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Mesozooplankton grazing during the *Phaeocystis globosa* bloom in the southern bight of the North Sea

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Abstract

During spring blooms 1998 and 1999, three complementary methods were used to evaluate the in situ feeding activities of the dominant copepod species of the Belgian coastal zone: gut pigment content analysis using HPLC, the ^{14}C tracer method, and cell count experiments. The results obtained by all three methods consistently showed that *Phaeocystis globosa* is not an adequate food source for the spring copepods in the Belgian coastal zone. Our results demonstrated that, among the potential prey, copepods strongly selected diatoms and microzooplankton, and that these types of prey accounted for the major part of the ingested carbon. However, diatoms and microzooplankton ingestion did not always seem sufficient in terms of carbon to avoid food limitation. Comparison of clearance rates exerted on different potential prey types during the *P. globosa* peak with those before and after the *P. globosa* peak showed that the copepods' feeding pressure on diatoms was reduced during the *P. globosa* peak while that on microzooplankton was not. The low grazing pressure on *P. globosa*, together with the preferential grazing on diatoms, which reduces the competition for nutrients, and the predation on microzooplankton organisms, which reduces the microzooplankton grazing pressure on *P. globosa* cells, are likely to favour the *P. globosa* bloom in the Southern Bight of the North Sea.

Keywords: *Phaeocystis*; copepods; grazing; feeding selectivity; diatoms; microzooplankton

1. Introduction

In the Southern Bight of the North Sea, explosive developments of *Phaeocystis globosa* gelatinous colonies dominate the phytoplankton community, contributing over 90% of cell numbers during spring (Lancelot and Mathot, 1987). One of the most visible effects of these blooms is the formation of foam observed at the sea surface and as massive foam banks on beaches. The fate of the enormous biomass reached by *P. globosa* (1–5 gC m^{-3}; Lancelot et al., 1991), although essential to the energy budget of the marine ecosystem, is still unclear. The organic material produced by *P. globosa* could pass through the food chain either via mesozooplankton to fish ('classical' food chain) or via a consortium of heterotrophic micro-organisms (bacteria, heterotrophic nanoflagellates, ciliates, etc.) to mesozooplankton ('microbial' food web) feeding actively on protozoa (Hansen et al., 1993). Alternatively, a considerable

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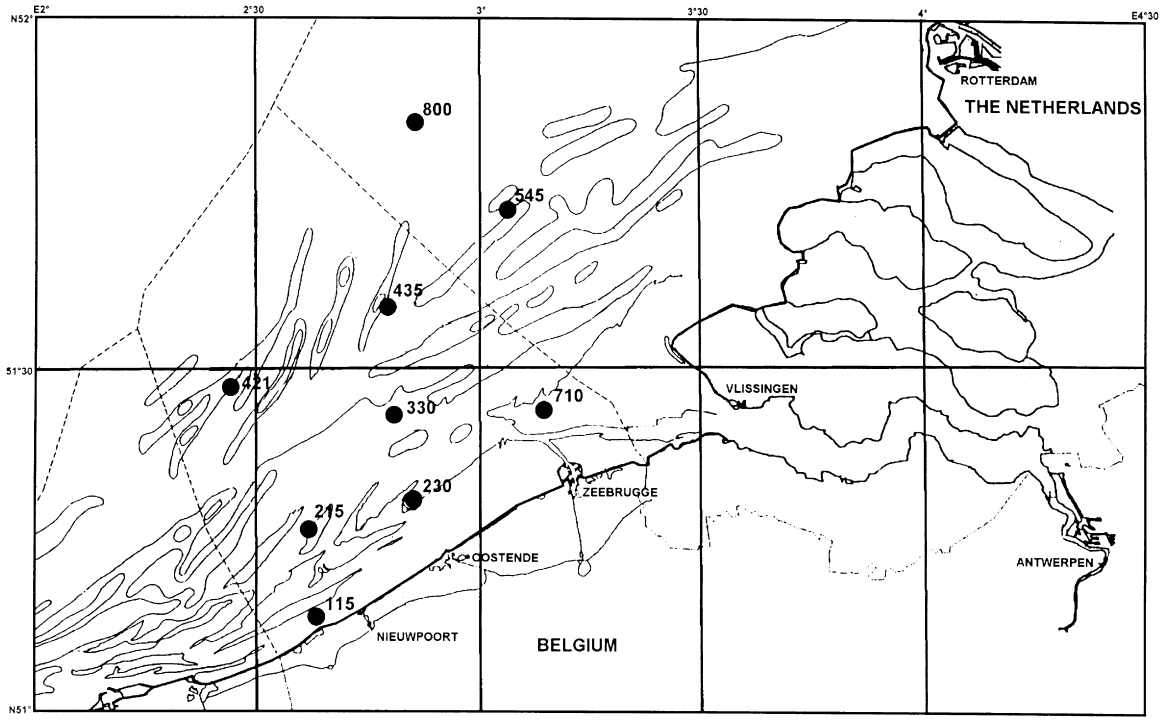

Fig. 1. Map of the Belgian coastal zone showing the sampling stations.

part of the *Phaeocystis* production might be unaffected by pelagic predation and sediment as detritus (Wassmann, 1994).

The degree to which copepods, which dominate mesozooplankton biomass in most marine systems, can eat *Phaeocystis* was originally debated (Joiris et al., 1982; Weisse, 1983). However, recent literature points to the importance of copepod size in determining their ability to consume *Phaeocystis* (Hansen et al., 1994; Weisse et al., 1994). Large copepod species (>1.5 mm) are indeed often reported to feed on *Phaeocystis* (Sargent et al., 1985; Huntley et al., 1987; Tande and Båmstedt, 1987; Eilertsen et al., 1989; Estep et al., 1990), whereas small copepod species (<1.5 mm) do not seem to feed efficiently on this alga (Daro, 1985; Verity and Smayda, 1989; Hansen and Van Boekel, 1991; Bautista et al., 1992).

Large copepods (mainly *Calanus* spp.) are abundant in the northern North Sea while small species such as *Acartia clausi*, *Centropages hamatus* and *Temora longicornis* dominate in the Southern Bight (Daro, 1988; Fransz et al., 1991; Williams et al., 1993). Consequently, while an important fraction of *Phaeocystis* production may enter the food chain through the mesozooplankton in the north, the direct transfer of *Phaeocystis* production to mesozooplankton in the south seems limited. Small copepod species may, however, indirectly benefit from *Phaeocystis* production (Fransz et al., 1992). For instance, microzooplankton is known to feed efficiently on *Phaeocystis* (Weisse and Scheffel-Möser, 1990) and Hansen and Van Boekel (1991) hypothesised that microzooplankton producing on *Phaeocystis* may in turn form an important prey to the mesozooplankton during *Phaeocystis* blooms. This hypothesis was later supported by laboratory experiments (Hansen et al., 1993), but to our knowledge, only one field study deals with this question (Brussaard et al., 1995), without distinction between mesozooplanktonic species.

In this study, we present in situ experimental data on the species-specific feeding activities of dominant copepods in the Belgian coastal zone during the spring

bloom. We used three complementary methods: pigment gut content analysis, the ^{14}C tracer method, and cell count experiments.

2. Methods

2.1. Sampling and environmental parameters

Sampling and experiments were carried out during field campaigns on *RV Belgica*, at various stations covering the whole Belgian coastal zone (Fig. 1). Samples were collected from March to June both in 1998 and 1999.

Zooplankton samples were collected using a 300 μm mesh plankton net for both determination of species abundance (unpublished data) and for use in the feeding experiments (tow duration <5 min). Additional samples were also collected using a 55-μm mesh plankton net for experiments including small copepodite stages.

Water samples were collected with a bucket to avoid *Phaeocystis* colonies disrupting. Subsamples were filtered on glass fibre filters for quantification of chlorophyll-*a* concentration and duplicate subsamples were fixed with 1% lugolglutaraldehyde solution for microscopic enumeration of planktonic microorganism and biomass estimations. The reader is referred to Rousseau et al. (2000) for details on the characteristics of the sampling locations and methodologies for biomass determination.

2.2. Gut pigment contents

The in situ gut pigment contents of adult copepods were analysed by high-performance liquid chromatography (HPLC). From each zooplankton sample, a subsample was taken with a piece of 300-μm net, wrapped in aluminium foil and immediately frozen in liquid nitrogen. In the laboratory, subsamples were stored in a deepfreeze at -85°C for no longer than six months. For analysis, each subsample was rinsed with filtered seawater and placed under a binocular microscope with a minimum light. Three replicates of 50 individuals per species and per station were sorted and placed into 0.5 cm^3 of 90% cold acetone. Replicates were then macerated with tissue grinders while being held on ice. After thorough grinding, they were refrigerated in the dark for 2 h, filtered on a syringe filter (Acrodisc CR PTFE 0.45 μm) to remove suspended particles, and injected into the HPLC system.

The HPLC system comprised a Waters Associates 600 Controller Pump, 717 Autosampler and injector, Photodiode Array Detector and 470 scanning fluorescence detector, connected via a Waters system Interface Module to a micro-computer running Waters Millennium Chromatography Manager software. The reversed-phased column used was Spherisorb ODS2, 25 cm × 4.6 mm ID, 5-μm particle size, packed by Australian Government Analytical Laboratories, Melbourne (90,000–14,000 plates m^{-1}). Fluorescence detection for chloropigments was done at 436 nm excitation and 676 emission. Our standard procedure consisted of the injection of 0.1 cm^3 of extract run through a 30-min gradient (A: 80:20 methanol: 0.5 M ammonium acetate aq. pH 7.2 v/v; B: 90:10 acetonitrile 210 nm UV cut-off grade: water (v/v); C: ethyl acetate HPLC grade; Flow rate was 1 cm^3 min^{-1}).

Pigments were identified by: (i) co-chromatography with standards commercially available from the International Agency for ^{14}C determination (Hørsholm, Denmark); (ii) comparing retention times of unknown peaks with published retention times of well-characterised pigments (SCOR Working Group 78, 1997, see Part IV Data sheets, and references therein); and (iii) photo diode-array detector.

Chlorophyll-*a* and chlorophyll-*a* derivatives in gut contents were used as an index of phytoplankton ingestion, whereas carotenoid pigments in gut contents were used as taxonomic indicators in order to characterise the ingested prey (Head and Harris, 1994). Assuming that phaeopigments-*a* detected in copepod guts originated from chlorophyll-*a* and were not originally present in the prey (Mackas and Bohrer, 1976), the amounts of phaeopigments and chlorophyll-*a* were summed and the results were expressed as chlorophyll-*a* equivalents.

2.3. ^{14}C experiments

Monospecific non-axenic algal cultures were prepared from natural communities sampled at station 330 (Fig. 1) during spring 1997. Strains were maintained in a culture medium at 8°C in a culture room under a 12 h light:12 h dark cycle at

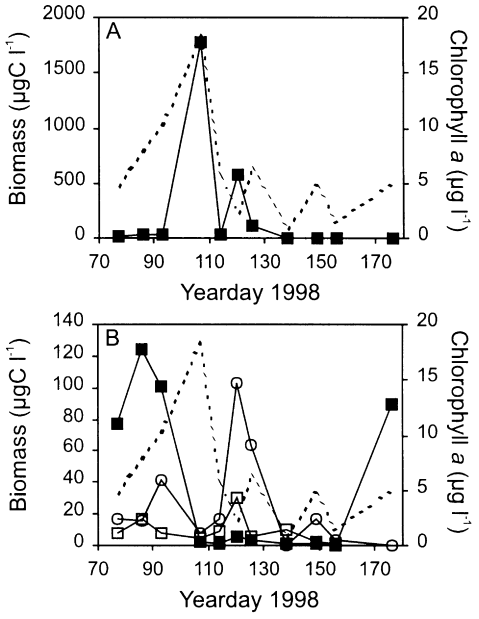

Fig. 2. Temporal variation in biomass of (A) *Phaeocystis globosa* (black squares), and (B) diatoms (black squares), dinoflagellates (open squares) and microzooplankton (open circles) together with chlorophyll-*a* concentrations (dotted lines) at station 330 (see Fig. 1) during spring 1998.

120 μmol quanta m^{-2} s^{-1}. The culture medium was prepared with sterile, filtered seawater enriched according to Veldhuis and Admiraal (1987) except for nitrate, ammonium and phosphate whose concentrations were respectively 50, 25 and 5 μM. Some 10 μM $Si(OH)_4$ (final concentration) were added for diatoms species. Four of these cultures, *P. globosa* small colonies (diameter <150 μm), large colonies (diameter >150 μm), *Chaetoceros socialis* (cell diameter: 4–15 μm) and a mixture of *Thalassiosira fallax* (cell diameter: 15–25 μm) and *T. Nordenskoldii* (cell diameter: 12–43 μm) were pre-labelled by adding 5 μCi $NaH^{14}CO_3$ to 50 cm^3 of culture. These were allowed to take up the ^{14}C for 24 to 48 h before the start of the experiments. On board, four bottles of 1 dm^3 were filled with freshly sampled seawater and 1 cm^3 of each labelled culture was added to each of the four bottles. A subsample (in duplicate) of 20–50 cm^3 was immediately filtered on GF/C filter in order to quantify the DPM (Disintegration Per Minutes) offered. The amount of culture cells added never exceeded 1/100 of the natural phytoplankton concentration, in order to preserve the zooplankton natural feeding behaviour. From a freshly caught zooplankton sample, about 50–70 animals (all species and stages mixed) were gently pipetted under binocular microscope and immediately added to each of the four bottles. Only animals with normal swimming behaviour were selected. Bottles were then placed in the dark, at seawater temperature, for not more than 1 h and 15 min. Then 20–50 cm^3 subsamples (in duplicates) of each of the four bottles were again filtered on a GF/C filter. The zooplankton was collected on a small piece of 50 μm plankton gaze, gently rinsed with GF/C filtered seawater, wrapped in aluminium foil, and stored at −20°C, together with the filters. In the laboratory, the filters were dissolved in 10 cm^3 scintillation cocktail, the animals were sorted per species and developmental stages under the binocular microscope, and put in the same scintillation cocktail. All samples were then counted in liquid scintillation counter for 50 min. Calculations of the clearance rates were done according to Daro and Baars (1986).

2.4. Cell count experiments

For the cell count experiments (Fuller and Clarke, 1936), twelve plastic bottles of 1 dm^3 were filled with 500 cm^3 of natural seawater. Four replicates of 30 adults of the same copepod species were gently pipetted under a binocular microscope and distributed to four of these bottles. Only animals with normal swimming behaviour were selected. Four bottles without copepods were immediately fixed in 2% glutaraldehyde (initial conditions), whereas the other bottles (four with and four without copepods) were incubated in a tank for 24 h with water circulation to maintain natural conditions of temperature. At the end of the incubation, copepod survival was visually controlled and the bottles were also fixed with 2% glutaraldehyde. In the laboratory, the samples were allowed to sediment for one week, and concentrated four to five times by pipetting the supernatant. Then the samples were gently mixed by inversion and 5 cm^3 subsamples were taken and stained with 2% acid lugol (final concentration) for phytoplankton and microzooplankton enumeration using an inverted microscope provided with phase contrast at 10 × 20 and 10 × 40 magnification.

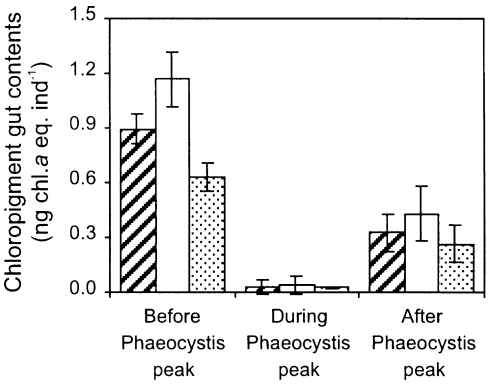

Fig. 3. Averaged day–night values (±standard errors) of chloropigment gut contents measured in adults and late copepodite stages of *Acartia clausi* (hatched bars), *Centropages hamatus* (white bars) and *Temora longicornis* (dotted bars), before, during and after the *Phaeocystis globosa* peak in 1998 spring.

Clearance rates (volume swept clear of prey/animal/unit of time) were quantified from the difference in prey concentration determined between control and experimental bottles, using the equations of Frost (1972).

Ingestion rates were calculated per copepod species for each potential prey by multiplying clearance rates by the corresponding prey biomass in the water (see Section 2.1). To calculate the daily ration in terms of carbon, copepod dry weight values measured in the Belgian coastal zone by Daro and Van Gijsegem (1984) were used, applying a dry weight–carbon conversion factor of 0.45.

3. Results

Spring was divided into three periods to describe copepod feeding activity: before the *P. globosa* peak, during the *P. globosa* peak (concentrations $>10{,}000$ cell cm^{-3}) and after the *P. globosa* peak. These three periods also correspond to different diatom concentrations (Fig. 2), diatoms being dominant before *P. globosa* peak (mainly *Chaetoceros socialis*), very scarce during the peak and relatively abundant again after the peak (mainly *Rhizosolenia delicatula* and *R. Stolterfothii*). *P. globosa* colonies were smaller during the fist period (70–810 μm, mean 374 μm) than during the second and the third periods (200–2175 μm, mean 790 μm and 145–2370 μm, mean 720 μm, respectively).

Averaged day–night values of copepod chlorophyll-*a* gut contents during these three periods are shown in Fig. 3. For the three species studied (*Acartia clausi*, *Centropages hamatus* and *Temora longicornis*), chlorophyll-*a* gut contents were relatively high before the *P. globosa* peak. During the *P. globosa* peak, chlorophyll-*a* gut contents were significantly lower (*t*-test, $p < 0.01$), indicating a very low phytoplankton ingestion. After the *P. globosa* peak, chlorophyll-*a* gut contents increased significantly (*t*-test, $p < 0.01$) but remained lower than during the first period. The general trend of chlorophyll-*a* gut contents contrasts with the variation of chlorophyll-*a* concentration in the water (Fig. 2), which mainly reflects the *P. globosa* concentration.

Among carotenoid pigments in the copepod guts, only three taxonomic indicators were detected: peridinin, fucoxanthin, and astaxanthin (Table 1). Peridinin corresponds to dinoflagellates. Detectable amounts of this pigment were found only during and after the *P. globosa* peak in *T. longicornis* but never in *A. clausi* and *C. hamatus*. On the other hand, fucoxanthin was always found in copepod guts. Fucoxanthin is present in both diatoms and prymnesiophytes. However, prymnesiophytes also contain 19′hexanoyl-fucoxanthin, which was never found in copepod guts. Consequently, most of the fucoxanthin found in copepod guts probably originated from diatoms. Astaxanthin is an animal pigment. It could potentially reflect microzooplankton ingestion. However, this pigment was also detected in starved copepods and it was not possible to separate the copepod astaxanthin from microzooplankton astaxanthin within the range of variability in the measurements.

Averaged day–night values of clearance rates obtained from the ^{14}C-experiments during *P. globosa* dominance are shown in Fig. 4. Clearance rates on small *P. globosa* colonies as well as on large *P. globosa* colonies (diameter >150 μm) were very low and often (24 among 26 values) not significantly different from zero (*t*-test, $p > 0.05$). Clearance rates on diatoms were much higher for all developmental stages of the three species (*t*-test, $p < 0.01$). Thus, it appears that even during the *P. globosa* dominance, copepods strongly selected diatoms.

The results of the cell count experiments are shown in Fig. 5. Clearance rates on *Phaeocystis* were always

Table 1
Carotenoid pigments detected in *Acartia clausi* (A), *Centropages hamatus* (C) and *Temora longicornis* (T), before, during and after the *Phaeocystis globosa* peak in 1998 and after 90 min of starvation in filtered seawater. Crosses in brackets correspond to detectable but very low amounts of pigment. Taxonomic groups corresponding to each pigment are also presented

Carotenoid pigment	Taxonomic group	Before *Phaeocystis* peak			During *Phaeocystis* peak			After *Phaeocystis* peak			After starvation		
		A	C	T	A	C	T	A	C	T	A	C	T
Peridinin	Dinoflagellates						(×)			(×)			
Fucoxanthin	Diatoms and Prymnesiophytes	×	×	×	(×)	(×)	(×)	×	×	×			
19′ Hexanoyl-Fucoxanthin	Prymnesiophytes												
Astaxanthin	Animals	×	×	×	×	×	×	×	×	×	×	×	×
Alloxanthin	Cryptophytes												
Lutein	Green algae												

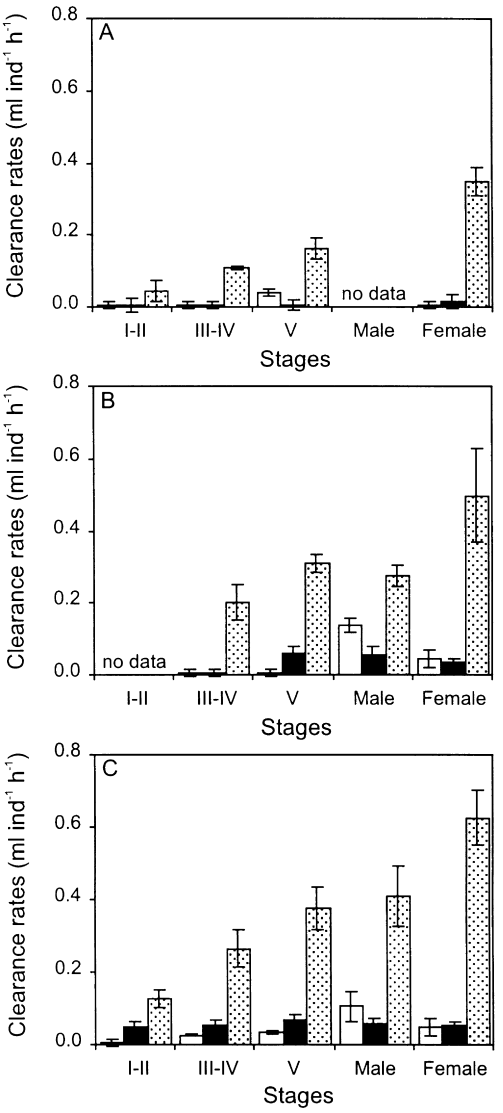

Fig. 4. Averaged day–night values (±standard errors) of clearance rates measured using the ^{14}C method for different developmental stages of (A) *Acartia clausi*, (B) *Centropages hamatus*and (C) *Temora longicornis* during the *Phaeocystis globosa* peak in 1999. White bars, black bars and dotted bars correspond to clearance rates on small (diameter <150 μm) *P. globosa* colonies, large (diameter >150 μm) *P. globosa* colonies and diatoms, respectively.

very low and not significantly different from zero (*t*-test, $p > 0.05$), whereas clearance rates on diatoms were much higher (*t*-test, $p < 0.01$). Furthermore, relatively high clearance rates on microzooplankton (mainly *Strombidium*-like

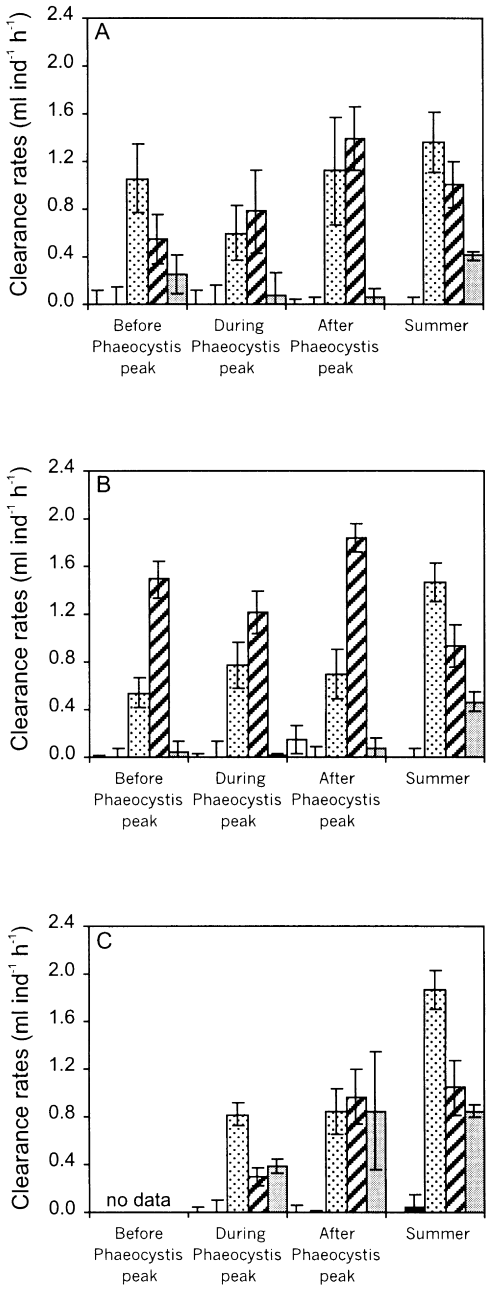

Fig. 5. Mean values (±standard errors) of clearance rates measured in the incubation experiments in adults of (A) *Acartia clausi*, (B) *Centropages hamatus* and (C) *Temora longicornis*, before, during and after the *Phaeocystis globosa* peak in spring 1998 and 1999 as well as in summer 1998 and 1999. White bars, black bars, dotted bars, hatched bars and gray bars correspond to clearance rates on *P. globosa*, nanoflagellates, diatoms, microzooplankton and dinoflagellates, respectively.

ciliates, tintinnids and rotifers) were also observed. In *C. hamatus*, these latter were even significantly higher than clearance rates on diatoms (*t*-test, $p < 0.01$). Clearance rates on dinoflagellates (mainly *Gymnodinium* spp.) were also relatively high in *T. longicornis* but relatively low and not significantly different from zero (*t*-test, $p > 0.05$) in *A. clausi* and *C. hamatus*.

For comparison, clearance rates obtained in summer are also shown in Fig. 5 together with clearance rates obtained in spring. From one period to another, somewhat different trends in the relative importance of the different clearance rates can be observed. In order to better understand this variability, clearance rate values were plotted against prey concentrations (Fig. 6). In such a graph, an increase is expected of clearance rate versus prey concentrations, followed by a decrease indicating that maximum ingestion rate is reached. During our experiments, we never observed a significant decrease in clearance rate as a function of prey concentration. On the contrary, we observed significant increases (*t*-test, $p < 0.05$) or no significant trend at all. This indicates that maximum ingestion rate was not reached during most of our experiments.

Furthermore, comparing values obtained during the *P. globosa* peak with values obtained before and after the peak (Fig. 6), we observed that for a given concentration of diatoms during *P. globosa* dominance clearance rates on diatoms were significantly lower (ANOVA, $p < 0.01$) than during the other periods. Such a trend was not observed for microzooplankton or dinoflagellates as prey.

Ingestion rates per copepod species obtained on different potential preys are shown in Fig. 7. The graph shows higher ingestion of diatoms before the *P. globosa* peak than during the other periods, very low diatom ingestion during the peak, and intermediate values after the peak. The share of microzooplankton in the diet of the copepods was relatively low before the *P. globosa* peak (11–40%) and rose considerably during and after the peak (50–96%). However, the amount of microzooplankton as well as of dinoflagellates ingested did not compensate for the decrease of diatom ingestion in terms of carbon. Indeed, total daily ingestion represented 27–50% of the adult copepod carbon weight before the peak, only 7–17% during the peak and 14–21% after the peak.

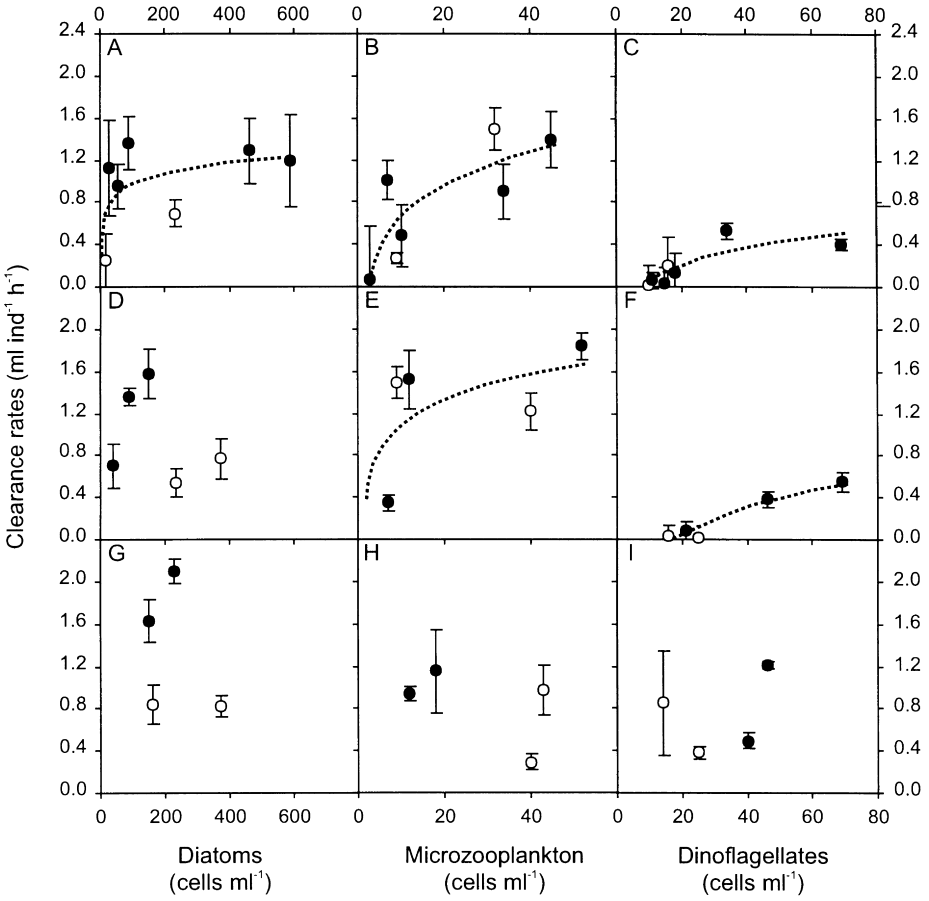

Fig. 6. Clearance rates measured in the incubation experiments for adults of *Acartia clausi* (A, B and C), *Centropages hamatus* (D, E and F) and *Temora longicornis* (G, H and I) as a function of the concentration of different prey types (mean of four replicates ± standard errors). White symbols: values obtained during the *P. globosa* peak (1998 and 1999); black symbols: values obtained before and after the peak (1998 and 1999). Dotted lines show log-linear regressions using all values.

4. Discussion

Each of the methods used in this study has its shortcomings and disadvantages (see Mauchline, 1998, for a review). Nevertheless, the concurrent use of three methods consistently confirms that *Phaeocystis globosa* is not an adequate food source for the small-sized spring copepods in the Belgian coastal zone. During the dominance of this alga, chloropigment gut contents were indeed much lower than during the periods of diatom dominance, indicating very low phytoplankton ingestion even if we consider a partial degradation of chloropigments into a colourless compound during their passage through the gut. Furthermore, no detectable amount of 19′hexanoyl-fucoxanthin was found in the copepod guts, although it is present in *P. globosa* cells (Bjørnland et al., 1988) and clearance rates on this prymnesiophyte, both measured by the ^{14}C method and in the cell count experiments, were always much lower than clearance rates on other food items.

In the literature, colony size compared to predator size has often been proposed to explain low grazing on *Phaeocystis* spp. by small copepods (Daro, 1985; Verity and Smayda, 1989; Bautista et al., 1992; Hansen et al., 1994). Nevertheless, factors other than size have also been considered. Copepods are known as chemosensory feeders (Poulet and Marsot,

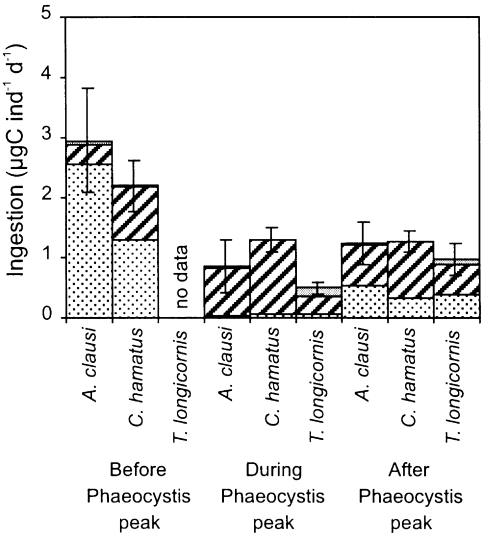

Fig. 7. Daily ingestion rate on diatoms (dotted bars), microzooplankton (hatched bars) and dinoflagellates (gray bars) by *Acartia clausi*, *Centropages hamatus* and *Temora longicornis* adults calculated from clearance rates and prey biomass in the water (see text) before, during and after the *Phaeocystis globosa* peak in 1998. Vertical lines correspond to the sum of standard errors.

1978). Although no toxic compounds were found in *Phaeocystis* spp. (Lancelot et al., 1994), some substances contained in it could have a repulsive property against copepods. In this respect, acrylic acid, dimethylsulphide as well as mucopolysaccharide have been proposed to play a role in *Phaeocystis* spp. avoidance by copepods (Verity and Smayda, 1989; Estep et al., 1990; Bautista et al., 1992). However, its ingestion by large copepods, at least in the absence of alternative food, suggests that *Phaeocystis* spp. is not chemically undesirable. A low nutritional value has also been proposed (Verity and Smayda, 1989; Estep et al., 1990; Bautista et al., 1992), but animals avoiding an abundant food source in a food-limited situation (see below), just because its nutritional value is low, seems improbable. Actually, a mechanical hindrance (size) appears to be the most probable and simple explanation of low grazing on this alga by small copepods, such as the spring species in the Belgian coastal zone. The gelatinous matrix of colonies could indeed clog the feeding appendages of copepods (Schnack et al., 1985) while filament produced by solitary cells (Chrétiennot-Dinet et al., 1997) could make it inconvenient to handle. In freshwater systems, where analogous developments of large colonies of Cyanobacteria, *Microcystis aeruginosa*, *Sphaerocystis* sp. or filamentous *Aphanizomenon* sp. are regularly observed, the formation of large mucilaginous colonies is often interpreted as a defence strategy against predation (Gliwicz, 1980; Gliwicz and Siedlar, 1980; Crumpton and Wetzel, 1982; De Bernardi and Giussani, 1990). Most of the copepods are unable to handle such large colonies (Gras et al., 1971). Even cladocerans, which are known to be less selective than copepods (De Mott and Moxter, 1991), are unable to handle such large colonies. When the largest among them, *Daphnia magna*, succeeds in ingesting them, the food is almost completely excreted (Lampert, 1987).

Among the potential prey other than *P. globosa*, we observed that copepods of the Belgian coastal zone strongly selected diatoms and microzooplankton. Before the *P. globosa* peak, diatoms accounted for the major part of the ingested carbon. This observation is not surprising since this food source was the most abundant during this period (Fig. 2). Then we observed that during the *P. globosa* peak diatom ingestion decreased dramatically in terms of carbon and that microzooplankton became the main food source. Low phytoplankton ingestion during *Phaeocystis* spp. dominance has already been observed in other field studies. Hansen and Van Boekel (1991) as well as Bautista et al. (1992) showed low gut fluorescence in *Temora longicornis* during *Phaeocystis* spp. dominance compared to gut fluorescence measured just before or just after its dominance. Daro (1985) also reported depressed feeding rates in *T. longicornis* during the *P. globosa* bloom in the Belgian coastal zone. Hansen and Van Boekel (1991) hypothesised that *T. longicornis* could switch to a heterotrophic food source during this period. Later this hypothesis was supported by laboratory studies showing high copepod predation rates on ciliates (Hansen et al., 1993). Our results appear to confirm this hypothesis in natural conditions for the three species studied. Thus, assuming that the microzooplankton uses *P. globosa* as food (Weisse and Scheffel-Möser, 1990), copepods appear to indirectly profit from *P. globosa* production. However, although microzooplankton ingestion could explain copepod survival in spite of low herbivory during the *P. globosa* dominance, it did

not seem sufficient in terms of carbon to compensate for the decrease of diatom ingestion. Consequently, either copepods were food limited during this period, or used detritus, originating, for instance, from decaying *P. globosa* colonies, to complement their diet. This latter possibility was unfortunately not tested during this study and will be subject to further investigation.

Low diatom ingestion during the *P. globosa* peak can be attributed both to the low diatom biomass (Fig. 2) and depressed clearance rates (Fig. 6). On the other hand, the insufficient microzooplankton ingestion seemed mainly due to the low abundance of this food source. It is intriguing that for a given prey concentration clearance rates on diatoms were lower during *P. globosa* dominance than during the other periods, whereas clearance rates on microzooplankton remained unchanged. It suggests that copepods were less hampered in their selection of microzooplankton than in their selection of diatoms during *P. globosa* dominance. Diatoms could be more easily trapped in the gelatinous matrix of *P. globosa* than motile protozoans, making them more difficult to obtain, or less desirable as food. Motile protozoans are probably also more easily detected by the copepods, by visual or tactile perception, even at high *P. globosa* concentrations. An alternative explanation could be that, in food-limited situations, copepods invest more energy in maintaining their predation on microzooplankton than in their grazing on diatoms. This latter hypothesis is in agreement with the optimal foraging theory (Lam and Frost, 1976; Lehman, 1976) as the nutritional value of microzooplankton has often been suggested to be higher than that of diatoms (Stoecker and Sanders, 1985; Gifford and Dagg, 1988; Stoecker and McDowell Capuzzo, 1990).

In spite of the possible food limitation mentioned above, copepod feeding activity is likely to favour the *P. globosa* bloom in the Southern Bight of the North Sea. Firstly, the low grazing pressure exerted on *this* colonial alga may contribute to its prodigious development. Moreover, preferential grazing on diatoms may result in a reduction of inter-specific competition for nitrate and phosphate among alga. Lastly, the selective removal of microzooplankton organisms by the copepods may limit their development and may subsequently reduce the microzooplankton grazing pressure on *Phaeocystis* cells (Weisse and Scheffel-Möser, 1990; Hansen et al., 1993). An evaluation of the consequences for the carbon budget of the Belgian coastal zone is presented in Rousseau et al. (2000).

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