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RESEARCH ARTICLE

Gaining integrated understanding of *Phaeocystis* spp. (Prymnesiophyceae) through model-driven laboratory and mesocosm studies

Stuart J. Whipple · Bernard C. Patten · Peter G. Verity · Marc E. Frischer · Jeremy D. Long · Jens C. Nejstgaard · Jon T. Anderson · Anita Jacobsen · Aud Larsen · Joaquin Martinez-Martinez · Stuart R. Borrett

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Abstract Knowledge of the complex life cycle of *Phaeocystis* is a key to understanding its role in marine ecosystems and global biogeochemistry. An existing life cycle model was modified and used to integrate understanding of the *Phaeocystis* life cycle. In model-driven research, models expose gaps in our understanding, empirical studies ensue, and feedback improves understanding. Following this scheme, three facets of the life cycle model were examined here. With four exceptions, the empirical studies described have been presented in other literature citations. The first facet involved testing for the existence of a process or producing its description. These studies included: demonstration of in vitro colony division in *Phaeocystis pouchetii*, description of in vitro change in colony shape for *P. pouchetii* associated with senescence, determining which *P. pouchetii* life stage is vulnerable to viral infection and lysis, and an experiment designed to determine whether the sediment could be a source of new *Phaeocystis* colonies to overlying waters; results suggested that more-detailed investigation of benthic particles as a physical substrate for colony formation is warranted. The second facet involved investigation of process rate quantification or process control parameters. Process rate quantification included measurements of colony division rate and growth rate using mesocosm-derived colonies. Process control experiments included testing diatom frustule enhancement of *P. pouchetii* colony formation from solitary cells, and investigation of mesozooplanktonic suppression and microzooplanktonic enhancement of *Phaeocystis globosa* colony formation by planktonic grazer infochemicals. The third facet

S. J. Whipple · P. G. Verity · M. E. Frischer
Skidaway Institute of Oceanography,
Savannah, GA, USA

S. J. Whipple (✉) · B. C. Patten
Institute of Ecology, University of Georgia, Athens,
GA, 30602, USA
e-mail: sjwhipple@earthlink.net

J. D. Long
Marine Science Center, Northeastern University,
Nahant, MA, USA

J. C. Nejstgaard · A. Jacobsen · A. Larsen
Department of Biology, University of Bergen, Bergen,
Norway

J. T. Anderson
Estuarine Research Center, Morgan State University,
St. Leonard, MD, USA

J. Martinez-Martinez
Plymouth Marine Laboratory,
Plymouth, Devon, UK

S. R. Borrett
Computational Learning Laboratory,
Stanford University, Stanford, CA, USA

pertained to the molecular identification of genetic differences between single cells and colonies of *P. globosa*. These studies were designed to provide insight to the question of control factors involved in the transition between single cell and colonial life stages. The life cycle model provided a ready place to incorporate new insights and understanding from empirical studies into an existing model, and can be used to improve simulation models of the direct and indirect effects of *Phaeocystis* on global biogeochemistry.

Keywords Conceptual model · Life cycle · Mesocosm · Model-driven research · *Phaeocystis*

Introduction

The genus *Phaeocystis* contains species that may play a significant role in global biogeochemistry (Smith Jr et al. 1991; Lancelot et al. 1994; Wassmann et al. 2005). They occur over extensive areas (Stefansson and Olafsson 1991; Lancelot and Rousseau 1994), supply significant portions of global dimethyl sulphide (DMS; Gabric et al. 1999; Ayers and Gillett 2000), and play a key role in planktonic ecosystems (Verity and Smetacek 1996; Lancelot et al. 1998). Life cycle processes of *Phaeocystis* may have significant effects on ecosystem biogeochemical processes including nutrient uptake and regeneration by life forms of *Phaeocystis*, nutrient release by viral lysis, nutrient release associated with zooplankton grazing, and nutrient release by senescent colonies. Details of the current state of knowledge of the *Phaeocystis* life cycle are comprehensively reviewed in Rousseau et al. (in press, this volume). In order to integrate understanding of the *Phaeocystis* life cycle, a conceptual model was constructed (Whipple et al. 2005a), although the existence of some life stages was uncertain and the controls on many of the processes were poorly understood. This exercise highlighted experiments which could provide a better understanding of the role of the life cycle in species dynamics and ecosystem processes.

Such enhanced understanding will be incorporated into a developing conceptual model (Whipple et al. 2005a), and also into an ecosystem model in which the *Phaeocystis* life cycle is only one set of biotic compartments (Whipple et al. unpubl.). In model-driven research, models expose gaps in our understanding of the *Phaeocystis* life cycle embedded in its ecosystem; empirical studies to address these gaps ensue, and the feedback from iteration of this cycle improves understanding. This paper presents examples of how a life cycle model of *Phaeocystis* has been used to direct research on the *Phaeocystis* life cycle and its ecology, and demonstrates how insight from these studies integrated into a conceptual model context enhances and integrates such empirical findings.

Model description

The *Phaeocystis* life cycle, which has been modified from the model presented in Whipple et al. (2005a), advances clockwise around Fig. 1 from the upper left with Diploid Solitary Cells, as the starting point. These cells flow to and from New Colonies, which is the critical transition stage between solitary and colonial life forms.

After new colonies cells first divide, they transfer to the growing small colonies compartment. Maturation continues through the size classes: small → medium → large via mitosis and mucus production of colony cells. There is also back-transfer from larger to smaller size classes by colony division (Whipple et al. 2005b).

When colonies begin to lose cells, growing colonies are transferred to corresponding size-based senescent colonies. Diploid or haploid solitary cells are released from these to complete the *Phaeocystis* life cycle. Of the four colony-forming *Phaeocystis* species, haploid flagellates have been documented only for *Phaeocystis globosa* (Eilertsen 1989; Jacobsen 2002; Medlin and Zingone in press, this volume; Rousseau et al. in press, this volume). The other life cycle input to diploid solitary cells comes from transformation of new colonies cells. Syngamy has not been documented in any *Phaeocystis* species; however, it has been included in the model since it is hypothesized as necessary to create diploid solitary cells from haploid cells prior to colony formation in *P. globosa* (Rousseau et al. in press, this volume). Since this