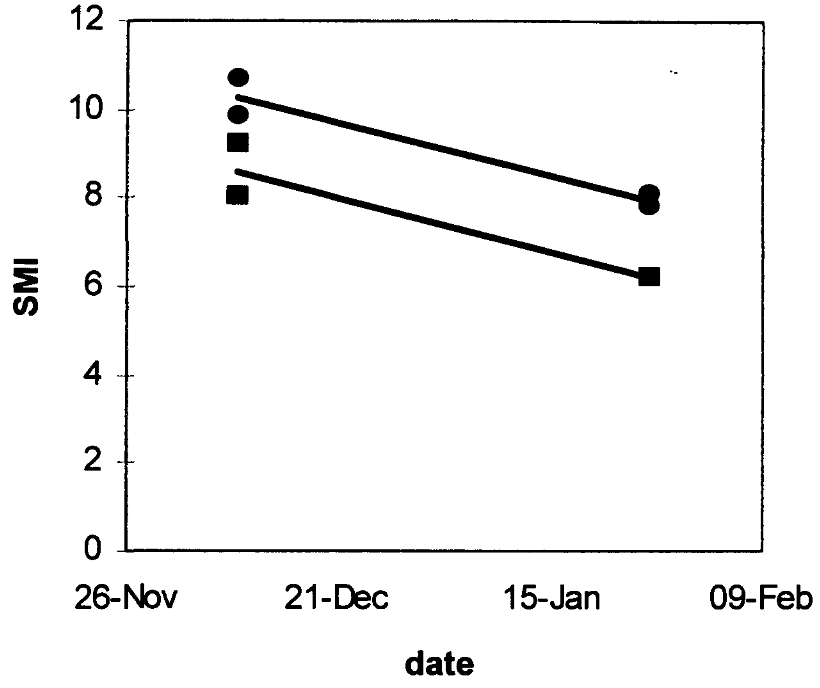


Fig. 6.5 Somatic mass index (mg*cm^{-3}) in the motif experiment. Circles stand for the cold treatment, squares for the warm treatment.

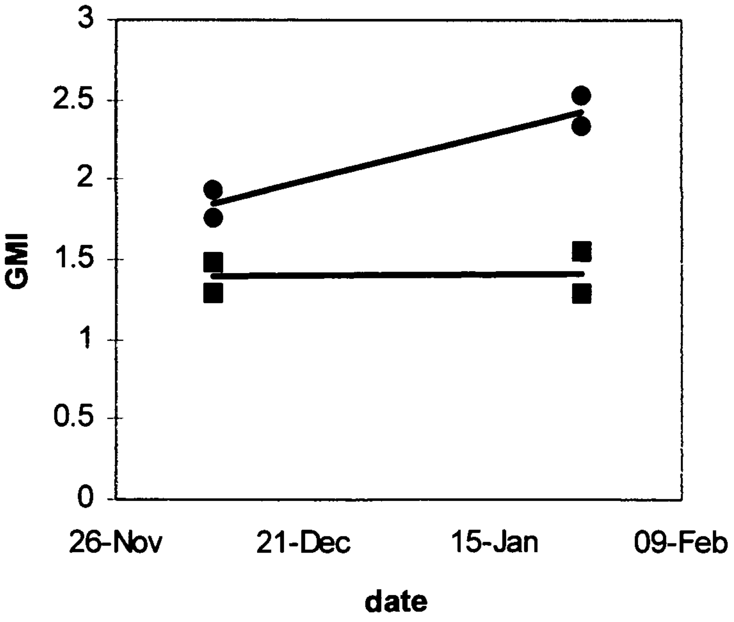


Fig. 6.6 The development of the gonadal mass index (mg*cm^{-3}) in the MOTIF experiment. Circles represent the cold treatment, squares the warm treatment.

This last experiment differs from previous ones in that the temperature manipulation is started in spring generating differences in BMI in summer, well before the moment of proposed egg-size determination. Earlier manipulation experiments started before or in October, generating differences in BMI in December, and no egg-size differences.

Fig. 6.4 shows the development of the BMI during winter. The level in the warm treatment is significantly lower than in the cold treatment, the decrease in BMI is the same for both treatments. When viewing the two components in which the BMI is split up the same pattern emerges for the SMI as for the BMI (Fig. 6.5). The cold treatment has a higher SMI than the warm treatment, whereas the decrease in SMI is similar. The gonadal index yields another picture (Fig. 6.6). The warm treatment shows no development of gonadal mass at all whereas in the cold treatment animals increase there gonadal tissue. The intercept is not statistically distinguishable whereas the interaction term is significant.

Egg-size variation does not show any relation with treatment. In a nested analysis most variation could be attributed to female, the only significant factor (Table 6.2).The highest egg production expressed as gonadal mass was found in the cold treatment. This result was to be expected as could be inferred from earlier observations. The proposed mechanism, however, does not match the results. In the beginning of the winter the GMI in both treatments is the same. Only during the winter things start to change. In the warm group the GMI remains the same whereas in the cold group the GMI increases.

Table 9.2 Results of a nested analysis of egg size variation in a model tidal flat system. A temperature treatment consisted of two levels with a difference of 4°C.

	df	ss	ms	F	p
treatment	1	210.8	210.8	7.18	>0.05
group	2	58.74	29.37	0.1	>0.05
motif	4	1171	292.8	1.21	>0.05
female	29	6998	241.3	17.3	<0.001
error	458	6389	13.95		

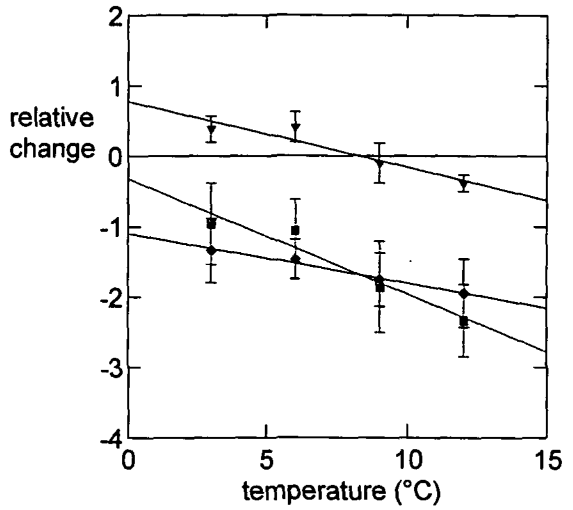


Fig. 6..7 Development of the gonadal mass (triangles), somatic mass (diamonds) and total body mass (squares) of *Macoma balthica* as a function of temperature while starved.

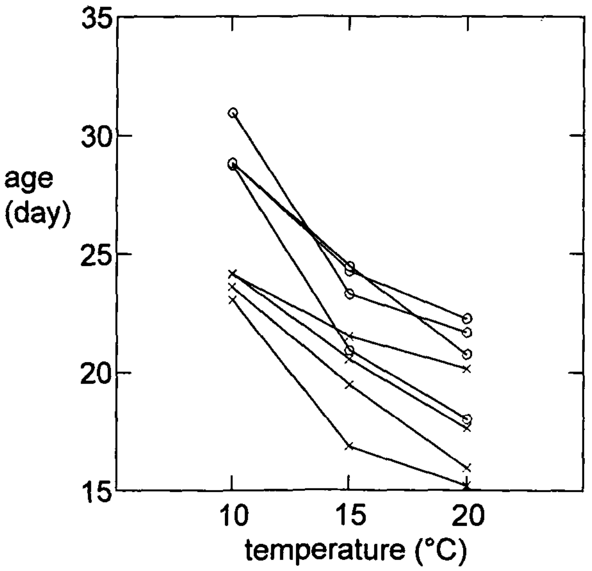


Fig. 6.8 Age when 50% of the larvae has developed a foot as a function of temperature. Larvae from Balsfjord are shown with a circle, larvae from Gironde with a cross

BMI levels were different but not the changes in BMI. This is contrary to earlier results of Honkoop & Beukema (1997) who found that the decrease in BMI is strongest in warm winters as compared to cold winters. The statistical power of this experimental set-up, however, is very limited.There was no effect of treatment found on egg-size, neither directly due to different temperatures of the environment nor indirect by BMI differences induced by temperature. The relationship between BMI in August and the egg-size in March of the following year, found in the field by Honkoop and Van der Meer (1998), is hard to understand. Eggs must be tuned to the environment in which they have to develop. This is the same for the groups between which this relationship was found by Honkoop & Van der Meer (1998). The BMI of the parent should not have anything to do with the optimal egg-size. That will only influence the egg number. Direct differences in the environment like temperature could cause a shift in the optimal egg-size and are much more probable. This response of egg-size is not found in the present study.

The final conclusion from this experiment is that the reproductive output depends on the BMI or the amount of reserves and the rate in which the reserves are being used for other processes than the production of eggs or sperm. Egg-size is not influenced by the BMI of the adult animal. The hypothesis that temperature acts as an environmental cue for the determination of egg-size does not get any support in this experiment.

The effect of temperature on gonadal development

Results of the above mentioned MOTIF experiment concerning the developments in body mass index (BMI), somatic mass index (SMI) and gonad mass index (GMI) were confirmed and elaborated on in another separate experiment. From January to April *Macoma balthica* were kept without food at four different temperatures. Four samples were taken through time. Somatic and gonadal tissue were separated and dry weights determined.

The development of total body mass, somatic body mass and gonadal body mass are plotted in Fig. 6.7. In all treatments the total body mass declines, the decline increases with temperature. The same is true for somatic body mass. The gonadal mass however increases in the lowest temperatures. At 9°C it remains constant, while at 12°C gonadal mass decreases in the same way as somatic mass.

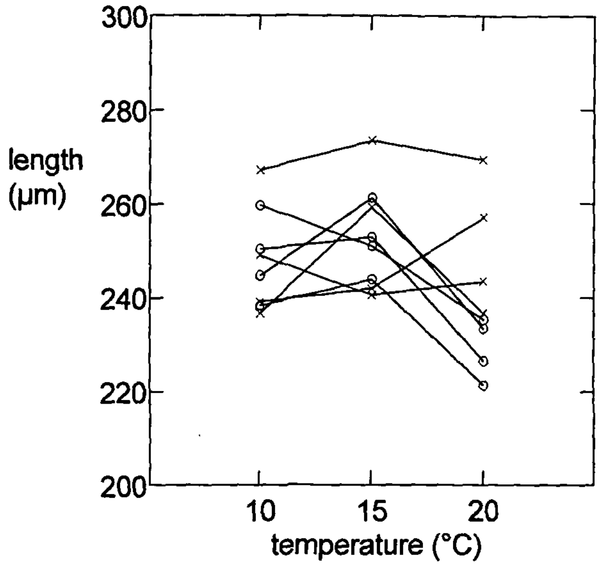


Fig. 6.9 Length at which 50% of the larvae from the Balsfjord (circles) and the Gironde (crosses) have developed a foot at three different temperatures.

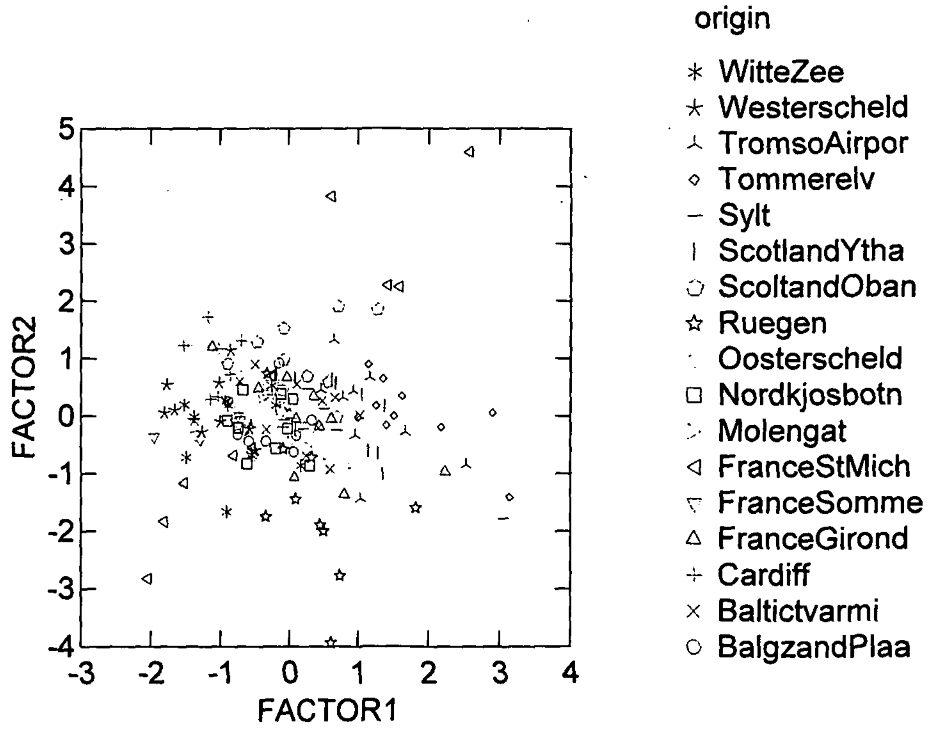


Fig. 6.10 Plot of factor 2 against factor 1 of a principal component analysis on 14 shell morphological characters from the European *Macoma balthica*

A decline of total body-mass is to be expected since no energy intake was possible. Reserves were used to survive. Under very low temperatures energy reserves are not only allocated towards maintenance processes but also to reproduction. At the highest temperature of 12°C not only the somatic mass is declining but also the gonadal mass. Energy which has first been allocated towards reproduction is redirected towards maintenance processes. This is an inefficient process. The conversion of energy into reproductive tissue will cause losses as the conversion back to a metabolizable form will induce losses to. The mechanism proposed by Honkoop & Van der Meer (1998) is therefore energetically inefficient and will only used as a rescue system in extreme conditions. Under normal conditions during winter energy reserves are allocated to maintenance processes and reproduction. The net amount of energy finally converted in eggs or sperm at the moment of spawning in spring is dependent on temperature in the preceeding winter.

The results show that when starving, *Macoma balthica* gonadal build-up will continue only under lower temperatures. At higher temperatures maintenance processes require all available energy. Field data show that the same processes operate in the wild as well.

Larval development: the effect of temperature and latitude.

In the first few weeks of their life *Macoma balthica* develop as planktonic larvae, before settling in the sediment. This is a crucial phase in the life history of *Macoma balthica* with high mortality rates. The larval phase is very important for the population dynamics. Once settled the mortality rates are more or less constant, the success of a year class is highly dependent on the pelagic phase (Van der Meer, 2001). Because settlement is such a risky part of life it can be expected that there is heavy selection pressure to reduce this dangerous period. This hypothesis was tested by experimentally comparing the development of Balsfjord and Gironde larvae under different temperatures.

The time at which 50% of the larvae had a foot was determined for each batch by fitting a logistic curve for the relationship between developmental stage and age. The results are plotted in Fig. 6.8. Under all temperatures the Balsfjord-group shows the slowest development of foot, taking approximately 5 days than the Gironde-group. In both groups elevated temperatures have a strong reducing effect on the development- time. There is no significant origing*temperature interaction.

The length of the shell with developing feet was also determined by fitting a logistic curve for the developmental stage-length relationship. The results (Fig. 6.9) show that origin alone does not have a significant effect on the size at metamorphosis. The origin*temperature interaction is significant. The factor temperature also significantly explains part of the variation.

Obviously the larvae from two different origins do not behave in the same way. The Gironde-group develops faster under all temperature treatments. At the same time the size at metamorphosis is similar or even larger in the Gironde-group, which means that they grow faster than the Balsfjord-larvae under further identical conditions. In some way or another the Gironde-larvae must be more efficient in converting the available food into growth. This could be the result of a higher food intake rate. At 20°C, a temperature never to be encountered in the Balsfjord, the smaller size at metamorphosis in the Balsfjord-larvae may indicate that this temperature acts as a stress-factor. In the other cases the size at metamorphosis is approximately the same. The results indicate that Gironde-larvae are better adapted to high developmental temperatures.

Shell morphology from different sites.

Beukema & Meehan (1985) observed latitudinal trends in a number of shell characteristics of *Macoma balthica*. In mussels as well as in oysters differences in shell characteristics make it possible to distinguish between species which are in first sight alike (McDonald, Seed et al. 1991; Day et al. 2000). If differences between species can be shown, patterns of population structuring within a species also might be visible in variations in shell morphology. From a large number of different sites in Europe samples of *Macoma balthica* were obtained. From twelve shells from each site fourteen different measures were taken. Dimensions and shape of the shell, muscle scars, pallial line, hinge and ligament were included. In a principal component analysis the data were reduced to three principal factors. Fig. 6.10 shows a plot of factor 1 against factor 2. No clear separations of geographic groups become clear. All groups are overlapping somehow. For all three factors the site of origin has a significant effect for the loadings, as tested by ANOVA.

There is a lot of site-specific variation in the shell morphology of *Macoma balthica*. At least part of the morphological differences have a genetic basis, as has been shown in laboratory breeding experiments (Luttikhuizen et al. in prep). There is no relationship with the resemblance in morphology and distance between the sites. Such a relationship might be expected, since populations living close together would have more gene flow than more distant populations.

Concluding, shell morphology does not envision a clear geographic structuring, at least not at the scale investigated in the present study. Possibly on a smaller scale patterns will emerge with habitat type as the explaining variable rather than distance.

6.4. General conclusion

Macoma balthica in the Gironde at the southern border of its distribution have a lower Body and Gonadal Mass Index, and a lower larvae growth development than living populations further north. This can be the effect of higher environmental temperatures, which is clearly demonstrated through experimental work. There is some evidence that there are differences in *Macoma balthica* between sites. Shell morphological studies show large differences but no clear pattern. Development of larvae from the Gironde are not affected at high temperatures like the Balsfjord larvae are. The results indicate that European population(s) of *Macoma balthica* will for sure be affected by higher temperatures. Populations now living further south are possibly better adapted to higher temperatures. Considering the dispersal abilities of *Macoma balthica* these populations might have a chance to move northwards when situations change.

7 MESOCOSM RESEARCH AND MODELLING: PROCESS RESEARCH ON EFFECTS OF TEMPERATURE AND WATER LEVEL ON TIDAL FLAT ECOSYSTEMS

7.1 Introduction

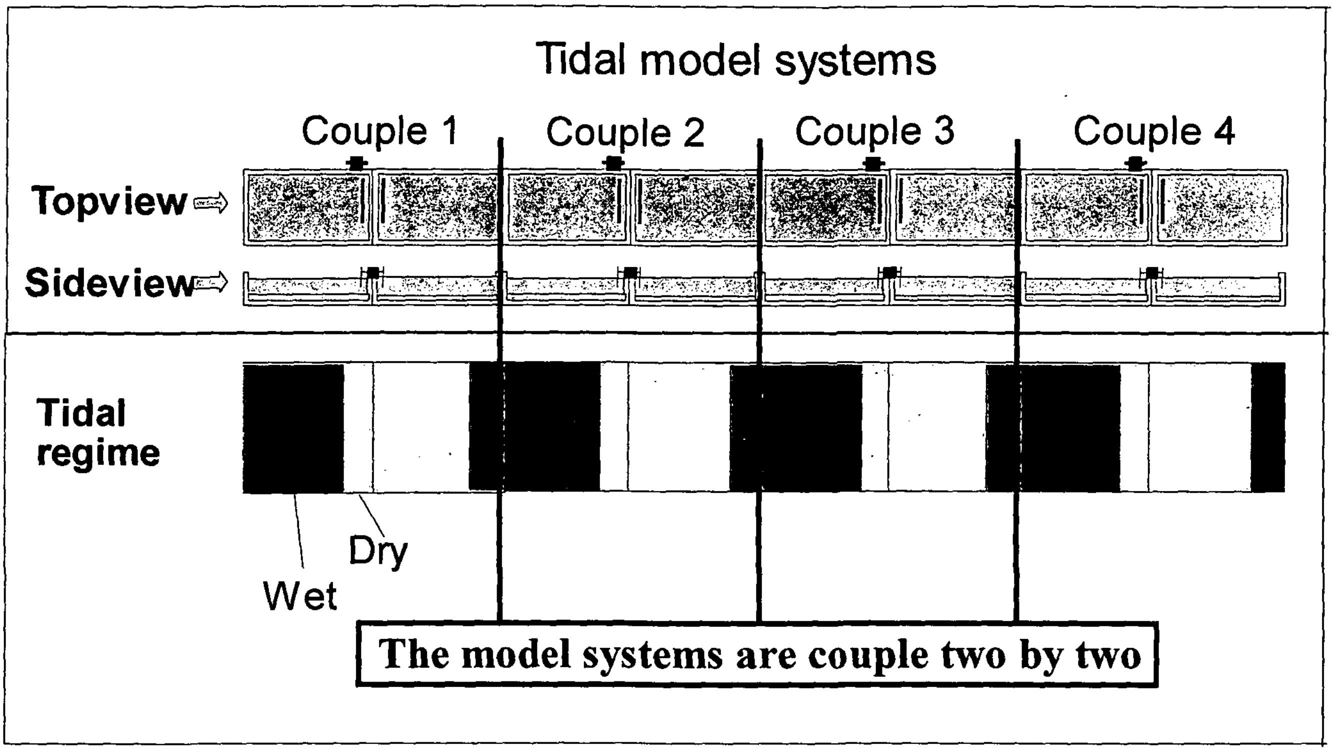
Global climate change can have important consequences for tidal flats in the Wadden Sea and elsewhere. Two aspects of the climate change, Sea Level Rise and Temperature Rise have been studied in MOTIFs (MOdel TIdal Flats) and are reported here. In situations without extra sedimentation a rise in sea level has the consequence that the period of inundation of the intertidal mudflats of the Wadden Sea increases In this subproject we assumed that there will be a change in inundation time and the effect of a difference in inundation time was studied. During NRP1 the effect of inundation time and winter temperature on the most common bivalves was studied. In the present study the development of the complete macrofauna community under different tidal regimes was studied in the period March to September. The effect of temperature was studied during a complete year from March to March.

7.2 Materials and methods

All experiments were carried out in MOTIFs, two concerning sea level rise (ExpSLR95 and ExpSLR97) and one concerning temperature rise (ExpTR98).

7.2.1 Description of the MOTIFs

The experiments were performed in eight MOTIFs, concrete basins measuring 6 metres long and 3.5 metres wide (Fig.7.1). A 45 cm high brick wall running the length of the basin separates a part to be filled with sediment (6x3 m) from a channel filled with water (6x0.5 m). The MOTIFs were coupled in pairs and the water was pumped from one MOTIF to the other, and back. The maximum water level was about 50 cm above the level of the sediment. High tide in one MOTIF coincided with low tide i.e. dry sediment surface in the neighbouring MOTIF. Additionally each MOTIF received a continuous flow of 40 litres of sea water per



1995, 1997: different tidal regimes (wet/dry period)
1998-1999: temperature increase of 4°C in half of the basins

Fig 7.1. Top-view and side-view of the tidal model system (MOTIF's). For warming up water, in the basins a heat exchanger was installed. The coupled basins have alternating high and low tide, which is outlined in the lower drawing.

hour. With a total water volume of 10 m^3 per pair of MOTIFs the supply resulted in a water residence time of about 5 days. In the first two experiments the supply water was taken directly from the intake of Marsdiep water. In the third experiment this direct input was blocked and supply water passed a series of settling tanks before being distributed over the MOTIFs. This change probably had consequences for the development of the macrobenthos communities in the MOTIFs, which will be discussed in the results.

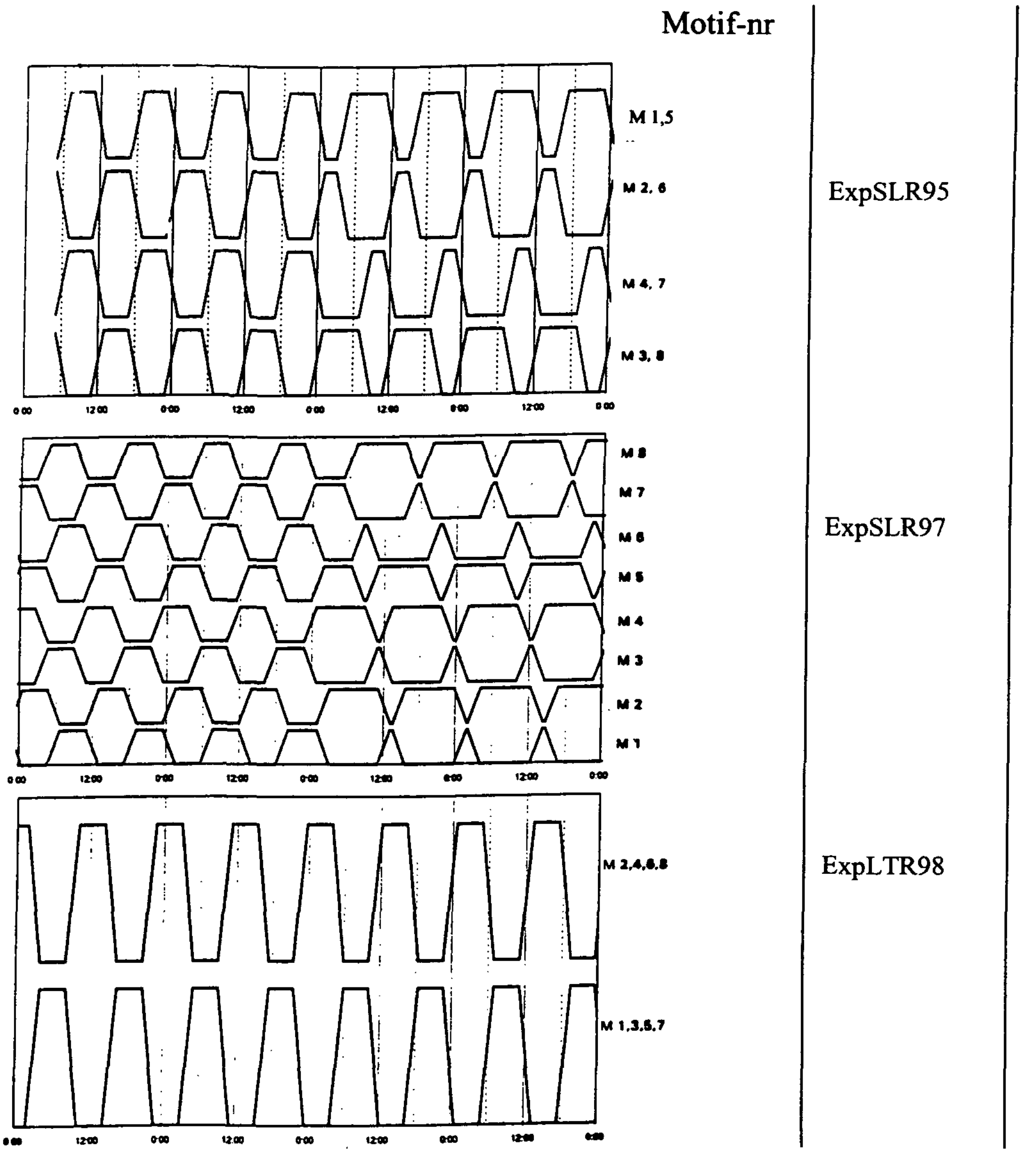
During all experiments the MOTIFs were filled with sediment up till the top of the 45 cm high brick wall. The sediment was collected from a natural tidal flat in the Mok Bay on the island of Texel. The sediment was collected some months before the start of the experiments and left dry exposed in the air to kill the infauna. After mixing, the sediment was placed into the MOTIFs in early February. The systems were filled with seawater and the tidal cycle was started. During March the MOTIFs were stocked with a selection of macrobenthic fauna in numbers similar to natural tidal flats. *Macoma balthica* and *Cerastoderma edule* were collected on natural tidal flats; *Arenicola marina* was obtained from a local fisherman. The organisms were evenly spread on the sediment of the MOTIFs. *Littorina littorina* were collected from hard substrate in a nearby harbour and placed on the sediment near the walls. During settlement all *Littorina* moved to the walls of the MOTIFs.

7.2.2 Sampling

The macrobenthic fauna was sampled by pushing a metal frame 50x50 cm into the sediment until it reached the concrete bottom of the MOTIF. The sediment within the frame was sieved through a 1 mm perforated metal sieve and the sediment was returned to the core before the frame was withdrawn. The material left on the sieve was flushed with seawater in the laboratory in a sieve with 1 mm plankton gauze. All organisms left on the sieve were transferred to flat white trays, from which the organisms were picked, counted and identified to the lowest reasonable taxonomic level. Except for the bivalves the organisms were placed immediately in porcelain crucibles and dried at 60 °C during 48 hours in a vented incubator. After weighting the crucibles were ashed during 2 hours at 560 °C and weighted again. The difference between the two weights, the ash-free dry weight, is considered to represent the organic matter of the organism. The bivalves were stored deep frozen for later treatment.

For bivalves the length-weight relationship was determined. The shell length was measured with a digital calliper. The content of the shells was excised after short heating in a microwave oven and the ash free dry weight was determined as described above.

At each sampling occasion three samples were taken. The sampling spots for the box cores were selected randomly from a grid of 0.25 m^2 squares. In order to avoid effects of previously sampled spots no sampling spots were allowed to lie side by side. This was accomplished by selecting the sampling spots from only the black fields of an imaginary chess board pattern. As a matter of course spots were never sampled for a second time. A strip of 25 cm from the



	ExpSLR95	ExpSLR97	ExpTR98
Tidal Period (hh:mm)	12:00	12:30	12:30
Low tide period pretreatment period (hh:mm)	4:00	4:15	4:15
Low tide period high tide MOTIFs (hh:mm)	2:00	0:30	4:15
Low tide period low tide MOTIFs (hh:mm)	6:00	8:00	4:15
Period of immersion high tide MOTIFs (hh:mm)	10:00	12:00	8:15
Period of immersion low tide MOTIFs (hh:mm)	6:00	4:30	8:15
High tide MOTIFs	1,3,5,8	2,4,5,8	
Low tide MOTIFs	2,4,6,7	1,3,6,7	
Transfer from low to high tide at noon/midnight	2,3,6,8		
Transfer from high to low tide at noon/midnight	1,4,5,7		

Fig 7.2 Tidal regimes in low tide and high tide MOTIFs in all three experiments described in this paper. Each experiment was preceded by 3 weeks of "normal" tides, i.e. 4 hours low tide and high tide in ExpSLR95 and 4.15 h in ExpSLR97 and ExpTR98, plus 2 hours transition time from low tide to high tide and reverse

walls or from the brick wall bordering the tidal channel was excluded from the sampling area. In this way the sampling spots were randomly chosen from 25 possible ones.

Corophium volutator and *Hydrobia ulvae* can be present in very high numbers (tens of thousands per m^2, Beukema 1974). Enumerating those organisms in the box core samples is not sensible. For these organisms 5 sub-samples were taken within the box corer with a tube sampler with an inner diameter of 4.5 cm to a depth of 10 cm. These samples were treated in the same way as the complete box core sample. The data were corrected for the difference in sampling surface.

7.2.3 Registration system

The MOTIFs were equipped with a registration and control system based on a Campbell CR10 data-logger. Directly and via multiplexers, different instruments and sensors were connected to the data-logger. In the second (ExpSLR97) and third (ExpTR98) experiment the data-logger was also used to regulate the tides and in the third experiment (ExpTR98) the temperature regulation was performed by the data-logger. The data-logger was connected to a PC in the main building of the institute. Via the PC the data-logger could be programmed, data could be retrieved and tidal pumps and heating could be switched on and off.

All signals were sampled every 30 seconds and stored as 15 minute averages. Light intensity was measured in the air as quanta and as energy with respectively a LACIER model LI192SB quantum sensor and a model LI200SB pyranometer sensor. Water depth of each MOTIF was measured with Ott model ODS4 pressure sensors. WTW model 600 trioxmatic oxygen electrodes were used to measure oxygen concentrations and water temperatures. In the second (ExpSLR97) and the third (ExpTR98) experiment sediment temperatures were measured with YSI thermistor sensors buried at a depth of three cm connected to the data logger system.

7.2.4 Tidal regime

In the first experiment the timing of the tides was regulated by 24 hour switching clocks. These clocks created two tidal cycles of exactly 12 hours each day. This set-up had the disadvantage that the tides were synchronised with the diurnal cycle, which could create differences between MOTIFs dependent on the timing of high and low tide. In the second and the third experiment the data-logger was used to create a more natural tidal cycle of 12 hours and 30 minutes. In this way the timing of high and low tide shifted 1 hour every day. This set-up prevented (at least diminished) differences between MOTIFs because of timing of the tidal cycle.

The transition from high tide to low tide took about 2 hours. After the start of the MOTIFs a symmetrical tidal regime was imposed upon each pair of MOTIFs. This resulted in a period of dry sediment of 4 hours in the first experiment and 4 hours and 15 minutes in the second and third experiment.

- In the first and second experiment the tidal regime was changed in such a way that half of the MOTIFs were set to a shorter period of dry sediment as a way to analyse the effect of sea level rise. These MOTIFs will be referred to as high tide MOTIFs. As a consequence the other MOTIFs received a longer period of dry sediment (the low tide MOTIFs). In the first experiment the middle of the transition of the tides was chosen at noon and midnight. This gave 4 MOTIFs with low tide (shortened or prolonged) before noon/midnight and 4 MOTIFs with low tide after noon/midnight. In the second experiment the transition time was chosen randomly within the tidal cycle, which as a whole shifted 1 hour each day. The first experiment ran from March, 1995 until October, 1995, the second one from march 1997 - October 1997.
- In the third experiment the symmetrical tidal regime was maintained. The experiment ran from March 1998 - March 1999.

The tidal regimes in each MOTIF are summarized in Fig. 7.2.

7.2.5 Temperature regulation

For the study of the effect of temperature rise a regulated heating system was created. In the small channel of the MOTIFs heat exchangers were installed. A constant flow of water through the heat exchangers was maintained. In front of the outflow of the heat exchangers the water temperature was measured and registered. In 4 of the 8 MOTIFs (the controls, low temperature MOTIFs) dummy heat exchangers were installed. The heat exchangers of the other MOTIFs (high temp MOTIFs) were connected via magnetic valves to a boiler. When the water temperature of one of the high temperature MOTIFs was less than 4 °C higher than the temperature of the controls the magnetic valve of the heat exchanger of that particular

MOTIF was opened. At the next scan of the data logger (scan interval 30 seconds) the temperature was again compared to the control temperature. If the temperature had increased to more than 4° above the control the valve was closed. If the temperature difference still was less than 4°, the valve was kept open for another period of 30 seconds.

7.2.6. Statistics

In the Sea Level Rise experiments differences were tested with a t-test for paired comparison (Sokal and Rohlf 1969). In the Temperature Rise experiment a t-test for means with unequal variances was used (Sokal & Rohlf 1969). Significance values were calculated for the two-tailed distribution. The tests were performed for each sampling occasion and for the averages for each MOTIF of all samples taken after the start of the differentiated treatment.

7.3 Results

7.3.1 Sea Level Rise Experiment

General

Two experiments were performed to test the effect of Sea Level Rise on the tidal mud flats. The first Sea Level Rise experiment ExpSLR95 did not reveal any significant effects of the experimentally induced difference in tidal regime. A combination of design shortcomings and technical problems probably masked the effects. Of the technical problems two important ones can be mentioned. Before filling the MOTIFs with sediment, the channel walls had to be repaired in one pair of the MOTIFs. These MOTIFs were completely dry when the sediment was dumped into them, whereas the other MOTIFs contained a shallow layer of water. After having filled the MOTIFs with seawater and running the tide for some days, the sediment of most MOTIFs looked like natural sediment with an oxidised surface layer and anoxic sediment at greater depths. However, in the aberrant pair the oxidised top layer was extraordinary thin and at times the surface was even anoxic. When the organisms were entered some weeks later they behaved differently in the aberrant pair of MOTIFs. *Arenicola* and *Macoma* stayed much longer on top of the sediment before burying, and had much higher mortality than in the other MOTIFs. The second problem was the tidal pump system of one of the pairs of MOTIFs. During the second half of the experiment it was impossible to lower

Table 7.1 T-test for paired comparison of high tide versus low tide MOTIFs

Numbers/m2

		Post	08/04/97	27/05/97	08/07/97	19/08/97	30/09/97
adult	ARENMARI	-0.943	0.312	-0.900	0.230	0.876	-0.053
adult	CERAEDUL	-0.200	-0.120	-0.505	-0.813	-0.441	-0.687
adult	MACOBALT	0.485	-0.256	-0.820	0.756	0.239	0.391
juv	ARENMARI	-0.948	0.391	0.353	-0.518	-0.885	1.000
juv	CERAEDUL	0.003		-0.194	-0.809	0.044	0.055
juv	MACOBALT	0.001	-0.391	0.080	0.056	0.009	0.888
	COROVOLU	0.058	-0.391	0.391	0.192	0.061	0.081
	HYDRULVA	0.081		0.391	0.388	0.280	0.053
	ENSIENSI	0.000			0.008	0.000	0.003
	LANICONC	0.049			0.156	0.068	0.072
	NEREDIVE	-0.382		0.391	0.037	-0.316	-0.403
	NEREVIRE	0.174			0.391	0.035	0.444
	SCOLARMI	0.018				0.103	0.215
	SPIOFILI	0.044			0.080	0.182	0.144

Species richness

Post	08/04/97	27/05/97	08/07/97	19/08/97	30/09/97
0.002	-0.391	0.014	0.015	0.011	0.103

Biomass/m2

		Post	08/04/97	27/05/97	08/07/97	19/08/97	30/09/97
	All species	0.001	-0.153	0.055	0.038	0.092	0.179
total	ARENMARI	0.041	-0.262	0.040	0.069	0.334	-0.713
adult	ARENMARI	0.080	-0.261	0.069	0.076	0.470	-0.189
juv	ARENMARI	0.056	0.391	0.061	0.374	0.070	0.219
total	CERAEDUL	0.111	-0.452	0.373	0.042	0.521	0.441
adult	CERAEDUL	0.148	-0.452	0.345	0.032	0.520	0.666
juv	CERAEDUL	0.083		-0.197	-0.964	0.673	0.133
total	MACOBALT	0.003	-0.790	0.619	0.262	0.077	0.159
adult	MACOBALT	0.005	-0.790	0.663	0.289	0.108	0.119
juv	MACOBALT	0.158	-0.391	0.141	0.207	0.054	-0.524
	COROVOLU	0.048			0.239	0.067	0.444
	HYDRULVA	0.061		0.320	0.504	0.287	0.065
	ENSIENSI	0.001			0.021	0.008	0.015
	LANICONC	0.080			0.154	0.172	0.050
	NEREDIVE	-0.289			0.087	-0.310	-0.447
	NEREVIRE	0.127			0.391	0.086	0.154
	SCOLARMI	0.193				0.238	0.290
	SPIOFILI	0.043			0.115	0.021	0.063

Individual weight

		Post	08/04/97	27/05/97	08/07/97	19/08/97	30/09/97
adult	ARENMARI	0.029	-0.138	0.019	0.012	0.157	-0.966
juv	ARENMARI	0.009	0.391	0.127	0.030	0.004	0.088
adult	CERAEDUL	0.004	0.238	0.013	0.003	0.016	0.028
juv	CERAEDUL	-0.025		-0.182	-0.697	-0.097	0.378
adult	MACOBALT	0.038	0.477	0.099	0.054	0.229	0.007
juv	MACOBALT	0.911		0.107	-0.212	-0.816	-0.571
	COROVOLU					-0.477	0.711
	HYDRULVA					-0.982	-0.770
	ENSIENSI						
	LANICONC						
	NEREDIVE						
	NEREVIRE						0.009
	SCOLARMI						
	SPIOFILI					0.053	0.009

Length

	Post	08/04/97	27/05/97	08/07/97	19/08/97	30/09/97
CERAEDUL	-0.003	0.246	0.014	0.001	0.009	0.003
MACOBALT	-0.318	0.812	0.240	0.051	0.151	0.039

Body Mass Index

	Post	08/04/97	27/05/97	08/07/97	19/08/97	30/09/97
CERAEDUL	0.766	0.508	0.002	-0.237	-0.411	-0.122
MACOBALT	-0.478	0.046	0.172	0.055	0.533	0.274

Table 7.1 (continued). T-test for paired comparison of high tide versus low tide MOTIFs

Relative increase biomass/m2

		Post	31/03/97	02/05/97	17/06/97	29/07/97	09/09/97
total	ARENMARI	-0.892	-0.329	0.075	0.978	-0.686	-0.380
adult	ARENMARI	-0.198	-0.329	0.105	0.810	-0.598	-0.164
juv	ARENMARI	-0.391		-0.391	-0.089	0.034	-0.442
total	CERAEDUL	0.323	-0.367	0.192	0.908	-0.430	0.757
adult	CERAEDUL	0.493	-0.367	0.189	0.981	-0.389	-0.983
juv	CERAEDUL					0.998	0.262
total	MACOBALT	0.190	-0.562	0.384	0.822	0.758	-0.243
adult	MACOBALT	0.171	-0.562	0.445	0.795	0.817	-0.411
juv	MACOBALT	0.391			-0.167	0.450	-0.058
	TOTAL	0.158	-0.188	0.071	0.891	-0.930	-0.764

Relative increase individual weight

		Post	31/03/97	02/05/97	17/06/97	29/07/97	09/09/97
total	ARENMARI	0.455	-0.151	0.003	0.753	-0.530	-0.378
adult	ARENMARI	0.744	-0.151	0.009	-0.017	-0.348	-0.469
juv	ARENMARI	-0.391		-0.391	-0.256	0.083	-0.060
total	CERAEDUL	-0.072	0.253	0.003	-0.108	-0.005	-0.506
adult	CERAEDUL	0.124	0.253	0.008	-0.080	-0.526	-0.215
juv	CERAEDUL					-0.633	0.094
total	MACOBALT	0.764	0.425	0.537	-0.308	0.879	0.267
adult	MACOBALT	0.705	0.425	0.395	-0.758	-0.456	0.904
juv	MACOBALT				-0.069	0.293	-0.458
	TOTAL	-0.204	0.920	0.065	-0.073	-0.997	-0.941

Increase in biomass/m2

		Post	31/03/97	02/05/97	17/06/97	29/07/97	09/09/97
total	ARENMARI	0.863	-0.262	0.051	0.702	-0.426	-0.282
adult	ARENMARI	-0.584	-0.261	0.081	0.660	-0.339	-0.271
juv	ARENMARI	0.220	0.391	0.061	-0.610	0.063	0.985
total	CERAEDUL	0.400	-0.452	0.274	0.292	-0.705	0.979
adult	CERAEDUL	0.610	-0.452	0.258	0.314	-0.629	-0.763
juv	CERAEDUL	0.133	-0.197	-0.197	0.608	0.660	0.344
total	MACOBALT	0.215	-0.790	0.480	0.813	0.652	-0.188
adult	MACOBALT	0.191	-0.790	0.531	0.803	0.734	-0.309
juv	MACOBALT	-0.652	-0.391	0.159	-0.485	0.043	-0.038
	TOTAL	0.160	-0.153	0.050	0.426	0.921	-0.548

Increase in induvidual weight

		Post	31/03/97	02/05/97	17/06/97	29/07/97	09/09/97
total	ARENMARI	0.192	-0.131	0.008	0.303	-0.145	-0.255
adult	ARENMARI	0.470	-0.138	0.016	-0.101	-0.329	-0.291
juv	ARENMARI	0.088	0.391	0.129	0.285	0.085	-0.192
total	CERAEDUL	-0.115	0.238	0.011	0.112	-0.007	-0.779
adult	CERAEDUL	0.028	0.238	0.008	0.053	0.818	-0.144
juv	CERAEDUL	0.378	-0.182	-0.182	0.633	-0.292	0.086
total	MACOBALT	0.422	0.477	0.237	-0.321	0.865	0.306
adult	MACOBALT	0.212	0.477	0.158	0.982	-0.435	-0.919
juv	MACOBALT	-0.571		0.107	-0.007	0.257	-0.537

the water level in either of the two MOTIFs to a level that the sediment became exposed to the air.

The design problem was twofold. As mentioned in Chapter 2 the tidal periods were synchronised with the daily 24 hour period. The timing of the tidal period was an extra variable of the experiments in addition to the tidal period. This timing could also create differences between the MOTIFs with the same tidal length. This extra variability might have hampered the detection of differences caused by the length of the tidal period. Another design choice was the difference in high and low tide period imposed on the individual MOTIFs of each pair. The imposed difference in immersion time (10 versus 6 hours) might have been too small to reveal differences in development

In the course of the experiments macroalgae (*Ulva* and *Enteromorpha*) entered the MOTIFs. The occurrence and development of the macroalgae was highly erratic and not related to the treatment. The presence of macroalgae seriously effects the functioning of the MOTIFs. It also hampers the sampling of the benthic fauna. In the first experiment the algae were allowed to develop for a too long time and reached a fairly high biomass. The removal of these algae probably effected the MOTIFs differently depending on the timing of the removal of the algae. It was a source of variability not related to the treatment and might have masked a possible effect. In the following experiments the macroalgae were removed as soon as they occurred in the MOTIFs. In this way mass development could be avoided.

The results of the second Sea Level Rise experiment are presented in the following sections. In the graphs the high tide MOTIFs are represented by closed symbols and the low tide MOTIFs by open symbols. The heavy and the thin lines represent the averages for the high tide and low tide MOTIFs respectively. For the different variables the statistical significance was determined and the results of the statistical tests are presented in Table 7.1.

Physical/chemical conditions

Oxygen concentrations in the water did not drop below 4 mg/dm and could reach maxima near 20 mg/l. As the water moved between each pair of high and low tide MOTIF, it is not surprising that there was no difference related to the treatment. In the low tide MOTIFs the sediment was exposed to the air for longer periods than in the high tide MOTIFs. During exposure the dry sediment lacks the heat buffering properties of the water. Consequently the sediment of the low tide MOTIFs experiences more extreme temperature variations. The results of the temperature measurements at 3-cm depth in the sediment are summarized in Table 7.2. The average sediment temperature for the period from the start of the differentiated tidal regime until the termination of the experiment was the same for low and high tide MOTIFs. The average daily amplitude, however, was more than twice as high in the low tide MOTIFs compared to high tide MOTIFs. The most extreme daily amplitude was 16.5 °C for the low tide MOTIFs and 8.5 °C for the high tide MOTIFs. The relatively harsh conditions in low tide MOTIFs may be an important parameter for the functioning of the community in addition to the reduced feeding time.

Table 7.2 Temperature variations at 3 cm depth in the sediment of low tide and high tide MOTIFs during the ExpSLR97 experiment

Temperatures		
	Low Tide MOTIFs	High Tide MOTIFs
Minimum during experiment	4.9	6.2
daily average minimum	14.5	16.4
Average during experiment	17.8	18.0
Daily average maximum	22.1	19.8
Maximum during experiment	33.6	30.0
Daily temperature amplitude		
Minimum	1.87	0.95
Average	7.63	3.43
Maximum	16.48	8.48

Macrobenthos

Numbers/m²

The differences in tidal regimes did not lead to changes in the numbers of the three main species in the MOTIFs (Fig. 7.3, Table 7.1). *Cerastoderma* and *Macoma* stayed virtually constant in numbers throughout the experiment, indicating very low mortality of these species. The mortality of the originally introduced *Arenicola* was considerable. Only between 11 and 50 % (average 26 %) of the original animals survived until the last sampling in

September. The mortality that was observed in this experiment was much higher than observed in the field by Beukema (1974) between July and February. In the high tide MOTIFs the mortality occurred mainly after July whereas in the low tide MOTIFs the mortality was rather constant over the experimental period. These observations have to be treated cautiously as there was a large variability in the observed numbers. The high mortality of *Arenicola* would lead to an extinction of the population within one year. The reason for this high mortality is not known. In the temperature rise experiment, discussed later, we found a much lower mortality, but still higher than 15% in half a year at Balgzand (Beukema 1974).

The population densities presented in Fig. 7.3 were restricted to the individuals that can be assumed to having been introduced into the MOTIFs at the start of the experiment. During the experiment young stages of all three species entered the MOTIFs. Juvenile *Arenicola* could easily be recognised by their size and colouration. For the two bivalve species the original specimens could be recognised from the size distribution (Fig. 7.4). The originally stocked bivalves had unimodal size distributions. *Cerastoderma* had a quite narrow size distribution, whereas *Macoma* had a wider variation, indicating the presence of different age classes. The original peaks could be traced until the end of the experiment. In the high tide MOTIFs the

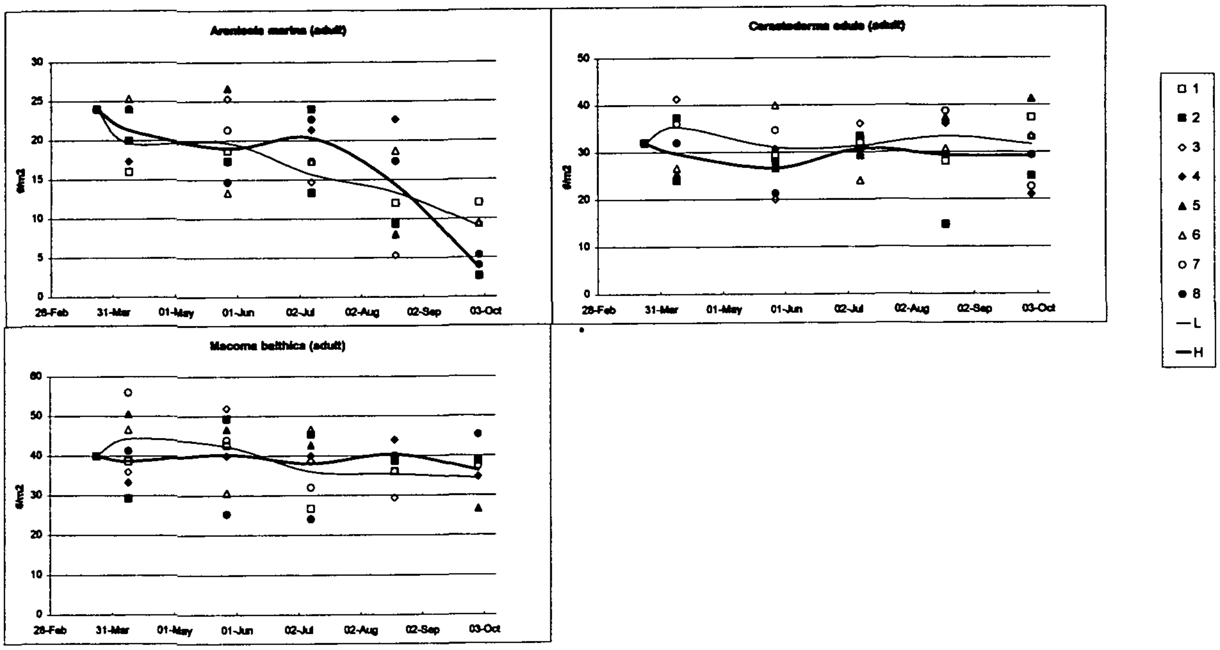


Fig. 7.3. Densities of *Cerastoderma, Macoma and Arenicola* in the MOTIFs under different tidal regimes during experiment ExpSLR97. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

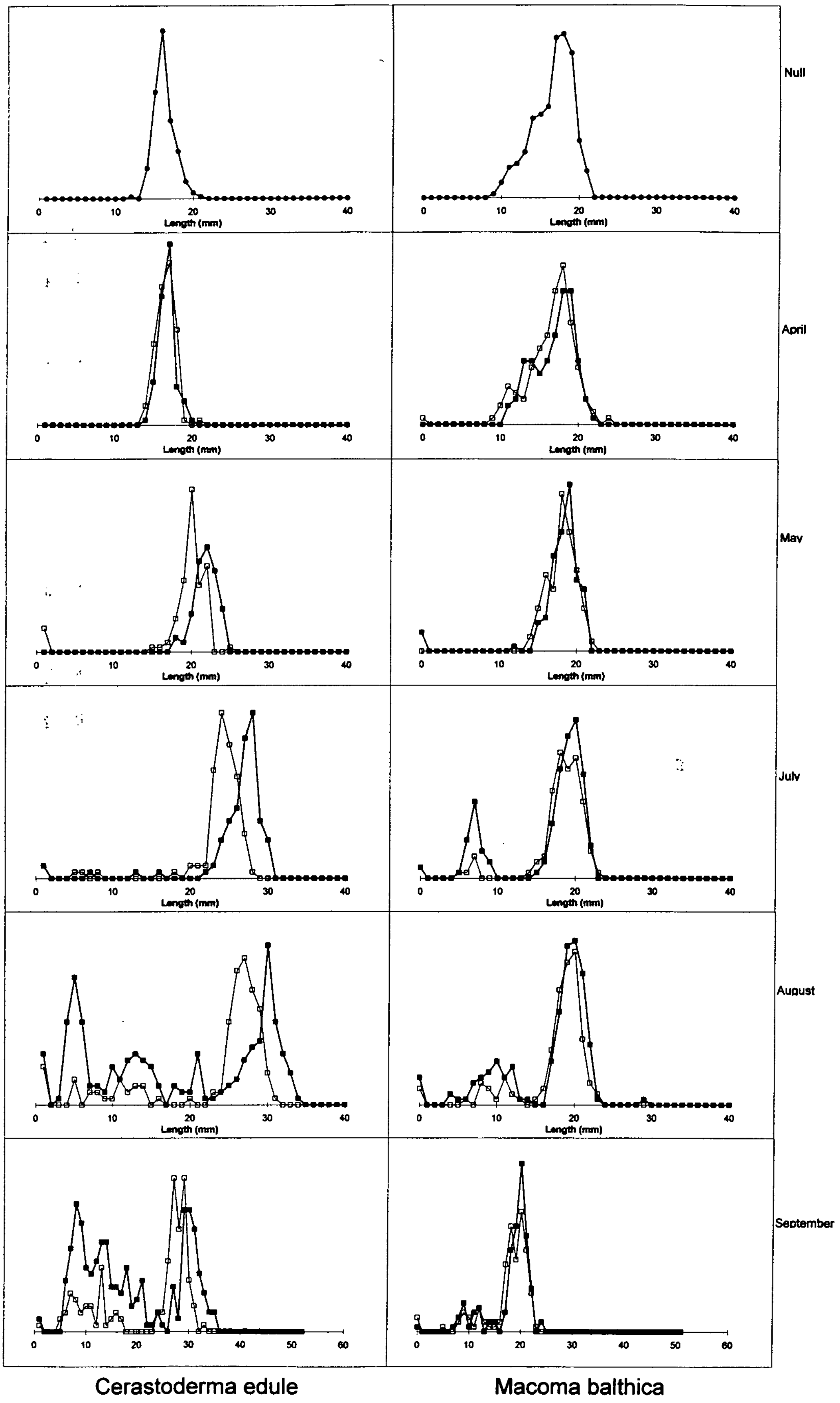


Fig. 7.4. Size distribution of *Cerastoderma edule* and *Macoma balthica* in the course of ExpSLR97. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols.

size distribution of *Cerastoderma* has shifted to higher sizes, indicating better growth in high tide MOTIFs. For *Macoma* this shift is also noticeable but much smaller. Small sized *Macoma* appear in July and small *Cerastoderma* in August. Growth differences between adults and juveniles will be presented and discussed separately.

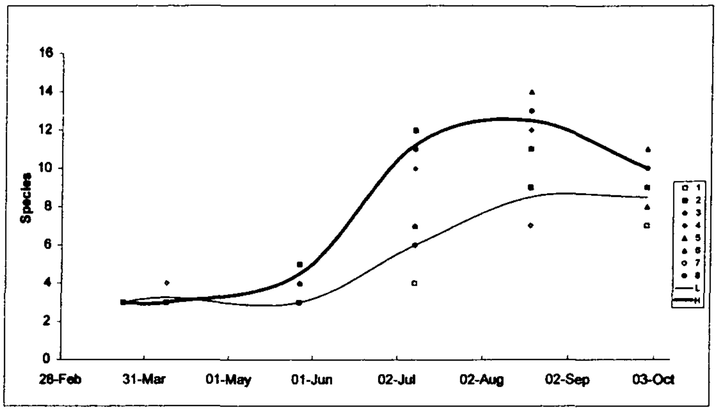


Fig. 7.5. Number of species in high tide and low tide MOTIFs in the course of the ExpSLR97 experiment. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

Apart from juvenile stages of the stocked species other species entered the MOTIFs as well. Hence the number of species increased during the experiment. In total 22 species were identified. The high tide MOTIFs developed a significantly higher species richness than the low tide MOTIFs (Fig. 7.5, Table 7.1). The development of the populations of the most important species is presented in Fig. 7.6. Three different patterns of development can be discerned. Juvenile *Arenicola* enters the MOTIFs in one invasion in equal numbers in the high and low tide MOTIFs. After the invasion the numbers stayed constant. Then there is a large group of organisms (juvenile *Cerastoderma*, juvenile *Macoma, Spio, Corophium* and *Hydrobia, Nereis virens*) that enter the high and the low tide MOTIFs with clearly higher numbers in the high tide MOTIFs. The differences between the high and the low tide MOTIFs are significant to highly significant (Table 7.1). The third group consists of *Ensis* and *Lanice* that almost exclusively are found in the high tide MOTIFs, and are virtually absent in the low tide MOTIFs. *Nereis diversicolor* is the only species that seems to prefer the low tide MOTIFs, but this is based on its presence in fairly high numbers in two low tide MOTIFs in August and one low tide MOTIF in September.

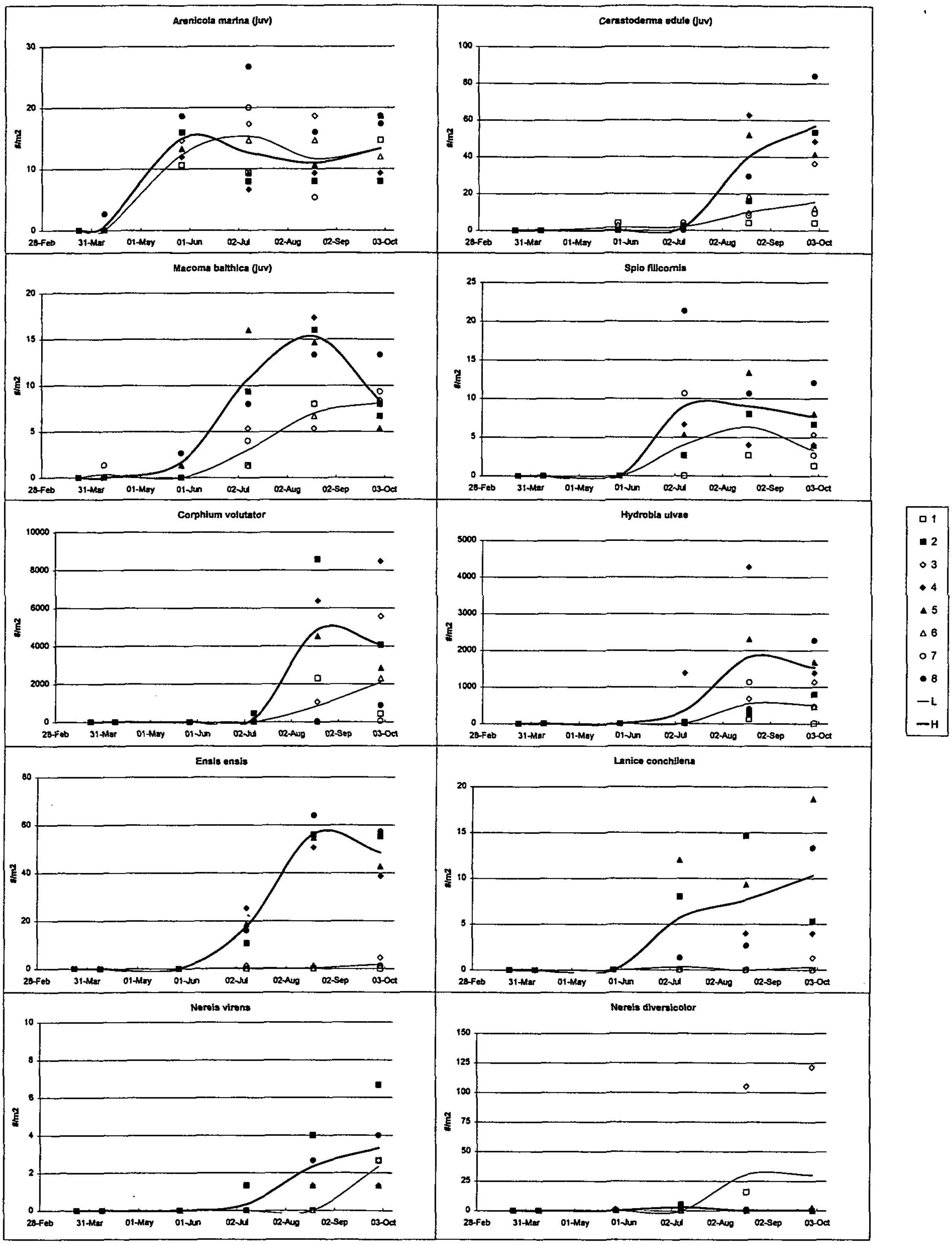


Fig. 7.6. The development of the populations of the most important species (n/m2) in high tide and low tide MOTIFs in the course of the ExpSLR97 experiment. Only those populations that have settled starting as larvae are shown here. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

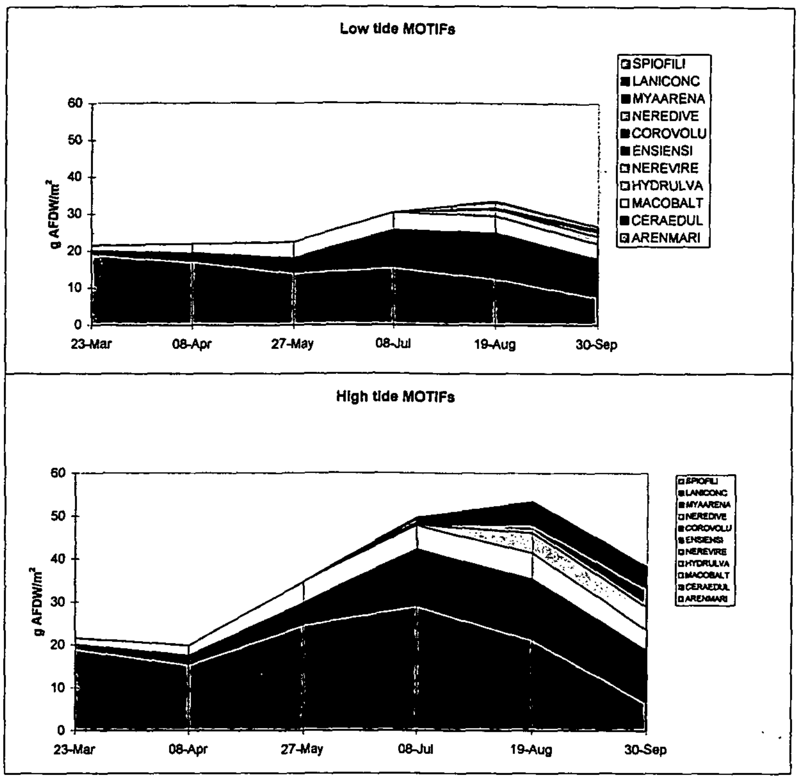


Fig. 7.7. Biomass of stocked and invaded macrobenthos species in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment

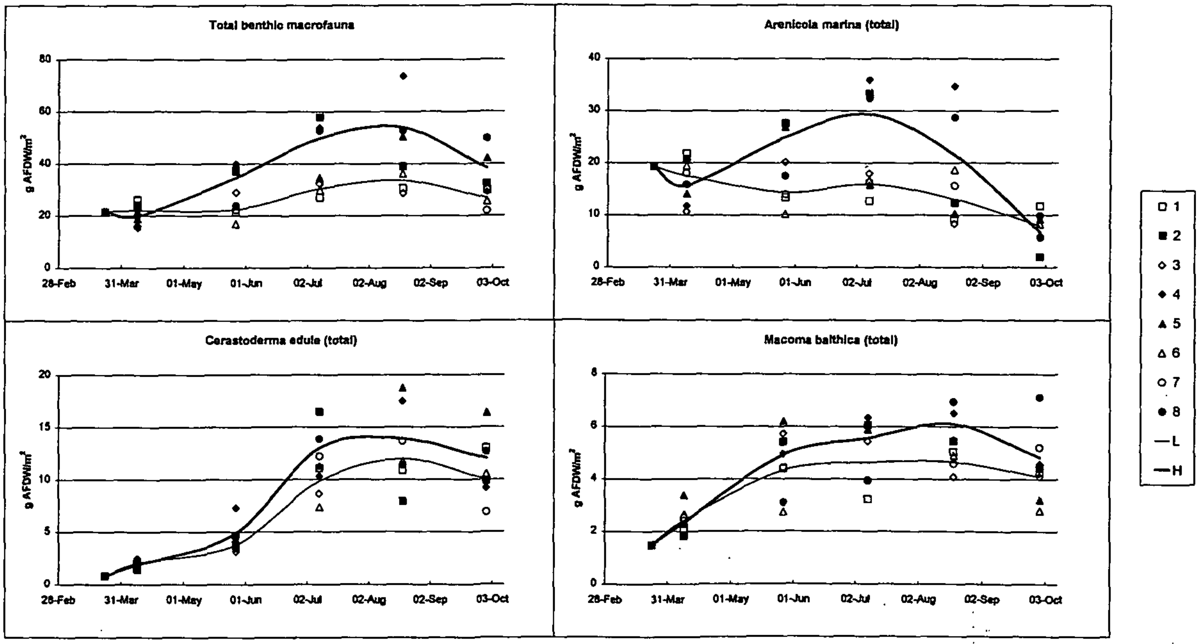


Fig. 7.8. Ash free dry weight (g AFDW/m2) of the three most important macrobenthos species in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

Biomass/m^2

The three introduced species remained the most abundant in terms of biomass (Fig.7.7). From June onwards the invaded species contributed significantly to the total biomass in the high tide MOTIFs (up to 40% in September). The share of these species in the low tide MOTIFs was about 20% (Fig 7.7).

The ash free dry weight of the total macrobenthic community and the three most important species is plotted against time in Fig. 7.8. From the start of the experiment there is a steady increase of the total biomass until August. Thereafter the biomass decreased again. This pattern in the MOTIFs is similar to that in the field (Beukema 1974). The graph clearly reveals that the low tide MOTIFs increased much less in benthic biomass than the high tide MOTIFs. There is quite some variation between the MOTIFs and the differences per sampling date are rarely significant. When the averages of the four sampling dates after the start of differentiated tidal regime are used, the difference between the high tide and the low tide MOTIFs is highly significant (Table 7.1).

The development of the biomass of the total *Arenicola* population was different between the high and the low tide MOTIFs. In the high tide MOTIFs the biomass increased until July and decreased thereafter. In the low tide MOTIFs there was a slow decrease in biomass throughout the experimental period. *Cerastoderma* and *Macoma* biomass increased strongly until July/August and decreased slightly thereafter. The highest biomass of all three species were found in the high tide MOTIFs, except for *Arenicola* at the last sampling.

In Fig. 7.9, the biomass data are presented separately for adults and juveniles. All species show a higher biomass in high tide MOTIF's. The results of the juveniles are quite variable. In September the *Arenicola* population in the high tide MOTIF's is dominated by the juveniles. The adults have nearly got extinct at that time. In the low tide MOTIFs the juvenile biomass also exceeded adult biomass, but the dominance is less extreme. The contribution of juvenile bivalves to the biomass is small in comparison to that of the adults. In September juvenile *Cerastoderma* contributed 2% to the *Cerastoderma* biomass in the low tide MOTIFs and 10% in the high tide MOTIFs. For *Macoma* the share of the juveniles at the last sampling was about 5%, irrespective of the tidal regime.

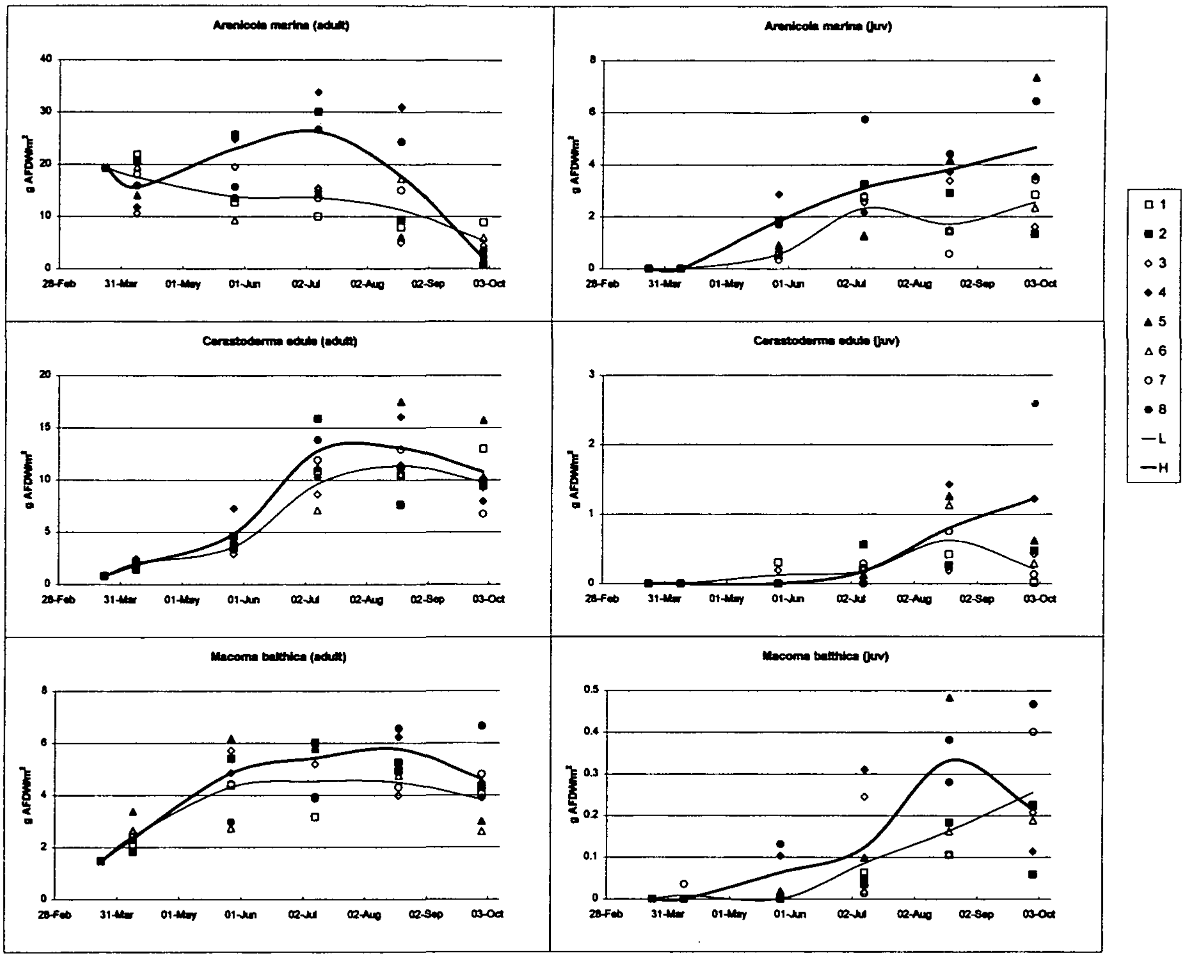


Fig. 7.9. Biomass (g AFDW/m2) of adult and juvenile stocked and invaded *Arenicola*, *Cerastoderma* and *Macoma* in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

Individual weight

Because the numbers of individuals are independent of the tidal regime and biomass is higher in high tide MOTIFs the weight of individual macrobenthic animals has to be related to the tidal regime. This is shown in Fig. 7.10. The plots of the juvenile bivalves are irregular, which is related to the continuous immigration of juveniles. Juvenile *Arenicola* invaded the MOTIFs during one single period. Afterwards their growth was related to the tidal regime. The individual weight of juveniles increased much more in the high tide MOTIFs than in the low tide MOTIFs, resulting in weights about twice as high during the last sampling.

Length

Another aspect of growth is shell length (Fig 7.11). The length of *Cerastoderma* is slightly, but highly significantly higher in high tide MOTIFs than in low tide MOTIFs. Because the average length increase was much smaller in *Macoma* the length difference between high and

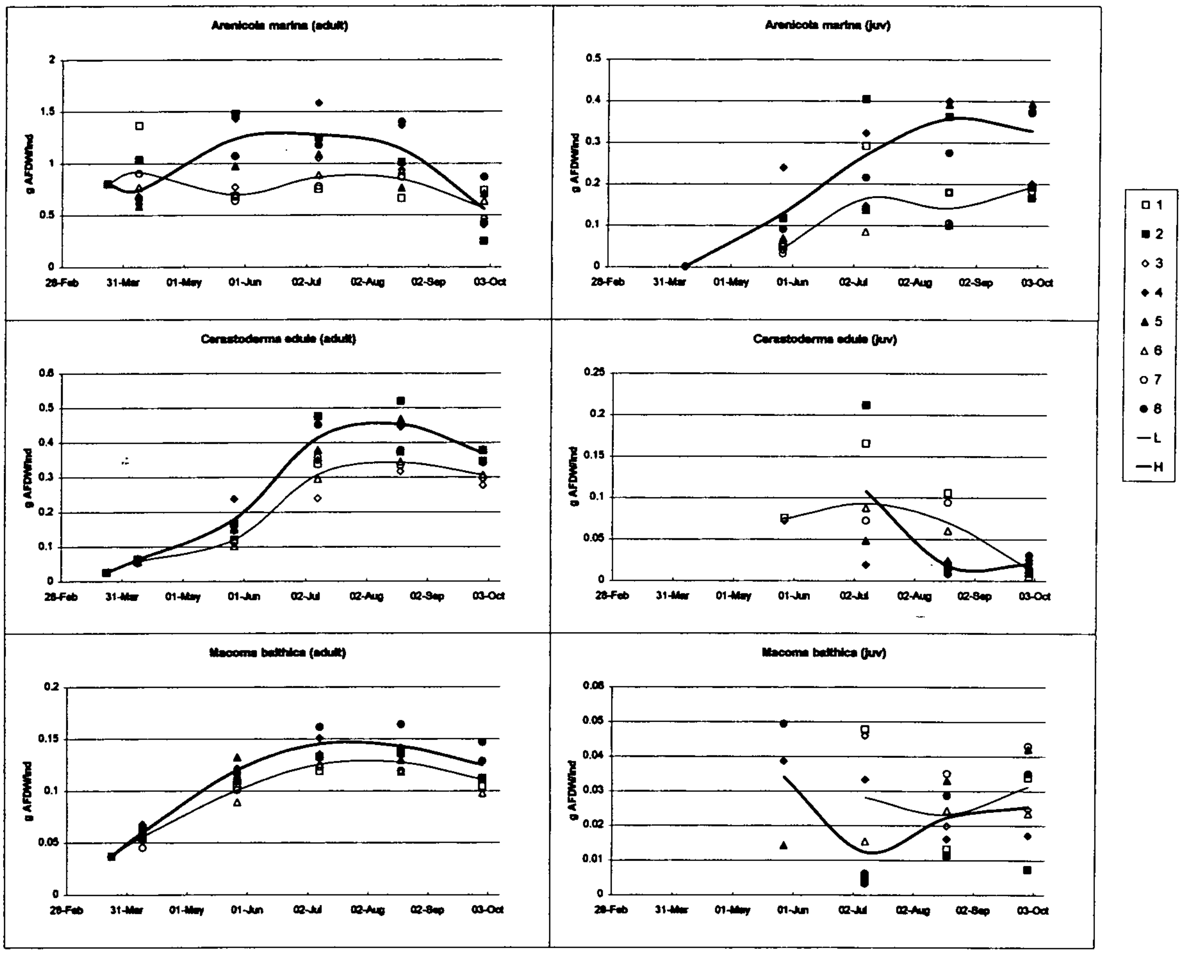


Fig. 7.10. Biomass (g AFDW/m2) of individual adult and juvenile *Arenicola*, *Cerastoderma* and *Macoma* in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment.

low tide MOTIFs was small and only significant on 2 sampling days. Adult *Macoma* in high tide MOTIFs becomes larger than in low tide MOTIFs.

Body Mass Index

The Body Mass Index (AFDW/length^3, mg cm^{-3}) is a measure of the condition of the bivalves (Fig 7.11). A high BMI indicates that an individual bivalve is in good condition. For *Macoma* a minimum BAI of 5.6 is required to spawn (Hencoop and Van der Mere 1997). Stress can have a negative effect on this condition factor. The results of the BAI do not indicate that the tidal regime creates stress for the bivalves. There was a difference in BAI for *Cerastoderma* in May and for *Macoma* in July, with higher BIS in high tide MOTIFs. Later during the experiment the differences disappeared again.

Individual growth

The main effect of the difference in tidal regime is a difference in the individual weight of the organisms. This difference must be brought about by a difference in growth rate. The growth

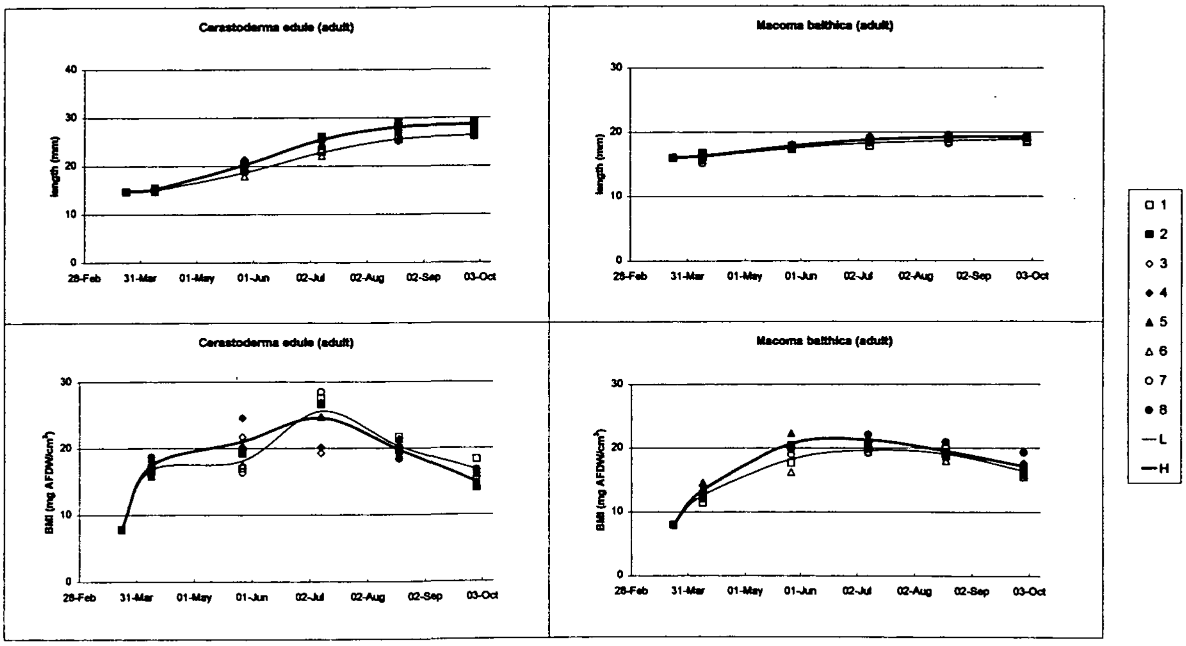


Fig. 7.11. Size (mm) and Body Size Index (AFDW/cm3) of individual adult *Cerastoderma* and *Macoma* in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment

rates are higher in high tide MOTIFs, but only during the period of active growth. In the period that the organisms stabilise their weight or decrease in weight this process is stronger in high tide MOTIF's. For *Arenicola* this effect is that strong that at the end of the experiment the individual weights in high tide MOTIFs have equalized those in low tide MOTIFs.

Discussion sea level rise experiment

The EcoWasp model, which was meant to be tested in the MOTIFs, assumes a direct proportionality between inundation of the sediment and the time filter feeders can collect food. Except when there is a food surplus the longer feeding time will lead to a higher food uptake and consequently a higher secondary production. The result of the Sea Level Rise experiment confirms that a longer inundation time leads to a higher production. Although immigration also is higher in the high tide Motifs the stimulation of individual growth is mainly responsible for the increase of production. The experiment also shows that this stimulation of production is not restricted to filter feeders, but is also found in deposit feeding *Arenicola*. The stimulation of the growth of deposit feeders might be related to an increased deposition of organic material in high tide MOTIFs. On the other hand the feeding activity of deposit feeders decreases or stops?? when the sediment is dry.

In the high tide MOTIFs the period the sediment is covered with water is about 2.6 times as long as compared to the low tide MOTIF's (Fig. 7.2). From the start of the ExpSLR97 experiment to the day maximum biomass was reached the total benthic macrofauna production was 32 g ash free dry weight m^{-2} for high tide MOTIFs and 12 g ash free dry weight/m^2 for low tide MOTIFs, also a factor of 2.6. The biomass increases of the three main species shows a different pattern. In this case the relationship between inundation time and production is no longer present.

The Body Mass Index of *Macoma* and *Cerastoderma* increased to high values in summer. These BMI values were higher than values generally measured for specimens sampled in the field (Zwarts, 1991). Dissection of the *Macoma* from the MOTIFs revealed that they had much larger siphons than specimens in the field. It is know that several predators feed on regenerating parts of preys (e.g. siphons of *Macoma*). The absence of predators in the MOTIFs may be responsible for these high BMI values.

The average sediment temperature is equal in all MOTIFs, but the extremes reach higher and lower levels in the low tide MOTIFs. The harsher conditions did not lead to a higher mortality in low tide MOTIFs. This leaves the difference in the length of the period the organisms can feed actively as the principle factor causing the differences between the MOTIFs. This effect was clearly observed for all organisms. It was surprising to see that the BMI was not effected by the difference in tidal regime. This suggests a balance between length growth and body mass increase, resulting in no difference in BMI. This finding contradicts the result from NRP 1. Honkoop and Beukema (1997) and Honkoop and van der Meer (1998) found no differences in length in their treatments. This result implies that differences in body mass resulted in differences in BMI. It is unclear why the results of the two studies differ in this way. The experimental conditions in the present experiments are more natural than the experiments during NRP1 (two tidal cycles per 24 hours versus 1, normal daylight versus complete darkness), but it is hard to understand why this would lead to the differences in response.

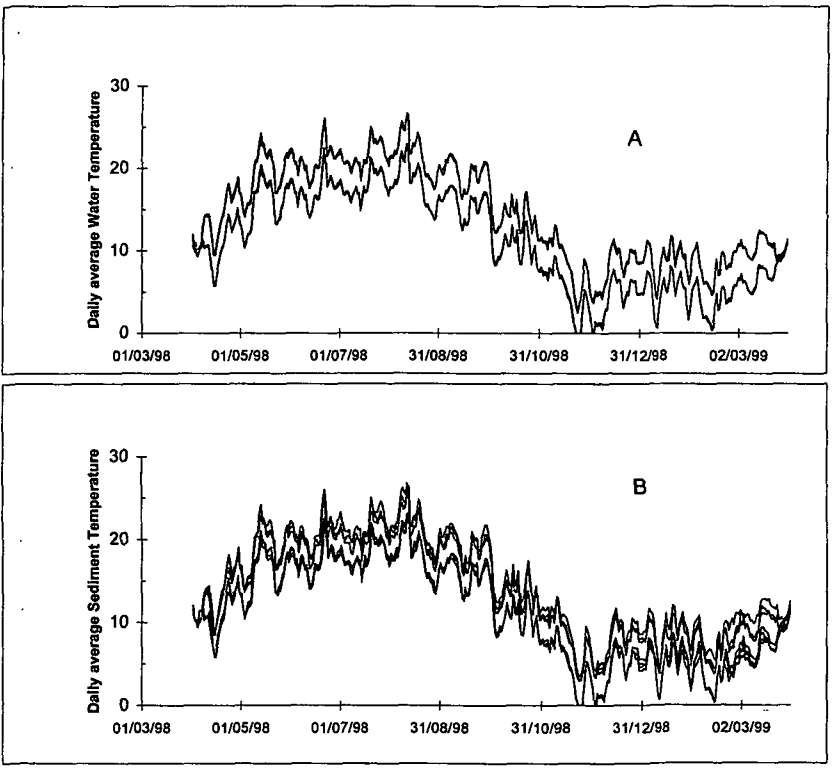


Fig. 7.12. Daily average temperatures in water (A) and sediment (B) in experimentally heated MOTIFs (upper lines) and control MOTIFs without heating (lower lines) in the course of the ExpTR98 experiment.

Predation pressure of birds is more intense on high mudflats than on the lower and longer immersed flats. On the other hand submersed flats experience higher predation from invertebrates and fish. Population densities in the field are the result of population increases and population losses due to predation. Both predation from birds and fish/invertebrates ultimately determine the consequences of sea level rise for the invertebrate benthic fauna. The experiment with the model tidal flats shows that there are differences in production and that differences in biomass in the field are at least partly the result of a bottom up mechanism. It is one of the important advantages of mesocosm studies that mechanisms can be singled out.

7.3.2. Temperature Rise Experiment

General

In the temperature experiment (ExpTR98) the tidal regimes were identical for all pairs of MOTIFs (Fig 7.2). The tidal period lasted 12 hours and 30 minutes, resulting in a one-hour shift of the timing of high and low tide each day. The temperature regulation started on April 7th 1998, immediately after the first sampling. MOTIFs 1,2,5,6 were used as controls whereas MOTIFs 3,4,7,8 were heated to a level of 4 °C above the temperature of the controls. In the graphs the high-temperature MOTIFs are indicated with closed symbols, controls MOTIFs by open symbols. The heavy lines are used for the average of all high temperature MOTIFs and the thin lines for the average of the controls. For technical reasons it was necessary to select pairs of MOTIFs to be heated. Strictly the two MOTIFs of a pair are not independent. Nevertheless, in this report the MOTIFs will be treated as independent units in the statistical analysis. The results of the statistical analysis for the different variables are summarised in Table 7.3.

Physical/chemical conditions

The temperature regulation functioned perfectly with a difference in water temperature of 4 °C (Fig. 7.12). The temperature regulation was restricted to the water phase of the MOTIFs. During low tide the sediment temperature of the heated MOTIFs tended to equalise with that of the unregulated MOTIFs. Hence, the average temperature difference for the sediment was smaller than the 4° of the water (Fig. 7.12), depending very much on the weather conditions during exposure. Consequently not only the temperature difference between heated and control MOTIFs was smaller than the difference in water temperature, it also was more variable.

During the first months of the experiment the oxygen regime was very dynamic, with oxygen concentrations varying from 2-18 mg dm^{-3}. There was no relation between the temperature treatment and the minimum or maximum oxygen concentrations. Although the minima were rather low it cannot be expected that this effected the experiments. Most species can temporarily tolerate low oxygen concentrations. Moreover, these adverse situations occurred in all MOTIFs and not specifically in one of the treatments. From October onwards the variation was much smaller, with minima of 6.8 mg dm^{-3} and maxima of 10 to 14 mg dm^{-3}. During this period the high temperature MOTIFs had slightly lower oxygen concentrations than the controls. This difference is easily explained by the difference in saturation values at the different temperatures. Large daily amplitudes during spring and summer indicate high primary production, which decreased in autumn and winter. The data do not allow for a more accurate calculation of productivity.

Macrobenthos

Numbers/m^2

In contrast to the previous experiment no juvenile stages of *Cerastoderma* and *Macoma* entered the MOTIFs. Only sporadically bivalves were found at sizes smaller than the originally stocked population (Fig. 7.13). On the other hand, juvenile *Arenicola* invaded the MOTIFs in huge numbers shortly after the start of the experiment (Fig. 7.14). In three of the four pairs the numbers were equally high, but in one control pair (MOTIF 1 and MOTIF 2) the numbers were much smaller. The difference persisted until the end of the experiment (Fig. 7.14). It is unclear why the numbers in MOTIF 1 and 2 were much lower than in the other MOTIFs The supply water was identical in all MOTIFs by leading supply water from a common header tank through equally long hoses to each MOTIF.

Tabel 7.3 T-test for paired comparison of high temperature versus control MOTIFs

Numbers/m2

	Post	06/04/98	25/05/98	13/07/98	31/08/98	19/10/98	07/12/98	27/01/99	15/03/99
ARENMARI	0.735	-0.222	0.692	-0.582	0.675	0.785	0.715	0.897	0.818
ARENMJUV	0.411	0.739	0.285	0.369	0.327	0.421	-0.994	0.337	0.319
ARENMTOT	0.410	-0.716	0.283	0.374	0.324	0.422	-0.996	0.339	0.311
CERAEDUL	-0.566	0.248	-0.430	-0.736	-0.828	0.373	0.534	0.936	-0.135
MACOBALT	-0.723	-0.537	-0.471	0.158	-0.726	0.595	-0.359	-0.681	-0.484
COROVOLU	-0.807	0.391	0.061	0.202	0.571	-0.033	-0.021	0.806	-0.262
GAMMSPEC	-0.187		0.298	-0.582	-0.584	-0.048	-0.006	0.254	0.853
HYDRULVA	0.045	0.266	0.248	0.276	0.436	0.410	0.345	0.284	0.297
TOTAL	-0.807	0.739	0.216	0.464	-0.961	-0.019	-0.081	0.206	0.576

Biomass/m2

	Post	06/04/98	25/05/98	13/07/98	31/08/98	19/10/98	07/12/98	27/01/99	15/03/99
All species	-0.490	-0.244	0.250	-0.850	-0.338	-0.256	-0.161	-0.408	-0.088
ARENMARI	-0.491	-0.194	0.850	-0.185	-0.552	-0.807	-0.569	-0.171	-0.483
ARENMJUV	0.550	0.442	0.144	0.623	0.551	-0.428	-0.841	0.625	-0.755
ARENMTOT	0.736	-0.194	0.194	0.829	0.672	-0.464	-0.724	0.948	-0.590
CERAEDUL	-0.034	0.265	-0.418	-0.125	-0.116	-0.402	-0.393	-0.205	-0.023
MACOBALT	-0.082	-0.622	-0.245	-0.527	-0.103	-0.150	-0.108	-0.180	-0.045
COROVOLU	-0.927	0.391	0.070	0.210	0.775	-0.016	-0.074	0.967	-0.230
GAMMSPEC	-0.208		0.393	-0.541	-0.423	-0.037	-0.058	0.204	0.848
HYDRULVA	0.071	0.312	0.366	0.237	0.247	0.450	0.298	0.302	0.316

Individual weight

	Post	06/04/98	25/05/98	13/07/98	31/08/98	19/10/98	07/12/98	27/01/99	15/03/99
ARENMARI	-0.155	-0.944	-0.436	-0.447	-0.333	-0.387	-0.197	-0.078	-0.114
ARENMJUV	-0.230	0.494	-0.338	-0.214	-0.213	-0.212	-0.294	-0.244	-0.233
ARENMTOT	-0.352	-0.513	-0.301	-0.209	-0.218	-0.213	-0.958	-0.691	-0.599
CERAEDUL	-0.017	0.888	0.754	-0.060	-0.017	-0.088	-0.009	-0.006	-0.027
MACOBALT	-0.015	-0.838	-0.423	-0.031	-0.026	-0.015	-0.080	-0.019	-0.013
COROVOLU	0.687		0.483	-0.698	0.829	-0.388	0.709	-0.437	0.829
GAMMSPEC	0.797		0.717	-0.353	-0.472	-0.738	0.357	0.777	0.555
HYDRULVA		-0.608			0.250	-0.126			
TOTAL	-0.440	-0.170	-0.240	-0.413	0.945	0.061	0.068	-0.265	-0.295

Length

	Post	06/04/98	25/05/98	13/07/98	31/08/98	19/10/98	07/12/98	27/01/99	15/03/99
CERAEDUL	-0.042	-0.194	0.663	-0.218	-0.006	-0.238	-0.010	-0.017	-0.188
MACOBALT	-0.087	-0.442	-0.384	-0.525	-0.076	-0.175	-0.407	-0.192	-0.111

Body Mass Index

	Post	06/04/98	25/05/98	13/07/98	31/08/98	19/10/98	07/12/98	27/01/99	15/03/99
CERAEDUL	-0.008	0.274	-0.902	-0.027	-0.209	-0.035	-0.015	-0.007	-0.016
MACOBALT	-0.006	0.195	-0.740	-0.034	-0.008	-0.016	-0.018	-0.026	-0.119

Relative increase biomass/m2

	Post	30/03/98	30/04/98	18/06/98	06/08/98	24/09/98	12/11/98	01/01/99	19/02/99
ARENMARI	-0.684	-0.210	0.392	-0.631	0.856	-0.995	-0.950	-0.658	-0.664
ARENMJUV	-0.210			-0.093	-0.754	-0.200	0.722	0.343	-0.230
ARENMTOT	-0.700	-0.211	0.105	-0.099	-0.923	-0.291	0.812	0.524	-0.423
CERAEDUL	-0.040	0.249	-0.291	-0.576	0.766	0.301	-0.660	-0.376	-0.542
MACOBALT	-0.261	-0.660	-0.779	0.542	-0.059	0.816	-0.804	0.915	0.888
TOTAL	-0.135	-0.251	0.141	-0.107	-0.630	-0.267	0.927	0.895	-0.293

Relative increase individual weight

	Post	30/03/98	30/04/98	18/06/98	06/08/98	24/09/98	12/11/98	01/01/99	19/02/99
ARENMARI	-0.095	-0.931	-0.607	-0.935	-0.588	0.844	-0.694	-0.578	-0.330
ARENMJUV	-0.170			-0.084	0.871	-0.625	0.189	-0.064	0.565
CERAEDUL	-0.034	0.767	-0.991	-0.011	0.636	-0.623	-0.428	-0.032	0.658
MACOBALT	-0.116	-0.917	-0.746	-0.045	-0.378	-0.271	0.159	0.878	0.679

Increase in biomass/m2

	Post	30/03/98	30/04/98	18/06/98	06/08/98	24/09/98	12/11/98	01/01/99	19/02/99
ARENMARI	0.586	-0.194	0.454	-0.550	0.634	0.737	-0.826	-0.704	-0.871
ARENMJUV	-0.703	0.442	0.144	-0.243	-0.781	-0.199	0.501	0.468	-0.210
ARENMTOT	0.903	-0.194	0.144	-0.158	-0.974	-0.262	0.577	0.627	-0.416
CERAEDUL	-0.017	0.265	-0.313	-0.248	-0.901	0.192	-0.878	-0.616	-0.473
MACOBALT	-0.414	-0.622	-0.790	0.807	-0.074	0.649	0.762	0.861	0.759
TOTAL	-0.128	-0.244	0.193	-0.136	-0.732	-0.331	0.635	0.677	-0.304

Increase in individual weight

	Post	30/03/98	30/04/98	18/06/98	06/08/98	24/09/98	12/11/98	01/01/99	19/02/99
ARENMARI	-0.115	-0.944	-0.551	-0.823	0.947	0.697	-0.681	-0.494	-0.348
ARENMJUV	-0.235		-0.340	-0.181	0.236	0.460	0.234	-0.324	-0.544
CERAEDUL	-0.018	0.888	0.787	-0.021	0.869	-0.808	-0.979	-0.135	0.227
MACOBALT	-0.114	-0.838	-0.681	-0.048	-0.569	-0.702	0.115	0.635	0.470

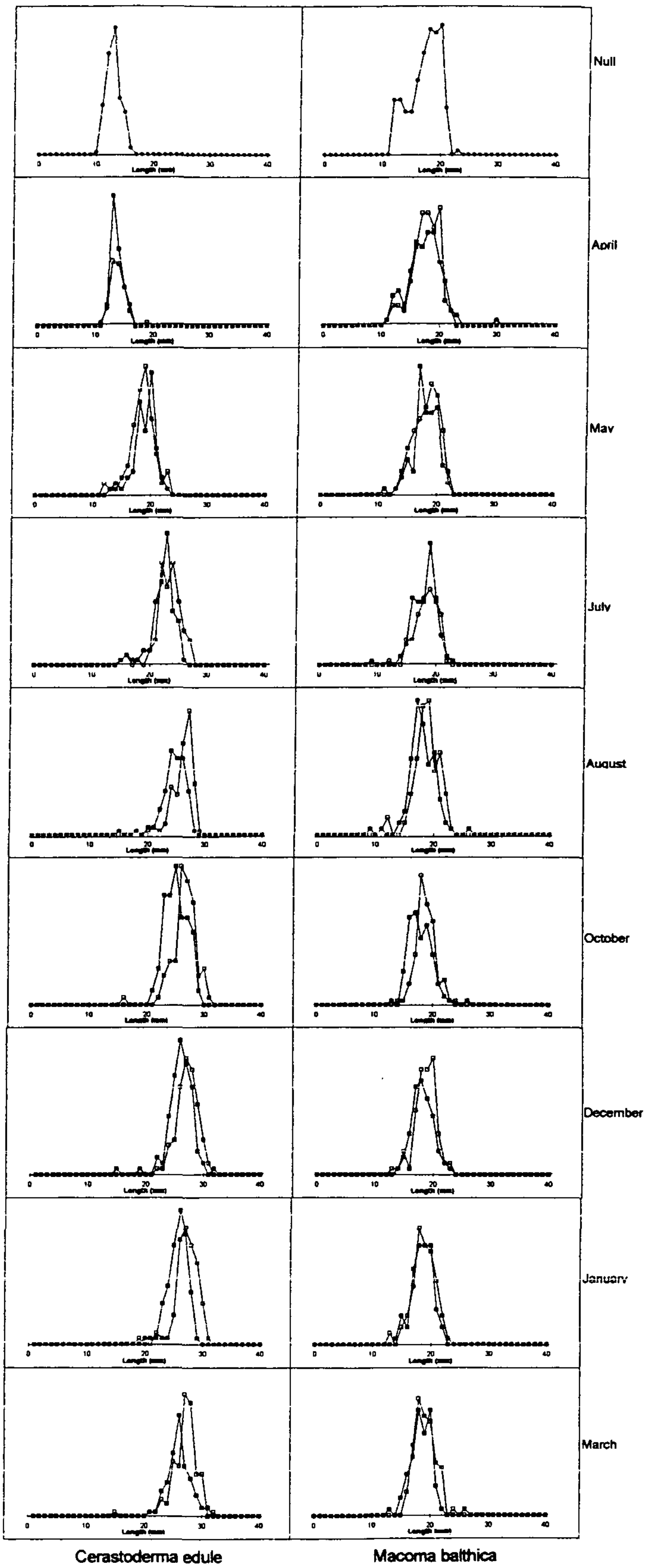


Fig. 7.13 Size distribution of *Cerastoderma edule* and *Macoma balthica* in the course of ExpTR98. High temperature MOTIFs are represented by closed symbols and control MOTIFs by open symbols.

Other species never became abundant during this experiment. In this respect this experiment (ExpTR98) differs from the previous experiment (ExpSLR97). The different can be explained by the change in the water supply. In experiment ExpSLR97 the water supply was directly connected to the intake pump of seawater. In experiment ExpTR98 this connection was blocked and the supply water in this experiment passed a series of settling basins where the seawater had a residence time of about three days. Apparently most species settled out in these basins, whereas juvenile *Arenicola* were able to keep suspended and pass the settling basins. The numbers of adult *Arenicola* decreased slowly throughout the experiment (Fig. 7.14). Juvenile *Arenicola* were fairly constant during the summer but numbers dropped suddenly in November in the high ature MOTIFs and in December in the controls (Fig. 7.14). *Cerastoderma* stayed constant in numbers until the end of the experiment indicating that mortality was very small (Fig. 7.14). *Macoma* numbers dropped considerably in April/May,

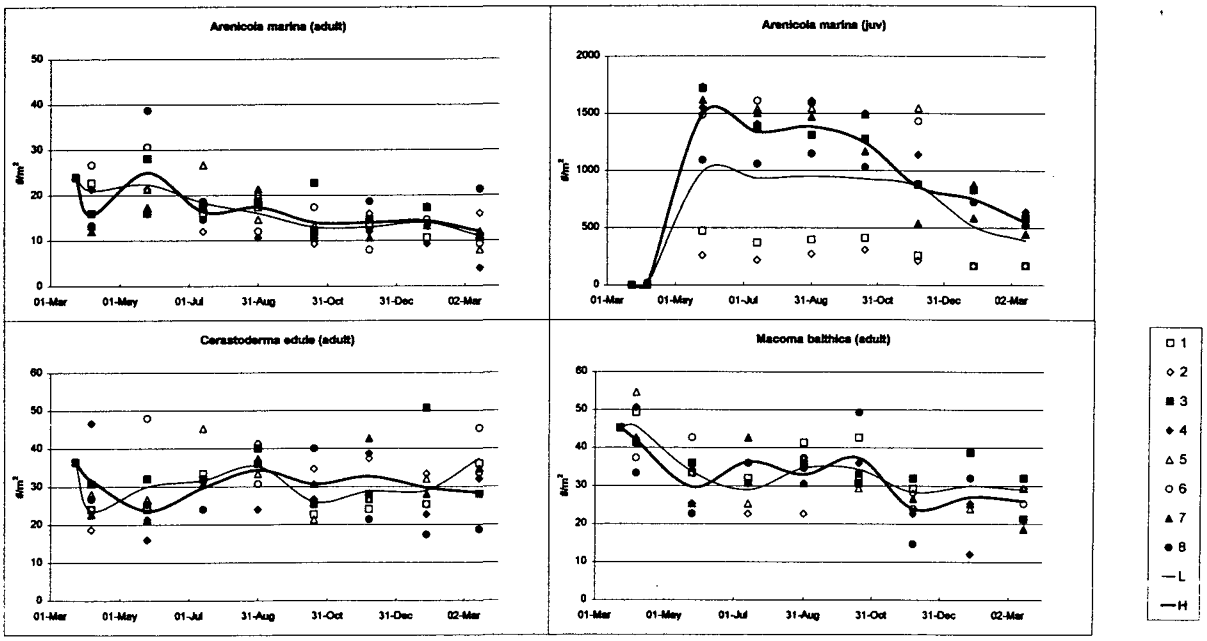


Fig. 7.14. The development of populations of adult (stocked) and juvenile (invaded) *Arenicola* and adult *Cerastoderma* and *Macoma* (n/m2) in high temperature and control MOTIFs in the course of the ExpTR98 experiment. High temperature MOTIFs are represented by closed symbols, control MOTIFs by open symbols. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

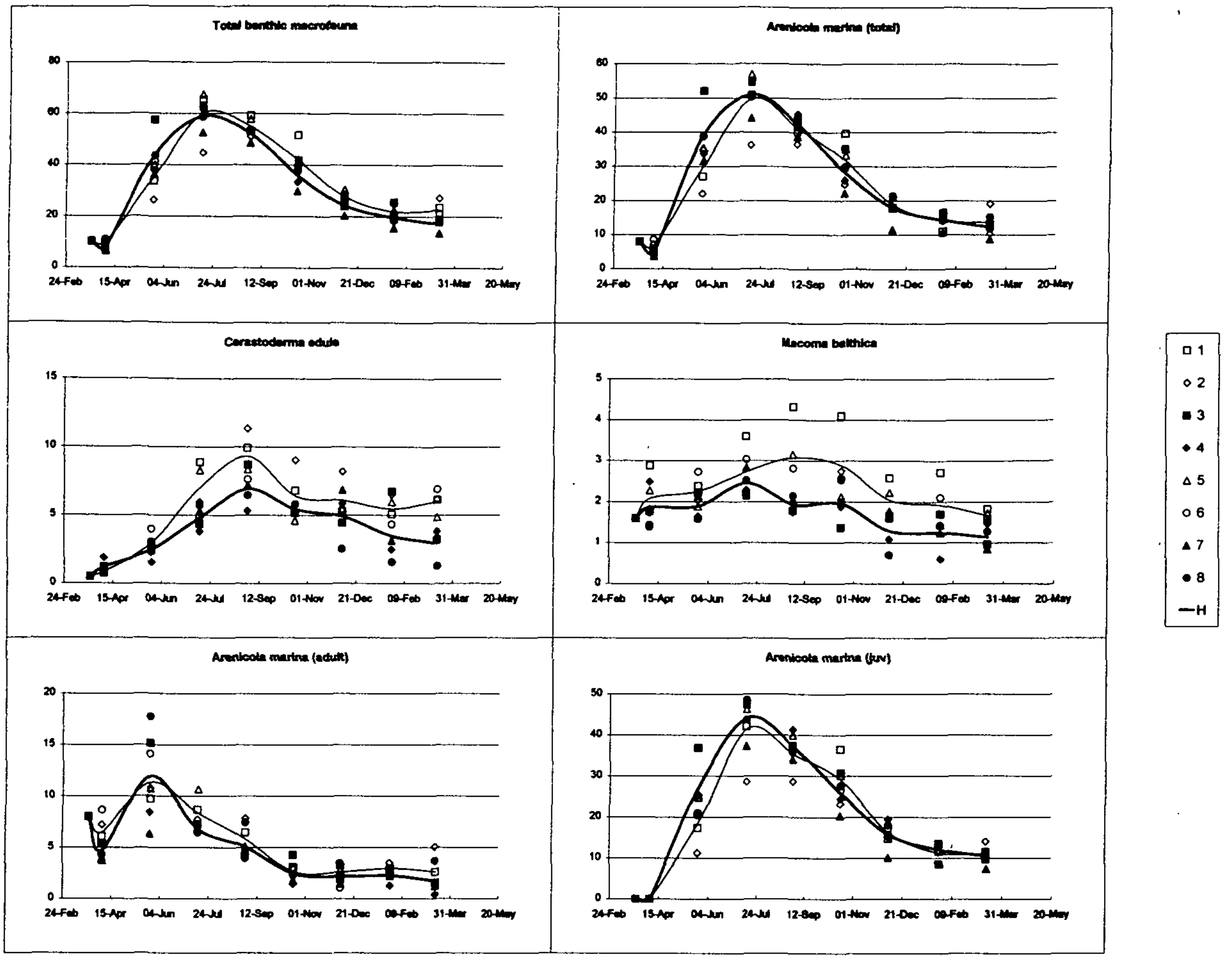


Fig. 7.15. Ash free dry weight (g AFDW/m2) of the total benthic macrofauna, adult and juvenile *Arenicola (combined), Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. High temperature MOTIFs are represented by closed symbols, control MOTIFs by open symbols. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

stayed constant during summer, and dropped again in November (Fig. 7.14). There were no differences in the numbers of any of these species that could be related to temperature increase.

Biomass/m^2

The total benthic macrofauna biomass (Fig. 7.15) rapidly increased from 10 g AFDW/m^2 at the start of the experiment to 59 g AFDW/m^2 in July. Thereafter the biomass slowly decreased until 20 g AFDW/m^2 in March, one year after stocking the MOTIFs. Juvenile *Arenicola* dominated the total biomass figures. Other species than those originally stocked hardly contributed to the biomass (Fig. 7.16). Although the numbers of juvenile *Arenicola*

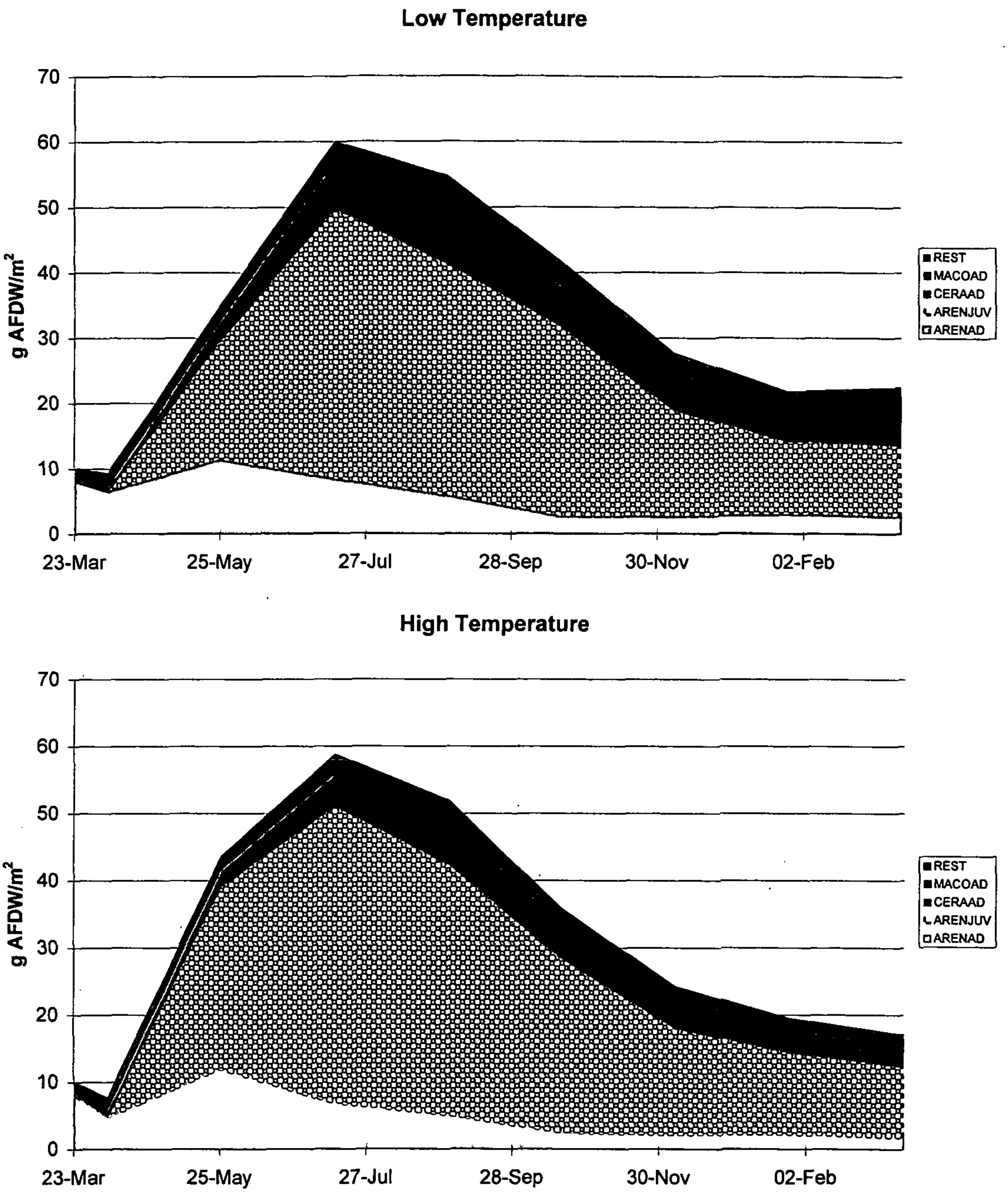


Fig. 7.16. Total biomass (in ash free dry weight, g AFDW/m2) of the total benthic macrofauna, mainly consisting of adult and juvenile *Arenicola, Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment.

were much lower in one pair of the controls (MOTIF 1 and 2), the biomass of juvenile *Arenicola* is virtually the same in all MOTIFs (Figs. 7.15, 7.16). Only on the first day of occurrence of juvenile *Arenicola* MOTIFs 1 and 2 had a lower biomass. Later during the experiment the juvenile *Arenicola* biomass equalised in all MOTIFs (Fig. 7.15). These

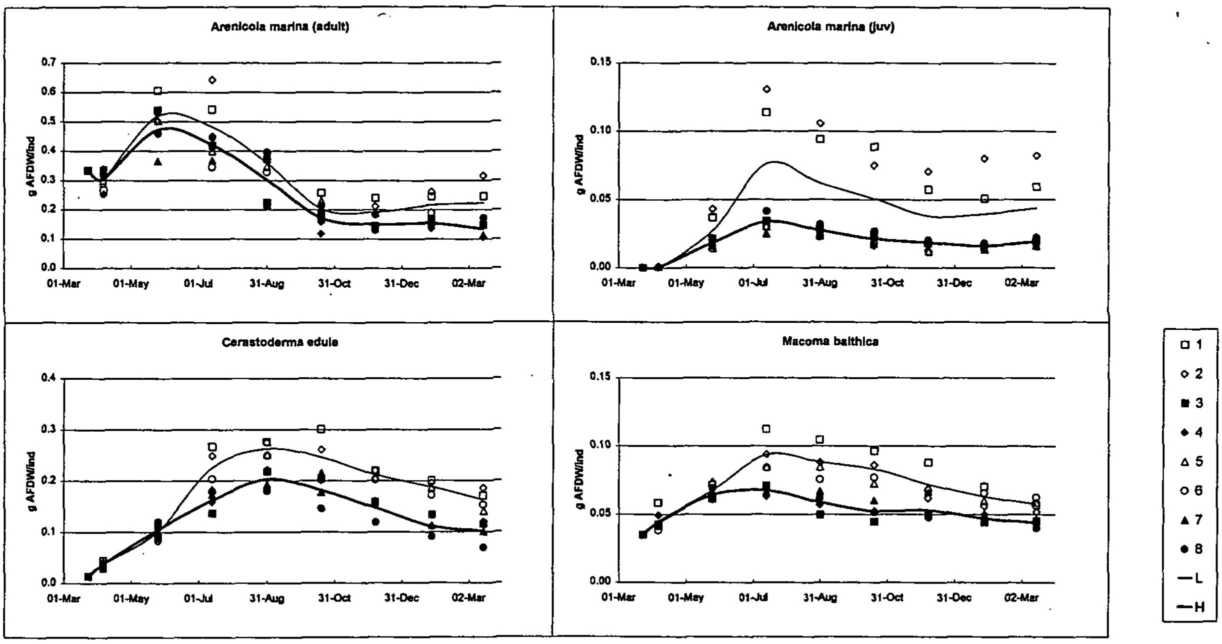


Fig. 7.17 Biomass (g AFDW/ind) of individual adult and juvenile *Arenicola*, *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

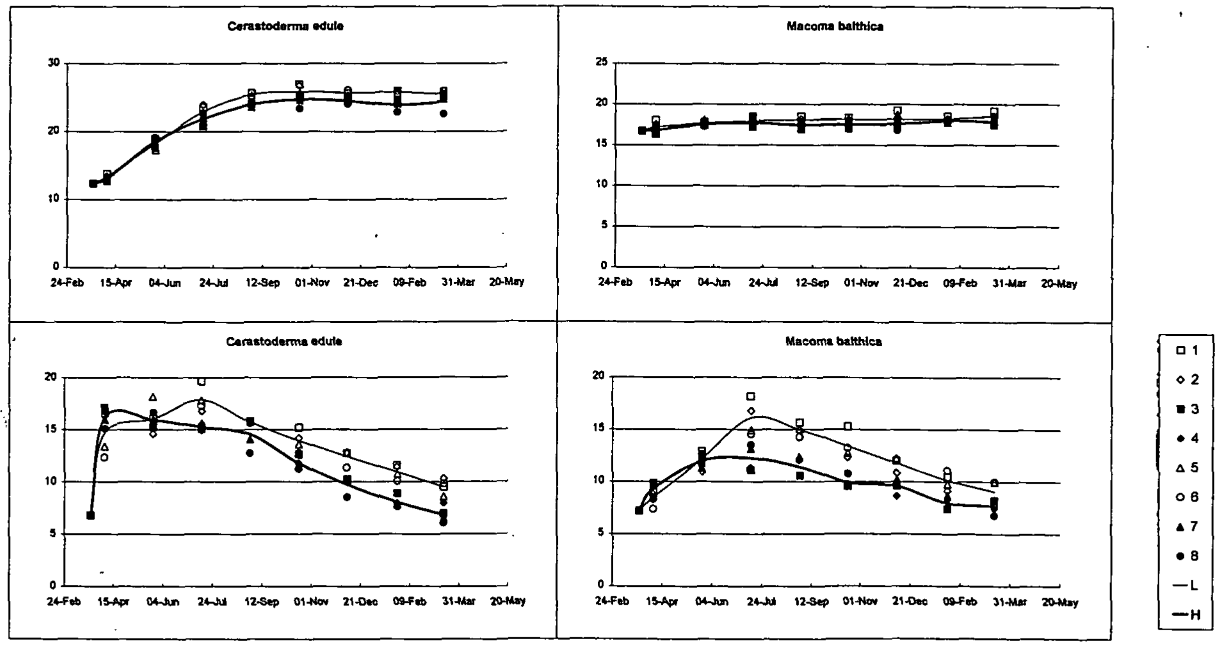


Fig. 7.18 Size (upper, mm) and Body Size Index (lower, AFDW/cm3) of individual adult *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

observations suggest that *Arenicola* biomass is limited by some factor (food availability, space ?). Not even the temperature difference evokes a difference in *Arenicola* biomass. On the other hand, the bivalve biomass is clearly depressed in the high temperature MOTIFs (Figs. 7.15, 7.16).

Individual weight

Weight data on individual *Arenicola* show reflect what has been discussed above (Fig. 7.17). Individual weight of juvenile *Arenicola* increased very rapidly in the aberrant MOTIFs and 2, and weights very closely alike in the other MOTIFs, irrespective of temperature regime. Even the individual weight of adult *Arenicola* in MOTIFs 1 and 2 was higher than in the other MOTIFs, but there was no difference related to the temperature regime *Cerastoderma* and *Macoma* clearly reveal the temperature effect on the individual organisms (Fig. 7.17). The differences in individual weights were highly significant when considering the whole treatment period. The difference was also significant on most of the sampling dates (Table 7.3).

Length

Cerastoderma showed better growth in the controls than in high temperature MOTIFs. The average growth of *Macoma* was much smaller because the sample which was used to stock the MOTIFs represented a fairly broad age distribution. There is an indication of growth suppression at higher temperatures (Fig. 7.18), but the observed differences, although consistent, were not significant.

Body Mass Index

The body mass index of both *Cerastoderma* and *Macoma* was affected by the temperature regime. In high temperature MOTIFs the was strongly and highly significantly depressed (Fig. 7.18). This depression indicates that higher temperatures exerted stress on the bivalves.

Individual growth

Individual growth, measured as the increase in individual ash-free dry weight, is plotted for the four groups of organisms in Fig. 7.19. Adult *Arenicola* have a growth pulse in late spring/early summer. Their growth rate is not effected by the difference in temperature regime. The juvenile *Arenicola* do not have as clear a growth pulse except for the aberrant

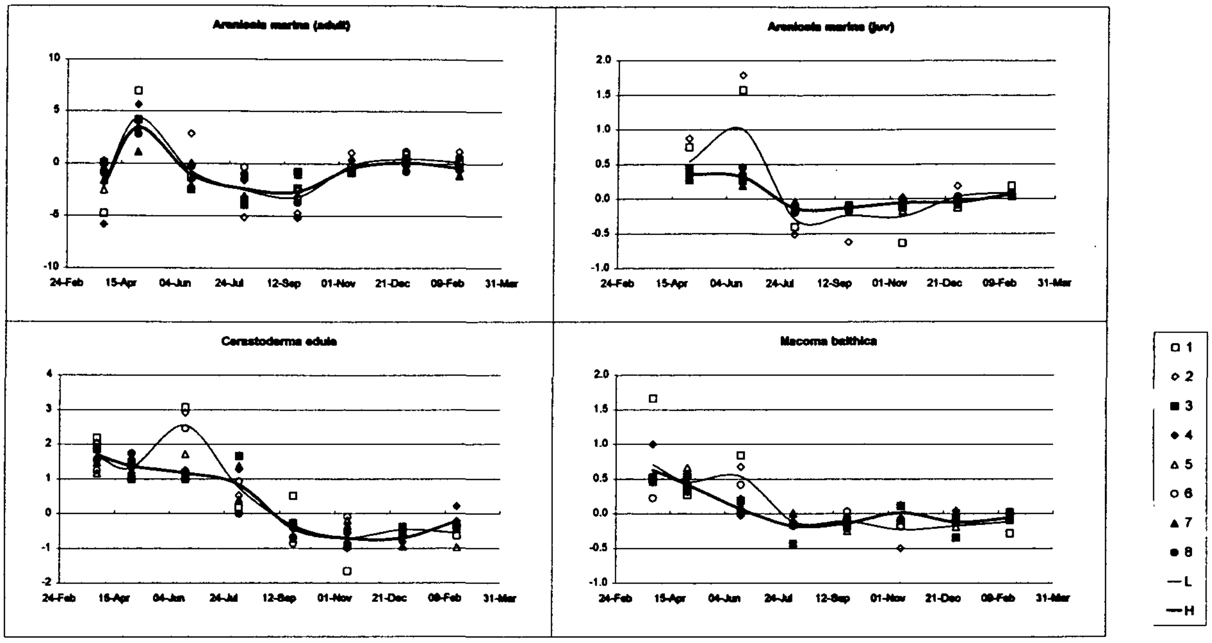


Fig. 7.19 Growth rates (expressed as ash free dry weight per individual) of adult and juvenile *Arenicola* and adult *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

MOTIFs 1 and 2. Later during the year the animals become leaner. At this stage this proceeds faster in MOTIFs 1 and 2. For the other six MOTIFs the individual growth rates of juvenile *Arenicola* are identical. The seasonal pattern of the individual growth of the bivalves is peculiar. In the controls there is a clear growth pulse between May and July, whereas this pulse is absent in the heated MOTIFs. During this period the difference in growth rate between controls and high temperature MOTIFs is significant. The differences vanish in the course of the experiment.

Discussion Temperature Rise Experiment

The increase of the average water temperature by about 4 °C resulted in an increase in average sediment temperature of 3.2 °C. The numbers of the at the start of the experiment introduced bivalves and Arenicola were not effected by the increased temperature. For Arenicola this was also valid for the juveniles that entered the MOTIFs between the first sampling in April, prior to the start of the heating, and the first sampling after that (May).

Arenicola production was not effected by this temperature difference. *Cerastoderma* and *Macoma* were very strongly effected. In the high temperature MOTIFs individual growth was reduced. This led to lower biomass of these species in the high temperature MOTIFs. The difference in individual weight was brought about by a reduced individual growth in the period between 25 May and 13 July. Once the difference in weight was established it persisted until the end of the experiment. This result contradicts the general idea that it are especially increased winter temperatures that are most critical.

For the population development reproduction is at least as important as mortality. The condition expressed as Body Mass Index, of *Cerastoderma* and *Macoma* at the end of the experiment was lower in the high temperature MOTIFs than in the controls. During NRP1 (Hencoop & Van der Mere, 1997; Hencoop et al. 1999) it was found that Macoma stopped producing eggs when the BAI was below 5.6 mg cm^{-3}. Above this threshold the number of eggs produced is proportional to the BAI. In the high temperature MOTIFs the average BAI at the last sampling in March was 7.7 compared to 9.1 in the controls. With the regression equations given by Hencoop & van der Mere (1997) the expected number of eggs can be calculated. This number was 50000 and 27000 per individual for the control and high temperature MOTIFs respectively. Although the difference is quite large the above mentioned authors also showed that the egg numbers were of minor importance for the recruitment of the population. For Cerastoderma the situation was more critical because the BAI values measured in the present experiment were above and below the threshold BAI for Cerastoderma. In the controls egg production would be small but in the high temperature MOTIFs the BAI was so low that no egg production could be expected on the basis of the results of Hencoop &Van der Mere (1997). So the temperature rise imposed on the MOTIFs could stop reproduction of Cerastoderma and that has large consequences for the population. This conclusion has to be taken cautiously because our last sampling was performed on March 15, about 2 months before spawning of Cerastoderma. During this period the Cerastoderma probably grows considerably.

7.4 General Discussion

The two aspects of climate change studied in the mesocosms, sea level rise and temperature rise, have an impact on the tidal flat macrobenthos community. In neither of the experiments the numbers of the organisms introduced into the MOTIFs at the start were affected by the treatment. In other words a difference in inundation period or an increase in temperature by 3 to 4 °C did not change the direct mortality of the organisms. In the sea level rise experiment the numbers of individuals of other species and younger stages of the originally introduced species indicated a difference in success of immigration. Immigration was more successful in the MOTIFs with a long inundation period, resulting in a higher species richness and higher biomass of invaders in the high tide MOTIFs. In the temperature rise experiment immigration was greatly diminished because of a change in the hydraulic situation and only juvenile Arenicola invaded in huge numbers. In the sea level rise experiment the three stocked species all had a higher growth rate in the high tide MOTIFs. As the numbers were not different the difference in production is solely based on differences in individual growth. Together with the

Table 7.4 Summary of effects

	Sea Level Rise	**Temperature Rise**
Number of species	Increase	?
Mortality		
Arenicola marina	No Effect	No Effect
Cerastoderma edule	No Effect	No Effect
Macoma balthica	No Effect	No Effect
Individual AFDW		
Arenicola marina	Increase	No Effect
Cerastoderma edule	Increase	Decrease
Macoma balthica	Increase	Decrease
Length		
Cerastoderma edule	Increase	Decrease
Macoma balthica	Increase ?	Decrease ?
BMI		
Cerastoderma edule	No Effect	Decrease
Macoma balthica	No Effect	Decrease
Inferred egg production		
Cerastoderma edule	No Effect	None
Macoma balthica	No Effect	Decrease

higher number of invaders that also showed higher individual growth rates the total benthic macrofauna production was higher in the high tide MOTIFs. There was an indication for a proportional relationship between the length of the inundation period and the biomass production. In the temperature experiment the bivalves showed a depressed individual weight in the high temperature MOTIFs. The temperature, on the other hand, did not effect Arenicola. As Arenicola, especially the juveniles, dominated the biomass there was no difference in total benthic macrofauna biomass between the control and the high temperature MOTIFs. For the bivalves the two aspects of climate change had opposite effects. Sea level rise, i.e. longer inundation period, stimulates while temperature rise depresses the bivalve production. The long-term effects for the populations cannot be deduced from the present experiments, as recruitment did not take place within the MOTIFs. The juvenile stages that were found in the MOTIFs entered the MOTIFs with the supply water. However, combining the present results with those from NRP1 indicates that a higher water temperature might have a negative effect on the bivalve recruitment and consequently the population development.

A summary of the observed effects is presented in Table 7.4

8 A FUZZY EXPERT SYSTEM FOR EFFECTS OF CLIMATE CHANGE ON THE WADDEN SEA ECOSYSTEM

8.1 Introduction

Climate change is rather slow: it acts in the time-domain of decades. As a consequence the analysis of the effects of climatic change addresses the change in the dominant processes, governing the large-scale behaviour of the morphological and ecological system. Given the present state of knowledge it is impossible to produce a quantitative model of all the processes and interactions fully describing the system. But the present knowledge can be organised in such a way that a qualitative / semi-quantitative evaluation of the functioning of the system can be achieved. One way to achieve this is to make use of an expert system. Expert systems in environmental assessments have been in use since many years (Waterman, 1986; Geraghty, 1993). One of the most promising techniques in expert systems for ecological assessments is fuzzy logic (Ecological Modelling, 1996).

This chapter describes the results of the development and implementation of an expert system for the effects of climate change on the Wadden Sea ecosystem. This study was part of the Dutch National Research Programme on Global Air Pollution and Climate Change (NRP-II project). Within the NRP-II project WL | Delft Hydraulics, in co-operation with the Dutch National Institute for Coastal and Marine Management, developed an expert system for assessing the effects of climate change on the Wadden Sea ecosystem. Specific objectives of this study were: (1) Develop an expert system for the effects of climate change on a large number of ecological parameters, (2) Present these results both in a qualitative as well as in a quantitative way and (3) Give the user the possibility to define and evaluate scenarios.

In order to develop a model for the whole ecosystem of the Wadden Sea, a modular, incremental approach was chosen. In this way, a variety of modules for different parameters could be prepared and subsequently integrated into a model of the complete ecosystem. The fuzzy expert system EcoFuzz contains knowledge rules on various ecosystem components and their behaviour under climate change for Mudflats, Phytoplankton, Microphytobenthos, Macrozoobenthos, Salt

Marshes and Oystercatchers. For the underlying reasoning used for the implementation of knowledge rules, fuzzy logic was used.

8.2 Concept of fuzzy logic

Fuzzy logic is an extension of conventional (Boolean) logic, that has been proposed by Zadeh in the 1960s (Zadeh, 1965) as a means to model uncertainty. Fuzzy logic introduces a concept of partial truth-values, that lie in between "completely true" and "completely false". The central concept of fuzzy logic is the *membership function*, which represents numerically the degree to which an element belongs to a set. In a classical set, a sharp or unambiguous distinction exists between the members and non-members of a set, while in a fuzzy set, the distinction between members and non-members is gradual. An element can be a member of a set to a certain degree and be at the same time member of a different set to a certain degree. The degree to which a member is element of a set is called the membership degree. Similar to traditional logic, in fuzzy logic membership values can be combined through operations on fuzzy sets, such as union, intersection and complement.

Fuzzy logic is often used for reasoning in knowledge-based systems, such as fuzzy expert systems. The knowledge is typically represented in terms of IF-THEN rules. An example is: IF A AND B THEN C. The IF-part of the rule is called the *premise* and the THEN-part the *consequent*. The truth value of the rule's premise describes to what degree the rule applies in a given situation. The so-called *fuzzy inference mechanism* is used to determine the consequent fuzzy set based on the truth value of the premise (this is often called the *degree of fulfillment*). Consequent fuzzy sets of individual rules are then combined (*aggregated*) into a single fuzzy set. In most practical applications, the resulting fuzzy set is converted (*defuzzified*) in to a real (*crisp*) value. The complete inference mechanism has five steps:

1. In the *fuzzification* step the membership degrees of the actual values of the premise variables are calculated.
2. Then the *degree of fulfilment* for the premise of each rule is computed, using fuzzy logic operators.

3. In the *inference* step, the degree of fulfilment of the premise of each rule is used to modify the consequent of that rule accordingly. This operation represents the If-Then implication, i.e. an intersection operator. Usually the minimum operator is used.
4. Then, the consequent fuzzy sets of all the rules are *aggregated* into a single fuzzy set, using an operator that represents the fact that the rules are valid simultaneously.
5. Finally, the resulting fuzzy set can be *defuzzified* to yield a crisp value. Defuzzification can be seen as an operator that replaces a fuzzy set by a representative value.

8.3 Knowledge sources

The Wadden Sea expert system was mainly constructed using information of human experts. The expert system was developed to formalise the (linguistic) knowledge of various experts and to combine this with the knowledge of (numeric) models. Literature and maps were supplementary collected on climate change, the morphology of the Wadden Sea, the different species and functional groups of the ecosystem of the Wadden Sea, their life history, ecotopes etc. The available literature formed the base knowledge in the interview sessions with experts. Existing models of (parts of) the hydro- and morphodynamic system and ecosystem of the Wadden Sea also contain a lot of knowledge that was translated into IF-THEN rules and integrated in the knowledge system. Additional knowledge on the effects of climate change on macrozoobenthos was gathered in mesocosm experiments carried out in the NRP-II project.

The implementation of expert knowledge from interviews was carried out in an iterative way. The assumptions on the systems behaviour were discussed with the experts and the expert knowledge was incorporated into EcoFuzz. Feedback from the experts resulted in the final implementation of the expert rules.

8.4 General structure of the expert system

For this study a fuzzy logic expert system was developed, called EcoFuzz. Many parts of the ecosystem are linked to each other and act upon each other. Therefore a modular structure for the expert system was chosen. The general structure of EcoFuzz consists of different modules for specific parts of the ecosystem, that together form a model of the complete ecosystem. The application of EcoFuzz made for the NRP II project contains ecosystem modules for the Wadden Sea with dedicated rules for the possible effects of climate change. The EcoFuzz expert system does not describe a dynamic development of the ecosystem over a period of 100 years, but gives a static presentation of expected changes in model variables that are valid after 100 years of climate change, i.e. in the year 2100.

To establish the knowledge on climate change, the expert system EcoFuzz contains the following elements (Fig. 8.1):

- *aspects;*
- *relational systems;*
- *relational schemes.*

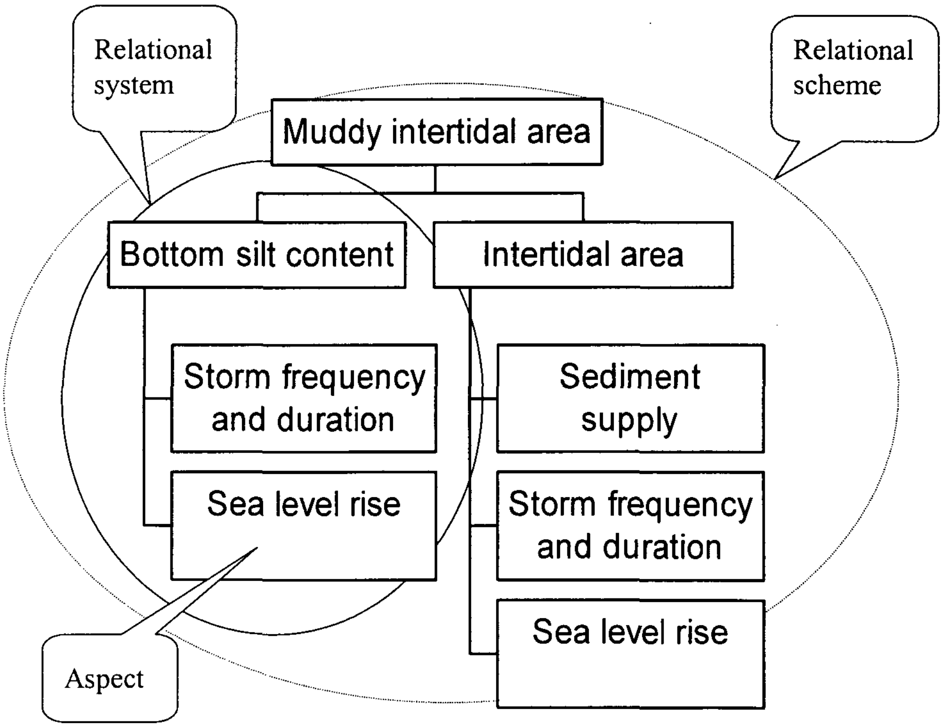


Figure 8.1. Elements in EcoFuzz.

8.4.1 Aspects

Aspects are the building blocks of the reasoning system. Each aspect is defined as a set of classes with fuzzy boundaries, so called fuzzy sets. Each value of an aspect has a membership degree for one or more of the fuzzy sets. As an example, the aspect 'Accelerated Sea Level Rise (SLR)' is presented in Figure 8.2. This aspect is classified into four classes: autonomous SLR, low accelerated SLR, intermediate accelerated SLR, and high accelerated SLR.

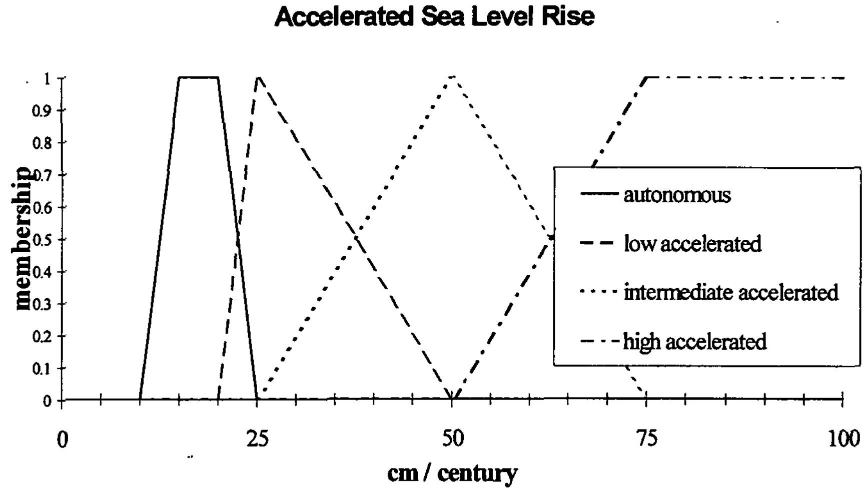


Figure 8.2. Membership functions for the aspect Accelerated Sea Level Rise.

8.4.2 Relational systems

The relationships between the aspects define the knowledge in the expert system. The way aspects relate to each other is defined in *relational systems*. A relational system contains the inference rules for the combination of the fuzzy sets, such as: IF A decreases AND B decreases THEN C decreases. A relational system can have one or more *affecting* aspects and always has one *affected* aspect.

As an example, the relational system for the Bottom Silt Content is presented. The aspect Bottom Silt Content has five fuzzy sets that denote the relative change in silt content compared to the present situation. The Bottom Silt Content in the Wadden Sea is affected by the Sea Level Rise and the Storm Frequency and Duration.

The latter aspect has four fuzzy sets that denote the relative change in storms compared to the present situation. The inference rules for the relational system are presented in Table 8.1.

Table 8.1. Relational system for Bottom Silt Content

Bottom Silt Content (% change)				
	Storm Frequency and Duration (% change)			
Sea Level Rise (cm/century)	decrease	present	increase	strong increase
present	present	present	present	decrease
low	present	present	present	decrease
intermediate	present	present	decrease	strong decrease
high	decrease	decrease	strong decrease	strong decrease

8.4.3 Relational schemes

A combination of systems is implemented into EcoFuzz as a *relational scheme*. As an example, the relational scheme for Mudflats is presented in Figure 8.1.

The fuzzy expert system EcoFuzz contains knowledge rules on various ecosystem components and their behaviour under climate change. In total six different schemes were implemented for Mudflats, Phytoplankton, Microphytobenthos, Macrozoobenthos, Salt Marshes and Oystercatchers. Due to the modular structure of EcoFuzz (parts of) these schemes can be connected to each other. This is typically the case for the description of higher organisms. The relational scheme for the Oystercatcher carrying capacity in the Wadden Sea for example contains (elements) of the schemes for macrozoobenthos, morphology and salt marshes. The macrozoobenthos scheme itself is connected to the primary production scheme. In this way the know-how of experts in their own fields of expertise can be coupled into an ecosystem model.

8.4.4 Example of EcoFuzz output

As an example, the resulting fuzzy output for the aspect Muddy Intertidal Area is presented in Figure 8.3. EcoFuzz presents the results of the computation as fuzzy memberships for the sets, or as defuzzified values.

Figure 8.3 shows that scenarios 2 and 4 have a membership degree of 1 for the *present* class. Scenario 5 is the result of a decrease in Intertidal Area and a decrease in Bottom Silt Content and results in a membership of 1 for the *strong decrease* class. Scenarios 1, 3 and 6 have membership degrees in three classes; 0.43 for *strong decrease*, 0.29 for *decrease* and 0.29 for *present*.

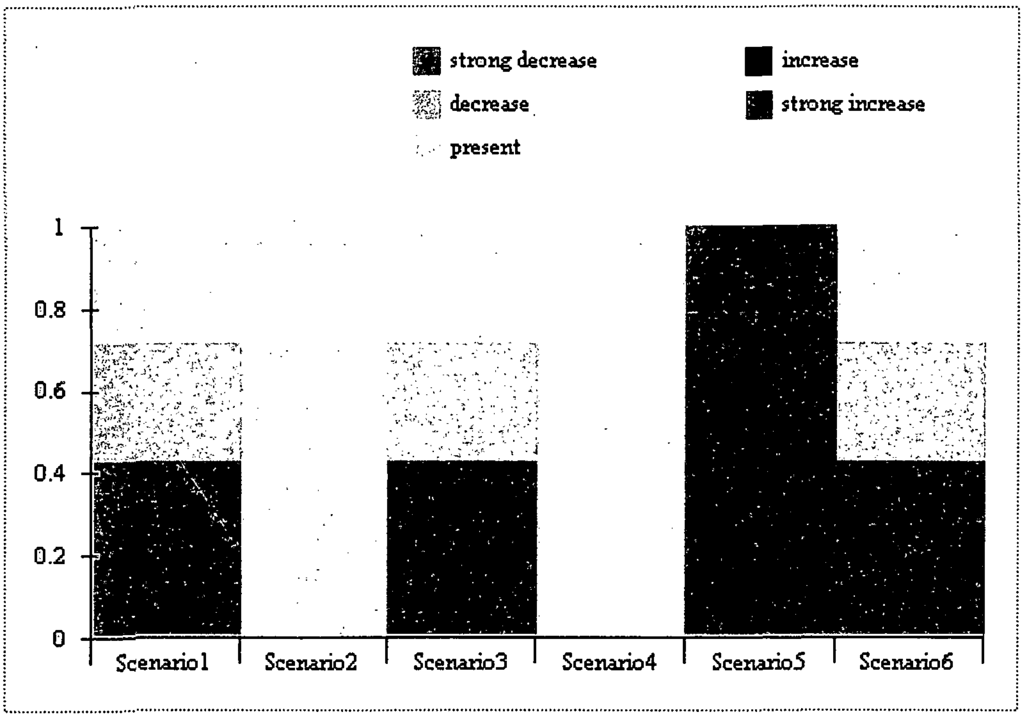


Figure 8.3. Fuzzy output for six scenarios of effects of climate change on relative change in the Muddy Intertidal Area.

Fuzzy inference

As an example of the fuzzy inference in this expert system, the outcome for scenarios 1, 3 and 6 is analysed. The combinations shown in Table 8.2 are relevant for the computation of the memberships for these scenarios. The relative changes of the Intertidal Area and the Bottom Silt Content, as a result of climate change, have membership degrees of 0.6 in the *decrease* class and 0.4 in the *present* class. The combination of the changes in these parameters defines the change in Muddy Intertidal Area..

Table 8.2. Relevant inference rules of the relational system for Muddy Intertidal Area.

Muddy Intertidal Area (% change)		
Intertidal Area (% change)	**Bottom Silt Content (% change)**	
	decrease: **0.6**	present: **0.4**
decrease: **0.6**	strong decrease	decrease
present: **0.4**	decrease	present

For both aspects the membership degree for the *decrease* class is 0.6 and for the *present* class is 0.4. The resulting membership degrees for Muddy Intertidal Area for the four combination rules of Table 8.3, using the MIN operator are:

strong decrease = MIN (0.6, 0.6) = 0.6
1. *decrease* = MIN (0.4, 0.6) = 0.4
2. *decrease* = MIN (0.6, 0.4) = 0.4
3. *present* = MIN (0.4, 0.4) = 0.4

Table 8.3. Climate change scenarios based on IPCC predictions.

	(1) baseline A	(2) stab 450	(3) baseline A rad	(4) stab 450 rad	(5) sea level extreme	(6) changing circulations
acc. sea level rise (cm/century)	65	50	65	50	110	65
mean winter temperature (°C)	+ 8	+ 4	+ 8	+ 4	+ 8	-1
mean summer temperature (°C)	+ 5	+3	+ 5	+3	+ 5	+ 6
summer irradiation (%change)	0	0	-4	-4	-4	-4
storm freq. and duration (%change)	0	0	0	0		0
sediment supply (insuff.-suff.=0-1)	1	1	1	1	1	1

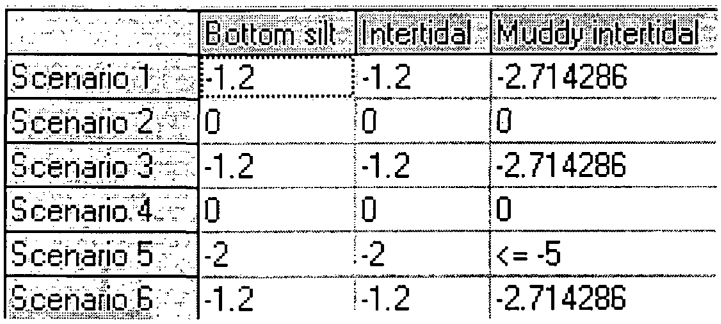
The aggregation of the membership degrees for these rules, using the MAX operator yield: *strong decrease* 0.6, *decrease* 0.4, *present* 0.4. These outcomes are subsequently scaled between 0 and 1, using the sum of scores, which is 1.4:

strong decrease = 0.6/1.4 = 0.4286;
decrease = 0.4/1.4 = 0.2857;
present = 0.4/1.4 = 0.2857.

Defuzzification

Using the membership functions of the individual aspects, the fuzzy results can be defuzzified into crisp values. Table 8.4 presents the defuzzified output for the Morphology scheme.

Table 8.4. Defuzzified output for the Morphology scheme.



	Bottom silt	Intertidal	Muddy intertidal
Scenario 1	-1.2	-1.2	-2.714286
Scenario 2	0	0	0
Scenario 3	-1.2	-1.2	-2.714286
Scenario 4	0	0	0
Scenario 5	-2	-2	<= -5
Scenario 6	-1.2	-1.2	-2.714286

All results are expressed as %change relative to present situation.

An example will clarify the process of defuzzification. For scenario 1 the membership degrees for the Muddy Intertidal Area classes are given by:

strong decrease = 0.4286;
decrease = 0.2857;
present = 0.2857.

The membership functions for Muddy Intertidal Area are presented in Figure 8.4.

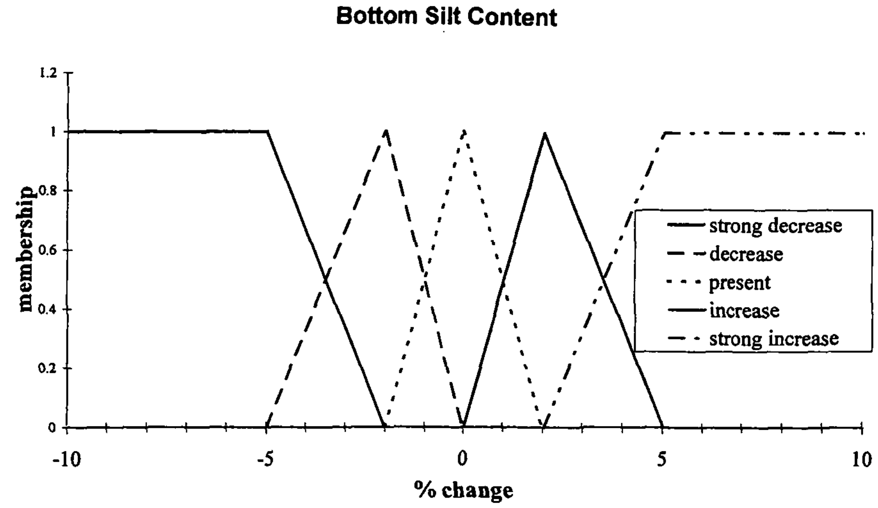


Figure 8.4. Membership functions for the aspect Muddy Intertidal Area.

In the defuzzification step, the centre of each membership class is used for functions that do not go to infinitely, and the right or left boundary values of membership values are used for functions that do go to infinitely. The crisp values of the membership classes are therefore:

strong decrease:	-5%
decrease:	-2%
present:	0%
increase:	+2%
strong increase:	+5%

The membership degrees for each class are then multiplied with the crisp class value. For the membership degrees of scenario 1 this yields:

0.4286*-5 + 0.2857 * -2 + 0.2857 * 0 = -2.71%.

8.5 Scenario computations

The completed expert system EcoFuzz was used to compute the effects of climate change on the functioning of the Wadden Sea Ecosystem. Six climate change scenarios were defined using assumptions on changes in accelerated sea level rise, mean winter and mean summer temperature, summer irradiation and storm frequency and duration (Table 8.2). The scenario definitions for these parameters are based on IPCC predictions. In all scenarios it was assumed that there is 'sufficient' sediment supply to the Wadden Sea. In these scenarios the sea level rise has a range between 50 cm/century and an extreme 110 cm/century, the mean winter temperatures rises considerably in most scenarios (4 or 8 degrees), the mean summer temperature rises in all scenarios, and the summer irradiation decreases in four scenarios. Although the storm frequency and duration and the sediment supply stay unchanged, knowledge on the effects of changes of these parameters is included.

8.6 Results

The results of the scenario computations denote the expected changes in the Wadden Sea ecosystem. These computations were carried out for the six relational schemes that were implemented in the EcoFuzz application, i.e. Mudflats, Phytoplankton, Microphytobenthos, Macrozoobenthos, Salt Marshes and Oystercatchers. A comprehensive analysis of the knowledge schemes and results are not subject of this chapter, but a summary of expected changes is given below.

8.6.1 Mudflats

The Mudflats relational scheme is already discussed in this chapter. The results of the scenario computations show that the area of intertidal mudflats will not be affected as long as the accelerated sea level rise velocity is less than 50 cm/century, the storm frequency and duration do not increase and as long as there is a sufficient sediment supply to the Wadden Sea basin. When these conditions are exceeded the relative decrease in the area of mudflats is limited to a couple of percents, unless there is an extreme sea level rise, than the relative decrease will be more than five percent.

8.6.2 Phytoplankton

The relational scheme for phytoplankton is simple, changes in summer temperature and summer irradiation affect the phytoplankton. Results of the scenario computations show that the phytoplankton biomass in the Wadden Sea will not be affected by the estimated rise in summer temperature and summer irradiation. The assumption that is made here is that the nutrient levels and salinity remain constant.

8.6.3 Microphytobenthos

The relational scheme for microphytobenthos consists of two parts. One part is the scheme for mudflats and denotes the preferable habitat of microphytobenthos. The other part denotes the changes in microphytobenthos density affected by the changes in summer temperature and summer irradiation. When the summer irradiation decreases, the primary production and density will decrease. When the summer temperature increases, the density will decrease as a result of a higher mortality rate. For all scenarios it is expected that the microphytobenthos biomass will decrease with a relative change between the 0.8% and 4.4% for the scenarios, with the exception of scenario 5 (extreme sea level rise) when the decrease is more than five percent.

8.6.4 Macrozoobenthos

The relational scheme for macrozoobenthos is a more complicated one. The area of mudflats and the biomass of benthos per square metre depict the relative change in total amount of benthos. The biomass of benthos is divided into a summer biomass and a winter biomass. Growth and reproduction depict the summer biomass and the winter biomass is depicted by winter mortality that is affected by the mean winter temperature. The mean summer temperature and the phytoplankton biomass depict the growth of benthos. The weight of adults in spring and the predation pressure on benthos in spring are both affected by the mean winter temperature and depict the reproduction.

A decreased mortality rate of macrozoobenthos in warmer winters will result in a higher biomass in winter, but a decreased growth and reproduction rate will cause a lower biomass in warmer summers. As a result the biomass of benthos per square metre will show a more stable seasonal pattern and a net increase. The scenario computations show that the total amount of macrozoobenthos in the Wadden Sea will increase with 6 percent for scenarios with limited sea level rise (50 cm/century) and higher temperatures. It will decrease slightly with about 1.5 percent for scenarios with an intermediate sea level rise (65 cm/century) or even 10 percent for extreme sea level rise (110 cm/century), primarily caused by the effects on their preferable habitat, the area of intertidal mudflats. In case of a combination of intermediate sea level rise and colder winters the total amount of macrozoobenthos will decrease with 19 percent.

8.6.5 Salt marshes

The relational scheme of salt marshes predicts the relative changes in the pioneer zone of the marshes. The bottom shear stress imposed on this zone and the vegetative growth depict the changes in the pioneer zone. The bottom shear stress is affected by the storm frequency and duration and the sea level rise. These parameters also affect the bottom silt content. The bottom silt content and the bottom shear stress together depict the vegetative growth. The vegetative growth will decrease in coarser sediments and in places with more scour.

The scenario computations show that the bottom shear stress will increase, the vegetative growth will decrease and as a result the area of salt marsh pioneer zone will show a decrease of more than five percent.

8.6.6 Oystercatchers

There are two relational schemes for Oystercatchers. The annual cycle in Oystercatcher abundance in the Wadden Sea was divided into a winter population and a summer population. The winter scheme predicts the changes in maximum carrying capacity for wintering birds. The mean winter temperature has a direct effect, through migration and mortality, and the food availability plays a role. The biomass of benthos in winter and the intertidal area depict the food availability. The summer scheme predicts the maximum carrying capacity in summer. The food availability in summer and the area of salt marshes depict the carrying capacity. The food availability is affected by the biomass of benthos in summer and the intertidal area.

Results of the scenario computations show that the carrying capacity of Oystercatchers in summer will decrease with more than ten percent for the first five scenarios, due to a decreased food availability and salt marsh area. The exceptional sixth scenario with colder winters results in a stabilisation of summer benthos biomass and shows therefore a decrease of only eight percent. The carrying capacity of Oystercatchers in winter will show a net increase for the first four scenarios, due to the increased food availability in warmer winters. The fifth scenario with extreme sea level rise shows the highest decrease in intertidal area, but this is compensated for by the increase in food availability and shows a net stabilisation of carrying capacity. The sixth scenario with colder winters shows a decrease in food availability and therefore a decrease in Oystercatcher carrying capacity.

8.7 Discussion and recommendations

8.7.1 Discussion

This project has integrated available knowledge on the functioning of the Wadden Sea ecosystem under climate change scenarios in an expert system. A new software tool was developed to aggregate this knowledge in a formalised way, using fuzzy set theory as a mathematical basis.

There are various knowledge sources used to feed the expert system with relevant information, of which interview sessions with experts were the most important. In these interview sessions experts were asked to give their opinion on the potential effects of climate change, each on their own field of expertise. The most difficult information to gather was a quantification of the magnitude of the effects. Most experts were able to present a probable direction into which the changes may take place, but the size of the effects was often difficult to estimate. Therefore, the quantification of the effects presented in this study must be interpreted with care.

The expert model that was developed in this project, EcoFuzz, is generally applicable for the implementation of other expert systems. This software has also been successfully used to model floating algae in the IJsselmeer (Vonk & Michielsen, 1998).

In this project a knowledge base of relevant parameters for the Wadden Sea ecosystem has been set up and filled with knowledge on systems behaviour under climate change scenarios. This expert system is able to handle knowledge from different domains on different time and spatial scales in a formalised way. The model can aggregate information to ecosystem level and is able to present a qualitative to semi-quantitative evaluation of the integrated effects of climate change on geomorphological and ecological processes.

The results of the climate change scenarios show the expected effects for different abiotic and biotic system components and the system as a whole, because the system components are linked to each other. A selection of species or functional groups was made, based either on relevance for the ecosystem or on available knowledge on the potential effects of climate change. Each system component was described in the most simple way, in order to minimise the amount of rules needed to describe the system and to keep the system behaviour understandable. When using expert systems, it is important for the experts to be able to follow the different steps in detail. Black-box systems are not appropriate.

8.7.2 Recommendations

Several recommendations can be made on the methodology of the Wadden Sea experts system and on the instrument itself.

The ecosystem of the Wadden Sea is described in a very simplified form. The mathematical methods used to describe the ecosystem of the Wadden Sea are linear functions on a limited number of parameters. The way these relations are implemented fits the way of thinking of experts. The problems of climate change are complex and in many cases knowledge is lacking to give a clear and complete overview of impacts. Experts must then rely on their gut-feelings and will provide an estimation of effects mainly in terms of general directions and magnitudes.

Another reason for a simplified description is that it makes the expert system transparent, so that an expert is able to follow each step and its consequence.

The question is to what extent EcoFuzz may be an oversimplification of truth. Many relationships in nature are non-linear, show feedback coupling and there are many dynamic processes on different time and spatial scales. EcoFuzz does not describe a dynamic development of the ecosystem, but merely gives a static presentation of expected changes in model variables that are valid after 100 years of climate change, without feedback loops. The model does not take into account extreme events, such as the introduction of invader species, or parasites. Furthermore EcoFuzz assumes a constant gene-pool in the faunal communities and does not take into account possible adaptive responses to climate changes.

A validation of the results of EcoFuzz has only partly been carried out. The knowledge that is incorporated into EcoFuzz mainly stems from interviews with experts that was presented to them once. Each consulted expert was given the possibility to review its own representation of expert knowledge on its own field of expertise. Afterwards, all available knowledge was related to each other and combined in the present version of EcoFuzz. Subsequently, the effects of the climate change scenarios were computed; these results have been presented in this study.
Regarding the way the Wadden Sea system is described in EcoFuzz it is recommended to:

4. present the model results of the climate change scenarios to the consulted experts;
5. validate the model results with expert knowledge of a different set of experts;
6. execute a sensitivity analysis of EcoFuzz;
7. improve the mathematical description of ecosystem behaviour.

In developing the software for the expert system a flexible user-interface is coupled to a modular build-up of ecosystem components and relationships. EcoFuzz makes use of external ASCII- files that contain the fuzzy membership functions for the aspects, the inference rules for the systems, the selection of systems into schemes, the scenario input and the model output. For the stand-alone user this is not always very user-friendly, but an advantage is that EcoFuzz can easily be coupled to other ecosystem models or incorporated in other software such as Decision Support Systems.

Regarding the software-instrument EcoFuzz, it is recommended to improve the user interface with respect to the use of external files.

9 INTEGRATION BY A DYNAMIC ECOSYSTEM MODEL: ECOWASP

9.1 Introduction

In the previous chapters we discussed general system characteristics (ch. 3), three types of system responses (responses of salt marshes and tidal flats, (ch. 4); responses of bird migration (ch. 5); responses of shell fish reproductive characteristics (ch. 6)) and one whole system study (ch. 7). In chapter 8, a first attempt to integrate knowledge on climate change effects in an expert system has been described.

In the present chapter, an integration of system processes in a dynamic ecosystem model is described. Climate change will influence a number of these processes; wind, precipitation and temperature are assumed (ch. 2) to be the most important driving forces.

In this chapter 9, the setup of the ecosystem model is briefly described; as is the tuning procedure. In chapter 10, scenario results are presented.

The EcoWasp ecosystem model is a dynamic model for the integrated simulation of biological, chemical and physical processes in a shallow tidal water system. Biological, physical and chemical key processes are modelled in detail. The model thus integrates formalized knowledge of ecosystem processes.

An essential feature of dynamical ecosystem models is that they usually are based upon mass budgets for all variables: nutrients, algae, fauna. Therefore, resource competition is a build-in feature, and contradicting use of resources is not possible.

Dynamic ecosystem modelling is based upon the numerical and dynamical solution of sets of differential equations. Models have grown from simple descriptions (Vollenweider, 1969) to more integrated system descriptions. DiToro et al (1971) were among the first to describe simultaneously nutrient, phytoplankton and zooplankton dynamics and feedbacks in an aquatic system. The phytoplankton-nutrient relationship was described by a Monod-type dependency; the zooplankton-phytoplankton coupling was Lotka-Volterra (Maynard-Smith, 1979) like. Many further developments have been based on similar approaches, and concerned the introduction of more algal functional groups and primary and secondary consumers (Radford, 1982; Radford et al, 1991; Baretta & Ruardij, 1988; EON-I, 1988; EON-II, 1988). Biomass (as ash free dry weight, or related components such as organic-C or organic-P) is the main biological state variable in these models. Sometimes bacterial dynamics are also part of a model (Baretta & Ruardij, 1988), but usually models intend to reproduce daily averages and do not deal with fast bacterial responses.

Size-dependent process descriptions, where also animal numbers and sizes play a role, are realized or discussed by e.g. Fransz et al (1991), Heral (1993), Raillard & Menesquen (1994) and partly in the ERSEM modelling project (Bryant et al, 1995). Such additional details are based upon general knowledge of biological processes (e.g. Reise,1985; Lampert & Sommer, 1993; and many others) or on the results of theoretical studies (e.g. Metz et al, 1988; Roos, 1989), and studies that emphasize the importance of animal sizes and development (e.g. Condrey & Fuller, 1985; Gerritsen & Kou, 1985; Peters,1983; Kooijman, 1993). Since ecosystem models deal with communities or functional groups rather than specific species, size development in a community may be caused by the development of other species, instead by the growth of individuals of one species. Aquatic ecology knows many documented examples of algal communities that show a clear abundance change from small opportunistic species towards larger, slower growing, less edible ones (Lehman, 1988; Metz et al, 1988; Mills & Forney, 1988; Reynolds, 1988, Sommer, 1988; Benndorf & Hennig, 1989; Burns et al,1989; Gaedke, 1992); size-related predation is an important aspect of such successions (DeMott, 1985; Haney & Trout, 1985; Gosling, 1992; Klepper, 1989).

Besides the exchange of matter between atmosphere and water (mainly oxygen, see e.g. Thomann & Mueller, 1987), or the implementation of atmospheric depository inputs. In shallow systems, a major development concerned the exchange between sediment and water (Berner, 1971, 1975,1980; Duursma & Hoede, 1967; Van Raaphorst & Brinkman, 1984; Håkanson & Jansson (1983)). Sediment may act as a storage of organic matter and nutrients in parts of a year, and/or as a source of such compounds in other parts of the year. The description of sediment processes sometimes is very simplified: only a storage function -without any depth structure- may be considered, with sedimentation as input process, mineralisation as transformation process and exchange with the overlying water as output process. Also, rather complex descriptions may be implemented, based upon detailed schematisations (e.g. Brinkman & Van Raaphorst, 1986; Ruardij & Van Raaphorst, 1995; Berner, 1980).

9.2 What makes the EcoWasp model different from other models?

Two major differences between the EcoWasp model and most other ecosystem models can be named: the details regarding sediment processes, and the implementation of size-dependency relationships including individual growth and mortality of fauna species. For the last feature average values for a number of age classes are used.

As in most other models, in EcoWasp ecological key processes in a tidal system are integrated: nutrient dynamics, benthic and pelagic primary production, mineralization, benthic and pelagic micro- and macrobenthos activities are implemented, as well as sediment/water exchange, air/water exchange, input from and output to adjacent land and sea and interactions between compartments.

A main reason to implement sizes and numbers of fauna element has been the believe that the model description should not deviate too far from real processes; some of these are already mentioned in the introduction. Experimental data and field observations mainly deal with animal sizes, numbers and activities (e.g. Thompson, 1984; Klepper, 1989; Peters, 1985; Bayne et al, 1988). Biomass based models get into trouble when experimental, size related results are to be translated into simulation process characteristics (e.g. Baretta & Ruardij, 1988), and, consequently, simulation results can not easily be compared with what happens in the field.

Many animals produce large amounts of small sized offspring, that may show activities exceeding that of the adults; not only related to body mass, but also on a population basis (Chardy et al, 1991; Radford et al, 1991); although this is not a generally accepted opinion. If true, it would imply that during some (probably short) period the system's response may be governed by the newly formed offspring, rather than by the adult animal communities. Whether this is really important or not is an important question to be answered, since such sudden, drastic changes in predation intensities upon certain organisms may appear as chaotic behaviour of the

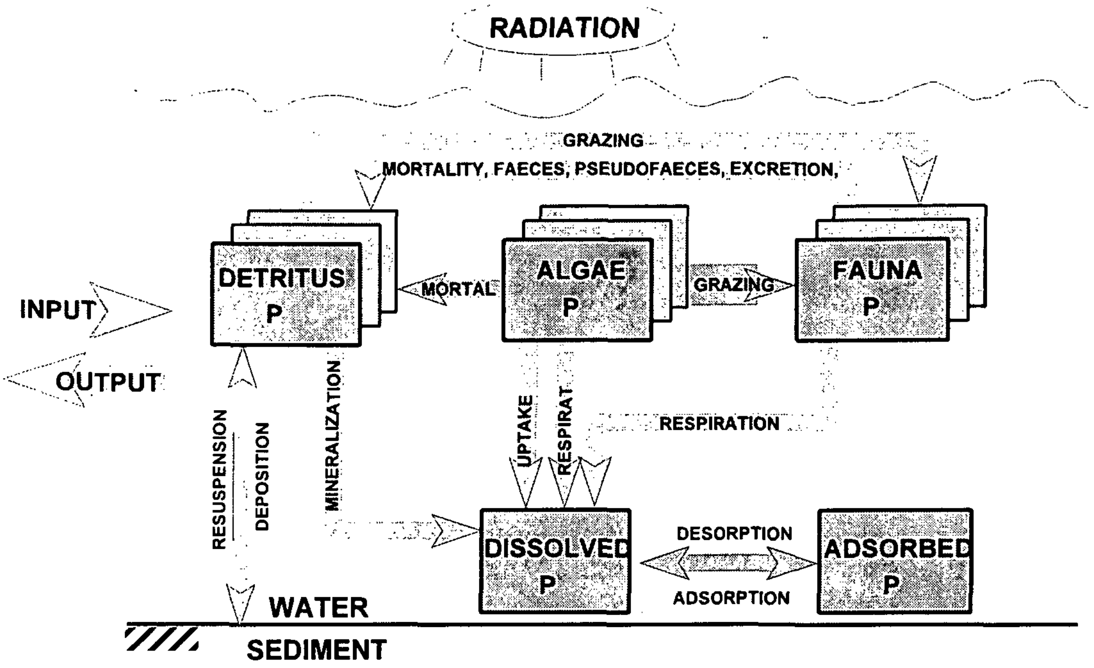


Fig. 9.1 Processes and state variables implemented in EcoWasp

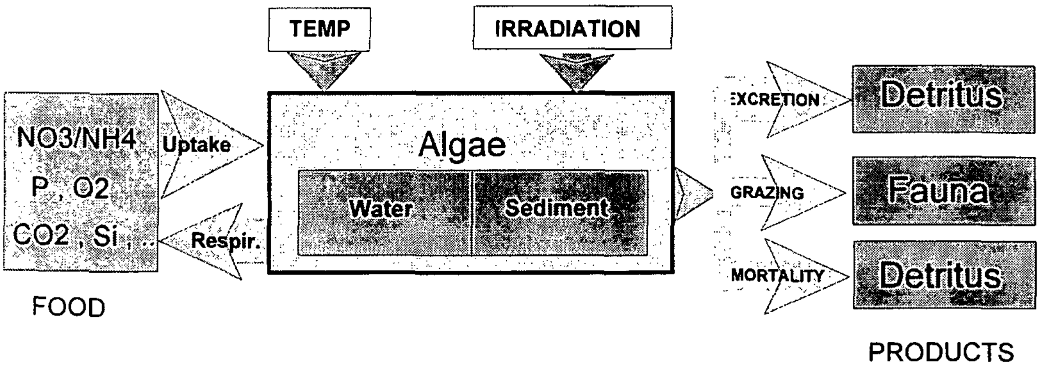


Fig. 9.2 Algae processes as implemented in the model

ecosystem.

The wish to deal with such characteristics has been an important reason to implement size related description of fauna processes in the EcoWasp model.

9.3 What makes the EcoWasp model suitable for the present study?

We believe that especially the size-number description, the possibility to assign a habitat suitability to boxes, plus the detail of the sediment process description make the model special for the present task. But also, since an adequate description of the resuspension/sedimentation process is lacking, the overall effect of storms and wind cannot be subject of the computations. Effects of wind and storms are therefor discussed more or less "off-line": their effects can only be implemented as a change in, for example, habitat suitability.

9.4 Outline of the model

General

The model, as an abstract description of natural processes, is defined by the choice of all the variables to be calculated, the processes and the parameters.

A schematic outline of the ecosystem model is given in Fig. 9.1. All the process types can basically be found in the water column as well as in the sediment. For example: algal processes also run in the deepest sediment layer; although there only loss processes are relevant, such as mortality.

A general dynamical description of algal processes (Fig. 9.2) is presented in text box 9.1, where the growth process (mean net uptake) is given in more detail.

Dead algae, as a result of mortality, excretion or fauna processes are assigned to detrital matter (Fig. 9.3), that degrades according to the description in text box 9.2.

The availability of appropriate electron acceptors is supposed to determine rates and products of the mineralization process; see the sediment part (page 165).

The description of fauna dynamics (Fig. 9.4) is based on numbers of animals and their average

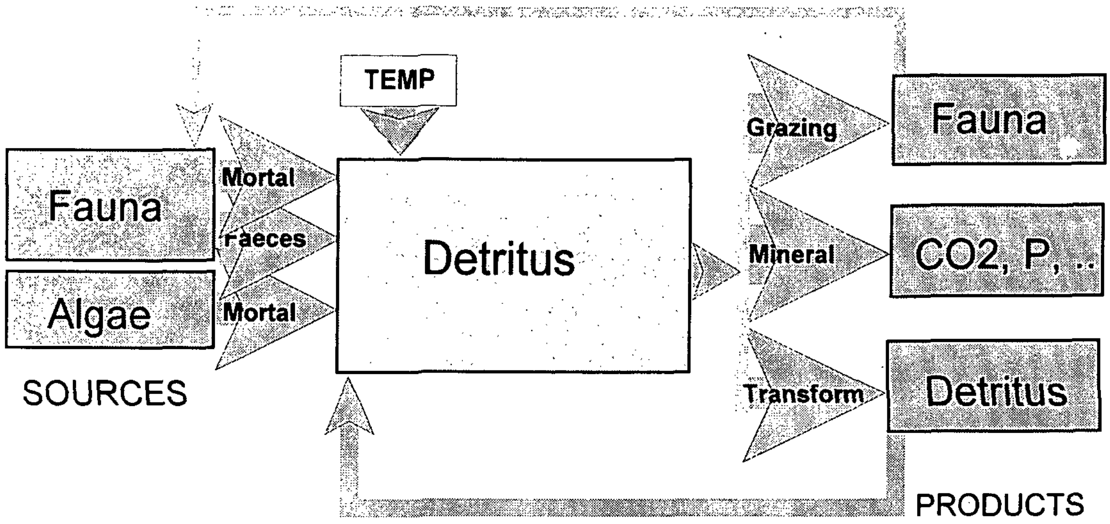


Fig. 9.3 Detritus processes in the EcoWasp ecosystem model

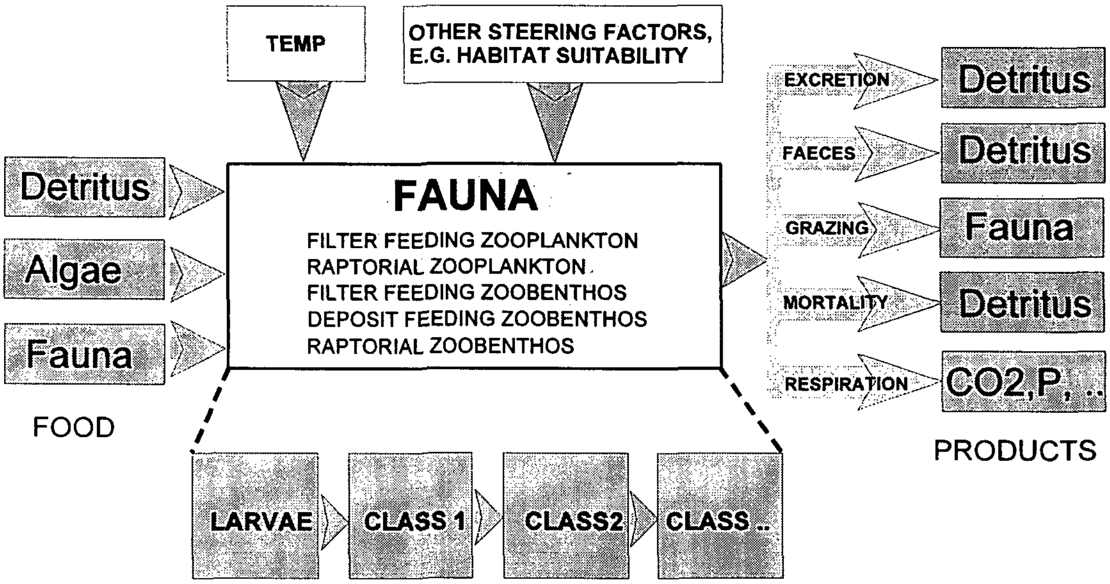


Fig. 9.4 Fauna processes implemented in EcoWasp

Algae

Generally, a dynamical description for the algal content in a system reads

$$\frac{\partial \overline{Alg_i}}{\partial t} = uptake + respiration +$$

$$+ excretion + mortality + grazing + \Sigma input - \Sigma output \qquad (g\ m^{-3}\ d^{-1})\ \ (9.1)$$

Each of these terms can be described in more detail.

For example, the uptake term from eq (1) reads

$$uptake = \mu_{max} \cdot F_1(NUT) \cdot F_2(T) \cdot F_3(RAD) \cdot \overline{Alg_i} \qquad (g\ m^{-3}\ d^{-1})\ \ (9.2)$$

where μ_{max} is a first order uptake constant, and F(NUT), F(T) and F(RAD) denote the dependency of uptake rate on nutrient availability, temperature and light climate, respectively. Temperature dependency is explained below. The nutrient availability relationship is described using a classical Monod-equation (see DiToro et al, 1971). Variable cell-quota descriptions are not implemented.
Light dependency is formulated using a Smith equation (e.g. Golterman, 1975) integrated over the depth of the water column. For benthic algae, an adapted equation has been used; effects of the tidally varying water depths are accounted for. All suspended particles in the water all have their own specific contribution to the light attenuation coefficient.
The other terms in eq 1 have similar, although somewhat less complex, descriptions. It is beyond the scope of this paper to give each detail of all formulations. A fixed size is assigned to algae, which is compulsory since grazing of fauna species is size related.

Text box 9.1 Basic specifications of dynamic descriptions of algae processes.

individual masses. Within each fauna group two or more classes may be distinguished. In text box 3 a general outline is given, with some detail in text box 4.

The computer program determines the constraints, since processes that are not programmed cannot be calculated. On the other hand, processes may be left out of the calculation by setting appropriate switches. The number and the kind of the variables to be calculated may be chosen in a similar way: the choice is free up to the limits set by the program.

Detritus

Generally, a description of the changes of the detritus content (Det) reads

$$\frac{\partial \overline{Det_i}}{\partial t} = formation + mineralization + grazing + \Sigma inputs + \Sigma outputs \qquad (\text{g DW m}^{-3}\ \text{d}^{-1})\ (9.4)$$

Formation of detritus is the result of algal mortality, excretion and of fauna mortality, faeces production and excretion, and of transformation of other detrital matter.

The mineralization rate is first order in detrital matter Det, but zero order in bacteria. Bacteria dynamics are *not* part of the model.

The mineralization rate of a detritus compound reads

$$mineralization = k_{max} \cdot F_4(T) \cdot F_5(electron\,acceptor) \cdot \overline{Det_i} \qquad (\text{g DW m}^{-3}\ \text{d}^{-1})\ (9.5)$$

where k_{max} is a first order decay rate constant, and F(T) and F(electron acceptor) denote the dependency on temperature and the type of electron acceptor, respectively.

Under oxygen availability, F(electron acceptor) equals 1. However, when other acceptors are needed (nitrate, e.g.), mineralization may slow down. Acceptors such as manganese (IV) and iron (III) are not considered in the model.

Text box 9.2 Basic specifications of dynamic descriptions of detritus processes.

An age and size structure was taken into account for four reasons:

1- a number of characteristics is size dependent, such as the productivity/biomass ratio of a population. By introducing size classes, the different behaviour of, for example, larvae is taken into account.

2- the description is much better related to the data that are collected during field surveys and laboratory experiments: the model may better serve as a bridge between population dynamic theory and ecosystem modelling.

3- the description is much better suited for future extensions.

4- the description is generic.

The classes are not chosen based upon a certain size or age range, but are defined according to the reproduction process (new born animals fill class 1, animals still present in class 1 shift to class 2, etc), the growth of animals (animals in a class grow or loose weight as a result of uptake and losses) and the change in numbers (animals die). It is assumed that there is no spread in

Fauna

Generally, a population biomass density is described by
where W_i is the average mass (g) of individual animals in class i, and N_i the number of animals per unit of

$$M_i = \overline{W_i} \cdot N_i \qquad (\mathrm{g\ m^{-3}})\ (9.6)$$

volume (number.m^{-3}). Changes in population biomass is a result from changes in both mass and numbers. Changes in animal average mass (W) follow from

$$\frac{\partial \overline{W_i}}{\partial t} = uptake + respiration + excretion + faeces + spawningW \qquad (\mathrm{g\ DW \cdot ind^{-1} \cdot d^{-1}})\ (9.7)$$

and changes in numbers N from

$$\frac{\partial N_i}{\partial t} = mortality + grazing + spawningN \qquad (\mathrm{ind\ m^{-3}\ s^{-1}})\ (9.8)$$

The conversion from the spawned biomass spawningW to spawned numbers SpawningN is done through the larval mass. The first born larvae get a start mass which is a model parameter. Later born larvae get the mass the already existing larvae already have reached as a result of uptake and losses. This construction avoids some numerical problems. Spawning occurs in certain periods, set by parameter values; presently it is not related to computed environmental conditions.
Since ion budgets are computed following N.dW/dt and W.dN/dt, a dW/dt . DN/dt-correction is implemented.

Text box 9.3 Basic explanation of fauna description in EcoWasp. Text box 4 gives some details

animal average mass in a single class. In case of shifting classes, the two largest classes are mixed up.

To each class, parameters are assigned that determine the position of the animal in the system, the position where it collects food, where it puts its faeces, where it respires, and where it puts its pseudo-faeces (Fig 9.5), if relevant. Maximum and minimum prey sizes are defined, relative to the body size of the animal. Food preference and utilization for each prey component is one of the parameters. Equations are given in text boxes 9.3 and 9.4.

The activity of the animals depends on their mass. For all the formulations given in text box 9.3 and 9.4 containing F(W), an allometric equation like

$$F(\overline{W}) = a \cdot Mass^{b} \qquad (-)\ (9.3)$$

should be read. The a- and b-value will be different for the several sub-processes.

Fauna (continued)

Each animals filters or searches a certain system volume per unit of time. This determines the grazing losses in terms of animal numbers (in case they are prey), and this times the prey masses, it determines the amount of food in terms of biomass that can be taken up by a predator animal.

As a short explanation, the uptake term is given in more detail.
Fauna uptake rate reads

$$uptake\ rate = up_{max} \cdot F_6(Food) \cdot F_7(T) \cdot F_8(\overline{W_i}) \cdot \overline{W_i} \qquad (\text{g DW ind}^{-1}\ \text{d}^{-1})\ (9.9)$$

where up_{max} is the maximum uptake rate constant. F(Food) and F(T) are the food and temperature dependency functions, $F_8(W)$ the allometric function that describes the weight dependency of uptake. Multiplication with W (as done here) gives the individual uptake rate.
The description of respiration consists of two terms: a basic metabolism term and an activity related term. The latter is zero when there is no feeding activity but it increases when the animal searches for food. Thus:

$$respiration = rest respiration + activity respiration \qquad (\text{g DW ind}^{-1}\ \text{d}^{-1}) \quad (9.10)$$

or:

$$respiration = -k_{rr} \cdot F_9(T) \cdot F_{10}(\overline{W_i}) - k_{ra} \cdot F_{11}(activity) \qquad (\text{g DW ind}^{-1}\ \text{d}^{-1}) \quad (9.11)$$

Parameters are k_{rr} (rest respiration constant) and k_{ra} (activity related respiration constant). Mind that they have different units and, thus, have different meanings. F(activity) is nothing else than the space that an individual has searched for food per until of time (m^3 ind^{-1} day^{-1}); the conversion factor k_{ra} thus describes the amount of energy (expressed in g DW in the model) needed per m^3 searched volume. One of the ideas is that this factor is more or less the same for all animals that show the same food collection behaviour.
Excretion is described similarly. Respiration is an oxygen demanding process, and the products are carbon dioxide and nutrients following the stoichiometric ratio of the animal. Chemically, respiration is the reverse reaction of growth (in the model). The product of excretion is some detrital matter; set through a model parameter.
Changes in numbers are describes following:

$$\frac{\partial N_i}{\partial t} = mortality + grazing + spawningN \qquad (\text{ind m}^{-3}\ \text{s}^{-1}) \quad (9.12)$$

The change in numbers by mortality is described by

$$mortality = -k_{mor} \cdot F_{12}(T) \cdot N_i \cdot F_{13}(age, condition, \overline{W_i}) \qquad (\text{ind m}^{-3}\ \text{day}^{-1})\ (9.13)$$

where k_{mor} is a rate constant (d^{-1}). This equation basically describes all the mortality not modelled in the term grazing (eq. 8). The terms k_{mor} and F(age, condition, mass) have to be reconsidered every time new predators are introduced in or removed from a model setup, or when other feeding parameters are changed.

Text box 9.4 Some fauna description details in EcoWasp

Since animal mass finally reaches some maximum value, b-values for respiration and excretion need to be larger than the one for uptake.

Animal length is computed using the relationship

$$Length = a'\cdot Mass^{\frac{1}{b'}} \qquad \text{(g) (9.14)}$$

where b' is about (but not exactly) 3.

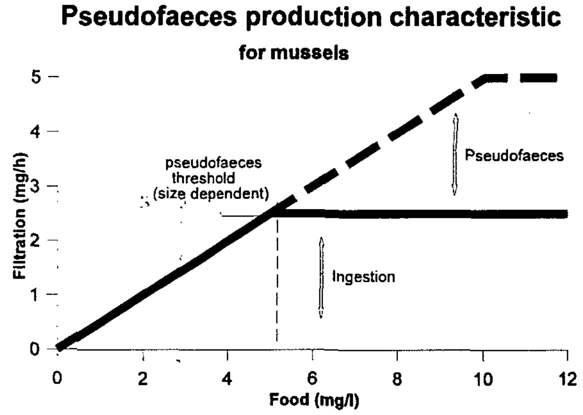


Fig. 9.5 Pseudofaeces production rules in the model

A special process for some filter feeding animals concerns pseudo-faeces production, being that part of food that is caught, but not taken up by the mussel (Fig. 9.5). This part is deposited on the sediment surface. Animals only start taking up food when sufficient food is available to compensate for the activity related losses. In the model, pseudo-faeces production does not start until maximum food uptake is reached. There is an upper pseudo-faeces production limit; when this limit is reached, the filtering rate slows down with a further increase of food availability. By this, the animal reduces its activity related energy expenses.

Temperature dependency of biological processes

A temperature relationship that describes the processes' response to temperature variations is implemented. We decided to use functions that easily allow a temperature discrimination. Standard Q_{10}- formulations e.g. (Begon et al, 1990) result in temperature related growth characteristics that do not differ very much for different choices for the parameters. We implemented the relationship from text box 9.5; it may give several shapes of temperature relationships, depending on the parameter values (Fig. 9.6). And thus, it better allows temperature dependent species competition.

The function used for all the biological processes reads

$$F(T) = \left(\begin{array}{ll} = \dfrac{(T-T_1)^2}{(T-T_2)^2 + (T-T_1)^2} & if\ T < T_2 \\ = \dfrac{(T-T_3)^2}{(T-T_2)^2 + (T-T_3)^2} & if\ T > T_2 \end{array} \right) ; \left(\begin{array}{l} = 0\ if \quad T<T_1 \vee T>T_3 \\ = 1\ if \left(\begin{array}{l} T_1 = T_2 \wedge T<T_2 \\ T_3 = T_2 \wedge T>T_2 \end{array} \right) \end{array} \right) \qquad (-) \quad (9.15)$$

where $F(T=T_2) = 1.0$. For $T<T_1$ and $T>T_3$ $F(T)=0$. When (T2-T1)= (T3-T2), then the function is symmetric around T2. Also, the area under the curve is 1.0, which is useful in a couple of cases. Important is that the shape of this function is very different for different parameter combinations (fig. 9.6), thus allowing temperature dependent species competition, or optimum temperatures for species occurrence. .

Text box 9.5 Temperature dependency function in EcoWasp. This function has a maximum of 1 at $T= T_2$

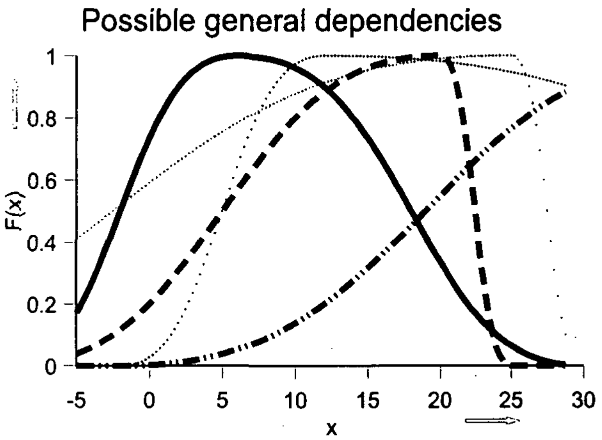


Fig. 9.6 Five different possibilities for a temperature dependency

Nutrient dynamics

All kinds of elements are allowed in the model, adding elements does not require an adaption of the source code. For all biological and chemical transformations, the elemental budget is computed. Each animal, algal, solid, detritus compound has a fixed stoichiometry. All biological activities (in each compartment, in each layer) together lead to negative or positive rates of addition to the dissolved nutrient concentrations. And, since these biological processes take place in the water as well as in the sediment, net kinetic contributions of biological activities to all nutrients in all layers of all compartments are known.

Sediment structure

The sediment is divided into a number of fixed layers, each having a known layer thickness. All solid (inorganic solids, detritus, algae, fauna) characteristics are computed with regard to these fixed layers. Pore water profiles for dissolved substances are computed using analytical solutions for standard first and/or zero order diffusion-reaction equations (Duursma & Hoede, 1967; Berner 1971, 1975, 1980; Brinkman and Van Raaphorst, 1986, Ruardij & Van Raaphorst,1995). Bioturbation acts upon distribution of solids. Algal, detrital and fauna process rates result in positive or negative production rates of all relevant dissolved pore water substances.

From the computed pore water profiles, the diffusive exchange between water and sediment is computed, through Fick's first law. Thus, reaction intensities in the sediment directly affect sediment-water exchanges and overlying water characteristics.

The biological activities of animals also transport dissolved and solid substances.

Habitat information

Although in a model like this, many process related information has been implemented, a number of relationships always remains without attention. A major example concerns information on where mussels find their preferred environment. In exposed areas, mussels cannot survive in the Wadden Sea, mainly as a result of physical disturbance. Such information is not generated by the model (as is information on food availability), and implemented through a habitat suitability parameter. He more it deviates from 1 -standing for normally suitable- , the higher the animal mortality. Thus, it influences the animal mortality term in textbox 9.4.

9.5 Parameter tuning

With small models (e.g. Maynard-Smith, 1979; Scheffer, 1990), having a few parameters, a true calibration can be done (Van Straten, 1986; Keesman,1989; Brinkman et al, 1995). Large, complex models like EcoWasp can not be truly calibrated. For all processes, sufficient field information has to be available, which is never the case. This lack of data implies that many parameters cannot be separated completely (or even: at all) from each other: and thus many interrelations exist. The only method to find more or less appropriate parameter values is to start with an interpretation of available literature results. And from separate detail studies, followed by an off-line parameter tuning, parameter best-guesses can be found. This does not give full information, but generally sets relatively narrow ranges. Within these ranges the modeller has

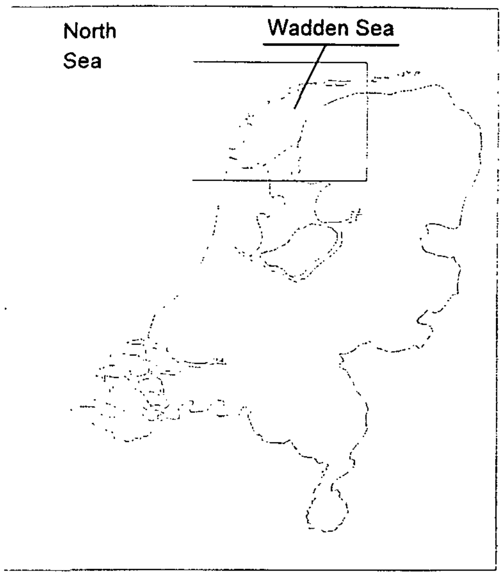


Fig. 9.7 Location of the Wadden Sea in the Netherlands

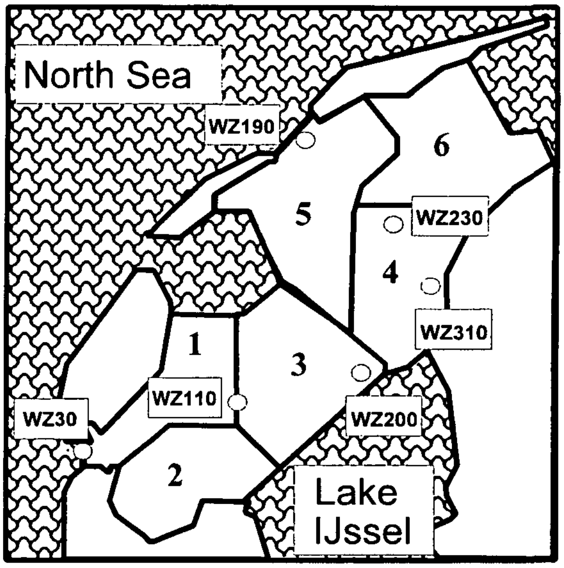


Fig. 9.8 Compartments and monitoring points in the western part of the Dutch Wadden Sea

Table 9.1. Mean depths (cm) of compartments from Fig. 9.8 and their sub-compartments. Mean depth is at mean tidal level.

Compart	flat	sub-tidal	channel	total
1	51.9	258	1480	789
2	53.1	215	642	203
3	76.5	261	923	344
4	72.1	243	701	202
5	60.4	247	1170	191
6	68.3	212	790	131

Table 9.2 Mean volume (m^3) of compartments (at mean tidal level)from Fig. 9.8 and their sub-compartments.

Compart	flat	sub-tidal	channel	total
1	6,68e+06	1,99e+08	1,08e+09	1,28e+09
2	3,88e+07	2,72e+08	1,38e+08	4,50e+08
3	2,22e+07	3,85e+08	3,20e+08	7,28e+08
4	4,45e+07	3,28e+08	3,60e+07	4,09e+08
5	7,82e+07	2,92e+08	1,22e+08	4,92e+08
6	9,84e+07	2,20e+08	8,92e+06	3,27e+08

some freedom for the final tuning, which is nothing else than making results to deviate not too much from the measurements.

These measurements themselves usually carry a large uncertainty. This has little to do with sampling errors, but merely with a non uniform distribution of all kinds of variables in the system: it is difficult to find really representative figures for a large tidal system.

Parameter values

In chapter 3, a number of parameter values has been presented. It is mainly this set of parameters that has been used for the simulations presented in this chapter 9.

9.6 Application: system description and model setup

Area

The model is applied to the western part of the Dutch Wadden Sea (Fig. 9.7) for the year 1980-1988. This period has been chosen because input data, and data for comparison were available; and in 1986 additional data were available from the EON study (EON-I, 1988; EON-II, 1988). For the ecosystem model computations, the area is divided into six water compartments (Fig. 9.8), each covering three areas with different depths: tidal flats (all areas above the mean low water level (MLW)), subtidal areas (from MLW down to MLW - 5 m) and channels. The twelve-compartment set-up from EON-I (1988) and EON-II (1988) has been recompiled, regarding water flows and volume exchange coefficients. These EON-data have been computed for an atmospherically quiet period in June, 1971 (Ridderinkhof, 1988). Average depths and compartment areas have been computed from GIS-information. In tables 9.1-9.4 these basic data have been listed.

The flow trajectory of fresh water is also computed during the EON study. The then derived characteristics have been compiled as well.

The sizes of the six compartments are of the same order (Table 9.2), which is necessary to avoid numerical inconveniences. The exchange between North Sea and Wadden Sea mainly is mainly driven by the tides (Tables 9.3 and 9.4). According to (Ridderinkhof, 1988), there is, on average,

Table 9.3 Water volume exchange rates ($m^3\ s^{-1}$) between the six Wadden Sea compartments, including the North Sea. Recalculated from EON-I (1988)

compart	1	2	3	4	5	6
1	0	4483	3232	0	0	0
2	4483	0	570	0	0	0
3	3232	570	0	467	864	0
4	0	0	467	0	550	516
5	0	0	864	550	0	1466
6	0	0	0	516	1466	0
Marsdiep	3144	0	0	0	0	0
Het Vlie	0	0	0	0	4011	0

The upper right triangle of the matrix equals the lower left triangle. Note that the columns Marsdiep en Het Vlie have been omitted.

Table 9.4 Water flows ($m^3\ s^{-1}$) between the six Wadden Sea compartments, including the North Sea. Recalculated from EON-I (1988)

compart	1	2	3	4	5	6
1	0	405	410	0	0	0
2	-405	0	405	0	0	0
3	-410	-405	0	-21	838	0
4	0	0	21	145	0	-166
5	0	0	-836	-145	0	106
6	0	0	0	166	-106	60
Marsdiep	815	0	0	0	0	0
Het Vlie	0	0	0	0	-875	0

A value denotes the flow from the column compartment number to the row compartment number. E.g., from Het Vlie into compartment 5, the flow is 875 $m^3 s^{-1}$. Note that Marsdiep and Het Vlie are not mentioned as columns, since the upper right triangle of the matrix has the same values (times -1) as the lower left triangle has. The diagonal values usually are 0, except Flow[6,6]. This values of 60 ($m^3\ s^{-1}$) means that in compartment 6 there is a sink flow; in this case to the adjacent tidal basin in the eastern part of the Dutch Wadden Sea.

a rest-flow from the North to the South.

For the exchange between the Vlie basin (North-East) and the Marsdiep basin (South-West), the rest flow is more important than the tidally induced exchange; both basins are more or less separated from each other.

Available input data

Data for the in-flowing fresh water and the adjacent North Sea have been supplied by the monthly monitoring programme by the National Institute for Coastal And Marine Management (RIKZ) and the National Institute of Public Health and the Environment (RIVM). Missing data are estimated as good as possible. The model performs an linear interpolation for all input time series data. Meteorological data (radiation, wind) are taken from monthly weather reviews by the Royal Netherlands Meteorological Institute (KNMI 1975-1993), for the nearby station De Kooy, Den Helder.

Available data for comparison

Chlorophyll concentrations, dissolved phosphorus, nitrogen compounds and silicate are used to compare computed and measured water quality characteristics. The measured values are taken from the monthly water quality monitoring program, already mentioned above. Chloride monitoring data are useful for testing the transport model. Benthic animal data are monitored locally (Beukema, 1976, 1982, 1989, 1991, 1993; Dekker, 1989, 1991,1992,1993, 1995, 1996); from these an estimate for benthic biomass densities have been derived. Alterra information (by it's predecessor RIN) on mussel growth rates in the field for the period 1983-1990 (unpublished results) allows an extra check on computed animal mass development. The EON-study in 1986 provided some primary production data (EON-I,1988; EON-II,1988).

9.7 Physical results

The mean residence time of Vlie basin rest flow water in the Marsdiep basin is about 34 days, computed as (total volume)/flow. But, residence time is a relative conception: the smaller the compartments, the shorter the residence times. To avoid such misinterpretations, we computed flushing characteristics for the separate compartments: what is the response of each compartment to stepwise changes in the adjacent North Sea water, or the Lake IJssel fresh water.

Table 9.5 shows the final content of North Sea and Lake IJssel water, as well as the day number when 67% of the changes are settled. This day number is referred to here as the characteristic refreshment time. Compartments nearby the fresh water input locations may contain up to 30-35 % fresh water; the refreshment time for compartment 5 (in the Vlie-basin) is not more then 5

Table 9.5. Mixing characteristics of the Wadden Sea, computed after an average inflow of fresh water and a standard exchange with the North Sea (Ridderinkhof; 1988). Tabulated are: i) starting with a 100% fresh water situation: the value after 60 days (% NZ-water), and the day number at which 67% of this final value is reached; and ii) starting with a 100% sea water situation: the value after 60 days (% fresh water) and the day number at which 67% of this final value is reached.

Comp	Dagnr	% NZ	Dagnr	%IJm
1	6	91.6	15	8.4
2	10	86.0	14	14.0
3	15	68.8	8	31.2
4	23	65.5	16	34.5
5	19	63.2	10	36.8
6	12	87.0	16	13.0
7	12	86.0	15	14.0
8	3	97.2	18	2.8
9	7	92.9	17	7.1
10	11	84.9	15	15.1
11	8	92.8	18	7.2
12	11	87.2	16	12.8

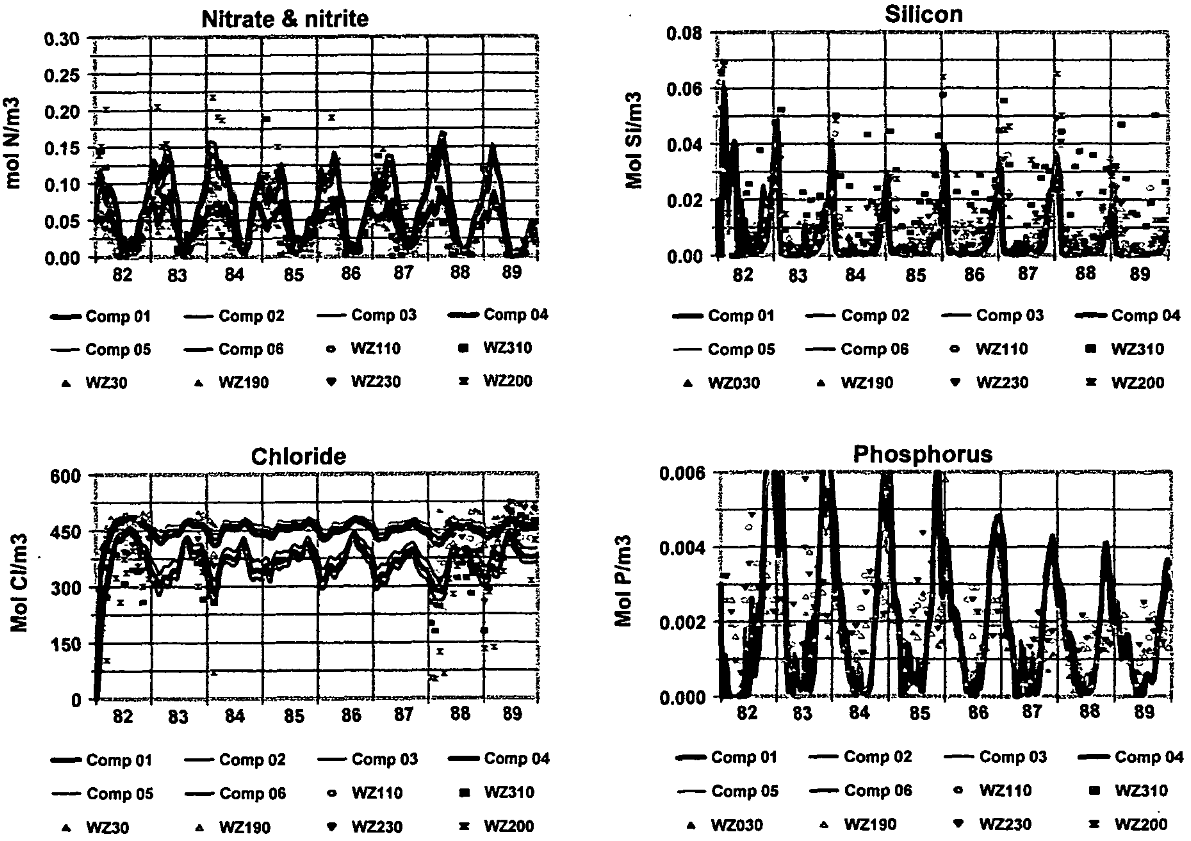


Fig. 9.9 Western Wadden Sea simulation results and measurements for compartments 1-6. The water bodies of the tidal flat, subtidal and channel sub-compartments are mixed up.

days. The pelagic characteristics are largely influenced by the North Sea inputs, because these refreshment figures are of the same order as those for pelagic processes such as net algae growth. More inner compartments are expected to show a more independent behaviour, with characteristic refreshment times of about three weeks.

9.8 Chemical results

With these data in mind, the results of the whole system simulations can better be understood. Fig 9.9 shows results and measured data for dissolved nitrate+nitrite, phosphorus, silicon and chloride. All measurements have been taken together, because we do not intend to discuss local differences; the overall view is our primary concern. Generally spoken, nitrate + nitrite (although NO_2^- is of minor importance) is nicely simulated. Also silicon shows a relatively good resemblance; especially the inner monitoring locations show higher [Si]-values than computed. The spread in data values also is relatively high is this case. At this the underlying governing process is not correctly quantified. For phosphorus, measurements and simulation values do not fit. Possibly the sedimentary P-release still can be improved. The chloride simulations show that an improvement may be expected from the realisation of a more detailed compartment setup. Six water body compartments obviously are not enough to account for the observed salinity variations.

9.9 Biological results

Chlorophyll-a (Fig. 9.10) is simulated more or less consistent with the measurements. When looking to details (e.g. 1986), then it is obvious that the inner compartments show

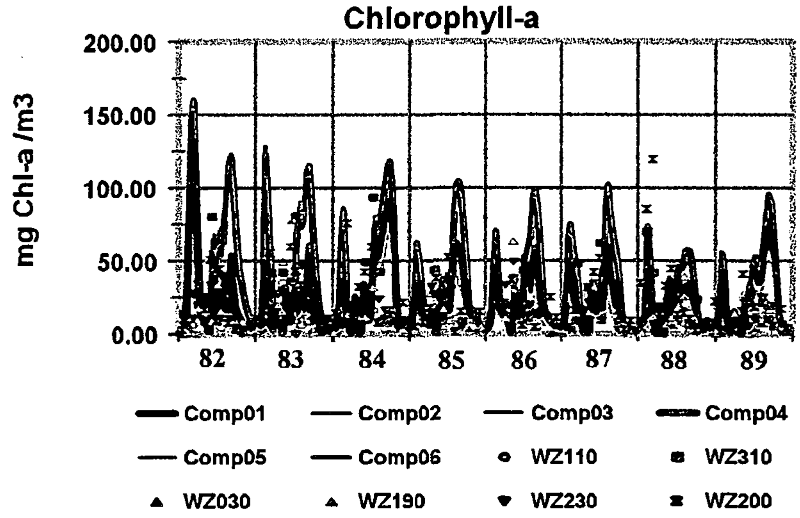


Fig. 9.10 Chlorophyll-content. Simulation and RIKZ- monitoring data

higher chlorophyll-a data then the outer compartments; the model computations show similar differences. The model still shows too strong algae development in the spring period.

Primary production follows a similar pattern, with low productivity in summer (Fig 9.11). Overall productivity is lower than the data summarised in Chapter 3, table 3.4. It turned out to be only possible to reach higher productions (up to 800-900 g DW m^{-2} a^{-1}) if only large adult filter feeders were present; thus, the relatively active class 1 and class 2 mussels should be absent. It is still possible then to reach high biomass densities. Here, the implementation of a (size,number)-description for fauna shows its advantages: not only primary production, but also growth and filtration characteristics should be OK. As was already mentioned in chapter 3, the

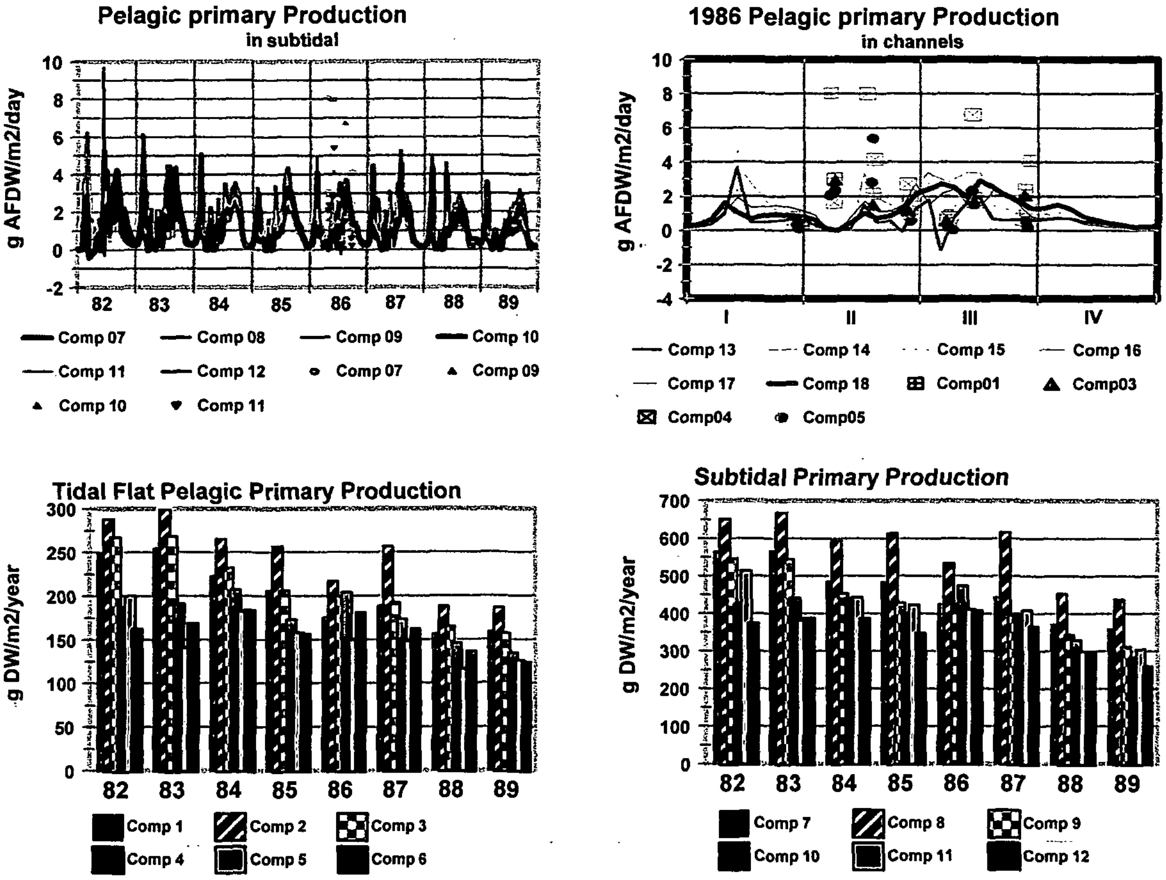


Fig. 9.11 Primary production simulated, and measured (1986 only, EON-I,II)

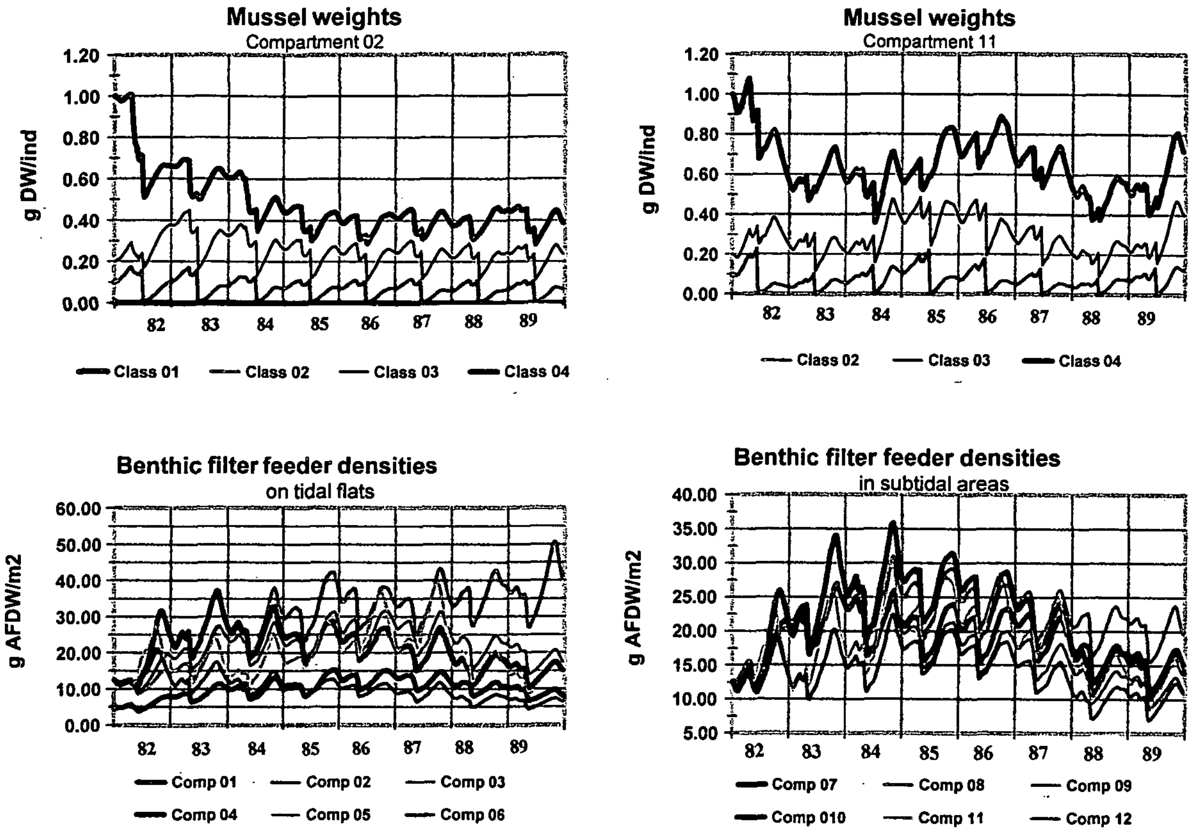


Fig. 9.12 Mussel weight development and mussel biomass densities on tidal flats and in the subtidal. Compartment 2 = flat; 11 = subtidal

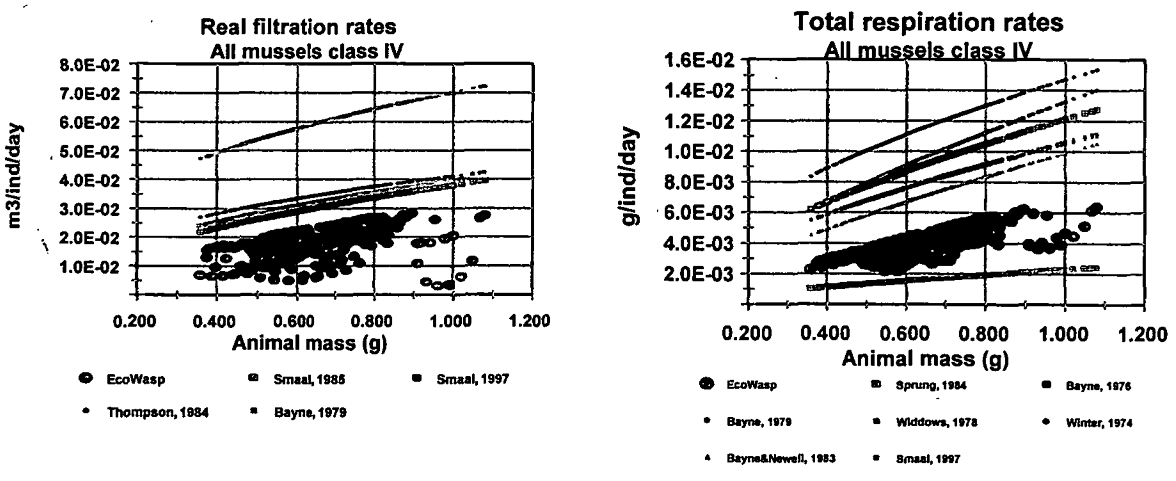


Fig. 9.13 Computed and measured filtration and respiration rates for filter feeders (mussels). Measurements are from laboratory experiments

all-year primary production measurement data resulted from extrapolations, and these suffer from some uncertainties. The computed primary production here is similar to the ones of the ERSEM computations for near coastal areas (Varela et al, 1995), which resulted in net primary productions of about 300-400 g DW m^{-2} a^{-1}. Probably, the simulation results are not that bad. Benthic macro fauna biomass densities (Fig. 9.12) are close to inventory estimates (Chapt. 3),

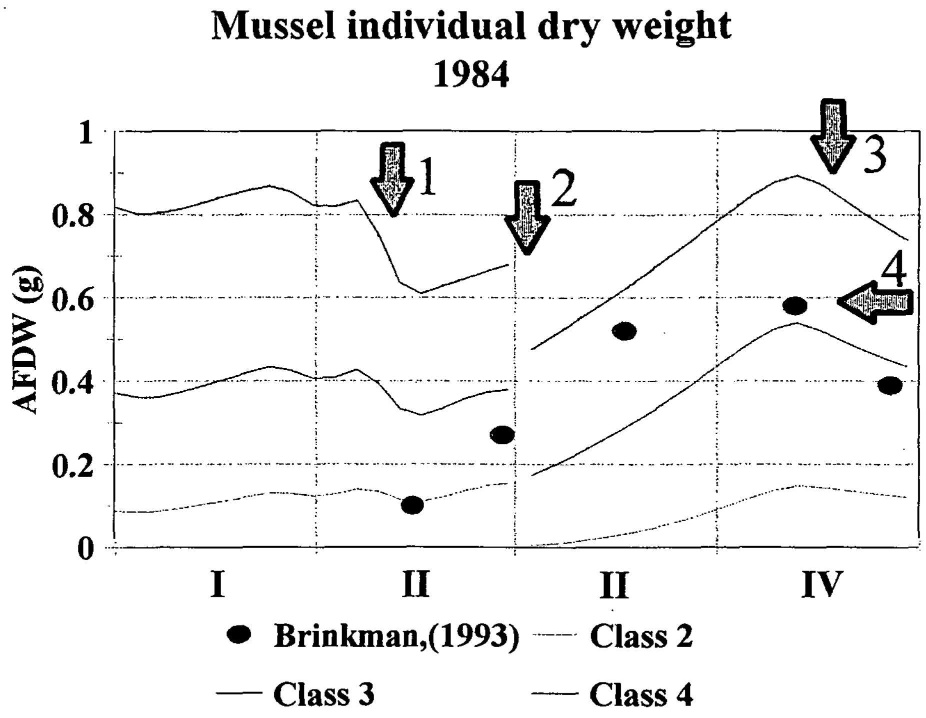


Fig. 9.14. Observed (dots) and computed mussel weight development in one year (1984). At time 1, reproduction takes place, causing weight decrease. At time 2, larvae settle, and cause a shift from class 1 to 2, etc. At time 3, the winter period starts, causing a slowly decreasing weight. This development is supported by the measurements (4). Between years there can be considerable differences.

although differences between compartments may be relatively large. These differences cannot be supported by data yet. Also filtration and respiration rates are close to measured values, although the latter differ widely, commonly a result of the experimental conditions during the laboratory research. (Fig. 9.13). Growth rates of filter feeders also come close to the observed values (Fig 9.14). At last, a comparison of measured uptake by filter feeders of organic matter (phytoplankton and particulate organic matter (POM)) (Asmus & Asmus, 1997) shows a fairly good agreement with computed values (Fig. 9.15).

These agreements show that the EcoWasp simulations produce results that are a good reflection of system characteristics.
In fig.9.16, limiting nutrients are shown, as computed with the model. Diatoms suffer from silicon shortage during large parts of the year. Nitrate and phosphorus both are limiting nutrients for and diatoms and non-diatoms during other periods. In some cases (fig.16, graph D) nutrient limitation can almost stop algae growth. Grazing pressure by filter feeders can be seriously affecting algae growth. Grazing rates may be up to 1 per day; that is, each water volume is filtered by a filter feeder once per day. But on average, this pressure is lower, and averages about once per 5 days.

In fig. 9.17, overall primary productions for a tidal flat and a channel compartments are shown, and for two subtidal compartments. The differences are large; primary production in channels is lower than in sub-tidal areas because of the depth; in lower channel parts the contribution to total primary production is negative. On tidal flats, pelagic primary production is only possible during submersion, and thus total year sums are lower than in the sub-tidal.

9.10 Evaluation of the model development

The development of simulation models as has roughly been sketched here is a process quite similar to developments in any other experimental or theoretical science; the search for better or more likely true descriptions still goes on. Because this chapter is meant as a presentation of the model and part of its features, an extensive discussion of applied model descriptions and simulation results is not appropriate here. We stress that to our opinion ecosystem models, because they act on the scale of whole systems, are the tool to be used to test research hypotheses or formal descriptions of ecological mechanisms.

As stated, parameter tuning of a complex model like EcoWasp always stays an object of discussion. However, one should not be too pessimistic about the used approach for finding

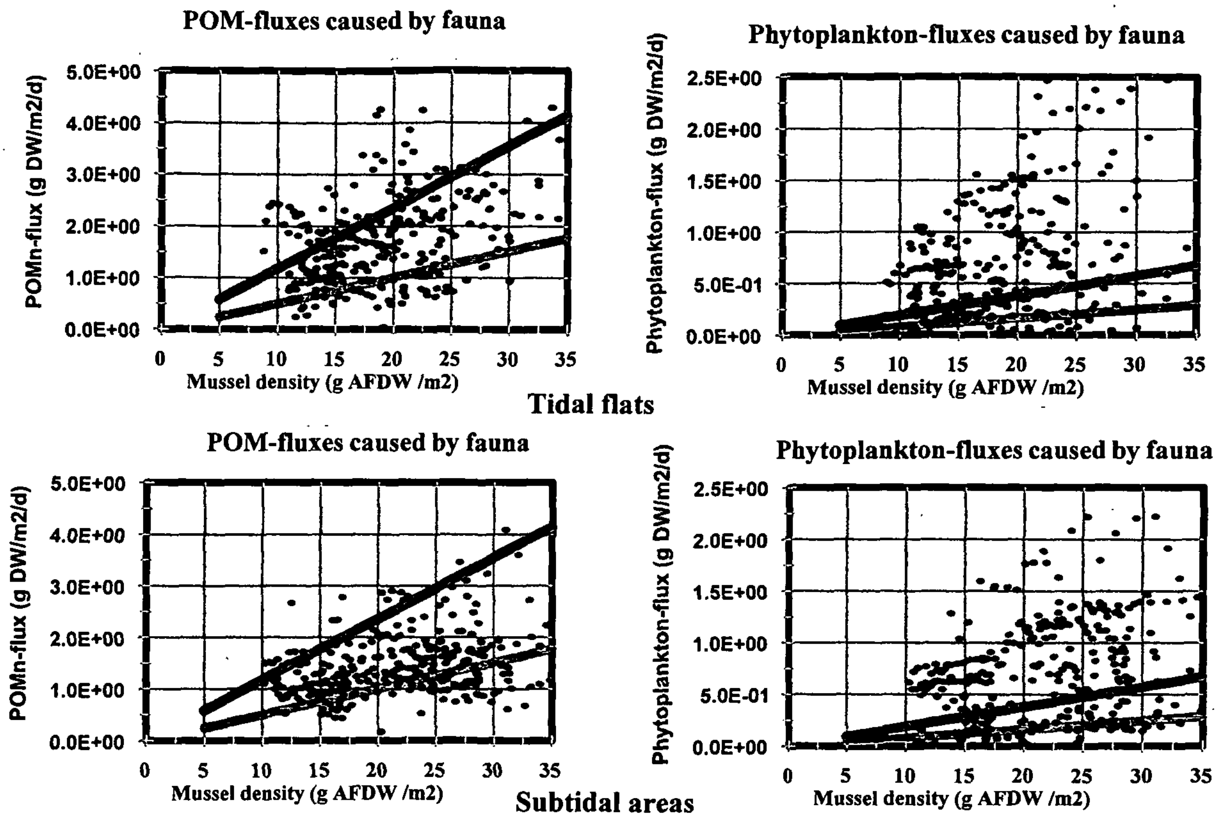


Fig. 9.15. Computed EcoWasp- filtatrion rates (dots) and measured filtration rates above a mussel beds (Asmus & Asmus, 1997). Red = maximum value, brown = minimum value. Field data have been extrapolated using average filter feeder densities in the Asmus-measurements.

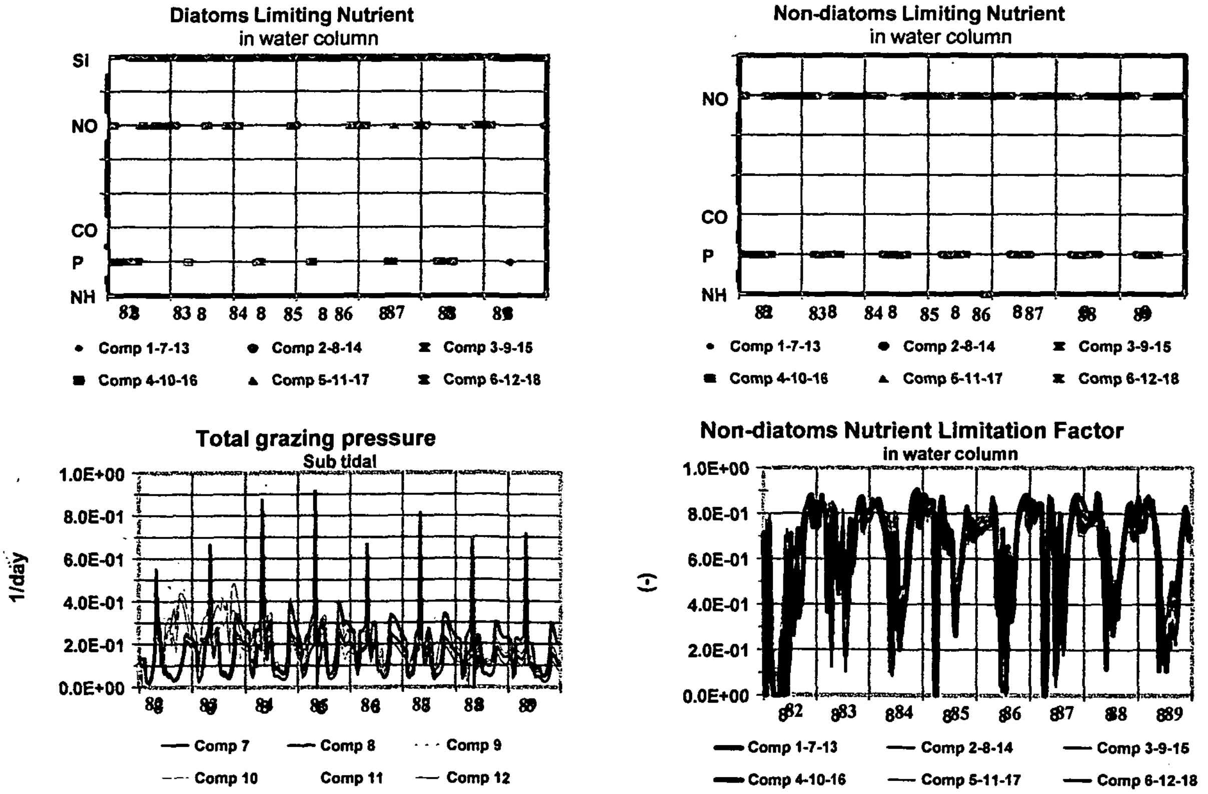


Fig. 9.16. Limiting nutrients, grazing pressure and non-diatoms nutrient growth limitation factor as computed by the basic EcoWasp-simulation

appropriate parameter values: the combined effect (the final simulation results) is not unreliable, but the more one wants to discuss details of the simulation, the larger the uncertainties will be. Each lowest-level process bears a large uncertainty, as do the related parameters, but the combination of all is much more reliable. This is opposite to a 'normal' addition or combination of uncertain quantities and shows how cautious one has to be with these uncertainty discussions.

Some processes are not yet fully implemented in the model. Especially the effects of predation by birds and other organisms, as well as fishery effects still have to be accounted for by adjustment of the mortality rate constant for one or some of the size classes. Thus, only a rough indication of an overall effect can be simulated; here the results of the project has not met the objectives.

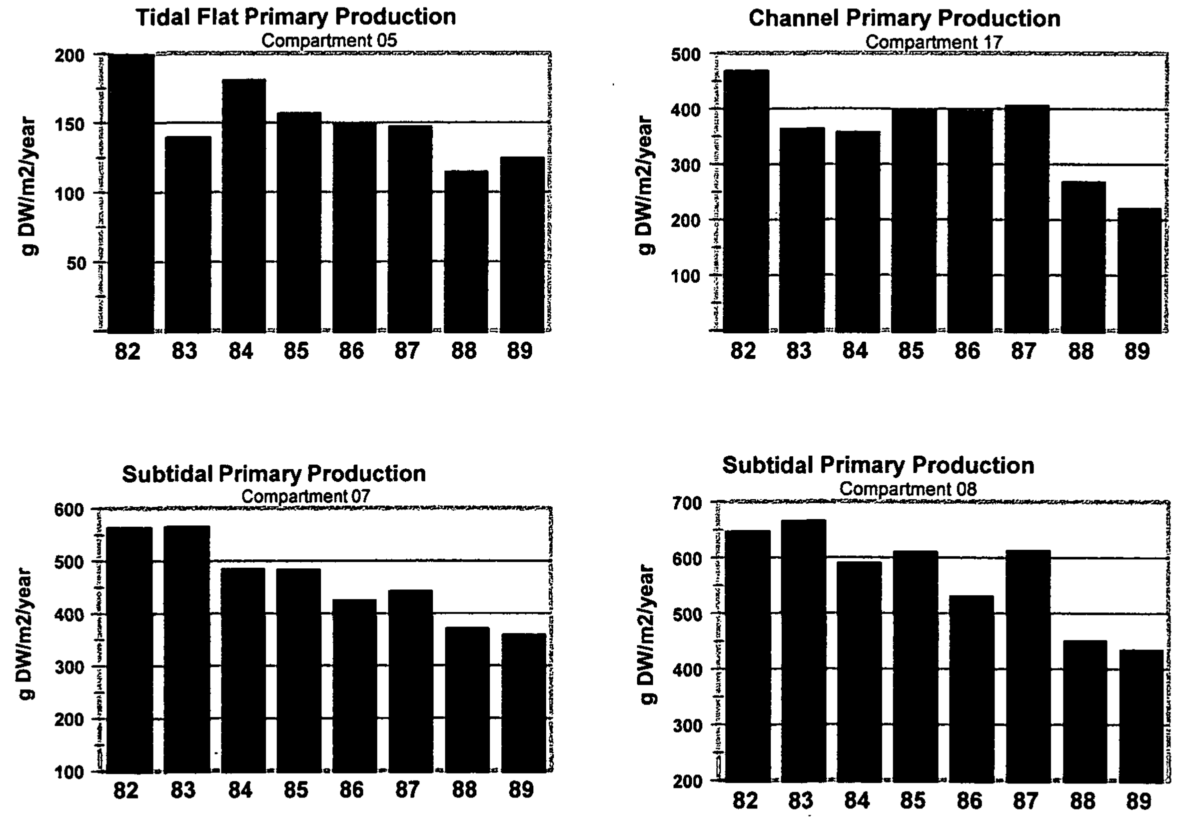


Fig. 9.17. Computed total primary production in a tidal flat compartment, a channel compartment, and two sub-tidal compartments.

9.11 Scenario simulations

9.11.1 Scenario overview

Based on the considerations mentioned in chapter 2, we investigated 11 different scenarios:

- temperature scenarios :

  TW4: for the winter period, we assumed a maximum temperature increase of 4 °C. This was reached at 9 February of a year, in fig. 9.18 an example is shown.

  T04: for the whole year, an increase of 4 °C is assumed.

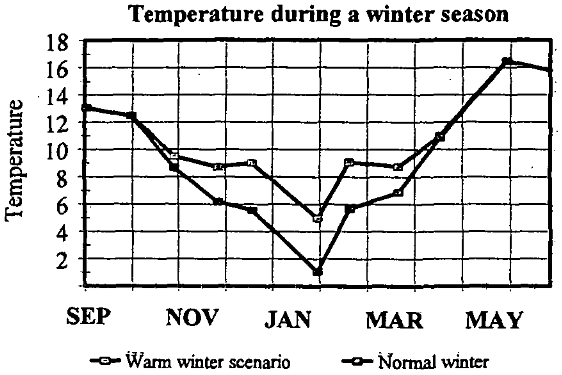


Fig. 9.18. Temperature differences between normal and warm winter, in temperature scenario tw4

- precipitation scenarios:

  Q06 : an increase of 6 % is assumed. This should be realized in the winter period only, but since summer outflow values for fresh water are not that important, we assumed an overall increase of 5% fresh water outflow from Lake IJssel.

  Q25: as Q06, but the increase is assumed to be 25%

- sea level rise scenarios. We assumed an increase of the average tidal level, without changing the tidal volume (see exchange scenarios), nor did we adjust t the borders of the compartments. This implies that a tidal flat partly becomes a sub-tidal area, although this is not visible in the compartment boundaries.

  L02 : an increase of 20 cm is assumed

  L04 : an increase of 40 cm is assumed

  L06 : an increase of 60 cm is assumed

  L10 : an increase of 1 metre is assumed..

- **E05** : exchange with the North Sea increases by 5%. This is to investigate the effects of an increasing tidal range.

  E25 : as E05, but increase of 25% instead.

- **C01** : if the North Sea circulation pattern changes, the North Sea boundary conditions will become different. It is assumed that the Marsdiep boundary has the same conditions as the Terschellinger boundary. The concentrations of nutrients and chlorophyll-a becomes considerably lower.

Beside these computation scenarios, some auxiliary effects will be discussed briefly.

In figs. 9.19-9.21, an overview of results is presented. We limited our explanation to average values for biomass of benthic fauna and algae, for pelagic algae and for primary production.

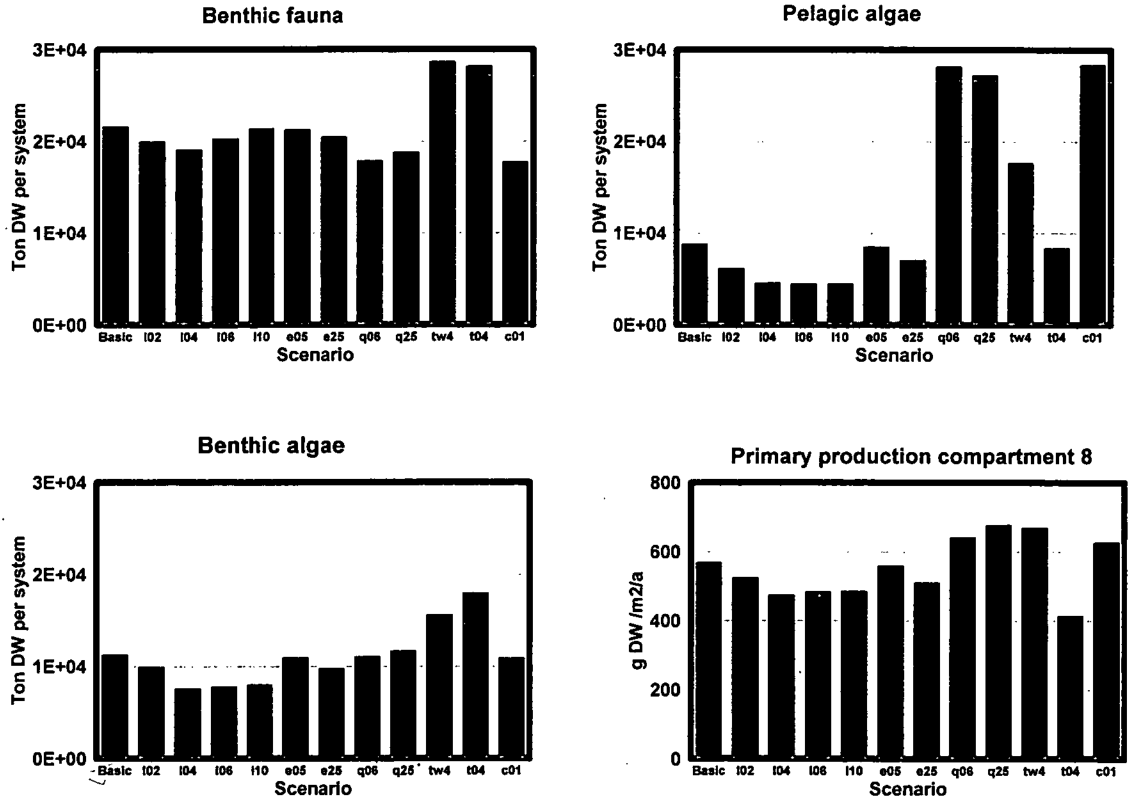


Fig. 9.19 Benthic fauna, pelagic and benthic algae plus primary production for the basic computations and the 11 scenarios 8-year averages

9.11.2 Temperature scenarios

Introduction

We had to deal with two main possible temperature variations: one concerns an overall rise in average daily temperature, throughout the year, the other covers a warmer winter period only. Since we did not expect a very clear response of the system in terms of productivity and biomass (species composition is not part of the EcoWasp simulations), we restricted ourselves to a relatively large increase of 4 degrees Celsius, the whole year, and only during the winter period, respectively.

Also, the temperature rise is effectuated by changing the water temperature in the input time series. In reality, changing solar radiation, long-wave back-radiation and air temperature are the main steering processes, but since a heat budget computation is not part of this project, we had to bypass these factors.

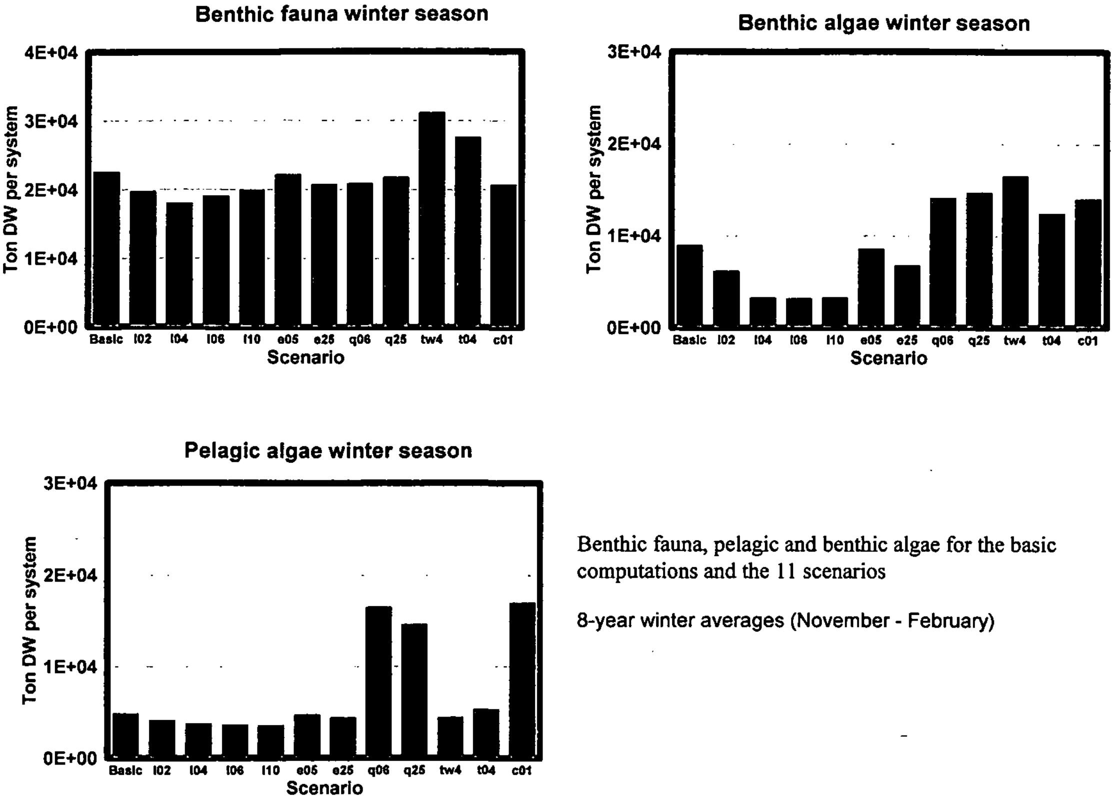
Results

The results of chapter 3 suggested that there will be only slight changes. The present scenario simulations, however, show a large effect on the Wadden Sea system. The main reason for this is that now we modelled animal growth, mortality and reproduction. The model computes a much lower reproduction, leaving more food for the 'existing' mussels. These can grow more, but their relative activity (relative to the biomass) is low. This means that on average, benthic biomass increases, but the number of young animals will be low. And thus, grazing intensities become low as well; therefore the pelagic algae can reach high values. This is especially the case when there is an overall temperature increase throughout the year. If only winter temperatures increase, the effect is much smaller.

9.11.3 Sea level rise

Introduction

The present rate is about 18 cm a^{-1}, a most likely rate in the coming century is about 40 cm a^{-1}, and 60 cm a^{-1} is a pessimistic value. The worse case scenario reads 100 cm a^{-1}.



Benthic fauna, pelagic and benthic algae for the basic computations and the 11 scenarios

8-year winter averages (November - February)

Fig. 9.20 Simulation results for winter season (Nov-Feb) averages,

The geographic boundaries of the compartments were kept the same, which means that a comparison with the standard situation is not completely fair. Especially benthic filter feeder biomass, being "forbidden" in the channel compartments, becomes possible in those areas of the formerly sub-tidal compartments that lie below MLWL- 5 mtr.

Results

Benthic diatoms suffer from an increasing water level. This is a very plausible result, since they have best chances on emerged areas. But also pelagic algae decrease somewhat, mainly because of the increasing average system depth. On the one hand, the area where pelagic primary production takes place stays more or less the same; only the production time increases somewhat in the tidal flat compartments. On the other hand, average water depth increases, and the part that is added is the low producing deeper part of the water column. Sometimes an extra, although low, production, in the sub-tidal and the channel areas this concerns a negative contribution to primary production. Overall, sea level rise results in a lower overall primary production.

The effect for filter feeders is small; their biomass increases a bit. EcoWasp also computed a shift of main occurrence from sub-tidal areas to those tidal flat compartments (that partly become sub-tidal as well). This phenomenon is not shown here.

9.11.4 Precipitation scenario

Introduction

Summer fresh water outflow values are relatively low, and therefore, precipitation changes are simulated by adding 6% and 25% respectively to the fresh water input from Lake IJssel.

Results

Algae profit from an extra fresh water input. From Fig. 9.16 is clear that the model computes a growth inhibition due to nutrient shortage. Since the lake IJssel fresh water contains much larger amounts of nitrate and silicate then the marine inputs do, such a shortage will partly be undone. In the model runs, diatoms already begin to grow during the winter season, and that is the reason for the positive effect on pelagic algae. During summer, there is also a tremendous effect on pelagic algae biomass; and a negative one on benthic algae. Despite the increase of pelagic algae, filter feeders hardly react when only biomass density is considered; but reproduction success is lower, and therefore the population shifts to larger, relatively less active animals.

9.11.5 Exchange scenarios

Introduction

Beside sea level rise, also a change in tidal volume might be an effect of climate change. Such a change implies that every tide a larger amount of water flows into and out of the area. And thus, the exchange with the North Sea becomes more intense. A 5 % and a 25% extra exchange has been subject of the simulations.

Results

Only a high extra exchange with North Sea coastal waters will show some effect: algae and filter feeders biomass decrease a bit. This is mainly due to the lower nutrient and algae content of the NS water: the higher the exchange, the higher the exchange loss factor for algae, and the less filter feeders can use as food.

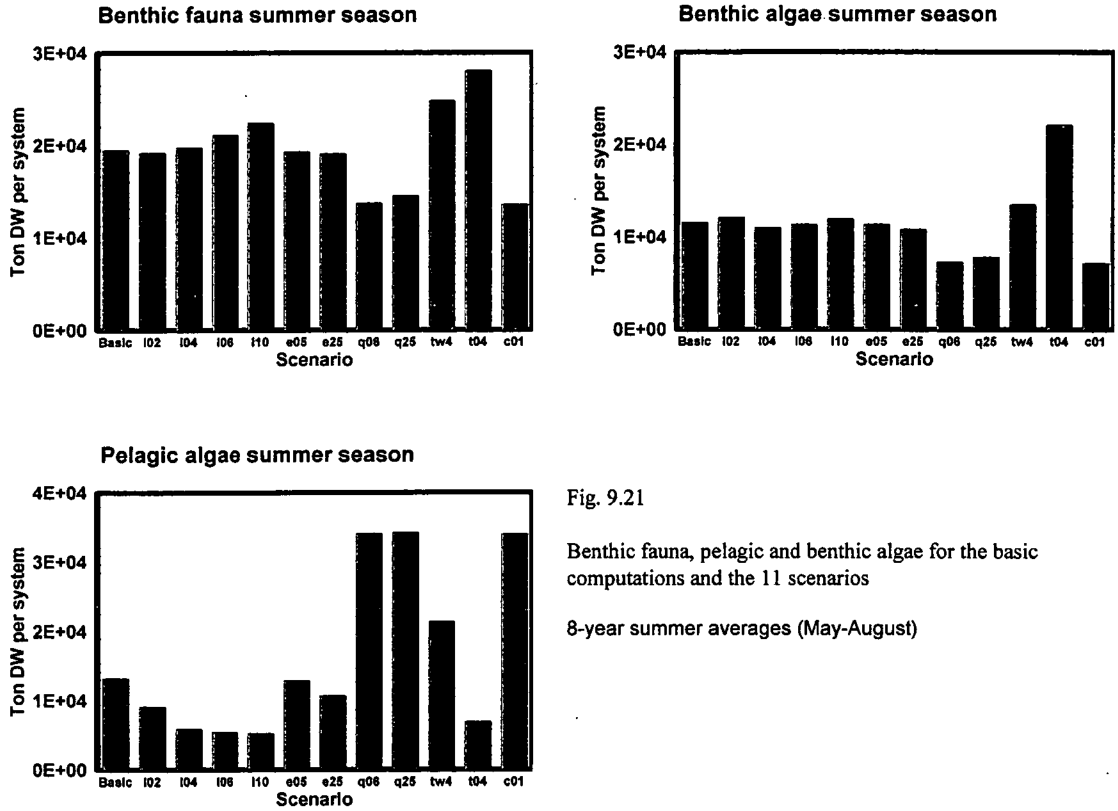


Fig. 9.21

Benthic fauna, pelagic and benthic algae for the basic computations and the 11 scenarios

8-year summer averages (May-August)

Fig. 9.21 Simulation results, summer averages (May-Sep)

9.11.6 North Sea circulation scenario

Introduction

If the boundary conditions in the North Sea coastal area is determined by a water flow from the north instead of from the south, the concentrations of algae and nutrients will be lower, on average. The input data for Terschelling have been used for the Marsdiep boundary conditions as well. Nutrients (especially silicon) content becomes lower.

Results

Benthic fauna biomass, benthic algae become a bit less; primary production increases a bit. A large effect is found for pelagic algae, that shows a tremendous increase. Unless silicon, nitrate is higher, and therefore the algae summer contents are higher. Filter feeders lack their spring food, and reproduce less. Thus, animals shift to less in number, but individuals grow larger during summer.

9.11.7 Auxiliary effects

Storms

Storms have not been directly part of the simulation, but their effects can be put in to the computation through a habitat suitability factor. What happens in that case is that especially the smaller sized mussels will be affected by such a decrease of habitat suitability, because it is this class is most vulnerable for increase hydrodynamic disturbances. In the beginning, this will lead to a decrease of grazing pressure, an increase of algae biomass, and an increase of large mussel individual mass. Later on, since old mussels will die, the new recruitment will be less than before. It is the quantification of this effect that has not been done (yet).

Through the mussel bed habitat suitability study done for the Ministry of Agriculture, Nature Management and Fisheries (Brinkman &Van Stralen, 1999), a first guess of the survival chances of mussel beds, related to storm effects (orbital velocities) has been made possible. It became clear that the best environment for mussel beds is that one that suffers less from waves. With increasing orbital velocities, mussel beds become more affected. Although year-to-year survival is very variable, overall recruitment will be influenced negatively by increasing storm frequency and storm strength.
But, since it is presently not clear at all what the future changes will be (more or even less storms), the effects on mussel beds will be as unclear.

Wind

Apart from storms (that have only effects during a short period), also winds may cause effects.

An increase of average wind velocities will result in a higher suspended matter content (silt, detritus, sand), and thus it will lower primary production in the system. Consequently, filter feeder biomass will be affected negatively. The main problem here is that suspended inorganic matter will also influence the filter feeding behaviour of mussels. This mechanism is not very well investigated in this case of EcoWasp; this has to be part of a future extension.

Biogenic sedimentation: a possibility to counteract sea level rise

We computed the total filtration possibility of filter feeders, in terms of mm sediment deposited on the sediment surface. This gives an estimation of the maximum contribution of filter feeders to undo effects of sea level rise. From the basic computations we did for this scenario study, we estimated an average deposition of about 2 g DW m^{-2} d^{-1} for detrital matter and up to 10 g DW m^{-2} d^{-1} for solids. This is 700 -3500 g DW m^{-2} a^{-1}, respectively. This is, with an average solids density of about 1.5-2.0 10^3 kg DW m^{-3}, an average biogenic sedimentation of 0.5 - 2.0 mm a^{-1}. When this happens in mussel beds alone it would cause in an annual accretion up to 100 mm. This is in agreement with the data mentioned in chapter 3.

9.12 Conclusions

The integrating ecosystem model EcoWasp has been improved considerably during the project, although some of the targets were not realized. Especially the activity description for benthic filter feeders turned out to be capable to describe and laboratory filtration and respiration measurements, individual mussels growth rates in the field and mussel bed grazing intensities upon algae and particulate matter. Thus the model integrated experimental data from completely different time and size scales. The effect of bird predation, however, was not directly implemented in the model, and needed to be part of a general mortality term.

The computations simulated benthic filter feeder biomass quite well; primary production remained lower than figures resulting from extrapolations from field experiments. Until now it has not been possible to compute together a good fit for chlorophyll-a (algae), and for benthic filter feeder biomass and primary production and benthic filter feeder growth and filtration activities. Only primary production remained underestimated by the model.

Effects of climate change have been estimated. The system seems to be sensitive to sea level changes, and temperature changes, especially to whole year temperature changes. With increasing winter temperatures, especially the tidal flat filter feeders lost biomass densities, probably because their individual budget is more under stress than sub-tidal mussels because of the tidal effects.

A matter of concern is the size development of animals. Now, the result is the combined effect of gain (by filtration) and losses (by respiration and excretion). Probably also phenomena not modelled here play a role. It might be necessary to introduce a certain maximum size value. In that case, problems with oversized animals will not occur.

9.13 Acknowledgements

The construction of EcoWasp has started around 1990 as a cooperation between IBN (Alterra's predecessor) and the Netherlands Institute for Sea Research (NIOZ). Afterwards, the IBN / Alterra continued its further development (Brinkman, 1993-a; Brinkman & Smit, 1993). Many programming has been done by J. Smit (NIOZ/IBN), reaching its present status during this NRP-project reported here.

B. Frederiks (National Institute for Coastal and Marine Management, RIKZ/RWS) provided most of the data from the Rijkswaterstaat databases WORSWRO and DONAR. S. Reents provided morphological data extracted and compiled from the IBN / Alterra Arc/Info-GIS system. Many technical and scientific discussions with Th. Fast and A. Wilhelm from the GKSS-research institute (Geesthacht, Germany) improved the model and enhanced the proper implementation of code.

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10 DENOUEMENT

10.1 Overview of results

During this climate change project, we focused on a number of characteristic processes, and thus we covered some morphological phenomena, shell fish processes and birds. We aplied three integrating methods: integration by a model ecosystem study, by the setup of an expert system, and by the further development and application of a dynamic ecosystem model.

We also choose a number of key steering factors to focus on. Temperature rise, water level rise and changing tidal volume, increasing strengths of wind and storms, and increasing fresh water inflow as a results of increasing precipitation in the more central sites of Europe.

The study on morphological processes in the salt marsh area and the tidal flats in front of these areas showed that local wave action determines whether the supplied sediment stays in suspension or is deposited within the sedimentation fields of the salt marshes. The height and maintenance of the brushwood groynes determines the wave action during calm weather condition. During storm surges, when the groynes are submerged, currents are still interrupted but the wave dampening effect reduces significantly.
A future increase in storm surge level and frequency will seriously affect salt marsh development. Salt marsh areas of the mainland coast of the Dutch Wadden Sea need a two-year period to recover from a year with many storm surges. At the moment, the salt marshes along the coast of Friesland attain a positive accretion budget so the effect of an increase in storm surges will lead to a decrease in accretion. The salt marshes along the coast of Groningen show growth stagnation so the effect of an increase in storm surges will directly lead to erosion in this area.

The study on bird migration focused on the improvement of bird models. Dynamic models as DEPLETE and LARGEPOP are applicable to investigate climate change effects in a foraging area (DEPLETE) or on a world wide scale (LARGEPOP). Analysis with DEPLETE, and with the habitat suitability model HABITAT both predict a decline of bird numbers in the Wadden Sea as a result of sea level rise. Loss of foraging possibilities is the main cause of such a decline. Because also conditions in breeding areas are affected, an overall view is needed; LARGEPOP predicts a world wide decline of the Brent geese population as a result of sea level rise and changing conditions during the breeding season.

Higher environmental temperatures may cause a lower Body and Gonadal Mass Index, and a lower larvae growth development for the baltic tellin *Macoma balthica*. This is demonstrated by the research on shell fish development and reproduction. We compared *M. baltica* from the Gironde, at the southern border of the distribution with populations living further north. Development of larvae from the Gironde are not affected at high temperatures like the Balsfjord larvae are. The results indicate that European population(s) of *Macoma balthica* will for sure be affected by higher temperatures. Populations now living further south are possibly better adapted to higher temperatures. Considering the dispersal abilities of *Macoma balthica* these populations might have a chance to move northwards when situations change.

The two aspects of climate change studied in the mesocosms, sea level rise and temperature rise, have an impact on the tidal flat macrobenthos community. In neither of the experiments the numbers of the organisms were affected by the treatment, not by the temperature rise, nor by a sea level rise. It seems that in situations with an increased water level, larvae settlement and growth was more successful. Also, in the high level situation, growth turned out to be better. The length of the inundation period and the biomass production showed a proportional relationship.

With an increased temperature, individual biomass of cockles was lower than in the normal situations. This did not occur during a winter period, but in the April-May period. The model systems were dominated by *Arenicola marina* (especially juveniles), that did not show any relationship with temperature. Therefore, an overall biomass density response to changing temperatures was not found.

For bivalves, the two major climate change aspects had opposite effects: sea level rise stimulated biomass and production, whereas temperature rise depressed bivalve production.

A long term effect cannot be deduced from these experiments; recruitment did not take place in the basins.

An attempt to integrate climate change related phenomena has been done by the development of an expert system. Such a tool also covers time scales that exceed the ones feasible for laboratory research or experiments in model systems or the field. In this expert system (EcoFuzz), experimental observations, model results and expert knowledge can be integrated and the results can be presented in both a qualitative and a quantitative way. Furthermore, the model offers the user the possibility to define and evaluate cases. In order to develop a model for the whole ecosystem of the Wadden Sea a modular, incremental approach was chosen, as was the application of fuzzy set theory. It provides a suitable means for the incorporation of ambiguities and lack of quantitative data into a classification scheme.
The functionality of EcoFuzz includes the definition of fuzzy membership functions for all relevant aspects, the definition of fuzzy inference rules, and the evaluation of scenarios in a graphical form. The input of this expert system consists of observations from mesocosm experiments, results of model computations, and expert knowledge.

The integrating ecosystem model EcoWasp has been improved considerably during the project, although some of the targets were not realized. Especially the activity description for benthic filter feeders turned out to be capable to describe and laboratory filtration and respiration measurements, individual mussels growth rates in the field and mussel bed grazing intensities upon algae and particulate matter. Thus the model integrated experimental data from completely different time and size scales. The effect of bird predation, however, was not directly implemented in the model, and needed to be part of a general mortality term. The computations simulated benthic filter feeder biomass quite well; primary production remained lower than figures resulting from extrapolations from field experiments. Until now it has not been possible to compute together a good fit for chlorophyll-a (algae), and for benthic filter feeder biomass and primary production and benthic filter feeder growth and filtration activities. Only primary production remained underestimated by the model.
Effects of climate change have been estimated. The system seems to be sensitive to sea level

changes, and temperature changes, especially to whole year temperature changes. With increasing winter temperatures, especially the tidal flat filter feeders lost biomass densities, probably because their individual budget is more under stress than sub-tidal mussels because of the tidal effects.

A matter of concern is the size development of animals. Now, the result is the combined effect of gain (by filtration) and losses (by respiration and excretion). Probably also phenomena not modelled here play a role. It might be necessary to introduce a certain maximum size value. In that case, problems with oversized animals will not occur.

The main picture resulting from the simulations is that the results are sensitive for timing aspects. Changing periods of development for algae and filter feeders cause large effects; as a result from different conditions for mussel larvae to feed to survive. Changing predation pressure caused by a different behavior of e.g. crabs and shrimps are still left out of the model; these probably will amplify such timing effects.

10.2 Concluding remarks: did we meet the targets?

At the end of such a project one has to compare the parts of the work that have been carried out and the results with the targets mentioned in the project proposal at the beginning of the project.

A main conclusion has to be that the project proposal does promise more than we finally realised: the implementation of bird migration and bird foraging mechanisms could not be realised. We consider this as a short-coming of our project. A major cause was already mentioned in chapter 2: the reduction of finances from the first proposal draft to the final project description has not been followed by a proportional reduction of the tasks. Especially the coordinating projects have financially been reduced much more than practically. Also, the modelling project now described in chapter 9 has been split up in two even smaller parts, thus allowing the project described in chapter 8. One must conclude that now both sub-projects have not been given enough opportunity to meet their targets completely.

On the other hand, in the whole project, we did study key processes in the Wadden Sea ecosystem, and we did provide the reader with new data, new evidence for ideas on the functioning of the system, biologically as well physically, and new insight in the way processes, inputs and mechanisms influence each other. Also, we presented where we might go as a consequence of a number of climate change related phenomena.

10.3 Suggestions for the future

Such a large project will always end up with new ideas for new research themes, or even enhancement of methods or new measurements. Although the list is not complete, a number of possible subjects can be named.

Regarding salt marsh development, it might be worth to integrate all present process knowledge on salt marsh accretion, with data on inputs through tidal inlets and with estimates of the active effect of benthic animals. This can be combined with estimates of dynamics of tidal flats; concerning silt as well as sand. Then, the insight of the silt and sand budget of the system can be improved. This will provide us also with new data on the possibilities of the system to catch more silt and sand.

Bird modelling, and the implementation of predation pressure in the dynamic model EcoWasp on benthic filter feeders is still on the list to be realised. It was at the beginning of the project, and still is. In principal, the model is suitable for it; and also a number of adaptations needed for this are implemented, but the final integration was not reached.

Model ecosystem research, as performed in mesocosms, is one of the few ways to be fully able to measure all ins and outs of a medium sized, fully functioning ecosystem. One is able to measure what comes in, what leaves the system, and what happens inside the system with the organisms or, what are sediment-water fluxes, or what is primary production in the water column and on the sediment surface. Especially such a complete set-up, closely connected with model computations and laboratory measurements (like in our project), can provide better possibilities for a combined theoretical-practical research. But then, and that was a draw-back of our investigations, the measurements should not be restricted to biological ones alone.

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GLOBAL CHANGE

April, 2001

Dutch National Research Programme on Global Air Pollution and Climate Change (second phase, 1995-2001)

The following reports document the research carried out (so far) in the Second Phase of the Dutch National Research Programme on Global Air Pollution and Climate Change (NRP). If you would like to see a list of the reports published in the First Phase of the NRP, please write us or visit us on the internet. All reports are free of charge. If you want to order a publication please write to Rose Marie de Haan. Programme Office, Dutch National Research Programme on Global Air Pollution and Climate Change (NRP), P.O. Box 1, 3720 BA Bilthoven, The Netherlands;
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THEME	I	Behaviour of the climate system as a whole and its component parts.
THEME	II	Vulnerability of natural and societal systems to climate change.
THEME	III	Societal causes and solutions.
THEME	IV	Integration and assessment.

Report no. (The number between [......] is the original corresponding NRP-projectnumber)

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