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*Phaeocystis: A Global Enigma*

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*Phaeocystis*, nutrients, iron, irradiance, bloom, carbon export, ocean acidification, grazing, genetic plasticity

**Abstract**

The genus *Phaeocystis* is globally distributed, with blooms commonly occurring on continental shelves. This unusual phytoplankter has two major morphologies: solitary cells and cells embedded in a gelatinous matrix. Only colonies form blooms. Their large size (commonly 2 mm but up to 3 cm) and mucilaginous envelope allow the colonies to escape predation, but data are inconsistent as to whether colonies are grazed. Cultured *Phaeocystis* can also inhibit the growth of co-occurring phytoplankton or the feeding of potential grazers. Colonies and solitary cells use nitrate as a nitrogen source, although solitary cells can also grow on ammonium. *Phaeocystis* colonies might be a major contributor to carbon flux to depth, but in most cases, colonies are rapidly remineralized in the upper 300 m. The occurrence of large *Phaeocystis* blooms is often associated with environments with low and highly variable light and high nitrate levels, with *Phaeocystis antarctica* blooms being linked additionally to high iron availability. Emerging results indicate that different clones of *Phaeocystis* have substantial genetic plasticity, which may explain its appearance in a variety of environments. Given the evidence of *Phaeocystis* appearing in new systems, this trend will likely continue in the near future.

## INTRODUCTION

Phytoplankton assemblages are extremely diverse, with large variations in size, shape, composition, environmental responses, and ecological roles. Some species can become major contributors to biomass at selected times and locations, forming blooms that are characterized by reduced diversity and large accumulation of biomass. Phytoplankton blooms can have inordinate impacts (both positive or negative) on local and regional food webs and greatly influence biogeochemical cycles. One genus that forms large blooms throughout the ocean is the haptophyte *Phaeocystis*. Its cosmopolitan distribution and potentially significant impacts on the environment require an assessment of the general characteristics of the genus, its role in marine systems, and its potential impacts in a climate-changed ocean (Lancelot et al. 1998, Schoemann et al. 2005), especially in view of the data acquired in the past two decades. *Phaeocystis* forms harmful algal blooms and accumulates at large biomass levels, which can lead to oxygen depletion at depth and mortality within the benthos (Cadée 1996, Doan et al. 2010). It also has hemolytic activity (van Rijssel et al. 2007), but no direct negative human impacts have yet been observed. *Phaeocystis* is an enigmatic species because it has multiple morphotypes and occurs from polar to tropical regions, and its colonial stage creates massive accumulations and immense surface foams in some locations (see the sidebar titled A Killer Phytoplankter along with **Figure 1**). However, there are many unknowns with respect to its ecophysiology, and in this review we explore the expanding data base on the genus and assess its role in ocean processes, particularly considering recent results.

### A KILLER PHYTOPLANKTER

*Phaeocystis globosa* and *Phaeocystis pouchetii* are often considered to be harmful algal bloom species, as they form dense accumulations of organic matter that can settle to the benthos and deplete oxygen, causing substantial deaths of benthic organisms and fish. They also form extensive quantities of surface foams (see **Figure 1**). In 2020, such foams were observed off the coast of the Netherlands, and three surfers—all experienced surfers and swimmers—presumably drowned after becoming lost within the coastal foam. Other plankton can kill humans directly via toxic reactions after ingestion of food contaminated with harmful species (e.g., ciguatera), and now *Phaeocystis* blooms have been implicated in fatal human activities.



**Figure 1**

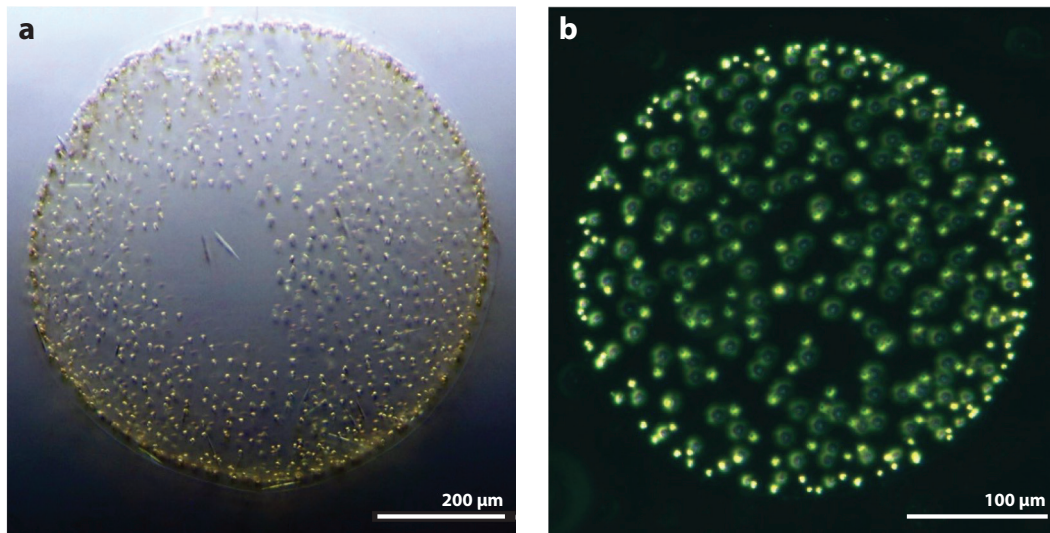
Foam produced by *Phaeocystis* in Yamba, Australia, August 2007. Photo copyright 2007 Icon Images.

At least three paradigms that involve *Phaeocystis* are present in the literature: (a) *Phaeocystis* releases substantial amounts of dimethylsulfoniopropionate (DMSP), which is oxidized in situ to dimethylsulfide (DMS) and thus plays a major role in the marine sulfur cycle; (b) *Phaeocystis* colonies are often ungrazed as a result of the colonial size and envelope composition; and (c) in situ assemblages of *Phaeocystis* have elevated C:N:P ratios and thus alter the elemental flux ratios to depth. However, the ubiquity of these paradigms in all environments, to all blooms, and to all species of the genus remains unclear.

## PHAEOCYSTIS LIFE HISTORY AND DISTRIBUTION

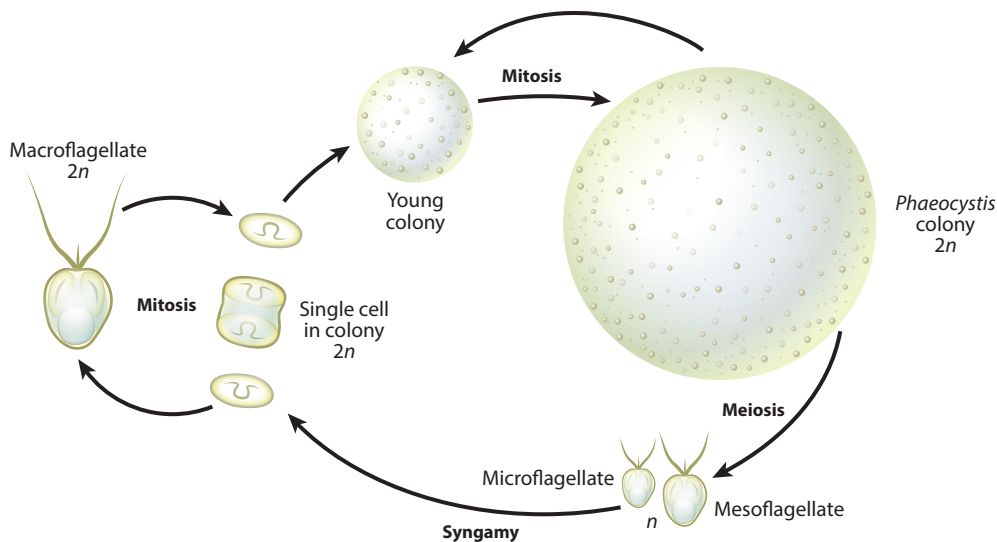
*Phaeocystis* has a complex, polymorphic life history with two prominent forms: small, biflagellated, solitary cells (approximately 5–10  $\mu\text{m}$  in size) and large colonies comprising hundreds of thousands of cells embedded in a gelatinous, mucopolysaccharide matrix, which has been described as a “thin, but tough skin” (Hamm et al. 1999, p. 101). Colonies are typically 100–200  $\mu\text{m}$  in diameter and are spherical in shape during active growth but can reach up to 3 cm in certain environments (Figure 2). Sexual reproduction occurs (Figure 3), although the frequency and importance of this process are unclear. A progression of various phases within the colonial stage have been observed. For example, relatively transparent colonies become translucent in the late stages of a bloom, suggesting that this might be an optical measure indicating the release of cells from the envelope, the development of flagellated solitary cells, and the formation of “ghost colonies” (Smith et al. 2017, p. 97; D.J. McGillicuddy Jr., H.M. Sosik, E.B. Olson & E.E. Peacock, unpublished information). Additional aspects of the life cycle have been debated (Gäbler-Schwarz et al. 2010), but the ecological and biogeochemical impacts of the two major forms remain clear—that is, solitary cells are members of the flagellated nanoplankton, while colonial forms are large net plankton.

Six described species of *Phaeocystis* have been distinguished using both microscopic and genetic analyses (Schoemann et al. 2005). Four of those species form colonies, and three have a



**Figure 2**

Micrographs of *Phaeocystis globosa* colonies (a) observed off the coast of France (provided by J. Toullec, Ghent University) and (b) from a culture (provided by P. Countway).

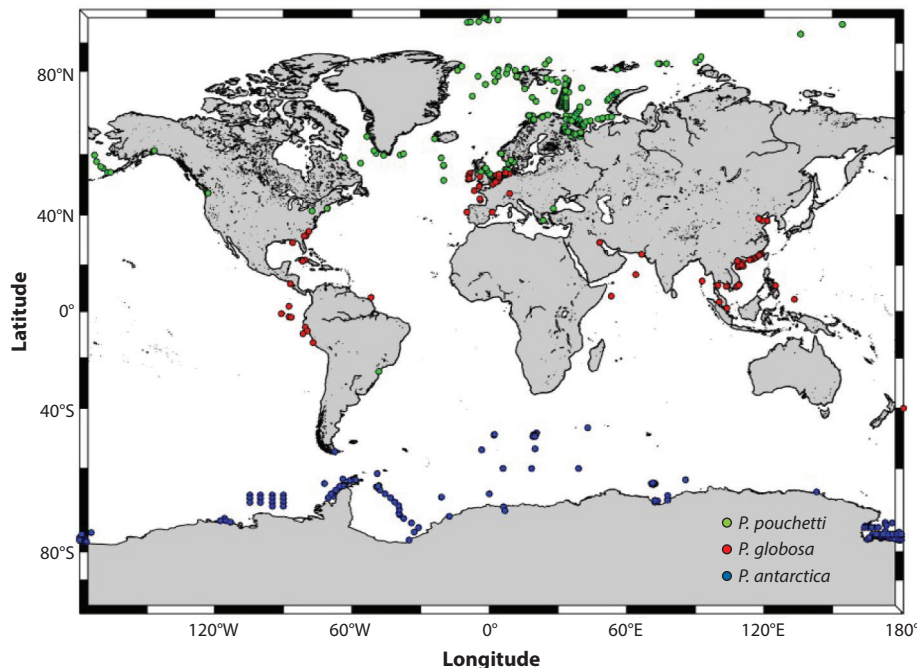


**Figure 3**

Schematic life cycle of *Phaeocystis* along with the number of chromosomes ( $n$ ) at each stage. Figure adapted with permission from Eikrem et al. (2016).

global distribution and form substantial blooms. The three bloom-forming species, *P. globosa*, *P. pouchetii*, and *P. antarctica*, occur largely in coastal waters, although blooms in deeper waters have been observed (Figure 4). *P. globosa* frequently blooms in temperate and tropical waters, whereas *P. pouchetii* occurs in temperate and polar waters, while blooms of *P. antarctica* are found mainly in the Southern Ocean (Figure 4). In this review, we focus on these bloom-forming species to synthesize and extrapolate what is known about the genus and its impacts.

The factors influencing colony formation have been intensively investigated, given the importance of colonial blooms, but no clear consensus has emerged from laboratory or field efforts. Veldhuis & Admiraal (1987) reported that phosphate controlled the formation of colonies from solitary cells, but more recent work has emphasized the role of nitrogen. Controlled culture studies have suggested that chemical cues released upon grazing by microzooplankton on solitary cells invoked a response in other cells to form colonies (which then became unavailable to smaller ciliates as prey) (Jakobsen & Tang 2002, Long et al. 2007), but an in situ investigation of allelopathic effects is unavailable. In a comprehensive metaproteomic investigation of *P. globosa* in Chinese coastal waters, the synthesis of glycosaminoglycans, a major component of the envelope, was greatly enhanced at the onset of colony formation; furthermore, temperature acted as an environmental cue to induce colony formation (Zhang et al. 2021, Cheng et al. 2023). In contrast, Mathot et al. (2000) found that *P. antarctica* in the Ross Sea first appeared as solitary cells during early spring but immediately shifted to colonial growth (although some solitary cells always remained in the water column). Bender et al. (2017) found that elevated iron concentrations ( $>0.14$  nM, a concentration that is always exceeded in austral spring) appeared to trigger a shift from solitary to colonial development in *P. antarctica* cultures. They also found extensive proteomic and transcriptomic differences between solitary and colonial forms, with iron playing a central role in the partitioning of cellular components. For example, lectins, fibrillins, and glycoproteins were found in one strain's colonial form, and actin and tubulin (components of flagella) were observed



**Figure 4**

Map depicting the distributions of *Phaeocystis* species derived from published and anecdotal reports. Green, red, and blue dots indicate locations where significant concentrations of *P. pouchetti*, *P. globosa*, and *P. antarctica* have been observed, respectively. Figure kindly provided by R. Meng.

in solitary cells, as were calcium-binding proteins. Their analysis of a Ross Sea bloom indicated the simultaneous presence of both forms, as did that of Smith et al. (2003a). The variety of potential colony-forming signals in different areas of the ocean suggests that the responses may be species dependent and/or that individual species are flexible in their responses to the environment.

## METHODOLOGICAL ISSUES

Because of its colonial nature, concerns have been expressed about the potential damage to colonies during sample processing and preservation. Kiene & Slezak (2006) found that vacuum filtration released substantial amounts of DMSP from *Phaeocystis* colonies and urged the use of gravity filtrations for studies of sulfur cycling. Similarly, another study found that dissolved organic carbon was enhanced in *Phaeocystis* blooms when filtering volumes larger than 100 mL under vacuum (C.A. Carlson, D.A. Hansell & W.O. Smith Jr., unpublished information). Despite these reservations, most studies have used gentle vacuum filtration (<1/3 atm) to assess the biological and chemical characteristics of *Phaeocystis*. Similarly, samples preserved (often with acid Lugol's solution) for microscopic enumeration can degrade colonies unless samples are counted soon after collection (unlike diatoms; Wassmann et al. 2005). Extreme care needs to be taken in handling and processing of cultures and samples with substantial concentrations of *Phaeocystis*. Molecular tools such as next-generation amplicon sequencing can detect the relative contribution of small-sized *Phaeocystis* forms in field samples but can also be disadvantageous because PCR biases and variable gene copy numbers can lead to inaccurate estimates (Wolf et al. 2016).

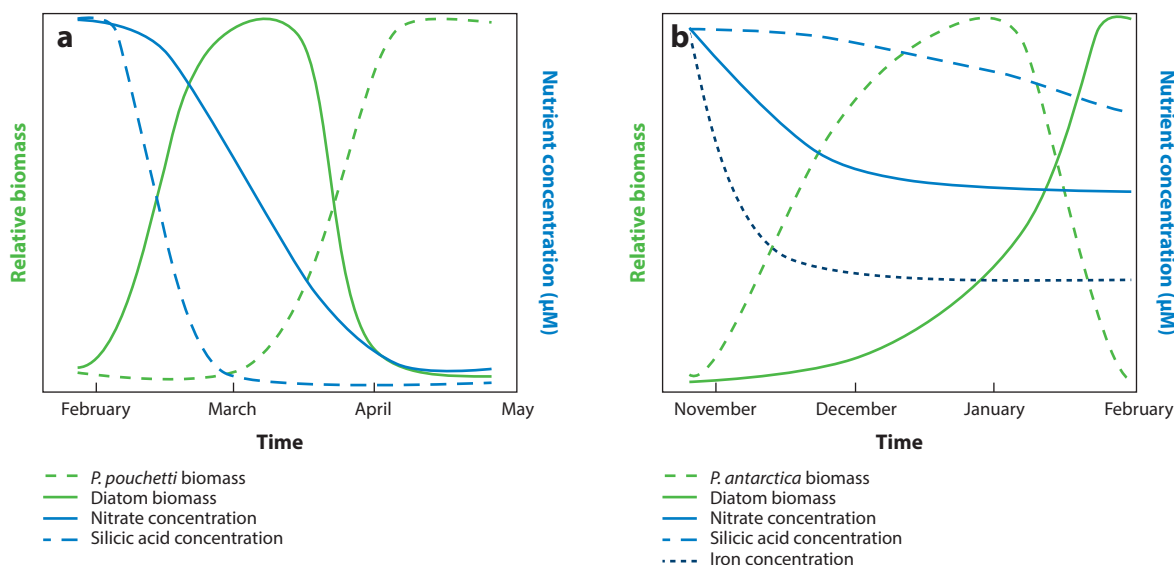


## DIFFERENCES AMONG THE THREE MAJOR SPECIES OF PHAEOCYSTIS

Many of the attributes of each of the three species have been studied in both field investigations and laboratory studies, which allows a comparison to illustrate mutual and dissimilar traits among the three.

### Nitrogen Utilization

Given that blooms of colonial *Phaeocystis* have been observed for decades (Gieskes et al. 2007) and have been found in regions of substantial riverine nutrient inputs, early investigations focused on the role of macronutrients in stimulating these blooms. Indeed, *P. pouchetii* and *P. globosa* have formed extreme blooms in the North Sea that were linked to anthropogenic eutrophication. Those blooms occurred after a diatom bloom in spring (**Figure 5a**); diatom growth reduction was attributed to silica limitation that then allowed haptophytes to grow under elevated nitrogen concentrations (Lancelot et al. 1998). The blooms resulted in not only large standing stocks of the alga but also extreme amounts of surface foam; these foams resulted from the partial degradation of colonial material and accumulation at the surface. In a pattern substantially different from that of the North Sea, *P. antarctica* blooms in the Ross Sea and Prydz Bay form prior to substantial diatom growth (Smith et al. 2000) (**Figure 5b**). Bloom formation of *P. antarctica* may depend primarily on iron availability (Bender et al. 2017, Rizkallah et al. 2020) and usually occurs in high-nitrate waters, as nitrate is rarely depleted in Antarctic waters.



**Figure 5**

Temporal progression of *Phaeocystis* and diatoms and the relative concentrations of nitrate, silicic acid, and iron in (a) the North Sea and (b) the Ross Sea. (a) Relative biomass of *Phaeocystis pouchetii* and diatoms (Lancelot et al. 1998) along with the approximate levels of nitrate (maximum concentration 30  $\mu\text{M}$ , minimum concentration 0.1  $\mu\text{M}$ ) and silicic acid (maximum concentration 15  $\mu\text{M}$ , minimum concentration 0.1  $\mu\text{M}$ ) (van der Zee & Chou 2005). The iron concentrations are unknown but are assumed to be well above saturation concentrations due to the shallow nature of the system. (b) Relative biomass of *Phaeocystis antarctica* and diatoms (Smith et al. 2014a) along with the approximate levels of nitrate (maximum concentration 30  $\mu\text{M}$ , minimum 16  $\mu\text{M}$ ) (Smith et al. 2003b), silicic acid (maximum concentration 80  $\mu\text{M}$ , minimum concentration 65  $\mu\text{M}$ ) (Smith et al. 2003b), and iron (maximum concentration 0.2 nM, minimum concentration 0.06 nM) (Sedwick et al. 2011).

Given the response to eutrophication—especially in the 1970s and 1980s, when anthropogenic nutrient loads were excessive due to riverine inputs into the North Sea—the impact of nutrients has been studied extensively (due to enhanced measures to restrict nutrient inputs, such inputs are no longer observed). In general, large phytoplankton (e.g., diatoms) tend to use nitrate, while small forms (cyanobacteria and flagellates) use ammonium (Probyn & Painting 1985). Given the two morphotypes of *Phaeocystis* (colonial versus solitary) and their size differences, it was initially unclear which nitrogenous form (oxidized or reduced) colonies and solitary cells would use. Since that time, colonial *P. antarctica* has been shown to utilize nitrate (Cochlan & Bronk 2001, Arrigo et al. 2002), and large *P. pouchetii* blooms have been shown to be associated with significant removal of nitrate in the North Sea (Tungaraza et al. 2003) and in mesocosms (colonies removed approximately 15  $\mu\text{mol}$  of nitrate over the course of a 10-day bloom; Sanderson et al. 2008). Blooms of *P. pouchetii* in the Fram Strait and Mid-Atlantic Bight also removed nitrate (Smith et al. 1991, 2021). *P. globosa* was associated with reductions of nitrate during summer upwelling (Doan et al. 2010).

Wang et al. (2011) studied three strains of *P. globosa* in culture and found that nitrate was favored among the solitary cells of all three strains and also supported active growth of colonies, a finding confirmed by Lv et al. (2019). Growth on ammonium or urea supported colonial growth but at slower rates than with nitrate (Wang et al. 2011). Solitary cells also used both nitrate and ammonium, but again, growth rates using ammonium were less than those with nitrate. Field observations have also suggested that nitrate supports *P. globosa* colonial growth (Veldhuis et al. 2005, Long et al. 2007). In summary, all studies of nitrogenous nutrition suggest that the growth of all *Phaeocystis* species and forms is supported by nitrate, with ammonium being utilized but less efficiently. The use of nitrate by smaller cells is unusual, but not without exception, as small cells ( $<5 \mu\text{m}$ ) removed nitrate in the North Pacific (Meyer et al. 2022a). Wassmann et al. (2005) found that large accumulations of solitary cell biomass can occasionally exceed those of colonies in the northeastern Atlantic, and while they did not study nitrogen assimilation, the timing of their cruise suggested that nitrate was supporting solitary cell growth. Nearly all *Phaeocystis* bloom studies in situ have been dominated by colonies when oceanographic conditions resulted in elevated nitrate concentrations (**Figure 3**).

## The Influence of Irradiance

*Phaeocystis* is often observed in spring and in turbulent environments (e.g., the Southern Ocean and North Atlantic). Studies have suggested that its photophysiological adaptations provided mechanisms by which it was able to grow in low-light environments (e.g., Lancelot et al. 1998). Field investigations indicate that *Phaeocystis* can occur under a wide range of light intensities, even in disphotic waters, suggesting its extraordinary ability to cope well with low and highly variable irradiance (Cota et al. 1994). Moisan & Mitchell (1998) found that cultured *P. antarctica* exhibited extreme pigment packaging per cell and had a 30-fold variation in quantum yield, which suggests that these features may allow *P. antarctica* to initiate blooms at the beginning of spring when in situ irradiance levels are low ( $<1\%$  of the incident surface irradiance). Large *P. pouchetii* and *P. antarctica* blooms were found under prevailing photon flux densities that were  $<1\%$  of the surface levels (Schofield et al. 2015, Assmy et al. 2017).

*P. antarctica* blooms regularly form in early spring in the Ross Sea, Antarctica (Smith et al. 2014b), and their distribution has been correlated with greater mixed-layer depths (and hence low irradiance levels; Arrigo et al. 1999, Smith et al. 2000, Smith & Jones 2015). Diatoms generally replace *P. antarctica* in early January, a period of strong water column stratification and low iron concentrations (**Figure 5b**). However, complete seasonal studies in the Ross Sea showed that increased mixed layers observed in late summer as a result of storms did not result in a switch

to haptophyte dominance from diatom assemblages. In accordance with this, short-term (hours) photosynthesis–irradiance responses were not significantly different between assemblages dominated by *P. antarctica* and diatoms (Smith & Donaldson 2015). Similarly, in an assessment of 449 stations in the Ross Sea, no difference was noted in the chlorophyll–mixed-layer relationship between stations dominated by *P. antarctica* or diatoms, suggesting that a simple relationship between mixing (and irradiance availability) and phytoplankton composition does not occur or is markedly influenced by other oceanographic conditions (such as iron concentrations). Mangoni et al. (2019) found that *P. antarctica* bloomed in stratified coastal waters in Terra Nova Bay during summer, indicating that this species can cope with a high-light environment. The authors hypothesized that the occurrence of *Phaeocystis* blooms (instead of diatoms) in summer was triggered by a wind-induced vertical mixing event, which may have introduced iron into the surface. They also speculated that only *P. antarctica* growth was promoted and that diatoms were colimited by iron and vitamin B<sub>12</sub>. The influence of colimitation of iron with another nutrient as a potential driver of phytoplankton succession of diatoms versus *P. antarctica* remains unresolved but needs resolution in future research, as there is growing evidence that colimitation with other nutrients (vitamin B<sub>12</sub> and manganese) can be critical to Southern Ocean phytoplankton dynamics (Bertrand et al. 2007; Balaguer et al. 2022, 2023).

In contrast to *P. antarctica* blooms, *P. globosa* blooms usually develop in the North Sea after the diatom bloom in late spring (Gieskes et al. 2007), when the ambient light levels are comparatively elevated (**Figure 5a**). *P. globosa* appears to possess efficient photosynthetic machinery that allows it to cope well at high light intensities. *P. antarctica* uses fast xanthophyll cycling under high light as a photoprotective mechanism (Kropuenske et al. 2009), but the xanthophyll activity is exhibited only when it is exposed to irradiances higher than those that support maximum growth rates (Kropuenske et al. 2009, Trimborn et al. 2019). Similarly, under conditions of high irradiance (33% of surface irradiance), *P. antarctica* abundance and colony biomass significantly increased relative to diatoms in assemblages grown in elevated iron concentrations (Feng et al. 2010). Colonial *P. globosa* cells also have an elevated tolerance to high-light conditions. They produce mucus as an energy dissipation mechanism and store fixed carbon in the form of polysaccharides in the mucoid matrix (Riegman & von Boeckel 1996). Solitary *P. antarctica* cells also appear to have a high light tolerance (Trimborn et al. 2017b). The abundance of solitary cells relative to colonial cells as well as the number of colonies of *P. antarctica* in a natural Antarctic phytoplankton assemblage was similar when exposed to medium and high daily light intensities (Heiden et al. 2019). Furthermore, high iron concentrations, especially when in concert with high irradiance levels, also promoted *P. antarctica* colonial growth relative to diatoms (Feng et al. 2010).

## Elemental and Cellular Composition

Accessory pigments of phytoplankton are often used to separate different broad groups within a single assemblage and to assign each group's contribution to the total chlorophyll concentration (e.g., Hayward et al. 2023). The pigments 19'-hexanoyl-oxyfucoxanthin (19-hex), 19'-butanoyloxyfucoxanthin (19-but), and chlorophyll *c*<sub>3</sub> (Chl *c*<sub>3</sub>) are considered the major diagnostic pigments for *Phaeocystis* (DiTullio et al. 2003, Wang et al. 2022), although all species contain fucoxanthin and other light-harvesting pigments (van Leeuwe et al. 2014). Variations among the three diagnostic pigments within bloom-forming species are substantial, and variability even among a single species is common. For example, *P. antarctica* contains substantial concentrations of all three diagnostic pigments, but 19-hex:Chl *a* ratios can vary by close to two orders of magnitude in strains from different locations (Wang et al. 2022). Similarly, *P. globosa* blooms in coastal Chinese waters have 19-but and Chl *c*<sub>3</sub> but no 19-hex, but strains isolated from the region



**Table 1** Summary of constituent ratios found in studies of *Phaeocystis*

Species	C:Chl	C:N	Sample location/growth conditions	Reference
—	—	6.625	Entire ocean	Redfield 1958
<i>P. pouchetii</i>	38	7.0 ± 0.5	Mid-Atlantic Bight, spring; initial NO <sub>3</sub> <sup>-</sup> 12 μM	Marra et al. 1994
	57–85	6.6	Culture; high nitrate, irradiance <85 μmol photons m <sup>-2</sup> s <sup>-1</sup>	Verity et al. 1991
	222 ± 174	5.89 ± 1.69	North Atlantic, spring, in situ bloom; initial NO <sub>3</sub> <sup>-</sup> 12 μM	Smith et al. 1991
	—	6.42	Norwegian mesocosms, spring; initial NO <sub>3</sub> <sup>-</sup> 400 μM	Verity et al. 2007
	—	8.85	Norwegian mesocosms, spring; initial NO <sub>3</sub> <sup>-</sup> 4 μM	Verity et al. 2007
	64 ± 32	—	Mid-Atlantic Bight, spring; NO <sub>3</sub> <sup>-</sup> <2 μM	Smith et al. 2021
	35–50	6.6–7.1	Barents Sea, in situ bloom, spring; NO <sub>3</sub> <sup>-</sup> 3–5 μM	Wassmann et al. 1990
	61–70	~16	Barents Sea, in situ bloom, spring; NO <sub>3</sub> <sup>-</sup> <1 μM	Wassmann et al. 1990
<i>P. antarctica</i>	204 ± 110	5.4 ± 0.82	Ross Sea mesocosms, spring; high light, NO <sub>3</sub> <sup>-</sup> >2 μM	Smith et al. 1998
	289 ± 165	6.2 ± 1.3	Ross Sea mesocosms, spring; high light, NO <sub>3</sub> <sup>-</sup> <2 μM	Smith et al. 1998
	62–118	6.7–7.3	Ross Sea, spring; initial NO <sub>3</sub> <sup>-</sup> 30 μM	Alderkamp et al. 2019
	—	7.4	Ross Sea, derived from nutrient deficits; initial NO <sub>3</sub> <sup>-</sup> 30 μM	Arrigo et al. 2002
	76 ± 14	7.64 ± 0.54	Ross Sea; irradiance 4–19 μmol photons m <sup>-2</sup> s <sup>-1</sup> , high iron	Feng et al. 2010
	269 ± 42	7.10 ± 0.31	Ross Sea; irradiance 17–91 μmol photons m <sup>-2</sup> s <sup>-1</sup> , high iron	Feng et al. 2010
	30–100	—	Ross Sea, in situ bloom	Jones & Smith 2017
	42.7 ± 42.6	—	Ross Sea, in situ bloom	Kaufman et al. 2017
29.8–47.9	7.7 ± 1.8	Ross Sea, in situ bloom	Smith et al. 2017	
<i>P. antarctica</i> , <i>P. globosa</i>	—	6.2–8.3	Cultures; irradiance 113 μmol photons m <sup>-2</sup> s <sup>-1</sup> , T = 4°C and 18°C	Solomon et al. 2003

Abbreviations: C:Chl, ratio of particulate organic carbon to chlorophyll; C:N, ratio of particulate organic carbon to particulate organic nitrogen; T, temperature; —, data not reported.

exhibit both 19-but and 19-hex (Wang et al. 2019). Strains of *P. pouchetii* also have both 19-but and 19-hex but exhibit substantial variations in their ratios to Chl *a* and each other (Zapata et al. 2004). Pigments are influenced by environmental conditions such as nutrients and light, but the variations among species and within a single species even under the same growth conditions are extreme, suggesting a broad molecular diversity within the *Phaeocystis* group.

The cellular carbon content of *P. globosa* and *P. antarctica* colonies was higher than that of single cells during blooms (Solomon et al. 2003). As colonies have a mucopolysaccharide envelope, it has been thought that the C:N ratios of assemblages dominated by colonies would be significantly elevated (e.g., Wassmann et al. 1990), although Solomon et al. (2003) suggested that the presence of amino sugars reduces this effect. Data from a variety of studies indicate that the C:N ratio is not greatly different from the Redfield ratio (Redfield 1958) (Table 1). Marra et al. (1994) found the C:N ratio in an Atlantic *P. pouchetii* bloom to be 7.0 ± 0.5, similar to those in cultures (Verity et al. 1991) and only slightly more than the ratio reported by Smith et al. (1991). They concluded that “the colonial form has a C:N ratio not significantly different from the canonical Redfield ratio, despite the gelatinous matrix of the colony” (Marra et al. 1994, p. 6638). Verity et al. (2007) found an average C:N ratio of 6.42 (although unamended mesocosm colonies had ratios of 8.85, which likely were influenced by nitrogen limitation). *P. antarctica* C:N ratios have also been found to be close to the Redfield stoichiometry. Smith et al. (1998) found molar ratios between 5.97 and 7.53 for *P. antarctica* within mesocosms, and Alderkamp et al. (2019) observed C:N ratios between 6.7 and 7.3 under a variety of iron and light levels in an assemblage dominated by *P. antarctica*. The measured C:N ratios in the Ross Sea included in a broad survey by Smith & Kaufman (2018) also fell within this range.

Arrigo et al. (2002) estimated nutrient ratios in *P. antarctica* from nutrient reductions in the euphotic zone. They found that N:P ratios averaged 18.8, significantly higher than the canonical Redfield ratio of 16; C:P ratios averaged 139 (versus the Redfield ratio of 116). The resulting C:N ratio estimated from these means for haptophyte assemblages was 7.4, not dramatically different from that found in direct measurements (**Table 1**). Similar estimates for other species of *Phaeocystis* are unavailable. In summary, despite the widespread view of a carbon-rich envelope having an impact on C:N ratios, the data suggest that these ratios in actively growing colonies and solitary cells are not significantly different from the canonical Redfield ratio.

The ratio of particulate organic carbon (POC) to chlorophyll (C:Chl) is often used as a broad index of physiological status, and actively growing algae generally have ratios between 30 and 50 (weight:weight) (Geider et al. 1998). Given the potential for the mucoid envelope to increase the nonphotosynthetic portion of POC, as well as the potential for photophysiological responses (enhanced chlorophyll synthesis at low irradiances) to modify this ratio, understanding the in situ and culture estimates may provide insights into acclimations of *Phaeocystis* to environmental changes (**Table 1**). Marra et al. (1994) found C:Chl ratios in a natural *P. pouchetii* bloom to average 38 (under elevated nitrate concentrations), and in another *P. pouchetii* bloom they averaged 62.7 (under low and potentially limiting nitrate levels) (Smith et al. 2021). Wassmann et al. (1990) found ratios of 45.5 and 71.4 at the start and end of a bloom of *P. pouchetii*, respectively.

Estimates of the C:Chl ratio are far more common for *P. antarctica* (**Table 1**). Alderkamp et al. (2019) found in mesocosms in which irradiance and iron were controlled that C:Chl ratios ranged from 62 to 118, with the highest ratios observed at high irradiances and low iron concentrations. In similar experiments, Feng et al. (2010) found ratios averaging  $76.4 \pm 14.3$  and  $269 \pm 42$  in low- and high-light (7% and 33% of surface irradiance) conditions, respectively, and Smith et al. (1998) measured mean ratios to be  $204 \pm 58.6$  in deck incubations (although the starting ratio of the in situ population was 42.3). In situ estimates of C:Chl ratios in *P. antarctica* blooms have included 30–100 (Jones & Smith 2017),  $42.7 \pm 42.6$  (Kaufman et al. 2017), and 29.8 and 47.9 (Smith et al. 2017). All of these values are consistent with the idea that in situ assemblages exist in low light and exhibit normal C:Chl ratios, and that when populations are placed in high (surface) irradiances (and possibly reduced iron concentrations) for extended periods of time, they acclimate by markedly increasing their C:Chl ratios.

## CONTRIBUTION OF PHAEOCYSTIS TO VERTICAL FLUX

*Phaeocystis* blooms reach very high biomass levels (chlorophyll concentrations up to  $20 \mu\text{g L}^{-1}$ ), and because vertical flux is often quantitatively related to surface-ocean biomass and productivity, it has been suggested that *Phaeocystis* blooms may be responsible for large amounts of carbon exported out of the euphotic zone to depth (e.g., Wassmann et al. 1990, Smith et al. 1991). Nissen & Vogt (2021) modeled the export of POC from the euphotic zone and concluded that *P. antarctica* was responsible for approximately 40% of total export of POC to a depth of 100 m south of 60°S, a conclusion similar to that of Wang & Moore (2011). Exporting POC to 100 m is a relatively short-term removal in terms of carbon sequestration; to remove the carbon for centuries, it must get to approximately 1,000 m (or into the sediments). After reviewing the available data for flux taken simultaneously with surface measurements of biomass and sediment trap accumulations in the upper 150 m of the water column, Reigstad & Wassmann (2007) concluded that “the overall contribution of *Phaeocystis* spp. to vertical carbon export. . . is small” (p. 217) as a result of extensive remineralization of *Phaeocystis*-derived POC in the upper 100 m. Using glider estimates of POC changes through time and depth to produce a carbon budget of the southern Ross Sea, Meyer et al. (2022b) also found little POC flux or accumulation at depths greater than 150 m during a

*P. antarctica* bloom and concluded that a large majority of *Phaeocystis*-derived POC was remineralized at shallower depths, consistent with other data (e.g., Jones & Smith 2017, Smith et al. 2017). Furthermore, no significant export of *Phaeocystis* was detected in sediment traps at 100 and 300 m at 52°S in the South Atlantic (Wolf et al. 2016).

There are contrasting observations that suggest that *Phaeocystis* can be important for deep export (and carbon sequestration), but they may be related to specific physical mixing processes or related to the physiological state of the *Phaeocystis* bloom. For example, in the Ross Sea, *P. antarctica*-derived POC (DMSP) was found in sediments during the spring bloom, suggesting that the *Phaeocystis*-derived material was exported efficiently to depth and that a “significant fraction” (an undefined amount; DiTullio et al. 2000, p. 597) of this POC escaped remineralization in the upper 100 m (DiTullio et al. 2000). Jones & Smith (2017) also found increased *P. antarctica* POC at depth during extreme mixing events. Thus, the mixed-layer pump (Dall’Omo et al. 2016) could explain the episodic injection of *Phaeocystis* cells (approximately 12% of the surface numbers were found at 550 m) to depth (DiTullio et al. 2000), especially since the area analyzed was close to the Ross Ice Shelf, a site of extreme katabatic winds during spring. Similarly, based on coupled <sup>234</sup>Th-based estimates of the POC flux with incubation-based estimates of primary production, the highest export efficiency below 100 m was found in a *P. pouchetii* bloom among the measured stations in the Arctic Ocean (Le Moigne et al. 2015).

Other factors can also increase *Phaeocystis* carbon export flux. For example, Lalande et al. (2011) reported ice-associated *Phaeocystis* carbon export due to deep mesoscale vertical transport and subduction associated with cyclonic eddy activity. Mineral ballasting with cryogenic gypsum has been reported to increase export flux (Wollenburg et al. 2018). *Phaeocystis* colonies release transparent exopolymer particles that facilitate the aggregation of suspended particles and form sinking marine snow (Hong et al. 1998, Passow 2002). In association with diatoms, *Phaeocystis* aggregates containing transparent exopolymer particles can sink and facilitate carbon export to depth (Le Moigne et al. 2015). Thus, while *Phaeocystis* POC flux is largely remineralized at shallow depths (much shallower than diatom POC), there are circumstances where export flux to greater depths can be significant.

## PHAEOCYSTIS LOSS PROCESSES AND CHEMICAL INTERACTIONS

It has been thought that grazing by microzooplankton was a factor in driving solitary cells to form colonies (e.g., Jakobsen & Tang 2002) and that grazing rates on colonies decreased due to either a size mismatch between prey and some (but not all) predators or palatability/handling issues imposed by colonies that precluded its consumption (Tang 2003, Nejstgaard et al. 2007, Ryderheim et al. 2022). However, results from multiple grazing experiments in a variety of oceanographic settings and controlled experiments are contradictory, and it is difficult to demonstrate a clear relationship between *Phaeocystis* and its potential grazers (Table 2).

Stable isotope and chemical analyses reveal that organic matter produced by *Phaeocystis* enters the food web (Falk-Petersen et al. 2009); however, a mechanistic understanding remains unresolved. Numerous examples of colonial *Phaeocystis* being ingested by various grazers have been reported (Nejstgaard et al. 2007, Saiz et al. 2013, Ray et al. 2016). Large copepods (mainly *Calanus* spp.), dinoflagellates, ciliates, tintinnids, and euphausiids have been reported to graze on *Phaeocystis* (Haberman et al. 2002, Saiz et al. 2013, Ryderheim et al. 2022), but other studies have reported reduced feeding and abundance within blooms (e.g., Estep et al. 1990, Long et al. 2007). An investigation using molecular tags of *P. pouchetii* found that they appeared in the guts of *Calanus* copepods, but the contribution to ingestion decreased as the abundance of the haptophyte increased (Ray et al. 2016). *Calanus* actively grazed colonial *P. pouchetii*, but its feeding rate was low (Saiz et al. 2013).

**Table 2** Selected literature that describes the biological impact of interactions within *Phaeocystis* assemblages

Species investigated	Effect	Grazing on solitary cells	Grazing on colonies	No grazing	Reference
<i>P. pouchetii</i>	Copepods actively ingested solitary cells and colonies in situ	X	X		Saiz et al. 2013
<i>P. pouchetii</i>	<i>Calanus finmarchicus</i> grazed on single cells and colonies	X	X		Tände & Båmstedt 1987
<i>P. pouchetii</i>	<i>Calanus glacialis</i> grazed on single cells and colonies	X	X		Estep et al. 1990
<i>P. pouchetii</i>	<i>Acartia longiremis</i> grazed on single cells and colonies <100 µm in size	X	X		Hansen et al. 1994
<i>P. globosa</i>	<i>Acartia tonsa</i> grazed on single cells and colonies	X	X		Tang et al. 2001
<i>P. globosa</i>	<i>Balanus crenatus</i> grazed on single cells and colonies	X	X		Hansen 1995
<i>P. antarctica</i>	<i>Euphausia superba</i> grazed on single cells and colonies <500 µm in size	X	X		Haberman et al. 2002
<i>P. globosa</i>	Dinoflagellates grazed on single cells	X			Nejstgaard et al. 2007
<i>P. antarctica</i>	Dinoflagellates grazed on single cells	X			Shields & Smith 2008
<i>P. pouchetii</i>	<i>Gadus morhua</i> larvae grazed on colonies		X		Krogstad 1989
<i>P. pouchetii</i>	<i>Calanus</i> ingested colonies		X		Ray et al. 2016
<i>P. antarctica</i>	<i>Metridia gerlachei</i> grazed on colonies 0.05–1.55 mm in diameter		X		Schnack 1983
<i>P. antarctica</i>	Microzooplankton grazed on colonies in natural bloom		X		Landry et al. 2002
<i>P. globosa</i>	Selection for diatoms versus single cells by microzooplankton			X	Nejstgaard et al. 2007
<i>P. globosa</i>	No haptophyte feeding by <i>Mesodinium</i> when dinoflagellate available as food			X	Tang et al. 2001
<i>P. globosa</i>	No feeding by ciliates in high concentrations of <i>Phaeocystis</i> cultures			X	Tang et al. 2001
<i>P. antarctica</i>	No grazing by microzooplankton on colonies in natural bloom			X	Caron et al. 2000
<i>P. pouchetii</i>	Reduced feeding by <i>Calanus</i> and <i>Metridia</i> in cultures	?	?	?	Estep et al. 1990
<i>P. globosa</i>	Copepod grazing efficiency decreased with increasing colony size	?	?	?	Ryderheim et al. 2022

Other reports have suggested that the impact of colonial forms of *P. pouchetii* on grazing may be a result of complex ecological interactions that influence the transition of *P. pouchetii* between solitary cells or colonies. For example, the presence of colonies may increase the grazing pressure on other algal species and microzooplankton, which in turn influence the abundance of solitary cells of *P. pouchetii* (Long et al. 2007). Chemical cues produced by *Acartia tonsa* copepods grazing on solitary *P. globosa* cells in culture inhibited colony formation by *P. globosa*, whereas chemical cues from the grazing ciliate *Euplotes* sp. enhanced colony formation (Long et al. 2007). In the presence of phagocytotic dinoflagellates (those that ingest smaller cells), *P. globosa* colonies significantly increase their size (Jakobsen & Tang 2002). Despite the many contradictory reports and the absence of clearly accepted (and defined) methods to estimate grazing, it appears that copepods

such as *Calanus*, *A. tonsa*, and *Temora longicornis* actively ingest colonial *Phaeocystis* (Saiz et al. 2013, Ryderheim et al. 2022). However, in situations when alternate prey such as ciliates or dinoflagellates are available, copepods preferentially remove the alternate prey first (Tang et al. 2001). Small copepods (e.g., *Oithona*) and copepodites, often found to be the major group responsible for phytoplankton mortality, do not efficiently graze on *Phaeocystis* colonies (Ryderheim et al. 2022). However, small copepods, ciliates, and other microzooplankton can be the primary consumers of solitary *Phaeocystis* cells (Tang et al. 2001, Long et al. 2007). A complete assessment of grazing on *Phaeocystis* using molecular techniques is needed within blooms of all three species.

Viruses are known to infect solitary *Phaeocystis* cells (Brussaard et al. 2004), but the colonial envelope may offer protection from infection (Jacobsen et al. 2007). It has been suggested that the formation of colonies from single cells may be a mechanism to avoid both zooplankton grazing (by increasing size) and viral infection (through protection by embedding cells in the matrix). The envelope may serve as an antiviral defense either from chemical release or by creating a simple mechanical barrier. The production of transparent exopolymer particles, produced during colony disintegration as well as photosynthesis, creates a sticky surface to which viruses adhere, thus reducing free viral numbers and subsequent encounter rates (Brussaard et al. 2007).

The release of chemicals by phytoplankton can alter seawater chemistry and thereby influence phytoplankton interactions and competition for resources. For instance, *P. antarctica* produces humic acid-like substances (Koch et al. 2019) that are important in binding iron and other trace metals (Schoemann et al. 2001, Hassler et al. 2012). The presence of these substances can stimulate phytoplankton growth by enhancing iron solubility and/or accelerating iron uptake (Schoemann et al. 2001, Hassler et al. 2012). Fieldwork has demonstrated that the highest iron uptake capacities are related to enhanced *P. antarctica* abundances in the field (Trimborn et al. 2015). However, the exact underlying mechanisms of iron-*Phaeocystis* interactions and the subsequent bloom dynamics remain uncertain and require further investigation.

Chemical deterrence by *Phaeocystis* represents a way to reduce grazing pressure as well as to minimize the physiological fitness competitor species via allelopathy. *Phaeocystis* produces DMSP and its cleavage products DMS and acrylate (Stefels & van Boekel 1993). Relative to solitary cells, colonial *P. globosa* cells actively upregulate the gene expression of acrylate production (Mars Brisbin & Mitarai 2019). Accumulation of acrylate within colonies can serve to deter grazers and heterotrophic bacteria (Noordkamp et al. 2000). Colonial *P. globosa* cells also upregulate different pathogen interaction pathways compared with solitary cells (Mars Brisbin & Mitarai 2019). Colonial *P. globosa* cells have a larger number of downregulated differentially expressed genes (7,234 out of 7,769 genes), which may balance the energetic cost of the increased defensive role associated with colony formation (Wang et al. 2015). The release of polyunsaturated aldehydes during a *P. pouchetii* bloom suppressed the growth of other phytoplankton species (Hansen & Eilertsen 2007), although this phenomenon was not observed in an early stage of the bloom. Allelopathic effects of *P. globosa* also reduce the growth of co-occurring phytoplankton (Sampaio et al. 2017) or the feeding of potential microzooplankton (Tang et al. 2001, Nejstgaard et al. 2007).

## PHAEOCYSTIS AND THE SULFUR CYCLE

The CLAW hypothesis (Charlson et al. 1987; the CLAW abbreviation comes from the authors' surnames) states that some phytoplankton species respond to climate forcing by producing DMS that increases cloud condensation nuclei (CCN) in the atmosphere, thus increasing cloud cover. The DMS feedback that increases albedo acts to stabilize the temperature of the Earth's atmosphere. The phytoplankton considered to be most responsible for this climate feedback are haptophytes—specifically, coccolithophorids and *Phaeocystis*. *Phaeocystis* can produce large amounts



of DMSP (Stefels & van Boekel 1993), which in turn is oxidized to DMS, a volatile gas that can enter the atmosphere (Liss et al. 1994, DiTullio et al. 2003, Kameyama et al. 2020). The CLAW hypothesis states that the reduction in solar irradiance associated with CCN production then reduces phytoplankton and DMSP production. While some data support the spatial relationship between DMS concentrations and CCN distribution, other data do not (Green & Hatton 2020). It is also noteworthy that Woodhouse et al. (2010) found a low sensitivity of CCN density to changes in the air–sea flux of DMS. Furthermore, they concluded that future marine DMS changes would result in an insignificant increase in CCN.

An additional complication to the CLAW hypothesis is whether all *Phaeocystis* blooms generate large DMS fluxes. It appears that *P. antarctica* and *P. pouchetii* consistently generate substantial concentrations of DMSP and DMS in waters where they attain high biomass (DiTullio & Smith 1996). The genes encoding proteins for DMSP biosynthesis and cleavage have been identified in *P. antarctica* (Alcolombri et al. 2015) and *P. globosa* (Mars Brisbin & Mitarai 2019). One *P. globosa* culture was found to have the enzymes for DMSP production, and some blooms of the species have been reported to generate significant DMSP concentrations (Mohapatra et al. 2013). However, some blooms of this species do not seem to produce DMS to the extent that blooms of other *Phaeocystis* species do (X. Wang, personal communication; W.O. Smith Jr., unpublished information), despite reaching substantial biomass levels. However, direct determinations of DMS from these blooms is lacking. In Antarctic coastal waters, Vance et al. (2013) detected elevated DMSP concentrations associated with high *P. antarctica* abundances over a period of days and hypothesized that they were an antioxidant response against solar radiation stress. They further hypothesized that the produced DMSP was rapidly converted and oxidized into compounds other than DMS, as DMS concentrations remained constantly low in their study. Rapid DMSP production and removal processes associated with *Phaeocystis* blooms could potentially explain the high variability in DMSP concentrations observed in high-chlorophyll waters. While a positive relationship among *Phaeocystis*, cloud formation, and the sulfur cycle may occur during some seasons and locations, it appears that the CLAW hypothesis is an oversimplification of the complex ocean–atmosphere interactions that naturally occur, and only part of that interaction involves DMS production via *Phaeocystis*. Further work on broader spatial and temporal scales is needed to completely resolve the uncertainties in this relationship.

## PHAEOCYSTIS AND THE FUTURE

*Phaeocystis* colonies have been observed in waters of the North Atlantic and North Sea since the 1920s (Gieskes et al. 2007). Long-term monitoring of *Phaeocystis* over six decades in the North Sea suggests a trend in which *Phaeocystis* blooms develop earlier in the year; whether earlier bloom events are due to climate-induced warming is not yet clear, but these blooms do not appear to be linked solely to nutrient inputs (Gieskes et al. 2007). Model simulations indicate that reduced nitrogen loads from riverine sources to the North Sea should decrease the occurrence and magnitude of *Phaeocystis* blooms, while lowered phosphate inputs negatively affect primarily diatoms (Gypens et al. 2007).

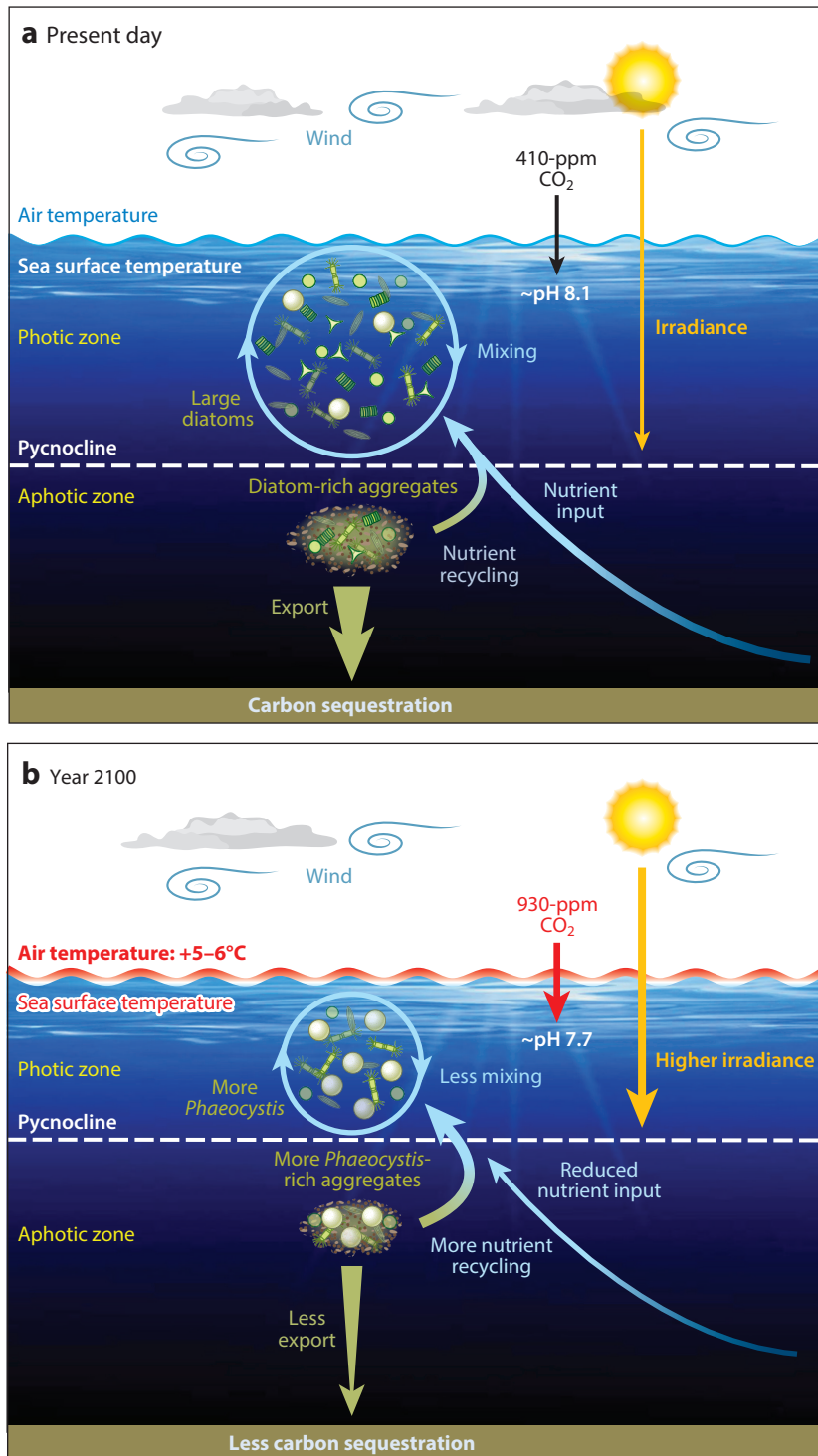
*P. pouchetii* has also been observed in New England waters for decades. Its appearance was considered to be a “novel appearance,” and it was established as a keystone species there in the 1970s (Smayda 1998, p. 566). Despite being prominent phytoplankton species in high-latitude systems, reports of *Phaeocystis* in environments where it has not previously been observed appear to be increasing. For example, *Phaeocystis* was first detected in the Arabian Sea in 1996 (Madhupratap et al. 1999) and has bloomed there frequently since that time (B. Queste, personal communication). *Phaeocystis* was first observed along the coast of Vietnam in 2002 (Tang et al. 2004), where it now

blooms every year in multiple locations. It was noted in southern Chinese waters in 1997 (Qi et al. 2004) and now forms prominent annual blooms in numerous Chinese locations (Song et al. 2020). Observations of *P. globosa* occurring in Thailand, Cambodia, Pakistan, Malaysia, and Myanmar coastal systems have been made as well. Whether the abrupt appearance of *Phaeocystis* in tropical waters is real or an artifact of previous poor sampling or detection remains unclear.

Climate models project that rising CO<sub>2</sub> emissions until the end of this century will result in a decrease in ocean pH by as much as 0.04 pH units and ocean warming of up to 5°C. The increase in upper-ocean stratification will result in lower nutrient delivery to the surface water and elevated surface irradiances [Bindoff et al. 2019, Representative Concentration Pathway 8.5 (RCP8.5) climate scenario] (**Figure 6**). Based on laboratory and field-based CO<sub>2</sub> manipulation experiments with either *P. globosa* isolates or *P. globosa*-dominated assemblages, growth of this species was stimulated by CO<sub>2</sub>-induced acidification (Wang et al. 2010, Keys et al. 2017, Taucher et al. 2018). Similarly, the only study on colonial *P. pouchetii*, which was a dominant species within an Arctic phytoplankton population, indicates that this species was tolerant to acidification, as it grew well even under a very low pH level of 7.4, which is far lower than the expected pH levels of approximately 7.7 until 2100 (Thoisen et al. 2015). Such a high pH tolerance seems to occur in all *Phaeocystis* species, as *P. antarctica* also grew well with acidification irrespective of its life stage (colonial versus solitary) (Feng et al. 2010; Trimborn et al. 2013, 2017a,b, 2019; Xu et al. 2014; Andrew et al. 2022). As *Phaeocystis* species usually thrive in coastal and sea-ice environments, phytoplankton cells are here frequently exposed to changes in pH and CO<sub>2</sub> on diurnal and seasonal scales as a result of photosynthetic activity. For instance, in spring, when sea ice begins to melt, elevated CO<sub>2</sub> seawater concentrations relative to atmospheric levels are common. In particular, the colonial form of *Phaeocystis* exhibits a greater ability to cope with variable CO<sub>2</sub> conditions such as those generated over the light–dark cycle (Flynn et al. 2012). The latter finding suggests a certain degree of plasticity within *Phaeocystis* species to thrive in elevated CO<sub>2</sub> levels, as projected for the end of this century. The tolerance of the genus *Phaeocystis* to ocean acidification is also noted when exposed to a broad range of light intensities, as it can tolerate both low (Wang et al. 2010, Keys et al. 2017, Trimborn et al. 2017b) and high irradiances (Feng et al. 2010, Trimborn et al. 2017b, Heiden et al. 2019, Pausch et al. 2022). In contrast to *Phaeocystis*, a number of diatom species are more susceptible to ocean acidification, especially in conjunction with high light levels that cause a decline in growth and/or carbon fixation rates (Gao & Campbell 2014, Heiden et al. 2019, Petrou et al. 2019). Due to the susceptibility of diatoms to ocean acidification together with high light levels (Gao & Campbell 2014, Heiden et al. 2019, Petrou et al. 2019), *Phaeocystis* may become increasingly important in more illuminated and acidified waters (**Figure 6**).

In addition to a lowered surface seawater pH and higher light availability by the end of this century, warming of surface waters will exert control on future distributions of *Phaeocystis*. In contrast to *P. globosa*, which can form blooms over a broad range of temperatures (4–32°C; Schoemann et al. 2005, Wang et al. 2010), the thermal tolerance of *P. antarctica* (–2–10°C) and *P. pouchetii* (0–14°C) is more restricted (Wang et al. 2010). Using remote sensing, Orkney et al. (2020) revealed that warming regions of the northern Fram Strait in the Arctic were associated with declines in diatoms and increases in *Phaeocystis*. In contrast, Ross Sea field surveys suggest that the temporal and spatial distributions of *P. antarctica* are negatively correlated with elevated temperatures (Liu & Smith 2012).

To resolve how the projected climatic changes (e.g., CO<sub>2</sub>, light, and temperature) may influence phytoplankton in the future, multiple-stressor incubation experiments can provide valuable insights, but only a few studies have examined all factors together. To date, the interactive effects of CO<sub>2</sub>, light, and temperature have been studied mainly for *P. antarctica* (Feng et al. 2010, Xu et al. 2014, Andrew et al. 2022) and not yet for *P. globosa* and *P. pouchetii*. In particular, prediction



(Caption appears on following page)

**Figure 6** (Figure appears on preceding page)

Schematic illustrating the biogeochemical impacts of *Phaeocystis* in (a) today's ocean and (b) a possible future climatic scenario as forecasted for the global ocean at the end of the twenty-first century (2100). (a) Under present-day climatic conditions, diatoms are considered to be the main contributors to carbon sequestration, with *Phaeocystis* being insignificant. (b) According to a current IPCC report [Bindoff et al. 2019, Representative Concentration Pathway 8.5 (RCP8.5) climate scenario], as a consequence of warming, the global ocean becomes more acidic and stratified, leading to reduced nutrient inputs from below and phytoplankton being trapped in warm, nutrient-poor, highly illuminated surface waters. Based on laboratory and field-based observations, these conditions could promote the growth of *Phaeocystis*. *Phaeocystis* aggregates are more prone to degradation, enhancing nutrient recycling and reducing carbon export and sequestration.

of the future occurrence of *P. antarctica* is even more complicated as its occurrence is linked to iron availability in addition to light and temperature. Laboratory multiple-stressor experiments (CO<sub>2</sub>, light, temperature, and iron) with *P. antarctica* indicate differential CO<sub>2</sub> effects, with high CO<sub>2</sub> becoming a stressor for this species when it was grown above its optimal temperature for growth (Xu et al. 2014, Andrew et al. 2022). Because these studies changed light and iron availability in addition to CO<sub>2</sub> and temperature, it is difficult to tease apart whether this response was due primarily to CO<sub>2</sub> and temperature or to all factors together. According to model predictions, the spatial and temporal occurrence of *P. antarctica* and diatoms in the Southern Ocean is controlled mainly by temperature and iron availability, with light also exerting control but more on a local scale (Nissen & Vogt 2021). In line with this, Kaufman et al. (2017) modeled the Ross Sea future conditions and suggested that due to the earlier disappearance of ice as a result of warming, a low-irradiance system will be created and extend the duration of *P. antarctica* blooms. Less and more sporadic ice cover, on the other hand, will increase deep vertical mixing as a result of more frequent storm events, conditions that should also promote the growth of *P. antarctica*. Recent publications on Southern Ocean phytoplankton further pinpoint that iron together with manganese or vitamin B<sub>12</sub> can be colimiting for Southern Ocean phytoplankton (Bertrand et al. 2007, Balaguer et al. 2022). These studies indicate that *P. antarctica* is different from diatoms in that it is not as susceptible to colimitation by iron and vitamin B<sub>12</sub> (Bertrand et al. 2007) or iron and manganese (Balaguer et al. 2022), as well as having the ability to cope with low manganese concentrations (Balaguer et al. 2023).

Due to the limited knowledge on the different *Phaeocystis* species, particularly *P. pouchetii*, and their response to the interactive effects of CO<sub>2</sub>, light, temperature, and nutrient availability, it is difficult to make realistic predictions of the future distribution, growth, and role of *Phaeocystis*. Understanding the occurrence and distribution of any species is challenging, and until global climate models include an accurate prediction of *Phaeocystis* blooms, it will be challenging to predict the regional and global changes of this genus.

## REMAINING UNCERTAINTIES AND FUTURE ISSUES

Despite the large amount of research that has been completed on *Phaeocystis*, our understanding of many of its features remains incomplete. Given its status as a harmful algal species, knowing how ongoing and future climate change will influence its distribution and abundance is paramount. But other unresolved questions remain.

### Potential for Mixotrophic or Heterotrophic Activity

It is now accepted that many phytoplankton, including other haptophytes, have the potential for mixotrophic activity (the use of reduced organic material for growth in addition to photosynthesis). Because *Phaeocystis* occurs in many environments that are not considered optimal for growth

(such as low irradiance), Koppelle et al. (2022) suggested that it might supplement its autotrophic growth via heterotrophic nutrition. They also found bacterial cells within individual *P. globosa* cells under low phosphate concentrations, suggesting that bacteria were ingested via phagocytosis to meet their phosphorus demand. However, a maximum of only 2% of all haptophyte cells contained bacteria, suggesting that prey consumption may not be a significant energy source for the entire population. The same study used a genomics-based model to predict phagocytosis in multiple *Phaeocystis* species, which suggested that *P. globosa* and *P. antarctica* have high phagocytosis probabilities. Rizkallah et al. (2020) detected the occurrence of genes that potentially code for mixotrophy (endocytosis) in solitary *P. antarctica* under iron limitation. Endocytosis in *P. antarctica* might represent an alternate pathway to acquire nutrients and thereby relieve the effects of iron limitation. The degree, magnitude, and importance of mixotrophy in the success of *Phaeocystis* are uncertain, but molecular insights suggest it may provide a means for the species to thrive in adverse oceanographic conditions.

### Genetic Diversity Within Assemblages and Strains of the Same Species

*Phaeocystis* blooms appear to be a relatively diverse mixture of different clones, each with the potential for different growth responses to environmental conditions (Gäbler et al. 2007, Gäbler-Schwarz et al. 2017, Luxem et al. 2017, Wang et al. 2022). Indeed, a diversity of growth responses, temperature tolerances, and toxicity have been found within a single sample of *P. globosa* (Hu et al. 2019), and these patterns seem to occur within blooms of *P. antarctica* and *P. pouchetii* as well (Luxem et al. 2017, Wang et al. 2019). The genetic diversity makes it difficult to generalize on results from cultures, and the intrapopulation variability appears to be substantial. Furthermore, studies of blooms in situ likely reflect the preponderance of the clone that has become dominant and may not adequately reflect the molecular mechanisms that allow a bloom to persist through time. Similarly, spatial variations may reflect the differential variable contribution of one clone to overall *Phaeocystis* abundance. The importance of intrapopulation genetic variability remains a major uncertainty in our understanding of *Phaeocystis* dynamics.

### Future Role of *Phaeocystis* in Global Biogeochemical Cycles

In view of the harmful attributes associated with *Phaeocystis* and the apparently large genetic plasticity of its species, understanding how those will be expressed in a warmer ocean is important. Climate change induces vast changes in the ocean and atmosphere, and a simple prediction based on a single effect will not adequately describe the most likely future changes in *Phaeocystis* distributions and biogeochemical impacts. It is uncertain whether the plasticity in *Phaeocystis* is similar to or greater than that of diatoms (or other functional groups), so the impacts of the molecular responses to future changes need to be established relative to those of other phytoplankton species and groups. The biogeochemical differences between *Phaeocystis* and diatoms are extreme (e.g., the lack of use of silicon by *Phaeocystis* and differences in elemental composition leading to alteration of deep-water chemistry upon remineralization), and future increases or decreases in *Phaeocystis* will have substantial impacts on biogeochemical cycles. Future research needs to understand the myriad consequences of such changes.

#### SUMMARY POINTS

1. *Phaeocystis* is one of the ocean's most important species. It forms large-scale blooms and contributes significantly to the carbon and sulfur cycle in marine systems.



2. The polymorphic growth pattern of *Phaeocystis* provides different pathways of energy and material to food webs, with solitary cells being part of the microbial food web and colonies likely contributing to the energetics of large animal food webs.
3. While patterns of growth exist throughout the ocean, *Phaeocystis* exhibits profound variations among species and within a single species, suggesting that it has a substantial genetic plasticity. This plasticity limits our ability to draw clear conclusions about environmental influences on its growth.
4. Despite the difficulty in drawing clear pan-species characteristics, increased occurrences of blooms in coastal regions are likely. Similarly, *Phaeocystis antarctica* abundance and distribution may increase in polar regions and alter globally important biogeochemical cycles.
5. Future changes in the distribution and magnitude of blooms are uncertain, but given the significant role of *Phaeocystis* in biogeochemical cycles, understanding these changes is of extreme importance.

## DISCLOSURE STATEMENT

The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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## Errata

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