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Research Article

PHYTOPLANKTON IN THE HEL UPWELLING REGION (THE BALTIC SEA)

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Abstract

The influence of upwelling on qualitative and quantitative phytoplankton composition was estimated based on the material collected during seven upwelling events along the northern seaside of the Hel Peninsula (the southern Baltic Sea) between April 2000 and August 2002.

As a result of disturbing upwelling effect on hydrological conditions, local changes in taxonomic composition, biovolume and species diversity of phytoplankton assemblages were observed. The most significant differences in phytoplankton taxonomic compositions were noted when the distance and the differences in water temperature between the upwelling centre and the reference area were the biggest. The number of identified taxa and phytoplankton biovolume were much lower in the upwelling centre as compared to the area outside the direct upwelling influence. However, in most cases a decrease in Hurlbert's index of species diversity was not found in the upwelling centre. In the upwelling centre, as a consequence of a considerably lower autotroph biovolume, an increase in heterotroph percentage in total biovolume of the identified organisms was also noted. When the upwelling evolution was directly preceded by phytoplankton bloom, both dominance and biovolume of the most abundant species were distinctly reduced.

INTRODUCTION

From an ecological point of view, vertical transport is the key of physical processes occurring in unstable frontal regions. The advective processes in upwelling systems are the dominant forces that control the biomass and potentially the composition of phytoplankton community (Smith *et al.* 1983). As the physical environment exerts strong control over the amount of light and nutrients experienced by phytoplankton (Collos 1986), it must also influence phytoplankton community structure. Vertical transport results both in an increased flux of nutrients to the surface waters and transport of phytoplankton communities which rate too rapid to track equilibrium (Martin *et al.* 2001).

Due to the notorious difficulties in making high-resolution measurements in the commonly occurring but ephemeral and highly dynamic upwellings in the Baltic Sea (Bychkova *et al.* 1988, Urbański 1995, Kowalewski 1998), there are only few phytoplankton observational studies (Kahru *et al.* 1984, Nõmmann *et al.* 1991, Uitto *et al.* 1997, Danielsen *et al.* 1998, Vahtera *et al.* 2005).

In the Gdańsk Basin region upwelling is observed at the coasts of the Hel Peninsula and the Vistula Spit. Phytoplankton composition in the Gdańsk Basin has been the subject of many investigations (Rumek 1948, 1950, Ringer 1973, 1975, Pliński *et al.* 1985; Pliński and Picińska 1986, Bralewska 1992, Witek *et al.* 1993, Wrzołek 1993, Pliński 1995, Wrzołek 1996, Niemkiewicz and Wrzołek 1998, Gromisz and Witek 2001). In these papers significant seasonal changes in phytoplankton abundance and species composition as well as spatial diversity depended on the distance to the Vistula River mouth or the open sea have been well documented. Some of the above authors concentrate on environmental factors, which affect phytoplankton taxonomic diversity. However, there are no literature data on qualitative and quantitative phytoplankton composition during upwelling events.

The aim of the present work was to determine the influence of coastal upwelling in the Hel Peninsula region on qualitative and quantitative composition of phytoplankton autotrophic and heterotrophic species.

MATERIAL AND METHODS

Research was carried out along the northern seaside of the Hel Peninsula (the southern Baltic Sea) between 2000 and 2002 in the warmer period of the year, from the mid of April till the mid of October. There were seven cruises during which taxonomical composition and biovolume of phytoplankton were determined at three main sites location of which depended on a given spatial water distribution occurring during each upwelling. The central station (U) was located in the pool of the cold, transparent water that emerged to the surface. The reference (outer) station (O) was chosen in the area sufficiently far from the station U where the surface waters were supposed not to be directly affected by the upwelling. Between them the transitional station (T) was situated. Information on geographical coordinates of the sampling stations as well as sampling time is listed in the paper of Matciak *et al.* (2005a).

The material collected at 0.5, 2.5 and 10 m depths using 30 dm^3 Niskin bottle was preserved with Lugol's solution (Edler 1979) and analyzed in an inverted microscope (Utermöhl 1958). Autotrophic dinoflagellates were distinguished from the heterotrophic ones using chlorophyll *a* autofluorescence excited with blue light. Thus, a separate water portion was preserved with alkaline Lugol's solution, 3 % $Na_2S_2O_3$ solution and alkaline formaldehyde and then it was frozen (Sherr and Sherr 1993). The material was slowly thawed in the laboratory and cell autofluorescence was observed under an Olympus IMT-2 inverted microscope with an IMT-2 RFL epifluorescence attachment.

During analysis the abundance was estimated for each species or higher systematic unit. When identification to species level was impossible, the organisms were classified to genus or higher systematic unit (*e.g.* Centrales, Oscilatoriales, Choanoflagellidea). Small monadal and coccal forms difficult taxonomically were combined and regarded as "other unidentified". Since the precise identification of heterotrophic dinoflagellates was impossible, they were assembled into groups of different cell length classes (*e.g.* 10-15 µm, 15-20 µm) such as "*Gymnodinium* spp./*Gyrodinium* spp." and "thecate dinoflagellates". Then, average cell volume was evaluated by geometric method according to Edler (1979). Using these data, the biovolume of each taxon was determined for each sample.

Hurlbert's index of species diversity (*PIE*) was calculated for every station. In the original version the index describes the probability of two randomly seen individuals belonging to different species (Hurlbert 1971) and is calculated using the abundance of each taxon. In this work, abundance was replaced by biovolume and species diversity was calculated as follows:

$$PIE = (\frac{B}{B-1}) \times (1 - \sum_{i=1}^{s} p_i^{\,2}) \tag{1}$$

where: B is total phytoplankton biovolume; p_i is contribution of species i in total phytoplankton biovolume.

The similarity of taxonomic composition between samples was estimated by hierarchical agglomerative clustering analysis according to Bray-Curtis measure of similarity using PRIMER v.5 programme. The analysis was based on each taxon percentage in the phytoplankton biovolume and was carried out in accordance with the Bray-Curtis similarity coefficient, which is defined as follows:

$$S_{jk} = 100\left\{1 - \left(\sum_{i=1}^{p}\left|y_{ij} - y_{ik}\right|\right) \Big/ \left(\sum_{i=1}^{p}\left(y_{ij} - y_{ik}\right)\right)\right\} \tag{2}$$

where: y_{ij} is percentage of the biovolume of species i in sample j, y_{ik} *is* percentage of the biovolume of species i in sample k ($i = 1, 2, \ldots, p; j = 1, 2, \ldots, n$).

In order to increase the significance of rare species in the phytoplankton biovolume, data logarithmic transformation (log (1+y)) was done before calculating the similarity. In order to present the results of clustering analysis in a graphic form, hierarchical agglomerative clustering was used, in which the similarity matrix was sorted according to group-average linkage strategy. The results of the hierarchical clustering were presented in the form of dendrograms, where the *x* axis represents the full set of samples and the *y* axis defines the similarity level at which two samples or group are considered to have fused (Clarke and Warwick 1994). Only autotrophic organisms were analyzed separately for each upwelling. On the obtained dendrograms separation for groups at 50% similarity level was accepted to be significant. This means that the phytoplankton similarity among the samples from different groups was lower than 50%, while within each group the phytoplankton similarity among the samples was greater than 50%.

The matching of biotic to environmental patterns was done by BIOENV program in the PRIMER package. In this procedure, Spearman rank correlation between biotic and abiotic similarity matrices was counted. The weighted Spearman coefficient (ρ_w) lies in the range (-1, +1), with the extremes of $\rho_w = -1$ and +1 corresponding to the cases where two sets of ranks are in complete opposition or complete agreement. The values of ρ_w around zero correspond to the absence of any match between two patterns (Clarke and Warwick 1994). In this work the values of Spearman coefficient were calculated for such abiotic parameters as temperature, salinity and distance between the upwelling centre and the outer (reference) station.

Hydrological conditions during every upwelling, used in the data interpretation, were given by Matciak *et al.* (2005a).

RESULTS

In the investigated region *ca.* 140 phytoplankton species belonging to main taxonomical groups (blue-green algae, diatoms, dinoflagellates, green algae, euglenoids and cryptophytes) were identified. The presence of 15 heterotrophic taxa (12 of them belonged to dinoflagellates, the rest - to flagellates) was also noted. Total biovolume of phytoplankton and the percentage of dominant taxa are presented in Table 1. As a result of clustering analysis, two or three phytoplankton groups for individual stations and depth levels were obtained in every upwelling event.

In spring two upwelling events (28.04.2000 and 13.05.2002) were observed. During the upwelling on 28 April 2000, at similarity level 51 %, the first group was formed by phytoplankton sampled at 0.5 m and 2.5 m depths of the upwelling (U) and transitory (T) stations (Fig. 1). The second group included the algae collected at all depths of the reference station (O) as well as at 10 m depth of the U and T stations. At all stations the highest percentage in phytoplankton biovolume was showed by the dinoflagellate, *Peridiniella catenata*. The species dominated at the reference (outer) station (68–95 %, according to the depth) whereas in the upwelling centre its percentage was 25-42 % (Table 1). In the second group the biovolume of phytoplankton taken at 10 m depth was distinguished by a high percentage of the ciliate, *Mesodinium rubrum* (20-53 %) that contained autotrophic endosymbionts.

The cluster analysis based on the data on the upwelling of 13 May 2002 did not reveal regularity in phytoplankton assemblages. In respect of taxonomic composition, phytoplankton collected at 10 m depth in the upwelling centre was the most distinct (Fig. 1). It was dominated by the ciliate, *M. rubrum* (94 %) (Table 1). *M. rubrum* was also characterized by the highest percentage in phytoplankton biovolume (49-74 %) at all depth levels in the upwelling centre, the transitional zone and the reference area. Dinoflagellates, *P. catenata* and *Amylax triacantha*, and the diatom, *Diatoma tenuis*, were also characteristic species of May upwelling.

In summer three upwelling events (8.07.2001, 2.08.2002 and 28.08.2002) were recorded. During the upwelling on 8 July 2001 the algae assembled (at *ca.* 50 % similarity level) into three groups representing individual stations (Fig. 1). *Aphanizomenon* sp. showed the highest percentage (25-42 %) at all depth levels of every station (Table 1). The outer (reference) station was characterized by the occurrence of the dinoflagellates, *Heterocapsa triquetra* (3-7 %) and cf. *Alexandrium* sp. (4-5 %). Blue-green alga, *Nodularia spumigena* (4-31 %), and a diatom, *Actinocyclus octonarius* (6-18 %), were typical of the upwelling centre (U). At the transitory station (T), apart from *Aphanizomenon* sp., *N. spumigena* and *A. octonarius*, the diatom, *Skeletonema costatum*, also appeared to be a dominant species.

In the upwelling event observed on 2 August 2002 the first group, at similarity level of 48 %, was formed by phytoplankton occurring in the whole water column of the upwelling centre as well as at 10 m depth at the T and O stations (Fig. 1). The second group was consisted of the algae taken at 0.5 and

Table 1

Total biovolume of phytoplankton and the percentage of dominant taxa during upwellings along the Hel Peninsula

Date	Station	Depth [m]	Biovolume [µg dm^{-3}]	Dominant taxa [% biovolume]
1	2	3	4	5
28.04.2000	U	0.5	91	un. 2-15 µm (39), *P. catenata* (25), *T. acuta* (6)
		2.5	186	*P. catenata (*43), un. 2-15 µm (24), *T. baltica* (8)
		10.0	783	*M. rubrum* (54), *P. catenata* (31), *T. baltica* (6)
	T	0.5	453	*P. catenata* (60), un. 2-15 µm (23), *P. prolonga* (4)
		2.5	725	*P. catenata* (70), un. 2-15 µm (9*), Aphanizomenon* sp. (7)
		10.0	3599	*P. catenata* (60), *M. rubrum* (20), *T. baltica* (17)
	O	0.5	6076	*P. catenata* (95), *Aphanizomenon* sp. (2), un. 2-15 µm (2)
		2.5	11288	*P. catenata* (91), *M. rubrum* (4), un. 2-15 µm (2)
		10.0	4274	*P. catenata* (68), *M. rubrum* (26), un. 2-15 µm (2)
13.05.2002	U	0.5	265	*M. rubrum* (49), *P. catenata* (12), *D. tenuis* (7)
		2.5	297	*M. rubrum* (74), *A. octonarius* (12), *P. catenata* (7)
		10.0	697	*M. rubrum* (94), *T. batlica* (3), *Glenodinium* sp. (1)
	T	0.5	306	*M. rubrum* (52), *D. tenuis* (17), *D. communis* (6)
		2.5	907	*M. rubrum* (72), *P. catenata* (20), *A. triacantha* (3)
		10.0	231	*M. rubrum* (64), *A. triacantha* (12), *P. catenata* (7)
	O	0.5	4008	*M. rubrum* (68), *P. catenata* (10), *D. tenuis* (6)
		2.5	1878	*M. rubrum* (55), *P. catenata* (10), *D. tenuis* (10)
		10.0	319	*M. rubrum* (59), *P. catenata* (11), *D. tenuis* (6)
08.07.2001	U	0.5	527	*N. spumigena* (31), *Aphanizomenon* sp. (28), un. 2-15 µm (14)
		2.5	322	*Aphanizomenon* sp. (32), *N. spumigena* (20), *A. octonarius* (6)
		10.0	76	*Aphanizomenon* sp. (32), *A. octonarius* (18), Oscilatoriales (6)
	T	0.5	1215	*Aphanizomenon* sp. (37), *N. spumigena* (21), un. 2-15 µm (9)
		2.5	1031	*N. spumigena* (48), *Aphanizomenon* sp. (34), Centrales 5-10 µm (5)
		10.0	187	*Aphanizomenon* sp. (25), *S. costatum* (17), *N. spumigena* (16)
	O	0.5	3671	*Aphanizomenon* sp. (26), un. 2-15 µm (7), *S. acuminatus* (6)
		2.5	4110	*Aphanizomenon* sp. (42), Oscilatoriales (13), cf. *Alexandrium* sp. (5)
		10.0	671	*Aphanizomenon* sp. (37), *H. triquetra* (7), *E.* cf. *gymnastica* (6)
02.08.2002	U	0.5	224	*Aphanizomenon* sp. (21), *A. octonarius* (21), *H. triquetra* (10)
		2.5	235	*Aphanizomenon* sp. (27), *E.* cf. *gymnastica* (12), *H. triquetra* (8)
		10.0	128	*Aphanizomenon* sp. (33), *T. acuta* (10), *D. didyma* (8)
	T	0.5	2678	*C. meneghiniana (36), Aphanizomenon sp. (20), N. spumigena (17)*
		2.5	996	*C. meneghiniana* (24), *Aphanizomenon* sp. (22), *N. spumigena* (12)
		10.0	342	*Aphanizomenon* sp. (70), *C. meneghiniana (4), M. rubrum* (2)
	O	0.5	4542	*C. meneghiniana* (58), *H. triquetra* (15), *E.* cf. *gymnastica* (8)
		2.5	1777	*C. meneghiniana* (48), *E.* cf. *gymnastica (15), Aphanizomenon* sp. (9)
		10.0	140	*C. meneghiniana (43), Aphanizomenon* sp. (9), *E.* cf. *gymnastica* (7)

1	2	3	4	5
28.08.2002	U	0.5	8	*S. lacustris* (10), *Nitzschia* sp. (10), *Aphanizomenon* sp. (10)
		2.5	27	*Aphanizomenon* sp. (65), *Anabaena* sp. (7), *H. triquetra* (5)
		10.0	18	*M. rubrum* (18), *D. didyma* (17), *Aphanizomenon* sp. (15)
	T	0.5	161	*Anabaena* sp. (38), *N. spumigena* (30), *Aphanizomenon* sp. (17)
		2.5	571	*N. spumigena* (62), *Anabaena* sp. (28), *Aphanizomenon* sp. (6)
		10.0	41	*Anabaena* sp. (41), *P. duplex* (35), *Planktothrix* sp. (8)
	O	0.5	1698	*C. meneghiniana* (55), *Aphanizomenon* sp.(9), *H. triquetra* (6)
		2.5	1252	*C. meneghiniana* (69), *Aphanizomenon* sp. (7), *Planktothrix* sp. (4)
		10.0	181	*C. meneghiniana* (42), *A. octonarius* (30), *A. granulata* (5)
18.09.2000	U	0.5	263	*C. granii* (93), *A. octonarius* (2), un. 2-15 µm (2)
		2.5	100	*C. granii* (89), *A. octonarius* (2), un. 2-15 µm (2)
		10.0	98	*C. granii* (91), *A. octonarius* (2), un. 2-15 µm (2)
	T	0.5	528	*T. acuta* (27), un. 2-15 µm (17), *C. granii* (11)
		2.5	345	*C. granii* (33), un. 2-15 µm (24), *E.* cf. *gymnastica* (11)
		10.0	150	*C. granii* (59), *C. meneghiniana* (9), *E.* cf. *gymnastica* (5)
	O	0.5	455	*C. meneghiniana* (47), un. 2-15 µm (17), *S. costatum* (14)
		2.5	467	*C. meneghiniana* (28), *S. costatum* (19), un. 2-15 µm (14)
		10.0	425	*C. meneghiniana* (34), *S. costatum* (14), *T. acuta* (12)
27.09.2001	U	2.5	234	*C. granii* (33), *M. rubrum* (21), *T. acuta* (10)
		10.0	115	*M. rubrum* (52), *T. acuta* (12), *P. prolonga* (8)
	T	0.5	129	*A. octonarius* (31), *M. rubrum* (14), *D. acuminata* (7)
		2.5	118	*A. octonarius* (18), *M. rubrum* (17), Centrales 5-10 µm (15)
		10.0	62	*M. rubrum* (25), *A. octonarius* (18), *D. acuminata* (11)
	O	0.5	224	*C. granii* (35), *E.* cf. *gymnastica* (12), *D. fragilissimus* (11)
		2.5	409	*C. granii* (55), *E.* cf. *gymnastica* (12), *A. octonarius* (10)
		10.0	163	*E.* cf. *gymnastica* (29), *A. octonarius* (16), *T. acuta* (11)

A. granulata - Aulacoseira granulata, A. octonarius – Actinocyclus octonarius,
A. triacantha - Amylax triacantha, C. granii – Coscinodiscus granii,
C. meneghiniana – Cyclotella meneghiniana, D. acuminata - Dinophysis acuminata,
D. communis - Desmodesmus communis, D. didyma - Diploneis didyma,
D. fragilissimus - Dactyliosolen fragilissimus, D. tenis - Diatoma tennis,
E. cf. *gymnastica – Eutreptiella* cf. *gymnastica, H. triquetra – Heterocapsa triquetra,*
N. spumigena – Nodularia spumigena, M. rubrum – Mesodinium rubrum,
P. catenata – Peridiniella catenata, P. duplex - Pediastrum duplex,
P. prolonga - Plagioselmis prolonga, S. acuminatus - Scenedesmus acuminatus,
S. costatum – Skeletonema costatum, S. lacustris - Snowella lacustris,
T. acuta - Teleaulax acuta, T. baltica - Thalassiosira baltica,
un. – other unidentified

U – upwelling station, T – transitional station, O – outer station

2.5 m depths in the transitional (T) and reference (O) zones. In the first group *Aphanizomenon* sp. showed the highest percentage (9-70%) in phytoplankton biovolume while in the second group domination of the diatom, *Cyclotella meneghiniana* (24-58%) was noted (Table 1).

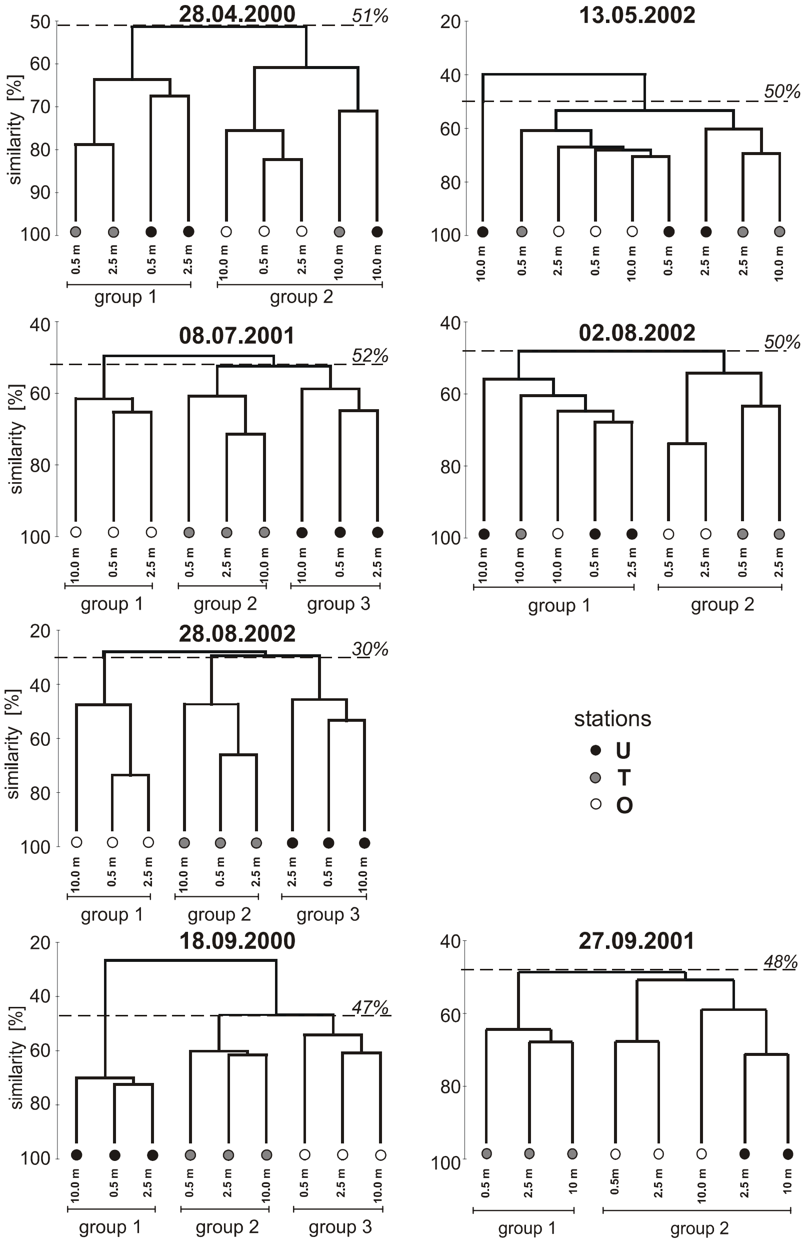

Fig. 1. Groups of phytoplankton distinguished by the clustering analysis during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

During the upwelling on 28 August 2002 the first group, at 28% similarity level, was formed by phytoplankton organisms from the reference station (O). In this group, the diatom, *C. meneghiniana*, was characterized by the highest percentage (42-69%) in phytoplankton biovolume (Fig. 1). The other characteristic species were the blue-green algae, *Aphanizomenon* sp. (3-9%) and *Planktotrix* sp. (6%), and the dinoflagellate, *Heterocapsa triquetra* (2-6%) (Table 1). In the second group, formed by the samples collected at the transitional station (T), a clear domination of the blue-green algae, *N. spumigena* (30-62%) and *Anabaena* sp. (28-41%), was found. The third group assembled the algae from the station situated in the upwelling centre. *Aphanizomenon* sp. showed the highest percentage (10-65%) in biovolume. *C. meneghiniana*, *Planktotrix* sp., *N. spumigena* and *Anabaena* sp. were not observed.

In autumn two upwelling events (18.09. 2000 and 27.09.2001) were found. In the upwelling event observed on 18 September 2000 phytoplankton from all levels of the U station formed the first group, even at 27% similarity (Fig. 1). The group was dominated by the diatoms, *Coscinodiscus granii* and *A. octonarius*. The former species reached maximum percentage in biovolume (89-93%) while the percentage of the latter one was 2-3% (Table 1). Phytoplankton occurring at all levels of the reference (outer) station formed the next group dominated by two other diatoms, *C. meneghiniana* (27-47%) and *S. costatum* (14-19%). In taxonomic composition of this group, the species typical of the upwelling centre (*C. granii* and *A. octonarius*) were not found. In the third group, formed by phytoplankton from the transitory station, the biovolumes of *C. meneghiniana* and *S. costatum* were much lower (6-9%), and the highest percentage was noted for *C. granii* (11-59%).

During the upwelling on 27 September 2001 one phytoplankton sample (the U station, 0.5 m depth) was missing. Hence, the interpretation of the dendrogram obtained (Fig. 1) encountered objective difficulties. The algae collected at the transitory station (T) formed the first group at a 48% similarity level. *A. octonarius* and *M. rubrum* showed the highest percentage in phytoplankton biovolume, 18-31% and 14-25%, respectively. The algae sampled at the O and U stations formed the second group. At 0.5 and 2.5 m depths *C. granii* domination (33-55%) was observed whereas at 10 m depth *M. rubrum*, the euglenoid, *Eutreptiella* cf. *gymnastica* and the cryptophyte, *Teleaulax acuta* attained the highest percentage in phytoplankton biovolume (Table 1).

The highest values of the weighted Spearman rank correlation (ρ_w) between abiotic parameters and biotic similarity matrices were noted during the upwelling on 18 September 2000 for temperature ($\rho_w = 0.90$) and U - O distance

(ρ_w=0.82) (Table 2). There was not any significant correlation between phytoplankton composition and salinity for all upwelling events (max ρ_w=0.38). The values of ρ_w were not calculated for upwelling on 27 September because one phytoplankton sample was missing.

Table 2

The values of weighted Spearman coefficient (ρ_w) for phytoplankton during upwellings along the Hel Peninsula

Date	Values of ρ_w		
	temperature	salinity	U-O distance
28.04.2000	0.33	0.38	0.33
13.05.2002	0.13	-0.001	0.23
08.07.2001	0.05	0.34	**0.61**
02.08.2002	**0.59**	-0.36	0.37
28.08.2002	0.21	-0.08	**0.58**
18.09.2000	**0.90**	-0.06	**0.82**

some data of 27.09.2001 were missing; U – upwelling station, O – outer station

Maximum and minimum values of phytoplankton biovolume were noted at the reference station and in the upwelling centre, respectively (Fig. 2). The only exception was observed on 13 May 2002 when, as a consequence of high *M. rubrum* abundance, biovolume at 10 m depth of the U station exceeded the value obtained at the same depth of the O station.

Generally, in the upwelling centre a 24-70% reduction in the number of phytoplankton taxa was observed as compared to the reference (outer) station (Fig. 3). Only during the upwellings in April 2000 and September 2001 the number of taxa did not show significant differences.

The values of species diversity index (*PIE*) increased and reached the maximum in the upwelling centre in April 2000 and August 2002 (Fig. 3). In July and September 2001 the index values at the U and O stations were similar, and in September 2000 and May 2002 the lowest values were noted at the U station.

Generally, the percentage of heterotrophic taxa in total biovolume of auto- and heterotrophs increased at the U station except for September upwellings (Table 3). It was especially distinct on 28 April 2000 and 13 May 2002 when heterotrophic taxa constituted 51 and 36% of total biovolume, respectively.

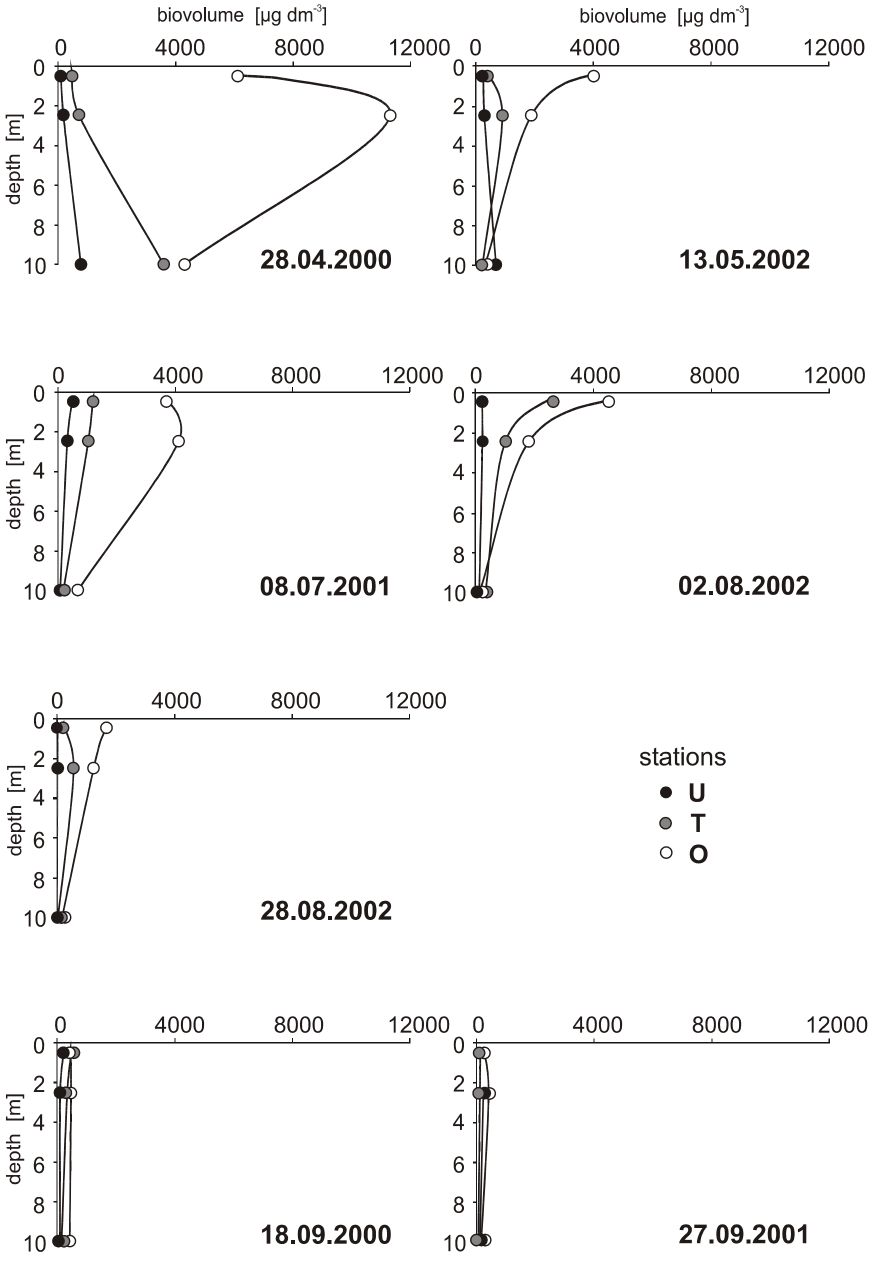

Fig. 2. Phytoplankton biovolumes during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

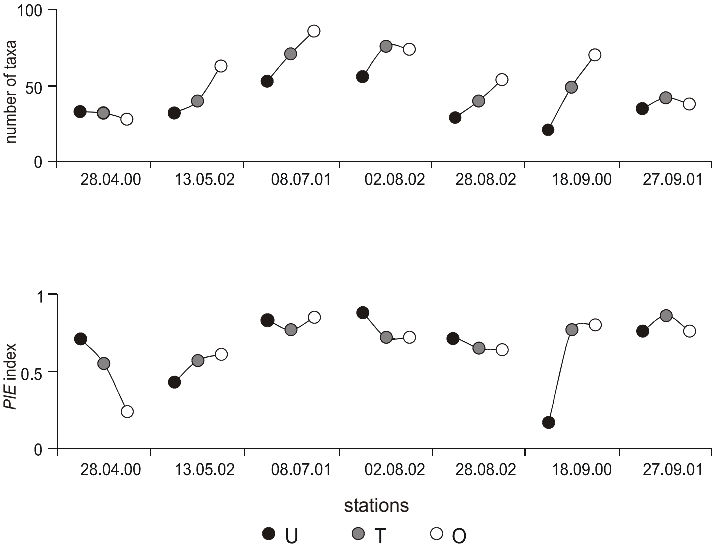

Fig. 3. Number of phytoplankton taxa and the values of Hurlbert's index of diversity (*PIE*) during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

Table 3

Percentage of heterotrophic species in total biovolume of auto- and heterotrophs during upwellings along the Hel Peninsula

Date	Station		
	U	T	O
	[% biovolume]		
28.04.2000	51	24	5
13.05.2002	36	26	10
08.07.2001	7	3	12
02.08.2002	17	4	6
28.08.2002	10	0	7
18.09.2000	1	16	21
27.09.2001	7	7	8

U – upwelling station, T – transitional station, O – outer station

The highest biovolume of heterotrophic taxa was observed on 28 April 2000 and 13 May 2002 (Fig. 4). During both upwellings the biovolumes of heterotrophs in the upwelling centre and the reference area were almost the same. In April the dinoflagellates, *Gyrodinium* sp. and *Protoperidinium bipes*, were characterized by the highest percentage in biovolume, 34-75% and 2-48%, respectively. In May, however, domination of athecate dinoflagellates, classified as *Gymnodinium* spp./*Gyrodinium* spp. (36-67%), *Gyrodinium* sp.(5-16%) and *Protoperidinium brevipes* (2-29%) was observed. In July 2001, August 2002 and September 2000 and 2001 the highest biovolumes were noted at the

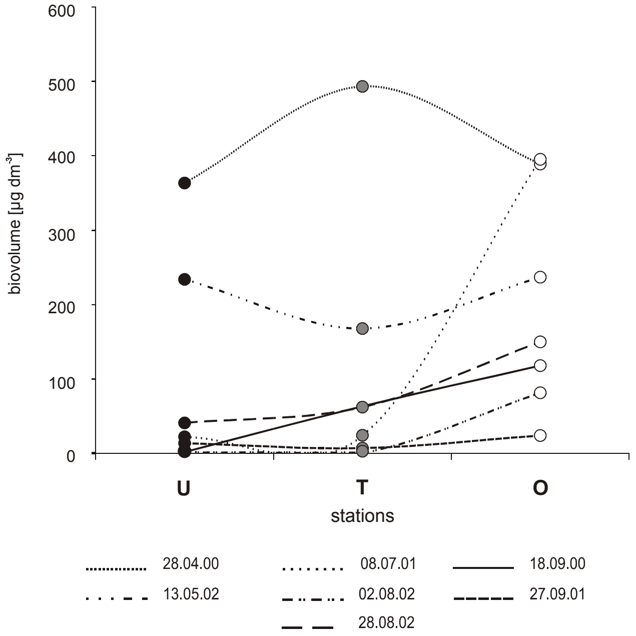

Fig. 4. Biovolume of heterotrophic phytoplankton species during upwellings along the Hel Peninsula; U - upwelling station, T - transitional station, O - outer station.

O station and the lowest at the U station. Such regularity was especially pronounced on 8 July 2001 when the biovolume of heterotrophs at the outer (reference) station was 18 times higher than in the upwelling centre. At that time thecate dinoflagellates (cell size 15-30 µm) dominated at the outer (reference) station (26-56%), and high percentage of *Ebria tripartita* (5-22%), the representative of Ebriidea class, was also noted. Dinoflagellates from Kolkwitziellaceae family and heterotrophic flagellates: *Leucocryptos marina* and taxonomically difficult flagellates (13-20 µm in size) dominated in the upwelling centre.

DISCUSSION

The comparison of qualitative and quantitative phytoplankton composition between the upwelling centre, the transitional zone and the reference area enabled one to distinguish the following patterns in formation of phytoplankton assemblages:

1. Phytoplankton from every station (in the whole water column) was a separate assemblage. Such situation was noted on 18 September 2000, 8 July 2001 and 28 August 2002.
2. Two assemblages were recognized in the study area. The first one was formed by phytoplankton occurring in the surface water layer (0.5 and 2.5 m) of two neighbouring stations. The second assemblage was composed of phytoplankton collected at those stations at 10 m depth and from the whole water column of the third station. It was found on 28 April 2000 and 2 August 2002.
3. There were no regularities in assembling of phytoplankton organisms from individual stations (13 May 2002).

Unfortunately, the results of the clustering analysis are not fully objective since many algae were not identified to species level. Moreover, the group called „other unidentified", consisting of monadal and coccal forms, made a great part of the investigated material. Such taxa as genus, family or the „other unidentified" group included a variable number of species. In this respect, similarity values of the distinguished groups are typical of the present paper and, without the comparison of phytoplankton identification method, they should not be compared to the values obtained by other authors. It seems, however, that the incomplete phytoplankton identification did not have a significant effect on the conclusions since the same method of phytoplankton analysis was applied.

During the upwellings characterized by the biggest distance between the upwelling centre and the reference area, three separate phytoplankton assemblages corresponding to individual stations (U, T and O) were recognized. Such upwellings were observed on 8 July 2001, 28 August 2002 and 18 September 2000 (Matciak *et al.* 2005a). The distance between the upwelling centre (U) and the reference (outer) station was *ca.* 9-10 km (9.7, 10.7 and 8.7, respectively). In the case of the above upwellings, the abiotic variable which best groups samples is U - O distance (ρ_w=0.61, 0.58 and 0.82, respectively). Only in September, apart from U - O distance, water temperature was also the variable, which accounts best for the formation of three separate phytoplankton assemblages corresponding to individual stations (ρ_w=0.9). In that case the first phytoplankton assemblage was formed at 27% similarity, and the next two assemblages only at 47% similarity level. In August water temperature had a very small effect on phytoplankton species assembling (ρ_w=0.21) and three assemblages were separated at *ca.* 30%. In July 2001, however, water temperature did not affect the formation of phytoplankton assemblages at all (ρ_w=0.05). At that time the assemblages corresponding to each station were separated only at *ca.* 50% similarity. When the transitional station (T) was situated closer to the reference station (O) than to the upwelling centre (U) (September 2000), the first assemblage was formed by the algae collected in the upwelling centre. This group was distinctly different from the other groups in respect of phytoplankton taxonomic composition. On the contrary, on 8 July and 28 August, the first assemblage was composed of phytoplankton collected at the reference station (O), which was situated at a greater distance from the T station.

When upwellings were characterized by the biggest area and the considerable temperature difference between the extreme stations (18 September 2000 and 28 August 2002), the species which showed maximum percentage in the first assemblage (at all station depths) was not observed in taxonomic composition of the corresponding extreme station. In September *C. granii*, the diatom typical of cooler waters, showed *ca.* 90% dominance in the upwelling centre whereas it was not observed at the outer (reference) station (O). Similarly in August, *C. meneghiniana* was not found at the U station, but attained the highest dominance in the reference area. However, in July, despite similar upwelling area, the dominant species at every station was *Aphanizomenon* sp. Optimum growth temperature for this species is 15-28°C (Pliński and Jóźwiak 1999). In July, when the differences in water temperature between the U (15.4°C) and O (19.9°C) stations were much lower, this species maintained its dominance over the whole area. Therefore, it could be concluded that the difference in water temperature between the upwelling centre and the reference (outer) station had a greater influence on phytoplankton taxonomic composition as compared to the effect of the upwelling spatial range.

Another pattern in the formation of phytoplankton assemblages was observed during the upwellings on 28 April 2000 and 2 August 2002 when the distances between two stations (U and O) were much shorter, 2.9 and 4 km, respectively. In those days the phytoplankton samples collected at two stations (at 0.5 and 2.5 m depths), which were situated closer to one another in relation to the remaining station and showed smaller difference in water temperature, fused into one assemblage. The second assemblage included the algae taken at the above stations at 10 m depth and from all levels of the other station. In August the abiotic variable which best groups phytoplankton species was temperature ($\rho_w = 0.59$). In April the analyzed environmental factors had only a slight influence on the formation of phytoplankton assemblages ($0.33 < \rho_w < 0.38$). In both upwellings the similarity in phytoplankton taxonomic composition between the assemblages was *ca.* 50%. The assemblages differed mainly in species, which showed the highest percentage in phytoplankton biovolume.

In May 2002, when there was not regularity in clustering of phytoplankton organisms, the difference between the upwelling centre (U) and the reference station (O) was in only 1.1 km. Nevertheless, there was a big temperature difference (8.5 °C) in the surface water at those stations.

During all upwellings the dependence of phytoplankton species clustering upon salinity (max $\rho_W = 0.38$) was insignificant. There was not any relationship between the patterns of phytoplankton assemblages grouping and season of the year as well.

It could be stated that the most significant differences in phytoplankton taxonomic composition are typical of upwellings which are characterized by the biggest area and the considerable temperature difference between the upwelling centre and its surroundings. At that time the similarity in phytoplankton taxonomic composition between the U, T and O stations reached the lowest level (27-28%). The clustering analysis of phytoplankton organisms collected in 1994-1997 in the Gulf of Gdańsk and the Pomeranian Bay and identified by the same method as in the present study showed that at almost the same similarity (25%) and irrespective of the season, only the phytoplankton taken in vicinity of the Vistula River mouth was distinguished (Gromisz and Witek 2001). Taxonomic composition of phytoplankton samples collected at a greater distance from the river mouth and on the open sea, at several days' intervals, showed the similarity level greater than 50%.

The phytoplankton biovolume was always lower in the upwelling centre (U) as compared to the reference area (O). The biggest differences observed on 28 August 2002 at 0.5 m depth coincided with the maximum difference in temperature of the surface water between the above stations. At that time the phytoplankton biovolume taken from 0.5 m depth at the reference (outer) station (1698 $\mu g\,dm^{-3}$) was as much as 212 times greater than at the upwelling centre (8 $\mu g\,dm^{-3}$). In April 2000 the biovolume was 66 times greater, and in the other cases – up to 20 times. The above results confirm the data obtained by Nõmmann *et al.* (1991) and Uitto *et al.* (1997) who observed a reduction in phytoplankton biovolume during upwellings in the Baltic Sea.

The only case of higher phytoplankton biovolume at the U station (10 m depth) than in the reference area (May 2002) resulted from an increase in abundance of the ciliate, *M rubrum*. In April 2000 this species dominated also in the upwelling centre at 10 m depth and caused an increase in phytoplankton biovolume compared to the surface water layer. In spite of its taxonomic position, this species is fully autotrophic due to endosymbiotic algal cells (Taylor *et al.* 1971). Therefore, from ecological point of view it belongs to phytoplankton (Laybourn-Parry 1992). High abundance of *M. rubrum* is frequently observed in the upwelling zone (Packard *et al.* 1978), and its blooms were also noted in the Baltic Sea (Fenchel 1968, Lindholm 1978). The increase in the biovolume of *M. rubrum* was observed in the upwelling water in the western part of the Gulf of Finland too (Vahtera *et al.* 2005).

The course of changes in phytoplankton biovolume represents a good consistence with the changes in chlorophyll *a* concentration and daily primary production level (Zalewski *et al.* 2005). The parameters describing the suspension in respect of quantity, mass and number ($C_{p\text{-}org}$, POC, PN, particle number and size) also indicate a clear impoverishment of the upwelling waters compared to the reference area (Bradtke *et al.* 2005).

Generally, a considerable decrease in phytoplankton biovolume in the upwelling centre (U) was accompanied by the lower number of taxa. The only exception was observed on 28 April 2000 when phytoplankton bloom occurred during the upwelling. At that time a very high phytoplankton biovolume, dominance of the dinoflagellate *P. catenata* (up to 90%), and low species diversity ($PIE = 0.2$) were noted outside the upwelling area. In the upwelling centre the phytoplankton biovolume and percentage of *P. catenata* (25-31%) were significantly lower. Although the numbers of identified taxa in the upwelling centre and the reference area were similar, *PIE* index in the upwelling centre increased up to 0.7. As a consequence of upwelling, a distinct increase in biovolume and dominance of blooming species as well as a decrease in phytoplankton species diversity were observed.

Only in two cases (September 2000 and May 2002) the smaller number of taxa at the U station corresponded to a decrease in diversity index (*PIE*) value. During the upwellings in July and September 2001 *PIE* was relatively stable over the study area. In August 2002, however, the lower number of taxa was accompanied by the highest value of species diversity index at the U station. It could be explained by a weaker dominance of single species, *i.e.* an increase in species evenness. Therefore, it could be concluded that in majority of analyzed upwellings (5 events) the lower number of taxa and smaller biovolume of phytoplankton in the upwelling centre were not accompanied by a decrease in the value of species diversity index.

An interesting situation was observed in September 2000. As a result of upwelling phytoplankton assemblage dominated by *C. granii*, which is typical of October and November (Gromisz and Witek 2001), appeared as early as in mid September. In the upwelling centre the percentage of the diatom in biovolume was 89-93%, while in the reference area *C. granii* was not found. The number of taxa identified in the upwelling region was by 70% lower than at the reference (outer) station, and species diversity index decreased from 0.8 to 0.2. Satellite images of the sea surface along the Hel Peninsula gave evidence of favourable conditions for the development of autumn phytoplankton assemblage in the upwelling water in September. Satellite-derived chlorophyll *a* concentration in optical light penetration layer was higher in the upwelling water than in the surrounding waters (Krężel *et al.* 2005). It could be attributed to an earlier appearance of autumn phytoplankton assemblage in the upwelling water resulting from a decrease in water temperature.

The highest and almost the same biovolume of heterotrophic taxa in the upwelling centre and at the outer (reference) station was noted in the latter part of April and in mid May when the maximum abundance of heterotrophic dinoflagellates in the Gulf of Gdańsk was observed (Witek *et al.* 1993, Bralewska and Witek 1995). In the other months the biovolume was clearly lower, and its value was smaller in the upwelling centre than in the reference area. An increase in heterotroph percentage at the U station, despite the same or lower biovolume of heterotrophs, resulted from a considerable reduction in autotroph biovolume.

Although the best conditions for phytoplankton development, *i.e.* high water transparency (Matciak *et al.* 2005b) and a significant increase in biogenic substance concentration (Burska and Szymelfenig 2005) occurred in the upwelling centre, the phytoplankton biovolume was lower than in the reference waters. It could be presumed that the reason for such situation was not only a decrease in water temperature (Matciak *et al.* 2005a) but also high dynamics of the upwelling waters that disturbed the formation of phytoplankton assemblages (Smith *et al.* 1983, Matciak *et al.* 2005a). The selection of geographic positions of the reference stations could also be a controvertible question. Although hydrological and optical conditions at the reference stations (*i.e.* the highest and constant water temperature, low water transparency) indicated the upwelling decay (Matciak *et al.* 2005a, b), an intensive phytoplankton development resulting from an increase in water temperature as well as a high concentration of biogenic substances brought by upwelling (Burska and Szymelfenig 2005) could be observed just over there.

The observations carried out by Vahtera *et al.* (2005) in the Gulf of Finland showed that in late summer mainly cyanobacteria received benefit by the enrichment of the upwelling waters with nutrients. During upwelling the authors demonstrated a distinct decrease in phytoplankton total biomass together with a slight increase in *Mesodinium rubrum, Eutreptiella* spp. and Prasinophyceae biomass. However, a lag time of about 2-3 weeks after upwelling relaxation was long enough for the successive cyanobacteria blooms to occur, mainly due to the enhanced phosphate concentration. Therefore, upwelling could intensify growth and prolong the period of toxic, nitrogen-fixing filamentous cyanobacteria persistence in different regions of the Baltic Sea.

Summing up, it could be concluded that upwelling modifies the phytoplankton composition, biovolume and species diversity through its disturbing effect on hydrological conditions in the environment. Such pattern is particularly well pronounced when upwelling is characterized by the biggest distance and considerable temperature difference between the upwelling centre and the reference area.

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