

Zooplankton grazing on *Phaeocystis*: a quantitative review and future challenges

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Received: 23 May 2006 / Accepted: 16 November 2006 / Published online: 20 April 2007
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Abstract The worldwide colony-forming haptophyte phytoplankton *Phaeocystis* spp. are key organisms in trophic and biogeochemical processes in the ocean. Many organisms from protists to fish ingest cells and/or colonies of *Phaeocystis*. Reports on specific mortality of *Phaeocystis* in natural plankton or mixed prey due to grazing by zooplankton, especially protozooplankton, are still limited. Reported feeding rates vary widely for both crustaceans and protists feeding on even the same *Phaeocystis* types and sizes. Quantitative analysis of available data showed that: (1) laboratory-derived crustacean grazing rates on monocultures of *Phaeocystis* may have been overestimated compared to feeding in natural plankton communities, and should be treated with caution;

(2) formation of colonies by *P. globosa* appeared to reduce predation by small copepods (e.g., *Acartia*, *Pseudocalanus*, *Temora* and *Centropages*), whereas large copepods (e.g., *Calanus* spp.) were able to feed on colonies of *Phaeocystis pouchetii*; (3) physiological differences between different growth states, species, strains, cell types, and laboratory culture versus natural assemblages may explain most of the variations in reported feeding rates; (4) chemical signaling between predator and prey may be a major factor controlling grazing on *Phaeocystis*; (5) it is unclear to what extent different zooplankton, especially protozooplankton, feed on the different life forms of *Phaeocystis* in situ. To better understand the mechanisms controlling zooplankton grazing in situ, future studies

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should aim at quantifying specific feeding rates on different *Phaeocystis* species, strains, cell types, prey sizes and growth states, and account for chemical signaling between the predator and prey. Recently developed molecular tools are promising approaches to achieve this goal in the future.

Keywords Colony formation · DMS · Gut pigment · Molecular methods · Microzooplankton · *Phaeocystis* · *antarctica* · Predator defense

Introduction

The haptophyte *Phaeocystis* is a dominant phytoplankton genus in tropical to polar seas (Baumann et al. 1994). They are key species in marine food webs and biogeochemical cycles, e.g., as major producers of carbon and climatically important sulfide compounds (Liss et al. 1994; Alderkamp et al. this volume; Stefels et al. this volume). Three major species: *P. globosa* Scherffel, *P. pouchetii* (Hariat) Lagerheim and *P. antarctica* Karsten (Medlin and Zingone this volume) exist in two main morphotypes: small single cells and mucilaginous colonies (see Rousseau et al. this volume for details on the different cell and morphotypes).

The success of *Phaeocystis* has been ascribed to a number of factors, including escaping from grazing by its dramatic ability to shift morphotype between solitary flagellates of a few micrometers to large mucous colonies up to several cm in diameter (Weisse et al. 1994; Chen et al. 2002; Schoemann et al. 2005; Veldhuis and Wassmann 2005; Rousseau et al. this volume). For a phytoplankton bloom to form, the sum of growth and accumulation must be larger than the sum of loss due to horizontal and vertical advection, sinking, lysis and predation (e.g., Smayda 1997; Banse 1994). Advection is beyond the control of all phytoplankton, and thus not likely to be a strong selective force for *Phaeocystis* (but see Seuront et al. this volume). Neither does the growth rate of *Phaeocystis* appear to be exceptionally high relative to other bloom-forming phytoplankton, such as diatoms (Hegarty and Villareal 1988). Indeed, in many field and mesocosm studies *Phaeocystis* blooms co-occurred with, or followed the demise of, diatom blooms (Peperzak et al. 1998; Goffart et al. 2000; Rousseau et al. 2002; Tungaraza et al. 2003; Larsen

et al. 2004). Sinking loss of *Phaeocystis* also seems to be small for the large colonies (Reigstad and Wassmann this volume). This could be partly due to the balloon-like characteristics of the colonies: colonial cells are embedded in a thin mucous skin whereas the interior of the colonies is hollow (van Rijssel et al. 1997). Although single cells are susceptible to viral lysis, an intact mucous skin may protect colonial *Phaeocystis* cells from viral lysis and other infections (reviewed by Brussaard et al. this volume). A remaining possible explanation for the success of *Phaeocystis* despite its moderate growth rate is its ability to reduce grazing mortality, which is the focus of this review article.

Grazing on *Phaeocystis* (mainly *P. globosa* and *P. pouchetii*) has been studied since the beginning of the last century (e.g., Lebour 1920, 1922), and a wide range of organisms have been reported to be able to ingest *Phaeocystis* (Table 1). Unfortunately, most of the early studies were based on light microscopy of gut contents of the grazers, and neither feeding rate nor detailed description of the prey species was available (see Notes in Table 1, and further discussion below). It was not until the 1980s that direct quantitative studies on zooplankton feeding on *Phaeocystis* were reported (reviewed in Peperzak 2002; Rousseau et al. 2000; Schoemann et al. 2005; Weisse et al. 1994). Published grazing rates span wide ranges even for the same predators feeding on the same *Phaeocystis* species, morphotype and food concentration. This indicates that the widely accepted view of grazing vulnerability as a function of predator-to-prey size ratio and prey abundance (Frost 1972; Hansen et al. 1994a) for a given predator type (Hansen et al. 1997) may be compounded by other factors controlling grazing on *Phaeocystis*.

Although copepods and other organisms may ingest *Phaeocystis* spp. (Table 1), at least when they are in palatable condition (Estep et al. 1990; Long and Hay 2006), there are also reports of reduced zooplankton feeding and abundance during blooms of *Phaeocystis* (Table 2) and low reproductive output in copepods, even when feeding rates are relatively high (Verity and Smayda 1989; Turner et al. 2002; Klein Breteler and Koski 2003; Long and Hay 2006). Several authors have previously reviewed various negative effects of *Phaeocystis* on different organisms (e.g., Weisse et al. 1994; Turner et al. 2002; Schoemann et al. 2005); and we provide an updated summary in Table 2. However,