

**Spatio-temporal decay
'hot spots' of stranded
wrack in a Baltic sandy
coastal system. Part I.
Comparative study of the
pattern: 1 type of wrack
vs 3 beach sites***

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Sandy beach
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Abstract

The significance of distance along the beach-dune transect and different moisture conditions as regards the decay of *Zostera marina* leaf litter was investigated in simple field experiments in three temperate, medium- to fine-quartz-sediment, sandy beaches of the Gulf of Gdańsk in Poland. 1800 replicate litterbags of freshly stranded *Zostera marina* leaves were placed in beach sediments at different strata and levels on each of the beaches. The litterbags were sampled after 5, 10, 50, 100 and 150 days in the field and the remaining material was then dried and weighed. Under similar conditions of sediment composition, salinity and wave inundation, ANOVA tests revealed significant differences in breakdown through time and site. Thus there were some differences in the decay process between the low and high

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beach. In the former, degradation proceeded rapidly in the initial stages and then stabilised, while in the latter it remained linear throughout the study period. Matter loss in each stratum was also seasonally dependent. This may, however, be more closely linked to successional changes in the chemistry and/or microflora of the beach wrack than to its physical breakdown. Differences between organic matter degradation in the high and low beaches may be explained by differences in the moisture regime and nutrient status, and not by differences in the decay processes themselves. Therefore, two decay centres were found in the beach-dune system: the low beach together with the strandline (wrack consumption 12–21 % day⁻¹ in the warm season, and 4–10 % day⁻¹ in the cold season) and the dune (active consumption 2–6 % day⁻¹ in the warm season only).

1. Introduction

The principles according to which sandy-shore ecosystems function are in general well known and numerous relevant concepts have been developed world-wide. These are set out in Brown & McLachlan (1990), although some revision of this book is now needed in the light of subsequent developments. Recent years have seen a greater research effort focused on European sandy shores: in comparison with other localities, these beaches had been neglected, and even now our knowledge of these systems extends only from the coast of Italy around to northern Sweden (e.g. Scapini 2002). Our understanding of sandy-beach systems in Poland is also on the increase (Węśławski et al. 2000).

The super-parameter that controls the ecology of Poland's tideless sandy-beaches and drives the ecological processes is wave action. The characteristics of the beach system depend essentially on interactions between this wave action and the particle size parameters. These physical interactions result in beach types ranging from reflective to fully dissipative, these two extremes representing different ecosystems and ecosystem functioning. Lacking a surf zone and primary production, and with an impoverished macrofauna, reflective beaches are probably importers of material from the sea. Conversely, dissipative beaches, which may enjoy a high level of primary production in their extensive surf zones and a much higher diversity and biomass, are exporters (McLachlan 1983, Brown & McLachlan 1990).

Dunes are essentially coastal terrestrial systems in which wind-driven sand transport is of key importance. Sand exchange with beaches and their surf zones links these environments. The dune systems on the Polish coast range from physically controlled, wind-dominated transgressive dune sheets with high rates of sand movement and salt spray, common along the shores of the Słowiński National Park at the mid-point of the Polish coast, to systems with a substantial biological structure, as evidenced by

the stable, vegetation-covered dunes characteristic of the Hel Peninsula. The most obvious feature of coastal dunes is the physical and biological gradient stretching landwards from the sea.

Variations in the distribution, composition and structure of sandy beach communities have been related to changes in environmental parameters and to beach morphodynamics. However, the results published by different authors are inconsistent, with the result that there is diversity of opinions on the subject, which has been approached from various angles. McLachlan et al. (1993, 1995) have demonstrated that sediment parameters, wave height and beach slope regulate the intertidal macrofauna of the sandy beaches. These authors have shown that there is an increase in species diversity, abundance, and biomass of the macrobenthos from reflective to dissipative beaches, and also from micro/mesotidal to macrotidal beaches. However, many studies of the physical influences on community structure do not take temporal variations into consideration (Defeo et al. 1992, Jaramillo et al. 1993). Investigations of this kind cannot be used as a basis for making generalisations because they are easily misinterpreted (Brazeiro & Defeo 1996). Moreover, studies involving monthly sampling at only one point on only one beach do not permit appropriate temporal comparison between communities (Brazeiro & Defeo 1996). Seasonal changes in community density have been related to the population biology of the dominant species rather than the physical environment (Velooso & Cardoso 2001).

The rationale for the present work was that if beaches with the same species composition exhibit the same pattern of variation, the processing of beach wrack would have the same pattern of spatio-temporal variation regardless of the different morphodynamic states. The present study was conducted along the beach-dune slope of each of three sandy beaches. The degradation rates of the eelgrass *Zostera marina* L. from litterbags during two different seasons were compared and discussed. The idea was to find some spatio-temporal decay centres ('hot spots'). Thus, the objective of this study was to analyse spatio-temporal macro- (between beaches) and mesoscale (within beaches) variations in the degradation of *Z. marina*. Two null hypotheses were tested: that the physical parameters do not affect degradation rates in sandy beach studies, and that time (represented as samples taken in different seasons) does not affect these rates.

2. Materials and methods

2.1. Study area

The study was carried out on the coast of Poland on three tideless sandy beaches (Fig. 1): Hel Great Beach and Hel Small Beach at the

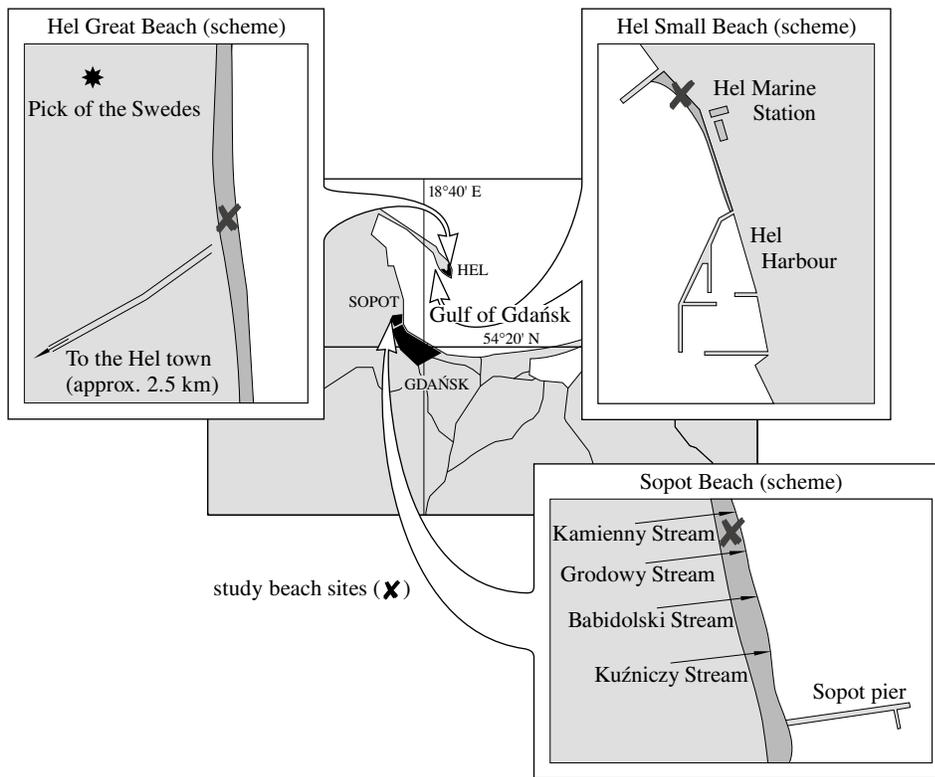


Fig. 1. Location of beach study sites

end of the Hel Peninsula, and Sopot Beach on the western shore of the Gulf of Gdańsk. They exhibit low gradients and broad surf zones in which most of the wave energy is dissipated, as well as large meteorological tidal ranges (astronomic tides of 0.03 m) with a maximum shore wave height of 0.35–0.6 m (Druet et al. 1972), the shoreline position being modified by wave and wind intensity and direction (Table 1). The studied section of sandy shore on the open sea side of the Hel Peninsula consists of foredunes (30 m wide and 4 m in height) formed by *Ammophila arenaria* – the uppermost boundary of the beach, a wide expanse of sand, and a surf zone between the exposed upper beach and the submerged sandy sea floor. The sandy shore, completely bereft of plant cover, is separated from the dune by a scarp representing the storm driftline. The beach appears to be barren but the shorebirds feeding along the surf edge betray the presence of other life forms. By contrast, small dunes and buildings back the Hel Small Beach and Sopot Beach, which are directly adjacent to the urban environment.

In the context of the LITUS project, the beach is the zone between the lowest and highest watermarks. Owing to the lack of tides in the Baltic Sea,

Table 1. The geographical location and physical characteristics of the beaches. The overall means are the values calculated from each stratum on each beach. The standard deviation is given in parentheses

Beaches characteristics	Hel Great Beach	Hel Small Beach	Sopot Beach
longitude	18°50'E	18°49'E	18°33'E
latitude	54°36'N	54°36'N	54°27'N
tidal regime	tideless	tideless	tideless
surf zone width [m]	100–150	10–25	70–110
beach width [m]	80–120	10–30	50–70
beach length [m]	10000	400	4000
beach slope ^a	1/25–1/40	1/15–1/30	1/25–1/35
sediment grain size [φ]	2.89 (0.03)	1.92 (0.08)	1.71 (0.07)
sediment textural group ^b	fine to very fine	medium to fine	medium to fine
sediment sorting [φ]	well-sorted 0.34 (0.06)	moderately-sorted 0.54 (0.05)	moderately-sorted 0.67 (0.09)
beach type ^c	ultra-dissipative	intermediate	dissipative
beach exposure ^d	very exposed, score = 15–18	exposed, score = 10–13	exposed, score = 12–15

^a slope = 1 mean gradient from above the driftline to the low tide swash region after McLachlan et al. (1993),

^b type of sand after Folk & Ward (1957),

^c *sensu* Short & Wright (1983),

^d according to McLachlan (1980) rating system.

it practically starts from the foot of the dune and extends to a water depth of approx. 1 m. Almost the entire Polish coastline consists of sandy beaches. The shores of the Gulf of Gdańsk are therefore a very popular holiday destination in Poland. Together with their surf-zones, the Hel Small Beach and Sopot Beach are ideal recreational areas. Hel Great Beach, however, is situated in a former restricted military area of the Marine Landscape Park, where human impact is relatively low. It was selected as an example of a relatively undisturbed Polish beach.

All three beaches have the same macrofauna communities, in which *Talitrus saltator* (Montague) – a talitrid amphipod, *Fucellia tergina* (Zett.) – an anthomyiid dipteran, *Stenus biguttatus* L. and *Paederus litoralis* (Graw.) – staphylinid beetles, *Ptenidium pusillum* (Gyll.) – a ptiliid,

Hister quadrinotatus Scriba – a histerid, and *Coccinella septempunctata* L., *Paramysia oblongoguttata* L. and *Coccinula quatuordecimpustulata* (L.) – coccinellids, are the dominant species (Jędrzejczak 2002b). This common feature provides the opportunity to compare the faunal influences on distinct type of beaches as a function of time.

2.2. Sampling design

The beaches were sampled during the spring/summer and autumn/winter seasons from 2000 to 2001 (April–September 2000 and October 2000–March 2001, respectively). Two transects extended from above the dune to below the swash line, and four sampling strata parallel to the water line were sampled according to a stratified random design (Fig. 2). The following zones were defined: (i) the dune zone, which corresponds to the foot of the first dune (stratum 4); (ii) the backshore zone, marked conventionally on the beach according to its morphology (stratum 3); (iii) the supralittoral zone, which corresponds to the subterrestrial fringe described by Dahl (1952) and to the zone of drying or dry sand (Salvat 1964), where organic material is stranded on the beach (stratum 2); and (iv) the intertidal zone, which corresponds to Dahl's midshore, located between the drift line and the water line (stratum 1). Strata 3 and 4 are described as high beach, and strata 1 and 2 as low beach. The distance between strata varied in accordance with the width of the beach. The overall width of the beach, including all the strata, was 83 m (Hel Great Beach), 25 m (Hel Small Beach), and 63 m (Sopot Beach).

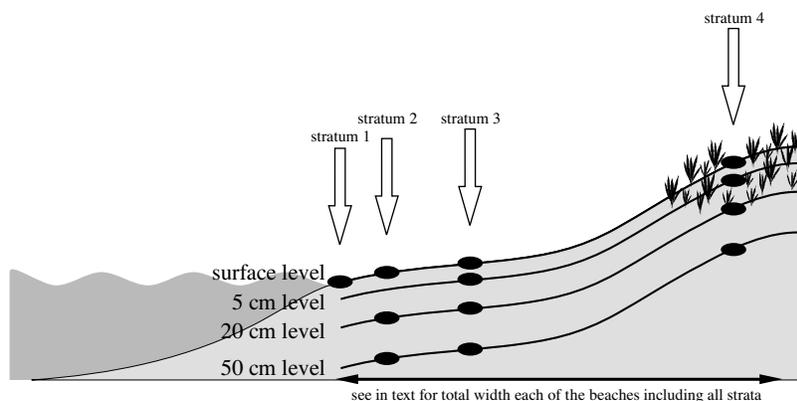


Fig. 2. Diagram of beach-dune slope showing the zones sampled (strata and depth levels) and the exposure of litterbags in the sand. The diagram is not to scale

2.3. Litterbag design and placement

This study was carried out following the previously adopted procedure (Inglis 1989, Jędrzejczak 1999, 2002a, b) modified to local conditions. Each transect trial ran for 150 days and was set up on the beach-dune profile. Made from 5-mm nylon mesh, the 225×105 mm litterbags were designed to allow all of the beach fauna access to the enclosed wrack material. Fresh *Zostera* was collected, blotted dry, and 60 g wet weight portions of leaves were placed inside the bags. Each litterbag was randomly assigned a plastic identification tag. Five replicate bags were positioned at random in each stratum from which existing wrack had been removed (Fig. 2). The surface bags were given just a light covering of sand. The sub-surface bags were positioned within the substrate using the following procedures. In stratum 2, a flat spade was inserted in the sediment to the requisite depth (20 or 50 cm, see Fig. 2 for details) and a bag slid into the sediment along the blade of the spade. The sediment was then pressed back around each bag. In the high-beach strata, trenches were dug and a bag placed horizontally in each hole at the requisite depth (5, 20 or 50 cm). The sediment removed by the burial was returned to the trench alongside the bag to ensure that the environment was as similar as possible to the original one. Having been assigned an identification number, each bag was inserted individually into the sediment. Litterbags were sampled 5, 10, 50, 100 and 150 days post-placement. Therefore, 1800 litterbags were used during the whole study (3 beaches \times 2 seasons \times 12 samples \times 5 replicates \times 5 retrievals).

In the laboratory the content of each litterbag was gently washed onto a 0.25-mm sieve to remove adhering sediment and surface fauna. The remaining vascular material was then dried for 3 days at 60°C and weighed. Final results were expressed as the percentage of initial wrack dry weight loss at the completion of the experiment and were analysed using ANOVA. In order to obtain the initial mass of *Z. marina*, five 60-g portions of fresh tissue were dried and weighed.

2.4. Decomposition model and statistics

Decomposition data derived from litterbag studies were expressed as the percentage of initial tissue dry weight loss and were compared using a four-way ANOVA procedure (Underwood 1981, StatSoft Inc. 1995, Fowler et al. 1998, Zar 1999) with time (days & season) and site (stratum/depth level & beach) as the main effects. F-tests were used to compare differences between individual site regressions for each stratum and level (full model) and a reduced model, where data from all sites, for each stratum and level were synthesised in one regression. F-tests were compared for each of three

regressions: Hel Great Beach, Hel Small Beach and Sopot Beach. To prevent a binomial distribution, all data were transformed to their arcsine. Then the resultant data had an underlying distribution that was nearly normal (Zar 1999). This transformation is presented in eq. (1):

$$p' = \arcsin(p)^{1/2}, \quad (1)$$

where

p – data proportion.

The final results were evaluated with a single exponential decay model (Jenny et al. 1949, Swift et al. 1979) according to eq. (2):

$$W_t = W_0 \cdot e^{-kt}, \quad (2)$$

where

W_t – dry weight (g) of litter sample remaining after time t ,

W_0 – initial dry weight (g) of litter sample,

e – base of natural logarithm,

k – decay coefficient (day^{-1}),

t – time (days).

The decay coefficient k permits comparison of decomposition rates between organic material types and among studies. The single-exponential model does not discriminate between soluble versus refractory material, nor does it distinguish microbial contributions (Wieder & Lang 1982).

The geostatistical gridding method of Kriging, which has proved useful and popular in many fields, was produced to do visually appealing contour and surface plots from irregularly spaced data. Within Surfer (Golden Software Inc. 1996), Kriging can be either an exact interpolator or a smoothing interpolator, depending on the user-specified parameters, to build a contour map, which was a plot of three values. The first two dimensions were the X, Y co-ordinates, and lines of equal value (the contour lines on the map) represented the third (Z). The shape of the surface is shown by the contour lines.

3. Results

Significant weight loss occurred in bags of all strata and depth levels (Table 2). The pattern of weight loss was similar at all beach sites and the eelgrass disintegrated in an approximately exponential fashion during most of the experimental periods. ANOVA tests revealed significant differences in degradation with respect to time (days and season) and site (strata and depth level). The main effects of stratum \times depth level were significantly greater for the stratum ($F_{\text{stratum}} = 63.107$, $P < 0.01$) than for the depth level ($F_{\text{depth}} = 21.473$, $P < 0.01$). The days \times season and stratum \times season

Table 2. Analysis of the proportion (arcsine transformation) of the dry weight loss of seagrass in the litterbags on five sampling days: (a) at different strata (stratum), and (b) at different levels (depth). Data are for three beach sites (beach) during two seasons (season). Significant effects are highlighted

a.

Source of variation	Trial			
	df	MS	<i>F</i> ratio	P
days	4	1.909	97.530	< 0.01
stratum	3	3.629	185.435	< 0.01
season	1	4.511	230.535	< 0.01
beach	2	0.024	1.242	0.291
days × stratum	12	0.022	1.122	0.342
days × season	4	0.115	5.867	< 0.01
stratum × season	3	0.164	8.374	< 0.01
days × beach	8	0.005	0.270	0.975
stratum × beach	6	0.015	0.795	0.574
season × beach	2	0.014	0.716	0.489
days × stratum × season	12	0.023	1.200	0.283
days × stratum × beach	24	0.002	0.123	1.00
days × season × beach	8	0.003	0.147	0.997
stratum × season × beach	6	0.012	0.634	0.702
days × stratum × season × beach	24	0.004	0.224	0.999
Bartlett's statistic	89	$\chi^2 = 191.552$		< 0.01
Cochran's statistic		C = 0.060		

b.

Source of variation	Trial			
	df	MS	<i>F</i> ratio	P
days	4	2.373	45.997	< 0.01
depth	3	1.271	24.643	< 0.01
season	1	4.782	92.692	< 0.01
beach	2	0.009	0.167	0.846
days × depth	12	0.012	0.226	0.997
days × season	4	0.159	3.088	0.017
depth × season	3	0.126	2.438	0.065
days × beach	8	0.004	0.081	0.999
depth × beach	6	0.005	0.092	0.997
season × beach	2	0.018	0.341	0.771
days × depth × season	12	0.008	0.164	0.999
days × depth × beach	24	0.002	0.049	1.00
days × season × beach	8	0.007	0.144	0.996
depth × season × beach	6	0.002	0.044	0.999
days × depth × season × beach	24	0.001	0.027	1.00
Bartlett's statistic	119	$\chi^2 = 153.615$		0.018
Cochran's statistic		C = 0.045		

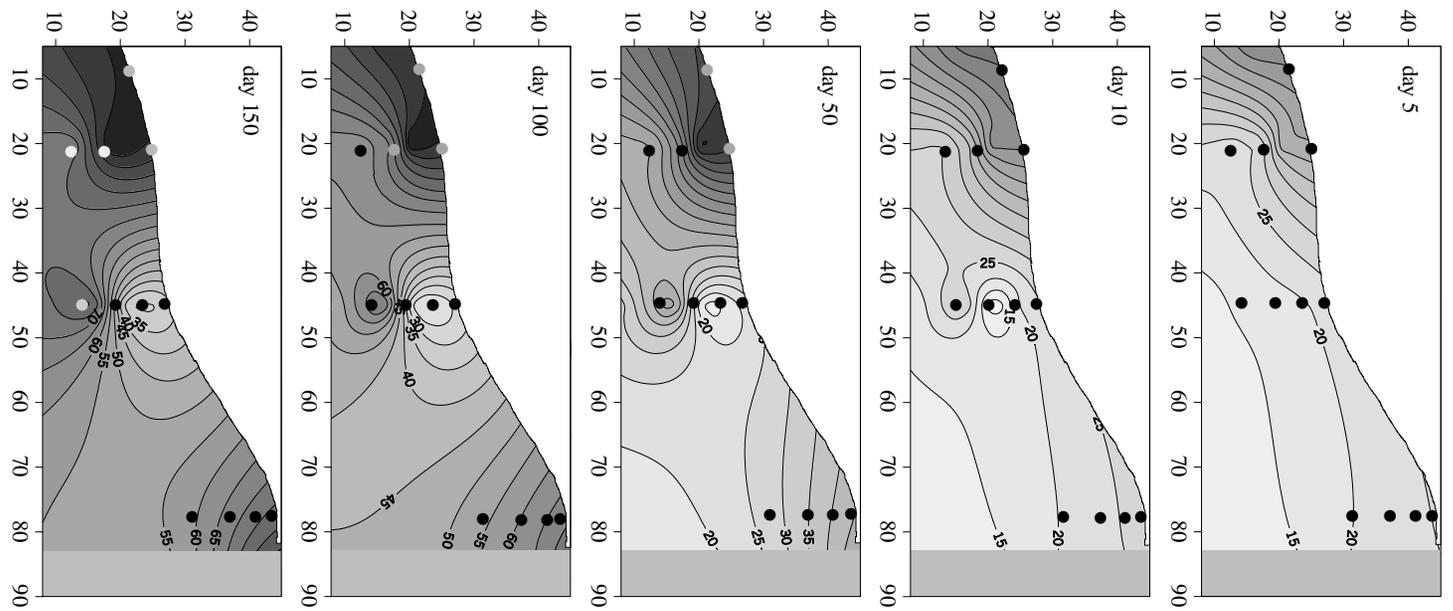


Fig. 3. Profiles of the slope of Hel Great Beach showing the zones sampled, the exposure of litterbags in the sand, and the estimated pattern of seagrass disintegration (Surfer Mapping System) on five sampling days in spring/summer. White indicates 0% dry matter loss, black 100% loss. Each line interval represents a loss of 5%. The diagrams are not to scale.

Surfer Mapping System: Spacing	# of lines
X direction 1.73	50
Y direction 1.76	20

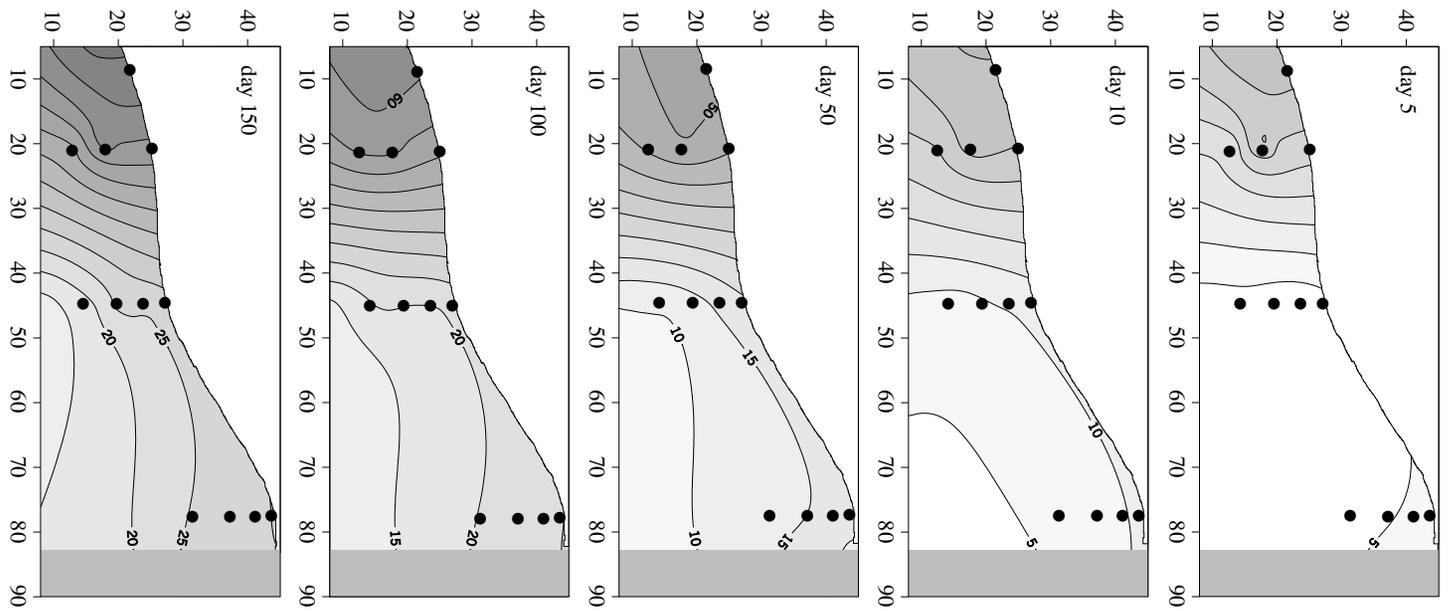


Fig. 4. Profiles of the slope of Hel Great Beach showing the zones sampled, the exposure of litterbags in the sand, and the estimated pattern of seagrass disintegration (Surfer Mapping System) on five sampling days in autumn/winter. Detailed descriptions are as in Fig. 3

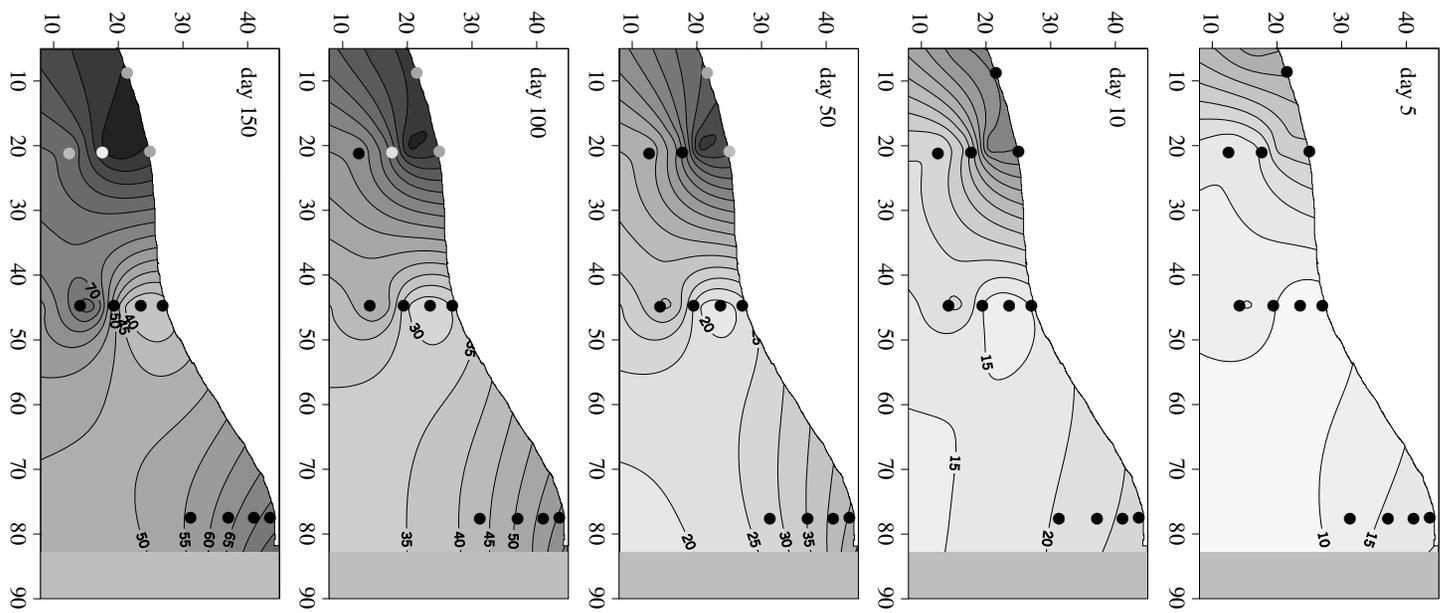


Fig. 5. Profiles of the slope of Hel Small Beach showing the zones sampled, the exposure of litterbags in the sand, and the estimated pattern of seagrass disintegration (Surfer Mapping System) on five sampling days in spring/summer. Detailed descriptions are as in Fig. 3

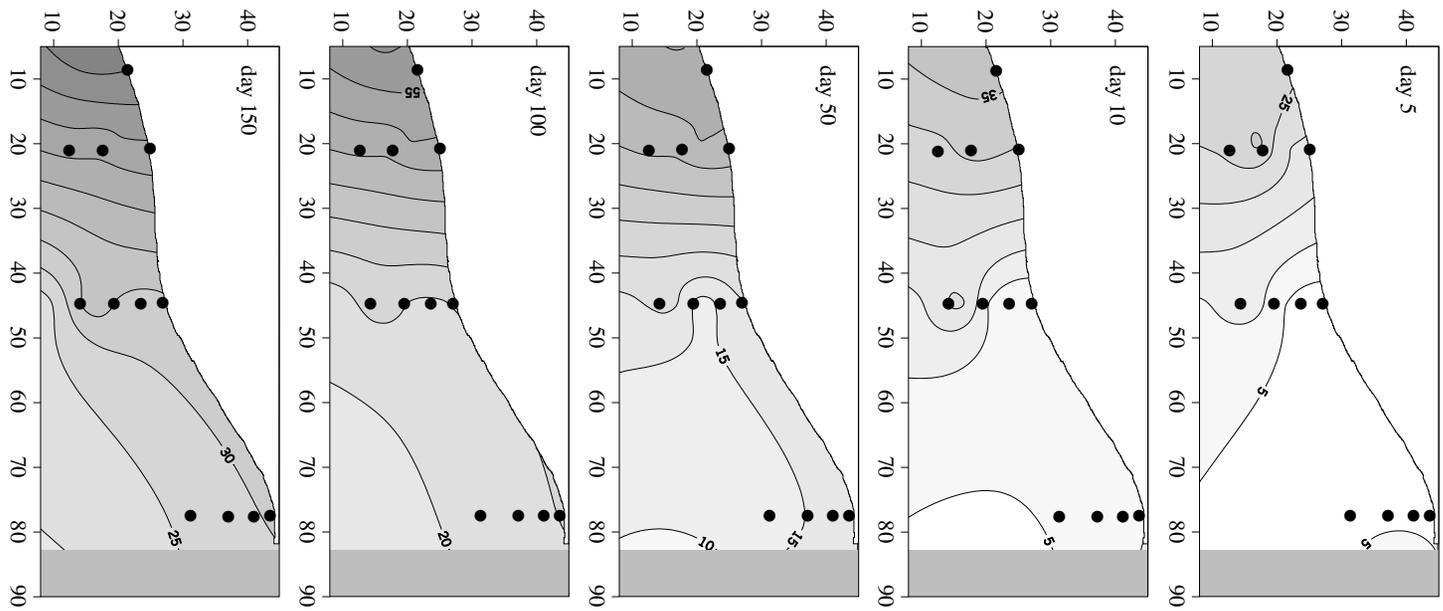


Fig. 6. Profiles of the slope of Hel Small Beach showing the zones sampled, the exposure of litterbags in the sand, and the estimated pattern of seagrass disintegration (Surfer Mapping System) on five sampling days in autumn/winter. Detailed descriptions are as in Fig. 3

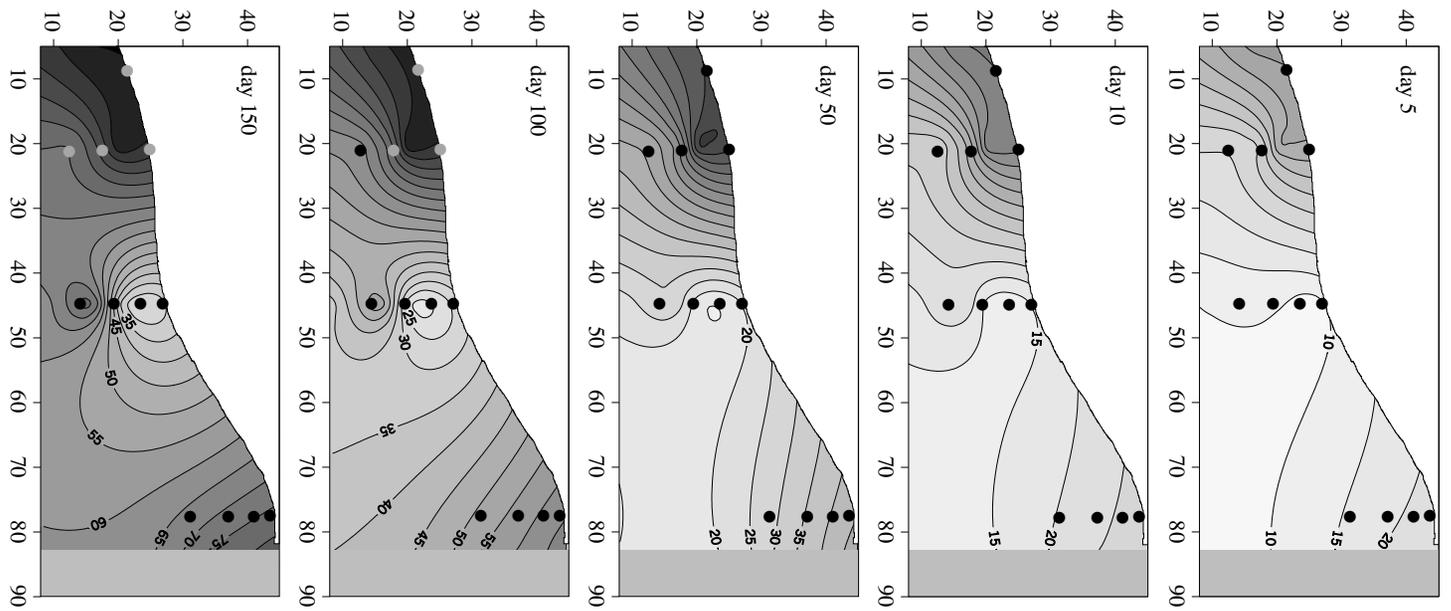


Fig. 7. Profiles of the slope of Sopot Beach showing the zones sampled, the exposure of litterbags in the sand, and the estimated pattern of seagrass disintegration (Surfer Mapping System) on five sampling days in spring/summer. Detailed descriptions are as in Fig. 3

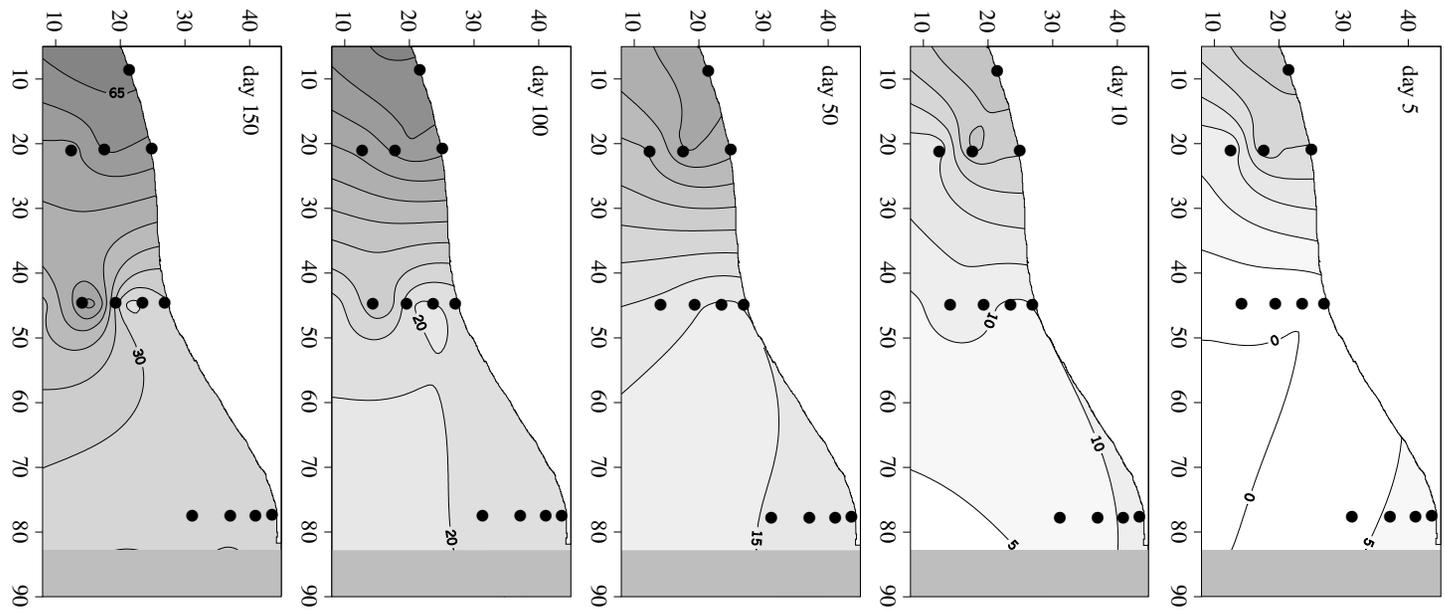


Fig. 8. Profiles of the slope of Sopot Beach showing the zones sampled, the exposure of litterbags in the sand, and the estimated pattern of seagrass disintegration (Surface Mapping System) on five sampling days in autumn/winter. Detailed descriptions are as in Fig. 3

Table 3. Average decay coefficients (k) of seagrass loss in the litterbags collected on Hel Great Beach. Data are for two seasons on five sampling days at different strata and depths

strata	depths [cm]	days	k [% day ⁻¹]	
			spring/summer season	fall/winter season
1	0	5	20.56	9.95
		10	12.74	5.14
		50	3.34	1.44
		100	2.60	0.99
		150	1.90	0.83
2	0	5	12.89	6.90
		10	9.47	4.60
		50	6.71	1.34
		100	9.21	0.79
		150	6.14	0.61
	20	5	6.57	9.50
		10	5.47	4.86
		50	2.41	1.38
		100	1.27	0.86
		150	2.65	0.66
50	5	5.29	4.94	
	10	3.57	3.65	
	50	1.39	1.27	
	100	1.00	0.86	
	150	0.85	0.46	
3	0	5	4.50	0.38
		10	2.36	1.15
		50	0.38	0.38
		100	0.25	0.23
		150	0.23	0.19
	5	5	4.01	0.34
		10	0.52	1.04
		50	0.26	0.30
		100	0.23	0.22
		150	0.25	0.21
	20	5	3.85	0.69
		10	3.75	0.82
		50	1.56	0.23
		100	1.29	0.23
		150	1.11	0.14
	50	5	2.66	0.50
		10	1.65	0.92
		50	0.66	0.22
		100	0.68	0.15
		150	0.88	0.09
4	0	5	5.70	1.07
		10	3.17	1.08
		50	1.75	0.26
		100	2.22	0.31
		150	2.17	0.23
	5	5	4.75	1.42
		10	2.38	1.03
		50	0.91	0.34
		100	0.78	0.23
		150	1.48	0.22
	20	5	6.35	1.64
		10	3.18	0.82
		50	0.75	0.46
		100	1.28	0.35
		150	0.67	0.29
	50	5	3.28	0.37
		10	1.64	0.35
		50	0.45	0.23
		100	0.71	0.18
		150	0.49	0.16

Table 4. Average decay coefficients (k) of seagrass loss in the litterbags collected on Hel Small Beach. Data are for two seasons on five sampling days at different strata and depths

strata	depths [cm]	days	k [% day ⁻¹]	
			spring/summer season	fall/winter season
1	0	5	14.85	6.73
		10	10.29	4.88
		50	2.71	1.40
		100	1.79	0.94
		150	1.73	0.80
2	0	5	7.95	4.75
		10	11.46	3.88
		50	5.20	1.21
		100	3.47	0.69
		150	6.14	0.52
	20	5	4.75	7.77
		10	5.16	4.04
		50	2.06	1.06
		100	1.48	0.62
		150	2.39	0.48
50	5	3.52	6.06	
	10	2.99	3.41	
	50	1.30	1.09	
	100	0.99	0.64	
	150	0.98	0.50	
3	0	5	1.07	0.41
		10	1.34	0.53
		50	0.41	0.41
		100	0.31	0.28
		150	0.28	0.27
	5	5	1.72	1.07
		10	1.14	0.85
		50	0.39	0.26
		100	0.31	0.28
		150	0.32	0.27
	20	5	3.42	2.75
		10	3.08	2.46
		50	1.08	0.49
		100	0.71	0.33
		150	1.05	0.32
	50	5	2.29	1.92
		10	2.03	1.30
		50	0.70	0.40
		100	0.51	0.24
		150	0.58	0.16
4	0	5	4.93	0.98
		10	3.36	1.29
		50	1.95	0.30
		100	1.59	0.28
		150	1.49	0.23
	5	5	4.59	1.27
		10	3.08	0.75
		50	0.77	0.26
		100	0.66	0.25
		150	0.97	0.20
	20	5	4.42	1.27
		10	2.99	0.85
		50	1.01	0.48
		100	0.70	0.36
		150	0.62	0.26
	50	5	1.50	0.50
		10	2.01	0.22
		50	0.49	0.17
		100	0.48	0.20
		150	0.46	0.16

Table 5. Average decay coefficients (k) of seagrass loss in the litterbags collected on Sopot Beach. Data are for two seasons on five sampling days at different strata and depths

strata	depths [cm]	days	k [% day ⁻¹]	
			spring/summer season	fall/winter season
1	0	5	16.55	8.03
		10	11.80	4.95
		50	3.30	1.44
		100	2.84	1.08
		150	4.21	0.80
2	0	5	14.11	5.97
		10	11.99	3.83
		50	5.09	1.39
		100	7.13	0.92
		150	6.14	0.63
	20	5	7.53	7.75
		10	6.66	4.97
		50	2.12	1.47
		100	1.57	0.85
		150	1.49	0.65
50	5	6.06	2.59	
	10	3.95	2.03	
	50	1.47	1.05	
	100	1.02	0.74	
	150	0.93	0.52	
3	0	5	1.48	0.02
		10	1.30	0.96
		50	0.35	0.30
		100	0.23	0.22
		150	0.19	0.22
	5	5	2.13	0.20
		10	1.19	1.07
		50	0.32	0.32
		100	0.19	0.21
		150	0.23	0.17
	20	5	2.60	0.42
		10	2.99	1.60
		50	0.72	0.40
		100	0.80	0.43
		150	1.02	0.58
50	5	2.12	0.17	
	10	1.88	0.89	
	50	0.49	0.45	
	100	0.39	0.25	
	150	0.63	0.32	
4	0	5	5.80	1.70
		10	3.60	1.19
		50	1.60	0.34
		100	1.56	0.28
		150	1.70	0.21
	5	5	4.51	1.51
		10	2.51	1.07
		50	0.93	0.39
		100	0.83	0.24
		150	1.02	0.23
	20	5	6.04	1.65
		10	3.73	0.86
		50	1.03	0.61
		100	1.17	0.37
		150	1.55	0.30
50	5	2.60	0.44	
	10	1.76	0.42	
	50	0.47	0.24	
	100	0.72	0.20	
	150	0.72	0.17	

interactions for dry weight loss were also significant. Therefore, the matter loss at each stratum with respect to days was seasonally dependent. The effect of depth \times season was only marginally significant. Other ANOVA proportions were not statistically significant. During 150 days in spring/summer, the material inside the litterbags lost between 30–100% of its initial dry weight at the Hel Great Beach (Table 3), 34–100% at the Hel Small Beach (Table 4), and 25–100% at the Sopot Beach (Table 5). The respective losses in the autumn/winter season were smaller: 12–71% (Table 3), 21–70% (Table 4) and 22–70% (Table 5).

Towards Day 150, there was a noticeable increase in the variability of material recovered from the litterbags. At this time the *Zostera* blades showed a tendency to laminate and, therefore, loss of fine particulate material was likely to be more variable than on earlier sampling dates. However, arcsine transformation of the data did not fail to remove significant error variance heterogeneity (Cochran's and Bartlett's statistics in Table 2), where treatment variances were deemed homogenous. Therefore this tendency of *Zostera* blades to laminate may not increase the probability of Type I error (Underwood 1981, Zar 1999), in contrast to the findings of Inglis (1989), where the lamination of *Macrocystis* blades caused such significant error variance heterogeneity. Therefore, it did not influence the conclusions of the present analysis.

The mean distribution of seagrass degradation on Hel Great Beach in the two seasons is shown in the Surfer diagrams presented in Figs. 3 and 4. Further Figs. 5 and 6 show the spatio-temporal distribution of the seagrass breakdown at Hel Small Beach from two seasons. The corresponding results for Sopot Beach are shown in Figs. 7 and 8. The breakdown pattern tended to focus on specific areas along the beach-dune slopes, and displayed different dynamics, with two distinct zones of strong degradation during spring and summer (the low beach with waterline and strandline, and the dune), but only one such zone during autumn and winter (the low beach).

4. Discussion

On a beach a complex interrelationship exists between a large number of physical, chemical, geological and biological factors, none of which can be controlled, and all of which vary. Differences between the decay of the same litter under identical climatic conditions, but at different sites, are normally minor. A common characteristic of all sandy beaches is high turbulence (Riedl 1971, Riedl & McMahan 1974, McLachlan 1979). Saturation and aeration play a major role within the sandy sediment on the beach (Eagle 1983, Brown & McLachlan 1990). The level of oxygen controls the redox equilibria maintained by some other elements, including nitrogen, sulphur,

iron and manganese and therefore influences the cycles of these elements. Thus, the discussion of oxygen is closely linked to that of the redox potential Eh. Fenchel & Riedl (1970) and McLachlan (1978) have shown the importance of Eh in sandy beaches. As a measure of the interstitial climate, Eh measurements were found to be more sensitive than oxygen availability, but this could have been due to the measurement methodology applied. The redox potential discontinuity (RPD) has been shown to be an area where significant changes in the oxygen cycle occur (McLachlan 1978). This is the layer where oxidising processes become displaced by reducing processes. It was also found to be the region of the highest organic matter concentration. Oxygen availability is relatively high in the surface layers of most beaches, but drops within the deeper layers (Eagle 1983). The breakdown of organics is thus greater on the surface than beneath the soil (Hackney 1987). A characteristic of some sandy beaches is the dark grey or black layer in the region of stagnation and oxygen deficiency, and results from the formation of iron and other sulphides under reducing conditions. Its depth beneath the surface is related to the penetration of oxygenated water into the interstitial spaces of the porous system (Massel 2001), and ranges from several metres in coarse sand and shell detritus subject to heavy surf, to a few millimetres in more protected areas of fine sand (Riedl & McMahan 1974, Dye 1981).

Another factor contributing to the oxygen levels in interstitial water is the filtration distance, i.e. the distance that this water travels within the interstices (Riedl 1971, McLachlan 1982). Large volumes of seawater are filtered by intertidal sand in that unsaturated sand is swash-flushed. The wave-driven water flow through the sand body is able to transport oxygen, and thus helps to maintain biological activity in the porous media (Massel 2001). Finer sands have greater surface areas for microbial colonisation and are also more efficient detritus traps. This, together with lower permeability, leads to greater oxygen uptake and mineralisation than in coarser sands. This is also a common and well-known phenomenon in freshwater systems (Eagle 1983).

Another common property is the high biological activity in the sediment surface layers. The depth of this highly active layer varies from 1 or 2 cm to more than 50 cm (McLachlan 1982). The main factors affecting this layer are the degree of oxygenation, sediment particle size and water flow-through rate (McLachlan 1979), desiccation (Dye 1980), and organic content (Koop et al. 1982). The oxygen level in beaches is also dependent on position on the beach. Day (1980) worked out oxygen budgets for two beaches with different exposures. In a more exposed beach, interstitial systems were found to account for 43% and macrofauna 57% of the oxygen consumed. In a more

sheltered beach, macrofauna used up only 3% of the oxygen budget, the rest being accounted for by interstitial organisms. Furthermore, Urban-Malinga & Opaliński (1999) noted that oxygen consumption decreased gradually from the saturated sand under the water in the surf zone to the backshore and seemed to be a function of distance from the waterline. Urban-Malinga & Opaliński (2001) also reported that oxygen consumption depended on the temperature and water content in the sand. They found a significant linear correlation between the oxygen consumption rates and water temperature ($r = 0.63$, $P < 0.05$), and the organic matter content in the sand ($r = -0.5$, $P < 0.05$).

In accordance with the above general scheme, three breakdown zones were distinguished in each of the beaches on the basis of mean experimental data:

- (1) a lower zone (Strata 1 and 2), which suffered the highest seagrass loss in both the warm and cold seasons,
- (2) a middle zone (Stratum 3), characterised by the lowest values of degradation,
- (3) an upper zone (Stratum 4), where the highest values occurred only in the warm season.

Short-term studies, both in the laboratory and on the beach itself, have led to suggestions that the faunal succession is not directly related to the degradation of the eelgrass tissue, which proceeded linearly throughout the study period (Koop & Lucas 1983, Inglis 1989, Jędrzejczak 2002a). However, the long-term study of the whole beach-dune slope suggests that exclusion of the fauna appeared to have had a greater effect on the rate of carrion breakdown (Jędrzejczak 1999). Interpretation of this phenomenon is difficult because not all the required data from Polish shores are available.

Thus, Wachendorf et al. (1997) and Jędrzejczak (1999) attributed the decay differences between sites to differences in the moisture regime. These authors claimed that leaching and microbiological activities exert separate influences on decay, the latter value being estimated from measurements of microbial biomass. The mass loss in the wet low-beach was due predominantly to the beach fauna, followed by loss from leaching. However, the breakdown in the dry high-beach resulted mainly from microbial respiration. Additionally, the findings of Jędrzejczak (1999, 2002a) seem to confirm that abiotic leaching and microbial decay play a more significant part in the breakdown of stranded seaweed than do the meio- and macrofauna community in the overall degradation process, although the significance of the meiofauna rises as the exposure time elapses. However, the latter can be linked with the fact that the meiofaunal forms tend to colonise old wrack (Jędrzejczak 2002b).

Seasonal variations in the zonation patterns have also been documented in this study. The observed seasonal variability could be related to seasonal variations in water and air temperatures, which in these beaches reach c. 12°C. Lower temperatures during autumn and winter would be the reason for the seasonal decrease in the degradation rate towards its lower decay level. The seasonal variability in the zonation pattern of seagrass disintegration has been also attributed to other causes, such as aggregated responses of sandy beach fauna or variations in other key physical variables such as sediment water content, sandy beach erosion and accretion (Brazeiro & Defeo 1996, Defeo et al. 1997).

5. Conclusions

This paper shows that there are differences in beach wrack degradation in the various beach zones, and that these are mainly due to diverse water regimes. However, the appearance of stranded *Z. marina* on the backshore and dune is less probable than on the low beach, where it is a natural phenomenon. Only during storms can material be carried up to the storm driftline at the foot of the dune. Hence, on the basis of these results, both hypotheses have turned out to be wrong. The degradation rates in the sandy beach studies are affected by physical parameters. The samples taken in different seasons indicate that degradation rates are also affected by time. Moreover, it is clear that individual parameters cannot be regarded as major controlling factors in a complex ecosystem. The type of material, temperature, microbial decay, leaching and decomposer activity, in that order, significantly alter the rate of weight loss. This may, however, be more intimately linked to successional changes in the chemistry and/or microflora of the beach wrack than to its physical breakdown. The differences in the processing of organics may be explained by variations in the moisture regime and nutrient status, and not by variations in the decay processes themselves. Therefore, two decay centres ('hot spots') can be marked out in the beach-dune system – the low beach together with the strandline, and the dune. The 'hot spot' in the supralittoral zone is active all year long; however, rapid degradation in the dune 'hot spot' occurs only during the warm season.

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