Ocean Sci. J. (2015) 50(2):283-289
http://dx.doi.org/10.1007/s12601-015-0025-1

Article

Available online at http://link.springer.com

SpringerLink

Ocean Science Journal

pISSN 1738-5261
eISSN 2005-7172

Theoretical Size Controls of the Giant *Phaeocystis globosa* Colonies

Xiao Liu[1,3]*, Walker O. Smith Jr.[1], Kam W. Tang[1,4], Nhu Hai Doan[2], and Ngoc Lam Nguyen[2]

[1]*Virginia Institute of Marine Science, College of William & Mary, Gloucester Point, VA 23062, USA*
[2]*Institute of Oceanography, Vietnam Academy of Science & Technology, 01 Cau Da, Nha Trang, Viet Nam*
[3]*Department of Earth Sciences, University of Southern California, Los Angeles, CA 90089, USA*
[4]*Department of Biosciences & Centre for Sustainable Aquatic Research (CSAR), Swansea University, Swansea SA1 8PP, UK*

Received 27 October 2014; Revised 28 February 2015; Accepted 8 April 2015

Abstract – An unusual characteristic of the cosmopolitan haptophyte *Phaeocystis globosa* is its ability to form colonies of strikingly large size-up to 3 cm in diameter. The large size and the presence of a mucoid envelope are believed to contribute to the formation of dense blooms in Southeast Asia. We collected colonies of different sizes in shallow coastal waters of Viet Nam and conducted a series of measurements and experiments on individual colonies. Using these empirical data, we developed a simple carbon-based model to predict the growth and maximal size of *P. globosa* colonies. Our model suggests that growth of a colony from 0.2 cm to 1.4 cm (the maximal size in our samples) would take 16 days. This number, however, is strongly influenced by the maximal photosynthetic rate and other physiological parameters used in the model. The model also returns a specific growth rate of 0.30 d^{-1} for colonial cells, comparable to satellite estimates, but lower than have been measured for unicellular *P. globosa* in batch culture at similar temperatures. We attribute this low growth rate to not only the model uncertainties, but factors such as self-shading and diffusive limitation of nutrient uptake.

Key words – carbon partitioning, *Phaeocystis globosa*, colonies, maximal size, growth

1. Introduction

Phaeocystis globosa (Prymnesiophyceae) produces dimethylsulfide (Stefels et al. 1995; Liss et al. 1994), a compound that promotes cloud formation, and has the ability to form blooms of large mucilaginous colonies in coastal and stratified oceanic waters, thereby impacting local ecosystems as well as providing feedbacks to the global climate (Schoemann et al. 2005; Rousseau et al. 2007). As part of the polymorphic life cycle, free-living solitary cells can form large colonies of non-flagellated cells distributed in an organic-rich envelope (van Rijssel et al. 1997; Hamm et al. 1999). Colony formation is thought to be triggered by various environmental factors (e.g. Jakobsen and Tang 2002; Wang et al. 2010; Wang et al. 2011), and the large colony size and presence of the mucoid envelope may substantially reduce grazing mortality and viral infection (Hamm et al. 1999; Ruardij et al. 2005), which in turn may facilitate the formation of large blooms under favorable conditions.

In Southeast Asia, *P. globosa* colonies of up to 3 cm in diameter have been reported (Chen et al. 2002), which places them among the largest phytoplankton in marine systems. Colonies of large size (>1 cm) have been found off the coasts of China, Viet Nam, Thailand, Malaysia, Myanmar, Pakistan and the Arabian Sea (Madhupratap et al. 2000; Qi et al. 2004; Doan et al. 2010; P. Harrison, pers. comm.; G. Usup, pers. comm), and may cause substantial ecological disruptions to fisheries and benthic ecosystems (Nguyen et al. 2012). However, few field investigations of these "giant" colonies have been conducted. Smith et al. (2014) found that the colonies had high sinking rates, that the envelope prevented rapid exchange of ions and organic material, and that dissolved organic carbon (DOC) was highly enriched in the intracolonial fluid. However, it remains unclear what factors are responsible for the giantism; furthermore, it is unknown what factors limit the maximal size of these colonies. For example, the substantial amount of organic material partitioned into the mucoid envelope and internal fluid must place a large demand on the photosynthetically generated carbon that may ultimately limit colony size. Conversely, if the mucoid envelope becomes

*Corresponding author. E-mail: liu284@usc.edu

thinner as colonies enlarge, the structural integrity of the envelope might be compromised and the colonies may break in turbulent environments.

The disadvantages of being large and immotile in aquatic systems are numerous. An average sinking rate of 189 m d^{-1} has been measured for giant (ca. 1 cm) *P. globosa* colonies in waters off south central Viet Nam (Smith et al. 2014), which poses a challenge for them to maintain their position in the euphotic zone. Unlike chain-forming diatoms, the spherical shape and large size decrease the effective surface area (relative to the total volume) of a *P. globosa* colony and may significantly hinder cellular nutrient uptake and gas exchange. Although Ploug et al. (1999) found that oxygen passed through *P. globosa* envelope at rates similar to diffusive rates in seawater, direct measurements on diffusion of salt across the mucoid envelope of giant colonies provided an estimate of diffusive coefficient similar to ions and low molecular-weight proteins in cytoplasm (Liu 2011), suggesting that the envelope is permeable, but potentially restricts the flux of nutrients and the growth of colonial cells. Furthermore, a substantially elevated concentration of DOC has been found in the intracolonial fluid (Smith et al. 2014), which suggested that DOC did not diffuse across the envelope quickly. However, this also provides evidence that this strain may use the internal fluid as a reservoir for organic materials that can be re-utilized during unfavorable conditions. Such mixotrophic growth has been found in other haptophytes and may be a common strategy for the group (Flynn et al. 2013). Sedimentation of giant colonies and microbial oxidation of mucilaginous and intracolonial carbon hence may be important in regional carbon cycles and the generation of hypoxia and die-off of benthic fauna in shallow waters (Cadée 1996; Nguyen et al. 2012). As such, understanding the *in situ* growth and control of maximal size of giant *P. globosa* colonies is of broad interest, particularly since cultured *P. globosa* strains do not reach the sizes observed *in situ*.

We developed a carbon-based model that assesses the size growth of individual *P. globosa* colonies, and performed a suite of sensitivity analyses to understand its control mechanisms. We conclude that the rate of excretion is an important parameter that regulates the colonial size growth, and also suggest that the maximal size for the Vietnamese *P. globosa* colonies is likely controlled by reduced thickness of the mucoid envelope, and the consequent susceptibility to physical disruption, grazing, microbial degradation and viral infection.

2. Methods

Photosynthetically Available Radiation (PAR)

In situ photosynthetically available radiation (PAR) was estimated using remote sensing techniques. Daily MODIS Aqua Level-3 PAR images at 4-km resolution were obtained from NASA Ocean Color Data Archive, which were first binned temporally through an 8-day period to include the date of sampling (August 23, 2010); a 3 × 3 spatial mask was then applied to compute the mean and standard error from pixels nearest to our sampling site (10.71°N, 108.00°E). A diel cycle with hourly resolution was constructed based on Meinel and Meinel (1976) as a function of latitude and day of the year (Fig. 1).

Model description

The model uses size-dependent functions of cell abundance, chlorophyll concentration, and particulate and dissolved organic carbon (POC, DOC) obtained from direct measurements, which we conducted on fresh colonies of a range of sizes collected in shallow coastal waters of Viet Nam. Methods and data were reported in more detail previously (Smith et al. 2014). The purpose of the model was to simulate the size growth of giant *P. globosa* colonies under varying physiological conditions and to predict the generation time of large blooms. Model parameters and empirical functions are provided in Table 1. Colony diameters of 0.2 and 1.4 cm were chosen as the initial and final sizes in the model, representing the smallest and largest colonies, respectively, that were measured for physiological parameters used in the model. Several

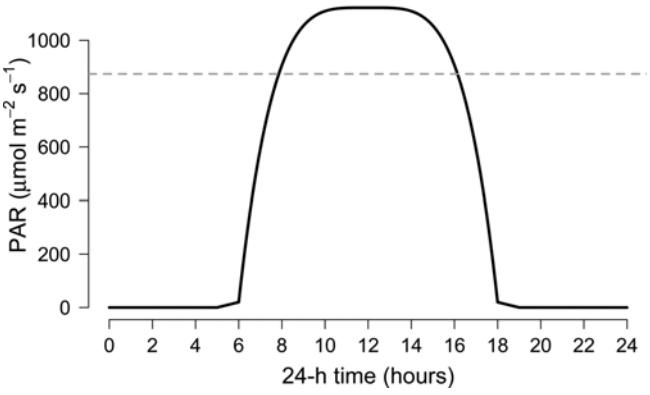

Fig. 1. Diel distribution of photosynthetically available radiation (PAR) at the sampling site (10.71°N, 108.00°E) during the sampling period (August 21-28, 2010). The dashed line indicates the 8-day averaged MODIS Aqua PAR (873.9 μmol m^{-2} s^{-1})

Table 1. Parameters used in the model

Parameter	Unit	Equation	References
Cellular carbon	pg C cell^{-1}	13.5 (constant)	Rousseau et al. (1990)
Cellular chlorophyll	pg Chl cell^{-1}	0.45 (constant)	Smith et al. (2014)
Cell density	10^6 cm^{-2}	$y = 0.408 * D^{0.444}$	Liu (2011)
Colonial surface area	cm^2	$y = \pi D$	
Intracolonial DOC	µg C	$y = 41.4 * D^{2.551}$	Liu (2011)
Maximum photosynthetic rate of colonial cells	µg C µg Chl^{-1} h^{-1}		Verity et al. (1991)

simplifying key assumptions were made:

1) Photosynthesis is the only source of organic carbon, and photosynthate is partitioned into the growth of colonial cells, the production of organic mucilage, and is released as DOC into the intracolonial and extracolonial environments;

2) Partition coefficients (% of total photosynthetic carbon) within different "carbon pools" in the colonies (i.e. cells, mucilage, DOC) are constant during each time step of active growth;

3) Hourly maximum photosynthetic rate (P_m^b) of a *Phaeocystis* colony was estimated as a function of total chlorophyll and PAR at 20°C (Verity et al. 1991) during 13:11 L:D photoperiods (Fig. 2). Although satellite measurements suggested a surface temperature of 28.1°C during our sampling period, it is assumed that the Vietnamese strain of *P. globosa* is well adapted to the ambient environment and its photosynthesis is not reduced by the warmer temperatures.

4) Dark respiratory loss (R) was initially set at 29% of the total photosynthetic carbon (Falkowski, 1992), but was also treated as a variable in the sensitivity analyses;

5) Cellular chlorophyll and carbon were held constant at 0.45 pg Chl cell^{-1} (Smith et al. 2014) and 13.5 pg C cell^{-1} (Rousseau et al. 1990), respectively;

6) Mucilage POC as a percentage of total colonial POC is described by γ, and is independent of colony size. γ was initially set at 77% based on direct measurements: total POC in colonial cells was calculated from multiplying cellular carbon by total number of colonial cells, and total mucilage was then derived by subtracting total cellular carbon from total colonial POC, the latter of which was measured directly via pyrolysis (Smith et al. 2014). γ was also treated as a variable in the sensitivity analyses.

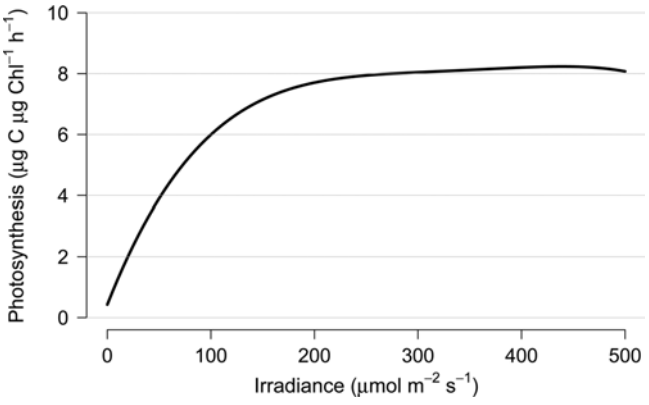

Fig. 2. Chlorophyll specific photosynthetic rate (P_m^b) of *Phaeocystis* colonies as a function of irradiance. Colonies were grown at 20°C. Reproduced from Verity et al. (1991)

To construct the density of colonial cells within the mucoid envelope, we used a size-dependent power function derived from direct measurements on giant colonies, allowing for an increase in cell density during size growth. This observed positive correlation is, however, in contrast to observations on the North Sea strain (e.g. Jakobsen and Tang 2002). Measurements of DOC in the intracolonial space were used to constrain the model's carbon partitioning. An unknown constant, β (the fraction of photosynthate that is released into the intracolonial space as DOC, equal to the amount of DOC that is released externally to the ambient seawater), was adjusted to satisfy two criteria: 1) colony diameter approaches 1.4 cm (± 5%) at the end of the growth period ($t = n$); and 2) time-integrated release of DOC into the intracolonial space during active growth ($t = 0 \rightarrow n$) is close to 97.0 µg C (± 5%; see Eq. 3 below).

Model simulation occurred in a series of time steps in hours. The first was to calculate the initial parameters at $t = 0$ (6H) for a 0.2 cm colony using known empirical functions (Table 1). Total colonial cell abundance equaled 4.9×10^4, total cellular carbon 0.662 µg C, total chlorophyll 0.022 µg Chl, and PAR 19.8 µmol m^{-2} s^{-1}. Maximum photosynthetic rate (P_m^b) at $t = 0$ is a function of chlorophyll and PAR, and equaled 2.12 µg C µg Chl^{-1} h^{-1}; total photosynthesis of the colony during the first time step ($t = 0 \rightarrow 1$) can be then calculated as $P_m^b * Chl * \Delta t$, or 0.024 µg C. Colonial growth occurs over discrete intervals of 1 *h*: at $t = 1$, for example, γ*(1-2β) of carbon fixation from total photosynthesis during the previous interval ($t = 0$) is added as mucilage and the

remaining (1-γ)*(1-2β) as colonial cell biomass. Since cellular carbon and chlorophyll are constant, total POC of colonial cells at $t = 1$ can be used to derive total cell abundance and total chlorophyll. Colony size in turn can be estimated from total cell abundance and cell density. According to Smith et al. (2014), cell density (ω) can be expressed as a power function of colony diameter (D; in cm):

$$\omega = 0.408 * D^{0.444} \quad (1)$$

and Eq. 1 becomes

$$D = 1.443 * N^{0.409} \pi^{-0.409} \quad (2)$$

Since total chlorophyll at $t = 1$ is known, total photosynthesis at $t = 2$ can be calculated in the same manner as in the first time step, and this is repeated through time, along with simultaneous tuning of β in the range of [10%, 90%] at increments of $\Delta\beta = 1\%$. During the 11-*h* dark period, photosynthesis is zero, and hourly respiratory loss (R) equals 29% of the mean maximum photosynthetic rate (P_m^b) over the previous 13-*h* light period. This amount is subtracted from total colonial carbon at each time step, allowing for a decrease in colony size owing to dark respiration.

When the two criteria of the model are both satisfied at $t = n$, colony diameter ($D_{t=n}$) should approach 1.4 cm and intracolonial DOC_t accumulated within $t = 0 \rightarrow n$ ($\int_0^n DOC_t\, dt$) should approach that estimated from the empirical equation:

$$\Delta DOC = 4.14 * (D_{t=n}^{2.551} - D_{t=0}^{2.551}) \quad (3)$$

where $D_{t=0} = 0.2$ cm, $D_{t=n} = 1.4$ cm, and n is the time (in hours) needed for a *P. globosa* colony to grow from 0.2 cm to 1.4 cm in diameter. As mentioned, ΔDOC should approach 97.0 μg C. Heterotrophic removal of intracolonial DOC is ignored to simplify the model.

Model sensitivity analyses

Two sets of independent sensitivity analyses were performed by altering rate of respiratory loss (R = 10-40% of total photosynthesis, at increments of 2%) and percentage of carbon incorporated into mucilage (γ = 30-90%, at increments of 10%) to assess the impact of modifications in physiological conditions on the size growth of *P. globosa* colonies.

3. Results and Discussion

Modeled size growth of *P. globosa* colonies

The model suggests that a *P. globosa* colony takes 385 hours, or 16 days, to grow from 0.2 cm to 1.4 cm in diameter. Predicted total chlorophyll and cell abundance per colony increases by approximately 2 orders of magnitude during this size growth. Model tuning yields a value of β = 20.5%, meaning approximately 41% of photosynthetic carbon is released into the intracolonial space. Assuming that an equal amount of carbon is released externally into the ambient seawater, a total of 20.5% of photosynthate is released as DOC. These estimates are greater than those commonly observed in phytoplankton (ca. 10% of productivity; Christian and Anderson, 2002), although high extracellular release has been reported for encased cells such as zooxanthellae in corals and assemblages experiencing sub-optimal conditions such as nutrient limitation or photoinhibition (e.g. Muscatine et al. 1984).

Applying the model-estimated total cell abundance at each time step to a theoretical exponential growth function ($N_{t=n} = N_{t=0} e^{\mu t}$) gives an estimate of specific growth rate of $\mu = 0.30$ d^{-1}, approximately 2-fold lower than laboratory measurements at similar temperatures (e.g. 0.59 ± 0.04 d^{-1}, Wang et al. 2010; 0.65-0.72 d^{-1}, Peperzak et al. 2000). To assess the *in situ* growth of giant *P. globosa* colonies, we retrieved daily chlorophyll concentrations at 1-km resolution from MODIS Aqua Level-2 images from late August through early September 2007, during when a large *P. globosa* bloom was observed, reaching a density of ~1,550 colonies L^{-1} (Doan et al. 2010). Despite cloud coverage, the satellite captured elevated chlorophyll concentrations on August 21 (2.80 ± 0.19 mg m^{-3}) and August 24 (6.23 ± 0.62 mg m^{-3}) at the investigated site, in contrast to the "pre-bloom" levels (e.g. July 30, 1.95 ± 0.04 mg m^{-3}; Fig. 3). Assuming that *P. globosa* colonies were the dominant contributor to the increased chlorophyll, and that chlorophyll per cell remained constant, the exponential growth function suggests a specific *in situ* net growth rate of $\mu = 0.27$ d^{-1}, comparable to our model estimate.

Model sensitivity analyses

One of the largest uncertainties in this model is the partitioning of mucilage carbon. The percentage of photosynthate that is incorporated into the mucilage (γ = 77%) was estimated from direct observations on giant colonies; critical steps in this estimate involved the measurement of total POC via filtration and pyrolysis, and estimation of total cellular carbon, which in turn employed an empirical value of cellular carbon content in *P. globosa* (13.5 pg C cell^{-1}; Rousseau et al. 1990). Considering

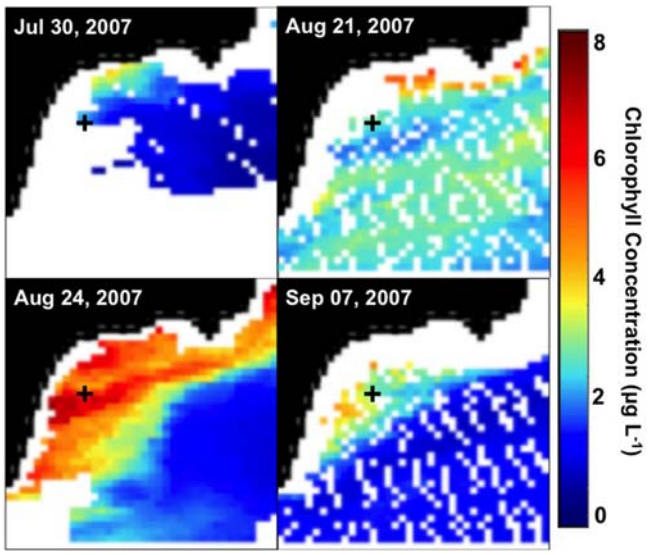

Fig. 3. MODIS Aqua chlorophyll maps (10.6-11.0°N, 108.0-108.4°E). In 2007, a large *P. globosa* bloom was observed at the site represented by the black cross on the maps (10.82°N, 108.11°E; Doan et al., 2010). July 30, August 21 and 24, and September 7 were chosen to represent the "pre-bloom", "bloom", and "post-bloom" conditions, respectively, and chlorophyll concentrations were retrieved from the site with a 3×3 mask

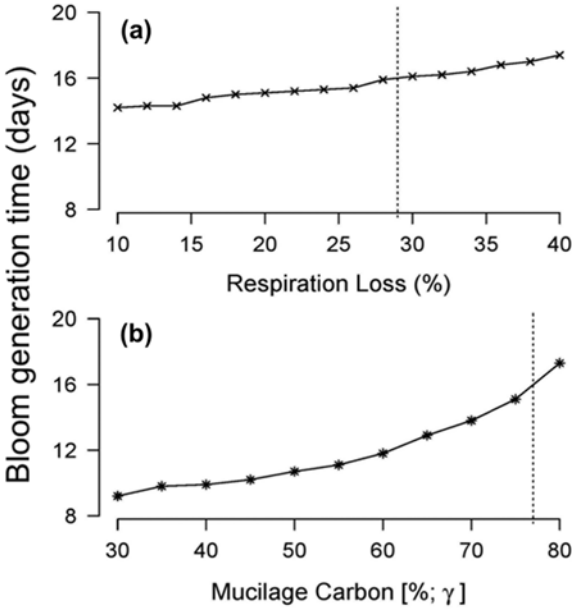

Fig. 4. Generation time of giant colonies (growth from a colony of 0.2 cm to its maximal size of 1.4 cm) predicted from model sensitivity analyses. Sensitivity analysis (a) used variable respiratory losses (10-40% of total photosynthesis), and (b) variable percentages of carbon that was incorporated into mucilage (γ = 30-80%). Dotted lines indicate values used in the original model calculation

that diameters of colonial cells for the Vietnamese strain (averaged 10.3 μm; Smith et al. 2014) were larger than literature values (5.6-8.3 μm; Peperzak et al. 2000), an underestimate of POC in colonial cells would yield an overestimate of mucilage carbon pool, and therefore an overestimate of γ. Sensitivity analyses suggested that colonial growth from 0.2 to 1.4 cm at γ = 80% would take much longer (17 days) than it would at γ = 30% (9 days; Fig. 4). The effect of varying respiratory loss is quantitatively less substantial, yet not negligible; sensitivity analyses showed that generation of giant colonies would take 14 days at a respiratory loss of 10%, but 17 days at 40% (Fig. 4). The temperature and dependence of maximal photosynthetic rate (P_m^b) also may introduce uncertainties to the model. Verity et al. (1991) found that *P. globosa* solitary and colonial cells synthesize carbon at 12.2 and 8.0 μg C μg Chl^{-1} h^{-1} at 20°C, respectively, both appreciably higher than have been measured at lower temperatures. We assumed in the model that the Vietnamese strain of *P. globosa* is well adapted to the ambient temperature (~28.1°C) and reduces carbon at the same rate as predicted by Verity et al. (1991)'s analysis at 20°C. However, it is unclear whether a warmer temperature would constrain or facilitate photosynthesis of the colonial cells. Satellite images are unable to resolve the temperature gradient in the coastal surf zone, where abundant giant colonies were observed and collected. Although the limitation in satellite SST measurements could have introduced errors to the estimate of *P. globosa* specific growth rate, those errors are relatively minor.

Controls on the maximal size of *P. globosa* colonies

Considering that a majority of colonies we observed were less than 1.4 cm (Smith et al. 2014), questions remain as to why larger colonies were not abundantly present, and how environmental and physiological conditions would limit the maximal size of *P. globosa* colonies. As a colony grows larger in diameter (D), the amount of carbon per unit area of the mucoid envelope (y) decreases (Fig. 5), and total mucilage carbon within the colony (y') can be estimated accordingly:

$$y = -33.8 * \ln(D) + 12.1 \quad (4)$$

$$y' = y\pi D^2 \quad (5)$$

Using Eqs. 4 and 5, the mucilaginous carbon is 66.5 μg C cm^{-2} (or 8.35 μg C $col.^{-1}$) for a 0.2 cm colony, and 0.73 μg C cm^{-2} (or 4.48 μg C $col.^{-1}$) for a colony of diameter 1.4 cm. A significant decrease in the mucilage areal carbon, and thereby envelope thickness, is likely to be accompanied by a decrease in colony

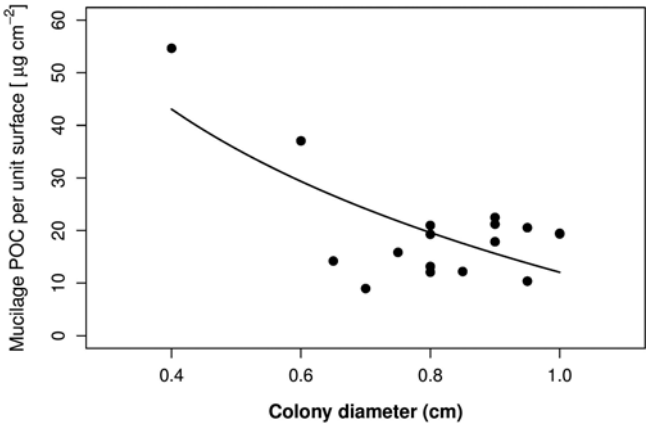

Fig. 5. Relationship between amount of POC per unit colony surface and colony size for the giant *P. globosa* colonies. The line represents the logarithmic correlation between the two variables ($y = -33.8 * \ln(D) + 12.1$ $y = -33.8 \ln(D) + 12.1$, $n = 17$, $r^2 = 0.49$). Modified from Smith et al. (2014)

integrity and susceptibility to grazing, microbial degradation, and physical disruption, particularly in shallow and turbulent environments where *P. globosa* blooms in Southeast Asia have often been observed. Eq. 4 gives a theoretical maximal size of 1.43 cm when mucilaginous carbon is zero ($D = 1.43$; $y = 0$). Although larger colonies have been observed in other regions (e.g. Qi et al. 2004; Nguyen, pers. comm.), this estimate is comparable to the largest colonies we collected in Viet Nam (1.4 cm). Furthermore, total mucilaginous carbon for a colony reaches its maximum at a size of 0.85 cm ($D = 0.85$; Eq. 5), indicating that larger colonies may indeed be susceptible to rapid carbon losses owing to factors mentioned above, and that the specific growth rate has been underestimated for the younger and smaller colonies, and overestimated for the older and larger ones. It is likely that colonies of moderate sizes, such as ones smaller than 0.85 cm, constitute a significant proportion of the biomass that is quickly accumulated during a *P. globosa* bloom.

4. Implications

The *P. globosa* population in Viet Nam forms giant colonies that are more than an order of magnitude larger than any *Phaeocystis* colonies previously discovered. Their strikingly large sizes and unusual characteristics in carbon partitioning force us to re-evaluate size constraints and adaptation strategy in regard to marine phytoplankton. We used empirical data to develop a carbon-based model, which simulates the growth of and theoretical size constraints on the colonies. Despite the simplifications and uncertainties of the model, this study represents an important initial step towards understanding how *P. globosa* reaches and attains its large size in nature. Sensitivity analyses suggest that physiological adaptations that allow the cells to minimize respiratory losses and modify carbon partitioning would facilitate the quick formation of large colonies and dense blooms. We also suggest that growth slows down, and eventually ceases, in old and large colonies due to the fact that photosynthetic carbon is insufficient to maintain the integrity of colonial mucoid envelope.

Acknowledgements

This study was supported by NSF Grant OCE 0850910 to WOS and KWT, and NAFOSTED (National Foundation of Science and Technology, Ministry of Science and Technology, Viet Nam) grant No. 106.13.2011.16 to Hai Doan-Nhu and Lam Nguyen-Ngoc. We acknowledge the invaluable help of Jennifer Dreyer from VIMS and Nguyen Chi Thoi from Institute of Oceanography, Nha Trang who assisted field samplings and laboratory analysis.

References

Cadée G (1996) Accumulation and sedimentation of *Phaeocystis globosa* in the Dutch Wadden Sea. J Sea Res **36**:321-327

Chen YQ, Wang N, Zhang P, Zhou H, Qu LH (2002) Molecular evidence identifies bloom-forming *Phaeocystis* (Prymnesiophyta) from coastal waters of southeast China as *Phaeocystis globosa*. Biochem Syst Ecol **30**:36-46

Christian JR, Anderson TR (2002) Modeling DOM biogeochemistry. In: Hansell DA, Carlson CA (ed) Biogeochemistry of marine dissolved organic matter. Academic Press, Orlando, pp 717-756

Doan NH, Nguyen NL, Dippner JW (2010) Development of *Phaeocystis globosa* blooms in the upwelling waters of the south central coast of Viet Nam. J Mar Syst **83**:253-261

Falkowski PG (1992) Molecular ecology of phytoplankton photosynthesis. In: Falkowski PG, Woodhead AD (eds) Primary productivity and biogeochemical cycles in the sea. Plenum Press, New York, pp 47-67

Flynn KJ, Stoecker DK, Mitra A, Raven JA, Glibert PM, Hansen PJ, Graneli E, Burkholder JM (2013) Misuse of the phytoplankton-zooplankton dichotomy: the need to assign organisms as mixotrophs within plankton functional types. J Plankton Res **35**:3-11

Hamm C, Simson D, Merkel R, Smetacek V (1999) Colonies of *Phaeocystis globosa* are protected by a thin but tough skin. Mar Ecol-Prog Ser **187**:101-111

Jakobsen HH, Tang KW (2002) Effects of protozoan grazing on

colony formation in Phaeocystis globosa (Prymnesiophyceae) and the potential costs and benefits. Aquat Microb Ecol **27**:261-273

Liu X (2011) Ecological, physiological and bio-optical characteristics of *Phaeocystis globosa* in coastal waters of south central Vietnam. M.S. Thesis, College of William and Mary, 142 p

Liss PS, Malin G, Turner SM, Holligan PM (1994) Dimethyl sulfide and *Phaeocystis*: a review. J Mar Syst **5**:41-53

Madhupratap M, Sawant S, Gauns M (2000) A first report on a bloom of the marine prymnesiophycean, *Phaeocystis globosa* from the Arabian Sea. Oceanol Acta **23**:83-90

Meinel AB, Meinel MP (1976) Applied solar energy: an introduction. Addison-Wesley, Reading, 650 p

Muscatine L, Falkowski PG, Porter JW, Dubinsky Z (1984) Fate of photosynthetic fixed carbon in light-and shade-adapted colonies of the symbiotic coral *Stylophora pistillata*. P Roy Soc Lond B **222**:181-202

Nguyen NV, Tung LT, Hoa LX, Thoa NV, Thanh NC, Hoa VM (2012) Red tides in Halong Bay, Viet Nam caused serious loss in aquaculture. In: Proceedings of the international conference on Bien Dong 2012 (Abstract), Nha Trang, pp 146

Peperzak L, Colijn F, Vrieling EG, Gieskes WWC, Peeters JCH (2000) Observations of flagellates in colonies of *Phaeocystis globosa* (Prymnesiophyceae): a hypothesis for their position in the life cycle. J Plankton Res **22**:2181-2203

Ploug H, Stolte W, Jorgensen BB (1999) Diffusive boundary layers of the colony-forming plankton alga *Phaeocystis* sp.: implications for nutrient uptake and cellular growth. Limnol Oceanogr **44**:1959-1967

Qi YZ, Chen JF, Wang ZH, Xu N, Wang Y, Shen PP, Lu SH, Hodgkiss IJ (2004) Some observations on harmful algal bloom (HAB) events along the coast of Guangdong, southern China in 1998. Hydrobiologia **512**:209-214

Rousseau V, Mathot S, Lancelot C (1990) Calculating carbon biomass of *Phaeocystis* sp. from microscopic observations. Mar Biol **107**:305-314

Rousseau V, Chretiennot-Dinet M, Jacobsen A, Verity P, Whipple S (2007) The life cycle of *Phaeocystis*: state of knowledge and presumptive role in ecology. Biogeochemistry **83**:29-47

Ruardij P, Veldhuis MJW, Brussaard CPD (2005) Modeling the bloom dynamics of the polymorphic phytoplankter *Phaeocystis globosa*: impact of grazers and viruses. Harmful Algae **4**:941-963

Schoemann V, Becquevort S, Stefels J, Rousseau W, Lancelot C (2005) *Phaeocystis* blooms in the global ocean and their controlling mechanisms: A review. J Sea Res **53**:43-66

Smith WO, Liu X, Tang KW, DeLizo LM, Doan NH, Nguyen NL, Wang X (2014) Giantism and its role in the harmful algal bloom species *Phaeocystis globosa*. Deep-Sea Res Pt II, **101**:95-106

Stefels J, Dijkhuizen L, Gieskes WWC (1995) DMSP-lyase activity in a spring phytoplankton bloom off the Dutch coast, related to *Phaeocystis* sp. abundance. Mar Ecol-Prog Ser **123**:235-243

van Rijssel M, Hamm CE, Gieskes WC (1997) *Phaeocystis globosa* (Prymnesiophyceae) colonies: hollow structures built with small amounts of polysaccharides. Eur J Phycol **32**:185-192

Verity PG, Smayda TJ, Sakshaug E (1991) Photosynthesis, excretion, and growth rates of *Phaeocystis* colonies and solitary cells. Polar Res **10**:117-128

Wang X, Wang Y, Smith WO Jr (2011) The role of nitrogen on the growth and colony development of *Phaeocystis globosa* (Prymnesiophyceae). Eur J Phycol **46**:305-314

Wang Y, Smith WO Jr, Wang X, Li S (2010) Subtle biological responses to increased CO_2 concentrations by *Phaeocystis globosa* Scherffel, a harmful algal bloom species. Geophys Res Lett **37**:L09604