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PHOTOSYNTHESIS AND RESPIRATION OF PLANTS FROM THE GULF OF GDAŃSK

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Photosynthesis-light intensity relationship in nanoplankton, net plankton, and benthic plants from the Gulf of Gdańsk were determined and the relevant curves plotted. Based on the curves, seasonal variability of some parameters characteristic of gas exchange, i.e. compensation point (P_c), I_k , photosynthesis saturation point (P_s), photosynthesis maximum (P_m), an respiration (R) were examined. Plants from the Gulf of Gdańsk were found to have low light requirements, which indicates their shadow tolerance.

INTRODUCTION

Phytoplankton and phytobenthos are two ecological formations in aquatic ecosystems responsible for organic matter production from simple inorganic substances. Their contributions to primary production differ. According to Steemann Nielsen (1975), 95% of the annual primary production in the seas and oceans is due to phytoplankton activity. Characteristic of most of the aquatic ecosystems is the seasonal variability of productivity with simultaneous changes in the species composition of producers. Productivity of plant communities depends on specific photosynthetic activity of individual species and is modified by environmental conditions and endogenous factors. In this situation, knowledge of photosynthesis-light intensity relationships is particularly important as an initial information on primary production. The aim of the present work was to determine photosynthesis-light intensity relationships for major producers of organic matter in the Gulf of Gdańsk. Comparisons were also made between seasons and species composition.

MATERIALS AND METHODS

Phytoplankton was collected from the surface water layer, within April–December, at station GN (54°32'N, 18°48'E; 35 m depth) situated in the central part of the Gulf of

Gdańsk. Materials were collected with an Apstein phytoplankton net. The algae collected were carried in thermos flasks to the laboratory where, after removing zooplankton with a micropipette, experiments were started immediately. At the end of each experiment, the algae were placed in a larger volume of water and fixed with Lugol's solution. Biomass was determined following Edler (1979).

Nanoplankton was collected at GN, too, with a 5 dm³ bathometer. The samples were filtered through a No. 25 net (60 µm mesh size) to remove net phytoplankton and then passed through GF/C glass filters (0.7 µm pores) to retain the nanoplankton. Discs of 5 mm diameter were cut out of the filters. Some discs were placed in the reaction micro-chamber in a drop of water. The remaining discs were covered with immersion oil and the cell number and biomass were determined under a microscope (Holmes 1962).

Measurements of the phytoplankton gas exchange rates were carried out at a temperature the same as that in the field.

Benthic plants were collected from underwater meadows situated in the western part of the Gulf of Gdańsk (the inner Puck Bay). The materials were collected during three periods differing in their light and temperature conditions (Findenegg 1943):

- I. April – May (spring): high radiation intensity, low temperature;
- II. July (summer): high radiation intensity, high temperature;
- III. October (autumn): low radiation intensity, high temperature.

Benthic plants were kept for some days and then examined at a temperature average for the given season: 5°C (spring); 18°C (summer); and 12°C (autumn), and at the light intensity of 2000 lx (= 27 µE/m² s) with a light: dark cycle of 16:8 h. Measurements were also performed at 5, 18, and 12°C. Thallus fragments of several mg wet weight were used for gas exchange measurements (fragments from the upper parts of multilayer thall were used). Brinkhuis (1977a, 1977b) examined several benthic algae and reported that the gas exchange rates of intact plants and thallus fragments showed a great similarity. Fragmentation of benthic plants was widely applied in different techniques of photosynthesis and respiration measurements (Kanwisher 1966; King and Schramm 1976a; Mathiesen and Dawes 1974; Merrill and Waaland 1979).

Gas exchange rates were determined using a volumetric microrespirometer (Zurzycki and Starzecki 1971). The method was adapted to assessment of photosynthetic and respiratory activities of small biological objects at gas exchange rates varying within 10⁻¹–10⁻⁴ µl O₂/h with an accuracy of ±5%. CO₂ concentration in the reaction micro-chamber was kept at a constant level with 35 µl 0.1 Warburg No. 10 carbonate buffer. The light source used was a Narva bulb (220 V, 250 W) with 39 klx maximum light intensity. Infra-red radiation was absorbed by a 50 mm thick liquid filter containing 140 g ferrous ammonium sulphate in dm³ of 2% H₂SO₄. Different light intensities were obtained with a combination of neutral filters and diaphragms of various diameters. Light intensity was measured with a JU-16 luxmeter. The luxmeter was addi-

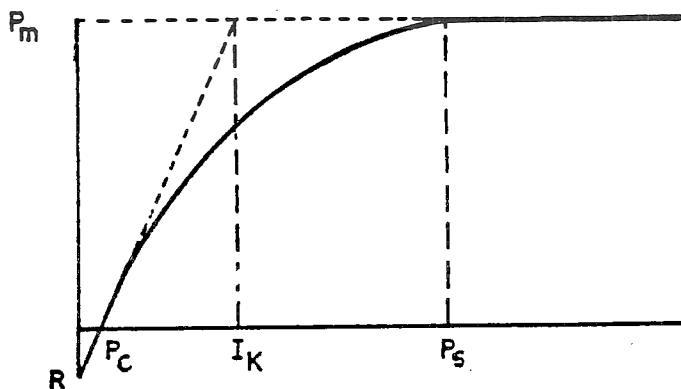


Fig. 1. Characteristic points of photosynthesis curve as a function of light intensity:

P_m = maximum photosynthesis; I_k = light intensity at the intersection of slope and horizontal sections of photosynthetic curve; P_s = saturation point; P_c = compensation point; R = dark respiration

tionally calibrated (using a Lambda Li-Cor Li-185 radiometer) in energy units characteristic of photosynthetic active radiation (PAR) range. It was calculated that for the optical micro-respirometer system used, 1 W/m^2 PAR corresponded to 205 lx.

The measurements were performed in 4–5 replicates and standard deviations did not exceed 10%. The same method, applied to different groups of plants such as small unicellular nanoplankton, net phytoplankton, multicellular benthic algae, and vascular plants as well as expression of the data obtained in comparable units ($\mu\text{l O}_2/\text{h mg}$ wet weight for benthic plants and $\mu\text{l O}_2/\text{h} \cdot \text{mm}^3$ for phytoplankton) enabled direct comparisons of photosynthesis and respiration rate.

Based on photosynthesis curves, changes of compensation point (P_c), I_k , saturation point (P_s), maximum photosynthesis (P_m), and respiration (R) were calculated (Fig. 1).

RESULTS

Comparison of the results obtained in each month of the growth season revealed sizable differences in the course of photosynthesis curves in the net phytoplankton. Fig. 2. presents such curves for the spring samples, photosynthesis being saturated with increasing light intensity up to 5000 lx (maximum at 10–12 klx). Results obtained in other periods of the growth season are given elsewhere (Latała 1982). Autumn samples characterized by diatom blooms showed photosynthesis saturation to occur even

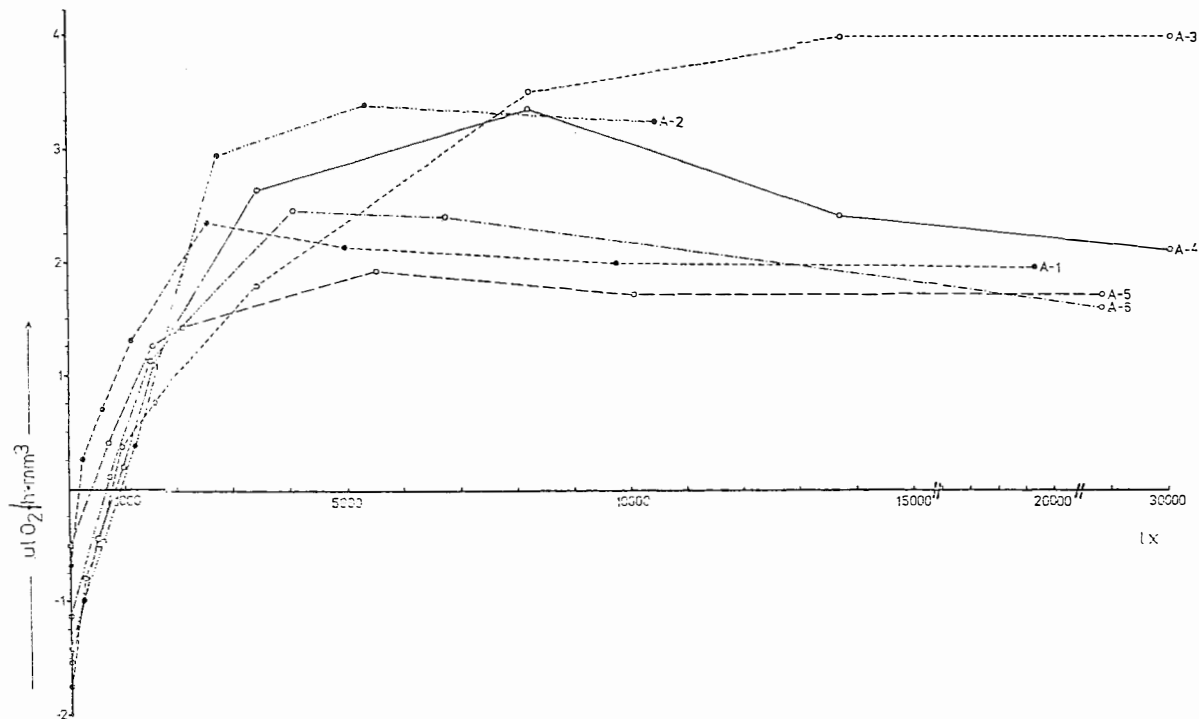


Fig. 2. Photosynthetic curves of spring net phytoplankton samples dominated by diatoms. Contribution of main species to total biomass (in %): A-1 - *Thalassiosira* sp. 46%; *Melosira* sp. 19%; *Chaetoceros* sp. 16%. A-2 - *Diatoma* sp. 30%, *Achnanthes taeniata* 20%; *Skeletonema costatum* 10%. A-3 - *Skeletonema costatum* 54%, *Diatoma* sp. 38%. A-4 - *Diatoma* sp. 42%; *Peridinium triquetra* 30%; *Skeletonema costatum* 10%. A-5. - *Achnanthes taeniata* 94%. A-6 - *Asterionella* sp. 37%; *Cyclotella* sp. 34%.

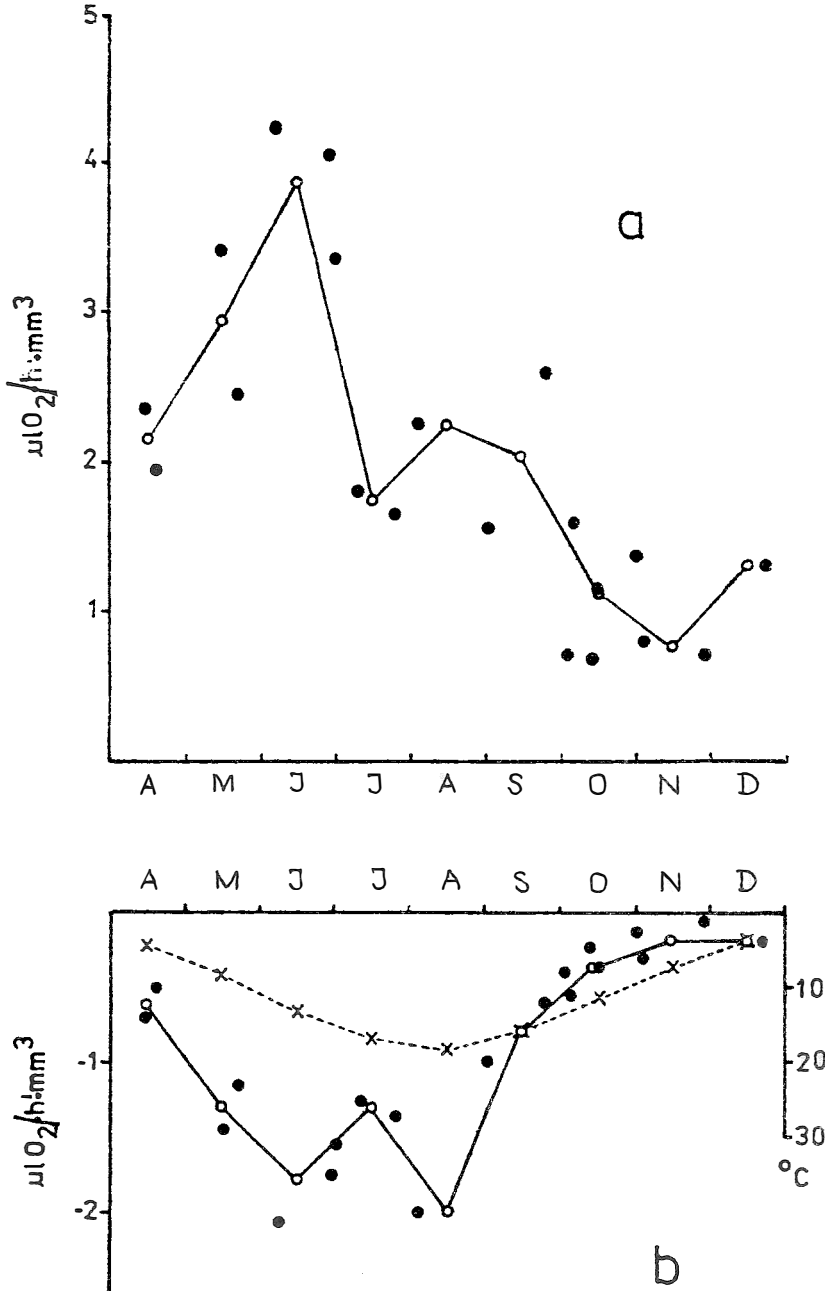


Fig. 3. Seasonal changes of maximum photosynthesis (a) and respiration (b) in net phytoplankton. Black circles = direct measurements; white circles = mean values for different months. Dashed line = seasonal changes of temperature

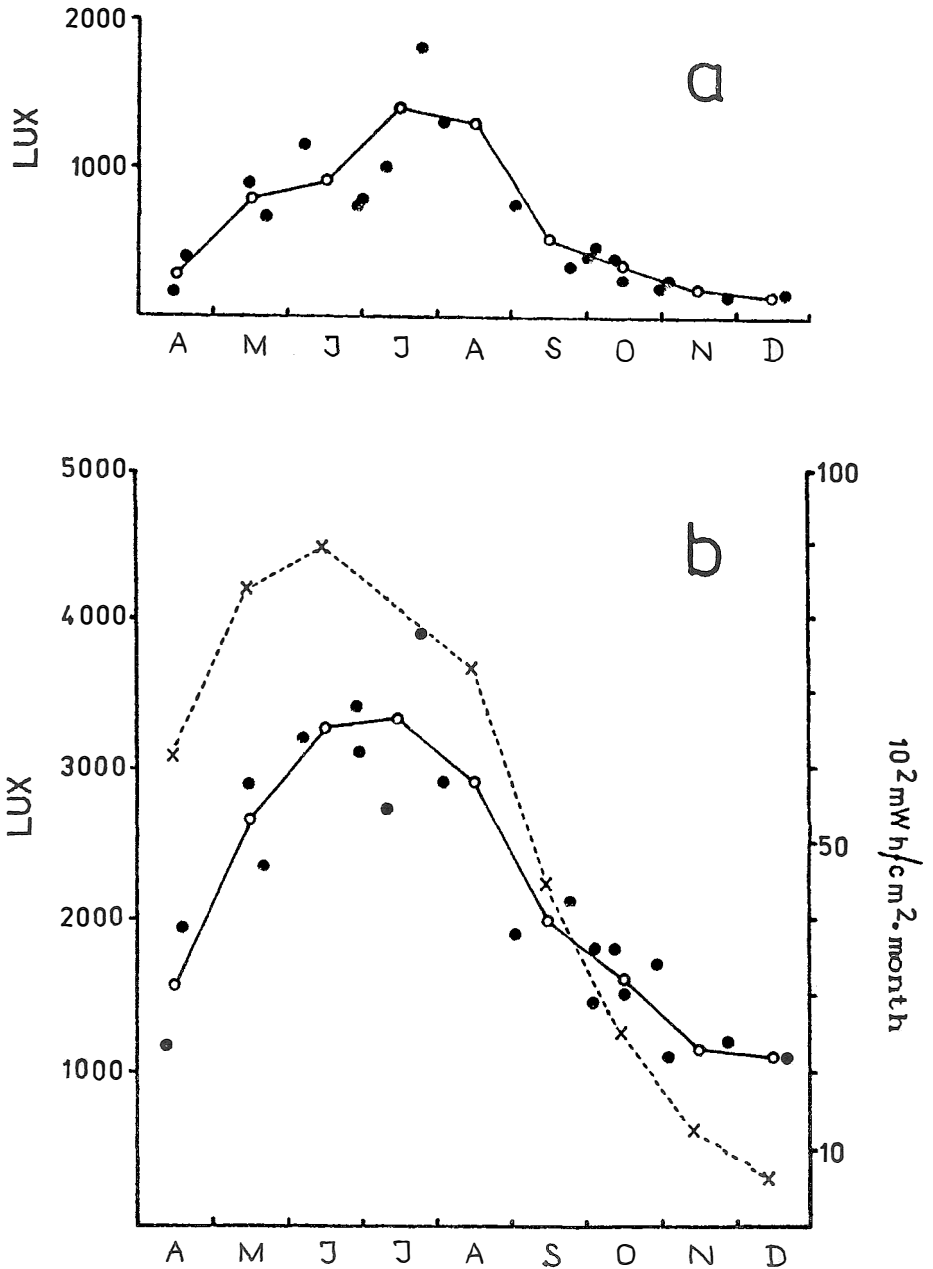


Fig. 4. Seasonal changes of compensation point (a) and I_k (b) in net phytoplankton. Black circles = direct measurements; white circles = means values for different months. Dashed line = changes of average totals of visible radiation reaching the environment in different months ($10^2 \text{ mWh/cm}^2 \cdot \text{month}^{-1}$) during 1965–74 (according to A. Krężel 1982)

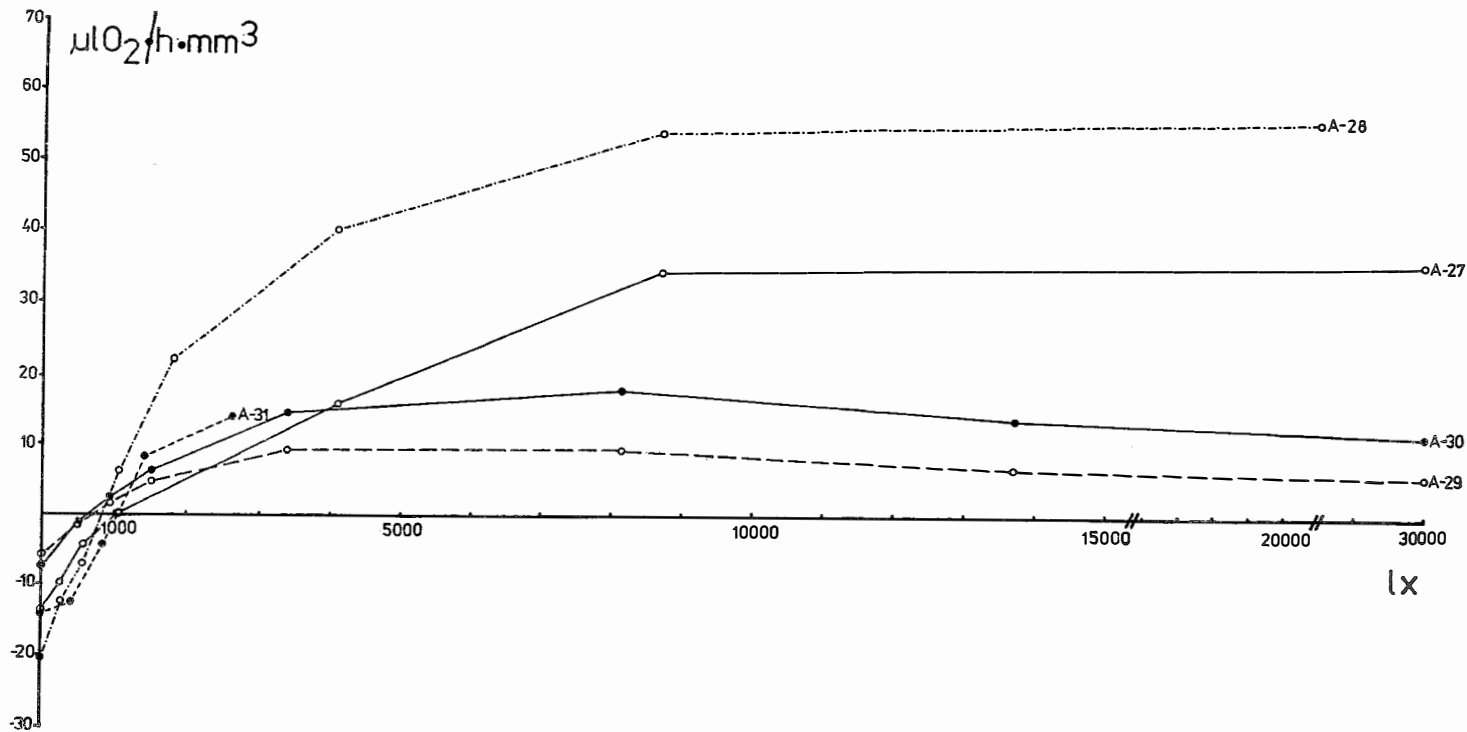


Fig. 5. Photosynthetic curves for nanoplankton. Contribution of main species to total biomass (in %): A-27 — *Cyclotella* sp. 52%; *Diatoma* sp. 18%; A-28 — *Cyclotella* sp. 46%; *Microcystis* sp. 26%. A-29 — *Peridinium triquetra* 72%; *Diatoma* sp. 15%; A-30 — *Peridinium triquetra* 72%; *Diatoma* sp. 15%. A-31 — *Dinophysis* sp. 48%; *Ebria tripartita* 17%; *Peridinium triquetra* 15%; *Skeletonema costatum* 10%

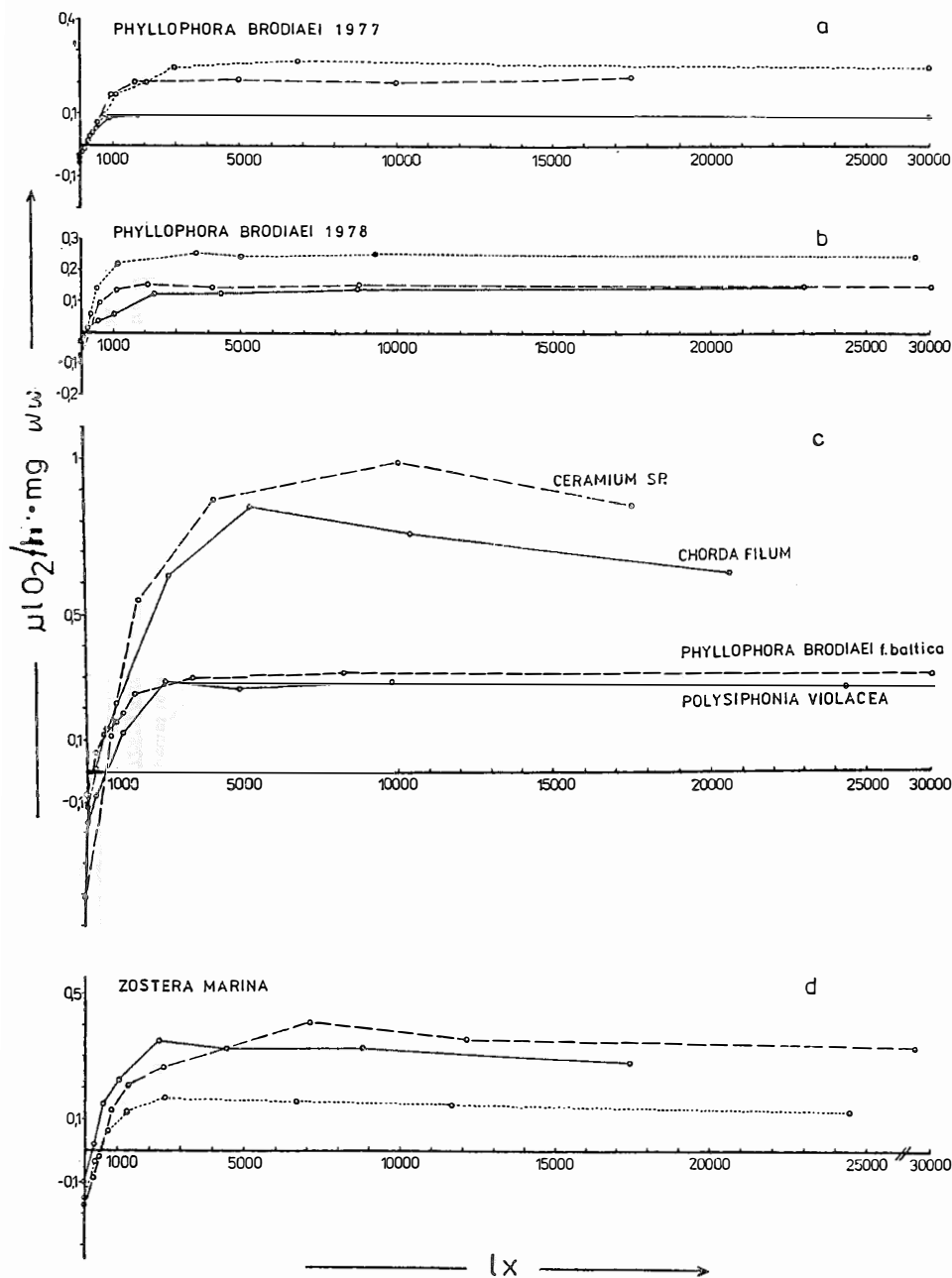


Fig. 6. Photosynthetic curves for benthic plants ($\mu\text{l O}_2 \text{ h}^{-1} \text{ mg}^{-1} \text{ w.w.}$).
 Continuous line = spring data; dashed line = summer data; dotted line = autumn data

at about 2500 lx. In many cases, a certain decrease in photosynthetic rate with increasing light intensity was observed. As shown in Fig. 3a, Pm in the net phytoplankton was in the range of 0.67 – 4.22 $\mu\text{l O}_2/\text{h}\cdot\text{mm}^3$. The rate increased in spring and – accompanied by diatom domination – attained the highest level in June following which a gradual decrease was recorded. Respiratory oxygen consumption changed within the range of –0.06 to –2.06 $\mu\text{l O}_2/\text{h}\cdot\text{mm}^3$ with the maximum values in June – August associated with the blue-green algae domination. The respiration rate values varied following the seasonal temperature changes (Fig. 3b). As can be seen from Fig. 4, the compensation point and Ik showed seasonal variability as well. Light intensity at the compensation point was in the range of 150–1700 lx and was lowest in early spring and autumn and highest in summer. The same trend was observed in Ik which ranged within 1100–3850 lx. Seasonal differences in the compensation point and Ik (Fig. 3b) are closely related to changes in average energy totals in the range of visible light reaching the environment during different months. In most cases, a doubled Ik value corresponded with the photosynthesis saturation point.

Nanoplankton was studied only in the season of its more abundant growth, i.e. in June and July. The photosynthesis curves are shown in Fig. 5. Photosynthesis maximum and respiration ranged within 8.95–55.54 and –5.58 to –20.31 $\mu\text{l O}_2/\text{h}\cdot\text{mm}^3$, respectively. The photosynthetic activity was significantly higher in samples dominated by diatoms (Fig. 5, curves A–27 and A–28) than in those dominated by dinoflagellates. The compensation point and Ik of nanoplankton ranged within 650–1000 and 2000–3200 lx, respectively.

The gas exchange was determined in the dominant or abundant benthic plant species from the Gulf of Gdańsk. Fig. 6 shows the photosynthesis curves of some species, the complete data being given elsewhere (Latała 1982). Table 1 summarizes the characteristic parameters of the gas exchange in all the species tested. The difference in Pm between individual species ranged within 0.105–3.23 $\mu\text{l O}_2/\text{h}\cdot\text{mg}$ wet weight. The lowest value was exhibited by the red alga *Phyllophora brodiaei*, whereas the highest one concerned the green alga *Enteromorpha* sp. The respiration rate ranged within –0.028 to –0.838 $\mu\text{l O}_2/\text{h}\cdot\text{mg}$ wet weight and, as in the case of Pm, the highest and the lowest values were found in the species mentioned above. Light intensity at the compensation point ranged within 150–900 lx. *Phyllophora brodiaei* exhibited a low demand for light, whereas *Myriophyllum spicatum*, a vascular plant, had a high demand. The light intensity at Ik changed from 700 lx (*Phyllophora brodiaei*) to 4000 lx (*Enteromorpha intestinalis*), photosynthesis being saturated at 1500–7000 lx. High light intensities (20–30 klx), as a rule, did not reduce the photosynthetic rate of the plants studied.

To facilitate comparisons of photosynthetic activity between different groups of plants from the Gulf of Gdańsk, gas exchange was measured with the same technique and the results were expressed in comparable units. The highest gas exchange rates

Table 1

Characteristic points of light-photosynthesis curves for benthic plants from Gdańsk Bay,
Pm, Ik, Pc, R as in Fig. 1

Species	Time	Pm ($\mu\text{O}_2 \cdot \text{h}^{-1} \cdot \text{mg}^{-1} \text{f wt}$)	R	Pc	Ik (lx)	Ps	Pm/R
1	2	3	4	5	6	7	8
<i>Chlorophyta</i>							
<i>Chaetomorpha linum</i>	IV 1978	0.621	-0.380	700	1900	3000	1.63
	VII	0.536	-0.157	300	1500	5000	3.40
	X	0.401	-0.070	250	1300	3000	5.72
<i>Cladophora albida</i>	VII. 1978	1.001	-0.232	450	2500	4500	4.31
<i>Cladophora rupestris</i>	V. 1977	0.377	-0.120	150	850	3000	3.15 +
	VII	0.612	-0.245	450	1800	4000	2.50
	X	0.789	-0.190	150	1150	4000	4.15
	IV. 1978	0.447	-0.101	200	1000	3500	4.41
	X	0.502	-0.295	350	1250	3500	1.70
<i>Cladophora serica</i>	VI. 1978	1.139	-0.250	250	1400	2000	4.56
<i>Cladophora sp.</i>	VII. 1977	1.476	-0.635	600	2000	6000	2.32
<i>Enteromorpha ahneriana</i>	X. 1978	3.231	-0.810	550	3400	7000	3.99
<i>Enteromorpha clathrata</i>	VII. 1978	0.552	-0.205	500	2000	3000	2.69
<i>Enteromorpha compressa</i>	VII. 1978	1.866	-0.349	300	2000	3000	5.35
	XI	3.158	-0.492	300	2300	5000	6.42
<i>Enteromorpha flexuosa</i>	X. 1978	1.134	-0.184	150	1400	3500	6.15
<i>Enteromorpha intestinalis</i>	IV. 1978	1.808	-0.495	800	4000	7000	3.65
	V	2.147	-0.479	250	1900	6000	4.48
	VII	1.606	-0.472	650	2900	7000	3.40
<i>Enteromorpha linza</i>	X. 1978	2.584	-0.404	150	1500	5000	6.39
<i>Enteromorpha sp.</i>	V. 1977	0.949	-0.247	300	1500	5000	3.43
	VII	2.362	-0.838	300	1300	5000	2.82
	X	1.499	-0.282	300	2100	4000	5.32

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1	2	3	4	5	6	7	8
<i>Ulothrix implexa</i>	IV. 1978	1.241	-0.381	500	2200	3000	3.26
<i>Phaeophyta</i>							
<i>Chorda filum</i>	V. 1978	0.845	-0.109	150	2400	5000	7.74 +
<i>Ectocarpus siliculosus</i>	VII. 1978	0.870	-0.250	650	2900	5000	3.48 +
<i>Fucus vesiculosus</i>	V. 1977	0.168	-0.065	300	1100	200	2.59
	VII	0.406	-0.169	300	1200	4000	2.39 +
	X	0.381	-0.204	300	1000	4000	1.87
	V. 1978	0.357	-0.357	500	1700	2000	2.78
	VII	0.408	-0.114	250	1400	4000	3.58
	X	0.455	-0.150	400	1700	4500	3.03
<i>Pilayella littoralis</i>	V. 1977	0.459	-0.126	400	1800	2000	3.65
	VII	0.579	-0.435	750	1700	2500	1.33
	X	0.541	-0.399	300	900	1500	1.35
	IV. 1978	0.507	-0.361	400	1000	2000	1.40
	X	1.055	-0.674	350	900	6000	1.56
	<i>Rhodophyta</i>						
<i>Ceramium sp.</i>	VII. 1977	0.985	-0.413	500	1900	7000	2.39
<i>Furcellaria fastigiata</i>	V. 1977	0.178	-0.074	200	800	1500	2.42 +
	VII	0.330	-0.098	300	1300	3000	3.36
	X	0.141	-0.054	150	800	2000	2.62
	IV. 1978	0.173	-0.100	250	900	2000	1.73 +
	VII	0.382	-0.074	200	1700	4000	5.02
	X	0.279	-0.097	400	1600	3000	2.88
<i>Phyllophora brodiaei</i>	V. 1977	0.105	-0.037	150	800	1500	2.86
	VII	0.223	-0.045	150	1100	1500	4.93
	X	0.269	-0.060	150	1300	3000	4.51
	V. 1978	0.154	-0.028	150	1000	2000	5.45
	VII	0.137	-0.079	250	800	1500	1.98
	X	0.262	-0.068	150	700	1500	3.85
<i>Phyllophora brodiaei f. baltica</i>	VI. 1978	0.313	-0.124	250	1100	2500	2.53
<i>Polysiphonia violacea</i>	IV. 1978	0.290	-0.162	500	1400	2500	1.79
<i>Vascular plants</i>							
<i>Myriophyllum spicatum</i>	V. 1978	0.378	-0.172	500	1900	3000	2.19
	VII	0.511	-0.392	900	2100	4000	1.30 +
	X	0.552	-0.183	400	2100	4000	3.01
<i>Potamogeton filiformis</i>	IV. 1978	0.160	-0.080	600	2000	2500	2.00
<i>Zostera marina</i>	IV. 1978	0.349	-0.099	200	1000	2500	3.51
	VII	0.406	-0.171	450	1500	6000	2.37
	X	0.168	-0.156	450	1000	2500	1.08 +

+ photosynthesis inhibition in strong light ($\approx 28 \text{ klx}$)

Table 2

Maximum values of net photosynthesis and respiration for different groups of plants from Gdańsk Bay		
	$\mu\text{l O}_2 \text{ h}^{-1} \cdot \text{mm}^3$	R
Nanonplankton	8.95 – 55.54	–5.85 – 20.30
Net phytoplankton	0.67 – 4.22	–0.06 – –2.06
	$\mu\text{l O}_2 \text{ h}^{-1} \cdot \text{mg}$	
Benthic plants	w.w.	
algae with thin thallus	0.10 – 3.23	–0.03 – –0.84
algae with thick thallus	0.40 – 3.23	–0.10 – –0.84
vascular plants	0.10 – 0.45	–0.03 – –0.20
	0.16 – 0.55	–0.08 – –0.39

were recorded in small nanoplanktonic organisms, whereas the lowest values were characteristic of perennial algae with multilayer thalli as well as of vascular plants (Table 2). The photosynthetic and respiration rates differed by the factor as high as 500 and more than 500, respectively.

DISCUSSION

Photosynthetic active radiation (PAR) constitutes about 45% of the total solar radiation (Kirk 1983) and does not exceed about 500 W/m^2 on a sunny day (Czopek 1971). The energy contained between the compensation and photosynthesis saturation points is of a great importance for efficient production of organic matter. Daniels (1956) reported that this energy ranged within $0.5 - 50 \text{ W/m}^2$. The present study yielded comparable results, i.e. $150 - 10,000 \text{ lx}$ ($= 0.7 - 49 \text{ W/m}^2$).

The ^{14}C method was employed to examine gas exchange rates of natural phytoplanktonic communities. The method does not, however, apply to respiration rate measurements, thus the values of respiration rate extrapolated from photosynthesis-light intensity curves (Steemann Nielsen and Hansen 1959a) are not accurate (Talling 1975). For this reason, relatively few data exist on respiration and light intensity at the compensation point in natural phytoplanktonic communities and the results obtained in the present work are therefore still more interesting. Steemann Nielsen and Hansen (1959b) reported P_c values in natural plankton communities. P_c of the surface phytoplankton growing at high light intensities ranged within $600 - 1200 \text{ lx}$, whereas the phytoplankton from lower parts of the euphotic zone was adapted to low light intensities, its P_c ranging within $200 - 450 \text{ lx}$. The present results concerning light intensity at the compensation point are similar to those obtained by Steemann Nielsen and Hansen (1959b). No data on seasonal variability of P_c (Fig. 3a) could be found in the literature.

During the growth season, phytoplankton exhibited a characteristic pattern of I_k values, with the highest I_k in summer and the lowest in winter (Gargas 1971; Jewson 1976; Steemann Nielsen and Hansen 1961; Talling 1957). A similar I_k curve was obtained in the present study. The light intensity values at I_k were relatively low throughout the growth season (1100–3850 lx) and conformed with the results of other authors concerning phytoplankton from the lower part of the euphotic zone and adapted to low light intensity.

The photosynthesis saturation of phytoplankton often occurs even at $100 \mu\text{E}/\text{m}^2 \text{ s}$ (= 5000 lx) and remains at a constant level in the light intensity range of $3 \times I_k$ (Harris 1978). Similar results were obtained by Jenkin (1937), Ryther (1956) and Talling (1960). In tropical waters and in the North Atlantic, photosynthesis saturation took place at 30 (Steemann Nielsen and Jensen 1957) and 6–13 klx (Steemann Nielsen and Hansen 1959b), respectively. Photosynthesis of the phytoplankton from lower parts of the euphotic zone is saturated at lower light intensities (often lower by half) as compared with the surface phytoplankton (Ichimura et al. 1962). Generally, phytoplankton from the Gulf of Gdańsk showed photosynthesis saturation at a relatively low light intensity of 5000 lx. The I_k or P_s values indicate that the material studied has low light requirements.

Light intensities higher than $3 \times I_k$ (Harris 1978) or exceeding photosynthesis saturation point by 10 klx (Ryther 1956) cause a significant inhibition of planktonic photosynthesis, particularly in marine organisms. An extensive review on the subject is given by Harris (1980). The results obtained here conform with the above-mentioned data. In most cases, the highest light intensity used (20–30 klx) reduced the rate of photosynthesis.

P_m values of the net phytoplankton ($2 \mu\text{l O}_2/\text{h} \cdot \text{mm}^3$ on the average) were much lower than those of the nanoplankton (Table 2). Malone (1980) reported that nanoplankton exhibited higher photosynthetic activity than did the net phytoplankton. He found that average gas exchange rate per chlorophyll unit was 2–3 times higher in nanoplankton than in the net phytoplankton. The results obtained here confirm the well-known principle: the smaller the organism, the higher its metabolic rate resulting from the higher ratio of chlorophyll *a* content and cell surface to the cell volume (Paasche 1960; Smayda 1965; Sournia 1982). The highest gas exchange was observed in the nanoplankton samples dominated by diatoms, whereas a decrease in the gas exchange rate was recorded in those samples dominated by dinoflagellates. This fact can be correlated with the opinion that diatoms show higher photosynthetic activity per C unit than other algal taxa (Chan 1980; Thomas et al. 1978).

Relatively few studies have been conducted on the gas exchange in Baltic plants. Some results obtained in the western (King and Schramm 1976b) and the northern (Wallentinus 1978, 1979) regions of the Baltic could be found only, information on the Southern Baltic lacking completely.

When comparing data reported in the papers mentioned above, concerning gas exchange rates in plants from different Baltic areas with results obtained in the Gulf of Gdańsk (Latała 1982), a close similarity could be seen in spite of different methods applied, whereas significant differences exist in the light requirements. King and Schramm (1976b) demonstrated that photosynthesis in most species was saturated at about 25 klx. According to Wallentinus (1978), photosynthesis saturation occurred in a wide range (1800–20,000 lx) and, similarly to the present work, she found the lowest values in the red algae *Phyllophora brodiaei* and *Furcellaria fastigiata*. The photosynthesis saturation in phytobenthic species from the Gulf of Gdańsk was in a narrower range of 1500–7000 lx. King and Schramm (1976b) found that light intensity at the compensation point ranged within 250–2150 lx, whereas lower values (150–900 lx) were obtained in the experiments presented. Photosynthesis inhibition at high light intensities has been observed only occasionally in the benthic plants. This is a significant difference with respect to planktonic communities (Stemann Nielsen 1975). Similar differences were observed in the present study.

Light requirements of different plant species result from phylogenetic and/or ontogenetic adaptations (Rabinowitch 1951). Different authors reported various light intensities characteristic of heliophilous and shadow-tolerant plants. According to Rabinowitch (1951) and Szennikow (1951), P_c in shadow tolerant and heliophilous plants is 2–50 lx and 500–700 lx, respectively, photosynthesis being saturated (P_s) at 200–2000 lx and 2000–8000 lx, respectively. Higher light intensities at the compensation point were suggested by Górski (1962): 100–300 lx for shadow-tolerant and 200–1000 lx for heliophilous plants. He reported the same values of light intensity in the case of saturation point. It appears from the above review that the plants from the Gulf of Gdańsk showed relatively low light requirements. Their shadow-tolerant nature results from adaptation of highly polluted and poorly transparent waters.

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