Microphytobenthic primary production along a non-tidal sandy beach gradient: an annual study from the Baltic Sea

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Abstract

The microphytobenthic primary production and chlorophyll *a* content were studied over the annual cycle (May 1998 – May 1999) on a non-tidal Baltic sandy beach at three stations along the beach gradient: littoral, waterline and splash zone. The chlorophyll *a* concentrations varied between 0.88 and 12.18 μg cm^{-3}. Net and gross primary production rates respectively lay within the ranges 0.1–31.4 mgC m^{-2} h^{-1} and 0.2–41.8 mgC m^{-2} h^{-1}. The highest values of both Chl *a* content and primary production were noted at the littoral station, the lowest ones at the waterline. The mean annual P/B ratio was highest at the waterline. The differences in Chl *a* content between stations were statistically significant and may be related to water dynamics, resuspension and water content. Production rates were highly variable on monthly time scales, and the highest results at all the study locations were noted in July. The gross photosynthetic rates were significantly correlated with water temperature.

The complete text of the paper is available at http://www.iopan.gda.pl/oceanologia/

1. Introduction

The part played by the microphytobenthos as a primary carbon source and an important component in the cycling of carbon and nutrients in coastal areas has generated very considerable interest in recent decades. Heip et al. (1995), MacIntyre et al. (1996) and Middelburg et al. (2000) have indicated a central role for the microphytobenthos in moderating carbon flow in coastal sediments. The majority of studies on microphytobenthos composition, distribution and functioning have concentrated on intertidal ecosystems (Cadée & Hegeman 1974, 1977, Barranguet et al. 1997, 1998, Conde et al. 1999, Middelburg et al. 2000, de Brouwer & Stal 2001, Montani et al. 2003).

The Baltic is a semi-enclosed, non-tidal sea. The available data on benthic primary productivity from the Baltic coast are limited to shallow waters (Wasmund 1989, Yap 1991, Meyercordt & Meyer-Reil 1999, Vilbaste et al. 2000, Köster & Meyer-Reil 2001), whereas there is a lack of information from sandy beaches – the dominant biotope on the southern Baltic coast.

A strong functional diversity on the beach slope (from the littoral towards the dune) has been demonstrated by Urban-Malinga & Opaliński (2001, 2002) and Jędrzejczak (1999, 2002), the differences in sediment metabolism and organic matter degradation rates between various points along the beach gradient being mostly attributed to the changing physical environment on the beach. In the present study we aimed to assess the rates of microphytobenthic production within the sandy beach and to evaluate the seasonal pattern of this process, our objective being to describe the variability of primary production along the beach gradient.

2. Materials and methods

Study site and sampling stations

The study was carried out on the non-tidal sandy beach at Sopot on the Gulf of Gdańsk – one of the open bays of the southern Baltic (Fig. 1). The 10-year mean annual photosynthetic active radiation (PAR) reaching the water surface in the Gulf of Gdańsk is 143 W m^{-2}, with a maximum of 193 W m^{-2} in early summer and a minimum of 4 W m^{-2} in winter (Kaczmarek & Dera 1998). The average salinity in the open Gulf of Gdańsk is 7–7.5 PSU; in the coastal zone, by contrast, values below 7 PSU are common (Cyberska 1990).

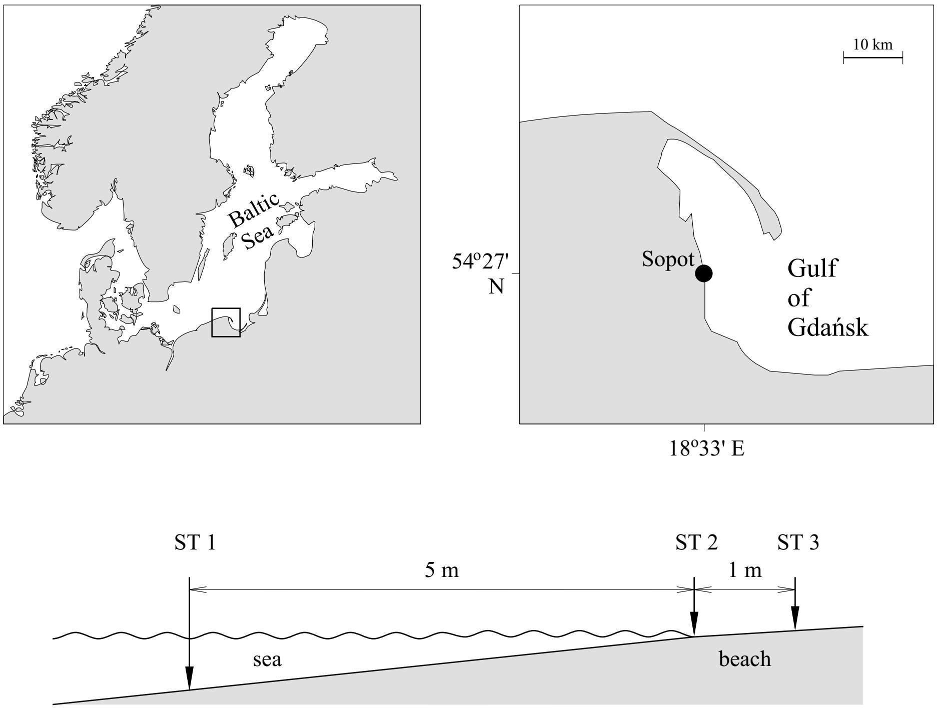

Fig. 1. Map of the study area; location of the stations on the beach profile

Table 1. Characteristics of the study sites – average water content and sediment parameters (sediment parameters given by Jankowska 2001 and Jędrzejczak 1999)

Sediment parameters	Station		
	1	2	3
average water content [%]	21.7	19.8	17.7
medium grain diameter	1.31	1.28	1.12
sorting index	1.04	1.08	0.98
kurtosis	4.54	17.8	3.54
skewness	–0.25	–3.41	–0.27
very fine sand [%]	3	1	1
fine sand [%]	30	23	60
medium sand [%]	35	55	60
coarse sand [%]	17	20	10
very coarse sand [%]	8	4	1

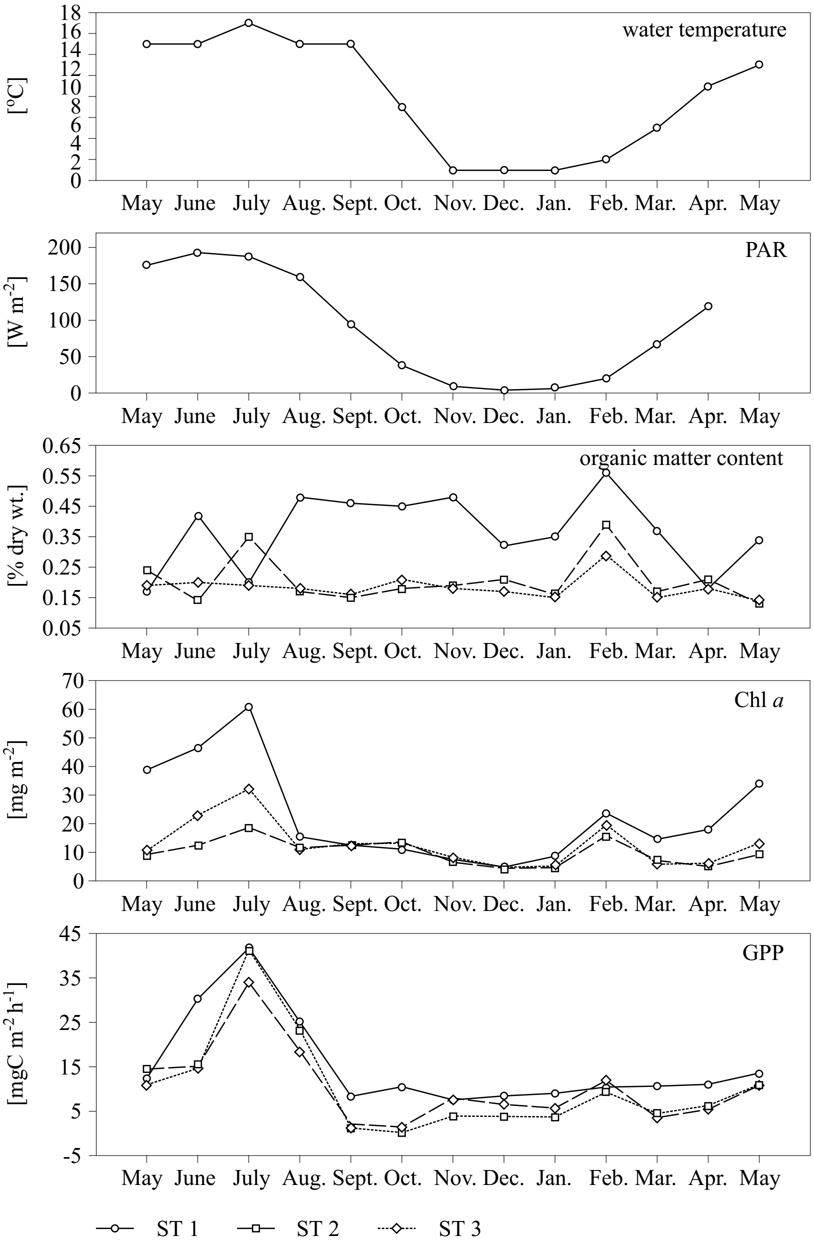

Fig. 2. Chlorophyll *a* content, gross primary production (GPP) and organic matter content in the sediment during the period of study. PAR values are given according to Kaczmarek & Dera (1998)

The beach investigated has a slope of 7 degrees and is 50 m wide. The sand consists mainly of fine and medium grains (Jędrzejczak 1999, Jankowska 2001). Both the sorting index and the percentage of fines increase towards the dunes (Table 1). During summer, the splash zone and waterline are loaded with massive deposits of decaying algae.

Sediment samples were collected from May 1998 until May 1999 at monthly intervals, at three stations along a transect: ST 1 – located under water at 0.5–1 m depth; ST 2 – at the waterline; ST 3 – in the splash zone (Fig. 2).

20 replicate sediment cores were taken at random at each study site with 2 cm diameter plastic tubes; however, only the top 0.5 cm of each core was retained. Replicates were pooled in order to obtain an averaged sample, as recommended by Kramer et al. (1994).

Parallel samples were taken in the same way for organic matter content analysis and pigment determination. The organic matter content was determined by loss of sediment weight on ignition.

Primary production measurements

Primary production measurements were carried out in the field by the oxygen method. A constant volume of sediment (10 cm^3) from each site was poured into 100 cm^3 Erlenmayer flasks, which were then filled with filtered sea water and tightly stoppered. Five replications of light and dark bottles (wrapped in aluminium foil) were placed in a special plexiglass (Perspex) stand. Bottles with sediment from ST 2 and ST 3 were incubated at waterline level under natural light and temperature conditions. Bottles with sediment from ST 1 were incubated on the sandy bottom at 0.5 m depth. Five control flasks with filtered sea water were incubated in order to assess the changes in oxygen concentration in the water itself during incubation. After 4 hours of incubation (always between 10:00 and 14:00 hrs) the oxygen content in the flasks was measured with an oxygen electrode.

The carbon production rate was calculated using the photosynthetic quotient PQ of 1.25, i.e. 1 mg of oxygen produced is equivalent to 0.3 mg of organic carbon assimilated (Pamatmat 1968, Dale 1978, Wasmund 1986).

Chlorophyll concentration

10 cm^3 sediment samples for Chl *a* estimation were frozen immediately after sampling, later to be extracted with 90% acetone and analysed spectrophotometrically. The Chl *a* concentration in the sand was calculated using the modified formula of Lorenzen (1967):

$$\mathrm{Chl}\ a\,(\mathrm{mg\ m^{-3}}) = (\mathrm{A}_{665} - \mathrm{A}_{750})\,26.7 \times \mathrm{v/V\,L},$$

where
A – extinction,
v – volume of acetone extract [cm^3],
V – volume of sand [dm^3],
L – length of cuvette [cm].

The gross primary production was used to calculate the production to biomass ratio (P/B).

In order to measure the penetration of light through the sediment, a metal cylinder was placed over the Li–190SA Quantum Sensor. The cylinder was then filled with measured quantities of sediment so that the thickness of the sediment layer in the cylinder increased in 1.0 mm steps; the light penetration through each new sediment layer was then measured.

3. Results

During the period of study, air temperatures varied between –5°C (November) and +23°C (July) (Table 2), and water temperatures ranged from +3°C (November) to +17°C (July) (Fig. 2).

The penetration of light through the sediment column was very low: at a sediment depth of 4–5 mm only 0.17% of the incident light was recorded.

The highest Chl *a* concentrations (annual mean = 4.5 μg cm^{-3}) were noted in the littoral (max 12.18 μg cm^{-3} in July) and the lowest at the waterline (annual mean = 2.0 μg cm^{-3}) (Table 2, Fig. 2). The differences in Chl *a* concentrations between stations were statistically significant (ANOVA: $F = 4.63$, $p = 0.016$).

The average annual net primary production was 7.0 mgC m^{-2} h^{-1}, with a minimum of 0.1 mgC m^{-2} h^{-1} recorded in the splash zone in October and a maximum of 31.4 mgC m^{-2} h^{-1} in July, also in the splash zone. The average annual gross primary production, with a minimum of 0.2 mgC m^{-2} h^{-1} noted in October in the splash zone and a maximum of 41.8 mgC m^{-2} h^{-1} in the littoral in July, was approximately 60% higher than the net production (Table 2). The gross photosynthetic rate in the sediments at stations ST 2 and ST 3 was significantly correlated ($p < 0.05$) with water temperature ($r = 0.68$ and $r = 0.72$ at ST 2 and ST 3 respectively). The highest results at all locations were recorded in July (Fig. 2). Variations in primary production over time in the littoral were less important in comparison with those in the splash zone (CV [%] of 74% vs 150% respectively).

P/B ranged between 0.02 (ST 3 in Oct.) and 2.12 mgC (mgChl *a*)$^{-1}$ h^{-1} (ST 3 in August). The highest yearly mean of 1.06 mgC (mgChl *a*)$^{-1}$ h^{-1} was recorded at the waterline (Table 2).

Table 2. Net and gross primary production, Chl *a* content and P/B ratio during the period of study. (ST – stations on the beach profile)

Month	Air temperature [°C]	ST	Net PP [mgC m^{-2} h^{-1}]	Gross PP [mgC m^{-2} h^{-1}]	Chl *a* [μg cm^{-3}]	P/B [mgC (mgChl *a*)$^{-1}$ h^{-1}]
M	16	1	6.3	12.5	7.77	0.32
		2	4.7	14.5	1.85	1.57
		3	2.4	11.0	2.12	1.04
J	15	1	12.0	30.3	9.30	0.65
		2	9.5	15.1	2.50	1.21
		3	8.8	14.7	4.60	0.64
J	23	1	26.1	41.8	12.18	0.69
		2	21.1	34.0	3.73	1.82
		3	31.4	41.3	6.43	1.29
A	17	1	*	*	3.08	*
		2	11.0	18.5	2.32	1.60
		3	18.9	23.3	2.20	2.12
S	17	1	4.8	8.4	2.50	0.67
		2	1.3	2.1	2.50	0.17
		3	0.8	1.2	2.60	0.09
O	10	1	5.9	10.5	2.22	0.95
		2	0.7	1.4	2.73	0.11
		3	0.1	0.2	2.63	0.02
N	–5	1	2.1	7.6	1.50	1.01
		2	4.1	8.0	1.30	1.23
		3	2.9	3.9	1.65	0.47

Table 2. (*continued*)

Month	Air temperature [°C]	ST	Net PP [mgC m^{-2} h^{-1}]	Gross PP [mgC m^{-2} h^{-1}]	Chl *a* [μg cm^{-3}]	P/B [mgC (mgChl *a*)$^{-1}$ h^{-1}]
D	6	1	4.2	8.5	0.97	1.74
		2	5.1	6.5	0.88	1.48
		3	3.5	3.8	0.95	0.80
J	4	1	5.6	9.0	1.73	1.04
		2	4.9	5.7	0.93	1.23
		3	3.7	3.7	1.04	0.72
F	4	1	8.9	10.4	4.73	0.44
		2	8.8	11.9	3.16	0.76
		3	7.2	9.3	3.92	0.47
M	8	1	8.4	10.7	2.91	0.73
		2	2.3	3.6	1.43	0.50
		3	1.9	4.5	1.17	0.77
A	12	1	7.5	11.1	3.60	0.61
		2	4.4	5.4	1.01	1.07
		3	2.6	6.3	1.24	1.01
M	16	1	7.4	13.6	6.80	0.40
		2	8.2	10.8	1.85	1.17
		3	2.4	11.0	2.65	0.83
yearly means		1	8.4 ± 6.2	14.6 ± 10.5	4.5 ± 3.6	0.80 ± 0.9
		2	6.5 ± 5.4	10.6 ± 8.8	2.0 ± 0.9	1.06 ± 0.6
		3	7.0 ± 8.2	10.3 ± 10.4	2.5 ± 1.6	0.79 ± 0.6

* no data

The differences in primary production between stations were statistically not significant, but they did vary significantly with water temperature (ANOVA: $F = 2.41$, $p = 0.044$).

Significant linear correlations were found between the Chl *a* concentration and the gross primary production ($r = 0.88$, $p < 0.001$ in the littoral; $r = 0.59$, $p = 0.033$ at the waterline and $r = 0.74$, $p = 0.003$ in the splash zone), and also between Chl *a* concentration and the net primary production ($r = 0.83$, $p = 0.001$ in the littoral; $r = 0.58$, $p = 0.039$ at the waterline and $r = 0.71$, $p = 0.006$ in the splash zone).

4. Discussion

The measured microphytobenthic photosynthetic rates and Chl *a* concentrations reported in the present study correspond to the results recorded in other coastal sediments of the Baltic Sea. They also lie within the ranges recorded in estuarine sediments well known for their high productivity (Table 3).

Chlorophyll *a* concentration

Expressed in terms of chlorophyll *a* content, the microphytobenthic biomass varied significantly along the beach gradient. The pattern of these changes is in agreement with studies reporting that the Chl *a* distribution is correlated with the abiotic environment and a combination of factors related to the degree of exposure and wave dynamics, such as grain size (Sundbäck 1984, Lucas & Holligan 1999). Already Steele & Baird (1968) found that vertical mixing and wave action are the major factors controlling diatom growth on an intertidal beach. Wave-generated turbulence and shear stress may cause resuspension of surface sediments and their associated microphytobenthos and, consequently, lower microalgae biomass (de Jonge & van Beusekom 1995). These factors can thus be taken to be the principal ones responsible for the lower Chl *a* concentrations at the air-exposed stations strongly affected by waves (waterline and splash zone) than in the littoral, where sediment mixing is less intensive. Furthermore, the littoral sediment can be effectively fuelled by phytoplankton blooms, which can also enhance the chlorophyll *a* concentration at this site and additionally stabilise the sediment.

On the other hand, it is noteworthy that chlorophyll concentrations were almost uniform on the beach slope during the cold period of the year, when winds and storms are more frequent. We suggest that the intensive water dynamics during these times of the year affect the sediment on the beach slope to the same degree, at least over the spatial range studied here, therefore rendering the microphytobenthic community more homogenous.

Table 3. Summary of primary productions and Chl *a* contents in different studies of coastal sediments (GPP/NPP – gross/net primary production)

Primary production	Chlorophyll *a*	Region	Author
0.77–1.78 mgC (mgChl a)$^{-1}$ h^{-1} (4.3–7.3 gC m^{-2} year^{-1})	0.5–2 μg g^{-1}	Sandy beach, Scotland	Steele & Baird (1968)
GPP 30 mgC m^{-2} h^{-1}		Highly eutrophic coastal lagoon, Kirr Bucht, Baltic	Meyercordt & Meyer-Reil (1999)
GPP 17.6 mgC m^{-2} h^{-1}		Moderately eutrophic coastal lagoon, Rassower Strom, Baltic	Meyercordt & Meyer-Reil (1999)
5–32 mgC m^{-2} h^{-1}		Tagus Estuary, Portugal	Brotas & Catarino (1995)
34.5 ($\pm$ 29.6) mgC m^{-2} h^{-1}	5.9–17.3 mg m^{-2}	Westerschelde Estuary	Barranquet et al. (1998)
21.45–30.0 mgC m^{-2} h^{-1}	6–9 μg cm^{-3}	Shallow coastal waters, southern Baltic	Wasmund (1989)
0.38–5.01 mgC m^{-2} h^{-1}	2.8–14.1 μg cm^{-3}	Estuarine littoral, southern Baltic	Yap (1991)
48–107 mgC m^{-2} h^{-1} 59–102 mgC m^{-2} h^{-1}	39.2 ($\pm$ 10.4) g m^{-2} 5.1 ($\pm$ 2.7) g m^{-2}	Silty site Sandy site Tidal flat, Scheldt Estuary	Middelburg et al. (2000)
	3.3–12.3 μg g^{-1}	Mudflat, Westerschelde Estuary	de Brouwer & Stal (2001)

Table 3. (*continued*)

Primary production	Chlorophyll *a*	Region	Author
	27–162 mg m^{-2} 0.7–9 mg m^{-2} (pelagial)	Laguna la Rocha, Uruguay	Conde et al. (1999)
	97.5 mg m^{-2}	Manukau Harbour, New Zealand	Cahoon & Safi (2002)
1.1–19 mgC m^{-2} h^{-1}	7–108 mg m^{-2} 0.6–6.3 mg m^{-3} (pelagial)	Wakaura estuary, Japan	Goto et al. (1998)
NPP 0.1–31.4 mgC m^{-2} h^{-1} GPP 0.2–41.8 mgC m^{-2} h^{-1}	0.88–12.18 μg cm^{-3} (4.4–60.92 mg m^{-2})	Sandy beach, Gulf of Gdańsk, Baltic	This study

The temporal evolution of Chl *a* concentrations may also be influenced by the sediment granulometry, which is subject to dynamic changes during the year (Barranguet et al. 1997).

The pattern of Chl *a* distribution on a beach slope can be also explained by the water content of the sediment. The relationship between the water content and Chl *a* concentration in sediments has been demonstrated in intertidal sediments by Riaux-Gobin & Bourgoin (2002, and the references therein). They showed that the upper intertidal zone is poorer in pigments than the lower part, which contains more water and associated microphytes. The pattern observed in the present study suggests that sediment water content could be an important factor influencing Chl *a* distribution along the beach gradient, especially in spring and summer (Fig. 2). However, the fact that water content measurements were performed only once during our study does not allow any general conclusions to be drawn in this respect.

Primary production

Light penetration measurements showed that the top 5 mm of sediment taken for measurements constitute the entire euphotic zone in the sediment studied, i.e. where photosynthesis is possible.

According to Barranguet et al. (1998) photosynthesis in microalgae appears to be regulated by very diverse environmental variables, like nutrient limitation, light, temperature, sediment grain size and stability. Seasonal changes in primary production in intertidal environments subject to large fluctuations of many different factors can mostly be explained by specific adaptations to light and temperature (Cadée & Hegeman 1974, Grant 1986, Blanchard et al. 1996, Barranguet et al. 1998). It seems that the same relations can be also attributed to a non-tidal beach: production and water temperature were correlated at all stations along the beach gradient. The relatively high P/B ratio at the waterline and in the splash zone, especially between April and August, can be attributed to the better light conditions at these stations than in the littoral. The increase in chlorophyll concentration towards the littoral station is probably balanced by the decrease in light that occurs especially at those times of the year when light penetration to the bottom may be severely restricted by phytoplankton blooms.

Changes in primary production rates from one season to the next can also be explained by changes in the density and composition of the microphytobenthic community. Different microphytobenthic groups may display a variety of photosynthetic features, which can lead to changes in primary production rates. The microphytobenthic community of the shallow littoral sediments of the Gulf of Gdańsk is dominated by epipsammic diatom species, but during late spring, summer and early autumn dinoflagellates, blue-green and green algae are present in the sediments in high densities (Pliński & Kwiatkowski 1996).

Furthermore, as has already been mentioned, resuspension reduces biomass, and hence the potential production of microphytobenthos. Waves are stronger and storms are more frequent in the autumn and winter, so that the role of physical advection in chlorophyll dynamics is most likely to be important during these seasons. In addition, low temperatures retard production.

In most cases, net primary production exceeds respiration in the top 0.5 cm of the sediment. However, the microphytobenthos is known to support heterotrophic processes in deeper sediments, and also in the water. Sediment mixing due to wave action may displace algae from the sediment surface to deeper layers (even by more than 10 cm) (Steele & Baird 1968, Cadée & Hegeman 1974), where they may be consumed by micro-, meio-, and macrofauna. On the other hand, resuspended microphytobenthos contributes significantly to the water column production (MacIntyre & Cullen 1995) and may be an important food source for suspension feeders (Herman et al. 1999).

It has been stressed by some authors that microphytobenthic production, which occurs in the top few millimetres of the sediment, can be as high per unit area as phytoplankton production in several metres of water (Charpy-Roubaud & Sournia 1990, and the references therein; Goto et al. 1998, Conde et al. 1999). Conde et al. (1999) found the Chl *a* concentration in the water to be approximately 18 times lower than in the sediment (0.7–9 vs 2.7–162 mg m^{-2}). Photosynthetic assimilation rates in the waters of the highly eutrophic southern Baltic and Gulf of Gdańsk vary from 1.59 to 6.81 $\text{mgC}\,(\text{mgChl}\,a)^{-1}\ \text{h}^{-1}$ with an average value of 3.31 $\text{mgC}\,(\text{mgChl}\,a)^{-1}\ \text{h}^{-1}$ (Renk & Ochocki 1998). In view of this fact, the production recorded in a sandy beach very exposed to environmental stress and often regarded as being completely barren seems significant. We therefore suggest that the part played by the microphytobenthos in the energy flow in a non-tidal sandy beach can be as important as in intertidal areas.

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