Photosynthesis, excretion, and growth rates of *Phaeocystis* colonies and solitary cells

PETER G. VERITY, THEODORE J. SMAYDA and EGIL SAKSHAUG

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Unialgal cultures of the prymnesiophyte, *Phaeocystis* cf. *pouchetii*, were isolated from Norwegian and United States coastal waters. Manipulation of the nutrient medium resulted in populations overwhelmingly dominated by either colonies or solitary cells of *Phaeocystis*. Both morphotypes were grown under a range of irradiances at 0°, 2°, 5°, 10° and 20°C. Photosynthesis was measured as incorporation of $H^{14}CO_3^-$, and excretion as accumulation of $DO^{14}C$ during 24-hour incubations; growth rates of solitary cells were determined concurrently from changes in abundance.

Both morphotypes exhibited temperature-dependent asymptotic increases in pigment-specific photosynthesis with irradiance. Saturation intensities increased with temperature. Cell division by *Phaeocystis* solitary cells exhibited a functional response similar to photosynthesis, although growth apparently saturated at lower irradiances. C:Chl*a* ratios were positively correlated with irradiance and inversely related to temperature, while C:N ratios were insensitive to these environmental parameters. Colonies had higher C:Chl*a* and C:N ratios than solitary cells. Pigment-specific excretion rates were linear functions of irradiance, and exhibited temperature-dependent positive correlations with photosynthesis. Percent extracellular release (PER) by both morphotypes was inversely related to temperature.

At low temperatures (0–5°C), solitary cells had higher photosynthesis rates than colonies at all irradiances. Their excretion rates, however, were also higher, such that the PER of solitary cells exceeded those of colonies at 0°C and low irradiances at 2°C. No differences were detectable at 5°C. At higher temperatures, photosynthesis by solitary cells still generally exceeded that by colonies, but the colonies excreted considerably more DOC. Thus, while solitary cells are more efficient at utilizing light for photosynthesis, they do not necessarily channel a larger proportion into biomass production. Colonies, however, appear to be particularly stressed by higher temperatures and irradiances.

Peter G. Verity, Skidaway Institute of Oceanography, P.O. Box 13687, Savannah, Georgia 31416, USA; Theodore J. Smayda, Graduate School of Oceanography, University of Rhode Island, Kingston, Rhode Island 02881, USA; Egil Sakshaug, Trondhjem Biological Station, University of Trondheim, Bynesveien 46, N-7018 Trondheim, Norway.

Introduction

Phaeocystis cf. *pouchetii* (Hariot) Lagerheim, a prymnesiophyte, is one of few marine phytoplankton taxa which exhibits phase alternations between free-living solitary cells and a gelatinous colonial aggregation of non-motile cells. While both stages are capable of rapid vegetative growth (Kornmann 1955; Kayser 1970), the colonies occur most prominently in the plankton. Thousands of non-motile cells (3–10 μm) may be contained within colonies up to 10–20 mm in diameter (Gieskes & Kraay 1975; Verity et al. 1988a, b; Weisse & Scheffel-Möser 1990). The free-living solitary cells, of similar size, can be released from colonies, may persist indefinitely in the plankton, and may initiate formation of new colonies. In addition, macrospheres and microspores have been described (Kornmann 1955; Parke et al. 1971) which behave like asexual gametes. While they persist in some cultures, they have not been reported from natural populations, and their function remains obscure.

Blooms of colonial *Phaeocystis* have been reported for 100 years (Pouchet 1892; Gran 1902). They are prominent in both coastal and oceanic waters, near the ice edge in both polar regions (Braarud 1935; Biggs 1982), and exhibit cross-shelf distributional gradients influenced by frontal dynamics (Iverson et al. 1979a, b). Colony blooms are particularly well documented in Norwegian fjords (Sakshaug 1972; Heimdal 1974; Eilertsen et al. 1981), in the Norwegian Sea (Smayda 1958; Paasche 1960), and in the North Sea (Cadee & Hegeman 1986). In contrast, archived samples from the Continuous Plankton Recorder (CPR) imply a long-term decline in *Phaeocystis* in all open sea areas of the North Sea (Owens et al.

1989). This trend, however, may be applicable only to colonies since the CPR mesh size (ca. 250 μm) excludes small colonies and all solitary cells.

This apparent conflict in historical trends of abundance emphasizes that the majority of the data are restricted to observations of *Phaeocystis* colonies, and that our knowledge of in situ behavior is based almost exclusively on colonial stage dynamics. The occurrence of solitary cells as an alternate planktonic stage complicates quantitation of *Phaeocystis* bloom inception and its environmental regulation. Although the role of life cycle phenomena has recently received attention (Verity et al. 1988b), the abundance and temporal development of solitary cells has not generally been assessed, primarily due to difficulties in recognition of living *Phaeocystis* in natural samples containing other phytoflagellates of similar size and morphology. This dearth of data biases our understanding of *Phaeocystis* bloom dynamics. For example, *Phaeocystis* is usually considered to be bipolar, with a preference for boreal and colder waters and the winter period in temperate seas (Kashkin 1963). It occurs extensively in polar seas up to the ice edge, and it has been reported from sea ice in both the Arctic (Hsiao 1980) and Antarctic (Whitaker 1977). But this bipolar nature is now suspect, as *Phaeocystis* cf. *pouchetti* also occurs in subtropical and tropical water (Guillard & Hellebust 1971; Leadbeater 1974; Estep et al. 1984; Verity unpubl. data). Yet it rarely (if at all) produces the prodigious blooms commonplace in cold waters. Why?

The major structural difference between colonial and solitary stages is the large gelatinous matrix of the former. Significant amounts of photosynthate are directed towards its manufacture (Guillard & Hellebust 1971; Lancelot & Mathot 1985; Veldhuis & Admiraal 1985) which, presumably, is energetically expensive. Surprisingly, though, little is known of the relative photosynthetic and excretion potentials of the two morphotypes. It was the purpose of this study to provide such data and to investigate the role of temperature and irradiance in influencing these parameters.

Methods

Unialgal cultures of *Phaeocystis* cf. *pouchetii* (see Sournia 1988) were isolated from the Tromsø sound near Tromsø, Norway, and grown in batch culture using polycarbonate flasks. Manipulation of nutrient concentrations in sterilized "f" medium (Guillard 1975) resulted in cultures overwhelmingly dominated by colonies (f/50 − Silicate) or by solitary cells (f/2 − Silicate). Similar responses to nutrient concentrations have been observed for other *Phaeocystis* clones (Guillard & Hellebust 1971; Verity & Smayda 1989; Turner et al. 1990). For both treatments, > 95% of all cells belonged to a single morphotype, e.g. colonies or solitary cells. All media were prepared from the same batch of seawater.

Colony cultures could not be cleaned entirely of their bacterial populations, probably due to their residual occurrence on the gelatinous sheaths of the colonies. Healthy colonies, however, have few bacteria attached to their surfaces (Verity et al. 1988b). Cultures of solitary cells were deliberately not made axenic in order to better intercompare results with colonies. In both cases bacterial abundances (determined in DAPI-stained epifluorescence microscope counts) were $< 2 \times 10^4$ cells/ml^{-1}, and bacterial biomass was an insignificant proportion of algal biomass.

Each morphotype was cultured at four to six irradiances and 14:10 L:D photoperiods at 0°, 2°, 5°, 10°, and 20° C. Cool-white fluorescent light was attenuated using neutral density screen, and irradiance was measured with a Biospherical Instruments QSL-100 quantum sensor. Cultures were adapted to experimental conditions for > 10 generations, after which identical aliquots were used to measure carbon, nitrogen, and chlorophyll *a* (chl *a*) contents; photosynthesis and excretion rates; and population growth rates (of solitary cells only).

For proximate analyses, samples were collected on 0.45 μm Gelman AE filters using low vacuum pressures (< 50 mm Hg difference between atmospheric pressure and vacuum pressure in the flask). Chl *a* was extracted in the dark after grinding in 90% acetone, and measured fluorometrically before and after acidification (Holm-Hansen et al. 1965). Filters for carbon (C) and nitrogen (N) determinations were pre-combusted at 400° C for 1 hour. Carbon and nitrogen were measured with a HP185B CHN analyzer (Sharp 1974).

Growth and photosynthesis were measured as follows: two sets of 250-ml polycarbonate bottles, previously soaked in dilute HCl and washed in

deionized water, were gently filled with aliquots of the acclimated stock cultures. One set received an inoculum of 1.85×10^5 Becquerels (5 μCi) of $NaH^{14}CO_3$ (New England Nuclear), prepared using trace metal clean techniques (Fitzwater et al. 1982). The other set was unaltered and was used to measure cell and colony size and abundance, as well as growth rates of solitary cells. Both sets were returned to their acclimation irradiances and incubated for 24 hours. In addition, an extra ^{14}C bottle was wrapped in aluminum foil to provide a dark control.

The ^{14}C incubations were terminated by collecting phytoplankton on Gelman 0.45 μm AE glass fiber filters in triplicate subsamples. The filters were rinsed, placed in glass vials, acidified for 1 hour with 0.1 ml of 5 N HCl to drive off residual inorganic ^{14}C, and suspended in 5 ml of Aquasol II scintillation cocktail. Release of dissolved organic carbon (DOC) was determined using methods modified after Verity (1981). Triplicate 8-ml aliquots of the ^{14}C filtrate from each bottle were pipetted into 10 ml glass test tubes. The pH was lowered to 3.0 by acidification with HCl, and samples were bubbled with air for 1 hour to purge inorganic carbon. Five ml of each replicate were counted in 16 ml of Aquasol II.

All samples were counted to an accuracy of at least 5% using a Beckman LS150 liquid scintillation counter. Quenching was corrected by the channels ratio method utilising a curve prepared from ^{14}C-toluene. An isotope discrimination factor of 1.05 was applied. Particulate and DOC production rates were corrected for dark bottle activity, which was always a small fraction of light bottle counts.

In colony cultures, the abundance of colonies in triplicate 50 ml samples was enumerated using a stereomicroscope. Cell abundance was calculated as (colony abundance) × (cells per colony), where cells per colony was determined as described in Verity et al. (1988a). In solitary cell cultures, cell abundance of triplicate subsamples was measured in Palmer-Maloney chambers using a Zeiss Photomicroscope II. Cell growth rates were expressed as population doublings according to $K(\text{doublings} \cdot d^{-1}) = (1/t)\log_2 (N_t/N_0)$, where N_t and N_0 were abundances at time t and 0. Carbon (C) growth rates were also calculated by normalizing colony and cell photosynthesis rates to their C content according to $K_c(\text{doubl.} \cdot d^{-1}) = (1/t) \log_2 [(C + \Delta C)/C]$, where C is the initial carbon content and ΔC is the production rate over time t (Eppley 1972). Note that ^{14}C uptake rates described here approximate net rather than gross particulate carbon production, due to the relatively long incubations (24 hours).

Statistical tests were conducted according to Sokal & Rohlf (1969), with significance levels of $P > 0.05$ unless otherwise noted. Correlations between photosynthesis and growth rates were analyzed by functional (geometric mean) regressions as both parameters were subject to independent errors in measurement (Ricker 1973; Laws & Archie 1981).

Results

Colonies

Chlorophyll *a*-specific photosynthesis increased asymptotically with irradiance in a temperature-dependent manner (Fig. 1). The slopes of the P-I curves increased with temperature (Table 1). Saturation apparently occurred at 100–200 μmol photons $m^{-2} s^{-1}$ at 0° and 2°C; at > 150 μmol $m^{-2} s^{-1}$ at 5°C; at > 200 μmol photons $m^{-2} s^{-1}$ at 10°C; and at > 250 μmol $m^{-2} s^{-1}$ at 20°C. Maximum observed photosynthetic rates were also temperature-dependent, ranging from 2.2 (0°C) to 8.1 (20°C) g C (g Chl*a*)$^{-1}$ h^{-1}.

Similar functional relationships are evident when photosynthesis is normalized to colony carbon (Fig. 2). Carbon-specific incorporation increased asymptotically with irradiance, but saturation apparently occurred at lower light levels than that observed for pigment-specific photosynthesis. Maximum rates ranged from 0.25 to 1.15 μg C · μg colony-C^{-1} · d^{-1}.

Table 1. Slopes of the light-limited portion (α^B, gC · g Chl*a*$^{-1}$ · h^{-1} · μmol photons^{-1} m^{-2} s^{-1}) of the P-I curves at each temperature. Bracketed values indicate 95% confidence intervals around slopes. Fits of these data to the exponential model yielded the following equations: α^B (of solitary cells) = $0.033e^{0.044(\text{temp.})}$ and α^B (of colonies) = $0.026e^{0.060(\text{temp.})}$

	α^B (± 95% CI)	
Temp. (°C)	Solitary Cells	Colonies
0	.032 (.006)	.025 (.005)
2	.035 (.008)	.029 (.006)
5	.040 (.007)	.031 (.006)
10	.065 (.012)	.063 (.025)
20	.073 (.022)	.077 (.012)

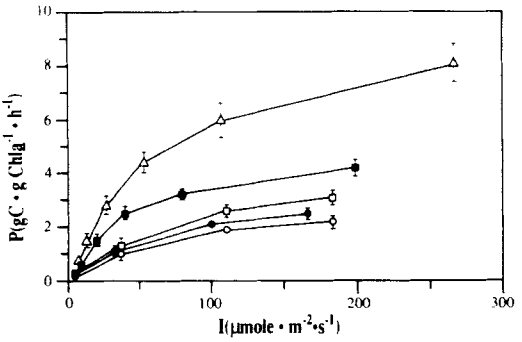

Fig. 1. Chl *a*-specific photosynthesis (P) of colonies as a function of irradiance (I). Colonies were grown at 0° (○), 2° (●), 5° (□), 10° (■), and 20° (△). Error bars represent 1 SD.

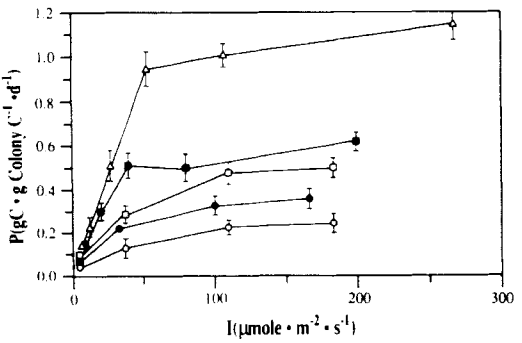

Fig. 2. Carbon-specific photosynthesis (P) of colonies as a function of irradiance (I). Symbols as in Fig. 1.

Carbon excretion was generally a small fraction of particulate fixation (Fig. 3). Percent extracolonial release (PER) was inversely related to temperature and ranged from 1–7% (20°C) to 6–19% (0°C). The highest relative release occurred at higher irradiances at all temperatures.

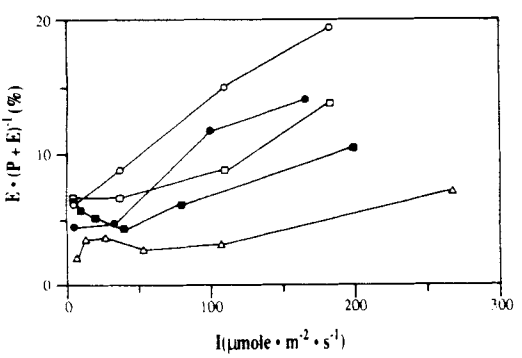

Fig. 3. Carbon excretion (E) of colonies expressed as the percent of total incorporation of ^{14}C into organic carbon (P + E). Symbols as in Fig. 1.

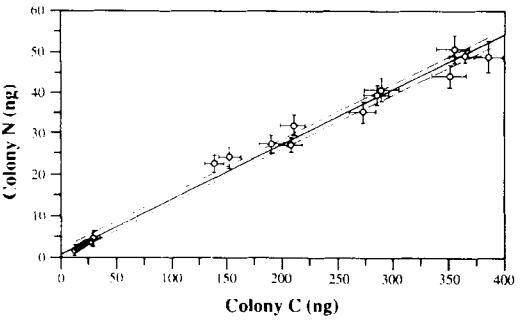

Fig. 4. Nitrogen (N) and carbon (C) contents of colonies grown at all temperatures and irradiances. Error bars represent 1 SD. Dashed lines illustrate 95% confidence intervals of regression slope. Geometric mean regression: Colony N (ng) = 0.587 + 0.135 (Colony C, ng); $r^2 = 0.991$, n = 24.

Colony carbon and nitrogen were linearly related and independent of irradiance, temperature, and colony size (Fig. 4). The regression slope is equivalent to a mean C:N (by weight) of 7.41. Colonies ranged from an average of 12 to 385 ng C, 2 to 49 ng N, and 228 to 2,560 cells per colony (data not shown), with the largest colonies occurring at low temperatures.

Ratios of C:Chl*a* (by weight) exhibited temperature-dependent asymptotic relationships with irradiance (Fig. 5). C:Chl*a* increased with irradiance, but this trend was most evident at low temperatures. Ratios ranged from 65–99 (20°C) to 109–159 (0°C). N:Chl *a* ranged from 9–13 (20°C) to 15–20 (0°C) in colonies containing 0.1–0.4 (20°C) and 1.9–2.4 (0°C) ng Chl*a* per colony (data not shown).

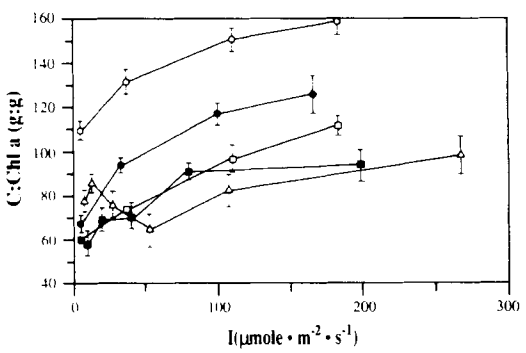

Fig. 5. The ratio in colonies of carbon to chlorophyll *a* (C:Chl *a*), by weight, as a function of irradiance (I). Symbols as in Fig. 1.

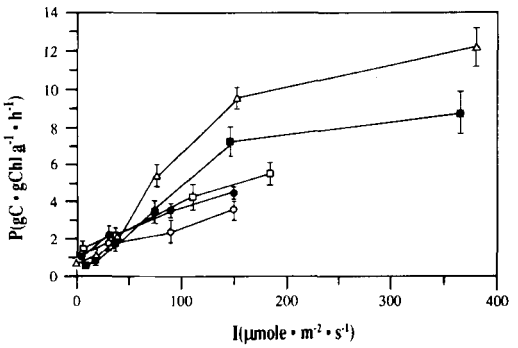

Fig. 6. Chl *a*-specific photosynthesis (P) of solitary cells as a function of irradiance (I). Symbols as in Fig. 1.

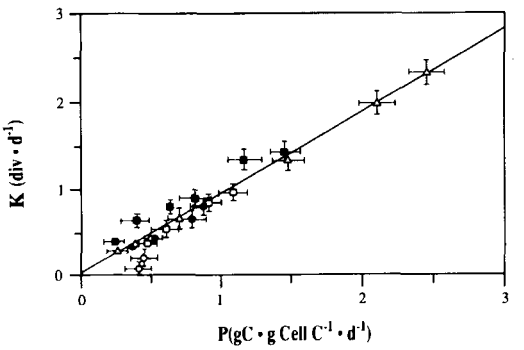

Fig. 8. Comparison between cell-based population growth (K) and carbon-based photosynthesis (P) of solitary cells. Symbols as in Fig. 1. Geometric mean regression: $K(div \cdot d^{-1}) = -0.023 + 0.986$ [P, gC · (g Cell C)$^{-1}$ · d^{-1}]; $r^2 = 0.944$, n = 24.

Solitary cells

Chlorophyll *a*-specific photosynthetic rates were temperature-dependent and increased with irradiance in a quasi-asymptotic manner (Fig. 6). The slopes of the P-I curves (α^B) (symbols as in Platt et al. 1980) increased with temperature (Table 1). Saturation was not clearly observed at the irradiances used at 0°, 2°, and 5°C, but was approached at 200–400 μmole photons · m^{-2} · s^{-1} at 10° and 20°C. Maximum observed photosynthetic rates increased from 2.7 (0°C) to 12.2 (20°C) gC (g Chl*a*)$^{-1}$ h^{-1}. Q_{10} values for these maximum rates were not calculated as they may not represent actual maximum rates (e.g. P_m^B).

Population growth rates of cells were also temperature-dependent and exhibited asymptotic relationships with irradiance (Fig. 7). Saturation of cell division occurred at lower light levels than did photosynthesis, as observed for carbon-specific photosynthesis of colonies. Maximum growth rates increased from 0.3 (0°C) to 2.3 (20°C) doublings per day. Photosynthesis measured in 24-hour incubations represents net carbon incorporation and, when normalized to cell carbon, is a measure of carbon growth rate. A comparison of this parameter to independently determined cell division rates (Fig. 8) shows a slope not significantly different from 1.0 and an intercept not significantly different from 0, indicating that the cells were in balanced growth.

As with colonies, carbon excretion was generally a small fraction of particulate fixation (Fig. 9). Percent extra-cellular release (PER) was an inverse function of temperature, ranging from 2% (20°C) to 10–20% (0°C). PER increased with irradiance only at the colder temperatures.

Cell carbon (C) and nitrogen (N) were linearly related independent of irradiance, temperature,

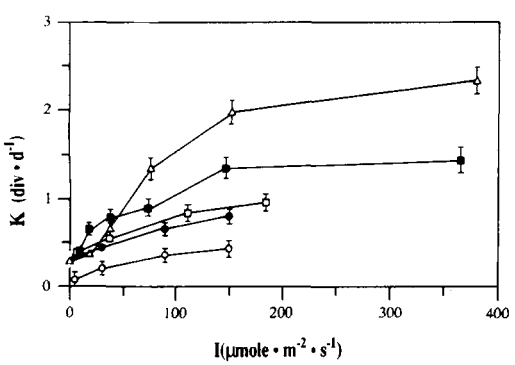

Fig. 7. Population growth rates of solitary cells (K) as a function of irradiance (I). Symbols as in Fig. 1.

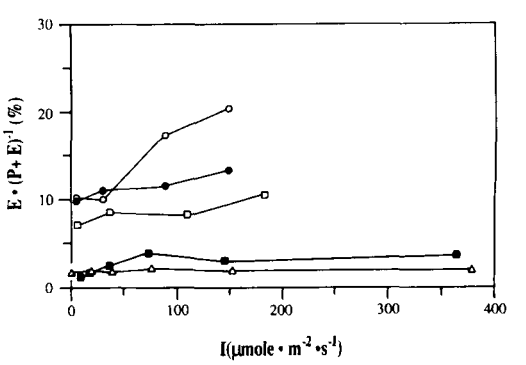

Fig. 9. Carbon excretion (E) of solitary cells expressed as the percent of total incorporation of ^{14}C into organic carbon (P + E). Symbols as in Fig. 1.

and cell size (Fig. 10). The regression slope is equivalent to a mean C : N ratio of 6.6 (by weight). Cells ranged from an average of 10–110 pg C, 1–16 pg N, and 0.1–1.9 pg Chl*a* per cell (data not shown). Weight ratios of C : Chl*a* exhibited temperature-dependent asymptotic increases with irradiance (Fig. 11), a trend particularly evident at lower temperatures. Ratios ranged from 39–70 (20°C) to 51–100 (0°C). N : Chl*a* ranged from 6–10 (20°C) to 9–16 (0°C) (data not shown).

Discussion

A major objective of this study was to evaluate the comparative physiological potential of solitary cells and colonies of *Phaeocystis*, as modulated by environmental parameters, to aid in understanding the bloom dynamics of this enigmatic alga. Despite a centennial of investigation (Pouchet 1892; Lagerheim 1893; Gran 1902), factors influencing the inception and regulation of *Phaeocystis* blooms are poorly understood and for several reasons: (1) taxonomic uncertainties and the question of physiological clones; (2) incomplete description of the life cycle; (3) lack of physiological data on life cycle stages within a single clone; and (4) inability to distinguish solitary *Phaeocystis* cells in natural assemblages of nanoplankton.

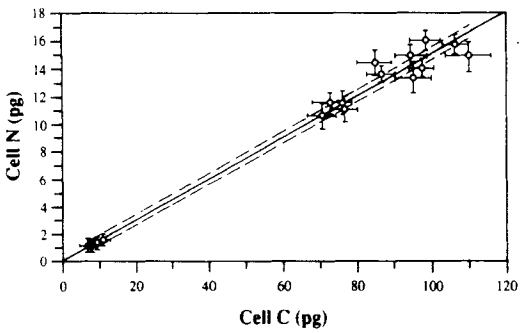

Fig. 10. Nitrogen (N) and carbon (C) contents of solitary cells grown at all temperatures and irradiances. Error bars represent 1 SD. Broken lines illustrate 95% confidence intervals of regression slope. Geometric mean regression: Cell N (pg) = 0.012 + 0.152 (Cell C, pg); $r^2 = 0.989$, n = 24.

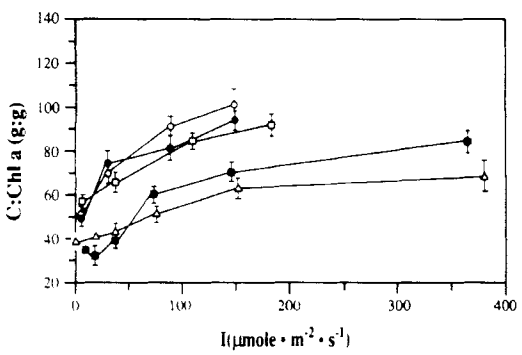

Fig. 11. The ratio in solitary cells of carbon to chlorophyll *a* (C : Chl*a*), by weight, as a function of irradiance (I). Symbols as in Fig. 1.

The taxonomic confusion centers around species designation. Although nine species have been described (Sournia 1988), most records of blooms have been attributed to *Phaeocystis* cf. *pouchetii* and *P. globosa*, based primarily on differences in colony morphology. On the basis of culture experiments, Kornmann (1955) concluded that *P. globosa* is a young stage (= Jugendstadium) of *P. pouchetii*. On the basis of ecological data, Gran (1902) favored their taxonomic separation. He characterized *P. pouchetii* as a cold-water form very sensitive to higher temperatures, and *P. globosa* as a hardier form which occurs during the warmest season. Guillard & Hellebust (1971) found that large colonies formed by their tropical clone resembled descriptions of *P. globosa*. This morphotype, absent in their cold water clones, occurred in natural populations collected near Woods Hole. The Norwegian clone in the present study reproduced spherical colonies, as did a U.S. east coast isolate (Verity et al. 1988b), although very large, old colonies of both clones would occasionally show more elongate or lobed shapes (e.g. Bätje & Michaelis 1986). We have insufficient evidence to definitively establish the identity of our clone or its relationship to the *P. pouchetii/globosa* debate, and we accept the recommendation of Sournia (1988) to refer to it as *Phaeocystis* cf. *pouchetii*.

Cell size, and hence carbon/nitrogen content, may also vary considerably among and within clones. Cells of *Phaeocystis* cf. *pouchetii* are typically 3–8 μm in diameter (Kornmann 1955; Parke et al. 1971; Chang 1984; Jahnke 1989). Distinctly larger cells up to 10–12 μm, however, have been reported (Ostenfeld 1904; Hallegraeff 1983; Tande & Båmstedt 1987). Mean size of solitary cells in the present study ranged from 3 μm to 10 μm and was inversely related to temperature. Carbon content was 10–110 pg per cell. These directly measured values compare to those of 15–35 pg per cell for 4–7 μm cells (Jahnke 1989), and

to calculated carbon contents of 9.5 pg cell^{-1} for 5 μm cells (Weisse & Scheffel-Möser 1990) and 258 pg cell^{-1} for 6–10 μm cells (Tande & Båmstedt 1987).

The uncertain relationship discussed above between systematics and morphological variability is exacerbated by the possible occurrence of physiological clones, specifically thermal clones (Guillard & Hellebust 1971; Guillard & Kilham 1977). Their cold-water clones grew between 4°C (lowest level tested) and 13°C, but not above 16°C, while a tropical clone grew between 17°C and 27°C, but died at 14°C. Kayser's (1970) cold-water clone grew best at 15°C (highest temperature tested), but with difficulty at 5°C. Similarly, *Phaeocystis* colonies from the North Sea could not be induced to grow below 5°C (Grimm & Weisse 1985; Weisse et al. 1986), and rapid multiplication was observed only above 7°C. Natural populations, however, occur at considerably lower temperatures (e.g. Smayda 1958; Eilertsen & Taasen 1984; Verity et al. 1988a, b). The clone in the present study could be cultured as distinct morphotypes over a broad temperature range, whereas another arctic clone of *P.* cf. *pouchetii* could not (Jahnke 1989). These apparent contradictions between lab data and field observations may reflect true physiological adaptations, inadequate culture methods or acclimation to growth conditions, or occurrence of multiple species. Resolution requires full description of the life cycle of *Phaeocystis* cf. *pouchetii* and definition of taxonomic status with respect to other species (Jahnke 1989).

The present data illustrate that different morphotypes of *Phaeocystis* vary in their physiological performance even within a single clone. While colonies and solitary cells exhibited similar functional responses to variations in irradiance and temperature, they differed substantially in magnitude. At 0–5°C, solitary cells were always more photosynthetically efficient than colonies at a given irradiance (Fig. 12). The slope of the light-limited portion of the P-I curve for solitary cells exceeded that for colonies at 0–5°C, although the differences were not significant at $p > 0.05$ (Table 1). This suggests that solitary cells were somewhat better adapted than colonies to low light and temperature. However, chlorophyll *a*-specific excretion by solitary cells also exceeded that of colonies (Fig. 13), such that solitary cells actually released larger portions of their photosynthate (PER), especially at 0°C and 2°C. The PER of

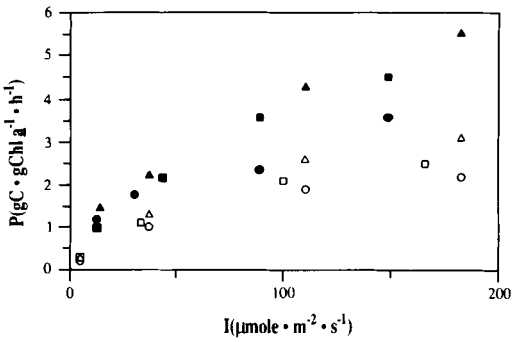

Fig. 12. Comparison of chl *a*-specific photosynthesis (P) of colonies (open symbols) and solitary cells (filled symbols), as a function or irradiance (I). Cultures were grown at 0° (○), 2° (□), and 5°C (△). Data from Figs. 1 and 6.

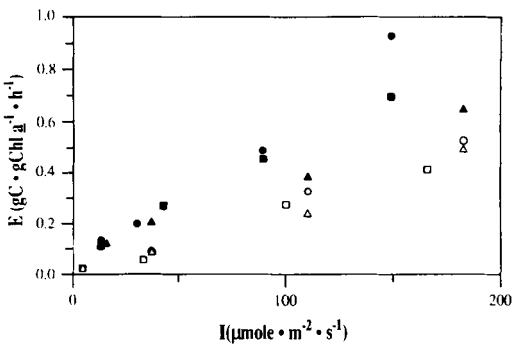

Fig. 13. Comparison of pigment-specific excretion (E) of colonies (open symbols) and solitary cells (filled symbols), as a function of irradiance (I). Cultures were grown at 0° (○), 2° (□), and 5°C (△).

both morphotypes were indistinguishable at 5°C. The α^B values were similar to those of natural *Phaeocystis* populations advected beneath sea ice (Palmisano et al. 1986) and support those authors' conclusion that this alga is capable of adapting to a broad range of irradiances at low temperatures.

The responses at higher temperatures were different. Photosynthesis by solitary cells still exceeded that of colonies at 10–20°C (Fig. 14), although the distinction was less than at 0–5°C. Values of α^B were indistinguishable at 10–20°C (Table 1). The most salient physiological shift was observed in carbon excretion rates (Fig. 15). Solitary cells excreted less carbon per unit of chlorophyll *a* than did colonies, particularly at higher irradiances. The net effect was that PER of colonies exceeded that of solitary cells at 10–20°C.

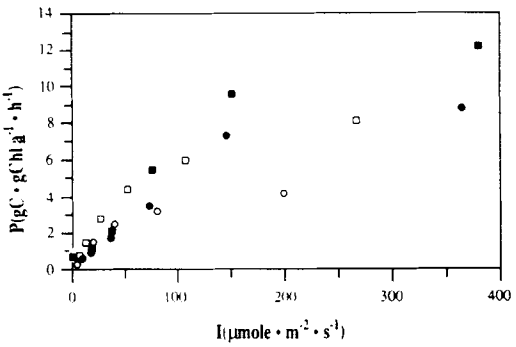

Fig. 14. As in Fig. 12, but cultures grown at 10° (○) and 20°C (□).

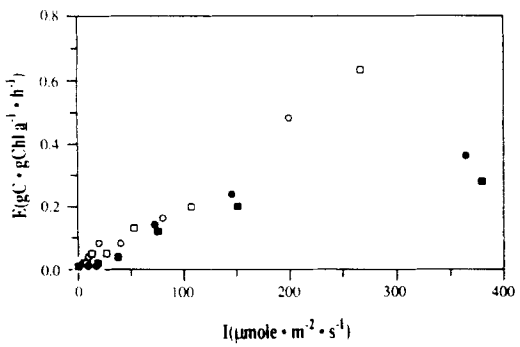

Fig. 15. As in Fig. 13, but cultures grown at 10° (○) and 20°C (□).

The major structural difference between these morphotypes is the large gelatinous matrix of the colonies (Chang 1984) which apparently serves as a storage depot for labile organic carbon (Lancelot & Mathot 1985; Veldhuis & Admiraal 1985; Lancelot et al. 1986). Release of DOC external to the colonies was generally only a small fraction of total incorporation. Previous high PER values for colonies of 16–64% (Guillard & Hellebust 1971) were not confirmed in the present study. This difference may reflect that very dense cultures were grown at low nutrient levels and high irradiances in the prior study. Assuming that substantial amounts of photosynthate are channeled into the gelatinous matrix of the colonies (Lancelot & Mathot 1985; Veldhuis & Admiraal 1985), the low rates of DOC release measured here indicate that organic carbon associated with colony mucus is retained on the glass fiber filters during low pressure filtration. This implies that biochemical parameters measured using filter-collected colonies (Figs. 4 and 5, 10 and 11; see also Verity et al. 1988a) accurately represent the carbon, nitrogen, and chlorophyll *a* contents of the entire cell-matrix complex. The relatively low and constant C:N ratio of colonies (7.4) in the present study implies that most of the colony carbon is in the form of cells, or that organic nitrogen is also being deposited in the matrix, as suggested elsewhere for field populations (Verity et al. 1988a). Calculations imply that colonies with an overall C:N ratio of 7.4, in which cells (C:N = 6.6: Fig. 10) contribute < 50% of total colony carbon, should have an average C:N composition of the gelatinous matrix of < 9.0 (Fig. 16).

Comparison of photosynthetic performances of colonies and solitary cells may offer insights into their latitudinal distributional patterns. From the perspective of light utilization and the gross partitioning of photosynthate, low temperatures and irradiances favor colonies. Solitary cells are more efficient at utilizing light for photosynthesis, but they release a larger fraction of it as DOC than do colonies. In contrast, high temperatures and irradiances favor solitary cells, and colonies appear to be more stressed. This stress may be reflected in the relatively low carbon growth rates of colonies at 10–20°C (Fig. 2). In addition to excreting more cabon, the colonies may be respiring more, perhaps associated with the incipient stages of a life cycle transition from non-motile colony cells to motile swarmers. These general conclusions may, in part, explain why blooms of colonies apparently occur almost exclusively in colder waters, or at lower temperatures in tem-

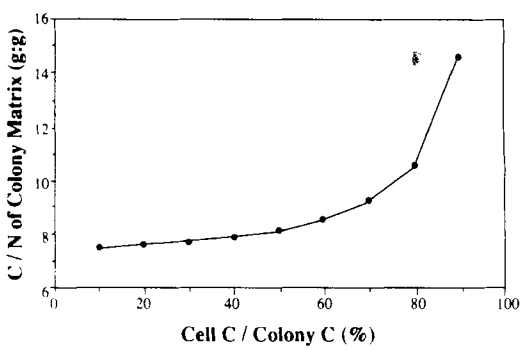

Fig. 16. The C:N ratios of colony gelatinous matrix required to produce an overall colony C:N ratio of 7.4 when cells within the colonies have a C:N ratio of 6.6. Colony matrix C:N ratios are plotted against the % contribution of cell carbon to total colony carbon.

perate regions. Similarly, solitary *Phaeocystis* cells are a ubiquitous component of tropical oceans, whereas colonies are rarely observed, and seldom in abundance.

A comparison of our data for *Phaeocystis* with data for cultures of large diatoms and *Phaeocystis*-dominated Barents Sea communities which contain diatoms (Table 2) reveals that all three differ significantly in terms of the Chl *a*:C ratio and photosynthetic parameters. The Barents Sea communities, not unexpectedly, exhibit properties somewhere between the two extremes: *Phaeocystis* colonies and shade-adapted large diatoms. Above all, large diatoms and *Phaeocystis* differ in that diatoms have a much higher Chl *a*:C ratio, which has been emphasized previously (see Sakshaug 1989 for review). On the other hand, P_m^B is 3–4 times higher for *Phaeocystis* than for large diatoms. A high Chl *a*:C ratio and a low P_m^B for the large diatoms, however, counteract each other such that the maximum carbon-normalized photosynthetic rate (P_m^C), which expresses the maximum hourly growth rate, becomes more similar for the three groups than individual Chl *a*:C ratio and P_m^B. The similarity between the three groups in terms of the maximum growth becomes even more evident when growth rate at optimum light (μ_{max}) is considered.

While the three groups of phytoplankton thus are not very different in terms of growth in strong light, the diatoms appear to be more efficient than *Phaeocystis* in low light. This can be inferred from the very high carbon-normalized photosynthetic efficiency α^c which again is due to the very high Chl *a*:C ratio. There is thus no support for the notion that *Phaeocystis* might dominate in cold

Table 2. Some properties of shade-adapted *Phaeocystis* (15–45 μmol m^{-2} s^{-1}) relative to other algae; 14 h day length. Chlorophyll-normalized (α^B, P_m^B) and carbon-normalized (α^C, P_m^C) photosynthetic parameters pertain to filtered samples. Values in brackets represent light-adapted cells.

	Temp	Solitary[1]	Colonies[1]	Large diatoms[2]		Barents Sea[3]	
Chl*a*:C	0°	0.014	0.008	0.048	[0.028]	0.031	[0.013]
	2°	0.013	0.011				
	5°	0.015	0.014				
α^B	0°	0.032	0.025	0.023	[0.025]	0.020	[0.026]
	2°	0.035	0.029				
	5°	0.040	0.031				
$\alpha^C(10^3)$	0°	0.45	0.20	1.1	[0.70]	0.62	[0.34]
	2°	0.46	0.32				
	5°	0.60	0.42				
P_m^B	0°	3.4	2.2	0.8	[1.7]	0.9	[1.6]
	2°	4.5	2.5				
	5°	5.5	3.1				
P_m^C	0°	0.048	0.018	0.038	[0.048]	0.028	[0.021]
	2°	0.059	0.028				
	5°	0.083	0.043				
I_k	0°	106	88	35	[68]	45	[62]
	2°	129	86				
	5°	138	100				
$\mu_m(d^{-1})$ (obs.)	0°	[0.28]	—	—	[0.33]	—	[0.29][4]
	2°	[0.44]	—				
	5°	[0.55]	—				

[1] This study

[2] *Thalassiosira nordenskioeldii* and *Chaetoceros furcellatus*; 25 and (brackets) 400 μmol m^{-2} s^{-1} (Sakshaug et al. 1991).

[3] *Phaeocystis*-dominated populations (viscous water) with diatoms, Barents Sea. Based on data from F. Rey presented in Sakshaug & Slagstad (1991 this volume); average for populations deeper than 70 m and (brackets) in the upper 20 m.

[4] Calculated as $P_m^C \cdot 14$

waters due to its particularly efficient utilization of low light. Rather, the frequent dominance of *Phaeocystis* in cold waters might be due to a high frequency of large initial stocks, or perhaps sedimentation and grazing rates may be particularly low for *Phaeocystis* during initial phases of blooms.

Inception of Phaeocystis blooms: a hypothesis

Temperature- or irradiance-dependent shifts in performance, however, do not explain the inception of colony blooms, for which two mechanisms are known. One, only recently documented (Verity et al. 1988b), is multiplication and enlargement of small colonies into larger ones, which then cleave into two daughter colonies of similar size and cell number. This process, however, is augmented by or secondary in importance to the formation of new colonies from single cells (Kormann 1955; Kayser 1970; Parke et al. 1971). Since the latter transformation occurs in nature at temperature and light conditions under which either morphotype can be maintained in culture, it is likely that additional factors are implicated.

Numerous environmental factors have been invoked as bloom triggers, including temperature (Jones & Haq 1963); decreased concentrations of silicate and phosphate (Jones & Spencer 1970; Gieskes & Kraay 1975; van Bennekom et al. 1975); trace metals (Morris 1971; Davidson & Marchant 1987); and edaphic effects (Jones & Haq 1963). Conclusive evidence in support of these hypotheses is lacking (Cadee & Hegeman 1986; Weisse et al. 1986). Nutrient concentrations per se do not appear to solely regulate dominance by or transitions among life cycle stages. For example, tropical waters, which tend to be oligotrophic, rarely show prodigious colony blooms, and chronic nutrient deprivation can also induce emigration of cells out of colonies, which suggests that low nutrient conditions favor solitary cells. However, colonies are inhibited and solitary cells are predominant when excess nutrients are added to cultures (see citations in Methods).

A key, consistent observation is that *Phaeocystis* colony blooms usually follow the spring diatom maximum, implying that perhaps chemical modification of seawater via biological conditioning or secretion of allelochemic substances (Smayda 1980) is a prerequisite for colony formation. In this regard, there is the provocative suggestion that some species of the diatom genus *Chaetoceros* produce a chemical compound which initiates the change from the motile to non-motile stage (Boalch 1984). Free-living *Phaeocystis* cells can attach to surfaces by means of their flagella (not haptonema) (Kornmann 1955; Parke et al. 1971), and 8-cell colonies are found attached to chain-forming diatoms, frequently *Chaetoceros* (Smayda & Verity unpubl. data).

We propose that *Phaeocystis* blooms develop through a two-step process requiring the sequential involvement of both stages in the life cycle. Solitary cells increase in abundance due to their rapid growth rates and small size which prevents efficient retention by suspension-feeding metazoan herbivores (Verity & Smayda 1989). Colonies develop from these cells, perhaps facilitated by the presence of diatoms, and in this stage *Phaeocystis* blooms accumulate gradually from slow-growing populations subjected to minimal population losses to predation. Thus, by altering its growth rates, chemical composition, size, and palatability to herbivores, *Phaeocystis* incorporates a suite of responses to physical, chemical, and biological stimuli representative of those of the entire phytoplankton community. The challenge for future studies is to resolve details of the induction and regulation of these processes in the context of the life cycle of *Phaeocystis*.

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