# The Wadden Sea 2010

The Wadden Sea – A Universally Outstanding Tidal Wetland

The Wadden Sea Quality Status Report
- Synthesis Report 2010

## Colophon

Publisher Common Wadden Sea Secretariat (CWSS), Wilhelmshaven, Germany;
Language support Seabury Salmon
Cover Photo Klaus Janke
Lay-out and technical editing Common Wadden Sea Secretariat
Graphic support Gerold Lüerßen
Published 2010
ISSN 0946-896X

This publication should be cited as:

Karsten Reise, Martin Baptist, Peter Burbridge, Norbert Dankers, Ludwig Fischer, Burghard Flemming, Albert P. Oost, Cor Smit, 2010. The Wadden Sea – A Universally Outstanding Tidal Wetland. Wadden Sea Ecosystem No. 29. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, page 7 – 24.

Wim J. Wolff, Jan P. Bakker, Karsten Laursen, Karsten Reise, 2010. The Wadden Sea Quality Status Report - Synthesis Report 2010. Wadden Sea Ecosystem No. 29. Common Wadden Sea Secretariat, Wilhelmshaven, Germany, page 25 – 74.

#### **Foreword**

The designation of the Dutch and German parts of the Wadden Sea Conservation Area as a World Heritage Site by UNESCO in June 2009 was a major step in formally recognizing the global importance of the Wadden Sea as a nature area. As such, it is managed through a joint effort of Denmark, Germany and The Netherlands. Therefore, the QSR Synthesis Report 2010 is preceded by a summary report of the universally outstanding and most significant natural values. This is based on the nomination dossier and is here extended to cover the entire Wadden Sea

In this Trilateral Wadden Sea Cooperation, the Trilateral Monitoring and Assessment Program (TMAP) plays a central role, providing the basis for a periodic assessment of the condition of the Wadden Sea ecosystem, and for an evaluation of progress towards the ecological targets set out in the Wadden Sea Plan.

This Quality Status Report 2009 (QSR 2009) was prepared to update the findings of the QSR

2004 and to provide input into the Trilateral Governmental Conference on Sylt on 18 March 2010. The work was coordinated by the Common Wadden Sea Secretariat and the Trilateral Monitoring and Assessment Group. Over 115 scientists from The Netherlands, Germany and Denmark contributed to this project during 2008–2009. They prepared 30 thematic reports which were published in November 2009 (http://www.waddensea-secretariat.org/QSR-2009/index.htm).

These thematic reports, together with findings from the 12<sup>th</sup> International Wadden Sea Symposium (Wilhelmshaven, 30 March – 3 April 2009) (Wadden Sea Ecosystem No. 26) provide the basis for the QSR synthesis report presented here. It summarizes the main findings of the QSR thematic reports and attempts to present an integrated assessment of the main ecosystem developments and identify main issues of concern and gaps of knowledge for science, management and policy.

Common Wadden Sea Secretariat

# The Wadden Sea 2010

# The Wadden Sea – A Universally Outstanding Tidal Wetland

Karsten Reise, Martin Baptist, Peter Burbridge, Norbert Dankers, Ludwig Fischer, Burghard Flemming, Albert P. Oost, Cor Smit \_\_\_\_\_ page 7

The Wadden Sea Quality Status Report
- Synthesis Report 2010

Wim J. Wolff, Jan P. Bakker, Karsten Laursen, Karsten Reise page 25

## WADDEN SEA ECOSYSTEM No. 29

# The Wadden Sea – A Universally Outstanding Tidal Wetland

Karsten Reise

**Martin Baptist** 

Peter Burbridge

**Norbert Dankers** 

**Ludwig Fischer** 

**Burghard Flemming** 

Albert P. Oost

**Cor Smit** 



#### **Abstract**



Bird flock on the Wadden Sea beach (Photo: J. van de Kam).

Along the North Sea shore, the largest coherent tidal flat area of the temperate world has evolved. Sediment supply from the sea has sufficiently balanced a slow sea-level rise in the last 8,000 years to maintain a coastal configuration of a seaward sandy barrier, extensive tidal flats and episodically flooded marshes. The Wadden Sea is unique in that it consists of vast (4,700 km<sup>2</sup>) bare sand and mud flats, emerging twice daily at low tide. Oceanic waters dominate river influence, and dynamic sandy shoals and dune islands provide a partial shelter against waves and winds of a rough sea. In the course of a year, the Wadden Sea is visited by an unparalleled 10-12 million birds for foraging and resting on their East Atlantic flyway. Food provision in the form of tidal flat fauna is 10-20 times higher than in adjacent deeper waters. When the tide is in, the flats serve as a rich nursery for shrimp and fish. The Wadden Sea

constitutes a gigantic biological filter between land and sea. This filter is primarily composed (1) of extensive beds of molluscan suspension feeders which filter the local tidal volume about twice a month, (2) of sediment kept permeable by bioturbating lugworms, and (3) of marsh vegetation which functions as a filter during episodic storm surges when waters are loaded with re-suspended fine particles. An impressive number of about 10,000 species of plants, fungi and animals thrive in the Wadden Sea. After a long phase of overexploitation, protection measures have triggered spectacular recoveries in breeding birds and seals. Large-scale land claims have ceased and the Wadden Sea is today highly rated for its serene beauty. Global warming with an accelerating sea-level rise, however, may threaten the sandy barrier and the extent of the tidal flats.

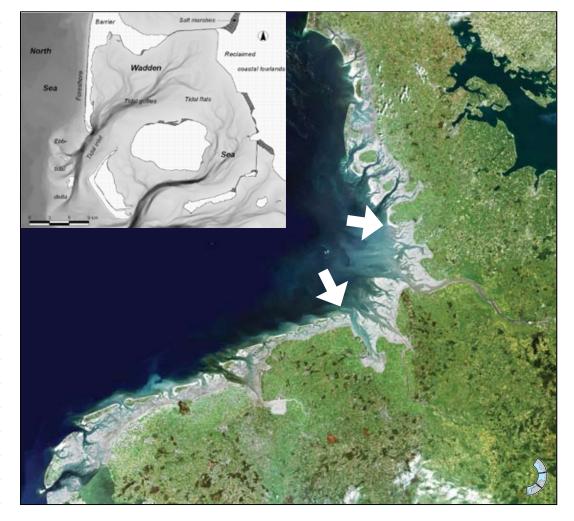
#### 1. Introduction

The earliest and most famous historical testimony of the Wadden Sea is recorded in the 'Historia Naturalis' by Plinius the Elder who visited the southern coast of the North Sea in the year 47 AD. He was amazed by the 'indistinctness' and 'immeasurable expanse' of land inundated by the sea twice daily. The intimate bond between the people and this changeable environment was quite incomprehensible to him. However, perception of pleasure was derived from the Wadden Sea when in the 18-19th centuries the 'aesthetics of the sublime' stimulated human senses to ascribe outstanding value to this serene coastal sea with land diving under water and water running off the land, with an open horizon and limitless sky, and a calm sea which may all of a sudden turn wild with an arising torrential storm (Fischer and Hasse, 2001).

The Wadden Sea is mostly shallow enough to wade across. The unique vastness of the tidal flats and shoals, fringing salt marshes, wide beaches and dune islands with a spectacular abundance of

wildlife has been the motivation for proposing the Wadden Sea as a UNESCO World Heritage Site. The following text is condensed from the description and justification chapters of the Dutch-German nomination dossier (CWSS, 2008, 2009), but here extended to cover the entire Wadden Sea area including the Danish part. The foremost question was: On which universally outstanding, most significant natural values should the inscription be based? We have employed major reviews of scientific knowledge (Wolff 1983), quality assessments (CWSS, 1991; De Jong, 1999; Essink et al., 2005; Marencic & de Vlas, 2009), and cite representative studies on the geomorphology, ecology and biology of the region from the 19th century onwards. Comparisons with other coasts of the world are based on Reineck and Singh (1980), Flemming (2002), Reise (2001) and own surveys (see annex 3 in CWSS, 2008). The purpose of this paper is to provide a concise overview on physical and biotic values which lend the Wadden Sea a universally outstanding status worthy for inscription as UNESCO World Heritage Site.

Figure 1: Satellite images taken in 2000-2002 and combined to show low tide conditions everywhere. In reality tidal waves progress counter-clockwise over a six-hour period through the Wadden Sea (Source: Eurimage, Common Wadden Sea Secretariat & Brockmann Consult). Arrows indicate boundaries between sub-regions. Inset shows tidal basins in the Northern Wadden Sea (modified from CPSL, 2005).



## 2. Physical Environment

The Wadden Sea has the world's largest continuous belt of bare tidal flats partially sheltered by a sandy barrier against a rough sea, with the latter's waters dominating river influence. When post-glacial sea level rise began to slow down about 8,000 years ago, the Wadden Sea emerged with a seaward barrier of dune islands and sandy shoals, and a landward area of tidal flats and salt marshes (Zagwijn, 1986; Flemming and Davis, 1994). The rates of sea-level rise and sediment supply varied over time and locality, causing continuous dynamics in the coastal morphology of the Wadden Sea. As a result, at times parts of the coast have grown where the sea tides and waves have washed in more sediment from the adjacent offshore zone than was needed to compensate for sea level rise. At other times, the coast retreated in some places when sediment supply has been unable to compensate for sea level rise. In this way, the Holocene history of sea level, climate, and depositional responses has been preserved in the stratigraphic record of the Wadden Sea (Streif, 1989; Bartholdy and Pejrup, 1994; Behre, 2003).

With the Wadden Sea, a universally outstanding coastal landscape has arisen at the southern and eastern shores of the North Sea (Figure 1). Along a coastal stretch of approximately 500 km, an uninterrupted belt of sand and mud flats with a total area of 4,700 km<sup>2</sup> is exposed to the air and then covered by water twice daily in the rhythm of the tides. This belt of tidal flats is dissected by more than 30 branching tidal inlets and five major estuaries. Such a vast and coherent intertidal area not covered by salt marsh vegetation is found nowhere else in the world.

There are many other sedimentary coasts which, in one way or another, resemble the Wadden Sea morphologically but are much smaller or differ in terms of climate, river influence, tides or waves. Other large tidal flats can be found in the Arctic, but there the tides tend to be smaller than in the Wadden Sea, and the shore is frozen and covered by ice most of the year. In tropical and subtropical climates, the tidal zone is often occupied by mangroves, whereas in the Wadden Sea tidal flats lack upright growing plants, except for salt marsh vegetation above mean high-tide level. On other coasts, most of the sediment is directly supplied from the hinterland by rivers, and salinity is ususally low or variable. Examples of such coasts are the Arctic Lena Delta, the temperate Mississippi Delta or tropical deltaic regions of the Amazon, Niger or Ganges. Also, the wide mud flats along the coasts of the Yellow Sea have been built up by rivers.

The Wadden Sea is special in that almost all of the sediments are supplied from the adjacent sea with only a minor or local river influence (Arends, 1833; van Straaten and Kuenen, 1957). Salinity ranges mostly between 20 and 30 psu, which is less than in the open ocean (34) but more than in estuaries (0-20), where most other intertidal flats are found in Europe. Large sand and mud flats occur along the NW African coast where the Banc d'Arguin covers an area of 630 km2 and which corresponds to 13% of the tidal flat area of the Wadden Sea (Wolff et al., 1993). These tidal flats constitute a relic from a former river delta, and are intimately linked to the Wadden Sea by its wading birds overwintering there (Wymenga et al., 1990). The Wadden Sea comprises about 60% of the intertidal area at the north-eastern Atlantic shores.

A further feature of the Wadden Sea is a seaward barrier of sandy islands and shoals which is a consequence of moderate tidal ranges, and sand having been supplied from the offshore by waves and subsequently moved by the wind (Oost and de Boer, 1994). Tides have increased with the rising level of the sea and today span from 1.5 to 4 m. Below a tidal range of about 0.5 m, unbroken barrier spits and lagoons develop and above about 3.5 m barrier islands no longer occur due to the large tidal prisms. The Wadden Sea may be divided into three morphological sub-regions (see arrows in Figure 1), based on tidal ranges between 1.5 to 3 m in the South and North, and >3 m in the central part, as well as on coastal orientation and river influence:

- In the Southern Wadden Sea, twelve major barrier islands located 5 to 15 km off the mainland shore, shelter the tidal area against waves generated by northwesterly and northerly winds. Sediment imported from the sea does not fully compensate for sea-level rise and islands migrate landwards. A large embayment, the former brackish Zuiderzee (3,600 km2), was part of the Southern Wadden Sea until it was separated by a dam in 1932. It was subsequently converted into a freshwater lake and arable land. Another embayment, the estuarine Dollard, still exists.
- In the Central Wadden Sea, tidal ranges often exceed 3 m and there are four estuaries causing a lower and more variable salinity than in the other two regions. A seaward chain of barrier islands is absent. Here, sediment import seems to balance sea-level rise. With the Jadebusen, a large embayment extends deep into the low-lying coastal marshland.

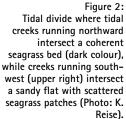
• In the Northern Wadden Sea, eight islands and elevated sand bars form a seaward barrier 5 to 25 km off the mainland. They provide shelter against waves generated by the prevailing westerly winds. Mostly, sediment supply does not compensate for sea-level rise, except for an oversupply between the islands of Rømø and Fanø. Several marsh islands are scattered across the tidal area. These are remnants of a coherent marshland which became drowned in late medieval times. In the North, some Pleistocene cliffs meet the sea.

A distinctive hydrological feature of the Wadden Sea is a series of tidal basins which are marine analogues to river catchments (Postma, 1954; Ehlers, 1988). However, flow direction alternates with the tides (see inset in Figure 1). The existence of tidal basins is interrelated with barrier islands and elevated sands. Between these, the tidal flow is compressed and scours deep tidal inlets with a mean flow of about 1 m s-1. Behind the barrier islands, most inlets branch into major tidal channels which, in turn, branch into successively smaller tidal creeks or runnels in a recurrent fractal pattern. In the back-barrier area, flood waters of adjacent tidal inlets meet at tidal divides (watersheds) where currents tend to calm down (Figure 2). Other than in lagoons, tidal divides allow for a direct lateral connection between basins. Seaward of tidal inlets, ebb-delta shoals are formed. Here, ebb currents interact with waves and a long-shore current which runs from southwest towards northeast.

The sediment distribution along deltaic coasts is typically from coarse materials inshore to progressively finer sediments offshore. In the Wadden

Sea, by contrast, the decrease in grain size is the other way round (van Straaten, 1954). This difference is caused by the sediment transport routes perpendicular to the shore running in opposite directions, whith the source either rivers or the sea. Along tropical and subtropical coasts, tidal flats may also develop behind a barrier of coralline reefs. Here the sediment particles primarily consist of biogenic carbonates, whereas in the Wadden Sea siliclastic sediments prevail.

Strong hydraulic and aeolian dynamics are an important characteristic of the Wadden Sea region. Twice a day the tides move an average volume of 15 km<sup>3</sup> of sea water through the tidal channels and inlets into the tidal basins where roughly the same volume remains at low tide, thus swelling up to some 30 km3 at high tide. A high exchange rate of tidal water masses secures the dominance of marine conditions in the back-barrier area (Postma, 1954). In the course of a tidal cycle, the sum of freshwater discharge is <1% of the tidal volume. The difference in tidal exchange between the phases of the moon amounts to only about 20% in the Wadden Sea. Instead, strong onshore winds may increase high tides up to 4 m above mean high tide. Strong offshore winds are less frequent and may push low tides down to 1.5 m below mean low tide level. Because of this asymmetry in wind speed and direction, tidal flats often remain submerged over several days due to prevailing westerly winds, whereas continuous emergence over several tidal cycles due to southerly or easterly winds is extremely rare (Weisse and Plüß, 2006). This contributes to the dominance of marine over terrestrial organisms in the tidal zone of the Wadden Sea.





### 3. Ecology



Figure 3: Bed of suspension feeding mussels (Mytilus edulis) bound together by byssal threads. Shells are partly overgrown by barnacles (mainly Elminius modestus), a few oysters (Crassostrea giggs), bladder wrack (Fucus vesiculosus forma mytili), and periwinkles (Littorina littorea) graze on microbial films (Photo: K. Reise).

Ecologically the Wadden Sea functions as a gigantic coastal filter of unique composition, and offers plenty of food to a rich aquatic nursery and to 10-12 million birds in the course of a year. The habitats of the Wadden Sea show in a fascinating way how physical forces and biological activities interact to generate conditions for life in a fragile balance. Along this coast physical forces are strong, biological activities high, and the basic materials are soft sediments and fluid waters. This combination makes the dynamic interactions between organisms and their environment readily apparent and attractive to study. Major habitats are arranged along an offshore-inshore gradient and from deep tidal inlets up to the highest dunes: an offshore belt seaward of the barrier islands, a tidal area with subtidal gullies and shoals, intertidal mud and sand, with seagrass meadows or mixed oyster and mussel beds, a few estuaries, salt marshes on islands and along the mainland coast, beaches and dunes mainly on the islands. These habitats are functionally interrelated and constitute a characteristic combination.

The offshore belt of the Wadden Sea is operationally defined as the zone seaward of the barrier islands and elevated outer sands, extending into the North Sea down to the -15 m depth contour. This belt has no tidal flats and drops off smoothly towards the open North Sea but does not fully comply with it in terms of the biota. There is a continuous exchange of both water and sediment with the tidal area. The sediment supply from the

offshore belt is vital for the resilience of the coast when responding to changes in tidal area, sea level and to disturbances caused by storm surges (Flemming and Bartholomä, 1997). Phytoplankton blooms often start in this belt because turbidity is low enough for sufficient light and nutrient concentrations are high (Postma, 1954; van Beusekom and de Jonge, 2002). Through the tidal channels and inlets this offshore primary production reaches the inshore zoobenthos. In the offshore belt, autotrophic production prevails and in the tidal area, heterotrophic production is dominant. Also larvae of benthic fauna and fish drift from the offshore belt further inshore. Shrimp, fish, diving birds, seals and harbour porpoises readily commute between offshore and inshore zones (Bückmann, 1934; Wolff and Zijlstra, 1980). In severe winters, the offshore belt provides an important refuge for the survival of populations otherwise confined to the tidal area.

Within the tidal area, the subtidal shoals and gullies similarly serve as a refuge for the intertidal fauna when conditions turn harsh. The subtidal fringe and low intertidal zone are the primary sites for beds of suspension feeders, mussels and oysters in particular (Hagmeier and Kändler, 1927). Mussels are kept in bottom cultures and also occur naturally in mixed beds with oysters (Figure 3; Dankers and Zuidema, 1995; Nehls et al., 2006). A native subtidal oyster has been driven to extinction by over-exploitation, while the introduced Pacific oyster recently invaded the intertidal mussel beds. Together with other suspension feeders, the entire volume of tidal waters is filtered within two weeks (Verwey, 1952). Mussels and oysters also stabilize the bottom and accrete fine sediments, accumulate large amounts of shell material, provide attachment for algae and sessile invertebrates, and shelter for mobile invertebrates and fish. This rich association served as a model for the community concept (biocoenosis) developed by Möbius (1877) with the assumption of balanced species interactions maintaining a community of organisms. This concept is still favoured in ecological textbooks.

Tidal elevation and sediment composition are two major determinants of benthic assemblages on the tidal flats (Thamdrup, 1935; Wohlenberg, 1937; Linke, 1939). Suspended fine particles, mostly comprising aggregates of mineral grains and organics, tend to accumulate on the landward side of the tidal flats (Postma, 1961; Dronkers, 1984). This general phenomenon was initially explained by van Straaten and Kuenen (1957) with a combination of settling lag and scour lag. The former is a time lag between the moment at which a decreasing current is no longer able to hold a particle in suspension and the moment at which this particle reaches the bottom. The latter is the time lag caused, among others, by the extracellular slime of the microalgal film on the bottom, binding settling particles so that stronger currents are required for re-suspension than the velocity at which deposition of the same particle had occurred. The vast tidal flats of the Wadden Sea serve as a primary example for this progressively shoreward-fining gradient in particle size.

The sediment surface is almost completely covered with microscopic algae and bacterial colonies. Some of these are mobile and once buried under new deposits, they crawl back to the surface. This behavior may generate a laminated structure of mud deposition until reworked by the occasional storm surges (Wohlenberg, 1953). Intertidal seagrass beds may also accumulate fine particles. However, most leaves are shed in autumn and then waves re-suspend the intermittent accretion. The most extensive seagrass meadows occur in the Northern Wadden Sea on approximately 10% of the tidal flat area, and these represent the largest intertidal seagrass beds in Europe (Figure 2; Reise and Kohlus, 2008).

A large proportion of the tidal flats of the Wadden Sea consist of wave-rippled sands. This habitat is maintained by the constant sediment reworking of lugworms (Figure 4). In analogy to Darwin who described the role of earthworms in the shaping of the landscape in England, lugworms shape the appearance of the tidal flats and the spatial relationship between mud and sand flats in the Wadden Sea. Their fecal mounds with coiled strings of sand are the most characteristic feature of the tidal flats in the Wadden Sea. The total population size may comprise about one billion worms and this is considered the largest

Figure 4:
Fecal castings of lugworms
(Arenicola marina) which
are reworking and irrigating
vast tidal flats in the Wadden Sea, thereby maintaining a permeable sandy
sediment (Photo: K. Reise).





Figure 5: Staging knots (Calidris canutus) probing intertidal sediments of the Wadden Sea for small molluscs. About 450,000 fly towards Greenland and Canada, and 340,000 fly towards Siberia for breeding. During winter, most stay in western Africa (Photo: K. Reise).

worldwide. Lugworms recycle the upper layer of the sediment 10-20 times per year through their guts (Cadée, 1976) and prevent clogging of the interstices of sand with organic material (Volkenborn et al., 2007). They also irrigate their burrows with water from above and build up an oxic environment in otherwise anoxic sediment. This increases bacterial activity and the permeable sand functions as an effective filter for the tidal waters.

The impressive ecological productivity of the tidal flats comprises high bacterial remineralisation rates, strong import of suspended microalgae, and a generally high productivity at the bottom by microscopic algae instead of large plants (Cadée and Hegeman, 1974; Loebl et al., 2007). Together this constitutes a readily consumable food supply for a zoobenthos which builds up an exceptionally high biomass, dominated by molluscan suspension feeders, followed by deposit feeding worms and small snails (Beukema, 1976; Beukema et al,. 2002; Asmus, 1987; Reise et al., 1994). These in turn provide plenty of food for small crabs, shrimp and fish which use the flats as a nursery when the tide is in (Smidt, 1951; Kuipers, 1977; Strasser, 2002), and for huge flocks of wading birds, gulls and ducks when the tide is out (Piersma, 1987; Scheiffarth and Nehls, 1997). These have the advantage of searching for prey on a very large intertidal area, with a fair chance of frequently encountering patches of a sufficient quality and quantity of accessible food. On the permanently

submerged bottom of the North Sea, the zoomass is 10-20 times lower than on the tidal flats. This is why the Wadden Sea can feed 10-12 million coastal birds in the course of a year (Blew et al., 2005). Most of these are migrants along the East Atlantic flyway and use the Wadden Sea as their central staging area to replenish energy lost during breeding and long-distance flights (Figure 5). Thus, the Wadden Sea feeds birds which travel to many other coasts or fly further inland. Similarly, the tidal flat fauna offers food for young fish which as adults migrate into the open sea or into the rivers. Seals and harbour porpoises are at the top of the aquatic food web, and birds of prey represent a link to the terrestrial food web (Baird et al., 2004). A diverse assemblage of parasites hitchhikes on these trophic pathways (Thieltges et al., 2006).

The estuaries as tidally influenced transition zones between marine and riverine environments are not a dominant feature and are small in size relative to the marine parts of the Wadden Sea (Harten and Vollmers, 1978). This is in contrast to most other tidal areas in Europe and the world. Nevertheless, these estuaries supply the Wadden Sea with nutrients, are pathways for diadromous fish and add habitats of low and variable salinity.

Mangroves and salt marshes dominate tidal areas along most tropical and temperate sedimentary coasts of the world. However, in the Wadden Sea, climate is too cold for mangroves and salt marshes are relegated to high-tide level and the episodically flooded supratidal zone. Thus, bare tidal flats prevail. In contrast, the Georgia Bight, on the other side of the Atlantic, represents a geomorphologically similar coast with many tidal areas and seaward barriers of sandy islands over a length of 1,200 km. However, bare mud flats comprise only 300 km<sup>2</sup>, whereas salt marshes occupy 4,200 km<sup>2</sup> (Dame et al., 2000). In the Wadden Sea this habitat ratio is reversed with tidal flats occupying 4,700 km<sup>2</sup> and salt marshes 400 km<sup>2</sup>. The reason for this difference is still open to debate. The Georgia Bight is warmer than the Wadden Sea which may be of particular benefit for the cord grass which dominates the marsh there. On the other hand, and unlike the Wadden Sea, the rivers along the east coast of North America supply huge amounts of fine-grained sediments which are trapped in the cord grass meadows, allowing these to expand. In addition, mean wave height in the Wadden Sea is twice that of the back-barrier area in the Georgia Bight. This may also explain why salt marshes are relegated towards high-tide level in the Wadden Sea.

Beaches and dunes are found along many coasts. However, in the Wadden Sea, numerous sandy barrier islands are aligned along the coast like strings of pearls. Sand blown by prevailing westerly winds from dry parts of the beach is trapped by pioneer plants. In the Wadden Sea, the main dune generating species is a marram grass (Ammophila arenaria) which is able to grow upwards with the accumulating sand (Figure 6). It does not stabilize the sand sufficiently to prevent further aeolian transport. Along retreating shorelines, one dune may therefore overtop another. When a dune height of 20 m is exceeded, the characteristically strong winds of the North Sea region overrule the marram grass and bare migrant dunes arise (Priesmeier, 1970). Without marram grass, the barrier islands would presumably look very different. This can be inferred from observations made along the coast of Oregon in the northwest of North America. There, marram grass was originally absent. After it had been introduced, it quickly generated a high and permanent fore-dune barrier behind the beach where none had been before.

Figure 6:
Dunes on Wadden Sea barrier islands are generated by an interplay between sand mobilizing wind and stabilizing marram grass (Ammophila arenaria) (Photo: K. Reise).



# 4. Biodiversity

The Wadden Sea displays a complex matrix of habitats across environmental gradients of depth and salinity, height and dryness, exposure to hydrodynamics and winds, and substrates modified by organisms. These habitats occur in dynamic sequences in a highly repetitive pattern due to the long chain of islands and shoals, tidal basins and estuaries, and together accommodate a high diversity of aquatic and terrestrial species. The Wadden Sea has a long tradition of research on the composition of the regional flora and fauna (Wolff, 1983; Gerlach, 2004; Niedringhaus et al.; 2008). It forms the habitat for about 2,700 species of marine origin and at least 5,100 semi-terrestrial and terrestrial species, mostly the flora and fauna of salt marshes and dunes on the islands (Table 1). Various unicellular groups and small metazoans such as terrestrial nematodes have not been included in the surveys. Adding these, we estimate that the Wadden Sea area is populated by about 10,000 taxa, not including bacteria and archaea.

Of the taxa recorded, phototrophic plants comprise about 2,300, macrofungi 1,300 and animals 4,200 species. With this impressive species richness the Wadden Sea helps to arrest the loss of coastal biodiversity in temperate coastal zones. Presumably a crucial factor for the high species richness is the repetitive sequences of dynamic habitats on a large scale. This is likely to reduce the risk of extinction. On a sandy beach and sand flat of the island of Sylt, extending 115 m between the high and low tide lines, altogether more than one million individuals have been examined and identified to species level. Most belong to the interstitial fauna, composed of metazoans small enough to move through the interstices of sand without having to push sand grains out of their

way. In toto, 652 species have been recorded, and for 148 of them it is the type locality where they have been described for the first time (Armonies and Reise, 2000). Contrary to larger marine organisms, the hot spot of diversity for the interstitial fauna lies in the intertidal zone rather than at greater depth (Figure 7). Adding estimates for unicellular algae, the territories of almost 1,000 species are trespassed when walking from high to low tide line at that site. Nowhere else in the world has species richness of a beach been analysed in such detail.

An incredible number of small arthropod species live in the salt marshes, mainly insects and spiders (Heydemann 1981). The main primary producers, the vascular plants, comprise only 45 species. Directly feeding on these plants are 6 species of waterfowl and 400 species of insects. Another 500 species have been found to feed on dead plant material, algae and fungi. Predaceous arthropods comprise 245 and parasites 250 species. To this spectrum we may add about 100 species of birds feeding and resting in salt marshes. The sum of all these species is almost 1,600. To these terrestrial organisms some 500 species of aquatic, mostly marine invertebrates of the meiofauna, have to be added. Again, considering unicellular organisms not included in the surveys, the grand total is about 2,300 taxa which may dwell in salt marshes of the Wadden Sea. This compares well with the species richness encountered in European temperate forests. More species occur in salt marshes than in beaches and sand flats because the vegetation generates a more complex habitat.

Of the 140-plus species of fish recorded in the Wadden Sea, 20 spend their entire life in the tidal

Marine aquatic organisms		Terrestrial, semi-terrestrial and freshwater organisms		
Vascular plants	2	Macrofungi (islands)	1,300	
Macroalgae	80	Lichens (islands)		
Pelagic microalgae	380	Mosses (islands)	338	
Benthic microalgae	260	Vascular plants	900	
Zooplankton	260	Molluses	70	
Benthic microfauna	1,200	Arthropods	2,000	
Benthic macrofauna	400	Birds		
Fish	149	Other vertebrates		
Marine mammals	3	Man	1	

Table 1: Overview of species richness in the Wadden Sea. In some groups, numbers have been estimated. Due to taxonomic uncertainties, not all species complexes have been analysed, and in terrestrial environments surveys on small soil fauna are incomplete. Rare visitors are left out. Most numbers are from lists of species in Wolff (1983).

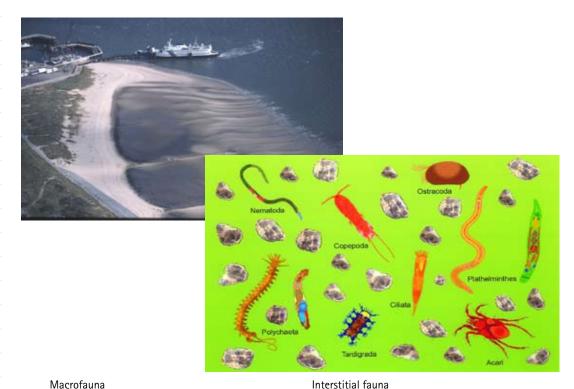
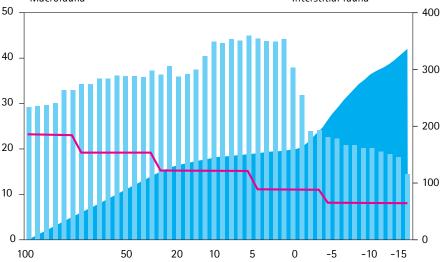


Figure 7: Across 120 m of a sheltered beach and intertidal sand flat (photo, top) the incredibly high species number of the small fauna in the interstices of sand (green panel) attains a maximum near mid tide level (bottom panal, columns, right scale), while macrofaunal species numbers gradually increase towards spring low tide line (red line, left scale). Horizontal acis indicates distance (m) from the bend (0) in the slope between the tide lines (modified after Armonies and Reise, 2000).



area. Plaice (*Pleuronectes platessa*) and sole (*Solea solea*) spawn in the North Sea and their pelagic eggs and larvae drift into the tidal area, metamorphose and settle on the mud flats. There they benefit from ample food and warm temperatures (Zijlstra, 1972). They leave the Wadden Sea as juveniles before their first winter. Also, juveniles of herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) occur in big shoals, particularly at night. Several diadromous species spawn in the rivers and merely pass through the Wadden Sea. Whiting (*Merlangius merlangus*) and cod (*Gadus morrhua*) have open sea nurseries, but in late summer and autumn of some years juveniles make incursions into the Wadden Sea with dramatic

effects on shrimp and small fish on which they prey (Jansen, 2002).

For coastal birds, the Wadden Sea is not only attractive because of the high availability of food. Some of the islands and high sands are without mammalian predators and human disturbance. Almost one million ground-breeding birds belonging to 31 species use these sites (Koffijberg et al., 2006). Of Eurasian spoonbill, avocet, gull-billed tern and sandwich tern more than 25% of the European populations breed in the Wadden Sea region. For 43 species, the Wadden Sea supports more than 1% of the flyway population, which is the criterion of the Ramsar Convention for identifying wetlands of international importance.

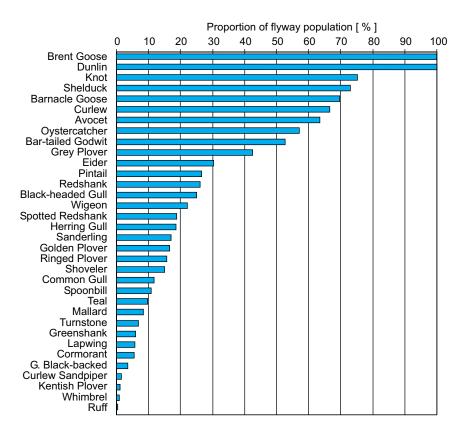


Figure 8: Maximum estimated numbers of migratory birds between 1992-2000 given as proportion of flyway populations for the entire Wadden Sea (from: Blew et al., 2005).

Of these, 4 are breeding in the Wadden Sea, 15 are only visiting during their seasonal migrations, and 24 do both. Almost the entire population of dark-bellied brent goose (Branta b. bernicla) and the entire European and West-Russian population of dunlin (Calidris alpina) use the Wadden Sea during periods of the annual cycle (Figure 8). An additional seven species are present with more than 50% and further 14 species with more than 10% of their flyway populations. In absolute numbers, it is estimated that dunlin reaches a seasonal maximum of 1.4 million, oystercatcher 582,000, black-headed gull 499,000, red knot 339,000 and wigeon 333,000. In late summer, almost all shelducks of Northern and Western Europe concentrate with about 200,000 birds for moulting in the least disturbed areas of the Wadden Sea (Blew et al., 2005). Many birds use the Wadden Sea only briefly, others do so for several months and use the area to gain enough energy for further migration. Other species spend the whole winter in the area. Hence, the numbers actually using the area

(10 to 12 million) are much higher than the total numbers present at any one moment. Nonetheless, the Wadden Sea is one of the most spectacular sites for coastal birds in the world.

Indigenous species of marine mammals in the Wadden Sea are common seal (Phoca vitulina), grey seal (Halichoerus grypus) and harbour porpoise (Phocoena phocoena). The Wadden Sea now sustains approximately 20% of the Northeast-Atlantic subspecies of common seal. Archaeological findings suggest that grey seals were the dominant seal species until medieval times and then vanished entirely. The cause was most probably the ease of hunting during whelping on the upper beaches. Recently grey seals have also started a comeback (Reijnders et al., 1995). During the moulting season, 20,250 common seals and 1,900 grey seals resting on sand bars have been counted from the air in 2008. In the Northern Wadden Sea, female harbour porpoise with offspring are observed with a density of 1-2 individuals per km<sup>2</sup>.

## 5. History and Outlook

Humans have always been present in the Wadden Sea region. Hunting and fishing seem to have driven large animals such as grey whale, Dalmatian pelican, sturgeon and salmon to extinction (Wolff, 2000). These will not come back without active support. Bird and seal populations have strikingly recovered when protection measures became effective in the course of the 20th century, but there is still room for more. Almost a thousand years ago, embanking of salt marsh areas commenced and culminated in the 20th century when also mud flats and entire embayments were cut off from the Wadden Sea by seawalls. This reduced the extent of salt marshes and nearshore mud flats, and at the same time interfered with a further deposition of silt and clay where the tidal zone became narrower and hydrodynamic energy increased per unit area (Flemming and Bartholomä, 1997). These distortions of natural processes constitute a major challenge to habitat restorations along the mainland coast.

In the 1950s and 1960s, pollutants in Wadden Sea organisms reached very high levels and caused incidences of mass mortalities in Eider ducks and sandwich terns, and reduced reproduction rates in seals (Brouwer *et al.*, 1989). Discharges of pollutants have decreased since then. Sublethal effects are hard to detect and persistent pollut-

ants are still in the sediments. Nutrient loads in the rivers debouching into or near the Wadden Sea reached a maximum in the 1970s, but have declined since then. However, they are still 2-5 fold above pre-industrial values. Enhanced algal blooms have been observed in the past and, although somewhat decreased, have not ceased altogether (van Beusekom 2005; Philippart et al., 2007). The question will be, how low do we wish to go with the nutrient loads?

North Sea fish have for a long time been subject to strong fishery pressure (Holm, 2005). After large fish had disappeared, fisheries in the Wadden Sea focused on shellfish and shrimp. This has affected the benthos in general: native oysters have vanished, subtidal mussels are mostly confined to culture lots, and intertidal beds are intermittently strongly decimated, while catches of shrimp (*Crangon crangon*) have been sustained (Lotze, 2005). Industrial cockle fishery has recently been banned completely. There seems to be a large potential for fish and shellfish recovery but management efforts are still in their infancy.

At least 60 alien aquatic species have been unintentionally introduced by shipping or with imported oysters. The Pacific oyster (*Crassostrea gigas*) became extremely abundant on mussel beds and beyond (Figure 9). This species, and others

Figure 9: Introduced Pacific oysters are spreading throughout the Wadden Sea. They have added new biogenic reefs and partially displaced native mussel beds (Photo: K. Reise).



introduced earlier, seem to particularly benefit from the current trend of warming (Nehring et al., 2009). Around the low-tide line, the epibenthic community is already dominated by alien species, giving rise to new functions and habitats. Preventative measures against further introductions are urgently needed.

In the long run, sea-level rise triggered by global warming is expected to exceed the adaptive capacity of the Wadden Sea. The rise could be of the order of 1 m until the end of this century (Rahmstorf, 2007). Along the mainland, seawalls prevent a landward shift of the tidal area in response to higher water levels, and sediment supply from the North Sea may not keep up with the speed of sea-level rise. A time lag in sediment transport from the offshore belt to the tidal area would result in the intertidal zone being drowned. As the tidal flats provide the core function and services of the Wadden Sea ecosystem, plans should be prepared on how to facilitate sediment supply from the North Sea into the tidal area, and how to trap suspended particles from the tidal waters even in embanked low marshes. This demands an innovative and interdisciplinary research agenda leading towards a strengthening of the regional identity in a changing world (Kabat et al., 2009).

#### Conclusions

As a universally outstanding combination of attributes, the Wadden Sea

(1) has the largest unbroken belt of bare intertidal mud and sand flats in the world,

- supplied with sediment primarily from the
- and a long chain of barrier islands providing shelter to the tidal area behind,
- adapting to sea-level rise by vertical accretion and by retreat of the sandy barrier,
- being subject to relatively high waves and strong seasonal storm surges,

- with tides doubling the volume of water twice daily,
- and a strong dominance of oceanic waters over their riverine counterparts;
- (2) functions as a gigantic coastal filter,
- composed of extensive molluscan beds,
- and the largest lugworm population in the world keeping sediments permeable,
- and salt marshes confined to areas near high-tide level, unable to encroach on the vast tidal flats;
- (3) offers a wide food availability based on
- phytoplankton imported from an offshore belt and on benthic microalgae,
- both readily consumed by an abundant benthic fauna.
- which provides food to an aquatic nursery of shrimp, fish and seals,
- and food to 10-12 million birds in the course of a year;
- (4) has a complex and repetitive habitat matrix
- with about 10,000 species of aquatic and terrestrial organisms,
- which is indispensible for 44 populations of 34 species of coastal birds,
- showing a recovery of bird and seal populations after centuries of exploitation,
- no longer threatened by land claim ambitions, and being protected by trilateral policy.

The Wadden Sea may thus be perceived as a coast of hope. Extraordinary flocks of coastal birds and abundant seals are indicative of a thriving tidal ecosystem in spite of a history of strong human impacts. Ongoing species introductions and climatic warming will inevitably change the species composition. Eventually, accelerating sea-level rise will threaten the large extent of the tidal flats. This will require nature protection and coastal defence agencies to join forces in a common management plan to maintain the natural values and at the same time to allow for a sustainable shared human use.

#### Acknowledgements

We are most grateful to the staff of the Common Wadden Sea Secretariat and the many civil servants of Dutch and German Nature Protection Agencies who have been involved in writing the nomination dossier and encouraged this manuscript.

#### References

Arends, J.R.L., 1833. Physische Geschichte der NordseeKüste und deren Veränderungen durch Sturmfluthen seit
der Cymbrischen Fluth bis jetzt. Facsimile print 1974, Verlag
Schuster, Leer.

Armonies, W., Reise, K., 2000. Faunal diversity across a sandy
shore. Mar. Ecol. Prog. Ser., 196, 49–57.

Asmus, H., 1987. Secondary production of an intertidal mussel
bed community related to its storage and turnover compartments. Mar. Ecol. Prog. Ser., 39, 251–266.

Baird, D., Asmus, H., Asmus, R., 2004. Energy flow of a boreal intertidal ecosystem, the Sylt-Rømø Bight. Mar. Ecol. Prog. Ser. 279, 45-61.

Bartholdy, J., Pejrup, M., 1994. Holocene evolution of the Danish Wadden Sea. Senckenbergiana maritima, 24, 187-209.

Behre, K.E., 2003. Eine neue Meeresspiegelkurve für die südliche Nordsee. Probleme der Küstenforschung im südlichen Nordseegebiet, 28, 9-63.

Beukema, J.J., 1976. Biomass and species richness of the macrobenthic animals living on the tidal flats of the Dutch Wadden Sea. Neth. J. Sea Res., 10, 236–261.

Beukema, J.J., Cadée, G.C., 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, 11–125.

Blew, J., Günther, K., Laursen, K., van Roomen, M., Südbeck, P., Eskildsen, K., Potel, P., Rösner, HU., 2005. Overview of numbers and trends of migratory waterbirds in the Wadden Sea 1980-2000. Wadden Sea Ecosystem No. 20, 8–148.

Brouwer, A., Reijnders, P.J.H., Koeman, J.H., 1989. Polychlorinated biphenyl (PCB) – contaminated fish induces vitamin A and thyroid hormone deficiency in the common seal (*Phoca vitulina*). Aquatic Toxicology, 15, 99–106.

Bückmann, A., 1934. Über die Jungschollenbevölkerung der deutschen Wattenküste der Nordsee. Ber. Dtsch. Wiss. Komm. Meeresforsch. NS, 7, 205–213.

Cadée, G.C., 1976. Sediment reworking by *Arenicola marina* on tidal flats in the Dutch Wadden Sea. Neth. J. Sea Res., 10, 440-460

Cadée, G.C., Hegeman, J., 1974. Primary production of the benthic microflora living on tidal flats in the Dutch Wadden Sea. Neth J. Sea Res., 8, 260-291.

CPSL, 2005. Coastal Protection and Sea Level Rise. Solutions for Sustainable Coastal Protection in the Wadden Sea Region. Wadden Sea Ecosystem No. 21. Common Wadden Sea Secretariat. Wilhelmshaven, Germany.

CWSS, 1991. The Wadden Sea status and developments in an international perspective. Report to the sixth Governmental Conference on the Protection of the Wadden Sea. National Forest and Nature Agency, the Ministry of the Environment, Denmark and The Common Wadden Sea Secretariat.

CWSS, 2008. Nomination of the Dutch-German Wadden Sea as World Heritage Site. Wadden Sea Ecosystem No. 24, 1-200. Common Wadden Sea Secretariat. Wilhelmshaven, Germany.

CWSS, 2009. Nomination of the Dutch-German Wadden Sea as World Heritage Site. Supplementary Information. Common Wadden Sea Secretariat. Wilhelmshaven, Germany.

Dame, M. et al., 2000. Estuaries of the South Atlantic Coast of North America: Their geographical signatures. Estuaries, 23, 793–819

Dankers, N., Zuidema D.R., 1995. The role of the mussel (*Mytilus edulis*) and mussel culture in the Dutch Wadden Sea. Estuaries, 18, 71–80.

De Jong, F., Bakker, J., van Berkel, K., Dankers, N., Dahl, K., Gätje, C., Marencic, H., Potel, P., 1999. Wadden Sea Quality Status Report. Wadden Sea Ecosystem No. 9, 1-259.

Dronkers, J., 1984. Import of fine marine sediment in tidal basins. In: Proc. Fourth International Wadden Sea Symposium 1983. Neth Inst for Sea Res Publ Ser 10, 83-106.

Ehlers, J., 1988. Morphodynamics of the Wadden Sea. Balkema, Rotterdam.

Essink, K., Dettmann, C., Farke, H., Laursen, K., Lüerßen, G., Marencic, H., Wiersinga, W., (Eds), 2005. Wadden Sea Quality Status Report 2004. Wadden Sea Ecosystem No. 19, 1–359.

Fischer, L., Hasse, J., 2001. Historical and current perceptions of landscapes in the Wadden Sea region. In: Vollmer, M. et al. (Eds.) Landscape and cultural heritage in the Wadden Sea region. Wadden Sea Ecosystem No. 12, 72–97.

Flemming, B.W., 2002. Geographic distribution of muddy coasts. In: Healy, T., Wang, Y., Healy J-A (eds) Muddy coasts of the world: processes, deposits and function. Elsevier Science, Amsterdam, 99-201.

Flemming, B.W., Bartholomä, A., 1997. Response of the Wadden Sea to a rising sea level: a predictive empirical model. German J. Hydrogr., 49, 343–353.

Flemming, B.W., Davis, R.A. Jr., 1994. Holocene evolution, morphodynamics and sedimentology of the Spiekeroog barrier island system (southern North Sea). Senckenbergiana maritima, 25, 117-155.

Gerlach, S.A., 2004. Checkliste der Mikro- und Meiofauna im schleswig-holsteinischen Wattenmeer. In: Bundesanstalt für Gewässerkunde (Ed.). Die Biodiversität in der deutschen Nord- und Ostsee. Bd. 2. Bericht BfG-1397, Koblenz.

Hagmeier, A., Kändler, R., 1927. Neue Untersuchungen im nordfriesischen Wattenmeer und auf den fiskalischen Austernbänken. Wiss. Meeresunters. (Helgoland), 16,1–90.

Harten, H., Vollmers, H., 1978. The estuaries of the German North Sea coast. Die Küste, 32, 50-65.

Heydemann, B., 1981. Ökologie und Schutz des Wattenmeeres. Schriftenreihe Bundesministerium Ernährung Landwirtschaft Forsten, Reihe A: Angewandte Wissenschaft, 255, 1–232.

Holm, P., 2005. Human impacts on fisheries resources and abundance in the Danish Wadden Sea, c1520 to the present. Helgol. Mar. Res., 59, 39-44

Jansen, S., 2002. Das Räuber-Beutesystem juveniler Gadiden, Grundeln und Garnelen im Wattenmeer nördlich von Sylt. PhD Thesis, Hamburg: University Hamburg, 154 pp.

Kabat, P., Bazelmans, J., van Dijk, J., Herman, P.M.J., Speelman, H., Deen, N.R.J., Hutjes, R.W.A., 2009. Knowledge for a sustainable future of the Wadden. Integrated research agenda oft he Wadden Academy-KNAW. The Netherlands, 1–124.

Koffijberg, K., Dijksen, L., Hälterlein, B., Laursen, K., Potel, P., Südbeck, P., 2006. Breeding birds in the Wadden Sea in 2001. Wadden Sea Ecosystem No. 22, 1-132.

Kuipers, B.R., 1977. On the ecology of juvenile plaice on a tidal flat in the Wadden Sea. J. Sea Res., 11, 56-91.

Linke, O., 1939. Die Biota des Jadebusens. Helgol. Wiss. Meeresunters., 1, 201-348.

Loebl, M., Dolch, T., van Beusekom, J.E.E., 2007. Annual dynamics of pelagic production and respiration in a shallow coastal basin. J. Sea Res., 58, 269–282.

Lotze, H.K., 2005. Radical changes in the Wadden Sea fauna and flora over the last 2,000 years. Helgol. Mar. Res., 59, 71–83.

Marencic, H. and de Vlas, J. (Eds), 2009. Quality Status Report 2009. Wadden Sea Ecosystem No. 25. Common Wadden Sea Secretariat, Trilateral Monitoring and Assessment Group, Wilhelmshaven, Germany.

Möbius, K., 1877. Die Auster und die Austernwirthschaft. Wiegandt, Hempel & Parey, Berlin.

Nehls, G., Diederich, S., Thieltges, DW., Strasser, M., 2006. Wadden Sea mussel beds invaded by oysters and slipper limpets: competition or climate control? Helgol. Mar. Res., 60, 135-143.

Nehring, S., Reise, K., Dankers, N., Kristensen, P.S., 2009. Alien species. Thematic Report No. 7. In: Marencic, H. & Vlas, J. de (Eds), 2009. Quality Status Report 2009. Wadden Sea Ecosystem No. 25.

Niedringhaus, R., Haeseler, V., Janiesch, P., (Eds.) 2008. Die Flora und Fauna der Ostfriesischen Inseln - Artenverzeichnisse und Auswertungen zur Biodiversität. Nationalpark Niedersächisches Wattenmeer, 11, 1-470.

Oost, A.P., de Boer, P.L., 1994. Sedimentology and development of barrier islands, ebbtidal deltas, inlets and backbarrier areas of the Dutch Wadden Sea. Senckenbergiana maritima, 25. 65-115.

Philippart, C.J.M., Beukema, J.J., Cadée, G.C., Dekker, R., Goedhart, P.W., van Iperen, J.M., Leopold, M.F., Herman, P.M.J., 2007. Impacts of nutrient reduction on coastal communities. Ecosystems, 10, 96-119.

Piersma, T., 1987. Production by intertidal benthic animals and limits to their predation by shorebirds: a heuristic model. Mar. Ecol. Prog. Ser., 38, 187-196.

Postma, H., 1954. Hydrography of the Dutch Wadden Sea. Archs. Néerl. Zool., 10, 405-511.

Postma, H., 1961. Transport and accumulation of suspended matter in the Dutch Wadden Sea. Neth. J. Sea Res., 1, 148-190.

Priesmeier, K., 1970. Form und Genese der Dünen des Listlandes auf Sylt. Schr. Naturw. Ver. Schlesw.-Holst., 40, 11-51.

Rahmstorf, S., 2007. A semi-empirical approach to projecting sea-level rise. Science, 315, 368-370.

Reijnders, P.J.H-, van Dijk, J., Kuiper, D., 1995. Recolonization of the Dutch Wadden Sea by the grey seal Halichoerus grypus. Biological Conservation, 71, 231-235.

Reineck, H.E., Singh, I.B. (Eds.) 1980. Depositional sedimentary environments. Springer-Verlag, Berlin.

Reise, K. (Ed.) 2001. Ecological comparisons of sedimentary shores. Ecological studies 151. Springer-Verlag, Berlin.

Reise, K., Herre, E., Sturm, M., 1994. Biomass and abundance of macrofauna in intertidal sediments of Königshafen in the northern Wadden Sea. Helgol. Meeresunters., 48, 201-215.

Reise, K., Kohlus, J., 2008. Seagrass recovery in the Northern Wadden Sea? Helgol. Mar. Res., 62, 77-84.

Scheiffarth, G., Nehls, G., 1997. Consumption of benthic carnivorous birds in the Wadden Sea. Helgol. Meeresunters., 51. 373-387.

Smidt, E.L.B., 1951. Animal production in the Danish Waddensea. Med. Kom. Danm. Fiskeri- og Havunders. Ser Fiskeri, 11(6), 1-151.

Strasser, M., 2002. Reduced epibenthic predation on intertidal bivalves after a severe winter in the European Wadden Sea. Mar. Ecol. Prog. Ser., 241, 113-123.

Streif, H., 1989. Barrier islands, tidal flats, and coastal marshes resulting from relative rise of sea level in East Frisia on the German North Sea coast. Proceedings KNGMG Symposium 'Coastal Lowlands, Geology and Geotechnology', 1987, 213-223.

Thamdrup, H.M., 1935. Beiträge zur Ökologie der Wattfauna. Medd. Dan. Fisk. Havunders., 10(2), 1-125.

Thieltges, D.W., Krakau, M., Andresen, H., Fottner, S., Reise, K., 2006. Macroparasite community in molluscs of a tidal basin in the Wadden Sea. Hegol. Mar. Res., 60, 307-316.

Van Beusekom, J.E.E., 2005. A historic perspective on Wadden Sea eutrophication. Helgol. Mar. Res., 59, 45-54.

Van Beusekom, J.E.E., de Jonge, V.N., 2002. Long-term changes in Wadden Sea nutrient cycles: importance of organic matter import from the North Sea. Hydrobiologia, 475/476, 185-194.

Van Straaten, L.M.J.U., 1954. Composition and structure of recent marine sediments in the Netherlands. Leidse Geol. Med. 19. 1-110.

Van Straaten, L.M.J.U., Kuenen, P.H., 1957. Accumulation of fine-grained sediments in the Dutch Wadden Sea. Geol Mijnbouw, 19, 329-354.

Verwey, J., 1952. On the ecology on the distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply. Archs néerl. Zool., 10, 171-239.

Volkenborn, N., Hedtkamp, S.I.C., van Beusekom, J.E.E., Reise, K., 2007. Effects of bioturbation and bioirrigation by lugworms (Arenicola marina) on physical and chemical sediment properties and implications for intertidal habitat succession. Estuar. Coast. Shelf Sci., 74, 331-343.

Weisse, R., Plüß, A., 2006. Storm-related sea level variations along the North Sea coast as simulated by a high-resolution model 1958-2002. Ocean Dynamics, 56, 16-25.

Wohlenberg, E., 1937. Die Wattenmeer-Lebensgemeinschaften im Königshafen von Sylt. Helgol. Wiss. Meeresunters., 1, 1-92.

Wohlenberg, E., 1953. Sinkstoff, Sediment und Anwachs am Hindenburgdamm. Die Küste, 2(2), 33-94.

Wolff, W.J. (Ed.) 1983. Ecology of the Wadden Sea. Balkema, Rotterdam, The Netherlands.

Wolff, W.J., 2000. Causes of extirpations in the Wadden Sea, an estuarine area in The Netherlands. Conservation Biology, 14.876-885.

Wolff, W.J., van der Land, J., Nienhuis, P.H., de Wilde, P.A.W.J., 1993. The functioning of the ecosystem of the Banc d'Arguin, Mauritania: a review. Hydrobiologia, 258, 211-222.

Wolff, W.J., Zijlstra, J.J., 1980. Management of the Wadden Sea. Helgol. Meeresunters., 33, 596-613.

Wymenga, E., Engelmoer, M., Smit, C.J., van Spanje, T.M., 1990. Geographical breeding origin and migration of waders wintering in West Africa. Ardea, 78, 83-112.

Zagwijn, W.H., 1986. Nederland in het Holoceen. Rijks Geol. Dienst, Haarlem, 46 pp.

Zijlstra, J.J., 1972. On the importance of the Waddensea as a nursery area in relation to the conservation of the southern North Sea fishery resources. Symp. Zool. Soc. Lond., 29, 233-258.