ECOLOGICAL COMPARISON OF TWO SANDY SHORES WITH DIFFERENT WAVE ENERGY AND MORPHODYNAMICS IN THE NORTH SEA

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View from the lab to the boat “Sandy beach”, List/Sylt

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1 GENERAL INTRODUCTION

Sandy beaches attract many people by a combination of phenomena. They provide views and settings, sea-scapes and waves, surf and swash, all dynamic and ever-changing scenes. Beaches provide the shore for walks and fishing, the dry beach for resting and playing, and the surf zone for those who wish to venture into the area of swash, wave bores, breaking waves and currents. From the scientific point of view exposed sandy shores are one of the most dynamic physical systems on the earth's surface. They may be regarded as typifying a physically controlled habitat to a large extent for the organisms which inhabit it. Wave energy associated with sediment particle size and tidal range has been emphasized as a major structuring force for beach morphology, and for the infaunal communities of these habitats (e.g., Brown & McLachlan 1990; Short 1999; Fig. 1). Thus, shore morphodynamics may considerably influence the biotic beach system. In turn, ecological interactions can exert direct and indirect influences on the physical nature of the beach (Short 1999).

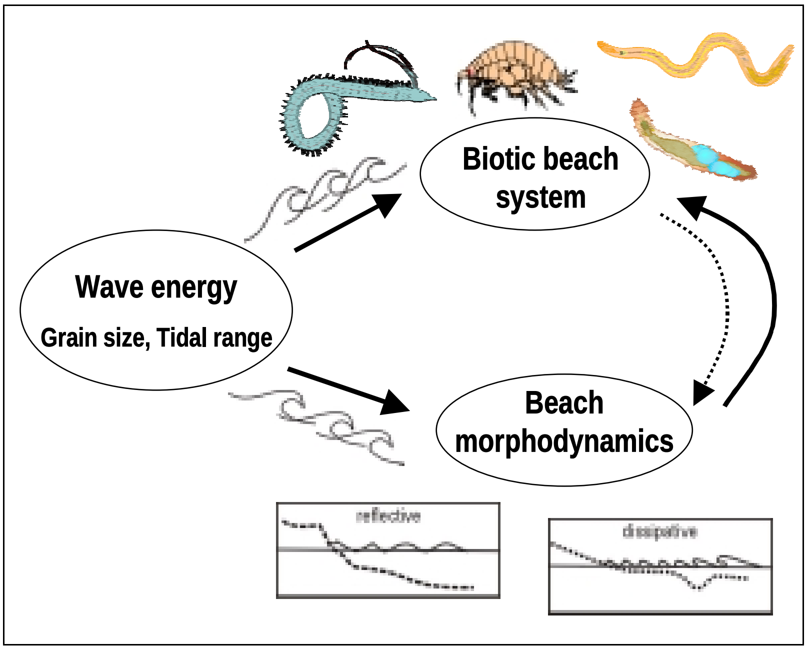


Fig. 1 Schematic model of interactions between wave energy, beach morphodynamics and the biotic components on sandy shores.

The present study is an ecological comparison between two exposed sandy shores of different wave energy and morphodynamics in the North Sea. It adresses the general question of the effect of wave energy on different infaunal components on sandy shores, and on the entire biological (and morphological) beach system. In view of increasing wave energy on sandy shores as a corollary of global warming (Bird 2000; Lozán et al. 2001) this question may become increasingly important in the coming decades. Simultaneously, the demand of beach management may increase in the foreseeable future (Nordstrom 2000), and its cost to physical features and ecological values of sandy shores should be evaluated. This is done for beach nourishment operations in the present study.

Studying beach ecology requires an understanding of shore morphodynamics. Therefore, the first section (1.1) of this general introduction includes a sandy beach definition (1.1.1), basic shore morphodynamics (1.1.2) and the mode of erosion (1.1.3). Then, a short overview of the history of biological beach research (1.1.4), and an introduction to the beach ecosystem (1.1.5) is given. Section 1.2 focusses on human interferences to this system, and finally, the hypotheses and the outline of this study (1.3) are presented.

1.1 Sandy beaches

1.1.1 Occurrence and definition

Sandy beaches occur on all sedimentary shorelines exposed to waves, wherever there is sufficient sediment for the waves to deposit it above sea level (Short 1999). They are essentially similar on coasts in various climatic environments, except in cold regions where wave action ceases, at least in winter, because of the freezing of the sea. Estimates of the proportion of sandy beaches on the world’s coastline range from 11% (53 000 km) to 34 % (170 000 km) (Short 1999). Existing beaches are geologically of recent origin, having formed as the Late Quaternary marine transgression slackened or came to a Holcene sea level stillstand: on most coasts about 6000 years.

Beaches can be defined in numerous ways and the term sandy beach has been often loosely used in the literature to cover a wide range of environments from high energy open ocean beaches to extremely sheltered estuarine sandy flats. For the purpose of this study the sandy beach/shore is defined according to Brown & McLachlan (1990). It is considered to be a marine sandy littoral area exposed to the sea including the zone of wave shoaling across the nearshore zone, wave breaking across the surf zone, and wave dissipation in the swash zone (Fig. 2).

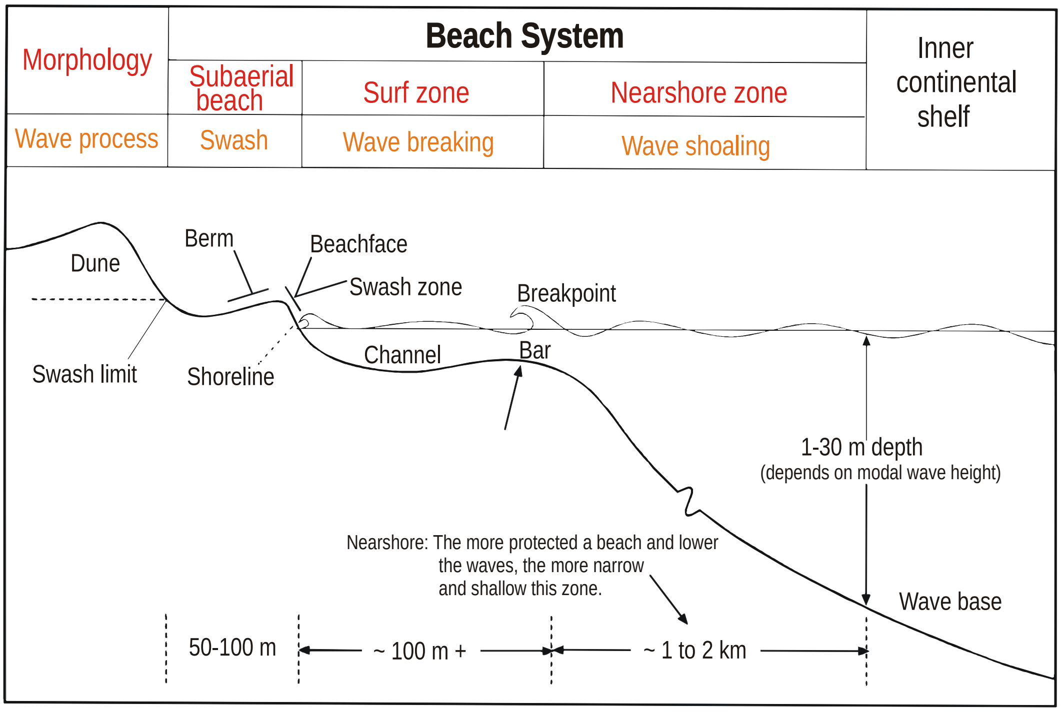


Fig. 2 Exposed, high energy sandy beach system (modified from Short 1999).

1.1.2 Morphology

Basically, shore morphology is a function of waves and sediment (Brown & McLachlan 1990; Short 1999). A range of additional processes, such as tide and wind, also influence the shore morphodynamics. Short & Wright (1983) categorized exposed sandy beaches in several types (Fig. 3). Dissipative beaches represent the high energy end of the beach spectrum. They are a product of large waves moving over fine sand, resulting in a flat beachface and wide surf zone. Spilling breakers dissipate their energy while traversing the surf zone as bores before expiring as swash on the beachface. Dissipative beaches tend to have relatively stable morphologies, and exhibit minimal shoreline change (Short & Hesp 1982; Short 1983). Textbook examples occur on the west coasts of Australia (Short 1996) and southern Africa (McLachlan et al. 1993).

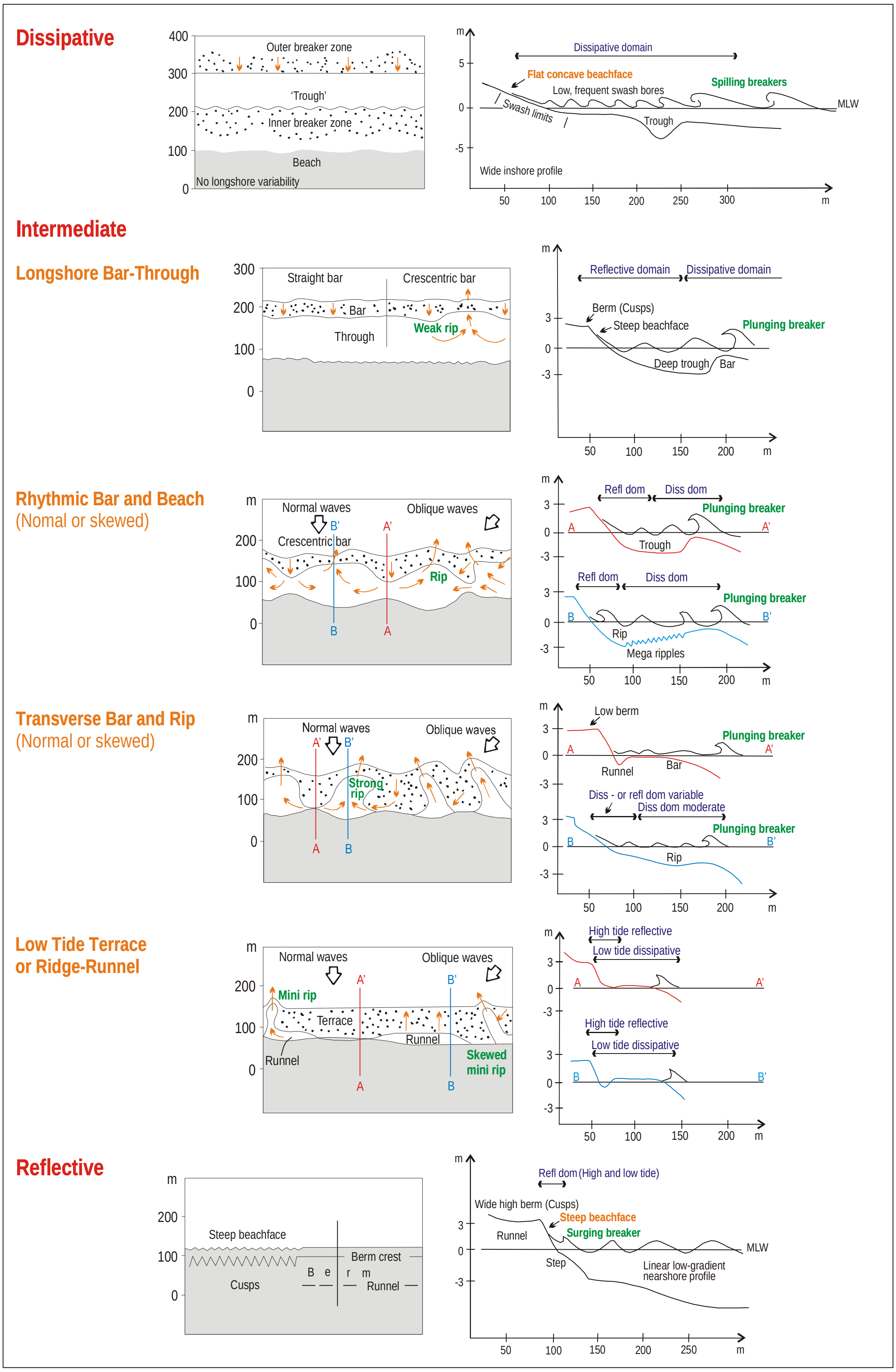


Fig. 3 Top view (left) and side profile (right) of wave-dominated beach types. Simplified from Short (1999). For more details see Short (1999). MLW = Mean low water.

Reflective beaches lie at the lower energy end of the spectrum, though not necessarily in areas of low waves (Short 1999). They are favoured by combinations of lower waves and/or longer periods or coarse sediments. Reflective beaches are always characterized by a relatively narrow beach and swash zone, and a absence of surf zone. Waves moves unbroken to the shore where they collapse or surge up the beachface. The latter is relatively steep and if there is a range of sand size, the coarsest sand will accumulate at the base of the swash zone as a step (Hughes & Cowell 1987; Bauer & Allen 1995). Sand is transported shoreward under these conditions and stored on the subaerial beachface. Thus, beach cusps are commonly present. Good examples can be found along shores of the North Sea and the English Channel (Mann 2000).

Intermediate beaches represent a transition from high energy dissipative to low energy reflective beaches (Short & Wright 1983). They occur under a wide range of environmental conditions, ranging from moderate to high waves (0.5 to 2.5 m), fine to medium sand, and longer wave periods. Four beach states were distinguished mainly in response to wave conditions. Immediately below the high energy dissipative type is the longshore bar and through, then the rhythmic bar and beach, next the transverse bar and rip and finally the low tide terrace (Wright & Short 1984). In intermediate systems, spatial wave transformation gradients are larger, nearshore slopes are steeper and incident waves tend to break trough plunging, particularly when they have a relatively low steepness. The most obvious characteristic of intermediate beaches is a pronounced longshore variability caused by alternating rip and bar topography. Dynamically they are characterized by increasing rip circulation. Intermediate shores are the most mobile in terms of sediment exchange and most common world-wide.

In nature beaches actually exist in a continuum of types, hence the states presented in figure 3. Where a particular beach usually resides in the spectrum is dependent on its modal wave height and sediment parameters (Short 1999).

1.1.3 Mode of erosion

Beaches are not locked into a single morphodynamic type and respond to changes in wave energy. For a given beach type, waves that are much larger than the average causes strong backwash and strong erosion. There is a general tendency for erosion to take place during storms (Fig. 4) and for this to be balanced by accretion during the rest of the year (Short 1999). Thus, in temperate climates where storms tend to be concentrated in winter, the general pattern for beaches is to be eroded during winter and built up again during spring and summer (Bird 1985). In winter they are closer to the dissipative type, and in summer closer to the reflective.

Fig. 4 Erosion of the exposed western side on the island of Sylt (Germany) in the North Sea after a winter storm 1998.

However, a net erosion has become widespread. More than 70 % by length of beach-fringed coastlines retreated over the past few decades, while less than 10 % prograded, and the remaining 20 to 30 % having shown no measurable change (Bird 2000). No single explanation can account for the modern prevalence of erosion of the world's beaches, or for the onset or acceleration of erosion on any particular beach. Erosion is not simply the outcome of human activities such as artificial structures and reduced riverine inputs, of sea level rise, an increase in storminess or the maturing of the system as the sediment supply from the sea floor dwindled during the Holocene stillstand. Instead, each of these factors may have contributed to beach erosion, to an extent which differs from place to place (Bird 2000).

However, the beach erosion problem will intensify if, as predicted, the global sea level rise increases in the next decades as a corollary of global warming (Leatherman 1987; Short 1999; Bird 2000; Lozán et al. 2001). Generally, a sea level rise will result in a deepening of nearshore water, so that larger waves break upon the shore, initiating erosion on beaches or accelerating it where it is already taking place. In most cases the high tide line will move landward as the result of submergence and accompanying erosion as the nearshore profile also migrates landward. Where the climatic changes that accompany the rising sea level lead to more frequent and severe storms, generating surges that penetrate further inland than they do now, erosion will further increase (Bird 2000). An increasing storminess occurred in the eastern North Sea, measured as elevated storm tide levels during the last three decades in correspondence to a North Atlantic climate anomaly (Siefert 1984; Führböter & Dette 1992; Hofstede 1997). The prediction that beach erosion will be initiated or accelerated by a rising sea level has to be reconciled with evidence that in the geological past some marine transgressions were accompanied by shoreward drifting of sea floor sediment, and that beaches formed and prograded on coastlines as sea level rise slackened and came to an end (Short 1999).

1.1.4 Historical overview of biological beach research

In contrast to studies on rocky shores the beach ecosystem was largely neglected until Remane (1933) started studies on a sheltered beach at the coast of Germany. Sandy shores at first sight are almost devoid of life, and observations of sandy beach infauna *in situ* is far more difficult than on the rocky shore. Additionally, the dynamics of the beach system precludes the performence of manipulative experiments. The research on beaches has spread from sheltered towards exposed shores and from early taxonomic and qualitative through quantitative ecology and physiology of important species towards more holistic approaches. Pioneering studies which represent a first qualitative attempt to evaluate a whole beach system were that of Pearse et al. (1942) and Hedgpeth (1957). The work on sandy beaches up to the late 80’s was reviewed by Brown & McLachlan (1990). Most biological studies concentrated on the intertidal infauna, while large gaps still occur on the ecology of surf zone biota of high energy sandy beaches. Within studies on the intertidal infauna, macrofauna has been far more intensively studied than the meio- and microfauna, caused by difficulties to collect and identify the latter. Studies of e.g., Remane (1933, 1940, 1952), Delamare Deboutteville (1960), Swedmark (1964), Ax (1966), Jansson (1966) Fenchel et al. (1967), Jansson (1967a+b, 1968), McInytre (1968), Schmidt (1968), McInytre (1969), Schmidt (1969), Ax (1969), McInytre (1971), and Fenchel (1978) are considered as basic sources on the ecology and systematics of sandy beach meiofauna.

A beach site where meiofauna research has been done with unrivaled intensity is a sheltered sandy beach at the east coast of the German Wadden Sea island Sylt. In a sequence of taxonomic and ecological surveys over more than 30 years almost all major taxa of interstitial fauna were investigated individually and all surveys followed a similar scheme introduced by Schmidt (1968, 1969) (e.g., Westheide 1966, 1967; Schmidt & Teuchert 1969; Ax 1971; Müller & Ax 1971; Ehlers 1972, Sopott 1972; Ehlers 1973; Hartwig 1973a+b; Sopott 1973; Blome 1974; Ehlers 1974, Faubel 1974a+b, 1976; Mielke 1975, 1976; Blome 1982, 1983; Armonies & Hellwig-Armonies 1987; Hoppenrath 2000a-d). Armonies & Reise (2000) integrated these data and produced an overview of the total number of species on this shore. There is probably no other beach site where the total number of species can be given at a similar level of completeness (Armonies & Reise 2000). Studies on the extensive (~ 40 km) exposed sandy shore at the west coast of Sylt were definitely more scarce and less systematic in comparison to that on the sheltered beach. The latter included sometimes on lower level of effort a sampling on the exposed shore (e.g., Westheide 1967; Schmidt 1968, 1969; Schmidt & Teuchert 1969; Hartwig 1973b; Bartsch & Schmidt 1979; Reise 1988; Wellner & Reise 1989).

1.1.5 Sandy beach ecosystem

The following short introduction to the beach ecosystem focusses mainly on the infauna. Analyses of the whole size spectrum of sandy beach benthic organisms consistently showed three size peaks corresponding to bacteria, meiofauna and macrofauna (Schwinghammer 1981; Warwick 1984), with discontinuities between grain colonisiers and interstitial forms and between interstitial forms and macrofaunal burrowers (Fig. 5). The benthic macrofauna of exposed sandy beaches is usually dominated by crustaceans, molluscs and polychaetes. In the meiofauna nematodes, copepods, plathelminths, polychaetes and ostracods are the major taxa (McIntyre 1977). Further biotic components of the beach ecosystem are epibenthic predators, such as shrimps, crabs, fishes and shorebirds, and water column organisms in the surf and nearshore zone.

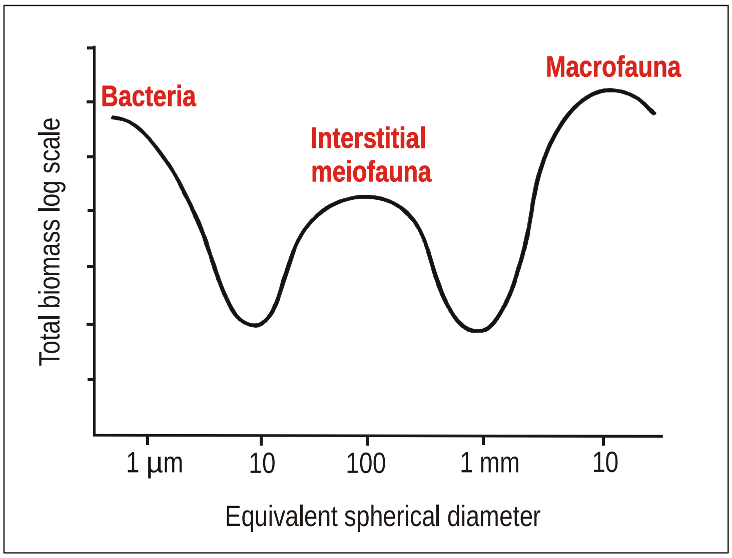


Fig. 5 Size spectrum of benthic biota on sandy beaches, based on Schwinghammer (1981) and Warwick (1984).

As mentioned above, sandy shores are physically dominated habitats in which wave energy interacting with sediment particle size may be the major controlling factor of the entire biotic beach system. However, for meio- and macroinfauna a divergent sensitivity to these abiotic factors is assumed, because they may represent, additionally to their difference in size, biologically and ecologically seperate groups of animals on sandy shores (McIntyre 1968, 1971; McLachlan 1977b). Wave exposure has strong adverse effects on macrofauna, resulting in an increase of macrofaunal abundance and diversity from reflective to dissipative shores (e.g., Shelton & Robertson 1981; McLachlan 1983; Jaramillo & Gonzales 1991; Jaramillo & McLachlan 1993). In contrast, wave exposure seems to be less important for meiofauna (McIntyre 1971; McLachlan 1977b; Mann 2000). Meiofauna may be somewhat buffered against the physical extremes of the seashore, because it tends to live below the sediment surface during the entire tidal cycle, as well as during their entire life (Armonies & Reise 2000). In contrast, most macrofaunal species tend to occur at or close to the sand surface, depending on the latter for feeding, respiration, larval settlement or migration among others.

Sandy beach infauna showes a highly patchy distribution across and along the shore. Intertidal macrofaunal zonation on sandy beaches has been studied by several authors (reviewed by McLachlan & Jaramillo 1995), resulting in two major zonation schemes: A biologically defined tripartite division of the intertidal shore primarily based on crustacean distribution (Dahl 1952), and a subdivision of four zones based on physical changes across the shore (Salvat 1964, 1967). For meiofauna a more complex three-dimensional distribution pattern determined by chemical gradients and interstitial moisture content was proposed (Fenchel & Riedl 1970; Pollock & Hummon 1971; McLachlan et al. 1979; McLachlan 1980b; Brown & McLachlan 1990; Giere 1993). Zonation is not only an intertidal phenomenon. However, only few authors studied zonation patterns from the intertidal towards the subtidal (e.g., McIntyre & Eleftheriou 1968; Knott et al. 1983; Reise 1985; Brown & McLachlan 1990). They reported an increase of macrofaunal species number, diversity and abundances in downshore direction, with a short interruption at the wave breaking point (Fig. 6). For meiofauna, a contrasting pattern is assumed with lower species number and abundances in the subtidal than in the intertidal (McIntyre & Murison 1973; McLachlan 1977a+b; Reise 1985; Armonies & Hellwig-Armonies 1987; Brown & McLachlan 1990; Giere 1993). Generally, a prediction of zonation schemes on sandy shores may be difficult due to a high variability of faunistic zones in time and space (Dexter 1984; Brown & McLachlan 1990; McLachlan & Jaramillo 1995; Brazeio & Defeo 1996; Giere 1993). Zonation is therefore often just valid for the period of investigation indicating that the long-term performence of the sandy beach ecosystem is poorly understood.

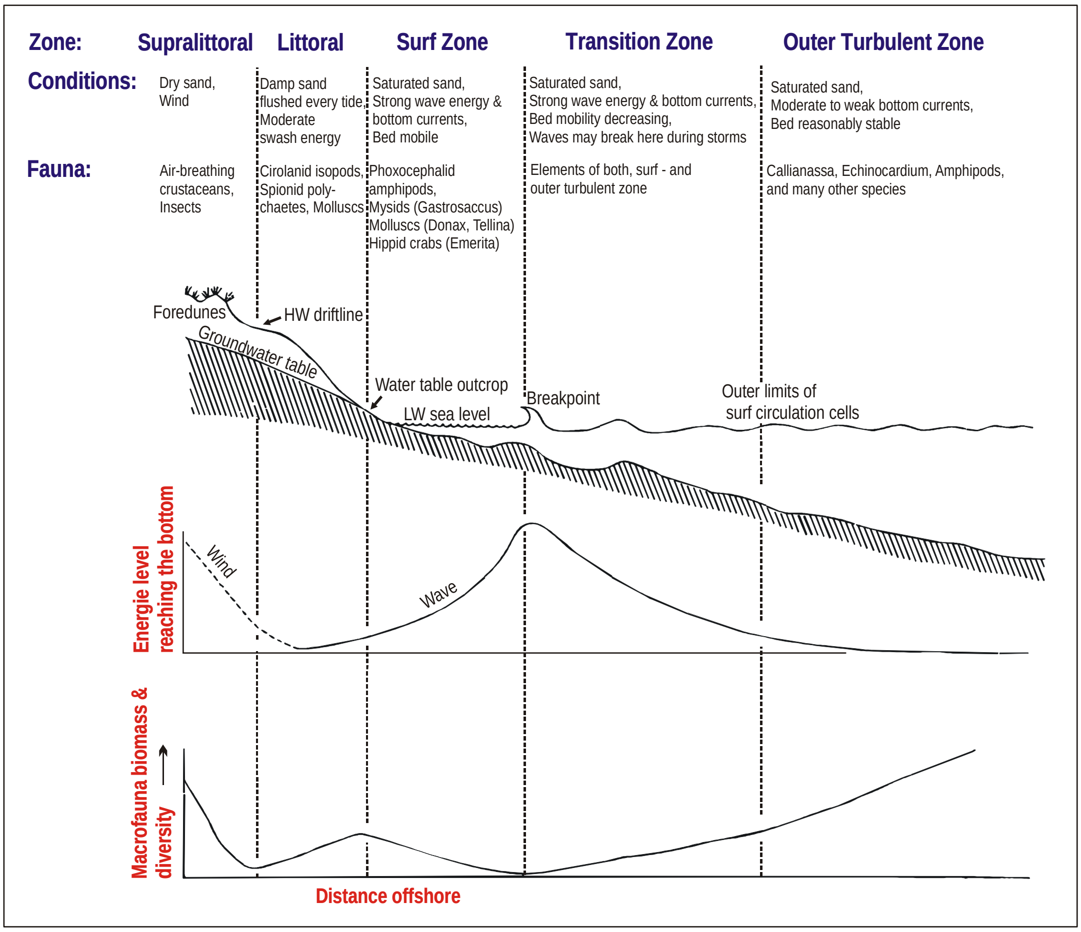


Fig. 6 Generalised scheme of macrofaunal zonation on sandy shores, including features of the schemes proposed by Dahl (1952) and Salvat (1964, 1967). Modified from Brown & McLachlan (1990).

1.2 Human interferences on sandy shores

Sandy beaches are prime recreational areas of great socio-economic importance as tourist attractions and for the local human population (Brown & McLachlan 1990; Nordstrom 2000). The use of sandy beaches as recreational areas is accompanied by many human interferences on the ecosystem (Fig. 7). The presence of people on the beach and swimming in the surf zone has marked effects on the activities of some members of the fauna, such as shorebirds, fishes and semi-terrestrial crustaceans (e.g. *Ocypode* sp.) (Brown & McLachlan 1990). Beach grooming (the removal of wrack, kelp and other detritus), a common practice on bathing beaches, may affect sand transport and fordune stability, as well as depriving some sandy beach animals of shelter or food, or both (Brown & McLachlan 1990; Mann 2000). Other forms of human interferences on sandy beaches include the driving of vehicles along them, the littering of the shore with debris and the polluting of the ecosystem with oil slick from oil platforms, pipelines, tankers etc. (McInytre 1977; Mann 2000; Nordstrom 2000). Open coast beaches are generally quite resilient, even to human traffic (Brown & McLachlan 1990). However, recreational activities increased dramatically during the last decades and there is no indication that the trend will be reversed (Nordstrom 2000). Thus, beaches are subjected to ever-increasing pressure from recreational activities, and litter left by human visitors has already become an escalating problem (Brown & McLachlan 1990).

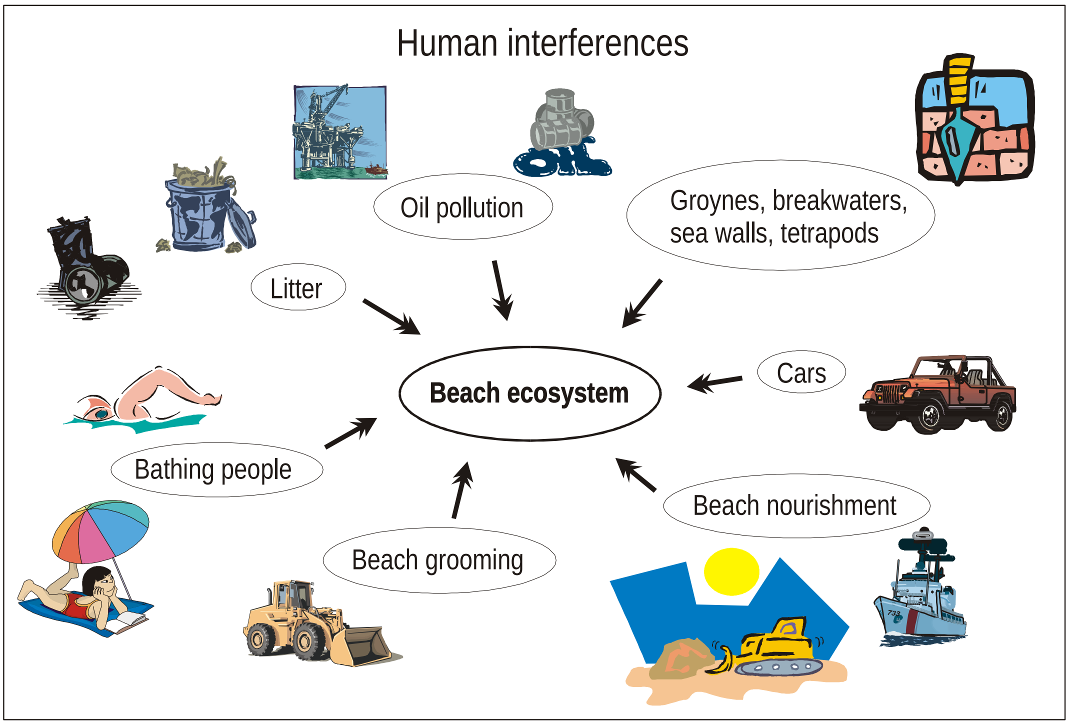


Fig. 7 Human impacts on the beach ecosystem.

However, on all beach types most severe effects are due to major engineering structures and other large scale disturbances, which disrupt sand movements and change wave and wind climates. Engineering structures, such as groynes, breakwaters, sea walls or the placement of tetrapods are a common response to beach erosion, especially where it threatens to undermine and destroy developed property such as roads and buildings

(Nordstrom 2000; Fig. 8). This led to littering of the world's coastline with an array of artificial structures of various kinds (Bird 2000). The east coast on the island Sylt (Germany) in the North Sea provides an example in case for such an development. Currently, 35 % of the coastline are artificially reinforced, and Lackschewitz et al. (2000) estimated an increase up to 77 % with increasing erosion when the recent policy of coastal management is continued.

Fig. 8 Sea wall associated with tetrapods on the exposed shore on the island of Sylt (Germany) in the North Sea.

Some of these "hard" defences were successful, but many have failed and became derelict; others have been found unsatisfactory due to hazards to beach users and lack of aethetic appeal (Walton & Sensabaugh 1979; Reilly & Bellis 1983; Pilkey & Wright 1989; Cooper 1998). In view of these limitations, beach nourishment as a "soft" defence has become a preferred method for dealing with shoreline erosion (Reilly & Bellis 1983; Nelson & Pullen 1985; Nelson 1993; Nordstrom 2000). The essential effect of this artificial sand deposition on the beach is to move the beach state back in time and to allow it to repeat an earlier sequence of erosion (Fig. 9). Initially, beach nourishment projects have been at seaside resorts that had eroding beaches and wanted them restored for recreational use. However, in recent years increasing awareness of the importance of beaches in absorbing wave energy resulted in increased use of beach nourishment to protect the coastline and prevent further cliff erosion or damage of coastal property. World-wide, its use rapidly increased in the last decades, and this was accompanied by an increasing volume of replenished material per project (Valverde et al. 1999).

Fig. 9 Nourished sediment forms a new cliff on the beach of approximately 2.5 to 3 m depending on the volume of nourished material (island of Sylt, Germany).

1.3 Thesis outline

We have seen that wave energy in combination with sediment grain size may be a major factor for the morphological and biological beach system, probably with different effects on the individual faunal components. If wave energy increases by increasing sea level rise as a corollary of global warming, questions of its effect on the biotic beach system become increasingly important: What are the ecological consequences of increasing wave energy on sandy shores? Will increasing wave energy result in a community shift on sandy beaches? Simultaneously, increasing wave energy affects beach morphodynamics and is expected to increase coastal erosion (Bird 2000). This may result in increasing beach management to combat erosion. Traditionally coastal management mainly focussed on the safety of people living near the coast and on the safety of developed property rather than on conservation or restoration of ecosystems. Management primarily meant managing the sand budget, while plants and animals were of secondary importance (Brown & McLachlan 1990). However, if the ecosystem status shall be maintained or re-established, ecological criteria must be taken into account, such as the consequences of nourishment operations for the beach ecosystem. Coastal management needs to reconcile socio-economic and environmental-conservational interests.

The proximity of two sandy shores in the North Sea with strongly differing wave energy and morphodynamics provides a natural experiment and a unique chance to reveal the effect of wave energy on cold-temperate beach ecosystems (Fig. 10). The shore on the island of Rømø is accreting, fine grained, flat profiled, receives low wave energy, and resembles a dissipative beach type constant during the entire year (Fig. 11). The beach on the neighbouring island Sylt (12 km distance) is eroding, coarse grained, steep profiled and receives high wave energy (Fig. 12). It resembles an intermediate beach type, with distinct seasonal morphodynamics. During winter it tends more towards “longshore bar-through” and “rhythmic bar and beach” types, and during summer it resembles more “transverse bar and rip” and “low tide terrace” beach types (see Fig. 3). Contrary to the Rømø shore, the Sylt shore is strongly controlled by wave energy. Both shores are important recreational sites. No beach management occurs at Rømø, while at Sylt erosion is managed by recurrent beach nourishment since 1988. This may enhance the dynamics of the Sylt beach system because it prevents the morphodynamic state to reach equilibrium (Short 1999).

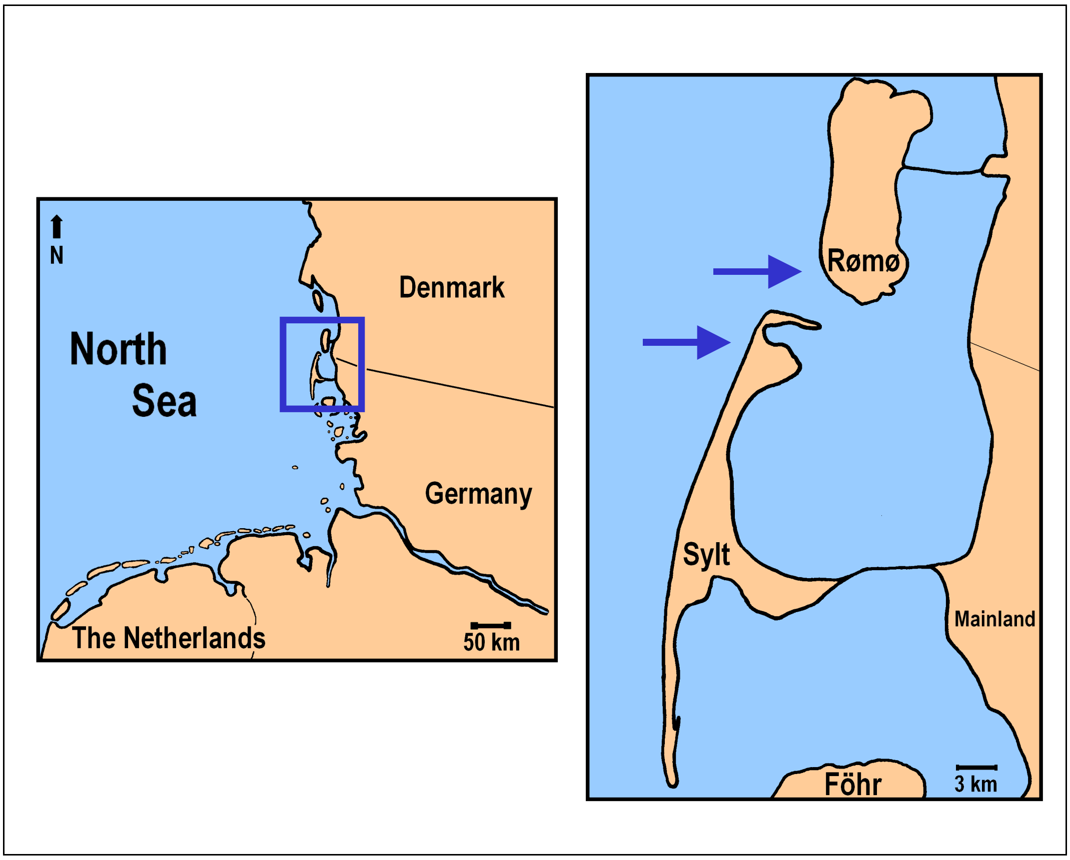


Fig. 10 Study sites (blue arrows) on the Wadden Sea islands Sylt (Germany) and Rømø (Denmark) in the eastern North Sea.

Fig. 11 Accreting beach with low wave energy on the island of Rømø (Denmark).

Fig. 12 Erosive shore with high wave energy on the island of Sylt (Germany) (Photo: K. Reise).

The primary objective of this thesis is on the effects of wave energy on meio- and macrofauna dwelling in the sediment. Simultaneous studies of these two faunal components on sandy shores are scarce, especially studies with meiofauna on species level. However, such a simultaneous and detailed look may provide insights on the ecological distinction between meio- and macrofauna in the biotic beach system. This objective is extented by studying temporal variability and zonation of these two faunal assemblages. In contrast to a focus of most sandy beach studies on the intertidal the present investigation includes inter- and subtidal sampling. Chapter 2 is focussed on the overall community structure and temporal variability of the meio- and macrofauna of the entire shore, while in chapter 3 across shore distribution of these faunal components is presented. A less abundant and less diverse infauna with more pronounced temporal variations was hypothesized on the shore with high wave energy, compared to the shore with low wave energy. Zonation of the two faunal components from the intertidal towards the subtidal may diverge, due to a high susceptibility of macrofauna to tidal emergence and hydrodynamic turbulence, while meiofauna, living at a different spatial scale, may be more responsive to the oxygen-sulfide chemocline within the sediment.

Wave energy and shore morphology may have implications on the entire beach ecosystem and predictions of community shifts on sandy shores due to a climatic change require a detailed knowledge of the *entire* faunal assemblage. To provide a more comprehensive picture of the food webs on the two shores, additionally to meio- and macroinfauna, parameters on food supply, aquatic epibenthos, and shorebirds are presented (chapter 4). For inferences on mineralisation, concentrations of dissolved inorganic nutrients in interstitial and surf waters are measured. Of course, the food webs are not complete. The biotic components of the water column are left aside and the supralitoral zone of the shores is not included in the infauna sampling.

In view of an increasing demand of coastal defence in the foreseeable future this thesis includes a study on the impact of beach nourishment on meio- and macroinfauna (chapter 5).

Thus, the present study comparing two sandy shore ecosystems differing in wave energy and morphodynamics, and including the effects of human interferences on the beach system, may offer first ideas on the ecological consequences of increasing hydrodynamic forces on exposed cold-temperate sandy shores in the North Sea in the next decades. Of course, this comparison of just two sandy shores in the North Sea cannot yield a general prediction of the sandy shore development due to a climatic change, neither morphologically nor biologically. The morphological pattern depends on local geological conditions, and a community shift may differ in different biogeographic regions.

2 MACRO- AND MEIOFAUNA ON TWO SANDY SHORES WITH LOW AND HIGH WAVE ENERGY: COMMUNITY COMPOSITION AND TEMPORAL VARIABILITY

ABSTRACT Meio- and macrofauna diverge in their sensitivity to wave energy on sandy shores. This is shown by a comparison of shores from the neighbouring barrier islands Sylt and Rømø in the North Sea, differing in wave energy, grain size and shore morphology. The Sylt shore is eroding, coarse grained, steep profiled and receives high wave energy, while the Rømø shore is accreting, fine grained, flat profiled and receives low wave energy. The former resembles highly dynamic intermediate beach types and the latter a stable dissipative beach. Meiofaunal abundance was similar on both shores, while species density and diversity of interstitial plathelminths and polychaetes were higher at Sylt than at Rømø. In contrast, macrofaunal abundance, species density, and diversity were all lower at Sylt than at Rømø. At Sylt the meiofauna was composed of roughly equal proportions of several major taxa, while at Rømø nematodes dominated strongly. Polychaetes were the most abundant macrofaunal taxon on both shores, followed by amphipods and isopods at Sylt, and by bivalves and amphipods at Rømø. Community analyses for both, meio- and macrofauna, revealed separate faunal assemblages for the two shores. In both faunal components highly mobile species were more prominent at Sylt than at Rømø. Temporal variability of meiofauna was higher at Sylt, while a higher temporal variability of macrofauna was observed at Rømø. In conclusion, high wave energy on the intermediate shore primarily affected the macrofauna, while the meiofauna diversified. Low wave energy on the stable, dissipative shore favoured macrofauna and nematodes adapted to low oxygen conditions.

Introduction

Sandy beaches are the most widely distributed intertidal habitat, dominating the temperate and tropical shorelines of the world (Dexter 1992). The morphology of a beach results from interactions between the available sediment and the energy of the waves impinging on the shoreline (Brown & McLachlan 1990; Short 1999). By combining wave energy and grain size, exposed sandy shores have been categorized into several types between dissipative and reflective beaches (Short & Wright 1983; Short 1999). Dissipative beaches are characterized by fine sand, a flat slope and a wide surf zone where waves break, and consequently, dissipate most of their energy before reaching the beachface. Reflective beaches, in contrast, have coarse sand, a steep slope and virtual absence of a surf zone. Thus, waves break directly on the beachface and reflect much energy back to the sea. Intermediate types can be distinguished between these two extremes. Several indices have been proposed to quantify the morphodynamic state of a beach by integrating parameters such as wave height, sediment fall velocity, and tidal range (e.g., fall velocity Ω, relative tidal range RTR, beach state index BSI) (McLachlan et al. 1993; Short 1999).

Studies in many parts of the world investigated sandy beach macrofauna and their responses to changes in physical factors, such as wave energy and sediment composition (see Trevallion et al. 1970; Eleftheriou & Nicholson 1975; McLachlan et al. 1981; Dexter 1983; McLachlan & Hesp 1984; Dexter 1990; Ismail 1990; Jaramillo & Gonzales 1991; McArdle & McLachlan 1992; Defeo et al. 1992; Jaramillo & McLachlan 1993; McLachlan et al. 1993; Souza & Gianuca 1995; Hacking 1998). Macrobenthic communities match well with the physical classification of sandy beaches, and the combined effect of wave energy, sand particle size and beach slope was proposed as the main factor determining the macrofauna assemblage (e.g., McLachlan et al. 1993; Jaramillo 1994). In this context, the “swash exclusion hypothesis” was proposed, explaining the control of intertidal macrofauna abundance and diversity by a “swash climate”, determined by wave height and beachface slope (McArdle & McLachlan 1992; McLachlan et al. 1993). Most investigations were limited to the intertidal zone and rarely included the meiofauna (e.g., Jansson 1967; McIntyre 1968, 1971; Gray & Rieger 1971; Hulings & Gray 1976; McLachlan 1977a, 1977b, 1980; McLachlan et al. 1981, 1984; Armonies & Reise 2000). Inclusion of the subtidal shore will provide a more complete picture, and since meio- and macrofauna form distinct communities on sandy shores, they may be controlled by different factors (McIntyre 1971; McLachlan 1977b).

The very different shores of two adjacent barrier islands in the North Sea provide a unique chance to reveal the effects of low and high wave energy on meio- and macrofauna from the mid shore down to subtidal level in the course of a year. One of the shores is eroding, coarse grained, steep profiled and receives high wave energy, while the other one is accreting, fine grained, flat profiled and receives low wave energy. By comparison, the first is strongly controlled by wave energy and shows distinct seasonal morphodynamics. Therefore a less abundant and less diverse fauna with more pronounced temporal variations was hypothesized on this shore, compared to the shore with low wave energy. This study focuses on the overall composition and temporal variability of the meio- and macrofauna of the entire shore, while the across shore distribution is presented in chapter 3.

Material and methods

Study sites

The study was conducted on shores of the island of Sylt (Germany) and the neighbouring island of Rømø (Denmark) in the North Sea (Fig. 1). Both shores are exposed to the west, which is the prevailing wind direction in the eastern North Sea. During the study period wave height and wave period in the adjoining North Sea varied between 3.03 m with 8.8 s, and 0.08 m with 3.8 s, respectively (ALR Husum 1999). The mean wave height was 0.73 ± 0.52 m. The shores are located in a cold-temperate region with an average seawater temperature of 4°C in winter and 15°C in summer. During the study period surf water salinity ranged between 27 to 33 ‰ PSU (practical salinity units) and salinity of the interstitial water was 27 to 29 ‰ PSU in 5-10 cm sediment depth on both beaches. Tides are semidiurnal with a mean range of 1.8 m, and little difference between neaps and springs.

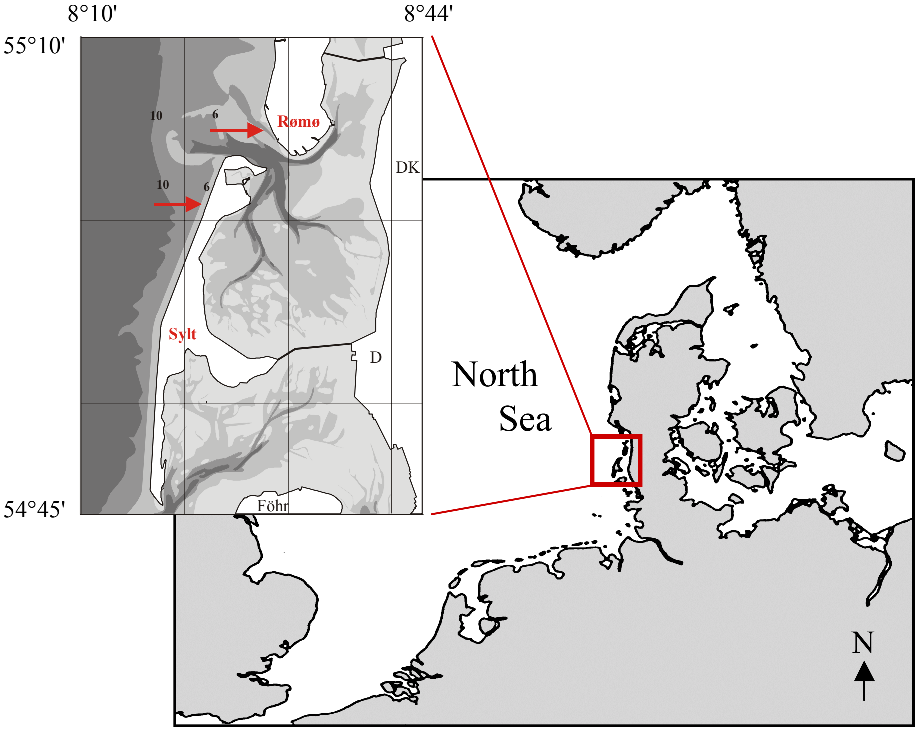
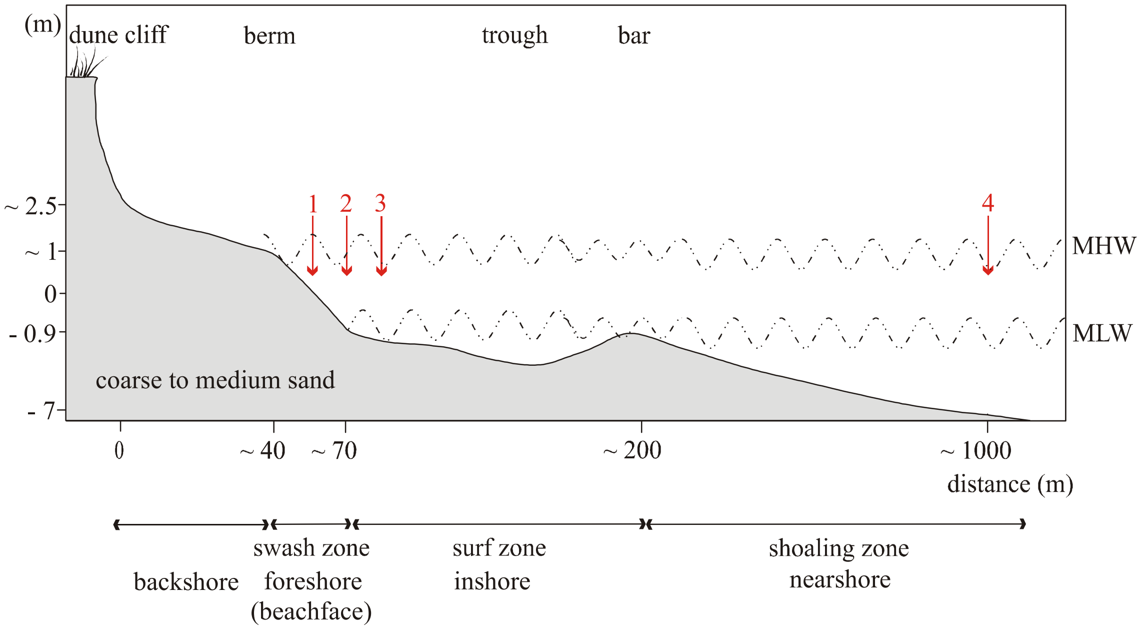


Fig. 1 Study sites (→) on the islands of Sylt and Rømø in the eastern North Sea. Shading refers to water depths (> 10, > 6, > 0 m: intertidal flats). DK = Denmark, D = Germany.

Sylt projects some 5 km further seaward than Rømø, and its shore retreated 1 to 2 m per year in the last century (Dette & Gärtner 1987), while the Rømø shore extended seaward at the same time (Bartholdy & Pejrup 1994). The eroding Sylt shore has a steep beachface with a slope of 2 to 4° (base of dune cliff to mean low tide line) and a horizontal distance between the mean high and low tide marks of 25 to 30 m (Fig. 2). This profile changes several times per year in response to actual wind and wave conditions. On average, the slope is flatter during winter and steeper during summer. Offshore from the mean low tide line, the profile flattens and an intermittent sand bar with a depth between -2.5 to -3.5 m below mean low tide line parallels the beach at a distance of about 200 m. Further offshore the profile becomes steeper again and the 6 m depth line occurs at 1 km distance from the shoreline. The accreting Rømø shore, in contrast, has a broad and flat beachface (slope $\leq 1°$), with a horizontal distance of 150 to 200 m between the mean high and low tide marks (Fig. 2). The profile remains rather constant during the year. Thirty meters offshore from mean low tide line the profile becomes steeper and a trough of 6-8 m depth occurs in front of this beach. This deep trough is part of the ebb tide delta of the tidal inlet between Sylt and Rømø. Further offshore the profile flattens again with a multiple bar and trough morphology. The 6 m depth line was about 5 km west of the shoreline.

Sylt: intermediate shore with high wave energy



Rømø: dissipative shore with low wave energy

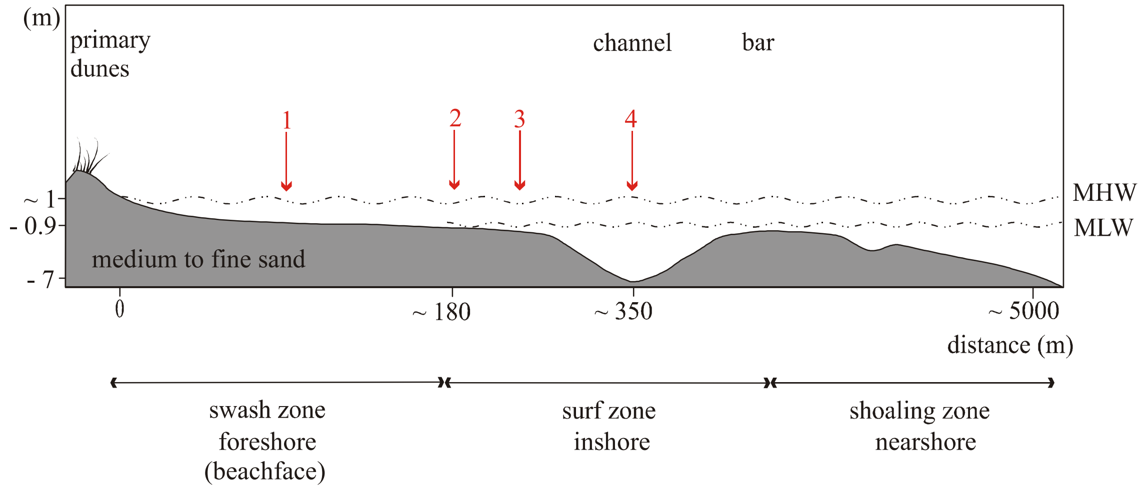


Fig. 2 Schematic illustration of profiles across the Sylt and Rømø shore including sample positions (→ 1-4) and terminology of zones across the shore according to Short (1999). 1= mid shore (middle between mean high (MHW) and mean low water (MLW)) = 0 m depth, 2 = mean low water (0.9 m depth), 3 = 1.4 m depth, 4 = 7 m depth.

These differences in the shore morphology between Sylt and Rømø are associated with marked differences in the wave energy profiles (Fig. 3).

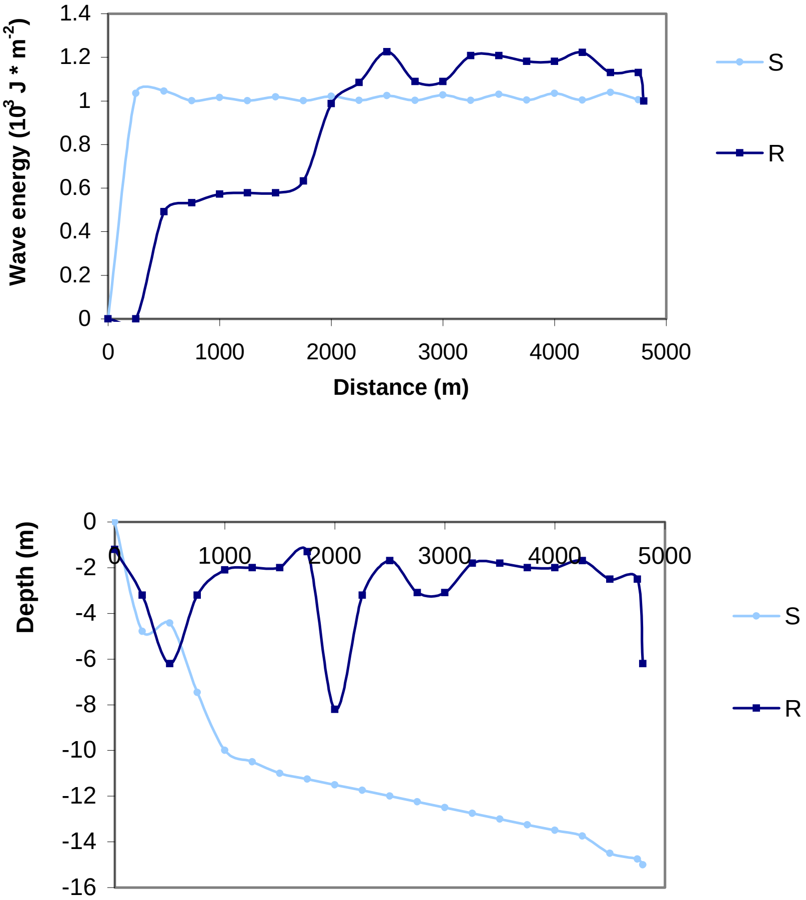


Fig. 3 Wave energy and depth profile across the Sylt (S) and Rømø (R) shore up to 5 km distance from mean low water (0 m). Wave energy was modelled according to Deigaard et al. (1986) with data from Ahrendt (unpubl., Geomar Kiel).

However, differences in wave energy only partially explain the different sediment granulometry between Sylt and Rømø. The sediment of the eroding shore is coarse to medium grained (median diameter (Md) = 0.56 ± 0.33 mm; Wentworth grade classification), moderately well sorted sand (quartile deviation (QD) = 0.56 ± 0.18 φ (phi); scale in Gray 1981), and devoid of a blackish sulphide layer during the entire year. The accreting shore consists of medium to fine grained sand (Md = 0.20 ± 0.05 mm), is very well sorted (QD = 0.33 ± 0.09 φ), and the blackish sulphide layer begins on average at 8 cm sediment depth. Temporal variation of sediment particle size and sorting coefficient on both shores is low and in no case statistically significant (Tab. 1). Differences in sediment composition between the shores are partially explained by the origin of the material supplied to the shores. The sand on the Sylt shore originates from an eroding Pleistocene and Tertiary cliff with coarse kaolinitic sand and some till 10 km south of the study site, transported northwards along the shoreline with the currents. The sand on the Rømø shore mainly originates from eroding Pleistocene deposits about 55 km north, which are transported southwards and turn progressively finer during this long passage (Bartholdy & Pejrup 1994).

Tab. 1 Temporal variation of median grain size (mm) and sorting coefficient (φ (phi)) on the Sylt and Rømø shore. Arithmetic means with standard deviations of four transect positions each with six replicates (n = 24).

Median grain size	**April**	**July**	**October**	**January**
Sylt	0.51 ± 0.29	0.68 ± 0.36	0.57 ± 0.37	0.48 ± 0.28
Rømø	0.19 ± 0.02	0.21 ± 0.05	0.20 ± 0.04	0.21 ± 0.06
Sorting coefficient	**April**	**July**	**October**	**January**
Sylt	0.57 ± 0.20	0.59 ± 0.17	0.56 ± 0.19	0.52 ± 0.17
Rømø	0.32 ± 0.06	0.33 ± 0.11	0.33 ± 0.08	0.34 ± 0.09

Thus, despite a similar exposure to the waves of the North Sea by both shores and their vicinity (12 km distance), the morphodynamic states of both shores are strongly contrasting (Tab. 2). According to the beach types of Short & Wright (1983), the Sylt shore can be characterized by intermediate types (more towards "longshore bar-through" and "rhythmic bar and beach" during winter, and more towards "transverse bar and rip" and "low tide terrace" during summer), which are the most dynamic ones (Short 1999). Presumably, recurrent beach nourishment on the Sylt shore during the last two decades enhanced these dynamics, because it prevents the morphodynamic state to reach equilibrium (Short 1999). The morphodynamic state of the Rømø shore resembles a dissipative type and is morphologically constant throughout the year.

Tab. 2 Relevant characteristics of wave energy, sediment, and morphology of the Sylt and Rømø shore. Morphodynamic states according to Short & Wright (1983).

Character	Sylt	Rømø
Wave energy at the beachface	high	low
Sediment balance	erosion	accretion
Sediment grain size	coarse to medium	medium to fine
Beachface	steep	flat
Sand bar	present	present
Near-/offshore slope	steep	flat
Morphodynamic state	intermediate	dissipative

Sampling

To assess the differences of meio- and macrofauna between shores, transects from mean tide line to 7 m depth composed of four positions were sampled (1: mid shore = middle between mean high and mean low water line = 0 m depth, 2: mean low water = 0.9 m depth, 3: 1.4 m depth, 4: 7 m depth; Fig. 2). At each study site six evenly spaced transects along 1 km of shoreline were sampled. At each position within transects, one core of 10 cm² cross area was collected to a sediment depth of 30 cm for meiofauna. For macrofauna, four cores of 50 cm² were taken at each position down to a depth of 20 cm and pooled to 200 cm² cross area. With respect to temporal variability, sampling surveys were conducted in April, July and October 1998 and January 1999.

In the laboratory, meiofauna was extracted from the sediment using the SMB-method of Noldt & Wehrenberg (1984) with a sieve of 63 µm mesh size. This method is specifically adapted to include soft-bodied meiofauna. The organisms were sorted to major taxa and counted. Plathelminths, polychaetes, nemerteans and bivalves were identified to species level, including juvenile macrofauna (= temporary meiofauna). Especially plathelminths and nemerteans need to be alive for species determination. This limits the amount of samples that can be handled. Due to very low abundances, nemerteans, oligochaetes, gastrotrichs and bivalves were summarized under “others”.

Macrofauna samples were sieved through 1 mm. The animals were sorted alive, counted and identified to species level whenever possible. This included *Crangon crangon*, *Carcinus maenas* (both Decapoda) and *Hydrobia ulvae* (Gastropoda) which all belong to the mobile surface fauna, but are also found burrowed in the sediment. In abundance "others" summarized decapods, nemerteans, cumaceans and gastropods.

For grain size analyses one additional core (10 cm^2 cross area to a depth of 10 cm) was collected at each transect position during each sampling survey. Granulometric analyses were carried out by dry sieving and the median grain sizes and sorting coefficients were calculated according to Buchanan (1984). The mean beach slope was measured using Emery's (1961) profiling technique.

Statistical analysis

The community structure on the two shores was characterized by the total number of species, species density (average number of species per 10 cm^2 for meiofauna and per 200 cm^2 for macrofauna), diversity (Shannon´s entropy $H' = -\sum n_i * ln n_i$, where n_i = proportion of individuals of the i-th species with i= 1,2,3,...S), and abundance per 10 and 200 cm^2, for meio- and macrofauna, respectively. To test for overall differences in meio- and macrofauna between the entire shores, data of the four transect positions each with six replicates and of the four sampling surveys were pooled per shore (n = 96), and one-way ANOVA (Analysis of variance) was used to test for differences in species density, diversity and abundance between the shores (statistical advice C. Hennig, Department for Mathematics, University of Hamburg). Cochran's test was used to test for homoscedasticity of variances, and data of the dependent variables were transformed once (square root transformation of macrofauna abundance at Rømø). When variances were not homogenous despite of the transformation, Wilcoxon's non-parametric U-Test (Sachs 1984) was used. Statistical significance was assumed at $p < 0.05$.

The temporal variability of the infauna within the shores was analysed using one-way ANOVA as well. These analyses were based on pooled data of the four transect positions each with six replicates per sampling survey (n = 24). Different levels within a significant parameter were analysed using Tukey's Honest-Significant-Difference (HSD) multiple comparison test. When variances remained heterogeneous despite of the transformation, the H-Test (Kruskal and Wallis), followed by pair-wise U-Tests was used. As before, statistical significance was assumed at $p < 0.05$ for ANOVA and H-

Test, and at $p < 0.008$ for the following U-Tests (Bonferroni-procedure for multiple comparisons; Sokal & Rohlf 1995). Zonation of the infauna on both shores is presented in chapter 3.

The infaunal assemblages were further analysed using the PRIMER software package from the Plymouth Marine Laboratory (PML). Multivariate analyses were carried out on non-transformed (macrofauna) and double square root transformed (meiofauna) data using the Bray-Curtis index and group average linkage for cluster analysis and non-metric multidimensional scaling (MDS). To point out temporal variations of the faunal assemblages, the analyses were based on a mean of the four transect positions each with six replicates per sampling survey. The discrimination of infaunal communities of the two shores was tested by one-way ANOSIM (Analysis of similarity) with the null hypothesis that similarities on an average will be the same between and within sites (Clarke 1993). The R statistic indicates the degree of discrimination between sites ($R = 1$ if all replicates within sites are more similar to each other than any replicates from different sites; $R \approx 0$ if the null hypothesis is true) and evidence to reject the null hypothesis is given by significance level p. For temporal variations of the communities within each shore similarities within and between sampling occasions were tested with ANOSIM. For meiofauna, the species number, species density and community analyses were based on plathelminths, polychaetes, nemerteans and bivalves. For macrofauna, all specimens were determined to species level with exception of nemerteans and cumaceans.

Results

Comparison of the meio- and macrofauna between the shores

Meiofaunal species density and diversity were significantly higher at Sylt than at Rømø, while total species number was higher at Rømø than at Sylt (64 versus 57; Tab. 3). Macrofaunal species density, diversity, and species number were higher at Rømø than at Sylt.

Tab. 3 Meio- and macrofaunal species number, species density and diversity on the Sylt and Rømø shore. Species density and diversity are presented as arithmetic means with standard deviations of four transect positions, each with six replicates, and of four sampling surveys (n = 96). Species density: number of species per 10 cm^2 and 200 cm^2 for meio- and macrofauna, respectively. U-test (U) and one-way ANOVA (A): df (degree of freedom) = 1.

Meiofauna	**Sylt**	**Rømø**	**p <**	**F**
Species number				
Total	57	64		
Plathelminthes	46	49		
Polychaeta	9	13		
Bivalvia	1	2		
Nemertini	1	0		
Species density	5.1 ± 2.4	3.0 ± 2.7	0.0001 (A)	31.63
Diversity H'	0.9 ± 0.5	0.6 ± 0.5	0.0001 (A)	17.05
Macrofauna	**Sylt**	**Rømø**	**p <**	**F**
Species number				
Total	16	28		
Polychaeta	10	19		
Crustacea	4	6		
Bivalvia	2	2		
Gastropoda	0	1		
Species density	1.3 ± 1.8	6.4 ± 2.5	0.0001 (U)	
Diversity H'	0.4 ± 0.5	1.3 ± 0.5	0.0001 (A)	286.80

Total meiofaunal abundance was similar on both shores, but the taxonomic composition differed strongly (Fig. 4). Nematodes were more abundant at Rømø than at Sylt, while the reverse was true for plathelminths, copepods, ostracods, and acarids (U-Test, df = 1, all $p < 0.001$). Abundances of polychaetes and "others" showed no differences between the shores. In terms of individual numbers, nematodes clearly dominated the meiofauna assemblage at Rømø (84 %), while at Sylt polychaetes (17 %), plathelminths (24 %), nematodes (22 %) and copepods (26 %) comprised fairly equal proportions. Among the meiofaunal taxa determined to species level (plathelminths, polychaetes, nemerteans and bivalves), the dominants differed completely between the two shores. At Rømø *Protodriloides symbioticus* (Polychaeta, 61 %), *Microstomum* sp. (Plathelminthes, 18 %), *Spio martinensis* (4 %), *Paromalostomum fusculum* (Plathelminthes, 3 %) and *Capitella minima* (2 %) accounted for about 88 % of total meiofaunal abundance. In contrast, at Sylt the dominants were *Notocaryoplanella glandulosa* (Plathelminthes, 50 %) and the polychaetes *Trilobodrilus axi* (25 %), *Hesionides arenaria* (10 %), and *Protodrilus* sp. (4 %).

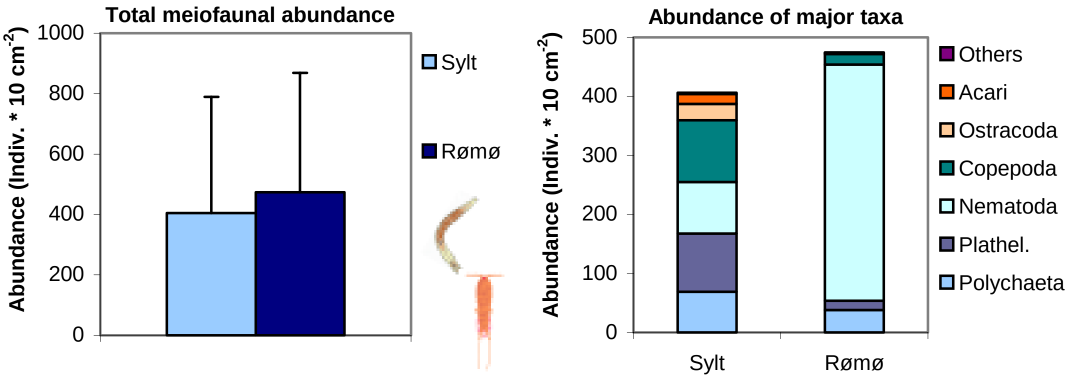


Fig. 4 Total meiofaunal abundance and abundance of major taxa per 10 cm^2 on the Sylt and Rømø shore. Arithmetic means with standard deviations of four transect positions, each six times replicated, and of four sampling surveys (n = 96). Others = nemerteans, oligochaetes, gastrotrichs and bivalves. Plathel. = Plathelminthes.

Total macrofaunal abundance was higher on the Rømø shore than on the Sylt shore (one-way ANOVA, df = 1, F = 63.22, $p < 0.0001$; square root transformation of data; Fig. 5). This was mainly caused by higher abundances of polychaetes and bivalves at Rømø than at Sylt (U-Test, df = 1, both $p < 0.0001$). Isopods occurred only at Sylt, and abundances of amphipods and "others" did not differ significantly between the shores. Polychaetes contributed 80 to 90 % to the macrofaunal abundance on both shores, followed by bivalves (4 %) and amphipods (2 %) at Rømø, and by amphipods (13 %) and isopods (3 %) at Sylt. On the Rømø shore the polychaetes *Spio martinensis* (28 %), *Scolelepis squamata* (19 %), *Scoloplos armiger* (13 %), *Capitella minima* (12 %), *Pygospio elegans* (10 %), *Capitella capitata* (5 %) and the bivalve *Macoma balthica* (4 %) accounted for 91 % of the total macrofaunal abundance. In contrast, on the Sylt shore *S. squamata* (51 %) was most abundant, followed by *S. martinensis* (25 %), *Bathyporeia* sp. (Amphipoda, 13 %), and *Eurydice pulchra* (Isopoda, 3 %). These species accounted for 92 % of the total macrofaunal abundance. All other species occurred with few individuals only, on both shores.

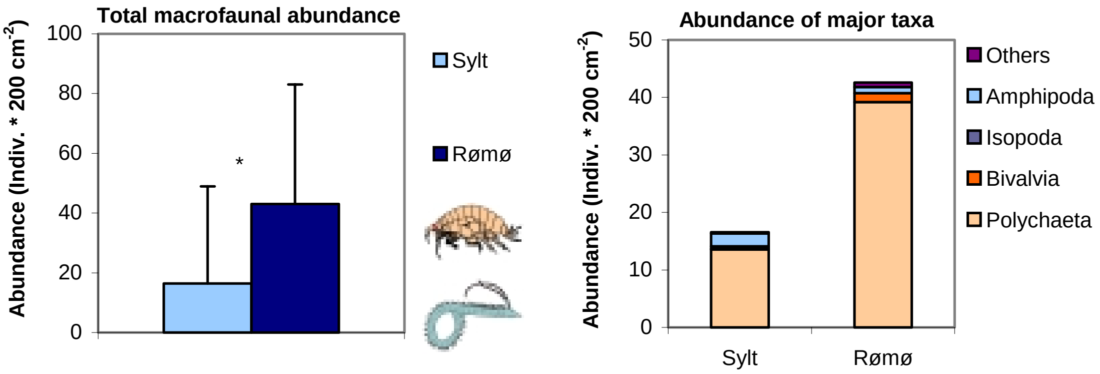


Fig. 5 Total macrofaunal abundance and abundance of major taxa per 200 cm^2 on the Sylt and Rømø shore. Arithmetic means with standard deviations of four transect positions, each six times replicated, and of four sampling surveys (n = 96). Others = decapods, nemerteans, cumaceans and gastropods. * = significant difference between the shores.

Temporal variability of the meio- and macrofauna within each shore

At Sylt, meiofaunal diversity was lowest in January, while no significant temporal differences in species density occurred (Tab. 4). At Rømø, no significant temporal variation of diversity and species density was detected. In the macrofauna, lowest diversity and species density occurred in January on the Sylt shore (Tab. 4). This contrasts with the Rømø shore, where diversity was lowest in October, while no significant temporal differences in species density were noticed.

Tab. 4 Temporal variation of meio- and macrofaunal species number, diversity, and species density on the Sylt and Rømø shore. Species density and diversity are presented as arithmetic means with standard deviations of four transect positions each with six replicates (n = 24). Species density: average number of species per 10 and 200 cm^2 for meio- and macrofauna, respectively. A = one-way ANOVA, H = H-Test, both df (degree of freedom) = 3; T = Tukey's Honest-Significant-Difference multiple comparison test; U = U-Test, df = 1. Significant differences are indicated by different letters; the same letters indicate non-significant differences.

Meiofauna	**April**	**July**	**October**	**January**	**p <**	**F**	**p <**
Sylt							
Species number	25	30	33	25			
Diversity H'	1.3 ± 0.3^{a}	1.1 ± 0.3^{a}	1.4 ± 0.2^{ab}	0.9 ± 0.3^{ac}	0.05 (A)	3.42	0.05 (T)
Species density	5.3 ± 1.8	5.6 ± 1.9	5.0 ± 3.1	4.5 ± 2.4			
Rømø							
Species number	26	23	29	36			
Diversity H'	1.2 ± 0.5	0.8 ± 0.3	1.3 ± 0.3	1.3 ± 0.7			
Species density	2.8 ± 2.7	2.2 ± 1.4	3.1 ± 2.5	4.1 ± 3.6			
Macrofauna	**April**	**July**	**October**	**January**	**p <**	**F**	**p <**
Sylt							
Species number	7	13	11	7			
Diversity H'	0.8 ± 0.5^{a}	1.0 ± 0.4^{ab}	0.7 ± 0.4^{a}	0.3 ± 0.2^{ac}	0.05 (A)	3.54	0.05 (T)
Species density	1.9 ± 1.8^{a}	1.8 ± 2.4^{a}	1.1 ± 1.8^{ab}	0.6 ± 0.7^{ac}	0.01 (H)		0.01 (U)
Rømø							
Species number	21	16	22	18			
Diversity H'	2.0 ± 0.2^{a}	1.8 ± 0.1^{a}	1.5 ± 0.2^{b}	1.8 ± 0.3^{ab}	0.01 (A)	7.10	0.05 (T)
Species density	6.8 ± 2.7	7.3 ± 2.4	5.9 ± 2.1	5.5 ± 2.6			

On the Sylt shore, total meiofaunal abundance was highest in July (Fig. 6; Tab. 5). This was due to the temporal course of polychaetes, ostracods and acarids, which all attained abundance maxima in July (polychaetes also in October). The same tendency occurred in copepod abundances. On the Rømø shore, highest meiofaunal abundance was detected in April and July. This was mainly brought about by nematodes, polychaetes and copepods, while plathelminths attained their maximum abundances earlier in the year (January/April). Nematodes dominated the meiofaunal abundance during all sampling surveys at Rømø, while the contribution of major taxa changed temporally at Sylt. In January and April, nematodes and plathelminths together accounted for about 70 % of the total abundance, while in July and October, copepods and polychaetes (50 to 60 % of the total abundance) took over. On species level of the investigated taxa, the polychaete *Protodriloides symbioticus* dominated the assemblage at Rømø during the entire year (60 to 70 % of the assemblage). At Sylt, the plathelminth

Notocaryoplanella glandulosa was most abundant in January, April, and July (50 to 70 %), while the polychaetes *Trilobodrilus axi* (32 %) and *Hesionides arenaria* (39 %) were more abundant in October.

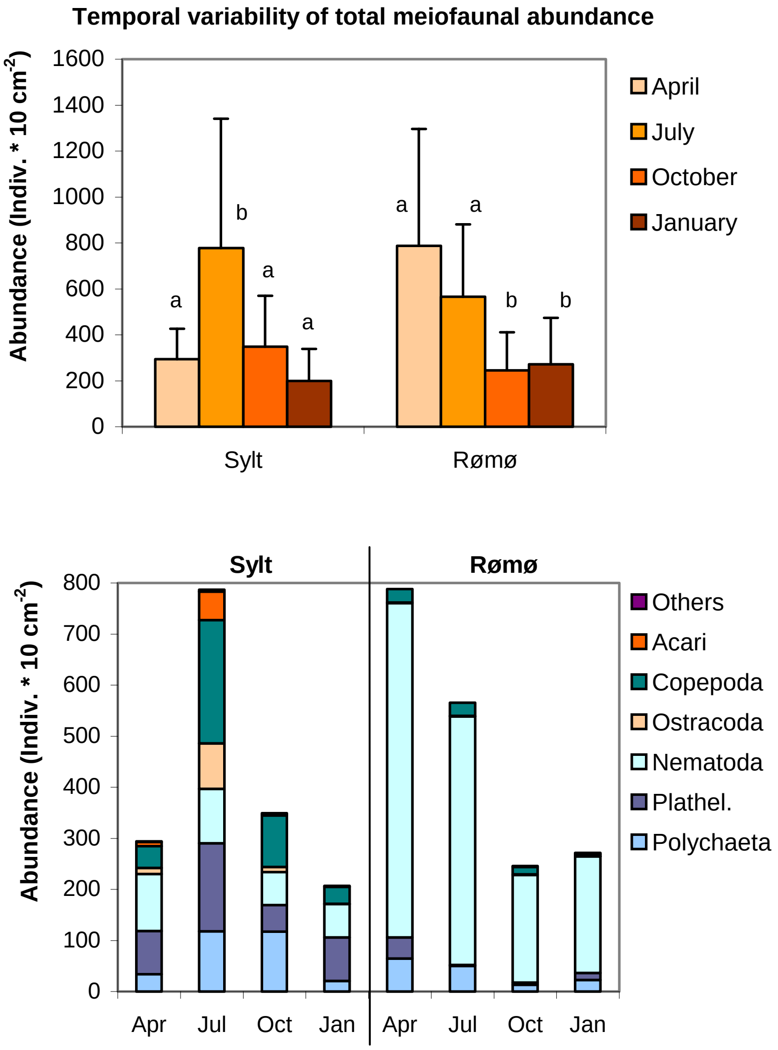


Fig. 6 Temporal variability of total meiofaunal abundance and major taxa abundance per 10 cm^2 on the Sylt and Rømø shore, presented as arithmetic means with standard deviations of four transect positions, each with six replicates (n = 24). Others = nemerteans, oligochaetes, gastrotrichs and bivalves; Plathel. = Plathelminthes. Significant differences are indicated by different letters; the same letters indicate non-significant differences.

Tab. 5 Statistics of temporal variability of total meio- and macrofaunal abundance and abundance of major taxa on the Sylt and Rømø shore. H-Test: df (degree of freedom) = 3, U-Test: df = 1. Jan = January, Apr = April, Jul = July, Oct = October.

Meiofauna	**H-Test**	**U-Test**	**p <**
Sylt			
Total	< 0.01	Jul/Apr; Jul/Oct; Jul/Jan	< 0.008
Polychaeta	< 0.001	Jul/Apr; Jul/Jan; Oct/Jan	< 0.008
Ostracoda	< 0.001	Jan/Apr; Jan/Jul; Jan/Oct	< 0.008
Acari	< 0.001	Apr/Jan; Jul/Oct; Jul/Jan	< 0.008
Copepoda	> 0.05	Apr/Jul; Jul/Jan	< 0.008
Rømø			
Total	< 0.0001	Apr/Oct; Apr/Jan; Jul/Oct; Jul/Jan	< 0.001
Nematoda	< 0.05	Apr/Oct; Apr/Jan; Jul/Oct; Jul/Jan	< 0.008
Polychaeta	< 0.01	Apr/Oct; Apr/Jan; Jul/Oct; Jul/Jan	< 0.008
Copepoda	< 0.01	Jul/Jan	< 0.008
Plathelminthes	< 0.001	Apr/Jul; Apr/Oct	< 0.0001
Bivalvia	< 0.01		
Nemertini	< 0.05		
Macrofauna	**H-Test**	**U-Test**	**p <**
Sylt			
Polychaeta	< 0.05	Apr/Oct	< 0.008
Amphipoda	< 0.01	Jul/Jan; Oct/Jan	< 0.008
Isopoda	< 0.05		> 0.008
Rømø			
Total	< 0.0001	Apr/Jul; Apr/Oct; Jul/Jan; Oct/Jan	< 0.001
Polychaeta	< 0.0001	Apr/Jul; Apr/Oct; Jul/Jan; Oct/Jan	< 0.001
Decapoda	< 0.0001	Apr/Jul	< 0.001
Cumacea	< 0.05		

Total macrofaunal abundance on the Sylt shore did not significantly vary temporarily. However, there was a minor temporal variability in abundances of polychaetes, amphipods and isopods (Fig. 7; Tab. 5). At Rømø, macrofaunal abundance attained a maximum in July and October, mainly caused by polychaetes. Polychaetes dominated the macrofaunal abundance during the entire year on the Rømø shore. The Sylt shore showed a similar pattern, with exception of April, when amphipods dominated the assemblage. However, at the species level, the ranking of dominants varied over the sampling surveys on both shores (Tab. 6).

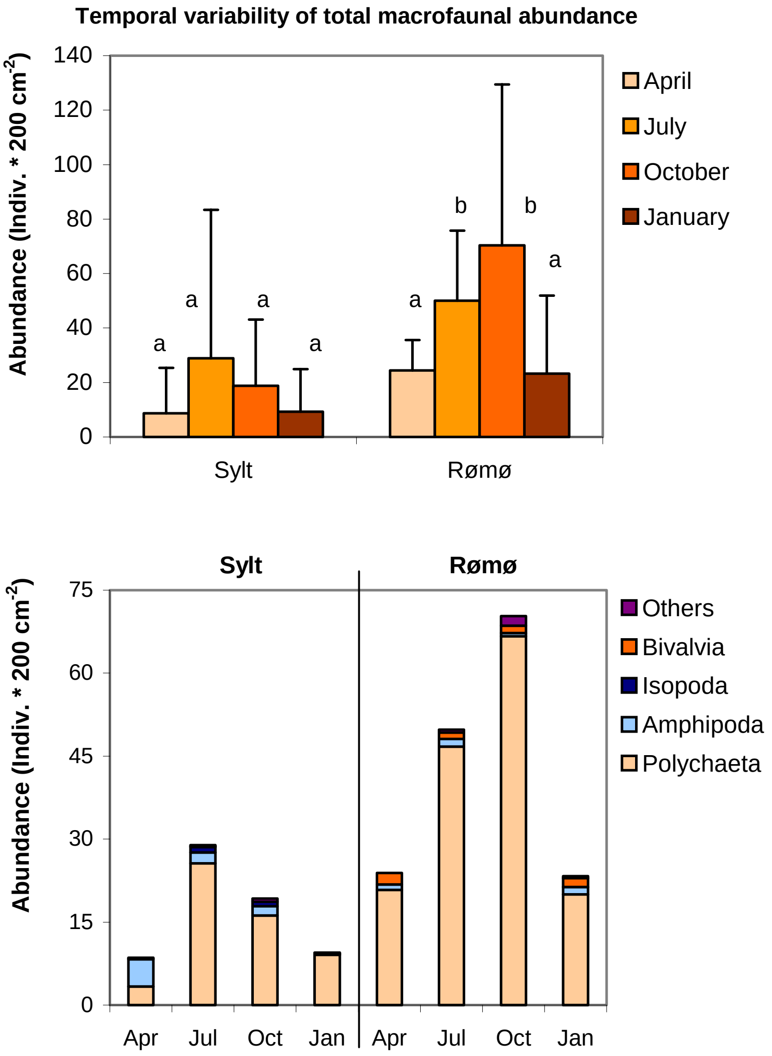


Fig. 7 Temporal variability of total macrofaunal abundance and abundance of major taxa per 200 cm^2 on the Sylt and Rømø shore, presented as arithmetic means with standard deviations of four transect positions, each with six replicates (n = 24). Others = decapods, nemerteans, cumaceans and gastropods. Further abbreviations see figure 6.

Tab. 6 Temporal variation of dominant macrobenthic species on the Sylt and Rømø shore, ranked in decreasing order of their contribution to the total abundance. Species contributing together 90 % to the total abundance are listed.

	Sylt	**Rømø**
April	*Bathyporeia* sp. (60 %)	*Scoloplos armiger* (21%)
	Scolelepis squamata (16 %)	*Capitella minima* (14 %)
	Spio martinensis (11 %)	*Scolelepis squamata* (13 %)
	Paraonis fulgens (7 %)	*Psammodrilus balanoglossoides* (10 %)
		Spio martinensis (10 %)
		Capitella capitata (8 %)
		Macoma balthica (7 %)
		Pygospio elegans (6 %)
July	*Spio martinenis* (52 %)	*Spio martinenis* (27 %)
	Scolelepis squamata (31 %)	*Pygospio elegans* (19 %)
	Bathyporeia sp. (7 %)	*Scolelepis squamata* (15 %)
		Scoloplos armiger (12 %)
		Capitella minima (11 %)
		Capitella capitata (6 %)
October	*Scolelepis squamata* (77 %)	*Spio martinenis* (39 %)
	Haustorius arenarius (5 %)	*Scolelepis squamata* (28 %)
	Eurydice pulchra (4 %)	*Scoloplos armiger* (8 %)
	Bathyporeia sp. (4 %)	*Capitella minima* (7 %)
		Pygospio elegans (7 %)
		Capitella capitata (2 %)
January	*Scolelepis squamata* (90 %)	*Capitella minima* (29 %)
		Scoloplos armiger (19 %)
		Spio martinensis (18 %)
		Macoma balthica (7 %)
		Scolelepis squamata (7 %)
		Capitella capitata (4 %)

Community analyses

Multivariate analyses of the meio- and macrofauna data (mean of the four transect positions with six replicates per sampling survey) separated the meiofaunal assemblages of the two shores at the highest level, while it revealed three clusters for the macrofauna (Fig. 8). The first macrofaunal cluster contained only one sample of the Sylt shore, the second cluster separated all samples of Rømø, which were associated with two samples of Sylt, and the third cluster contained all remaining samples of the Sylt shore. ANOSIM confirmed the similarity of the data within each shore (Tab. 7).

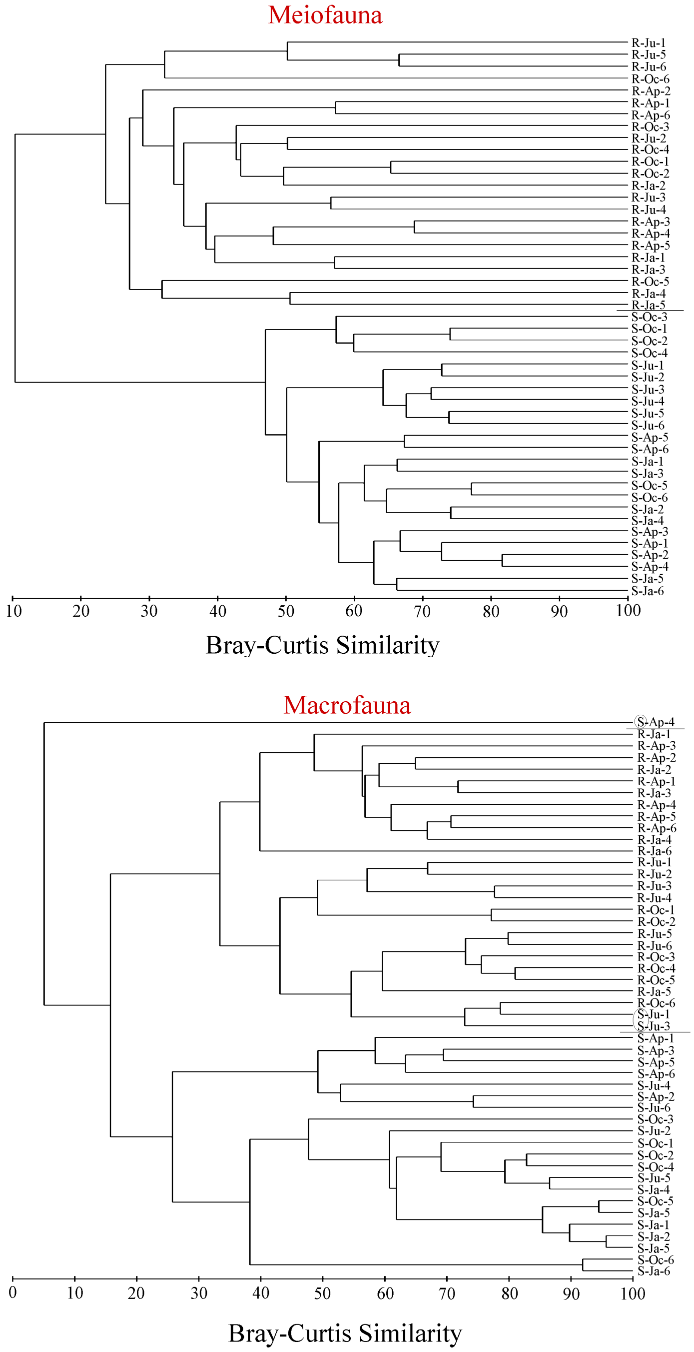


Fig. 8 Dendrogram of Bray-Curtis similarity for meio- and macrofauna of the Sylt (S) and Rømø (R) shore, surveyed in April (Ap), July (Ju), October (Oc) and January (Ja). Numbers behind symbols of sampling surveys refer to replicate transects.

Besides separating the assemblages of the two shores, cluster analyses produced lower order clusters within each shore. This distinction of faunal groups within each shore is further illustrated with MDS plots. For meiofauna, the cluster analyses on the Sylt shore separated the sampling occasions, while there was only a weak relation to the sampling surveys on the Rømø shore (Fig. 9; Tab. 7). For macrofauna, these clusters did not clearly relate to the sampling occasions at Sylt, although January was almost completely grouped into one cluster separated from April and July, but less so from October (Fig. 9; Tab. 7). In contrast, at Rømø the clusters were better related to the sampling occasions, with one cluster including July and October and another one including January and April.

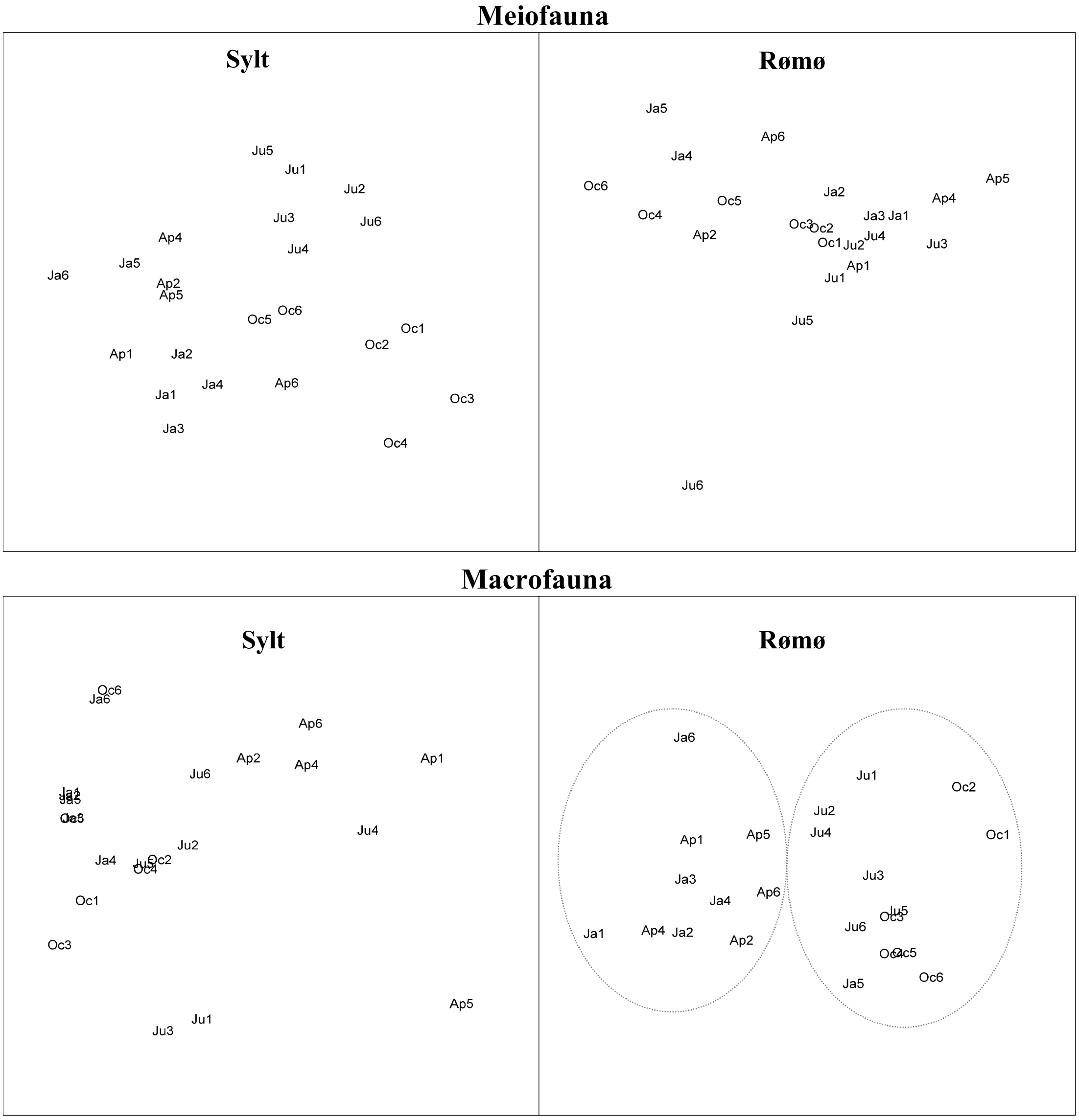


Fig. 9 MDS plots for meio- and macrofauna on the Sylt and Rømø shore, surveyed in April, July, October and January. Abbreviations see figure 8. Stress values: Meiofauna: 0.18 (Sylt) and 0.11 (Rømø); macrofauna: 0.10 (Sylt) and 0.13 (Rømø).

Tab. 7 ANOSIM (Analysis of similarity) results of the multivariate analyses of meio- and macrofauna data between shores and between sampling surveys within each shore. Total = ANOSIM over all surveys within one shore. Jan = January; Apr = April; Jul = July; Oct = October.

between shores			**between surveys**					
			Meiofauna			**Macrofauna**		
	R	p		R	p		R	p
Meiofauna	0.9	0.001	Sylt Total	0.8	0.001	Sylt Total	0.4	0.001
Macrofauna	0.8	0.001	Rømø Total	0.2	0.02	Jan/Apr	0.8	0.002
						Jan/Jul	0.7	0.002
						Jan/Oct	0.3	0.04
						Rømø Total	0.5	0.001
						Jul/Oct	0.1	0.2
						Jan/Apr	0.2	0.09

Discussion

Meiofauna

Meiofauna is structured by a multifactorial network of biotic and abiotic factors interacting with each other in many ways and creating complex systems (Giere 1993). A higher meiofaunal diversity was reported in coarser sediment and under well oxygenated conditions, in contrast to finer sediment and more sulphidic conditions (Gray & Rieger 1971; Giere 1993; McIntyre & Murison 1973; McLachlan 1977a). This is supported by the results of this study, focusing on interstitial plathelminths and polychaetes. Diversity does not necessarily correlate negatively with physical harshness, because this is often counterbalanced by chemically benign conditions (i.e. oxic versus sulphidic conditions; Giere 1993). The interstitial climate at Sylt was more physically controlled, with strong hydrodynamics, strong changes in pore moisture, and where organisms must tolerate movement and grinding of sand grains. However, no oxygen limitation was indicated on this shore. In contrast, the interstitial system at Rømø may be physically more stable, but oxygen supply was limited, with increasingly sulphidic conditions indicated by the blackish sulfid layer in the sediment (Reise & Ax 1979). Thus, the physical harshness of the intermediate shore may be counterbalanced by a weak chemocline (Powell et al. 1983; Giere 1993) at Sylt. The effects of this are exemplified by plathelminths and polychaetes, and it is assumed that other major taxa follow the pattern. The dominance of nematodes at Rømø, in contrast to a co-dominance of several major taxa at Sylt, may be caused by the differences in the interstitial climate between the shores. Higher abundances of nematodes in finer, less oxygenated sediments than in coarser ones, and a reverse pattern for copepods are well known, because the latter are more sensitive to low oxygen (McLachlan 1983; Coull 1985).

Similar meiofaunal abundances on both shores were not expected. A grain size of about 0.2 to 0.3 mm, i.e. as on the Rømø shore, has been suggested to be an optimum for the development of high abundances (McIntyre & Murison 1973; McLachlan 1977b). However, the richest meiofauna was found in habitats with a balance between organic input and oxygenation (Brown & McLachlan 1990; Armonies & Reise 2000). The overall balance may be similar on both shores. Evidently, it was more favourable for nematodes than for other taxa on the dissipative shore, while similarily favourable for plathelminths, polychaetes, copepods, nematodes, and ostracods on the intermediate shore.

Differences between the two shores were also expressed on lower taxonomic levels. A dominance of Proseriata in plathelminths assemblages of exposed habitats (*Notocaryoplanella glandulosa* and *Nematoplana coelogynoporoides*, in our case) is well known (e.g., Reise 1988; Wellner & Reise 1989). Many proseriate species are long, slender, very quick moving, and often equipped with special adhesive organs. In contrast, sheltered habitats are often dominated by Macrostomida (*Paromalostomum fusculum*, *Microstomum* sp., in our case), Acoela and Dalyellioida with a stout shape (Reise 1988). McLachlan et al. (1981) also reported larger meiofauna organisms on very exposed, coarse grained beaches than on less exposed ones. The polychaete assemblages also differed between shores. *Trilobodrilus axi* is characteristic of exposed beaches avoiding habitats with fine sand, while such sediment is preferred by *Protodriloides symbioticus* (Schmidt 1969). However, these species are not always separated. They co-exist in high abundances on a coarse to medium grained shore on the sheltered side of Sylt (Schmidt 1969), which has a profile that consists of an upper steep part and a lower one with a dissipative tidal flat (Armonies & Reise 2000). A pronounced dominance of single species occurred in both assemblages. This may result from “extreme” interstitial climates on both shores, caused by physical harshness at Sylt, and by a strong chemocline at Rømø.

Temperate meiofauna usually show highest abundances in summer (McIntyre & Murison 1973; McLachlan 1983; Coull 1988). This is explained by temporal changes in recruitment, temperature, wave energy, water percolation, oxygenation, benthic primary production and related factors (McIntyre & Murison 1973; McLachlan 1983; Alongi 1990; McLachlan 1990). The Sylt shore showed the expected maximum of abundances in summer, which were mainly caused by interstitial polychaetes and copepods. However, the Rømø shore attained maximum abundances already in April, mainly brought about by nematodes, which frequently show an earlier maximum of abundances than copepods (Harris 1972). At Sylt, the temporal change in community structure of the investigated taxa was closely related to the population dynamics of the dominant species (*N. glandulosa*, *T. axi, Hesionides arenaria*), while species richness did not varied temporarily. Such temporal variations were not observed on the Rømø shore.

Macrofauna

Many parameters have been claimed to structure the macrofauna inhabiting sandy shores. Although most studies have focused on intertidal communities, these conclusions also apply to this investigation, which included the subtidal zone. Higher abundance and species richness have been reported from shores with fine sediments, flat slopes, and low wave energy, rather than from shores with coarse sand, steep profiles, and high wave energy (Shelton & Robertson 1981; McLachlan 1983; Jaramillo & Gonzales 1991; Jaramillo & McLachlan 1993). Coarse sand at a steep beachface may limit macrofauna, because its high permeability may lead to desiccation. It also hinders burrowing of macrofauna and in combination with steep slopes and high wave energy it produces general habitat instability (Croker 1977; McLachlan 1977b; McLachlan et al. 1981; Shelton & Robertson 1981; McLachlan et al. 1984). Thus, physical harshness on the intermediate shore may limit macrofauna.

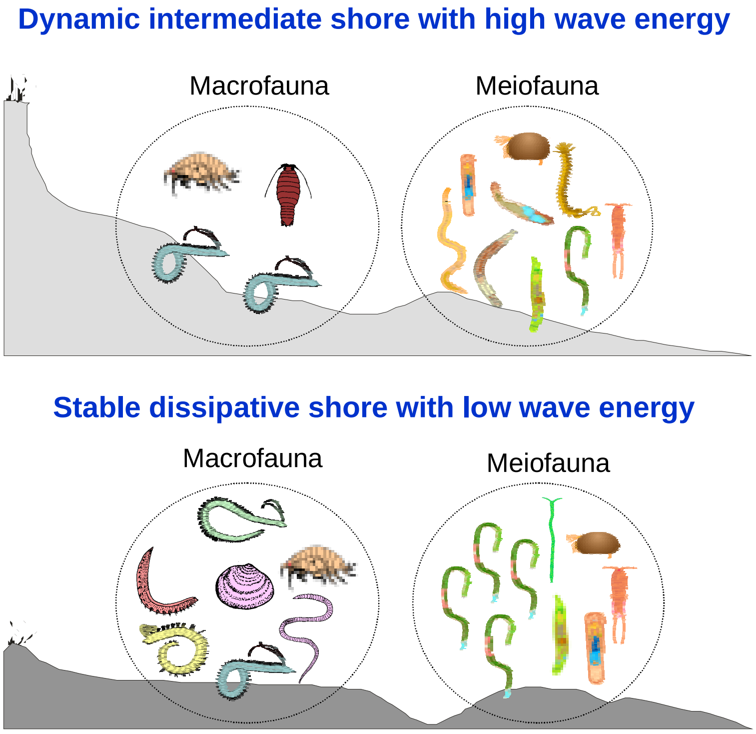
The differing environmental conditions between the two shores may explain the relative share of major macrofaunal groups. Polychaete abundances usually increase with increasing physical stability, while many crustaceans seem to prefer exposed localities

(McIntyre et al. 1970; Seed & Lowry 1973; McLachlan et al. 1981; Dexter 1983; McLachlan 1983; Dexter 1984; Jaramillo & Gonzales 1991). This matches with the macrofaunal composition found at Sylt and Rømø. Conditions are further reflected by different dominant species. This brings about distinct communities at Sylt and Rømø as shown by multivariate analyses. Macrofauna on the Sylt shore was characterized by very mobile organisms such as *Scolelepis squamata*, *Bathyporeia* sp. and *Eurydice pulchra*, while the Rømø shore also haboured less mobile animals (e.g., *Capitella minima, Capitella capitata* and *Macoma balthica*). A predominance of active swimmers is known from shores with strong hydrodynamics. *E. pulchra* has been suggested as a useful indicator for shores with high wave energy (Seed & Lowry 1973; Eleftheriou & Nicholson 1975). *S. squamata* was the dominant species at Sylt, while several species occurred with fairly even proportions at Rømø. Such a strong dominance of a single species is well known from habitats with one environmental factor attaining extreme values, i.e. wave energy (Shelton & Robertson 1981). This contrasts with low dominance in habitats with a lower wave energy.

Sandy shores are dynamic habitats with temporal changes in morphology, temperature, grain size, and other environmental factors, which may cause variations in the macrofauna (Salvat 1966; Ansell et al. 1972; McLusky et al. 1975; McLachlan 1983; Brown & McLachlan 1990). Population dynamics of dominant species and active/passive migrations of organisms may also change the community (Holland & Polgar 1976; Brown & McLachlan 1990; Ismail 1990; Haynes & Quinn 1995; Degraer et al. 1999; Armonies 2000). A pronounced temporal variability of the macrofauna was noticed on the dissipative shore, which is of high physical stability. The variation mainly resulted from changes in abundance of the dominant species. On the other hand, low temporal variability in the macrofauna occurred on the highly dynamic intermediate shore. The only change was caused by a strong dominance of *S. squamata* in January. However, the low species density in winter indicates that several species probably moved out of the habitat in winter. This may be caused by increased wave energy in the winter season. When habitats become unsuitable (e.g. temperature decline, storms) some macrofauna may simply leave to the adjacent subtidal zone or retreat to deeper sediment layers (Leber 1982; Brown & McLachlan 1990; Jaramillo et al. 1996).

Conclusions

The dynamic intermediate shore with high wave energy is characterized by an impoverished macrofauna, but an abundant meiofauna of high evenness between major taxa, and high diversity of interstitial plathelminths and polychaetes (Fig. 10). This may be a result of shore instability on a scale limiting macrofauna, while on the meiofaunal scale there may be still a favourable balance between physical and chemical factors. The physically more stable dissipative shore with low wave energy is characterized by a rich macrofauna and an abundant meiofauna (Fig. 10). The latter is strongly dominated by nematodes, and of lower diversity of plathelminths and small polychaetes. Physical stability on a macro-scale benefits the larger benthic organisms, while the concomitant chemical conditions below the sediment surface are unfavourable for the interstitial plathelminths and polychaetes. Thus, the boundary between physically and chemically controlled habitats seems to differ for meio- and macrofauna on sandy shores. In addition to body size, a fundamental difference between meio- and macrofauna may be a divergent sensitivity to chemoclines and physical harshness on sandy shores.


Dynamic intermediate shore with high wave energy

Stable dissipative shore with low wave energy

Fig. 10 Schematic illustration of the meio- and macrofauna composition on two cold-temperate sandy shores differing in wave energy, grain size, and shore morphology.

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3 ZONATION OF MACRO- AND MEIOFAUNA ON TWO SANDY SHORES WITH LOW AND HIGH WAVE ENERGY

ABSTRACT Spatial patterns of meio- and macrofauna, from intertidal to subtidal, were compared for two sandy shores of adjacent barrier islands in the eastern North Sea which differed in wave energy, grain size, and shore morphology. The shore on the island of Sylt is eroding, coarse grained, steep profiled, with high wave energy, and resembles intermediate beach types. The shore on the island of Rømø is accreting, fine grained, flat profiled, with low wave energy, and resembles a dissipative beach. In addition to body size, meio- and macrofauna may differ in their response to hydrodynamic forces on sandy shores, causing divergent zonation patterns. Meiofauna was abundant in the intertidal at Sylt, dominated by plathelminths and copepods. In contrast, it was fairly even abundant across the entire Rømø shore, dominated by nematodes. Species density of interstitial plathelminths and polychaetes peaked at mean low water and in the shallow subtidal at Sylt, while it reached the maximum at the mid shore at Rømø. Macrofauna was abundant and of high species density in the subtidal at Sylt, and evenly distributed across the Rømø shore. Community analyses revealed distinct zonation of meio- and macrofauna at Sylt, corresponding to a pronounced habitat sequence on this intermediate shore. Communities and habitats changed gradually across the flat, dissipative Rømø shore. No distinct faunal boundary occurred between inter- and subtidal zones on both shores. It is suggested that strong hydrodynamic forces at the steep intertidal on the dynamic intermediate shore limited the macrofauna, but had weak effects on the meiofauna. Less hydrodynamic forces across the entire flat, stable dissipative shore resulted in a evenly distributed macrofauna and a nematode dominance in the meiofaunal assemblage.

Introduction

Faunal zonation on sandy shores is not as readily visible as on rocky shores, and only few studies described spatial patterns of meio- or macrofauna from intertidal towards deeper subtidal zones (McIntyre & Eleftheriou 1968; McIntyre & Murison 1973; McLachlan 1977a, 1977b; Knott et al. 1983; Reise 1985; Armonies & Hellwig 1987; Brown & McLachlan 1990; Armonies & Reise 2000). For macrofauna, a general increase in species number, diversity, and abundance is reported in downshore direction, with a short interruption at the wave breaking zone, seaward of the beachface. Tidal submergence is suggested as the determining factor for macrofaunal zonation, because most species depend on the sediment surface for feeding, respiration, larval settlement, or migration among others. However, hydrodynamic turbulence, sediment composition, and species interactions may also influence the spatial variation of the macrofauna (Field 1971; Reise 1985; Brown & McLachlan 1990; Armonies & Reise 2000). A contrasting zonation pattern is proposed for meiofauna (McIntyre & Murison 1973; McLachlan 1977b; Reise 1985; Armonies & Hellwig 1987; Brown & McLachlan 1990; Giere 1993). Since most meiofauna tends to live below the sediment surface during the entire tidal cycle, as well as their life cycle, it may be less influenced by tidal submergence, and is thus somewhat buffered against the physical extremes of the seashore (Bally 1983; Armonies & Reise 2000). The chemocline within the sediment, food availability, degree of desiccation, and sediment composition are suggested as major determinants of meiofaunal spatial variation (Schmidt 1969; Harris 1972; McLachlan 1977b; Giere 1993). Thus, spatial patterns of meio- and macrofauna across sandy shores may be very different. A fundamental divergence between these two faunal components is assumed in their response to chemoclines and physical harshness on sandy shores (chapter 2), which may also affect their zonation patterns.

The proximity of two exposed sandy shores of different morphodynamic types enabled us to compare zonation patterns of meio- and macrofauna perpendicular to these shorelines. The shore on the island of Sylt is eroding, steep profiled, coarse grained, and has high wave energy. It corresponds to intermediate beach types (see Short 1999). The shore on the adjacent island of Rømø is accreting, flat profiled, fine grained, and with low wave energy. This one is a dissipative beach type. A divergent zonation pattern of meio- and macrofauna is hypothesized, due to a high susceptibility of macrofauna to tidal emergence and hydrodynamic turbulence. Meiofauna, living at a different spatial scale, may be more responsive to the oxygen-sulfide chemocline within the sediment than the macrofauna. The overall community change perpendicular to the shoreline is expected to be more distinct on the steep, intermediate shore type than on the flat, dissipative one.

Material and methods

Study sites

The studied shores are located on the exposed western sides of the neighbouring barrier islands of Sylt (Germany) and Rømø (Denmark) in the eastern North Sea (Fig. 1). Despite their vicinity (12 km distance) and a similar exposure to the North Sea waves (mean wave height in the adjoining North Sea during the study period: 0.7 ± 0.5 m; ALR 1999), the morphodynamic beach state of the two shores contrasts strongly. This is illustrated in detail in figure 2.

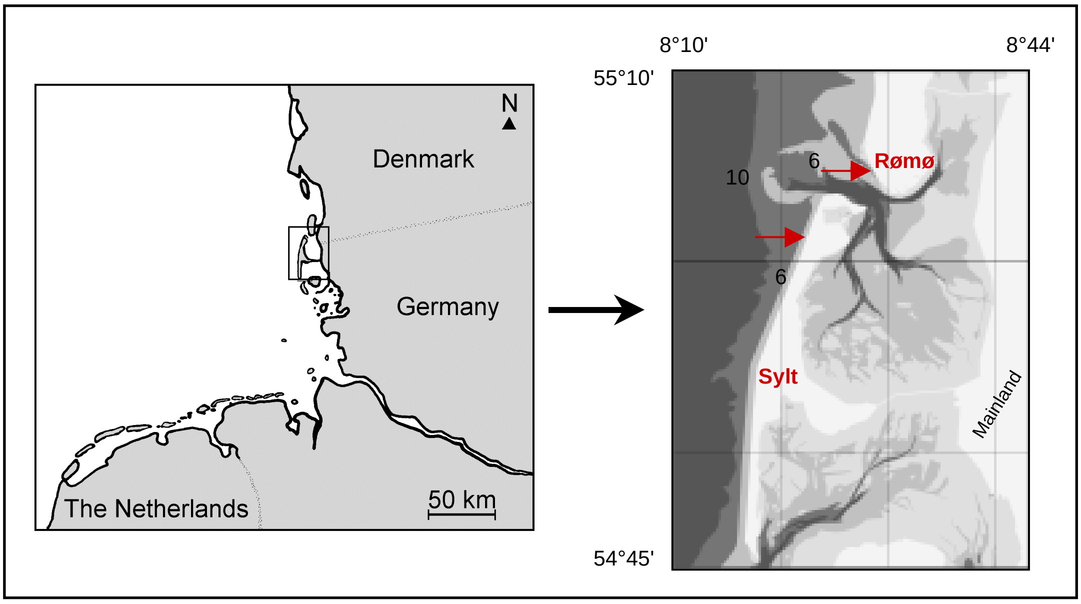


Fig. 1 Study sites (→) on the neighbouring barrier islands of Sylt and Rømø in the eastern North Sea. Average sea water temperature of this cold-temperate region is 4°C in winter and 15°C in summer. Water salinity is the range of 27 to 33 ‰ PSU. Tides are semidiurnal with a mean range of 1.8 m. Shading refers to water depths (> 10 m, > 6 m, > 0 m: intertidal flats).

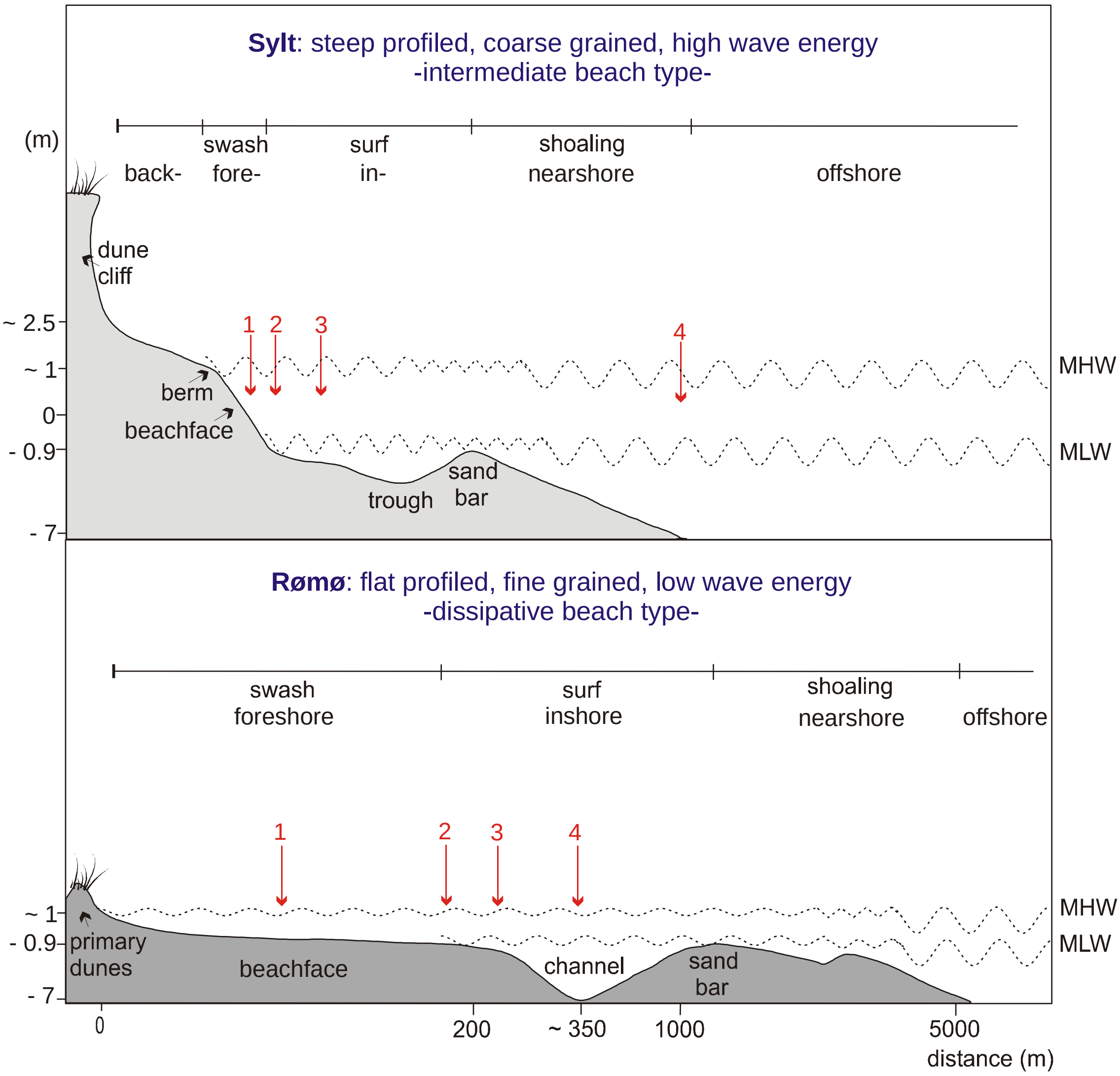


Fig. 2 Schematic illustration of the profile across the Sylt and Rømø shore, resembling intermediate beach types with high wave energy and a dissipative beach with low wave energy (see Short & Wright 1983), respectively. Additionally, sample positions (→ 1-4), and terminology of different zones across the shore according to Short (1999) are marked. 1= mid shore (middle between mean high (MHW) and mean low water line (MLT)) = 0 m depth; 2 = mean low water (0.9 m depth); 3 = 1.4 m depth; 4 = 7 m depth. Shading refers to grain size: light grey = coarse to medium sand; dark grey = medium to fine sand.

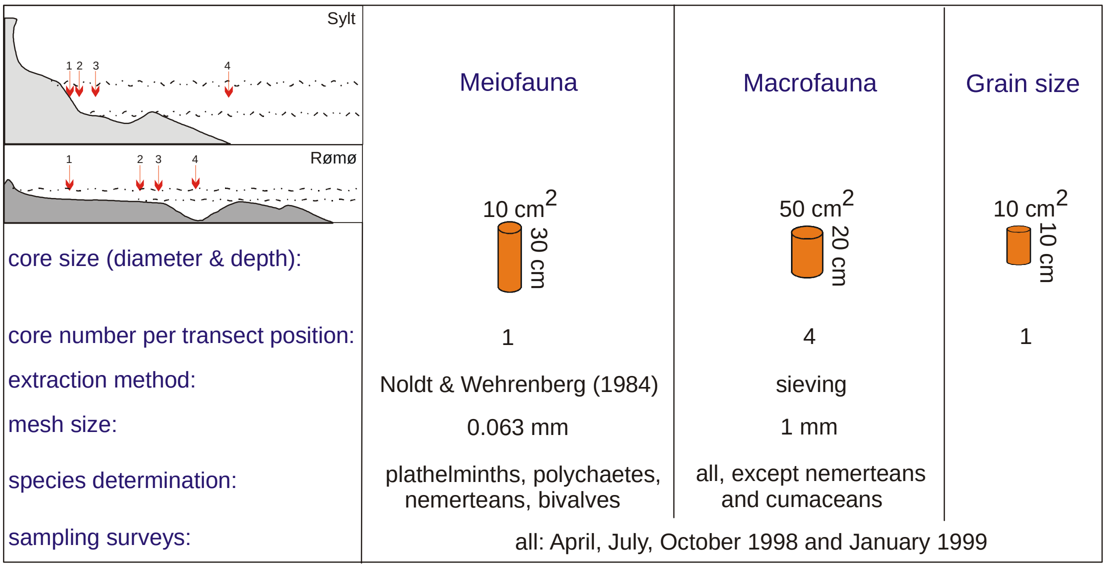
Associated with wave energy, sediment granulometry differs between Sylt and Rømø. The sediment at Sylt consists of medium to coarse sand (Wentworth grade classification) with a decrease in grain size towards the subtidal (Tab. 1). It is moderately well sorted in the intertidal and well sorted in the subtidal (sorting classes according to Gray 1981). The upper three transect positions (Fig. 2) are devoid of a blackish sulphide layer, while such a layer starts at 8 cm sediment depth on average at the 7 m depth line. The Rømø shore consists of fine to medium sand, but it is coarser grained and less sorted at 7 m depth in the channel (Tab. 1). A blackish sulphide layer is present at all transect positions, beginning at 10 cm sediment depth at mid shore, and at 7 cm at the other three sample positions. A more detailed description of the study area and of both shores is given in chapter 2.

Tab. 1 Median grain size (mm) and sorting coefficient (φ (phi)) at four transect positions on the Sylt and Rømø shore presented as arithmetic means with standard deviations calculated over six replicates per position and four sampling surveys (n = 24). Significant differences are indicated by different letters; the same letters indicate non-significant differences. MLW = mean low water line; A = one-way ANOVA, df (degree of freedom) = 3; HSD = Tukey's Honest-Significant-Difference multiple comparison test; H = H-Test, df = 3; U = U-Test, df = 1.

Median grain size	**Sylt**	**Rømø**	**Sorting coefficient**	**Sylt**	**Rømø**
Mid shore	0.95 ± 0.28^{a}	0.19 ± 0.02^{a}	*Mid shore*	0.67 ± 0.12^{a}	0.32 ± 0.07^{a}
MLW	0.59 ± 0.23^{b}	0.18 ± 0.01^{a}	*MLW*	0.66 ± 0.15^{a}	0.28 ± 0.02^{a}
1.4 m depth	0.44 ± 0.21^{c}	0.18 ± 0.01^{a}	*1.4 m depth*	0.48 ± 0.19^{b}	0.31 ± 0.06^{a}
7 m depth	0.26 ± 0.13^{d}	0.27 ± 0.06^{b}	*7 m depth*	0.42 ± 0.13^{b}	0.44 ± 0.09^{b}
H-Test $p <$	0.00001	0.001	$p <$	0.00001 (A)	0.001 (H)
U-Test $p <$	0.001	0.0001	F	17.11	

Sampling

To assess the infauna zonation meio- and macrofauna core samples were taken at four positions across a transect from the mean tide line to 7 m depth (Fig. 2). On each shore six evenly spaced transects were sampled along 1 km of shoreline. Additionally to infauna, samples for grain size analyses were collected. The sampling scheme is summarized in figure 3 and a detailed description is given in chapter 2.



	Meiofauna	Macrofauna	Grain size
core size (diameter & depth):	10 cm^2 30 cm	50 cm^2 20 cm	10 cm^2 10 cm
core number per transect position:	1	4	1
extraction method:	Noldt & Wehrenberg (1984)	sieving	
mesh size:	0.063 mm	1 mm	
species determination:	plathelminths, polychaetes, nemerteans, bivalves	all, except nemerteans and cumaceans	
sampling surveys:	all: April, July, October 1998 and January 1999		

Fig. 3 Sampling for meio- and macrofauna, and grain size analyses across the Sylt and Rømø shore. In the macrofauna the four cores (50 cm^2) per transect position were pooled to 200 cm^2. After extraction from the sediment both faunal components were sorted to major taxa and counted, followed by species detemination. Temporary meiofauna (= juvenile macrofauna) was included in the meiofauna. *Crangon crangon*, *Carcinus maenas* (both Decapoda) and *Hydrobia ulvae* (Gastropoda) were included in the macrofauna. Sediment analyses were carried out by dry sieving and mean grain sizes and sorting coefficent were calculated according to Buchanan (1984).

Statistical analyses

Spatial patterns of the infauna, perpendicular to the shoreline, were described by total number of species, species density, diversity, and abundance. Species density is the average number of species per 10 cm^2 for meiofauna, and per 200 cm^2 for macrofauna. Diversity is calculated according to Shannon Wiener Index $H' = -\sum n_i * ln n_i$, where n_i = proportion of individuals of the i-th species with i = 1, 2, 3,...S). For statistical analyses of differences in these parameters between the transect positions within each shore, one-way ANOVA (Analysis of variance) was used (statistical advice C. Hennig, Department for Mathematics, University of Hamburg). These analyses were based on pooled data of six replicates per transect position and of four sampling surveys (n = 24). Different levels within a significant parameter were analysed using Tukey's Honest-Significant-Difference (HSD) multiple comparison test. Cochran's test was used to test for homoscedasticity of variances. When variances were not homogeneous they always remained heterogeneous, despite of transformations. In this case the H-Test (Kruskal and Wallis) followed by pair-wise U-Tests (Sachs 1984) was used. Statistical significance was assumed at $p < 0.05$ for ANOVA and H-Test, and at $p < 0.008$ for the pairwise U-Tests (Bonferroni-procedure for multiple comparisons; Sokal & Rohlf 1995).

Spatial patterns of the infauna across the shores were further analysed by multivariate analyses using non-metric multidimensional scaling (MDS) (PRIMER software package, Plymouth Marine Laboratory). These analyses were carried out on non-transformed (Rømø meiofauna) and double square root transformed (Sylt meiofauna; both sites macrofauna) data, and were based on means calculated over six replicates per position and four sampling surveys. The discrimination of infaunal communities was tested by one-way ANOSIM (Analysis of similarity; Clarke 1993). Temporal variability of meio- and macrofauna on both shores was analysed in chapter 2, where further statistical details were described.

In meiofauna, species number, species density, and community analysis were based on plathelminths, polychaetes, nemerteans, and bivalves. In macrofauna all specimens were determined to species level, except nemerteans and cumaceans.

Results

Species density and diversity

At Sylt, total meiofaunal species number and diversity were lowest at mid shore, while species density peaked at the intermediate positions (Fig. 4; Tab. 2). At Rømø, in contrast, total species number and species density were highest at mid shore, while diversity showed no significant differences between the transect positions.

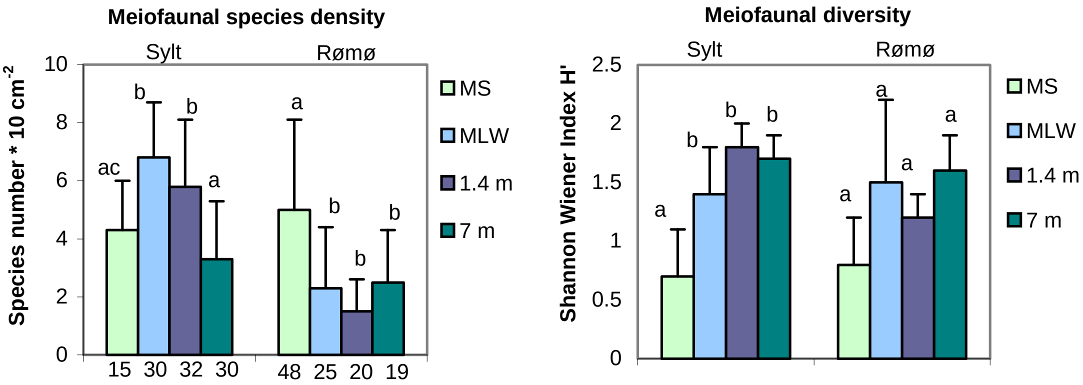


Fig. 4 Meiofaunal species density and diversity along a transect on the Sylt and Rømø shore. Arithmetic means with standard deviations calculated over six replicates per position and four sampling occasions (n = 24). Total species number is mentioned below each column. Same letters within a transect indicate non-significance; significant differences are indicated by different letters. MS = mid shore, MLW = mean low water, 1.4 and 7 m = 1.4 and 7 m depth.

Tab. 2 Statistics of spatial patterns of meio- and macrofaunal species density and diversity across the Sylt and Rømø shore. ANO = one-way ANOVA, df (degree of freedom) = 3; HSD = Tukey's Honest-Significant-Difference multiple comparison test. H-Test: df = 3, U-Test: df = 1.

	Meiofauna	**ANO**	**F**	**HSD**	**H-Test**	**U-Test**
		p <		p <	p <	p <
Sylt	Species density	0.001	13.86	0.001		
	Diversity	0.001	11.63	0.05		
Rømø	Species density				0.00001	0.001
	Diversity	0.1	2.66			
	Macrofauna	**ANO**	**F**	**HSD**	**H-Test**	**U-Test**
		p <		p <	p <	p <
Sylt	Species density				0.00001	0.001
	Diversity				0.05	= 0.01
Rømø	Species density	0.00001	14.63	0.001		
	Diversity	= 0.7	0.45			

Total macrofaunal species number increased downshore at Sylt, and species density was also higher in the subtidal than in the intertidal (Fig. 5, Tab. 2). Diversity showed significant differences among all sample positions, with a tendency towards higher indices downshore. At Rømø, macrofaunal species number also increased down to 1.4 m depth, but then decreased at 7 m depth in the channel. There, the lowest species density was found. Diversity showed no significant differences between the sample positions.

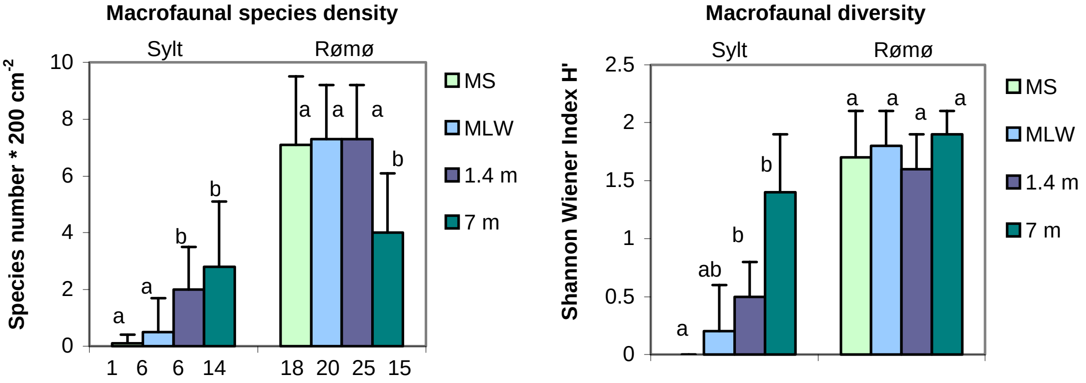


Fig. 5 Macrofaunal species density and diversity at four transect positions on the Sylt and Rømø shore presented as arithmetic means with standard deviations calculated over six replicates per position and four sampling surveys (n = 24). Total species number is mentioned below each column. Same letters within a transect indicate non-significance; significant differences are indicated by different letters, except diversity at Sylt, where different letters indicate a tendency (p = 0.01). Abbreviations see Fig. 4.

Abundance

At Sylt, total meiofaunal abundance was higher at the intertidal than at the subtidal positions (Fig. 6, Tab. 3). This was mainly caused by plathelminth and copepod abundances. Nematodes showed highest abundances at 7 m depth, where polychaetes, ostracods, and oligochaetes attained minimum abundances. All other taxa showed less (nemerteans) or no (acarids and bivalves) statistically significant spatial patterns perpendicular to the shoreline. At Rømø, a minimum of total meiofaunal abundance occurred at 7 m depth in the channel. Nematode abundances decreased significantly at this position. Polychaetes and plathelminths attained maximum abundances at mid shore. Ostracods showed less zonation across the shore and the abundance of copepods, acarids, oligochaetes, nemerteans, and bivalves did not differ between the four transect positions.

At Sylt, plathelminths contributed 50 % to the total meiofaunal abundance at mid shore. Further downshore, first copepods and then nematodes took over (Fig. 6). At Rømø, in contrast, nematodes contributed 70 to 90 % to the total meiofauna abundance at all sample positions.

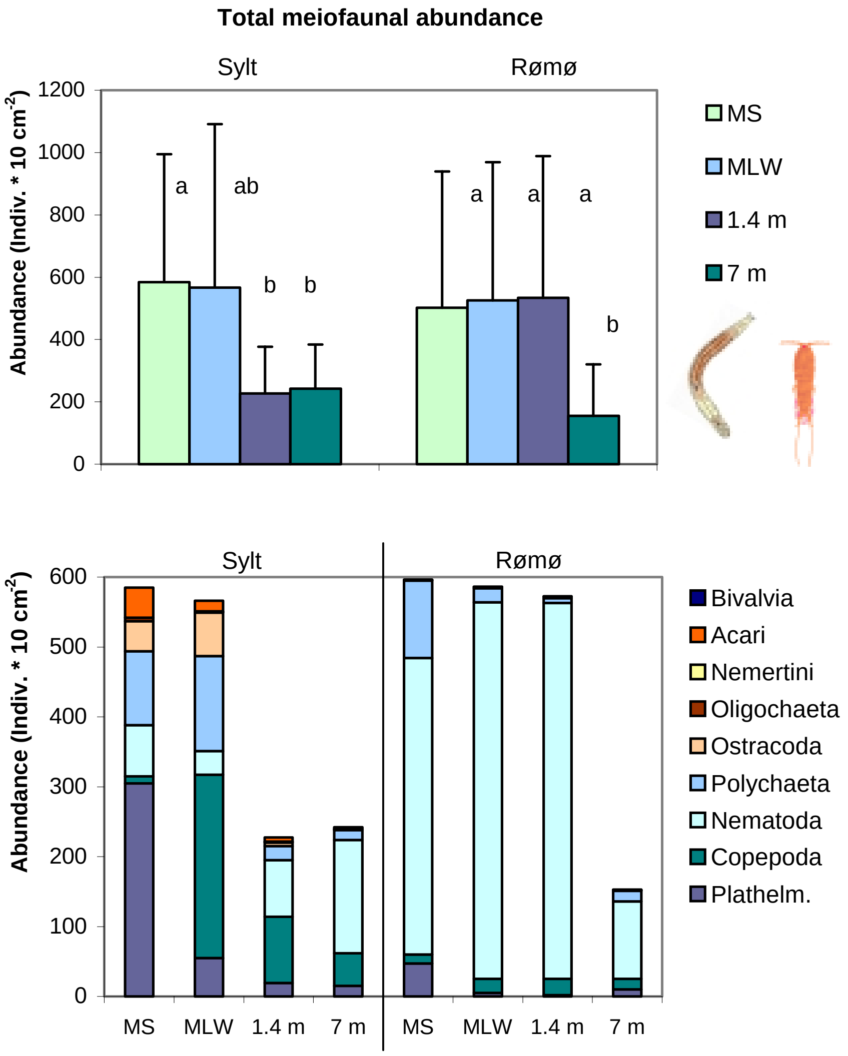


Fig. 6 Total meiofaunal abundance and abundances of single meiofaunal groups at four transect positions on the Sylt and Rømø shore presented as arithmetic means with standard deviations calculated over six replicates per position and four sampling surveys (n = 24). Plathelm. = Plathelminthes. Further abbreviations see figure 4.

At Sylt, the meiobenthic community of the investigated taxa was strongly dominated by the plathelminth *Notocaryoplanella glandulosa* at mid shore. Further downshore, the distinct dominance of one single species decreased and the dominants replaced each other (Tab. 4). At Rømø, the intertidal sites were strongly dominated by the archiannelid *Protodriloides symbioticus*, while in the subtidal a more equal contribution of single species to the meiofaunal abundance was observed.

Tab. 4 Dominant meiofaunal species at the four transect positions on the Sylt and Rømø shore ranked in decreasing order of their contribution to the total meiofauna abundance. Species contributing together 90 % to the total abundance are listed. Pl = Plathelminthes, Po = Polychaeta.

Sylt	Rømø
Mid shore	
Notocaryoplanella glandulosa (Pl) 72 %	*Protodriloides symbioticus* (Po) 70 %
Trilobodrilus axi (Po) 15 %	Microstomida sp. (Pl)23 %
Hesionides arenarea (Po) 11%	
Mean low water	
Trilobodrilus axi (Po) 54 %	*Protodriloides symbioticus* (Po) 73 %
Notocaryoplanella glandulosa (Pl) 18 %	*Paromalostomum fusculum* (Pl) 8 %
Hesionids arenarea (Po)10 %	*Scoloplos armiger* (Po) 6 %
Protodrilus sp. (Po) 7 %	Microstomida sp. (Pl) 5 %
Nematoplana coelogynoporoides (Pl) 6 %	
1.4 m depth	
Protodrilus sp. (Po) 25 %	*Protodriloides symbioticus* (Po) 44 %
Protodriloides symbioticus (Po) 23 %	*Capitella minima* (Po) 16 %
Parotoplanina germinoducta (Pl) 11 %	*Spio martinensis* (Po) 15 %
Hesionides arenarea (Po) 8 %	*Paromalostomum fusculum* (Pl) 6 %
Nematoplana coelogynoporoides (Pl) 8 %	*Cheliplanilla caudata* (Pl) 3 %
Kataplana mesopharynx (Pl) 5 %	*Scoloplos armiger* (Po) 3 %
	Scanorhynchus forcipatus (Pl) 3 %
7 m depth	
Thyphloplanoida sp. (Pl) 25 %	*Spio martinensis* (Po) 24 %
Spio martinensis (Po) 19 %	*Micropthalmus szercowii* (Po) 14 %
Trilobodrilus axi (Po) 13 %	*Archimonocelis oostendensis* (Pl) 13 %
Protodrilus sp. (Po) 8 %	*Capitella minima* (Po) 12 %
Scolelepis squamata (Po) 5 %	*Microphthalmus aberrans* (Po) 9 %
Carenscoila bidentata (Pl) 4 %	*Carenscoila bidentata* (Pl) 8 %
Nematoplana coelogynoporoides (Pl) 3 %	*Neoschizorhynchus parvorostro* (Pl) 6 %
Proschizorhynchus gullmarensis (Pl) 3 %	*Proschizorhynchus gullmarensis* (Pl) 2 %
	Psammorhynchus tubulipenis (Pl) 2 %
	Schizochilus choriurus (Pl) 2 %

Tab. 3 Statistics of the zonation of total meio- and macrofaunal abundance, and major taxa abundance across the Sylt and Rømø shore. H-Test: df (degree of freedom) = 3, U-Test: df = 1.

Meiofauna	**H-Test**	**U-Test**	**Macrofauna**	**H-Test**	**U-Test**
Sylt	p <	p <	*Sylt*	p <	p <
Total	0.001	0.008	Total	0.00001	0.008
Plathelminthes	0.001	0.008	Polychaeta	0.00001	0.008
Copepoda	0.001	0.008	Amphipoda	0.00001	0.008
Nematoda	0.05	0.008	Isopoda	0.00001	0.008
Polychaeta	0.05	0.008	Bivalvia	0.05	> 0.008
Ostracoda	0.05	0.008			
Oligochaeta	0.05	0.008			
Nemertini	0.05	> 0.008			
Rømø	p <	p <	*Rømø*	p <	p <
Total	0.0001	0.008	Total	0.001	0.008
Nematoda	0.0001	0.008	Polychaeta	0.001	0.008
Polychaeta	0.001	0.001	Amphipoda	0.001	0.008
Plathelminthes	0.001	0.001	Nemertini	0.001	0.008
Ostracoda	0.05	> 0.008			

In contrast to meiofauna, total macrofaunal abundance was higher at the subtidal than at the intertidal positions on the Sylt shore (Fig. 7, Tab. 3). This was mainly brought about by polychaetes and amphipods. Isopods attained maximum abundances at 1.4 m depth, while bivalve abundances showed no clear pattern. At Rømø, macrofaunal abundance showed a significant minimum at 7 m depth, which was mainly caused by a scarcity of polychaetes. The same pattern was noticed in abundances of amphipods and nemerteans. No zonation across the shore was detected in abundances of bivalves, decapods, gastropods, and cumaceans. Polychaetes contributed most (> 80 %) to the macrofaunal abundance at all transect positions on both shores. An exception was the mid shore at Sylt, where only isopods occurred.

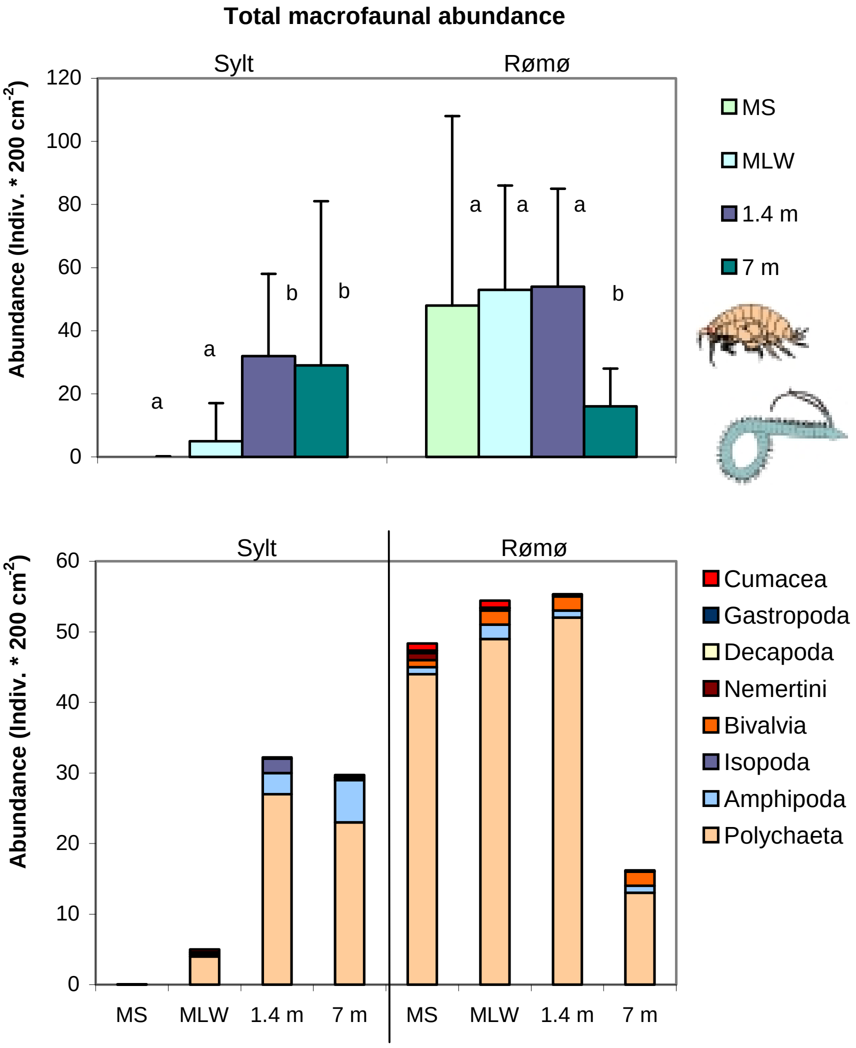


Fig. 7 Total macrofaunal abundance and abundance of major taxa along a transect on the Sylt and Rømø shore. Arithmetic means with standard deviations calculated over six replicates per position and four sampling surveys (n = 24). Abbreviations see figure 4.

The macrofaunal assemblages at the upper transect positions on the Sylt shore were strongly dominated by one species each, while evenness was higher at 7 m (Tab. 5). In contrast, at Rømø the contribution of single species to the macrofaunal abundance was more balanced across the entire shore, although the ranking of the dominant species changed.

Tab. 5 Dominant macrofaunal species at the four transect positions on the Sylt and Rømø shore ranked in decreasing order of their contribution to the total macrofaunal abundance. Species contributing together 90 % to the total abundance are listed. P = Polychaeta, I = Isopoda, A = Amphipoda, B = Bivalvia.

Sylt	**Rømø**
Mid shore	
Eurydice pulchra (I) 100%	*Scolelepis squamata* (P) 58 %
	Scoloplos armiger (P) 10 %
	Pygospio elegans (P) 9 %
	Eteone longa (P) 4 %
	Capitella minima (P) 3 %
	Bathyporeia sp. (A) 3 %
	Paraonis fulgens (P) 3 %
Mean low water	
Scolelepis squamata (P) 81 %	*Spio martinensis* (P) 40 %
Bathyporeia sp. (A) 6 %	*Pygospio elegans* (P) 14 %
Eteone longa (P) 6 %	*Scoloplos armiger* (P) 14 %
	Capitella minima (P) 9 %
	Scolelepis squamata (P) 7 %
	Macoma balthica (B) 3 %
	Bathyporeia sp. (A) 3 %
1.4 m depth	
Scolelepis squamata (P) 86 %	*Spio martinensis* (P) 41 %
Bathyporeia sp. (A) 6 %	*Capitella minima* (P) 25 %
	Scoloplos armiger (P) 11 %
	Pygospio elegans (P) 8 %
	Capitella capitata (P) 5 %
7 m depth	
Spio martinensis (P) 55 %	*Capitella capitata* (P) 25 %
Bathyporeia sp. (A) 21 %	*Scoloplos armiger* (P) 24 %
Scolelepis squamata (P) 8 %	*Spio martinensis* (P) 20 %
Ophelia limacina (P) 4 %	*Macoma balthica* (B) 10 %
Nephtys hombergii (P) 3%	*Capitella minima* (P) 8 %
	Nephtys hombergii (P) 3 %

Community analyses

Multivariate analyses of the meio- and macrofauna data separated faunal assemblages, which are illustrated with MDS plots. For meio- and macrofauna the ANOSIM results revealed no clear relation of clusters to the transect positions on both shores (Fig. 8 and 9, Tab. 6). However, in both faunal components and on both shores the assemblage at 7 m depth was separated from the assemblage at the mid shore. Additionally, at Sylt in meio- and macrofauna a more distinct separation of communities between transect positions is indicated, in contrast to that at Rømø.

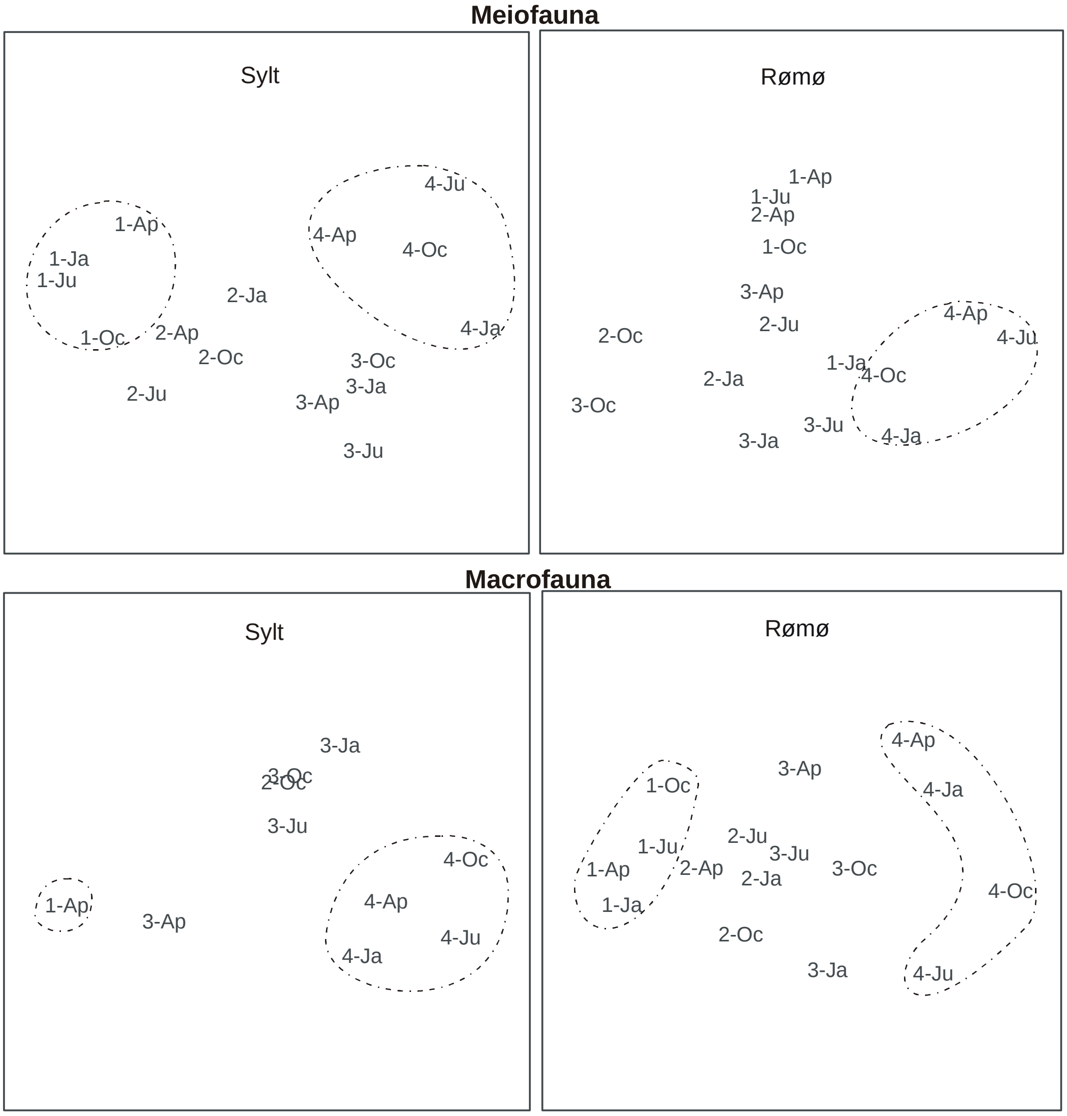


Fig. 8 MDS plots for the meio- and macrofauna on the Sylt and Rømø shore as surveyed at four transect positions (1 = mid shore, 2 = mean low water, 3 = 1.4 m depth, 4 = 7 m depth) in four sampling surveys (April-Ap, July-Ju, October-Oc and January-Ja). Stress values: Meiofauna: 0.10 (Sylt), 0.11 (Rømø); macrofauna: 0.04 (Sylt) and 0.13 (Rømø). On both shores and in both faunal components the assemblage at 7 m depth was separated from that at the mid shore.

Tab. 6 ANOSIM (Analysis of Similarity) results of multivariate analysis of meio- and macrofauna data between sampling positions within each shore. Null hypothesis: similarities on an average between and within positions will be the same. *R* indicates the degree of discrimination between positions: R = 1, if all replicates within positions are more similar to each other than any replicates from different positions; R ≈ 0, if the null hypothesis is true. Evidence to reject the null hypothesis is given by significance level *p*. Total = ANOSIM over all positions.

Meiofauna	**R**	**p =**	**Macrofauna**	**R**	**p =**
Sylt Total	0.56	0.001	Sylt Total	0.60	0.003
7 m depth/mid shore	0.89	0.03	7 m depth/mid shore	1.0	0.2
Rømø Total	0.44	0.002	Rømø Total	0.65	0.001
7 m depth/mid shore	0.99	0.03	7 m depth/mid shore	1.0	0.03

Discussion

Causes of zonation

In addition to their difference in size, meio- and macrofauna may diverge in their response to chemoclines and physical harshness on sandy shores (chapter 2), which may also cause a divergent zonation pattern of these two faunal components.

Meiofauna - For meiofauna, species number and abundance usually seem to be higher in the intertidal than in the subtidal (McIntyre & Murison 1973; McLachlan 1977b; Reise 1985; Armonies & Hellwig 1987; Brown & McLachlan 1990; Giere 1993). Meiofaunal abundance at Sylt and Rømø confirmed this pattern, while species density of interstitial plathelminths and polychaetes showed a different zonation. Several factors, as degree of desiccation, oxygen, food availability, particle size, temperature, and salinity, all interacting with each other, have been proposed as causes of meiofaunal zonation (Schmidt 1969; Harris 1972; McLachlan 1977b, Moore 1979; McLachlan 1980; Brown & McLachlan 1990; Giere 1993). At Sylt at mid shore, desiccation due to a high duration of emergence and coarse sediment may have limited meiofaunal species density (Schmidt 1969; Gray & Rieger 1971; Giere 1993; Armonies & Reise 2000). The core depth of 30 cm in this study may have influenced species density at this position, too. Some species are known to occur down to ground water level (~ 50 cm) on this beach (Schmidt 1968). At the downshore transect positions, this core depth is likely to contain almost all meiofauna. In contrast to the mid shore position, at 7 m depth at Sylt interstitial plathelminths and polychaetes may be mainly limited by reduced oxygen availability, respectively a high sulfide concentration. The latter was indicated by a blackish sulfide layer of the finer sediment at this position (Reise & Ax 1979; McLachlan 1980). Thus, the intermediate transect positions represent the optimum conditions for the plathelminths and small polychaetes, viz. a high availability of oxygen, moist sand throughout the entire tidal cycle, and a medium grain size (McLachlan 1977b; Brown & McLachlan 1990; Armonies & Reise 2000). Strong hydrodynamic turbulence, which occurred at mean low water at Sylt, may not be a limiting factor for the meiofauna, as it was suggested in previous studies (McIntyre 1971; McLachlan et al. 1984; Sherman & Coull 1980; Armonies & Reise 2000; chapter 2). The suggestion of a higher sensitivity of meiofauna to chemoclines than to physical harshness on sandy shores is supported by the results at Rømø, too. Species density did not differ between mean low water, 1.4 m and 7 m depth, despite of strong currents at 7 m depth in the channel. The latter are indicated by a coarser grain size at this position, which tends to be a result of stronger hydrodynamics (e.g., Brown & McLachlan 1990). Optimum conditions for the investigated taxa seem to occur at mid shore at Rømø. This may be due to a highest oxygen availability at this position, indicated by a deeper beginning of the blackish sulfide layer there than at the other transect positions. Oxygen availability as a major determinant of meiofaunal zonation is suggested by e.g., Schmidt (1969) and McLachlan (1978, 1980), too.

Macrofauna - In contrast to the meiofauna, macrofauna seems to be more sensible to physical harshness than to characteristics of the chemocline on sandy shores (chapter 2). This is supported by the spatial patterns observed at Sylt and Rømø. At Sylt, macrofaunal species density, diversity, and abundance increased from the intertidal towards the subtidal, as reported in previous studies (McIntyre & Eleftheriou 1968; Christie 1976; Eleftheriou & McIntyre 1976; Knott et al. 1983; Reise 1985; Brown & McLachlan 1990; Defeo et al. 1992). Less hydrodynamic turbulence in the subtidal at Sylt, indicated by finer grain sizes and the presence of a blackish sulfide layer, may be a prime cause for this zonation (Brown & McLachlan 1990). An increasing feeding time, a smaller temperature range and an absence of desiccation in the sub- than in the intertidal have also been proposed as major causes of this zonation pattern

(McLachlan 1977b; Brown & McLachlan 1990; Armonies & Reise 2000). The macrofaunal zonation at Rømø primarily supports the prevalence of hydrodynamic forces as a limiting factor to the macrofauna. Macrofauna showed little zonation on this shore, except at 7 m depth in the tidal channel, where macrofauna was poorly represented in contrast to the other transect positions. This could primarily be the result of strong currents in this channel of the tidal inlet which separates the two islands. Low macrofaunal abundances in such channels are also reported by Riesen & Reise (1982) and Reise & Schubert (1987). However, coarser grain sizes at this position also cause a variation in the macrofauna, but at the same time stronger hydrodynamics tend to cause coarser grain sizes (e.g., Brown & McLachlan 1990). Thus, macrofauna and hydrodynamic forces are negatively correlated, which was also suggested by Christie (1976) and Brown & McLachlan (1990). This is supported by Lackschewitz & Reise (1998), reporting low macrofaunal diversity and abundance on flood delta shoals subjected to strong hydrodynamics and with highly unstable sediments, contrasting with the rich macrofauna of stable sandy flats.

Further, the results of this study indicate a minor influence of submergence time and grain size on the zonation of meio- and macrofauna on sandy shores. This support the importance of chemoclines and physical harshness for the zonation of meio- and macrofauna, respectively. While the submergence time increased from the mid shore to 1.4 m depth, the spatial variability of meio- and macrofauna were incompatible to this pattern on both shores. Bally (1983) also suggested less influence of the submergence time on the meiofauna, while several authors assumed that this factor may have a high importance for the macrofauna (e.g., Brown & McLachlan 1990). However, the latter was not confirmed on the two shores in this study. Similarily, a lack of correlation between the spatial patterns of the sediment composition and both faunal components was observed at Sylt and Rømø. Thus, sand particle size may be unlikely to directly affect meio- and macrofaunal zonation in general. Less effect of grain size on the spatial variability of meio- (Schmidt 1969; Harris 1972) and macrofauna (McLachlan & Jaramillo 1995) has also been suggested in previous studies.

Spatial pattern

Several studies proposed faunal zonation schemes perpendicular to the shoreline. Some of them suggested a distinct faunal boundary at low tide line (Dörjes et al. 1969; Croker 1977; Dexter 1983, 1984), while others assumed a gradual change of the faunal assemblage across the shore (McIntyre & Eleftheriou 1968; Reise 1985; Armonies & Hellwig 1987). Knott et al. (1993) observed a distinct difference in the macrofauna between inter- and subtidal zones, but noted that many of the numerically dominant species are prevalent in both zones. An abrupt faunal boundary at low tide line was not apparent in this study. However, at Sylt, distinct community changes across the shore were noticed for both faunal components by multivariate analyses. This may be a result of distinct habitat changes on the meio- and macrofaunal scale across this intermediate shore. The tidal levels at which meio- and macrofaunal communities change may differ, due to a different boundary of physically and chemically controlled habitats of these two faunal components (chapter 2). In contrast, at Rømø the community changed more gradually, in line with more gradual habitat changes across this dissipative shore.

A dominance of isopods, such as *Eurydice pulchra* at mid shore at Sylt, agrees with the results of several studies on high energy beaches (McLachlan & Jaramillo 1995). Increasing polychaete abundance and species number in downshore direction on this shore may be a result of increasing physical stability (McLachlan 1983; Knott et al. 1993). In meiofauna, nematode abundances increased downshore, while copepod abundance showed a reversed pattern, due to decreasing grain size, less turbulence, and less oxygen availability in downshore direction (Gray & Rieger 1971; McLachlan 1978, 1983; Coull 1985; Armonies & Hellwig 1987; Raffaelli 1987). As shown at Sylt, several authors reported a dominance of the highly mobile polychaete *Scolelepis squamata* in the lower intertidal and shallow subtidal on sandy shores (Wolter 1987; Knott et al. 1993; Souza & Gianuca 1995). The same is true for the dominance of the Otoplanid *Notocaryoplanella glandulosa* (Plathelminthes) at mid shore (Schmidt 1969; Reise 1988; Wellner & Reise 1989).

At Rømø at all transect positions, polychaetes were most abundant in the macrofauna and nematodes in the meiofauna. This may be due to less wave energy, finer sediment, and lower oxygen availability across the entire shore (McLachlan 1983; Giere 1993;

Knott et al. 1993). On the species level, numerically dominant macrofaunal species showed a wide distribution throughout the inter- and subtidal, while the ranking of dominant species changed. This was also reported by Knott et al. (1983) and Brown & McLachlan (1990). In the meiofauna, a gradual community change across the Rømø shore resulted from changing species composition, with the exception of the polychaete *Protodriloides symbioticus*, which remained dominant at the upper transect positions.

Conclusion

The dynamic intermediate shore with high wave energy is characterized by an abundant meiofauna at the intertidal beachface, dominated by plathelminths and copepods, and high species density of interstitial plathelminths and polychaetes at mean low water and in the shallow subtidal (Fig. 9). Macrofaunal abundance and species density peaked in the subtidal. On the physically more stable dissipative shore with low wave energy, meiofauna dominated by nematodes is homogenously abundant across the shore, except at a deep channel with strong hydrodynamics and coarser grain sizes (Fig. 9). Species density of plathelminths and small polychaetes peaked at mid shore. Macrofauna is fairly even in abundance and species density, except at the channel. The divergent zonation patterns of meio- and macrofauna on the studied shores give further evidence for a divergent sensitivity to chemoclines and physical harshness of this two faunal components, as proposed in chapter 2. Strong hydrodynamic forces primarily affect the macrofauna at the steep intertidal on the dynamic intermediate shore and at the deep tidal channel on the dissipative shore. Meiofauna primarily responses to chemoclines, present at the deeper subtidal only on the intermediate shore and across the entire dissipative shore. Tidal submergence and sediment composition may be of minor importance on the infaunal zonation on the studied shores.

As a corollary of a global climate change, sea level will continue to rise. This will often be followed by increasing hydrodynamic energy at the world’s coastline (Bruun & Asce 1962; Führböter 1989; Lozán et al. 2001). Thus, the effect of hydrodynamic forces on faunal zonation on sandy shores may become increasingly important in the coming decades. This study on the zonation of the infauna on two cold-temperate sandy shores of different wave energy, grain size and shore morphology gives first ideas of the consequences. With increasing hydrodynamics and the associated physical and morphological changes, the macrofauna of cold-temperate sandy beaches may shift towards deeper shore levels, where wave forces are diminished. Meiofaunal plathelminths and polychaetes will probably remain high on the shore.

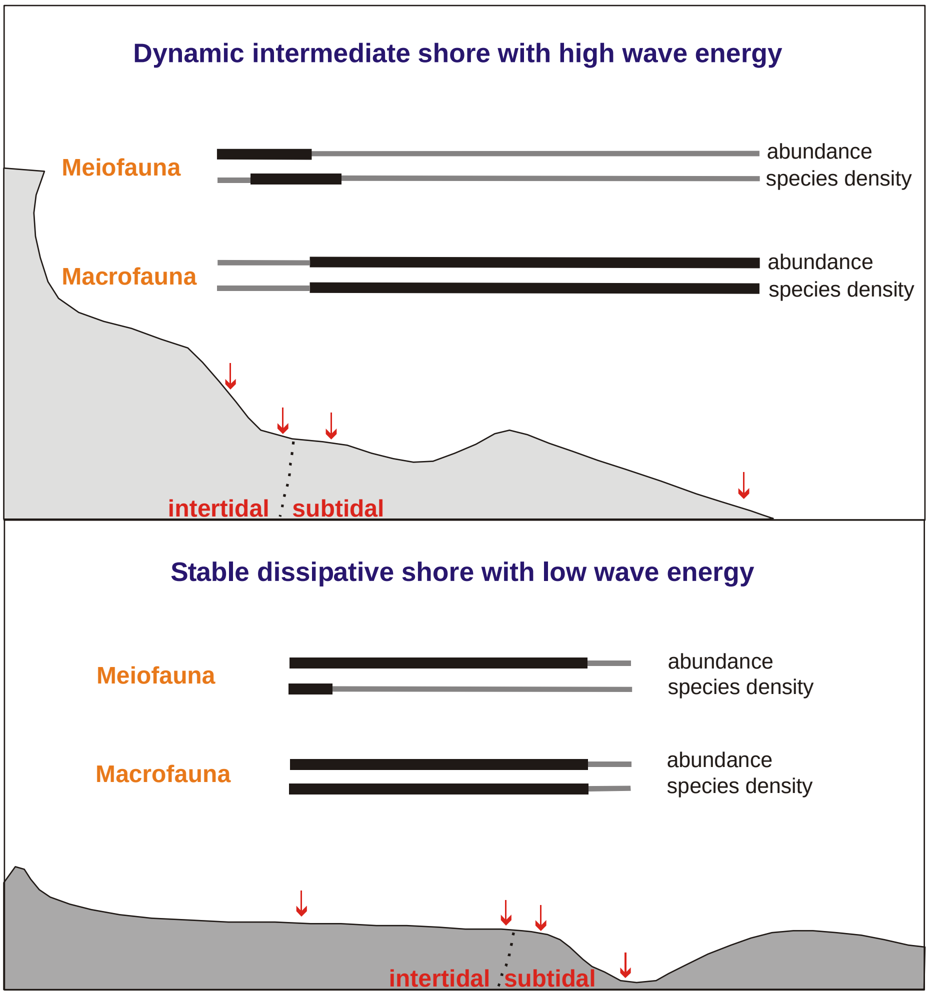


Fig. 9 Schematic illustration of the infaunal zonation on the Sylt and Rømø shore. Meiofaunal species density included plathelminths, polychaetes, nemerteans and bivalves. In macrofauna all specimens were determined to species level, except cumaceans and nemerteans. Black bars indicate a higher abundance and species density, respectively, at the associated transect positions, in contrast to that of grey bars.

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4 BEACH MORPHOLOGY AND FOOD WEB STRUCTURE: COMPARISON OF AN ERODING AND AN ACCRETING SANDY SHORE IN THE NORTH SEA

ABSTRACT Food web components and inorganic nutrients were studied on two sandy shores of the adjacent barrier islands Sylt and Rømø in the North Sea, differing in morphodynamics. Implications of high and low wave energy on the food web structure were assessed. The Sylt shore represents a dynamic intermediate beach type, while the Rømø shore is morphologically stable and dissipative. On the steep profiled, coarse grained Sylt shore, strong hydrodynamics resulted in erosion and high fluxes of organic material through the beach, but prevented any storage of food sources. Contrary to that, the flat profiled, fine grained Rømø shore with low wave energy and accretion accumulated organic carbon from surf waters. At Sylt oxic nutrient regeneration prevailed, while anoxic mineralisation was more important at Rømø. Macrofauna on the Sylt shore was impoverished compared to the community at Rømø. Correspondingly, abundances of epibenthic predators such as shrimps, crabs, fish, and shorebirds were also lower at Sylt. Meiofauna was abundant on both shores, but differed in taxonomic composition. Several major taxa comprised fairly equal proportions of individual numbers on the well oxygenated Sylt shore, while nematodes strongly dominated the assemblage at Rømø. Thus, on cold-temperate, highly dynamic intermediate shores with high wave energy and subject to erosion, a “small food web” takes over. Organisms are agile and quickly exploit fresh organic material. Larger organisms and nematodes abound under stable, dissipative and accreting shore conditions where some food materials may accumulate and zoomass builds up to support abundant visitors from higher trophic levels.

Introduction

Exposed sandy shores are often considered to be merely an edge of the sea or the land, but they also constitute an important ecotone with food chains based on decomposers, grazers and suspension feeders (McLachlan 1980; McLachlan et al. 1981a). High wave energy renders beaches to be inhospitable for many benthic species, but at the same time transforms a physical interface into a productive ecosystem. Exposed sandy shores are usually characterized by surf and epipsammic diatoms as main producers, while attached macroalgae are missing. In addition to microalgae, the food web is based on dissolved and particulate organic matter such as detritus and carrion, with the latter being of minor importance (Steele et al. 1970; McLachlan et al. 1981b; Brown & McLachlan 1990) except when marine mammals are stranded. Two partially separated food webs are based on these energy sources. The "small food web" consists of bacteria, protists and meiofauna. The main components of the "large food web" are macrobenthos and epibenthic predators such as shrimps, crabs, fishes and shorebirds. Both food webs are important in processing the organics washed ashore from the sea to which most production is returned (McLachlan 1980, 1983). The presence of these food web components and their relative importance in the system differ between beach types (Brown & McLachlan 1990). Two main types are distinguished, interface beaches and self sustaining beach and surf zone systems. The former have no surf zone and no primary producers. Their interstitial biota are far more important than the macrofauna and they depend on marine inputs. The latter are characterized by well developed surf zones with significant primary production and a well developed, large food web. Such beaches are self-sustaining, i.e. not depending on offshore marine inputs.

The vicinity of two exposed sandy shores divergent in morphodynamics, provided the opportunity to assess the effects of eroding and accreting conditions on the food web structure on cold-temperate shores in the North Sea. The eroding shore is coarse grained, steep profiled and receives high wave energy, while the accreting shore is fine grained, flat profiled and receives less wave energy. The former resembles dynamic intermediate beach types, and the latter a dissipative beach type (Short & Wright 1983). A comprehensive approach included parameters of food supply (chl *a*, particulate organic carbon, C/N ratio and organic content as loss-on-ignition), meio-, macro- and epibenthos and shorebirds. Concentrations of dissolved inorganic nutrients in interstitial and surf waters were determined for inferences on mineralisation. In particular, the following questions are posed: What are the implications of shore morphology on the food availability for the benthic fauna and on the composition of the meio- and macrofauna assemblage and finally, for the visiting crabs, fishes, and birds?

Material and methods

Study sites

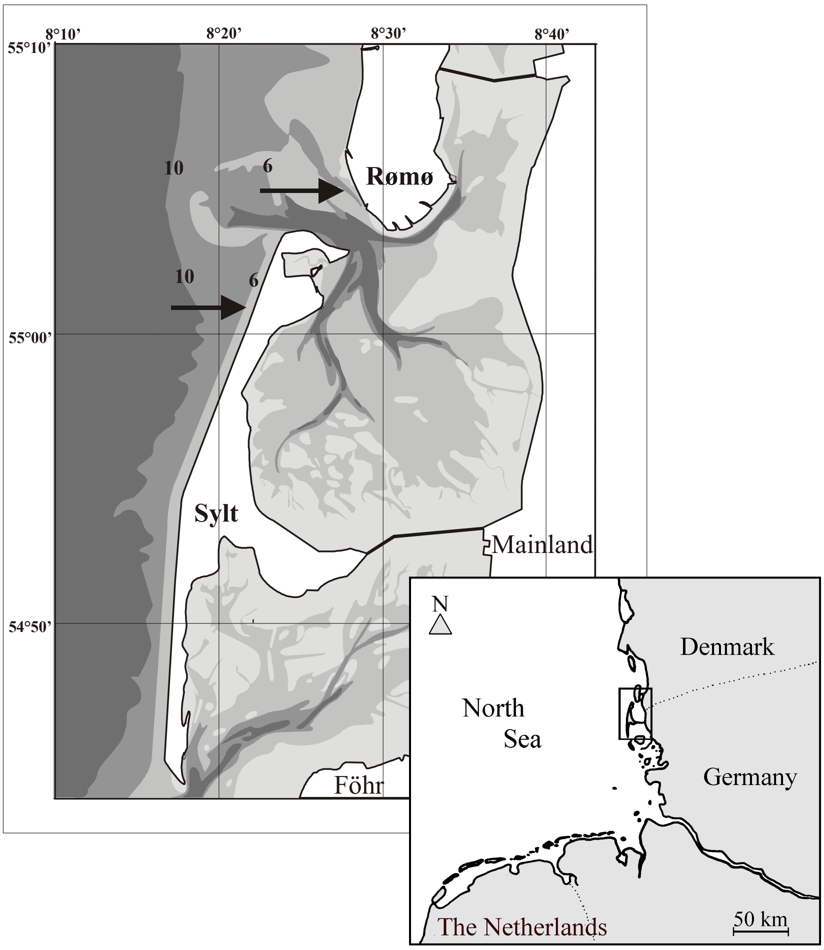
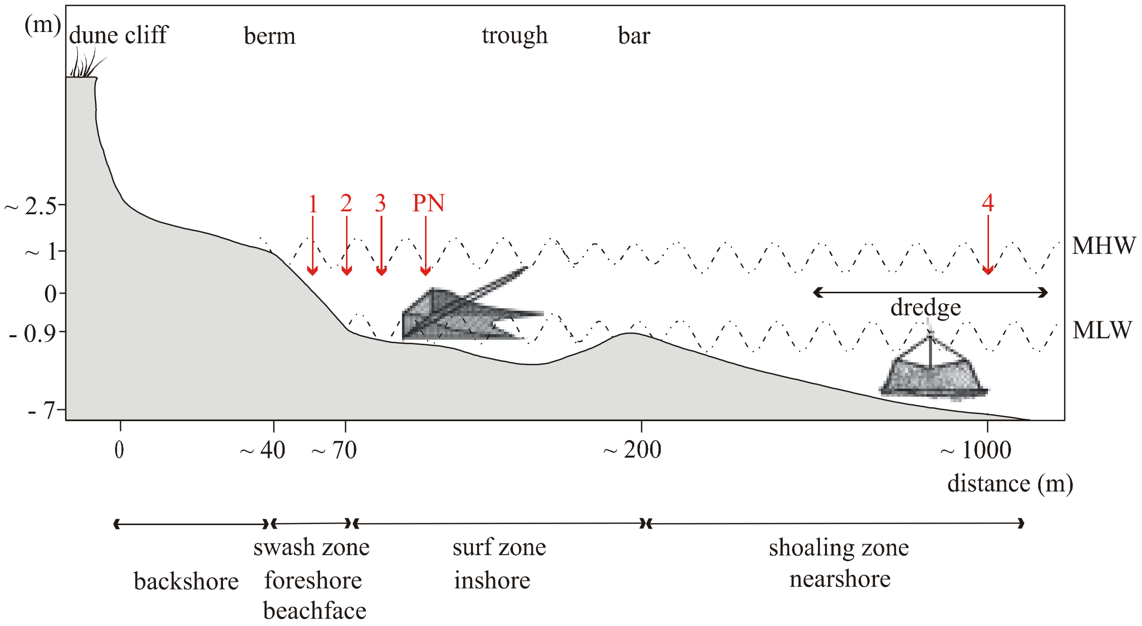


Fig. 1 Study sites (→) on the barrier islands of Sylt (Germany) and Rømø (Denmark) in the eastern North Sea. Shading refers to different water depths (> 10 m, > 6 m, > 0 m: intertidal flats).

The study was conducted on shores of the exposed western sides of the neighbouring barrier islands of Sylt (Germany) and Rømø (Denmark) in the eastern North Sea (Fig. 1). The tides are semidiurnal with a mean range of 1.8 m, and neaps and springs are almost equal. Waves varied during the study period between a maximum height of 3 m with a period of 9 s and a minimum height of 0.1 m with a period of 4 s. Mean wave height was 0.7 ± 0.5 m (ALR Husum 1999). Salinity was in the range of 27 to 33 ‰ PSU. The average water temperature of this cold-temperate region is 4 °C in winter and 15 °C in summer.

Sylt projects some 5 km further seaward than Rømø and the beach retreated 1 to 2 m per year in the last century, while the Rømø beach was progressing seaward at the same time (Dette & Gärtner 1987; Bartholdy & Pejrup 1994). The eroding Sylt shore has a steep beachface (slope of 2 to 4°) and intermittent sand bars parallel the beach at a horizontal distance of about 200 m from mean low water line (Fig. 2). Further offshore, the profile is rather steep with the 6 m depth contour within 1 km distance from the shoreline. The sediment on the Sylt shore is coarse to medium (median diameter (Md) = 0.56 ± 0.33 mm; Wentworth grade classification), moderately well sorted (quartile deviation (QD) = 0.56 ± 0.18 φ (phi); sorting classes: Gray 1981), and devoid of a blackish sulfide layer during the whole year. In contrast, the accreting Rømø shore has a wide and flat beachface (slope ≤ 1°) and a trough of 6-8 m depth directly seaward of the mean low water line. The latter is part of the ebb tide delta of the tidal inlet between Sylt and Rømø. Further offshore, the profile is flat with the 6 m depth contour occurring 5 km west of the shoreline. Much wave energy dissipates on this broad and flat offshore profile, and may explain why the Rømø beachface receives less wave energy than the Sylt beachface (cite summarizing data from Ahrendt, pers. comm.). The sediment at Rømø consists of medium to fine sand (Md = 0.20 ± 0.05), is well sorted (QD = 0.33 ± 0.09 φ), and there is a blackish sulfide layer beginning at 8 cm sediment depth on an annual average. According to the beach classification of Short & Wright (1983) the morphodynamic state of the Sylt shore resembles intermediate types ("longshore bar-through" and "rhythmic bar and beach" during winter; "transverse bar and rip" and "low tide terrace" during summer). These are the most dynamic ones (Short 1999) and periodic beach nourishments at Sylt enhance these dynamics, resulting in a non-equilibrium morphodynamic state. The Rømø shore resembles a dissipative type and was morphologically constant throughout the study period.

Sylt: eroding, intermediate shore with high wave energy



Rømø: accreting, dissipative shore with low wave energy

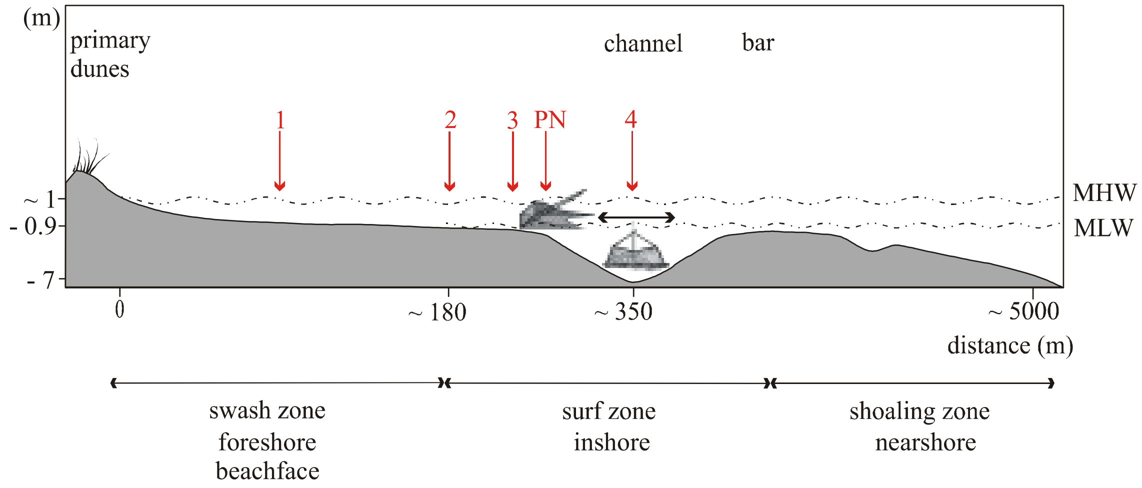


Fig. 2 Schematic illustration of profiles across the Sylt and Rømø shore including sampling positions: 1 = mid shore (middle between mean high (MHW) and low water line (MLW)) = 0 m depth, 2 = mean low water (0.9 m depth), 3 = 1.4 m depth, PN = 1.9 m depth, 4 = 7 m depth, dregde = 3 to 8 m depth. Core sampling of meio- and macrobenthos: position 1-4; sediment sampling for determination of particulate organic matter: position 1-3; sediment sampling for determination of chl *a* and sampling of interstitial waters for inorganic nutrients: position 2; sampling of surf waters for chl *a* and inorganic nutrients: position 3. PN = push-net sampling; dredge = dredge sampling. Shading refers to grain size: light grey = coarse to medium sand; dark grey = medium to fine sand. Terminology of different zones across the shore is according to Short (1999).

Sampling

To determine the **chlorophyll *a*** (chl *a*) content in surf waters and in the sediment, samples were collected on both shores in July and August 1999 (Fig. 2). Surf water samples were taken at 1.4 m water depth, and 100 ml were filtered (Whatman GF/F glass microfibre filters) for analysis. Sediment samples of 2 cm depth were collected at mean low water line using cores of 5 cm^2 and 2 cm^2 cross area at Sylt and Rømø, respectively. Surveys were conducted around low tide during midday. On each shore and during each sampling occasion, 10 replicates were taken along 1 km of shoreline, with the exception of sediment sampling in July when 20 replicates were collected. Chlorophyll *a* was measured spectrophotometrically after aceton extraction, and chl *a* concentrations were calculated according to Lorenzen (1967).

For particulate organic matter (**POM**), particulate organic carbon (**POC**) and particulate nitrogen (**PN**) in the sediment, samples were taken in August 1999 at three water depths (position 1 to 3; Fig. 2). At each position 8 replicates of surface sediment samples were taken along 1 km of shoreline. Carbon and nitrogen analysis were carried out using a C/N analyser (Heraeus Elementar vario EL). Organic matter in the sediment was further measured as loss-on-ignition (LOI) after 12 h at 550 °C, and is expressed as percentage of sediment dry weight. This sampling was done in April 1999, collecting sediment samples at three water depths, as mentioned above, each with six replicates on both shores.

To assess **nutrient concentrations in surf and interstitial waters**, parallel samples were taken at Sylt and Rømø in July and August 1999. Sampling was conducted during low water by taking surf water samples at 1.4 m depth and interstitial water samples at mean low water line (Fig. 2). Interstitial water was extracted from surface sediments (5 to 10 cm depth) through ceramic cups and sucked into evacuated glass bottles (van Katjwijk, pers. comm.). During both occasions, replicates (July surf water: 15, interstitial water: 20; August surf and interstitial water: 10) were collected along 1 km of shoreline. Nutrient analysis (ammonium, nitrite, nitrate, phosphate and silicate) were carried out following the methods described by Graßhoff et al. (1983). Due to very low nitrite concentrations (< 0.3 µmol* l^{-1}) in relation to nitrate (> 1 µmol* l^{-1}), both were pooled to nitrite plus nitrate (NO_x) concentrations.

Meio- and macrofauna were sampled on both shores at four positions along a transect from mean tide line to 7 m depth (Fig. 2). The transects were 6-fold replicated, evenly distributed along 1 km of shoreline. At each position one core for meiofauna (cross area: 10 cm²) down to a sediment depth of 30 cm was taken and four cores for macrofauna (cross area: 50 cm²) down to a depth of 20 cm, which were pooled to 200 cm². With respect to temporal variability, sampling was repeated 4 times: in April, July and October 1998 and in January 1999. The meiofauna was extracted from the sediment using the SMB-method of Noldt & Wehrenberg (1984; sieve mesh size: 63 µm), sorted to major taxa, and counted. Due to very low abundances nemerteans, oligochaetes, gastrotrichs and bivalves are summarized under “others”. Macrofauna samples were sieved (1 mm mesh size), the animals sorted alive, counted and identified to species level whenever possible. The abundance category “others” comprises decapods, nemerteans, cumaceans and gastropods. A more detailed description of meio- and macrobenthos sampling on both shores is reported in chapter 2.

“Small” epibenthos was collected using a Riley push-net (Eleftheriou & Holme 1984) equipped with a 1.90 m net bag of 1.5 mm mesh size kept open by a rectangular frame of 1.50 x 0.30 m. The survey was carried out in July and August 1999 with 10 hauls of 70 m length per shore during each sampling survey. In July sampling was conducted at sunrise and nightfall, in August during day and night. All hauls were taken around low tide, and arranged alongshore at 1.90 m water depth, with respect to mid shore = 0 m depth (duration of each haul: ~ 1 minute; Fig. 2). All organisms in the net were counted and identified to species level whenever possible. Sometimes the entire net was filled with green algae. In such cases, half of the content was sorted for species, and counts of individuals were multiplied by 2. Then the entire content was sorted for rare species.

“Large” epibenthos was sampled with a traditional oyster dredge of 1 cm mesh size. The dredge had a wrought-iron blade of 1 m in width at its lower edge. The 0.5 m long net bag was kept open by a rectangular frame of 1 x 0.5 m. The survey was carried out in June and July 1999 by taking 12 hauls of 500 m length on both shores during each sampling. The hauls were collected at 3 to 8 m water depth around low tide in the morning (Fig. 2). All organisms in the net were counted and identified to species level whenever possible. Beside living epibenthos, the dredge content was composed of shell gravel with some stones, and occasionally with clumps of clay or peat. Sometimes shell gravel or *Lanice conchilega* tubes filled the entire net bag. In these cases, half of the total content was sorted for species, and counts of individuals were multiplied by 2. The entire content was then sorted for rare species. Because of their small size relative to the mesh size of the dredge, amphipods and mobile polychaetes were disregarded. Macroscopic epigrowth on organisms was also recorded, counted as a colony and added to the total abundance of "large" epibenthos. The abundance category "Moll/Echinod" comprises molluscs and echinoderms, and "Cnidar/Bryoz" comprises cnidarien and bryozoen colonies. Flatfish (mostly < 5 cm in length) in dredge and push-net samples were summarized as "juvenile flatfish". These dredge and push-net samples are regarded as semi-quantitative, because dredges sometimes bounce up and down on the bottom (Field 1970). Efficiency of push-net samples may be low with respect to *Carcinus maenas*, because this crab may quickly burrow into the sediment when approached by a net (Hermann et al. 1998).

During preliminary studies, resting and **feeding birds** were recorded on both shorelines, indicating sanderlings (*Calidris alba*) as the most numerous migrants on the Sylt and Rømø shores. To get an impression of avian predation pressure, feeding sanderlings were counted along 1 km of shoreline. Counts were related to shoreline instead of area, because sanderlings trail the water's edge and forage whenever a wave has receded (Myers et al. 1980; Roberts & Evans 1993). A survey was carried out in May 1999, because many sanderlings visit the Wadden Sea during spring migration and peak in mid-late May (Meltofte et al. 1994). On five days with similar weather conditions the birds were counted every 15 minutes during 5 hours around low tide when the intertidal area of the shores was exposed (4 hours before and 1 hour after low tide). Additionally, this time range was chosen, because McLachlan et al. (1980) reported feeding sanderlings throughout the day and Crove (pers. comm.) reported a main feeding time around low tide.

The main thrust of this study was on meio- and macrofauna dwelling in the sediment (chapter 2 and 3). All other measurements reported are at a lower level of effort. They are presented here to provide a comprehensive picture of the diverging food webs of the two shores for which the infauna may serve as an indicator.

Statistics

One-way ANOVA (analysis of variance) was used to test for differences in abundances of meio-, macro- and epibenthos as well as in concentrations of chl *a*, particulate organic matter and inorganic nutrients between the shores. To test for homoscedasticity of variances Cochran's test was used, and data of the dependent variables were transformed once (square root transformation of macrobenthos abundance). When variances were not homogenous despite of the transformation, Wilcoxon, Mann and Whitney's non-parametric U-Test (Sachs 1984) was used (statistical advice C. Hennig, Department for Mathematics, University of Hamburg). Statistical significance was assumed at $p < 0.05$ for ANOVA and U-Test, and at $p < 0.025$ for multiple U-Test (comparison of inorganic nutrient concentrations between and within the shores; Bonferroni-procedure for multiple comparisons; Sokal & Rohlf 1995). To test for overall differences of meio- and macrofaunal abundances between shores, data of the four transect positions each with six replicates and of the four sampling surveys were pooled ($n = 96$). Temporal and spatial variability of the infauna is presented in chapter 2 and 3. Different sampling occasions of chl *a*, inorganic nutrients and epibenthos (e.g., June, July, August, sunrise, nightfall, day, night) were analysed separately. The same was done with sedimentary C/N and organic matter as loss-on-ignition (LOI) with three sample positions at different water depths, each with 8 and 6 replicates, respectively. In "large" epibenthos the hauls from within the depth range of 3 to 8 m were pooled ($n = 12$) for analysis. For testing on differences in abundances of feeding sanderlings along the shorelines, mean abundance per counting day was calculated and used in the analysis.

Results

Chlorophyll *a*, particulate organic matter and inorganic nutrients

Chl *a* values in surf waters showed no significant differences between the Sylt and the Rømø shore in July and August, while the sediment at Rømø contained significantly higher chl *a* concentrations than that at Sylt in both months (Fig. 3).

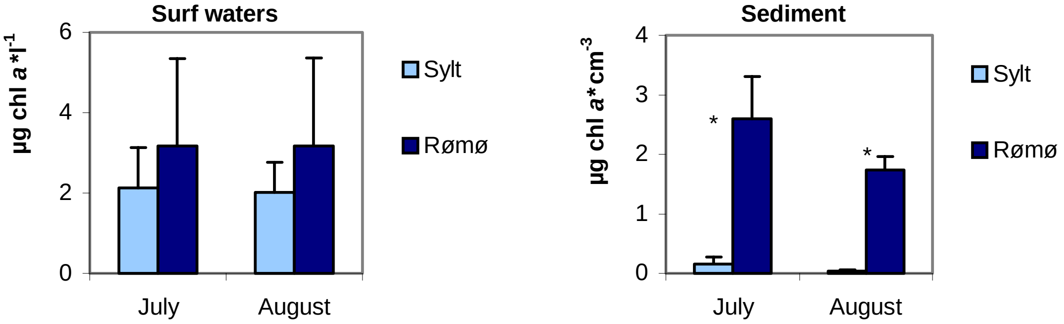


Fig. 3 Chlorophyll *a* concentrations of surf waters and sediment on the Sylt and Rømø shore in July and August 1999. Arithmetic means with standard deviations of 10 replicates per sampling occasion (with exception of sediment sampling in July: n = 20). * = significant differences between shores within each sampling survey; both U-Test, $p < 0.001$, df (degree of freedom) = 1.

Particulate organic carbon and C/N ratios were at all sample positions significantly higher on the Rømø than on the Sylt shore (Fig. 4). Organic content as loss-on-ignition (LOI) was also at all positions higher at Rømø than at Sylt (Rømø/Sylt [%]: mid shore 0.19 ± 0.08/0.13 ± 0.03; mean low water 0.24 ± 0.1/0.16 ± 0.04; 1.4 m depth 0.23 ± 0.07/0.16 ± 0.06; all U-Test, $p < 0.05$, df = 1).

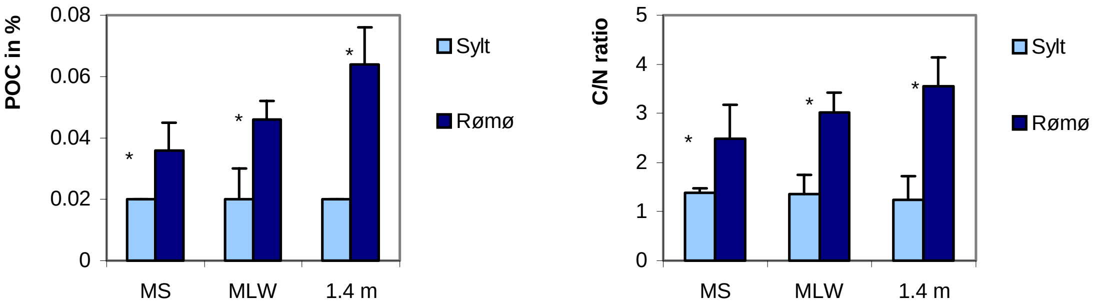


Fig. 4 Particulate organic carbon (POC) and C/N ratio of sediment on the Sylt and Rømø shore in August 1999. Arithmetic means with standard deviations calculated over 8 replicates per position. MS = mid shore; MLW = mean low water; 1.4 m depth line. * = significant differences between shores; all U-Test, $p < 0.01$, df = 1.

In surf waters no differences of phosphate and silicate concentrations between the shores were detected during both sampling surveys. Ammonium concentration showed no difference in July, but were significantly higher at Rømø than at Sylt in August (Fig. 5). Conversely, nitrite plus nitrate (NO_x) concentrations in surf waters were lower at Rømø during both sampling occasions. In interstitial waters, concentrations of all nutrients differed between the shores in July and August (Fig. 5). Phosphate, silicate and ammonium were significantly higher at Rømø than at Sylt, while NO_x showed a reversed pattern.

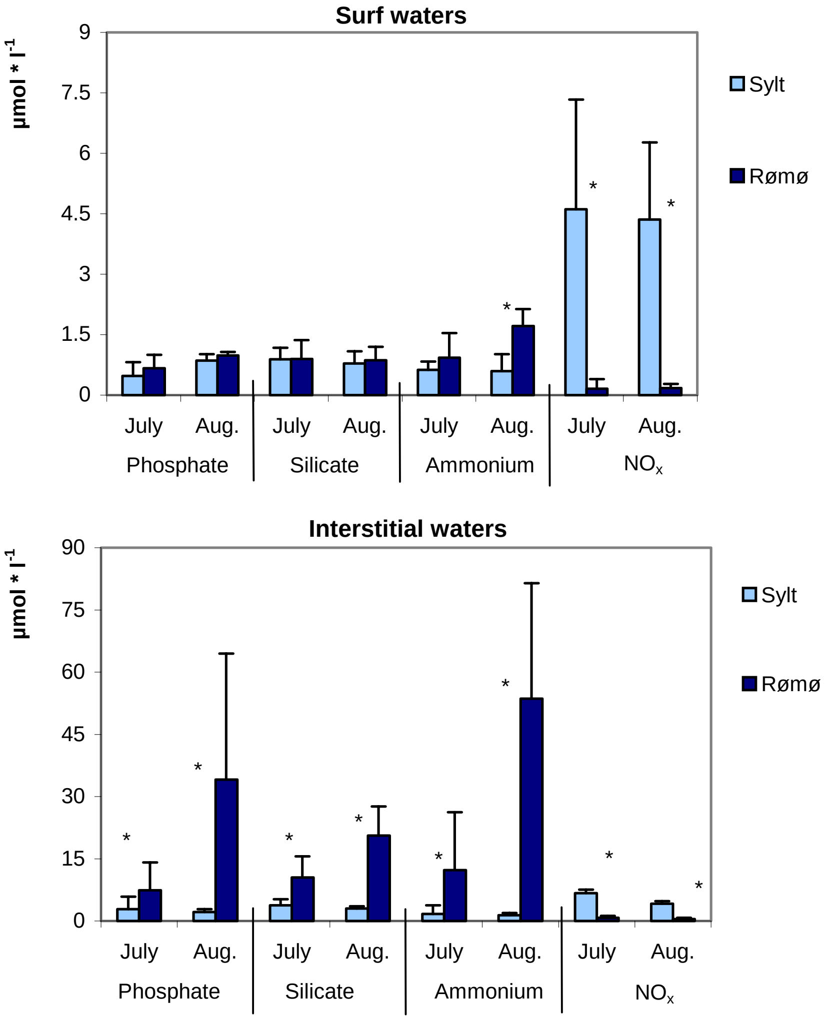


Fig. 5 Inorganic nutrient concentrations in surf and interstitial waters at Sylt in contrast to Rømø in July and August (Aug.) 1999. Arithmetic means with standard deviations calculated over replicates per sampling survey (July: surf water n = 15, interstitial water n = 20; August: both n = 10). NO_x = nitrite plus nitrate. * = significant differences between shores within each sampling occasion; all U-Test, $p < 0.025$, df = 1. Note the difference in scale between surf and interstitial water.

Nutrient concentrations in interstitial waters were higher than in surf waters on both shores during both sampling periods (Fig. 6). Exceptions with no difference between interstitial and surf waters were ammonium (July, Sylt) and NO_x (August, Sylt).

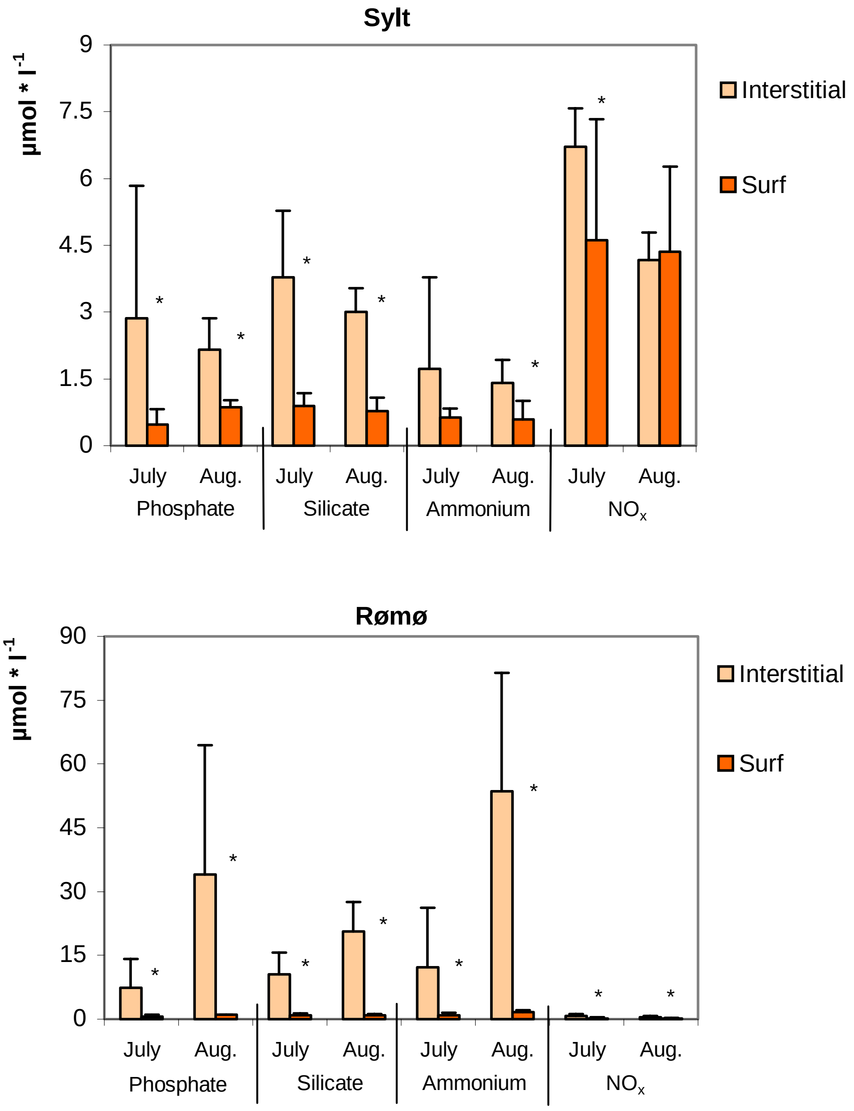


Fig. 6 Inorganic nutrient concentrations in surf in contrast to interstitial waters on the Sylt and Rømø shore in July and August 1999. Arithmetic means with standard deviations calculated over replicates per sampling (July: surf water n = 15, interstitial water n = 20, August: both n = 10). Surf = surf waters, interstitial = interstitial waters. * = significant differences between interstitial and surf waters within shores and within each sampling survey; all U-Test, $p < 0.025$, df = 1. Note the difference in scale between Sylt and Rømø.

Meio- and macrofauna

Total meiofaunal abundance did not differ between the Sylt and the Rømø shore, but there were differences in terms of individual numbers of major taxa (Fig. 7). Abundances of nematodes were significantly higher at Rømø than at Sylt, while the reverse was true for abundances of plathelminths, copepods, ostracods, and acarids (all U-Test, $p < 0.001$, $df = 1$). Abundances of polychaetes and minor taxa showed no differences between the shores. Nematodes (84 %) clearly dominated the meiofaunal assemblage on the Rømø shore, while on the Sylt shore polychaetes (17 %), plathelminths (24 %), nematodes (22 %) and copepods (26 %) comprised fairly equal proportions. Total abundance of macrofauna organisms was significantly higher at Rømø than at Sylt (one-way ANOVA, $p < 0.0001$, $F = 63.22$, $df = 1$; Fig. 7). This was mainly caused by higher abundances of polychaetes and bivalves on the Rømø shore. Isopods occurred only at Sylt (all U-Test, $p < 0.0001$, $df = 1$). A detailed description of the meio- and macrofaunal communities is given in chapter 2 and 3.

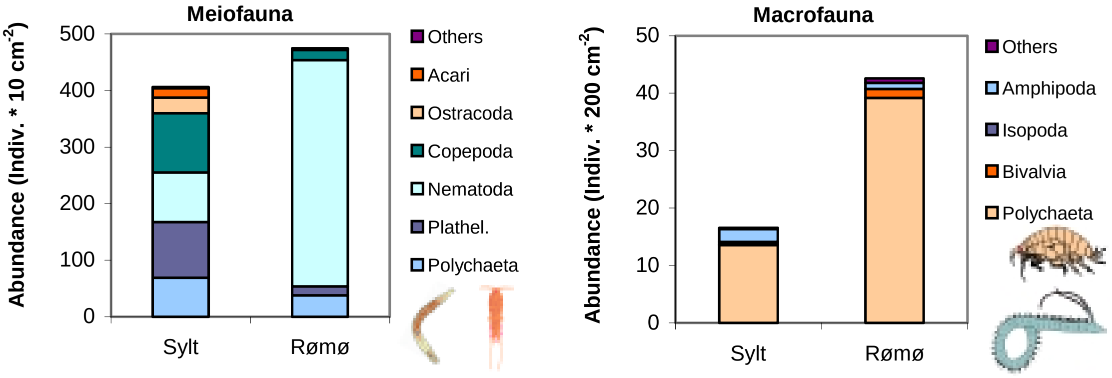


Fig. 7 Total meio- and macrofaunal abundance and abundance of major taxa on the Sylt and Rømø shore. Arithmetic means of four transect positions each with six replicates and of four sampling surveys ($n = 96$). “Others” includes nemerteans, oligochaetes, gastrotrichs and bivalves in meiofauna, and decapods, nemerteans, cumaceans and gastropods in macrofauna. Plathel. = Plathelminthes.

Epibenthos and sanderlings

Total abundance of "small" epibenthos was significantly higher on the Rømø than on the Sylt shore during both sampling occasions in July and in day-sampling in August (Fig. 8). Night-sampling in August showed no statistically significant differences between the shores. On both shores Nilsson's pipe fish (*Syngnathus rostellatus*), sand goby (*Pomatoschistus minutus*), brown shrimp (*Crangon crangon*) and shore crab (*Carcinus maenas*) were the dominant fish and crustacean species. The differences between the shores in July were mainly brought about by sand goby (*P. minutus*) and brown shrimp (*C. crangon*). In August in day-sampling higher crustacean abundances, particularly brown shrimp, at Rømø than at Sylt caused the difference of total epibenthos abundance between the shores (all U-Test, $p < 0.05$, df = 1). All other taxa showed no statistically significant differences in abundances between the shores.

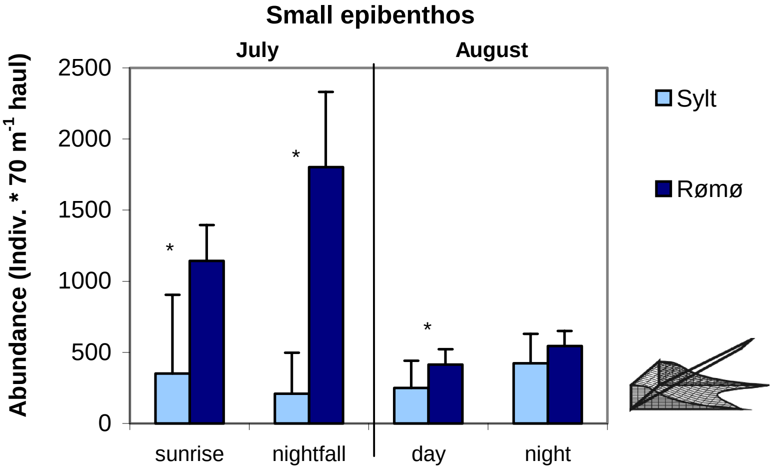


Fig. 8 Total abundance of "small" epibenthos per 70 m push-net haul on the Sylt and Rømø shore in July and August presented as arithmetic means with standard deviations of 10 hauls at 1.90 m water depth. * = significant differences between shores within each sampling; all one-way ANOVA, $p < 0.05$, df = 1, July: sunrise F = 13.61, nighfall F = 55.97, August: day F = 5.23.

Total abundance of "large" epibenthos was significantly higher on the Rømø than on the Sylt shore in June and July (Fig. 9). Densities of molluscs/echinoderms, barnacles, and cnidariens/bryozoans were higher at Rømø than at Sylt during both sampling occasions. Decapod abundance was only in July significantly higher at Rømø than at Sylt.

However, decapod abundance in June without *C. crangon* revealed a significant difference between the shores. The ranking of dominant species in each taxa was similar at Rømø and Sylt (Tab. 1).

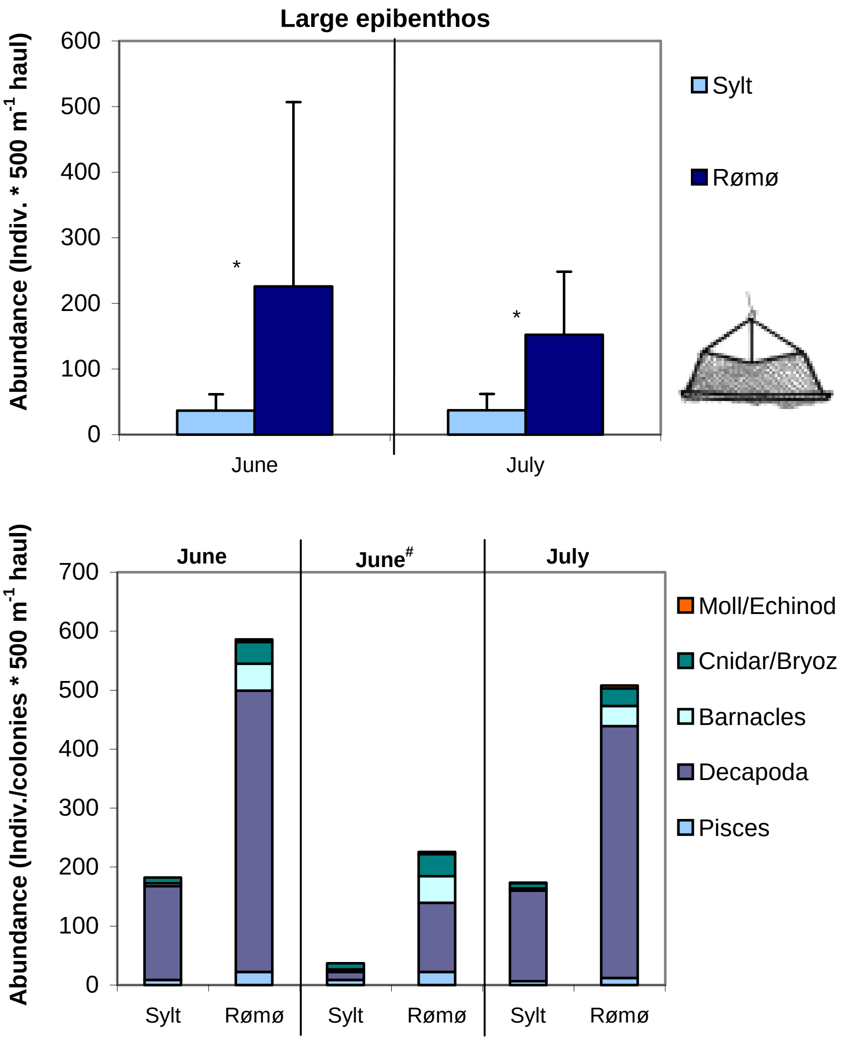


Fig. 9 Total abundance and abundance of major taxa of "large" epibenthos per 500 m dredge haul on the Sylt and Rømø shore in June and July presented as arithmetic means with standard deviations of 12 hauls within 3 to 8 m water depth. Moll/Echinod = total of Mollusca and Echinodermata, Cnidar/Bryoz = total of cnidarian and bryozoen colonies. June# = crustacean abundances without *Crangon crangon*. * = significant differences between shores within each sampling survey; total abundance: both U-Test, $p < 0.05$, df = 1; taxa abundance: all U-Test, $p < 0.01$, df = 1.

Tab. 1 Ranking of species of “large” epifauna on the Sylt and the Rømø shore in June and July 1999. Species contributing 90 % to the total abundance per taxa are listed.

Sylt June	**%**	**Rømø June**	**%**	**Sylt July**	**%**	**Rømø July**	**%**
Pisces							
Juv. flatfish	55	Juv. flatfish	31	*Pleuronectes platessa*	74	*Pleuronectes platessa*	47
Pleuronectes platessa	28	*Syngnathus rostellatus*	20	Juv. flatfish	13	*Merlangius merlangus*	13
		Sprattus sprattus	17			*Sprattus sprattus*	13
		Pomatoschistus minutus	12			*Pomatoschistus minutus*	10
Crustacea							
Crangon crangon	89	*Crangon crangon*	69	*Crangon crangon*	85	*Crangon crangon*	77
Pagurus bernhardus	5	*Pagurus bernhardus*	10	*Pagurus bernhardus*	10	Barnacle colonies	7
		Barnacle colonies	9			*Pagurus bernhardus*	6
Mollusca							
		Macoma balthica	69	*Crepidula fornicata*	50	*Crepidula fornicata*	65
		Cerastoderma edule	19	*Mytilus edulis*	50	*Macoma balthica*	28
Cnidaria							
Hydractinia echinata	65	*Hydractinia echinata*	63	*Hydractinia echinata*	99	*Hydractinia echinata*	57
Obelia longissima	22	*Obelia longissima*	25			*Obelia longissima*	22
Obelia sp.	11					*Obelia* sp.	16
Bryozoa							
Electra pilosa	50	*Electra pilosa*	50	*Electra pilosa*	75	*Electra pilosa*	56
Bowerbankia imbricata	43	*Bowerbankia imbricata*	43	*Alcyonidium* sp.	25	*Alcyonidium* sp.	24

Feeding sanderlings (*Calidris alba*) showed significantly higher abundances on the Rømø than on the Sylt shoreline (U-Test, $p < 0.01$, df = 1; Fig. 10).

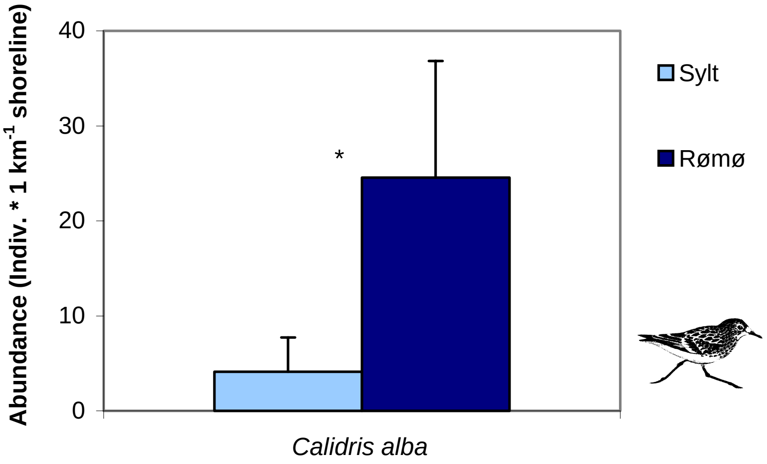


Fig. 10 Abundance of sanderlings (*Calidris alba*) along 1 km of shoreline on the Sylt and Rømø shore in May 1999 presented as arithmetic means with standard deviations of five counting days each with five hours of counting. * = significant differences between shores.

Discussion

The presence of food web components on sandy shores differs between beach types due to different shore morphology and associated grain size and wave energy (Fig. 11).

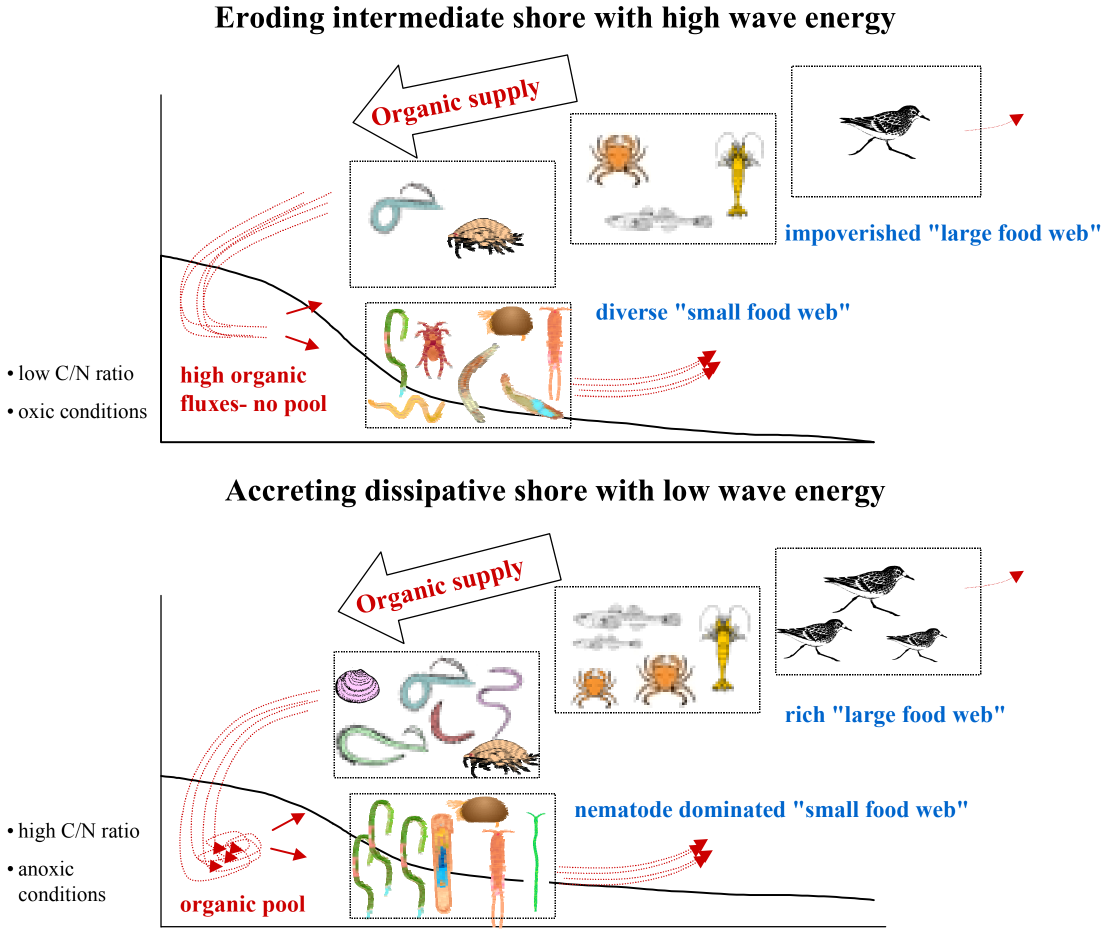


Fig. 11 Food web structure on cold-temperate shores. Highly dynamic, intermediate shores with high wave energy and subject to erosion are characterized by high fluxes of organic material through the beach, but without storage of food sources in the sediment. On these shores the “small food web” of agile organisms dominates, while organic storage and the “large food web” is important on stable, dissipative and accreting shores. Arrows indicate flow of organic and mineralized substances.

“Large food web” (macrobenthos-epibenthos-shorebirds)

Food sources for the macrobenthos on sandy shores are surf and epipsammic diatoms, particulate and dissolved organic matter, detritus and carrion (Brown & McLachlan 1990). However, the major food available for the macrobenthos may differ between the studied shores as a result of their different morphodynamic states. The Rømø shore apparently stores food sources in the sediment, which is indicated by a higher amount of particulate organic carbon and chl *a* in the sediment at Rømø than at Sylt. Less wave energy and finer sand grains at Rømø may enhance the accumulation of organic material from the surf waters. Furthermore, higher C/N ratios indicate a higher amount of refractive material at Rømø than at Sylt. In contrast, at Sylt high hydrodynamics and erosion may prevent any storage of organic carbon in the sediment. But this shore may filter higher volumes of sea water than the Rømø shore due to coarser sediment, steeper profile and higher wave energy resulting in higher fluxes of particulate organic matter on this shore, despite of similar chl *a* concentrations (and probably particulate organic matter) in the surf waters on both shores. Thus, the sediment at Rømø is probably a richer food source for deposit feeders. This is supported by a higher abundance of macrofauna on this shore. Cammen (1982) also assumed that fine grained sediment was a richer food source for deposit feeders. In contrast, higher fluxes of particulate organic matter at Sylt may support filter feeders as it was shown on shores in South Africa (McLachlan 1980; McLachlan et al. 1981a). However, compared to Rømø, the Sylt macrofauna is impoverished. Physical disturbance by high wave energy is proposed as the major limitation for the macrofauna on the intermediate Sylt shore, while food availability may be no limiting factor due to high fluxes of particulate organic matter on this shore. Accordingly, oxygen availability is unlikely to limit the macrofauna at Sylt. A negative correlation of macrofauna with strong hydrodynamics and unstable sediments was also reported e.g. by Brown & McLachlan (1990), Christie (1976) and Lackschewitz & Reise (1998). While severe hydrodynamic turbulence seems to exclude filter feeders from cold-temperate shores, such populations (e.g. surf clams *Donax* spp.; hippoid crabs *Emerita* spp.) are able to cope with such conditions on warm-temperate to tropical shores (Steele 1976; McLachlan et al. 1981a). Apparently, this niche of agile filter feeders is not occupied in the eastern North Sea due to low temperature which may restrict the mobility of these poikilotherme organisms. The same may be true for agile scavengers (e.g. *Bullia* spp.). Under low hydrodynamic conditions the benthic macrofauna of the nearshore zone also colonizes the beachface of cold-temperate shores.

The inshore zone of sandy shores may act as a feeding ground for epibenthic species and, especially for juvenile fish, as nursery areas rich in food (McIntyre & Eleftheriou 1968; Lasiak 1981; Brown & McLachlan 1990). The most abundant epibenthic predators at Sylt and Rømø (brown shrimp, shore crab, sand goby, juv. flatfish, pipe fish) are opportunistic carnivores, mainly feeding on infauna selected on the basis of relative availability (Pihl 1985). Newly recruited individuals feed on zooplankton and, to some extent, on meiobenthos, while older stages feed on small macroinvertebrates such as epibenthic mysids and crustaceans, polychaetes, or bivalve siphons (Edwards et al. 1970; Mehner 1992; Pihl 1985; Hamerlynck & Cattrijsse 1994). The only exception in the study area was Nilssons's pipe fish which is mainly planctivore (Hermann et al. 1998). Lower epibenthic abundances at Sylt than at Rømø are probably a result of low food availabilty. This may be indicated by an impoverished macrofauna at Sylt in contrast to Rømø, although absolute abundances of benthic prey species are not necessarily an adequate measure of their availability to predators (Ansell & Gibson 1990). Low abundances of macro- and epibenthos will in turn affect shorebirds foraging on invertebrates on sandy shores (Myers et al. 1982; Hockey et al. 1983), which is indicated by lower sanderling abundances at Sylt than at Rømø. Sanderlings feeding on crustaceans, gastropods, bivalves and insects were the most numerous visitors on sandy shores in the study area as it was also reported from shores in South Africa (Voous 1962; McLachlan et al. 1980; Myers et al. 1980).

“Small food web” (micro- and meiofauna)

The interstitial food chain consisting of bacteria, protists and meiofauna is partially separated from the macrobenthos-epibenthos-shorebird food web. The main energy flow through this system goes through bacteria utilizing dissolved and particulate organic matter received from the sea (Steele et al. 1970). Remineralized nutrients support microphytobenthos. Protozoans feed on bacteria and miroalgae, and also consume dissolved and particulate organic matter. Food sources for meiofauna are all these components and meiofauna itself (McIntyre et al. 1970; Munro et al. 1978; Alongi 1988; Brown & McLachlan 1990). Total meiofaunal abundance did not differ between Sylt and Rømø. This may indicate a similar food availability on both shores. However, at Sylt agile meiofaunal organisms (i.e. most plathelminths, copepods, polychaetes) were most abundant, while the Rømø shore was dominated by sluggish organisms (i.e. most nematodes). This may result from differences in the interstitial climate between the shores. The physical harshness of the eroding, intermediate shore may be counterbalanced by oxygen-rich conditions. On the accreting, dissipative shore a pronounced chemocline favours a dominance of nematodes (see chapter 2 and 3). As is the case for the macrofauna, differences in availability of major food sources between the shores may also affect the meiofauna. At Sylt, meiofauna needs to be able to quickly use fresh organic matter pathing through the beach under high oxic conditions resulting in the dominance of agile meiofaunal organisms. In contrast, at Rømø meiofauna may primarily exploit accumulated refractive organic material under low oxic or even anoxic conditions. Many nematodes are well adapted to this functional role (Heip et al. 1985; Giere 1993).

Meiofauna linked to almost all trophic compartments in the interstitial system attains a significant position within the “small food web”. However, meiofauna represents no dead end in the food chain, because there are several meiofauna-macrofauna interrelations. Meiofauna feeds on juvenile macrofauna and itself serves to some extent as food for macrofauna (Reise 1979; Giere 1993). Thus, the meiofauna may have a central position in the entire benthic food web of exposed sandy shores. However, there is still a large gap in knowledge on the meiofauna food web and meiofauna-macrofauna interactions on sandy shores. This warrants further studies on this subject.

Nutrient regeneration

Sandy beaches have long been considered to be active in nutrient recycling by mineralising organic matter received from the sea (Pearse et al. 1942). Several authors proposed a great importance of sandy beaches in the inshore zone’s self-purifying and regeneration mechanisms (Oliff et al. 1970; McLachlan 1979, 1982; Liebezeit & Velimirov 1984), while Hayes (1974) reported a rather insignificant nutrient efflux from beaches. At Sylt and Rømø nutrient concentrations were higher in interstitial than in surf waters, indicating that both beaches are sources of nutrients originating from mineralisation of organic matter. This is supported by the correspondence of an ammonium dominance in surf and interstitial waters at Rømø with anoxic sediment layers, and the nitrate dominance at Sylt with oxic conditions throughout. The results of this study enable no quantitative conclusions on efflux rates. Higher nutrient concentrations in interstitial waters on the dissipative shore than on the intermediate one may result primarily from a lower permeability of the finer sediment at Rømø. High permeability due to coarse sediment at Sylt prevents any accumulation of nutrients. However, Huettel et al. (1998) proposed a high turnover rather than a low activity in non-accumulating sandy bottoms. Thus, the different nutrient concentrations in interstitial waters provide no evidence for a differential mineralisation rate of the shores. Higher N-values (ammonium or nitrate, respectively) in surf waters on both shores than in the Sylt-Rømø Bight during the study period may indicate a high turnover on both shores (van Beusekom, pers. comm.).

Conclusion

The biotic system of the eroding, intermediate shore with high wave energy is mainly supplied by the actual organic loading from surf waters pathing through the beach (Fig. 11). Meiobenthos is abundant and mainly composed of agile organisms, while macrobenthos, epibenthic predators, fish and shorebirds are all impoverished. On the accreting, dissipative shore with low wave energy, part of the input is stored as organic carbon in the sediment, which then supports the biotic system. Meiobenthos is abundant, but sluggish organisms (many nematodes) dominate the assemblage. Macrobenthos, epibenthic predators and shorebirds are abundant. The intermediate shore may be characterized by an oxic nutrient regeneration, while on the dissipative shore also anoxic mineralisation occurs.

As a corollary of global warming sea level rise may accelerate, resulting in increasing hydrodynamic forces and enhanced erosion on the world's sandy shorelines (Bruun & Asce 1962; Bird 1987; Führböter 1989; Lozán et al. 2001). This may enhance beach nourishment to combat erosion. Beach nourishment attempts to keep the shoreline at the same position, but it may also interrupt natural changes from reflective to dissipative shores (Short 1999). Thus, highly dynamic intermediate shores away from equilibrium state may be a result. On cold-temperate shorelines, such shores may be characterized by high fluxes of organic matter through the beach, but without storage of food sources in the sediment. They may primarily be used by a well developed “small food web” of agile organisms which are able to quickly exploit fresh organic material under high oxic conditions, while the “large food web” will impoverish.

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5 BURRIED ALIVE:

EFFECTS OF BEACH NOURISHMENT ON THE INFAUNA OF AN EROSIVE SHORE IN THE NORTH SEA

ABSTRACT Artificial beach nourishment as a “soft” defence has become the preferred method to combat shoreline erosion. However, the beach infauna may be affected by such a disturbance. Up to 3 m of sand have been piled upon beaches, followed by enhanced sediment dynamics. The impact of two nourishment operations of different magnitude (159,000 and 351,000 m^3/2 km) on meio- and macrofauna across a shore on the island of Sylt (North Sea) has been studied between 1999 and 2001. No significant effect on meiofauna was noticed after the smaller operation in 1999, while a decreased copepod abundance in the shallow subtidal and a reduced polychaete species density at mid shore occurred 4 months after the larger nourishment. In the macrofauna, a short-term reduction of the two dominants, the isopod *Eurydice pulchra* and the polychaete *Scolelepis squamata*, in the shallow subtidal was noticed in 1999. A stronger and more lasting negative effect was caused by the larger operation in 2000. Macrofaunal abundance and species density in the deeper subtidal zone were lower even 9 months after the nourishment compared to a reference site. However, these infaunal responses to both beach nourishments are not considered as dramatic relative to natural changes along the shore and between years. From an ecological perspective, sand replenishments may be regarded as an acceptable method for coastal defence, provided intervals between succeeding operations last at least three years at a given site.

Introduction

Coastal erosion threatens to become an unrelenting problem due to the combined effects of coastal development and rising sea level (Leatherman 1987; Charlier & de Meyer 1995; Lozán et al. 2001). To combat coastal erosion the traditional approach has been the construction of groynes, breakwaters, sea walls, the placement of tetrapods etc.. These “hard” defences have frequently been found unsatisfactory due to hazards to beach users, lack of esthetic appeal, occasionally enhanced erosion further downshore, and high costs coupled with limited effectiveness (Walton & Sensabaugh 1979; Reilly & Bellis 1983; Pilkey & Wright 1989; Cooper 1998). In view of these limitations, sand replenishment as a “soft” defence has now become the preferred method for dealing with shoreline erosion (Reilly & Bellis 1983; Nelson & Pullen 1985; Nelson 1993; Nordstrom 2000). The essential effect of this method is to move the beach state back in time and to allow it to repeat an earlier sequence of erosion.

The use of sand replenishment has been rapidly increased in the last decades accompanied by an increasing amount of replenished material per project (Valverde et al. 1999). This raises challenging questions about the consequences of these large-scale disturbances to the beach ecosystem. How do effects vary with the amount of replenished sand and the spatial scale of the operation? The immediate impact on the benthos is in many cases a massive burial by 1 to 3 m of sand on the upper shore (Rakocinski et al. 1996). After the operation, hydrodynamics gradually restore the shore’s original morphology, concomitant with an increased sediment mobility (Brown & McLachlan 1990). This may also affect the infauna seaward of the upper shore. Studies on ecological consequences of beach nourishment rarely have found their way into pre-reviewed literature (Nelson 1993), and most dealt with macrofauna only, while concurrent studies on meiofauna are scarce. Due to a focus on fore- and inshore macrofauna, possible effects on the adjacent subtidal communities have rarely been studied (e.g. Essink 1997).

The growing scale of beach nourishments and the paucity of information on its ecological effects compelled us to study the consequences for both meio- and macrofauna, and from the intertidal towards the subtidal shoaling zone. On the island of Sylt (Germany) two operations differing in the amount of supplied sand were investigated: at a beach length of 2 km 159,000 m^3 were deposited in 1999 and a further amount of 351,000 m^3 was added to the same site in 2000. A nearby undisturbed beach was simultaneoulsy studied for comparison and to account for seasonal effects. Lower infaunal abundances and species densities at the nourished site after the operation compared to the reference site are defined as negative effects, provided no lower values already occurred before the nourishment. Recommendations for beach nourishments are given to keep the ecological impact low. Generally, a smaller impact on meiofauna than on macrofauna is hypothesized. Meiofauna seems to be better adapted to mobile shore sediments than most macrofauna (McIntyre 1971; McLachlan et al. 1984; chapter 2 and 3). Effects at the adjacent subtidal may increase with the amount of sand supplied to the backshore and beachface.

Material and Methods

Study site

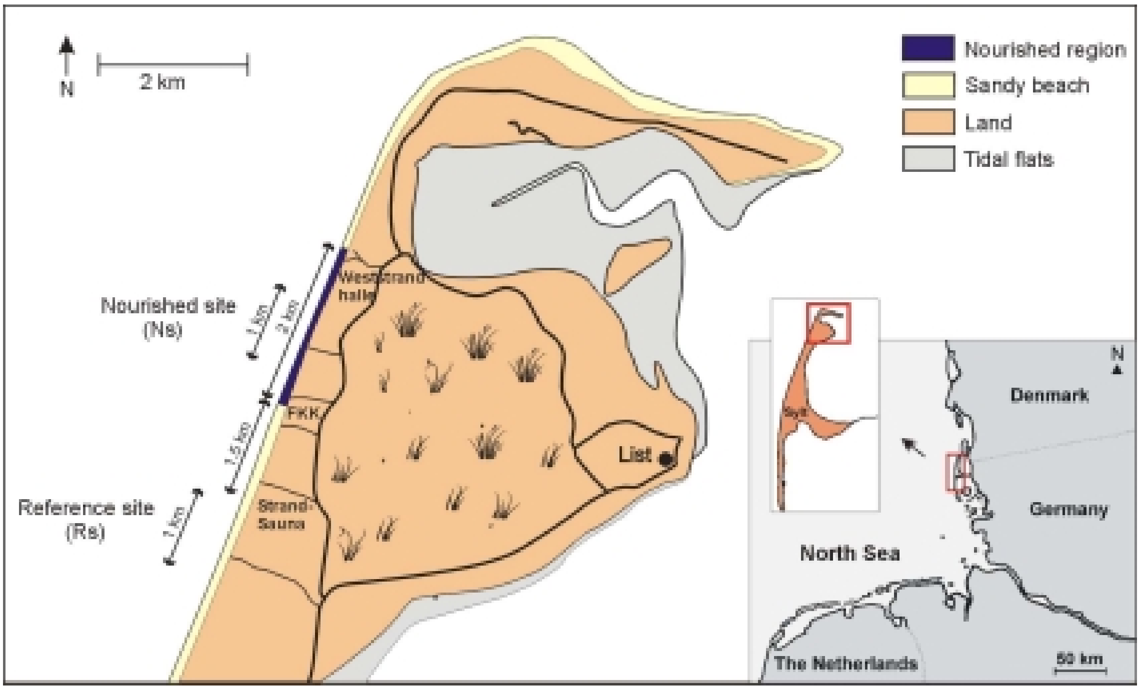

Fig. 1 Study sites at the northern part of the barrier island of Sylt in the eastern North Sea. Nourished (Ns) and reference site (Rs) are 1 km in shorelength. The nourished region is 2 km in shorelength, with replenishments in the summers of 1999 and 2000. The reference site begins 1.5 km south of the nourished region.

The studied shore is at the exposed western side of the barrier island of Sylt (Germany) in the eastern North Sea (Fig. 1). Average water temperature of this cold-temperate region is 4 °C in winter and 15 °C in summer. During the study period surf water salinity was in the range of 27 to 33 ‰ PSU (Practical Salinity Units) and interstitial water was 27 to 29 ‰ PSU. Tides are semidiurnal with a mean range of 1.8 m, and little difference between neaps and springs. Two sites at the nothern part of Sylt, each 1 km in shorelength, were studied (Fig. 1). The nourished site (Ns) is located in a nourished region, which is 2 km long. Replenishments took place in the summers of 1999 and 2000. Earlier, this region was already nourished 1988 and 1993. The selected reference site (Rs) begins 1.5 km south from the nourished region. This site was nourished once in 1992. Residual longshore currents are directed northward. Before sand replenishments started, the shoreline retreated by 1 to 2 m per year in the last century (Dette & Gärtner 1987). The studied areas are characterized by a steep beachface (slope of 2 to 4°). An intermittent sand bar parallels the beach at a horizontal distance of about 200 m from mean low water line (Fig. 2). Further offshore, the profile is rather steep, with the 6 m depth contour positioned within 1 km from the shoreline. The morphodynamic states of the shore resemble intermediate types ("longshore bar-through" and "rhythmic bar and beach" during winter; "transverse bar and rip" and "low tide terrace" during summer), which are assumed to be the most dynamic ones (Short & Wright 1983; Short 1999). Dynamics become enhanced by the beach nourishment, which constitutes to a morphodynamic state away from equilibrium. The sediment of the shore consists of medium to coarse sand (median diameter (Md) = 0.56 ± 0.33 mm; Wentworth grade classification) with a decrease in grain size towards the subtidal (chapter 3). It is moderately well sorted in the intertidal and well sorted in the subtidal (sorting classes according to Gray 1981). A blackish sulphide layer in the sediment is apparent in the deeper subtidal only (chapter 3).

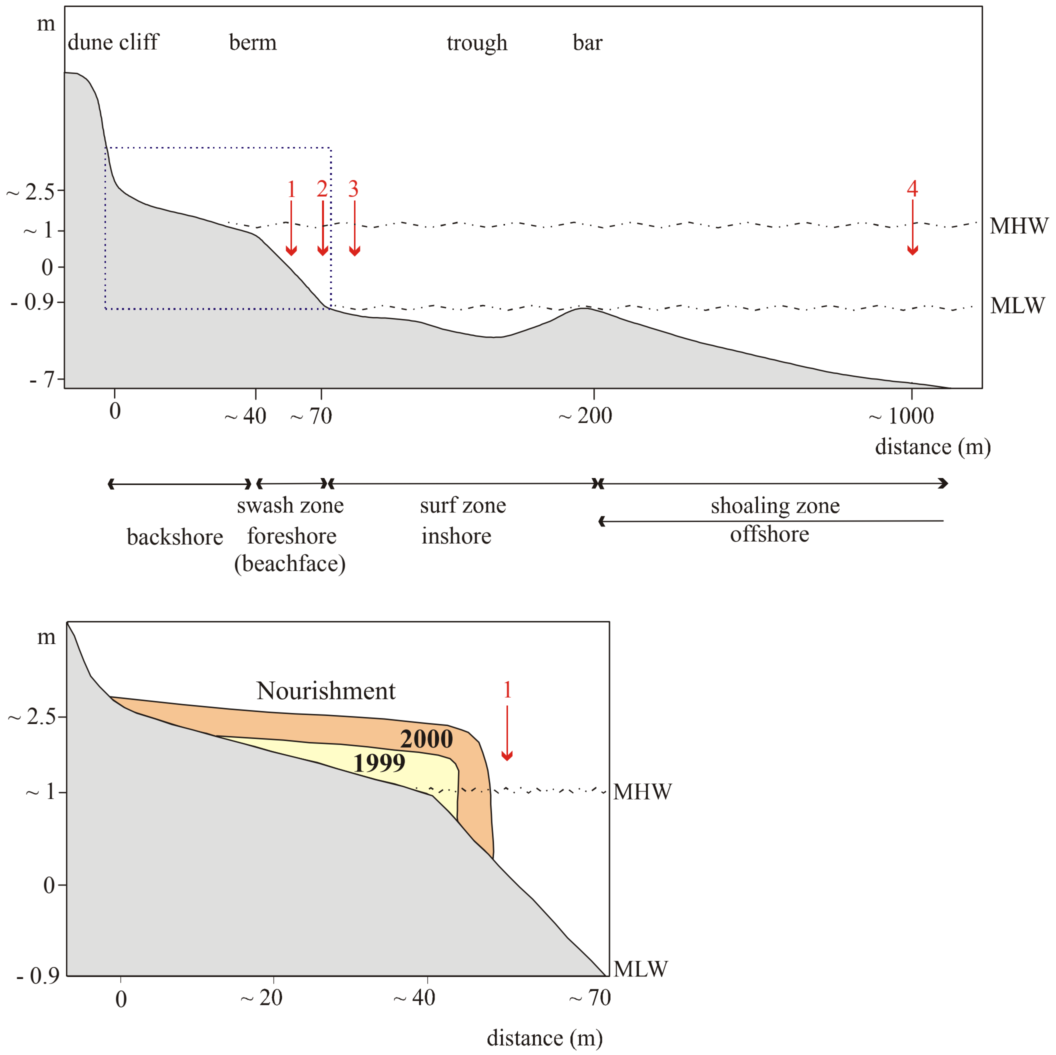

Fig. 2 Schematic profile across the Sylt shore with sampling sites (→ 1-4), and terminology for zones according to Short (1999). In the detail below, the amount of replenished sand and the resulting beach profiles in 1999 and 2000 are indicated. 1 = mid shore (middle between mean high (MHW) and mean low water line (MLW)) = 0 m depth; 2 = mean low water (0.9 m depth); 3 = 1.4 m depth; 4 = 7 m depth.

Beach nourishment

The beach nourishment in 1999 was completed over a period of 6 weeks (May 18 to July 30). During this phase 159,000 m^3 of dredged sand were hydraulically deposited directly onto the beach along 2 km of shoreline. The material was dredged 6 km offshore at Westerland II by a hopper bagger, transported to the beach and pumped as a water slurry via a movable pipeline onto the beach. The sediment-water slurry was released from a diffuser head at the end of the pipeline into a basin on the beach, prepared by bulldozers. The water flowed back into the sea, while the sediment stayed and a new beach profile was modelled by the bulldozers. In 2000 (May 22 to June 20) a nourishment of 351,000 m^3 was conducted in the same way as in 1999. After the completion of the operations, a new cliff of approximately 1.5 m height in 1999 and of 2.5 to 3 m height in 2000 developed (Fig. 2). The beach immediately began to restore its original morphology. The steeper profiles from the sediment filling cause beach morphometries to become more reflective, thereby potentially increasing wave disturbance and sediment transport dynamics (Brown & McLachlan 1990; Rakocinski et al. 1996). The nourished material was moderately well sorted sand with a medium grain size of 0.45 ± 0.16 mm and 0.36 ± 0.18 mm in 1999 and 2000, respectively. In both years these grain sizes were close to the mean of the resident sediment of the entire shore (1999: 0.51 ± 0.29 mm; 2000: 0.54 ± 0.27). The nourished material was grey and black, indicating that it came from a reduced sediment layer. It contained no living meio- and macrofauna.

Sampling

To assess the impact of beach nourishment on the infauna, an "area by time" design (see Nelson 1993) was used. A nourished site and a reference site were studied simultaneously. The selected reference site was approximately 1.5 km south of the nourished region (Fig. 1). Since residual currents transport sediment northward, any impact by the nourishment is unlikely to occur. Interspersion of nourished and reference sites was impossible, having only a single impact site available. In 1999 a pre-nourishment survey of meio- and macrofauna was conducted in April, 1 month before the operation began. In October, 3 months after the completion of the operation, the first post-nourishment sampling for meio- and macrofauna was done. Macrofauna was also sampled 9 months (April 2000) after the impact. Then, somewhat unexpectedly, the financial support for this study was extended just before the second nourishment was started. Therefore, meiofauna pre-sampling was done just before (May 2000) the impact and for macrofauna the last post-nourishment sampling in April 2000 was then taken as pre-nourishment sampling for the second replenishment. Post-nourishment sampling for meio- and macrofauna was done 4 months (October 2000) after the nourishment and macrofauna was also sampled 9 months (March 2001) after the operation.

To assess the effect of the operations on the infauna from mid shore to 7 m depth, four positions were sampled: (1) mid shore (0 m), (2) mean low water (0.9 m depth), (3) 1.4 m depth, (4) 7 m depth (Fig. 2). During all sampling occasions these positions were located seaward of the new cliff, which developed immediately after the nourishments. Each position was replicated randomly six times within 1 km of shoreline length. For meiofauna replicates were taken using a core of 10 cm^2 cross area to a sediment depth of 30 cm. Macrofauna was sampled at 1.4 m and 7 m depths in 1999, and in 2000/2001 also at mean low water (0.9 m depth). This was, because at this beach macrofauna is of very low abundance above mean low water (chapter 3). Each replicate consisted of 4 cores of 50 cm^2, pooled to 200 cm^2 cross area, down to a depth of 20 cm.

In the laboratory, meiofauna was extracted from the sediment using the SMB-method by Noldt & Wehrenberg (1984), which is specifically adapted to include soft-bodied meiofauna. A mesh size of 63 µm was used. Major taxa were sorted and plathelminths and polychaetes were identified to species level. “Meiofauna” here includes permanent and temporary meiofauna (juvenile polychaetes). Due to low abundances acarids, oligochaetes, nemerteans, bivalves and gastrotrichs were summarized under “others” in 1999. In 2000, abundance category “others” comprises oligochaetes and nemerteans only. This was due to missing acarids, bivalves and gastrotrichs during this sampling period.

Macrofauna samples were sieved trough a 1 mm mesh. The animals were sorted alive, counted and identified to species level whenever possible. *Crangon crangon* and *Carcinus maenas* (both Decapoda) belong to the mobile surface fauna, but also burrow in the sediment were included in the analysis. In 1999/2000, macrofaunal nemerteans, decapods and bivalves were summarized under “others”, while in 2000/2001 abundance category “others” comprises decapodes and bivalves.

In both years replenished material was directly collected from the diffuser head of the pipeline and searched for living meio- and macrofauna (800 cm^3 for meiofauna, 8000 cm^3 for macrofauna).

Simultaneously to all meio- and macrofauna sampling occasions sediment samples (one core of 10 cm^2 cross area to 10 cm sediment depth) were taken for grain size analysis at the same sampling positions as for the infauna. Further, 14 replicates of the replenished material were sampled for grain size analysis. Granulometric analyses were carried out by dry sieving. Mean grain sizes and sorting coefficients were calculated according to Buchanan (1984).

Statistical analysis

Average numbers of individuals (= abundance) and species (= species density) per 10 and 200 cm^2 for meio- and macrofauna, respectively, were calculated for each sampling occasion at the nourished and reference site. Each transect position was considered separately. For meiofauna, species density was based on plathelminths and polychaetes, while for macrofauna all specimens were determined to species level. Analysis of variance (ANOVA) was used to test for differences in abundances, species density and grain size between sites within each survey and between sampling occasions within each site (statistical advice C. Hennig, Department for Mathematics, University of Hamburg). Different levels within a significant parameter were analysed using Tukey's Honest-Significant-Difference (HSD) multiple comparison test. To test for homoscedasticity of variances Cochran's test was used, and data of the dependent variables were transformed (Tab. 3, 4, 6 and 7). When variances remained heterogeneous despite of the transformation, the H-Test (Kruskal and Wallis), followed by pair-wise Wilcoxon's non-parametric U-Tests, were used (Sachs 1984; statistical advice C. Hennig, Depart. for Mathematics, Univ. of Hamburg). Statistical significance was assumed at $p < 0.025$ for ANOVA (Bonferroni-procedure for multiple comparisons; Sokal & Rohlf 1995), at $p < 0.05$ for H-Test, and at $p < 0.025/0.017$ (meio-/macrofauna) for the following pairwise U-Tests.

Results

Grain size in 1999/2000

After the nourishment in 1999, the sediment at mean low water (MLW) was coarser at the nourished than at the reference site (Fig. 3, Tab. 1). No differences in grain size between sites was detected before the operation. However, grain size had increased at both sites. Also at 7 m depth, the sediment was coarser at the nourished site than at the reference site. This was already the case before replenishment. No differences in grain size between sites and surveys were noticed at mid shore and 1.4 m depth.

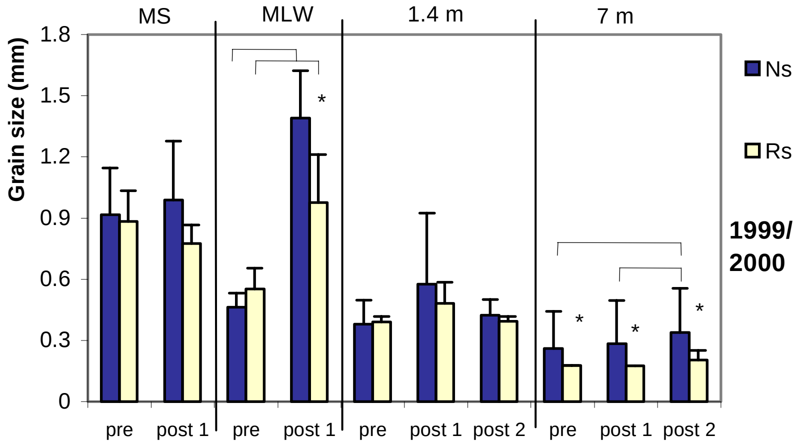

Fig. 3 Grain size at nourished (Ns) and reference site (Rs) across the shore in 1999/2000 presented as arithmetic means with standard deviations of 6 replicates per survey. Pre = pre-survey in April, 1 month before nourishment; post 1 + 2 = post-surveys in October 1999 and April 2000, 3 and 9 months after nourishment. MS = mid shore (0 m depth), MLW = mean low water (0.9 m depth), 1.4 m and 7 m depth line. * = significant differences between sites within surveys. ┌─┐ = significant differences between sampling dates within sites.

Grain size in 2000/2001

In the meiofauna study in 2000, grain size was finer at MLW at the nourished than the reference site after replenishment (Fig. 4, Tab. 1). No difference in grain size between sites was noticed in the pre-survey. Grain size decreased at the nourished site, while it remained the same at the reference site. At 7 m depth sediment was coarser at the nourished site in all surveys. No differences in grain size between sites were detected at mid shore and 1.4 m depth.

Similarly in the macrofauna study in 2000/2001, the sediment at MLW was finer at the nourished than the reference site in the first post-sampling (same data as in the meiofauna figure; Fig. 4, Tab. 1). No difference in grain size between sites was noticed in the pre- and second post-survey. Also, grain size showed no significant difference between the sampling occasions at the nourished site. At the reference site, however, grain size was finer in the second post-survey compared to both previous surveys. At 7 m depth grain size was different between sites, but not consistent between surveys. At 1.4 m no difference of grain size between sites and surveys was noticed.

In summary, at MLW both nourishments affected mean grain size, and at 7 m depth the sites were different in grain size already before the operation.

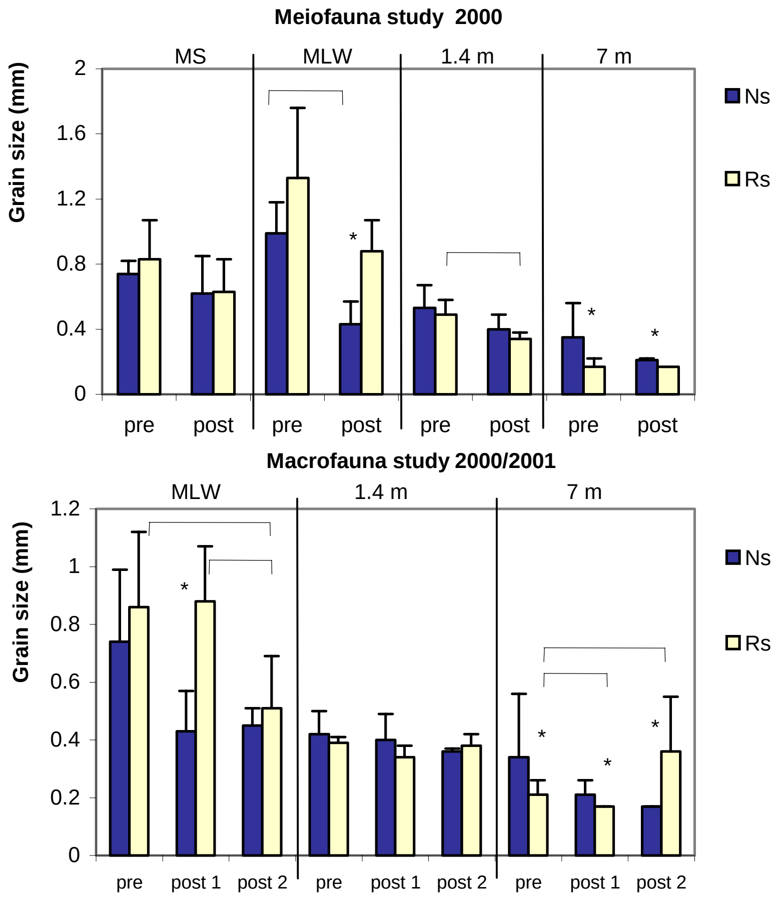

Fig. 4 Grain size at nourished (Ns) and reference site (Rs) across the shore in the meio- and macrofauna surveys in 2000/2001. Arithmetic means with standard deviations of 6 replicates per survey. Meiofauna: pre = pre-survey in May, just before nourishment; post = post-survey in October, 4 months after nourishment. Macrofauna: pre = pre-survey in April, 1 month before the operation; post 1 + 2 = post-surveys in October 2000 and March 2001, 4 and 9 months after the impact. Abbrevations see figure 3.

Tab. 1 Statistics of medium grain size comparisons at the nourished (Ns) and the reference site (Rs) in 1999/2000 and 2000/2001. ANO = one-way ANOVA, df = degree of freedom, HSD = Tukey's Honest-Significant-Difference multiple comparison test. H-Test: df = 3, U-Test: df = 1. 1999/2000: pre = prey-survey, 1 month before the operation; post 1 + 2 = post-surveys, 3 and 9 months after the impact. 2000/2001: Meiofauna: Pre = pre-survey, just before nourishment; post = post-survey, 3 months after the operation. Macrofauna: Pre = pre-survey, 1 month before nourishment; post 1 + 2 = post-surveys, 4 and 9 months after the impact.

Medium grain size	**ANO**	**df**	**F**	**HSD**	**H-Test**	**U-Test**
1999/2000						
Mean low water	p <				p <	p <
post 1 Ns/Rs	0.01	1	9.53			
Ns pre/post	0.00001	1	112.83			
Rs pre/post	0.01	1	16.49			
7 m depth						
pre Ns/Rs						0.017
post 1 Ns/Rs						0.017
post 2 Ns/Rs						0.017
Rs pre/post 1					0.001	0.01
Rs post 1/post 2					0.001	0.01
2000/2001						
Meiofauna	p <			p <	p <	p <
Mean low water						
post Ns/Rs	0.001	1	21.41			
Ns pre/post	0.001	1	32.50			
1.4 m depth						
Rs pre/post	0.01	1	14.34			
7 m depth						
pre Ns/Rs						0.01
post Ns/Rs						0.01
Macrofauna	p <			p <	p <	p <
Mean low water						
post 1 Ns/Rs	0.001	1	21.41			
Rs pre/post 1	0.001	3	12.00	0.01		
Rs post 1/post 2	0.001	3	12.00	0.01		
1.4 m depth						
Rs pre/post 1	0.01	3	6.58	0.01		
7 m depth						
pre Ns/Rs						0.01
post 1 Ns/Rs						0.01
post 2 Ns/Rs						0.01
Rs pre/post 1					0.001	0.01
Rs pre/post 2					0.001	0.01

Meiofauna

There is no consistent trend in meiofaunal abundance and species density between the nourished and the reference site (Tab. 2). Some major taxa were more abundant at the reference site before the nourishment took place, and in one case copepods were more abundant thereafter. Species density of plathelminths and polychaetes was higher at the nourished site at two positions after the first nourishment in 1999, while no differences were shown before the operation. In the surveys 2000 species density of polychaetes was higher at the nourished site at 1.4 m depth before the operation, while it was higher at the reference site at mid shore after the nourishment.

Tab. 2 Summary for meiofauna: Significant differences in abundance and species density of plathelminths and polychaetes between nourished and reference site per survey. For explanations to positions and surveys see Fig. 2 and Tab. 1, respectively. R = higher values of total meiofaunal abundance or species density (plathelminths and polychaetes) at the reference site; N = higher values of these parameters at the nourished site; - = no difference between sites. Letters below R and N indicate differences of single taxa between sites: O = Ostracoda, C = Copepoda, P = Polychaeta, N = Nematoda, Pl = Plathelminthes.

Abundance	**1999**		**2000**		**Species density**	**1999**		**2000**	
Position	*pre*	*post*	*pre*	*post*	Position	*pre*	*post*	*pre*	*post*
MS	R_O	-	-	-	*MS*	-	N	-	R_P
MLW	$R_{C,P,O}$	-	-	-	*MLW*	-	-	-	-
1.4 m	-	-	-	R_C	*1.4 m*	-	-	N_P	-
7 m	R_N	-	-	-	*7 m*	-	N_{Pl}	-	-

Nourishment 1999: abundance

No difference in meiofaunal abundance at mid shore, MLW and 7 m depth was detected between the nourished and the reference site after the operation 1999 (Fig. 5, Tab. 3). However, abundance was lower at the nourished than at the reference site already before the nourishment. At mid shore, ostracods showed a significant difference between the sites in the pre-survey. At both sites a decrease of abundances from pre- to post sampling was noticed, caused by copepods and plathelminths at the nourished site and also by polychaetes, ostracods and "others" at the reference site. At MLW copepod, polychaete and ostracod abundances were lower at the nourished than the reference site already before the operation. At this position abundance increased at the nourished site after replenishment, mainly caused by interstitial polychaetes (*Hesionides arenarea* and *Trilobodrilus axi*). At the reference site no differences were noticed. At 7 m depth, nematodes caused a difference of abundances between sites in the pre-survey, as well as a decrease of abundances at the reference site thereafter. Meiofaunal abundances at 1.4 m depth showed no differences between sites and surveys.

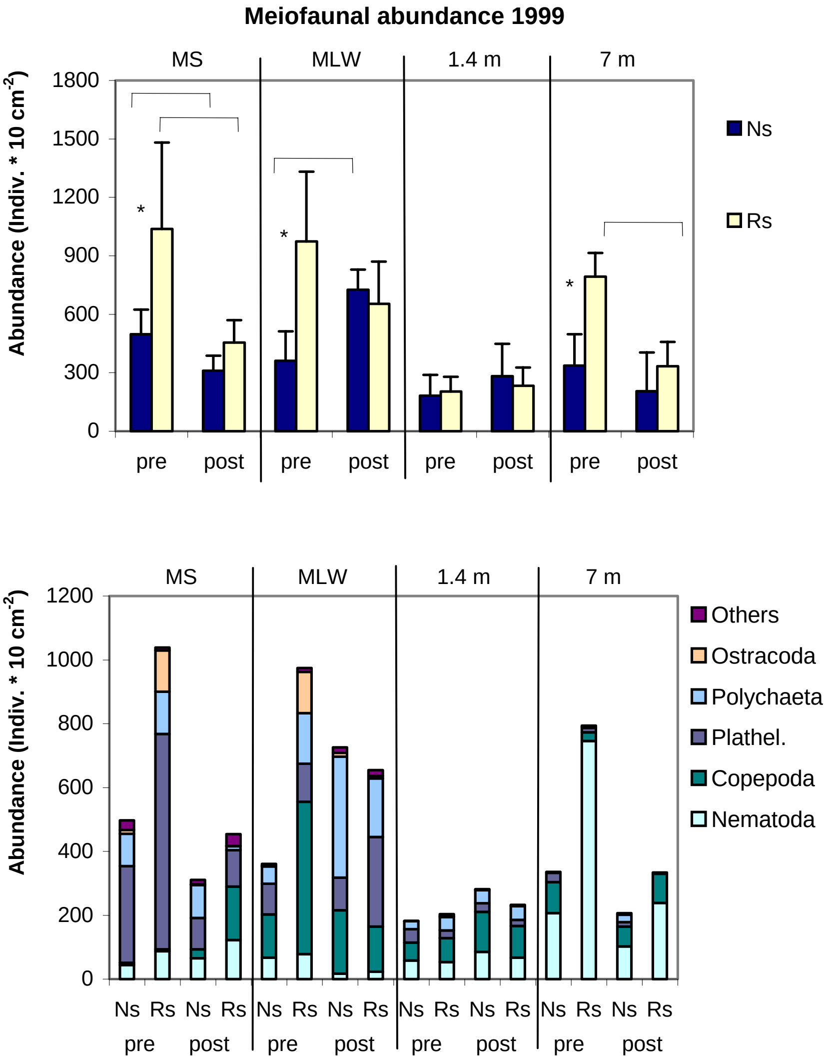

Fig. 5 Total meiofaunal abundance and abundance of major taxa per 10 cm^2 at nourished (Ns) and reference site (Rs) across the shore in 1999. Arithmetic means with standard deviations of 6 replicates per survey. Plathel. = Plathelminthes. Others = acarids, oligochaetes, nemerteans, bivalves and gastrotrichs. Further abbreviations see figure 3.

Nourishment 2000: abundance

In 2000, total meiofaunal abundance at 1.4 m depth was lower at the nourished compared to the reference site in the post-survey, due to the copepods (Fig. 6, Tab. 3).

No difference of total abundance between sites was noticed in the pre-survey, although abundances of nematodes, plathelminths, polychaetes and ostracods differed between sites. At the nourished site abundance decreased after the impact, while it remained constant at the reference site. At the former, abundances of nematodes, copepods, polychaetes and ostracodes differed between sampling occasions. At mid shore, MLW and 7 m depth total abundance showed no difference between sites in both sampling occasions. A decrease of abundances from pre- to post-nourishment surveys was noticed at both sites at mid shore and MLW.

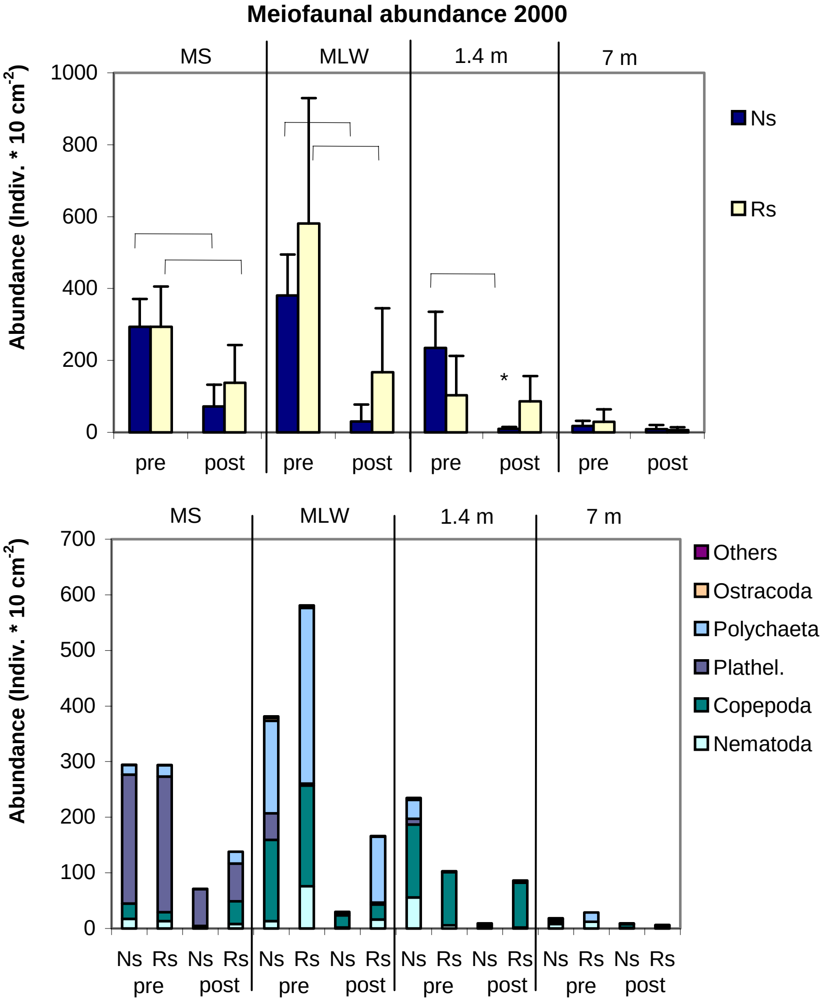

Fig. 6 Total meiofaunal abundance and abundance of major taxa per 10 cm^2 at nourished (Ns) and reference site (Rs) at 4 sampling positions in 2000, presented as arithmetic means with standard deviations of 6 replicates per survey. Others = oligochaetes and nemerteans. Further abbreviations see figure 3, and for surveys figure 4.

Tab. 3 Statistics of total meiofaunal abundance and abundance of major taxa per 10 cm^2 at the nourished (Ns) and reference site (Rs) in the studies 1999 and 2000. MLW = mean low water, Trans = data transformation, Sq.r. = square root, LN = natural logarithm, Ostrac. = Ostracoda, Copep. = Copepoda, Plathel. = Plathelminthes, Nemat. = Nematoda, Polych. = Polychaeta. * = assumed to indicate a tendency. No significant differences between sites and surveys were noticed at 1.4 m depth in 1999 and at 7 m depth in 2000. Further abbrevations see table 1.

1999

Abundance	**ANO**	**F**	**Trans**	**U-**
Mid shore	p <			p <
pre Total	0.01	9.89	sq.r.	
pre Ostrac.	0.025	7.82	sq.r.	
Ns Total	0.025	9.41		
Ns Copep.	0.025	8.12		
Ns Plathel.	0.01	15.07	LN	
Rs Total	0.01	12.89	LN	
Rs Copep.				0.01
Rs Plathel.	0.001	28.85	LN	
Rs Polych.	0.01	9.97	sq.r.	
Rs Ostrac.				0.01
Rs Others	0.01	19.22		
MLW				
pre Total	0.01	14.94		
pre Copep.	0.01	11.75		
pre Polych.	0.01	10.80		
pre Ostrac.				0.01
post Polych.	0.03*	5.15		
Ns Total	0.001	23.70		
Ns Nemat.	0.01	20.49		
Ns Polych.	0.001	27.15	sq.r.	
7 m depth				
pre Total	0.001	30.92		
pre Nemat.	0.0001	77.77		
pre Plathel.	0.01	16.11	sq.r.	
Rs Total	0.0001	42.33		
Rs Nemat.	0.00001	63.49		
Rs Copep.	0.01	11.96		
Rs Plathel.				0.01

2000

Abundance	**ANO**	**F**	**Trans**	**U-**
Mid shore	p <			p <
Ns Total	0.001	30.82		
Ns Plathel.	0.01	13.14		
Ns Nemat.	0.01	9.76		
Ns Polych.				0.025
Rs Total	0.03*	6.21		
Rs Plathel.	0.01	10.11		
MLW				
Ns Total	0.001	48.97		
Ns Polych.	0.0001	52.70	sq.r.	
Ns Copep.	0.01	12.89	sq.r.	
Ns Plathel.	0.0001	73.48	sq.r.	
Ns Ostrac.				0.025
Ns Others				0.025
Rs Total	0.025	6.72		
Rs Polych.	0.03*	5.79	sq.r.	
1.4 m depth				
pre Nemat.				0.01
pre Plathel.				0.01
pre Polych.	0.001	19.20	sq.r.	
pre Ostrac.				0.01
post Total	0.025	8.84		
post Copep.				0.03*
Ns Total				0.01
Ns Nemat.	0.01			
Ns Copep.	0.0001	41.28	sq.r.	
Ns Polych.	0.01			
Ns Ostrac.	0.01			

Nourishment 1999: species density

Meiofaunal species density of plathelminths and polychaetes at mid shore and 7 m depth was higher at the nourished than at the reference site after replenishment in 1999 (Fig. 7 , Tab. 4). No significant difference in species density between the sites was noticed before the impact. At 7 m depth the difference in the post-survey was mainly caused by plathelminths. A decrease from pre- to post-survey in species density was noticed at mid shore at the reference site and at MLW, 1.4 m and 7 m depth at both sites.

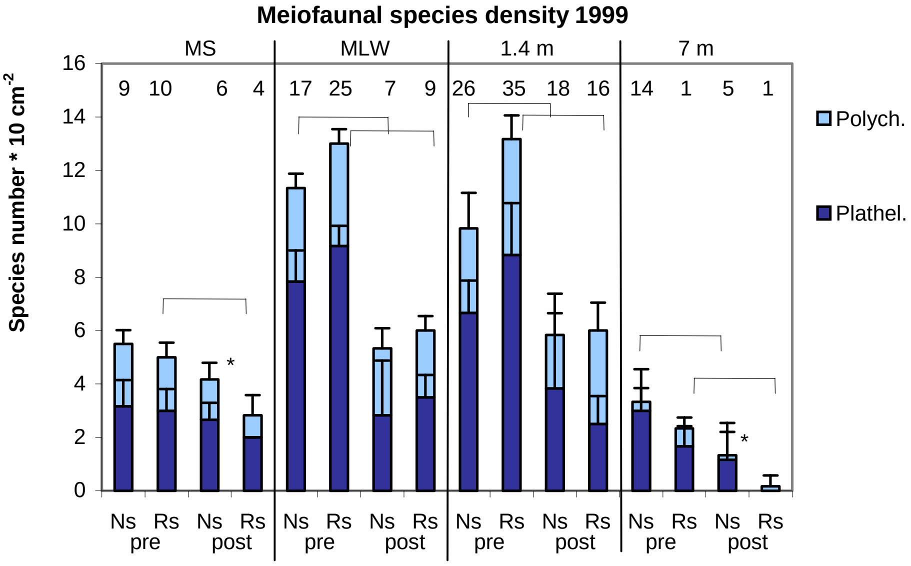

Fig. 7 Meiofaunal species density of plathelminths and polychaetes per 10 cm^2 at nourished (Ns) and reference site (Rs) across the shore in 1999, presented as arithmetic means with standard deviations of 6 replicates per survey. Above each column total species number is given. Abbreviations see figure 3.

Nourishment 2000: species density

In 2000, meiofaunal species density at mid shore was lower at the nourished than the reference site after replenishment (Fig. 8, Tab. 4). No difference in species density between sites was noticed in the pre-survey. At 1.4 m depth, species density was higher at the nourished than the reference site before the operation, while no difference was detected in the post-survey. A significant decrease from pre- to post-survey in species density was noticed at the nourished site at mid shore, MLW and 1.4 m depth, while it remained constant at the reference site. All these differences in species density were caused by polychaetes. At the nourished mid shore, particularly the missing archiannelids (*Trilobodrilus axi*, *Protodrilus* sp.) caused the difference between the sites in the post-survey. At MLW and 7 m depth, no differences in species density between sites within surveys were noticed.

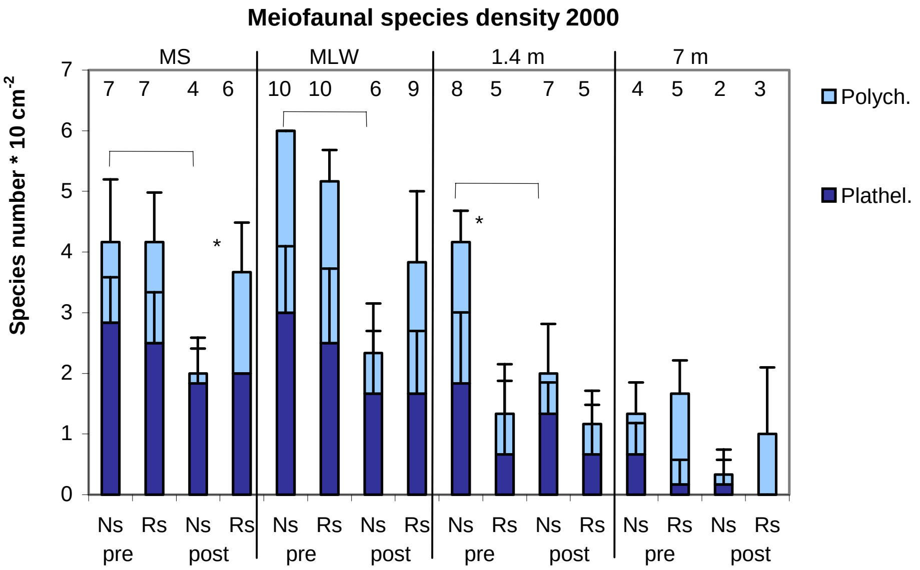

Fig. 8 Meiofaunal species density of plathelminths and polychaetes per 10 cm^2 at nourished (Ns) and reference site (Rs) across the shore in 2000. Arithmetic means with standard deviations of 6 replicates per survey. Above each column total species number is given. Further abbreviations see Fig. 3, and for surveys Fig. 4.

Tab. 4 Statistics of meiofaunal species density (plathelminths and polychaetes) per 10 cm^2 at the nourished (Ns) and the reference site (Rs) in the studies in 1999 and 2000. Total = total of plathelminths and polychaetes. Further abbrevations see Tab. 1 (statistics, surveys) and 3 (positions, taxa). Square root transformation: 1.4 m depth Rs Plathel., 7 m depth Ns Total and Rs Total. No significant differences between sites and surveys were detected at 7 m depth in 2000.

1999	**ANO**	**F**	**U-**	**2000**	**ANO**	**F**	**U-**
Mid shore	p <		p <	*Mid shore*	p <		p <
post Total	0.025	6.96		post Total	0.01	12.37	
Ns Polych.	0.025	7.35		post Polych.	0.01	16.20	
Rs Total	0.01	15.94		Ns Total	0.01	11.95	
Rs Polych.	0.025	8.45		Ns Polych.	0.025	6.62	
MLW				*MLW*			
Ns Total	0.0001	45.17		Ns Total	0.001	26.30	
Ns Polych.	0.01	10.00		Ns Polych.			0.01
Ns Plathel.	0.00001	77.59		*1.4 m depth*			
Rs Total	0.001	43.24		pre Total	0.01	9.97	
Rs Polych.	0.01	12.31		pre Polych.	0.01	17.86	
Rs Plathel.	0.0001	39.59		Ns Total	0.01	13.00	
1.4 m depth				Ns Polych.	0.01	17.86	
Ns Total	0.025	8.24					
Ns Plathel.	0.025	9.20					
Rs Total	0.01	17.74					
Rs Plathel.	0.001	22.65					
7 m depth							
post Total	0.001	26.65					
post Plathel.			0.01				
Ns Total	0.01	11.50					
Ns Plathel.	0.025	6.80					
Rs Total	0.01	12.05					
Rs Plathel.			0.01				

Macrofauna

Primarily, a summary of significant differences in macrofaunal abundances and species densities revealed lower values for polychaetes at the offshore position of the nourished site after the replenishment 2000 (Tab. 5).

Tab. 5 Summary for macrofauna: Significant differences in abundance and species density between nourished and reference site per survey. For explanations to positions and surveys see figure 2 and table 1, respectively. R = higher values of total abundance or total species density at the reference site; N = higher values of these parameters at the nourished site; - = no difference between sites. Letters below R and N indicate differences of single taxa between sites: I = Isopoda, P = Polychaeta, A = Amphipoda. / = this positions was not sampled in 1999.

Abundance		**1999/2000**			**2000/2001**	
Position	*pre*	*post 1*	*post 2*	*pre*	*post 1*	*post 2*
MLW	/	/	/	-	-	N_P
1.4 m	-	$R_{I,P}$	N	N	-	-
7 m	-	-	-	-	R_P	R_P
Species density		**1999/2000**			**2000/2001**	
Position	*pre*	*post 1*	*post 2*	*pre*	*post 1*	*post 2*
MLW	/	/	/	-	-	N
1.4 m	-	-	-	-	R_A	-
7 m	-	-	-	-	R_P	R_P

Nourishment 1999: abundance

Macrofaunal abundance at 1.4 m depth was lower abundance at the nourished than at the reference site in the first post-sampling (Fig. 9, Tab. 6) caused by the isopod *Eurydice pulchra* and the polychaete *Scolelepis squamata*. No difference in abundance between the sites was detected before the operation. In the second post-sampling abundance was higher at the nourished than at the reference site. However, at both sites abundances in the second post-survey were lower than in previous sampling occasions. At 7 m depth no differences in abundances between sites and surveys were noticed.

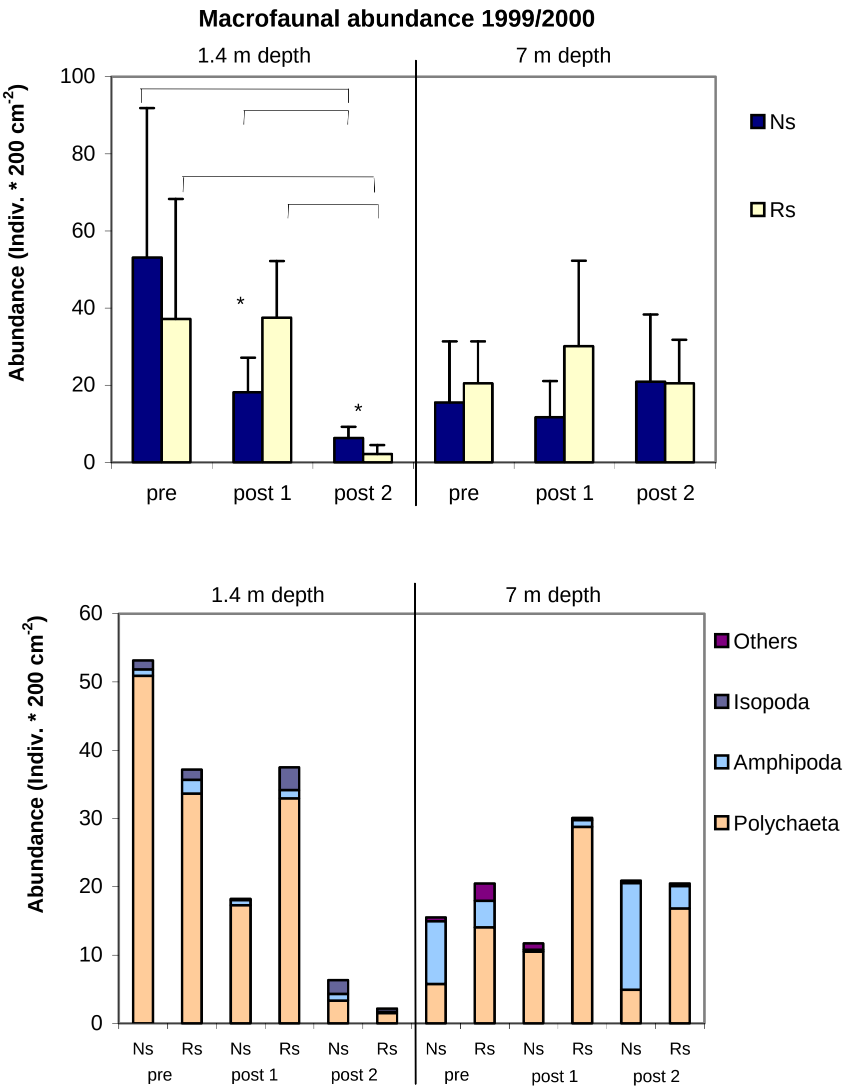

Fig. 9 Total macrofaunal abundance and abundance of major taxa per 200 cm^2 at nourished (Ns) and reference site (Rs) at 1.4 m and 7 m depth in 1999/2000. Arithmetic means with standard deviations of 6 replicates per survey. Others = nemerteans, decapods and bivalves. Further abbreviations see figure 3.

Nourishment 2000: abundance

Macrofaunal abundance at MLW was higher at the nourished than at the reference site in the second post-survey, mainly caused by the polychaete *S. squamata*. No difference between sites was noticed before (Fig. 10, Tab. 6). At 1.4 m depth no difference in abundance between the sites was detected in both post-surveys, while macrofaunal abundance was already higher at the nourished than the reference site in the pre-survey. However, abundance had increased at the reference site until the first post-survey. No such increase occurred at the nourished site. At 7 m depth total abundance was lower at the nourished than the reference site in both post-surveys, while it was similar before the operation. This was caused by varying polychaete abundances. At the nourished site abundances decreased from the pre- to both post-nourishment samplings, because of an almost total collapse of Amphipods as well as by reduced polychaete abundances. No difference in abundances between surveys was detected at the reference site.

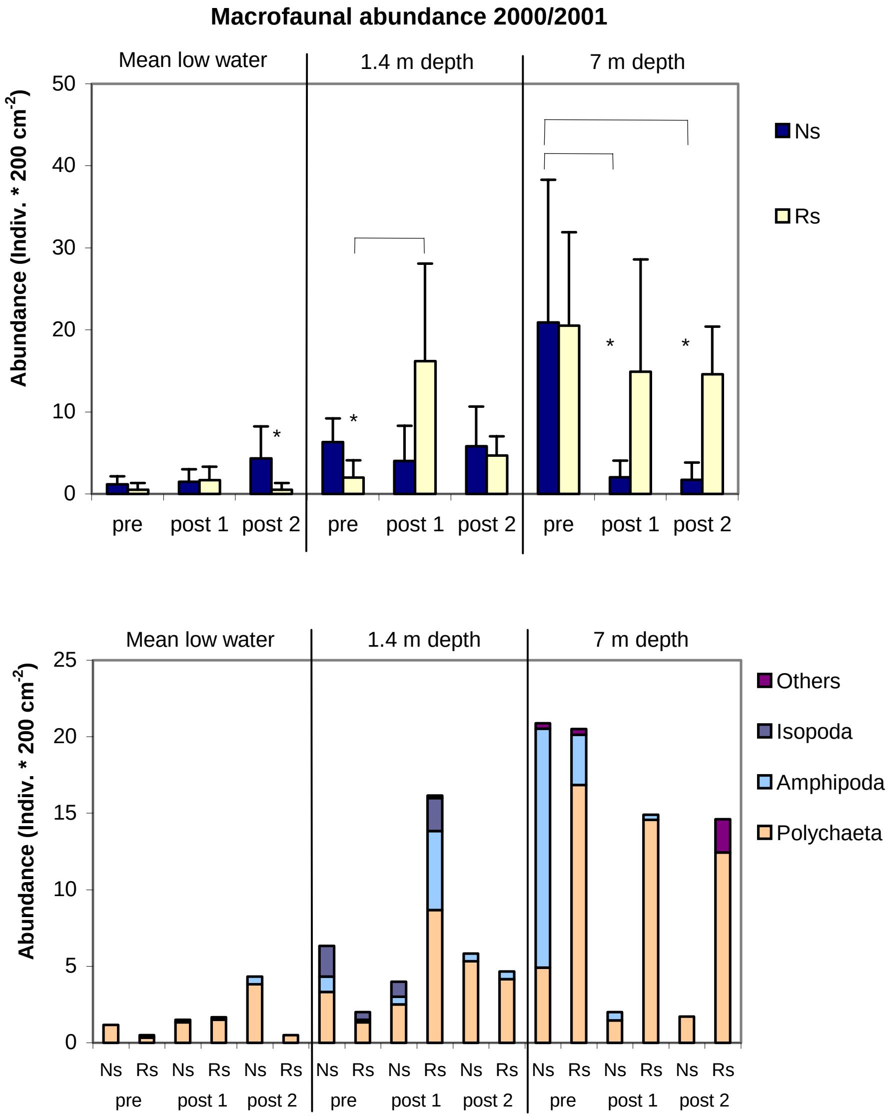

Fig. 10 Total macrofaunal abundance and abundance of major taxa per 200 cm^2 at nourished (Ns) and reference site (Rs) at 3 sampling positions in 2000/2001. Arithmetic means with standard deviations of 6 replicates per survey. Others = decapods and bivalves. pre = pre-survey in April, 1 month before the operation; post 1 + 2 = post-surveys in October 2000 and March 2001, 4 and 9 months after the impact. Further abbrevations see figure 3.

Tab. 6 Statistics of total macrofaunal abundance and abundance of major taxa per 200 cm^2 at the nourished (Ns) and the reference site (Rs) in the studies in 1999/2000 and in 2000/2001. Trans = data transformation; sq.r. = square root. * = assumed to indicate a tendency. Further abbrevations see table 1. No significant differences between sites and surveys were noticed at 7 m depth in 1999.

Abundance	**ANO**	**df**	**F**	**HSD**	**Trans**	**H-**	**U-**
1999/2000	p <			p <		p <	p <
1.4 m depth							
post 1 Total	0.02	1	7.55				
post 1 Isopoda	0.01	1	11.01		sq.r.		
post 1 Polychaeta	0.03*	1	4.61				
post 2 Total	0.02	1	7.64				
Ns Total pre/post 2						0.01	0.01
Ns Total post 1/post 2						0.01	0.01
Ns pre/post 2 Polychaeta						0.01	0.01
Ns post 1/post 2 Polychaeta						0.01	0.01
Rs Total pre/post 2						0.01	0.001
Rs Total post 1/post 2						0.01	0.001
Rs pre/post 2 Polychaeta						0.01	0.01
Rs pre/post 2 Amphipoda	0.025	3	4.85	0.017			
Rs post 1/post 2 Polychaeta						0.01	0.01
2000/2001							
Mean low water							
post 2	0.01	1	9.31				
post 2 Polychaeta	0.025	1	6.74				
1.4 m depth							
pre	0.025	1	8.89				
Rs pre/post 1	0.01	3	7.14	0.01	sq.r.		
Rs pre/post 1 Polychaeta	0.01	3	7.03	0.01	sq.r.		
Rs pre/post 1 Amphipoda							0.017
7 m depth							
post 1 Total	0.01	1	14.70		sq.r.		
post 1 Polychaeta							0.01
post 2 Total	0.0001	1	51.26		sq.r.		
post 2 Polychaeta	0.001	1	29.60				
Ns Total pre/post 1	0.01	3	9.31	0.01	sq.r.		
Ns Total pre/post 2	0.01	3	9.31	0.01	sq.r.		
Ns pre/post 1 Polychaeta	0.01	3	9.54	0.01			
Ns pre/post 2 Polychaeta	0.01	3	9.54	0.01			
Ns pre/post 2 Amphipoda	0.01	3	5.74	0.025	sq.r.		

Species density

Macrofaunal species density and that of major taxa showed no significant differences between sites and surveys in 1999/2000 (Fig. 11).

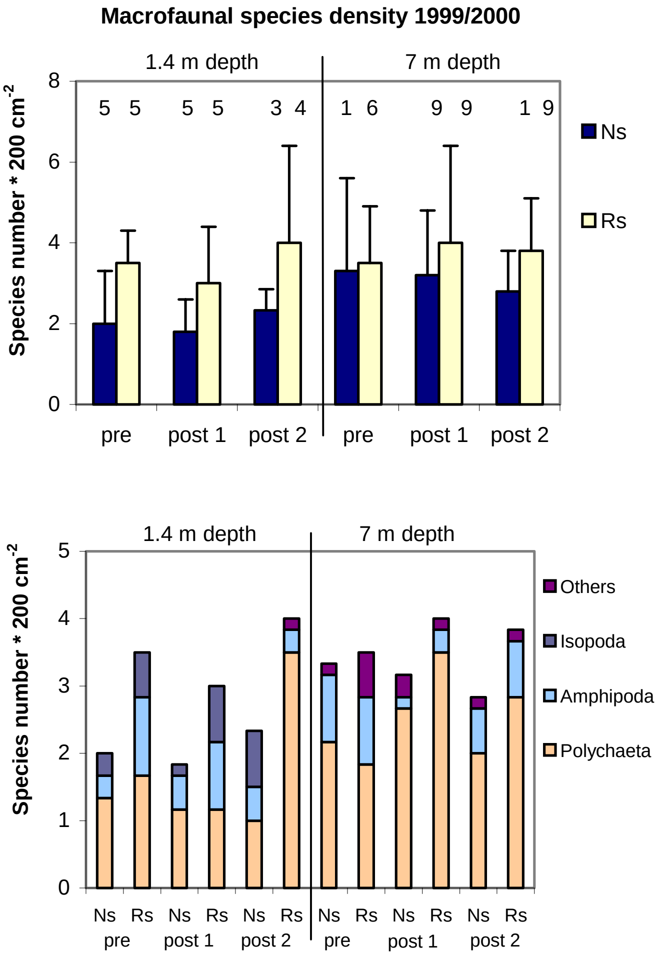

Fig. 11 Total macrofaunal species density and species density of major taxa per 200 cm^2 at nourished (Ns) and reference site (Rs) at 1.4 m and 7 m depth in 1999/2000. Arithmetic means with standard deviations of 6 replicates per survey. Above each column total species number is given. Others = nemerteans, decapods and bivalves. Further abbrevations see Fig. 3.

With regard to the operation in 2000, macrofaunal species density at MLW was higher at the nourished than the reference site in the second post-survey (Fig. 12, Tab. 7). No other differences were noticed at this position. At 1.4 m depth, species density was lower at the nourished than the reference site 3 months after the operation. This was mainly caused by amphipod species density. No difference of species density between sites was detected before and 9 months after nourishment. Species density was similar at the nourished site in all surveys, while it increased until the first post-survey at the reference site. At 7 m depth, species density was lower at the nourished than the reference site in both post-surveys, while no difference was noticed in the pre-survey. This was caused by polychaete species density. No difference of species density between surveys was detected at the reference site, while at the nourished site species density declined.

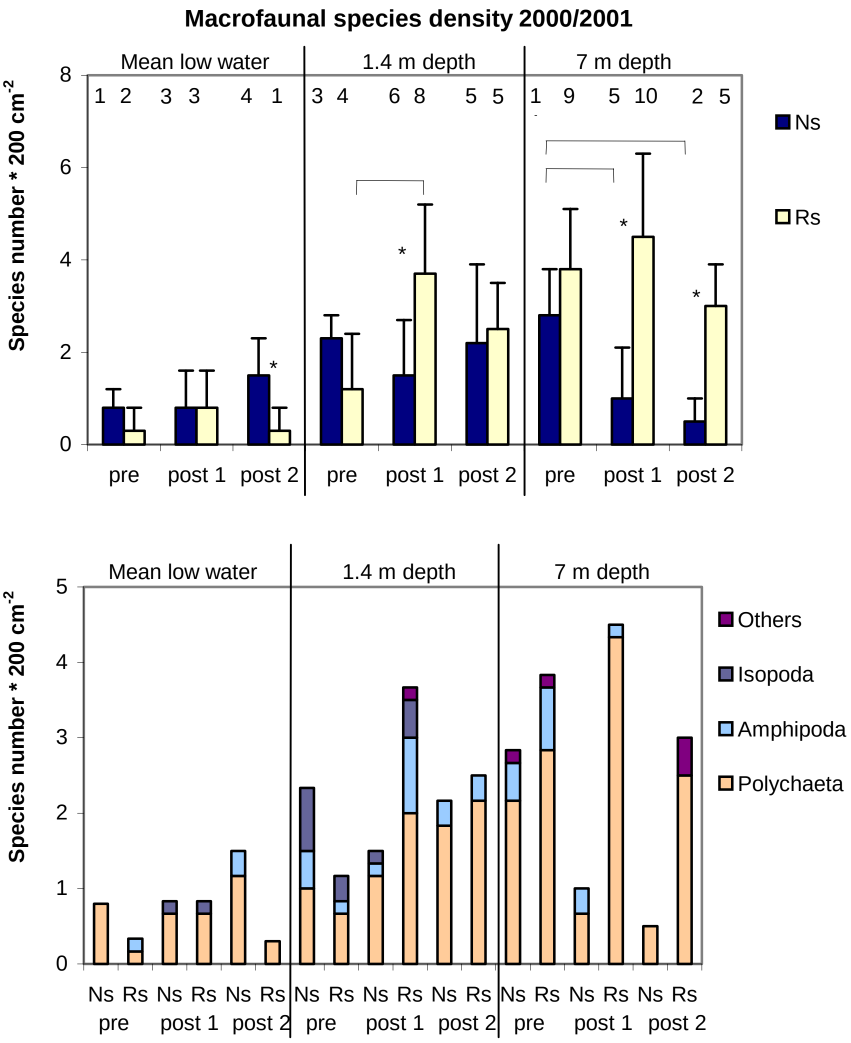

Fig. 12 Total macrofaunal species density and species density of major taxa per 200 cm^2 at nourished (Ns) and reference site (Rs) at 3 sampling positions in 2000/2001. Arithmetic means with standard deviations of 6 replicates per survey. Above each column total species number is given. Others = decapods and bivalves. Further abbreviations see figure 3, and for surveys figure 4.

Tab. 7 Statistics of total macrofaunal species density and species density of major taxa per 200 cm^2 at the nourished (Ns) and the reference site (Rs) in the study 2000/2001. Amph. = Amphipoda; Polych. = Polychaeta. * = assumed to indicate a tendency. Further abbrevations see Tab. 1. Square root transformation: 7 m depth post 1 Polychaeta.

Species density	**ANO**	**df**	**F**	**HSD**
Mean low water	p <			p <
post 2	0.025	1	8.45	
1.4 m depth				
post 1	0.025	1	7.48	
post 1 Amph.	0.025	1	7.35	
Rs pre/post 1	0.01	3	5.95	0.01
Rs pre/post 1 Amph.	0.01	3	4.20	0.03*
7 m depth				
post 1 Total	0.01	1	17.09	
post 1 Polych.	0.001	1	26.04	
post 2 Total	0.001	1	34.09	
post 2 Polych.	0.001	1	40.00	
Ns Total pre/post 1	0.001	3	11.01	0.01
Ns Total pre/post 2	0.001	3	11.01	0.01
Ns pre/post 1 Polych.	0.01	3	9.89	0.01
Ns pre/post 2 Polych.	0.01	3	9.89	0.01

Discussion

Effects on the meiofauna community

The meiofauna living high on the beach is buried by a sand deposit of 1 to 3 m in height by the nourishment operation. Due to sparse meiofaunal populations in the backshore region (Schmidt 1968; own observations) this study focused on effects on the meiofauna occuring seaward of the sand deposition. The organisms in the lower intertidal and subtidal may be affected by altered wave disturbance and sediment transport regimes as a result of the modified shape of the backshore (Brown & McLachlan 1990; Rakocinski et al. 1996). However, the results from 1999 indicate no negative impact on the meiofauna (Tab. 2). In 2000, copepod abundance at 1.4 m depth and polychaete species density at mid shore were reduced 4 months after the operation. These effects could have been caused by the nourishment, but it remained in the range of magnitude observed generally between adjacent sites along the beach. It is assumed that most meiofaunal taxa occurring on an intermediate beach type with high wave energy, are generally well adapted to shifting sediments and hydrodynamic turbulences (McIntyre 1971; McLachlan et al. 1984; Armonies & Reise 2000; chapter 2 and 3). Meiofauna seems to rapidly recover at the nourished site, presumably because many species are fast reproducing and often are highly mobile, such as the dominant plathelminth *Notocaryoplanella glandulosa* in the intertidal at the Sylt shore. Recovery of meiofauna may depend on both, active migration and passive resuspension into the water column (Palmer 1988; Fegley 1988; Schratzenberger & Thiel 1995; Armonies 1988). It may be further enhanced by the high dynamics of the intermediate beach system.

Schratzenberger & Thiel (1995) reported also minor short-term effects on the meiofauna by a beach nourishment, primarily on copepods (harpacticoids), as shown in this study too.

Effects on the macrofauna community

A minor short-term negative impact by the nourishment 1999 on the macrofauna in the shallow subtidal was indicated by reduced abundances of *Eurydice pulchra* and *Scolelepis squamata* in the first post-survey, while 9 months after the operation no more differences in abundances between nourished and reference site were detected (Tab. 5). The larger nourishment in 2000 revealed a longer-term effect on the macrofauna in the deeper subtidal. Polychaete abundances and species density at 7 m depth were still reduced 9 months after the operation. Increasing wave disturbance and sediment transport initiated by the nourishment (Brown & McLachlan 1990; Rakocinski et al. 1996) may directly affect the macrofaunal organisms. Also, their recruitment may be affected due to a coincidence of both operations with the reproductive season (see Naylor 1972; pers. comm. A. Rodriguez). The time of the nourishment is proposed by several authors as an important factor determining the effects of the operation and the duration of the recovery (Reilly & Bellis 1983; Adriaanse & Coosen 1991; Löffler & Coosen 1995; Essink 1997; Peterson et al. 2000).

Minor negative effects by beach nourishment on the macrofauna in the lower intertidal and shallow subtidal accompanied by a fairly rapid recovery, as it was shown in 1999, were also reported from other studies in Denmark, Germany, Belgium, The Netherlands and Florida (Culter & Mahadevan 1982; Saloman & Naughton 1984; Gorzelany & Nelson 1987; Birklund et al. 1996; Le Roy et al. 1996; Rakocinski et al. 1996; van Dalfsen & Essink 1997; Grotjahn & Liebezeit 1997). To some extent macrofauna at high energy beaches may be well adapted to rapid morphological changes (Nelson 1993; Löffler & Coosen 1995). Most of these macrofaunal species are opportunistic with a short life cycle and a large reproductive potential. As in meiofauna, the organisms are often characterized by a high mobility, i.e. the dominants on the Sylt beach *S. squamata* and *E. pulchra*. These characteristica are important for the recovery, which depends on a recruitment from pelagic larvae or immigration by mobile adults from adjacent sites.

In contrast to the macrofauna in the intertidal and shallow subtidal, that in the deeper subtidal may have a higher sensitivity to disturbances. This is likely to result from a higher abundance of long lived species and a higher diversity in the deeper subtidal than in the highly dynamic intertidal communities (McIntyre & Eleftheriou 1968; Knott et al. 1983; Reise 1985; Brown & McLachlan 1990; chapter 3). This is supported by the results of the study in 2000. A greater adverse impact on offshore than on intertidal communities is also assumed by Parr et al. (1978) and Rakocinski et al. (1996). A comparison of the results in 1999 and in 2000 indicates that the sediment transport initiated by the nourishment in 1999 may not have extended up to the 7 m depth line. A steeper profile after the larger nourishment in 2000 made beach morphometries more reflective than in 1999. This may have increased wave disturbance and sediment transport, as it is reported by Brown & McLachlan (1990). Ahrendt (1994) also reported sediment transport dynamics down to about 7 m depth by a nourishment on the Sylt shore.

The temporary reduction of polychaetes by the larger operation in 2000 may have affected subtidal consumers. However, considering the spatial extension of the subtidal offshore habitat this may have no overall significance. Moderate effects by beach nourishment on migrating consumers are also reported in other studies (Löffler & Coosen 1995; van Dalfsen & Essink 1997). However, harmful consequences may be observed in shores with higher secondary production than at Sylt due to a reduced energy transfer to higher trophic levels (Reilly & Bellis 1983; van Dalfsen & Essink 1997; Petersen et al. 2000).

The match of grain size

Grain size of the nourished material is assumed by several authors as an important factor determining the effects of beach nourishment on the macrofauna (e.g. Hayden & Dolan 1974; Nelson 1993; Löffler & Coosen 1995; Peterson et al. 2000). Sediment composition is also often mentioned as one factor determining the meiofauna (Gray & Rieger 1971; Gray 1974; Jansson 1967; Giere 1993). The results of the grain size analyses in 1999/2000 and 2000/2001 indicate a good match of grain sizes between the replenished material and the shore sediment. Only at mean low water, grain size differed 3 months after both operations. However, at this position no negative impact on the infauna was noticed, while the infauna was affected in the subtidal despite of a good match of grain size. Similar results were reported by Rakocinski et al. (1996). Thus, a good match of grain size may enhance a rapid recovery of the infauna, but it may not be the key to determine the impact on the biota.

Effects of recurrent nourishments

A comparison of the infauna between 1999/2000 and 2000/2001 revealed a lower macrofaunal abundance at 1.4 m depth and reduced meiofaunal abundances and species densities of plathelminths and polychaetes at the 4 transect positions in October 2000 than in 1999 (Tab. 8). These differences in infauna were also noticed by a comparison between 2000 and an earlier investigation in 1998 at the same beach (chapter 3). This may be interpreted as a year by year variability rather than a long-term effect of the two-fold beach nourishment, because the differences in the infauna between the surveys occurred at the nourished and the reference site alike. Additionally, the survey in 1999 indicates a complete recovery before the operation in 2000 began. If the recovery is not completed before the next nourishment begins at the same site, larger and longer-term effects are to be expected. In contrast to the study 1999/2000, the study 2000/2001 indicates no recovery of the macrofauna until nine month after the operation. Van Dalfsen & Essink (1997) reported a recovery of the macrofauna within 1 to 2 years after a shoreface nourishment. Thus, it is recommended to replenish a given site no more often than at intervals of 3 years to allow the macrobenthos to recover sufficiently.

Tab. 8 Comparison of the infauna between the studies in 1999, 2000 and 1998. Presented are significant differences of total macrofaunal abundance per 200 cm^2 and of total meiofaunal abundance and species density per 10 cm^2 between the sampling in October 1999 and 2000, and between the October surveys in 1998 and 2000. Ns = nourished site; Rs = reference site. To test for differences Wilcoxon's non parametric U-Test (degree of freedom = 1) was used. Significance was assumed at $p < 0.05$.

	Site	**1999**	**2000**	**1998**	**1999/2000**	**1998/2000**
Macrofauna			*Abundance*		p <	p <
1.4 m depth	Ns	18 ± 9	4 ± 4	49 ± 27	0.01	0.01
	Rs	38 ± 15	16 ± 12	49 ± 27	0.025	0.025
Meiofauna			*Abundance*			
Mid shore	Ns	311 ± 77	72 ± 61	522 ± 137	0.01	0.01
	Rs	455 ± 115	138 ± 105	522 ± 137	0.01	0.01
MLW	Ns	726 ± 103	30 ± 47	517 ± 224	0.01	0.01
	Rs	654 ± 217	167 ± 178	517 ± 224	0.01	0.025
1.4 m depth	Ns	282 ± 167	10 ± 6	194 ± 62	0.01	0.01
	Rs	233 ± 94	86 ± 71	194 ± 62	0.025	0.01
7 m depth	Ns	206 ± 198	9 ± 11	161 ± 110	0.01	0.01
	Rs	334 ± 125	6 ± 8	161 ± 110	0.01	0.01
Meiofauna			*Species density*		p <	p <
Mid shore	Ns	2 ± 0	2 ± 1	6 ± 1	0.01	0.01
	Rs	5 ± 8	4 ± 1	6 ± 1	-	0.01
MLW	Ns	3 ± 1	2 ± 1	7 ± 2	0.01	0.01
	Rs	3 ± 1	4 ± 2	7 ± 2	0.01	0.01
1.4 m depth	Ns	2 ± 0	2 ± 1	5 ± 1	0.01	0.01
	Rs	3 ± 1	1 ± 1	5 ± 1	0.01	0.01
7 m depth	Ns	1 ± 0	1 ± 1	4 ± 2	0.05	0.01
	Rs	0 ± 0	1 ± 1	4 ± 2	-	0.025

Effects of different nourishment operations

Beach nourishment operations require relatively calm weather conditions, which tend to be limited to the summer season. This may therefore interfere with recruitment of the benthos in spring and summer. However, important effects to the beach system will occur only if replenishments are performed all at once along the entire beach of an island, which is rather unlikely to take place at an island as long as Sylt. Van Dalfsen & Essink (1997) proposed shoreface nourishment as an alternative to beach nourishment. This could be done outside the recruitment and recreational season and they reported relatively small effects on the macrobenthos with a recovery after 1 to 2 years. However, shoreface nourishment may be less effective at Sylt due to high hydrodynamics at the in- and foreshore regions as a result of a steep offshore profile (pers. comm. K. Ahrendt, Geomar Kiel). This may also prevent a realization of nourishment outside calm weather conditions in summer. Furthermore, the results of this study indicate a high sensitivity of the subtidal benthos, which may be more affected by shoreface than by beach nourishment. In contrast to beach and shoreface nourishment, draining the beach as an alternative way of beach protection, as it is conducted in Denmark (Geoteknisk 2001), may result in large negative effects on the infauna. Especially the meiofauna, which occurs in high abundances in the intertidal, may be negatively affected by dewatering of the beach at low tide. However, a respective investigation has not yet been done.

Conclusion

In conclusion, the beach nourishments in 1999 and 2000 at Sylt had no dramatic, long-lasting effects on the infauna on the shore, and may be regarded as an acceptable method of coastal defence from an ecological perspective. The meiofauna is generally less affected by such operations than the macrofauna. Nourishments on a larger scale than the operation in 2000 may become critical for the benthos at the deeper subtidal zone adjacent to the beach. Different results were foundin other impact studies on sand nourishments indicating the requirement of site-specific investigations.

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6 GENERAL DISCUSSION

The aim of this final chapter is to put the findings of the previous sections together and to provide an overall picture of two beach systems in the North Sea differing in wave energy and morphodynamics. On the basis of the comparison of these two beach systems, ideas on the consequences of increasing hydrodynamic forces on exposed sandy shores in cold-temperate regions are suggested, including the effects of beach nourishment on the beach system.

The chapter starts with a discussion of the effects of wave energy on the infaunal components, and on the entire beach system (6.1), followed by a description of the overall picture of the two studied shores (6.2). Some critical remarks of faunal predictions based on beach types classified by dimensionless indices are presented in section 6.3. Disturbances to the beach system are discussed (6.4), and finally, possible consequences due to an increasing pressure of such disturbances in the coming decades (6.5).

6.1 Effects of wave energy on the sandy beach ecosystem

The differences in the biotic components between the studied shores and the faunal zonation across each shore, point out that wave energy is a major parameter determining the macroinfaunal community on sandy beaches. This physical harshness may directly affect the macrofauna, as was suggested by several authors (e.g., Croker 1977; McLachlan 1977b; McLachlan et al. 1981; Shelton & Robertson 1981; McLachlan et al. 1984). However, the results reveal a minor direct influence of wave energy on the meiofauna, living on a different spatial scale than the macrofauna. This supports the concept of McIntyre (1968, 1971) and McLachlan (1977b) of two quite distinct metazoan faunas on sandy shores controlled by different factors, additionally to the difference in size and different micro habitats occupied by meio- and macrofauna. The distinction between these faunal components is coupled with differences in metabolic rates, generation times and turnovers (McLachlan 1977b). However, despite of the distinction between meio- and macrofauna on sandy shores, there are links between these faunal groups (Giere 1993), and interactions between them may not be negligible.

McLachlan (1983) suggested that large burrowing meiofauna in finer sediment tend to bridge the size group and may fasciliate energy flow between these two components. Scarce information on the meiofauna food web and of interactions between meio- and macrofauna on sandy shores warrants further studies on this subject.

Wave energy is proposed as the key parameter controlling the entire beach system, including beach morphology and ecology, and driving energy flow and nutrient cycling on the shores (Brown & McLachlan 1990). The beach morphodynamic state is mainly determined by interactions between wave energy, tides and sediment particle size (Short 1999). Brown & McLachlan (1990) reported a corresponding difference in the presence and relative importance of the biotic components - primary producers, macrofauna, interstitial biota and water-column microbes - between beach types and proposed a conceptual model (Fig. 1). The importance of macrofauna and the microbial loop increases from reflective to dissipative beaches, while meiofauna was of similar importance in all beach types. Due to this influence of the physical beach state on the biotic components they distinguished two main beach systems, with an occurrence of several intermediate states. Interface beach systems have little or no surf zone, no primary producers or microbial loop, an interstitial biota far more important than the macrofauna, a dependence on inputs from the sea and generally a low total biomass (Brown & McLachlan 1990). In contrast, self-sustaining beach and surf zone systems are characterized by well developed surf zones with significant primary production and all three food chain compartments. Such beaches are self-sustaining, not dependent on inputs from the sea, and may have their energetics dominated by the microbial loop (McLachlan 1980a; McLachlan et al. 1981). Interface beaches process materials derived from the sea and recycle nutrients to the sea, whereas self-sustaining beaches tend to recycle materials within their own boundaries.

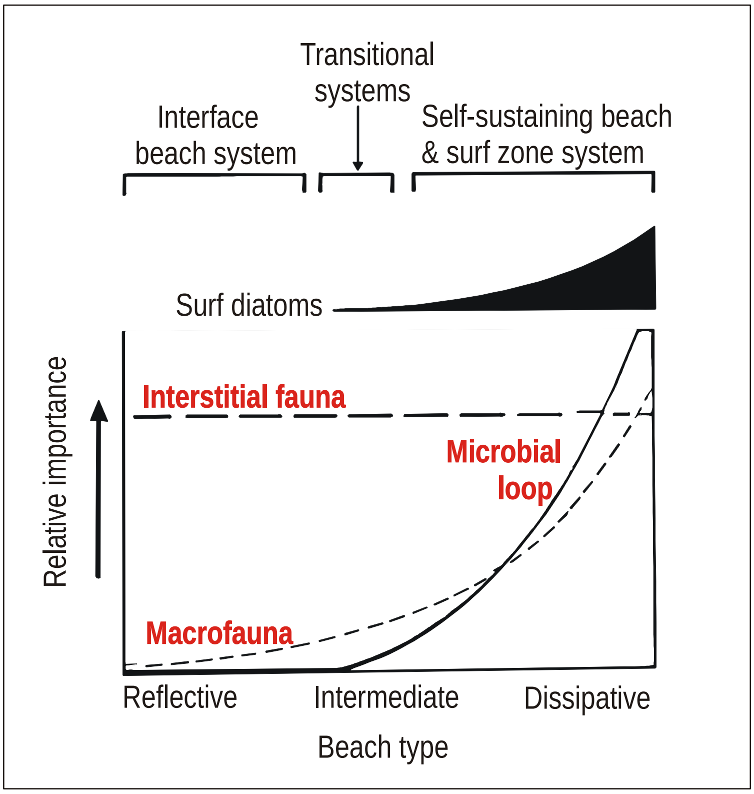

Fig. 1 Conceptual model on the relative importance of the three food chains across a spectrum of beach morphodynamic types encountered on open sandy shores. The relative significance of surf zone diatoms and the two major types of beach systems are also indicated (after Brown & McLachlan 1990).

The results of this study support the general trend of an increase in macrofaunal species richness and total abundance from reflective to dissipative beaches, which is suggested by several authors (e.g., Brown & McLachlan 1990; Jaramillo & Gonzales 1991; Jaramillo & McLachlan 1993; McLachlan 1990). It also supports the assumption of a similar importance (in terms of total abundance) of the meiofauna on all beach types (Brown & McLachlan 1990). However, diversity of interstitial plathelminths and small polychaetes differed distinctly between the studied shores. This may indicate a different importance of single meiofaunal taxa in each beach type, and probably of meiofauna in general. Therefore, a more complex picture of the interstitial biota in the conceptual model is assumed than suggested by Brown & McLachlan (1990). To enable final conclusions all meiofauna should be determined to species level, especially nematodes because they were the dominant taxon on the dissipative shore.

6.2 The overall picture

The present study also provides some further evidence for the general beach systems proposed by Brown & McLachlan (1990). The highly dynamic, intermediate shore with high wave energy corresponds with the interface beach system of Brown & McLachlan (1990). It is mainly supplied by the actual organic loading from surf waters pathing through the beach, and characterized by oxic nutrient regeneration (Fig. 2). Meiobenthos is far more important than the macrofauna, in which the latter includes macrobenthos and mobile epibenthic predators, such as fishes, crabs and shorebirds. Based on the results of this study the characterization of such beach systems of Brown & McLachlan (1990) can be completed for cold-temperate regions. These may be characterized by a dominance of agile meiofaunal taxa and very mobile macrofaunal organisms, such as the polychaete *Scolelepis squamata*, the amphipod *Bathyporeia* sp. and the isopod *Eurydice pulchra*. In the interstitial plathelminth assemblage a dominance of Proseriata may occur. This is well known for exposed habitats (here *Notocaryoplanella glandulosa* and *Nematoplana coelogynoporoides*; e.g., Remane 1940; Reise 1988; Wellner & Reise 1989). The former are often long, slender, very quickly moving, and equipped with special adhesive organs, which may reduce the washout of such small animals by waves and during severe stroms (Giere 1993).

In contrast, the more stable, dissipative shore with low wave energy stored part of the input as organic carbon in the sediment, and additionally to oxic nutrient regeneration there is also anoxic mineralisation in this beach system (Fig. 2). Meiobenthos, macrobenthos, aquatic epibenthic predators and shorebirds are all abundant. In the meiofauna sluggish taxa (many nematodes) dominate the assemblage. In addition to mobile macrofaunal organisms it also harboured less mobile animals, e.g. the polychaetes *Capitella minima, Capitella capitata* and the bivalve *Macoma balthica*. The interstitial plathelminth assemblage may be dominated by Macrostomida (here *Paromalostomum fusculum*, *Microstomum* sp.), Acoela and Dalyellioida with a stout shape, which is reported for more sheltered habitats (Reise 1988).

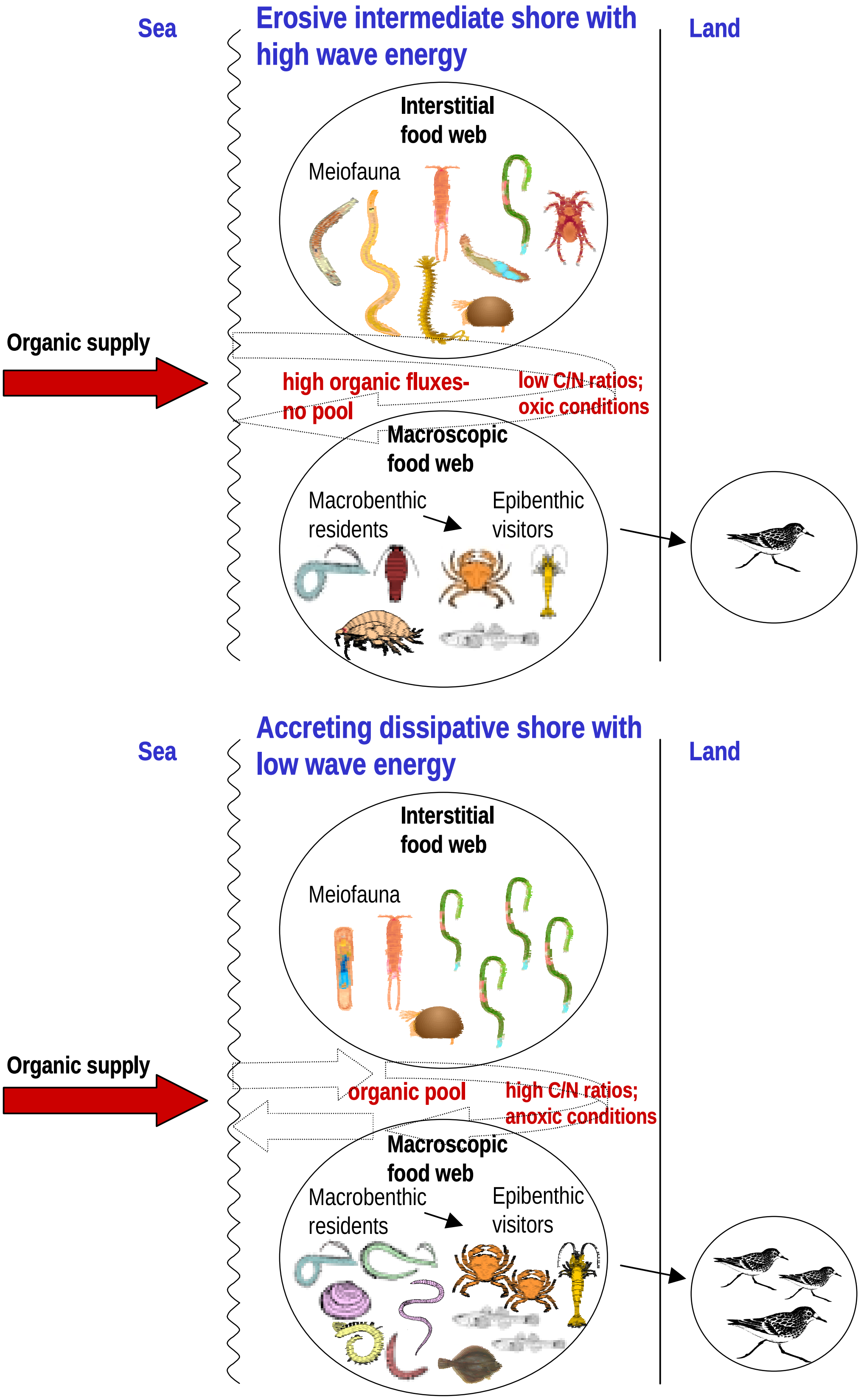

Fig. 2 Schematic model of the two studied beach systems with high and low wave energy in the cold-temperate region of the North Sea.

This beach system is tending more towards the self-sustaining beach and surf zone system proposed for dissipative shores by Brown & McLachlan (1990). However, a self-sustainment, respectively a development of an semi-enclosed beach system is not assumed for sandy shores in the North Sea. In oligotrophic waters as in South Africa self-sustaining beach and surf zone systems tend to recycle materials within their own boundaries. Nutrients remineralised in the beach significantly support the primary production in the surf zone, which in turn supports the biotic components on the beach (e.g., McLachlan 1980a; McLachlan et al. 1981). In contrast, North Sea waters are generally characterized by high nutrient concentrations, and there is no nutrient limitation for primary producers (Körner & Weichart 1992; DeJong et al. 1999). This may prevent the development of a really "self-sustaining" beach system. However, the results of the nutrient concentrations in interstitial and surf waters in this study indicate that both beach systems may act intermittently as a nutrient sink and also recycle nutrients to the surf zone. The former suggestion is in contrast to that of McLachlan (1983). There is considerable scope for further research to clarify mineralisation processes and nutrient fluxes on sandy shores.

Deposit feeders (e.g. *S. squamata*, *C. minima*) and suspension feeders (e.g. *Bathyporeia* sp., *M. balthica*) are the major group of sandy beach invertebrates (Dexter 1979) occurring in both beach systems. Scavengers (*E. pulchra*) were more restricted to the dynamic intermediate shore with high wave energy. Generally, sandy beach invertebrates were characterized as fast growing and short lived organisms with broad niches (Holland & Polgar 1976; Dexter 1979; McLachlan 1983). However, this may only apply to more reflective/intermediate shores with high wave energy, while increasingly more slowly growing and long lived species intermingle as the beaches approach the dissipative side of the spectrum.

6.3 Beach type classification and faunal predictions

The above section demonstrates a strong relationship between morphodynamic beach types and the presence and relative importance of the biotic components. Several dimensionless indices have been proposed to describe the beach morphodynamic state

(Tab. 1, Fig. 3). For macrofauna a predictable relationship between the beach morphodynamic state (calculated by such indices) and species richness, abundance and biomass were reported (e.g., McLachlan 1990; McLachlan et al. 1993, 1996; Hacking 1998; McLachlan 2001). In contrast, for meiofauna such studies and thus such relationships are lacking, probably a result of the difficulty in meiofauna species identification.

Tab. 1 Examples of dimensionless indices for calculations of the beach morphodynamic state. H_b = modal wave height, T = modal wave period, W_s = sediment fall velocity, M = maximum tide range, E = maximum theoretical equilibrium tide (for a theoretical earth covered by water, E = 0.8), MSR = mean spring tide range.

Index	**Calculation**	**Source**
fall velocity Ω	$\Omega = H_b/W_s{*}T$	Gourlay (1968); Wright & Short (1984)
beach state index BSI	$BSI = \log(H_bM/W_s{*}TE) + 1)$	McLachlan et al. (1993)
relative tidal range RTR	$RTR = MSR/H_b$	Masselink & Short (1993)

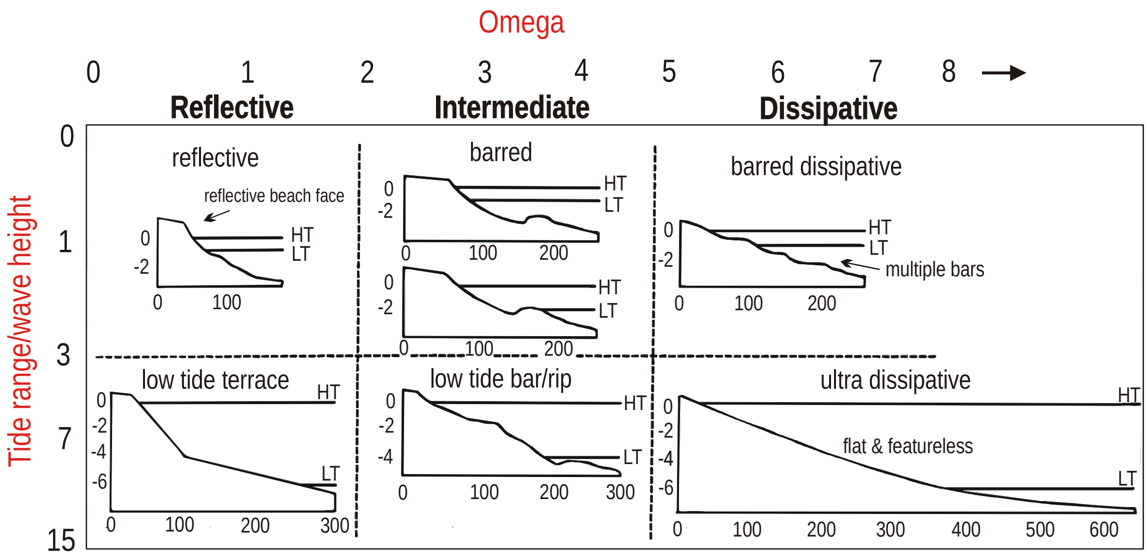

Fig. 3 Classification of beaches on the basis of the modal breaker height H_b and period T, the sediment fall velocity W_s and the mean spring tide range MSR. These four morphodynamic variables are represented by two dimensionless parameters: dimensionless fall velocity $\Omega = H_b/W_s{*}T$ and the relative tide range $RTR = MSR/H_b$. Distances are in meters (modified from Short 1999).

However, caution is adviced to general predictions of beach fauna based on a beach type classification from calculations of indices. The “modal wave height H_b” of an area, which is one of the central parameters of the calculations, requires a long-time series data set of the wave height, which is rarely available to beach ecologists. Thus, often short-time measurements were used for the calculations. However, as shown in the study area wave height could be a highly variable parameter (maximum: 3.03 m, minimum: 0.08 m, mean: 0.73 ± 0.52 m; ALR Husum 1999), resulting in a high variability of Ω, for example. For the Sylt shore Ω varied during the study period between a minimum of 0.2 and a maximum of 4.9, corresponding to a reflective and an intermediate beach type (see Fig. 3). For the Rømø shore a minimum of 0.3 (reflective) and a maximum of 10.5 (dissipative) was calculated. Calculations of Ω by Ahrendt (1994) for the Sylt shore showed a clear tendency towards the dissipative side of the spectrum. These calculations for the studied shores may show that Ω is just valid for a certain time and state until the wave climate changes again. Thus, snapshot calculations of Ω may result in misleading beach classifications and hence relationships to the infauna (Jaramillo et al. 1996b).

Further, calculated indices neglect the local dynamics, such as sediment supply to the system, which may sometimes maintain the morphodynamic beach state. For example, beach nourishment may distinctly enhance the dynamics of the Sylt shore providing environmental conditions which are probably more towards the reflective side of the spectrum than indicated by the calculated fall velocity index. On the Rømø shore the continuous accretion of fine to medium sand may be a major reason for the constant beach state during the entire year, despite of a high variable fall velocity. This indicates again that faunal predictions based on beach type classifications from calculations of indices should be treated with some caution.

6.4 Disturbances to the beach ecosystem

Disturbance is one of the key factors that structure marine communities (Sousa 1984). It refers to damage, displacement, or mortality caused by physical or biotic agents. Thus, disturbance removes biomass, and it is known to represent an important causative factor for spatial heterogenity, and consequently for the structure and dynamics of natural communities. In many soft-substrate habitats physical disturbances, refering to abiotic disturbances such as storms, far outweight the influence of biological disturbances

(Grant 1981). The former do not only remove or kill the infauna, but may simultaneously change the sediment structure, its chemistry and the food resources, which may result in indirect effects on species populations (Sousa 1984). After disturbance, recolonization proceeds over days and months, with opportunistic species initially occupying the defaunated habitat. Thus, a major consequence of disturbance in soft sediments is that most communities are best envisioned as a mosaic of patches in different stages of recovery from disturbances (Bertness 1999).

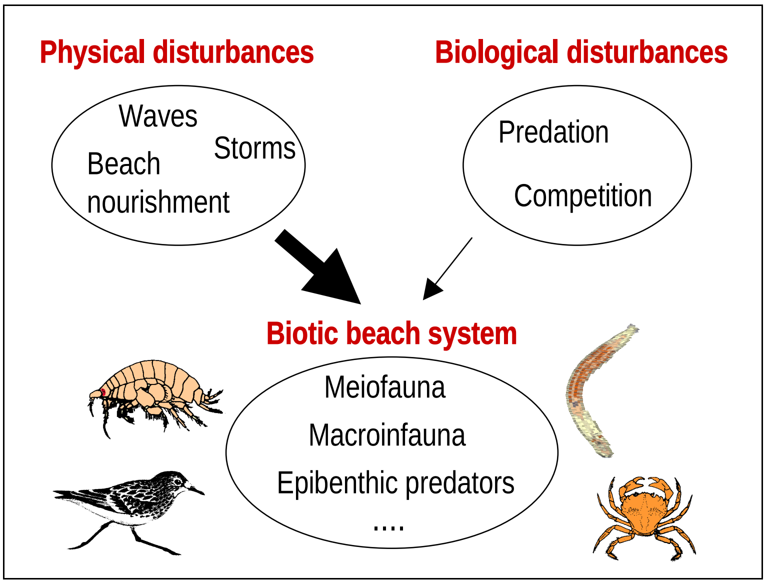

Fig. 4 Schematic model of the influence of physical and biological disturbances to the biotic beach system.

For exposed sandy shores physical disturbances, ranging from individual waves impinging on the shoreline on a small scale to severe stroms and human impacts (e.g., beach grooming and beach nourishment) on a larger scale, are proposed as the major structuring force of the ecosystem (Fig. 4). Competition and predation may be less important because there seems to be no shortage of space and no food limitation (Peterson 1979; Brown & McLachlan 1990; McLachlan 2001). Competition by interferences may be minimized by the particular three-dimensional nature of the substratum, coupled with the fact that all species can burrow into it. Further, most animals are opportunistic feeders, which decrease the likelihood of competition as an important factor. Progressing along the gradient from reflective, wave-dominated beaches to macrotidal flats where tidal factors are more important than waves, increasing stability of the substrate leads to the formation of permanent burrows and more complex communities with often more specialized and less opportunistic species and thus, with greater scope for biological interactions (McLachlan 2001).

Thus, sandy shores may be characterized by low environmental constancy and predictability, but they may have a high resistance and resilience to disturbances. Many taxa on sandy beaches exhibit morphological and behavioural adaptions which reduce the likelihood of washout by waves and during severe storms (Brown & McLachlan 1990; Giere 1993; Hall 1994). In addition, most sandy beach animals are highly mobile, opportunistic, short living and with high reproductive rates adapted to quickly recover from local extinctions caused by the environmental fluctuations. For meiofauna a rapid recovery after small-scale disturbances was reported by several authors (e.g., Sherman & Coull 1980; Thistle 1980; Colangelo et al. 1996). Others pointed out less impact on macrofauna by larger-scale disturbances such as recreational activities and beach “restoration” (Gorzelany & Nelson 1987; Jaramillo et al. 1996a; Peterson et al. 2000). The present study also revealed a rapid recovery of meio- and macrofauna on the highly dynamic intermediate shore after large-scale disturbances by beach nourishment. However, I suspect “recovery“ in the present study was mainly due to mobility enhanced by the dynamics of the beach system and not by rapid reproduction.

6.5 Consequences of increasing physical disturbances

An increasing pressure of physical disturbances on sandy beaches is assumed in the foreseeable future. Wave energy and storm surges may increase as a corollary of global warming (Siefert 1984, Führböter & Dette 1992; Hofstede 1997; Bird 2000; Lozán et al. 2001). Furthermore, disturbances by human interferences on sandy beaches may increase due to the modern prevalence of shore erosion resulting in an increase of coastal defences, e.g. beach nourishment (Nordstrom 2000). Additionally, beach management focussing on the value of beaches as recreation platforms may increase, because sandy beaches are subjected to ever-increasing pressure from recreational activities. Disturbances, particularly multiple events that occur in rapid succession, are recognized as prime initiators of shifts in community structure between alternate compositional stages, which may or may not be persistent (Sousa 1984). Such shifts are increasingly possible as the rate and severity of physical and anthropogenic disturbances increase. Thus, the increasing pressure of physical disturbances on sandy shores in the coming decades may initiate a community shift in the beach ecosystem, associated with changes of the morphological beach state.

Scenarios on morphological and ecological changes on sandy shores due to a climatic change do not have real predictive value if human activity is not included. Erosion on sandy shores may generally cause a development towards dissipative beach types (Short 1999). However, beach nourishment may interrupt this general development, resulting in highly dynamic intermediate beaches with high wave energy away from equilibrium state (Fig. 5). For this beach state the studied Sylt shore may be an example.

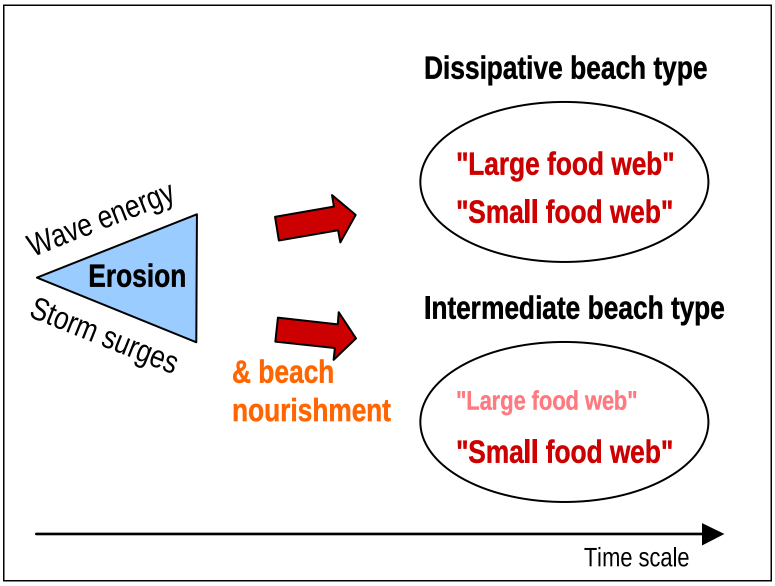

Fig. 5 Increasing erosion on sandy shores followed by an increasing use of beach nourishment to combat the erosion will result in highly dynamic intermediate shores away from equilibrium state. The biotic system of these shores may be characterized by an impoverished “large food web”, while meiofauna is abundant, of high evenness between major taxa and of high diversity in interstitial plathelminths and polychaetes.

Thus, the present study comparing a dissipative shore with low wave energy and a highly dynamic intermediate shore with high wave energy and artificially nourished, may offer first ideas on the consequences on cold-temperate exposed sandy shores by increasing physical disturbances. The macrofauna may be strongly affected by increasing wave energy in contrast to the meiofauna. The former will be impoverished and shift towards deeper shore levels where wave forces are diminished. Thus, the food availability for epibenthic predators in the swash and surf zone, such as juvenile fishes and shorebirds, will decrease. In summary, the entire “large food web” will become impoverished (Fig. 5). In contrast, meiofauna will remain abundant, of high evenness between major taxa, and of high diversity in interstitial plathelminths and polychaetes. As described above, these beach systems are mainly supplied by the actual loading from surf waters, and may have an entirely oxic nutrient regeneration. Disturbances by beach nourishment operations have minor impacts on the infauna in such dynamic systems. However, the scale of the nourishment operation determines the effects. To keep the impact on a low level, no larger operations than studied in the year 2000 on the island of Sylt are recommended, associated with a regeneration time of at least two years between these disturbances.

7 LITERATURE CITED IN THE GENERAL INTRODUCTION AND DISCUSSION

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8 SUMMARY

Exposed sandy beaches are physically harsh and highly dynamic environments. Waves, tides and sediment type form a largely physically controlled habitat for the sandy beach organisms. The present study is an ecological comparison of two sandy shores differing in wave energy and morphodynamics. The study sites were located in the eastern North Sea on the German island of Sylt and the neighbouring Danish island of Rømø. The Sylt shore is coarse grained, steep profiled, and receives high wave energy. Beach nourishment is used to counterbalance erosion. It is a highly dynamic, intermediate beach type. In contrast, the Rømø shore is fine grained, flat profiled, accreting and with low wave energy. It represents a relatively stable, dissipative beach type.

The primary objective of this thesis are the effects of wave energy and sandy shore morphology on the biotic community and its food supply. The studied community components include the meio- and macroinfauna, aquatic epibenthos, and shorebirds. A simultaneous and detailed analysis of the first two provides insights on the ecological distinction between meio- and macrofauna in the beach system including their temporal variability and spatial zonation across the shore. In addition, the ecological consequences of beach nourishment on the infauna were studied.

Overall meiofaunal abundances (average of inter- and subtidal) were similar on both shores, but the taxonomic composition differed. On the intermediate shore with high wave energy, meiofauna was composed of roughly equal proportions of several major taxa, while there was a strong numerical dominance of nematodes on the dissipative shore with low wave energy. Meiofaunal zonation on the intermediate shore showed higher abundances in the intertidal than in the subtidal, while meiofauna was more evenly abundant across the entire dissipative shore. Species density and diversity of interstitial plathelminths and polychaetes were higher at Sylt than at Rømø. Both numbers peaked at mean low water and in the shallow subtidal at Sylt, while the maximum occurred at the mid shore at Rømø.

In contrast to meiofauna, overall macrofaunal abundance, species density, and diversity were all lower on the intermediate than on the dissipative shore. Polychaetes were the most abundant taxon on both shores, followed by amphipods and isopods at Sylt, and by bivalves and amphipods at Rømø. Zonation revealed higher macrofaunal abundance and

species density in the subtidal than in the intertidal at Sylt and a even distribution across the Rømø shore.

Temporal variability of meiofaunal abundances was higher on the intermediate shore, while this was the case with macrofauna on the dissipative shore. In both faunal components highly mobile species were more prominent at Sylt than at Rømø.

Corresponding to the impoverished macrofauna on the intermediate shore, abundances of epibenthic predators, such as shrimps, crabs, fishes, and shorebirds were also lower at Sylt than at Rømø. Additionally, the concentrations of Chlorophyll *a* and particulate organic carbon and the C/N ratio in the sediment were all lower on the intermediate than on the dissipative shore. Nutrient concentrations in interstitial and surf waters indicate oxic nutrient regeneration at Sylt, while at Rømø also anoxic mineralisation occurs.

In conclusion, high wave energy on the eroding, dynamic intermediate shore limited the macrofauna, particularly at the steep intertidal slope, while it had weak effects on the meiofauna. The latter is abundant and of high evenness between major taxa. Further, it is mainly composed of agile taxa, which are able to quickly exploit the fresh organic material pathing through the beach under high oxic conditions. Low wave energy across the accreting, dissipative shore favoured macrofauna, and nematodes adapted to low oxygen conditions. Organic materials may intermittently accumulate on this shore and zoomass builds up to support abundant visitors from higher trophic levels.

This comparison of two sandy beaches differing in wave energy offers first ideas on the consequences of increasing wave energy and erosion on exposed sandy shores. Such increases are expected as a corollary of global warming and the concomitant sea level rise. This is likely to provoke an increasing use of beach nourishment to combat erosion, creating highly dynamic intermediate shores away from morphodynamic equilibrium. The Sylt shore with its described ecosystem may be an example for this future beach state. A “small food web” takes over on such shores, particularly in the cold-temperate region of the North Sea, while the “large food web” will be impoverished. Disturbances by nourishment operations had minor impacts on the infauna of this dynamic system. Thus, from an ecological perspective, beach nourishments may be regarded as an acceptable method of coastal defence. However, no larger operations than the ones studied (350,000 m^3/2 km) and intervals between those disturbances of at least two years at a given site are recommended.

9 KURZFASSUNG

Exponierte Sandstrände sind physikalisch harsche und äußerst dynamische Lebensräume, deren Morphologie maßgeblich durch die Energie der auflaufenden Welle, den Tidehub und den Sedimenttyp bestimmt werden. Für ihre Bewohner stellen sie ein stark physikalisch kontrolliertes Habitat dar, in dem die Wellenenergie als bestimmender Faktor gilt.

Die vorliegende Arbeit ist ein ökologischer Vergleich von zwei exponierten Sandstränden, die durch unterschiedliche Wellenenergie und Morphodynamik charakterisiert sind. Die untersuchten Strände befinden sich in der östlichen Nordsee auf Sylt und der Nachbarinsel Rømø. Der Sylter Strand ist durch groben Sand, ein steiles Profil und hohe Wellenenergie gekennzeichnet (Abb. 1). Um der Erosion entgegen zu wirken, werden auf Sylt seit 1988 in unregelmäßigen Abständen Sandvorspülungen durchgeführt. Nach der morphodynamischen Strandklassifizierung von Short & Wright (1983) ist der Sylter Strand ein dynamischer, intermediärer Strandtyp. Der Strand auf Rømø hingegen ist durch feineren Sand, ein flaches Profil, geringe Wellenenergie und dauerhafte Sanddeposition charakterisiert (Abb. 1). Es ist ein relativ stabiler, dissipativer Strand.

Abb. 1 Links: Erosiver, hoch dynamischer, intermediärer Sandstrand auf der Nordseeinsel Sylt (Foto: K. Reise). Rechts: Depositärer, relativ stabiler, dissipativer Strand der Insel Rømø.

Schwerpunkt der vorliegenden Arbeit waren die Effekte der Wellenenergie und Strandmorphologie auf die im Sand lebenden Organismen (Meio- und Makrobenthos). Parallele Studien dieser beiden Faunenkomponenten sind an Stränden selten, insbesondere Untersuchungen in denen die Meiofauna („Sandlückenfauna”) bis zur Art bestimmt wurde. Gerade eine gleichzeitige und detaillierte Analyse dieser beiden Tiergruppen kann jedoch weitere Hinweise auf eine ökologische Trennung von Meio- und Makrofauna in den Stränden liefern. Neben dem Unterschied in ihrer Größe werden die Gemeinschaften der Meio- und Makrofauna im Strand vermutlich auch durch unterschiedliche Faktoren maßgeblich bestimmt. Daher wurde auch ihre zeitliche Variabilität und räumliche Zonierung von Eu- zu Sublitoral untersucht. Um den Einfluß der Wellenenergie und Strandmorphologie im Hinblick auf das gesamte Ökosystem zu klären, wurden zusätzlich die Nahrungsverfügbarkeit für die Fauna in den Stränden, das aquatische Epibenthos und die Vögel betrachtet. Weiterhin schließt diese Arbeit eine Untersuchung der ökologischen Effekte von Sandvorspülungen auf das Meio- und Makrobenthos ein.

Die Individuendichte der Meiofauna (im Mittelwert aus Eu- und Sublitoral) war in beiden Stränden ähnlich, aber die taxonomische Zusammensetzung war unterschiedlich. Am Strand mit hoher Wellenergie setzte sich die Gesamtindividuendichte der Meiofauna aus zahlreichen Taxa mit nahezu gleichen Anteilen zusammen, während am Strand mit geringer Wellenenergie Nematoden deutlich dominierten. Die räumliche Zonierung zeigte am Sylter Strand eine signifikant höhere Meiofauna-Individuendichte im Eu- als im Sublitoral. Auf Rømø hingegen wurde eine gleichförmige Verteilung von Eu- zu Sublitoral festgestellt. Die Artendichte und Diversität der im Sandlückensystem lebenden Plathelminthen und Polychaeten war am Strand mit hoher Wellenergie signifikant höher als am Strand mit geringer Wellenenergie. Auf Sylt waren Artendichte und Diversität dieser Platt- und Borstenwürmer an der mittleren Niedrigwasserline und im flachen Sublitoral am höchsten, während auf Rømø am höher gelegenen mittleren Strandhang die höchsten Werte gefunden wurden.

Die Verteilung der Makrofauna unterschied sich deutlich von der der Meiofauna. Individuen-, Artendichte und Diversität waren am Sylter Strand signifikant geringer als am Rømø Strand. Polychaeten stellten die individuenreichste Gruppe an beiden Stränden, gefolgt von Amphipoden und Isopoden auf Sylt und von Bivalvien und Amphipoden auf Rømø. Die Zonierung zeigte auf Sylt eine deutlich höhere Individuen- und Artendichte der Makrofauna im Sub- als im Eulitoral. Auf Rømø hingegen waren ähnliche Individuen- und Artendichten von Eu- zu Sublitoral zu beobachten.

Die zeitliche Variabilität der Meiofauna-Individuendichte war am dynamischen Strand mit hoher Wellenenergie ausgeprägter, während dies für die Makrofauna am stabileren Strand mit geringer Wellenenergie der Fall war. In beiden Tiergruppen waren hoch bewegliche Arten besonders auf Sylt vertreten.

Einhergehend mit der verarmten Makrofauna-Gemeinschaft am Sylter Strand wurden geringere Individuendichten epibenthischer Räuber, wie Fische, Krabben, Garnelen und Vögel, auf Sylt als auf Rømø festgestellt. Zusätzlich waren die Konzentrationen an Chlorophyll *a* und partikulärem organischem Kohlenstoff (POC), sowie das C/N-Verhältnis im Sediment auf Sylt geringer als auf Rømø. Dies weist auf eine periodische Anhäufung von organischem Material am stabileren Strand mit geringer Wellenenergie hin, während am dynamischen Strand mit hoher Wellenenergie kein „Nahrungspool” vorhanden ist. Vergleiche der Konzentrationen anorganischer Nährstoffe im Poren- und Brandungswasser deuteten auf eine oxische Nährstoff Regeneration am Sylter Strand hin, während am Rømø Strand auch eine anoxische Mineralisation vorhanden war.

Zusammenfassend zeigen die Ergebnisse, daß die hohe Wellenenergie am erodierenden, dynamischen Sylter Strand die Makrofauna besonders im steilen Eulitoral limitiert, während sie einen geringen Einfluß auf die Meiofauna besitzt (Abb. 2). Letztere ist an diesem Strand individuenreich und setzt sich aus zahlreichen Taxa mit gleichmäßigen Anteilen zusammen. Weiterhin sind hauptsächlich hoch bewegliche Taxa vertreten, die fähig sind frisches organisches Material welches den Strand „durchströmt” unter den vorhandenen sauerstoffreichen Bedingungen schnell zu nutzen. Die niedrigere Wellenenergie entlang des gesamten stabileren dissipativen Rømø Strandes fördert die Entwicklung einer individuen- und artenreichen Makrofauna, sowie eine Dominanz von Nematoden innerhalb der Meiofauna (Abb. 2). Letztere sind häufig an geringe Sauerstoffkonzentrationen angepasst. Unter solchen Strandbedingungen kann sich organisches Material zeitweise anhäufen und sich mehr Zoomasse aufbauen, die wiederum Besucher höherer trophischer Ebenen, wie Krabben, Fische und Vögel, fördert.

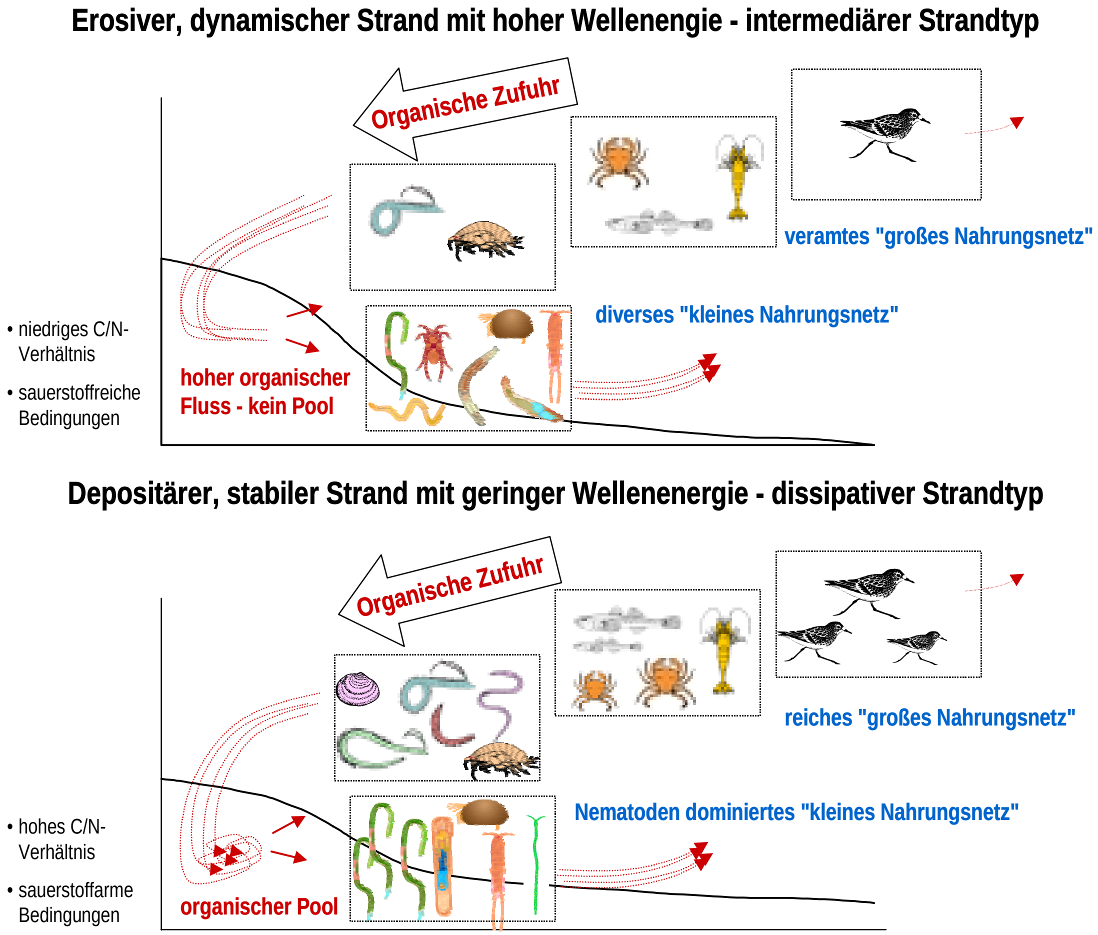

Abb. 2 Nahrungsnetz zweier Sandstrände mit unterschiedlicher Wellenenergie in der kalt-temperierten Region der östlichen Nordsee. Der dynamische, intermediäre Strand mit hoher Wellenenergie ist durch hohe Flüsse organischen Materials durch den Strand charakterisiert, speichert jedoch keine Nahrungsresourcen. An diesen Stränden dominiert das „kleine Nahrungsnetz" mit hoch beweglichen Tieren. Am stabileren, dissipativen Strand mit geringer Wellenenergie akkumuliert zweitweise organisches Material und das „große Nahrungsnetz" ist bedeutend. Pfeile deuten den Fluss organischer und mineralisierter Substanzen an.

Der vorliegende Vergleich der Ökosysteme zweier Strände mit unterschiedlicher Wellenenergie liefert erste Ideen möglicher Konsequenzen einer steigenden Wellenenergie und Erosion an exponierten Sandstränden. Solche Zunahmen werden im Zusammenhang mit einer globalen Klimaerwärmung und einem damit verbundenen Meerespiegelanstieg erwartet. Gleichzeitig wird, um die Strände zu stabilisieren, von einer Zunahme an Sandvorspülungen ausgegangen. Daraus resultieren vermutlich hoch dynamische Strände eines intermediären Strandtypes, die sich in einem morphodynamischen Ungleichgewicht befinden. Der Sylter Strand mit seinem beschriebenen Ökosystem ist für diesen Strandtyp ein Beispiel. In der kalt-temperierten

Region der Nordsee dominiert in solchen Systemen das „kleine Nahrungsnetz” (Meiofauna), während das „große Nahrungsnetz” (Makrobenthos-Epibenthos-Vögel) verarmt. Sandvorspülungen haben geringe negative Einflüsse auf das Benthos in diesem dynamischen System. Aus ökologischer Sicht können sie als eine akzeptable Methode des Küstenschutzes angesehen werden. Der Umfang der Maßnahme spielt jedoch eine entscheidende Rolle. Um eine Verträglichkeit für das Ökosystem zu gewährleisten werden keine größeren Maßnahmen als die in dieser Arbeit untersuchten (350,000 m^3 auf 2 km) und Ruhepausen zwischen solchen Störungen von mindestens zwei Jahren an einem Strand empfohlen.

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