Estimation of carbon release from phytoplankton cells during photosynthesis in the Gulf of Gdańsk

OCEANOLOGIA, No. 34
pp. 49–56, 1993.
PL ISSN 0078–3234

Carbon released
from phytoplankton
Primary production
Baltic Sea
Gulf of Gdańsk

HENRYK RENK
Marine Biology Centre,
Polish Academy of Sciences,
Gdynia

Manuscript received June 8, 1993, in final form November 5, 1993.

Abstract

The results of daily primary production determined by the ^{14}C method in the Gulf of Gdańsk are presented. The amount of carbon released from phytoplankton cells during photosynthesis was calculated from the difference between the daily primary production of separate morning and afternoon incubations and that of all-day incubation. The largest quantity of matter, *ca.* 25% of the primary production, was released from phytoplankton cells in May, whereas during the other spring and summer months (April to September) carbon release varied between 6 and 10% of primary production.

1. Introduction

The isotope method of estimating primary production (Steemann Nielsen, 1952, 1965) has been used for many years and basically measures the carbon incorporated in phytoplankton cells. For years it has been stated that some organic matter is excreted into the environment during photosynthesis (Fogg, 1977, 1983; Anderson and Zeutschel, 1970; Thomas, 1971; Berman and Holm-Hansen, 1974; Sharp, 1977). According to Fogg (1966), 5–35% carbon photosynthetically fixed by phytoplankton may be released almost immediately into the environment in this way. Carbon in the form of organic compounds excreted by phytoplankton may become a feeding basis for bacteria in the environment, thus starting a subsidiary link in the food-chain (Larsson and Hagström, 1979, 1982; Laanbroek *et al.*, 1985; Bratbak and Thingstad, 1985). For this reason the amount of matter released from cells during photosynthesis is of much interest to scientists. The matter released from phytoplankton cells in the Baltic Sea has up till now been

almost an unknown link in the energy and marine organic matter balance. There now follows an attempt to estimate the quantity of matter released during photosynthesis.

2. Material and methods

The experimental material was collected during cruises aboard the research vessels of the Sea Fisheries Institute, Gdynia. The results below have never been published before and were obtained as a by-product of other research programmes. This material comprises the results of primary production measurements made during incubations in the morning – P_1, afternoon – P_2 and all day – P_3 at three stations located in the Gulf of Gdańsk – Tab. 1.

Table 1. Sampling stations

Station	Region	Position		Depth
		N	E	[m]
G_2	Gdańsk Deep	54°50'	19°20'	116
J	Puck Bay	54°35'	18°45'	55
H	Hel	54°35'30"	18°45'36"	41

The primary production was measured by the radioisotope method (Steemann Nielsen, 1952) at a depth of 0.5 m and, occasionally, also at 5 m, 10 m and 20 m. The details of this method are specified elsewhere (Renk, 1983, 1990).

3. Results and discussion

The results of primary production measurements are shown in Tab. 2. The expression $P_1 + P_2$ is the sum of the primary productions measured in the morning and afternoon, whereas P_3 stands for the primary production measured during an all-day incubation. These results prove that the primary production measured during two consecutive time intervals, in the morning and afternoon, is greater than that measured during an all-day incubation. The difference is presumably caused by carbon release from phytoplankton cells.

At the initial stage of *in situ* phytoplankton incubation in the presence of carbon–14 (^{14}C) (in the bottle), the cells contain natural carbon; only after some time do they start releasing ^{14}C incorporated during photosynthesis at the time of the experiment. The concentration of ^{14}C in phytoplankton cells depends on the incubation time, and the amount of ^{14}C released from

the cells is proportional to its concentration in them. The differences in ^{14}C concentrations in cells caused by different incubation times may helpful in calculating the amount of carbon released from cells during photosynthesis.

Table 2. Primary production and carbon released from phytoplankton cells

Date	Station	E	$P_1 + P_2$	P_3	δ	λ
	Incubation time (day length) D = 16 h					
May 16	G_2	1.42	25.6	9.2	2.28	0.22
May 17	G_2	6.22	18.3	15.3	1.20	0.05
May 18	G_2	19.54	39.1	11.4	3.43	0.36
May 19	G_2	13.76	13.9	2.9	4.79	0.47
May 20	G_2	21.36	19.8	4.7	4.21	0.42
May 24	H	12.51	74.9	19.9	3.76	0.38
May 25	H	14.69	14.1	9.0	1.57	0.12
May 26	H	22.25	8.0	4.6	1.74	0.15
May 28	H	16.17	24.9	22.2	1.12	0.03
	Incubation time (day length) D = 16 h					
May 29	H	13.16	26.4	12.5	2.11	0.20
May 24	H	* 5 m	38.5	17.4	2.21	0.22
May 25	H	* 5 m	6.1	1.0	6.10	0.56
May 26	H	* 5 m	9.0	4.6	1.96	0.18
May 29	H	* 5 m	44.5	26.1	1.70	0.15
June 23	G_2	17.27	55.4	48.0	1.15	0.04
June 24	G_2	12.56	78.9	66.4	1.19	0.05
June 25	G_2	22.4	81.6	59.5	1.37	0.08
June 28	G_2	9.8	88.9	61.6	1.44	0.10
June 23	G_2	* 5 m	37.1	19.6	1.89	0.17
June 23	G_2	* 10 m	13.8	10.8	1.28	0.06
June 23	G_2	* 20 m	1.5	1.0	1.50	0.10
Aug 15	G_2	23.13	48.7	43.2	1.13	0.03
Aug 16	G_2	16.96	58.8	39.8	1.48	0.10
Aug 17	G_2	10.11	60.3	36.6	1.65	0.13
Aug 18	G_2	8.27	87.4	69.6	1.26	0.06
	Incubation time (day length) D = 14 h					
Apr 9	J	21.54	651.5	479.4	1.36	0.08
Apr 10	J	11.99	552.6	376.4	1.47	0.11
Apr 11	J	11.88	203.6	120.4	1.69	0.16
Apr 12	J	18.49	124.2	79.3	1.57	0.13
Apr 13	J	14.21	145.6	126.6	1.15	0.04
Apr 14	J	7.31	100.0	56.1	1.78	0.17
Apr 15	J	17.32	44.7	43.6	1.02	0.01

Table 2. (continued)

Date	Station	E	P_1+P_2	P_3	δ	λ
Apr 15	J	6.39	251.5	185.2	1.36	0.09
Apr 16	J	8.59	205.9	191.4	1.08	0.03
Apr 16	J	*5 m	92.8	72.8	1.27	0.06
Sep 8	J	12.21	101.2	72.0	1.43	0.10
Incubation time (day length) D = 8 h						
Jan 16	H	2.68	16.0	9.5	1.68	0.14
Jan 17	H	1.51	18.9	18.3	1.03	0.02
Nov 18	H	0.84	3.4	2.0	1.70	0.28
Nov 19	H	1.80	8.1	7.9	1.03	0.015
Nov 20	H	1.77	7.1	7.1	1.00	0.00
Nov 21	H	2.19	6.9	5.6	1.23	0.07
Incubation time (day length) D = 7.7 h						
Dec 16	J	0.94	17.0	12.3	1.38	0.17
Dec 17	J	1.30	18.2	14.4	1.26	0.12

* measurement at 5 m, 10 m, 20 m depth, other measurements – in surface water,

E – diurnal dose of solar irradiance energy [MJ m^2 day^{-1}],

P_1+P_2 – daily primary production measured in two incubation intervals [mgC $m^{-3}d^{-1}$],

P_1 – from sunrise to true noon,

P_2 – from true noon to sunset,

P_3 – daily primary production measured during all-day incubation [mgC $m^{-3}d^{-1}$],

$\delta = (P_1 + P_2)/P_3$,

λ = quantity of carbon released from phytoplankton cells (relative to primary production).

The following indices are introduced to calculate the relative amount of carbon released from phytoplankton cells (with reference to phytoplankton production) in unit time:

A – phytoplankton radioactivity after an incubation time t,

ΔA – loss of phytoplankton activity due to carbon release from the cells in time Δt.

The relative amount of carbon released in unit time can thus be expressed by

$$\lambda = \frac{\Delta A}{A \Delta t}. \qquad (1)$$

Changes in phytoplankton radioactivity during incubation are caused by primary production $[p_h\, I(t)\,/\alpha]$ and activity loss due to release $[\lambda\, A]$, *i.e.*

$$\frac{dA}{dt} = \frac{p_h\, I(t)}{\alpha} - \lambda\, A, \tag{2}$$

where

p_h – the rate of primary production expressed as the amount of assimilated carbon in 1 m^3 of water at an irradiance of 1 [MJ m^{-2}],

$I(t)$ – solar radiation dose in time t,

$\alpha = \frac{Prod}{A}$ – the relationship betweeen primary production and phytoplankton radioactivity in the experiment.

To make the calculations easier, it is assumed here that primary production is a linear function of irradiance (of only limited validity). The calculations are for a standard day, when the diurnal changes in irradiance can be expressed by the function (Renk *et al.*, 1983)

$$I(t) = \frac{1}{2} I_m (1 - \cos \omega t), \tag{3}$$

where

I_m – the highest irradiance intensity in this water layer at the Sun's culmination (at midday),

t – time measured since sunrise,

$\omega = \frac{2\pi}{D}$,

D – day length.

Substituting expression (3) in eq. (2) yields

$$\frac{dA}{dt} = \frac{p_h\, I_m}{2d}(1 - \cos \omega t) - \lambda A. \tag{4}$$

This differential eqation enables the activity of a phytoplankton filter after a determined incubation time to be calculated. Since the filter activity is known from the experiment, it is easy to calculate the unknown quantity λ (describing carbon release from phytoplankton cells).

In order to solve differential eq. (4) the integration limits for particular experiments – the incubations (Tab. 3) – must be stated. The solution to differential eq. (4), not given here, leads to the following algebraic expression for filter activity after different incubation times:

$$A_1 = \frac{p_h I_m}{2\alpha} e^{-\lambda \frac{D}{2}} \left[\frac{1}{\lambda} e^{\lambda t} - \frac{e^{\lambda t}}{\lambda^2 + \omega^2} (\lambda \cos \omega t + \omega \sin \omega t) \right] \Bigg|_0^{\frac{D}{2}}$$

$$A_2 = \frac{p_h I_m}{2\alpha} e^{-\lambda D} \left[\frac{1}{\lambda} e^{\lambda t} - \frac{e^{\lambda t}}{\lambda^2 + \omega^2} (\lambda \cos \omega t + \omega \sin \omega t) \right] \Bigg|_{\frac{D}{2}}^{D} \tag{5}$$

$$A_3 = \frac{p_h I_m}{2\alpha} e^{-\lambda D} \left[\frac{1}{\lambda} e^{\lambda t} - \frac{e^{\lambda t}}{\lambda^2 + \omega^2} (\lambda \cos \omega t + \omega \sin \omega t) \right] \Bigg|_0^{D},$$

in which t, the incubation time, should be substituted by the appropriate differential limits of integration (Tab. 3).

Table 3. Integration limits for eq. (5)

Measurement-incubation	Incubation start Time	Incubation start Activity	Incubation end Time	Incubation end Activity
in the morning	$t=0$	$A=0$	$t=\frac{D}{2}$	$A=A_1$
in the afternoon	$t=\frac{D}{2}$	$A=0$	$t=D$	$A=A_2$
all day	$t=0$	$A=0$	$t=D$	$A=A_3$

An additional quantity δ is introduced in order to establish λ, the relative quantity of carbon released from phytoplankton cells. It denotes the ratio of primary production summed over two D/2 hour intervals to primary production from one time interval of D hours and is expressed as

$$\delta = \frac{P_1 + P_2}{P_3} = \frac{A_1 + A_2}{A_3}, \tag{6}$$

Substituting expression (5) in formula (6) yields

$$\delta = \frac{\frac{2}{\lambda}\left(1 - e^{-\lambda \frac{D}{2}}\right)}{\left(\frac{1}{\lambda} - \frac{\lambda}{\lambda^2+\omega^2}\right)\left(1 - e^{-\lambda D}\right)}, \tag{7}$$

or after transformation

$$\delta = \frac{2(\lambda^2 + \omega^2)}{\omega^2 (1 + e^{\frac{-\lambda D}{2}})}. \tag{8}$$

λ can be determined from eq. (8) as the other quantities are known. The calculated values of λ are given in Tab. 2 next to the primary production quantities.

As Tab. 2 shows, the relative quantities of carbon released from phytoplankton cells are within the range from 0 to 0.56, which means from 0 to 56% of primary production. Sorting these values according to months, we obtain the following mean values for particular months: January – 0.08,

April – 0.09, May – 0.25, June – 0.09, August – 0.08, September – 0.10, November – 0.09, and December – 0.14. The May results are distinctly different and indicate a threefold greater carbon release from phytoplankton cells than in other months. So it is just after the spring phytoplankton bloom that abundant release of organic matter takes place. During the year nutrient concentrations, especially those of inorganic nitrogen, are lowest during this period (Trzosińska, 1977, 1990), and then primary production in the Baltic is usually limited by nitrogen deficiency (Renk *et al.*, 1992). The finding that organic matter release from phytoplankton cells is higher when primary production is limited has been confirmed by other authors in their papers based on observations made at times of nutrient shortage (Wetzel, 1969; Myklestad, 1977; Bratbak and Thingstad, 1985). It has also been noted that the release of matter from cells is relatively greater in oligotrophic waters (Anderson and Zeutschel, 1970; Thomas, 1971; Berman and Holm-Hansen, 1974).

Harris (1978) states that the quantity of matter released from cells is greater in bright light. Our results, however, do not confirm this hypothesis. The mean values of λ for May are 0.24 at the surface and 0.28 at a depth of 5 m (the light intensity at this depth is less than at the surface). Slight differences between the λ values at various depths can be put down to 'experimental error'. Shailaja and Pant (1986) observed, moreover, that the light's spectral composition affects the intensity of release. Many papers (Sharp, 1977; Fogg, 1983) point out that the release of matter from phytoplankton cells is increased under stress conditions. In the southern Baltic such stress conditions occur, for example, when the summer N:P ratio in the water is unfavourable. The normal N:P ratio is 16:1 whereas in summer in the southern Baltic it often falls to 5:1 or less (Renk, 1983; Trzosińska, 1977, 1990).

References

Anderson G. C., Zeutschel R. P., 1970, *Release of dissolved organic matter by marine phytoplankton in coastal and offshore areas of the north-east Pacific Ocean*, Limnol. Oceanogr., 15, 402–407.

Berman T., Holm-Hansen O., 1974, *Release of photoassimilated carbon as dissolved organic matter by marine phytoplankton*, Mar. Biol., 28, 305–310.

Bratbak G., Thingstad T. F., 1985, *Phytoplankton-bacteria interactions an apparent paradox? Analysis of a model system with both competition and commensalism*, Mar. Biol. Progr. Ser., 25, 23–30.

Fogg G. E., 1966, *The extracellular products of algae*, Oceanogr. Mar. Biol. Ann. Rev., 4, 195–212.

Fogg G. E., 1977, *Excretion of organic matter by phytoplankton*, Limnol. Oceanogr., 22, 576–577.

Fogg G. E., 1983, *The ecological significance of extracellular products of phytoplankton photosynthesis*, Botanica Mar., 26, 3–14.

Harris G. P., 1978, *Photosynthesis, productivity and growth: the physiological ecology of phytoplankton*, Arch. Hydrobiol. Beih. Ergebn. Limnol., 10, 1–171.

Laanbroek H. J., Verplanke J. V., de Visscher P. R. M., de Vuyst R., 1985, *Distribution of phyto- and bacterioplankton growth and biomass parameters, dissolved inorganic nutrients and free amino acids during the spring bloom in the Oosterschelde basin*, Netherlands. Mar. Biol. Progr. Ser., 25, 1–11.

Larsson U., Hagström A., 1979, *Phytoplankton exudate release as an energy source for the growth of pelagic bacteria*, Mar. Biol., 52, 199–206.

Larsson U., Hagström A., 1982, *Fractionated phytoplankton primary production in the Baltic eutrophication gradient*, Mar. Biol., 67, 57–70.

Myklestad S., 1977, *Production of carbohydrates by marine planktonic diatoms*, J. Exp. Mar. Biol. Ecol., 29, 161–179.

Renk H., 1983, *Light conditions, chlorophyll a distribution and primary production in the southern Baltic*, Pol. Ecol. Stud., 9, 311–329.

Renk H., 1990, *Primary production of the southern Baltic in 1979–1983*, Oceanologia, 29, 51–75.

Renk H., Nakonieczny J., Ochocki S., Ficek D., Majchrowski R.,1992, *Some factors regulating primary production in the southern Baltic*, ICES Biol. Oceanogr. Comm. L:12.

Renk H., Ochocki S., Pytel H., 1983, *Short-term fluctuations of primary production and chlorophyll a concentration at the Gdańsk Deep*, Pol. Ecol. Stud., 9, 341–359.

Sharp J. H., 1977, *Excretion of organic matter by marine phytoplankton. Do healthy cells do it?*, Limnol. Oceanogr., 22, 381–398.

Shailaja M. S., Pant A., 1986, *Relationship between particulate and extracellular carbon compounds of phytoplankton photosynthesis in a tropical estuary*, Mar. Ecol. Progr. Ser., 32, 161–167.

Steemann Nielsen E., 1952, *The use of radiocarbon ^{14}C for measuring organic production in the sea*, J. Cons. Int. Explor. Mer, 18, 117–140.

Steemann Nielsen E., 1965, *On the determination of the activity in ^{14}C ampoules for measuring primary production*, Limnol. Oceanogr., 10-Suppl., R247–R252.

Thomas J. P., 1971, *Release of dissolved organic matter from natural populations of marine phytoplankton*, Mar. Biol., 11, 311–323.

Trzosińska A., 1977, *Factors controlling the nutrient balance in the Baltic Sea*, Thalassia Jugosl., 13, 301–312.

Trzosińska A., 1990, *Seasonal fluctuations and long-term trends of nutrient concentrations in the Polish zone of the Baltic Sea*, Oceanologia, 29, 27–50.