

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

7.1 Introduction

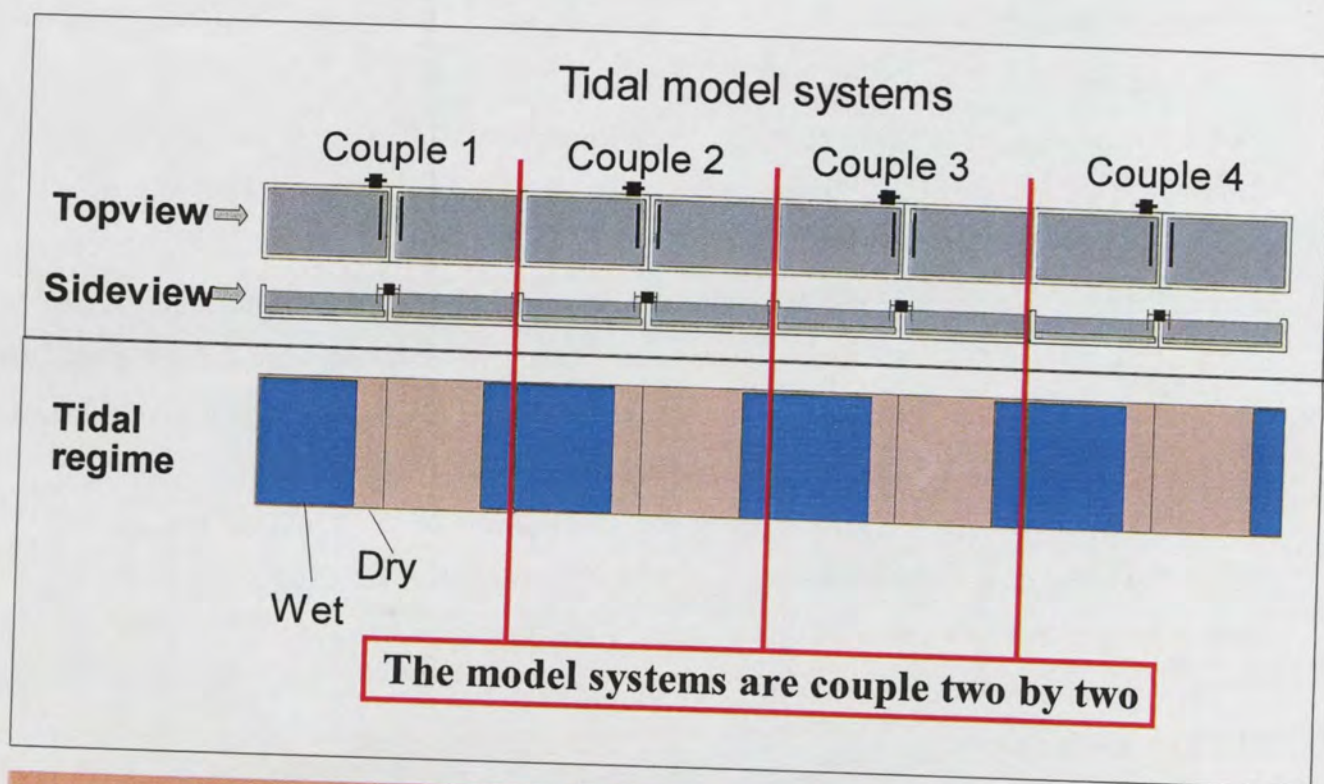
Global climate change can have important consequences for tidal flats in the Wadden Sea and elsewhere. Two aspects of the climate change, Sea Level Rise and Temperature Rise have been studied in MOTIFs (MOdel TIdal Flats) and are reported here. In situations without extra sedimentation a rise in sea 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 m³ 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

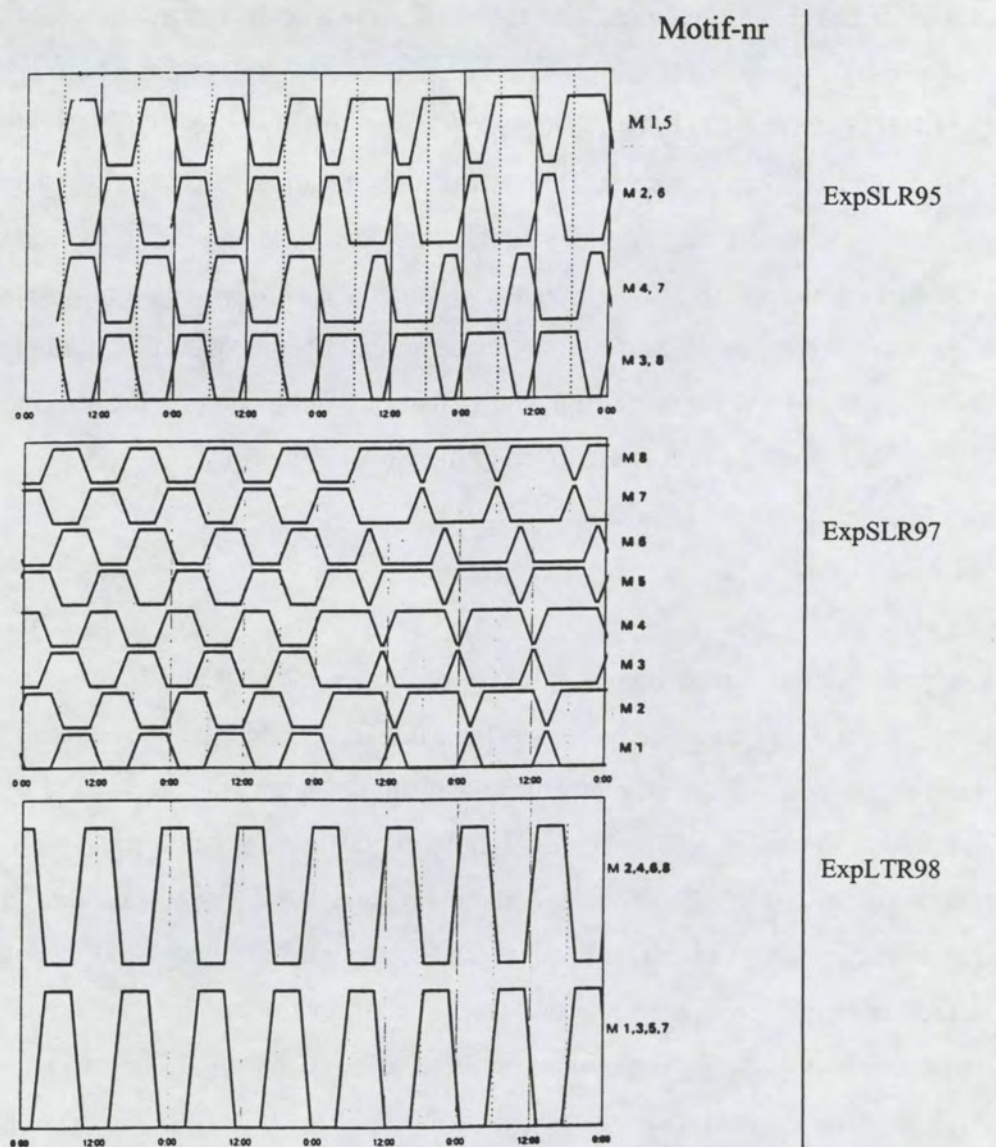
island of Texel. The sediment was collected some months before the start of the experiments and left dry exposed in the air to kill the infauna. After mixing, the sediment was placed into the MOTIFs in early February. The systems were filled with seawater and the tidal cycle was started. During March 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 m² 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 m², 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
	SPIOFILII	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
	SPIOFILII	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						
	SPIOFILII					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 individual 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

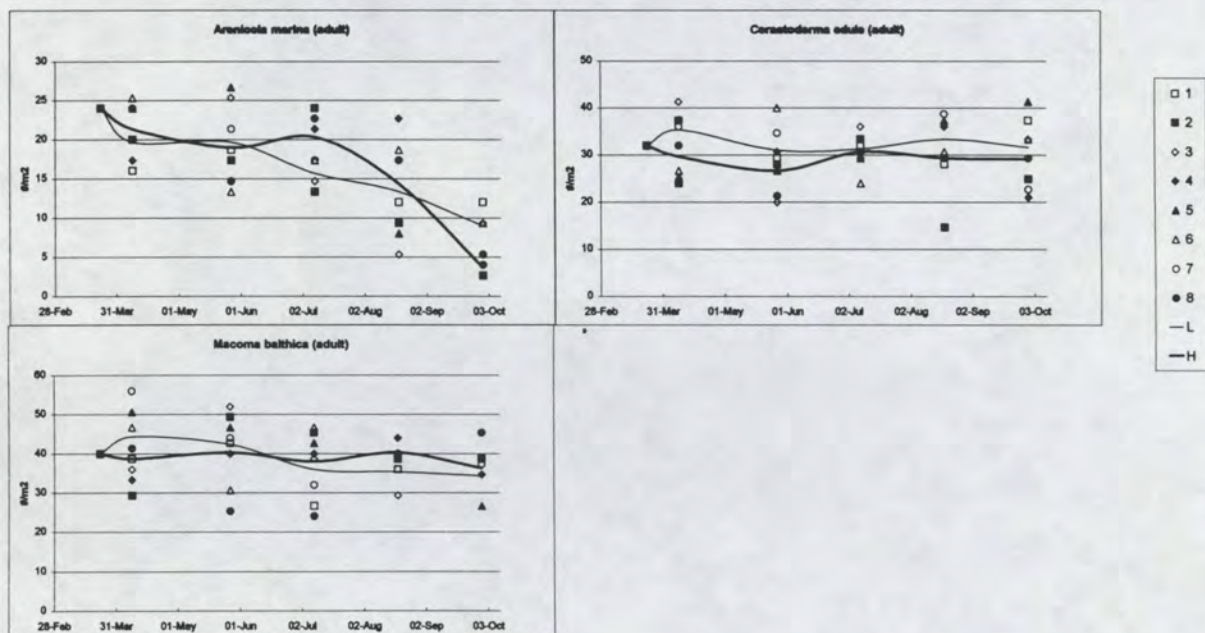


Fig. 7.3. Densities of *Cerastoderma*, *Macoma* and *Arenicola* in the MOTIFs under different tidal regimes during experiment ExpSLR97. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages for high tide and low tide MOTIFs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

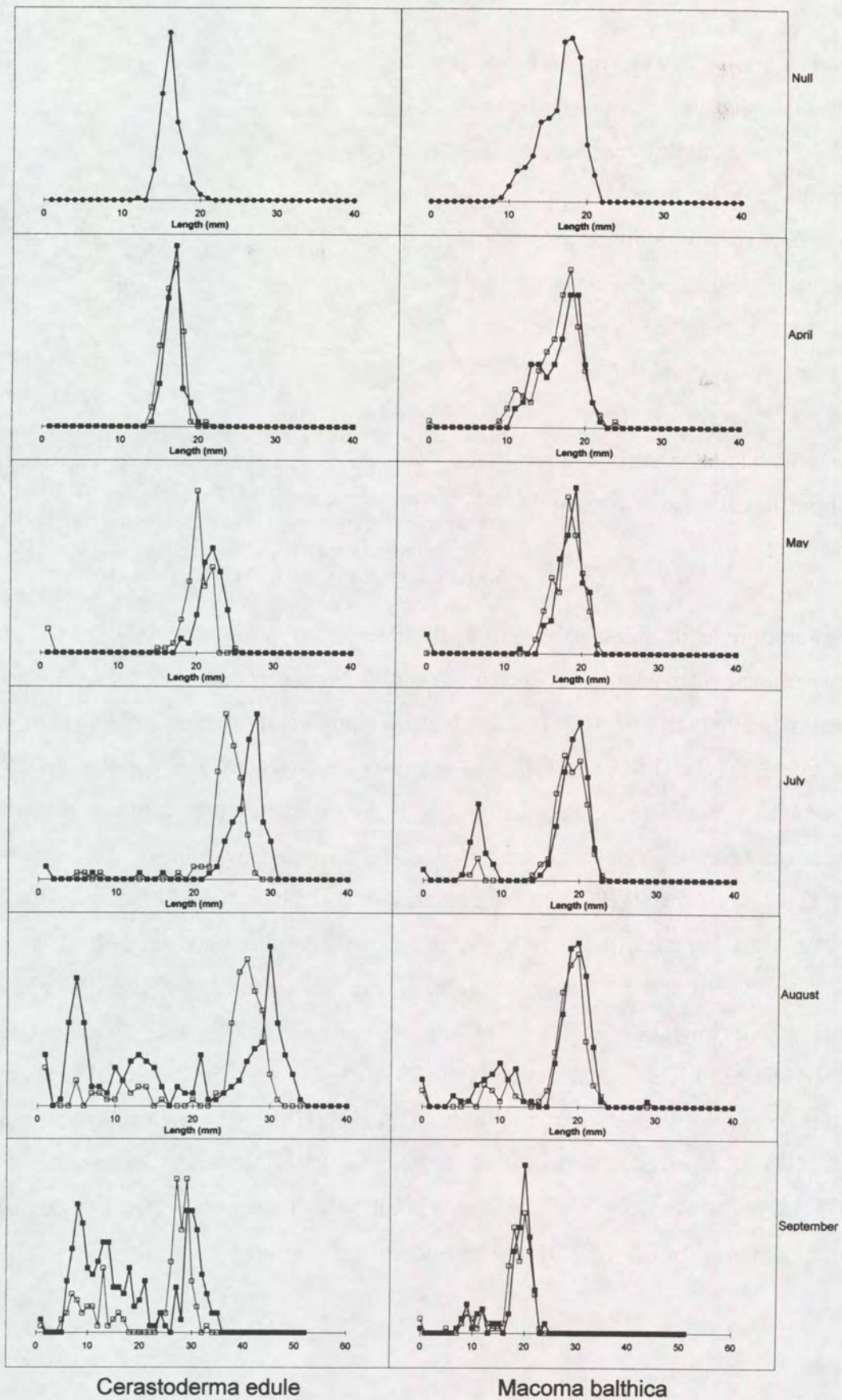


Fig. 7.4. Size distribution of *Cerastoderma edule* and *Macoma balthica* in the course of ExpSLR97. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols.

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.

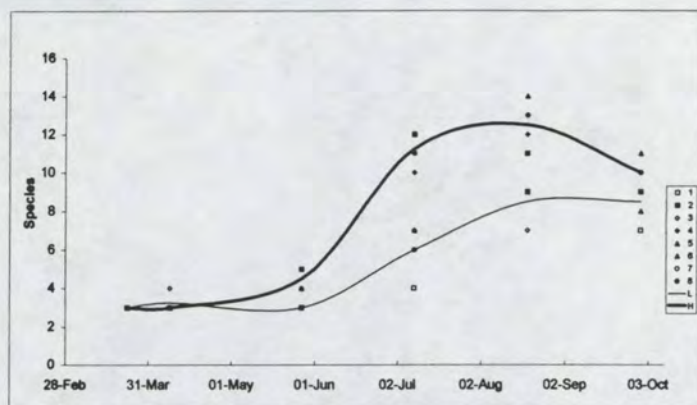


Fig. 7.5. Number of species in high tide and low tide MOTIFs in the course of the ExpSLR97 experiment. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

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.

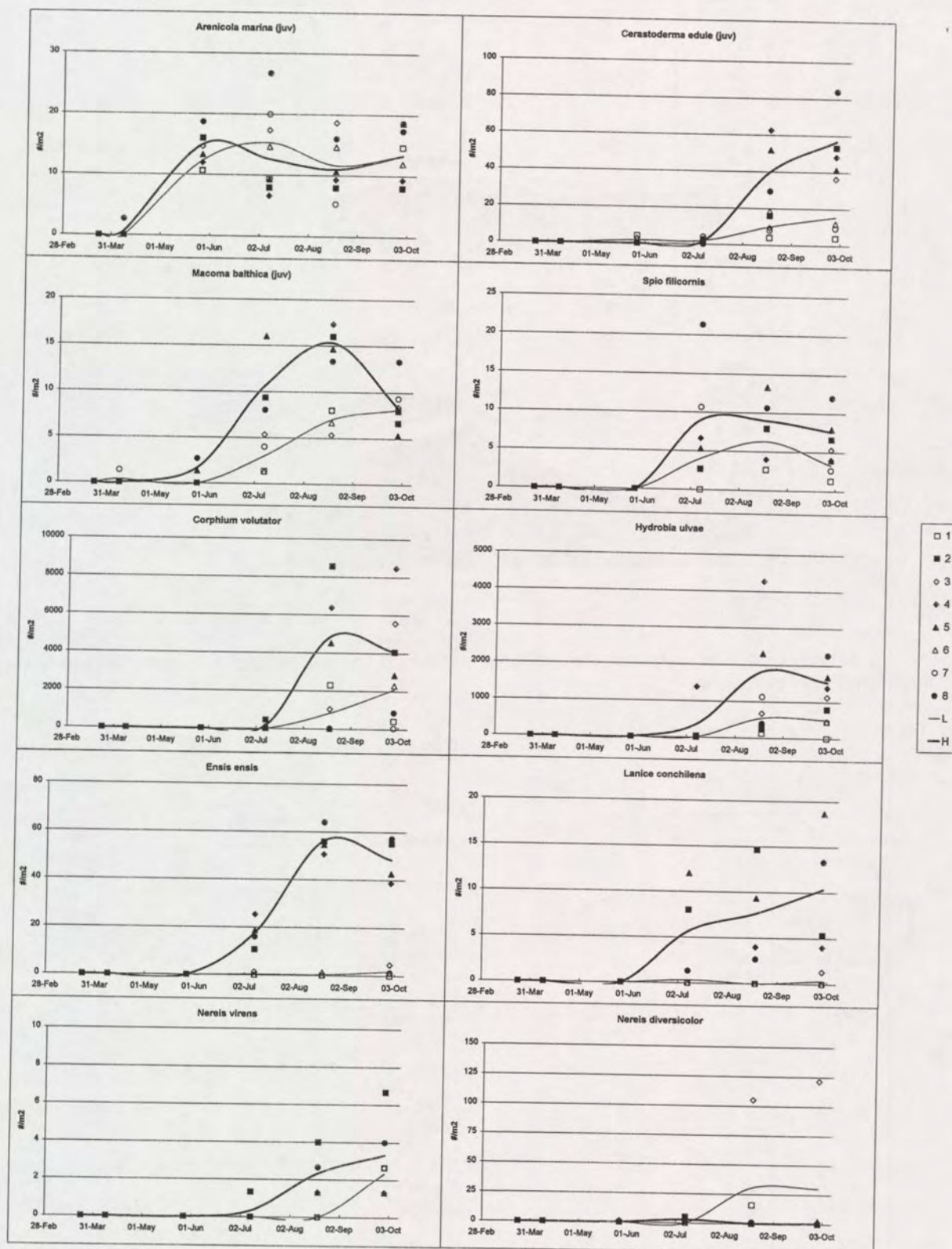


Fig. 7.6. The development of the populations of the most important species (n/m2) in high tide and low tide MOTIFs in the course of the ExpSLR97 experiment. Only those populations that have settled starting as larvae are shown here. High tide MOTIFs are represented by closed symbols and low tide MOTIFs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

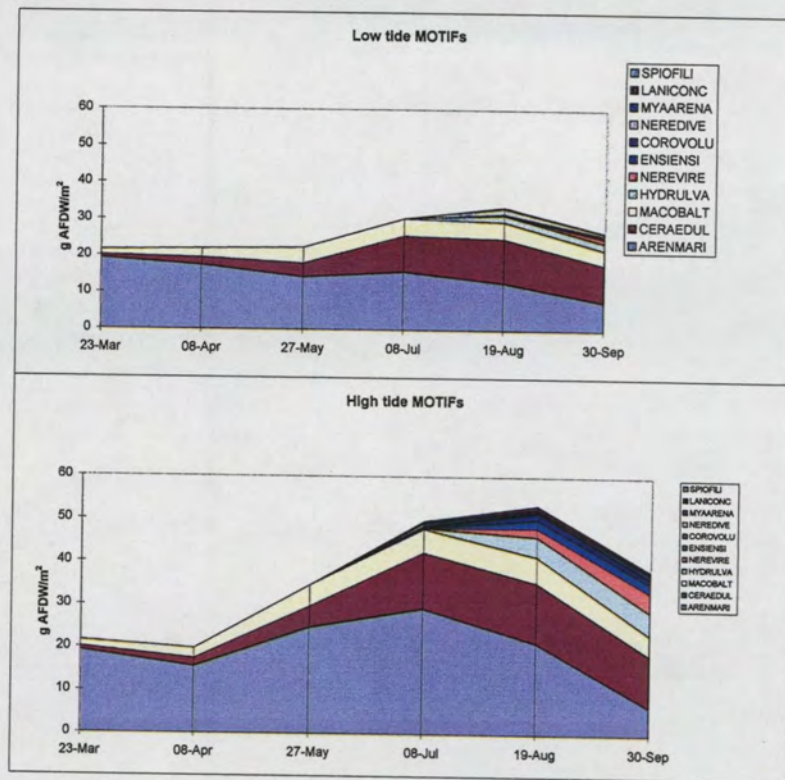


Fig. 7.7. Biomass of stocked and invaded macrobenthos species in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment

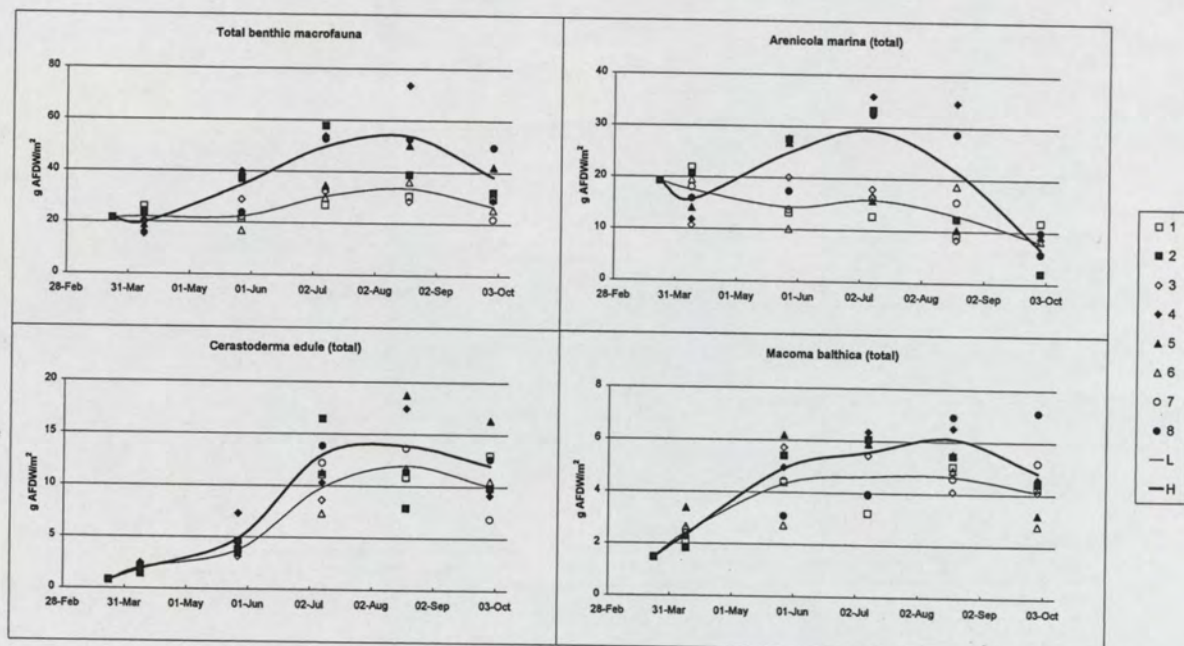


Fig. 7.8. Ash free dry weight (g AFDW/m²) of the three most important macrobenthos species in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment. High tide MOTIFs are represented by closed symbols and low tide MOTIFs by open symbols. The heavy and thin lines represent the averages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

Biomass/m²

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.

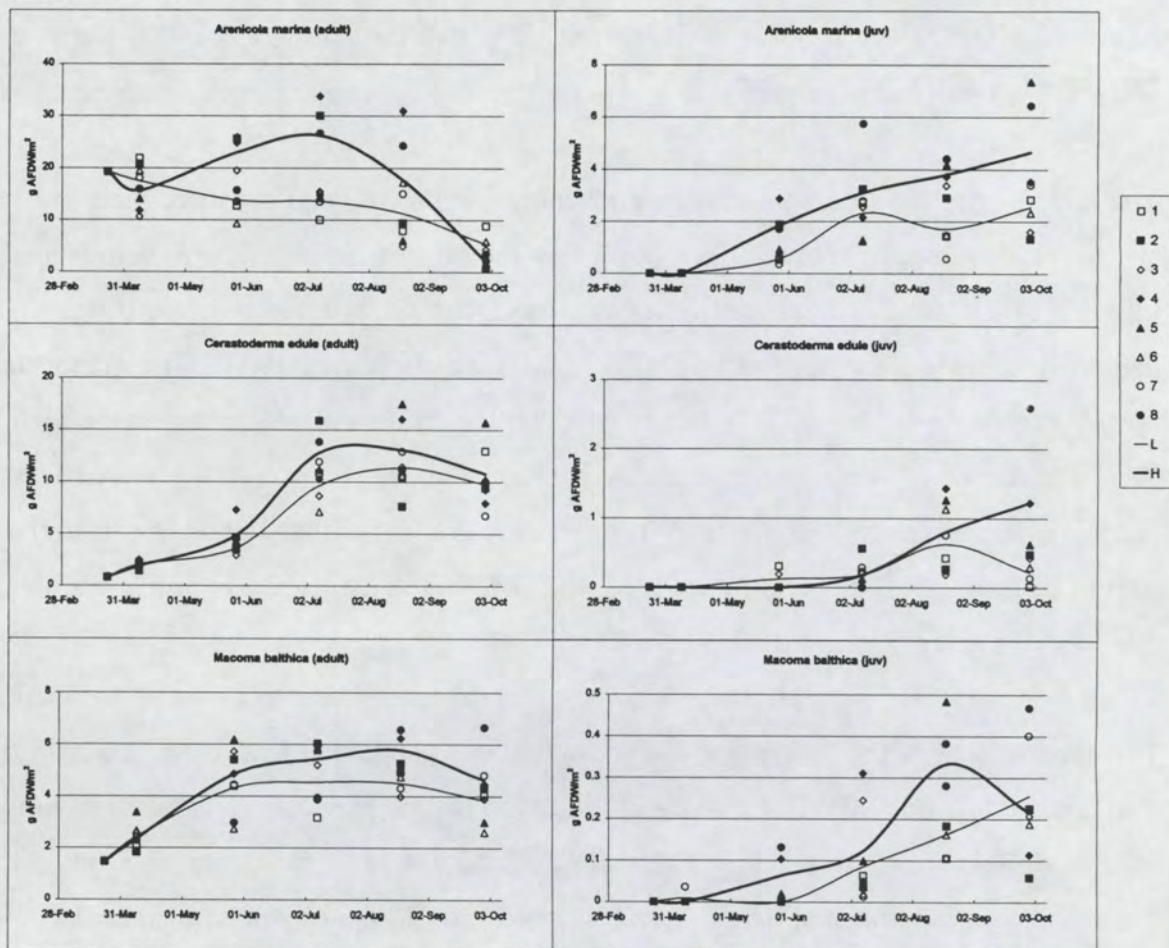


Fig. 7.9. Biomass (g AFDW/m²) of adult and juvenile stocked and invaded *Arenicola*, *Cerastoderma* and *Macoma* in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment. The heavy and thin lines represent the averages for high tide and low tide MOTIFs respectively

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

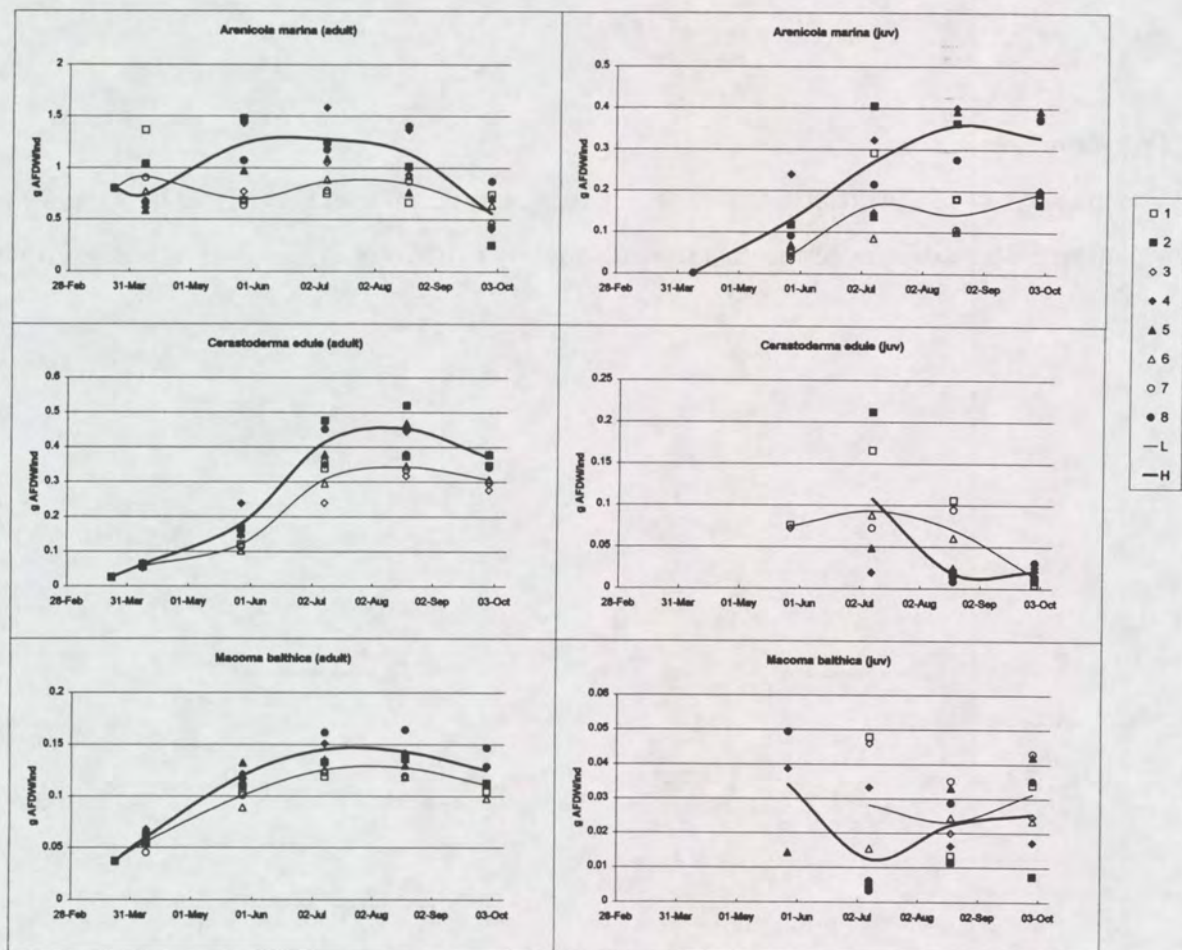


Fig. 7.10. Biomass (g AFDW/m²) of individual adult and juvenile *Arenicola*, *Cerastoderma* and *Macoma* in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment.

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 ($\text{AFDW}/\text{length}^3$, 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

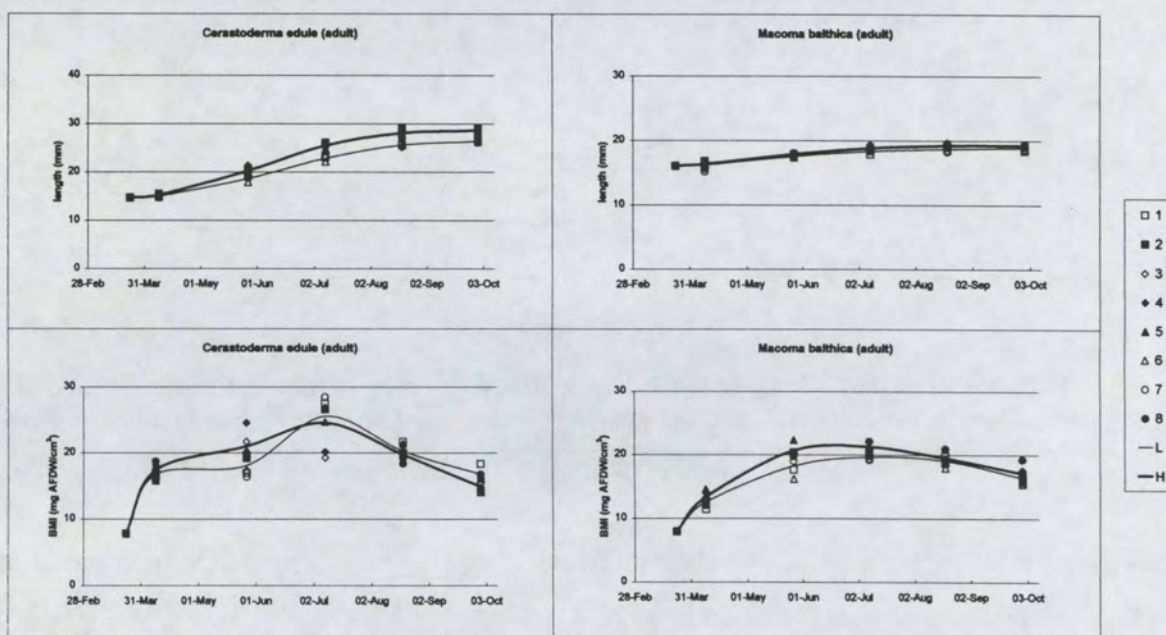


Fig. 7.11. Size (mm) and Body Size Index (AFDW/cm³) of individual adult *Cerastoderma* and *Macoma* in low tide and high tide MOTIFs in the course of the ExpSLR97 experiment

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/m² 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.

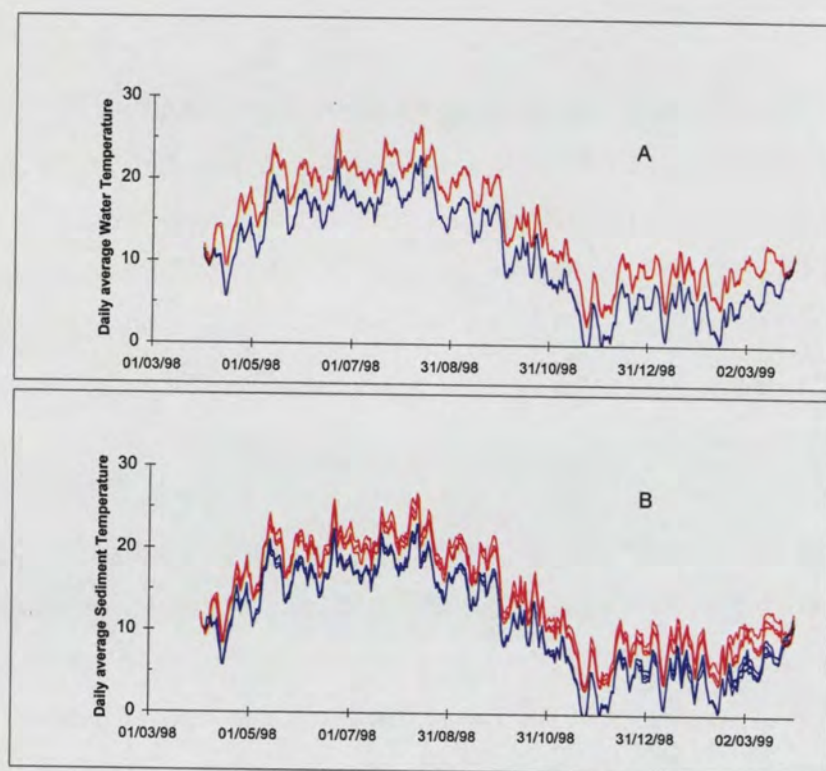


Fig. 7.12. Daily average temperatures in water (A) and sediment (B) in experimentally heated MOTIFs (upper lines) and control MOTIFs without heating (lower lines) in the course of the ExpTR98 experiment.

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/m²

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.

Table 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

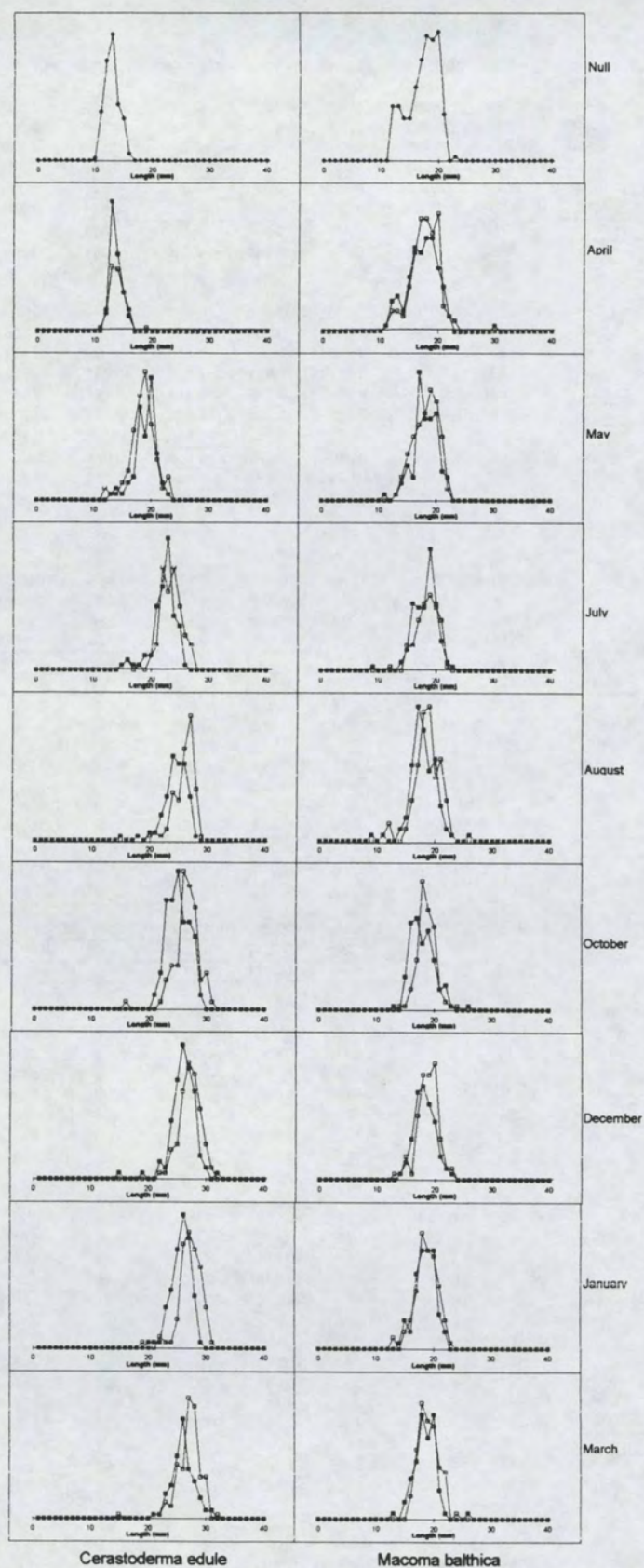


Fig. 7.13 Size distribution of *Cerastoderma edule* and *Macoma balthica* in the course of ExpTR98. High temperature MOTIFs are represented by closed symbols and control MOTIFs by open symbols.

Other species never became abundant during this experiment. In this respect this experiment (ExpTR98) differs from the previous experiment (ExpSLR97). The difference 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 temperature 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,

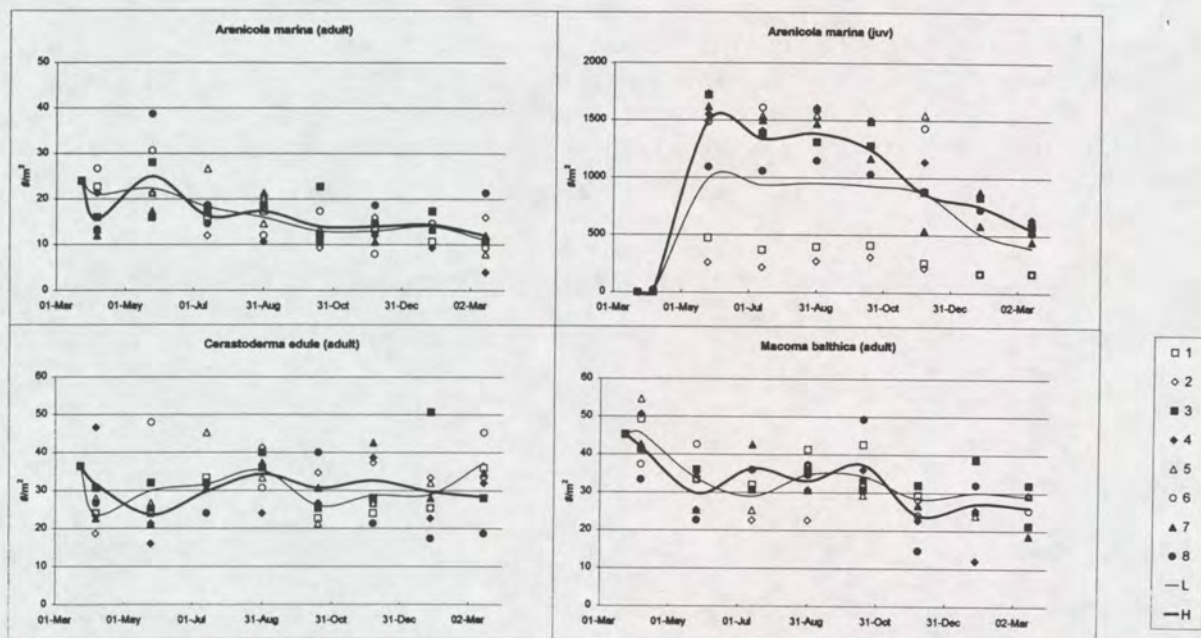


Fig. 7.14. The development of populations of adult (stocked) and juvenile (invaded) *Arenicola* and adult *Cerastoderma* and *Macoma* (n/m^2) in high temperature and control MOTIFs in the course of the ExpTR98 experiment. High temperature MOTIFs are represented by closed symbols, control MOTIFs by open symbols. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

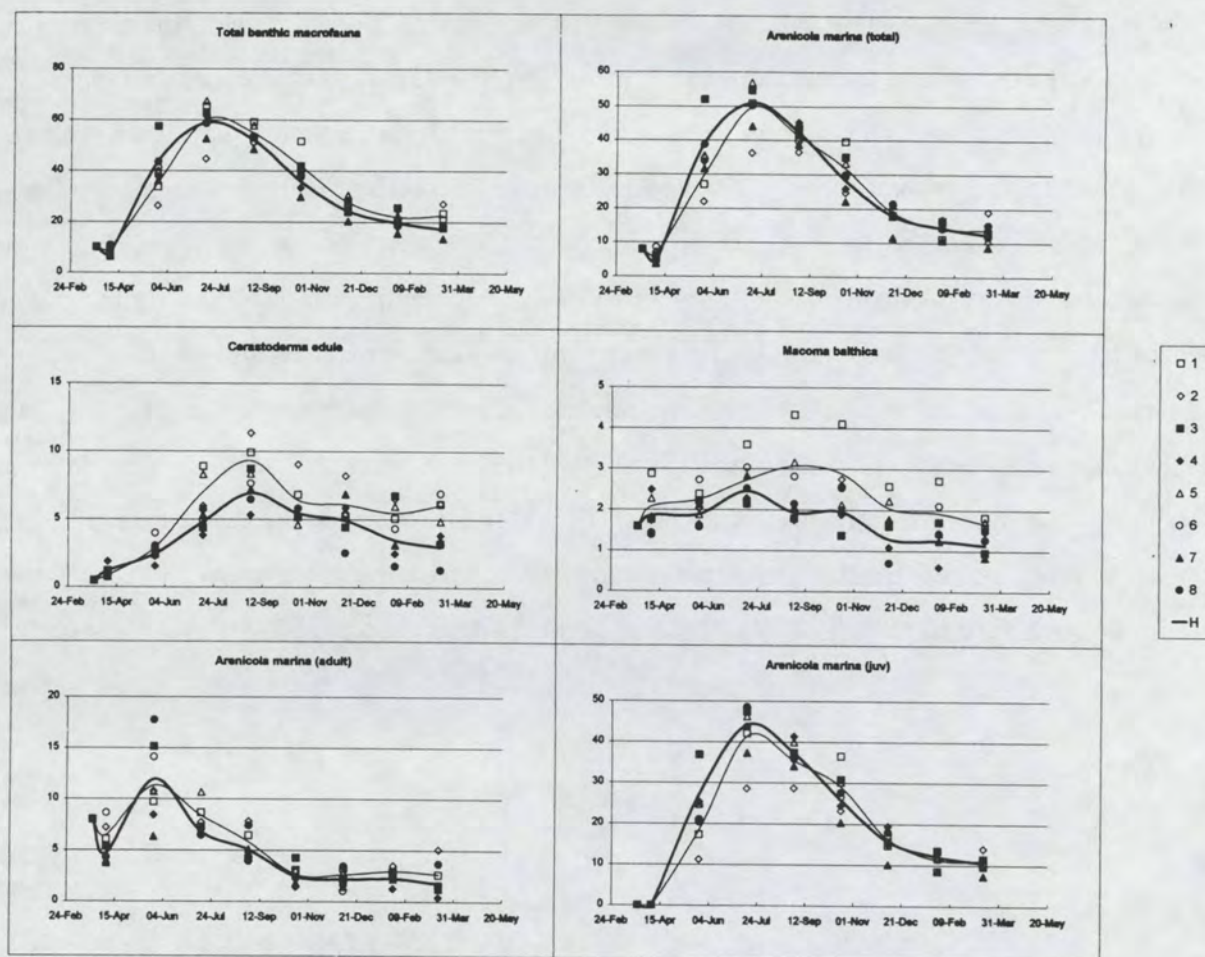


Fig. 7.15. Ash free dry weight (g AFDW/m²) of the total benthic macrofauna, adult and juvenile *Arenicola* (combined), *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. High temperature MOTIFs are represented by closed symbols, control MOTIFs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

The total benthic macrofauna biomass (Fig. 7.15) rapidly increased from 10 g AFDW/m² at the start of the experiment to 59 g AFDW/m² in July. Thereafter the biomass slowly decreased until 20 g AFDW/m² 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*

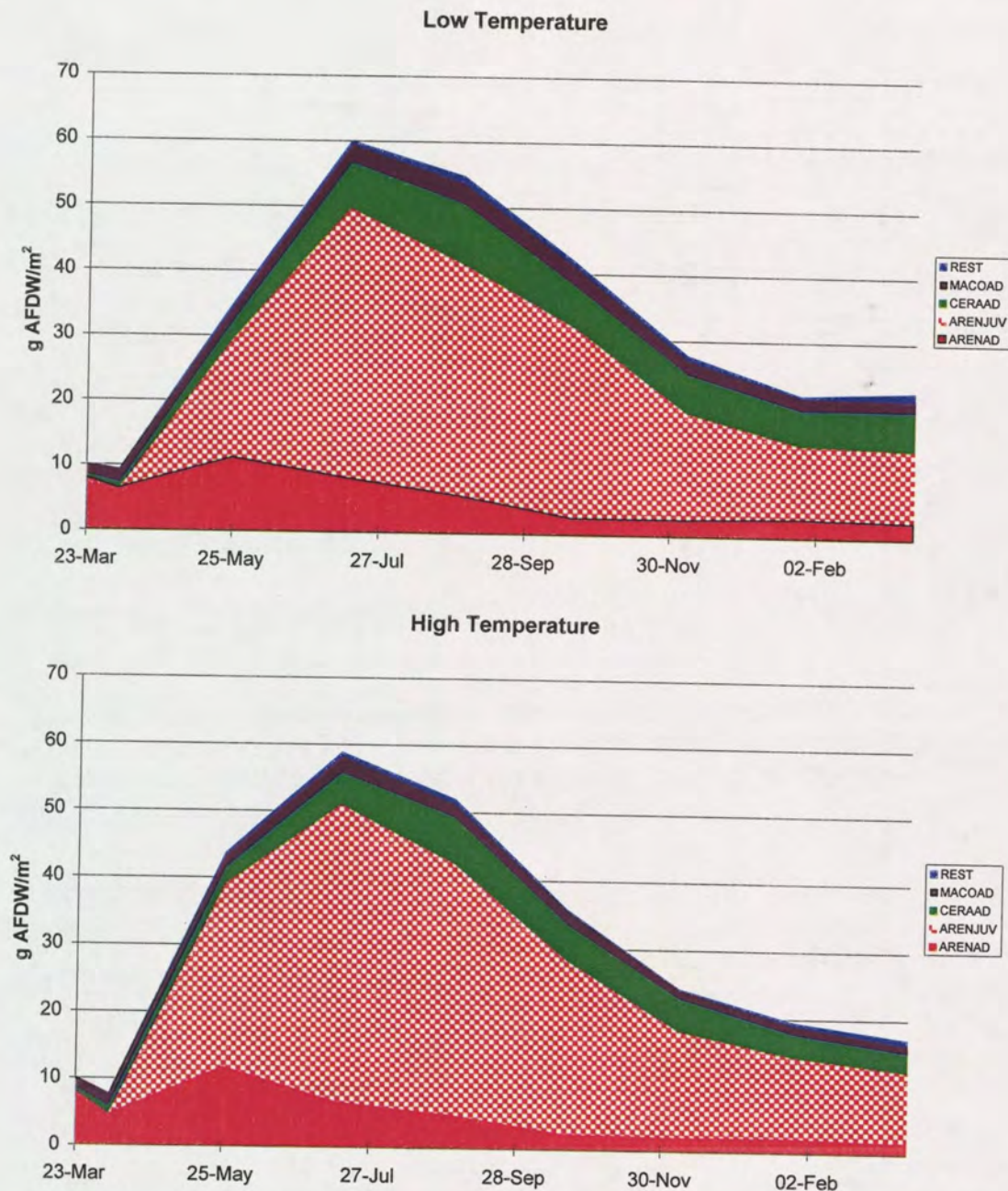


Fig. 7.16. Total biomass (in ash free dry weight, g AFDW/m²) of the total benthic macrofauna, mainly consisting of adult and juvenile *Arenicola*, *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment.

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

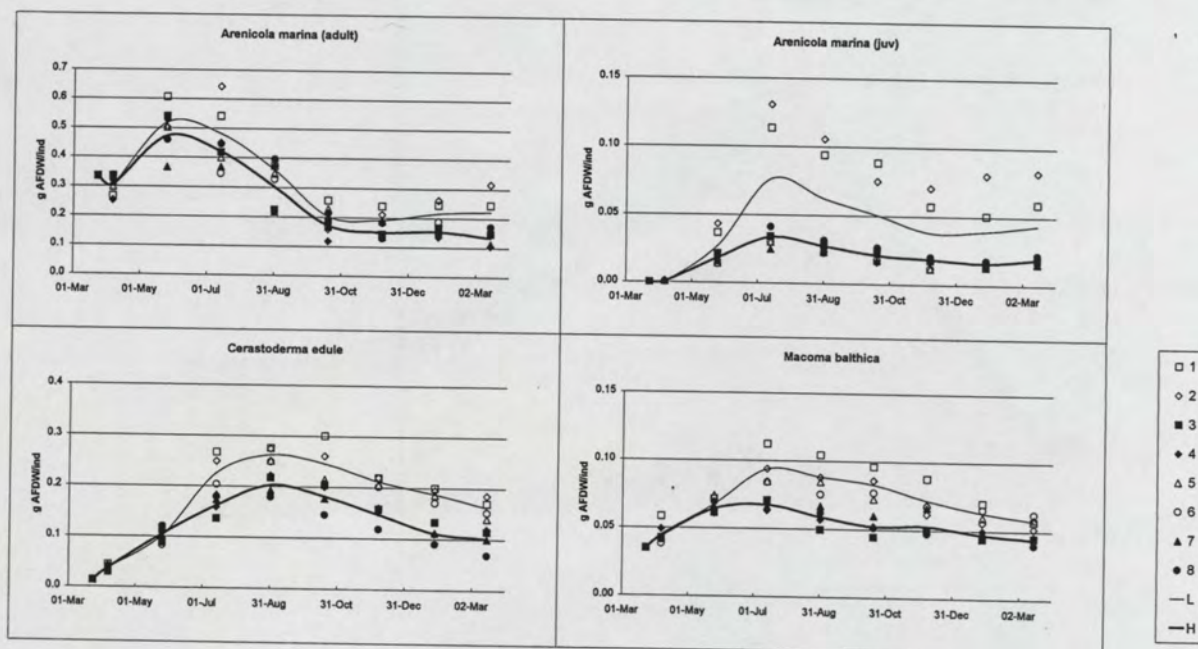


Fig. 7.17 Biomass (g AFDW/ind) of individual adult and juvenile *Arenicola*, *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

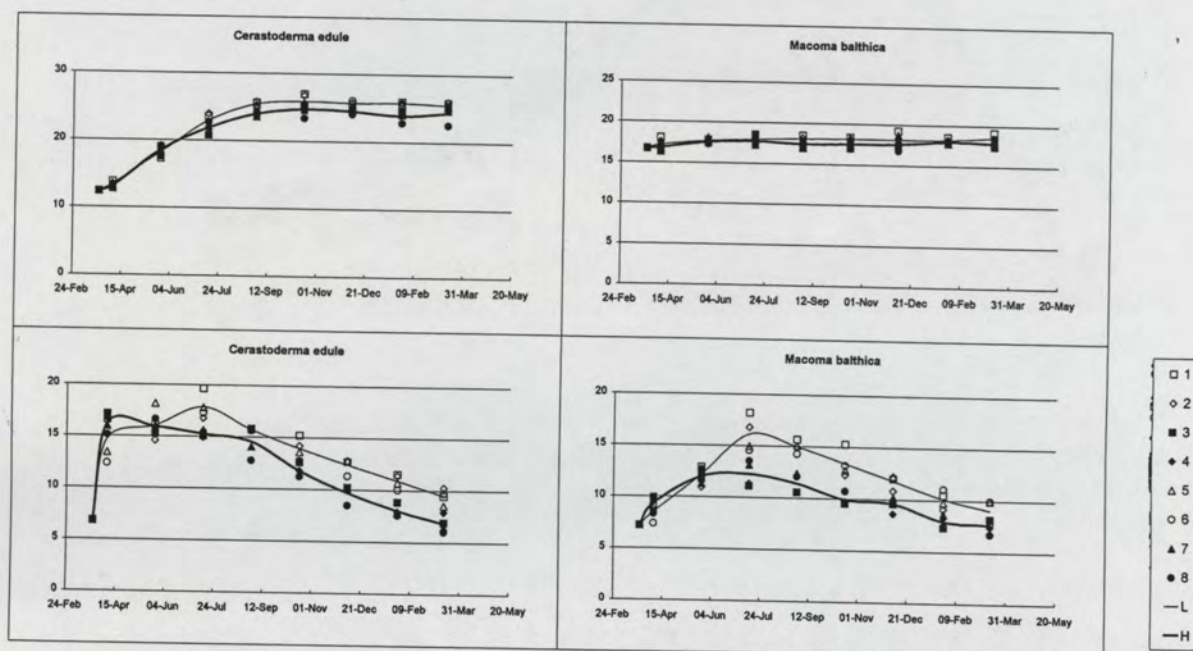


Fig. 7.18 Size (upper, mm) and Body Size Index (lower, AFDW/cm³) of individual adult *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. The heavy and thin lines represent averages for high temperature and control MOTIFs respectively

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

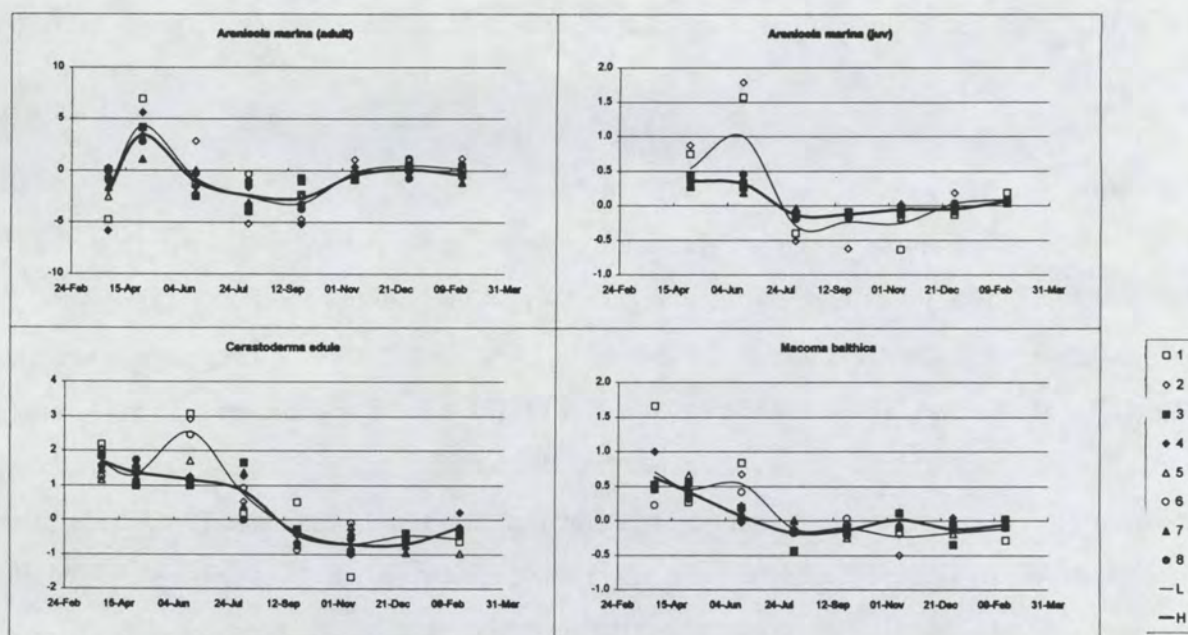


Fig. 7.19 Growth rates (expressed as ash free dry weight per individual) of adult and juvenile *Arenicola* and adult *Cerastoderma* and *Macoma* in high temperature and control MOTIFs in the course of the ExpTR98 experiment. The heavy and thin lines represent averages for high temperature and control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

Table 7.4 Summary of effects

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

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

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*.

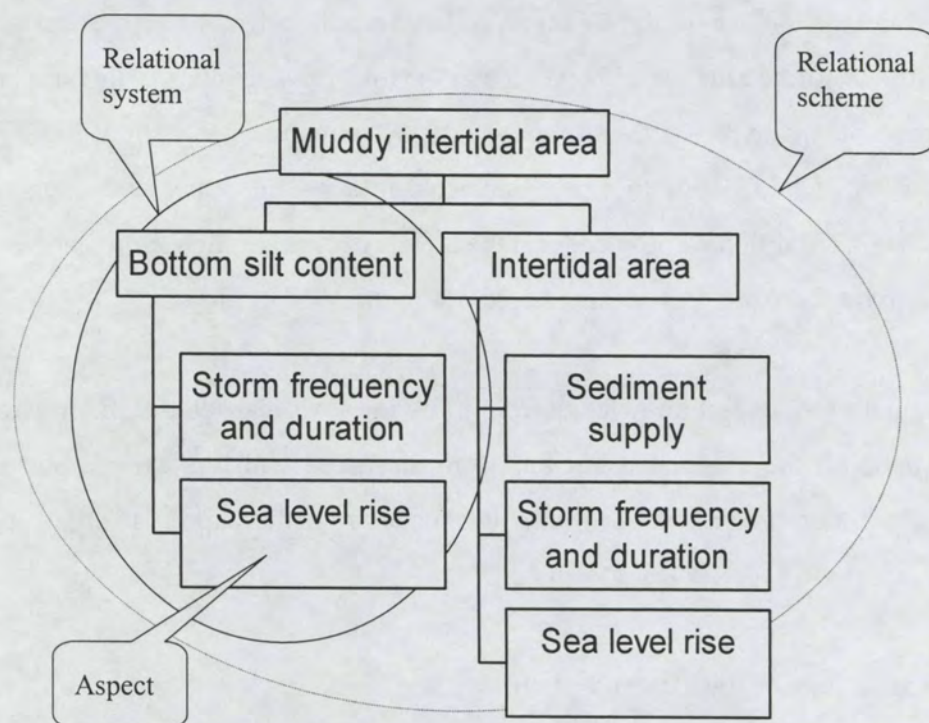


Figure 8.1. Elements in EcoFuzz.

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.

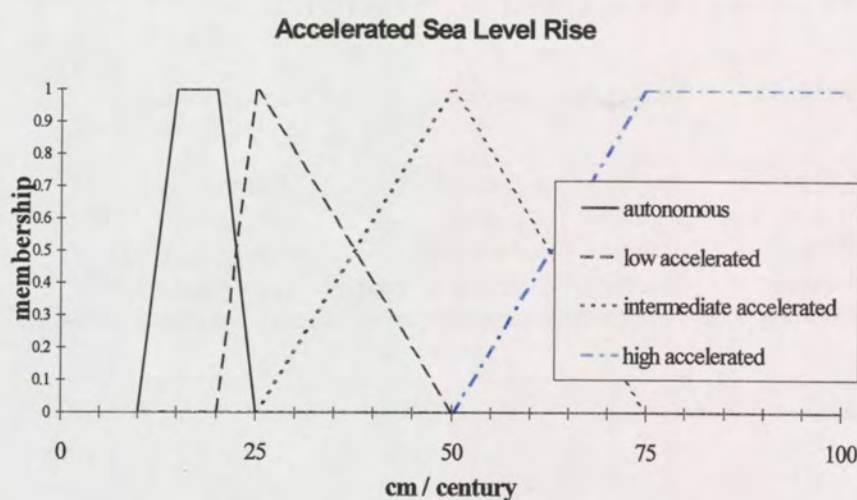


Figure 8.2. Membership functions for the aspect Accelerated Sea Level Rise.

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)				
Sea Level Rise (cm/century)	Storm Frequency and Duration (% change)			
	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*.

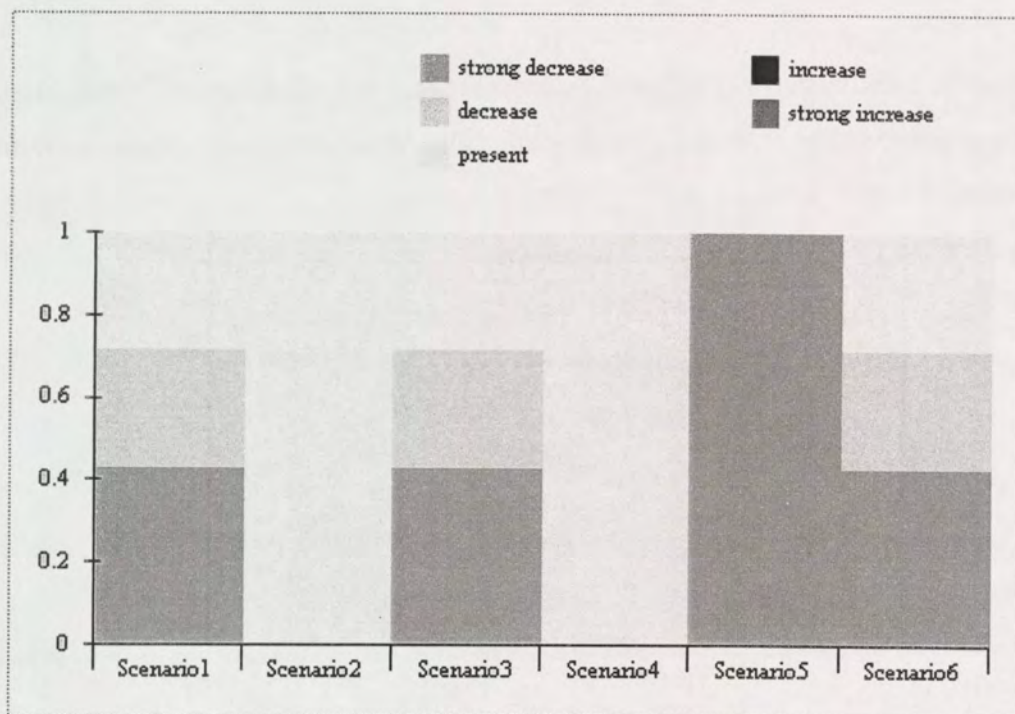


Figure 8.3. Fuzzy output for six scenarios of effects of climate change on relative change in the Muddy Intertidal Area.

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:

$$\text{strong decrease} = 0.6/1.4 = 0.4286;$$

$$\text{decrease} = 0.4/1.4 = 0.2857;$$

$$\text{present} = 0.4/1.4 = 0.2857.$$

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:

$$\text{strong decrease} = 0.4286;$$

$$\text{decrease} = 0.2857;$$

$$\text{present} = 0.2857.$$

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

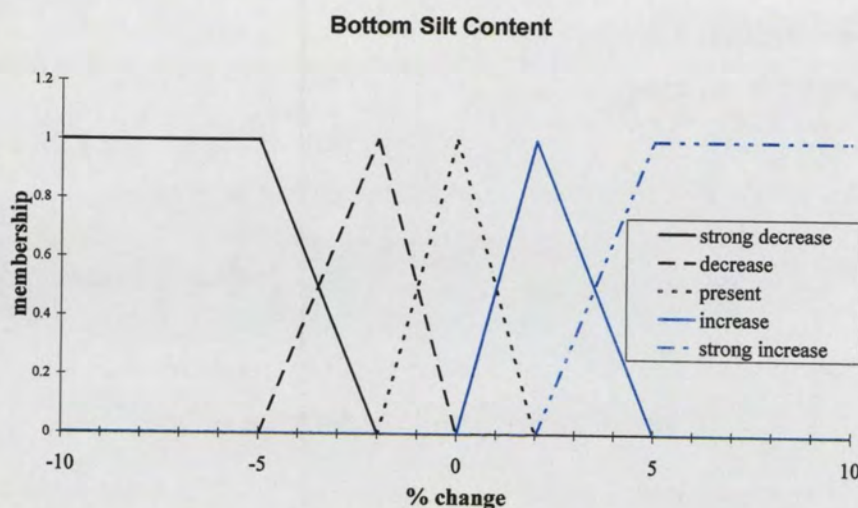


Figure 8.4. Membership functions for the aspect Muddy Intertidal Area.

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:

<i>strong decrease</i> :	-5%
<i>decrease</i> :	-2%
<i>present</i> :	0%
<i>increase</i> :	+2%
<i>strong increase</i> :	+5%

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

$$0.4286 \cdot -5 + 0.2857 \cdot -2 + 0.2857 \cdot 0 = -2.71\%.$$

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. Frasz 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; Ruurdij & 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 & Ruurdij, 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

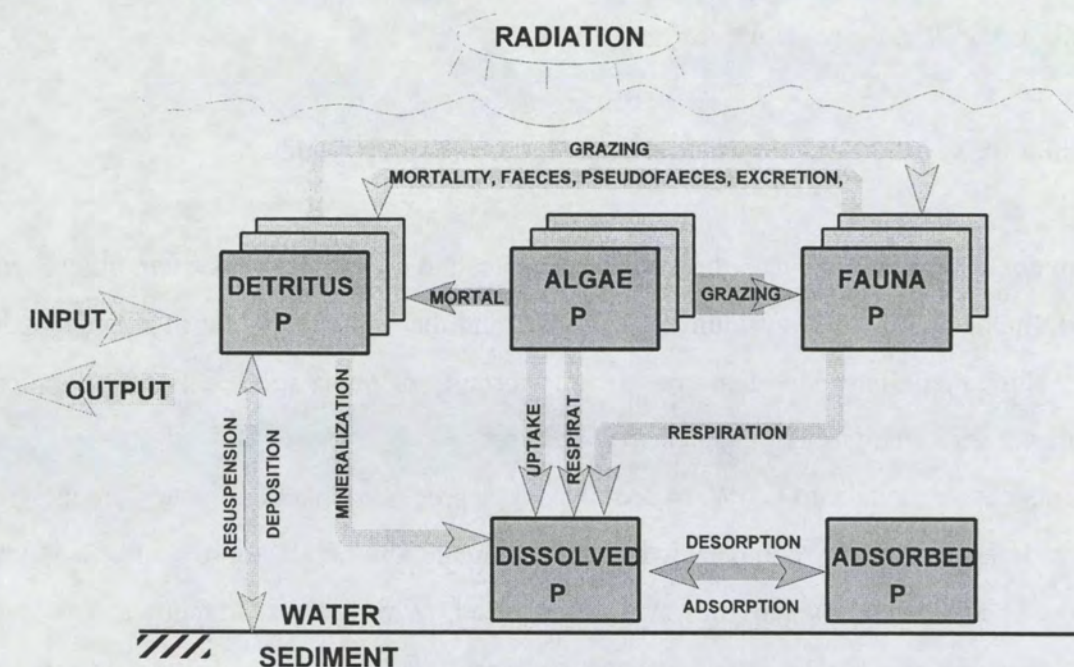


Fig. 9.1 Processes and state variables implemented in EcoWasp

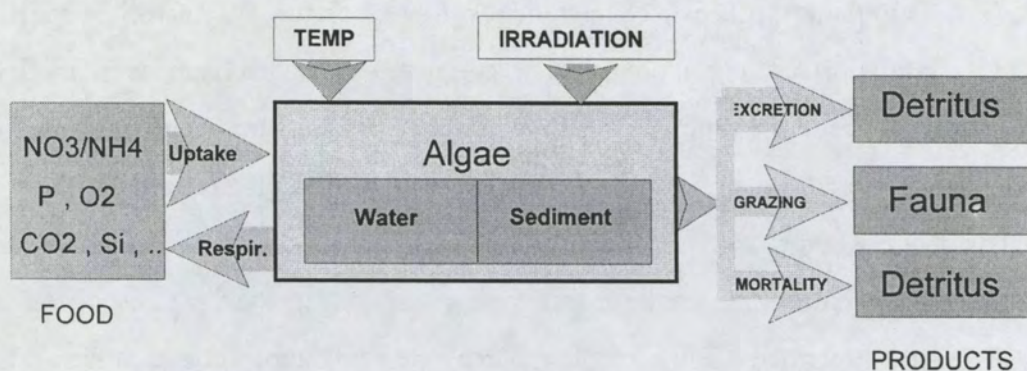


Fig. 9.2 Algae processes as implemented in the model

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

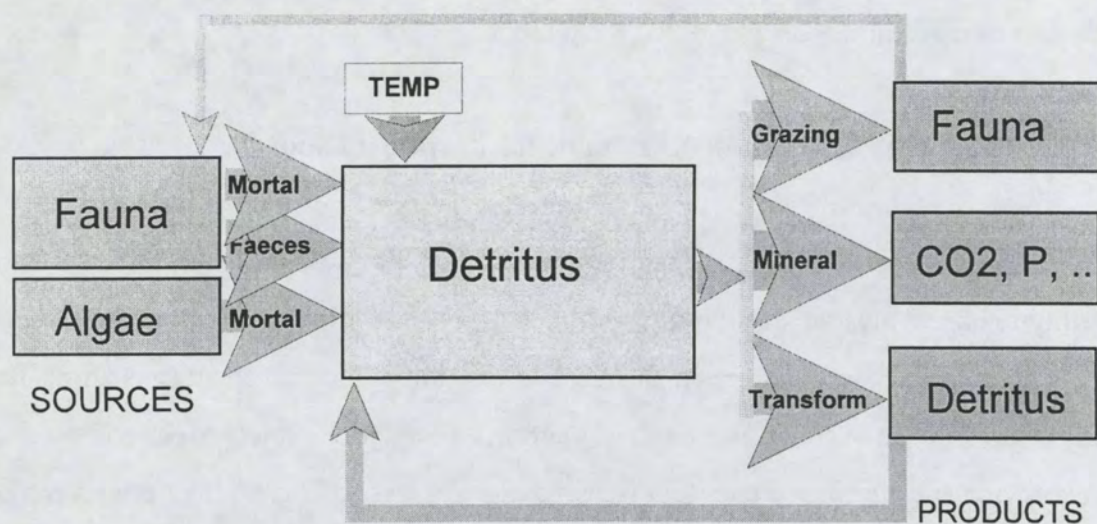


Fig. 9.3 Detritus processes in the EcoWasp ecosystem model

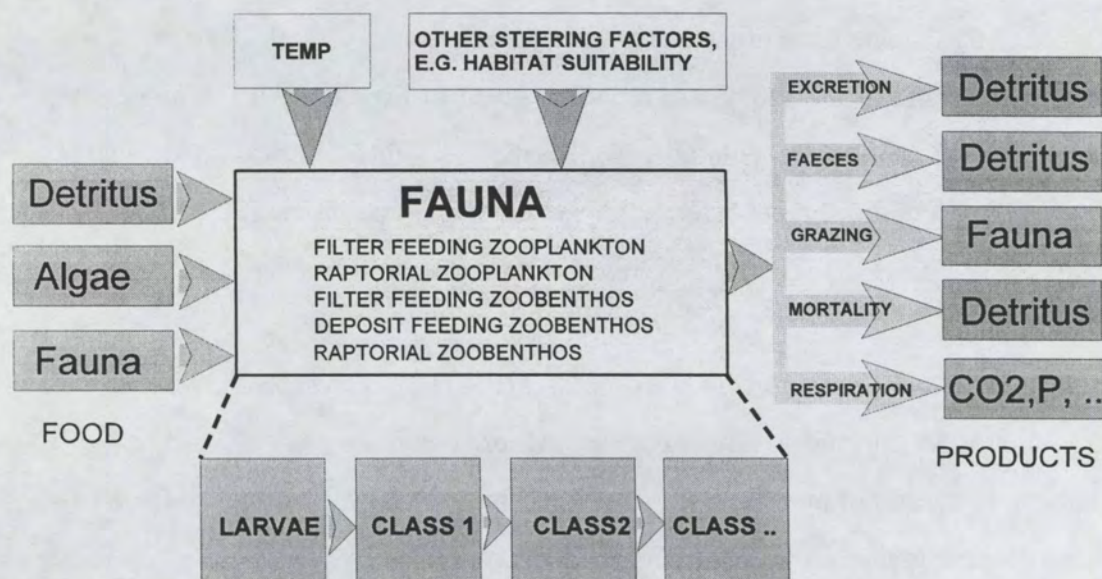


Fig. 9.4 Fauna processes implemented in EcoWasp

Algae

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

$$\frac{\partial \overline{Alg}_i}{\partial t} = \text{uptake} + \text{respiration} + \\ + \text{excretion} + \text{mortality} + \text{grazing} + \Sigma \text{input} - \Sigma \text{output} \quad (\text{g m}^{-3} \text{ d}^{-1}) \quad (9.1)$$

Each of these terms can be described in more detail.

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

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

where μ_{\max} is a first order uptake constant, and $F(\text{NUT})$, $F(T)$ and $F(\text{RAD})$ 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

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

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

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

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

Under oxygen availability, $F(\text{electron acceptor})$ 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

$$M_i = \overline{W}_i \cdot N_i \quad (\text{g m}^{-3}) \quad (9.6)$$

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

$$\frac{\partial \overline{W}_i}{\partial t} = \text{uptake} + \text{respiration} + \text{excretion} + \text{faeces} + \text{spawning}W \quad (\text{g DW} \cdot \text{ind}^{-1} \cdot \text{d}^{-1}) \quad (9.7)$$

and changes in numbers N from

$$\frac{\partial N_i}{\partial t} = \text{mortality} + \text{grazing} + \text{spawning}N \quad (\text{ind m}^{-3} \text{ s}^{-1}) \quad (9.8)$$

The conversion from the spawned biomass spawning W to spawned numbers Spawning N 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 $N \cdot dW/dt$ and $W \cdot dN/dt$, a $dW/dt \cdot dN/dt$ -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 respire, 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

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

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

Fauna (continued)

Each animal 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

$$\text{uptake rate} = \text{up}_{\max} \cdot F_6(\text{Food}) \cdot F_7(T) \cdot F_8(\overline{W}_i) \cdot \overline{W}_i \quad (\text{g DW ind}^{-1} \text{ d}^{-1}) \quad (9.9)$$

where up_{\max} is the maximum uptake rate constant. $F(\text{Food})$ 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:

$$\text{respiration} = \text{restrespiration} + \text{activityrespiration} \quad (\text{g DW ind}^{-1} \text{ d}^{-1}) \quad (9.10)$$

or:

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

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. $F(\text{activity})$ is nothing else than the space that an individual has searched for food per unit of time ($\text{m}^3 \text{ ind}^{-1} \text{ day}^{-1}$); 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 described following:

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

The change in numbers by mortality is described by

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

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 $F(\text{age, condition, mass})$ 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

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

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

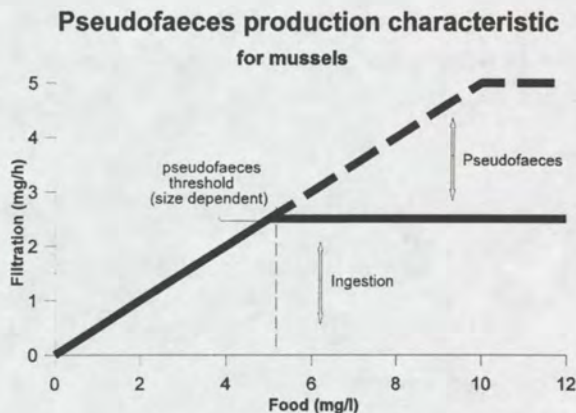


Fig. 9.5 Pseudofaeces production rules in the model

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

$$F(T) = \begin{cases} = \frac{(T-T_1)^2}{(T-T_2)^2 + (T-T_1)^2} & \text{if } T < T_2 \\ = \frac{(T-T_3)^2}{(T-T_2)^2 + (T-T_3)^2} & \text{if } T > T_2 \end{cases} ; \begin{cases} = 0 & \text{if } T < T_1 \vee T > T_3 \\ = 1 & \text{if } \begin{pmatrix} T_1 = T_2 \wedge T < T_2 \\ T_3 = T_2 \wedge T > T_2 \end{pmatrix} \end{cases} \quad (-) \quad (9.15)$$

where $F(T=T_2)=1.0$. For $T < T_1$ and $T > T_3$ $F(T)=0$. When $(T_2-T_1)=(T_3-T_2)$, then the function is symmetric around T_2 . 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 $T=T_2$

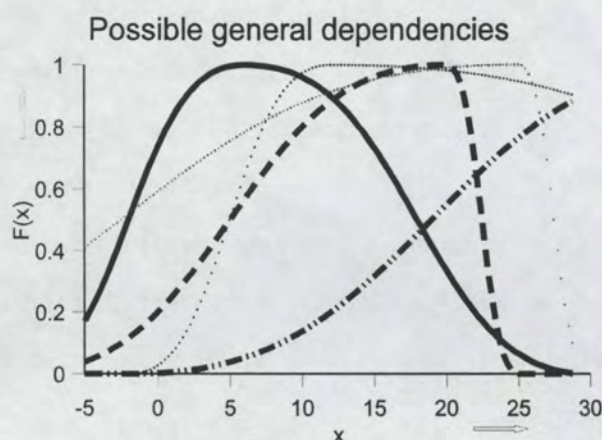


Fig. 9.6 Five different possibilities for a temperature dependency

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. The 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

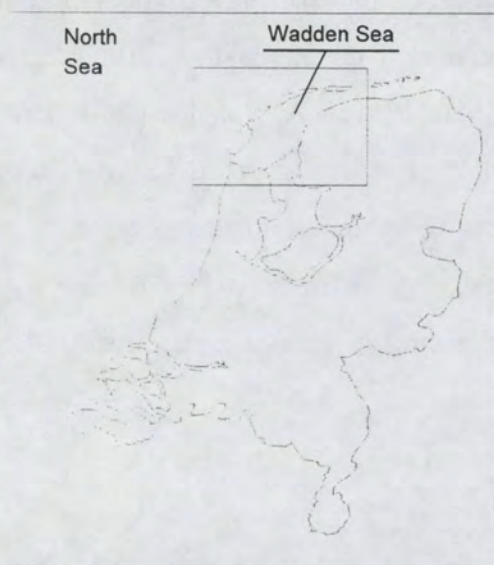


Fig. 9.7 Location of the Wadden Sea in the Netherlands

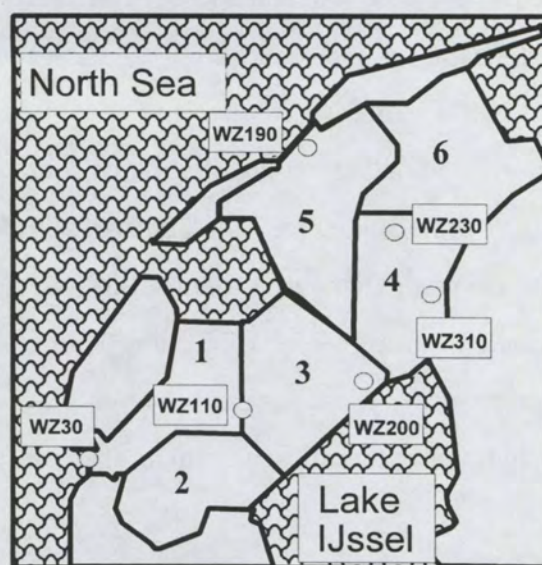


Fig. 9.8 Compartments and monitoring points in the western part of the Dutch Wadden Sea

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

Compartment	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 (m³) of compartments (at mean tidal level) from Fig. 9.8 and their sub-compartments.

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

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

compartment	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 $875 \text{ m}^3 \text{s}^{-1}$. 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 value of 60 ($\text{m}^3 \text{s}^{-1}$) 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

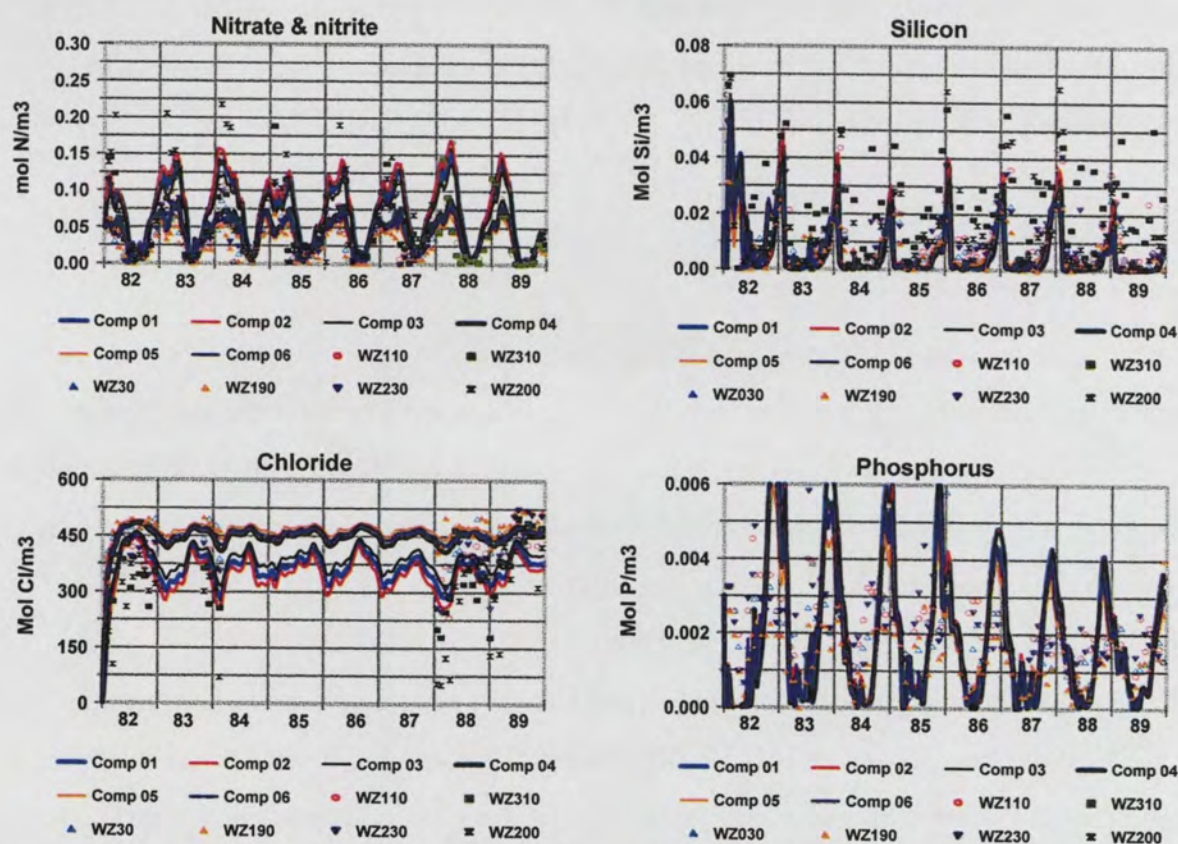


Fig. 9.9 Western Wadden Sea simulation results and measurements for compartments 1-6. The water bodies of the tidal flat, subtidal and channel sub-compartments are mixed up.

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 in 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

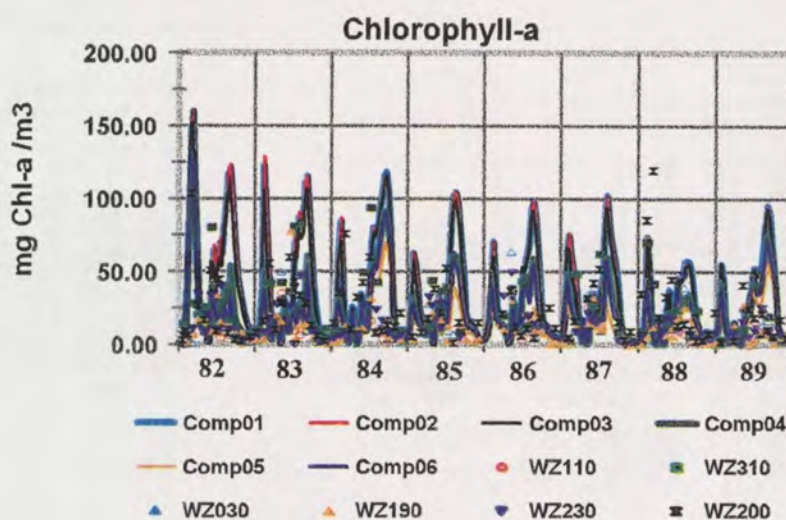


Fig. 9.10 Chlorophyll-content. Simulation and RIKZ- monitoring data

higher chlorophyll-a data than 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

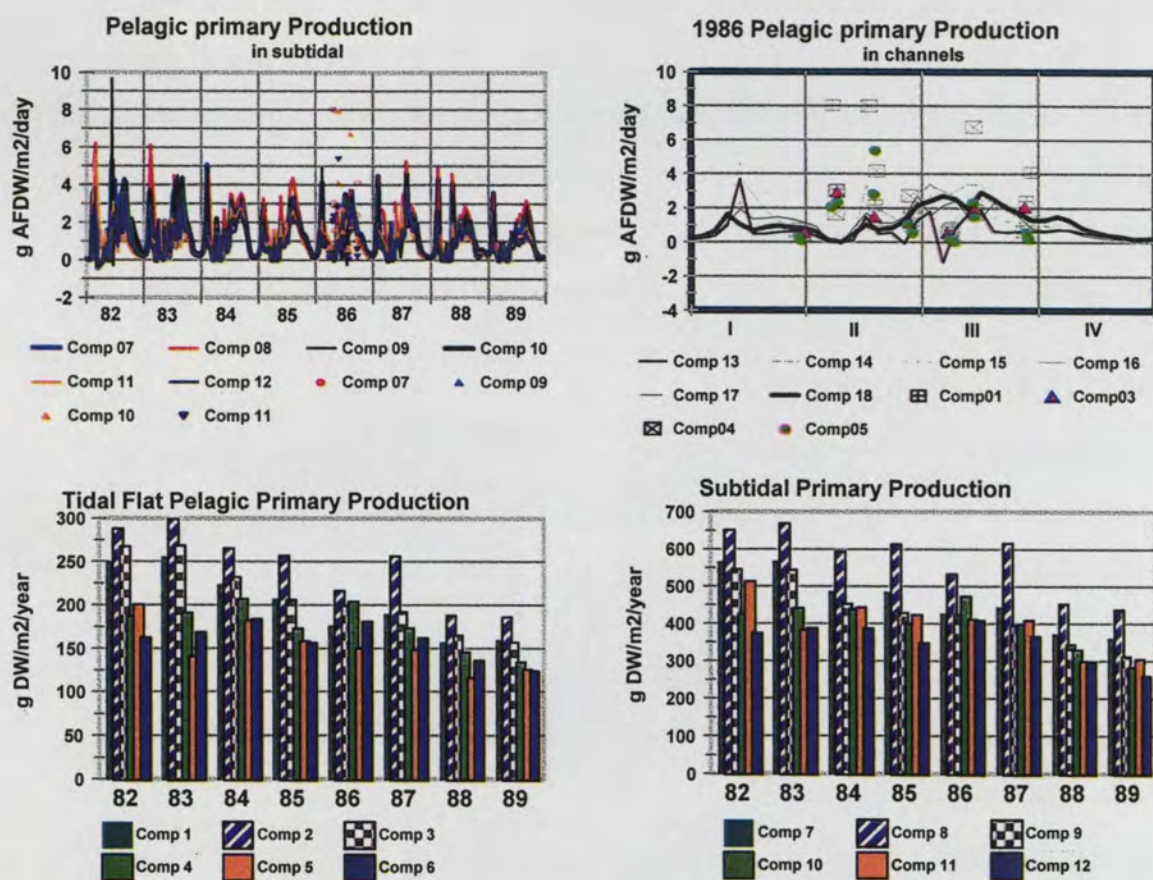


Fig. 9.11 Primary production simulated, and measured (1986 only, EON-I,II)

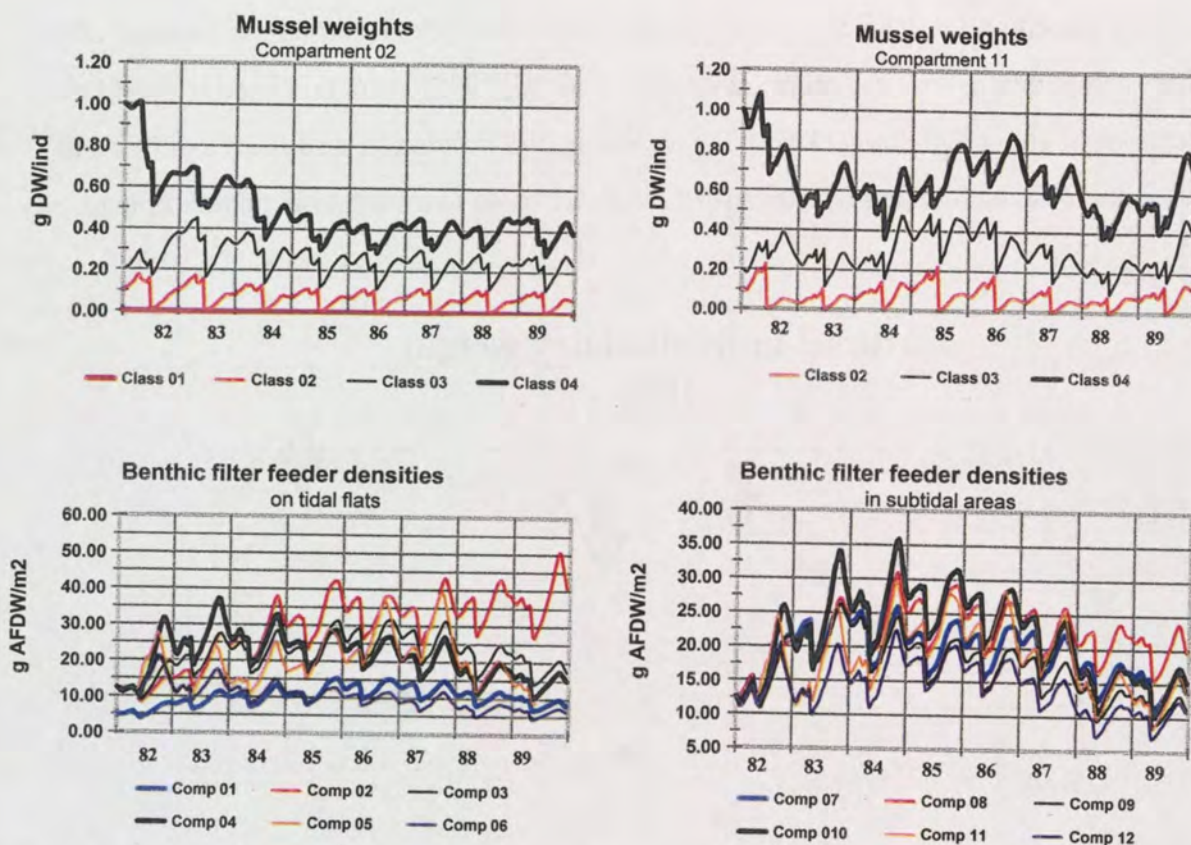


Fig. 9.12 Mussel weight development and mussel biomass densities on tidal flats and in the subtidal. Compartment 2 = flat; 11 = subtidal

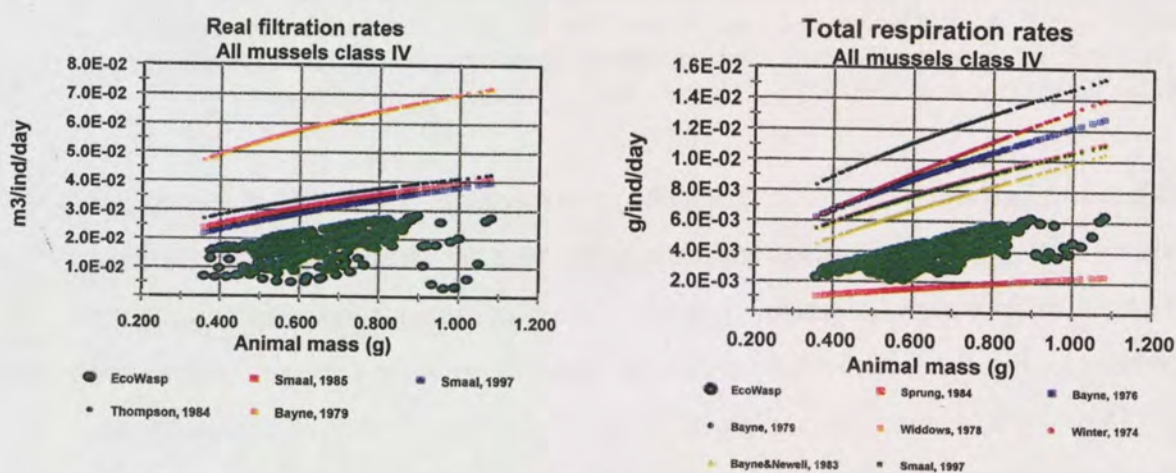


Fig. 9.13 Computed and measured filtration and respiration rates for filter feeders (mussels). Measurements are from laboratory experiments

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),

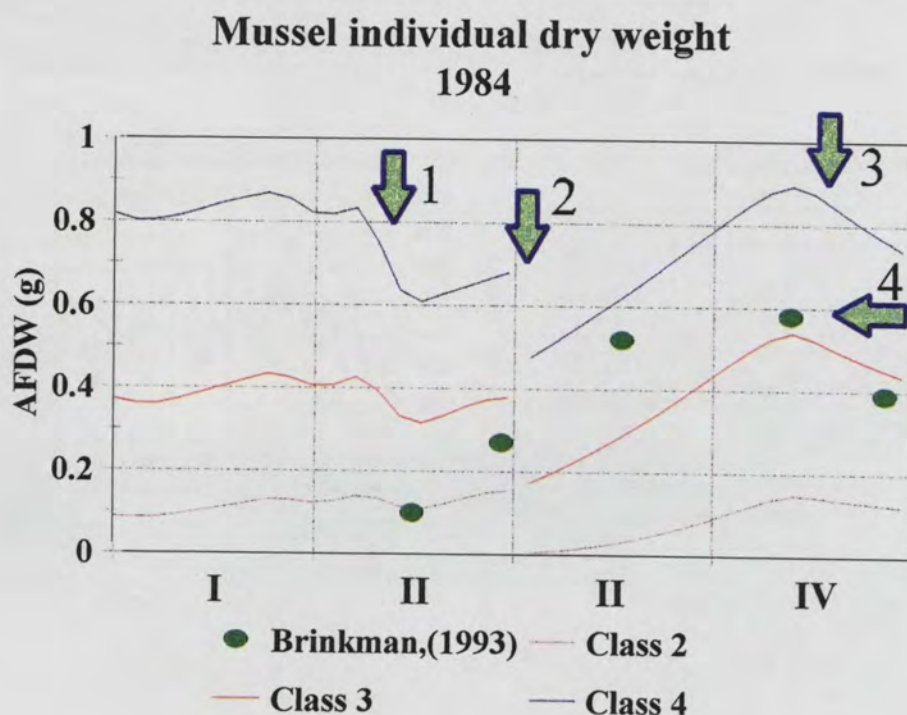


Fig. 9.14. Observed (dots) and computed mussel weight development in one year (1984). At time 1, reproduction takes place, causing weight decrease. At time 2, larvae settle, and cause a shift from class 1 to 2, etc. At time 3, the winter period starts, causing a slowly decreasing weight. This development 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

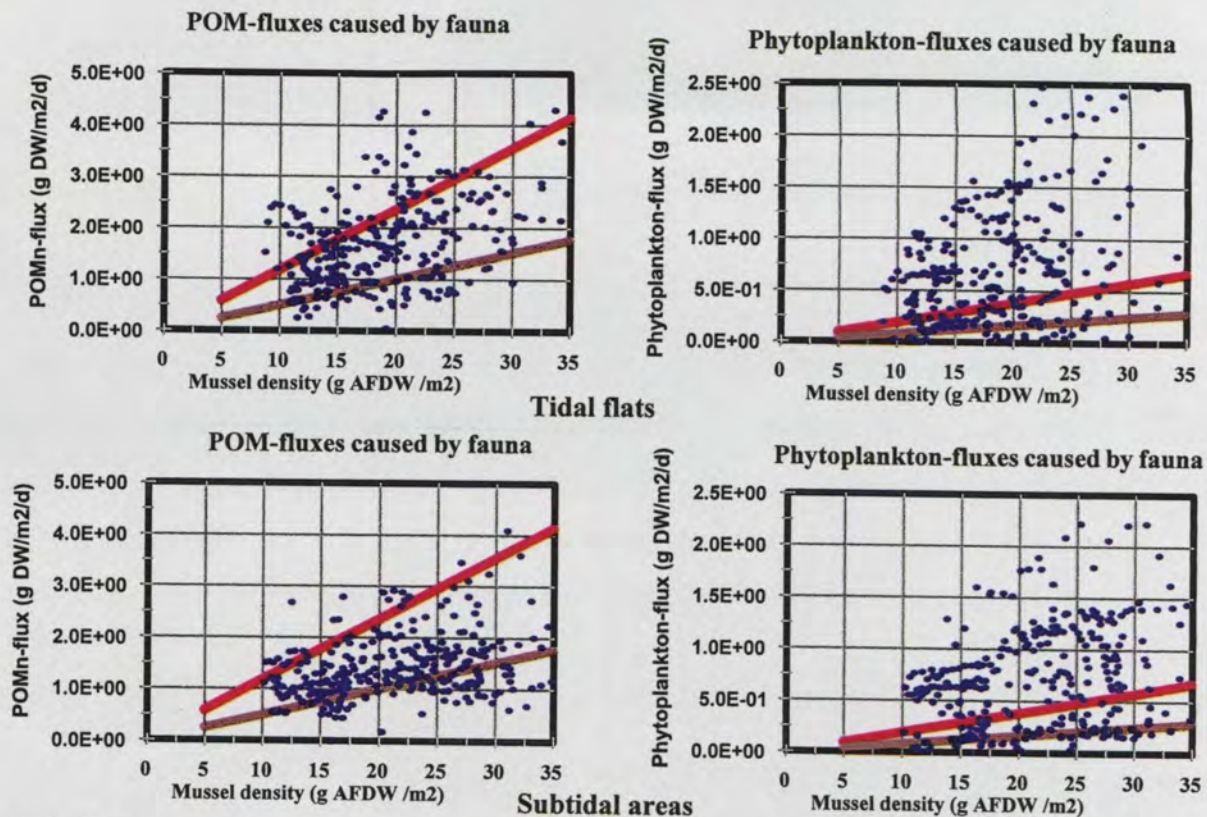


Fig. 9.15. Computed EcoWasp- filtration rates (dots) and measured filtration rates above a mussel beds (Asmus & Asmus, 1997). Red = maximum value, brown = minimum value. Field data have been extrapolated using average filter feeder densities in the Asmus-measurements.

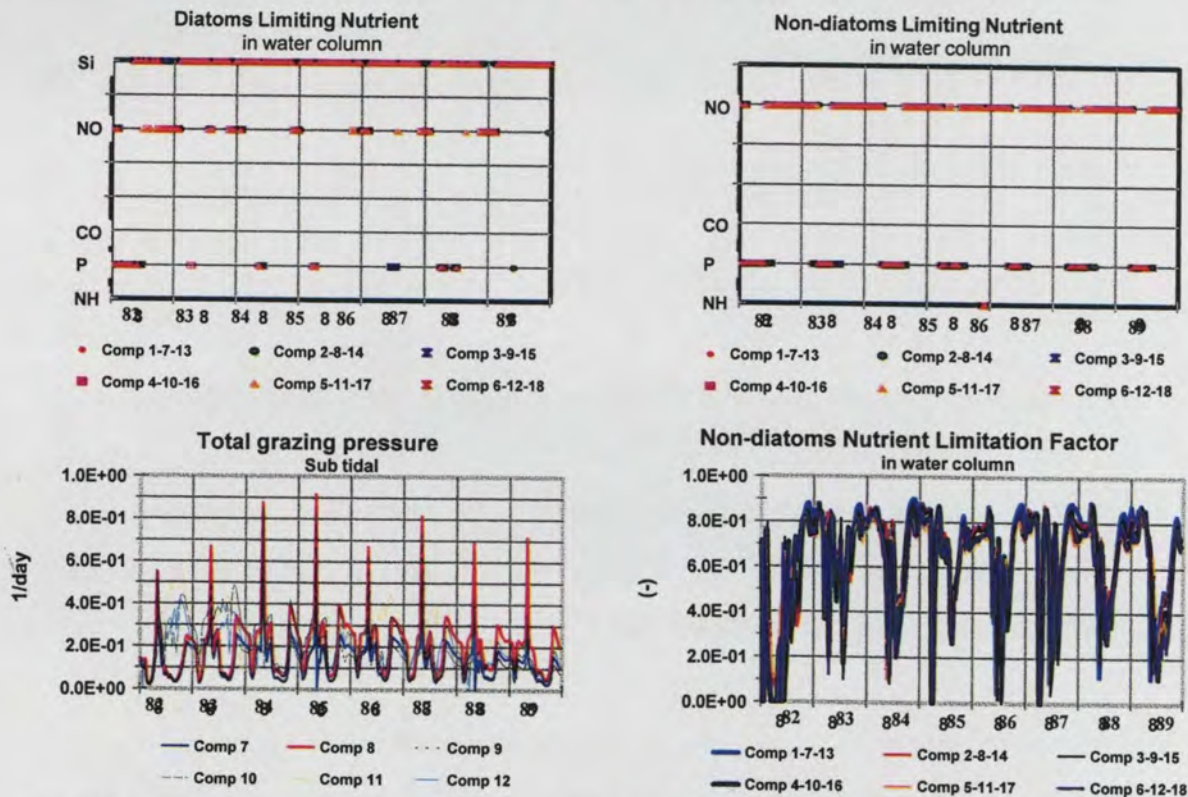


Fig. 9.16. Limiting nutrients, grazing pressure and non-diatoms nutrient growth limitation factor as computed by the basic EcoWasp-simulation

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.

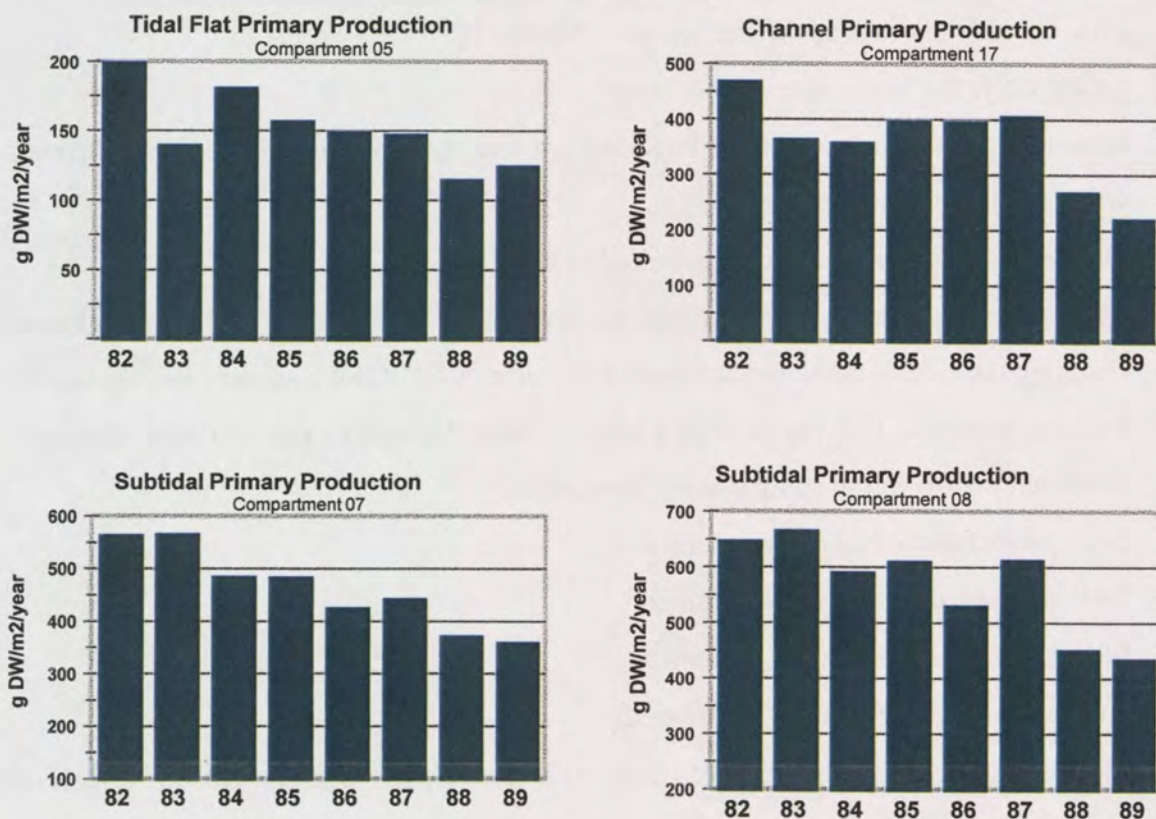


Fig. 9.17. Computed total primary production in a tidal flat compartment, a channel compartment, and two sub-tidal compartments.

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.

– 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 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

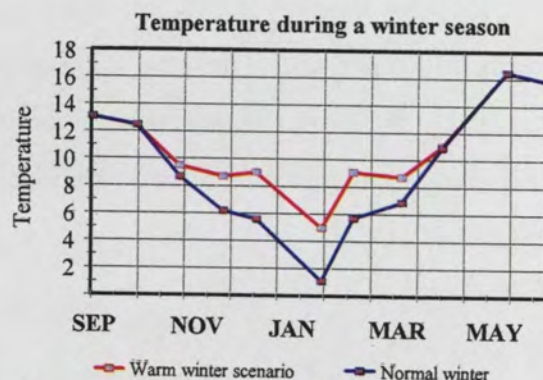


Fig. 9.18. Temperature differences between normal and warm winter, in temperature scenario tw4

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.

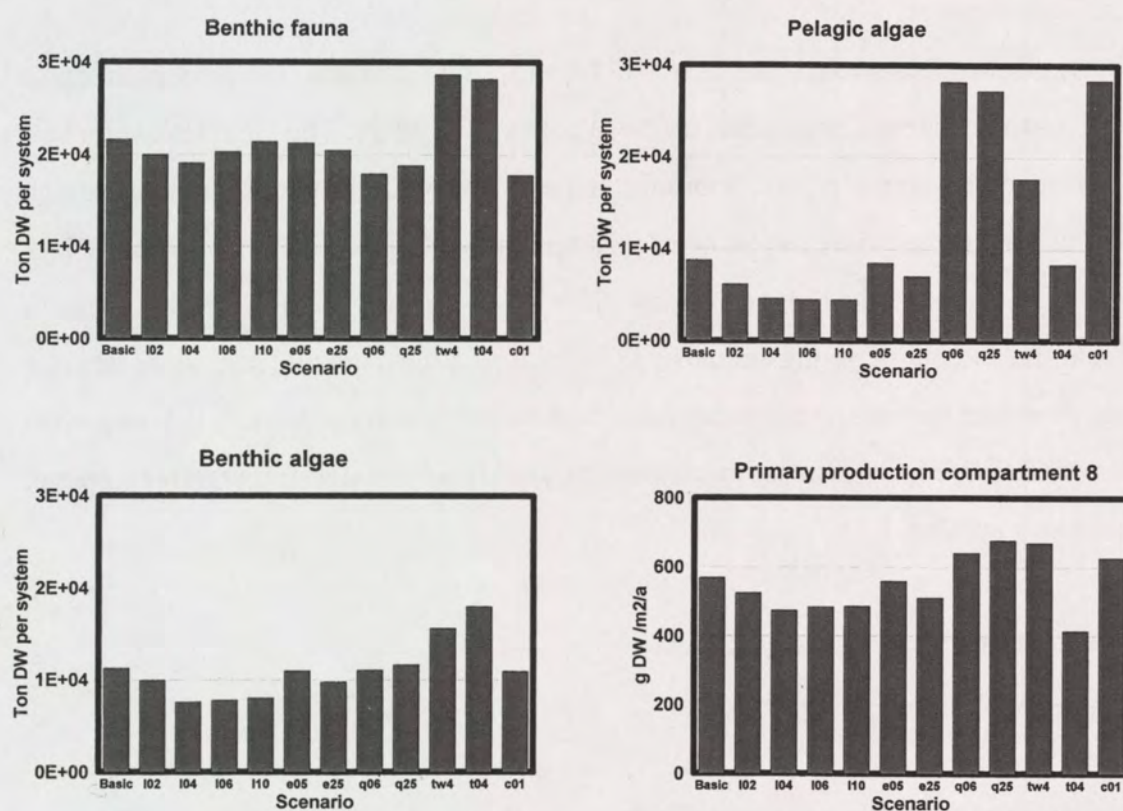


Fig. 9.19 Benthic fauna, pelagic and benthic algae plus primary production for the basic computations and the 11 scenarios 8-year averages

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.

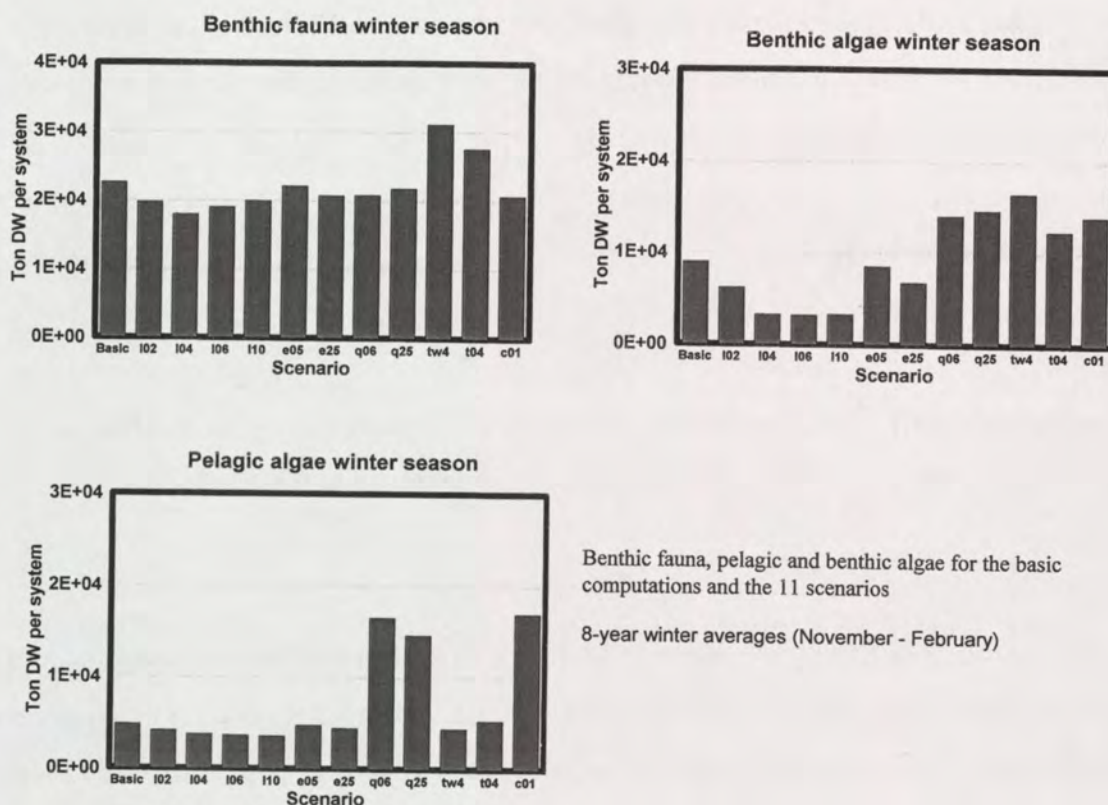


Fig. 9.20 Simulation results for winter season (Nov-Feb) averages,

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 than 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.

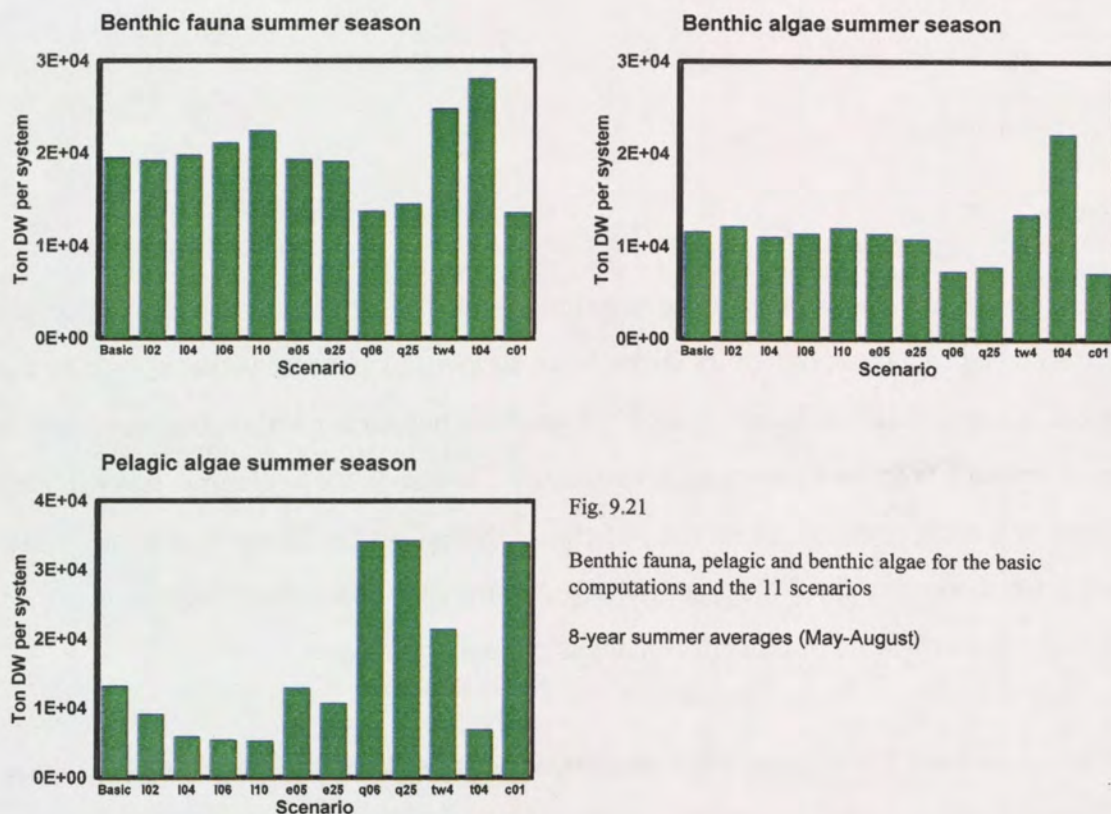


Fig. 9.21

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.

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.

H Asmus and R. Asmus (Alfred Wegener Institut für Polar- und Meeresforschung, List/Sylt) made data from their field experiments available.

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 $2 \text{ g DW m}^{-2} \text{ d}^{-1}$ for detrital matter and up to $10 \text{ g DW m}^{-2} \text{ d}^{-1}$ for solids. This is $700 - 3500 \text{ g DW m}^{-2} \text{ a}^{-1}$, respectively. This is, with an average solids density of about $1.5 - 2.0 \cdot 10^3 \text{ kg DW m}^{-3}$, an average biogenic sedimentation of $0.5 - 2.0 \text{ mm a}^{-1}$. 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.

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 applied 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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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.

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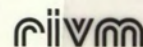
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