

**Zonation of macrofauna
across sandy beaches and
surf zones along the
Dutch coast***

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Abstract

On nine beaches and two transects in the surf zone along the Dutch coast the presence of benthic macrofauna was studied in relation to basic abiotic characteristics. According to Short's classification system, Dutch beaches are mesotidal and dissipative ($\Omega = 8.6$), and the RTR is low (1.52–1.27), which means that they are not tide-dominated. BSI ranged from 1.4 to 1.1 for the northern and western Dutch coasts respectively and had an overall value of 1.2. The rates of exposure of the beaches varied between 8 and 12, and are therefore regarded as sheltered to moderately exposed. The Dutch beaches display a geographical trend in beach types. Those of the Wadden Sea islands in the northern part of the Netherlands are dissipative, flat, fine-grained, and host high densities of many species of benthic macrofauna. The beaches along the western Dutch coast are less dissipative, steeper, with a higher mean grain size; the species diversity and abundance there are lower. Species diversity and abundance on the beaches increase from the high- to the low-water line. The maximum number of species was found

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between 0 and -1 m relative to the mean tidal level. The abundance peaks just above the mean tidal level, while the biomass reaches a maximum at the mean tidal level.

Species diversity and abundance are low in the surf zone, but increase towards deeper water. Species numbers are high and the abundance is very high in the trough between the two bars.

The relation between the diversity and abundance of macrobenthic species on the one hand, and the sediment composition, water column depth, and position between the bars on the other show a clear pattern of zonation for the beach, surf zone and near-shore: (1) a supralittoral zone with insects and air-breathing crustaceans, (2) a midshore zone, with intertidal species, (3) a lower shore zone, whose species extend into the shallow surf zone, and (4) a zone of sublittoral fauna in the trough between the two breaker bars within the surf zone.

1. Introduction

For 82% of its total length (432 km) the Dutch coast consists of sandy shores. This coast is part of the sandy coastal ecosystem of the North Sea extending from Cap Blanc Nez in France as far as Northern Jutland in Denmark. The Dutch coast can be divided into three physically different parts: the Wadden Sea islands in the north, the Schelde delta in the south, and in between, the central and western coasts, a sand barrier system fronted by beach and surf zones containing 2 or 3 bars. The beaches and surf zones are the products of wind-generated waves interacting with the medium to fine shore face sands in a mesotidal environment (Short 1992). The seemingly considerable difference between the high and low-water levels (1.4–3.8 m) contributes little to the variation in beach morphology. In fact, this is influenced mainly by breaker height, which ranges from 1.0 m (summer mean) to 1.7 m (winter mean) along the Dutch coast. Dunes, beaches and surf zones have always protected the land against flooding by the sea. However, a sandy coast is more than just a pile of sand providing a natural defence against the sea. The protection of the coastal environment is laid down in (inter)national legislation and regulations, such as the EU Water Framework Directive, the EU Bird and Habitat Directive, and in international treaties and recommendations. Examples are the global Biodiversity Treaty and the recommendation to set up an international network of protected coastal and marine areas to protect the marine environment. According to a recent EU recommendation, the management of the coast will also have to be based on an ecosystem approach. In order to protect the coastal environment, one has to know what to protect: What are its characteristics? Which organisms live in it? What functions does it fulfil? With respect to the Dutch coast, we assume that the main long-term threats are linked on the one hand with climate change and

on the other with the social and economic use of the land on or immediately behind the dunes. In the short-term, sand nourishment to counter erosion, the mechanical cleaning of beaches, and disturbance by vehicles and tourists – all the consequences of increasing recreational pressure – are important potential threats. Moreover, the enrichment of coastal waters with nutrients has very likely exerted a significant influence in the last 20–30 years. In this paper we present the results of our investigations on the zonation of the benthic macrofauna of the beaches and surf zone along the coasts of the Netherlands. We also examine the variations in terms of zoogeographic patterns and different beach types.

2. Material and methods

In June 2002 seven localities perpendicular to the waterline were sampled on each of nine beaches along the Dutch coast (Fig. 1). Five of the localities were tidal. The actual position of the sampling locality on the beach was determined on the basis of the predicted tidal curve in such a way that flooding time was spread equally over the intertidal localities. Locality 1 was positioned at the high-water line (HW), locality 5 at the low-water line (LW). Locality 2 was flooded for $\frac{1}{4}$ of a tide; locality 3 was flooded for $\frac{1}{2}$ of a tide and locality 4 experienced $\frac{3}{4}$ tidal flooding time. Locality 0 was situated 40 cm above the HW line and locality 6 was 40 cm below the LW

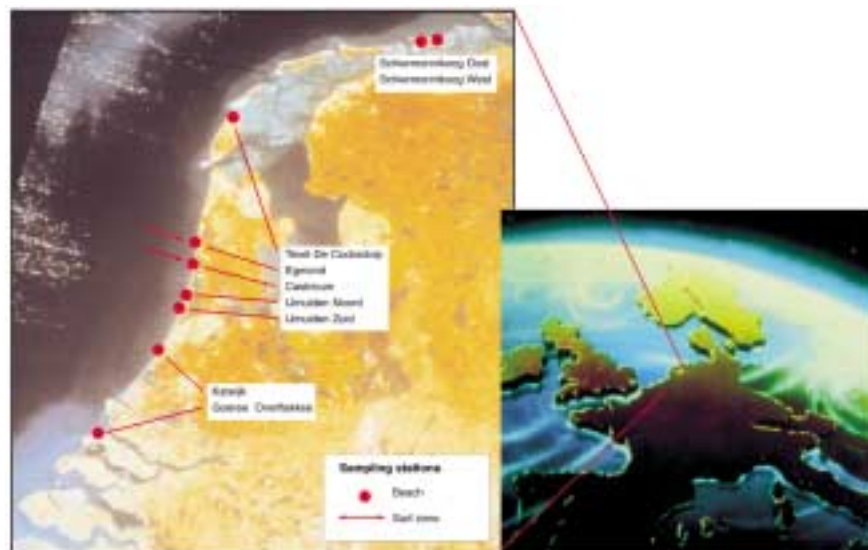


Fig. 1. Sampling stations on the Dutch coast; 2 surf zone transects and 9 beach sampling stations

line. The elevation could then be calculated on site using satellite equipment (Scorpio 6502 MK LRK-receiver).

The following parameters were measured on each beach: macrobenthos (abundance, diversity and biomass), sediment (grain size, sorting and carbonate), slope, penetrability of the sediment, position of the anaerobic layer and the presence or absence of stable burrows of macrobenthic animals.

Macrofauna was sampled to a depth of 30 cm using a stainless steel corer with a surface area of 78.5 cm². 10 subsamples were collected at each locality. In all cases a 1 mm-mesh sieve was used to separate the macrozoobenthos from the sediment. The organisms then were fixed using 3.8% formaldehyde.

Two samples were collected at each locality for sediment analysis using a 20 cm² plastic corer sunk to a depth of 10 cm. Before analysis the samples were stored at -20°C. All samples were treated with H₂O₂ and HCl and analysed with the Malvern-laser technique to determine the grain size, sorting and carbonate.

The penetrability was measured 10 times at each locality using a metal probe (Eijkelpkamp Agrisearch Equipment). The rod was pushed 30 cm into the sediment at constant speed by hand (2 cm sec⁻¹). The required pressure was expressed in [N cm⁻¹].

The slope of the tidal area was calculated from the difference between heights and distances between the low-water and the high-water lines.

The depth at which the anaerobic layer first appears was measured as the distance between the top layer of the sediment and the position where the sediment was coloured black. If this black layer was not yet visible at a depth of 30 cm, the anaerobic layer was assumed to be absent. The presence or absence of stable burrows was assessed visually.

Transects in the surf zone were sampled in two localities (Fig. 1) using a large tripod on wheels. The surf zone was sampled to a maximum water depth of 7 m. The geographical position and the depth at which the samples were taken were determined by satellite equipment and presented relative to the mean tidal level. The samples were taken with a 200 cm² Van Veen Grab to a depth of 0.25 m. A small subsample was taken with a 20 cm² plastic corer from the Van Veen Grab sample for sediment analysis.

3. Results

3.1. Beaches

3.1.1. General description

The Dutch beaches can be described using Dean's dimensionless parameter (Ω) and the relative tidal range (RTR). According to Short's

(1996) classification system, the Dutch beaches are mesotidal and dissipative ($\Omega = 8.6$). Nevertheless, there are local differences (Table 1). While the beaches of the west coast ($\Omega = 6.6$) are of the dissipative type ($5 < \Omega < 9$), those of the north coast are ultra-dissipative ($\Omega = 11.5$). The RTR is low (1.52–1.27), which means that the geomorphologies of these beaches are not tide-dominated. The beach state index (BSI) (McLachlan et al. 1993) ranges from 1.4 to 1.1 for the northern and the western Dutch coasts respectively; the overall value for the Dutch coast is 1.2. The rate of exposure, based on a rating system for beaches on a 20 point scale (Brown & McLachlan 1990), was calculated on the basis of wave action, length of the surf zone, percentage of very fine sand, grain size, slope, depth of the anaerobic layer, and the presence or absence of stable burrows of benthic animals. The beach of Schiermonnikoog-West is sheltered (score 8). All the other beaches can be regarded as moderately exposed with scores between 11 and 12. Generally speaking, then, we can describe the Dutch beaches as mesotidal, barred, dissipative, and moderately exposed.

Table 1. Dean's parameter (Ω), relative tidal range (RTR), beach state index (BSI) and exposure of the northern Dutch coast (Wadden Sea), the western Dutch coast and the mean values for the total Dutch coast

	Wadden Sea coast	Western coast	Dutch coast
Ω	11.5	6.6	8.6
RTR	1.52	1.27	1.65
BSI	1.4	1.1	1.2
exposure	8–11	11–12	8–12

3.1.2. Variation between beaches

An inventory of the beaches shows clear differences between the beaches of the Dutch mainland coast and those of the Dutch Wadden Sea islands (Table 2). Despite some significant local differences, the latter beaches are characterised by fine sand that is poor in carbonate and readily penetrated. The sediment is poorly sorted, i.e. it contains a mixture of sand grains of all sizes. Those beaches are flat and host high densities of many kinds of animals. Along the west coast of the Netherlands, the beaches are steeper and consist of coarser but better sorted sand. The carbonate content in the sediment of the beaches south of Egmond is higher than that of the northern beaches. Penetrating the sediment requires greater strength, and the species richness and specimen numbers are not as high as on the beaches of the Dutch Wadden Sea islands.

Table 2. Grain size, sorting, penetration, carbonate content, slope, diversity, abundance, Shannon-Wiener index and biomass for nine beaches along the Dutch coast (mean of all 7 localities)

Beach	Grain size [μm]	Sorting [ϕ]	Penetration	Carbonate content [%]	Slope [$1/x$]	Diversity [number of species]	Abundance [indiv. m^{-2}]	Shannon-Wiener	Biomass [g AFDW m^{-2}]
Schier Oost	208	4.0	288	2	96	20	1352	1.77	1.5
Schier West	202	4.1	202	2	89	28	4166	1.36	4.7
Texel	261	3.5	261	2	21	23	306	2.23	1.1
Egmond	305	3.5	305	2	42	7	347	0.89	1.9
Castricum	314	3.1	314	25	31	6	451	0.99	2.9
IJmuiden57	257	3.1	257	13	77	5	1179	0.14	1.5
IJmuiden60	328	3.2	328	8	32	8	553	1.08	4.1
Katwijk	359	2.8	359	12	36	8	471	1.2	2.2
Goeree	218	3.6	218	6	96	10	222	1.48	0.7

A total of 49 species was found on the beaches, from 5 to 28 per beach, with abundances ranging from 222 to 4166 indiv. m^{-2} . Fig. 2 shows a kite-diagram of the abundance of the different species (log scale) at each locality.

The most common species on the beaches is the bristle worm *Scolelepis squamata*, an important food source for the Sanderling *Caldris alba*, which is protected under the EU Bird Directive. Two other characteristic species are *Bathyporeia pilosa* – the sand digger shrimp, and *Euridice pulchra*, the speckled sea louse.

3.1.3. Variation within beaches

By taking the results of all nine beaches together, it is possible to describe the spatial variation on the beach perpendicular to the water line.

High up on the beach, near the high-water line, the grain size is small, the sorting poor, the content of carbonate low and the strength needed to penetrate the sand high (Table 3). The sediment near the low-water line is more easily penetrated owing to the greater water content, better sorting, and the larger average grain size. Both the number of species and their abundance increases towards the low-water line.

Fig. 3 shows the number of species found at each locality on each beach plotted against the elevation of the locality compared to the mean tidal level. It shows that the maximum number of species was found between 0 and -1 m relative to the mean tidal level.



Fig. 2. Kite diagram of mean macrobenthos abundance over all 9 beaches. Locality 1 = HW-level; locality 5 = LW-level

Table 3. Grain size, sorting, penetration, carbonate content, slope, diversity, abundance, Shannon-Wiener index and biomass for each of 7 localities on the beach (mean of all nine beaches)

Locality	Grain size [μm]	Sorting [ϕ]	Penetration	Carbonate content [%]	Diversity [number of species]	Abundance [indiv. m^{-2}]	Shannon-Wiener	Biomass [g AFDW m^{-2}]
0	265	3.6	516	4.4	7	146	0.5	0.2
1	258	3.7	533	3.9	10	30	1.1	0.2
2	253	3.4	564	5.2	14	639	1.4	1.3
3	270	3.4	486	10.2	19	1581	1.5	5.8
4	298	3.2	385	11.6	28	729	1.7	3.7
5	279	3.5	250	6.9	12	624	1.4	2.3
6	279	3.4	269	10.9	29	484	2.5	2.5

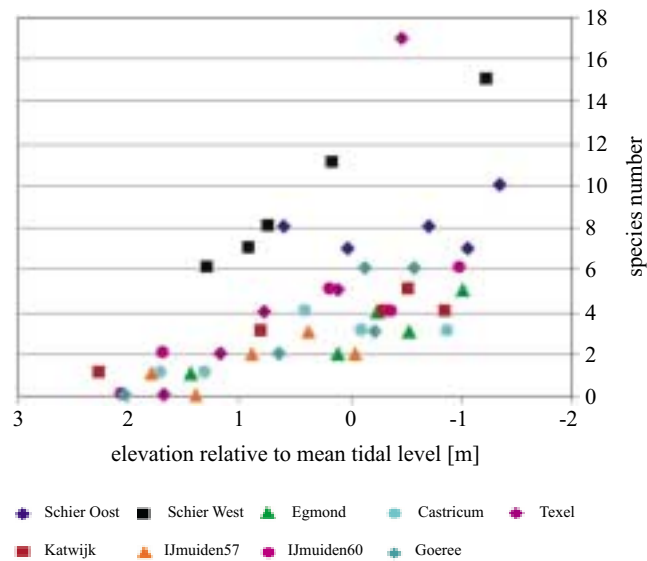


Fig. 3. Relation between the number of species found at each locality on all beaches, and elevations relative to mean tidal level

Fig. 4 shows the abundance plotted against elevation relative to the mean tidal level. The abundance peaks just above the mean tidal level, while the biomass reaches a maximum at this level (Table 3). The mean biomass on the Dutch beaches is 2.3 g AFDW m^{-2} . This is low compared

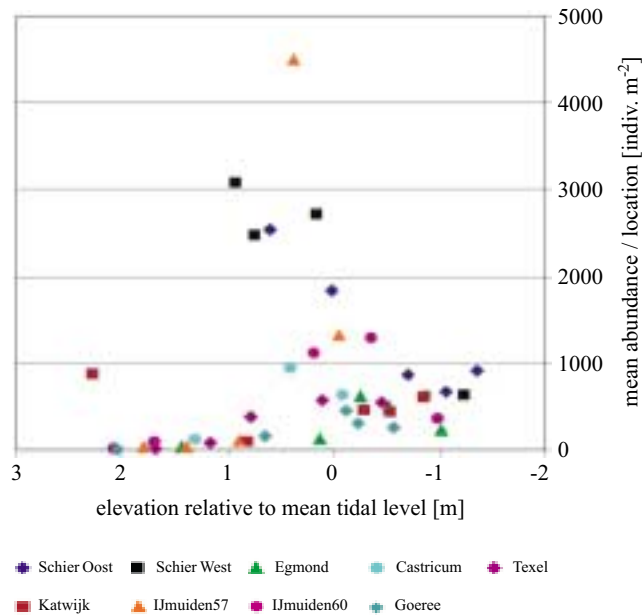


Fig. 4. Relation between abundance and elevation, and mean tidal level

to the value of 27 g AFDW m⁻² that Beukema (1981) found on the tidal flats of the Wadden Sea.

The relation between diversity and abundance on the one hand, and grain size and slope on the other, are in accordance with the relation given by Brown & McLachlan (1990): the numbers of species and their abundance both increase as the grain size and slope decrease (Tables 2 and 3).

3.2. Surf zone

3.2.1. General description

The results of sampling the surf zone along the Dutch coast show that there are two breaker banks (bars). One is approximately 150 m from the shoreline (low-water line), the other c. 400 m from the shore. Between them lies a trough, the bottom of which is at a depth of -5 m (Fig. 8). Table 4 combines the results of the sampling stations at Egmond and Castricum.

In the area within 200 m of the low-water line, the grains vary in size from 246 to 377 μm and are not well sorted. The sediment in the trough is coarse-grained, well-sorted sand with high carbonate and silt contents. Beyond the surf zone, the sand varies in grain size from 170 to 252 μm , is poorly sorted, and has a low silt content. Species numbers in the surf zone are low (2–7 species), as is the abundance (c. 100–1000 indiv. m⁻²). Beyond

Table 4. Grain size, sorting, carbonate content, silt, density and abundance, depth and distance from the low-water line (LW) for two transects in the surf zone (Castricum and Egmond)

Beach	Distance from LW	Depth [m]	Grain size [μm]	Sorting [ϕ]	Carbonate content [%]	Silt [%]	Diversity [number of species]	Abundance [indiv. m^{-2}]
Castricum	0	-1.4	341	2.3	37.0	0.4	3	400
Egmond	0	-1.5	298	3.7	3.1	0.5	6	85
Egmond	0	-1.5	302	3.7	3.5	0.2	4	130
Castricum	32	-2.9	267	3.5	22.4	0.6	3	80
Egmond	32	-3.0	335	3.3	6.2	0.4	2	25
Castricum	61	-1.4	377	2.5	59.5	0.3	2	2080
Egmond	64	-3.0	334	3.0	10.9	0.4	3	95
Egmond	96	-2.9	249	4.0	5.4	0.8	4	60
Castricum	121	-2.7	266	3.7	9.8	0.6	2	80
Egmond	128	-2.3	246	3.8	5.7	0.7	5	35
Egmond	160	-3.0	279	3.6	6.0	0.6	4	55
Castricum	181	-4.8	787	1.1	71.2	0.4	4	520
Egmond	192	-4.0	285	3.7	5.0	0.5	5	160
Egmond	224	-5.3	553	1.3	22.2	0.4	2	15
Castricum	241	-4.9	230	5.6	37.1	1.2	16	256 800
Egmond	256	-5.3	344	1.4	30.4	2.2	6	40 545
Egmond	288	-5.5	632	1.4	36.6	0.2	3	800
Egmond	320	-5.5	762	1.3	41.2	7.0	3	1560
Egmond	320	-5.6	717	1.2	54.2	0.5	2	520
Egmond	397	-3.7	241	3.8	5.5	0.8	4	55
Castricum	422	-3.8	231	3.9	9.3	0.8	6	120
Egmond	438	-4.2	252	3.8	7.0	0.8	4	45
Egmond	438	-4.4	252	3.8	6.8	0.6	4	65
Castricum	482	-5.6	186	4.2	8.9	1.2	8	150
Egmond	492	-5.8	223	3.9	7.4	0.9	11	925
Egmond	510	-6.2	228	3.9	7.6	0.9	8	1535
Castricum	542	-6.2	199	4.1	11.4	1.2	12	1020
Egmond	542	-6.5	207	4.0	8.6	0.9	10	1150
Egmond	596	-6.8	212	3.9	9.2	0.9	9	585
Castricum	602	-6.3	182	4.3	10.1	1.0	13	2415
Egmond	604	-6.9	198	4.0	9.1	0.9	14	1075
Castricum	724	-6.7	172	4.3	10.6	1.5	16	1015
Castricum	737	-6.7	170	4.4	11.9	1.2	15	440

Fig. 5. Kite diagram of mean macrobenthos abundance at Castricum; distance from the low-water line (LW) = 0

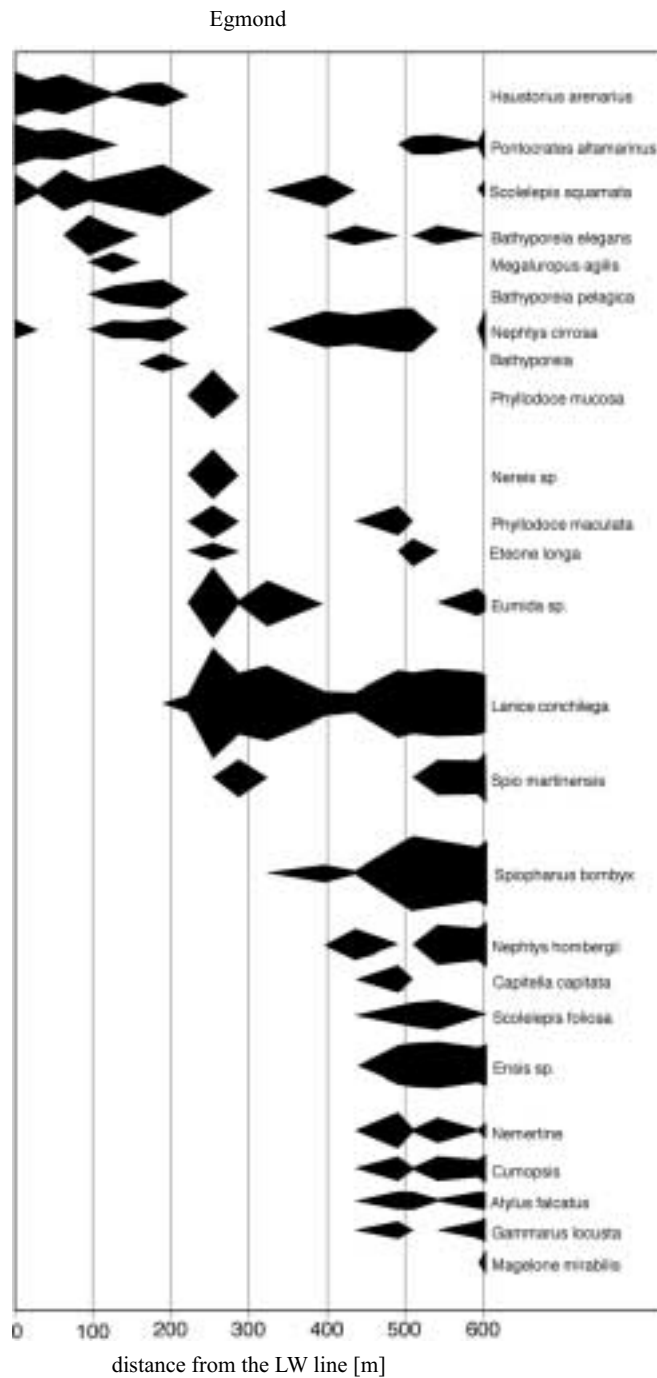


Fig. 6. Kite diagram of mean macrobenthos abundance at Egmond; distance from the low-water line (LW) = 0

the surf zone, species diversity and abundance increase to approximately 16 species and 1000 indiv. m^{-2} at a distance of more than 700 m from the low-water line. In the trough between the two bars, species numbers are high (16 at Castricum) and the abundance is very high (c. 100 000 indiv. m^{-2}).

Figs 5 and 6 present the relative abundance of macrobenthic species at Castricum and Egmond in the form of kite-diagrams. Polychaetes are dominant. Seawards of the second breaker bank and hosting a higher number of species than the surf zone, the outer zone is inhabited primarily by amphipods, bivalves and echinoderms.

'Typical' beach species like *S. squamata*, *Haustorius arenarius* and *B. pilosa* occur in the part of the surf zone nearest to the beach. A number of characteristic animals inhabit the trough, some 200–300 m from the beach, most specifically, the sand mason (*Lanice conchilega*). We may therefore infer that the trough is a special zone within the surf zone, and that the surf zone is itself very distinct from the offshore area beyond, where *Spiophanes bombyx* is the most abundant species.

3.3. Zonation of the beach and surf zones

For the purposes of cluster analysis, the beach and surf zone data were combined into a single set (Ward's Distance Metric: Squared Euclidean). Cluster analysis of the abundance of macrobenthos indicates an obvious zonation at a distance of 0.6 (Fig. 7). Higher-beach localities group

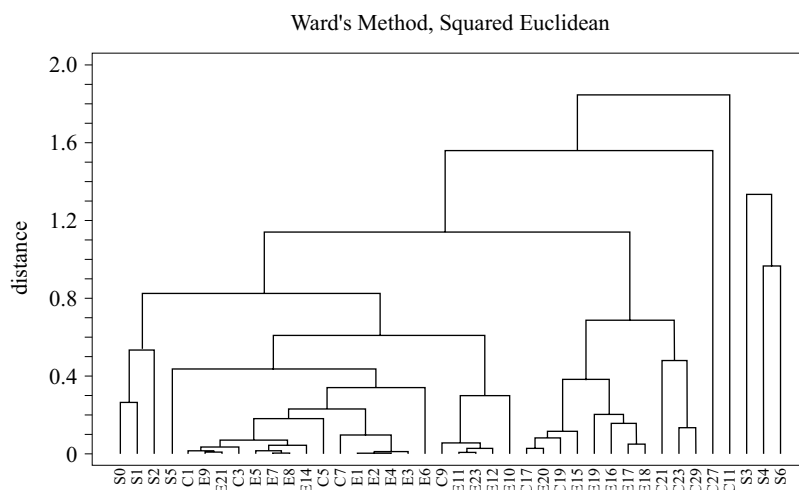


Fig. 7. Cluster analysis (Ward's Euclidian) of the abundance of all species. Beach samples (S0–S6); S1 = HW; S5 = LW. Surf zone samples – Egmond (E1–E23) and Castricum (C1–C29); E1 and C1 are close to the low-water line; E23 and C29 are farthest away from the low-water line

together, as do lower-beach localities. It is also clear that the localities in the surf zone and those beyond it form two separate groups. The latter group splits into two subgroups: the Egmond and the Castricum localities. We can therefore conclude that the zonation of the sandy shores in the Netherlands is as follows: (1) a supralittoral zone with insects and air-breathing crustaceans, (2) a midshore zone with intertidal species, (3) a lower-shore zone, whose species extend into the shallow surf zone, and

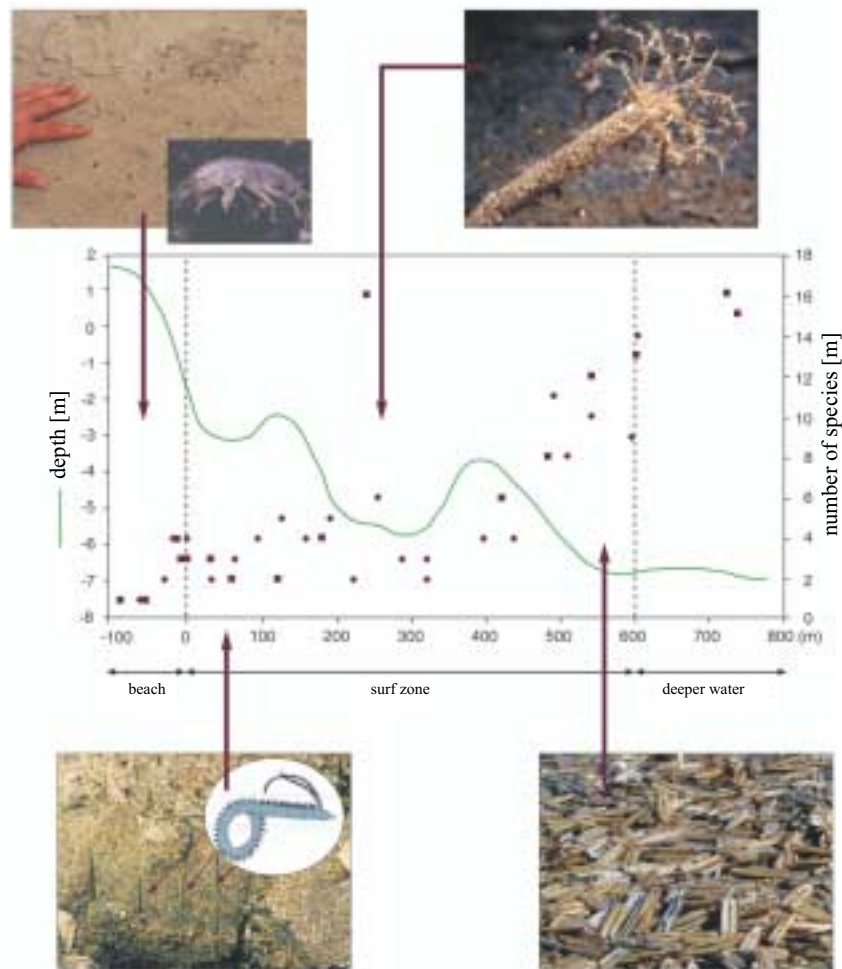


Fig. 8. Number of species in the beach and surf zones in relation to depth and distance from the low-water line. Characteristic species are shown: *Talitrus saltator* sand hopper (beach); *Scolelepis squamata* (beach and surf zone); *Lanice conchilega* sand mason (trough between the two bars); *Ensis americanus* razor clam (deeper water)

(4) a zone of sublittoral fauna in the trough between the two breaker bars within the surf zone.

Fig. 8 presents a general scheme in which the number of species has been plotted against distance to the low-water line and depth relative to the mean water line. It also shows some characteristic species of the different parts of the Dutch sandy shore. To this end, the sampling data from the surf zones at Castricum and Egmond were combined with the beach data of those two places; the data from the other Dutch beaches were omitted.

4. Discussion

4.1. Beach

The Dutch beaches show a geographical trend in beach types. The beaches of the Wadden Sea islands in the northern part of the Netherlands are dissipative, flat, fine grained, and host high densities of many species of benthic macrofauna. The beaches of the Dutch west coast are less dissipative, steeper, with a larger mean grain size, but where species diversity and abundance are lower. Degreear et al. (2003) describe Belgian beaches as ultra-dissipative, low-tide bar/rip beaches. They report values of Ω between 2.6–7.0, RTR between 8.5–10 and BSI between 1.8–4.2. In this paper the corresponding mean values for the Dutch beaches are $\Omega = 8.6$, RTL = 1.65 and BSI = 1.2. Compared to the Belgian beaches, then, Dutch beaches are influenced more by wind/wave action than by tide.

By taking the results of all nine beaches together, it was possible to describe the spatial variation on the beach perpendicular to the water line. High up on the beach, near the high-tide mark, the grain size is the smallest, the sorting the poorest, the carbonate content the lowest and the strength required to penetrate the sand the highest. For interstitial organisms this means that the environment is more favourable lower down on the beach than higher up. Towards the low-water line the sediment is more easily penetrated owing to the greater water content, better sorting and the larger average size of the grains. All this results in an increasing number of species towards the low-water line. The number of individuals is low near the high-water line and is the highest around the mean-tidal level. For birds foraging on the beach it is important that they can easily penetrate the sand with their bills and that food such as worms is readily available. The relation between the presence of organisms and sediment characteristics that we found for the Dutch beaches corresponds with what is known from the literature about the ecology of sandy coasts elsewhere in the world (Brown & McLachlan 1990). The differences in slope, grain size and BSI are small within the limited area of the Dutch coastline. However, the general trend of

higher species diversity and abundance at the dissipative, flat, fine-grained end of the spectrum compared to the lower species diversity and abundance at the more reflective end of the line, is also applicable to the Dutch beaches.

Based on the kite-diagram of the beach data, one can assume that the community of species above the high-water mark differs from that found between the high- and low-water lines. Above the high-water lines, it is mainly terrestrial organisms such as insects and the sand hopper that are found. According to kite and cluster analysis, we can assume not only that a specific group of organisms exists above the high-water line, but also that the tidal beach may be split into a zone above the mean water level and a zone below it. The organisms in the upper zone are complemented by a number of extra species in the lower zone. In particular, amphipods, polychaetes and isopods are found on the beach. Surveys of many European beaches have shown that there is a tendency towards three or four zones (McLachlan & Jaramillo 1995). From the results of the present study, we have come to the conclusion that three zones can be distinguished on Dutch beaches: (1) a supralittoral zone with insects and air-breathing crustaceans, (2) a midshore zone with intertidal species, and (3) a lower shore zone whose species extend into the shallow surf zone. These zones correspond to Dahl's scheme (1952) of the zonation of sandy-beach fauna. The number of species increases from the high-water line to the low-water line. The same trend was found on Belgian beaches (Degraer et al. 2003) and in the tidal flat area of the Dutch Wadden Sea (Beukema 2002). Moreover, these results correspond with the hypothetical pattern of species diversity across a beach/surf zone system as presented by Brown & McLachlan (1990). According to Beukema (2002), the maximum number of species can be found 20 to 40 cm below the mean water level. Moreover, there is a smaller decrease in species numbers towards the mean low-water line than towards the high-water line. Beukema states that this relation is independent of locality and sediment composition in the Wadden Sea. The results of this study of sandy beaches indicate that the relation found by Beukema is also valid for the sandy intertidal beaches in the Netherlands.

Both abundance and biomass reach maximum values at the mean tidal level, a result also obtained by Beukema (2002) on the tidal flats of the Dutch Wadden Sea. On Belgian beaches Degraer et al. (2003) recorded a maximum macrobenthic abundance not only in the upper intertidal zone but also on several beaches at the midtidal level, as compared with the Dutch beaches. According to Beukema (2002), the relatively low abundance and biomass of benthic animals at higher intertidal levels is probably due to the harsh environmental conditions there. These levels are characterised by strong fluctuations and extremes of such factors as

temperature and salinity, combined with short immersion periods, limiting the time for activities in marine organisms. At the same time the relatively low abundance of benthic macrofauna at the low-water line may be related to unfavourable environmental conditions like mobile sediments and higher predation pressure on the part of shrimps, crabs and young fish.

4.2. Surf zone

Surf zones have been neglected in ecological studies of the sea. But this is an understandable lapse in view of the logistical problems of working in such environments (McLachlan et al. 1984). While some authors have studied the hyper- and epibenthos (Beyst et al. 2001), information on the endobenthos is extremely scarce. Because the surf zone is inaccessible to ships and the standard sampling gear, sampling endobenthic animals there is logistically restricted. The tripod used in this study – a vehicle with three large wheels – can move about and sample in the surf zone in good and bad weather. In the surf zone, where the hydrodynamic conditions are harsh, species numbers are limited. But beyond the surf zone, towards the deeper water, these increase rapidly. It is not known at what distance or depth this increase stabilises. To produce a general scheme of the diversity along a gradient from the high-water level on the beach down to a water depth of minus 7 m beyond the surf zone, the data from the two beaches where the surf zone was also sampled – at Castricum and Egmond – had to be combined. This may have led to an underestimation of the number of species on the beach, since the total sampling area per beach was small for temperate dissipative beaches (Jaramillo et al. 1995). This may explain the aberration of this scheme from the hypothetical pattern of species diversity across a beach/surf zone system as presented by Brown & McLachlan (1990), who showed a decline in species diversity in the surf zone compared to the lower part of the beach.

The zonation pattern found on the two-barred dissipative sandy shores of the western coast of the Netherlands shows good correspondence with the zonation scheme suggested by McLachlan et al. (1984). They presented a diagram of the zonation of the intertidal and sublittoral macrofauna on high-energy sandy coasts of south-eastern Africa. The supralittoral zone, the midshore intertidal zone, and the surf zone found on the Dutch beaches correspond well with the supralittoral, midlittoral and inner turbulent zones found by McLachlan et al. (1984). From the present study it is not quite clear whether beyond the surf zone, where species diversity increases, other zones can be distinguished, as is the case for the beaches of south-eastern Africa.

The conditions in the trough between the two bars are very different from the rest of the surf zone. Owing to the limited number of samples only an indication of these conditions can be given. Even though the differences between Egmond and Castricum indicate that local differences may be large, a general pattern in abiotic and biotic variables arises from the data. The high percentage of silt and the high numbers of species and their abundance indicate relatively shallow conditions in which large numbers of the sand mason dominate the sediment. The trough seems to be a special area of local diversity and abundance and should therefore be treated with caution, as it is part of a conservation area under the European Water Framework Directive.

References

- Beukema J. J., 1981, *Quantitative data on the benthos of the Wadden Sea proper*, [in:] *Report 4 of the Wadden Sea working group*, N. Dankers, H. Kuhl & W. J. Wolff (eds.), Stichting Veth tot Steun aan Waddenonderzoek, Leiden, 134–142.
- Beukema J. J., 2002, *Expected changes in the benthic fauna of Wadden Sea tidal flats as a result of sea-level rise or bottom subsidence*, J. Sea Res., 47(1), 25–39.
- Brown A. C., McLachlan A., 1990, *Ecology of sandy shores*, Elsevier, Amsterdam, 1–328.
- Beyst B., Buysse D., Dewicke A., Mees J., 2001, *Surf zone hyperbenthos of Belgian sandy beaches: seasonal patterns*, Estuar. Coast. Shelf Sci., 53(6), 877–895.
- Dahl E., 1952, *Some aspects of the ecology and zonation of the fauna on sandy beaches*, Oikos, 4, 1–27.
- Degraer S., Volckaert A., Vincx M., 2003, *Macrobenthic zonation patterns along a morphodynamical continuum of macrotidal, low tide bar/rip and ultra-dissipative sandy beaches*, Estuar. Coast. Shelf Sci., 56(3)–(4), 459–468.
- Jaramillo E., McLachlan A., Dugan J., 1995, *Total sample area and estimates of species richness in exposed sandy beaches*, Mar. Ecol. Prog. Ser., 119, 311–314.
- McLachlan A., Cockcroft A. C., Malan D. E., 1984, *Benthic faunal response to a high energy gradient*, Mar. Ecol. Prog. Ser., 16, 51–63.
- McLachlan A., Jaramillo E., 1995, *Zonation on sandy beaches*, Oceanogr. Mar. Biol. Ann. Rev., 33, 305–335.
- McLachlan A., Jaramillo E., Donn T. E., Wessels F., 1993, *Sandy beach macrofauna communities and their control by the physical environment: a geographical comparison*, J. Coastal Res., 15, 27–38.
- Short A. D., 1992, *Beach systems of the central Netherlands coast: processes, morphology and structural impacts in a storm driven multi-bar system*, Mar. Geol., 107, 103–137.
- Short A. D., 1996, *The role of wave height, period, slope, tide range and embaymentisation in beach classifications: a review*, Rev. Chil. Hist. Nat., 69, 589–604.