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Dynamics of a *Phaeocystis*-dominated spring bloom in Belgian coastal waters. I. Phytoplanktonic activities and related parameters

C. Lancelot & S. Mathot

Groupe de Microbiologie des Milieux Aquatiques, Université Libre de Bruxelles, avenue F. D. Roosevelt 50, B-1050 Brussels, Belgium

ABSTRACT: Phytoplanktonic activities were measured weekly during spring 1984 in Belgian coastal waters almost entirely dominated by *Phaeocystis pouchetii* colonies. Accurate methods were developed to measure photosynthesis and growth rates by colonial *P. pouchetii* cells, mucus secretion and excretion from colonies. Photosynthetic properties, although quite different for cellular photosynthesis and mucus secretion, were found to be independent of changes in environmental conditions. Maximal photosynthetic rates were respectively 0.09 and 0.16 h^{-1} for cells and mucus. Cellular specific growth rate, on the other hand, was inversely correlated to the level of ambient inorganic nitrogen. Extreme values for cell turnover rates were 0.12 and 0.38 d^{-1}. A budget of metabolic activities of *P. pouchetii* colonies was established for the period of their bloom. The colonies photo-assimilated 94 g C m^{-2} mo^{-1}. From this, a maximum of 84 g C m^{-2} mo^{-1} was devoted to colonial biomass production and 7.5 g C m^{-2} mo^{-1} was excreted from the colonies.

INTRODUCTION

It is now well established that inorganic carbon assimilated by phytoplankton during the photosynthetic process is not entirely devoted to biomass production, i.e. what is commonly called net primary production or growth. Rather, some photosynthetic products are excreted from the cells, mainly in the form of small molecules directly utilizable by planktonic bacteria (see review by Lancelot & Billen 1986). Also some photosynthetic products are catabolized and provide energy and carbon skeletons for the synthesis of cellular material which can then proceed during the night as well as during the day (Cook 1966, Foy & Smith 1980, Cuhel et al. 1984, Lancelot & Mathot 1985a, Lancelot et al. 1986). These energy storage substrates occur mainly as reserve polysaccharides (Cook 1966, Foy & Smith 1980, Lancelot & Mathot 1985a). However, in the particular case of colonial algae such as *Phaeocystis pouchetii*, this physiological function is performed by the mucilaginous compounds which compose the colonial matrix (Lancelot & Mathot 1985b). Protein synthesis, combined with an accurate cellular C/N ratio, would therefore be recommended as a better index of phytoplankton growth than photosynthetic C assimilation.

For this reason, Lancelot et al. (1986) established a simple mathematical model to estimate *Phaeocystis pouchetii* cell growth in the water column. It is based on double control, by ambient inorganic nitrogen and light, of the light and dark protein synthesis rates.

Complementary to this model, we present in this paper data on measurements of photosynthesis rate by *Phaeocystis pouchetii* colonies. We show that these estimates, combined with those of *P. pouchetii* cell growth (Lancelot et al. 1986), give a maximal value for *P. pouchetii* colony growth in the water column. However, because of the particular mucilaginous structure of colonies, common methods for measurement of phytoplankton biomass and photosynthesis were not suit-

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able. The filtration procedure universally used for isolation of phytoplankton cells disrupts the colonies and solubilizes the mucus into seawater. At the present time, no gentle mechanical procedure exists for specific isolation of intact mucilaginous colonies. Filtrations on membranes of specific porosity combined with classical biochemical procedures (Lancelot 1983, Lancelot & Mathot 1985a, Lancelot et al. 1986) were therefore recently developed during time-course studies of ^{14}C incorporation. This methodology allows distinction between photosynthesis rate and growth of cells, and also allows estimates of mucus secretion and of extracellular release of organic molecules from the colonies together with the latter's utilization by bacteria.

This paper reports results of such measurements conducted weekly during spring 1984 in Belgian coastal waters where spectacularly high biomasses of *Phaeocystis pouchetii* colonies follow a moderate bloom of diatoms. In addition to the establishment of the photosynthetic properties of these 2 phytoplanktonic communities, parallel measurements of seawater temperature, incident available light intensity and major nutrients were made in order to determine the environmental factors associated with the onset of the *P. pouchetii* bloom and the control of its main metabolic activities. From these, specific mathematical sub-models are used to estimate the growth of colonies in the water column. Finally we present a tentative budget of phytoplankton activities for the whole period of the *P. pouchetii* bloom.

MATERIAL AND METHODS

Sample collection. Experiments were performed in Belgian coastal waters at Lat. 51°21' N, Long. 2°48' E, during spring 1984. Water samples were collected at sunrise at a depth of 3 m with 5 l Niskin bottles. One l was immediately filtered on a GF/F Whatman filter for chlorophyll *a* determination and the filtrates were frozen for subsequent analysis. A further 100 ml of seawater was fixed with Lugol's solution for phytoplankton determination.

Integrated measurements of total incident solar radiation were collected every 30 min by the 'Institut Royal Météorologique de Belgique' 10 km from the sampled station.

Chemical analysis. Chlorophyll *a* was measured by the spectrophotometric method of Lorenzen (1967). Nitrate and nitrite were determined according to the procedure described by Armstrong et al. (1967). Ammonium was measured by the phenol hypochlorite method of Slawyk & McIsaac (1972). The method for silica determination was adapted from the procedure described in Technicon Industrial Methods.

Phytoplanktonic activities measurement. ***Photosynthesis.*** Daily integrated carbon photo-assimilation by phytoplankton was calculated by means of the Platt et al. (1980) model from the experimental characterization of the photosynthesis-light relation for each sampled phytoplankton community.

The light-dependence of photosynthetic processes was experimentally determined by short-term ^{14}C-bicarbonate incubations of natural colonies run around noon, under simulated *in situ* conditions on deck for different fractions (0, 6, 10, 18, 32, 44, 56, 76, 100 %) of the incident light intensity. Four incubation times (0.5, 1, 2, 4 h) were used to test the importance of catabolic losses as a function of incubation time together with the adaptability of the colonies to maximal light intensities.

After incubation phytoplankton cells were separated from mucous substances and excreted products by means of GF/F Whatman filters. Filtrates were acidified to pH 2.5 and bubbled for 30 min in order to remove inorganic ^{14}C.

Ultrafiltrations with 500 dalton membranes were used to separate exopolymeric mucilaginous substances from organic compounds released in the external medium by the colonies.

Cellular growth, catabolism and excretion of organic molecules. Daily integrated cellular growth was calculated by means of the mathematical model of protein synthesis by *Phaeocystis pouchetii* cells as previously described in Lancelot et al. (1986). Physiological parameters which express the control of protein synthesis were determined from data of long-term kinetics of ^{14}C incorporation into specific classes of intra- and extracellular products, run under simulated *in situ* at maximum light intensity from noon to sunrise. As previously described (Lancelot et al. 1986), such kinetics allow estimating the absolute rate of light and dark protein synthesis. Moreover, these time-course studies clearly showed catabolic losses of intracellular reserve products or exopolymeric substances, the relative rate of which is calculated by means of the mathematical model developed in Lancelot & Mathot (1985a).

Experiments and biochemical procedures used for specific isolation of the different classes of metabolite are described in Lancelot & Mathot (1985a) and Lancelot et al. (1986).

Heterotrophic utilization of phytoplankton-excreted products. Successive filtrations on filters of different nominal porosity (2 µm, 0.2 µm) were performed in parallel with time-course studies of phytoplankton metabolism, in order to estimate the uptake by bacteria of phytoplankton-excreted products. Experimental procedure is that described by Wolter (1982). Antibiotic controls were simultaneously incubated in parallel.

RESULTS

Temporal changes of environmental factors and phytoplankton biomass during spring bloom

Fig. 1, 2 & 3 show changes in seawater temperature, major nutrients and phytoplankton biomass, as measured in Belgian coastal waters during the course of the spring bloom 1984. Dominant phytoplanktonic species are also indicated. Seawater temperature was 7 °C at the beginning of the spring bloom and increased by 3 C° during its course (Fig. 1). The spring bloom was

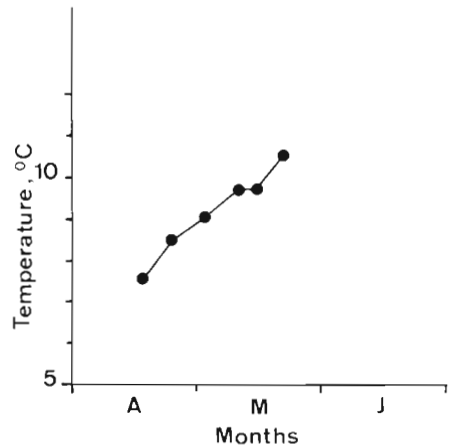

Fig. 1. Seawater temperature in Belgian coastal waters during spring 1984

clearly characterized by 2 peaks of phytoplankton biomass corresponding to the blooming of 2 distinct populations (Fig. 3). The first one, composed for the most part of the colonial diatom *Chaetoceros socialis,* culminated around 9 µg Chl *a* l^{-1} in early April when the temperature was lower than 8 °C. The second one, more important, culminated 1 mo later, when seawater temperature had gained 2 C°. Biomass was very high, around 20 µg Chl *a* l^{-1} and was 95 % attributable to the bloom of *Phaeocystis pouchetii* colonies, the remainder being composed of diatoms. After the decline of *P. pouchetii* the phytoplanktonic community was composed of a few small flagellates.

The decline of *Chaetoceros socialis* corresponded to the depletion of ambient silicon, concentrations of which (Fig. 2b), although high in winter (about 20 µmole l^{-1}), are lower than the Michaelis constant reported for silicon uptake by *Chaetoceros* sp. (0.5 to 2.2 µmole l^{-1}) (see review by Paasche 1980). Fig. 2b shows, in addition, that silicon concentrations were kept at a very low level during the whole spring bloom. *Phaeocystis pouchetii* colonies, on the other hand, do not require silicic acid and their growth should be controlled either by inorganic nitrogen or phosphate. Unfortunately, no data on phosphate concentration in our area during spring 1984 are available. However, measurements performed in the Belgian coastal zone in 1977 to 1979 (Mommaerts pers. comm.) never

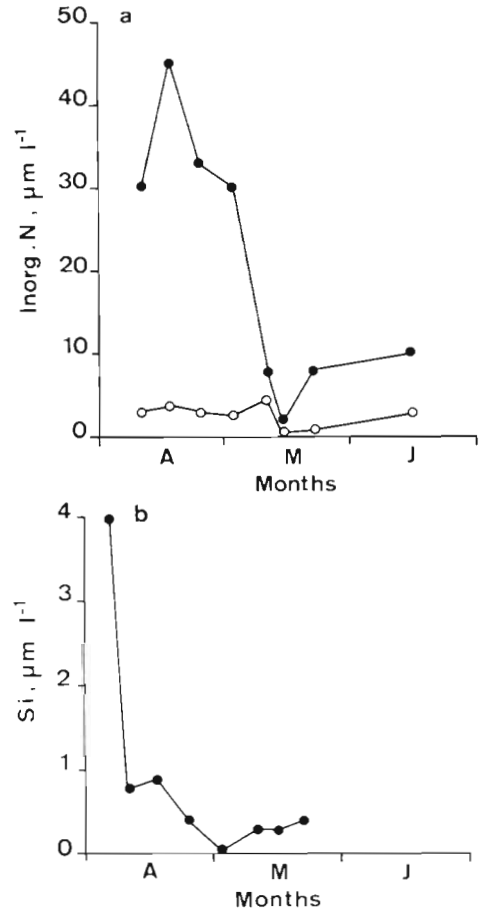

Fig. 2. Inorganic nutrients in Belgian coastal waters during spring 1984. (a) Nitrate (●); ammonium (○). (b) Silicon

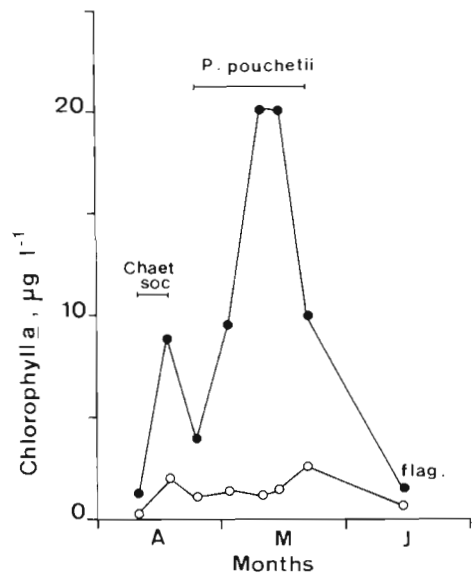

Fig. 3. Chlorophyll *a* (●) and degraded products (○) in Belgian coastal waters during spring 1984

showed very sharp seasonal variations in phosphate concentrations which were always higher than 0.5 µmole l^{-1}, even during the spring bloom. In contrast, nitrate and ammonium concentrations decreased very rapidly during the outburst of the *P. pouchetii* bloom and reached values significantly lower than the Michaelis constant for nitrogen assimilation by *P. pouchetii* (i.e. 4 µmole l^{-1}; Lancelot et al. 1986). After the decline of *P. pouchetii* colonies, ambient inorganic nitrogen concentrations reached non-limiting levels again.

Phytoplanktonic activities

Photosynthetic parameters

Fig. 4 & 5 give 2 typical examples of the short-term time dependence of the photosynthesis-light relation of a phytoplanktonic community dominated respectively by *Chaetoceros socialis* and *Phaeocystis pouchetii* colonies.

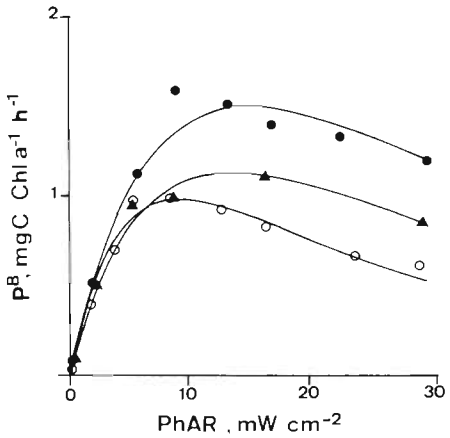

Fig. 4. *Chaetoceros socialis*-dominated phytoplankton population. Relation between specific photosynthetic rate (P^B) and photosynthetically active radiation (PhAR) for different incubation times: (●) 0.58 h; (▲) 1.16 h; (○) 4.16 h

Changes with incubation time of the photosynthesis-light relation by *Chaetoceros socialis* (Fig. 4) are typical of that generally encountered for diatoms (Marra 1980), i.e. low but constant photosynthesis rates over time at low light intensities and strong photoinhibition at high light intensities, increasing over time. In contrast, the photosynthesis-light relation of *Phaeocystis pouchetii* colonies does not show significant changes with increasing incubation times (Fig. 5a, b). However, the major trend of photosynthetic properties of *P. pouchetii* colonies lies in the quite significant difference existing between the control by light of cellular carbon photo-assimilation rate (Fig. 5a) and mucus

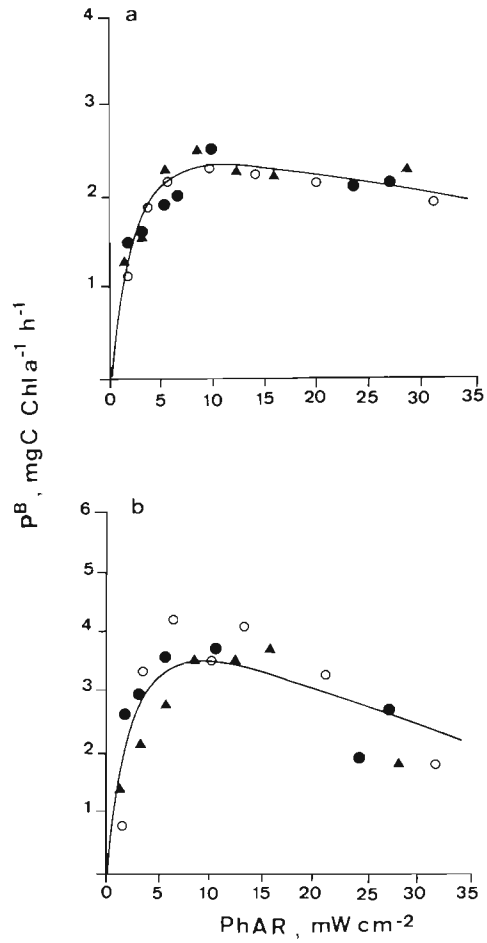

Fig. 5. *Phaeocystis pouchetii* colonies-dominated phytoplanktonic population. Relation between specific photosynthetic rate (P^B) and photosynthetically active radiation (PhAR) for different incubation times: (●) 0.8 h; (▲) 1.3 h; (○) 4.3 h. (a) Cellular photosynthesis; (b) mucus secretion

secretion (Fig. 5b). The latter photosynthetic process, although enhanced at intermediate light intensities, was strongly photoinhibited by high light intensities. Cellular photosynthesis, on the other hand, reached maximal rates at low light intensities and was not photoinhibited. Considering that *P. pouchetii* colonies act as biological entities and that mucus constitutes an energetic substrate for cell growth (Lancelot & Mathot 1985b), this agrees well with previous work (see review by Morris 1980), which shows that photosynthesis of storage products is enhanced at high light intensities. In addition, the severe photoinhibition of mucus secretion occurring at high light intensities would suggest that high light specifically represses one of the steps leading to the synthesis of mucus.

The mathematical formulation by Platt et al. (1980) of the light saturation curve was found to provide the best fit of experimental data relative to spring phytoplankton in Belgian coastal waters. Values of charac-

teristic photosynthetic parameters and derived parameters are reported in Table 1. This table shows that *Chaetoceros socialis* cells had a lower efficiency in utilizing light intensity than *Phaeocystis pouchetii* cells. Photosynthetic parameters characterizing *P. pouchetii* colonies did not change significantly during the course of the bloom. This means that photosynthesis rates by these colonies, in contrast to their growth (Lancelot et al. 1986), were not dependent on changes in temperature and ambient inorganic nutrients, which, however, occurred during the course of their blooming (Fig. 1 & 2).

Photosynthetic parameters of *Phaeocystis pouchetii* cells (Table 1) were typical of phytoplankton adapted to low light intensities (Platt et al. 1980), except that significant photoinhibition did not occur at high light intensities, possibly because of the presence of a mucus envelope surrounding the cells. High saturation parameters are very similar to those reported for *P. pouchetii* colonies growing in the Ems-Dollart Estuary (Colijn 1983). Maximal cellular photosynthetic rates, on the other hand, are far lower than those reported for the same *P. pouchetii* community, probably as a result of lower *in situ* temperature. Attention must be paid to the photosynthetic parameters of the 24 April sample which clearly illustrate the simultaneous presence of the 2 phytoplanktonic populations.

Parameters which characterize the control by light of mucus secretion, on the other hand, are to our knowledge the first reported. From Table 1, it can be seen that maximal synthesis rates of mucus were twice as high as those of cellular photosynthesis. Also saturating light intensities of mucus secretion were higher, close to those of *Chaetoceros socialis* cells. Moreover, photoinhibition of mucus secretion at high light intensities is a significant process, which must be taken into account for the calculation of daily photosynthetic rates.

Daily integrated photosynthesis rates during spring bloom

Daily integrated photosynthesis rates by phytoplankton during the spring bloom 1984 were calculated by means of the equation of Platt et al. (1980) from the photosynthetic parameters reported in Table 1, the hourly photosynthetically active radiation (PhAR) and the vertical light attenuation coefficient.

Results of these calculations are shown in Fig. 6a to c, which give seasonal changes of respectively cellular photosynthesis rates (Fig. 6a), mucus secretion (Fig. 6b) and excretion of small molecules from the colonies (Fig. 6c). Comparison of Fig. 3 & 6 shows that spring primary production is almost entirely due to *Phaeocystis pouchetii* colonies, which photo-assimilate more than 5 g C m^{-2} d^{-1} at the peak of the bloom, in close agreement with maxima reached in the Ems-Dollart Estuary (Colijn 1983). Maximal daily photosynthetic rates by *Chaetoceros socialis* – the dominant phytoplankton of mid-April – were 0.5 g C m^{-2} d^{-1}, i.e. 10 % of that reached by *P. pouchetii*.

Table 1. *Chaetoceros socialis*, and *Phaeocystis pouchetii* colonies. Photosynthetic parameters and their derived parameters as calculated from Platt et al. (1980) 's equation[a]

Date (1984)	Dominant species	Cells					Exopolymers				
		α^b	$P_m^{B\,c}$	β^b	$I_\phi{}^d$	$I_k{}^e$	α^b	$P_m^{B\,c}$	β^b	$I_\phi{}^d$	$I_k{}^e$
10 Apr	*Chaetoceros socialis*	0.2	11.5	0.031	371	57.5	Not determined				
17 Apr	*C. socialis* (0.5 h incubation)	0.03	3	0.009	333	100	Not determined				
	C. socialis (4 h incubation)	0.03	1.7	0.007	242	57	Not determined				
24 Apr	*Chaetoceros sociales* + *Phaeocystis pouchetii*	0.18	9.3	0.012	708	47	0.62	3.4	0.01	310	50
2 May	*Phaeocystis pouchetii*	0.11	2.7	0.001	2454	24.5	0.055	4.2	0.008	525	76
10 May	*Phaeocystis pouchetii*	0.14	2.5	0.003	833	18	0.085	5	0.006	833	59
14 May	*Phaeocystis pouchetii*	0.10	2.6	0.002	1300	26	0.14	4.5	0.009	500	32
21 May	*Phaeocystis pouchetii*	0.10	2.6	0.001	2600	26	0.08	5.4	0.011	491	67

[a] $P^b = P_m^B \cdot (1-e^{-\alpha I/P_m^B})\, e^{-\beta I/P_m^B}$

where P^B = specific photosynthetic rate
P_m^B = maximum specific photosynthetic rate
α, β = parameters characterizing respectively the quantum efficiency and photoinhibition of the photosynthetic process

[b] α, β = mgC Chl*a*$^{-1}$ h^{-1} $(W\,m^{-2})^{-1}$
[c] P_m^B = mgC Chl*a*$^{-1}$ h^{-1}
[d,e] I_k, I_ϕ = derived parameters respectively characteristic of the light and photoinhibition process ($W\,m^{-2}$)

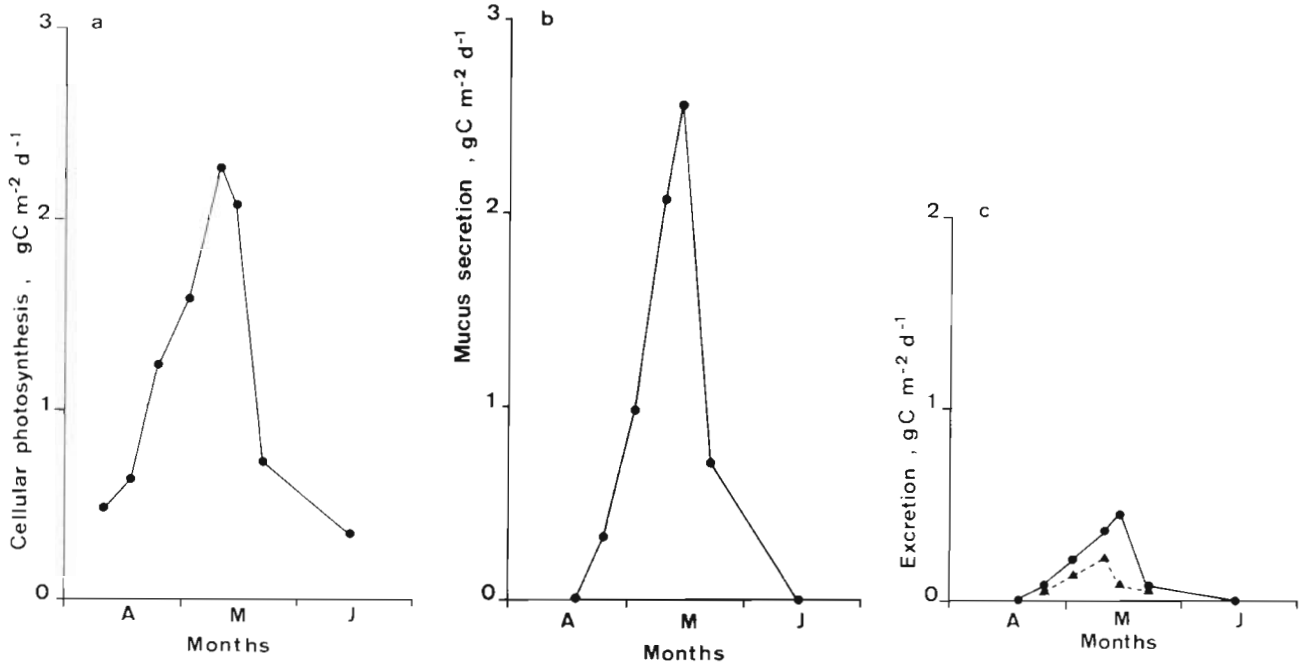

Fig. 6. *Phaeocystis pouchetii* colonies. Daylight photosynthesis rates during spring 1984. (a) Cells; (b) mucus; (c) excretion (●) and direct utilization of excreted products by bacteria (▲)

At the most developed stage of *Phaeocystis pouchetii*, where ambient inorganic nitrogen reached its lowest level (Fig. 2), daily rates of mucus secretion (Fig. 6b) were higher than carbon assimilation rates by colonial cells (Fig. 6a), in close agreement with previous results (Lancelot 1983). Excretion rate (Fig. 6c), on the other hand, was never an important process amounting to between 0 and less than 10 % of the total photosynthetic rate, in accordance with the recent review by Lancelot & Billen (1986).

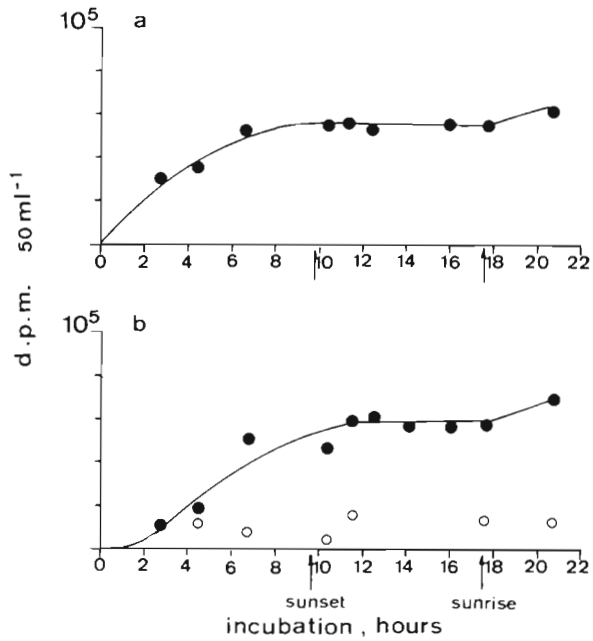

Fig. 7. *Phaeocystis pouchetii*. (a) Long-term kinetics of ^{14}C-bicarbonate incorporation into excreted product by colonies. (b) Long-term kinetics of uptake by bacteria of ^{14}C excreted products by *P. pouchetii* colonies. (○) Antibiotic control

Uptake by bacteria of phytoplankton-excreted products was deduced from data on successive filtrations, performed on planktonic communities incubated at maximal light intensity during a natural light:dark cycle, assuming that excreted products were in isotopic equilibrium with external ^{14}C-bicarbonate. Fig. 7, which illustrates such experiments, shows clearly a close coupling between excretion of organic molecules by phytoplankton and their use by bacteria. Daily uptake by bacteria of phytoplankton-excreted products in the water column was then calculated from daily excretion rates, assuming that the proportion of excreted products taken up by bacteria observed during incubation at maximal light intensity remains the same at the other light intensities. Results of these calculations (Fig. 6c) show that bacteria utilize from 16 to 90 % of phytoplankton-excreted products.

Growth and catabolism

Daily *Phaeocystis pouchetii* cell growth in the water column was calculated by means of the mathematical model of protein synthesis previously described by Lancelot et al. (1986) from data of biomass, ambient

inorganic nitrogen, hourly incident photosynthetically active radiation (PhAR) and vertical light attenuation coefficient. Physiological parameters, which express the control of protein synthesis, were those reported in Lancelot et al. (1986). Fig. 8 gives the seasonal changes

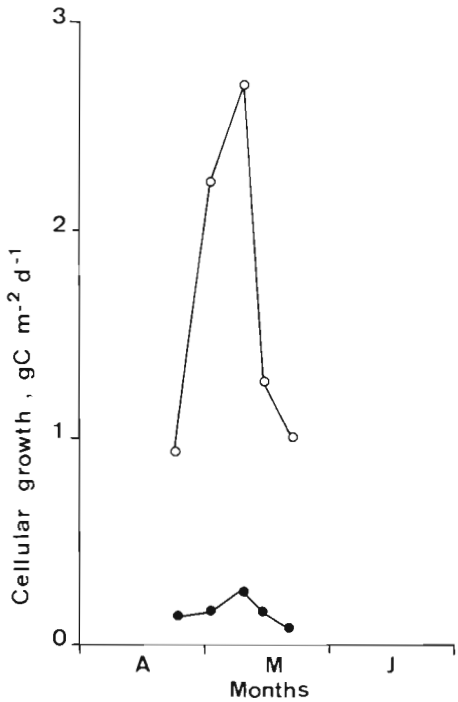

Fig. 8. *Phaeocystis pouchetii*. Daily (i.e. 24 h) (○) and dark (●) cellular growth during spring bloom 1984

of daily and dark *P. pouchetii* cell growth during the spring bloom 1984. It shows that dark growth, although sometimes as important as light growth in surface waters (Lancelot et al. 1986), is never an important process when integrated over the water column. It accounts for 7 to 15 % of total daily growth in the water column. Indeed, the high turbidity which characterizes Belgian coastal waters reduces the vertical light penetration, diminishing the size of photosynthetized energetic substrates, catabolic products of which are required for the dark growth of the cells.

As discussed previously (Lancelot et al. 1986), daily (i.e. 24 h) cellular growth rate was generally lower than cellular photosynthesis except at high levels of ambient inorganic nitrogen, where significantly higher daily growth rates were calculated. This is a special property of colonial algae, the energetic substrates of which are mainly exopolymeric.

Turnover rates of *Phaeocystis pouchetii* cells could be calculated from data on growth rate (Fig. 8) and chlorophyll *a* (Fig. 3), assuming a C/Chl *a* ratio of 30 for *P. pouchetii* cells (Lancelot-Van Beveren 1980). Calculated values, significantly correlated to ambient inorganic nitrogen ($r = 0.98$) range between 0.12 and 0.38 d^{-1} in close agreement with those reported by Eilertsen & Taasen (1983) for Norwegian coastal waters.

Relative rates of dark catabolism of exopolymeric substances were calculated from ^{14}C kinetics, during a 24 h cycle (see Lancelot et al. 1986), by means of the model developed in Lancelot & Mathot (1985a). In this model, catabolism of storage products is assumed to obey first-order kinetics. Results of these calculations are reported in Table 2. This table shows important

Table 2. *Phaeocystis pouchetii*. Relative rate of dark catabolism of mucus as calculated from the kinetics described in Lancelot et al. (1986) by means of the model developed in Lancelot & Mathot (1985a)

Samples	Dark catabolism (h^{-1})
24 Apr 84	0.2
2 Apr 84	0.1
10 Apr 84	0.02
14 Apr 84	0.2
21 Apr 84	0.1

catabolism relative rates, similar to that calculated for intracellular reserve polysaccharides of diatoms (Lancelot & Mathot 1985a). Unfortunately, absolute rates of dark catabolism of *Phaeocystis pouchetii* mucilaginous substances and hence net secretion of mucus matrix cannot be estimated at the present time, because the specific radioactivity of exopolymeric storage products is unknown, due to the lack of accurate chemical methods for isolation and determination of these compounds.

DISCUSSION AND CONCLUSIONS

Phaeocystis pouchetii is a very common spring alga of northern coastal and estuarine waters where spectacularly high biomasses of colonial forms are reported almost every year (Table 3). As shown by Table 4, which summarizes available literature data on environmental factors related to the presence of *P. pouchetii* colonies, this Haptophycea, which appears after diatoms, seems to be able to grow under very varied environmental conditions. However, paradoxically, in spite of the ubiquity of this species, little is known on its growth and the factors controlling it.

This paper, which reports measurements of photosynthesis and growth rates during the course of a *Phaeocystis pouchetii* bloom, indicates clearly the lack of parallelism between photosynthesis rate and growth rate. Photosynthesis rates by *P. pouchetii* cells and

Table 3. *Phaeocystis pouchetii*. Bloom period and biomass maxima in Northern Atlantic waters

Biotopes	Spring bloom period (mo)	Chl*a* ($\mu g\ l^{-1}$)	Cells (no. l^{-1})	Colonies (no. l^{-1})	Source
Balsfjorden (Northern Norway)	1.5[a]	ND	10^6	ND	Eilertsen et al. (1981a)
Eastern Irish Sea	1.5	ND	10^6	5000	Jones & Haq (1963), Cadée (1982)
Wadden Sea (Westernost Inlet)	[b]	40–120	10^6	ND	Cadée & Hegeman (1986)
Wadden Sea of Sylt (German Bight)					Weisse et al. (1986)
1975–1976	1.5		10^7		
1981	1.5	25		30 000	
Oosterschelde	1	6	10^7	ND	Laanbroek et al. (1985)
Ems-Dollart Estuary	1	10–30	$>10^6$	ND	Colijn (1983)
Dutch coastal waters					
1975	1.5	10	ND	ND	Gieskes & Kraay (1975)
1984	1	11	10^6	ND	Veldhuis et al. 1986
Belgian coastal waters	1–1.5	20	ND	ND	This paper

ND: not determined; [a] presence: 8 mo; [b] presence: 6 mo

Table 4. *Phaeocystis pouchetii* bloom and environmental parameters in Northern Atlantic waters

Biotopes	Salinity (‰)	Temp. (°C)	η^a (m^{-1})	Inorg. N (μg-at l^{-1})	Inorg. P (μg-at l^{-1})	Previous dominant diatom	Source
Balsfjorden (Northern Norway)	32.8–34	3–10	0.13	6–1	2–0.6	*Chaetoceros socialis* *Nitzschia grunowi*	Eilertsen et al. (1981a, b) Eilertsen & Taasen (1983)
Eastern Irish Sea		8–11			16–1	*Chaetoceros* sp. *Skeletonema* costatum	Jones & Haq (1963) Van Bennekom et al. (1975)
Wadden Sea (Westernost Inlet)	30	3–12	1	30–4		*Chaetoceros socialis*	Cadée & Hegeman (1986)
Wadden sea of Sylt (German Bight)		8–12		2–und.	0.4–und.		Weisse et al. 1986
Oosterschelde	27			40–60	1.5–0.6	*Skeletonema costatum* *Thalassiosira* sp.	Laanbroek et al. (1985)
Ems-Dollart Estuary	20–29	18	1.6	30		*Skeletonema costatum* *Asterionella glacialis*	Colijn (1983)
Dutch coastal waters 1975	30–33	8				*Biddulphia* *Chaetoceros* sp.	Gieskes & Kraay (1975)
1984		7.5–11.5			1.3–0.6	*Nitzschia grunowi* *Asterionella glacialis* *Skeleronema costatum*	Veldhuis et al. (1986)
Belgian coastal waters 1984	30	8.5–10.5	0.5	45–2.6	0.5–5	*Chaetoceros socialis*	This paper

[a] Light attenuation coefficient; und.: undetectable

colonial matrix secretion were found to be independent of temperature and ambient inorganic nutrient, at least in the range of variation fixed by the environment. Also the laws which govern photosynthetic processes for *P. pouchetii* cells and for their mucus envelope were found to be independent. Maximal specific photosynthetic rates were respectively 0.09 and 0.16 h^{-1} for cells and mucus. Similarly, light-saturation parameters of mucus were about twice as high as those of cells. Growth rate of *P. pouchetii* cells, on the other hand, was found to be directly correlated to the level of ambient inorganic nitrogen. Turnover rates of *P. pouchetii* cells were shown to vary between 0.38 d^{-1} with high external inorganic nitrogen and 0.12 d^{-1} when nitrogen was at its lowest level.

With the knowledge of photosynthesis and growth by *Phaeocystis pouchetii* colonies and their control by environmental variables, it was possible to establish a budget of their metabolism for the spring bloom 1984. This was deduced by integration of Fig. 6 & 8 for the whole period of the *P. pouchetii* bloom, i.e. from 24 April to 21 May. Results of these calculations are reported in Table 5. This table shows that 94 g C m^{-2} were photo-assimilated by *P. pouchetii* colonies during the spring bloom. Of this, 41.5 % was secreted as mucilaginous substances composing the colonial matrix, and 8 % was excreted directly as small molecules from the colonies and was directly usable by bacteria. Integration of Fig. 6c gives an estimate of up to 40 % bacterial utilization of these products. Growth rate of *P. pouchetii* cells, on the other hand, was estimated to 50.6 g C m^{-2}. Of this, 89 % i.e. 45 g C m^{-2} proceeded during the photoperiod, the remainder occurring during the dark at the expense of mucilaginous substances as previously described (Lancelot & Mathot 1985b). Direct comparison between photosynthetic rates and light and dark growth rates allows estimation of cellular and mucous catabolic losses. Indeed, cellular respiration during the light period could be deduced from the difference between cellular photosynthesis and cellular growth during the photoperiod. The result of this calculation shows that cellular respiration accounts for 5 % of cellular photosynthesis. In a similar way, a minimum value for catabolic losses of mucus can be deduced from night cellular growth which results from dark mobilization of mucus itself. A maximum estimate of net mucus secretion is therefore given by the difference between mucus photosynthesis rate and night cellular growth, i.e. 33.4 g C m^{-2}. This latter value combined with that of colonial cell growth rate gives an estimate for *P. pouchetii* colonies growth in Belgian coastal waters of 84 g C m^{-2} mo^{-1}.

Table 5. *Phaeocystis pouchetii*. Metabolic activities by colonies in Belgian coastal waters during the spring bloom 1984

Process	Structure	Activity (g C m^{-2} mo^{-1})
Photosynthesis	Colonies	94
	Cells	47.5
	Mucus	39
	Excretion	7.5
Respiration	Cells	2.5
	Mucus	?
Growth	Colonies	$\leq$ 84
	Cells	50.6
	Mucus	$\leq$ 33.4
Mortality	Cells	47.3

Finally, mortality rate of *Phaeocystis pouchetii* cells resulting mostly from physiological death or sedimentation in the absence of significant zooplankton grazing at this period of the year (Joiris et al. 1982, Fransz & Gieskes 1984) could be estimated by comparing daily growth rate (Fig. 7) and the rate of change of phytoplankton biomass (Fig. 3). Results of these calculations show that the relative rate of mortality ranges from 0.15 to 0.29 d^{-1}, in good agreement with the range of turnover rates. From these, mortality of *P. pouchetii* cells was estimated at 47 g C m^{-2} mo^{-1}.

Such an estimate of the budget of metabolic activities by *Phaeocystis pouchetii* colonies constitutes an essential step for the understanding of organic matter cycling at the first trophic levels of the food web of a coastal marine system entirely dominated by *P. pouchetii* during its spring bloom. Billen & Fontigny (Part II of this series; p. 249–257) discuss the utilization of organic matter by planktonic bacteria during the same bloom of *P. pouchetii*.

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