

8. Tidal Area



(Photo: K. Janke)

The Tidal Area covers all tidal flats (the littoral) and subtidal areas (the sublittoral). The seaward delimitation of the Tidal Area is formed by lines connecting the tips of the outer Wadden Sea islands. The landward delimitation is the pioneer zone of the salt marshes in front of the mainland, or, where salt marshes are not present, the mean high water level at spring tides. In estuaries, the upper limit is formed by the mean 10 psu isohaline at high water in the winter situation.

8.1 Hydrology – Geomorphology

Karel Essink



North Frisian islands,
Halligen and sand banks
(Satellite image:
Brockmann Consult).

8.1.1 Introduction

The Tidal Area and the Offshore Area form a coherent system. There is intensive water exchange through the tidal inlets between the islands. Sea level rise causes sand to be transported from the foreshore of the islands and the seabed in the Offshore Area to the Wadden Sea (see chapter 3 'Climate'). Since historic times this has caused the islands to migrate in the direction of the mainland. Before the mainland coast was fixed by dikes, the coastline reacted to such sea level rise by receding. Since dike building started, the Wadden Sea was progressively squeezed between these fixed sea dikes and the landward migrating islands (e.g., Flemming and Davis, 1994; Mai and Bartholomä, 2000).

Target

An increased area of geomorphologically and biologically undisturbed tidal flats and subtidal areas.

In the 1999 QSR the effects of this coastal squeeze on the geomorphology of the Wadden Sea were not described, notwithstanding two directly related Targets. Furthermore, continued deepening of shipping channels in estuaries may lead to hydrological and geomorphological changes. Little has been documented so far for the estuaries in the Wadden Sea.

8.1.2 Coastal squeeze

The most important cause of coastal squeeze in the Wadden Sea, undoubtedly, is the long-term

land reclamation by successive endikement of salt marshes and embayments. The historic loss of salt marshes since 1600 in the Dutch Wadden Sea was documented by Dijkema (1987). Reconstructions of historic coastlines of the Niedersachsen Wadden Sea show that 58% of potentially available tidal mud flats have disappeared (Delafontaine *et al.*, 2000). Along the Dutch coast of the Wadden Sea even larger areas have been lost, compared to hardly any loss along the Danish coast because of the elevated Pleistocene grounds directly bordering the Wadden Sea (*cf.* Mai and Bartholomä, 2000). As the Wadden Sea between the mainland and the islands narrowed, concomitant changes occurred in sediment type distribution typically showing lower grain size close to the mainland coast as a consequence of settling velocity gradients over the tidal flats between island and mainland (Figure 9 in Mai and Bartholomä, 2000). In the course of sea level rise, especially after dike building and land reclamation had begun, these settling velocity gradients have changed, allowing less mud to be deposited near the mainland coast, resulting a general depletion of fine-grained material (Dellwig *et al.*, 2000). Continued sea level rise will lead to a further depletion of fine-grained sediment and organic matter, and may eventually lead to the complete disappearance of tidal flats (see the model in Flemming and Nyandwi, 1994).

These fine-grained, organically rich sediments are assumed to play an important role in the recruitment success of bivalves (see chapter 8.2).

As a combined result of sea level rise and man-

made fixing of the mainland coast by dikes and successive endikements and land reclamations, the space between the islands and the mainland coast has become narrower (coastal squeeze). This has resulted in loss of mud flats along the mainland coast, which are important as a settling habitat for juvenile bivalves.

This loss of fine-grained sediment is considered a deviation from the natural dynamics in geomorphology because it has been caused by progressive endikement and land reclamation. Moreover, there is a deviation from the targets 'natural dynamic situation' and 'increased area of geomorphologically undisturbed tidal flats'.

8.1.3 Tidal regime and geomorphology of estuaries

Deepening of tidal channels in estuaries to promote shipping to sea ports that are located at a distance from the mouth of the estuary causes hydraulic changes. High water levels tend to become higher, and low water levels to become lower, as shown for the Ems, Weser and Elbe by Jensen *et al.* (2003). Hydraulic changes, however, do not stand alone. Increased deepening of the shipping channels to the port of Antwerp (Belgium) has changed the geomorphology of the Western

Scheldt, causing significant losses of salt marsh, intertidal mudflats and shallow water, particularly in the eastern part (*e.g.*, Huys, 1995; Vroon *et al.*, 1997).

It is not fully known to what extent the progressive deepening of the estuaries of the Ems, Weser and Elbe has caused changes in the geomorphology similar to those described for the Western Scheldt.

Effects on the intertidal geomorphology in the Grådyb tidal basin of deepening the shipping channel to the harbour of Esbjerg by 4 m in 1993 have been very small and hardly measurable (Pejrup *et al.*, 1993).

8.1.4 Recommendations

- The changes in distribution of high mudflats should be followed more precisely, especially in areas with relatively recent land reclamations/endikements, because of their importance as settling habitat for juvenile bivalves.
- A study should be made to provide insight in the effects of progressive deepening by dredging on estuarine geomorphology and consequently on the ecological functions of estuaries in the Wadden Sea.

References

Delafontaine, M.T., Flemming, B.W. and Mai, S., 2000. The Wadden Sea squeeze as a cause of decreasing sedimentary organic loading. In: Flemming, B.W., Delafontaine, M.T. and Liebezeit, G. (Eds.). *Muddy coast dynamics and resource management*. Elsevier Science, pp. 273-286.

Dellwig, O., Hinrichs, J., Hild, A. and Brumsack, H.-J., 2000. Changing sedimentation in tidal flat sediments of the southern North Sea from the Holocene to present: a geochemical approach. *J. Sea. Res.* 44: 195-208.

Dijkema, K.S., 1987. Changes in salt-marsh area in the Netherlands Wadden Sea after 1600. In: Huiskes, A.H.L., Blom, C.W.P.M. and Rozema, J. (Eds.). *Vegetation between land and sea*. W. Junk. Publ., Dordrecht, pp. 42-49.

Flemming, B.W. and Davis, R.A., 1994. Holocene evolution, morphodynamics and sedimentology of the Spiekeroog barrier island system (southern North Sea). *Senckenberg maritima* 24: 117-155.

Flemming, B.W. and Nyandwi, N., 1994. Land reclamation as a cause of fine-grained sediment depletion in backbarrier tidal flats, southern North Sea. *Neth. J. Aquat. Ecol.* 28: 299-307.

Huys, S.W.E., 1995. Geomorphological development of the intertidal in the Westerschelde 1935-1989. Institute for Marine and Atmospheric Research, Utrecht. Report R 95-3 (in Dutch).

Jensen, J., Mudersbach, C. and Blasi, C., 2003. Hydrological changes in tidal estuaries due to natural and anthropogenic effects. In: *Proceedings of the 6th International MEDCOAST 2003 Conference*, Ravenna, Italy.

Mai, S. and Bartholomä, A., 2000. The missing mud flats of the Wadden Sea: a reconstruction of sediments and accommodation space lost in the wake of land reclamation. In: Flemming, B.W., Delafontaine, M.T. and Liebezeit, G., (Eds.). *Muddy coast dynamics and resource management*. Elsevier Science, pp. 257-272.

Pejrup, M., Jensen, A., Zyserman, J., Rønberg, J.K., Birklund, J., Rasmussen, E.K. and Bartholdy, J., 1993. Miljømessig vurdering af uddybning af Grådyb. *Konsekvensvurdering*. Dansk Hydraulisk Institut, Vandkvalitetsinstitutet og Geografisk Institut, Hørsholm.

Vroon, J., Storm, C., and Coosen, J., 1997. Westerschelde, stram of struis? Eindrapport van het Project Oostwest, een studie naar de beïnvloeding van fysische en verwante biologische patronen in een estuarium. National Institute for Coastal and Marine Management/RIKZ, Den Haag. Report RIKZ-97.023.

8.2 Macrozoobenthos

Karel Essink



(Photo: M. Stock)

8.2.1 Introduction

In the 1999 QSR, an account was given of the development of three immigrant bivalve species. An update on these and other introduced species is given in chapter 6 of this report.

Also in the 1999 QSR, an attempt was made to clarify the possible causes of long-term changes in total biomass of the intertidal macrozoobenthic community as measured at selected monitoring locations within the Wadden Sea. Severity of winter and eutrophic conditions were mentioned as major regulating factors. In addition, the possible negative effects of mechanized shellfish fisheries were briefly introduced. The present chapter presents an update based on TMAP monitoring data and recently published information. New data on immigrant species (e.g. *Ensis americanus*, *Marenzelleria* cf. *viridis*, *Crassostrea gigas*) is presented in chapter 6 'Introduced species'.

Target

An increased area of geomorphologically and biologically undisturbed tidal flats and subtidal areas.

No trilateral Target was developed with respect to macrozoobenthos of soft sediments in the Tidal Area of the Wadden Sea. However, the general Target of 'an increased area of geomorphologically and biologically undisturbed tidal flats and subtidal areas' applies.

8.2.2 Recruitment, distribution and winter character

During cold winters, higher proportions of young (~5 mm shell length) bivalve *Macoma balthica* migrate from high coastal flats to low and/or offshore areas than in mild winters. This phenomenon, documented as early as the 1980s, was reaffirmed by new evidence obtained in different parts of the Dutch Wadden Sea (Beukema and Dekker, 2003; Hiddink and Wolff, 2002). This causes a redistribution of *Macoma balthica* over the different depth zones of the Wadden Sea and the offshore area, and needs to be taken into account when analyzing long-term data sets of macrozoobenthos from stations either in the littoral or the sublittoral parts of the Wadden Sea.

Another effect of cold winters is that the reproduction success of bivalves in the subsequent summer is usually better than after mild winters. This already known phenomenon was further investigated, both experimentally and through analyzing long-term data sets (Beukema *et al.*, 2001; Philippart *et al.*, 2003; Strasser *et al.*, 2001, 2002). In *Macoma balthica*, mild winters cause low egg production. Survival of post-larvae during the first few months of benthic life, however, plays a more prominent role in the recruitment process (Beukema *et al.*, 1998). At the tidal flats of the Wadden Sea and other shallow coastal waters bivalve spat is eaten by both shrimps and shore crabs. This predation pressure substantially reduces numbers of bivalve spat (Flach, 2003; Hiddink *et al.*, 2002; Strasser, 2002). After a severe winter, predators

such as the shore crab may return to the Wadden Sea too late to effectively prey upon bivalve spat, thus enabling a good recruitment (Strasser and Günther, 2001). Recruitment failures in the cockle (*Cerastoderma edule*), sandgaper (*Mya arenaria*) and Baltic tellin (*Macoma balthica*) were more frequent during the last approximately 15 years, especially at lower intertidal levels, and were negatively correlated to the quantities of shrimps present at the time of settlement of bivalve post-larvae (Beukema and Dekker, 2005). Such a relationship was not found for recruitment at higher intertidal levels, where shrimp abundance is low.

This difference in recruitment success between lower and higher intertidal flats is explained mainly by differential predation pressure on post-larvae with these high flats serving as a refuge in years of high predator abundances, although at the same time the sediment at the lower flats tended to become coarser (Beukema and Dekker, 2004). As a consequence, the centers of distribution of the three bivalve species were found to shift to higher intertidal levels with muddier sediments. Such a change in distribution at a local scale (Balgzand, Groninger Wad) was found for cockle beds also on the scale of the entire Dutch Wadden Sea (Anon., 2003; Zwarts *et al.*, 2003). Changes in sediment composition may have been caused by the large scale disappearance of blue mussel beds (*Mytilus edulis*) from the intertidal flats of the Dutch Wadden Sea in 1990 due to a combination of prolonged recruitment failure and intensive shellfish fishery (Dankers *et al.*, 2003). Mussel beds cause increased contents of mud and organic matter in the surrounding sediments up to a distance of about one km (Kröncke, 1996; Zwarts, 2003). Intertidal mussel beds started to reappear in 1995, but are still largely absent from the western part of the Dutch Wadden Sea (Anon., 2003; Dankers *et al.*, 2003) making the most sandy sediments unsuitable for successful recruitment of cockles (Beukema and Dekker, 2004).

After a severe winter, recruitment success in three bivalve species was found to be different between the northern (north of Eiderstedt) and southern (west of the Jade Bay) Wadden Sea (Strasser *et al.*, 2002). These regional differences may be related to the different topography (orientation of islands and tidal inlets) and related differential effects of wind induced currents on bivalve recruitment, and/or to differences in parent stocks, larval supply or epibenthic predation.

In the shallow subtidal (10–20 m depth) of the offshore area of the Wadden Sea synchronous winter effects have already been described by Beu-

kema *et al.* (1988). For the Norderney area Kröncke *et al.* (2001) report significant effects of cold winters on benthic community structure. Moreover, a clear shift has become noticeable since 1988, when climatic conditions were different as indicated by higher values of the North Atlantic Oscillation Index (NAOI). High NAOI values are accompanied by effects including higher seawater temperatures, particularly in winter and spring. For the Sylt area, Armonies *et al.* (2001) suggest that the slow recovery after severe winters, which are often characterized by long spells of easterly winds, may also be caused by loss of larvae and juveniles drifting away to deeper North Sea waters.

A more extensive overview of the effects of climate change is given in chapter 3 'Climate'.

8.2.3 Effects of shellfish fisheries

The apparently decreased suitability of lower and sandy flats in the Dutch Wadden Sea to support bivalve recruitment described above could not unequivocally be attributed to bottom disturbing activities of fisheries for cockles, blue mussels or lugworms (Beukema and Dekker, 2004; Zwarts *et al.*, 2003). A long-term experimental study to verify or disprove the assumed negative impact of cockle fisheries through changes in sediment composition on bivalve recruitment (see Piersma *et al.*, 2001) was not undertaken as part of the EVA-II project evaluating the effects of shellfish fisheries. A longer lasting negative effect of cockle dredging on bivalve recruitment was only found in sediments with low mud contents (Piersma *et al.*, 2001) and was absent in an area with higher mud contents (Hiddink, 2003). In the final scientific report on the effects of Dutch shellfish fishery the results described below are presented (Ens *et al.*, 2004)

During the past ten years, cockle dredges touched each year on average 25% of the surface area of the cockle beds present in areas open to cockle fishery. This resulted in an ever-increasing proportion of the adult cockle stock being found in the areas closed for shellfish fishing. Cockle fishery caused considerable direct mortality (up to tens of percent) of shallow living non-target benthic fauna and also removed dispersed blue mussels from the tidal flats.

On a small spatial scale, cockle fishery caused a decrease in recruitment success of blue mussels. On the scale of the Dutch Wadden Sea, however, there is no evidence of such an effect. In the areas open to cockle fishery, fewer cockle spat per m² recruited than in the closed areas. This difference had disappeared by 2000; since then mean

recruitment density of cockles has even been slightly higher in the open than in the closed areas. This may be explained by a negative effect of high adult cockle densities on recruitment (cf. Beukema and Cadée, 1999) and by the fact that high densities of adult cockles increasingly occurred in the areas closed for fishing.

Effects of shellfish fishery on mussel beds will be treated in chapters 8.3 'Intertidal blue mussel beds' and 8.5.2 'Subtidal blue mussel beds'.

8.2.4 Eutrophication

In the 1999 QSR it was concluded that differences in eutrophic states within the Wadden Sea are not clearly reflected in differences in biomass of intertidal macrozoobenthos. A consistently increasing trend in biomass of polychaetes could not be related to nutrient input data (Essink *et al.*, 1998). This may partly be due to limitations of the data sets.

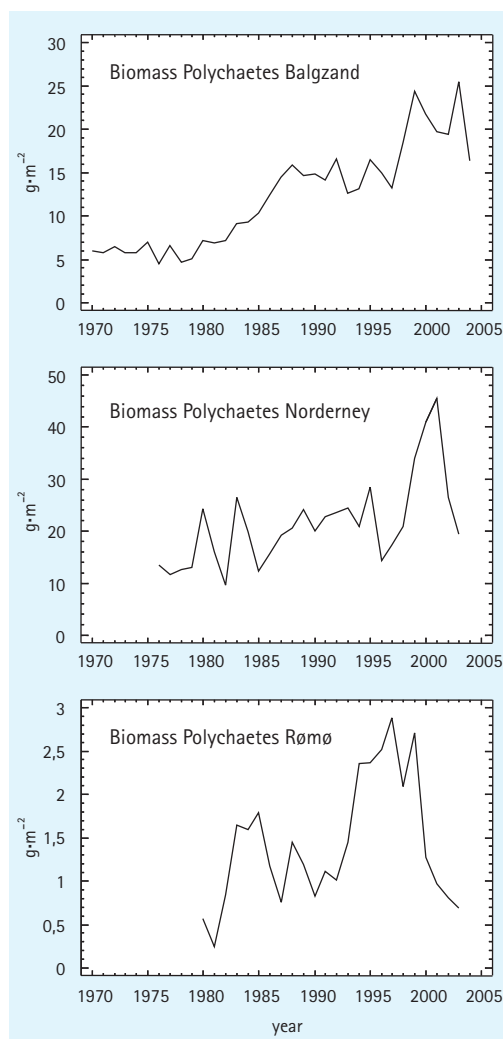
In a recent analysis of their long-term data sets

on phytoplankton, chlorophyll and intertidal macrozoobenthos in the Marsdiep-Balgzand area, Beukema *et al.* (2002) made comparisons between three decades, viz. the 1970s, 1980s and 1990s. It was around 1980 that a sudden and persistent increase occurred of phytoplankton cells, chlorophyll and of densities and biomass of zoobenthos, showing, however, considerable year-to-year variability. Their analyses show a significant positive correlation between chlorophyll concentration and density and biomass of zoobenthos, especially at places with already high biomass values. Apparently, here food supply was strongly limiting. In addition, the response to changes in phytoplankton food supply was strong only in suspension and deposit feeders, *i.e.* functional groups directly dependent on algal food, not in carnivorous species. Smaller polychaetes in particular became very abundant during the 1980s and 1990s. These developments indicate that not only the western Dutch Wadden Sea, but probably the entire Wadden Sea has been in an early stage of eutrophication (cf. Gray, 1992) during the last two decades. Any further development of eutrophication was probably prevented by environmental conditions such as strong tidal mixing preventing anoxia (e.g. 'black spots'), and severe winters as overriding regulators of zoobenthos abundance and biomass. In the Danish Wadden Sea no zoobenthos mass kills due to eutrophication related oxygen depletion were observed (Ærtebjerg *et al.*, 2003). In other parts of the Wadden Sea, such large-scale kills have been rare.

8.2.5 Are polychaetous worms taking over?

In the 1999 QSR, a consistently increasing trend in biomass of polychaetes in part of the Wadden Sea could not be related to nutrient input data. Data collected within the TMAP shows that the increasing trend in biomass of polychaetous worms for intertidal flat locations in the Dutch (Balgzand) and Niedersachsen (Norderney) Wadden Sea continued until 2004 (Fig 8.2.1) and also on parts of the locations monitored at Groningen intertidal flats. In the 1999 QSR, no such increasing trend was observed in the Danish Wadden Sea. After an update with recent data, there is still no significant trend (Figure 8.2.1). It must be noted that the Danish data refers to four polychaete species only, and not to all polychaetes present in the samples, which explains the low biomass values as compared with those present in other parts of the Wadden Sea.

Figure 8.2.1: Development of annual mean biomass (gram ash-free dry weight m^{-2}) of polychaetous worms at intertidal flats in different parts of the Wadden Sea. Note: Danish data (Rømø) refers to 4 species only, viz. *Arenicola marina*, *Heteromastus filiformis*, *Nereis diversicolor* and *Scoloplos armiger*.



Reise (1982) was the first to signal this increasing trend of polychaetes. He argued that the trend might have started even before the onset of eutrophication in the Wadden Sea, but could not give a clue as to the cause. Beukema *et al.* (2002) reported that at Balgzand intertidal flats (western Dutch Wadden Sea) small-sized worms became very abundant during the 1980s and 1990s. In the Dutch EVA-II project evaluating the effects of shellfish fisheries, it was hypothesized that bottom disturbance by cockle dredging favors the development of polychaetes. Extensive data collected provided indications that the densities of the ragworm *Nereis diversicolor* may have increased as a result of cockle fishery, but did not allow for clear conclusions (Anon., 2003). Finally, one might think of a process in which worms, generally having a r-type life strategy (relatively short-lived, regular reproduction), are developing whereas the K-type strategist bivalves (long-lived, irregular reproduction) are declining. Whether there is a causal or even a feedback relationship remains to be resolved. Perhaps we are facing a change of alternate stable states within the benthic system of the Wadden Sea (*cf.* van de Koppel *et al.*, 2001).

An explanation of the difference in trend of polychaete biomass between the northern (Denmark) and southern (Niedersachsen, The Netherlands) Wadden Sea cannot be easily presented. A difference in organic matter cycling processes between these major regions of the Wadden Sea, as suggested in chapter 5 'Eutrophication', might be a possibility. Further research into the possibility of having two sub-systems within the Wadden Sea is needed.

8.2.6 Are isolated populations endangered?

Most species occurring in the Wadden Sea belong to populations with a large geographical expansion along the western European coasts, e.g. *Mytilus edulis*, *Macoma balthica* and *Arenicola marina*. These populations have low genetic differentiation, typical of the absence of any kind of geographical isolation (Hummel, 2003). There are, however, several species with a disjunct distribution. One example is the lagoon cockle (*Cerastoderma lamarcki*) of which small populations have been observed in salt-marsh habitats at the island of Texel and Schiermonnikoog (The Netherlands) (Kuiper, 2000) and in salt-marsh creeks, ditches and brackish ponds in the northern Wadden Sea (Germany/Denmark) (Reise, 2003). The lagoon cockle has apparently disappeared from the intertidal zone of the northern Wadden Sea around



Eroded sediment showing tubes of *Lanice conchilega* (Photo: K. Reise).

1980, whereas it occurred at several sites in the 1960s and 1970s; it survived the severe winter of 1978/79 which killed almost all intertidal cockles (*Cerastoderma edule*). Seagrass beds in the upper intertidal were the preferred habitat, also connecting scattered occurrences in salt marsh ditches, creeks and ponds. The disappearance of these seagrass occurrences after 1980, together with increased storm surge frequencies (Hofstede, 1999) may have caused the lagoon cockle to vanish from the upper intertidal, leaving refuge only in sheltered salt marsh habitats (Reise, 2003).

Several species, such as the gastropods *Phytia myosotis*, *Alderia modesta* and *Hydrobia ventrosa*, the bivalve *Abra tenuis* and the isopod *Cyathura carinata* (see Reise, 2003), have disjunct distribution patterns, with isolated populations occurring in estuaries and lagoons. Little is known about the dispersal potential of these species and, therefore, of the risk of extinction of these populations. Presence or absence of these populations may play an important role in the assessment of ecological quality of coastal and transitional waters under the Water Framework Directive.



Nereis diversicolor (Photo: K.-E. Heers).

8.2.7 Conclusions

The observed decline in bivalve recruitment success over the last approximately 15 years, which is accompanied by a shoreward shift of their centres of distribution, may be explained largely by increasing predation pressure on the newly settled post-larvae by shrimps and shore crabs. This effect is clearest at lower intertidal levels, has been observed in different parts of the Wadden Sea and coincides with the occurrence of mild winters. This indicates the power of climatic factors in governing recruitment, and therefore population sizes of bivalves in the Wadden Sea. Continued global warming will therefore cause a declining trend of bivalve stocks.

On a more regional scale, however, deterioration of sedimentary conditions may play a role, especially on the more sandy lower tidal flats. Possible causes are the removal of mussel beds by fishery and sediment disturbance by cockle dredging. Mechanised fishery for cockles in the Dutch Wadden Sea had negative effects on recruitment of cockles and non-target species living in intertidal flats. There is an indication that the ragworm *Nereis diversicolor* and other small worms have increased in abundance.

It is concluded that during the last two decades the Wadden Sea has been in an early stage of eutrophication, almost without the occurrence of harmful anoxia except under patches of green algae. In the intertidal flats in The Netherlands and

Niedersachsen, biomass of polychaetous worms has continued to increase. Such a trend was not observed in the Danish Wadden Sea, with this restriction, however, that biomass data was not available for all worm species. Trends in polychaete biomass cannot be related to nutrient input data. The difference in trends between southern and Danish Wadden Sea may be related to supposed differences in organic matter cycling processes.

Isolated populations of benthic invertebrates in estuarine and brackish habitats may be endangered. These populations need further attention in order to elucidate their status.

8.2.8 Target evaluation

There is evidence of a loss of undisturbed tidal flat areas as a settling habitat for juvenile bivalves due to, for example, coarsening of the sediment.

Estuarine and brackish habitats, currently giving refuge to isolated invertebrate populations, seem too small to safeguard these populations.

8.2.9 Recommendations

- Further research into shifting centres of bivalve recruitment and their causes;
- Elucidation of the status of isolated estuarine and brackish invertebrate populations;
- Find an explanation for observed trends in polychaete biomass, and the differences in these trends within the Wadden Sea.

References

- Anonymous, 2003. Results Scientific Research EVA II – Public version. Ministerie van Landbouw, Natuur en Voedselkwaliteit, Directie Visserij, Den Haag pp. 37.
- Armonies, W., Herre, E. and Sturm, M., 2001. Effects of the severe winter 1995/96 on the benthic macrofauna of the Wadden Sea and the coastal North Sea near the island of Sylt. *Helgol. Mar. Res.* 55: 170-175.
- Ærtebjerg, G., Andersen, J.H. and Schou Hansen, O., (Eds.), 2003. Nutrients and eutrophication in Danish marine waters. A challenge for science and management. National Environmental Research Institute, Roskilde, pp. 125.
- Beukema, J.J., Dörjes, J. and Essink, K., 1988. Latitudinal differences in survival during a severe winter in macrozoobenthic species sensitive to low temperatures. *Senckenbergiana marit.* 20: 19-30.
- Beukema, J.J., Hopkoop, P.J.C. and Dekker, R., 1998. Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiol.* 375/376: 23-34.
- Beukema, J.J. and Cadée, G.C., 1999. An estimate of sustainable rate of shell extraction from the Dutch Wadden Sea. *J. Appl. Ecol.* 36: 49-58.
- Beukema, J.J., Dekker, R., Essink, K. and Michaelis, H., 2001. Synchronized reproductive success of the main bivalve species in the Wadden Sea: causes and consequences. *Mar. Ecol. Progr. Ser.* 211: 143-153.
- Beukema, J.J., Cadée, G.C. and Dekker, R., 2002. Zoobenthic biomass limited by phytoplankton abundance: evidence from parallel changes in two long-term data series in the Wadden Sea. *J. Sea Res.* 48: 111-125.
- Beukema, J.J. and Dekker, R., 2003. Redistribution of spat-sized *Macoma balthica* in the Wadden Sea in cold and mild winters. *Mar. Ecol. Progr. Ser.* 265: 117-122.
- Beukema, J.J. and Dekker, R., 2005. Decline of recruitment success in cockles and other bivalves in the Wadden Sea: possible role of climate change, predation on postlarvae and fisheries. *Mar. Ecol. Progr. Ser.* 287, 149-167.
- Dankers, N.M.J.A., Meijboom, A., Cremer, J.S.M., Dijkman, E.M., Heremes, Y. and Te Marvelde, L., 2003. Historische ontwikkeling van droogvallende mosselbanken in de Nederlandse Waddenzee. *Alterra rapport 876*, Alterra, Wageningen, pp. 114.
- Ens, B.J., Smaal, A.C. and de Vlas, J., 2004. The effects of shellfish fishery on the ecosystems of the Dutch Wadden Sea and Oosterschelde; Final report on the second phase of the scientific evaluation of the Dutch shellfish fishery policy (EVA II). *Alterra-report 1011*. Alterra, Wageningen.
- Essink, K., Beukema, J.J., Madsen, P.B., Michaelis, H. and Vedel, G., 1998. Long-term development of biomass of intertidal macrozoobenthos in different parts of the Wadden Sea. Governed by nutrient loads? *Senckenbergiana marit.* 29: 25-35.
- Flach, E.C., 2003. The separate and combined effects of epibenthic predation and presence of macro-infauna on the recruitment success of bivalves in shallow soft-bottom areas on the Swedish west coast. *J. Sea Res.* 49: 59-67.
- Gray, J.S., 1992. Eutrophication in the sea. In: Colombo, G., Ferrari, I., Ceccherelli, V.U. and Rossi, R., (Eds.). *Marine eutrophication and population dynamics*. Olsen and Olsen, Fredensborg: 3-15.
- Hiddink, J.G., 2003. Effects of suction-dredging for cockles on non-target fauna in the Wadden Sea. *J. Sea Res.* 50: 315-323.
- Hiddink, J.G. and Wolff, W.J., 2002. Changes in the distribution and decrease in numbers during migration of the bivalve *Macoma balthica*. *Mar. Ecol. Progr. Ser.* 233: 117-130.
- Hiddink, J.G., Marijnissen, S.A.E., Troost, K. and Wolff, W.J., 2002. Predation on 0-group and older yearclasses of the bivalve *Macoma balthica*: interaction of size selection and intertidal distribution of epibenthic predators. *J. Exp. Mar. Biol. Ecol.* 269: 233-248.
- Hofstede, J., 1999. Process-response analysis for Hörnum tidal inlet in the German sector of the Wadden Sea. *Quaternary International* 60: 107-117.
- Hummel, H., 2003. Geographical patterns of dominant bivalves and a polychaete in Europe: no metapopulations in the marine coastal zone? *Helgol. Mar. Res.* 56: 247-251.
- Koppel, J. van de, Herman, P.M.J., Thoolen, P. and Heip, C.H.R., 2001. Do alternate stable states occur in natural ecosystems? Evidence from a tidal flat. *Ecology* 82: 3449-3461.
- Kuiper, W., 2000. De weekdieren van de Nederlandse Brakwatergebieden (Mollusca). *Nederl. Faun. Meded.* 12: 41-120.
- Kröncke, I., 1996. Impact of biodeposition on macrofaunal communities in intertidal sandflats. *PSZNI: Marine Ecology* 17: 159-174.
- Kröncke, I., Zeis, B. and Rensing, C., 2001. Long-term variability in macrofauna species composition off the island of Norderney (East Frisia, Germany) in relation to changes in climatic and environmental conditions. *Senckenbergiana Marit.* 31: 65-82.
- Philippart, C.J.M., van Aken, H.M., Beukema, J.J., Bos, O.G., Cadée, G.C., Dekker, R., 2003. Climate-related changes in recruitment of the bivalve *Macoma balthica*. *Limnol. Oceanogr.* 48: 2171-2185.
- Piersma, T., Koolhaas, A., Dekinga, A., Beukema, J.J., Dekker, R. and Essink, K., 2001. Long-term indirect effects of mechanical cockle-dredging on intertidal bivalve stocks in the Wadden Sea. *J. Appl. Ecol.* 38: 976-990.
- Reise, K., 1982. Long-term changes in the macrobenthic invertebrate fauna of the Wadden Sea: are polychaetes about to take over? *Neth. J. Sea Res.* 16: 29-36.
- Reise, K., 2003. Metapopulation structure in the lagoon cockle *Cerastoderma lamarcki* in the northern Wadden Sea. *Helgol. Mar. Res.* 56: 252-258.
- Strasser, M., 2002. Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. *Mar. Ecol. Progr. Ser.* 241: 113-123.
- Strasser, M. and Günther, C.-P., 2001. Larval supply of predator and prey: a temporal mismatch between crabs and bivalves after a severe winter in the Wadden Sea. *J. Sea Res.* 46: 57-67.
- Strasser, M., Hertlein, A. and Reise, K., 2001. Differential recruitment of bivalve species in the northern Wadden Sea after the severe winter of 1995/96 and of subsequent milder winters. *Helgol. Mar. Res.* 55: 182-189.
- Strasser, M., Dekker, R., Essink, K., Günther, C.-P., Jaklin, S., Kröncke, I., Brinch Madsen P., Michaelis, M. and Vedel, G., 2002. How predictable is high bivalve recruitment in the Wadden Sea after a severe winter? *J. Sea Res.* 49: 47-57.
- Zwarts, L. et al., 2004. Bodemgesteldheid en mechanische kokkelvisserij in de Waddenzee. *Rijkswaterstaat-RIZA, Lelystad*.