

Trophic interactions between zooplankton and *Phaeocystis* cf. *globosa*

F. C. Hansen

Netherlands Institute for Sea Research; PO Box 59, 1790 AB Den Burg, The Netherlands

ABSTRACT: Mesozooplankton grazing on *Phaeocystis* cf. *globosa* was investigated by laboratory and field studies. Tests on 18 different species by means of laboratory incubation experiments, carried out at the Biologische Anstalt Helgoland, revealed that *Phaeocystis* was ingested by 5 meroplanktonic and 6 holoplanktonic species; filtering and ingestion rates of the latter were determined. Among copepods, the highest feeding rates were found for *Calanus helgolandicus* and *Temora longicornis*. Copepods fed on all size-classes of *Phaeocystis* offered (generally 4–500 µm equivalent spherical diameter [ESD]), but they preferred the colonies. Female *C. helgolandicus* and female *T. longicornis* preferably fed on larger colonies (ESD > 200 µm and ESD > 100 µm, respectively). However, a field study, carried out in the Marsdiep (Dutch Wadden Sea) showed phytoplankton grazing by the dominant copepod *Temora longicornis* to be negligible during the *Phaeocystis* spring bloom. *T. longicornis* gut fluorescence was inversely related to *Phaeocystis* dominance. The hypothesis has been put forward that *T. longicornis* preferentially feeds on microzooplankton and by this may enhance rather than depress *Phaeocystis* blooms. Results from laboratory incubation experiments, including three trophic levels – *Phaeocystis* cf. *globosa* (algae), *Strombidinopsis* sp (ciliate) and *Temora longicornis* (copepod) – support this hypothesis.

INTRODUCTION

The colony-forming prymnesiophyte *Phaeocystis* cf. *globosa* builds up high bio-masses in the continental coastal areas of the North Sea during intense phytoplankton blooms in spring and summer, where it can be the dominant species (Joiris et al., 1982; Veldhuis et al., 1986). A long-term monitoring study in Dutch coastal water indicates an increase in abundance of these blooms as well as an increase in their duration (Cadée, 1990). Algae of the genus *Phaeocystis* are not regarded as toxic, but they contribute to some environmental problems, and therefore have attracted widespread interest (Lancelot et al., 1987). *Phaeocystis* is, for example, an effective dimethylsulfoniopropionate (DMSP)-producer and due to this, contributes to the acid-rain problem (Barnard et al., 1984; Keller, 1988).

The understanding of the causes and consequences of *Phaeocystis* blooms, as well as their effect on the pelagic system, is still incomplete. For a better understanding, it is necessary to have knowledge of the trophic relationships between *Phaeocystis* and other members of the food web. However, the literature on the use of *Phaeocystis* as food for higher trophic levels is contradictory. Some studies indicate that *Phaeocystis* single cells and colonies can serve as food for zooplankton; whereas other studies indicate *Phaeocystis* to be unsuitable food (Weisse et al., 1994 and references cited therein). Its suitability as

food for copepods can also be dependent on the physiological state of the algae (Estep et al., 1990).

In this paper, results of laboratory and field measurements on the trophic relationships between *Phaeocystis* and zooplankton are presented. This study was an integrated part of the European Communities (EC) project "Dynamics of *Phaeocystis* blooms in nutrient-enriched coastal zones of the North Sea" (1988–1991).

MATERIALS AND METHODS

Laboratory grazing experiments at Helgoland

Between 6th April 1988 and 12th October 1989, different zooplankton species caught in the German Bight off Helgoland were tested for grazing on *Phaeocystis* cf. *globosa*-cultures by means of incubation experiments carried out in the laboratory at the marine station of the Biologische Anstalt Helgoland on Helgoland. These experiments were described in detail by Hansen (1992) and a brief description is given here. The animals were caught with a net of 280 μm mesh-size at the Helgoland Roads sampling station (54° 11.3'N, 07° 50.0'E), sorted, and transferred to gently aerated beaker-glasses in which they were adapted to experimental conditions for 24 h. In the grazing experiments, which lasted 24 or 48 h, they were fed cultured *Phaeocystis* cf. *globosa* (which was cultured semi-continuously) containing both flagellated and non-flagellated single cells of 3 to 8 μm equivalent spherical diameter (ESD, determined by microscopical size-measurements) as well as colonies (diameter: 10 to 500 μm). Filtration and ingestion rates were derived from differences in *Phaeocystis* cell densities and chl-*a* contents at the beginning and end of the experiments in the incubation vessels, using the equations given by Frost (1972). Measurements were performed by applying the Utermöhl-sedimentation technique (Utermöhl, 1958) and by fluorescence determinations after Holm-Hansen et al. (1965). The Wilcoxon test for non-related samples (Sokal & Rohlf, 1981) was used to test whether the grazing of certain species was statistically significant or not.

Field study in the Dutch tidal inlet Marsdiep

Between 30th March and 11th May 1990, the phytoplankton-grazing impact by *Temora* during a *Phaeocystis* bloom in the tidal inlet Marsdiep was estimated and related to the abundance and succession of phytoplankton development. The applied methods were described in detail by Hansen & van Boekel (1991). Copepods were collected off Texel (53° 00.2'N, 4° 47.6'E) by gentle filtration of surface water through a 300 μm -sieve. Copepods were sorted, their length measured and their gut pigment determined by fluorescence measurements. Copepod weights were calculated using length-weight relationships given by Klein Breteler & Gonzalez (1988). Gut pigment values were converted to ingestion rates (Mackas & Bohrer, 1976), using temperature-dependent rates of gut clearance given by Dam & Peterson (1988).

Combined grazing experiment including the ciliate *Strombidinopsis*

This grazing experiment was performed in a similar manner to the Helgoland laboratory experiments described above, but zooplankton organisms were obtained from cultures. The oligotrichous ciliate *Strombidinopsis acuminatum* was isolated from the Marsdiep out of *Phaeocystis* cf. *globosa* colonies and continuously cultured in a chemostat using the prymnesiophyte flagellate *Isochrysis galbana* as food organism. *Temora longicornis* copepods (C6, females) were obtained from cultures of Dr. W. C. M. Klein Breteler and N. Schogt (Klein Breteler, 1980). During the 24 h incubation experiment, the ciliates and the copepods (individually as well as in combination) were offered *Phaeocystis* single cells. Ingestion rates were calculated from changes in cell densities, and the biovolumes of *Phaeocystis* and *Strombidinopsis* were measured with a coulter-counter. For converting the biovolume to carbon, a factor of $0.11 \text{ pg C } \mu\text{m}^{-3}$ was used (Strathmann, 1967; Smetacek, 1975). *Temora* carbon content was taken as 40% of its ash-free dry weight (Omori, 1969), which was calculated from the length-measurements (see above).

RESULTS

In the Helgoland incubation experiments, most of the zooplankton species tested did graze on cultured *Phaeocystis*-colonial as well as single cells – i.e. 5 out of 10 meroplanktonic and 6 out of 8 holoplanktonic species (Table 1). There were no obvious differences in grazing response between taxonomic classes, but there was a distinct difference between species within the classes. Copepods are regarded to be of special importance because of their high grazing activity and their abundance (Fransz et al., 1991). Among copepods, the highest ingestion rates of *Phaeocystis* cells (measured under comparable conditions) were found for *Temora longicornis* and *Calanus helgolandicus* (Fig. 1). The latter, however, is much bigger than the other four species.

Copepods fed on all size-classes of *Phaeocystis* offered (generally 4 to 500 μm ESD), but they preferred the colonies. Female *T. longicornis* preferred larger colonies (ESD > 100 μm). In a 2-day incubation experiment, the vessel with predominantly male *Temora* had about the same size-distribution of *Phaeocystis*-colonies as the controls (with no copepods present); whereas in the experimental vessel with predominantly female *Temora*, only the smallest size fraction (ESD \leq 100 μm) was left over (Fig. 2). This result was confirmed by a second experiment, and a similar result was obtained in experiments with female *Calanus helgolandicus*, which grazed away all colonies larger than 200 μm ESD.

The grazing-impact of the dominant copepod *Temora longicornis* on a *Phaeocystis* bloom was investigated during a field study in the Dutch tidal inlet Marsdiep in spring 1990. The gut pigment content of males, females and smaller copepods, did not resemble the seasonal course of the chlorophyll-*a* concentration in the water (Figs 3, 4). It was inversely correlated with the dominance of *Phaeocystis* (Figs 4, 5). Calculated ingestion of phytoplankton was negligible during the *Phaeocystis* bloom and far too low to fulfil *Temora*'s metabolic needs, which were estimated from its biomass increase (Hansen & van Boekel, 1991).

It was concluded that *Temora* had switched to a heterotrophic food source and it has been suggested that this could have been a bloom of ciliates present during the

Table 1. Grazing response, maximum filtration and maximum ingestion rates (incl. corresponding experimental conditions) of 18 different zooplankton species (>280 µm, except *Noctiluca*) fed *Phaeocystis* cf. *globosa*. n. s. = grazing not significant; +: p = 0.05; *: p < 0.05; **: p < 0.01; ***: p < 0.001

Grazer-species	Grazing on <i>Phaeocystis</i>	Level of significance	Maximum filtration rate (ml/[ind. dl])	Maximum ingestion rate (ng chl- <i>a</i> /[ind. dl])	Temperature (°C)	Grazer-density (ind./l)	Mean algae concentration (µg chl- <i>a</i> /l)
Meroplankton							
Polychaeta:							
<i>Polydora pulchra</i>	yes	n. s.	1.1	2.4	17	47	2.2
Spionidae 2	no						
Cirripedia:							
<i>Semibalanus balanoides</i>	no						
<i>Balanus crenatus</i>	yes	+	1.9	2.6	17	160	1.3
Decapoda:							
<i>Upogebia deltaura</i>	no						
<i>Galathea intermedia</i>	yes	+	14.9	28.3	17	3	1.9
<i>Pagurus pubescens</i>	?		40.4	82.3	17	9	2.0
<i>Carcinus maenas</i>	no						
<i>Portunus depurator</i>	yes	n. s.	4.6	7.7	12	24	1.6
<i>Portunus holsatus</i>	yes	n. s.	39.2	44.6	17	10	2.2
Holoplankton							
Copepoda:							
<i>Acartia clausi</i>	no						
<i>Temora longicornis</i>	yes	***	26.1	32.2	9	154	21.4
<i>T. longicornis nauplii</i>	?		0.2	1.1	16	109	5.5
<i>Centropages hamatus</i>	yes	**	17.2	33.1	12	16	1.9
<i>Pseudocalanus elongatus</i>	yes	+	14.4	16.5	17	28	1.1
<i>Calanus helgolandicus</i>	yes	***	36.4	156.1	17	3	4.3
other holoplankton:							
<i>Noctiluca scintillans</i>	yes	n. s.	0.1	2.3	9	5970	19.7
<i>Tomopteris</i> sp.	yes	n. s.	6.9	1.1	15	10	0.2
<i>Evadne nordmanni</i>	?		2.0	5.8	12	87	2.9

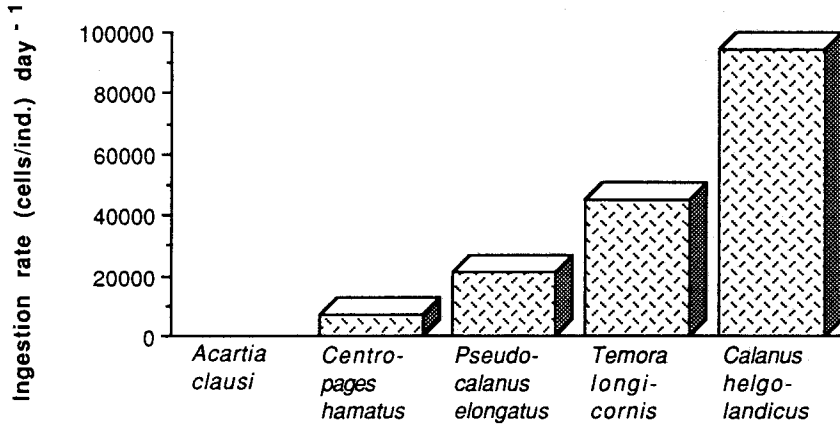


Fig. 1. Daily ingestion of *Phaeocystis* single and colonial cells ($3.9 \pm 0.5 \mu\text{g chl a l}^{-1}$) by 5 calanoid copepod species (copepods $> 280 \mu\text{m}$; density: 10 copepods l^{-1} for *C. helgolandicus*; 74 ± 15 copepods l^{-1} for other species). Temperature: $16.0 \pm 0.9^\circ\text{C}$

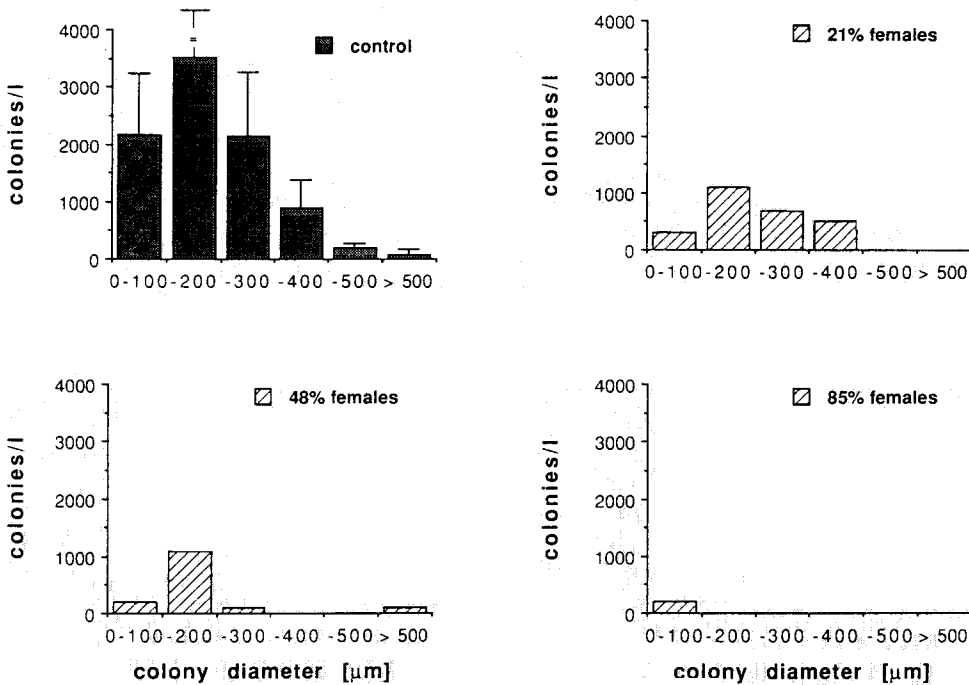
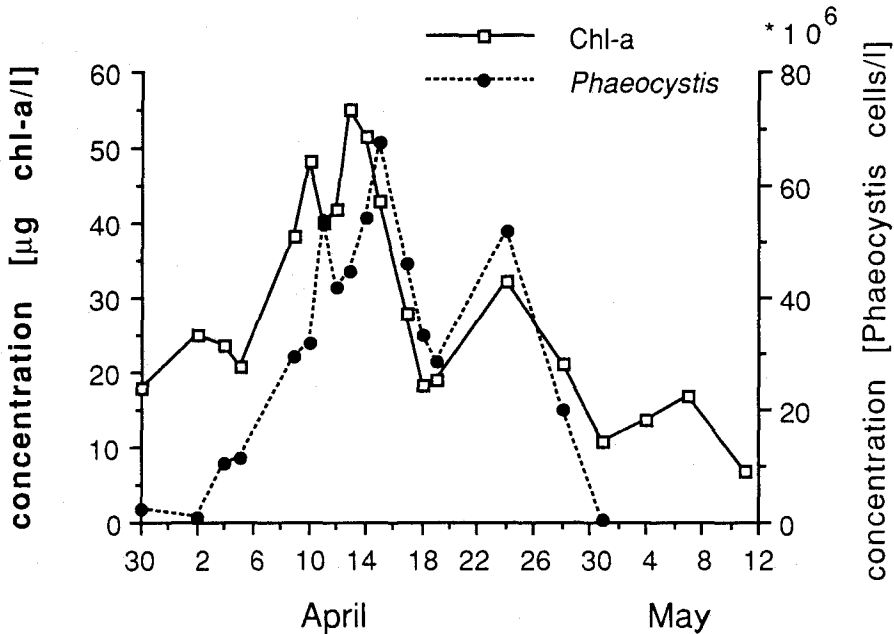


Fig. 2. Size-distribution of *Phaeocystis* colonies after 2 days of incubation without (control) and with *Temora longicornis* copepods $> 280 \mu\text{m}$ of different sex ratios. Mean and standard deviation for $n = 6$ (control)



(after Hansen & van Boekel, 1991)

Fig. 3. Phytoplankton spring development in the Marsdiep from 30th March to 11th May 1990: chl-a and *Phaeocystis* cell concentrations

Phaeocystis-dominated period of the phytoplankton spring bloom (van Boekel et al., 1992). The hypothesis is put forward that *T. longicornis* preferentially feeds on microzooplankton and by this may enhance, rather than depress, *Phaeocystis* blooms.

Results from three laboratory incubation experiments, each including three trophic levels – *Phaeocystis*, a herbivorous protozoan, and the copepod *Temora* – support this hypothesis (Hansen et al., 1993). The densities of *Phaeocystis* single cells in experimental vessels before and after 24-h incubation with *Temora* or/and the oligotrichous ciliate *Strombidinopsis* sp. is shown in Figure 6. There was almost no reduction in *Phaeocystis* cell concentration by *Temora*, but a strong reduction by *Strombidinopsis* as the only grazer. Derived rates of *Phaeocystis*-ingestion per unit body carbon of the grazer (specific daily ration) were about twice as high for the ciliate (34%/day) compared to the copepod (18%/day). When all three species were incubated together, *Temora* greatly preferred the ciliates. During the experiments, ciliate biomass (265 $\mu\text{g C/l}$) was reduced by 60% in the presence of copepods; whereas ciliate biomass increased to 318 $\mu\text{g C}$ in the controls (without copepods), resulting in a highly specific daily ration of copepods feeding on the ciliates of 276% (body-C/day). As expected from the hypothesis, the reduction of the *Phaeocystis* biomass in the incubations with ciliated and copepods was less than with ciliates alone: that means a decrease in overall grazing-pressure on *Phaeocystis* by the copepods.

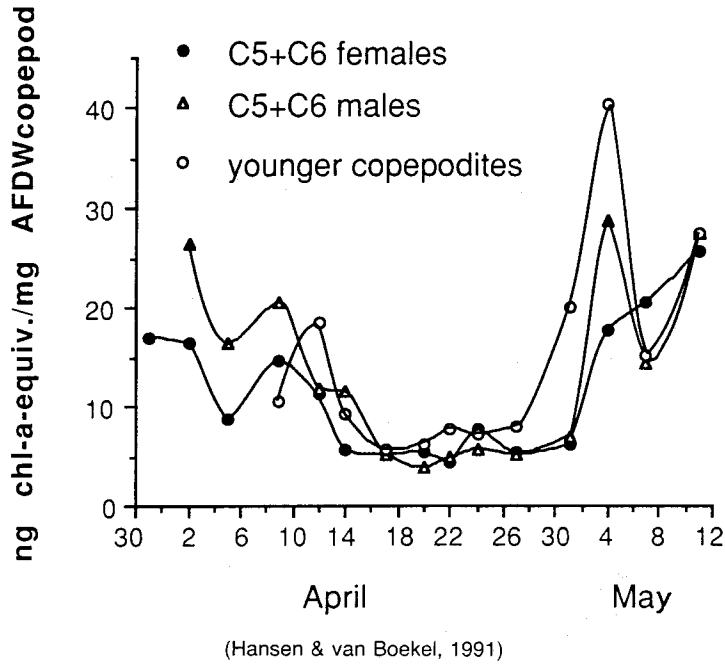


Fig. 4. *Temora longicornis*. Weight-specific gut fluorescence of 3 age and sex classes in the Marsdiep during spring 1990. Mean concentrations of stages > 300 μ m

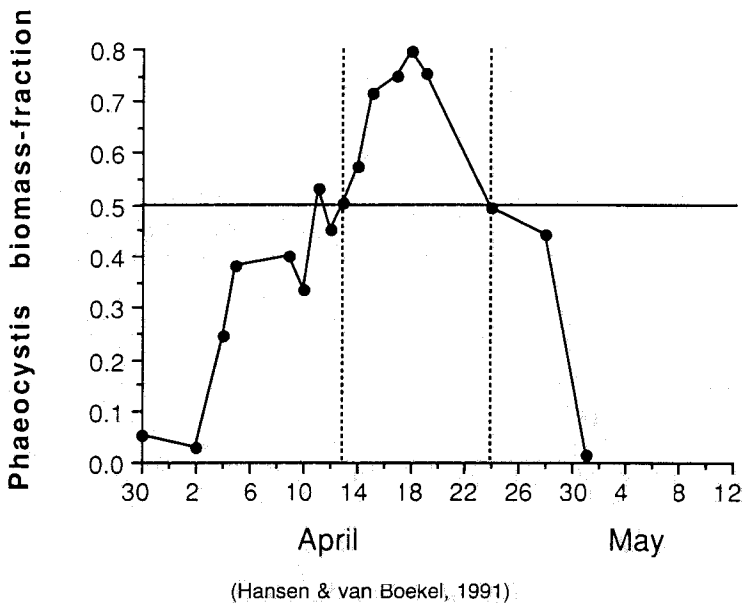


Fig. 5. *Phaeocystis* fraction of total phytoplankton biomass in Marsdiep in spring 1990. Vertical lines indicate period of *Phaeocystis* dominance

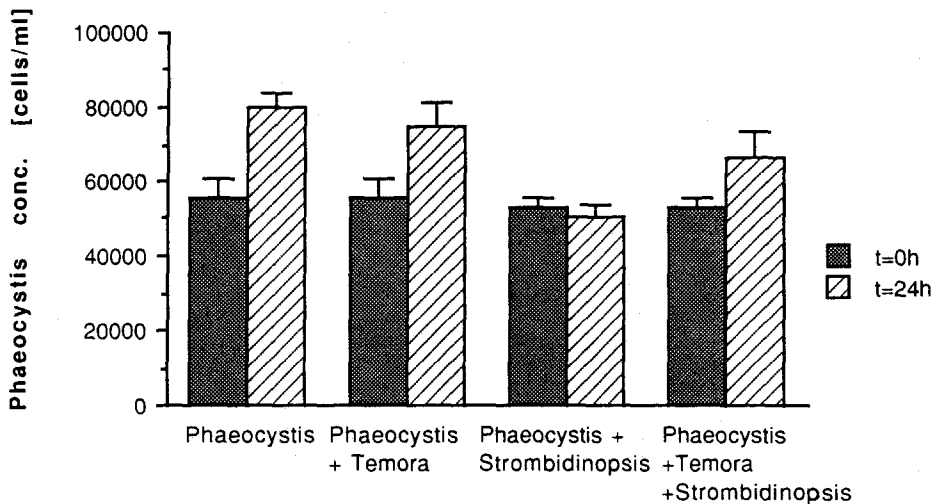


Fig. 6. *Phaeocystis* concentration (single cells) at the beginning ($t = 0$) and after a 24-h incubation at 12°C with *Temora longicornis* (C6, females) and *Strombidinopsis acuminatum*. Means and standard deviations for $n = 3$

DISCUSSION

The incubation experiments have shown that *Phaeocystis* can serve as a potential food source for many zooplankton organisms. An overestimation of copepod filtration and ingestion rates due to algae growth enhancement by nutrient excretion of the zooplankton organisms cannot be excluded, but is regarded unlikely, because of the high concentrations of nutrients contained in $f/2$ and $f/8$ enriched seawater (Guillard & Ryther, 1962) used in the experiments. The ingestion rates measured are comparable to rates found for other phytoplankton food (e.g. Nicolajsen et al., 1983; Baars & Fransz, 1984; Tande & Båmstedt, 1985), but are too low to allow high growth rates of the copepods. Based on the spring biomass increase of *T. longicornis*, Hansen & van Boekel (1991) calculated a required ingestion of 70 to 140% body weight daily, which is well in agreement with results from laboratory growth experiments (Klein Breteler et al., 1990).

In contrast to the results of the experiments in which only algal food was present, *Phaeocystis* was avoided by *Temora* in the more complex field situation, where alternative food sources were available. Suppressed feeding rates on phytoplankton during *Phaeocystis*-blooms were also reported by Daro (1986) as well as in a recent study by Bautista et al. (1992). We have suggested that *Temora* fed on co-occurring ciliates instead (Hansen & van Boekel, 1991).

There is much evidence that microzooplankton is a suitable food for copepods (Klein Breteler, 1980; Stoecker & McDowell Capuzzo, 1990 and references cited therein), in contrast to the low nutritional value reported for *Phaeocystis* (Claustre et al., 1990). Moreover, *Temora* is an omnivorous copepod, even able to ingest its own larvae (Daan et al., 1988). Thus, a positive selectivity for microzooplankton by *Temora*, as described for

other small omnivorous copepods (Wiadnyana & Rassoulzadegan, 1989), seems likely to occur. This is supported by the results from our combined experiment with *Temora*, the ciliate *Strombidinopsis* and *Phaeocystis* single cells.

Ciliates are thought to be the major predator on *Phaeocystis* single cells (Weisse & Scheffel-Möser, 1990). In the case of *Strombidinopsis*, feeding on colonial cells was observed by fluorescence microscopy. Admiraal & Venekamp (1986) observed grazing on colonial cells by tintinnids, which were extremely abundant during the *Phaeocystis* bloom. Assuming that the major grazing pressure on *Phaeocystis* is caused by microzooplankton organisms, which itself is the preferred food for the dominant mesozooplankton organisms, i.e. omnivorous copepods, these copepods would enhance the blooming of *Phaeocystis*. This scenario, as demonstrated in the experiment, is also likely to occur in the field under similar circumstances. Such a situation might be the late stage of a *Phaeocystis* spring bloom. At this time a considerable part of total *Phaeocystis* cells are comprised of flagellates, the colonies decay and are colonized by bacteria and microheterotrophs, and the copepods have also reached higher densities.

Our Marsdiep data suggest that most of the *Phaeocystis*-carbon is probably channelled to higher trophic levels via members of the microbial food chain (van Boekel et al., 1992). In future grazing studies, the coupling between mesozooplankton and the microbial loop should be taken into consideration.

Acknowledgements. This study was financially supported by the EC and is a contribution to the EC project on the "Dynamics of *Phaeocystis* blooms in nutrient-enriched coastal zones" [Contract Nos. B/89000615 & EV4V-0102-B (GDF)]. The ciliate grazing experiments were performed in cooperation with M. Reckermann. I thank Prof. Dr. J. Lenz, Dr. E. Hagmeier and Dr. W. C. M. Klein Breteler for their supervision. Thanks are also due to Dr. R. Riegman for valuable discussions on this topic. I thank all staff members of the Institut für Meereskunde Kiel (IFM), Meeresstation Biologische Anstalt Helgoland (BAH) and Nederlands Instituut voor Onderzoek der Zee (NIOZ), who supported this study. Language improvements on the manuscript by T. McCollin are gratefully acknowledged.

LITERATURE CITED

- Admiraal, W. & Venekamp, L. A. H., 1986. Significance of tintinnid grazing during blooms of *Phaeocystis pouchetii* (Haptophyceae) in Dutch coastal waters. – Neth. J. Sea Res. 20, 61–66.
- Baars, M. A. & Fransz, H. G., 1984. Grazing pressure of copepods on the phytoplankton stock of the central North Sea. – Neth. J. Sea Res. 18, 120–142.
- Barnard, W. R., Meinrat, O. A. & Iverson, R. L., 1984. Dimethylsulfide and *Phaeocystis pouchetii* in the southeastern Bering Sea. – Cont. Shelf Res. 3, 103–113.
- Bautista, B., Harris, R. P., Tranter, P. R. G. & Harbour, D., 1992. In-situ copepod feeding and grazing rates during a spring bloom dominated by *Phaeocystis* sp. in the English Channel. – J. Plankt. Res. 14, 691–703.
- Boekel, W. H. M. van, Hansen, F. C., Riegmann, R. & Bak, R., 1992. Lysis induced decline of the *Phaeocystis* bloom in the Marsdiep area of the North Sea and coupling with the microbial food chain. – Mar. Ecol. Prog. Ser. 81, 269–276.
- Cadée, G. C., 1990. Increased bloom (Note). – Nature, Lond. 346, 418.
- Claustre, H., Poulet, S. A., Williams, R., Marty, J.-C., Coombs, S., Ben Mlih, F., Hapette, A. M. & Martin-Jezequel, V., 1990. A biochemical investigation of a *Phaeocystis* sp. bloom in the Irish Sea. – J. mar. biol. Ass. U.K. 70, 197–207.
- Daan, R., Gonzalez, S. R. & Klein Breteler, W. C. M., 1988. Cannibalism in omnivorous calanoid copepods. – Mar. Ecol. Prog. Ser. 47, 45–54.
- Dam, H. G. & Peterson, W. T., 1988. The effect of temperature on the gut clearance rate constant of planktonic copepods. – J. exp. mar. Biol. Ecol. 123, 1–14.

- Eberlein, K., Leal, M. T., Hammer, K. D. & Hickel, W., 1985. Dissolved organic substances during a dense *Phaeocystis pouchetii* bloom in the German Bight (North Sea). – *Mar. Biol.* 89, 311–316.
- Estep, K. W., Nejstgaard, J. C., Skjoldal, H. R. & Rey, F., 1990. Predation by copepods upon natural populations of *Phaeocystis pouchetii* as a function of the physiological state of the prey. – *Mar. Ecol. Prog. Ser.* 67, 235–249.
- Fransz, H. G., Colebrook, J. M., Gamble, J. C. & Krause, M., 1991. The zooplankton of the North Sea. – *Neth. J. Sea Res.* 28, 1–52.
- Frost, B. W., 1972. Effects of size and concentration of food particles on the feeding behavior of the marine planktonic copepod *Calanus pacificus*. – *Limnol. Oceanogr.* 17, 805–815.
- Guillard, R. R. L. & Ryther, J. H., 1962. Studies of marine planktonic diatoms. I. *Cyclotella nana* Hustedt and *Detonula confervacea* Cleve. *Gran.* – *Can. J. Microbiol.* 8, 229–239.
- Hansen, F. C., 1992. Zooplankton Grazing an *Phaeocystis* mit besonderer Berücksichtigung der calanoiden Copepoden. Diss., Univ. Kiel, Ber. Inst. Meeresk. Kiel 229, 137 pp.
- Hansen, F. C. & van Boekel, W. H. M., 1991. Grazing pressure of the calanoid copepod *Temora longicornis* on a *Phaeocystis* dominated spring bloom in a Dutch tidal inlet. – *Mar. Ecol. Prog. Ser.* 78, 123–129.
- Hansen, F. C., Reckermann, M., Klein Breteler, W. C. M. & Riegman, R., 1993. *Phaeocystis* blooming enhanced by copepod predation on protozoa: evidence from incubation experiments. *Mar. Ecol. Prog. Ser.* 102, 51–57.
- Holm-Hansen, O., Lorenzen, C. J., Holmes, R. W. & Strickland, J. D. H., 1965. Fluorometric determination of chlorophyll. – *J. Cons. perm. int. Explor. Mer* 30, 3–15.
- Joiris, C., Billen, G., Lancelot, C., Daro, M. H., Mommaerts, J. P., Bertels, A., Bossicart, M. & Nijs, J., 1982. A budget of carbon cycling in the Belgian coastal zone: relative roles of zooplankton, bacterioplankton and benthos in the utilization of primary production. – *Neth. J. Sea Res.* 16, 260–275.
- Keller, M. D., 1988. Dimethyl sulfide production and marine phytoplankton: the importance of species composition and cell size. – *Biol. Oceanogr.* 6, 375–382.
- Klein Breteler, W. C. M., 1980. Continuous breeding of marine pelagic copepods in the presence of heterotrophic dinoflagellates. – *Mar. Ecol. Prog. Ser.* 2, 229–233.
- Klein Breteler, W. C. M. & Gonzalez, S. R., 1988. Influence of temperature and food concentration on body size, weight and lipid content of two calanoid copepod species. – *Hydrobiologia* 167/168, 201–210.
- Klein Breteler, W. C. M., Schogt, N. & Gonzalez, S. R., 1990. On the role of food quality in grazing and development of life stages, and genetic change of body size during cultivation of pelagic copepods. – *J. exp. mar. Biol. Ecol.* 135, 177–189.
- Lancelot, C., Billen, G., Sournia, A., Weisse, T., Colijn, F., Veldhuis, M. J. W., Davies, A. & Wassmann, P., 1987. *Phaeocystis* blooms and nutrient enrichment in the continental coastal zones of the North Sea. – *Ambio* 16, 38–46.
- Mackas, D. & Bohrer, R., 1976. Fluorescence analysis of zooplankton gut contents and an investigation of diel feeding patterns. – *J. exp. mar. Biol. Ecol.* 25, 77–85.
- Nicolajsen, H., Møhlenberg, F. & Kjørboe, T., 1983. Algal grazing by the planktonic copepods *Centropages hamatus* and *Pseudocalanus* sp.: diurnal and seasonal variation during the spring phytoplankton bloom in the Øresund. – *Ophelia* 22, 15–31.
- Omori, M., 1969. Weight and chemical composition of some important oceanic zooplankton in the north Pacific Ocean. – *Mar. Biol.* 3, 4–10.
- Smetacek, V., 1975. Die Sukzession des Phytoplankton in der westlichen Kieler Bucht. Diss., Univ. Kiel, 151 pp.
- Sokal, R. R. & Rohlf, F. J., 1981. *Biometry*. Freeman, San Francisco, 859 pp.
- Stoecker, D. K. & McDowell Capuzzo, J., 1990. Predation on protozoa: its importance to zooplankton. – *J. Plankt. Res.* 12, 891–908.
- Strathmann, R. R., 1967. Estimating the organic carbon content of phytoplankton from cell volume or plasma volume. – *Limnol. Oceanogr.* 12, 411–418.
- Tande, K. S. & Båmstedt, U., 1985. Grazing rates of the copepods *Calanus glacialis* and *C. finmarchicus* in arctic waters of the Barents Sea. – *Mar. Biol.* 87, 251–258.
- Utermöhl, H., 1958. Zur Vervollkommnung der quantitativen Phytoplankton-Methodik. – *Mitt. int. Verein. theor. angew. Limnol.* 9, 1–38.

- Veldhuis, M. J. W., Colijn, F. & Venekamp, L. A. H., 1986. The spring bloom of *Phaeocystis pouchetii* (Haptophyceae) in Dutch coastal waters. – Neth. J. Sea Res. 20, 37–48.
- Weisse, T., Tande, K. S., Verity, P. G., Hansen, F. C. & Gieskes, W. W. C., 1994. The trophic significance of *Phaeocystis* blooms. – J. mar. Systems 5, 67–79.
- Weisse, T. & Scheffel-Möser, U., 1990. Growth and grazing loss rates in single-celled *Phaeocystis* sp. (Prymnesiophyceae). – Mar. Biol. 106, 153–158.
- Wiadnyana, N. N. & Rassoulzadegan, F., 1989. Selective feeding of *Acartia clausi* and *Centropages typicus* on microzooplankton. – Mar. Ecol. Prog. Ser. 53, 37–45.