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REVIEW

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

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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* (Hariot) 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,

**Table 1** Organisms recorded to ingest *Phaeocystis* spp.

| Grazer | Developmental stage | *Phaeocystis* species | type/stage | Obervation method | References |
|---|---|---|---|---|---|
| *Dinoflagellates* | | | | | |
| *Amphidinium* sp. | – | sp. | "remains of spores" | in situ gut microscopy | Lebour (1922) |
| *Gymnodinium rhomboides* Schütt | – | sp. | – | in situ gut microscopy | Lebour (1922) |
| *Gymnodinium* sp. | – | *globosa* | single cells | incubation experiments | Tang et al. (2001) |
| *Gymnodinium triangularis* Lebour | – | sp. | – | in situ gut microscopy | Lebour (1922) |
| *Gyrodinium dominans* Hulburt | – | *globosa* | single cells | incubation experiments | Tang et al. (2001) |
| *Gyrodinium* cf. *spirale* | – | *globosa* | small colony | photomicrograph | Stelfox-Widdicombe et al. (2004) |
| *Noctiluca scintillans* (Macartney) Kofoid & Swezy | – | cf. *globosa* | single cells and colonies | incubation experiments and microscopy | Hansen (1992, 1995), Jakobsen and Tang (2002), Weisse et al. (1994) |
| *Oxyrrhis marina* Dujardin | – | cf. *globosa* | single cells | incubation experiments | Hansen et al. (1993) |
| *Ciliates* | | | | | |
| *Euplotes* sp. | – | *antarctica* | single cells and colonies | fluorescently labeled algae | Shields and Smith (2005) |
| *Euplotes* sp. | – | *globosa* | single cells and colonies | incubation experiments | Long (2004) |
| *Helicostomella subulata* (Ehrenberg) | – | *globosa* | single cells | live microscopy | Admiraal and Venekamp (1986) |
| *Lohmanniella oviformis* Leegaard | – | *globosa* | single cells | incubation experiments | Tang et al. (2001) |
| *Rimostrombidium conicum* (Kahl) Petz & Foissner | – | *globosa* | single cells | incubation experiments | Tang et al. (2001) |
| *Strombidinopsis acuminatum* Fauré-Fremiet | – | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1995, 1993) |
| *Strombidium* sp. | – | *globosa* | single cells | incubation experiments | Verity (2000) |
| *Strombidium vestitum* Leegaard | – | *globosa* | single cells | incubation experiments | Tang et al. (2001) |
| *Tintinnopsis beroidea* Stein | – | *globosa* | single cells | live microscopy | Admiraal and Venekamp (1986) |
| *Rotifers* | | | | | |
| *Syncaheta vorax* Rousselet | – | *globosa* | eating at colonies | live microscopy | Hollowday (1949) |
| *Polychaets* | | | | | |
| *Polydora pulchra* Carazzi | nectochaeta larvae | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| *Tomopteris* sp. | Larvae | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| *Molluscs* | | | | | |
| *Macoma balthica* (L) | Mussels?? | sp. | ingest single cells | laboratory incubation | Kamermans (1994) |
| *Mytilus edulis* L. | Mussels 33–58 mm | cf. *globosa* | cultured, ingested single cells | flow chamber, cell counts | Smaal and Twisk (1997) |

**Table 1** continued

| Grazer | Developmental stage | *Phaeocystis* species | type/stage | Obervation method | References |
|---|---|---|---|---|---|
| *Mytilus edulis* L. | Mussels > 3 cm | *globosa* | able to filter colonies | ? | Petri and Vareschi (1997) |
| *Nassarius reticulatus* (L) | veliger larvae | *pouchetii* | cultured, probably single cells | incubation, visual inspection | Fretter and Montgomery (1968) |
| *Rissoa inconspicua* Alder | veliger larvae | *pouchetii* | cultured, probably single cells | incubation, visual inspection | Fretter and Montgomery (1968) |
| *Cladocerans* | | | | | |
| *Evadne nordmanni* Lovén | – | sp. | cells and "spores" | in situ gut microscopy | Lebour (1922) |
| *Copepods, calanoids* | | | | | |
| *Acartia clausi* (Gunn.) | copepodites ? | sp. | "green remains, probably *Phaeocystis* in many" | in situ gut microscopy | Lebour (1922) |
| *Acartia hudsonica* Pinhey | CVI female | *pouchetii* | single cells and colonies | incubation experiments | Verity and Smayda (1989) |
| *Acartia longiremis* (Lilljeborg) | CVI female | *pouchetii* | ingested only colonies < 100 µm | incubation experiments | Hansen et al. (1994b) |
| *Acartia tonsa* Dana | CVI female | *globosa, pouchetii* | single cells and colonies | incubation experiments | Tang et al. (2001), Tang and Simó (2003), Verity (2000), Verity and Smayda (1989) |
| *Anomalocera pattersoni* Tempelton | copepodites ? | sp. | "*Phaeocystis*" | in situ gut microscopy | Lebour (1922) |
| *Calanoides* sp. | Copepodites | *Antarctica* | fluorescently labeled single cells | gut microscopy | K. Tang unpublished |
| *Calanus finmarchicus* (Gunn.) | copepodites ? | sp. | cells and "remains" | in situ gut microscopy | Lebour (1922) |
| *Calanus finmarchicus* (Gunn.) | CI-V | *pouchetii* | single cells and colonies | incubation experiments | Hansen et al. (1990), Tande and Båmstedt (1987) |
| *Calanus glacialis* Jaschnov | CIII-CV | *pouchetii* | colonies | incubation experiments | Estep et al. (1990) |
| *Calanus helgolandicus* (Claus) | copepodites > 280 µm | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995), Turner et al. (2002) |
| *Calanus hyperboreus* (Krøyer) | CIV-CVI female | *pouchetii* | single cells and colonies | incubation experiments | Estep et al. (1990), Huntley et al. (1987), Tande and Båmstedt (1987) |
| *Centropages hamatus* Lilljeborg | copepodites > 280 µm | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1995) |
| *Centropages hamatus* Lilljeborg | copepodites ? | cf. *globosa* | colonies? "*Phaeocystis* bladders" | in situ gut microscopy | Jones and Haq (1963) |
| *Centropages typicus* Krøyer | copepodites ? | sp. | "spores" | in situ gut microscopy | Lebour (1922) |
| *Eucalanus pileatus* Giesbrecht | CVI female | *globosa* | single cells and colonies | incubation experiments | Long and Hay (2006) |
| *Metridia gerlachi* Giesbrecht | copepodites ? | *pouchetii* (in Antarctica) | colonies 0.05–1.5 mm | incubation experiments | Schnack (1983) |

**Table 1** continued

| Grazer | Developmental stage | *Phaeocystis* species | type/stage | Obervation method | References |
|---|---|---|---|---|---|
| *Microcalanus* sp. | Copepodites | *antarctica* | fluorescently labeled single cells | gut microscopy | K. Tang unpublished |
| *Pareuchaeta antarctica* (Giesbrecht) | copepodites ? | *pouchetii* (in Antarctica) | colonies 0.05–1.5 mm | incubation experiments | Schnack (1983) |
| *Pseudocalanus elongatus* (Boeck) | copepodites > 280 μm | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| *Pseudodiaptomus pelagicus* Herrick | CVI female | *globosa* | single cells and colonies | incubation experiments | Long and Hay (2006) |
| *Temora longicornis* Müller | nauplii to adults | *globosa* | single cells and colonies | incubation experiments | Dutz and Koski (2006), Koski et al. (2005), Hansen (1992, 1995) |
| *Temora longicornis* Müller | copepodites ? | cf. *globosa* | colonies? "*Phaeocystis* bladders" | in situ gut microscopy | Jones and Haq (1963) |
| *Temora longicornis* Müller | copepodites ? | sp. | "green cells, probably *Phaeocystis"* | in situ gut microscopy | Lebour (1922) |
| *Temora stylifera* Dana | adult female | appeared similar to *globosa* | cultured single cells and colonies | incubation experiments | Turner et al. (2002) |
| *Copepods, cyclopoids* | | | | | |
| *Corycaeus anglicus* Lubbock | copepodites ? | sp. | "*Phaeocystis* in several" | in situ gut microscopy | Lebour (1922) |
| *Oithona nana* Giesbrecht | copepodites ? | cf. *globosa* | colonies? "*Phaeocystis* bladders" | in situ gut microscopy | Jones and Haq (1963) |
| *Oithona* sp. | copepodites | *antarctica* | fluorescently labeled single cells | gut microscopy | K. Tang unpublished |
| *Oncaea curvata* (Gunn.) | adult female | cf. *pouchetii* (in Antarctica) | colonies | incubation experiments | Metz (1998) |
| *Copepods, harpacticoids* | | | | | |
| *Euterpina acutifrons* (Dana) | copepodites ? | sp. | "flagellates...especially *Phaeocystis*" | in situ gut microscopy | Lebour (1922) |
| *Cirripedes* | | | | | |
| *Balanus crenatus* Bruguière | nauplii | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| "Cirripedes" | nauplii | sp. | "probably *Phaeocystis*" | in situ gut microscopy | Lebour (1922) |
| *Longipeda minor* T. & A. Scott | adult female | sp. | colonies | incubation, visual inspection | Nicholls (1935) |
| *Longipeda scotti* G.O.Sars | adult female | sp. | colonies | incubation, visual inspection | Nicholls (1935) |

**Table 1** continued

| Grazer | Developmental stage | *Phaeocystis* species | type/stage | Obervation method | References |
|---|---|---|---|---|---|
| *Amphipods* | | | | | |
| *Pontogeneia antarctica* Chevreux | hatchilings (2 mm)-adults | *antarctica* | "green plastidic debris... probably indicate ingestion of *Phaeocystis antarctica*" | in situ gut microscopy | Richardson and Whitaker (1979) |
| *Euphausiids* | | | | | |
| *Euphausia superba* Dana | | *sp.* | | in situ gut microscopy | Sieburth (1960) |
| *Euphausia superba* Dana | 35–45 mm | *antarctica* | single cells and colonies < 500 µm | incubation experiments | Haberman et al. (2003) |
| *Thysanoessa inermis* (Krøyer) | carapace ca 5 mm | *pouchetii* | ingested only colonies > 20 µm | incubation experiments | Hansen et al. (1994b) |
| *Thysanoessa raschii* (M. Sars) | carapace ca 5 mm | *pouchetii* | ingested only colonies > 20 µm | incubation experiments | Hansen et al. (1994b) |
| *Decapods* | | | | | |
| Crab (unidentified) | zoëa | sp. | "*Phaeocystis*" | in situ gut microscopy | Lebour (1922) |
| *Galathea intermedia* Lilljeborg | megalopa | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| *Porcellana* sp. | "larva" | sp. | "green spores, probably *Phaeocystis*" | in situ gut microscopy | Lebour (1922) |
| *Portunus depurator* (Linnaeus) | zoëa III-V | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| *Portunus holsatus* (Fabricius) | megalopa | cf. *globosa* | single cells and colonies | incubation experiments | Hansen (1992, 1995) |
| *Appendicularians* | | | | | |
| *Megalocercus huxleyi* (Ritter) | - | sp. | small colony | in situ faecal pellet microscopy | Gorsky et al. (1999) |
| *Fish* | | | | | |
| *Gadus morhua* L. | larvae < 0.2 mg/4 mm | *pouchetii* | colonies | in situ gut microscopy | Krogstad (1989), Løken (1990) |
| *Pleuronectes flesus* L. | larvae < 11 mm | sp. | colonies | incubation, visual inspection and in situ gut microscopy | Lebour (1920) |
| *Scomber scombrus* L. | large from fish catches | *globosa* | *"phytoplankton chiefly P. globosa"* associated with jelly probably colonies | in situ gut microscopy | Bullen (1908) |

(−) denotes no information/not applicable. (?) denotes likely but unclear. Note that species composition within the genus *Phaeocystis* has been debated (Baumann et al. 1994; Sournia 1988). Because the solitary cells of *P. globosa*, *P. pouchetii* and others may not be distinguishable by light microscopy, reports before 1980 could be misleading [e.g., the species in Antarctica reported by Schnack (1983) and Metz (1998) may likely be *P. antarctica*, rather than *P. pouchetii*]. Where multiple references are available (mostly for calanoid copepods) only selected representative references are shown here. See text for more references.

some of these data were derived from ecologically unrealistic organisms or assays and should be interpreted with caution (see discussion below). Further, positive correlations between *Phaeocystis* abundance and mesozooplankton in the field have also been reported, and some of the negative effects have been debated and ascribed to other organisms (see Notes in Table 2). Furthermore, results from fatty acid analysis indicate that dominating crustacean zooplankton may derive a major part of their diet from *P. pouchetii* in northern latitudes (Sargent et al. 1985) and from *P. globosa* in lower latitudes (Hamm and Rousseau 2003), suggesting that *Phaeocystis* do enter the food web.

A number of factors have been shown to control predation on this enigmatic genus: predator-to-prey size ratio, predator species and stage, prey species, morphotype, growth state and abundance (reviewed in Weisse et al. 1994; Rousseau et al. 2000; Peperzak 2002; Schoemann et al. 2005). However, to our knowledge, a quantitative analysis of the interactive effect of these factors has not been attempted. Using available literature, we attempt to quantify the relative importance and interactions among some of these factors in controlling zooplankton grazing on *Phaeocystis* spp. We also review recent findings on various unique aspects of the life history and physiology of *Phaeocystis* spp., and how they affect zooplankton grazing. Last, we discuss the need for new methodological approaches to address some of the remaining questions concerning zooplankton grazing on *Phaeocystis*.

## Grazing on *Phaeocystis*: quantitative patterns in published data

Reports on copepods and other crustaceans dominate available zooplankton grazing data on *Phaeocystis* spp. These data show a wide range of rates, even for similar predator-prey combinations. We therefore attempt to summarize available quantitative data in relation to some of the mechanisms proposed to control the feeding on *Phaeocystis*. The shortage of quantitative feeding studies on microzooplankton and *Phaeocystis* was pointed out already a decade ago (Weisse et al. 1994), and the number of such studies is still limited, especially for protozoan microzooplankton, whether using laboratory cultures (Table 3) or natural plankton assemblages (Table 4) as food. Due to the shortage of protozooplankton data a general statistical analysis of the factors controlling their grazing on *Phaeocystis* cannot yet be performed, but the available data will be discussed further below.

### Crustacean zooplankton grazing on *Phaeocystis*: is there a general pattern?

It is generally assumed that a shift from single cell to colony may be part of *Phaeocystis* defense against grazing by microzooplankton (Weisse et al. 1994; Rousseau et al. 2000; Peperzak 2002; Schoemann et al. 2005). Because of the ability of *Phaeocystis* to vary its functional prey size by forming colonies, it is often considered as dual species (sensu Turner et al. 2002): colonies can be referred to as macroplankton and are assumed to be suitable food for zooplankton and nekton, while the solitary nanoplankton are assumed to be vigorously grazed by microzooplankton (Lebour 1922; Hollowday 1949; Admiraal and Venekamp 1986; Weisse and Scheffel-Möser 1990). On the other hand an increase in size may result in a more suitable prey size range for larger predators such as crustacean zooplankton. For palatable prey, ingestion rates generally increase from small prey to the optimum prey size before the prey becomes too large to handle or ingest (Frost 1972; Hansen et al. 1994a). Thus, size may be a major factor controlling predation on *Phaeocystis*.

Many studies showed that the size of *Phaeocystis* strongly influences the feeding rates of differently sized metazoan predators. Hansen et al. (1990) reported that *Calanus finmarchicus* copepodites (CI-V) showed lower feeding rate on *P. pouchetii* colonies of >100 μm than similarly sized diatoms, while in the 30–100 μm size range feeding rates on diatoms and colonies were similar. Tande and Båmstedt (1987) showed that copepodite stage V of *C. finmarchicus* fed equally well on *P. pouchetii* single cells and the diatom *Chaetoceros furcellatus*, whereas Huntley et al. (1987), using the larger copepod *C. hyperboreus* CIV-V, reported much higher grazing rates on colonies 25–200 μm and >200 μm than on single cells of *P. pouchetii* or the diatom *Chaetoceros socialis*. In a study with grazers of different sizes feeding on *P. pouchetii*, Hansen et al. (1994b) observed an optimal predator-to-prey size ratio for feeding and an upper size ratio above which no ingestion

**Table 2** Negative effects on various organisms ascribed to *Phaeocystis* spp., with notes on contradictory reports

| Effect | Note | References |
|---|---|---|
| *Protists and other microbes* | | |
| Defence against viral attacks by intact colony membranes | | Reviewed by Brussaard et al. (this volume) |
| Antibiotic to bacteria in the acid environment of penguin guts. | A | Sieburth (1960, 1961) |
| Haemolytic activity in laboratory, or correlated with abundance of *P. pouchetii* during blooms of natural planktonin mesocosms | | Stabell et al. (1999), van Rijssel et al. (this volume) |
| Suggested allelopathy, e.g., possible negative intercations by *P. pouchetii* on *T. nordenskioeldii* and *Skeletonema costatum* in vitro. Rapid decrease in abundance of *Thalassiosira nordenskioeldii* and *Ebria* sp. during a bloom of *P. pouchetii*. | | Barnard et al. (1984), Smayda (1973) |
| Allelopathy, filtrates from mesocosm blooms of *P. pouchetii* and laboratory cultures of *P. globosa* resulting in reduced growth and lysis of the cryptophyte phytoplankton *Rhodomonas baltica*. | | Long (Unpublished data) |
| Lack of feeding of the ciliates *Mesodinium pulex* and *Strombidium elegans* in laboratory experiments despite high concentrations of *P. globosa* and no alternative food. | | Hansen et al. (1993), Tang et al. (2001) |
| Low biomass of bacteria and protozooplankton during blooms of colonial *Phaeocystis* | B | van Boekel et al. (1992) |
| *Metazooplankton* | | |
| Many copepods show low abundances, development, gut content and/or much lower feeding activity compared to alternative food such as diatoms, during blooms of *Phaeocystis* | C | Bautista et al. (1992), Breton et al. (1999), Daro (1985), Davies et al. (1992), Frangoulis et al. (2001), Gasparini et al. (2000), Hansen and van Boekel (1991), Turner (1994), Weisse et al. (1994) |
| Low feeding by *Calanus* spp. and *Metridia longa* on actively growing colonies of *P. pouchetii* | D | Estep et al. (1990) |
| Low feeding by nauplii on some cell types of *P. globosa* | | Dutz and Koski (2006) |
| Low reproductive output from *Acartia* spp., *Temora longicornis, Pseudodiaptomus pelagicus* and *Eucalanus pileatus* feeding on *Phaeocystis*, despite sometimes high ingestion rates. | E | Klein Breteler and Koski (2003), Long and Hay (2006), Tang et al. (2001), Turner et al. (2002), Verity and Smayda (1989) |
| Inhibiting copepod feeding by transparent exopolymer particles (TEP) derived from a *Phaeocystis globosa*. | | Dutz et al. (2005) |
| Suggested reduction of zooplankton feeding due to mucus secretion from colonies of *P. globosa*. | | Seuront et al. (this volume) |
| Not a good food organism for the barnacle *Balanus balanoides* | | Cook and Gabbott (1972) |
| *Other organisms* | | |
| Oxygen deficiency due to sedimenting *Phaeocystis* killing less mobile fauna in the sediments. | | Rogers and Lockwood (1990) |
| Colonies clogging gills and thus reducing feeding in several mussels, especielly smaller, e.g., *P. globosa* colonies reduced feeding in *Mytilus edulis* <3 cm, while larger where able to filter colonies. | | Blauw (this volume), Kopp (1978), Meixner (1981), Petri et al. (1999), Pieters et al. (1980), Smaal and Twisk (1997) |
| Inhibited growth in the bryozoan *Electra pilosa* possibly due to *Phaeocystis.* | | Jebram (1980) |
| Toxic to sea urchin larvae | | Hansen et al. (2003, 2004) |
| Toxic to blowflies (*Calliphora omitoria*) | | Stabell et al. (1999) |

**Table 2** continued

| Effect | Note | References |
|---|---|---|
| Migrating herring hindered by a "barrier" of *Phaeocystis* blooms | F | Savage (1930, 1932) |
| Toxic to cod larvae | | Aanesen et al. (1998), Eilertsen and Raa (1995), Hansen et al. (2004) |
| Skin and eye irritation of humans | | Dunne et al. (1984) |

*Notes*:

A: It has also been reported that the high concentrations of acrylate in *Phaeocystis* colonies do not inhibit surrounding bacteria and may be absorbed to the mucus matrix (Noordkamp et al. 2000)

B: But when solitary cells are abundant during blooms (Admiraal and Venekamp 1986; Weisse and Scheffel-Möser 1990), or during the breakdown (van Boekel et al. 1992), microzooplankton such as ciliates may be numerous

C: There are also some reports on apparently increased abundances of mesozooplankton during periods of blooms of *Phaeocystis* (Fransz and Gieskes 1984; Fransz et al. 1992; Weisse et al. 1986)

D: But in a later bloom stage the copeods switch to selectively feed upon the senescent *P. pouchetii*, rather than the diatoms (Estep et al. 1990)

**Table 3** Quantitative laboratory studies on protozooplankton grazing on *Phaeocystis*

| Grazer | Alternative prey | Feeding on *P. globosa* | References |
|---|---|---|---|
| *Oxyrrhis marina* | No | Yes | Hansen et al. (1993) |
| *Strombidinopsis acuminatum* | No | Yes | Hansen et al. (1993) |
| *Strombidium elegans* | No | No | Hansen et al. (1993) |
| *Strombidium* sp. | No | Yes | Verity (2000) |
| *Noctiluca scintillans* | No | Yes | Jakobsen and Tang (2002) |
| *Gyrodinium dominans* | No | Yes | Tang and Simó (2003) |
| *Lohmanniella oviformis* | *Isochrysis galbana* | Lower | Tang et al. (2001) |
| *Rimostrombidium conicum* | *Isochrysis galbana* | Higher | Tang et al. (2001) |
| *Strombidium vestitum* | *Isochrysis galbana* | Higher | Tang et al. (2001) |
| *Gyrodinium dominans* | *Isochrysis galbana* | Higher | Tang et al. (2001) |
| *Gymnodinium* sp. | *Isochrysis galbana* | Lower | Tang et al. (2001) |
| *Mesodinium pulex* | *Gymnodinium* sp. | No | Tang et al. (2001) |

All experiments are based on particle disappearance and cell counts of cultured *P. globosa*, or cf. *globosa* in Hansen et al. (1993). Notes are given on whether the grazer feed (yes) or not at all (no) on *Phaeocystis*, or showed higher or lower feeding rates on Phaeocystis, compared to alternative prey offered in parallel single prey species incubations

occurs. These results were also supported by Levinsen et al. (2000), who reported ingestion of single *P. pouchetii* by the smaller females of *C. finmarchus* but not by the larger *C. glacialis* and *C. hyperboreus*. Also, the krill *Euphausia superba* (35–40 mm) showed similar feeding on 50–100 µm *P. antarctica* colonies compared to the diatom *Thalassiosira antarctica*, whereas both single cells and larger colonies of *P. antarctica* were grazed at lower rates compared to the diatom (Haberman et al. 2003). Thus, data such as these support the notion that substantial shifts in size between *Phaeocystis* life forms affect grazing by differently sized predators. However, there is still a considerable variation in feeding rates on various forms of *Phaeocystis*, ranging from zero to expected maximum rates (sensu Hansen et al. 1997) for a number of predators (reviewed in Weisse et al. 1994; Schoemann et al. 2005).

In order to evaluate the relative importance of factors other than size and how they may help explain the observed variations in grazing rates, we compiled the available quantitative data, converted them into carbon units, and performed a series of correspondence and cluster analyses described below.

**Table 4** Literature inferring quantitative evidence of microzooplankton community grazing (g) and grazing impact (percentage of average standing stock (SS) removed $d^{-1}$) on *Phaeocystis* solitary cells in natural plankton

| *Phaeocystis* spp. | Area | Time | Analysis | $\mu$ ($d^{-1}$) | $g$ ($d^{-1}$) | Impact (% SS $d^{-1}$) | Note | References |
|---|---|---|---|---|---|---|---|---|
| *MESOCOSM (natural plankton indoor tank)* | | | | | | | | |
| *globosa* | South North Sea | Sep | Cell Counts | ? – 0.3 – ? | 0.3–0.7 | 26–48 | | Brussard et al. (2005) |
| *FIELD* | | | | | | | | |
| *cf. globosa?* | South North Sea | Apr–May | Cell Counts | 0.8–2.3 | 0.9–4.2 | 59–98 | A | Weisse and Scheffel-Möser (1990) |
| *cf. globosa?* | South North Sea | Feb–Jul | Total Chl *a* | −0.3–0.4 | 0.0–0.6 | 0–46 | B | Brussard et al. (1995) |
| *globosa* | South North Sea | April | Total Chl *a* | 0.1–0.7 | 0.3–1.1 | 24–68 | | Stelfox-Widdicombe et al. (2004) |
| *pouchetii* | North Norway fjord | April | Total Chl *a* | 0.3–0.5 | 0.21–0.36 | 19–30 | C | Archer et al. (2000) |
| *pouchetii* | Labrador Sea | May–Jun | Total Chl *a* | 0.2–0.9 | 0.0–0.3 | 0–27 | D | Wolfe et al. (2000) |
| *antarctica* | Ross Sea | Oct–Apr | Chl *a* HPLC FC | ? | 0–0.23 | 0–21 | E | Caron et al. (2000) |
| *antarctica* | Antarctica | Nov–Mar | Chl *a* HPLC FC | 0.1–0.6 | 0.1–0.3 | 14–26 | E | Landry et al. (2002) |
| *antarctica* | Antarctica | Dec | Chl *a* HPLC FC | 0.2–0.9 | 0.1–1.0 | 10–63 | E | Selph et al. (2001) |

Specific phytoplankton growth rate ($\mu$) is also shown. All rates are quantified by the dilution technique (Landry and Hassett 1982). Prey concentrations were analyzed by cell counts, total chlorophyll *a* fractions (Total Chl *a*), high-performance liquid chromatography (HPLC), or flow cytometry (FC)

A: Incubation time only 5–14 h during the day

B: Instantaneous grazing (g) max $\leq 0.1$ $d^{-1}$ when the phytoplankton was dominated by *Phaeocystis*

C: Additional experiment with FLA (*Chlorella*). Only 5 of 13 tested ciliates ingested the labeled phytoplankton

D: Also measured dimethyl sulphide (DMS) dynamics. During *P. pouchetii* bloom *g* was 0.0 and 0.3

E: No notes on specific *Phaeocystis* rates

## Treatment of literature data

Many reports of crustacean grazing on *Phaeocystis* spp. are based on non-prey-specific gut fluorescence during blooms of *Phaeocystis*. An unknown fraction of such fluorescence may stem from prey other than *Phaeocystis*. Indeed, the often co-occurring diatoms may even be a preferred prey (Gasparini et al. 2000). In addition, more than half the total biomass (and chlorophyll) of the *Phaeocystis* colony may be due to diatoms and other organisms living in and on the colonies during late bloom stages (Sazhin et al. this volume). Therefore, we exclude data based on non-specific gut pigments of grazers feeding on mixed or natural food suspensions. We converted all grazing rate measurements into common currency of carbon units, using either (in the preferred order): (1) directly reported data, (2) data reported in accompanying papers, (3) personal communications with the authors, or (4) common conversion factors (such as those used in Hansen et al. 1997). For quantitative and statistical analyses we included only grazing data from studies that reported experiment location (field or laboratory study), grazer species, stage or size, and *Phaeocystis* average size (or size range). To be included in the statistical analysis the sources also must have reported *Phaeocystis* species, abundance, morphotype and growth state (exponential or stationary—either given in the text or assumed from the state of the bloom). See Table 5 for further details on the variables. The sources used are listed in Table 6.

## Statistical methods

To investigate relationships between crustacean grazing rates on *Phaeocystis* and experimental conditions, a multiple correspondence analysis (MCA) followed by a hierarchical cluster analysis (HCA) was performed using SPAD 3.5 software (Lebart et al. 1988). The combination of MCA and cluster analysis is a common way to explore relationships among a large number of variables and to facilitate interpretation of the correspondence analysis results (Lebart et al. 2000). MCA uses a contingency table as data, which provides a simultaneous representation of the observations (rows) and variables (column) in a factorial space. This form of multivariate analysis describes the total inertia (or variability) of a multidimensional

**Table 5** Active structural variables used in the multiple correspondence analysis (MCA). *n* denotes the number of observations from each source

| Description of variables: modalities | Label | *n* |
|---|---|---|
| *Experiment location* | | |
| Field | Field | 91 |
| Laboratory | Laboratory | 205 |
| *Crustacean predators* | | |
| *Acartia clausi* | Acl | 13 |
| *Acartia hudsonica* | Ahu | 5 |
| *Acartia tonsa* | Ato | 12 |
| *Pseudocalanus elongatus* | Pel | 13 |
| *Temora longicornis* | Tlo | 35 |
| *Temora stylifera* | Tst | 15 |
| *Metridia longa* | Mlo | 1 |
| *Centropages hamatus* | Cha | 14 |
| *Calanus finmarchicus* | Cfi | 105 |
| *Calanus glacialis* | Cgl | 8 |
| *Calanus hyperboreus* | Chy | 75 |
| Phaeocystis *species* | | |
| *globosa* | *P. globosa* | 107 |
| *pouchetii* | *P. pouchetii* | 189 |
| *Phaeocystis growth* | | |
| Exponential | Exponential | 277 |
| Stationary | Stationary | 19 |
| Phaeocystis *abundance* (Ab, µg C $l^{-1}$) | | |
| 0.1–125 | Ab1 | 81 |
| 125–250 | Ab2 | 91 |
| 250–500 | Ab3 | 37 |
| 500–1000 | Ab4 | 71 |
| 1000–1810 | Ab5 | 16 |
| *C-specific ingestion* (CI, $d^{-1}$) | | |
| 0–0.01 | CI1 | 83 |
| 0.01–0.1 | CI2 | 151 |
| 0.1–1.5 | CI3 | 62 |
| Phaeocystis *selection* | | |
| Positive selection | For | 14 |
| Negative selection | Against | 76 |
| Null selection | Null | 5 |
| Single prey | Single | 201 |
| *Predator-to-prey size ratio (P:p)* | | |
| 0.8–4 | P:p1 | 57 |
| 4–16 | P:p2 | 90 |
| 16–64 | P:p3 | 49 |
| 64–256 | P:p4 | 25 |
| 256–1120 | P:p5 | 75 |

**Table 6** Sources of data used for the multiple correspondence analysis (MCA) and hierarchical cluster analysis (HCA) presented in Fig. 1, and quantitative summary in Fig. 2, respectively

| References | Location | *Phaeocystis* | Fig. 1 *n* | Fig. 2 *n* |
|---|---|---|---|---|
| Antajan unpublished | Field | *globosa* | 6 | 6 |
| Dutz and Koski (2006) | Lab | *globosa* | 7 | 7 |
| Estep et al. (1990) | Field | *pouchetii* | 25 | 25 |
| Gasparini et al. (2000) | Field | *globosa* | 55 | 55 |
| Haberman et al. (2003) | Lab | *antartica* | | 3 |
| Hansen et al. (1990) | Lab | *pouchetii* | 62 | 62 |
| Hansen et al. (1993) | Lab | *globosa* | 5 | 5 |
| Hansen et al. (1994b) | Lab | *pouchetii* | | 20 |
| Huntley et al (1987) | Lab | *pouchetii* | 4 | 4 |
| Klein Breteler and Koski (2003) | Field | *globosa* | | 4 |
| Koski et al. (2005) | Field | *globosa* | 2 | 6 |
| Koski unpublished | Field | *pouchetii* | 3 | 3 |
| Tande and Båmstedt (1987) | Lab | *pouchetii* | 95 | 95 |
| Tang et al (2001) | Lab | *globosa* | | 4 |
| Turner et al. (2002) | Lab | *globosa* | 15 | 15 |
| Verity and Smayda (1989) | Lab | *globosa* | 9 | 9 |
| Verity (2000) | Lab | *globosa* | 8 | 12 |
| Weisse (1983) | Lab | *globosa* | | 18 |

*n* denotes the number of observations from each source

set of data, in a sample of fewer dimensions (or axes) that is the best summary of the information contained in the data (Greenacre 1984; Everitt and Dunn 2001). Our data set contains both categorical and continuous variables that were used in the MCA as active (Table 5) and illustrative variables (PL, ESD, CI and Ab defined below), respectively. The factorial axes of the MCA were computed using active (categorical) variables whereas the continuous illustrative (or supplementary) variables were simply projected into this factorial plane without participating in its computation. The location of these continuous illustrative variables, is shown as arrows along the factorial axes in Fig. 1A, and expresses their linkage to the pattern of the categorical active variables displayed by the factorial axes (Lebart et al. 2000). Observations with missing data for carbon-specific ingestion and experimental characteristics were excluded from the MCA. Only four observations with *Phaeocystis antartica* were available, and were therefore also excluded. A data matrix of the remaining 296 observations with eight active and four illustrative variables were used for the analyses (Table 5). The size of predators (prosome length; PL) and prey (equivalent spherical diameter; ESD) were treated as illustrative variables. These continuous variables were used to calculate a predator-to-prey size ratio (P:p) with five categories (or modalities) used in the statistical treatment. Similarly, C-specific ingestion (CI) and *Phaeocystis* abundance (Ab) were transformed into categorical variables of three and five categories, respectively, to be tested both as illustrative and active variables in the MCA. The metric used in the MCA is based on the $\chi^2$. This was also the metric used in the following cluster analysis. The type of HCA used here is an agglomerative clustering, i.e., a procedure that successively groups the closest objects into clusters, which then are grouped into larger clusters of higher rank (Legendre and Legendre 1998). The programme identifies: (i) the cluster (group of observations) which has the smallest within-group variance and the greater variance between groups, and (ii) the descriptors (variables) that are highly representative of each cluster. The descriptors of the observations used in the clustering were their factorial coordinates on the first six axes obtained in the MCA. These first six axes explained about 58% of the total variability (inertia) in the data, and the additional amount of variability explained by the axes decreased markedly after the first six axes.

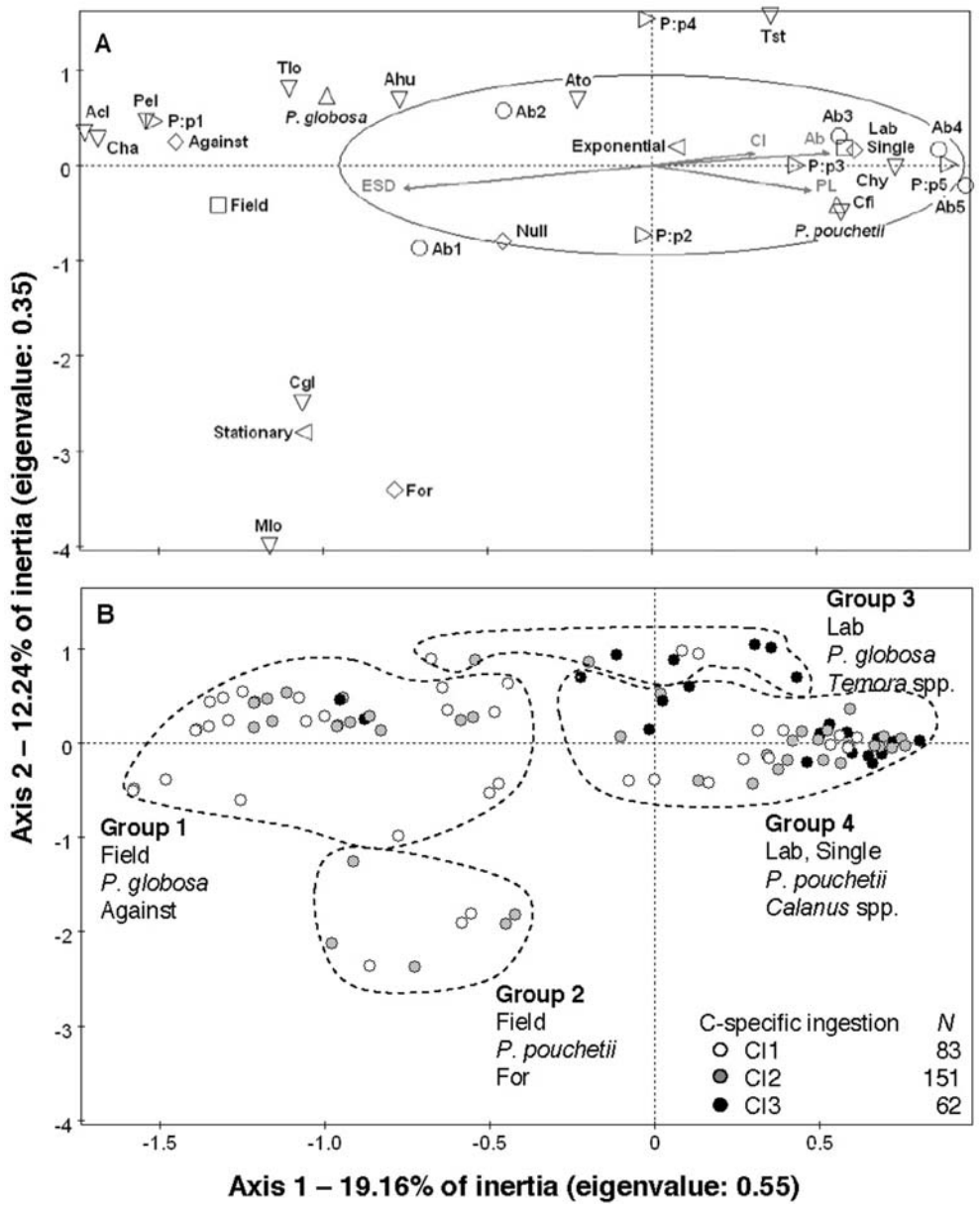


**Fig. 1** First factorial plane of MCA of data on crustacean grazing experiment on *Phaeocystis*. (**A**) Projections of continuous illustrative variables in the correlation circle (radius 1) and ordination of active variables: *Phaeocystis* species (Δ), growth (◁) and abundance (○), crustacean species (∇), predator-to-prey size ratio (▷), experiment location (□), selection (◇). (**B**) Ordination of data (○) labelled according to their C-specific ingestion characteristic and delimitation of the four groups designed by the hierarchical clustering ($\chi^2$ distance). See Table 5 for label identification

## Results from statistical analysis

The result of the MCA indicated that the first and second axes accumulate about 19% and 12% of the total variability, respectively (Fig. 1A). Two variables basically contribute to the first axis: the selection ("Against" and "Single", cumulated 18% of the contribution to axis 1) and the experiment location ("Lab" and "Field", cumulated 17.5% of the contribution). Thus, this axis differentiates laboratory experiments where *Phaeocystis* was the only prey ("Single"), as opposed to field experiments where

**Table 7** Characterization of the most typical properties of the four groups designed by the hierachical cluster analysis defined in Fig. 1 panel B

| Group *n* | 1 | | | 2 | | | 3 | | | 4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 82 | | | 15 | | | 27 | | | 172 | | |
| | Modality | gr/mod | mod/gr | Modality | gr/mod | mod/gr | Modality | gr/mod | mod/gr | Modality | gr/mod | mod/gr |
| Group characteristics | Against | 95 | 88 | For | 100 | 93 | P:p4 | 96 | 89 | Single | 84 | 98 |
| | *Field* | 80 | 89 | Stationary | 79 | 100 | Tst | 100 | 56 | *P. pouchetii* | 87 | 95 |
| | P:p1 | 96 | 67 | Ab1 | 19 | 100 | *P. globosa* | 25 | 100 | Lab | 82 | 98 |
| | *P. globosa* | 66 | 87 | Field | 16 | 100 | Tlo | 34 | 44 | P:p5 | 100 | 44 |
| | CI1 | 55 | 56 | P:p2 | 14 | 87 | Lab | 13 | 100 | Chy | 96 | 42 |
| | Cha | 100 | 17 | Cgl | 38 | 20 | CI3 | 19 | 44 | Cfi | 88 | 53 |
| | Acl | 100 | 16 | *P. pouchetii* | 7 | 93 | | | | Ab4 | 86 | 35 |
| | Pel | 100 | 16 | | | | | | | Exponential | 62 | 100 |
| | Ab1 | 48 | 48 | | | | | | | P:p3 | 88 | 25 |
| | Tlo | 63 | 27 | | | | | | | Ab5 | 100 | 9 |
| | Ab2 | 44 | 49 | | | | | | | CI3 | 77 | 28 |
| | | | | | | | | | | CI2 | 66 | 58 |

Gr/mod corresponds to the percentage of the modality belonging to the group, and mod/gr corresponds to the percentage of the group belonging to the modality. Modality label as in Table 5. *n* denotes the number of observations

alternative prey were available and *Phaeocystis* was selected against ("Against"). The predator-to-prey size ratio modality "P:p1" (size ratio < 4) also has an important contribution to the first axis (10%), showing that small copepods (such as *Centropages hamatus*, *Acartia clausi* and *Pseudocalanus elongatus*) tend to reject *Phaeocystis* in situ. On axis 2, the two modalities "Stationary" and "For" have the greatest contribution (18% and 20%, respectively). This axis separates grazing experiments where *Phaeocystis* in a stationary growth phase was selected positively by predators in situ. In the first factorial plane we also observed that *Phaeocystis* concentration and predator-to-prey size ratio in lab experiments were higher than what was generally observed in situ (Fig. 1A) and that higher carbon-specific ingestions were mostly related to laboratory experiments (Fig. 1B).

The combined analysis of the MCA and HCA clearly distinguished four groups of observations (Fig. 1B and Table 7). Groups 1 and 2 bring together 97% of the grazing experiments performed in the field and are separated from groups 3 and 4, which comprise 96% of the lab experiments with *Phaeocystis* provided as single prey. Group 1 consists of field experiments with small-size copepods selecting against *P. globosa*. Group 2 includes all field experiments with positive selection for *P. pouchetii* (93% of the group), and is characterized by a slightly higher predator-to-prey size ratio (87% of them had a P:p-ratio of 4–16, "P:p2"). In these experiments *Phaeocystis* was in the stationary growth phase and in relatively low abundance ("Ab1" = abundance between 0.1 and 125 μg C $l^{-1}$). The group 3 is characterized by lab grazing experiments of *Temora* spp. on *P. globosa*. The predator-to-prey size ratio in these laboratory experiments was higher (89% of them had a P:p ratio of 64–256, "P:p4") than what was commonly observed in grazing experiments on natural plankton. Similarly we observed higher carbon-specific ingestion than what was observed in situ for this copepod genus (group 1). Group 4 brings together the lab grazing experiments on *P. pouchetii* by larger copepods (*Calanus* spp.). This group includes the highest *Phaeocystis* abundance and predator-to-prey size ratio tested in lab experiments and grouped the highest carbon-specific ingestion estimates.

In conclusion, the MCA and the HCA analyses suggested that: (1) the lowest grazing rates from the field (often zero) were recorded for small copepods (*Acartia*, *Pseudocalanus*, *Temora* and *Centropages*) in blooms of *Phaeocystis globosa* colonies, (2) large copepods (e.g., *Calanus*) feeding on *Phaeocystis pouchetii* had higher grazing rates, especially in lab studies, when no alternative food was present and (3)

*P. pouchetii* in a stationary growth phase was positively selected by large copepods.

It is important to note that grazing data for large copepods (*Calanus* spp. and *Metridia longa*) were only available for *P. pouchetii*, whereas grazing studies with small copepods (*Acartia*, *Centropages*, *Pseudocalanus* and *Temora*) were limited to *P. globosa*. Thus, the presently available data do not allow us to determine whether the different results for *P. pouchetii* and *P. globosa* are due to differences between the two species, or differences between the predators. In order to test for species-specific differences, we need to compare grazing on both species simultaneously using similar methodologies in future studies.

## Quantitative results from data on crustacean grazing

Because the statistical analysis suggested a large difference between feeding rates in laboratory and field investigations, we compared the average specific ingestion rates in all available field and laboratory experiments (Table 6), and for five groups of predator-to-prey size ratios separately (Fig. 2). These comparisons revealed that: (1) overall feeding (carbon specific ingestion) on *Phaeocystis* spp. was significantly lower [$p < 10^{-8}$, analysis of variation (ANOVA)] in all field (average 2.5% $d^{-1}$) studies with natural plankton, compared to laboratory studies (average 11% $d^{-1}$), (2) the highest average carbon-specific ingestion rate (23% $d^{-1}$) on *Phaeocystis* spp. was found when the predator-to-prey size ratio (P:p) was 4–16 in lab studies, whereas there was no clear size ratio trend in field studies, and (3) ingestion was low ($\leq$2% $d^{-1}$) when P:p was < 4 in both lab and field, indicating that the upper effective size limit for prey equivalent spherical diameter was ¼ of the predator prosome length.

Thus, crustacean grazers show a much lower grazing on *Phaeocystis* in the field than in the laboratory. One reason for this discrepancy could be that fewer than 5% of the laboratory studies offered the copepods alternative prey to *Phaeocystis* whereas alternative prey were available in the field. Alternatively, laboratory cultures might not display the same chemical grazing cues (and possible grazing deterrents) as *Phaeocystis* growing in natural plankton. Haptophytes may lose their inhibitory effects in vitro, and toxicity may be species-, strain- or growth-condition-

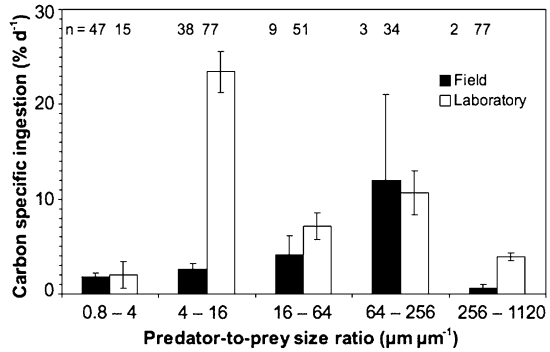


**Fig. 2** Crustaceans (all stages of copepods and krill) grazing on *Phaeocystis pouchetii*, *P. globosa* or *P. antarctica*, in laboratory and field experiments. Average daily carbon-specific ingestion rates (percent µg C µg $C^{-1}$ $d^{-1}$) are presented for five different predator-to-prey size categories [derived from predator prosome or carapace length and average equivalent spherical diameter (ESD) of the *Phaeocystis* prey, solitary cells or colonies]. Error bars denote the standard error (SE) of the average; the number of observations (*n*) for each category are given above each column. Note the high daily ration for P:p size ratio 64–256 in the field is due to a single (30%) value (with that value excluded, the rate is 3.0 ± 1.0 %)

specific (Edvardsen and Paasche 1998). Support for this hypothesis comes from laboratory studies that failed to recreate toxicity in the lab that was observed in the field, even with haptophytes isolated from highly toxic blooms, such as the *Chrysochromulina polylepis* bloom in 1988 (Nielsen et al. 1990). Likewise, the antipredation effect revealed by Estep et al. (1990) in actively growing field-collected *Phaeocystis pouchetii* apparently disappeared during the first 12 h in experimental containers. It may be that laboratory or other in vitro studies underestimate the negative effects of potentially toxic haptophytes in situ, but this requires explicit evaluation.

Ideally, future investigations on the ecology of zooplankton feeding should preferably be conducted in situ, although laboratory experiments are needed to investigate the effects of potentially important signaling substances between *Phaeocystis* and different predators in presence of realistic alternative prey.

## Grazing by protozooplankton and other microzooplankton

General trends in grazing by protozoan microzooplankton on *Phaeocystis* are difficult to assess since the number of quantitative investigations is limited (Tables 3 and 4). Very few studies have investigated

**Table 8** Microzooplankton grazing on *Phaeocystis globosa* solitary cells during blooms in the English Channel off northen France May 2003 and April 2004 (JC Nejstgaard, AF Sazhin and LF Artigas unpubl.)

| Date | Prey type (μm) | $r^2$ | $\mu$ ($d^{-1}$) | $G$ ($d^{-1}$) | Grazing impact (% SS $d^{-1}$) |
|---|---|---|---|---|---|
| Apr 2003 | Chl *a* (>0.45) | 0.58 | $0.24 \pm 0.07^{**}$ | $0.61 \pm 0.14^{***}$ | 46 |
| | Diatoms (5-99) | 0.45 | $1.34 \pm 0.18^{***}$ | $1.24 \pm 0.40^{**}$ | 71 |
| | *Phaeocystis* (2-8) | 0.04 | $0.08 \pm 0.16$ ns | $0.21 \pm 0.30$ ns | 19 |
| May 2004 | Chl *a* (>0.45) | 0.13 | $-1.17 \pm 0.12^{***}$ | $0.18 \pm 0.18$ ns | 17 |
| | Diatoms (5-99) | 0.18 | $0.16 \pm 0.09$ ns | $0.19 \pm 0.13$ ns | 18 |
| | *Phaeocystis* (2-8) | 0.04 | $-1.14 \pm 0.20^{***}$ | $-0.23 \pm 0.34$ ns | 0 |

Dilution experiments were performed and analyzed as decribed in Nejstgaard et al. (2001). Specific phytoplankton growth rate ($\mu$), microzooplankton grazing coefficient ($g$), grazing impact (percentage of average standing stock removed $d^{-1}$ ). ±SE for the mean. * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$ for $\mu$ or $g = 0$. Prey types are given with equivalent spherical diameter size ranges (μm)

microzooplankton as potential grazers on colonial *Phaeocystis* spp. The colonies are protected by a tough skin (Hamm et al. 1999) and microzooplankters are generally assumed to be too small to prey actively on colonial forms of *Phaeocystis* (Hansen et al. 1994a; Weisse et al. 1994; Tang 2003). In accordance, Irigoien et al. (2003) reported that nauplii of *Calanus finmarchicus* did not ingest colonies of *Phaeocystis* in the Irminger sea. However, the protists *Noctiluca scintillans* (Weisse et al. 1994; Jakobsen and Tang 2002) and apparently *Gyrodinium cf. spirale* (Stelfox-Widdicombe et al. 2004) are able to ingest small colonies, while some tintinnids and rotifers "attack" and "hover around colonies", possibly ingesting released cells (Hollowday 1949; Admiraal and Venekamp 1986). The abundance of microzooplankton has also been reported to decline or remain low during natural blooms of colonial *Phaeocystis*, but increases rapidly during the breakdown of the colonies at the end of the bloom (e.g., Peperzak et al. 1998; van Boekel et al. 1992). This suggests that actively growing colonies are inferior prey for microzooplankton, while single cells released from decaying colonies may be a suitable food source. However, an alternative explanation for the low microzooplankton abundance during *Phaeocystis* blooms is the strong selective predation pressure from larger zooplankton such as copepods (Hansen et al. 1993; Gasparini et al. 2000).

It is clear from the literature that at least some microzooplankton may readily ingest single-celled *Phaeocystis* (Tables 3 and 4), and chemical cues from microzooplankton grazing have been shown to induce colony formation (Long and Hay 2006) and enlargement in *P. globosa* (Tang 2003), supporting the assumption that microzooplankton graze on the single cells but not the colonies. However, some of the reported grazing rates in laboratory studies were low, with or without alternative prey present (Table 3). Also, in several incubation experiments with natural plankton the microzooplankton community grazing rates were very low ($\leq 0.1\ d^{-1}$) during dominance of *Phaeocystis* (Table 4). It is well known that some microzooplankton feed selectively (e.g., Verity 1988; González et al. 1990; Strom and Loukos 1998; Archer et al. 2000), and it was recently shown that copepod nauplii ingest some clones and cell morphotypes of *P. globosa* at low rates (Dutz and Koski 2006). Results showing selection against single cells by microzooplankton in the sea was obtained in recent dilution experiments in the English Channel (Table 8). These experiments yielded zero or close to zero microzooplankton grazing rates on single-celled *P. globosa*, but high microzooplankton grazing rates on diatoms based on cell counts, while bulk measurements of chlorophyll *a* (as used in most of the experiments in Table 4) indicated intermediate grazing values. This suggests that microzooplankton feeding on *Phaeocystis* may be highly variable in the sea, and reliable grazing rate measurements will therefore require taxon-specific quantitative methods, rather than bulk measurements (see further discussion under Future challenges).

## Cell-type and life-stage-specific interactions with grazers

In the species *P. globosa*, three solitary, flagellated cell types (micro-, meso, and macroflagellates)

differing in size and morphology have been described (Kornmann 1955; Peperzak et al. 2000). The ecological roles of these different cell types are largely unknown, partly due to difficulties in the identification and quantification of the flagellated cell type in field samples (Rousseau et al. 1994; Peperzak et al. 2000; Schoemann et al. 2005; Rousseau et al. this volume). A recent study showed that the grazing mortality of single cells may depend on the cell type, with moderate to high ingestion by *Temora longicornis* nauplii on non-flagellated cell types, but rejection of a flagellate type (Dutz and Koski 2006). This rejection was ascribed to the production of chitinous threads and the cohesion of threads into pentagonal star-like structures which are a typical feature of mesoflagellates (Chretiennot-Dinet et al. 1997; Peperzak et al. 2000).

The variable cell-type-specific grazing mortality of *P. globosa* offers important insight into the natural history of this phytoplankton species. Although flagellated and non-flagellated cell types co-occur throughout the year, blooms of *Phaeocystis* in temperate waters are generally dominated by the colonial cell type and by colonies (Peperzak et al. 2000; Rousseau et al. this volume). At the end of such blooms, single cells are released from the colonies presumably due to nutrient deficiency or irradiance limitation. The liberated cells appear to suffer a high mortality due to microzooplankton grazing, cell lysis and/or perhaps sedimentation (van Boekel et al. 1992; Brussaard et al. 1995; Riebesell et al. 1995; Brussaard et al. this volume; Reigstad & Wassmann this volume). Concurrent to the liberation and disappearance of single cells, an increasing abundance of micro/mesoflagellates has been observed in mesocosms and in the field (Veldhuis et al. 1986; Peperzak et al. 2000; Escaravage et al. 1995; Nejstgaard et al. 2006). The formation of intracolonial flagellated cells may bridge the disappearance of colonial cells and the appearance of flagellated cells (Peperzak et al. 2000). These haploid micro/mesoflagellates probably function as gametes or spores to survive unfavourable conditions during the warm summer months (Veldhuis et al. 1986; Peperzak et al. 2000). Reduced vulnerability of these cells to microzooplankton grazing could explain the accumulation of single flagellated cells despite a high grazing pressure at the end of *Phaeocystis* blooms, and be part of these phytoplankters' strategy to increase survival and foster bloom formation when favorable conditions return. Future studies should investigate the relevance of cell type- and life-stage-specific selection on wider range of zooplankton organisms.

## Colony formation and its potential role in morphological defense

The presence of the two distinctly different morphotypes in *Phaeocystis* has long intrigued scientists, and much remains unknown about their respective biological roles and regulation of transition between morphotypes (Rousseau et al. 1994; Lancelot et al. 1998; Rousseau et al. this volume). The prevalence of both morphotypes in natural *Phaeocystis* blooms in contrasting water types prompts the idea that *Phaeocystis* colony development is regulated by common factors (Lancelot and Rousseau 1994) and contributes to the success of the genus in marine systems (Rousseau et al. 1994; Lancelot et al. 1998; Rousseau et al. this volume). The production of the mucilaginous structure represents a substantial energy investment by the cells; the mucilaginous matrix may account for >50% of the total organic carbon of a *Phaeocystis* population (Rousseau et al. 1990; Mathot et al. 2000). The large colony size may also pose a problem of diffusion limitation to nutrient and oxygen uptake, although a modeling study shows that the colonies are unlikely to be limited by diffusion (Ploug et al. 1999). Thus, compared to solitary *Phaeocystis* cells, it is likely that the formation of colonies involves some additional costs, but that the drastic increase in size may be an effective defense mechanism against (relatively) small grazers, not unlike the highly successful freshwater colonial chlorophyte *Scenedesmus* (Lürling 2003; e.g., Lürling and Van Donk 1997), cyanobacteria *Microcystis aeruginosa* and *Sphaerocystis* sp. (e.g., De Bernardi and Giussani 1990), and for different copepods feeding on the large colony-forming diatom *Thalassiosira partheneia* (Schnack 1983).

Some studies suggest that microzooplankton prefer and perform better on single cells than on colonies. When incubated with a mixture of *Phaeocystis globosa* single cells and colonies, microzooplankton reduced the single cells to very low abundance, and the grazer population subsequently declined even when colonies were abundant, presumably due to starvation (Jakobsen and Tang 2002). When restricted

to a single diet of either single cells or colonies, the ciliate *Euplotes* grew three times faster on single cells (Long 2004). In contrast, the copepod *Acartia tonsa* and mixed mesozooplankton had higher feeding rates on colonies compared to single cells (Long and Hay 2006). The differential susceptibility of morphologies to grazers could allow *Phaeocystis* to use transformations as an adaptive, inducible response towards grazers. Two recent studies tested the role of chemical cues for inducing transformations using either incubators separated by a permeable membrane (Tang 2003) or filtrate experiments (Long 2004). In one study chemical cues from grazers triggered colony enlargement (Tang 2003). In the other study microzooplankton cues enhanced colony formation while cues from macrozooplankton suppressed colony formation (Long 2004). These observations point to the involvement of a grazing-related chemical signal in morphological defense, but the chemical characteristics of this signal remain unknown (Long and Hay 2006; Tang 2003). Colony formation by *Phaeocystis* could affect grazing even after the demise of a bloom. For example, the degrading colony matrix, making the surrounding water gelatinous, may continue to prevent grazing losses of single cells by microzooplankton (Seuront et al. this volume), and similarly, transparent exopolymer particles formed by coagulation of colony-derived carbohydrates could also inhibit copepod grazing (Dutz et al. 2005).

## Chemical defense

Macroalgae commonly use chemical defense against grazers (Hay and Fenical 1988; Pohnert 2004), and similar examples may exist in phytoplankton (see review by Pohnert 2004; and further examples in Yoshida et al. 2004; Pohnert 2005). A few observations suggest that chemical defense could be important for survival of *Phaeocystis* during exponential growth (Weisse et al. 1994; Estep et al. 1990; Long and Hay 2006). Recently, a number of toxins have been isolated from *Phaeocystis* (reviewed by van Rijssel et al. this volume), and *Phaeocystis* is reportedly toxic to some aquatic organisms, including phytoplankton, sea urchin and cod larvae (Table 2). However, specific chemical zooplankton feeding deterrents from *Phaeocystis* have not yet been isolated and characterized so their existence is still hypothetical. Several of the reported toxic effects were obtained using organisms (or even extracts) that do not interact in nature, and the ecological relevance of such results is unknown.

## Does DMS affect grazing on *Phaeocystis*?

*Phaeocystis* is a prominent producer of the secondary metabolite dimethylsulphoniopropionate (DMSP) that can be enzymatically cleaved to acrylate and the volatile trace gas dimethyl sulphide (DMS; Keller et al. 1989; Schoemann et al. 2005; Stefels et al. this volume). DMSP is a multifunctional compound that probably assists several physiological processes related to salinity-, temperature- and light-stress in algal cells (Stefels 2000). This compound and its cleavage products have also been suggested to function as grazing deterrents (Strom et al. 2003; Wolfe et al. 1997) and it is possible that they provide a competitive advantage to *Phaeocystis* when non-DMSP-producing alternative prey are available to potential predators. Microzooplankton grazing greatly increases the production of DMS in *Emiliania huxleyi* (Wolfe and Steinke 1996) and microzooplankton are suspected to have caused the conversion of *Phaeocystis*-DMSP to DMS in the southern North Sea (Archer et al. 2003). The grazing-induced production of DMS may be analogous to the production of volatile infochemicals during herbivore grazing on terrestrial plants that utilize such trace gases to attract carnivores (Dicke and Sabelis 1988; Steinke et al. 2002; Hay et al. 2004). Such indirect defense mechanisms involve interactions on three trophic levels that include plants, herbivores and carnivores. Seabirds are attracted by gradients of DMS in the atmosphere (Nevitt et al. 1995; Nevitt and Bonadonna 2005), and copepods are chemosensitive to DMS and react with search behavior when encountering plumes of this compound (Steinke et al. 2006). If DMS produced during grazing makes the microzooplankton grazers more susceptible to predation by copepods, then investment into such an indirect defense mechanism could be beneficial for the phytoplankton.

However, the ecological consequences of the production of DMS and associated compounds are controversial and explicit tests of possible defensive functions for *Phaeocystis* are required. For example, Tang and Simó (2003) did not observe negative

effects when the heterotrophic dinoflagellate *Gyrodinium dominans* grazed on *P. globosa* single cells, and the grazers retained >40% of the ingested DMSP. Furthermore, the grazing-induced production of DMS by unicellular phytoplankton is a result of grazing on individual cells and, as a consequence, these ingested cells will not directly benefit from the potential signaling to carnivorous enemies of the microzooplankton. It is possible that such indirect defense mechanisms are beneficial for *Phaeocystis* populations but they would also be of benefit to other members of the phytoplankton community that may not invest in chemical defenses (the cheater problem: Lewis 1986). One may argue that the cheater problem does not exist within a bloom of genetically closely related cells. However, molecular studies have shown that the genetic variation in phytoplankton populations is high, even within a monospecific diatom bloom (Rynearson and Armbrust 2005). It is impossible to predict functional diversity from such molecular data and there is very little information on the effect of genetic variation on the ecophysiological fitness in *Phaeocystis*.

Evidence is accumulating that chemical communication influences the composition and dynamics of pelagic communities (Pohnert 2004). The production of DMSP in *Phaeocystis* is probably only one example where a secondary metabolite benefits the physiology of individual cells and its catabolic products could affect the structure and function of *Phaeocystis*-dominated food webs. This is a complex research area that needs to be addressed with more detailed studies in the future.

## Does nutritional value affect grazing on *Phaeocystis*?

Copepods may feed selectively based on nutritional quality of the prey (e.g., Houde and Roman 1987). However, it is not clear how food quality of the different forms of *Phaeocystis* affects zooplankton grazing. It has been suggested that *Phaeocystis* spp. are of low nutritional value due to their low content of polyunsaturated fatty acids (PUFA) (Al-Hasan et al. 1990; Claustre et al. 1990; Rogers and Lockwood 1990; Nichols et al. 1991; Cotonnec et al. 2001; Tang et al. 2001; Turner et al. 2002). This contrasts with the high survival and development rates observed in other studies (Verity and Smayda 1989), at least for some strains of *P. globosa* (Dutz and Koski 2006). High amounts of $C_{18}$-PUFA were detected in a *P. globosa* bloom in the North Sea (Hamm and Rousseau 2003) and in a *P. pouchetii* bloom in Balsfjorden in northern Norway (Hamm et al. 2001). The mucus produced by colonies is generally considered to be of low nutritional value, refractory (Thingstad and Billen 1994), and of low carbohydrate content (van Rijssel et al. 1997). However, the composition of the mucus material may vary during a bloom cycle (Alderkamp et al. 2006), and colonization of this material by pennate diatoms and other organisms on and inside older colonies (Hamm and Rousseau 2003; Sazhin et al. this volume) may increase its nutritional value. Besides PUFA and carbohydrates, the effects of other important nutritional components of *Phaeocystis* such as amino acids, sterols and vitamins, on copepod feeding and reproduction are still poorly known.

## Survival of gut passage?

Some phytoplankton can survive gut passage, a trait that is often overlooked in zooplankton studies. For instance, large fractions of the chlorophytes *Chlamydomonas reinhardtii* and *Selenastrum capricornutum* survive passing the guts of *Daphnia*. This is considered a defense mechanism by the algae to reduce grazing pressure when their growth rates are low (van Donk et al. 1997). Further, the colonial chlorophyte *Sphaerocystis schroeteri* survives gut passage in *Daphnia* and benefits from grazer-released nutrients. This interaction is hypothesized to affect bloom formation in this species (Porter 1976). If cells of *Phaeocystis* may survive gut passage of zooplankton, this would have significant implications for the understanding of the grazing interactions. Because, net removal rates of the prey from the population will decrease, and if cells may produce defense chemicals upon predation and surviving gut passage it would affect the chemical antipredatory mechanisms suggested above. But, to our knowledge there are no such studies for *Phaeocystis* or any other haptophyte phytoplankton. However, small intact colonies of *P. pouchetii* have been observed fluorescing inside copepod pellets in the Barents Sea (P. Verity and P. Wassmann, personal communication) suggesting that surviving gut passage might be possible for *Phaeocystis*.

## Conclusions and future challenges

Although over 100 publications have examined zooplankton grazing on *Phaeocystis* spp., more than 90% report on copepods or other crustacean grazers, so quantitative data for other grazers are limited. Grazing on *Phaeocystis* was often determined by feeding on only single types of cultured phytoplankton in the laboratory. Field reports often do not provide enough information to evaluate even some of the most basic factors known to affect zooplankton grazing simultaneously, such as predator-to-prey size ratio, food concentration and feeding rates on alternative prey. Further, most reports on crustacean grazing in the field are based on non-prey-specific grazing estimations such as bulk gut pigments, that cannot be used to determine specific feeding on *Phaeocystis* in the mixed natural plankton assemblages.

Nevertheless, our analysis of the present literature suggests 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.

In the present literature there is a dichotomy between data showing high feeding rates on both single cells and colonies of *Phaeocystis pouchetii* by larger copepods, especially in the laboratory studies, and avoidance of colonies of *Phaeocystis globosa* by other smaller copepods in the field. This imbalance in basic quantitative data could initially be remedied by applying classical bottle incubation methods with a range of predators, preferably using natural plankton in situ, analyzed with methods that resolve the feeding rates on the different life forms (and prey sizes) of different species of *Phaeocystis* from alternative prey types. Such analyses could be done by microscopy (Verity and Paffenhöfer 1996; Båmstedt et al. 2000) corrected for food web cascades (Nejstgaard et al. 2001), and/or possibly analyzed by a combination of more recent methods such as flow cytometry (Collier and Campbell 1999; Jonker et al. 2000), computer/video-aided plankton counting devices (See et al. 2005), and specific molecular probing (Caron 2005) to increase the taxonomic precision. However, the ability of chemical cues to rapidly alter colony formation indicates that grazing estimates based on cell counts could grossly misrepresent actual grazing rates.

For example, zooplankton grazing may induce or suppress colony formation and enlargement (Tang 2003; Long 2004; Long and Hay 2006), and accumulating data suggests that chemical signaling between different levels of predators of prey can play an important role influencing the dynamics in pelagic communities (e.g., reviewed by Pohnert 2004; Yoshida et al. 2004). This suggests that chemical signaling in artificially increased grazer densities over long incubations could confound data from bottle experiments by changing the relative abundance of different life forms in the grazing bottle due to factors other than direct ingestion of the cells. Further, recent results suggesting that feeding on *Phaeocystis* may even be cell type- or life-stage-specific (Dutz and Koski 2006), and that new methods accounting for such differences are necessary.

Thus, the ideal way to assess feeding on *Phaeocystis* would be a direct quantification of feeding rates on specific prey by assessing individual predators that have been feeding undisturbed in situ. Molecular quantitative analysis of the prey in the guts and faecal pellets of the predators could potentially achieve this. Such approaches are already common in studies of e.g., terrestrial arthropods (Sheppard and Harwood 2005; Symondson 2002), and it has been shown that prey DNA from haptophyte phytoplankton can be detected in copepod guts and fecal pellets by standard polymerase chain reaction (PCR) targeting 18S ribosomal DNA (Nejstgaard et al. 2003). More recently, it was also shown that carnivorous diet may be inferred from the content of copepod fecal pellets using standard PCR (Vestheim et al. 2005), and that different phytoplankton DNA, including *Phaeocystis*, may be quantified in guts and fecal pellets from both appendicularians

and copepods using quantitative real-time PCR (Nejstgaard et al. 2005; Troedsson et al. 2007).

Thus the rapidly developing molecular approaches may help us obtain more-realistic ingestion rates of *Phaeocystis* and other live prey in situ. However, to further reveal and quantify mechanisms controlling the complex trophic interactions between *Phaeocystis* and its predators, new approaches need to be developed. In concert with the recent review by Pohnert (2004) we conclude that such development will probably be as complex as the interactions it tries to reveal. Developing successful innovative approaches and better quantitative analytical tools will depend largely upon multidisciplinary efforts between chemists, molecular biologists and plankton ecologists.

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