JOURNAL OF PLANKTON RESEARCH | VOLUME 23 | NUMBER 1 | PAGES 75–88 | 2001

Dynamics of copepod faecal pellets in relation to a *Phaeocystis* dominated phytoplankton bloom: characteristics, production and flux

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[1]TO WHOM CORRESPONDENCE SHOULD BE ADDRESSED

Copepod faecal pellet characteristics and production were measured in spring 1995, 1996 and 1997 in the North Sea Southern Bight in order to define changes due to the development of the phytoplankton bloom. Changes were related to the succession from diatoms to a Phaeocystis sp. bloom. Mean monthly pellet production decreased during the Phaeocystis bloom development to 0.27 pellets ind.$^{-1}$ h^{-1}, approximately 80% lower than before and after the bloom. Although phytoplanktonic pigments showed significant differences between inshore and offshore stations, there was no such significant difference for faecal pellet production. Faecal pellet sinking-rate decreased from 100 to 70 m day^{-1} during the transition from a diatom- to a Phaeocystis-dominated bloom. This was due to a decrease in pellet density and/or a decrease of the pellet volume. These results supported the idea of lower feeding of copepods under Phaeocystis bloom conditions. As mean seasonal density of copepod faecal pellets was higher (1.37 g cm^{-3}) than in other seas, accidental ingestion of sedimentary material as the cause of this high density is discussed.

INTRODUCTION

The most potentially important process accelerating vertical fluxes of phytoplankton organic matter could be the compaction and packing of phytoplankton into faecal pellets by herbivorous zooplankton (Smayda, 1971). This flux may fluctuate widely and vary non-linearly with depth according to faecal pellet characteristics and environmental factors (Karl and Knauer, 1984). Pellets may sink to reach the bottom and pass to the benthic ecosystem (Fowler *et al.*, 1987), or remain in the mixed layer and stay in the pelagic food chain (Krause, 1981). In shallow turbulent ecosystems, only a few faecal pellets reach the sea floor, as they are mostly consumed or degraded in the water column (Lane *et al.*, 1994).

As zooplankton constitute the most numerically abundant animal forms in the pelagic zones of the oceans, overall faecal pellet production of these organisms must be the highest of all marine animals (Turner and Ferrante, 1979). Consequently, in a biologically productive sea such as the North Sea, zooplankton faecal pellets could transport important quantities of organic matter. In the southern North Sea, where herbivorous copepods constitute 70–80% of the total zooplankton biomass and consume 40% (on an annual basis) of the net particulate production (Joiris *et al.*, 1982), they could produce a major part of the faecal pellets. This is the case in the Norwegian Sea where most of the suspended and sedimented faecal pellets appear to be produced by copepods (Bathmann *et al.*, 1987).

The eutrophic coastal area of the southern Bight of the North Sea exhibits, in spring, algal succession from diatoms to a *Phaeocystis* sp. bloom (Althuis *et al.*, 1994). The *Phaeocystis* sp. strain of the southern Bight of the North Sea has specific pigment differences, allowing it to be distinguished from other *Phaeocystis* sp. Buma *et al.* (Buma *et al.*, 1991) observed in a North Sea Southern Bight strain of *Phaeocystis* sp. a ratio of 19′ hexanoyloxyfucoxanthine to chlorophyll *a* (19′HF/Chl *a*) close to 1%, while *Phaeocystis* sp. of other areas had a higher ratio of 19′HF/Chl *a* (Jeffrey, 1997).

In northern Norway, vertical transport of bloom-derived organic matter during *Phaeocystis* sp. dominance has already been shown to be dominated by faecal pellet sedimentation (Riebesell *et al.*, 1995). The authors suggested that loss of the colony-forming prymnesiophyte *Phaeocystis* sp. from the surface layer is partly or completely due to zooplankton grazing. During the *Phaeocystis* bloom, however, this prymnesiophyte is known to inhibit the feeding of copepods (Daro, 1986; Hansen and Boekel, 1991; Bautista *et al.*, 1992). As a consequence of these events, copepod pellet production and the resulting flux could be affected.

The aim of this study was to define the role of copepod faecal pellets in the transfer of organic matter, and as a possible indicator of changes in copepod feeding activity during the phytoplankton bloom in the North Sea Southern Bight. As this area has several water masses [channel water, continental coastal water, southern North Sea water (Becker *et al.*, 1993)], differences in the transfer of the organic matter between these water masses are possible. In order to estimate the faecal pellet flux variation over time and space, several processes must be measured (production, sedimentation, decomposition) at short time intervals. This study endeavoured to develop an assay allowing the measurement of copepod faecal pellet production and sedimentation over short time scales.

METHOD

Samples were collected from the southern North Sea (Figure 1) during eight cruises on board the RV Belgica: 2–11 May 1995; 28 June–7 July 1995; 22–29 February 1996; 18–29 March 1996; 15–26 April 1996; 17–31 June 1996; 17–21 March 1997; and 28–30 April 1997. Temperature and salinity were measured using a computerized acquisition system (pump inlet at a depth of –2 m). Data were divided into two groups according to water masses (Figure 1): continental coastal water (CCW, 31–34 psu and 0–20°C) along the Belgian and southern Dutch coast; or southern North Sea water (SNSW, 34–34.75 psu and 4–14°C) offshore (Becker *et al.*, 1993). Separation was not considered for June 1996 as stations were at the limit between the two water masses. Channel water mass was not encountered in the sampling stations.

Phytoplankton analysis

Water samples for phytoplankton analysis were collected in spring 1996. For HPLC analysis of phytoplankton pigments, 250–1000 ml water samples taken at 3 m depth were filtered through a 47 mm Whatman GF/C filter and stored at –20°C. The analysis was conducted by the method described by Mantoura and Llewellyn (Mantoura and Llewellyn, 1983) as adapted by Goffart and Hecq (Goffart and Hecq, 1989). Among the pigments detected, as well as chlorophyll *a* (Chl *a*) as a measure of phytoplankton biomass, we examined only those (including their ratio to Chl *a*) whose changes could allow us to locate the *Phaeocystis* sp. bloom in the southern North Sea, i.e. 19′ hexanoyloxyfucoxanthin, fucoxanthin (Buma *et al.*, 1991) and chlorophyll c_3 (Althuis *et al.*, 1994).

Data from microscopic analysis of *Phaeocystis* (V. Rousseau, personal communication) are from samples taken at station 330 (Figure 1) on 26 April 1996, 6 May 1996 and 22 May 1996. Colony size was determined according to the method described by Rousseau *et al.* (Rousseau *et al.*, 1990) and was expressed in equivalent spherical diameter units.

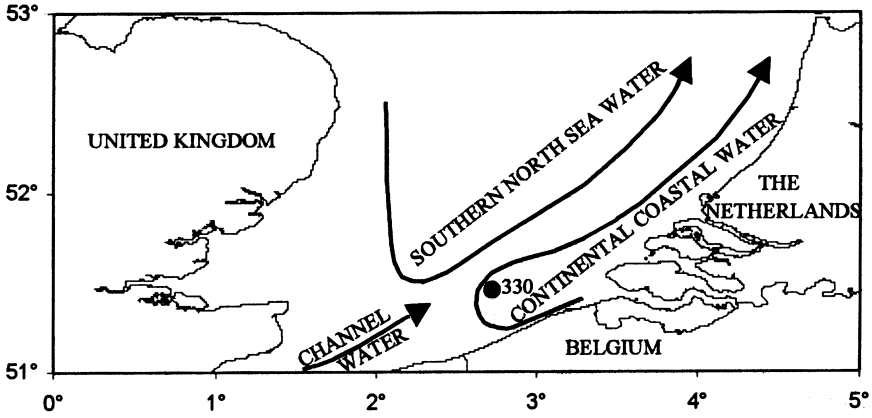

Fig. 1. Map of the study site with schematic diagram of general circulation adapted from Nihoul and Hecq (Nihoul and Hecq, 1984) and Becker *et al.* (Becker *et al.*, 1993) and location of station 330.

Copepod species composition, abundance and weight

Zooplankton was collected using a 200 µm mesh net drawn just below the seawater surface. After elimination of large organisms and debris retained on a 1 mm mesh net, copepods were isolated using a 200 µm mesh net. After weighing, two fractions of the sample were taken. The first was observed under a binocular microscope for species proportion (adults and copepodites) and body length determination. The second was used to determine the dry weight (DW) to wet weight ratio, by weighing the fraction before and after drying at 40ºC for 24 h. Then, the mean length of each copepod species at each station was converted to mean species dry weight using the relationship between the body length and dry weight of each species (Klein Breteler *et al.*, 1982). By using the proportions of each species in the sample, the mean copepod dry weight per station was established. Finally, abundance (ind. m^{-3}) was estimated by dividing the total biomass (mg DW m^{-3}) by the mean copepod dry weight.

Faecal pellet production rates determination

Immediately after zooplankton collection, a small fraction was isolated in a 60 ml transparent flask filled with natural sea water for the faecal pellet production rate experiment. The remaining fraction of the zooplankton was used for pellet collection. The total number of faecal pellets produced was counted in the flask under a binocular microscope every 5 min over a period of 1 h. The number of pellets versus time evolved according to a sigmoid curve, the slope of which gave the faecal pellet production rate (Belkhiria *et al.*, 1996). After 1 h, the sample was fixed in 5% formalin. Possible stress effects due to overcrowding in the sample were tested, and no correlation was found between the number of copepods in the flask and pellet production rate ($r^2 = 0.04$).

Faecal pellet flux (mg C day^{-1} m^{-2}) was estimated using copepod abundance (ind. m^{-3}) and faecal pellet production rate (pellets $ind.^{-1}$ h^{-1}). A value of 140 ng C per pellet of 2.5 10^5 μm^3 volume was used, based on measurements carried out with *Acartia clausi* feeding on natural food (Honjo and Roman, 1978). This value was adapted to each pellet volume (determined as described in the next section). A mean water depth of 15 m was considered.

Sinking rate determination

For the sinking rate determination, copepod faecal pellets were collected using a modification of the device described by Small *et al.* (Small *et al.*, 1979). It consisted of a hollow cylinder with the bottom covered by 200 µm netting. This retained the copepods but not their faecal pellets. The device was suspended in a covered container filled with 25 µm-filtered sea water, which was continuously renewed. This provided darkness, appropriate water temperature and aeration for the animals. The experiment lasted approximately 5 h, after which the content of the plastic flask was fixed in 5% formalin in order to avoid pellet degradation during long cruises.

Sinking rate experiments were based on a method modified from Turner (Turner, 1977). A large glass burette (85 cm high, 6.5 cm inside diameter) was filled with filtered sea water (31 psu at 19ºC) and left to stabilize for a minimum of 1 h. Several pellets at a time were gently released under the water surface using a Pasteur pipette. A 200 µm netting was placed 5 cm below the water surface in order to retain aggregates of faecal pellets. After the pellets had passed through, the netting was slowly removed and a stopwatch was started once the pellets had sunk 5 cm. After a delay of 2–3 min, the cock of the burette was opened and 1.5 ml samples were taken in an Ependorf tube every 20 s. This procedure lasted approximately 30 min. The sinking rate was calculated to take into account the decrease in height of the water column due to sampling. Intact pellets in each sample were counted and measured (length and width) under a binocular microscope. Their volume was calculated assuming pellets to be cylindrical.

Estimations of pellet density under laboratory conditions were obtained using a modified form of Stokes relationship for calculating sinking rates adapted to cylindrical particles (Komar *et al.*, 1981). The possible effect of fixation by formalin on the pellet density was studied, comparing samples of fresh pellets (preserved at 5°C for less than 24 h) or those fixed in 5% formalin. Mean estimated pellet density showed no significant difference.

Statistical methods

Differences in plankton data between water mass origin and/or sampling periods (cruises) were sought using the non-parametric Kruskal–Wallis test (H). When significant differences were obtained between water mass origin and/or sampling periods, the non-parametric Newman–Keuls–Student (NKS) comparison procedure adapted for unequal samples (Noether, 1976) was subsequently used to establish which sampling periods were different.

RESULTS

Phytoplanktonic analysis

Phytoplankton was studied only in 1996. Chlorophyll *a* concentration was significantly higher ($P < 0.01$) in April compared with February in both water masses, reaching a peak of 6.66 µg l^{-1} in the continental coastal water (CCW)

and 3.35 µg l^{-1} in the southern North Sea water (SNSW) (Figure 2a, Table I). High values for Chl *a* continued to be observed in May 1996 in both water masses, as reported by Borges and Frankignoulle (Borges and Frankignoulle, 1999) (Figure 2a). This pigment concentration was always significantly higher in the CCW (all $P < 0.05$, Kruskal–Wallis H = 4.79 in February, 3.85 in March and 4.08 in April). Chlorophyll c_3 (Chl c_3) was rare, not exceeding 32 ng l^{-1} in both water masses in February and March (Figure 2b). In the CCW, it was found in only one of 11 stations in February and one of four stations in March. On the contrary, it was always present during April and June in both water masses. Chl c_3 concentration was significantly higher in the CCW than in the SNSW only in April ($P < 0.05$, Kruskal–Wallis H = 5.33), with a maximum value of 190 ng l^{-1}. The ratio 19′HF/Chl *a* followed inversely the tendency of the previous pigments, decreasing significantly in April compared with February and June in the CCW ($P < 0.05$, Table I) to values of less than 3% (Figure 2c). The fucoxanthin to Chl *a* ratio (fuco/Chl *a*) decreased significantly only in the CCW in June ($P < 0.05$, Table I) compared with February. Both these ratios were higher in the CCW than in the SNSW in February (both $P < 0.01$, Kruskal-Wallis H = 8.56 for 19′HF/Chl *a* and 6.90 for fuco/Chl *a*).

Data from microscopic analysis of *Phaeocystis* sp. (V. Rousseau, personal communication) are shown in Figure 3. From late April to early May, colony range of size increased (Figure 3a) and more elongate than spherical forms were observed (Figure 3b). During this period, colony abundance was close to 2600 colonies l^{-1}. In late May, colony abundance decreased to 800 colonies l^{-1}. Only small and spherical forms of colonies were encountered.

Copepod species composition, abundance and weight

Zooplankton was largely dominated by copepods that constituted more than 90% of mesozooplankton biomass (which varied from 0.22 to 183 mg DW m^{-3}). Copepod abundance showed a significant increase of one order of magnitude in June (Figure 4a, Table II) compared with all previous months in both water masses, except compared with February in the SNSW (all $P < 0.05$, Table I).

Copepod abundance was higher in the CCW than in the SNSW in March and April (both $P < 0.05$, Kruskal–Wallis H = 7.51 and 4.20, respectively). For the studied period, *Temora longicornis* and *Pseudocalanus elongatus* were the two dominant species, *T. longicornis* dominating in February and June, and *P. elongatus* in March and April (Figure 4b). They were followed in abundance by *Acartia clausi* and *Centropages hamatus*. *Calanus* sp. was present occasionally in small numbers (less than 20 ind. m^{-3}).

Copepod mean weight (Figure 4c) was higher in the CCW than in the SNSW in February and March (both $P < 0.001$, Kruskal–Wallis H = 11.02 and 13.98, respectively), and higher in the SNSW than in the CCW in April ($P < 0.001$, Kruskal–Wallis H = 22.86). Only *T. longicornis* weight shows similar changes (all $P < 0.05$, Kruskal–Wallis H = 9.97, 36.86 and 6.84 in February, March and April, respectively). When the same water mass was compared at different periods, the copepod mean weight in the CCW decreased significantly from February to June, and from April to June, and increased from March to April (Table I). In the SNSW, copepod mean weight shows significantly higher values in February and March than in April and June (Table I).

Faecal pellet production rate and estimated flux

Few of our measurements were done during the night and in order to limit a possible variability due to diel variation, we limited our study of the seasonal variability of pellet production rate to values obtained during the day (Figure 5). Pellet production varied generally between 0.1 and 3.0 pellets $ind.^{-1}$ h^{-1}, with no significant difference between the two water masses. In 1996, this rate was significantly lower in April in both water masses compared with February and June (all $P < 0.05$, Table I), with values approximately five times lower. The pellet production rate was also significantly lower in May 1995 (CCW) compared with February and June 1996 (Kruskall–Wallis H = 16.13, $P < 0.05$, Newman–Keuls–Student NKS = 2.65 and 2.85, respectively, both $P < 0.05$). The estimated pellet flux (Table II) increased significantly in June 1996 compared with all other periods (all $P < 0.05$, Table I), except compared with February in the SNSW. Pellet production rate and pellet flux showed no significant difference between the two water masses.

Faecal pellet sinking rates, volume and estimated density

In the sinking rate experiments, when the total number of pellets counted exceeded 150, the correlation between pellet volume and sinking rate decreased with the number of pellets (perhaps due to aggregate formation). Therefore, only experiments with less than 150 pellets counted were considered. All sinking rate measure experiments gave a positive correlation ($r^2 > 0.5$) between pellet volume and sinking rate (Figure 6). Mean sinking rates were high until mid-March, between 100 and 120 m day^{-1}, after which they decreased to approximately 70 m day^{-1} (Figure 7). All periods after mid-March had significantly lower faecal pellet sinking rates than February and mid-March (all $P < 0.05$, Tables III and IV). This was also the case for both pellet volume and estimated density in 1996 (all $P < 0.05$, Tables III and IV).

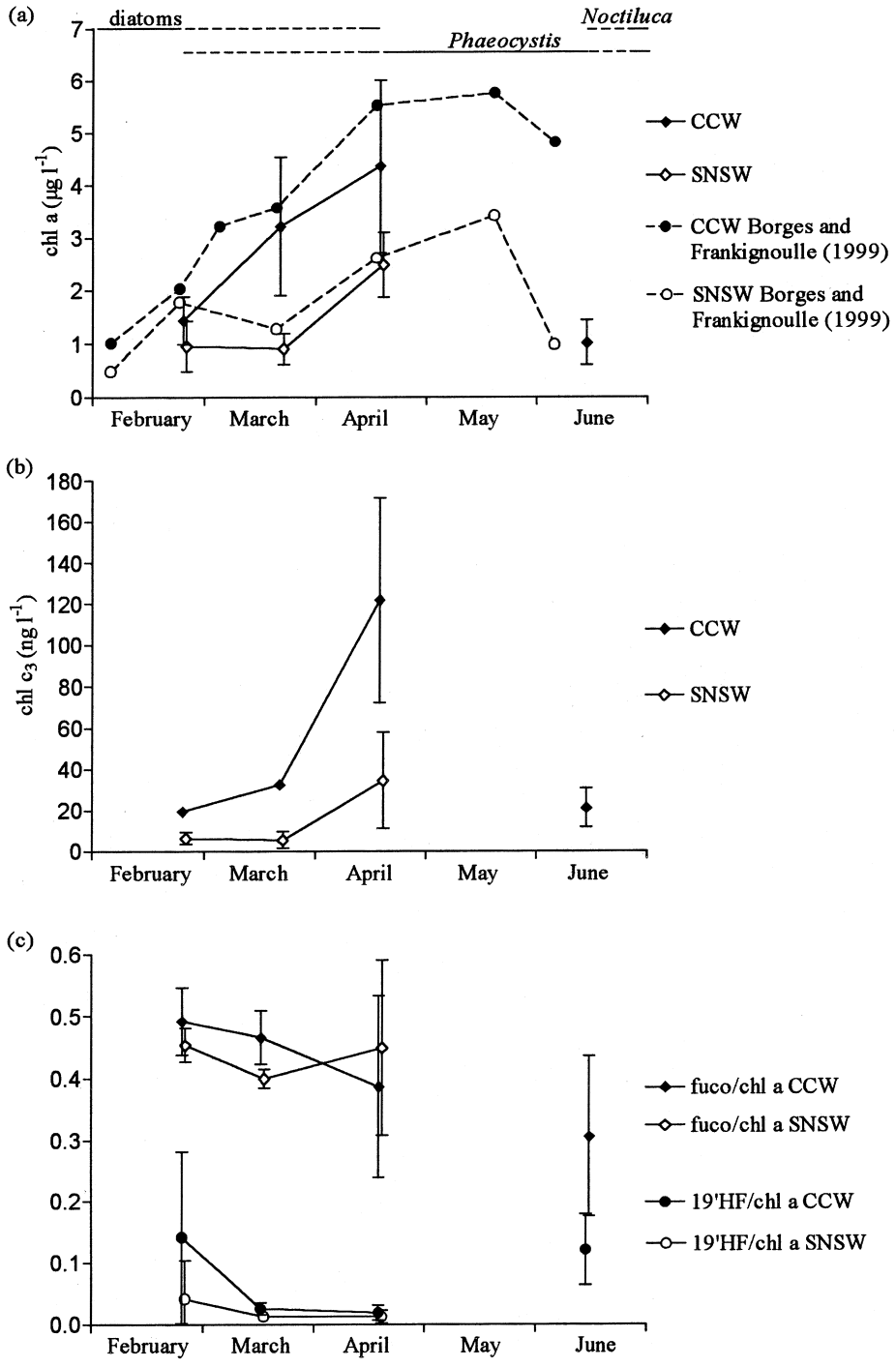

Fig. 2. (**a**) Mean Chl *a* concentration, (**b**) mean Chl c_3 concentration and (**c**) pigment to Chl *a* ratios during spring 1996 in the southern North Sea. Chl *a* combines data from the present study with data from Borges and Frankignoulle (Borges and Frankignoulle, 1999). CCW: continental coastal water; SNSW: southern North Sea water. In June, data were not separated in water masses (see text). Vertical bars show standard deviation. Number of observations shown in Table I.

*Table I: Statistical comparison of phytoplanktonic pigments, copepod abundance (CA), mean copepod weight (CW), faecal pellet production (P) and faecal pellet flux (PF) in the southern North Sea in 1996. H (P) = result of the Kruskal–Wallis test; NKS (P) = result of the non-parametric Newman–Keuls–Student comparison procedure. *P < 0.05; **P < 0.01; ***P < 0.001; ns: P > 0.05. F: February; M: March; A: April; J: June. n_F,n_M,n_A,n_J: number of measurements in February, March, April and June, respectively. CCW: continental coastal water; SNSW: southern North Sea water*

Water mass	Test	Periods compared	Chl *a*	Chl *c*3	19′HF/Chl *a*	fuco/Chl *a*	CA	CW	P	PF
CCW	H		17.79 (**)	7.98 (*)	13.52 (**)	8.09 (*)	15.25 (**)	28.83 (***)	9.37 (*)	13.71 (**)
		F–M	–2.08 (ns)	–0.85 (ns)	2.02 (ns)	1.34 (ns)	–1.30 (ns)	1.77 (ns)	0.61 (ns)	–0.32 (ns)
		F–A	–2.70 (*)	–1.75 (ns)	3.01 (*)	1.43 (ns)	0.26 (ns)	–2.20 (ns)	2.67 (*)	1.07 (ns)
		F–J	1.09 (ns)	–0.17 (ns)	–0.41 (ns)	2.71 (*)	–3.61 (**)	3.02 (***)	–0.73 (ns)	–3.07 (**)
	NKS	M–A	–0.29 (ns)	–0.67 (ns)	0.58 (ns)	–0.05 (ns)	1.29 (ns)	–3.84 (***)	2.30 (ns)	1.31 (ns)
		M–J	2.66 (*)	0.94 (ns)	–2.10 (ns)	0.81 (ns)	–2.78 (*)	1.17 (ns)	–1.22 (ns)	–2.85 (*)
		A–J	3.23 (*)	2.65 (*)	–2.95 (*)	0.93 (ns)	–3.30 (**)	5.03 (***)	–2.92 (*)	–3.27 (**)
	nF, nM, nA, nJ		11,4,4,5	1,1,4,5	11,4,4,5	11,4,4,5	12,16,5,5	23,28,15,42	11,12,4,5	10,11,3,5
SNSW	H		9.91 (*)	12.31 (**)	12.99 (**)	4.66 (ns)	21.82 (***)	60.58 (***)	14.29 (**)	22.35 (***)
		F–M	0.04 (ns)	0.24 (ns)	1.54 (ns)	–	2.37 (ns)	0.80 (ns)	0.72 (ns)	1.59 (ns)
		F–A	–3.06 (**)	–2.79 (*)	1.60 (ns)	–	2.71 (*)	6.41 (***)	3.66 (**)	3.22 (**)
	NKS	F–J	–0.35 (ns)	–2.36 (ns)	–2.21 (ns)	–	–2.04 (ns)	5.50 (***)	0.27 (ns)	–1.98 (ns)
		M–A	–2.31 (ns)	–2.45 (ns)	–0.09 (ns)	–	0.47 (ns)	5.29 (***)	2.45 (ns)	1.33 (ns)
		M–J	–0.29 (ns)	–2.07 (ns)	–2.94 (*)	–	–3.78 (***)	4.41 (***)	–0.35 (ns)	–3.06 (**)
		A–J	2.32 (ns)	0.54 (ns)	–3.10 (**)	–	–4.02 (***)	–1.06 (ns)	–2.69 (*)	–4.42 (***)
	nF, nM, nA, nJ		14,4,4,5	8,4,4,5	14,4,4,5	14,4,4,5	13,10,8,5	30,26,40,42	13,6,7,5	12,6,7,5

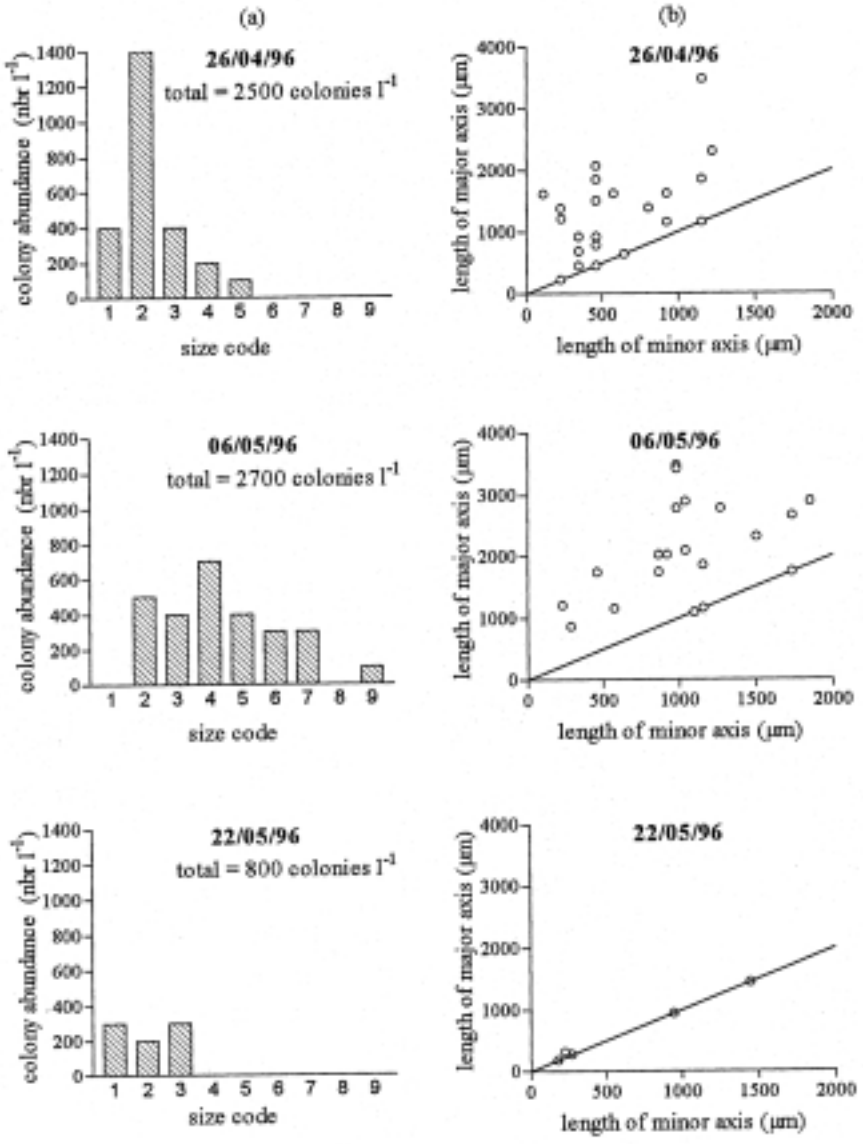

Fig. 3. (**a**) Size distribution of *Phaeocystis* sp. colony abundance. Sizes are expressed in terms of equivalent spherical diameter. Colonial diameter (µm) code is as follows : (1) <200; (2) 200–400; (3) 400–600; (4) 600–800; (5) 800-1000; (6) 1000–1200; (7) 1200–1400; (8) 1400–1600; (9) 1600–1800. (**b**) Shape of *Phaeocystis* sp. colonies expressed as the relation between the length of the major and minor axis. The straight line corresponds to the spherical form.

Table II: Copepod mean ±SD abundance (CA) and mean ±SD estimated faecal pellet flux (PF) during spring 1996 in the southern North Sea. Symbols as in Table I

Period	February		March		April		June
Water mass	CCW	SNSW	CCW	SNSW	CCW	SNSW	CCW+SNSW
CA (ind m^{-3})	550 ± 535	897 ± 664	995 ± 761	321 ± 361	421 ± 342	182 ± 126	7406 ± 4861
PF (mg C d^{-1} m^{-2})	61.8 ± 66.8	111 ± 115	54.7 ± 44.9	34.1 ± 46.7	20.5 ± 29.2	3.91 ± 4.16	606 ± 402
n	10	12	11	6	3	7	5

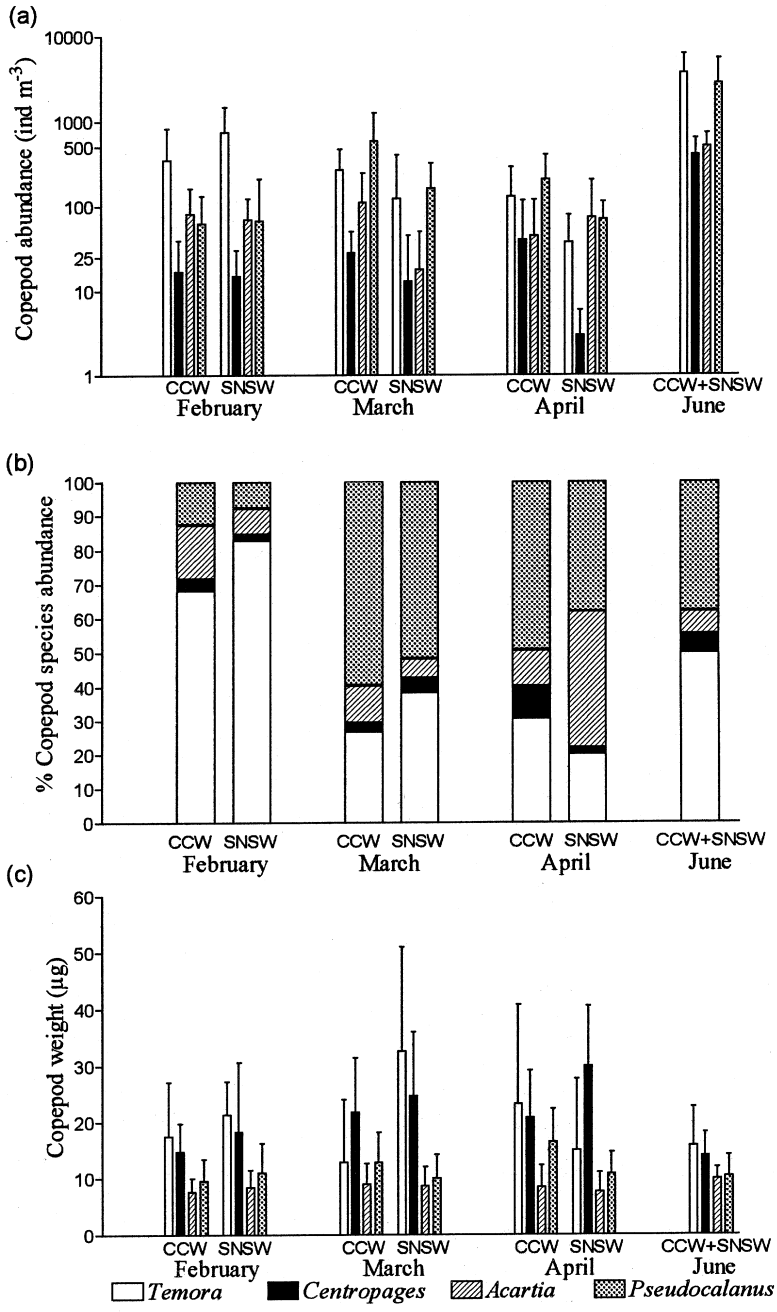

Fig. 4. Copepods (**a**) mean abundance, (**b**) composition and (**c**) mean weight during spring 1996 in the southern North Sea. In June, data were not separated in water masses (see text). Vertical bars show standard deviation. Number of observations shown in Table I. Symbols as in Figure 2.

DISCUSSION

An increase in total Chl *a* concentration between February and April, followed by a decrease between April and June, allowed us to locate the phytoplankton bloom between February and June with a peak in May, as reported by Borges and Frankignoulle (Borges and Frankignoulle, 1999). This bloom corresponds to that described by other authors (Billen *et al.*, 1990; Bautista *et al.*, 1992; Mills *et al.*, 1994; Becquevort *et al.*, 1998; Boon *et al.*, 1998; Schoemann *et al.*, 1998). However, it commences earlier in the continental coastal water mass than that described by Fransz (Fransz, 1975). The bloom is known to show a diatom to *Phaeocystis* transition between

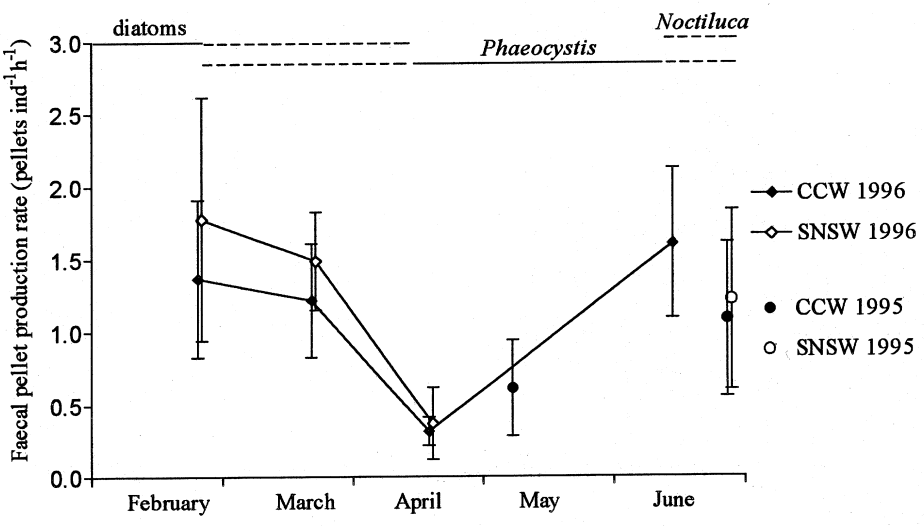

Fig. 5. Mean daytime faecal pellet production rate in the southern North Sea during spring 1995 and 1996. In June 1996, data were not separated in water masses (see text). Vertical bars show standard deviation. Number of observations from CCW in 1995 were five in May, eight in June and nine in SNSW in June. Number of observations in 1996 shown in Table I.

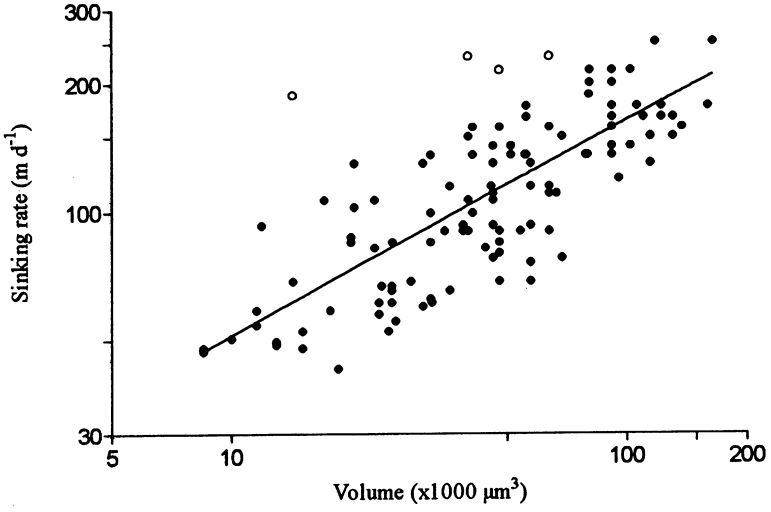

Fig. 6. Relationship between faecal pellet sinking rate (S) and volume (V) for pellets produced by copepods collected from the southern North Sea on 18 March 1996. Regression equation is $S = 55.20\ V^{0.48}–3.88$ ($r^2 = 0.62$, if open circle points which are outside the 99% interval are ignored).

Table III: Copepod faecal pellet mean ±SD length, width, volume and estimated density in the southern North Sea in 1996 and 1997

	February 1996	mid-March 1996	mid-March 1997	end-March 1996	April 1997	June 1996
Length (µm)	209 ± 72.1	201 ± 77.3	178 ± 63.2	180 ± 82.4	168 ± 52.2	167 ± 49.2
Width (µm)	53.2 ± 14.1	56.5 ± 13.4	52.3 ± 18.1	46.4 ± 12.2	41.3 ± 8.5	59.4 ± 11.2
Volume (x1000 µm^3)	529 ± 380	540 ± 347	451 ± 366	353 ± 309	243 ± 171	338 ± 217
Density (g cm^{-3})	1.37 ± 0.13	1.40 ± 0.14	1.42 ± 0.18	1.31 ± 0.11	1.45 ± 0.24	1.34 ± 0.17
n	132	118	69	49	103	136

Table IV: Summary statistics comparison of copepod faecal pellet volume, sinking rate and estimated density in the southern North Sea continental coastal water in 1996. F: February; mid M: mid-March; end M: end-March; J: June. Other symbols as in Table I

Test	Periods compared	Volume	Sinking rate	Density
H		28.94 (***)	89.79 (***)	20.12 (***)
NKS	F-end M	2.65 (*)	4.77 (***)	2.90 (*)
	F-mid M	–1.07 (ns)	–2.88 (*)	–1.01 (ns)
	F–J	3.78 (***)	5.44 (***)	3.42 (**)
	mid M–end M	3.16 (**)	6.84 (***)	3.71 (***)
	mid M–J	4.75 (***)	8.18 (***)	4.34 (***)
	end M–J	0.36 (ns)	–0.80 (ns)	–0.40 (ns)

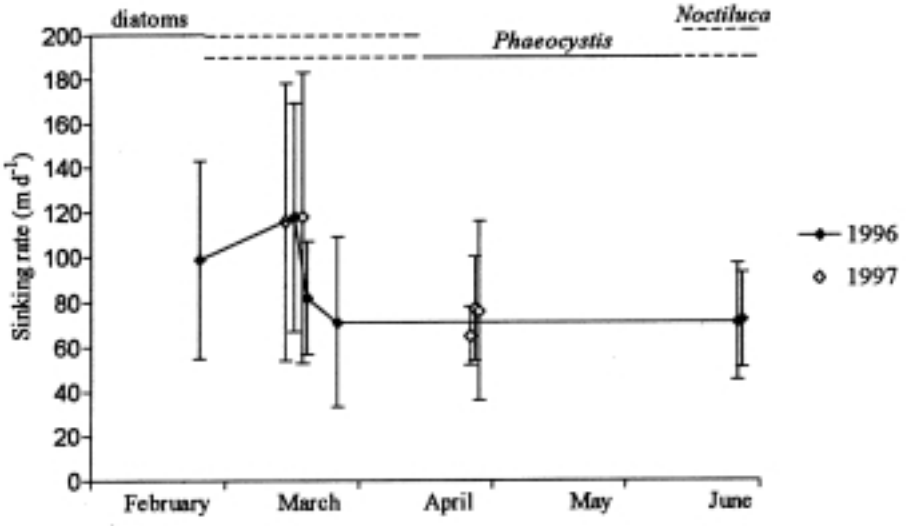

Fig. 7. Mean faecal pellet sinking rate in the southern North Sea continental coastal water in 1996 and 1997. Vertical bars show standard deviation. Number of observations shown in Table III.

March and April, followed by a *Phaeocystis* to dinoflagellate (*Noctiluca miliaris*) transition between May and June (Lancelot *et al.*, 1986; Althuis *et al.*, 1994; Boon *et al.*, 1998; Schoemann *et al.*, 1998). In this study, the *Phaeocystis* sp. bloom was located using specific pigment ratios of the southern North Sea *Phaeocystis* sp. strain. The North Sea Southern Bight strain of *Phaeocystis* sp. shows a ratio of 19′HF/Chl *a* close to 1% (Buma *et al.*, 1991), much lower than that of *Phaeocystis* sp. of other regions (Jeffrey, 1997).

In our study, the 19′HF/Chl *a* ratio decreased to values of less than 3% from February to April, increasing again in June, and the fuco/Chl *a* ratio was close to 30% in April (Figure 1c). These values are close to those obtained by Buma *et al.* (Buma *et al.*, 1991) from cultures of a North Sea Southern Bight clone of *Phaeocystis* sp., and allows the location of the *Phaeocystis* sp. bloom between February and June, with a peak between April and May. In addition, the rare appearance of Chl c_3 in February and March corresponds to the observations of Althuis *et al.* (Althuis *et al.*, 1994) in the same region of high concentrations of Chl c_3 during *Phaeocystis* sp. dominance. We confirm the suggestion of Althuis *et al.* (Althuis *et al.*, 1994) that this pigment could be typical of the *Phaeocystis* sp. of this region. These assumptions were supported by inverted light microscope observations, which showed higher values of *Phaeocystis* sp. colony abundance in April and early May than in late May.

The beginning of the zooplankton bloom occurred at least as early as June. Hecq and Gaspar described the

beginning of the zooplankton bloom in the coastal zone of the North Sea Southern Bight as occurring in May (Hecq and Gaspar, 1980; Hecq, 1982). This may also have been the case in 1996, but no data were obtained in May to confirm it.

Pellet production rate

In our study, the pellet production rate showed a mean value of 1.2 pellets ind.$^{-1}$ h^{-1}. This mean is close to, although lower than, the gut passage times obtained by Baars and Oosterhuis (Baars and Oosterhuis, 1984) working with the same species (except *Acartia clausi*) in May. Our lower values could be explained by the fact that the Baars and Oosterhuis's experiments were carried out in the evening when higher values could occur. Faecal pellet production is known to be positively related to the producer (copepod) weight (Paffenhöfer and Knowles, 1979) and to the ingestion rate (Gamble, 1978). In laboratory studies, the copepod species found in this study show different ingestion rates on cultured *Phaeocystis* (Weisse, 1983; Hansen and van Boekel, 1991; Weisse *et al.*, 1994). Therefore, changes in copepod species weight and percentage of the total copepod abundance can affect faecal pellet production. This was not the case in our study, as significant changes of these parameters between different periods or water masses (Figure 4) were not related (or not always in the same manner) to significant differences in faecal pellet production (Figure 5, Table I). Therefore, these relationships cannot explain the changes in faecal pellet production in our study. It should be noted that Daro and van Gijsegem (Daro and van Gijsegem, 1984), who reported seasonal variation in the weight of adult copepods during an annual cycle (except February and March) in the same study area, observed an increase between January and April and highest values in April.

On the other hand, faecal pellet production can be positively related to food quantity (Paffenhöfer and Knowles, 1979; Martens and Krause, 1990). In our case, there is an apparent negative relation to food as faecal pellet production seems negatively related to Chl *a*. This situation is the opposite of that found in the northern North Sea, where the maximum number of pellets per individual coincides with the phytoplankton bloom (Krause, 1981) dominated by diatoms. In fact, our study suggests different food quality, as the significant decrease in pellet production in April (Figure 5, Table I) could be explained by the *Phaeocystis* sp. expansion at that moment.

This can be shown by microscopic observations. From April to early May, when the lower pellet production rate is observed, a *Phaeocystis* sp. colony range of size increases (Figure 3a), and more elongate forms are encountered. Colony size can be linked to the age of the colony, as size is known to increase with colony age (Rousseau *et al.*, 1990). *Phaeocystis pouchetii* colonies become unpalatable for the mesozooplankton for a size–age above 350 µm, according to laboratory experiments (Weisse, 1983). Therefore, low pellet production could be explained by a lower grazing of *Phaeocystis* sp. during this period, due to a mismatch between the size of colonies and most mesozooplankton. A similar observation was made in the German Bight, where the *Phaeocystis* sp. biovolume fraction of total phytoplankton biomass was inversely related to the pigment content in the gut of *T. longicornis* (Hansen and Boekel, 1991). *Phaeocystis* sp. is also known to inhibit the feeding of copepods in the English Channel (Bautista *et al.*, 1992) and in the Southern Bight of the North Sea (Daro and van Gijsegem, 1984; Daro, 1986; Gasparini *et al.*, 2000).

In late May, colony size seems to decrease and the shape approaches a spherical form. This is different from other studies, where *Phaeocystis* sp. showed a large range of colony size and the spherical form was less frequent at the end of the bloom (Rousseau *et al.*, 1994). Due to the low number of colonies examined, the data on size and shape in late May are probably not representative.

In laboratory grazing studies, Marshall and Orr (Marshall and Orr, 1966) in the Clyde Sea found that *T. longicornis* grazed at least twice as much as the other dominant species we observed, and Weisse (Weisse, 1983) found an almost twice as high ingestion rate of *Phaeocystis* colonies (50–350 µm) by *T. longicornis* than by *Acartia clausi*.

Therefore, we assume that *T. longicornis* is responsible for the major part of pellet production, as it is one of the two dominant species of copepods during the period studied. As *T. longicornis* continues to dominate during summer in the Southern Bight of the North Sea (Daan, 1989), it could also explain the larger part of faecal pellet production during summer.

Pellet sinking rate

Faecal pellet sinking rates were proportional to pellet volume (Figure 6). This relationship has been shown in other studies on faecal pellets of unknown origin in Rhode Island (Smayda, 1969), and for copepod faecal pellets in Texas (Turner, 1977) and Southern France (Small *et al.*, 1979), although Bienfang (Bienfang, 1980) did not find such a relationship.

A seasonal decrease in the mean sinking rate of faecal pellets after mid March follows the transition from a diatom-dominated to a *Phaeocystis* sp.-dominated bloom (Figures 2 and 7). In 1996, this change in sinking rate was due to a decrease in pellet density and pellet volume (Tables III and IV). All these observations argue in favour of a diet effect on pellet density and size at the first transition. Such a negative effect of diet transition from diatoms to flagellates on the pellet sinking rate has already been shown in copepod cultures (Bienfang, 1980).

However, the effect of the seasonal phytoplankton bloom succession on the pellet sinking rate has not yet been described, probably due to the difficulty in obtaining enough data for a seasonal variation study, using individual pellet sinking measurements. In fact, wide variations in sinking rates for pellets of the same volume are observed in copepod pellet sinking rate measurements (Fowler and Small, 1972; Wiebe *et al.*, 1976; Turner, 1977; Small *et al*., 1979; Bienfang, 1980). Although our experiments also showed such large variations, the high number of pellets studied (between 50 and 150) allowed us to obtain significant seasonal differences.

Turner attributed the large variations in faecal pellet sinking rates to the small density and volume of the copepod pellet, which makes it sensitive to the microstructural variations in the water column (Turner, 1977). On the other hand, Bienfang (Bienfang, 1980) attributed the scatter in the sinking rate/volume relationship to the fact that pellet orientation during sinking is random, due to the faecal pellets' sinking system which is viscous (Reynolds number $\ll 1$). Turner also observed such variations in orientation, but also in the sinking rate for the same pellet (Turner, 1977). Finally, Fowler and Small (Fowler and Small, 1972) observed no such variations with larger-sized pellets, such as euphausiid faecal pellets.

In our study, a second reason for the sinking rate variation could be the use of pellets from different copepod species in the same sinking experiment. Therefore, according to Wiebe *et al.* (Wiebe *et al.*, 1976), sinking rate variation could also be attributed to differences in density of pellets of the same volume due to different diets of the species producing these pellets. In fact, density will depend upon the type, concentration and packing of food ingested, which could vary among species (Fowler and Small, 1972; Turner, 1977; Honjo and Roman, 1978; Small *et al.*, 1979; Bienfang, 1980; Dagg and Walser, 1986; Urban *et al.*, 1993; Hansen *et al.*, 1996).

Finally, the shape of the faecal pellet can also influence the vertical speed (Sasaki *et al.*, 1988), but as the pellets we observed were almost all of cylindrical form, with few pellets being elliptical, this effect should be disregarded in our experiments compared with both the previous ones.

Using the relationship of Komar *et al.* (Komar *et al.*, 1981) for calculating copepod faecal pellet density, our pellet density estimation averaged 6%, significantly higher ($P < 0.001$, Kruskal–Wallis H test = 62.01) than that obtained by Komar *et al.* on copepod pellets from mixed small copepods collected near Monaco (1.37 versus 1.28 g cm^{-3}). This difference could be due to the geographic origin of the pellets. Urban *et al.* (Urban *et al.*, 1993) measured densities of copepod faecal pellets collected in Newfoundland (Canada) and found that they were 10% lower than those estimated by Komar *et al*. These density values confirm the possible influence of the origin of the pellet. In fact, the mean pellet density value used by Komar *et al.* (Komar *et al.*, 1981) was based on data from copepod pellets collected near Monaco and thus, in an oligotrophic sea (Small *et al.*, 1979). Copepod faecal pellets coming from the southern North Sea, a eutrophic area, are expected to be denser than Mediterranean pellets. We can assume that in our study area, which is known to be highly turbid due to strong tidal mixing and the Scheldt river imports, a contamination of pellets with ingested sedimentary material is possible. Turner (Turner, 1984) observed that the major component of pellets of the plume of the Mississippi River was riverine sediment, and Smayda (Smayda, 1969) suggested that faecal pellets produced in the benthos could contain ingested sedimentary material, leading to a higher density.

Pellet flux

In the southern North Sea, pellet flux showed an important increase in June to a level one order of magnitude higher than for the previous months. This change was mostly the result of the increase in zooplankton abundance. Pellet flux estimation from February to April displayed values close to those for the same region (Joiris *et al.*, 1982) and in Western Norway (Skjoldal and Wassmann, 1986). However, our calculations may underestimate the total flux as only daytime measurements of pellet production rates were used in the calculations.

In our flux estimate, pellet sinking rate was not taken into account because sinking rate can be ignored in flux estimations in this region. In a shallow region such as the southern North Sea, strongly stirred by tidal and wind-driven currents, the shear-induced turbulence in the tidal bottom currents can make the bottom boundary layer overlap with the upper mixed layer, thus contributing to further mixing. This suggests that in this region, vertical transport by copepod faecal pellets is minimal. If we compare the characteristic time for settling and for turbulent diffusion (Lick, 1982; Alldredge *et al.*, 1987) in this shallow area (with a classical mean coefficient of vertical diffusivity of 0.01 m^2 s^{-1}), we get a characteristic time of turbulent diffusion almost an order of magnitude lower than the characteristic time for settling. This means that small particles such as copepod faecal pellets are continuously circulating in the water column. In addition, the mechanical degradation of pellets due to turbulent conditions (Alldredge *et al.*, 1987), as well as biodegradation by micro-organisms (Hansen *et al.*, 1996) and zooplankton itself (Lampitt *et al.*, 1990; Noji *et al.*, 1991), contribute to maintaining the organic matter that originates from the faecal pellets in the water column. Thus, although zooplankton faecal pellets are known to accelerate the downward vertical transport of organic matter (Wiebe *et al.*, 1976; Honjo and Roman, 1978;

Honjo, 1979), they do not always sink out of the layer of their production (Krause, 1981; Bathmann *et al.*, 1987; Martens and Krause, 1990), and do not reach the sea floor even in a very shallow ecosystem (Hofmann *et al.*, 1981; Lane *et al.* 1994) such as the one we studied.

The results of our study indicate that changes from one phytoplanktonic group to another affect copepod diet quantitatively and qualitatively, as shown by the changes in pellet volume and mean monthly values in pellet production. Results confirm that the *Phaeocystis* sp. bloom reflects inadequate food conditions, with low ingestion rates for copepods in the southern North Sea. The sinking rates of copepod faecal pellets in this region are too low to allow an efficient vertical export of organic matter and thus, they remain in the mixed layer and pass into the pelagic food chain.

ACKNOWLEDGEMENTS

This study was supported by the Belgian Impulse Programme for Marine Sciences (MS/12/090). We thank: Alberto Borges and Michel Frankignoulle for providing chlorophyll *a* data; Véronique Rousseau for providing microscopic data; the officers and crew of R.V. Belgica for their helpful collaboration; and Alberto Borges, Patrick Dauby, Khalid El Kalay, Gilles Lepoint, John Pinnegard, Nikos Skliris, Sandi Toomey, Kristell Van Hove and six anonymous readers for helpful comments.

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Received on February 22, 2000; accepted on October 13, 2000