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Daily irradiance governs growth rate and colony formation of *Phaeocystis* (Prymnesiophyceae)

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Abstract. *Phaeocystis* was cultured at a range of ecologically significant daily irradiances under nutrient-replete conditions. Below a threshold of 100 W h m^{-2} day^{-1}, the cells were small and flagellated, and remained solitary. Above this threshold, the cells were larger and able to form colonies. Growth rate and colony formation were maximum at sea surface irradiances (>700 W h m^{-2} day^{-1}). Presumably, colonial growth is a strategy to maintain optimum growth rates in the water column. Sinking, nutrient-stressed colonies reach low irradiances and colonial cells can transform into small solitary flagellated cells. These observations are important in understanding the ecology and life cycle of *Phaeocystis*.

Introduction

Phaeocystis (Haptophyta, Prymnesiophyceae) is a common phytoplankton genus in temperate and polar seas, occurring as solitary cells or colonies. Colonial blooms may play an important role in global carbon and sulfur fluxes (Gibson *et al.*, 1990; Smith *et al.*, 1991). In the North Sea, *Phaeocystis* is considered to be a major nuisance alga (Lancelot *et al.*, 1987). Because its life cycle is imperfectly understood (Kornmann, 1955; Veldhuis, 1987), there are several hypotheses for the triggering of blooms. They include temperature, salinity, freshwater run-off and nutrient discharge, but none of these hypotheses has been conclusive (Lancelot *et al.*, 1987; Verity *et al.*, 1988b). Long-term variation in the occurrence of *Phaeocystis* colonies in the northeast Atlantic is probably related to climatic change (Owens *et al.*, 1989).

These different suppositions do not rule out a common cause for the start of *Phaeocystis* blooms, such as the amount of light energy received. For instance, Arctic and Antarctic blooms follow the retreating ice caps in summer, when meltwater-induced stratification reduces mixing depth and consequently increases mean irradiance in the surface layer of the water column (Heimdal, 1989; Marchant *et al.*, 1991). In the Southern Bight of the North Sea, the spring diatom bloom starts when the increase in solar radiation results in a mean water column irradiance of 9.5 W m^{-2} (Gieskes and Kraay, 1975). The *Phaeocystis* spring bloom starts 1–2 months later (Leewis, 1985; Veldhuis, 1987), when incident solar radiation has increased considerably. A comparable delay in the blooming of *Phaeocystis* has been found in the Ems–Dollard estuary (Colijn, 1983). It has also been shown that *Phaeocystis* colonies may develop in the laboratory, i.e. at increased daily irradiances, in North Sea water samples taken before the spring diatom bloom (Kornmann, 1955; Veldhuis, 1987).

Previous investigations on the relationship of irradiance and *Phaeocystis* were mostly focused on the short-term process of photosynthetic production. The responses reported vary (Davidson and Marchant, 1992), but some general

abstractions can be made. For instance, *Phaeocystis* is capable of rapid carbon incorporation at relatively low irradiances, while at high irradiances photoinhibition may be less severe than in diatoms (Colijn, 1983; Lancelot and Mathot, 1987), or even absent (Verity *et al.*, 1988a). It has also been shown that the amount of photosynthetic products excreted by colonial cells, mainly macromolecular carbohydrates used for the colony matrix, increases with the amount of light energy (Guillard and Hellebust, 1971; Colijn, 1983; Lancelot and Mathot, 1985; Veldhuis, 1987). *Phaeocystis* also seems able to adapt to a wide range of light climates (Davidson and Marchant, 1992).

However, the rate of photosynthetic production versus irradiance or photon flux density is something quite different than growth rate as a function of daily irradiance. Of course, these two can be linked in a model, but to do so much more information on species-specific variables must be available (Bannister, 1990). Furthermore, differing environmental factors encountered in the field, and the occurrence of different *Phaeocystis* cell types, will impede this relationship (Jahnke, 1989; Madariaga, 1992). In the case of *Phaeocystis*, especially, there is a clear lack of parallelism between the photosynthesis rate and growth rate (Lancelot and Mathot, 1987).

The effect of daily irradiance on *Phaeocystis* in monocultures has indirectly been studied by Kornmann (1955). Over the course of several years, his batch cultures underwent seasonal changes in irradiance because his culture vessels were placed in a northern-facing window. The nutrient concentrations will also have varied considerably. Several life cycle stadia of *Phaeocystis* were described, but unfortunately the amount of daily irradiance and nutrient concentrations were not measured. A second study was performed by Jahnke (1989) using a range of daily irradiances and temperatures. However, in this study no life cycle events were apparently observed. An important conclusion was that the temperate *Phaeocystis* cf. *globosa* would outcompete diatoms only under ample nutrient conditions, near its optimum temperature (14°C) and at high irradiances. This agrees well with Langdon (1988) who found diatoms, as a group compared with a.o. haptophytes, to be the species best adapted to grow at low light.

To investigate the role of light in the vernal bloom of *Phaeocystis* more thoroughly, it was cultured at a range of daily irradiances that represented an ecologically significant sequence of the values encountered from winter to summer in the Southern Bight of the North Sea.

Method

Mean water column daily irradiance was calculated for early January (week 1) to late June (week 26) along the 'Noordwijk' transect (cf. Peeters and Peperzak, 1990), perpendicular to the Dutch coast, as follows. Global radiation data for 1980–1988, obtained from the Royal Dutch Meteorological Institute, were averaged to weekly values and converted to W h m^{-2} day^{-1} for comparison with experimental irradiances. Multiplying by 0.45 gave photosynthetically active radiation (I_0, PAR). Mean water column PAR (I_m) was calculated as:

$$I_m = I_0 (1 - e^{-\epsilon \times z})/(\epsilon \times z) \quad (1)$$

where ϵ = attenuation coefficient (m^{-1}) and z = water column depth (m).

In situ ϵ measurements, obtained in spring and summer in four consecutive years at Noordwijk stations 2, 10, 20 and 70 km offshore (H.Haas, personal communication), were averaged: N2: $\epsilon = 1.05 \pm 0.58$, $z = 13$; N10: $\epsilon = 0.55 \pm 0.26$, $z = 19$; N20: $\epsilon = 0.43 \pm 0.23$, $z = 21$; N70: $\epsilon = 0.22 \pm 0.06$, $z = 32$.

Assuming a homogeneous water column, depth-dependent irradiances at 5 m intervals for N70 were calculated as:

$$I_z = I_0 \times e^{-\epsilon \times z} \quad (2)$$

Phaeocystis clone Ph91 (non-axenic), originating from the North Sea, was grown at 15°C in f/2 culture medium without added silicon. To investigate the effect of daily irradiance on growth rate and colony formation, the following experiment was set up. In several timer-controlled incubators (daylength = 8, 13, 15 and 18 h day^{-1}), different irradiances (4, 8, 10, 18, 32, 55, 70 and 101 W m^{-2}, measured with a Photodyne XLA photometer with a spherical sensor) were obtained with neutral-density filters. Solitary cells were obtained by sieving through 20 μm gauze (Veldhuis, 1987). Their concentrations at the start of the experiment were 10^5 or 10^6 cells l^{-1} (two runs were made). Cultures were shaken gently once daily, before sampling. Growth was monitored by measuring *in vivo* chlorophyll fluorescence with a Turner Design model-10 fluorometer. Cells were kept in exponential growth phase by dilution with fresh culture medium and were therefore assumed to be nutrient replete. Growth rates were calculated after linear regression analysis of log-transformed fluorescence values. Statistically significant regressions ($P < 0.05$) were used for the equation:

$$\mu = (\log f_t - \log f_0) \times 3.32 \times t^{-1} \ (day^{-1}) \quad (3)$$

where $f_{t,0}$ = fluorescence on day t and day 0, respectively.

Colony formation was monitored by examining 2 ml non-fixed subsamples at 63× and 160× magnification on an inverted microscope. To estimate the amount of colonial cells, samples were taken during the exponential growth phase. One part was fixed with acid Lugol's iodine solution (Throndsen, 1978); the remainder was fixed after being sieved through 20 μm gauze. In unfiltered samples, colonies were destroyed by vigorous shaking. Cell counts were done microscopically. The percentage colonial cells was calculated as:

$$((\text{total } c\ l^{-1}) - (c\ l^{-1} < 20\ \mu m)/(\text{total } c\ l^{-1})) \times 100\% \quad (4)$$

Results

The large temporal and spatial range in daily irradiance from January through June in the Southern Bight of the North Sea is shown in Figure 1a. Although water depth decreases offshore to coast, the simultaneous increase in water

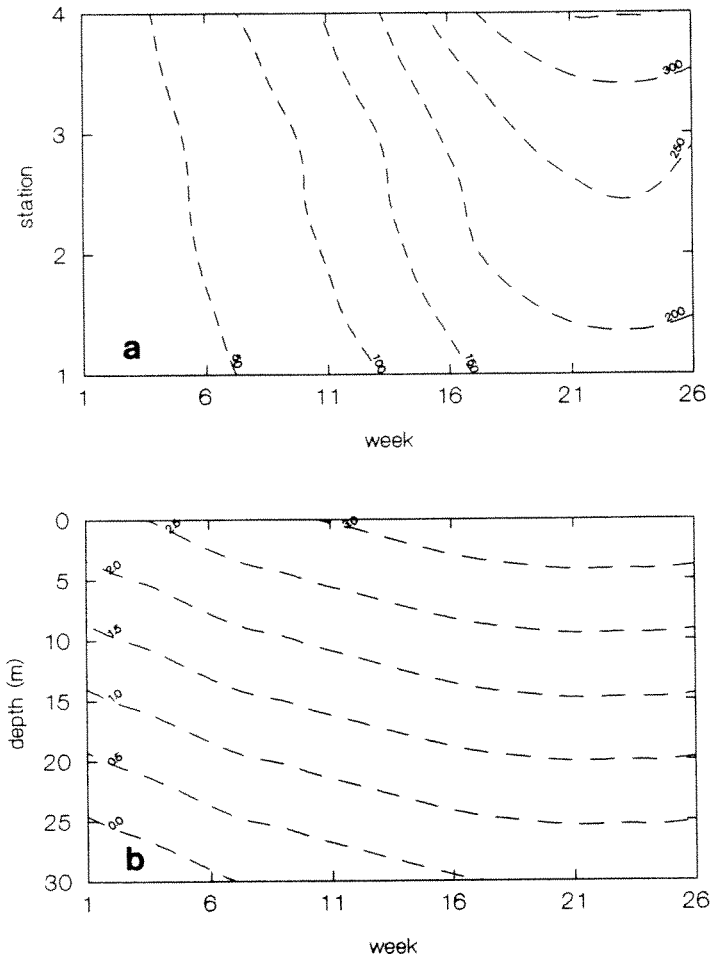

Fig. 1. Development of water column irradiance, January–June, in the Southern Bight of the North Sea. (**a**) Mean water column daily irradiance in W h m^{-2} day^{-1}, along the 'Noordwijk' transect perpendicular to the Dutch coast. Stations 1–4 are, respectively, 2, 10, 20 and 70 km offshore; (**b**) depth-dependent daily irradiance in log W h m^{-2} day^{-1} at station 4 (70 km offshore).

turbidity (Gieskes and Kraay, 1975) is the reason why mean daily irradiance at the inshore stations never exceeds 250 W h m^{-2} day^{-1}. There is also a large vertical gradient because irradiance decreases exponentially down through the water column (Figure 1b).

Figures 2 and 3 show the growth rate and percentage of colonial cells of *Phaeocystis* when cultured in such gradients. At daily irradiances <100 W h m^{-2} day^{-1}, no colony formation could be observed. Cells were small (~4 μm) and flagellated (Figure 4a). Above this value, growth rates increased from 0.5 day^{-1} to a maximum of 2.0 day^{-1}, reached at 700 W h m^{-2} day^{-1}. These rates are slightly smaller than those of Jahnke (1989), probably because his cultures were

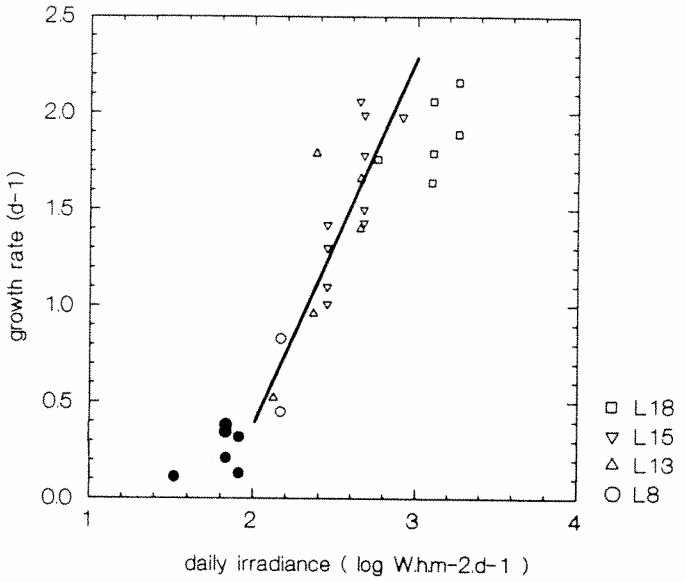

Fig. 2. Growth rate as a function of daily irradiance for *Phaeocystis*, cultured at different light:dark cycles: 8:16 (○), 13:11 (△), 15:9 (▽) and 18:6 (□) h day^{-1} and at several irradiances per cycle; closed symbols: no colony formation.

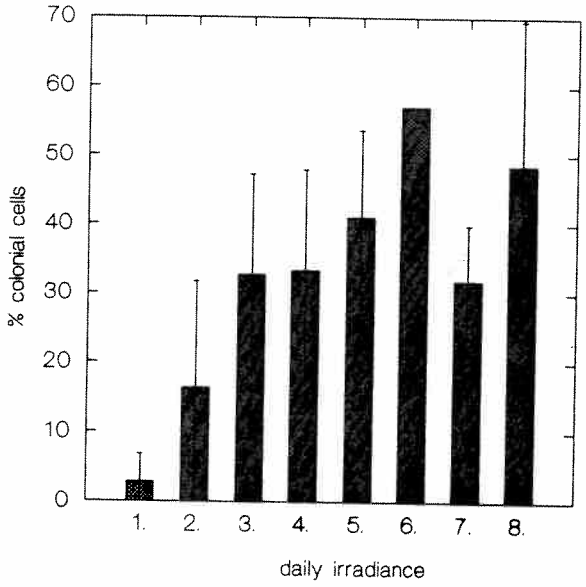

Fig. 3. Percentage of colonial cells as a function of daily irradiance (means ±1 SE). **1.** 0–100 (n = 6); **2.** 100–200 (n = 6); **3.** 200–300 (n = 10); **4.** 400–500 (n = 12); **5.** 500–600 (n = 2); **6.** 800–900 (n = 1); **7.** 1200–1300 (n = 6); **8.** 1800–1900 (n = 6) W h m^{-2} day^{-1}.

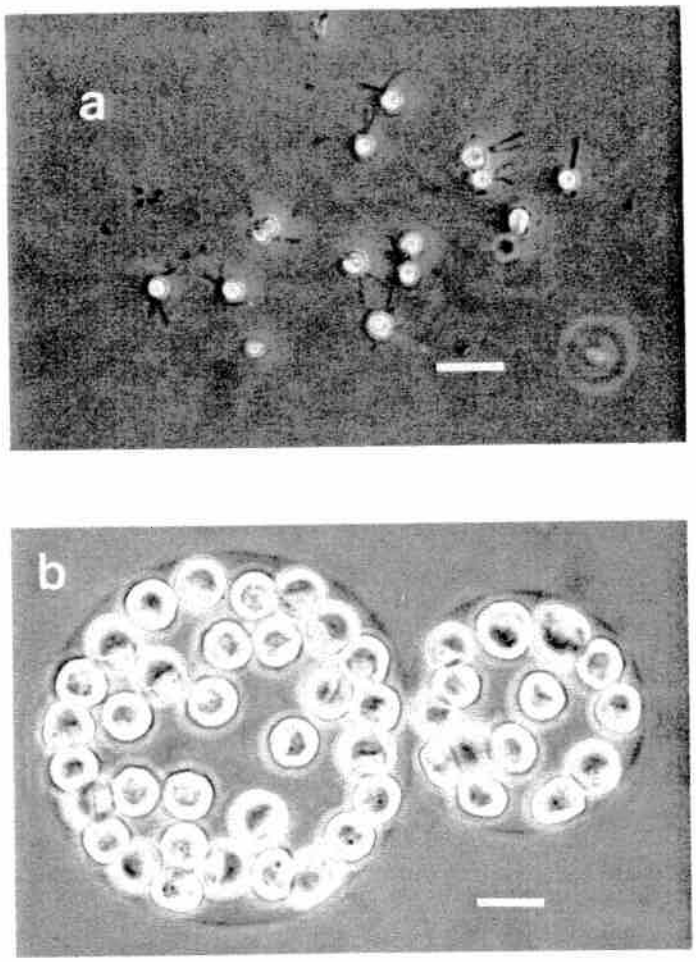

Fig. 4. Phase-contrast photomicrographs of: (**a**) solitary flagellated cells grown at 80 W h m^{-2} day^{-1}; (**b**) colonies of non-flagellated cells, cultured at 620 W h m^{-2} day^{-1}. Bar, 10 μm. Sample (a) was fixed with acid Lugol's iodine solution; (b) was not fixed.

aerated (L.Peperzak, unpublished). A statistically significant regression line could be fitted for $2 < \log DI < 3$:

$$\mu = -3.33 + 1.87 \times \log DI,\ r^2 = 0.72\ (P < 0.001)$$

Cells were large (~8 μm) and capable of forming colonies (Figure 4b). The globular form of the colony, the regularly distributed cells and the high growth rate at this temperature (15°C) are characteristic for the temperate *Phaeocystis* cf. *globosa* (Jahnke and Baumann, 1987).

The percentages of cells in colonies followed a similar trend to the growth rate (Figure 3), but the data contained too much variation to give a statistically

significant relationship with daily irradiance. The trend that larger colonies are formed at increasing daily irradiance is, however, in line with physiological (photosynthesis) data (see Introduction). The method employed overestimates the percentage colonial cells because the gauze may retain ~5% of the solitary cells (Veldhuis *et al.*, 1991). This accounts for the apparent colony formation (<5%) at daily irradiance <100 W h m^{-2} day^{-1} (Figure 3).

Discussion

Phaeocystis clone Ph91 formed colonies above a 100 W h m^{-2} day^{-1} threshold, under nutrient-replete conditions. This seems to agree well with *in situ* and laboratory observations. In winter, irradiance is too low (Figure 1) to form the colonial matrix and cells remain free-swimminig (Kornmann, 1955; Eilertsen *et al.*, 1989). However, a temporary increase in irradiance in shallow water could induce colony formation, even at sub-zero temperatures (Veldhuis, 1987). This may explain the low concentrations of colonies in the Wadden Sea during winter (Cadée and Hegeman, 1986). Kornmann (1955) observed colonies after increasing irradiance to a culture of 'Mikro-zoosporen', small flagellates apparently similar to those observed in this study below 100 W h m^{-2} day^{-1} (Figure 4a). Solitary cells adhering to solid surfaces may not detach and evolve into colonies on substrates such as seawater-rinsed glass (Kornmann, 1955) or on diatoms (Veldhuis, 1987; Cadée and Hegeman, 1991).

In the North Sea, the temporal development of phytoplankton blooms follows the coastward irradiance gradient, and *Phaeocystis* normally blooms after the first diatom bloom (Gieskes and Kraay, 1975; Colijn, 1983; Leewis, 1985; Veldhuis, 1987). The increase in irradiance in this temperate sea is slower (Figure 1a) than in polar regions. In high latitudes, the increase in daily solar radiation is faster than in temperate ones (Kirk, 1983). Enhanced by meltwater-induced stratification (Heimdal, 1988; Marchant *et al.*, 1991), daily water column irradiance will rise much more steeply. This may explain why *Phaeocystis* is one of the first species to bloom in polar seas (Wassman *et al.*, 1990; Davidson and Marchant, 1992). The intrusion of deep water on a continental shelf may also trigger colony development (Atkinson *et al.*, 1978). Davies *et al.* (1992) studied the *Phaeocystis* spring bloom in the English Channel in 1990. The *Phaeocystis* concentration increased after a marked rise in mean daily radiation, when the water column was not stratified and nutrient concentrations were high. Using data from their Table I and assuming that: (i) daylength is 12 h day^{-1} on 21 March and 12.5 h day^{-1} on 28 March; (ii) the carbon fixation was measured near midday and mean daily surface irradiance = 0.5 × surface irradiance during measurements; and (iii) 1 μE m^{-2} s^{-1} = 0.22 W m^{-2}, it can be calculated that the mean water column (z = 0–72 m) daily irradiance rose from 50 to 400 W h m^{-2} day^{-1}. This amply satisfies the light energy requirement for colony formation (Figure 2), although growth rates presumably were low due to a subsequent decline in mean surface irradiance. Just before, and during the bloom, daily irradiance was high again.

At daily irradiances >100 W h m^{-2} day^{-1}, non-colonial *Phaeocystis* cells may contribute 50% of total cell numbers, in culture (Figure 3) as well as *in situ* (Weisse and Scheffel-Möser, 1990). These solitary cells may be non-flagellated, in which case they resemble colonial cells in form and size, or flagellated, in which case they are smaller and different in cell shape (macroflagellate, not shown). The third cell type is the small microflagellate observed at $DI < 100$ W h m^{-2} day^{-1} (Figure 4a); it is significantly smaller and is considerably morphologically different from the macroflagellates (L.Peperzak, unpublished).

Phaeocystis colonies (Figure 4b) should be regarded as entities that store organic carbon, phosphate and nitrogen in the colony matrix when the light supply is sufficient (Lancelot *et al.*, 1987; Verity *et al.*, 1988b; Veldhuis *et al.*, 1991). The colonial cells might use these substances at night to sustain growth (Lancelot and Mathot, 1985). However, the measured maximum growth rate of 2 divisions day^{-1} (Figure 2) is equal to the mean of maximum growth rates of non-colonial marine microflagellates in laboratory cultures (Furnas, 1990), and is in the range of *in situ* growth rates of non-colonial *Phaeocystis* cells (Weiss and Scheffel-Möser, 1990). Above all, the calculated *in situ* dark growth rate of colonial cells can be very small compared to the daily (24 h) growth rate (Lancelot and Mathot, 1987). Therefore, the storage of energetically valuable carbohydrates in the colonial matrix seems not to be primarily aimed at the purpose of dark growth. This implies that colony formation is a multi-purpose strategy. It has also been suggested that the large size of the colonies compared with solitary cells, and the colony membrane, both serve to protect against zooplankton grazing (Lancelot *et al.*, 1987). This, however, does not prevent several micro-, meso- and metazooplankton groups from grazing on *Phaeocystis* colonies (Weisse and Scheffel-Möser, 1990; Sournia, 1991; Davidson and Marchant, 1992).

The mean water column irradiance in the North Sea never reaches the 700 W h m^{-2} day^{-1} (Figure 1a) necessary for the maximum growth rate. This implies that colonies should be able to position themselves at a certain optimum level, high in the water column (Figure 1b). *Phaeocystis* colonies from Norwegian fjords were found to be buoyant, enabling them to remain near the surface (Skreslet, 1988). Spring blooms in Arctic fjords, in the absence of a density gradient, could only be explained by assuming that the phytoplankton stratified itself; two of the dominant species in this area were *Phaeocystis* and the diatom *Chaetoceros socialis* (Eilertsen *et al.*, 1989). *Chaetoceros socialis* has also been observed before and during the spring *Phaeocystis* bloom in the North Sea (Gieskes and Kraay, 1975; Lancelot and Mathot, 1987), and may possibly use a similar strategy. Its weakly silicified, small cells excrete mucus and form colonies in the same size range as *Phaeocystis* (Drebes, 1974), and recently buoyancy of *C.socialis* colonies has been observed (Riegman *et al.*, 1992).

Unfortunately, studies of the vertical distribution of phytoplankton in the Southern Bight of the North Sea are scarce because the water column is assumed to be homogeneous throughout the year (Gieskes and Kraay, 1975; Leewis, 1985; Weisse and Scheffel-Möser, 1990). Normally, only surface samples are taken. However, in April 1926, a *Phaeocystis* bloom in the Southern Bight was

investigated at depth intervals of 10 m. Large differences in vertical distribution were found, and it was suggested that *Phaeocystis* blooms in surface waters and later sinks to the bottom (Savage and Hardy, 1934). Recent observations in this area also showed post-bloom sinking and the formation of colonial microflagellates (L.Peperzak, unpublished). In general, rates at which algal cells sink increase under physiological stress (Bienfang, 1981) and the buoyancy of *Phaeocystis* colonies decreases under nutrient stress (Skreslet, 1988). Van Boekel *et al.* (1992) could not find a clear relationship between the sinking rate of *Phaeocystis* colonies and the stage of bloom development, although they did observe a slight increase during the bloom decline. However, the colonies were obtained from surface samples and may not have been representative of the North Sea *Phaeocystis* population as a whole (cf. Skreslet, 1988). Once North Sea phytoplankton, notably *Phaeocystis*, is deposited on the sea floor, there is little resuspension despite high mean current velocities (Jennes and Duineveld, 1985).

The spring *Phaeocystis* bloom in the North Sea depletes either phosphate (Veldhuis, 1987) or nitrogen (Lancelot and Mathot, 1987; Van Boekel *et al.*, 1992). Presumably, sedimentation is enhanced by detritus or other planktonic forms adhering to the colonial mucus (Drebes, 1974; Wassman *et al.*, 1990). Bloom sedimentations have been described in several temperate and polar seas (Jennes and Duineveld, 1985; Lancelot *et al.*, 1987; Rogers and Lockwood, 1990; Wassman *et al.*, 1990). Sinking *Phaeocystis* colonies will eventually reach zones with very low irradiance (Figure 1b). As a result, colonial cells may transform into small flagellates (Figure 4a). Small solitary flagellates have been observed in North Sea surface samples after bloom collapse (Veldhuis, 1987; Lancelot and Mathot, 1987; L.Peperzak, unpublished) and in laboratory cultures after reducing irradiance, in combination with nutrient stress (Peperzak *et al.*, in preparation). The reduction in irradiance experienced by a surface *Phaeocystis* bloom advected under the fast Antarctic ice in nutrient-replete conditions did not result in such a transformation (Palmisano *et al.*, 1986). It seems that both reduced light energy and nutrient stress are needed to trigger the phenomenon.

The emigration of flagellated cells from nitrogen-stressed colonies in a mesocosm experiment, leading to so-called 'ghost' colonies, was ascribed to a rapid drop in temperature (Verity *et al.*, 1988b). However, irradiance decreased concomitantly because surface ice was formed and daily solar radiation decreased (Verity *et al.*, 1988b), and this important variable was not taken into account. In a recent mesocosm experiment, phosphate-stressed colonies were observed to sink to low irradiances. This also led to the release of small flagellates and the formation of 'ghost' colonies (V.Escaravage, personal communication). Davies *et al.* (1992) observed an increase of small *Phaeocystis* flagellates under the seasonal thermocline (40 m), after the decline of the surface (10 m) spring bloom. This was ascribed to downward migration of the flagellates, possibly due to photophobotaxis. An alternative explanation is that the colonies lost buoyancy control after nitrate became limiting (Davies *et al.*, 1992). Under the assumptions made earlier, daily irradiance at these depths was

500 W h m^{-2} day^{-1} (10 m) and 2 W h m^{-2} day^{-1} (40 m). During descent, colonies would pass the 100 W h m^{-2} day^{-1} threshold and this would have triggered the release of small *Phaeocystis* flagellates (Peperzak *et al.*, in preparation). It also explains the large concentration of small *Phaeocystis* flagellates at this depth, compared with the surface.

Presumably, colonial sedimentation is an adaptive response to nutrient limitation. Small and motile solitary *Phaeocystis* cells will be better able to compete for scarce nutrients and they may recolonize the water column. Colonial development will start when both nutrient concentration and daily irradiance are adequate again.

It has been suggested that summer blooms in the Wadden Sea started in 1978 after a lowering of the nitrogen:phosphorus discharge ratio, and because *Phaeocystis* may outcompete other species at low nitrogen concentrations (Riegman *et al.*, 1992). However, summer blooms had already occurred before 1978, e.g. 1974, 1975 and 1976 (Cadée and Hegeman, 1986), and the ratio shifted due to an unequal increase of both phosphorus and nitrogen discharge (Riegman *et al.*, 1992). Also, the colonial membrane and mucus act as a diffusion barrier for phosphate (Veldhuis *et al.*, 1991), and it is unlikely that this would not be so for nitrogen. Therefore, it is plausible that summer blooms are initially still light controlled. The supply of the first nutrient to limit growth rate will govern the peak and duration of the bloom (Jahnke, 1989; Peeters and Peperzak, 1990). The notion that oligotrophic tropical waters may not be an environment conducive to the development of *Phaeocystis* blooms (Davidson and Marchant, 1992) may well be attributable, therefore, to the inherent difficulty of colonies to compete for nutrients when these are scarce. For instance, the anthropogenic eutrophication of the bay of Kuwait has led to the blooming of *Phaeocystis* (Al-Hasan *et al.*, 1990). The reverse, oligotrophication, has occurred in the Oosterschelde estuary. The strong reduction of nutrient loads, notably nitrogen, has led to the poor development or absence of *Phaeocystis* colonies (Bakker *et al.*, 1993).

Owens *et al.* (1989) related the changes in abundance of *Phaeocystis* colonies in the northeast Atlantic Ocean since the 1940s to climatic change. The most pronounced physical change in this period has been an increase in northerly winds and gales, delaying the time at which the critical depth exceeds the depth of mixing (Cushing, 1990). Given the strong dependence of *Phaeocystis* colony formation on underwater light climate, the relationship as assumed by Owens *et al.* (1989) seems plausible. This is corroborated by observations of Davies (cited in Lancelot *et al.*, 1991). He noticed that the development of the *Phaeocystis* spring bloom was delayed by periods of strong wind that prevented long-term stratification.

The coherent observations on the ecology of *Phaeocystis* presented here form the basis for the description of its life cycle (Peperzak *et al.*, in preparation). The relatively high requirements for light energy and nutrients, in conjunction with species-specific temperature optima (Jahnke and Baumann, 1987), seem to define the geographical and temporal distribution of colonial blooms. Supplementary research with other, e.g. polar and tropical, strains or species should

confirm this. However, a role for other environmental factors, such as organic nutrients or the use of diatoms as a substratum for colonial growth *in situ* (Lancelot *et al.*, 1991), should not be ruled out.

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