

**The impact of the
River Odra on
the phytoplankton
composition and biomass
in the Pomeranian Bay***

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Abstract

The article is based on the analysis of phytoplankton samples collected in the Pomeranian Bay during five cruises in the years 1993, 1996 and 1997.

In each season a number of phytoplankton assemblages were formed under the impact of the hydrological and hydrochemical conditions gradually changing along an axis from the outlets of the Szczecin Lagoon towards the open sea. The most distinct assemblages could be described as ‘river-mouth’, ‘open-Bay’ and ‘open-sea’ assemblages.

The highest phytoplankton biomass was noted near the mouth of the Świna Strait in the ‘river-mouth’ assemblages, where the concentration of chlorophyll *a* was 4 to 5 five times higher in comparison with the ‘open-sea’ values. The phytoplankton biomass in the ‘open-Bay’ assemblages was roughly twice as high as that in the ‘open-sea’ assemblages.

Because of the high N:P ratio in the Odra waters, phosphorus was very probably the factor limiting phytoplankton primary production in the Pomeranian Bay during periods of intensified inflow of riverine waters.

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The species dominating the phytoplankton of the Pomeranian Bay during the present study were found to be the same as those recorded in this region 40 years earlier.

1. Introduction

The ecosystem of the Pomeranian Bay is subject to the constant influence of agricultural and industrial waste transported from its inland drainage area by the River Odra (Oder) and of sewage produced in the ports and conurbations of Szczecin and Świnoujście. Unlike the Gulf of Gdańsk, where the Wisła flows directly into the sea, the estuary of the Odra forms a vast stretch of brackish water – the Szczecin Lagoon. The waters of the Lagoon flowing into the Bay via three straits – the Dziwna, Świna and Peene – are thus not typical river waters. Furthermore, direct contact with the waters of the Baltic Proper and the influence of the waters of the North Sea via the Danish Straits have an impact on the hydrological regime of the Bay.

The annual loads of total nitrogen discharged by the Odra into its estuary in 1996–1997 ranged from 75 to 84 kt and the annual loads of total phosphorus over the same time period varied from 6.3 to 7.1 kt (Niemirycz & Bogacka 1997, Niemirycz & Bierawska 1998).

Larger quantities of nutrients directly affect phytoplankton growth in the Pomeranian Bay, particularly at the mouth of the Świna (Nakonieczny *et al.* 1991, Renk *et al.* 1992, Ochocki *et al.* 1995a, Pollehne *et al.* 1995). Nitrogen compounds reach the Pomeranian Bay in excess in relation to phosphorus compounds, in which situation phosphorus becomes the factor limiting phytoplankton growth. In this respect the position is the reverse of that in the waters of the Baltic Proper, where the element limiting primary production is nitrogen (Trzosińska & Łysiak-Pastuszak 1996). This may in turn affect the phytoplankton composition in the Pomeranian Bay.

Most of the earlier observations of phytoplankton in the Pomeranian Bay, carried out before 1993, were rather scanty since they came from individual sampling sites visited only occasionally during cruises encompassing the whole of the southern Baltic Sea (Nakonieczny *et al.* 1991, Renk *et al.* 1992, Wiktor & Kruk-Dowgiałło 1992). Only Zembrzuska (1973), who described the phytoplankton composition in the Pomeranian Bay in the period 1956–1958, gathered a more comprehensive collection of material.

Interest in the Pomeranian Bay has grown in the nineties, since the commencement of interdisciplinary research in the region by teams of German and Polish specialists. The pilot studies were performed in autumn 1993. During this phase analyses of phytoplankton composition and measurements of primary production were carried out in the Świna

(Pollehne *et al.* 1995) and in the open waters of the Bay (Ochocki *et al.* 1995a). The Polish research project was expanded in 1996–1997 to include a number of research cruises undertaken in different seasons of the annual cycle. The phytoplankton composition and biomass in the southern part of the Pomeranian Bay were also investigated in summer 1997 as part of a short-term project, the principal aim of which was to assess the effects of the disastrous flood in the Odra basin (Brandt *et al.* 1998, Gromisz *et al.* 1998, Niemkiewicz 1998).

This present paper describes the results of Polish research on the phytoplankton of the Pomeranian Bay carried out in 1993–1997. The main aim was to assess the impact of Odra waters on the composition and biomass of the phytoplankton in different seasons and to compare the dominant phytoplankton species in the nineties with the results obtained 40 years earlier by Zembruska (1973).

2. Material and method

The samples used to assess the species composition and biomass of the phytoplankton were collected during five cruises on board r/v 'Baltica' in the Pomeranian Bay in 1993, 1996 and 1997. Samples were collected in September 1993 (9 sampling sites), in March (18 sampling sites) and July

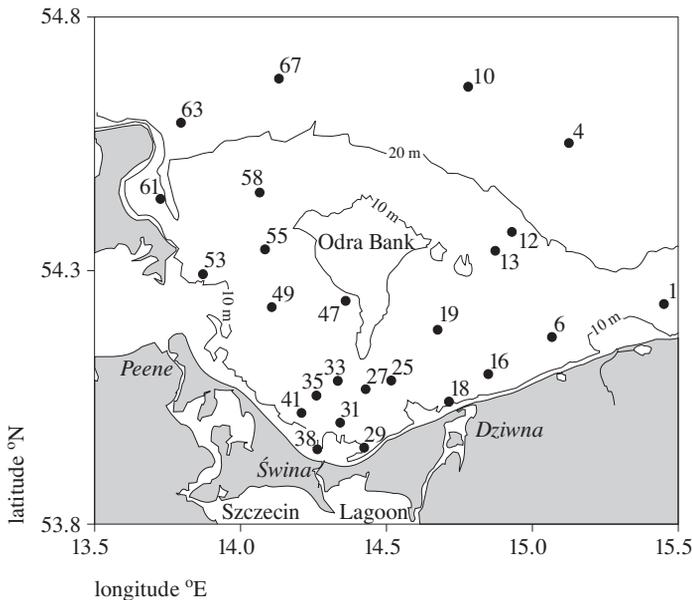


Fig. 1. Location of sampling sites in the Pomeranian Bay

1996 (24 sampling sites) and in May (24 sampling sites) and October 1997 (19 sampling sites). The location of all the sampling sites in the Bay is shown in Fig. 1, while the sites visited during subsequent cruises are listed in Table 1.

In 1993, samples were collected only in the surface layer of the water while in all the subsequent cruises they were collected both from the surface layer and from a depth of 10 m. All samples were preserved in Lugol solution (Edler 1979). In the laboratory the samples were integrated by mixing equal amounts of water from the two levels (with the exception of sampling stations 38 and 18, located near the strait mouths, where surface samples and those collected from 10 m depth were analysed separately and average results were subsequently calculated) and analysed with an Olympus inverted microscope (Utermöhl 1958). The abundance was estimated for each species or higher-order systematic unit (whenever species identification was impossible) and with the aid of the geometric method the average cell volume was also assessed. On the basis of these data it was possible to calculate the biovolume of each taxon at each sampling site.

Subsequently, hierarchical agglomerative clustering analysis utilising the Bray-Curtis similarity coefficient was carried out for each cruise with the aid of the PRIMER (Plymouth Routines in Multivariate Ecological Research) computer package. The results of the hierarchical clustering are presented in the form of dendrograms, with the x axis representing the full set of samples and the y axis defining the similarity level at which two samples or groups are considered to have fused (Clarke & Warwick 1994). The analysis was based on the percentage of each taxon in the total biovolume of the phytoplankton.

Furthermore, for each sampling site the value of the *PIE* (probability of interspecific encounters) diversity index was also calculated. This index specifies the probability that two randomly encountered individuals belong to different species. It was calculated by means of the following formula:

$$PIE = B/(B + 1)(1 - \sum pi^2),$$

where B is the total phytoplankton biovolume and pi is the percentage of species i in the total phytoplankton biovolume (Lampert & Sommer 1996).

Additionally, hydrochemical data collected during the cruises were used in the interpretation of the results (Pastuszak *et al.* in preparation), as were data on chlorophyll concentration (Ochocki *et al.* 1999, this volume).

Table 1. Dominant phytoplankton taxa in particular areas for each cruise. Numbers in brackets: (5 – 76–100%; 4 – 51–75%; 3 – 26–50%; 2 – 11–25%; 1 – 1–10%; 0 – <1% percentage in phytoplankton biovolume)

Groups	Stations	Description of area	Dominant species
September 1993			
1	27, 31, 38	river mouth (Świna)	<i>Prorocentrum minimum</i> (4–5), <i>Snowella</i> spp. (1), <i>Coscinodiscus granii</i> + <i>Actinocyclus octonarius</i> (1), cryptophytes (1), others (1), <i>Dinophysis acuminata</i> (0–1)
2	13, 18, 35, 55, 67	open Bay	<i>Prorocentrum minimum</i> (1–3), <i>Coscinodiscus granii</i> + <i>Actinocyclus octonarius</i> (2), cryptophytes (1–3), others (1–2), centrales (1), <i>Mesosodinium rubrum</i> (0–3), <i>Heterocapsa rotundata</i> (0–1) cryptophytes (3), <i>Heterocapsa rotundata</i> (2),
3	4	open sea	<i>Pyramimonas</i> spp. (2), <i>Eutreptiella gymmastica</i> (2), others (2), <i>Mesosodinium rubrum</i> (1), <i>Prorocentrum minimum</i> (1)

Table 1. (continued)

Groups	Stations	Description of area	Dominant species
March 1996			
1		Bay	
1.1	38	river mouth (Świna)	<i>Thalassiosira</i> spp. (3), cryptophytes (2), <i>Mesodinium rubrum</i> (2), flagellates+ <i>Dinobryon</i> sp. (2), <i>Peridiniella catenata</i> (1), others(1), <i>Melosira arctica</i> (1)
1.2	12	open Bay (E)	<i>Thalassiosira</i> spp. (4), <i>Mesodinium rubrum</i> (2), cryptophytes (1), <i>Peridiniella catenata</i> (1), flagellates+ <i>Dinobryon</i> sp. (1), <i>Melosira arctica</i> (1)
1.3	18, 19, 25, 27, 29, 31, 33, 41, 47, 49, 55, 58, 63, 67	open Bay (S,W)	<i>Thalassiosira</i> spp. (4-5), cryptophytes (1-2), <i>Skeletonema costatum</i> (0-2), <i>Melosira arctica</i> (1), <i>Mesodinium rubrum</i> (0-1), others (0-1), <i>Chaetoceros</i> spp. (0-1)
2	4, 10	open sea	<i>Mesodinium rubrum</i> (3), <i>Peridiniella catenata</i> (2-3), cryptophytes (2), <i>Thalassiosira</i> spp. (1-2), others (1), <i>Coscinodiscus</i> sp.+ <i>C. granii</i> (1)

Table 1. (continued)

Groups	Stations	Description of area	Dominant species
July 1996			
1		river mouth	
1.1	6, 18, 38, 41	Świna, Dziwna	cryptophytes (2-3), <i>Coscinodiscus</i> sp.+ <i>C. granii</i> (1-3), <i>Cylindrotheca closterium</i> (1-3), <i>Actinocyclus octonarius</i> +centrales (1-2), others (1) <i>Pyramimonas</i> spp. (1)
1.2	16		<i>Nodularia spumigena</i> (2), <i>Coscinodiscus</i> sp.+ <i>C. granii</i> (2), cryptophytes (2), <i>Aphanizomenon</i> sp. (2), others (1), <i>Actinocyclus octonarius</i> +centrales (1)
2		Bay	
2.1	25		cryptophytes (4), others (2), <i>Coscinodiscus</i> sp.+ <i>C. granii</i> (1), <i>Aphanizomenon</i> sp. (1), <i>Actinocyclus octonarius</i> +centrales (1), <i>Heterocapsa rotundata</i> (1), <i>Pyramimonas</i> spp. (1)
2.2	1, 13, 19, 29, 31, 35	transition area (S, E)	cryptophytes (2-3), others (2), <i>Pyramimonas</i> spp. (1-2), <i>Heterocapsa rotundata</i> (1), <i>Actinocyclus octonarius</i> +centrales (0-2), <i>Aphanizomenon</i> sp. (0-2)
2.3	4, 10, 27, 33, 47, 49, 53, 55, 58, 61, 63, 67	open Bay	others (2-4), cryptophytes (1-3), <i>Aphanizomenon</i> sp. (1-3), <i>Pyramimonas</i> spp. (1-2), <i>Nodularia spumigena</i> (0-2), <i>Heterocapsa rotundata</i> (0-2)

Table 1. (continued)

Groups	Stations	Description of area	Dominant species
May 1997			
1		transition area	
1.1	18	Dziwna	cryptophytes (3), others (2), <i>Pediastrum boryanum</i> (1), <i>Actinocyclus octonarius</i> +centrales (1), <i>Fragilaria crotonensis</i> + <i>F. pinnata</i> (1), <i>Skeletonema subsalsum</i> (1)
1.2	41, 47		cryptophytes (2-3), <i>Heterocapsa rotundata</i> (2), <i>Pyramimonas</i> spp. (1-2), others (1-2), <i>Skeletonema subsalsum</i> (1-2), <i>Eutreptiella gymnastica</i> (1)
2		Bay	
2.1	29, 31, 38	river mouth (Świna)	cryptophytes (2-4), others (1-3), <i>Heterocapsa rotundata</i> (1-2), <i>Mesodinium rubrum</i> (1-2), <i>Pyramimonas</i> spp. (1), <i>Monoraphidium contortum</i> (1)
2.2	13	open Bay (NE)	cryptophytes (3), others (2), <i>Pyramimonas</i> spp. (2), <i>Mesodinium rubrum</i> (1), <i>Actinocyclus octonarius</i> +centrales (1), <i>Heterocapsa rotundata</i> (1)
2.3	1, 6	open Bay (E)	cryptophytes (3-4), <i>Actinocyclus octonarius</i> +centrales (1-2), <i>Pyramimonas</i> spp. (1), others (1), <i>Mesodinium rubrum</i> (1), <i>Heterocapsa rotundata</i> (1)
2.4	16, 19, 25, 27, 33, 35, 49, 53, 55, 58, 61, 63	open Bay (S, W)	cryptophytes (2-4), others (1-3), <i>Pyramimonas</i> spp. (1-3), <i>Heterocapsa rotundata</i> (1-2), <i>Mesodinium rubrum</i> (0-1), <i>Actinocyclus octonarius</i> +centrales (0-1)
3	4, 10, 67	open sea	others (2), <i>Heterocapsa rotundata</i> (2), <i>Pyramimonas</i> spp. (1-3), cryptophytes (1-2), <i>Aphanizomenon</i> sp. (1-2), <i>Mesodinium rubrum</i> (1-2), <i>Dimophysis norvegica</i> (1)

Table 1. (continued)

Groups	Stations	Description of area	Dominant species
October 1997			
1		river mouth	
1.1	38	Świna	<i>Actinocyclus octonarius</i> (5), <i>Coscinodiscus</i> sp.+ <i>C. granii</i> (1), cryptophytes (1), <i>Mesodinium rubrum</i> (1), others (1)
1.2	29, 41		<i>Actinocyclus octonarius</i> (2-4), <i>Coscinodiscus</i> sp.+ <i>C. granii</i> (2-3), cryptophytes (2), others (1), <i>Mesodinium rubrum</i> (1), <i>Prorocentrum minimum</i> (1) <i>Heterocapsa rotundata</i> (1)
2		Bay	
2.1	6, 18, 25, 27, 33	transition area	<i>Coscinodiscus</i> sp.+ <i>C. granii</i> (4-5), cryptophytes (2), others (1), <i>Actinocyclus octonarius</i> (0-1), <i>Heterocapsa rotundata</i> (0-1), <i>Eutreptiella gymnastica</i> (0-1)
		(Dziwna, S)	<i>Prorocentrum minimum</i> (0-1), <i>Pyrainimonas</i> spp. (0-1), <i>Dinophysis acuminata</i> (0-1)
2.2	31		<i>Coscinodiscus</i> sp.+ <i>C. granii</i> (4), <i>Actinocyclus octonarius</i> (2), cryptophytes (1), others (1)
2.3	1, 4, 13, 19, 49, 53, 58, 61, 63, 67	open Bay	<i>Coscinodiscus</i> sp.+ <i>C. granii</i> (4-5), cryptophytes (1-2), others (1), <i>Mesodinium rubrum</i> (0-1), <i>Pyrainimonas</i> spp. (0-1)

3. Results

Implementation of the clustering analysis method for each of the cruises yielded dendrograms grouping sampling sites according to the similarities in the composition and the percentage of individual species or higher-order phytoplankton systematic units in the biovolume (Fig. 2). The main groups were distinguished (*e.g.* 1, 2, 3) as well as subgroups, when greater diversification within the main groups necessitated subtler distinctions (*e.g.* 2.1, 2.2, 2.3, 2.4). The similarities between the main groups distinguished during all the cruises did not diverge substantially. The lowest values were noted in March (49%) and July 1996 (51%), the highest ones in September 1993 (63%), and in May (57%) and October 1997 (57%).

Table 1 lists the sampling sites belonging to the groups and subgroups distinguished by clustering analysis for each of the cruises. The table also gives the names of the dominant species or higher-order phytoplankton systematic units. The chief factor determining the association of sampling sites into groups and subgroups was their location in the waters investigated. Four regions were distinguished, which correlated closely with the usual groups of sites. The first region comprised the sampling sites located off the Świna mouth and was called the 'river-mouth' area, the second one was a 'transition' area, the third one comprised the 'open-Bay' waters (the 'open-Bay' area), and the fourth one was located on the outer margins of the Bay (the 'open-sea') area (Table 1). During each cruise the boundaries between these areas varied somewhat, some of them being distinguishable only during some of the cruises, but the general layout remained basically the same.

The 'river-mouth' area was discernible during all the cruises. In September 1993, July 1996 and October 1997 it made up the main group, during the other cruises a subgroup associated with the 'open-Bay' area. Here the salinity was usually lower, a fact directly indicative of the impact of river waters on the phytoplankton composition and biomass. September 1993 was an exceptional month in this respect, since the salinity remained high in the whole Bay, including the vicinity of the Świna mouth. The region of the Dziwna mouth (sampling site 18) was associated with the sites near the Świna mouth only in July. During the remaining cruises the phytoplankton composition was similar there to that of the 'open-Bay' area (September 1993, March 1996) or the 'transition' area (May 1997, October 1997).

In July 1996 and October 1997 the 'transition' area was distinguished as a subgroup of the same main group that comprised the 'open-Bay' area. In May 1997 three sampling sites included in the 'transition' area constituted the main group. They were, however, largely isolated from each other and

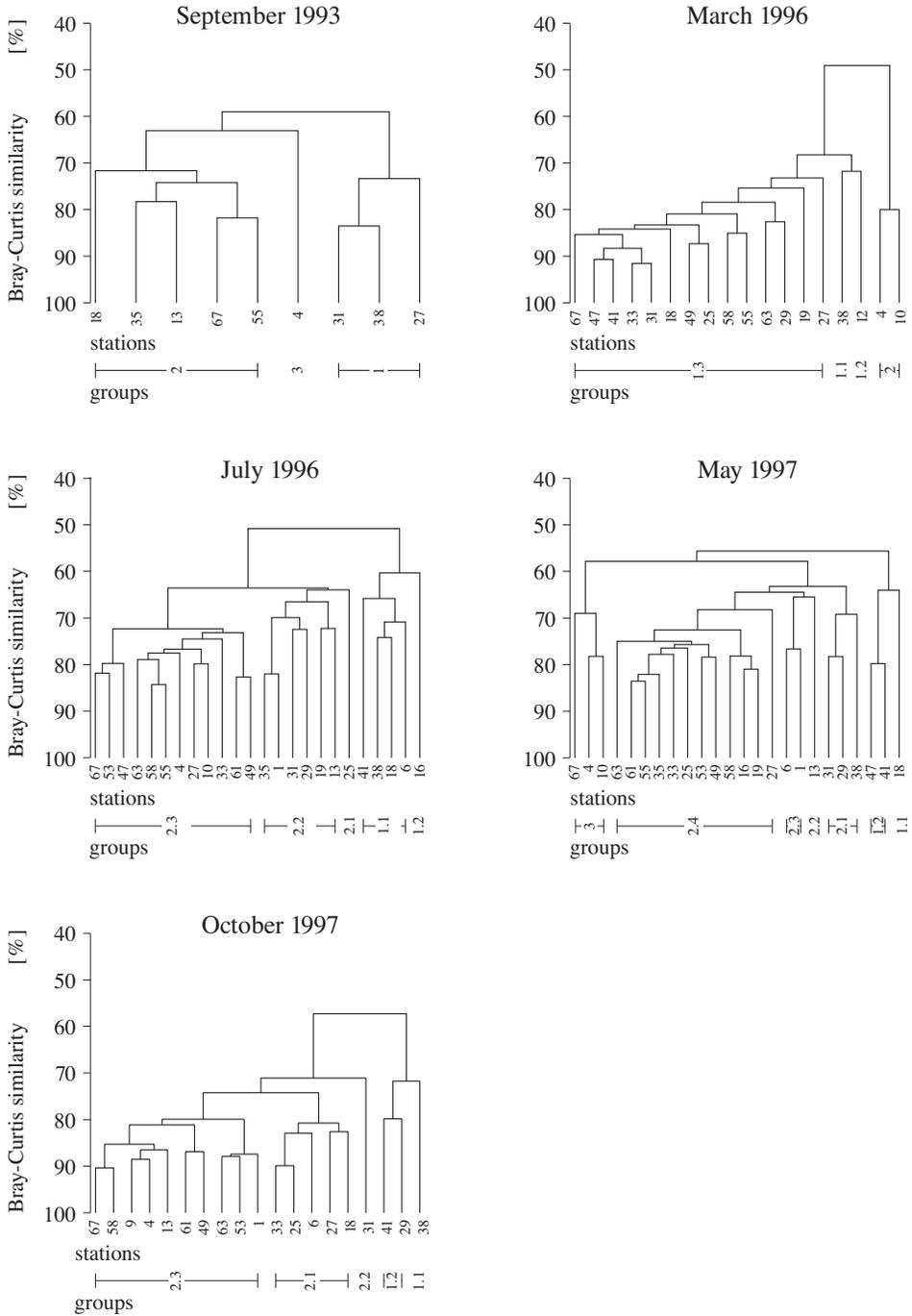


Fig. 2. Dendrograms of stations from five cruises in the Pomeranian Bay, derived from the hierarchical agglomerative clustering analysis utilising the Bray-Curtis similarity coefficient based on percentage of taxa in the biovolume

one of them (site 18 located near the mouth of the Dziwna) was classified as a separate subgroup.

The 'open-Bay' area was distinct during all the cruises, though as a main group only in September 1993. In 1996 and October 1997 this region formed a subgroup of the same main group that made up the 'transition' area. During the last two cruises different regions of the 'open-Bay' area were distinguishable as separate subgroups.

The 'open-sea' area was discernible during three cruises only (September 1993, March 1996, May 1997) though always as a main group.

Occasionally, individual sampling sites constituted separate subgroups that were difficult to classify. This applied to sites 16 and 25 in July 1996 and to site 31 in October 1997.

In expectation of a large vertical diversification of the phytoplankton composition in the vicinity of the Świna and Dziwna mouths (sampling sites 38 and 18), during three cruises (July 1996, May 1997, October 1997) surface samples and those collected at 10 m depth were analysed separately. A variant of clustering analysis was applied in the calculations, the aim being to treat the two layers as separate sampling sites. In 1996 and October 1997 there were no significant differences in the associations of the surface samples and the samples collected at 10 m depth. On the other hand, in May 1997, at sampling site 18 off the Dziwna mouth, normally (*i.e.* after sample integration) associated with the 'transition' area, the surface sample was identified as a separate main group (39% similarity), whereas the 10 m sample was included in the 'open-Bay'.

Figure 3 illustrates the salinity ranges, as well as the ranges of phosphate and nitrate concentrations, chlorophyll *a* concentrations and the species diversity index for the areas delineated during the cruises. The figure also shows the percentage changes in the biovolume of the dominant species or higher-order phytoplankton systematic units. Fig. 4 highlights the differences in the percentage of the main taxonomic groups in the biovolume of the phytoplankton in the areas established during each cruise.

In September 1993 the salinity of the entire Bay was stable and high (7.28–7.72 PSU); it was not lower even in the 'river-mouth' area, where the highest phosphate concentrations were noted. Nitrate concentrations were low everywhere in the Bay; indeed, nitrogen could well be the factor limiting phytoplankton growth in the 'open-sea' area. Phytoplankton biomasses were highest in the 'river-mouth' area ($4.4\text{--}13.8\text{ mg m}^{-3}$), gradually decreasing in the direction of the open sea ($1.3\text{--}3.2\text{ mg m}^{-3}$). In this cruise, dinoflagellates were the dominant phytoplankton group throughout the study area. Diatoms and cryptophytes were also among the dominant species in the 'open-Bay' area, as were cryptophytes in

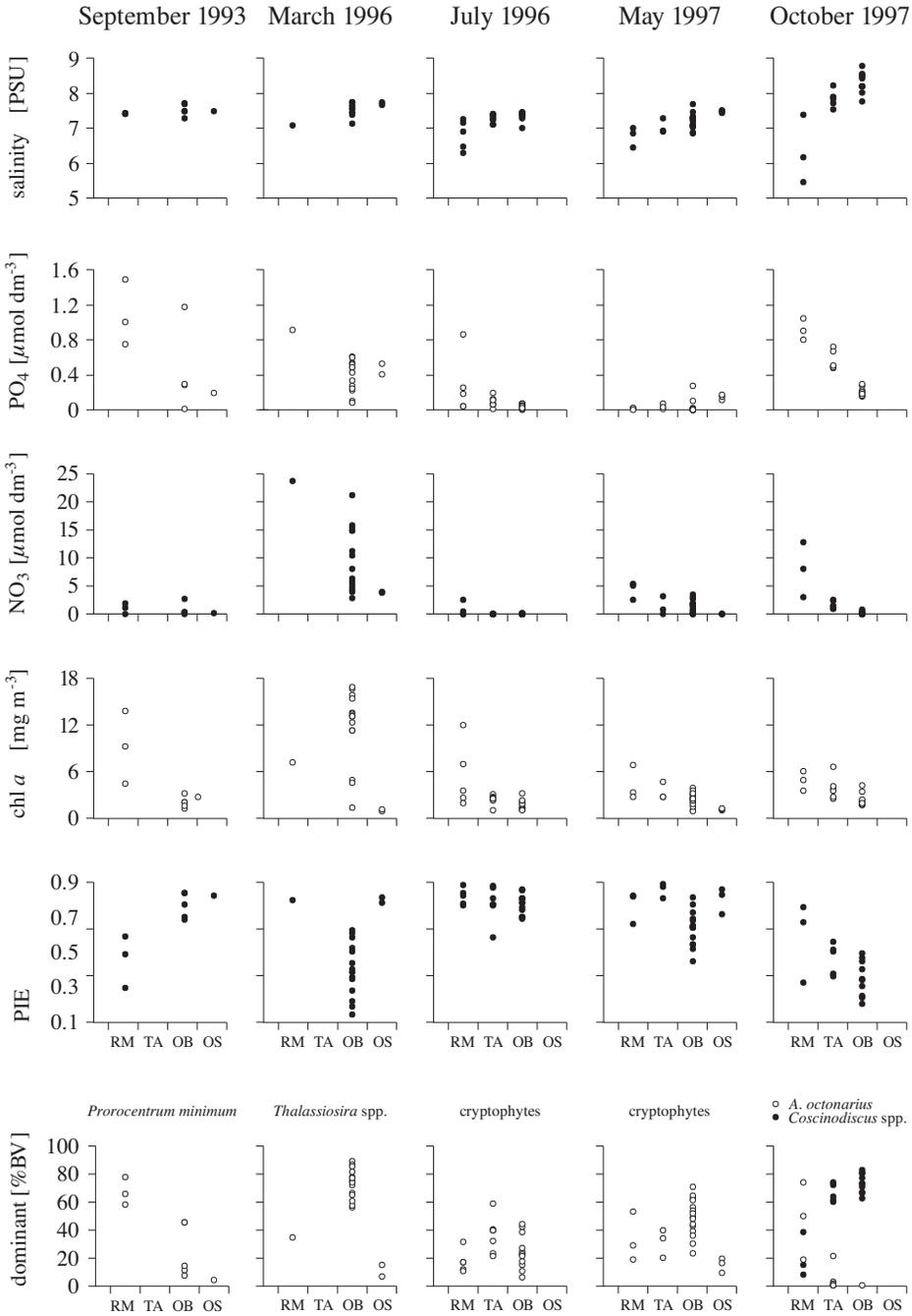


Fig. 3. Values of salinity, nutrients and chlorophyll *a* concentrations, *PIE* diversity index and percentage of dominant species in phytoplankton biovolume for each cruise; RM – ‘river-mouth’ area, TA – ‘transition’ area, OB – ‘open-Bay’ area, OS – ‘open-sea’ area

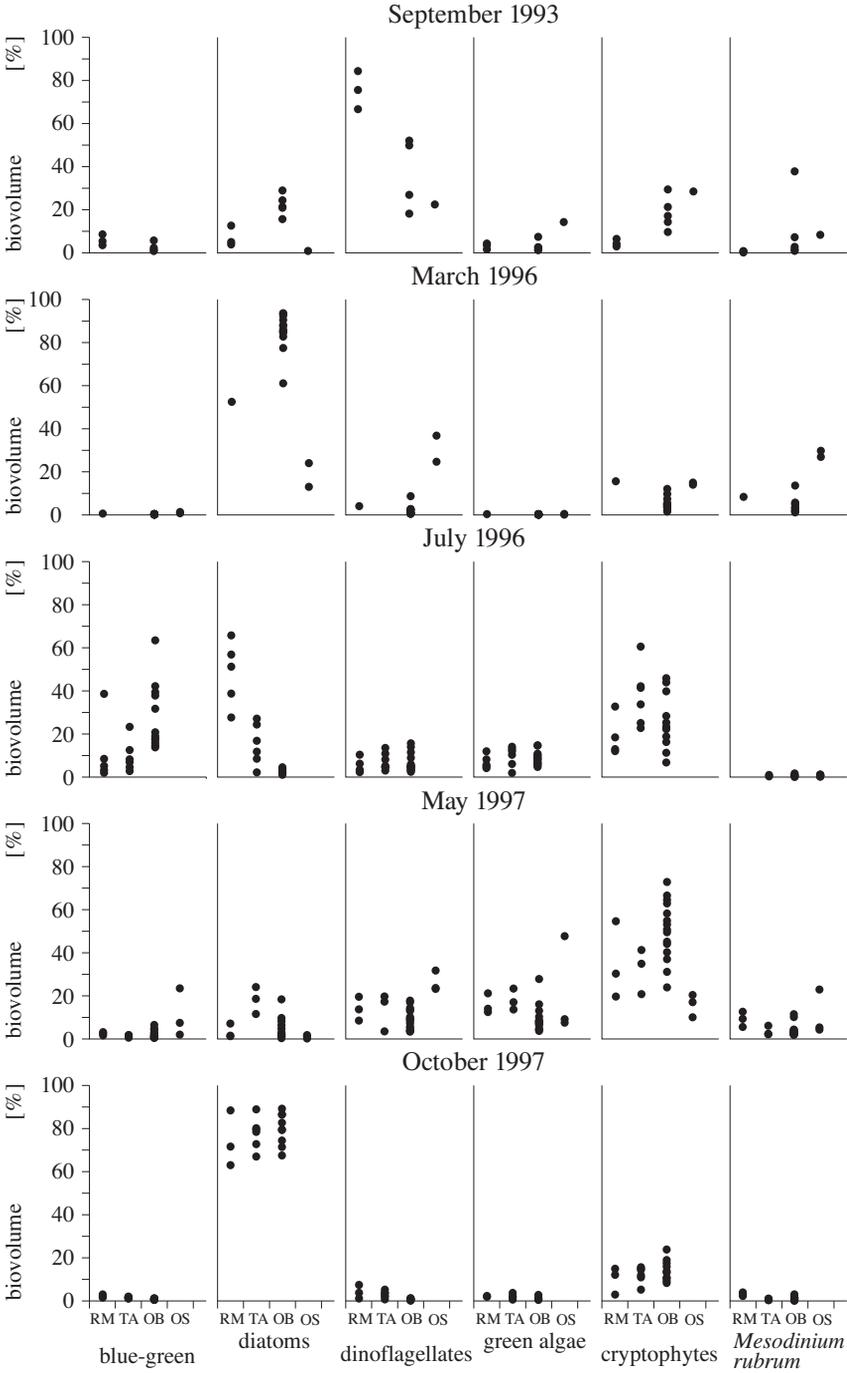


Fig. 4. Percentage biovolume composition of the main phytoplankton groups in the various areas in 1993–1997; RM – ‘river-mouth’ area, TA – ‘transition’ area, OB – ‘open-Bay’ area, OS – ‘open-sea’ area

the 'open-sea' area. In the 'open-Bay' and 'open-sea' areas the species diversity index was high (0.7–0.8). The drop in *PIE* in the 'river-mouth' area (0.3–0.6) was due to the mass occurrence of the dinoflagellate *Prorocentrum minimum* (62–83%). Another characteristic feature of the 'river-mouth' area was the presence of the blue-green algae (*Snowella* spp.) and *Dinophysis acuminata* (dinoflagellates). 'Open-sea' area sampling sites were dominated by *Pyramimonas* spp. (green algae) and *Eutreptiella gymnastica* (euglenophytes); moreover, the lowest percentage of diatoms and the dinoflagellate *P. minimum* in the phytoplankton biovolume were recorded there.

In March 1996 the salinity in the 'river-mouth' area was slightly reduced (7.08 PSU), but the concentration of nutrients was high. Elsewhere, the salinity remained at a relatively high level (7.13–7.74 PSU), while phosphate and nitrate concentrations clearly decreased in the offshore direction. Moreover, the reserves of phosphates in the 'open-Bay' area became depleted earlier than in the 'open-sea' area. Concentrations of chlorophyll were high mainly in the 'open-Bay' area and minimum phytoplankton biomasses (0.9–1.1 mg m⁻³) were characteristic of the 'open-sea' area. Off the mouth of the Świna and in the 'open-Bay' the percentage of diatoms in the phytoplankton biovolume was very high. They included *Thalassiosira* spp. in particular, which made up 60–92% of this biovolume in the 'open-Bay' area and consequently contributed to a significant reduction in the *PIE* species diversity index (0.15–0.6). In the 'river-mouth' and 'open-sea' areas *PIE* was high (approx. 0.8). This was mainly a consequence of the reduced percentage of diatoms in the biovolume and the simultaneously rising significance of dinoflagellates and cryptophytes. In March 1996 the phytoplankton species composition of the 'open-sea' area was significantly different in comparison to the other areas (Table 1). There, *Mesodinium rubrum* and the dinoflagellate *Peridiniella catenata* were the most abundant species. In the other two regions *Thalassiosira* spp. were dominant. The phytoplankton of the 'river-mouth' area, apart from *Thalassiosira* spp., was also composed of difficult-to-identify flagellates and *Dinobryon* spp., while in the 'open-Bay', diatoms such as *Skeletonema costatum* and *Chaetoceros* spp. accompanied the absolutely dominant *Thalassiosira* spp.

In July 1996 the lowest salinity was noted in the 'river-mouth' area (6.28 PSU). In the other areas, salinities were rather high (7.01–7.46 PSU). The concentration of nutrients (particularly nitrates) was very low throughout the study area, although slightly higher values were noted in the 'river-mouth' area in the immediate neighbourhood of the Świna mouth. It is also there that the highest phytoplankton biomass was noted (12 mg m⁻³), while in the remaining areas it was relatively low (1–3.2 mg m⁻³), owing

to a shortage of nitrogen and phosphorus. Cryptophytes, diatoms and blue-green algae were prevalent in the phytoplankton biovolume in that month, and the diversity index was quite high in the entire study area (0.7–0.9). Only at sampling site 25 did it fall to the minimum of 0.6. This was a consequence of the highest percentage of cryptophytes in the phytoplankton biovolume (61%) recorded during that cruise, which resulted in this site being set apart as a separate subgroup. Moreover, the percentage of diatoms was evidently decreasing away from the river mouth towards the open sea, unlike the blue-green algae, whose percentage in the phytoplankton biovolume attained maximum values in the ‘open-Bay’. Off the Świna and Dziwna mouths the dominant diatoms were *Coscinodiscus* sp. and *Coscinodiscus granii*, as well as a typical freshwater representative of the Pennales, *Cylindrotheca closterium*. Elsewhere, the dominant species included the dinoflagellate *Heterocapsa rotundata*.

In May 1997 the salinity gradually rose from the Świna mouth towards the open sea: minimum values were noted in the ‘river-mouth’ area (6.44 PSU), maximum values in the ‘open-Bay’ (7.7 PSU) and ‘open-sea’ (7.5 PSU) areas. In all the zones nutrient concentrations were low. Concentrations of nitrates decreased towards the open sea, where at the deep-water sampling sites nitrogen was very probably the principal element limiting phytoplankton growth. Phosphorus could well play a similar role near the mouth of the Świna and in the ‘transition’ area, where phosphate concentrations were lowest. The phytoplankton biomass also decreased away from the Świna mouth towards the open sea. Maximum values were noted in the ‘river-mouth’ area (6.9 mg m^{-3}), minima in the ‘open-sea’ area. In this cruise cryptophytes comprised the highest percentage of phytoplankton biovolume (20–74%) in all areas except in ‘open-sea’. There, the phytoplankton biovolume was dominated by dinoflagellates (*H. rotundata*) and green algae (*Pyramimonas* spp.). In comparison with the other areas the proportion of cryptophytes in the phytoplankton biovolume was here at its lowest, while that of blue-green algae was at its highest. Diatoms (*Actinocyclus octonarius*) were absolutely dominant in the ‘transition’ area. The *PIE* index in all the areas except the ‘open-Bay’ was especially high (0.7–0.9). The decrease in the species diversity here was caused by the conspicuous dominance of cryptophytes. Apart from these, other estuarine species were typically found in the ‘river-mouth’ and ‘transition’ areas, namely green algae such as *Pediastrum boryanum* and *Monoraphidium contortum*, diatoms *Skeletonema subsalsum*, *Fragilaria crotonensis* and *F. pinnata* as well as the euglenophyte *E. gymnastica*. At the deep-water sampling sites the dominant species also included blue-green algae (*Aphanizomenon* sp.) and dinoflagellates (*Dinophysis norvegica*).

In comparison with the other cruises, the salinity in the Bay in October 1997 displayed the greatest variation. Values fell to a minimum in the 'river-mouth' area (5.45 PSU), while maximum values were recorded in the 'open-Bay' area (8.58 PSU). High concentrations of nutrients near the mouth of the Świna decreased in the direction of the open sea, where the very low nitrogen concentration was probably the factor limiting phytoplankton growth. In spite of the obvious salinity and nutrient concentration gradients, the phytoplankton biomass in the Bay was not very highly diversified. Chlorophyll concentrations were slightly higher in the 'river-mouth' area but dropped to a minimum in the open Bay. The phytoplankton biovolume in all areas was very clearly dominated by diatoms. In this cruise, just as during the March 1996 one, species diversity indices were the lowest recorded (0.2–0.6), this being a consequence of the very high percentages of a few diatom species in the phytoplankton biovolume (63–89%). Only in the 'river-mouth' area was *PIE* higher (with the exception of site 38), owing to the increase in the proportion of dinoflagellates and blue-green algae there. Here the diatom *A. octonarius* dominated the phytoplankton biovolume. Elsewhere, its percentage in the phytoplankton biovolume was much lower, while the proportion of other diatom species, notably *Coscinodiscus* sp. and *C. granii*, was higher. At sites near the Świna mouth, the characteristic species also included *E. gymnastica* and *D. acuminata*.

4. Discussion

Quite predictably, salinities in the Pomeranian Bay were lowest in the 'river-mouth' area in the immediate neighbourhood of the Świna mouth. The salinity increased in the direction of the open sea and reached maximum values in the 'open-sea' area. However, in comparison with the Gulf of Gdańsk (Grelowski & Wojewódzki 1996), this parameter varied but moderately in the study area. This was largely a consequence of the fact that the volume of water discharged by the Odra is smaller than that of the Wisła, even though the two bays are comparable in size. Furthermore, the waters of the Odra undergo initial mixing with seawater in the Szczecin Lagoon. The fact that Pomeranian Bay waters are subject to intensive exchange with those of the Baltic Proper cannot be ignored. Further, because it is closer to the Danish Straits and so more susceptible to the influence of the North Sea, the Pomeranian Bay exhibits a greater variability in maximum salinities. For example, in October 1997, this value substantially exceeded 8 PSU, while during the remaining cruises it was no greater than 7.74 PSU.

The waters transported by the Odra primarily enrich the Pomeranian Bay with nitrogen, the element which in the Baltic Proper limits primary production (Trzosińska & Łysiak-Pastuszek 1996). In spring, when the

inflow of nitrogen compounds with the river waters is usually at its peak, there have been cases of local phosphorus depletion (*e.g.* in May 1997); this would suggest that it plays a part in limiting phytoplankton growth. Such a limitation due to phosphorus shortage has also been reported in estuarine waters of the eastern Gulf of Finland (Pitkaenen *et al.* 1993). In the second half of the growing season, enrichment of the Pomeranian Bay waters in nitrogen compounds was not so evident. During that period nitrogen was the major factor limiting primary production over large sectors of the Bay, as was the case in the open sea. A similar situation was also reported from the Gulf of Riga (Poder & Jaanus 1997). Phosphates not utilised by phytoplankton were present in relatively large concentrations in the second half of the growing season. Their presence may have been due to their regeneration in the sediment of Szczecin Lagoon and Pomeranian Bay (Grelowski *et al.* in press).

With the exception of early spring (March 1996), the phytoplankton biomass was high only in the 'river-mouth' area ($6.1\text{--}13.8\text{ mg m}^{-3}$); it was also high at the mouth of the Dziwna (6.7 mg m^{-3}) in October 1997. Chlorophyll *a* concentrations were minimal in the 'open-sea' area, where they ranged from 1 to 2.7 mg m^{-3} . In the other areas of the Pomeranian Bay they did not exceed 5 mg m^{-3} . Hence, the phytoplankton biomass in the 'river-mouth' area was 2 to 4 times higher than in the 'open-Bay' area and 4 to 5 times higher than in the 'open-sea' area. A similar comparison between the 'open-Bay' area and the 'open-sea' area shows that the biomass in the former area was about twice as high as that at the sampling sites located in its outer reaches. During the two cruises when the 'open-sea' area could not be delimited, the deep-water sampling sites were linked with the 'open-Bay' area. In October 1997 the phytoplankton biomass at these sites was lower than elsewhere in the 'open-Bay' area, as was the case during the other cruises; in July 1996, however, it was very slightly higher (1.5 times). The area with a higher phytoplankton biomass in September 1993 and July 1996 was limited to the 'river-mouth' area, whereas in March 1996 and May 1997 it extended to the greater part of the 'open-Bay' area. This was particularly conspicuous in March, when low temperatures retarded the phytoplankton growth and the corresponding utilisation of nutrients. This, in turn, greatly facilitated the propagation of spring diatom bloom over most of the Bay. In October 1997 the phytoplankton biomass was least diversified; higher concentrations of chlorophyll were present also in the 'transition' area.

In the wake of the August 1997 flood wave, which discharged into the Pomeranian Bay 2.2 times more nitrogen and 3 times more phosphorus than in the corresponding period of 1995 (Mohrholz *et al.* 1998), the phytoplankton biomass rose considerably throughout the study area

(Gromisz *et al.* 1998). Within a radius of 30 kilometres from the mouth of the Świna, chlorophyll concentrations were 3–4 times as high and in the other areas twice as high as in July 1996.

In the colder periods, *i.e.* in early spring and autumn, diatoms were prevalent in the phytoplankton biomass. In March 1996 this consisted mainly of small forms such as *Thalassiosira* spp., but in October 1997 of large ones – *Coscinodiscus* sp., *C. granii* and *A. octonarius*. In the warmer seasons the percentage of diatoms in the biovolume decreased and flagellated forms of cryptophytes, dinoflagellates (*P. minimum*, *H. rotundata*) and green algae (*Pyramimonas* spp.) played a more conspicuous role. A high biomass of nanoplanktonic cryptophytes in early summer was also noted in the coastal waters of Estonia (Päärsoo 1997) and in the Gulf of Riga (Poder & Jaanus 1997). In the summer, during the July 1996 cruise, apart from the species just mentioned, a large percentage of blue-green algae such as *Aphanizomenon* sp. and *Nodularia spumigena* could also be discerned in the phytoplankton biovolume. In July the dominant species did not include *M. rubrum* which, during the remaining cruises, particularly in March 1996 and May 1997, made up a relatively high percentage of the phytoplankton biovolume. This pattern of phytoplankton seasonal succession in the Pomeranian Bay was very similar to the one described in the Gulf of Gdańsk (Pliński & Picińska 1986, Witek *et al.* 1993, Pliński 1995).

In 1956–1958, the phytoplankton composition of the Pomeranian Bay as described by Zembrzuska (1973) was also dominated by diatoms in the colder seasons. In early spring these were representatives of the *Chaetoceros* genus, and in the autumn, *C. granii*, as in our studies. Such species as *A. octonarius* and *Melosira arctica* were as significant in the phytoplankton composition in the fifties as they were in our materials. The most numerous species in July mentioned by Zembrzuska was the blue-green alga *N. spumigena*, which likewise made up a large percentage of the phytoplankton biovolume in July 1996. Only in the case of dinoflagellates were there clear-cut differences. In no season during the period 1956–1958 did dinoflagellates form a substantial portion of the phytoplankton composition, owing to their relatively low frequency. In contrast, during each of our cruises, dinoflagellates could always be found among the dominant species, and in September 1993 *P. minimum* even became the most abundant species in the phytoplankton biovolume. The low abundance of dinoflagellates in Zembrzuska's samples could, however, have been a consequence of the method she employed to collect the samples (Copenhagen type net), which may well have failed to collect all the nanoplankton species present in the phytoplankton. In conclusion,

a comparison of the dominant species of the nineties with those of forty years earlier does not reveal any substantial changes in the phytoplankton composition in the Pomeranian Bay.

During three cruises (March 1996, May 1997, October 1997), the phytoplankton species diversity in the open Pomeranian Bay was lower than that of the adjoining regions. This was a consequence of the strong domination of individual algae taxa in the 'open-Bay' area. Although the phytoplankton diversity in the 'open-sea' area was at its highest, it was associated with a low biomass. In the 'river-mouth' areas *PIE* values were frequently high, in spite of the quite high phytoplankton biomass values. Only in September 1993 was the phytoplankton diversity in the 'river-mouth' area rather low, but as has already been mentioned, the high salinities measured there during the September cruise did not indicate the presence of larger quantities of riverine waters. Interestingly, the high *PIE* values at the mouth of the Świna were matched by the largest number of phytoplankton species identified in the samples, whereas in the 'open-sea' area high values of *PIE* were associated with the equal abundance of the species and not with their number.

During the year the degree of phytoplankton composition separateness fluctuated in the separate areas of the Bay with their respective phytoplankton assemblages. The division into 'open-sea' assemblages and 'open-Bay' assemblages was most noticeable in the first half of the growing season (March 1996 and May 1997). This was most probably a consequence of earlier and more intense phytoplankton growth in the Pomeranian Bay than in the open sea, which was facilitated by the faster warming up and possibly stronger stratification in the Bay, and reinforced by the impact of lighter riverine waters. The division into 'river-mouth' and 'open-Bay' assemblages was more clear-cut in the warmer half of the growing season (September 1993, July 1996 and October 1997). In that period, when phytoplankton metabolic rates are typically high, the effect of riverine water enrichment on the Bay's ecosystem was relatively short-lived and, after the swift depletion of nutrients, restricted to the immediate vicinity of the mouth of the Świna and the Dziwna outlet in July too.

Taking into account the data collected during all the cruises it can be concluded that the phytoplankton composition in the Pomeranian Bay was subject to a distinct seasonal fluctuation. Compared to the variations observed between different cruises, the differences between the assemblages in the areas delimited were less substantial during a single cruise. Greater diversification of the phytoplankton composition in individual areas was presumably precluded by the strong advective mixing of water and by the

fact that the water masses involved are never isolated for any significant length of time.

Summing up the results of the research on the impact of the waters of the River Odra on the phytoplankton composition and biomass in the Pomeranian Bay one can draw the following conclusions:

- The nutrient load transported by the Odra brought about a four- or fivefold increase in phytoplankton biomass near the mouth of the Świna and an approximately twofold increase in the open Pomeranian Bay as compared to the 'open-sea' zone.
- The N:P ratio in the Odra waters is relatively high, so when river water inflow into the Bay is rapid, nitrogen presumably ceases to function as the factor limiting primary production there and this role is taken over by phosphorus.
- Variability in the hydrological and hydrochemical conditions along the axis from the Świna mouth towards the open sea caused the phytoplankton composition to diversify with the formation of a number of assemblages, the most distinctive of them being the 'river-mouth', 'open-Bay' and 'open-sea' assemblages.
- In the open part of the Pomeranian Bay the phytoplankton species diversity was much reduced in comparison to both the 'river-mouth' and 'open-sea' areas.

On the basis of differences in the phytoplankton species composition Zembrzuska (1973) suggested dividing the Pomeranian Bay into three areas. The first of these would be located in the immediate neighbourhood of the Świna mouth; the second one would include the south-western part of the Bay and the third the waters over the Odra Bank together with the area to the north and east of it. Furthermore, after the disastrous flood in the Odra basin in summer 1997, the Bay could be divided on the basis of the phytoplankton composition and biomass into a region lying off the mouth of the Świna and two others covering the inner and outer parts of the Bay (Gromisz *et al.* 1998). In both of these divisions the most clearly delimited phytoplankton assemblage was the one associated with the Świna mouth, designated in this paper as the 'river-mouth' assemblage. The other two areas distinguished in the above papers may correspond to the 'Bay' assemblage, within whose boundaries two areas – the 'transition' and the 'open-Bay' assemblages – can be further distinguished in some seasons. However, neither of these two projects analysed phytoplankton samples from sites in the outer reaches of the Bay beyond the 20 m isobath.

On the basis of clustering analysis Rokicka-Praxmajer *et al.* (1998) divided the Pomeranian Bay into areas associated with meiobenthos

communities. In this division the species composition in the area adjoining the mouth of the Świna was clearly distinct from those in the rest of the Bay (Bray-Curtis similarity – 62%).

In the Gulf of Gdańsk, where a similar research project on phytoplankton composition in different seasons of the year had already been completed (Gromisz *et al.* unpubl.), there was a closer correlation than in the case of the Pomeranian Bay between the division into phytoplankton assemblages and such factors as salinity and nutrient concentration. Groups of sampling sites distinguished on the basis of phytoplankton composition have been described as ‘estuary class A’ types (salinity < 3.5 PSU), ‘estuary class B’ types (salinity 3.5–7.1 PSU) and ‘marine’ types (salinity > 7.1 PSU). ‘Estuary A’ sites were most distinctive (Bray-Curtis similarity 20–45%), being characterised by a very high phytoplankton biomass (20–58 mgchl m⁻³) and a permanent dominance of diatoms and green algae, regardless of the season of the year. In the ‘river-mouth’ assemblage in the Pomeranian Bay diatoms were present during all the cruises but only as one of the dominant groups. However, the range of the ‘estuary A’ assemblage in the Gulf of Gdańsk was limited to a small area within a radius of a few kilometres from the mouth of the Wisła. In the Pomeranian Bay no phytoplankton assemblage analogous to an ‘estuary class A’ assemblage was identified; this could be explained by the impact of the Szczecin Lagoon, which initially modifies both the nutrient content and the phytoplankton composition of waters discharged into the sea. ‘Estuary B’ and ‘marine’ assemblages were distinguishable in the rest of the Gulf of Gdańsk. In general these were less distinct from each other (they separated on the level of 55–70% of similarity) than the main assemblages identified in the Pomeranian Bay (separation on the level of 47–63% similarity).

The maximum concentrations of chlorophyll *a*, noted in the summer season near the mouth of the Świna, did not differ markedly from those obtained in earlier years. The earlier values ranged from 10 to 20 mg m⁻³ (Nakonieczny *et al.* 1991, Pollehne *et al.* 1995). Similar maximum values (6–18 mg m⁻³) were also recorded in summer in the coastal zone near the mouth of the Curonian Lagoon (Olenina & Kavolyte 1996) where, as in the Szczecin Lagoon, riverine and sea waters are initially mixed. In the Gulf of Gdańsk, where the Wisła flows directly into the sea, the maximum phytoplankton biomass was > 20 mgchl m⁻³ (Nakonieczny *et al.* 1991, Gromisz *et al.* unpubl., Ochocki *et al.* 1995b) and occasionally amounted to over 100 mgchl m⁻³ (Renk 1972, Latała 1996). Equally high chlorophyll concentrations were noted in a similar estuary in south-eastern Baltic – Parnu Bay in the Gulf of Riga (Tenson 1995, Olli 1996). Summing up, we may conclude that in estuaries where riverine and sea waters are

initially mixed in lagoons there are smaller differences in the phytoplankton composition between the areas immediately adjoining the lagoon outlet and the rest of the bay as compared to estuaries of rivers directly flowing into the sea. Areas in the immediate vicinity of lagoon mouths were also characterised by a generally lower phytoplankton biomass and by a smaller percentage of diatoms and green algae in the biovolume than areas in the direct neighbourhood of river mouths without a lagoon system.

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