La mer 35: 49-68, 1997
Société franco-japonaise d'océanographie, Tokyo

Nutrients limiting the Algal Growth Potential (AGP) in the Gulf of Riga, eastern Baltic Sea, in spring and early summer 1996

Serge Y. MAESTRINI*, Maija BALODE**, Christian BÉCHEMIN*
Ingrida PURINA** and Céline VÉRITÉ*

Abstract: In May, June and July 1996, samples were collected along one transect greatly influenced by river discharge (eastern side of the gulf), along one transect slightly influence by river discharge (western side), at one station located in the mouth of the main river (River Daugava), at one station located in the center of the Gulf and at several nearshore locations of the western side. Ratios of molecular concentrations of *in situ* dissolved inorganic nitrogen, phosphorus and silicon, as well as enrichment bioassays were used to determine which nutrient (s) limited the potential biomass of phytoplankton. Both comparison of $(NO_3+NO_2+NH_4)$: PO_4 (DIN : DIP) values with Redfield's ratio and bioassay inspection led to the same conclusions. Phosphorus was clearly the nutrient most limiting for the potential biomass of test species in nitrogen-rich waters, which occurred in mid spring, in the upper layer of the southern-eastern part of the Gulf which is greatly influenced by river discharge. In late spring, with the decrease of the total DIN reserve, nitrogen and phosphorus showed an equal limiting role. In deeper layers of this area and out of the river plume (western side and central part of the gulf), nitrogen was the limiting nutrient. In summer, when river discharge was the lowest, all DIN concentrations but one ranged between 1.6 and 2.6 μM, and the whole area was nitrogen-limited for both the cyanobacterial and the algal test strains. In 74% of the samples for which nitrogen was the limiting nutrient, phosphorus was recorded to be the second potentially limiting nutrient. In contrast, silicon never appeared as limiting the growth potential of either *Microcystis aeruginosa* or *Phaeodactylum tricornutum*; phosphorus was the limiting nutrient when DIN : SiO_3 values were >1 (in May), but DIN : SiO_3 was <1 when nitrogen was limiting (June and July). The authors conclude that the recently reported decrease of silicon loading in coastal waters and its subsequent enhanced importance in pushing the outcome of species competition towards harmful species may not yet be the most important factor for the Gulf of Riga. Iron appeared for 12% of the tests in the list of nutrients limiting the potential biomass. Tentative results also indicated that a significant fraction of the nitrogen ($\sim 4\,\mu$g-atom $N\,l^{-1}$) taken up by *Microcystis aeruginosa* may have been in the form of dissolved organic nitrogen (DON). It is thus also suggested tentatively that more attention be paid to these nutrients during further research in the Gulf of Riga.

1. Introduction

In recent decades, noxious algal events have emerged as a major environmental problem in the Baltic Sea (HORSTMANN, 1975; NIEMI, 1979; NEHRING, 1992), as well as in many other coastal waters (NIXON, 1990; DEDEREN, 1992; HALLEGRAEFF, 1995). Increase in nutrient concentration resulting from river discharges and varied loadings has been suggested as responsible for both macroalgal and phytoplankton biomass increases (BOIKOVA, 1986; ROSENBERG *et al.*, 1990; ANDRUCHAITIS *et al.*, 1993, 1995; PITKÄNEN *et al.*, 1993; YURKOVSKIS *et al.*, 1993). Bottom-water oxygen deficiencies and subsequent faunal mortality have been the most commonly observable consequences of excess in algal biomass in summer (BADEN *et al.*, 1990; RICHARDSON, 1990). Changes in phytoplankton population structure have been also marked (SCHULZ and KAISER 1986, WULFF *et al.*, 1986;

*Centre de Recherche en Ecologie Marine et Aquaculture de L'Houmeau (CNRS-IFREMER), B. P. 5, 17137 L'Houmeau, France
E-mail: smaestri-@ifremer. fr
**Institute of Aquatic Ecology, University of Latvia, Miera Iela 3, LV-2169 Salaspils, Latvia

CEDERWALL and ELMGREN, 1990; BALODE, 1996).

Nitrogen has been invoked most as the principal nutrient limiting algal growth potential in seawater when light and temperature are adequate and losses do not prevail (RYTHER and DUNSTAN, 1971; HCKY and KILHAM, 1988; HOWARTH, 1988; GRANÉLI *et al.*, 1990). Accordingly, one might expect that the more nitrogen were present, the more algal biomass would develop (RUDEK *et al.*, 1991). Several authors, however, have reported either co-occurring or successive limiting nutrients (SMAYDA, 1974; BERLAND *et al.*, 1978; LEVASSEUR *et al.*, 1990; FISHER *et al.*, 1992). In addition, the growth potentials of different species in the same assemblage may be limited by different nutrients (MAESTRINI and BONIN, 1981).

Human activities have significantly increased the input of algal nitrogenous and phosphorus nutrients to estuarine and coastal waters. In contrast, the silicon concentration has remained constant or has even decreased in river loadings, as a result of its absence in human wastewater and the secondary effect of eutrophication in freshwater, which leads to larger blooms of diatoms and subsequent exhaustion of the silicate content before discharge into the sea (SCHELSCKE and STOERMER, 1972; EGGE and AKNES, 1992). Hence, altogether, along with increased eutrophication in coastal water, N : Si and P : Si nutrient ratios have increased (RAHM *et al.*, 1996), and silicon limitation has become potentially more likely (OFFICER and RYTHER, 1980; Conley *et al.*, 1993; RAGUENEAU *et al.*, 1994).

Cyanobacteria have been the taxon most frequently cited as giving harmful blooms in the Baltic Sea in summer (EDLER *et al.*, 1985; KONONEN, 1992; BALODE, 1993; HEISKANEN and KONONEN, 1994; LEPPÄNEN *et al.*, 1995; TENSON, 1995). Moreover, their presence seems to have increased in the past decades both in space and time (KAHRU *et al.*, 1994). Toxin-producing dinoflagellates, which develop in waters of low nutrient concentrations, and which can be harmful at low biomass levels, have also been recently reported in the same area (WILLÉN *et al.*, 1990; CARPENTER *et al.*, 1995; BALODE and PURINA, 1996). Thus, the present situation might concur with the above-mentioned assumption that the continuous relative depletion of silicon in freshwater would lead to diatoms being replaced by non-siliceous forms such as cyanobacteria and green algae (SCHELSKE and STOERMER, 1972).

On this basis, we have endeavored to investigate whether uptake of dissolved organic compounds might favor the growth potential of toxic cyanobacteria and dinoflagellates in the same assemblage. Here we report an investigation of the nutrients limiting the growth potential in one cyanobacterium and one diatom, both grown in water collected from spring to summer in the Gulf of Riga. Data provided by bioassays have also been tentatively used to estimate the fraction of nitrogen taken up by these strains which might have been provided by dissolved organic matter

2. Material and methods

Samples were collected following two different strategies: (i) In early May, early June and early July 1996, seawater was taken at varied depths along two transects (Fig. 1); the first transect started from Saulkrasti, on the south-eastern coast of the gulf, while the second one started from Melluzi, on the south-western coast. In addition, one sample was collected in the mouth of the river Daugava, and another in the central part of the gulf. Seawater was sampled with Niskin bottles, filtered on glass-fiber filters (GF/C, 0.8 μm pore equivalent), and stored deep-frozen until use on 10 July. (ii) On 19 July 1996, nearshore surface water was collected with a bucket at various stations on the southern coast. Samples were filtered on glass-fiber filters (GF/C, 0.8 μm pore equivalent), then kept overnight at 4°C and used for experiment on 20 July.

Ammonium (KOROLEFF, 1969) and phosphate (MURPHY and RILEY, 1962) concentrations were immediately measured by using manual protocols. Other nutrients were analysed later on deep-frozen subsamples by using a Skalar autoanalyzer: nitrate (reduction to nitrite according to protocols of STRICKLAND and PARSONS, 1972), nitrite (BENDSCHNEIDER and ROBINSON, 1952), silicate (MULLIN and RILEY, 1965), urea (KOROLEFF, 1976). Total nitrogen and total phosphorus were obtained after

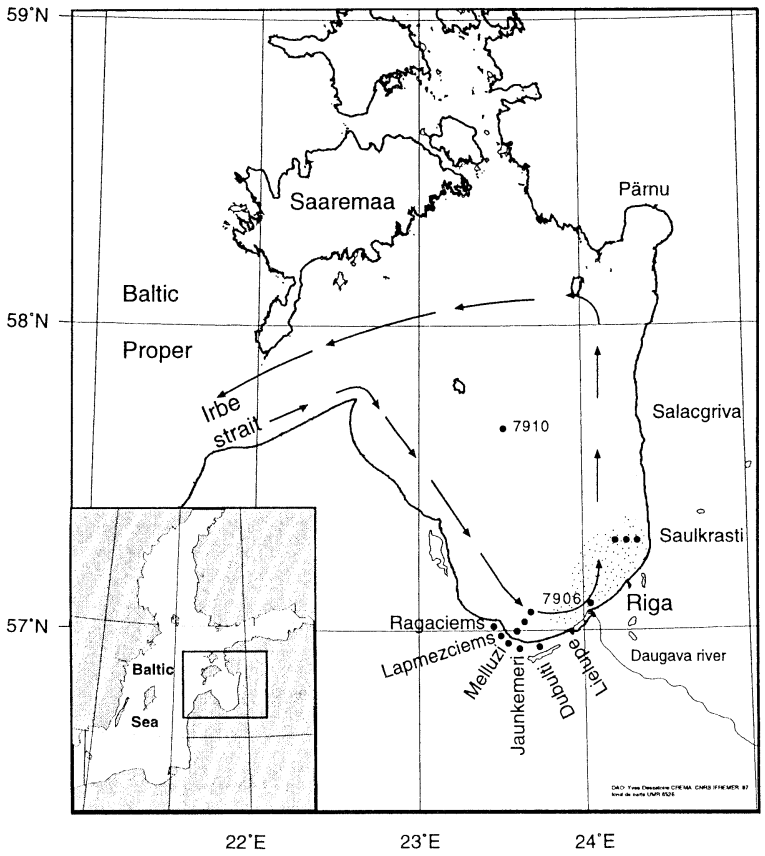

Fig. 1. Study area and positions of sampling stations.

ultraviolet oxidation under successive acid and alkaline conditions (COLLOS and MORNET, 1993), and then treated as for soluble reactive nitrogen and phosphorus.

Bioassays for nutrient (s) limiting growth potential.

Aliquots (30 ml) of either unfrozen or subsequently thawed samples were placed in 33-ml polycarbonate tubes, and the respective enrichment mixtures (Table 1) were added in volumes of 1 ml. Initial nutrient concentrations in the spike-enriched media were assumed to be low enough not to change the ecophysiological adaptation of the test algae and to be high enough to sustain an algal biomass significantly higher than that sustained by the unenriched control, thereby making clear which nutrients, if any, were present *in situ* at concentrations sufficiently high to sustain growth and which were not (for detailed discussion, see MAESTRINI *et al.*, 1984). Two cultured strains were used as test organisms: *Microcystis aeruginosa* (strain: Station Marine d'Endoume, France, courtesy of Dr B. BERLAND) was chosen for being a dominant summer component of local planktonic communities (BALODE and PURINA, 1996); *Phaeodactylum tricornutum* (strain: Plymouth Marine Biological Laboratory, England, courtesy of Dr. M. PARKE) was chosen for its capability to take up nutrients at extremely low concentrations (BONIN *et al.*, 1986). Test cells were inoculated in maximum volumes of 250 μl, in numbers to give an initial cell density of 136×10^6 cells. l^{-1} (experiment of 10 July) or 557×10^6 cells. l^{-1} (experiment of 20 July) of *Microcystis aeruginosa*, and 6.9×10^6 cells. l^{-1} (experiment of 10 July) or 9.2×10^6 cells. l^{-1} (experiment of 20 July) of *Phaeodactylum tricornutum*; these cells

Table 1. List and composition of spike enrichments used to bioassay the nutrient (s) limiting the growth potential of *Microcystis aeruginosa* and *Phaeodactylum tricornutum*; initial nutrient concentrations in the test cultures (equivalent to the enrichments alone) are indicated within parentheses.

1	Nothing	12	All–N
2	Nothing	13	All–P
3	Nothing	14	All–P
4	Nothing	15	All–Si
5	Nothing	16	All–Si
6	All	17	All–(Fe–EDTA)
7	All	18	All–(Fe–EDTA)
8	All–N	19	All–vitamin mix(Vit)
9	All–N	20	All–vitamin mix
10	All–N	21	All+metal mix(M)
11	All–N	22	All+metal mix

All=N (50 μM) +P (3.4 μM) +Si (60 μM) +Fe (200 nM) +EDTA (1.2 μM) +Metal mix=Co (5 nM) +Mn (100 nM) +Mo (100nM) +Vitamin mix=biotin (410 pM) +cyanocobalamin (135 pM) +thiamin (150 nM)

had been previously nutrient–depleted by culture for 2–3 days in nutrient–poor water. Incubation of the test cultures was carried out by placing the tubes before a north–facing window; light period was roughly 14 hours' light and 10 hours dark, at circa 100 μmole. $m^{-2}. s^{-1}$; temperature varied between 18 ℃ and 22 ℃ within a circadian period. *In vivo* fluorescence was moni-tored daily, during 6–10 days, with a R10 Turner Fluorometer (BRAND *et al.*, 1981), up to the respective maximum growth. Respective fluorescence values were then used to produce bar diagrams, with the value obtained after all-nutrient enrichment defined as 100%.

Data sets were first inspected by comparing the different enriched–culture fluorescence values to those of the unenriched and all–nutrient enriched controls. For each set (one water sample–one test species), it resulted in a number and a rank for each limiting nutrient. Then, in order to quantity the limiting role of each nutrient, the ratio of fluorescence in the "All minus one nutrient" enriched aliquots to the fluorescence in the unenriched control (abridged "All–X/control") was also calculated. In other words, for each particular nutrient missing in the spike and therefore present in the culture medium at its *in situ* concentration, this ratio is the increase in the coefficient of the natural AGP sustained by that nutrient. Hence, the lower the coefficient, the greater limiting effect, and vice versa. All included, 35 bioassay sets were done with 28 water samples and two test strains. All test cultures but four grew well, thus indicating no adverse chemical condition.

Bioassays for indirect estimation of the uptake of dissolved organic nitrogen.

Aliquots (30 ml) of unfrozen or thawed samples were distributed in 33–ml polycarbonate tubes. For *Microcystis aeruginosa*, five aliquots were left unenriched, and five others were enriched with the "All – N" mixture. With *Phaeodactylum tricornutum* only, five unenriched aliquots were grown. Growth and maximal biomass were estimated as for the differentially enriched bioassays. Mean values and standard deviations were calculated for each set of five biomass values; samples which differed by more than 50% of the standard deviation were discarded; others were pooled and used for analysis of DIN (NO_3, NO_2, NH_4). Nitrogen uptake was calculated as being the difference between concentration at time zero and the respective concentration at the time of maximum biomass. The biomass was estimated after filtration on glassfiber filters (nominally 0.45 μm), by analysis of the content of protein (PETTY *et al.*, 1982) for *M. aeruginosa*, or chlorophyll *a* (JESPERSEN and CHRISTOFFERSEN, 1987) for *P. tricornutum*.

Table 2. Nutrient concentrations (μM) in samples collected at different depths along transects on 1–5 May, 4 June and 3-4 July, as well as samples collected on 19 July at different nearshore stations. SA: transect from Saulkrasti, ME: transect from Melluzi.

Stations	Z (m)	S %	NO_3 (μM)	NO_2 (μM)	NH_4 (μM)	Urea (μM)	DIN (μM)	PO4 (μM)	DIN : P	SiO_3 (μM)	DIN : Si
Sampling of 1–5 May											
SA–03	0	3.64	35.8	0.7	0.5	3.6	36.9	0.22	167.8	10.1	3.7
SA–10	0	4.16	26.4	0.7	0.3	2.8	27.4	0.26	105.4	9.6	2.9
SA–30	5	3.70	37.5	0.6	1.0	4.3	39.1	0.34	115.1	12.6	3.2
SA–30	30	5.93	14.1	0.2	2.7	5.6	17.0	1.11	15.3	27.4	0.6
ME–10	0	5.38	8.7	0.2	0.6	1.3	9.5	0.45	21.7	2.2	4.3
ME–30	0	3.88	43.4	0.5	0.6	1.6	44.3	0.59	75.0	5.1	8.7
ME–30	10	5.17	4.7	0.7	0.6	1.9	6.0	0.73	8.1	0.4	15.0
ME–30	20	5.58	10.6	0.6	1.1	1.6	12.2	0.82	14.9	7.6	1.6
ME–30	30	6.00	12.5	0.4	1.7	3.3	14.7	1.20	12.3	20.9	0.7
7906	5	1.97	108.3	0.9	2.1	-	111.3	0.75	148.4	4.5	24.7
7910	0	5.42	5.5	0.7	0.2	1.7	6.4	0.33	19.5	3.0	2.1
Sampling of 4 June											
SA–10	0	4.01	5.6	0.5	0.7	0	6.8	0.05	135.4	1.3	5.2
SA–30	0	4.50	1.4	0.2	0.4	3.8	2.0	0.40	49.0	2.2	0.9
SA–30	5	4.95	0.4	0.1	0.4	2.8	0.9	0.03	0.5	1.8	0.5
SA–30	10	5.00	1.1	0.1	0.4	1.9	1.6	0.003	1.0	1.6	1.0
SA–30	30	5.94	11.4	0.2	1.9	7.0	13.4	0.18	103.4	19.5	0.7
Sampling of 3–4 July											
SA–05	0		1.0	0.4	1.0	4.5	2.4	0.23	10.4	3.3	0.7
SA–10	0		0.9	0.3	0.8	4.4	2.0	0.17	11.6	3.2	0.6
SA–20	0		0.7	0.3	1.0	4.2	1.9	0.15	12.8	3.1	0.6
SA–30	2.5		0.6	0.3	1.6	2.4	2.5	0.20	12.4	3.1	0.8
SA–30	5		0.5	0.2	1.7	2.9	2.4	0.15	16.2	2.6	1.0
SA–30	10		0.5	0.1	1.0	3.3	1.6	0.25	6.2	2.0	0.8
Sampling of 19 July											
Dubulti	0	4.14	0.7	0.7	0.4	5.6	2.3	0.38	6.1	6.3	0.4
Jaunkemeri	0	4.57	0.3	0.6	0.4	1.7	1.6	0.23	7.0	3.4	0.5
Lapmezciems	0	2.28	0.7	0.6	0.5	2.9	2.3	0.42	5.4	6.8	0.3
Lielupe	0	3.36	8.1	1.7	0.3	5.5	10.4	1.14	9.1	8.4	1.2
Melluzi	0	3.97	0.9	0.8	0.5	4.1	2.6	0.39	6.5	6.6	0.4
Ragciems	0	4.90	0.3	0.6	0.6	2.1	2.1	0.28	7.5	5.4	0.4

3. Results

An important decrease in the nutrient concentration occurred between spring and summer. In early May, waters were nitrogen-rich; most values of total dissolved inorganic nitrogen concentration ($DIN = NO_3 + NO_2 + NH_4$) ranged between 4.7 μM and 43.4 μM (Table 2), and the mean value was 19.9 μM (s=14.5, N=10). There was also an exceptional value of 108.3 μM recorded with water (station 7906) sampled in the plume of River Daugava. Although the absolute values were rather high (concentrations ranged between 0.22 and 1.20 μM; mean value was 0.62 μM; s=0.34; N=11), the phosphorus content was relatively not as high; most values of the ratio $DIN : PO_4$ (DIN: DIP) were greater than 16. The silicon content was also low relative to that of inorganic nitrogen. Only two values of the $DIN : SiO_3$ ratio were lower than 1; the others ranged between 1.6 and 15.

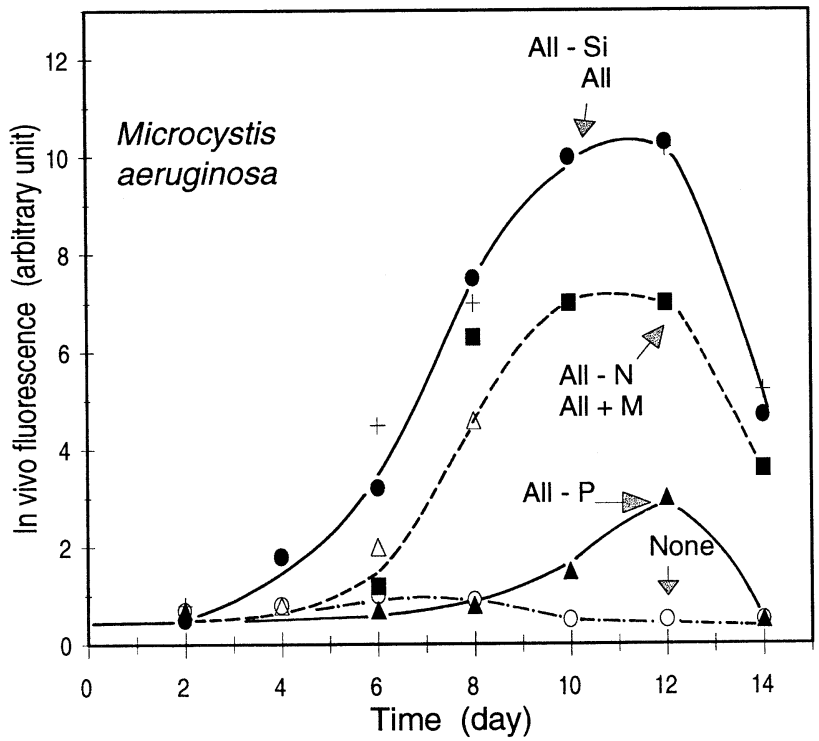

Fig. 2. *In vivo* fluorescence (arbitrary units) versus time, in differentially-enriched aliquot cultures of *Microcystis aeruginosa* (to allow the software to draw the figure, few missing data have been replaced by the mean of preceding and following values). Example of sample collected in early May 1996, at surface, at station 30 meters of the Melluzi transect.

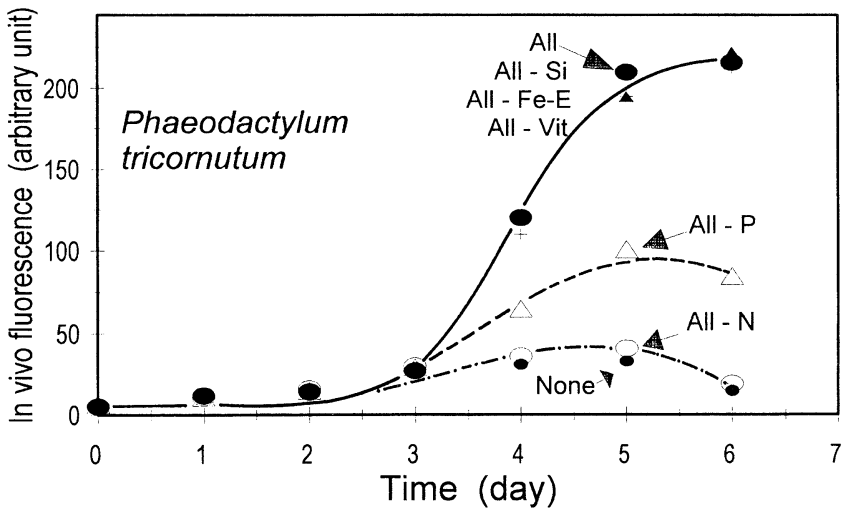

Fig. 3. *In vivo* fluorescence (arbitrary units) versus time, in differentially-enriched aliquot cultures of *Phaeodactylum tricornutum* (to allow the software to draw the figure, few missing data have been replaced by the mean of preceding and following values). Example of sample collected on 19 July 1996, at Lielupe station.

Table 3. Mean relative growth in unenriched seawater expressed as a percentage of that in the best nutrient enrichment, of *Microcystis aeruginosa* and *Phaeodactylum tricornutum* cultured in water sampled from early May to early July 1996 along Saulkrasti and Melluzi transects, and/or water collected nearshore on 19 July at different locations.

	Transect May–July	Sampling of 19 July	
	M. aeruginosa	*M. aeruginosa*	*P. tricornutum*
Mean	20.4	6.6	6.7
Standard deviation	16.8	2.8	4.8
N	20	6	6

In early June, the nutrient content had already decreased significantly. Values of DIN concentration for the upper waters ranged between 0.9 and 6.8 μM ($\bar{x}$=2.8; s=2.7; N=4), and those for phosphorus ranged between 0.03 and 0.40 μM ($\bar{x}$=0.13; s=0.18). A sharp decrease in silicon concentration ($\bar{x}$=1.7 μM; s=0.4) was also observed. Near the bottom (30–m depth) the ammonium and nitrate concentrations were much higher than in near–surface waters: 1.9 and 11.4 μM, respectively. Most values of DIN : DIP were still greater than 16, however. The silicon concentration was also high (19.5 μM).

In summer, (early July), all the coastal stations along the Saulkrasti transect, and all nearshore stations visited on 19 July (except one) were nitrogen–poor: the mean concentration of DIN was 2.2 μM (s=0.3; N=11). The Lielupe station (near the mouth of the river Lielupe and also close to the mouth of Daugava River), however, showed high DIN, 10.4 μM (Table 2). In contrast, concentrations of phosphorus and silicon had not decreased as much: mean values recorded were 0.26 μM (s=0.10) and 4.2 μM (s=1.7), respectively; at the Lielupe station, recorded values were 1.14 μM PO_4 and 8.4 μM SiO_3. Accordingly, all values of the DIN: PO_4 ratio were <16 and those of the DIN : SiO_3 ratio were <1, again except at Lielupe.

For reasons not apparent, water from two samples did not support growth and water from a further two samples supported only weak growth. Water from all the other samples, however, supported good growth. In growth trials started on 10 July, there was a two-day lag phase which prompted us to increase the initial cell density for trials started on 20 July. Overall, growth rate of *Phaeodactylum tricornutum*, as reflected by the increase of *in vivo* fluorescence, was higher than that of *Microcystis aeruginosa*.

Except for a single sample in which nutrient concentrations were extremely high (i.e. 108 μM NO_3, 1 May at station 7906), nutrientspiked test cultures showed a significant increase in the final biomass compared with unspiked cultures (Fig. 2 and 3). With surface samples collected on 19 July, the maximum biomass in the unspiked controls averaged no more than 6.6% for *M. aeruginosa* and 6.7% for *P. tricornutum*, of the spiked culture giving the best growth. With waters taken during transects in early May, June and July, the unenriched aliquots sustained a biomass in *M. aeruginosa* averaging 20.4% of that in the best enrichments (Table 3). Growth was only slightly enhanced, however, when nitrogen or phosphorus were absent in the enrichments (Fig. 4). Omission of phosphorus alone (All–N) usually gave a smaller biomass than did omission of nitrogen alone (All–P), however. The absence of chelated iron had similar consequences in only four cases. Omission of silicon and vitamins from the enriching mixtures did not decrease the yield of either the cyanobacterium and the diatom. On the other hand, the addition of Co, Mn and Mo clearly did not promote growth, and even slightly inhibited growth in both test species (Fig. 4).

Inspection of the bioassay sets showed that in all cases but a few, the AGP was limited by at least two nutrients; in only 4 samples was nitrogen the single limiting nutrient, although there was also one sample for which no nutrient was limiting (Table 4). Over the 31 sets of bioassays which led to clear results, three simultaneous limiting factors were found in only

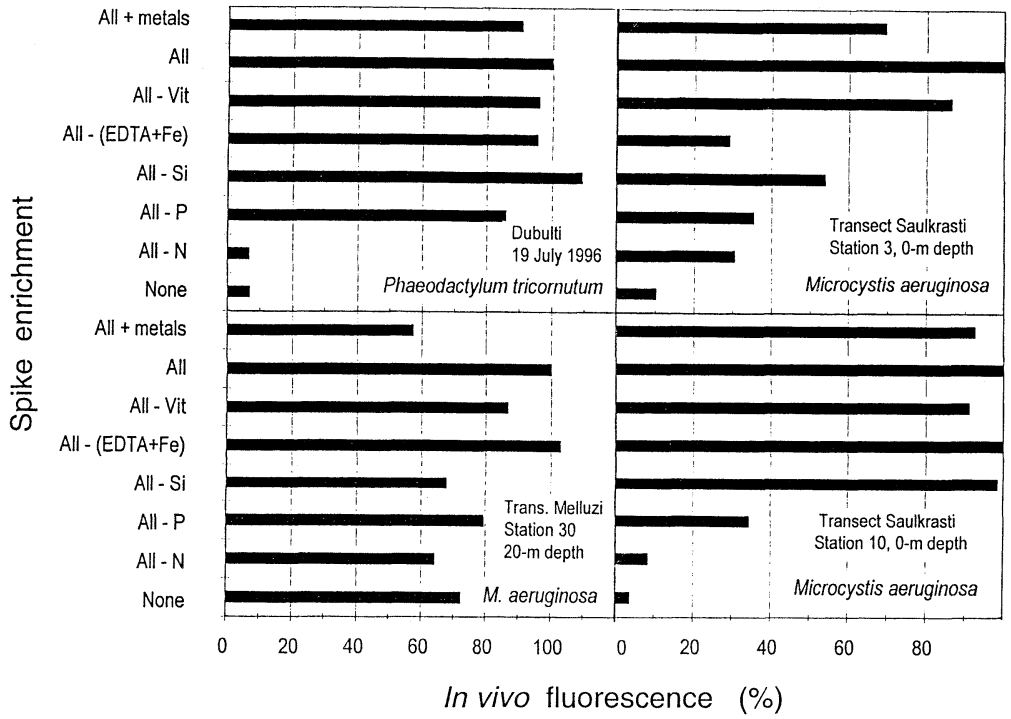

Fig. 4. Relative maximum algal biomass (%) versus spike enrichment; typical sets of data used for empirical analysis of nutrient limitation of AGP. *Phaeodactylum tricornutum* (top, left): N only is limiting; *Microcystis aeruginosa*: (top, right): N and Fe–EDTA are equally limiting, P is the third limiting nutrient; (bottom, left): inconclusive data; (bottom, right): N is first limiting, P is the second limiting nutrient.

6 samples. For both test species, nitrogen was found to be the primary limiting nutrient in 68% samples, but phosphorus in only 13%, colimitation by N and P in 19% (all for *M. aeruginosa*), and one case for which Fe–EDTA was equally as limiting as N and P. When nitrogen or phosphorus was not the first limiting nutrient, it was the second, except for one case of co-limitation at the second rank by nitrogen and iron. Equal third as the most limiting nutrient were iron and the vitamins, each in two samples over the 31 sets of bioassays. Silicon never appeared to limit the growth potential of the test species.

The nature of nutrients limiting the growth potential of test species changed from spring to summer. In early May, over nine samples (Table 4), phosphorus was the first limiting nutrient for *M. aeruginosa* growth in three samples and was co-limiting with nitrogen in a further four. In one sample, phosphorus was also first limiting for *P. tricornutum*. In contrast, nitrogen was the first limiting nutrient in all samples collected on 19 July, for both *M. aeruginosa* and *P. tricornutum*.

Mean values of the coefficient reflecting the limiting effect of each nutrient ranged between 0.2 and 2.2 for nitrogen (Table 5), between 2.2 and 6.3 for phosphorus, between 7.7 and 34.8 for silicon, between 7.1 and 25.6 for iron and Fe+EDTA, and between 3.3 and 32.4 for the vitamin pool. Addition of trace metals decreased the growth potential, however, values of the index varying between 3.8 and 32.8, while those related to the mixture containing all nutrients but metals ranged between 8.1 and 35.0.

Biomass formed in control cultures was low, especially in July water (Table 3). Accordingly, plots of biomass formation versus DIN uptake were scattered. In contrast, sample aliquots which were nutrient-enriched with all nutrients but nitrogen led to more homogene-

Table 4. Nutrients limiting the potential biomass of the cyanobacterium *Microcystis aeruginosa* and the diatom *Phaeodactylum tricornutum* in seawater sampled in the Gulf of Riga, from early May to 19 July 1996, with indication of respective DIN : PO_4. Growth : as increase of biomass in best promoting mixtures versus: +++ : 15–20 fold increase or more; ++ : 10–15 fold; + : 5–10 fold.

Station	Depth(m)	Growth	Limiting nutrient			DIN : PO_4
			1st	2nd	3rd	
		1 May – *P. tricornutum*				
7910	0	+++	P	N		19.5
		1 May – *M. aeruginosa*				
7906	0	+++	Inconclusive			148.4
7910	0	0	Inconclusive			19.5
		Transect Melluzi, 1–5 May – *M. aeruginosa*				
10	0	++	N	P		21.7
30	0	++	P	(N, Fe-EDTA)		75.0
30	10	+++	N	P		8.0
30	20	++	None			14.9
30	30	++	N			12.3
		Transect Saulkrasti, 3–4 May – *M. aeruginosa*				
03	0	+++	(N, Fe-EDTA, P)			167.8
10	0	+++	P	N		105.4
30	5	+++	P	N		115.1
30	30	++	N			15.3
		Transect Saulkrasti, 4 June – *M. aeruginosa*				
10	0	++	N	P		135.4
30		+++	N			49.0
30	0	++	(N, P)			0.5
30	5	+	(N, P)		Fe-EDTA	1.0
30		++	(N, P)			103.4
		Transect Saulkrasti, 3–4 July – *M. aeruginosa*				
05	0	++	(N, P)			
10	0	++	N	P		
20	0	++	N	P		
30	2.5	++	N	P		
30	5	+	Inconlusive			
30	10	++	N	P		
		Nearshore stations, 19 July – *M. aeruginosa*				
Dubulti	0	+++	N	P		6.1
Jaunkemeri	0	+++	N	P	Vit	7.0
Lapmezciems	0	+++	N	P	Vit	5.4
Lielupe	0	++	N			9.1
Melluzi	0	+++	N	P		6.5
Ragciems	0	0	Inconclusive			7.5
		Nearshore stations, 19 July – *P. tricornutum*				
Dubulti	0	+++	N			6.1
Jaunkemeri	0	+++	N	P	Fe-EDTA	7.0
Lapmezciems	0	+++	N	P		5.4
Lielupe	0	+++	N	P		9.1
Melluzi	0	+++	N	P		6.5
Ragciems	0	+++	N	P		7.5

Table 5. Mean growth (relative to that in unenriched water) when enriched with the following substances: All; All+metals; All except the component marked, in *Microcystis aeruginosa* and *Phaeodactylum tricornutum*. In water sampled from early May to early July 1996 along Saulkrasti and Melluzi transects, and water collected nearshore on 19 July at different locations. Parentheses indicate standard deviation.

Presence of	Absence of	Transects of May-early July	Nearshore samples of 19 July	
		M. aeruginosa (N=21)	*M. aeruginosa* (N=6)	*P. tricornutum* (N=7)
All		8.1 (2.5)	12.4 (16.7)	35.0 (30.1)
All+metals		7.2 (2.1)	3.8 (02.5)	32.8 (29.0)
	N	2.2 (0.8)	0.2 (00.5)	1.5 (00.7)
	P	3.2 (1.3)	2.2 (03.5)	6.3 (04.8)
	Si	7.7 (2.3)	9.9 (10.9)	34.8 (29.9)
	Fe-EDTA	7.1 (2.1)	8.2 (07.5)	25.6 (25.8)
	Vitamins	8.0 (1.6)	3.3 (02.4)	32.4 (28.2)

ous plots. All nutrients out of nitrogen being present in excess in these samples, the mean biomass formation was higher than that in the control (Table 5). The overall plot of data obtained with *M. aeruginosa* grown in transect samples cuts the X axis at roughly -4 (Fig. 5), thus suggesting that an average amount of$\sim$ 4 μg atom nitrogen per liter was taken up by the cells under a chemical form other than NO_3, NO_2 and NH_4 (DIN). Since in most samples the available volume of water was insufficient, similar plots for *P. tricornutum* are unavailable.

4. Discussion

REDFIELD (1934) observed that N-NO_3 and P-PO_4 are taken up by phytoplankton at a constant atomic ratio of 16 : 1, and FLEMING (1940) pointed out that this value is also that of the elemental composition of phytoplankton. It has since been agreed that ratios lower than 16 : 1 in the natural nutrient reservoir indicates nitrogen limitation, while a value higher than 16 reflects limitation by phosphorus. This concept must be used with care, because it applies to algal growth as crop, not as growth rate. On the other hand, differential enrichments (bioassays) apply to the potential maximum biomass, not to the actual biomass which can be first limited by the rate of losses. Nevertheless, determining the nutrient(s) limiting the potential biomass greatly helps to focus on the proper nutrient(s) and mechanisms leading to the situation of interest.

According to the respective nutrient contents of the water samples collected, it might be expected that at the time of the spring bloom (early May) the first limiting nutrient would be phosphorus in upper waters of the eastern eutrophicated part of the gulf, and nitrogen near the bottom. DIN : DIP values were indeed greatly >16 for samples taken at the surface and at a depth of 5 m depth, and <16 for the water collected at 30 m (Saulkrasti transect). Results given by the bioassays indicated exactly the same order of importance for the two main limiting nutrients (Table 4). At the same time, on the western side of the gulf, free from river discharge (Melluzi transect), the situation was different. Here nitrogen was the overall limiting nutrient, while phosphorus was limiting in only one sample for which DIN: DIP=75; Redfield's ratio and the bioassays furthermore led to exactly the same conclusions for all waters collected near the shore in July: DIN : DIP values ranged between 5.4 and 16.2 ($\bar{x}=9.3$; $s=3.4$; $N=12$), thus indicating that nitrogen was the first limiting nutrient, which was confirmed by bioassay.

Overall, it is clear that phosphorus was the most limiting nutrient for cyanobacterial growth potential in the nitrogen-rich waters. These conditions prevailed in spring, in the upper layer of the southern-eastern part of the Gulf, which is greatly influenced by river discharge. In late spring, with the decrease of the total DIN reserve, from $>17\,\mu$M to $<13\,\mu$M

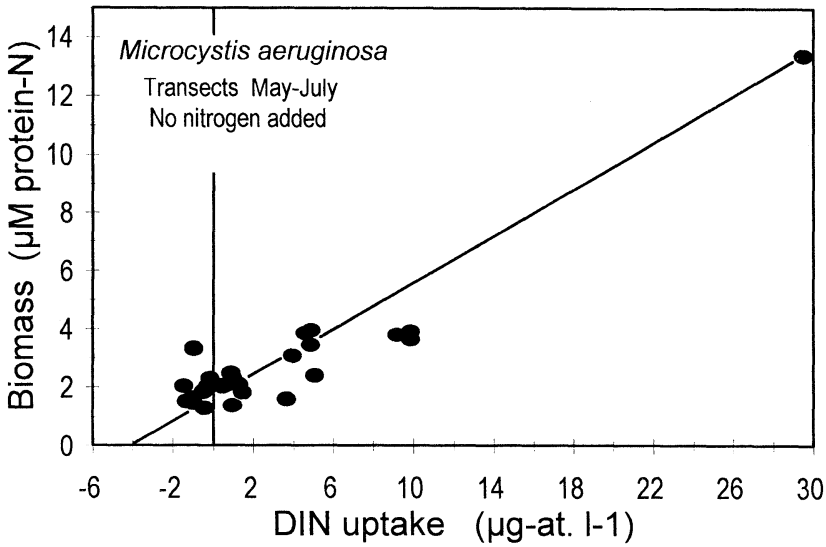

Fig. 5. Biomass (protein N) formed versus dissolved inorganic nitrogen taken up by the cyanobacterium *Microcystis aeruginosa* grown in waters collected in the Gulf of Riga, from early May to mid July, and nutrient-enriched with all nutrients but nitrogen.

(Table 2), nitrogen and phosphorus then played a similar role. In deeper layers of this area and out of the river plume, nitrogen was the limiting nutrient. It is likely that these differences are related to the circulation regime; although there are both cyclonic and anticyclonic currents and turnovers, the general trend of the circulation is that saline water of high salinity from the Baltic Proper enters into the gulf through the Strait of Irbe and flows south eastwards along the western coast (Fig. 1), while water of low-salinity having received fresh water from the River Daugava is flowing northwards along the eastern coast (BERZINSH, 1995). In summer, when the river discharge is the lowest, all DIN concentrations but one ranged between 1.6 and 2.6 µM, and the whole area was nitrogen-limited for both the cyanobacterium and the diatom test strains.

YURKOVSKIS *et al.* (1993), who sampled along the 20-m isobath and at greater depths from February to October 1989, reported mean monthly DIN : DIP values from 19 to 56. On this basis, they inferred that the phytoplankton of the whole gulf was phosphorus-limited. In contrast, at one station located in the Baltic Proper, mean DIN : DIP values for the same period ranged between 2.9 and 7.1, leading to the conclusion that nitrogen was the limiting nutrient. From these results as well as from those showing that the open-sea waters on the Baltic are presently nitrogen-limited (GRANÉLI *et al.*, 1990; KIVI *et al.*, 1993), PÖDER and JAANUS (1995) hypothesized that the shift from DIN : DIP values >16 to those <16 should be observed in the Irbe Strait area which separates the Gulf of Riga and the Baltic Proper. Samples they collected in summer 1993-94, along transects from the strait towards the gulf and the open sea, showed that most DIN : DIP values were <3; only for August waters, a few ranged between 5 and 10. Accordingly, the authors concluded there was no shift from phosphorus to nitrogen limitation from the gulf to the open sea, and concluded that nitrogen was the limiting nutrient in both the Baltic Proper and the Gulf of Riga. Further records on nutrient concentrations and comparison with previous long-term data led YURKOVSKIS *et al.* (1996) to show that drastic changes have occurred in the Gulf of Riga in the 90s. Since late 80s-early 90s, nitrate concentration has continuously decreased: from $\sim$18 µM in1991 to $\sim$10 µM in 1993, in the upper (0-10 m) layer, in February; and from $\sim$3.5 µM in 1989 to $\sim$0.5 µM in 1994, in the same layer, in August, while in deeper (20-50 m)

waters in August, they have decreased from ~22 μM in 1991 to ~5 μM in 1994. During the same period, concentrations of phosphorus have risen, leading to a situation of nitrogen limitation. Hence, all results agree. Most of the Gulf of Riga is now clearly nitrogen-limited in late spring and summer. In contrast, for small and shallow areas, whether nitrogen or phosphorus is limiting is an open question, because river discharges significantly influence salinity and nutrient concentrations, particularly in surface waters.

Important changes in nutrient reserves, nutrient ratios and the species composition of natural phytoplankton assemblages occur along salinity gradients from river mouths to the open sea. SAKSHAUG and MYKLESTAD (1973) and SAKSHAUG *et al.* (1983) found a permanent phosphorus limitation of phytoplankton biomass in the inner section of the Trondheim Fjord, but a clear nitrogen limitation in high-salinity waters; with DIN : DIP values falling from 50 to 10–12. In ponds and coastal waters of Massachusetts, bioassays showed that in low-salinity ponds (0 – 6.5 psu) phytoplankton biomass was phosphorus limited, while nitrogen addition stimulated phytoplankton growth only in the most saline ponds (31 psu) and the open sea; in ponds of intermediate salinity, phytoplankton biomass was limited both by nitrogen and phosphorus (CARACO *et al.*, 1987; CARACO, 1988).

Similar features have been reported for the Baltic Sea. LIGNELL *et al.* (1992) observed that phytoplankton carbon uptake rate and biomass were P-limited in a fjord-like inlet with low salinity on the south-west coast of Finland, whereas in the open sea both nitrogen and phosphorus were limiting. PITKÄNEN and TAMMINEN (1995) have shown that, in summer, from the river Neva to the open part of the Gulf of Finland, there was an associated gradient for salinity, nutrient concentrations and DIN : DIP. Both DIN : DIP values and bioassays indicated that phosphorus was limiting the potential biomass of phytoplankton in the river; then, phosphorus was first limiting and nitrogen was the second limiting nutrient in the estuary, and nitrogen was first limiting and phosphorus was the second limiting nutrient in the transition zone, whilst nitrogen was the single limiting nutrient in the open gulf.

Although technical limitations did not allow us to take more than two samples on the transect from the river Daugava to the open sea, our results as a whole agree with the scheme of gradual changes from river water to the open sea. Accordingly, the shift between DIN : DIP values >16 (freshwater-influenced waters) and those <16 (typical marine waters) that PÖDER and JAANUS (1995) endeavored to observe in the Strait of Irbe should be searched inside the Gulf of Riga, at the limit of the river plume. Controlled by the river discharge regime, the transition area would not have a fixed area and limits, however, and important seasonal variations are likely, as already observed for other areas. In the Patuxent River estuary (Chesapeake Bay), D'ELIA *et al.* (1986) reported great seasonal variability in river flow, nutrient regimes, and the response of natural phytoplankton assemblages to nutrient addition. During the high-flow season, in late winter, DIN : DIP typically exceeded 90, and addition of phosphorus stimulated growth. In late summer, DIN : DIP in nutrient standing stocks was characteristically <5; so when nitrogen was added the growth response was very rapid, reflecting nitrogen limitation. In the southern Baltic, GRANÉLI *et al.* (1988) have compared different coastal waters sampled outside Warnemünde, Rostock, Sopot and Falsterbo. Although the nutrient levels of their samples were different, there were no significant differences between the different locations for nutrients limiting the potential biomass. During winter, before the spring phytoplankton bloom had started, phosphorus was the most limiting nutrient for phytoplankton biomass formation; after the bloom, nitrogen appeared to be the most limiting nutrient.

Whether in nutrient-poor or in nutrient-rich waters, important variations in the nature of the limiting nutrient have been also observed with species. In oligotrophic coastal Mediterranean water, BERLAND *et al.* (1978) reported that the diatom *Skeletonema costatum* was phosphoruslimited, especially from February to June, whereas *Cylindrotheca closterium* was limited according to a complex succession invol-

ving nitrogen, phosphorus, silicon, and vitamins. In the Trondheim Fjord, (SAKSHAUG, 1987; GRANÉLI *et al.*, 1988) showed that phosphorus was the limiting nutrient for *Skeletonema costatum* when DIN: DIP=12, and for most the other species only when DIN : DIP=18–25.

In the Helsinki archipelago, RINNE and TARKIAINEN (1978) reported a nitrogen limitation for potential phytoplankton biomass, except for the nitrogen-fixing cyanobacterium *Nodularia spumigena* which showed phosphorus limitation. Similar findings were reported by TAMMINEN *et al.* (1985) who ran *in situ* mesocosm experiments at the entrance to the Gulf of Finland, in an area not directly influenced by large sewage discharge; addition of ammonium significantly increased the total phytoplankton biomass, while phosphate addition stimulated the growth of nitrogen-fixing cyanobacteria. Other authors have also reported that addition of phosphorus stimulated the growth of *Nodularia spumigena* (HUBER, 1986; LUKATELICH and MCCOMB, 1986), thus supporting HORSTMANN's (1975) contention that blooms of this species are a consequence of phosphorus loading. Furthermore, KONONEN *et al.* (1996) have inferred that *N. spumigena* blooms in a frontal region at the entrance of the Gulf of Finland benefited from the low DIN: DIP value which prevailed in surface water at the onset of the bloom. Blooms of *Aphanizomenon flos-aquae* and *N. spumigena* in the Gulf of Gdansk have been also related to low values of DIN : DIP (PLINSKI and JOZWIAK, 1996).

Since the 90s, blooms of the nitrogen-fixing species *Aphanizomenon flos-aquae* and *Nodularia spumigena* have also occurred in the Gulf of Riga, in summer (BALODE and PURINA, 1996). Their appearance was related to the decrease of the DIN : DIP ratio (YURKOVSKIS *et al.*,1996). This is in agreement with the overall nitrogen limitation we observed; species such as diatoms or non-nitrogen-fixing cyanobacterium such as *Microcystis aeruginosa* that we used as test species were nitrogen-limited. In contrast, *N. spumigena* were not nitrogen - limited, and therefore may take the upper hand in the assemblage, although diatoms appear not to be silicon-limited.

Silicon never appeared to be limiting for either of the two strains we used for bioassays. This might be a consequence of the absence of silicon requirement for *M. aeruginosa* and the very low needs of *Phaeodactylum tricornutum* (BONIN *et al.*, 1986). On the other hand, DIN : SiO_3 was <1 in June and July, and phosphorus was the limiting nutrient when DIN : SiO_3 values were >1 (Table 2); hence silicon could never be more limiting than nitrogen or phosphorus. YURKOVSKIS *et al.* (1993) found no silicate limitation in the Gulf of Riga in the 80s, but recent data have shown silicon acting as a limiting nutrient during the spring bloom (YURKOVSKIS, personal communication). Nevertheless, it is likely that altogether the recently reported decrease of silicon loading in coastal waters and its subsequent enhanced importance in pushing the outcome of species competition towards summer harmful species (SMAYDA, 1990; SOMMER, 1996) may not yet be critically important for the Gulf of Riga.

In four cases, iron appeared to be in the list of nutrients limiting potential biomass (Table 2). This appears to be the first report indicating finding iron to limit Baltic phytoplankton. Although role of iron has been stressed mostly for low-chlorophyll-high-nutrient regions (JENNINGS *et al.*, 1984; MARTIN and FITZWATER, 1988; ZETTLER *et al.*, 1996), it has also been found to be limiting on occasion in coastal waters; namely, in the Gulf of Maine (GRAN, 1933; GLOVER, 1978; WALLS *et al*, 1991), the coast of Oregon (GLOOSCHENKO and CURL, 1971), and the north-west Australian coast (Tranter and Newel, 1963). Moreover, iron is required for N_2 fixation by diazotrophic cyanobacteria (RUETER *et al.*, 1998; PAERL *et al.*, 1994), whereas it has been reported that at least 40–90% of the iron transported by freshwater aggregated and sedimented when salinity reaches 4–5 psu in the estuary of the Öve River, western Baltic (FORSGREN *et al.*, 1996). More research on the role of iron as a nutrient in the Gulf of Riga may thus be desirable.

Our results suggest that a significant fraction of the nitrogen taken up by the two test species may have been as dissolved organic nitrogen (DON). It is estimated that an average of $\sim 4\,\mu$g-atom N l^{-1} was taken up by *Microcystis aeruginosa*. This amount is close to the

mean concentration of urea we recorded ($\bar{x}$ =3.3; s=1.5; N=26; range 1.3 to 7.0 μM). Similar estimations have been made in oyster ponds of the French Atlantic coast (MAESTRINI and ROBERT, 1981), where diatom test species were found to take up 0.6 to 30.7 μg-atom l^{-1} of DON, and which, results suggested, had the capacity to take up six times more DON than DIN. These findings agree with current knowledge on nutritional capabilities of phytoplankton.

Several algae have been reported to grow in culture with organic compounds as the sole source of nitrogen and phosphorus (TERNETZ, 1912; DROOP, 1961; KUENTZLER and PERRAS, 1965; FLYNN and BUTLER, 1986; BERMAN *et al.*, 1991). Field research also shown that half-saturation values (K) for urea falls within natural urea concentrations (McCARTHY, 1972); accordingly, urea has been considered as an important potential nitrogen source for phytoplankton in various coastal waters (KRISTIANSEN, 1983; IGNATIADES, 1986; KOKKINAKIS and WHEELER, 1988; PRICE and HARRISON, 1988; FERNANDEZ *et al.*, 1996). In mesocosm experiment carried out *in situ*, in water of the western coast of the Baltic Sea, SÖRENSSON *et al.* (1989) reported an uptake rate for urea up to five times faster than that for nitrate. TAMMINEN and IRMISCH (1996) showed that urea uptake dominated that of total nitrogen in an incubation experiment with size-fractionated assemblages collected in summer at the entrance of the Gulf of Finland; urea appeared to be a particularly important nitrogen source during the regenerated phase of plankton succession. Also, dissolved free amino-acids have been reported to sustain a significant part of algal growth in the Chesapeake Bay (GLIBERT *et al.*, 1991). Moreover, PALENIK *et al.* (1988-89) have shown that some phytoplankters are able to use various forms of DON without initial transport into the cell, by using cell-surface enzymes to degrade these forms of nitrogen to NH_4, and TRANVIK *et al.*, (1993) observed the ingestion of proteins such as ferritin, casein and albumin by heterotrophic flagellates.

Suggestion has also been made that organic compounds from land-drainage origin, such as humic acids, have favored harmful dinoflagellate growth versus that of harmless species (CARLSSON and GRANÉLI, 1993; CARLSSON *et al.*, 1995; LARA *et al.*, 1993; MORAN and HODSON, 1994). Some results are conflicting, however. For instance, during a drogue experiment in the Baltic proper, SÖORENSSON and SAHLSTEN (1987) recorded no uptake of DOM whose molar C : N was >20, which they inferred was refractive. These results led them to believe the nitrogen fixers, mostly *N. spumigena*, relied mainly on N_2 for their nitrogen demand.

The cyanobacterium we used as test species, *Microcystis aeruginosa*, is not a N_2-fixing species. Accordingly, whether or not DOM is a significant factor in triggering the onset of toxic blooms in the Gulf of Riga is still an open question and should be a focus for further research.

Acknowledgements

This study was partly supported by the "Programme National Efflorescences Algales Toxiques" (France); mission in Latvia of French co-authors was supported by the "Ministère des Affaires Etrangères; crédits réservés à l' IFREMER". We warmly thank Dr Uldis BOTVA for providing some of nutrient data; Dr Aivars YURKOVSKIS for stimulating comments; and Dr Ian JENKINSON (ACRO, La Roche Canillac) for improving the English version.

References

ANDRUSHAITIS, A., M. BALODE and G. LAGZDINS (1993): Eutrophication of the Gulf of Riga. *In*: Measurement of Primary Production from the Molecular to the Global Scale, W.K.W. LI and S.Y. MAESTRINI (eds.), ICES mar. Sci. Symp., **197**, 260.

ANDRUSHAITIS, A., Z. SEISUMA, M. Legzdina and E. LENSHS (1995): River load of eutrophying substances and heavy metals into the Gulf of Riga. *In*, Ecosystem of the Gulf of Riga between 1920 and 1990, E. OJAVEER (ed.), Estonian Academy Publishers, Tallinn, 32-40.

BADEN, S.P., L.-O. LOO, L. PIHL and R. ROSENBERG (1990): Effects of eutrophication on benthic communities including fish: Swedish West Coast. Ambio, **19**, 113-122.

BALODE, M. (1993): Bloom dynamics of toxic blue green algae *in* the Baltic Sea, Gulf of Riga. In: Sixth International Conference on Toxic Marine Phytoplankton, 18-22 October 1993, Nantes, France, Abstracts, 27.

BALODE, M. (1996): Long-term changes of summer autumn phytoplankton community in the Gulf of Riga. *In*, A Comparative Ecological Approach of Coastal Environments and Paralic Ecosystems, O. GUELORGET and O. LEFEBVRE (eds.), 96–99.

BALODE, M. and I. PURINA (1996): Harmful phytoplankton in the Gulf of Riga (the Baltic Sea). *In*, Harmful and Toxic Algal Blooms, T. YASUMOTO, Y. OSHIMA and Y. FUKUYO (eds.), Intergovernmental Oceanographic Commission of UNESCO, Paris, 69–72.

BERLAND, B.R., D.J. BONIN and S.Y. MAESTRINI (1978): Facteurs limitant la production primaire des eaux oligotrophes d'une aire côtière méditerranéenne (Calanque d'En-Vau, Marseille). Int. Rev. ges. Hydrobiol., **63**, 501–531.

BERMAN, T., S. CHAVA, B. KAPLAN and D. WYNNE (1991): Dissolved organic substrates as phosphorus and nitrogen sources for axenic batch cultures of freshwater green algae. Phycologia, **30**, 339–345.

BERZINSK, V. (1995): Hydrological regime. *In*, Ecosystem of the Gulf of Riga between 1920 and 1990 E. DJAVEER (ed..), Estonian Academy Publishers, Tallinn, 7–31.

BOIKOVA, E. (1986): Nannoplankton-its distribution and role in eutrophication of the Baltic Sea. *In*: Ecological Investigations of the Baltic Sea Environment. Proceed. Internat. Conf. Riga, 16–19 March 1983, Baltic Marine Environmental Protection Commission (ed.), 240–254.

BONIN, D.J., M.R. DROOP, S.Y. MAESTRINI and M.-C. BONIN (1986): Physiological features of six micro algae to be used as indicators of seawater quality. Cryptogam. Algol., **7**, 23–83.

BRAND, L.E., R.R.L. GUILLARD and L.S. MURPHY (1981): A method for the rapid and precise determination of acclimated phytoplankton reproduction rates. J. Plankt. Res., **3**, 193–201.

CARACO, N. (1988): What is the mechanism behind the seasonal switch between N an P limitation in estuaries ? Can J. Fish. aquat. Sci., **45**, 381–382.

CARACO, N., A. TAMSE, O. BOUTROS and I. VALIELA (1987): Nutrient limitation of phytoplankton growth in brackish coastal ponds. Can J. Fish. aquat. Sci., **44**, 473–476.

CARLSSON, P. and E. GRANÉLI (1993): Availability of humic bound nitrogen for coastal phytoplankton. Estuar. Coast. Shelf Sci., **36**, 433–447.

CARLSSON, P., E. GRANÉLI, P. TESTER and L. BONI (1995): Influences of riverine humic substances on bacteria, protozoa, phytoplankton, and copepods in a coastal plankton community. Mar. Ecol. Prog. Ser., **127**, 213–221.

CARPENTER, E.J., S. JANSON, R. BOJE, F. POLLEHNE and J. CHANG (1995): The dinoflagellate *Dinophysis norvegica*: biological and ecological observations in the Baltic Sea. Eur. J. Phycol., **30**, 1–9.

CEDERWALL, H. and R. ELMGREN (1990): Biological effects of eutrophication in the Baltic Sea, particularly the coastal zone. Ambio, **19**, 109–112.

COLLOS, Y. and F. MORNET (1993): Automated procedure for determination of dissolved organic nitrogen and phosphorus in aquatic environments. Mar. Biol., **116**, 685–688.

CONLEY, D.J., C.L. SCHELSKE and E.F. STOERMER (1993): Modification of the biogeochemical cycle of silica with eutrophisation. Mar. Ecol. Progr. Ser., **101**, 179–192.

CONOVER, S.A.M. (1975): Nitrogen utilization during spring blooms of marine phytoplankton in Bedford Basin, Nova Scotia, Canada. Mar. Biol., **32**, 247–261.

D'ELIA, C.F., J.G. SANDERS and W.R. BOYNTON (1986): Nutrient enrichment studies in a coastal plain estuary: phytoplankton growth in large-scale, continuous cultures. Can J. Fish. aquat. Sci., **43**, 397–406.

DEDEREN, L.H.T. (1992): Marine eutrophication in Europe : similarities and regional differences in appearance. *In*: Marine Coastal Eutrophication. The response of marine transitional systems to human impact : problems and perspectives for restoration. Proceed. Intern. Conf., Bologna, Italy, 21–24 March 1990, 1310 p., R.A. VOLLENWEIDER, R. MARCHETTI and R. VIVIANI (eds.), Elsevier Sci. Publish., Amsterdam, 663–672.

DROOP, M.R. (1961): *Haematococcus pluviatilis* and its allies; III: organic nutrition. Rev. Algologique, **4**, 247–259.

EDLER, L., S. FERNÖ M.G. LIND, R. LUNDBERG and P.O. NILSSON (1985): Mortality of dogs associated with a bloom of the cyanobacterium *Nodularia spumigena* in the Baltic Sea. Ophelia, **24**, 103–109.

FERNANDEZ, E., E. MARANON, D.S. HARBOUR, S. KRISTIANSEN and B.R. HEIMDAL (1996): Patterns of carbon and nitrogen uptake during blooms of *Emiliania huxleyi* in two Norwegian fjords. J. Plankt. Res., **18**, 2349–2366.

FISHER, T.R., E.R. PEELE, J.W. AMMERMAN and L.W. Jr. HARDING (1992): Nutrient limitation of phytoplankton in Chesapeake Bay. Mar. Ecol. Prog. Ser., **82**, 51–63.

FLEMING, R.H. (1940): The composition of plankton and units for reporting populations and production. *In*: Proceedings 6th Pacific Scientific Congress, 1939, 3.

FLYNN, K.J. and I. BUTLER (1986): Nitrogen sources for the growth of marine microalgae: role of dissolved free amino acids. Mar. Ecol. Prog. Ser., **34**,

281–304.

FORSGREN, G., M. JANSSON and P. NILSSON (1996): Aggregation and sedimentation of iron, phosphorus and organic carbon in experimental mixtures of freshwater and estuarine water. Estuar. coastal mar. Sci., **43**, 259–268.

GLIBERT, P.M., C. GARSIDE, J.A. FUHRMAN and M.R. ROMAN (1991): Time-dependent coupling of inorganic and organic nitrogen uptake and regeneration in the plume of the Chesapeake Bay estuary and its regulation by large heterotrophs. Limnol. Oceanogr., **36**, 895–909.

GLOOSCHENKO, W.A. and H. Jr. CURL (1971): Influence of nutrient enrichment on photosynthesis and assimilation ratios in natural North Pacific phytoplankton communities. J. Fish. Res. Bd Can., **28**, 790–793.

GLOVER, H. (1978): Iron in Maine coastal waters; seasonal variations and its apparent correlation with a dinoflagellate bloom. Limnol. Oceanogr., **23**, 534–537.

GRAN, H.H. (1933): Studies on the biology and chemistry of the Gulf of Maine. II. Distribution of phytoplankton in August 1932. Biol. Bull., **64**, 159–181.

GRANÉLI, E., S. SCHULZ, U. SCHIEWER, D. GEDZIOROWSKA, W. KAISER and M. PLINSKI (1988): Is the same nutrient limiting potential phytoplankton biomass formation in different coastal areas of the Southern Baltic ?. Kieler Meeresforsch., **6**, 191–202.

GRANÉLI, E., K. WALLSTRÖM, U. LARSSON, W. GRANÉLI and R. ELMGREN (1990): Nutrient limitation of primary production in the Baltic Sea area. Oceanology, **19**, 142–151.

GRASSHOFF, K. (1976): Determination of nitrite. *In*, Methods of Seawater Analysis GRASSHOFF K., M. EHRHARDT and K. KREMLING (eds.), Verlag Chemie, Weinheim, Germany, 139–142.

HALLEGRAEFF, G.M. (1995): Harmful algal blooms: A global overview. *In*, Manual on Harmful Marine Microalgae, G.M. HALLEGRAEFF, D.M. ANDERSON and A.D. CEMBELLA (eds.), IOC Manuals and Guides N°**33**, UNESCO, Paris, 1–22.

HECKY, R.E. and P. KILHAM (1988): Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. Limnol. Oceanogr., **33**, 796–822.

HEISKANEN, A.-S. and K. KONONEN (1994): Sedimentation of vernal and late summer phytoplankton communities in the coastal Baltic Sea. Arch. Hydrobiol., **131**, 175–198.

HOLMES, R.W., P.M. WILLIAMS and R.W. EPPLEY (1967): Red water in La Jolla Bay. Limnol. Oceanogr., **12**, 503–512.

HORSTMANN, U. (1975): Eutrophication and mass occurence of blue-green algae in the Baltic. Merentutkimulslait. Julk. Havsforskningsinstr. Skr, **239**, 83–90.

HOWARTH, R.W. (1988): Nutrient limitation of net primary productivity in marine systems. Ann. Rev. Ecol. Syst., **19**, 89–110.

HUBER, A.L. (1986): Nitrogen fixation by *Nodularia spumigena* Mertens (Cyanobacteriaceae). 1: Field studies and the contribution of blooms to the nitrogen budget of the Peel-Harvey estuary, western Australia. Hydrobiologia, **131**, 193–203.

IGNATIADES, L. (1986): Annual variability of (^{14}C)urea utilization by natural marine phytoplankton. Br. phycol. J., **21**, 209–215.

JENNINGS, J.C.Jr., L.I. GORDON and D.M. NELSON (1984): Nutrient depletion indicates high primary productivity in the Weddell Sea. Nature, **308**, 51–54.

KAHRU, M., U. HORSTMANN and O. RUD (1994): Satellite detection of increased cyanobacteria blooms in the Baltic Sea: natural fluctuation or ecosystem change?. Oceanology, **23**, 469–472.

KIVI, K., S. KAITALA, H. KUOSA, J. KUPARINEN, E. LESKINEN, R. LIGNELL, B. MARCUSSEN and T. TAMMINEN (1993): Nutrient limitation and grazing control of the Baltic plankton community during annual succession. Limnol. Oceanogr., **38**, 893–905.

KOKKINAKIS, S.A. and P.A. WHEELER (1988): Uptake of ammonium and urea in the northeast Pacific: comparison between netplankton and nanoplankton. Mar. Ecol. Prog. Ser., **43**, 113–124.

KONONEN, K. (1992): Dynamics of the toxic cyanobacterial blooms in the Baltic Sea. Finn. Mar. Res., **261**, 3–36.

KONONEN, K., J. KUPARINEN, K. MÄKELÄ, J. LAANEMETS, J. PAVELSON and S. NÄMMANN (1996): Initiation of cyanobacterial blooms in a frontal region at the entrance to the Gulf of Finland, Baltic Sea. Limnol. Oceanogr., **41**, 98–112.

KOROLEFF, F. (1976): Determination of ammonia. *In*, Methods of Seawater Analysis, GRASSHOFF K., M. EHRHARDT and K. KREMLING (eds.), Verlag Chemie, Weinheim, Germany, 126–133.

KOROLEFF, F. (1976): Determination of urea. *In*, Methods of Seawater Analysis, GRASSHOFF K., M. EHRHARDT and K. KREMLING (eds.), Verlag Chemie, Weinheim, Germany, 158–162.

KRISTIANSEN, S. (1983): Urea as a nitrogen source for the phytoplankton in the Oslofjord. Mar. Biol., **74**, 17–24.

KUENZLER, E.J. and J.P. PERRAS (1965): Phosphatases of marine algae. Biol. Bull., **128**, 271–284.

LARA, R.J., U. HUBBERTEN and G. KATTNER (1993): Contribution of humic substances to the dissolved

nitrogen pool. Br. phycol. J., **25**, 103–115.

LEPPÄNEN, J.-M., E. RANTAJÄRVI, S. HÄLLFORS, M. KRUSKOPF and V. LAINE (1995): Unattended monitoring of potentially toxic phytoplankton species in the Baltic Sea in 1993. J. Plankt. Res., **17**, 891–902.

LEVASSEUR, M.E., P.J. HARRISON, B.R. HEIMDAL and J.C. THERRIAULT (1990): Simultaneous nitrogen and silicate deficiency of a plytoplankton community in a coastal jet–front. Mar. Biol., **104**, 329–338.

LIGNELL, R., S. KAITALA and H. KUOSA (1992): Factors controlling phyto– and bacterioplankton in late spring on a salinity gradient in the northern Baltic. Mar. Ecol. Prog. Ser., **84**, 121–131.

LUKATELICH, R.J. and A.J. MCCOMB (1986): Nutrient levels and the development of diatom and blue green algal blooms in a shallow Australian estuary. J. Plankt. Res., **8**, 597–618.

MAESTRINI, S.Y. and D.J. BONIN (1981): Competition among phytoplankton based on inorganic macronutrients. *In*: Physiological bases of phytoplankton ecology, T. PLATT(ed.), Can. Bull. Fish. aquat. Sci., **210**, 264–278.

MAESTRINI, S.Y., D.J. BONIN and M.R. DROOP (1984): Phytoplankton as indicators of seawater quality: bioassay approaches and protocols. *In*: "Algae as ecological indicators", E. SHUBERT (ed.), Acad Press Inc., London, 71–132.

MAESTRINI, S.Y. and J.-M. ROBERT (1981): Rendements d'utilisation des sels nutritifs et variations de l' état des cellules de trois diatomées de claires à huîres de Vendée. Oceanol. Acta, **4**, 13–21.

MARTIN, J.H. and S.E. FITZWATER (1988): Iron deficiency limits phytoplankton growth in the north east Pacific Subarctic. Nature, **331**, 341–343.

MCCARTHY, J.J. (1972): The uptake of urea by natural populations of marine phytoplankton. Limnol. Oceanogr., **17**, 738–748.

MORAN, M.A. and R.E. HODSON (1994): Dissolved humic substances of vascular plant origin in a coastal marine environment. Limnol. Oceanogr., **39**, 762–771.

MULLIN, J.B. and J.P. RILEY (1965): The spectrophotometric determination of silicate–silicon in natural waters with special reference to sea water. Analytica chim. Acta, **46**, 491–501.

MURPHY, J. and J.P. RILEY (1962): A modified single solution method for the determination of phosphate in natral waters. Analytica chim. Acta, **27**, 31–36.

NEHRING, D. (1992): Eutrophication in the Baltic Sea. *In*: Marine Coastal Eutrophication. The response of marine transitional systems to human impact: problems and perspectives for restoration. Proceed. Intern. Conf., Bologna, Italy, 21–24 March 1990, 1310 p., R. A. VOLLENWEIDER, R. MARCHETTI and R. VIVIANI (eds.), Elsevier Sci. Publish., Amsterdam, 673–682.

NIEMI (1979): Blue–green algal blooms and N : P ratio in the Baltic Sea. Acta Bot. Fenn., **110**, 57–61.

NIXON, S. (1990): Marine eutrophication: a growing international problem. Ambio, **19**, 101.

OFFICER, C.B. and J.H. RYTHER (1980): The possible importance of silicon in marine eutrophication. Mar. Ecol. Prog. Ser., **3**, 83–91.

PAERL, H.W., L.E. PRUFERT–BEBOUT and C. GUO (1994): Iron–stimulated N_2 fixation and growth in natural and cultured populations of the planktonic marine cyanobacteria *Trichodesmium* spp. Appl. Environ. Microbiol., **60**, 1044–1047.

PALENIK, B., D.J. KIEBER and F.M.M. MOREL (1988/1989): Dissolved organic nitrogen use by phytoplankton: the role of cell–surface enzymes. Biol. Oceanogr., **6**, 347–354.

PETTY, R.L., W.C. MICHEL, J.P. SNOW and K.S. JOHNSON (1982): Determination of total primary amines in seawater and plant nectar with flow injection sample processing and fluorescence detection. Analytica chim. Acta, **142**, 299–304.

PITKÄNEN, H. and T. TAMMINEN (1995): Nitrogen and phosphorus as production limiting factors in the estuarine waters of the eastern Gulf of Finland. Mar. Ecol. Prog. Ser., **129**, 283–294.

PITKÄNEN, H., T. TAMMINEN, P. KANGAS, T. HUTTULA, K. KIVI, H. KUOSA, J. SARKKULA, K. ELOHEIMO, P. Kauppila and B. Skakalsky (1993): Late summer trophic conditions in the north–east Gulf of Finland and the River Neva Estuary, Baltic Sea. Estuar. Coast. Shelf Sci., **37**, 453–474.

PLINSKI, M. and T. JOZWIAK (1996): Dynamics of heterocystous cyanobacteria growth in the brackish water. *In*, Harmful and Toxic Algal Blooms T. YASUMOTO, Y. OSHIMA and Y. FUKUYO (eds.), Intergovernmental Oceanographic Commission of UNESCO, Paris, 549–551.

PÖDER, T. and A. JAANUS (1995): Nutrient concentrations and phytoplankton variables in the Gulf of Riga and Baltic proper water mixing area: an attempt to test the dichotomy of limiting nutrient. *In*: 14th Baltic Marine Biologists Symposium, 5–8 September 1995, Pärnu, Estonia, 1–8.

PRICE, N.M. and P.J. HARRISON (1988): Uptake of urea C and urea N by the coastal marine diatom *Thalassiosira pseudonana*. Limnol. Oceanogr., **33**, 528–537.

RAGUENEAU, O., E. De Blas VARELA, P. TRÉGUER, B. QUÉGUINER and Y. Del AMO (1994): Phytoplankton dynamics in relation to the biogeochemical cycle of silicon in a coastal ecosystem of western

Europe. Mar. Ecol. Progr. Ser., **106**, 157–172.

RAHM, L., D. CONLEY, P. SANDÉN, F. WULFF and P. STALNACKE (1996): Time series analysis of nutrient inputs to the Baltic Sea and changing DSi: DIN ratios. Mar. Ecol. Prog. Ser., **130**, 221–228.

REDIFIELD, A.C. (1934): On the proportions of organic derivatives in sea water and their relation to the composition of plankton. *In*, James Johnstone Memorial Volume R.J. DANIEL (ed.), The University Press, Liverpool, 176–192.

RICHARDSON, K. (1990): Eutrophication in the Baltic: An overview of the problem. In: Water Pollution Research Report 16 – Eutrophication-related phenomena in the Adriatic Sea and in other Mediterranean coastal zones, H. BARTH and L. FEGAN (eds.), Commission of the European Communities, Bruxelles, 149–167.

RINNE, I. and E. TARKIAINEN (1978): Algal tests used to study the chemical factors regulating the growth of planktonic algae in the Helsinki sea area. Mitt. Internat. Verein. Limnol., **21**, 527–546.

ROSENBERG, R., R. ELMGREN, S. FLEISCHER, P. JONSSON, G. PERSSON and H. DAHLIN (1990): Marine eutrophication case studies in Sweden. Ambio, **19**, 102–108.

RUBEK, J., H.W. PAERL, M.A. MALLIN and P.W. BATES (1991): Seasonal and hydrological control of phytoplankton nutrient limitation in the lower Neuse River Estuary, North Carolina. Mar. Ecol. Prog. Ser., **75**, 133–142.

RUETER, J.G. (1988): Iron stimulation of photosynthesis and nitrogen fixation in Anabaena 7120 and *Trichodesmium* (Cyanophyceae). J. Phycol., **24**, 249–254.

RYTHER, J.H. and W.M. DUNSTAN (1971): Nitrogen, phosphorus, and eutrophication in the coastal marine environment. Science, **171**, 1008–1013.

SAKSHAUG, E., K. ANDRESEN, S. MYKLESTAD and Y. OLSEN (1983): Nutrient status of phytoplankton communities in Norwegian waters (marine, brackish, and fresh) as revealed by their chemical composition. J. Plankt. Res., **5**, 175–196.

SAKSHAUG, E. and S. MYKLESTAD (1973): Studies on the phytoplankton ecology of the Trondheimsfjord. III. Dynamics of phytoplankton blooms in relation to environmental factors, bioassay experiments and parameters for the physiological state of the populations. J. Expl Mar. Biol. Ecol., **11**, 157–188.

SCHELSKE, C.L. and E.F. STOERMER (1972): Phosphorus, silica, and eutrophication of Lake Michigan. *In*: Nutrients and Eutrophication: The Limiting-Nutrient Controversy, G.E. LIKENS (ed.), Limnol. Oceanogr., Special Symposia, I, 157–171.

SCHULZ, S. and W. KAISER (1986): Increasing trends in plankton variables in the Baltic Sea – A further sign of eutrophication? Appl. Environ. Microbiol., **4** (Supplement), 249–257.

SMAYDA, T.J. (1974): Bioassay of the growth potential of the surface water of lower Narragansett Bay over an annual cycle using the diatom *Thalassiosira pseudonana* (oceanic clone, 13–1). Limnol. Oceanogr., **19**, 889–901.

SMAYDA, T.J. (1990): Novel and nuisance phytoplankton blooms in the sea: evidence for a global epidemic. *In*: Toxic Marine Phytoplankton, E. GRANÉLI, B. SUNDSTRÖM, L. EDLER and D.M. ANDERSON (eds.), Elsevier Sci. Publish., New York, 29–40.

SMITH, S.V. and M.J. ATKINSON (1984): Phosphorus limitation of net production in a confined aquatic ecosystem. Nature, **307**, 626–627.

SOMMER, U. (1996): Nutrient competition experiments with periphyton from the Baltic Sea. Mar. Ecol. Prog. Ser., **140**, 161–167.

SÖRENSSON, F., K. PETTERSSON, J.S. SELMER and E. SAHLSTEN (1989): Flows of nitrogen in a mesocosm experiment in the Baltic Sea. Mar. Ecol. Prog. Ser., **58**, 77–88.

SÖRENSSON, F. and E. SAHLSTEN (1987): Nitrogen dynamics of a cyanobacteria bloom in the Baltic Sea: new versus regenerated production. Mar. Ecol. Prog. Ser., **37**, 277–284.

STRICKLAND, J.D.H. and T.R. PARSONS (1972): A practical hand-book of seawater analysis. Bull. Fish. Res. Bd Can., **167**, 2nd ed., 310 p.

TAMMINEN, T. and A. IRMISCH (1996): Urea uptake kinetics of an midsummer planktonic community on the SW coast of Finland. Mar. Ecol. Prog. Ser., **130**, 201–211.

TAMMINEN, T., S. KAITALA, K. KIVI and J. KUPARINEN (1985): Response of a planktonic brackish water community to single and combined additions of ammonia and phosphate in a factorial mesocosm experiment. *In*, Marine Biology of Polar regions and Effects of Stress on Marine Organisms J.S. GRAY and M.E. CRISTIANSEN (eds.), John Wiley & Sons Ltd, 363–378.

TENSON, J. (1995): Phytoplankton and primary production. *In*, Ecosystem of the Gulf of Riga between 1920 and 1990 E., OJAVEER (ed.), Estonian Academy Publishers, Tallinn, 104–126.

TERNETZ, C. (1912): Beiträge zur Morphologie und Physiologie der Euglena gracilis Klebs. Jahr. Wiss. Bot, **51**, 435–514.

TRANTER, D.J. and B.S. NEWELL (1963): Enrichment experiments in the Indian Ocean. Deep-Sea Res., **10**, 1–9.

TRANVIK, L.J., E.B. SHERR and B.F. SHERR (1993): Uptake and utilization of "colloidal DOM" by

heterotrophic flagellates in seawater. Mar. Ecol. Prog. Ser., **92**, 301–309.

WATRAS, C.J., V.C. GARCON, R.J. OLSON, S.W. CHISHOLM and D.M. ANDERSON (1985): The effect of zooplankton grazing on estuarine blooms of the toxic dinoflagellate *Gonyaulax tamarensis*. J. Plankt. Res., **7**, 891–908.

WELLS, M.L., L.M. MAYER and R.R.L. GUILLARD (1991): Evaluation of iron as a triggering factor for red tide blooms. Mar. Ecol. Prog. Ser., **69**, 93–102.

WETZEL, R.G. (1965): Nutritional aspects of algal productivity in marl lakes with particular reference to enrichment bioassays and their interpretation. Mem.Ist. Ital. Idrobiol., **18**, 137–157.

WILLÉN T.K. and, KONONEN, U. HORSTMANN (1990) Phytoplankton biomass and species composition, Baltic Sea Environnment Proc document. Baltic marine environment protection commission, Helsinki Commission, N°35 B (432 p.), 167–181.

WULFF, F., G. AERTEBJERG, G. NICOLAUS, A. NIEMI, P. CISZEWSKI, S. SCHULZ and W. KAISER (1986): The changing pelagic ecosystem of the Baltic Sea. Ophelia, **4** (Supplement), 299–319.

YURKOVSKIS, A., M. MAZMACHS and R. MODRIS (1996): Present state and historical changes of the nutrient system in the Gotland Basin and the Gulf of Riga (Baltic Sea). In, A Comparative Ecological Approach of Coastal Environments and Paralic Ecosystems, O. GUELORGET and O. LEFEBVRE (eds.), 78–81.

YURKOVSKIS, A., F. WULFF, L. RAHM, A. ANDRUZAITIS and M. RODRIGUEZ-MEDINA (1993): A nutrient budget of the gulf of Riga; Baltic Sea. Estuar. Coast. Shelf Sci., **37**, 113–127.

ZETTLER, E.R., R.J. OLSON, B.J. BINDER, S.W. CHISHOLM, S.E. FITZWATER and R.M. GORDON (1996): Iron-enrichment bottle experiments in the equatorial Pacific: responses of individual phytoplankton cells. Deep-Sea Res., **43** (Topical Studies In Oceanography), 1017–1029.

Received April 14,1997
Accepted May 8,1997

Résumé-Nutriment (s) limitant la biomasse potentielle (《AGP》) dans le Golfe de Riga, est Mer Baltique : bioessais conduits avec la cyanobactérie *Microcystis aeruginosa* et la diatomée *Phaeodactylum tricornutum*.

Des échantillons ont été recueillis début mai, juin et juillet 1996, le long de deux radiales situées, l' une dans la partie sud-est du golfe fortement influencée par les eaux fluviatiles, l' autre dans la partie sud ouest recevant peu d' eau douce, à une station située dans le panache de la principale rivière (Daugava), au mileu du golfe ; mi-juillet, des eaux proches du rivage ont été prélevés à différentes stations de la côte ouest. Les valeurs relatives des concentrations ioniques *in situ* en azote, phosphore et silicium et des bioessais (enrichissements différentiels) conduits en laboratoire ont été utilisées pour déterminer les nutriments limitant la biomasse potentielle. Les deux méthodes ont montré que le phosphore était le nutriment limitant pour les deux espéces tests dans les eaux de surface riches en azote minéral recueillies en début mai dans la partie sud-est du golfe; en fin de printemps, l'azote et le phosphore avaient un rôle équivalent. Dans les couches plus profondes de la partie est et dans toute les autres parties du golfe peu influencées par les eaux fluvialtiles, l'azote était le nutriment limitant. En été au moment du plus faible débit des rivières, pour toutes les stations échantillonnées, la concentration en azote minéral était comprise entre 1,6 et 2,6 μM et l'azote était le nutriment limitant. Pour 74% des échantillons où l'azote était le nutriment limitant, le phosphore est apparu comme étant potentiellement le nutriment limitant venant en second. En revanche, le silicium n'est jamais apparu comme pouvant limiter la biomasse, aussi bien pour la cyanobactérie que pour la diatomée tests ; le phosphore était limitant quand le rapport $NO_3+NO_2+NH_4$: SiO_3 était >1, en mai, et <1 en juin et juillet quand l' azote était limitant. Les auteurs estiment que l'accroissement en importance du rôle silicium pour la compétition interspécifique au sein du phytoplancton au bénéice des espéces toxiques non silicifiées récemment mis en exergue pour d'autres eaux côtiéres n'est pas encore significatif pour le golfe de Riga. Le fer est apparu dans la liste des nutriments limitants pour 12% des test. En outre, bien que les valeurs absolues soient entâchées d'imprécision, certains résultats indiquent qu'une faction non néligeable de l'azote prélevé ($\sim$4 μg-atom N l^{-1}) pourrait l'avoir été sous une forme organique. Les auteurs suggérent de prêter attention â ces deux facteurs pour les recherches â venir.

Биогены лимитирующие потенциал роста водорослей в Рижском заливе, Восточной части Балтийского моря (весна-лето, 1996).

С. У. Маестрини, М.Балоде, С.Бешемин, И.Пурина, С.Верите

Резюме: Пробы воды были собраны в мае, июне, июле 1996 года на трёх разрезах: первом- с сильным воздействием речного стока (восточное побережье), втором- без речного воздействия (западное побережье), третьем- против устья реки Даугава (на станциях у самого устья реки и в открытой части залива); а также на нескольких литоральных станциях западного побережья. Для выявления элемента, лимитирующего потенциальный рост фитопланктона, были использованы отношения растворимого азота, фосфора и кремния *in situ* и тесты биогенного лимитирования. Сравнение отношений растворимого неорганического азота к растворимому неорганическому фосфору (DIN/DIP) с отношением Редфилда и результаты экспериментов биогенного лимитирования привели к идентичным выводам. Фосфор выявлен как главный элемент лимитирующий потенциальный рост фитопланктона весной в богатых азотом поверхностных слоях вод юго-восточной части Рижского залива, где наблюдается сильное воздействие речного стока. В конце весны- начале лета наблюдается уменьшение резервов DIN. В это время как фосфор, так и азот становятся лимитирующими элементами. В более глубоких водных слоях этого района и в западной части залива, где не наблюдается воздействие речного стока, лимитирующим элементом был азот. Летом, когда наблюдается наименьшее воздействие пресных вод, концентрации DIN достигали 1.6-2.6μM, что обусловливало азотное лимитирование исследуемого района на что указывает также биотесты проведенные цианобактериями и диатомовыми. В 74% проб, где азот был лимитирующим элементом, фосфор выявлен как второй более значимый элемент. В то же время кремний не ограничивал рост *Microcystis aeruginosa* и *Phaeodactylum tricornutum* ни при отношении DIN к SiO3 >1 (в мае), когда фосфор был лимитирующим элементом, ни при отношении DIN к SiO3 <1 (в июне, июле), когда лимитирующим был азот. Железо в 12% проб лимитировало потенциал роста фитопланктона. Результаты исследований показывают, что тестовые культуры могут ассимилировать некоторое количество азота (~4μg-atomN/l) в форме растворимого органического вещества. Этому факту следует уделить больше внимания в последующих исследованиях фитопланктона Рижского залива.