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The trophic significance of *Phaeocystis* blooms

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Abstract

Both colonies and solitary cells of the prymnesiophyte *Phaeocystis* are ingested by a wide array of marine vertebrates. Grazers include protozoa, bivalves, amphipods, euphausiids and many copepod species. Common fish species such as mackerel (*Scomber scombrus*) and flounder (*Pleuronectus flesus*) have also been reported to feed upon *Phaeocystis*. While qualitative observations on the potential trophic significance of *Phaeocystis* exist for a long time, attempts to quantify feeding rates on *Phaeocystis* have begun only during the last decade. In feeding experiments, copepods have received most attention. Many copepod species appear to consume *Phaeocystis* colonies and solitary cells in the North Atlantic and in polar seas. Ingestion rates are highly variable depending on size and physiological state of *Phaeocystis* as well as on copepod species. Within the same species, large variations in individual feeding rates have been reported from different areas and investigators. When *Phaeocystis* co-occurs with larger amounts of diatoms, the latter seem to be preferred by some copepod species while others do not select against *Phaeocystis*. At present it is unclear whether this is primarily due to unsuitable size of *Phaeocystis* or because it is poor quality food. The relative nutritive value of *Phaeocystis* single cells and colonies should be investigated in more detail. Feeding of protozoa on *Phaeocystis* has been little studied. Ciliates and the giant dinoflagellate *Noctiluca* are known to consume *Phaeocystis* solitary cells. Protozoa might efficiently control *Phaeocystis* blooms during their initial phases when the share of solitary cells relative to total *Phaeocystis* biomass is higher than during later stages of the bloom. By switching their food preference towards heterotrophic food, copepods might benefit from enhanced protozoan biomass during *Phaeocystis* blooms. The potential succession of protozoan and metazoan grazers in the course of a *Phaeocystis* bloom awaits further research.

1. Introduction

The dynamics of *Phaeocystis* blooms have recently been intensively studied (Lancelot, 1984; Eberlein et al., 1985; Weisse et al., 1986). However, distinct indications of their trophic significance in the food webs are scarce, with considerable contradictory evidence. Whereas some authors point to the nutritive value of *Phaeocystis*

(e.g. Claustre et al., 1990), others reported diverse adverse effects of *Phaeocystis* blooms on the ecosystem, including growth inhibition of bacteria and certain algae (Sieburth, 1959, 1960, 1961, 1964; Smayda, 1973), clogging of mussel gills and copepod mouth parts leading to decreased effective feeding by these organisms (Kopp, 1978; Pieters et al., 1980; Meixner, 1981), and oxygen deficiency caused by the respiration

of living *Phaeocystis* cells and by bacterial degradation of sedimented material (Kopp, 1978). Commercially, the clogging of fishing nets leading to reduced catches has been a problem since the beginning of this century (Hardy, 1926).

In order to clarify our present knowledge of the significance of *Phaeocystis* blooms as food for plankton and benthos organisms, this article is a review of literature derived from field studies and laboratory investigations. The issue of species number within the genus *Phaeocystis* has long been debated in the literature (Sournia, 1988; Baumann et al., 1994). The results summarized here deal with *P. pouchetii* (Hariot) Lagerheim and *P. globosa* (Scherffel) which apparently differ in temperature tolerance and colony morphology (cf. Baumann et al., 1994). The niches of both species overlap in the North Sea (Rick and Aletsee, 1989), from where much information on the trophic significance of *Phaeocystis* originated. Since authority cannot be attributed unequivocally to some of the older records, and because the single cells of both species cannot be separated microscopically, they are not differentiated in this review. Rather, the grazing of various zooplankton species is discussed in relation to the size of the respective *Phaeocystis* colonies. Recent reports on the conversion of *Phaeocystis* material through the microbial food web are also discussed.

2. *Phaeocystis* and Metazoan grazers: an historical perspective

2.1. Observations and qualitative studies

Early observations of ecological impacts of *Phaeocystis* blooms on the pelagic food web were made during the first decades of this century in the waters off Plymouth, England. These observations were part of investigations into relationships between the occurrence of plankton and commercially important fish. In 1908, large quantities of *Phaeocystis* were found in mackerel stomachs (Bullen, 1908). Some years later, Lebour (1919) showed that young flounders also feed largely on *Phaeocystis*. Broadening her investigations into

the nutrition of Plymouth zooplankton, Lebour reported from gut examinations that "*Phaeocystis* serves as food for many of the plankton organisms, including *Calanus*, *Temora* and *Evadne*" (Lebour, 1922, p. 646). However, Hardy (1926) identified an inverse relationship between *Phaeocystis* and herring catches. This was the first description of adverse effects of *Phaeocystis* blooms on certain members of the pelagic food web. Shortly thereafter Savage (1930, 1932) reported that in the southern North Sea, *Phaeocystis* blooms "acted as a very effective barrier to the migration of herring" (Savage, 1932, p. 332). These observations were supported by Mielck (1933), although, in contrast to Savage, Mielck was not convinced of a causal relationship between the inverse occurrence of *Phaeocystis* and herring. Rather, Mielck believed that other phenomena associated with the water masses might be responsible for avoidance of herring swarms. Lucas and Henderson (1936) suggested an avoidance by the herring of large numbers of jelly-fish which at some stations was associated with dense patches of *Phaeocystis*. Guided by his own observations from the German Bight, Wulff (1934) likewise questioned Savage's hypothesis, which has often been cited as an indication of harmful effects of *Phaeocystis* blooms on the ecosystem.

Mary Lebour's hypothesis that *Phaeocystis* constitutes an important food organism for zooplankton was later supported by several other authors. Nicholls (1935) gave a detailed description of the ingestion of *Phaeocystis* colonies by *Longipedia scotti* and *L. minor* from the Clyde Sea area. Entire *Phaeocystis* colonies were broken apart by the copepod mandibles and "as much as possible" ingested. Jones and Haq (1963) showed from gut observations, that the copepods *Temora longicornis*, *Centropages hamatus* and *Oithona nana* fed on *Phaeocystis* colonies in the eastern Irish Sea. *Phaeocystis* had no adverse effects on other planktonic forms. Fretter and Montgomery (1968) found veliger larvae of the prosobranch *Nassarius reticulatus* in the waters off Plymouth which fed on *Phaeocystis*. *Phaeocystis* was cultured by these authors, and successfully offered as food for *Nassarius reticulatus* and *Rissoa inconspicua*. At Signy Island (Antarctic), the

amphipod *Pontogeneia antarctica* ingested *Phaeocystis* cells (Richardson and Whitaker, 1979), although the species was quoted as *Phaeocystis antarctica* and grouped within the cyanophyceae. Sieburth (1960) reported the grazing by Antarctic euphausiids upon *Phaeocystis* without adverse effect. This positive result is significant, as Sieburth related in a series of papers (Sieburth, 1959, 1960, 1961, 1964) antibacterial activity with acrylic acid released by *Phaeocystis*. Although the antibacterial nature was dependent upon low pH values occurring in the guts of penguins, where this phenomenon was first observed, and Sieburth stated that "the function of acrylic acid synthesis in *P. pouchetii* is probably for purposes other than its antibacterial activity" (Sieburth, 1961, p. 79), it became the widely quoted legend that

acrylic acid may inhibit the growth of other planktonic and benthic organisms.

Schnack (1983) showed that Antarctic copepods with a raptorial feeding mode (*Metridia gerlachi* and *Pareuchaeta antarctica*) could feed upon *Phaeocystis*, whereas filter feeding copepods were unable to ingest *Phaeocystis* colonies. Positive correlations between *Phaeocystis* biomass and the abundance of the dominant mesozooplankton species further imply an important role of *Phaeocystis* as a food organism in the North Sea (Fransz and Gieskes, 1984; Weisse et al., 1986; Fransz et al., 1992).

Besides these direct observations, some indirect evidence supports the potential trophic significance of *Phaeocystis* blooms. In the Ems–Dollard estuary (Dutch–German Wadden Sea, North

Table 1
Reports of fish and zooplankton grazing on *Phaeocystis*

Areas	Species feeding on *Phaeocystis*	Authors
North Atlantic		
English Channel	Mackerel (*Scomber scombrus*) [1]	Bullen (1908)
English Channel	Flounder (*Pleuronectes flesus*) [1,2]	Lebour (1919)
English Channel	*Acartia, Temora, Centropages, Calanus* and other copepods, cirripede and decapod larvae [1]	Lebour (1922)
English Channel	*Nassarius reticulatus* and *Rissoa inconspicua* larvae [1,2]	Fretter and Montgomery (1968)
Clyde Sea	*Longipedia scotti* and *L. minor* [2]	Nicholls (1935)
Eastern Irish Sea	*Temora longicornis, Centropages hamatus* and *Oithona nana* [1]	Jones and Haq (1963)
Southern North Sea	Natural zooplankton populations [2]	Joiris et al. (1982)
Northern North Sea	*Temora longicornis, Acartia clausi* [1,2]	Weisse (1983)
High latitudes		
Northern Norwegian fjords	*Calanus finmarchicus, Thysanoessa inermis, T. raschi* [3]	Sargent et al. (1985)
		Tande and Båmstedt (1987)
	Calanus finmarchicus [2]	Huntley et al. (1987)
	Canalus hyperboreus	Hansen et al. (1990)
Barents Sea	*Calanus finmarchicus, C. hyperboreus, C. glacialis, Metridia longa* [2], *Gadus morhua*, larvae [1]	Estep et al. (1991)
		Løken (1990)
		Krogstad (1989)
Fram Strait	*Calanus hyperboreus, C. finmarchicus* [3]	G. Kattner (unpublished data)
Arctic Seas	*Calanus hyperboreus, C. glacialis* [1,2]	S. Diel (unpublished data)
Antarctica	*Euphausia superba* [1]	Sieburth (1960)
Signy Island	*Pontogeneia antarctica* [1]	Richardson and Whitaker (1979)
Bransfield Strait	*Metridia gerlachei, Pareuchaeta antarctica* [2]	Schnack (1983)

[1] Analyses of gut and stomach contents.
[2] Feeding experiments.
[3] Fatty acid analyses.

Sea), tintinnid populations were very dense (up to 78 animals ml^{-1}) during the spring bloom of *Phaeocystis* Admiraal and Venekamp (1986). *Phaeocystis* may also serve as food for copepods in high latitudes. In northern Norwegian fjords Sargent et al. (1985) measured similar poly-unsaturated fatty acids in *Phaeocystis pouchetii* blooms and in the neutral lipids of major zooplanktonic herbivores such as *Calanus finmarchicus, Thysanoessa inermis* and *T. raschi.* These findings were supported by G. Kattner (pers. commun.), who analyzed the fatty acid composition of *Calanus hyberboreus* and *C. finmarchicus* from the Fram Strait, indicating the ingestion of diatoms or *Phaeocystis.*

The reports of fish and zooplankton grazing on natural *Phaeocystis* populations are summarized in Table 1.

2.2. Adverse effects on potential consumers

Laboratory studies to date have not determined whether the apparent unsuitability of *Phaeocystis* colonies as food for certain herbivores is due to chemical or size-related effects. Since the early studies by Hardy (1926) and Savage (1930, 1932) it has been assumed that *Phaeocystis* blooms may exert negative impacts on the marine ecosystem: (1) clogging gills of filter feeders, especially of mussels, and thus reducing their feeding activity (Kopp, 1978; Pieters et al., 1980; Meixner, 1981); (2) acting as a barrier for the migration of fish (Savage, 1930, 1932); (3) inhibiting diatom populations through release of allelo-

pathic substances (Smayda, 1973; Barnard et al., 1984) and (4) fouling beaches (e.g. Dunne et al., 1984). Whereas the first two of these impacts are of mechanical type, the two latter are chemical. Further potential effects such as oxygen deficiency after sedimentation (Kopp, 1978) are not well documented. Finally, indirect effects, such as starvation, are possible, as smaller herbivores might not find enough food during a *Phaeocystis* bloom, if large colonies are predominant and single cells are scarce (Martens, 1981).

The various reports of adverse effects of *Phaeocystis* blooms are summarized in Table 2. The acrylic acid studies by Sieburth (1959, 1960, 1961, 1964) are not listed as these investigations do not strictly deal with in situ observations. For further information on acrylic acid and dimethyl-sulfide (DMS) production and their ecological significance the reader is referred to Thingstad and Billen (1994) and Liss et al. (1994).

2.3. Pre 1980 laboratory studies

The literature reviewed so far has mainly treated the ecological importance of *Phaeocystis* in a primarily qualitative manner. Grazing studies with cultured *Phaeocystis* cells are scarcer than reports from field studies. It was already mentioned that Fretter and Montgomery (1968) were able to feed two prosobranch species successfully with *Phaeocystis.* Nicholls' (1935) observations of *Longipedia* grazing on *Phaeocystis* were described above. Jebram (1980) reported on toxic effects of *Phaeocystis* in feeding experiments with

Table 2
Literature reports on negative effects of *Phaeocystis* blooms

Areas	Harmful effects reported	Authors
Southern North Sea	Avoidance of *Phaeocystis* blooms by migrating herring	Savage (1930, 1932)
Narragansett Bay	Decrease in numbers of other algae, morphological cellular changes	Smayda (1973)
Seine Bight	Clogging of mussel gills, oxygen deficiency after sedimentation	Kopp (1978)
Dutch Wadden Sea	Adherence of *Phaeocystis* colonies to mussel gills	Pieters et al. (1980)
East Frisian Wadden Sea (North Sea)	Feeding of cockle *Cardium edule* hindered by a *Phaeocystis* bloom	Meixner (1981)
South coast of Ireland	Fouling beaches, skin and eye irritations	Dunne et al. (1984)

the bryozoan *Electra pilosa*. Unfortunately, these harmful effects were not further specified, so that the mechanism by which *Phaeocystis* inhibited the growth of *E. pilosa* remains speculative. Cook and Gabbot (1972) reported that *Balanus balanoides* at Menai Bridge, England thrives better during the spring diatom than during the summer *Phaeocystis* bloom, because "*Phaeocystis* in not a good food organism" (Cook and Gabbot, 1972, p. 811). They offered natural phytoplankton populations as food for the barnacles kept in aquaria in the laboratory.

2.4. Recent approaches to quantify metazoan grazing on Phaeocystis

Investigations with a more quantitative approach have been reported since 1980. These studies were motivated by trophodynamic considerations, where blooms of *Phaeocystis* often co-occurred in time with the most intensive growth and productive period of important herbivorous copepods both in temperate and subarctic waters. For example, this situation prevails in coastal waters of northern Norway and in the Barents Sea (Fig. 1), where *Calanus finmarchicus* is considered a key herbivore (Tande, 1991).

In laboratory grazing experiments, Weisse (1983) found that *Phaeocystis* colonies between 50 and 350 μm were ingested by *Acartia clausi* and *Temora longicornis* at approximately the same rate concentrations as other phytoplankton at comparable studies. Laboratory experiments in flow-through chambers conducted documented that solitary cells (in the size range from 5–8 μm equivalent spherical diameter, ESD) of *Phaeocystis* cultured under laboratory conditions were consumed by CV *Calanus finmarchicus* (Tande and Båmstedt, 1987). Although clearance rates were low (from 0.2–2.8 ml h^{-1} individual^{-1}), the estimated daily rations varied from 0.4 to 14.6% of body carbon, due to high algal specific carbon content. The authors concluded that solitary cells may be as suitable as the diatom *Chaetoceros furcellatus* as food for *Calanus* species from fjord areas in northern Norway. In this study, *C. hyperboreus* were also fed freshly isolated colonies (> 200 μm ESD) from the seawater in the con-
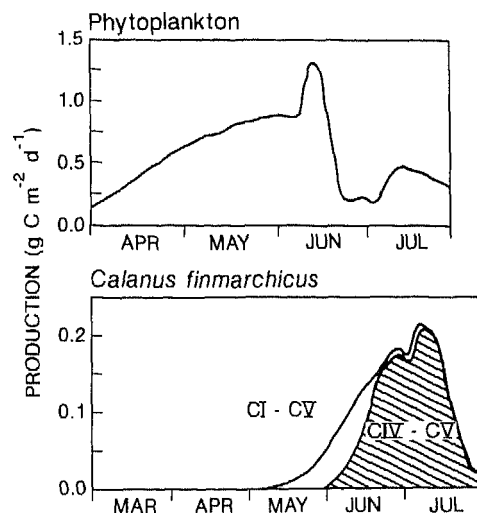

Fig. 1. The cycle of primary production and productivity of *Calanus finmarchicus* in Atlantic waters of the Barents Sea. Model simulation from 1 March to 1 August (from Tande, 1991).

centration range from 124 to 282 μg C l^{-1}, and clearance rates were estimated to 10 ml h^{-1} individual^{-1} (± 10.66, $n = 22$). These results emphasized that colonies of *Phaeocystis* may also be an important food source for these copepod species during the productive period in high latitudes.

In a contemporary study (Huntley et al., 1987), copepods obtained much greater daily rations when fed two sizes of colonies (25–200 μm, and > 200 μm ESD) than when fed either *Phaeocystis* flagellates or mixed diatoms (primarily *Chaetoceros socialis* and *Nitzschia grunowii*). Daily rations of copepods feeding on colonies ranged from 8.1 to 12.4% day^{-1} when exposed to food concentration of approx. 1 mg C l^{-1}. They concluded that a diet of *Phaeocystis* colonies should sustain the metabolic demand and growth requirements of *Calanus hyperboreus* copepodites. These two studies clearly demonstrated that *Phaeocystis* in fjords of northern Norway is eaten by co-occurring mesozooplankton.

The above studies only described the occurrence of feeding on *Phaeocystis*, and did not

address feeding mechanisms, zooplankton behavior, or prey preference. In the Antarctic, Schnack (1983) found that *Calanus propinquus, Rhincalanus gigas* and *Eucalanus* spp. would not feed on 0.5–1.5 mm colonies of *Phaeocystis*. It was thus relevant to ask if there was some upper limit of colony size which is difficult for copepods to handle and ingest, or if those results of Schnack (1983) and Schnack et al. (1985) reflected species-specific feeding behavior. In response, more systematic studies investigated dynamic interactions between various size categories of grazers (i.e. copepodite stage I–V *Calanus finmarchicus*), diatoms and colonies of *Phaeocystis* (Hansen et al., 1990). Clearance as a function of algal concentration (1–30 μg plant pigment l^{-1}) was described in juvenile stages of *C. finmarchicus* fed laboratory cultured diatoms *Thalassiosira nordenskioeldii* (ca. 20 μm ESD), *Porosira glacialis* (ca. 40 μm ESD) and two size categories (30–100 and > 100 μm ESD) of *Phaeocystis*. At unialgal diets, diatoms were more readily consumed than the larger size fraction of colonies of *Phaeocystis* by copepodite stage I–III *Calanus finmarchicus*. But offered smaller colonies, *C. finmarchicus* grazed both diatoms and colonies of gelatinous algae at equal rates. A linear relationship was found between gut content and food concentration up to 10 μg chlorophyll l^{-1}. Hansen et al. (1990) concluded that ingestion rate in *C. finmarchicus* was directly proportional to the ambient food concentration during the most productive period in high latitudes (May and June), irrespective of the algal species present. The colonies offered as food in this study grew in a wide variety of morphologies, from intact spherical to more disrupted colonies. Although this reduces the ecological significance of the size fractions, the results indicate that copepodite instars of *C. finmarchicus* are potentially grazers on colonies of *Phaeocystis*, although to a variable extent. An upper colony size limit was not established for *C. finmarchicus* in this investigation.

The studies described above have given tentative estimates of carbon fluxes between *Phaeocystis* and metazooplankton species from the continental shelf in temperate and boreal waters in Europe. The data generally support the con-

tention that colonies and solitary cells are consumed both under laboratory and field conditions. Recently, questions related to the quality of *Phaeocystis* as prey organisms has been addressed in two papers. Verity and Smayda (1989) considered the capability of two size classes of *Phaeocystis* (i.e. colonies of ca. 200 μm ESD and solitary cells ca. 5 μm ESD) to sustain egg production in *Acartia tonsa* and *A. hudsonica*, and growth of their nauplii. Their results showed that egg production by *Acartia* females fed unialgal cultures of *Phaeocystis*, either colonies or solitary cells, was not significantly different from that of starved copepods. In multialgal experiments, *Acartia* exhibited significantly greater ingestion of chain-forming diatoms (*Skeletonema*) than of *Phaeocystis*. The presence of *Phaeocystis* did not reduce ingestion of diatoms, nor did the co-availability of diatoms increase feeding on *Phaeocystis*. Since *Acartia* nauplii grew well on unialgal diets of *Phaeocystis*, Verity and Smayda (1989) suggest that the adult responses may reflect that solitary cells are too small and most colonies too large for these intermediate-sized (1 mm) copepods. Thus, grazing by *Acartia* and other copepods with similar prey size efficiencies may contribute to the development of *Phaeocystis* blooms by removing competing phytoplankton.

By adopting image analysis and epifluorescence microscope techniques, Estep et al. (1990) related grazing rates of four different copepod species (i.e. *Calanus finmarchicus, C. hyperboreus, C. glacialis* and *Metridia longa*) to colonies of *Phaeocystis* of different physiological state during a cruise in May 1989 in the Barents Sea. Natural phytoplankton contained *Phaeocystis* colonies in association with varying amounts of diatoms. Results from the grazing studies indicated that diatoms were actively preyed on in all experiments, with long chain-forming species as the preferred food. Healthy colonies were not consumed, while disintegrating and weakly fluorescent colonies were consumed at rates 2–10 times those for chain-forming diatoms.

In recent laboratory grazing studies, Hansen (1992) measured the uptake of *Phaeocystis* solitary cells and colonies by several species of meroplanktonic larvae and calanoid copepods in the
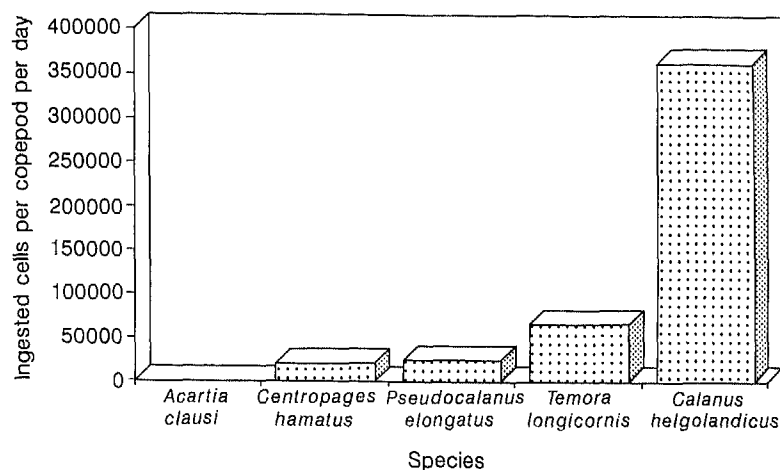
Fig. 2. Ingestion rates of five calanoid copepods on cultured *Phaeocystis* (solitary and colonial cells) at food concentrations of 4.1 ± 0.5 μg Chl *a* l^{-1}. Older copepodite stages selected from the size fraction < 280 μm of natural zooplankton sampled off Helgoland (German Bight, North Sea) were incubated at 16°C (± 0.9°C) for 48 h. Copepod numbers were either 10 individuals l^{-1} (*C. helgolandicus*) or 68 ± 17 individuals l^{-1} (other species) (from Hansen and van Boekel, 1991).

Dutch coastal area of the North Sea. Among copepods, ingestion rates were highest in *Calanus helgolandicus* and *Temora longicornis* (Fig. 2). However, plant pigment content in the guts of *T. longicornis* was inversely related to the dominance of *Phaeocystis* (Figs. 3 and 4) during the phytoplankton spring bloom in Dutch coastal waters (Hansen and van Boeckel, 1991). Grazing was very low during the *Phaeocystis* bloom (2%

day^{-1}), and Hansen and van Boekel hypothesized that *T. longicornis* switched to a heterotrophic food source, which could have been a bloom of ciliates present in that period (van Boekel et al., 1992). Depressed feeding rates in *T. longicornis* during a *Phaeocystis* bloom were also observed in Belgian coastal waters by Daro (1986).
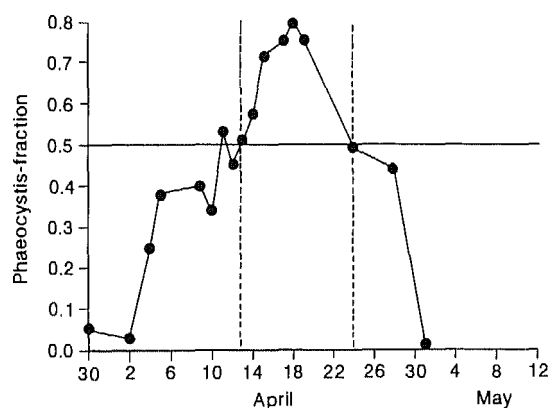

Fig. 3. *Phaeocystis* biovolume fraction of total phytoplankton biomass in the Marsdiep (a Dutch tidal inlet). Vertical lines indicate the period of *Phaeocystis* dominance.
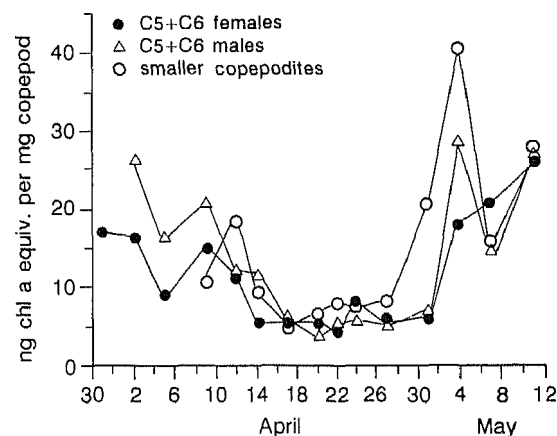

Fig. 4. *Temora longicornis*. Weight-specific gut fluorescence of three age and sex classes in the Marsdiep during spring 1990 (mean concentrations of all stages concentrated on 300 μm gauze).

3. Protozoa as consumers of *Phaeocystis*

The number of colonial cells usually far exceeds the abundance of free-living single cells during *Phaeocystis* blooms. The question arises whether this is inherent in the algal life cycle or due to control mechanisms that keep the single cells at low numbers.

As previously discussed, formation of large colonies may prevent grazing. The production of small free-living single cells, however, may also result in a refuge from grazing. Martens (1981) and Verity and Smayda (1989) concluded that the size of solitary cells is at the lower limit for efficient retention of many suspension-feeding copepods which dominate in coastal areas where the *Phaeocystis* blooms are most pronounced. In contrast to food size preferences of adult copepods and other macrozooplankton, single cells are in the optimal feeding size range of microzooplankton such as protozoa, rotifers and copepod nauplii. Therefore, efficient grazing control of single cells may well reflect the feeding of microzooplankton.

Admiraal and Venekamp (1986) measured the potential significance of protozoa as consumers of *Phaeocystis* cells. These authors found high numbers of tintinnids (up to 118,000 cells dm^{-3}) in the Dutch Wadden Sea and the coastal North Sea during a dense *Phaeocystis* bloom. They observed tintinnids grazing on *Phaeocystis* under the microscope. The tintinnids, mainly *Helicostomella subulata*, captured free-swimming single cells. They also appeared to grasp single cells from the surface of bladder-like colonies, but were unable to disrupt the colonies. Admiraal and Venekamp (1986) also mentioned that the tintinnids needed about 30 min for the digestion of *Phaeocystis*.

The first attempt to measure the grazing impact of natural protozoan zooplankton on single *Phaeocystis* cells has been made by Weisse and Scheffel-Möser (1990). Using a seawater dilution technique, growth and grazing loss rates of natural *Phaeocystis* populations from the North Sea were quantified. Grazing rates ranged from 0.037 to 0.174 h^{-1}. The relative feeding impact increased during the course of the bloom and exceeded the phytoplankton rates at the end. Based on the composition of the zooplankton present during the experiments, Weisse and Scheffel-Möser concluded that protozoa, such as ciliates and heterotrophic dinoflagellates, were the primary consumers of the single cells during the initial phase of the bloom. Grazing and clearance rates on *Phaeocystis* calculated for the ciliate assemblage were similar to laboratory results obtained for individual ciliate species and other food algae. Due to their distinctly lower community biomass, heterotrophic dinoflagellates were considered of minor importance compared to ciliates. Yet, Weisse and Scheffel-Möser (1990) noted that the giant *Noctiluca scintillans*, which became abundant when the *Phaeocystis* concentration had increased to higher levels, may be an important consumer of solitary cells. This conjecture was supported by laboratory experiments using natural *Phaeocystis* and *N. scintillans* isolated from the waters off the island of Helgoland in the German Bight. In those experimental flasks where *N. scintillans* was added to *Phaeocystis*, the number of *Phaeocystis* single cells decreased relative to controls (Fig. 5). Using epifluorescence microscopy and DAPI staining, *Phaeocystis* single cells could be visualized entrapped in the mucous slime (Weisse and Scheffel-Möser, unpubl.) which is produced by *N. scintillans* when feeding collectively (Omori and Hamner, 1982). *N. scintillans* apparently ingested *Phaeocystis* even at low food concentrations (about 50 μg C l^{-1}). The highest individual ingestion rate of *N. scintillans* found in these experiments was about 2300 cells d^{-1} and thus exceeded the maximal uptake rate of an average ciliate roughly by ten times. The maximum specific ingestion rate of *N. scintillans* was, however, much lower (0.17 body C ingested d^{-1}) compared to ciliates (1.82 body C ingested d^{-1}) at the food concentrations tested. This protozoan needs high food concentrations in order to multiply rapidly (Hanslik, 1987). It is, therefore, questionable whether this species could thrive on a diet of *Phaeocystis* single cells alone. Yet, due to its enormous individual biomass which is roughly two orders of magnitude higher than the individual biomass of a medium-sized ciliate, *N. scintillans* is likely to play an important role as con-
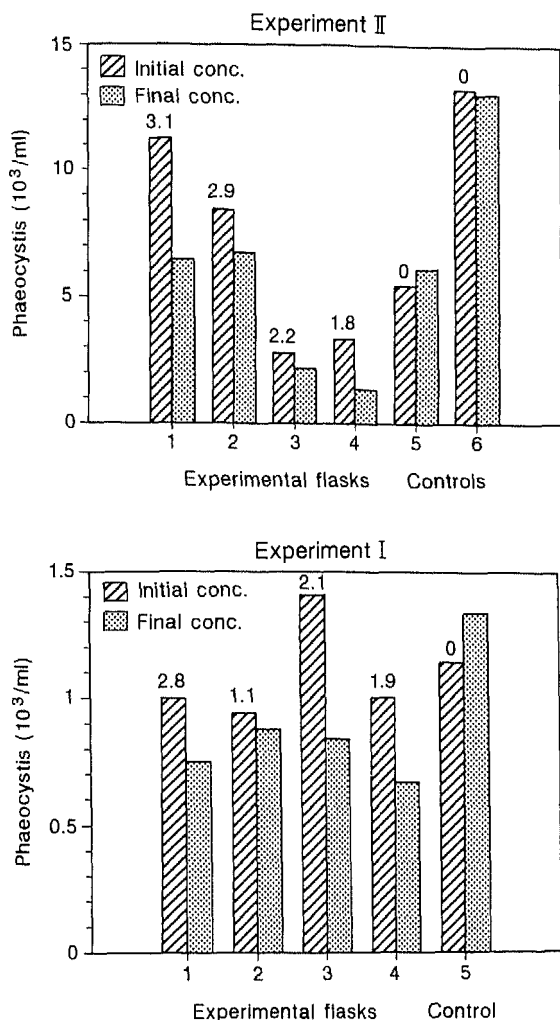
Experiment II

Experiment I

Fig. 5. Laboratory feeding experiments with natural *Noctiluca scintillans* and *Phaeocystis* sp. single cells. Samples were taken from Helgoland Roads (German Bight, North Sea) in 1 and 5 m water depth and incubated for 24 h in the dark at the in situ temperatures (11–13°C). Numbers on top of the bars denote the abundance of *Noctiluca* ml^{-1} (Weisse and Sheffel-Möser, unpubl. results).

sumer of *Phaeocystis* single cells during shorter time periods. If those preliminary results are applied to the natural situation in the North Sea, *N. scintillans* may be of comparable importance as a consumer of *Phaeocystis* single cells if its concentration equals about 10% of the ciliate numbers. In the North Sea, this is often reached during the

waning phase of the spring *Phaeocystis* bloom and during the later summer blooms.

Compared to metazooplankton, the current knowledge on the significance of protozoa and other microzooplankton as consumers of *Phaeocystis* is restricted. The results reported above suggest that protozoa might efficiently control the abundance of *Phaeocystis* single cells. In the laboratory, *Noctiluca scintillans* has also been observed to ingest smaller *Phaeocystis* colonies (G. Uhlig and G. Sahling, pers. commun.) and also parts of larger colonies (Hansen, 1992). Yet, at present the quantitative significance of protozoan grazing on colonies remains unknown. Evidently, more detailed experimental work is needed to elucidate the potential feeding impact of protozoa on *Phaeocystis* in various marine areas. Since the ultimate goal is to quantify the overall grazing impact on *Phaeocystis*, such experiments should be conducted in parallel to feeding experiments with larger zooplankton.

4. Discussion

Uncertainty in the interpretation of the ecological role of *Phaeocystis* mainly originates from its great morphological and physiological variability. Single cells of some 3–8 μm diameter (Kornmann, 1955; Parke et al., 1971) and large colonies of up to 2 mm diameter consisting of several hundreds of cells (see Bougard, 1979) usually coexist during a bloom (cf. Rousseau et al., 1994). With respect to grazing by zooplankton and benthic filter feeders, single cells and colonies of *Phaeocystis* function as different phytoplankton species. Any negative impact by mechanical clogging of gills of filter feeders is related to *Phaeocystis* mucilage, whereas any chemical effects are likely features originating from cells. Moreover, chemical effects may vary depending upon whether the cells are free swimming or embedded in a matrix. Therefore, a *Phaeocystis* bloom may vary in ecological role in relation to the different bloom phases and the varying proportions of the single cells and colonies. However, a zooplankton community is affected both by single cells and by colonies, so that it would be advantageous to be

able to select the preferred food item and to avoid the less favorable of even harmful ones. Therefore, it is not surprising that copepods such as *Acartia* and *Temora*, which are opportunistic particle feeders and can switch between different modes of ingestion, thrive in areas where dense *Phaeocystis* blooms regularly occur.

Mesozooplankton may also indirectly benefit from *Phaeocystis* blooms, by feeding on detritus-particles or heterotrophic microzooplankton. Vast amounts of detritus in the form of decaying colonies (probably coated with bacteria and colonized by microheterotrophs) appear in the water-column during the decline phase of *Phaeo-cystis* blooms. Although copepod grazing on detritus has been reported (e.g. reviewed by Poulet, 1983), information on the use of this alternative food source remains scarce. It has been shown that during *Phaeocystis* blooms, ciliates are numerous, and probably the most important grazers of solitary cells, which usually exceed colonial cells in abundance (Admiraal and Venekamp, 1986; Weisse and Scheffel-Möser, 1990). van Boekel et al. (1992) observed a strong increase in bacterioplankton and microzooplankton biomass following the release of DOC by lysis of *Phaeo-cystis* cell during a declining *Phaeocystis* bloom. This microzooplankton could have been grazed by the predominant copepod *Temora longicornis*, as hypothesized by Hansen and van Boekel (1991). The potential importance of microzooplankton as food for copepods has been shown by several recent studies (e.g. reviewed by Stoecker and McDowell Capuzzo, 1990; Kleppel et al., 1991). Thus, it seems likely that the biomass produced by *Phaeocystis* may also enter higher trophic levels through alternative pathways.

The functional role of *Phaeocystis* in the pelagic system may be similar to that of other colony-forming phytoplankton species, such as the diatoms *Chaetoceros socialis*, *C. radians*, *Thalas-siosira partheneia* and *T. subtilis* (Margalef, 1978). *Thalassiosira partheneia*, a species characteristic of the northwest African upwelling area (Schra-der, 1972), resembles *Phaeocystis* with regard to its resistance to grazing due to the enormous size of its colonies (Schnack, 1983). Furthermore, some of the organisms associated with the big *T.*

artheneia colonies (e.g. colorless flagellates, amoeba and ciliates), were also described from within colonies of *Phaeocystis* (Elbrächter and Boje, 1978).

5. Conclusions and perspectives

Stomach content analyses and laboratory feeding experiments have demonstrated the suitability of *Phaeocystis* colonies as food for herbivores of appropriate size or feeding efficiency, belonging to several taxonomic groups. The relative food value of solitary *Phaeocystis* cells has been less adequately examined. Very few experimental investigations have included comparisons of *Phaeo-cystis* with other phytoplankton, so that it remains uncertain whether, although ingested, *Phaeocystis* represents a nutritionally satisfactory food source. Moreover, apparent adverse effects may be chemically-included or size-related. It should be investigated whether *Phaeocystis* excretes specific allelopathic substances which inhibit grazing by zooplankton and growth of bacteria and phytoplankton.

At the present state of knowledge, it remains an open question whether the single cells of the co-occurring species, *Phaeocystis pouchetii* and *P. globosa*, differ with respect to their nutritional value and their vulnerability to grazing. *Phaeocys-tis* blooms in nature must be studied in relation to the various life cycle stages and associated size distributions. Authors should exercise care in quoting and generalizing results obtained by former investigators under specific conditions. The uncritical quoting of acrylic acid as a main feature of *Phaeocystis* blooms commonly leading to adverse effects on the ecosystem is such an example. Although our present knowledge of the trophic significance of *Phaeocystis* blooms and their functioning within the pelagic system is poor compared to other phytoplankton species, this organism offers fascinating possibilities for future research. It appears that the wax and wane of *Phaeocystis* blooms form an integral part of more complex, size-dependent trophic changes within the whole system. Therefore, complete understanding of the trophic significance of *Phaeocystis*

requires a comprehensive approach at an inter-disciplinary level, involving microbial, planktonic, biochemical and sedimentation studies. Only then will we be able to understand and eventually predict the ecological role of this enigmatic alga.

6. Notes added in proof

Recently, the importance of the relative sizes of *Phaeocystis* and grazing zooplankton was investigated using natural populations of *Phaeocystis* and co-occurring crustacean zooplankton from Norwegian fjords (Hansen et al., 1994). Phytoplankton communities dominated by colonial and solitary cells of *Phaeocystis* were incubated with added zooplankton spanning five orders of magnitude in biomass, including the euphausiids *Thysanoessa* spp. and the calanoid copepods *Calanus hyperboreus* Kroyer (CV), *C. finmarchicus* Gunnerus (CIV-V) and *Acartia longiremis* Liljeborg (adult females). Grazing was determined from changes in concentrations of four size classes of chlorophyll *a*, *Phaeocystis* cells and colonies. Clearance and optimum prey size range were both proportional to grazer size. Diatoms were grazed more than *Phaeocystis* by euphausiids and *A. longiremis*. Comparison of clearance estimated from colony disappearance to those from changes in chlorophyll *a* and *Phaeocystis* cell number indicated that the feeding/swimming activities of *Thysanoessa* spp. and *Calanus* spp. resulted in fragmentation of colonies into smaller size classes. Measurements of *Phaeocystis* cell abundance and size using an image analysis system, showed distinct differences in cell size between colony cells and solitary cells, which provided further evidence of colony disruption independent of ingestion. The data indicated that the role of *Phaeocystis* in planktonic food webs is highly dependent upon a continual match between the size structure of *Phaeocystis* populations and the collection efficiency of co-occurring zooplanton.

The earlier conjectures that protozoa are important consumers of *Phaeocystis* single cells (Weisse and Scheffel-Möser, 1990) and serve as a major food source for copepods during *Phaeocystis* blooms (Hansen and van Boekel, 1991) have been supported by a recent laboratory investigation. Hansen et al. (1993) compared the feeding potential of two ciliates, *Strombidinopsis acuminatum* and *Strombidium elegans* and one dinoflagellate species, *Oxyrrhis marina*, to that of the copepod *Temora longicornis*. *Strombidinopsis* and *Oxyrrhis* ingested *Phaeocystis* single cells at much higher rates than did the copepod, but specific protozoan ingestion and growth rates were lower than maximal rates obtained for the respective species with alternate algal food. *Strombidium* did not feed on *Phaeocystis* under experimental conditions, but grew well in cultures containing decaying colonies or added bacteria. *Temora* preferred the protozoans over *Phaeocystis* single cells thus relieving *Phaeocystis* from the protozoan grazing pressure. Hansen et al. (1993) calculated that copepod predation on ciliates could reduce the ciliate grazing pressure on *Phaeo-*

cystis single cells to 5% of the standing stock per day. These results further explain why copepods in spite of low herbivory survive during *Phaeocystis* blooms in the North Sea and the English Channel (van Boekel et al., 1992; Bautista et al., 1992; Davies et al., 1992). In Dutch coastal waters the egg production per *Temora* female even peaked at the highest *Phaeocystis* density (Fransz et al., 1992).

The potential significance of protozoa was also implied in Antarctic coastal waters where microheterotroph abundance peaked during or immediately after a *Phaeocystis* bloom (Davidson and Marchant, 1992).

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