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Research Article

PRIMARY PRODUCTION AND CHLOROPHYLL *a* CONCENTRATION DURING UPWELLING EVENTS ALONG THE HEL PENINSULA (THE BALTIC SEA)

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Abstract

The measurements of chlorophyll *a* concentration and primary production were carried out during seven upwelling events along the northern seaside of the Hel Peninsula (the southern Baltic Sea) between April 2000 and August 2002. Daily primary production was estimated by simulated *in situ* method. The maximum rates of phytoplankton photosynthesis derived from photosynthetic light curves were used for calculations. The values of chlorophyll *a* concentration and primary production depended directly on the level and distribution of phytoplankton biomass. The lowest chlorophyll *a* concentration and primary production were found in the upwelling centre and increased with the distance from its centre towards the reference area. Gradients of chlorophyll *a* concentration and primary production varied with the changes in upwelling intensity and the season of the year. In autumn the differences between the upwelling centre and the reference area were significantly smaller than in spring and summer. In spring and summer chlorophyll *a* concentration and primary production showed 20-fold and 7-fold increase, respectively, as compared to the results obtained in autumn. High values of assimilation numbers were found in the upwelling centre, what indicates favourable conditions for phytoplankton development. Therefore, it could be suggested that optimum thermal, light and trophic conditions enhance primary production at a certain distance from the upwelling centre and during upwelling relaxation.

INTRODUCTION

Primary production associated with nitrate uptake has been termed "new" production by Dugdale and Goering (1967) to distinguish between the utilization of allochtonous nitrogenous nutrients and regenerated production due to the assimilation of autochtonous nitrogen produced by food web recycling. Vertical advection results in the transport of deep nutrient-rich water into the surface euphotic zone. Hence, upwelling is a major mechanism to enhance primary production and to increase "new" production. Although the coastal upwellings constitute relatively small part of the global ocean surface, they are the sites of the highest rates of new production.

In spite of the fact that almost 30 upwellings were identified in the Baltic Sea (Bychkova and Viktorov 1987, Bychkova *et al.* 1988, Urbański 1995, Kowalewski 1998, Myrberg and Andrejev 2003), their influence on biological productivity is poorly recognized. The results obtained from *in situ* observations, satellite images and modelling provide only preliminary and fragmentary data on chlorophyll concentration, phytoplankton and zooplankton (Kahru *et al.* 1984, Kostrichkina and Yurkovskis 1986, Nõmmann *et al.* 1991, Semovsky *et al.* 1999, Siegel *et al.* 1999, Ennet *et al.* 2000).

It is commonly known that the coastal upwellings observed along continental shelves increase primary production and play a significant role in organic matter transport to the adjacent oligotrophic oceanic waters (Chavez *et al.* 1991, Gabric *et al.* 1993, Joint *et al.* 2001, Álvarez-Salgado *et al.* 2002). However, in fertile Baltic Sea the problem of "new" primary production input is still to be solved. It is important to know, whether and to what degree nutrients, previously occurring in deeper sea layers and introduced to food web by upwelling activity, contribute to eutrophication increase.

Coastal upwellings observed along the Polish coast of the Baltic Sea are characterized by different frequency and intensity (Urbański 1995, Krężel 1997b, Kowalewski and Ostrowski 2005). Therefore, their influence on primary production should be investigated.

In the present work, an attempt was made to determine chlorophyll *a* concentration and daily primary production in the upwelled water plume along the Hel Peninsula.

MATERIAL AND METHODS

The investigations were carried out along the seaside of the Hel Peninsula (the southern Baltic Sea) between 2000 and 2002 in the warmer period of the year. Chlorophyll *a* concentration and primary production were determined on seven upwelling events. On every upwelling three stations were chosen. The central station (U) was situated in the upwelling centre. The outer (reference) station (O) was set sufficiently far from the station U where the surface waters were not directly affected by upwelling. The transitional station (T) was situated between the U and O stations. The above stations were localized based on hydrological measurements of each upwelling. Geographical coordinates of the sampling stations as well as sampling times are given by Matciak *et al.* (2005a).

Water samples for chlorophyll measurements were collected, depended on the depth at the station, from levels of 0.5, 2.5, 5, 10, 15, 20, 30, 40, 50, 60 m and near the bottom using 30 dm^3 Niskin bottle. Chlorophyll *a* concentration was measured fluorometrically. The samples were filtered through Whatman GF/F filters and extracted with 90% acetone (24 h) in darkness, at *ca.* 4°C (Evans *et al.* 1987).

Primary production measurements of the samples collected basically at 0.5, 2.5 and 10 m depths were carried out in an incubator, in artificial light (313 kJ $m^{-2} h^{-1}$) for 2 h. To determine the parameters of the light curves, a system of filters and mirrors was used for samples taken at 2.5 m depth. PAR values were equal to 1, 10, 25, 50, 70 and 175% of the basic value. The samples were incubated at mean temperature value measured *in situ* at 2.5 and 5 m depths.

Photosynthetic intensity was determined radioisotopically (Ærtebjerg Nielsen and Bresta 1984, BMEPC 1988) with the use of ^{14}C - 150 kBq activity per incubated sample. The incubation of samples was carried out in 50 cm^3 glass bottles. After incubation each sample was filtered through Whatman GF/F filter. The activity of phytoplankton samples were measured with a liquid scintillation counter (Beckman LS-6000IC).

Inorganic carbon (necessary for primary production calculations) was estimated by pH measurements of the water samples before and after acidifying with 0.01 N HCl (1 : 4 v/v) (BMEPC 1988).

Photosynthetically active radiation (PAR), necessary for determination of attenuation coefficients in the euphotic zone, was registered at every measuring station. Daily total energy [kJ $m^{-2} d^{-1}$] was calculated using the model of solar energy input to the sea surface (Krężel 1997a, 1997b, Krężel and Kozłowski 2001).

Daily primary production was estimated by so-called simulated *in situ* method. The calculations were based on light curve parameters and *in situ* measurements – combination of light curve parameters with daily irradiance and water transparency (Lohrentz 1993, Tilzer *et al.* 1993, Renk 2000, Renk *et al.* 2000).

RESULTS

Irrespective of measuring time (Fig. 1), the lowest mean chlorophyll *a* concentrations, 0.26-2.05 mg m^{-3} at 0–10 m depth, were noted at the U stations situated in the upwelling centre. The highest values with a peak of 12.39 mg m^{-3} were found in April 2000 at the reference station (O) situated outside direct upwelling influence (Table 1). The differences in chlorophyll *a* concentrations between the U, T and O stations decreased with an increase in depth and they were insignificant below 20 m. Vertical variability in chlorophyll *a* concentration at 0–20 m depth depended on station location in relation to the upwelling plume area (Fig. 2). At the transitional (T) and reference (O) stations maximum values were found just below the surface water and they decreased with an increase in depth. On the other hand, chlorophyll *a* concentrations in the upwelling centre (the U stations) were similar throughout the water column, from the surface to the bottom, irrespective of observation time. The only exception was noted at the beginning of August 2002 when the upwelling was least intense (Fig. 2).

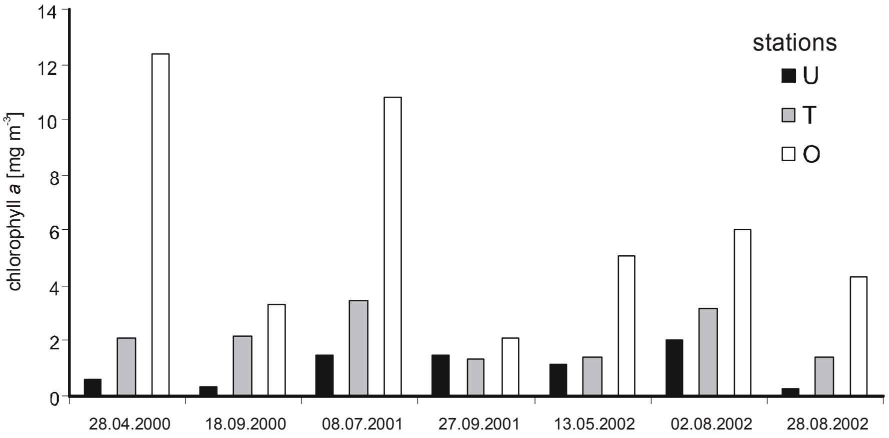

Fig. 1. Mean values of depth-integrated chlorophyll *a* concentration (0-10 m) during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

Table 1

Parameters for daily primary production estimation by simulated *in situ* method the values calculated from photosynthetic light curve mean chlorophyll *a* concentration (0-10 m depth) during upwellings along the Hel Peninsula

Date	Station	AN	E_m	Chlorophyll *a*	E_d (PAR)	k	PPobl (E_d)
		values calculated from photosynthetic light curve		mean 0-10 m			
		[mg C mg chl^{-1} h^{-1}]	[kJ m^{-2} h^{-1}]	[mg m^{-3}]	[kJ m^{-2} d^{-1}]	[m^{-1}]	[mg C m^{-2} d^{-1}]
28.04.2000	U	5.05	282	0.58	11946	0.252	349
	T	4.45	329	2.10	11946	0.272	1000
	O	3.82	330	12.39	11946	0.542	2543
18.09.2000	U	3.80	372	0.34	7835	0.279	103
	T	3.33	381	2.17	7835	0.337	474
	O	3.45	369	3.31	7835	0.810	315
08.07.2001	U	2.70	472	1.50	10167	0.257	425
	T	2.56	662	3.42	10167	0.277	732
	O	1.76	314	10.83	10167	0.398	1481
27.09.2001	U	2.60	373	1.47	5288	0.208	342
	T	2.40	366	1.32	5288	0.185	454
	O	2.93	274	2.11	5288	0.237	547
13.05.2002	U	1.74	330	1.14	2906	0.256	126
	T	1.74	327	1.40	2906	0.236	169
	O	1.67	276	5.07	2906	0.232	666
02.08.2002	U	6.13	550	2.05	9175	0.342	855
	T	4.73	416	3.21	9175	0.269	1472
	O	5.03	456	6.04	9175	0.321	2384
28.08.2002	U	3.55	528	0.26	7465	0.197	95
	T	2.17	274	1.43	7465	0.209	383
	O	2.50	336	4.30	7465	0.357	735

where:

AN - assimilation number corresponding to light saturation

E_m - PAR intensity corresponding to photosynthesis saturation

Chlorophyll *a* - depth-integrated chlorophyll *a* concentration (0-10 m)

E_d (PAR) - daily dose of PAR in the subsurface sea layer

k - diffusive coefficient of scalar PAR attenuation in water

PPobl (E_d) - daily primary production

U - upwelling station

T - transitional station

O - outer station

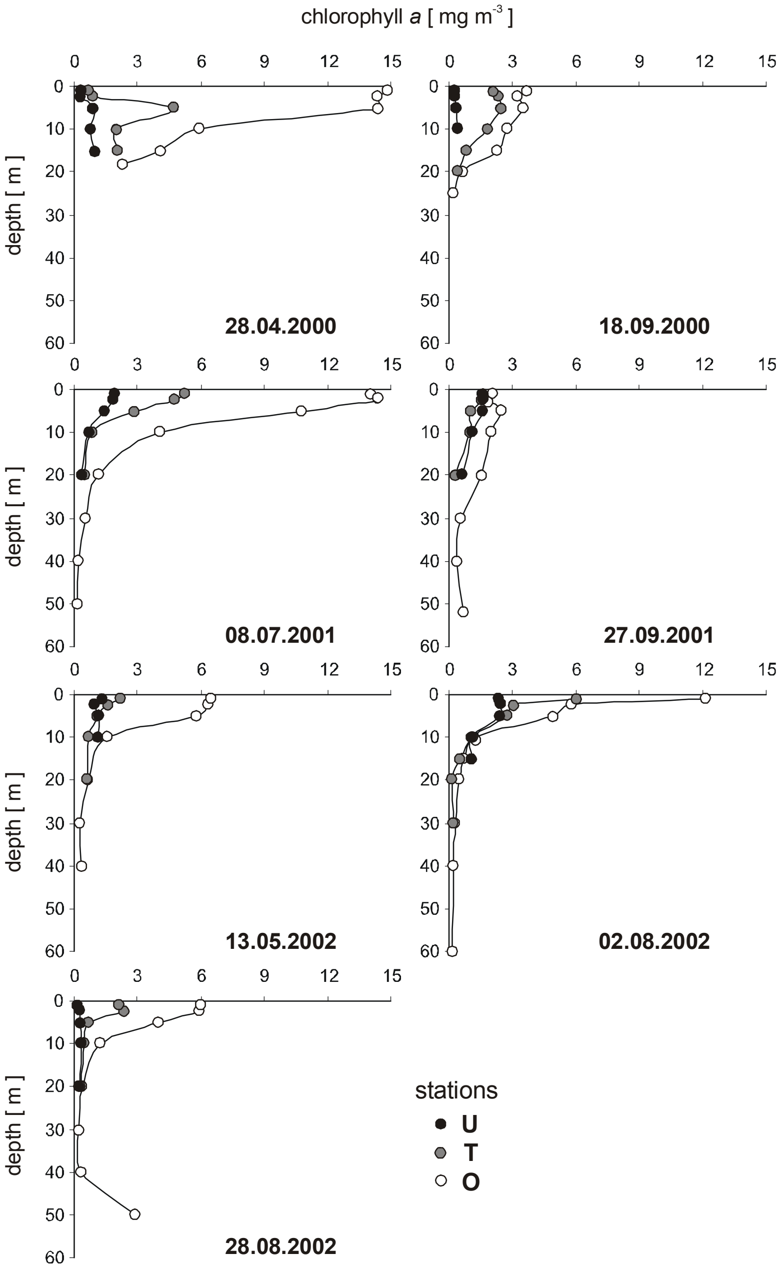

Fig. 2. Vertical profiles of chlorophyll *a* concentration during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

Similarly as in the case of mean chlorophyll *a* concentrations, the highest values of daily primary production estimated by simulated *in situ* method were usually obtained outside the zone of direct upwelling influence (the O stations), irrespective of observation time. The maximum value, 2543 mgC m^{-2} d^{-1}, was noted on the 28th of April, 2000 (Fig. 3). The measurements performed on the 18th of September, 2000 were an exception from the above regime since the estimated primary production at the reference station appeared to be lower than at the T station situated in the upwelling transitional zone (Fig. 3). Minimum values of daily primary production were typical of the U stations situated in the upwelling centre (Table 1, Fig. 3). The highest values of potential primary production were noted outside the region of direct upwelling influence (the O stations) with a peak between 0 and 5 m depth. The values decreased with an increase in water depth. The minimum values of potential primary production, similarly as daily primary production estimates, were observed in the upwelling centre (the U stations, Fig. 4). The estimated correlation between chlorophyll *a* concentration and primary production also points at interdependence of both parameters. R^2 values for potential primary production and chlorophyll *a* concentration, and for daily primary production (estimated by simulated *in situ* method) and mean chlorophyll *a* concentrations (0-10 m depth) were 0.8355 and 0.6358, respectively. Regression lines and R^2 coefficients were determined with an assumption that primary production was zero when chlorophyll *a* was absent (Fig. 5). Assimilation numbers (ANs) calculated from the light curves

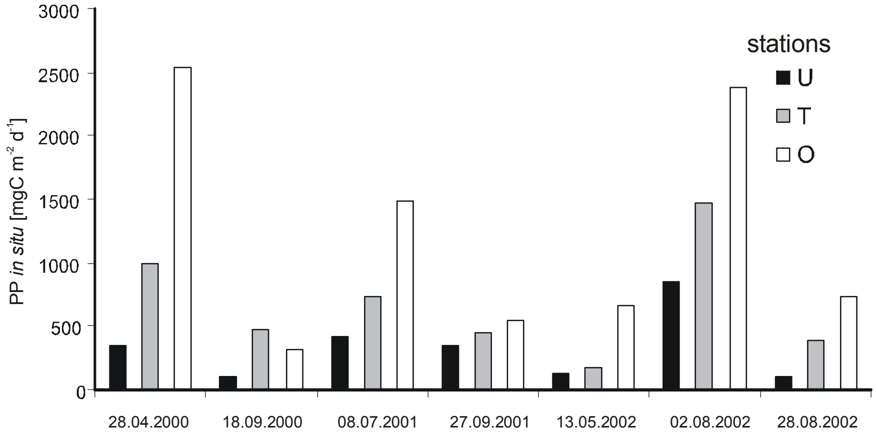

Fig. 3. Daily primary production estimated by simulated *in situ* method during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

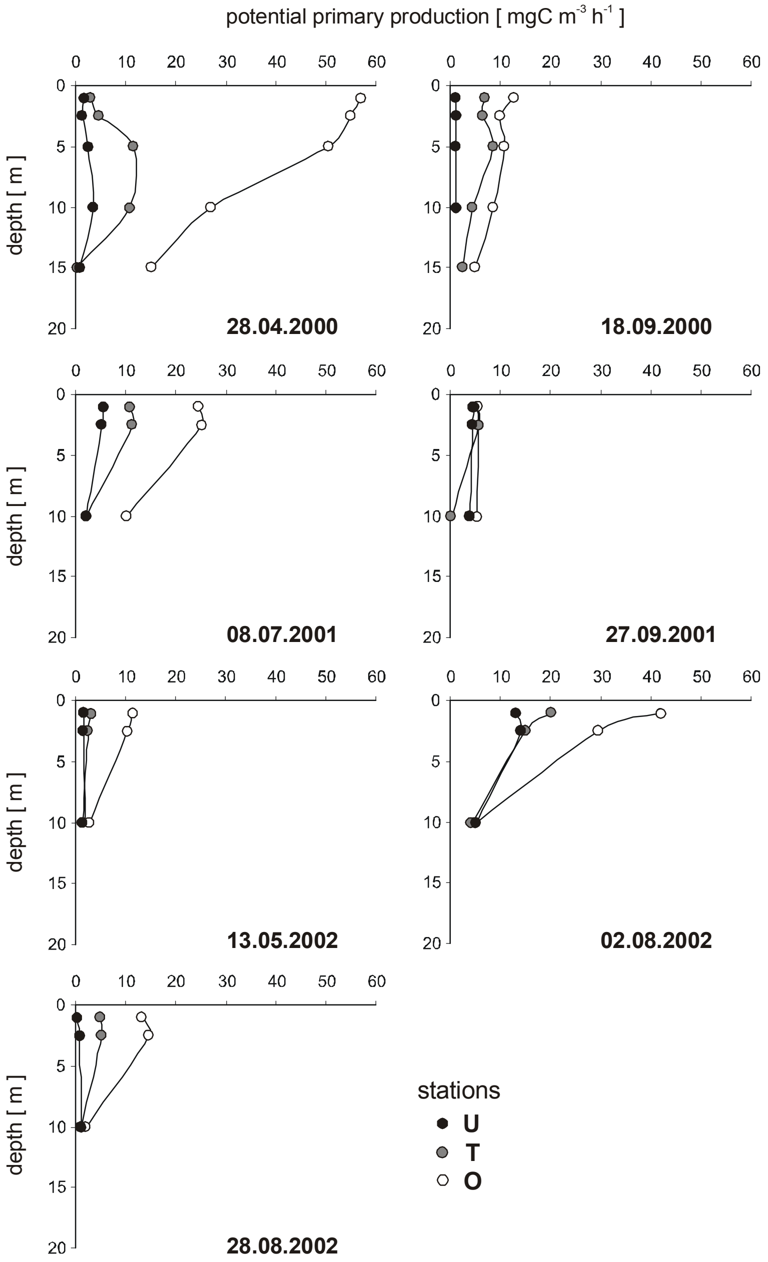

Fig. 4. Vertical profiles of potential primary production during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

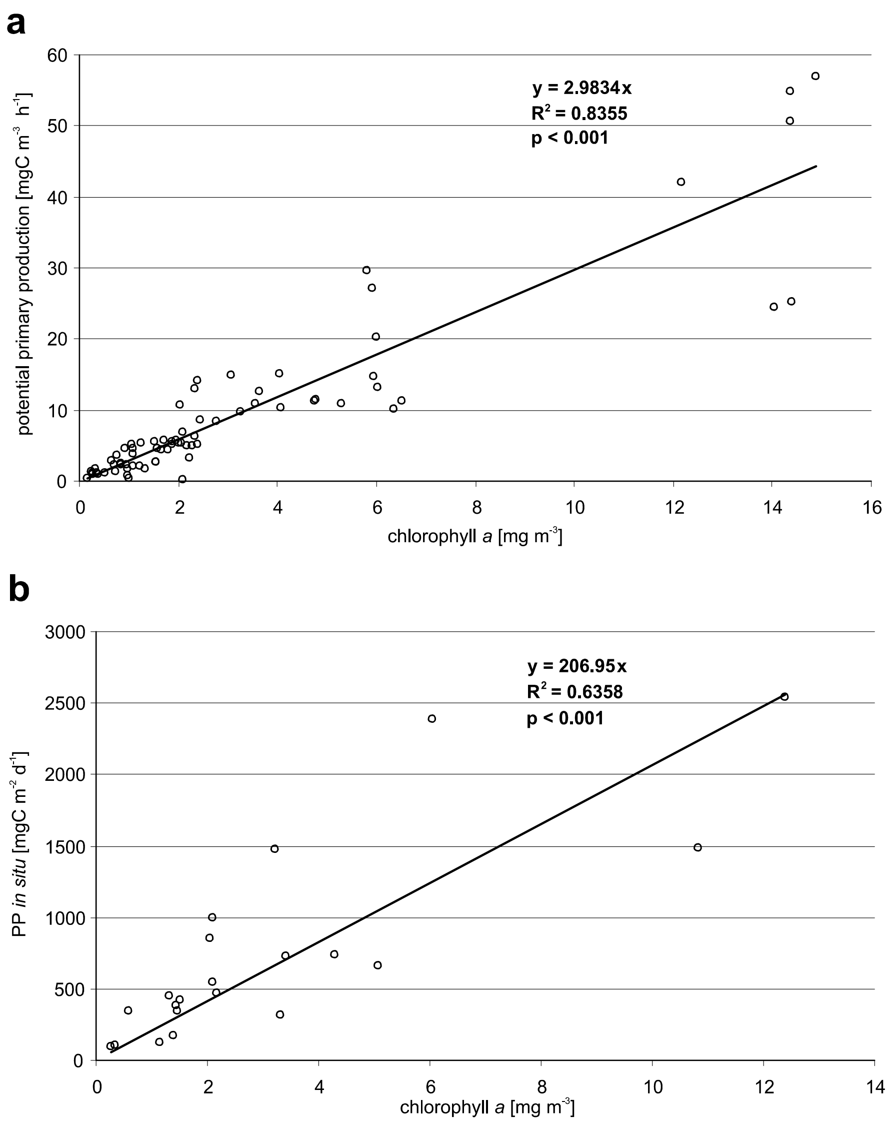

Fig. 5. Correlation between chlorophyll *a* concentrations and potential primary production (a) and correlation between average chlorophyll *a* concentrations (0-10 m) and daily primary production estimated by simulated *in situ* method (b) during upwellings along the Hel Peninsula.

(values estimated for optimum light conditions) usually showed maximum values in the upwelling centre (the U stations, Fig. 6). The above regularity was not found in two cases. On the 13th of May, 2002 assimilation numbers at the U and T stations were the same whereas on the 27th of September, 2001 assimilation number at the reference station (O) was higher than at the U station (Table 1, Fig. 6).

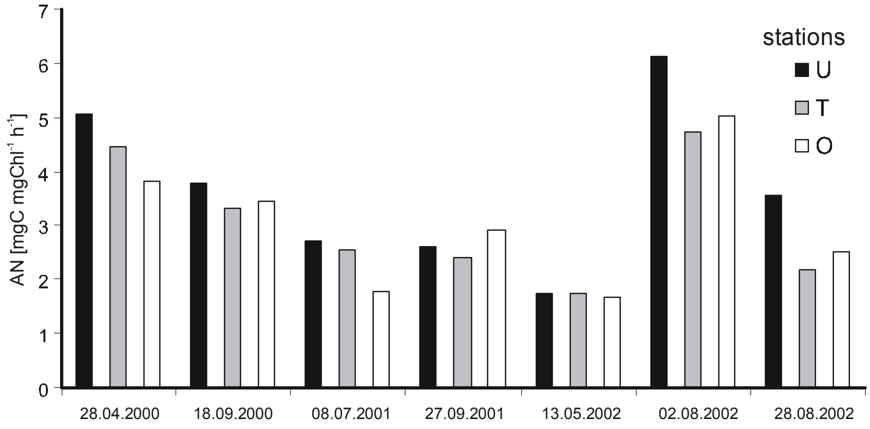

Fig. 6. Calculated assimilation numbers (ANs) under optimum light conditions during upwellings along the Hel Peninsula; U - upwelling station, T – transitional station, O - outer station.

DISCUSSION

Low chlorophyll *a* concentration and water temperature in the Hel upwelling water correspond to low primary production and phytoplankton biovolume (Gromisz and Szymelfenig 2005). Additionally, low water temperature may limit phytoplankton growth (Renk *et al.* 1999). However, an increase in temperature in the upwelling plume, even by several degrees, accelerates phytoplankton growth and may result in multiple increase in chlorophyll *a* concentration over a period of a few days (Nõmmann *et al.* 1991). The Hel upwelling is characterized by unfavourable thermal conditions since water temperature decreases, even by more than 10 °C (Matciak *et al.* 2005a). On the other hand, new primary production could be promoted by an increase in nutrients inflow (Burska and Szymelfenig 2005) and water transparency (Matciak *et al.* 2005b). The upwelling range and intensity estimated by the differences in the surface water temperature between the measuring stations is clearly reflected in horizontal and vertical distributions of chlorophyll *a* concentration. The more intense upwelling, the lower and more uniform chlorophyll *a* concentration in the water column of the upwelling centre. During intense upwellings chlorophyll *a* concentration in the surface water layer (0-2.5 m) was significantly higher at the transitional (T) and reference (O) stations as compared to the upwelling centre (the U stations) - the amount of phytoplankton in water upwelled from deeper layers is much lower than in the surface layer. The differences between the upwelling centre and the transitional and reference regions were almost 10-fold and over 20-fold, respectively. The maximum chlorophyll *a* concentration (12.4 mg m^{-3}) observed at the O station was almost three times higher than in the Gulf of Gdańsk in summer (4.5 mg m^{-3}) (EEA 2001). The differences in chlorophyll *a* concentrations between the upwelling centre and the reference zone were also markedly affected by the season of the year. In autumn chlorophyll *a* concentration in the reference area was significantly lower than in spring and summer. Therefore, the differences between the stations appeared to be smaller. Higher chlorophyll *a* concentrations observed in the upwelling water plume in autumn could be influenced by the occurrence of typical phytoplankton community which was observed as early as in mid September (Gromisz and Szymelfenig 2005).

Primary production depends strongly on chlorophyll *a* concentration, light conditions, temperature and nutrients availability (Renk *et al.* 2000). The combined effect of the above factors affects primary production within the area of direct upwelling influence (the U stations), the transitional zone (the T stations) and the reference area (the O stations).

The results obtained indicate that in the whole study area primary production depended, first of all, on chlorophyll *a* concentration (Fig. 5). In the regions of high chlorophyll *a* concentration both daily primary production estimated by simulated *in situ* method as well as potential primary production reached the highest values (Figs. 3, 4 and 5). When chlorophyll *a* concentration was low, *i.e.* in the region of the U stations, the primary production level could not be compensated by higher values of assimilation numbers (Figs. 3 and 6). In this case, chlorophyll *a* concentration affected primary production according to the feedback mechanism, *i.e.* primary production increased with an increase in phytoplankton biomass (Renk and Ochocki 1998).

When chlorophyll *a* concentrations are similar, primary production is influenced by light and temperature (Renk *et al.* 2000). Although, on the 18th of September, 2000 chlorophyll *a* concentration at the O station was higher (by *ca.* 30%) than at the T station, daily primary production estimated by simulated *in situ* method appeared to be lower. In this case the daily primary production level depended on the value of light attenuation coefficient, which was over three times higher at the O station (Table 1, Figs. 1 and 3).

Assimilation number values (determined for light saturation conditions) point at higher photosynthesis rate in the upwelling region (the U stations) as compared to the other regions. According to Renk (2000), the value of assimilation number depends on thermal, trophic and light conditions as well as phytoplankton species composition. The combined effect of the above factors influences the variability of the obtained assimilation numbers (Table 1, Fig. 6). It could be presumed that trophic conditions in the region of the U stations resulted in high values of assimilation number compared to the transitional and reference regions.

The upwelled near-bottom waters show a distinct impoverishment in organic matter what was manifested by lower particle number (3-5 times) as well as smaller amount of phytoplankton-derived carbon as compared to the reference area (Bradtke *et al.* 2005). This is also revealed in phytoplankton taxonomic composition (Gromisz and Szymelfenig 2005) and lower production level during upwelling event, similarly as in the other Baltic regions (Kahru *et al.* 1984, Ennet *et al.* 2000).

The Hel upwelling could be distinguished by similar properties as the other upwellings in various world regions, *e.g.* Punta San Hipolio, Baja California (Walsh *et al.* 1974), 15°S at the coast of Peru (MacIsaac *et al.* 1985), Point Conception, California (Wilkerson and Dugdale 1987), Benguela in South Africa (Shillington *et al.* 1990). The upwelling centre situated close to the shore is characterized by low temperature (Matciak *et al.* 2005a), high water transparency (Matciak *et al.* 2005b), high nutrients level (Burska and Szymelfenig 2005) but low chlorophyll *a* concentration and primary production. As the distance from the centre increases, the waters in the upwelling plume gets warmer, chlorophyll *a* concentration is higher and a decrease in nutrients is observed.

According to MacIsaac *et al.* (1985), four zones of physiological conditions could be distinguished along the axis of the upwelling plume. In zone I phytoplankton upwelled with nutrient-rich water is initially „shifted-down"; in zone II it undergoes light-induced „shift-up" to increased nutrient uptake, photosynthesis and synthesis of macromolecules. In zone III ambient nutrient concentration is rapidly reduced, there is a rapid accumulation of phytoplankton biomass in the water column and the processes proceed at maximum rates. In zone IV ambient nutrient concentration is significantly decreased, phytoplankton remains high, and limitation of phytoplankton processes is observed. At 15° S on the coast of Peru, in time and space domain where this entire sequence occurs, the cycle from initial upwelling to „shift-down" was completed in 8 to 10 days within 30 to 60 km off the coast (MacIsaac *et al.* 1985).

The area of Hel upwelling is much smaller. It is usually some or several kilometers in width and sometimes it could reach 30 km (Urbański 1995). However, the upwelling duration varies over a fairly broad range, from a few tens of hours to almost 30 days (Urbański 1995). The obtained spatial distributions of chlorophyll *a* concentration and primary production show a good agreement with I and II zones described by MacIsaac *et al.* (1985). It also seems that the conditions at the reference stations, assumed to be situated outside direct upwelling influence, represent a good correlation with the conditions in zone III.

In various coastal regions the frequent temporal and spatial displacement between high nutrient and chlorophyll concentrations, especially during strong upwelling events (Small and Menzies 1981, MacIsaac *et al.* 1985, Dugdale and Wilkerson 1989), suggests a lag in phytoplankton response to enhanced nutrient concentration. The observed lag phase depends not only on wind strength, which induces upwelling evolution (Pinazo *et al.* 1996, Carr 1998) and nutrient concentrations (Zimmerman *et al.* 1987) but also on adaptation period of phytoplankton cells to temperature, light and nutrient concentrations (Collos 1986). Therefore, maximum chlorophyll concentration could be observed even during the relaxation period (Dugdale and Wilkerson 1989). It could be supposed that in the region of Hel upwelling the highest production rates may be associated with relaxation events as well.

It is important to note that one of the biggest Baltic rivers, the Vistula, flows to the Gulf of Gdańsk. The river waters could frequently reach the coast of the Hel Peninsula from the side of the open sea (Majewski 1972). In this case the separation of allochtonous and upwelling sources of substances and the estimation of their effect on new primary production would appear to be a difficult task. It will be also difficult to distinguish upwelling new production from total primary production since the Hel upwelling occurs very close to the coast (Urbański 1995, Kowalewski 1998, Matciak *et al.* 2005a) and, depending on its intensity, the upwelled waters are mixed with the coastal surface waters.

Summing up, the results of primary production and chlorophyll *a* concentration measurements, which were obtained in the Hel upwelling region, indicate the following regularities:

- upwelling range and intensity were reflected in horizontal and vertical distributions of chlorophyll *a* concentrations;
- minimum concentrations of chlorophyll *a* and low values of primary production were observed in the upwelling centre (the U station region);

- maximum concentrations of chlorophyll *a* and high values of primary production were noted in the region of the O station, which was situated in the reference area, outside the direct influence of upwelling waters;
- the values of potential primary production and daily primary production (estimated by simulated *in situ* method) depended mainly on chlorophyll *a* concentration;
- the differences in chlorophyll *a* concentrations and primary production values between the upwelling centre and the reference area were significantly lower in autumn than in spring and summer;
- high values of assimilation numbers (determined for light saturation conditions) point at favourable trophic conditions in the upwelling centre (the U station region) as compared to assimilation numbers obtained for the transitional and reference areas.

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