

Current understanding of *Phaeocystis* ecology and biogeochemistry, and perspectives for future research

Peter G. Verity · Corina P. Brussaard ·
Jens C. Nejstgaard · Maria A. van Leeuwe ·
Christiane Lancelot · Linda K. Medlin

Received: 1 June 2006 / Accepted: 13 September 2006 / Published online: 16 March 2007
© Springer Science+Business Media B.V. 2007

Abstract The phytoplankton genus *Phaeocystis* has well-documented, spatially and temporally extensive blooms of gelatinous colonies; these are associated with release of copious amounts of dimethyl sulphide (an important climate-cooling aerosol) and alterations of material flows among trophic levels and export from the upper ocean. A potentially salient property of the importance

of *Phaeocystis* in the marine ecosystem is its physiological capability to transform between solitary cell and gelatinous colonial life cycle stages, a process that changes organism biovolume by 6–9 orders of magnitude, and which appears to be activated or stimulated under certain circumstances by chemical communication. Both life-cycle stages can exhibit rapid, phased ultradian growth. The colony skin apparently confers protection against, or at least reduces losses to, smaller zooplankton grazers and perhaps viruses. There are indications that *Phaeocystis* utilizes chemistry and/or changes in size as defenses against predation, and its ability to create refuges from biological attack is known to stabilize predator–prey dynamics in model systems. Thus the life cycle form in which it occurs, and particularly associated interactions with viruses, determines whether *Phaeocystis* production flows through the traditional “great fisheries” food chain, the more regenerative microbial food web, or is exported from the mixed layer of the ocean.

Despite this plethora of information regarding the physiological ecology of *Phaeocystis*, fundamental interactions between life history traits and system ecology are poorly understood. Research summarized here, and described in the various papers in this special issue, derives from a central question: how do physical (light, temperature, particle distributions, hydrodynamics), chemical (nutrient resources, infochemistry,

P. G. Verity (✉)
Skidaway Institute of Oceanography,
10 Ocean Science Circle, Savannah, GA, 31411, USA
e-mail: Peter.Verity@skio.usg.edu

C. P. Brussaard
Royal Netherlands Institute for Sea Research,
P.O. Box 59, 1790 AB Den Burg, The Netherlands

J. C. Nejstgaard
UNIFOB AS, Department of Biology,
University of Bergen, Bergen High Technology
Centre, 5020 Bergen, Norway

M. A. van Leeuwe
University of Groningen, Biological Centre,
P.O. Box 14, 9750 AA Haren, The Netherlands

C. Lancelot
Ecologie des Systèmes Aquatiques, Université Libre
de Bruxelles, Campus de la Plaine – C.P. 221,
Bd. du Triomphe, 1050 Bruxelles, Belgium

L. K. Medlin
Alfred Wegener Institute for Polar and Marine
Research, Am Handelshafen 12, 27570 Bremerhaven,
Germany

allelopathy), biological (grazers, viruses, bacteria, other phytoplankton), and self-organizational mechanisms (stability, indirect effects) interact with life-cycle transformations of *Phaeocystis* to mediate ecosystem patterns of trophic structure, biodiversity, and biogeochemical fluxes? Ultimately the goal is to understand and thus predict why *Phaeocystis* occurs when and where it does, and the bio-feedbacks between this keystone species and the multitrophic level ecosystem.

Keywords Biocomplexity · Plankton life cycles · *Phaeocystis* · Viruses · Zooplankton

Introduction

The assembly of phytoplankton communities is a continuous process in which instantaneous external assessments, e.g., species abundances, diversity, and bulk constituents, reflect the outcome of a host of physical, chemical, and biological processes operating at a hierarchy of temporal and spatial scales. The absolute abundance of a given taxon increases according to growth, immigration, physical concentration, and other mechanisms, whereas losses including grazing, lysis, sedimentation, dilution, and emigration act to stabilize population fluctuations. In this manner, many species generally compete yet coexist in a water mass of seemingly similar properties. That one species becomes numerically dominant, much less forms a near monospecific bloom, is a remarkable phenomenon, especially given that many loss processes are density dependent in nature. To do so regularly, over large spatial and long temporal scales, is indicative of a life-history strategy more successful than the competition. It may also indicate that one species is more genetically diverse than another, and that diversity enables it to exist over these scales as one suite of genotypes gives way to another suite of genotypes to perpetuate the bloom. From this perspective, each suite of genotypes conceivably thrives in a discrete set of environmental parameters.

The genus *Phaeocystis* is one such taxon. Whereas it contains at least six species (Medlin and Zingone this volume; Rousseau et al. this volume), it is ecologically acknowledged that the

blooms are typically caused by the two cold water species, *P. pouchetii* (high boreal and arctic waters) and *P. antarctica* (Southern Ocean), and by *P. globosa* (primarily cold north temperate waters). What is unusual in marine ecosystems is that such blooms are primarily a life cycle event: these *Phaeocystis* species transform from a tiny single-celled morphotype into a colonial stage in which hundreds or thousands of cells are embedded within a gelatinous matrix and protected behind an elastic but solute-permeable community membrane. Something about this transformation and/or the characteristics of the colony life-cycle stage (Lancelot and Rousseau 1994; Lancelot et al. 1998) permit *Phaeocystis* to out-compete other phytoplankton, which belong to a variety of algal classes with diverse strategies for competing for light and nutrients, but without a functionally comparable gelatinous house. At sufficiently high concentrations, colony blooms have been associated with a variety of ecosystem changes and negative effects on fisheries and fish farming (Lancelot et al. 1987; Schoemann et al. 2005; Nejstgaard et al. this volume), such that blooms of *Phaeocystis* colonies are considered as harmful algal blooms (HABs, e.g., Anderson et al. 1998, Veldhuis and Wassmann 2005). Less is known about the occurrence and significance of solitary cell stages of *Phaeocystis*, primarily because these small nanoplankton require specific careful methods for quantification. However, blooms of solitary cells have been reported on occasion, e.g., Ratkova and Wassmann (2002) and Wassmann et al. (2005), and thus the temporal and spatial distribution of *Phaeocystis* may have been under-sampled. Solitary cells may also be important to over-wintering strategies (see below) but relevant quantitative studies are lacking. Nevertheless, given that colonies derive from solitary cells, knowledge of their dynamics and mechanisms influencing their occurrence are important to understanding the success of this genus (Reigstad and Wassmann, this volume).

Thus the causes of life-cycle alterations in *Phaeocystis* may be under environmental controls, whether abiotic or biotic, and elucidation of these controls will shed light on the fundamental processes that regulate ecosystem organization and biogeochemical flows. Research attempting