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RESEARCH ARTICLE

Phytoplankton production and community respiration in different zones of the Curonian lagoon during the midsummer vegetation period

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Abstract

1 - Phytoplankton structure, primary production, extracellular release of dissolved organic carbon and pelagic community respiration were investigated in different zones of the Curonian Lagoon in July 2002-2004.

2 - Phytoplankton biomass and primary production rates in different zones varied from 10.3 to 30.2 mg l^{-1} and from 530 to 2300 mg C m^{-3} d^{-1}, respectively. Photosynthetic activity during the period of investigation on average was 2 times lower in the zone of seawater influence (Klaipeda Strait) than in the central part.

3 - The greatest differences in phytoplankton biomass and the rate of primary production in the investigated areas were registered during an intensive *Aphanizomenon* bloom. Total phytoplankton exudation ranged from 5 to 24 % (on average 12 %) of the total organic carbon production.

4 - The rates of production processes exceeded decomposition processes, thus stimulating the accumulation of autochthonic organic matter in the Curonian Lagoon during the midsummer vegetation period.

Keywords: phytoplankton, primary production, exudation, community respiration, Curonian Lagoon

Introduction

Eutrophication remains the main ecological problem in the Baltic coastal lagoons and estuaries (Schernewski, Schiewer, 2002). Inflow of nutrients increases primary production and causes summer cyanobacteria blooms in these ecosystems. Besides primary production, allochtonous organic matter may also contribute to system metabolism (Jassby *et al.*, 1993). It has been noted that in the summer period community respiration may be higher than primary production in estuaries because of allochtonous organic matter inflow with river water (Witek *et al.*, 1999).

The Curonian Lagoon is the largest and almost the most eutrophicated coastal lagoon in the Baltic Sea. It receives water from the Nemunas River, which is the third-largest contributor (after the Vistula and Oder Rivers) of total nitrogen and phosphorus to the Baltic Sea (Stalnäcke *et al.*, 1999). Even after a recent obvious decline in the use of fertilizers in Lithuania, nutrient concentrations did not decrease in the Lithuanian part of the lagoon (Olenina, Olenin, 2002), nor did the intensive cyanobacterial blooms in summer.

The production and fate of organic matter in this transitional water body has always been of a great interest (Sulijiene, 1990). On the basis of long-term (1974-1986) seasonal investigations, very high values of midsummer phytoplankton biomass and production-decomposition rates were detected. The investigations of the functioning of planktonic organisms were mostly carried out in the northern part of the lagoon (Jankevicius *et al.*, 1990). However, high variability of environmental conditions in such transitional water bodies exists. The structural and functional characteristics of communities can differ noticeably in various zones, especially in the river outlet and/or irregular marine water inflow zones. Detailed information on phytoplankton primary production and organic matter decomposition rates specifically regarding the environmental conditions in the Curonian Lagoon is still lacking.

The objectives of this study were to investigate how midsummer phytoplankton structure, primary production and community respiration rates vary under diverse hydroecological conditions in the Curonian Lagoon as well as evaluate the contribution of phytoplankton exudates to the total primary production.

Materials and Methods

Study site.

The Curonian Lagoon is a shallow (surface area - 1584 km^2, mean depth - 3.7 m) transitory water basin located in the south-eastern part of the Baltic Sea. The Nemunas River and several minor streams discharge into the Curonian Lagoon, resulting in a mean water residence time in this ecosystem of about three months. The Klaipeda Strait connecting the lagoon with the sea allows saltwater intrusion into a limited area in the northern part, where salinity varies from 0 to 8 PSU (Zaromskis, 1996).

Investigations were carried out in the Nemunas River Delta, in the central part and in the fresh-brackish water mixing zone (Klaipeda Strait) in July 2002 – 2004 (Fig.1). In addition, the rate of production-decomposition processes were also studied on the whole water area (11 stations) of the Lagoon on 2-3 August 2004. Samples were collected in the pelagic zone from the upper water layer (0.5 m) using a Ruttner collector.

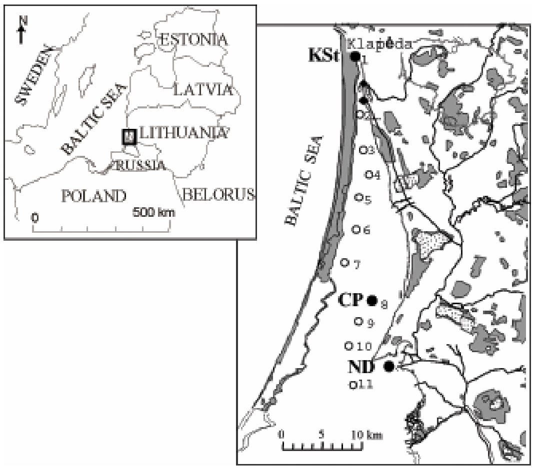

Figure 1. Situation of the Curonian Lagoon in the Baltic Sea and location of sampling stations in the Lithuanian part of the lagoon (KSt – Klaipeda Strait, CP – Central part, ND – Nemunas Delta)

Abiotic parameters.

Temperature, dissolved oxygen concentration and pH were determined *in situ* with a WTW MultiLine F/Set 3. Nutrient and DOC analyses were performed according to Merkiene . Ceponyte (1994). Phosphate-P was analysed by acid digestion followed by the molybdate ascorbic acid method; the same procedure was followed for total-P, following persulphate-H_2SO_4 digestion. Nitrate-N was determined using potassium persulfate-$K_2S_2O_8$ following Cd reduction to NO_2; total-N was analysed by the Kjeldahl method. DOC was measured by the dichromate oxidation method.

Phytoplankton community structure.

Half-litre samples for phytoplankton analysis were preserved with formaldehyde (4 % final concentration), concentrated by sedimentation (20-30 ml) and analysed under a Biolar light microscope (magnification 600×). Algae were counted (more than 500 counting units) in a Nageotte chamber, biomass was estimated from cell numbers and specific volumes (Olrik *et al.*, 1998). Chlorophyll *a* was extracted with 90 % acetone and analysed spectrophotometrically (Jeffrey. Humphrey, 1975).

Primary production and plankton community respiration.

The rates of primary production were investigated by ^{14}C and oxygen methods. In particular, the oxygen method was used not only to measure the rate of photosynthesis and community respiration, but also to evaluate the ratio between these parameters. The dissolved oxygen concentration in initial and in light- and dark-incubated (*in situ* for 24 h) bottles was determined by the Winkler method. Rates of photosynthesis (net production of oxygen) were estimated by the difference in the amount of oxygen in light and dark bottles. The rate of oxygen consumption (which corresponds to the rate of organic matter decomposition during community respiration) was evaluated by the difference in the amount of oxygen in initial and dark bottles. The values obtained were converted to carbon by factor 0.32 (Winberg, 1960).

Estimates of particulate production and extracellular release for phytoplankton.

The investigation of different fractions of total organic carbon production (TP) was carried out by applying labelled ^{14}C (Steeman-Nielsen, 1952) and selective filtration techniques (Vadstein *et al.*, 1989). 0.5 ml $NaH^{14}CO_3$ (activity 2 x 10^5 Bq/ml) was added to 100 ml samples. The samples (three light and one dark bottles) were incubated *in situ* for 4 h. The differentiation of separate fractions was performed by filtration using 1.5 and 0.17 μm polycarbonate filters (Synpor). The samples on filters were placed in HCl fumes for 5 min, while for liquid samples, inorganic ^{14}C was eliminated by adding HCl (pH ~ 2) and bubbling with air for 30 min. Radioactivity was measured by a liquid scintillation counter (Beckman Instruments Inc.). Particulate organic carbon production (PP) was determined by filtering an aliquot of 25 ml on 1.5 μm filters. ^{14}C on the 0.17 μm filter and in the 0.17 μm filtrate was taken to represent exudates incorporated by bacteria (EOC_i) and free dissolved phytoplankton exudates (EOC_d), respectively. The total exudation rate (EOC_t) was calculated as EOC_d+ EOC_i (including 40 % of respiration losses).

Results

Environmental conditions.

Due to mass development of phytoplankton (max. chlorophyll *a* – 246.2 μg/l in 2002) the water transparency was very low during active vegetation periods in July (Table 1). The Secchi disc depth was mainly less than 1 m except in the Klaipeda Strait area where values exceeded 1.2 m. It was only in the very north part of the Curonian Lagoon, where elevation of water salinity was registered. It ranged between 1.5 and 3.4 PSU at different sampling times. Higher concentration of inorganic nitrogen, predominantly in the form of ammonium, was found in the central part and the Klaipeda Strait. During an *Aphanizomenon flos-aquae* bloom (in July 2002) nitrate concentration was analytically immeasurable, while the concentration of ammonium was high (0.88 mg N l^{-1}). In contrast, under non-blooming conditions (in July 2003–2004), nitrate concentration ranged from 0.1 to 0.37 mg N l^{-1}, while ammonium values were 38 times lower (on average 0.023 mg N l^{-1}). In accordance with three year average data, DOC and phosphate concentration increased from the Klaipeda Strait towards the Nemunas River with the highest values in the delta area.

Structure of phytoplankton.

Phytoplankton biomass varied from 10.3 to 30.2 mg l^{-1} reaching the highest values during an intense *A.*
flos-aquae bloom in 2002 (Fig. 2). Algae biomass was maximal in the central part (18.6 mg l^{-1} on average throughout the study years). Three algal classes – *Cyanophyceae*, *Bacillariophyceae* and *Chlorophyceae* – made up

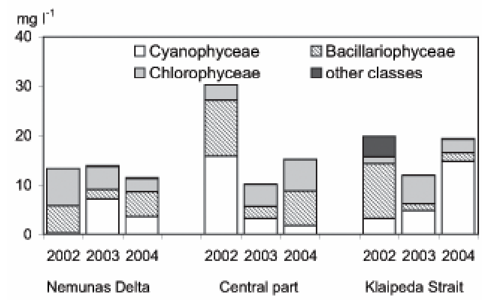

Figure 2. Phytoplankton composition and biomass in different zones of the Curonian Lagoon, July 2002-2004

the highest contribution to phytoplankton biomass in the Curonian Lagoon. The dominant algae species were most similar in the central part and the Klaipeda Strait in the same year. In both study sites *A. flos-aquae Cyclotella* sp. prevailed in 2002, *Woronichinia compacta*, *Pediastrum duplex*, *Closterium aciculare* in 2003, *Actinocyclus normanii* and *Oocystis submarina* in 2004, whereas the dominant species in the Nemunas Delta differed from the other studied sites significantly.

Table 1. Physical - chemical conditions in the upper water layer (0.5 m) of the Curonian Lagoon, July 2002-2004 mean values

Parameters /Sample site	Nemunas Delta	Central part	Klaipeda Strait
Depth, m	4.7 ± 0.3	4.0 ± 1.3	7.5 ± 4.3
Secchi depth, m	0.7 ± 0.1	0.6 ± 0.1	1.1 ± 0.1
Temperature, ^{o}C	20.2 ± 0.2	19.0 ± 0.9	19.0 ± 0.5
pH	8.1 ± 0.2	8.7 ± 0.2	8.4 ± 0.05
O_2, mg l^{-1}	7.0 ± 1.6	10.3 ± 1.9	9.2 ± 1.7
NO_3^-, mg N l^{-1}	0.1 ± 0.07	0.08 ± 0.05	0.22 ± 0.14
NO_2^-, mg N l^{-1}	0.003 ± 0.001	0.003 ± 0.002	0.003 ± 0.001
NH_4^+, mg N l^{-1}	0.11 ± 0.08	0.31 ± 0.38	0.22 ± 0.001
N_{total}, mg N l^{-1}	2.3 ± 1.2	2.05 ± 0.7	2.2 ± 0.7
PO_4^{3-}, mg P l^{-1}	0.043 ± 0.027	0.033 ± 0.015	0.027 ± 0.010
P_{total}, mg P l^{-1}	0.123 ± 0.04	0.125 ± 0.02	0.11 ± 0.06
DOC, mg l^{-1}	17.0 ± 4.5	14.0 ± 0.9	9.2 ± 1.0
BOD_7, mg O_2 l^{-1}	6.4 ± 2.5	6.3 ± 0.8	3.7 ± 0.2
Chlorophyll *a*, μg l^{-1}	23.7 ± 5.0	112.9 ± 88.8	42.8 ±21.3

Table 2. Dominant algae species in midsummer phytoplankton of the Curonian Lagoon (% of biomass)

	Nemunas Delta	Central part	Klaipeda Strait
2002	*Pediastrum boryanum* (Turpin) Meneghinii (21 %) *Chlamydomonas* sp. (11 %) *Scenedesmus quadricauda* (Turpin) Brébisson (5 %)	*Aphanizomenon flos-aquae* (L.) Ralfs (45 %) *Cyclotella* sp. (17 %)	*Diatoma* sp. (35 %) *Heterocapsa triquetra* (Ehrenb.) Stein (18 %) *A. flos-aquae* (14 %) *Cyclotella* sp. (6 %)
2003	*Planktothrix agardhii* (Gomont) Anagnostidis et Komárek (58 %) *Pediastrum duplex* Meyen (16 %)	*Woronichinia. compacta* (Lemmerm.) Komárek et Hindák (28 %) *P. duplex* (12 %) *Closterium aciculare* T. West (8 %)	*W. compacta* (44 %), *P. duplex* (14 %) *Cl. aciculare* (7 %) *Planctonema lauterbornei* Schmidle (7 %)
2004	*P. agardhii* (31 %) *Cyclotella meneghiniana* Kützing (15 %) *Stephanodiscus hantzshii* Grunov (10 %)	*Actinocyclus normanii* (Greg. in Grev.) Hustet (36 %) *Oocystis submarina* Lagerheimii (21 %)	*A. flos-aquae* (31 %) *A. normanii* (8 %) *O. submarina* (6 %)

Primary production and pelagic community respiration.

The rates of primary production (oxygen method) varied between 530–2300 mg C m-3 d-1 in the investigated areas. The maximal values of primary production during the investigation periods were registered in the central part (up to 2300 mgCm-3d-1), and the lowest (530–870 mg C m-3 d-1) in the fresh- and brackish water mixing zone (Figure 3 A).

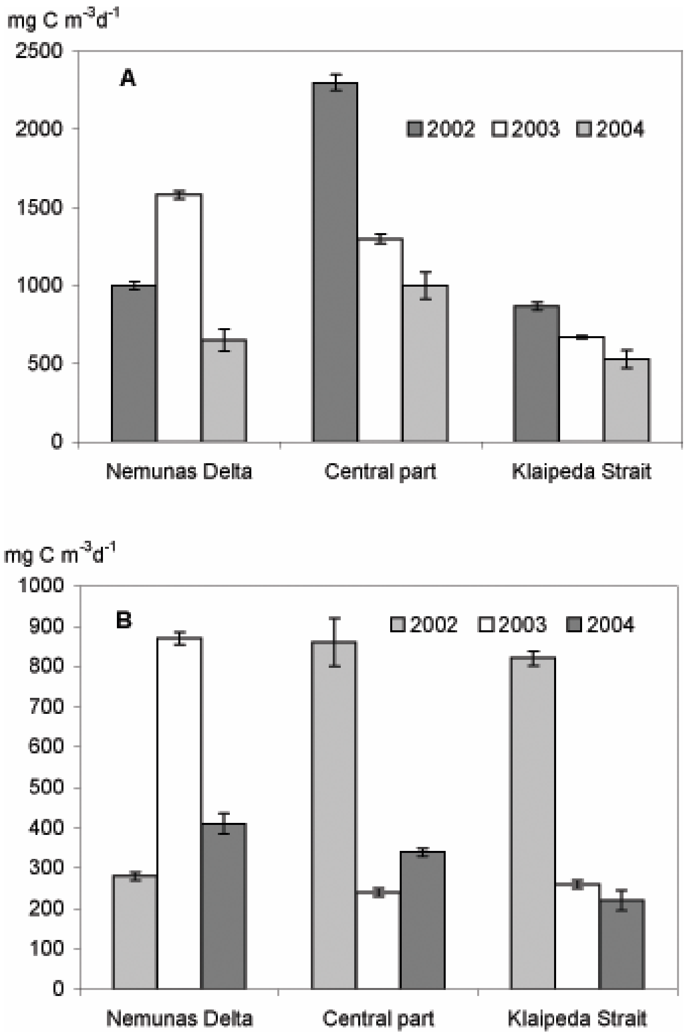

Figure 3. Phytoplankton primary production (A) and pelagic community respiration (B) in different zones of the Curonian Lagoon, July 2002-2004

The biggest spatial differences in phytoplankton productivity (the same as phytoplankton biomass) were observed during the *A. flos-aquae* bloom. In this period, the primary production in the central part was twofold and threefold higher than in the areas of the Nemunas Delta and in the Klaipeda Strait, respectively. The temporal variability of midsummer primary production in each site was also evident. Despite some exceptions (municipal wastewaters impact zone, 2nd station), in general phytoplankton primary productivity had a tendency to increase towards the southern part of the investigated area (Figure 4).

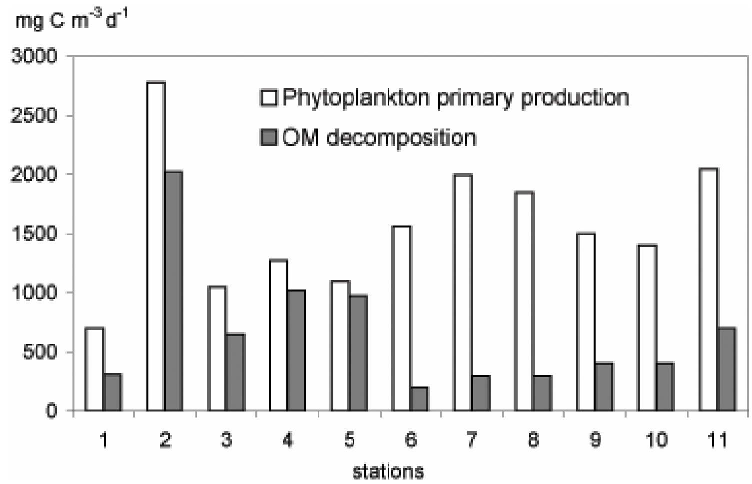

Figure 4. Spatial change in intensity of organic matter production and decomposition processes in the Curonian Lagoon on 2-3 August, 2004

The rate of community respiration in different zones and periods of investigations also varied widely (Fig. 3 B). However, the average respiration rate (like DOC concentration) increased from the Klaipeda Strait towards the Nemunas River, with the highest values (on average 520 mg C m^{-3} d^{-1}) in the Nemunas Delta. The net photosynthesis exceeded community respiration in all investigated places. The maximum ratio of organic matter production to decomposition (2.7–5.4) was found in the central part, whereas it ranged between 1.6–3.5 and 1–2.6 in the Nemunas Delta and the Klaipeda Strait, respectively. Total organic carbon production (particulate organic carbon production and total phytoplankton exudation) was also evaluated by applying the ^{14}C method with considerably shorter time of exposure. The mean values (two years) of midsummer particulate production and total phytoplankton exudation show a considerable difference for these parameters between the investigated sites, with lower values, both of particulate production and exudation, in the Klaipeda Strait (Figure 5). The rates of total phytoplankton exudation were found to have a positive relationship with the particulate production (R^2 = 0.70, $p<0.05$, n=12). Extracellular release of dissolved organic carbon by phytoplankton in different zones varied from 5 to 24 % and amounted on average to 12 % of total organic carbon production (Table 3). The parallel investigations of net primary production by the oxygen method and particulate primary production by the ^{14}C method were carried out in July of 2002 and 2003 under equal conditions of exposure *in situ* for 24 hours. The results in Table 4 show that despite quite significant fluctuation the mean PP_{oxygen}/PP_{carbon} ratio was 0.96, i.e. close to 1. These fluctuations may be related to the sensitivity of the methods as well as to the fact that the ^{14}C-method determines carbon flux, whereas the oxygen method gives results that are more closely associated with energy flux (Williams *et al*., 1979). It should be noted that in hydrobiological investigations both the oxygen and the ^{14}C methods are equally used for the determination of primary production.

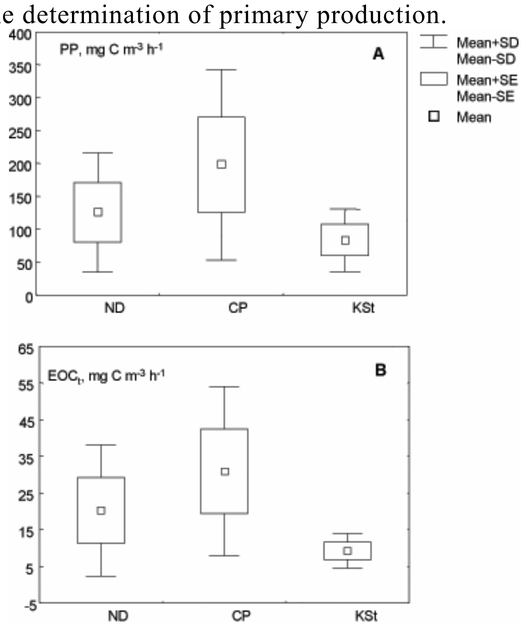

Figure 5. Particulate organic carbon production (A) and the total exudation of phytoplankton (B) in different zones of

the Curonian Lagoon (ND – Nemunas Delta, CP – Central part, KSt – Klaipeda Strait), 27-29 July 2002 and 16-17 July 2003 mean values

The advantages and limitations of each of them, as well as the ratio between the parameters obtained by the two methods have been widely discussed (e.g. Williams *et al.*, 1979, Bender *et al.*, 1987).

Table 3. Total organic carbon production (TP) and phytoplankton exudation (EOC_t) in the Curonian Lagoon, July 2002 and 2003 mean values

Sampling site	n	TP, mg C m^{-3} h^{-1}	EOC_t	
			mg C m^{-3} h^{-1}	% TP
Nemunas Delta	4	137.6 ± 86.4	20.5 ± 16.0	15.0
Central part	4	252.5 ± 169.6	31.7 ± 19.9	12.6
Klaipeda Strait	4	92.4 ± 37.1	9.2 ± 4.1	10.0

Table 4. Net primary production rates (mg C m^{-3} d^{-1}) measured by oxygen and ^{14}C methods (incubated *in situ* for 24 h)

Sampling site	Date	O_2 method	^{14} C method	$O_2/^{14}C$
Nemunas Delta	27 July 02	1061 ±25	1179 ± 33.0	0.90
Central part	29 July 02	2300 ±50	3141 ± 52.0	0.73
	17 July 03	1300 ±25	920 ± 7.6	1.41
Klaipeda Strait	29 July 02	870 ±25	803 ± 17.0	1,08
	17 July 03	670 ±0	1005 ± 12.0	0.67

Discussion

High concentrations of nutrients in the Curonian Lagoon seems to be among the main causes of the high intensity of phytoplankton primary production and other processes related to eutrophication. In midsummer 2002–2004, phytoplankton biomass in the Curonian Lagoon (10.3–30.2 mg l^{-1}) was similar to the values in the eutrophic Vistula Lagoon (44 mg l^{-1}) (Dmitrieva, 2005) and was five times higher than in the Neva Estuary (1.8–6 mg l^{-1}) (Nikulina, 2003). Cyanobacteria make a significant contribution to phytoplankton in the shallow low-salinity estuaries and lagoons of the Baltic (Carsten *et al.*, 2004). Usually, cyanobacteria (mostly *Aphanizomenon flos-aquae*) blooms are observed from the end of July to October in the Curonian Lagoon (Olenina, 1998). Under high nutrient content, the level and period of blooming depend on meteorological conditions, i.e. temperature and wind direction. Oliver anḍ Ganf (2000) and Kanoshina anḍ Lips (2003) stated that wind speed had a stronger impact on cyanobacteria abundance than water temperature during the summer period. Intensive blooming of cyanobacteria in the Curonian Lagoon was observed in July during the very warm summer of 2002. In the summer of 2003-2004, when the temperature did not reach high values and the wind direction changed frequently, cyanobacteria blooming was absent in July.

Long-term investigations of phytoplankton primary production by means of both oxygen and ^{14}C methods indicate that in the Lithuanian part of the Curonian Lagoon the intensity of this process may achieve 2500-4000 mg C m^{-3} d^{-1} during the “blooming” period. Similar values (3500-4200 mg C m^{-3} d^{-1}) were registered in the salty (4 ‰) Vistula Lagoon (Aleksandrov

2003). The maximum values of primary production were much higher (in the summer of 2002 up to 16100 mg C m^{-3} d^{-1}) in the Russian part of the Curonian Lagoon, where the impact of river discharges is lower and the inflow of sea water is absent (Aleksandrov 2003).

Due to the heterogeneity of the hydrological and chemical regime in the Lithuanian part of the lagoon, the spatial distribution of phytoplankton biomass and production were dissimilar. During all periods of investigation the values of primary production as well as the ratio of production to community respiration increased in direction from the Nemunas River Delta to the main part of the lagoon and were markedly lower in the zone of seawater influence (the Klaipeda Strait). In the northern part of the lagoon, where the impact of sea water is stronger, phytoplankton biomass and the intensity of production processes can vary from 2 to 26 times depending on the degree of marine water intrusion during midsummer (Sulijiene, 1990).

Extracellular release of dissolved organic carbon by phytoplankton on average made up 12 % of total primary production. Similar values have been found in other coastal eutrophic ecosystem (Marañon *et al*., 2004). In other regions of the Baltic Sea, the average annual exudate release has been estimated at 5 % (Witek *et al*., 1997), 7% (Lignell, 1990) and 12-16% (Larson, Hangstrom, 1982) of total primary production.

The ratio of production to decomposition of organic matter is close to one in sustainable water ecosystems (Boulion, 1983). During our investigations phytoplankton photosynthesis was intensive and the A/R ratio was higher than 1. So, in the Curonian Lagoon during the active vegetation period production-decomposition processes are biased towards production accumulation. On the other hand, during the salt water intrusion time to the lagoon, the amount of phytoplankton as well as photosynthetic activity decreases and decomposition processes dominate (A/R ratio – 0.1-0.4) in the northern part of the lagoon and especially in the Klaipeda Strait (Sulijiene, 1990).

Comparison of the results of the current investigation with others carried out previously indicates that the primary production values have not changed significantly in the Klaipeda Strait, but slightly increased in the central part over the period of two decades (Table 5). The values for primary production in the Nemunas River Delta significantly differed from those measured in July 1985 and 1991.

Table 5. Secchi disc depth (S) and primary production rates (PP) in July in different periods of investigation in the Curonian Lagoon (in brackets – mean values)

Sampling site	Years	S, m	PP, mg C m^{-3} d^{-1}
Klaipeda Strait	1985 – 1987	0.45 – 2.3 (1.3)	597 – 1650 (793)
	1991 – 1993	0.7 – 1.45 (1.0)	378 – 1387 (726)
	1996 – 1997	1.0 – 2.0 (1.5)	53 – 1230 (695)
	2002 – 2004	1.0 – 1.2 (1.0)	530 – 870 (690)
Central part	1985 –1987	0.45 – 0.8 (0.6)	1113 – 1273 (1201)
	1991 – 1993	0.8 – 0.9 (0.87)	600 – 1127 (980)
	1996 – 1997	0.5 – 0.9 (0.7)	1840 – 3820 (2830)
	2002 –2004	0.4 – 1.0 (0.7)	1002 – 2300 (1540)
Nemunas River Delta	1985	0.55	2250
	1991	0.5	4587
	2002 -2004	0.6 – 0.8 (0.7)	650 – 1580 (1077)

Thus, the high heterogeneity of hydrological – hydrochemical conditions in the Curonian Lagoon as a transitory water basin influences a fairly diverse spatial distribution of midsummer phytoplankton biomass and production. The greatest differences in these parameters were registered between the zones influenced by river runoff and marine water inflow and the more hydrologically stable central part of the lagoon during cyanobacteria blooming.

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