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High turnover rates of copepod fecal pellets due to *Noctiluca scintillans* grazing

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ABSTRACT: Copepod fecal pellet production and vertical flux, as well as vertical distributions of copepods, fecal pellets and the heterotrophic dinoflagellate *Noctiluca scintillans* were monitored in an upwelling plume off the coast of Brazil during 5 d in austral spring. Less than half (20 to 45 %) of the pellets produced in the overlying water column reached sediment traps positioned at 30 to 60 m depth, and specific sinking losses computed from steady-state considerations varied inversely with trap depth between 0.3 and 2.9 d^{-1}. Total specific losses varied between 0.6 and 16 d^{-1}, and the major part of these losses were thus unaccounted for by sinking and must have been due to remineralization in the water column; estimated specific remineralization rates increased with the ageing of the plume and varied between 0.3 and 13 d^{-1}. *N. scintillans* occurred in increasing concentrations in the upwelling plume as the latter aged, up to 5×10^5 cells m^{-2}, and fecal pellets occurred commonly in the food vacuoles of *N. scintillans*. Specific fecal pellet remineralization rates were linearly related to the abundance of *N. scintillans*. This relation can be quantitatively accounted for if *N. scintillans* clears the water for fecal pellets at about 0.6 l $cell^{-1}$ d^{-1}. A simple encounter model suggests that such high clearance rates are feasible. Since *N. scintillans* occurs at typical abundances of about 10^6 cells m^{-2} in temperate seas during spring, summer and autumn, it may contribute significantly to the recycling of rapidly sinking fecal pellets in the water column.

KEY WORDS: Copepod fecal pellets · Turnover · Flux · Pellet grazing

INTRODUCTION

Copepod fecal pellets, once thought to be important vehicles for vertical organic matter transport, are now believed to often become remineralised in the upper ocean rather than sedimenting to the seafloor, even in shallow water (e.g. Smetacek 1980, Viitasalo et al. 1999). The evidence stems mainly from the scarcity of fecal pellets in sediment traps relative to the rate at which pellets are produced in the overlying water column (Turner 2002). Since fecal pellets sink rapidly (~100 m d^{-1}), their residence time in the surface layer is typically less than a day, and remineralization therefore must be rapid to significantly reduce sinking losses. A number of mechanisms for pellet degradation have been suggested, including leakage of solutes (Jumars et al. 1989, Urban-Rich 1999), solubilization by colonizing bacteria (Jacobsen & Azam 1984, Hansen & Bech 1996), and metazoan coprorhexy and coprophageous feeding (Lampitt et al. 1991, Noji et al. 1991). Dense populations of flux feeding *Oithona similis* copepods, for example, may at times provide a very efficient 'coprophageous filter' that remineralizes most pellet material in the upper ocean (Gonzales & Smetacek 1994).

Another likely important fecal pellet feeder is *Noctiluca scintillans*. This heterotrophic dinoflagellate is omnivorous and has been reported to feed on almost anything from small phytoplankton cells to aggregates and detrital particles, including fecal pellets (Enomoto 1956, Prasad 1958). *N. scintillans* encounters prey particles either by intercepting prey as it itself ascends in the water column (Kiørboe & Titelman 1998), or by colonizing and feeding on diatom aggregates (Tiselius & Kiørboe 1998). Solitary *N. scintillans* cells secrete mm- to cm-long mucus threads on which prey particles

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are captured. These threads also facilitate the formation of mucoid feeding associations when cells are occurring at high concentrations (Omori & Hamner 1982, Shanks & Walters 1996). The long mucus threads and/or the mucoid feeding associations may also prove efficient in collecting fluxing particles, such as sinking copepod fecal pellets. Since *N. scintillans* may occur in very high concentrations, particularly during and in the aftermath of diatom blooms (Kiørboe & Titelman 1998, Dela-Cruz et al. 2002), it may potentially contribute significantly to the rapid turnover of sinking pellets in such environments.

Here I report on a study of copepod fecal pellet production, vertical flux, and turnover conducted in an upwelling plume in coastal waters off the Brazilian coast. *Noctiluca scintillans* occurred in increasing abundance in the ageing plume and I examine the hypothesis that *N. scintillans* contributes to the turnover of sinking copepod fecal pellets in the upper water column.

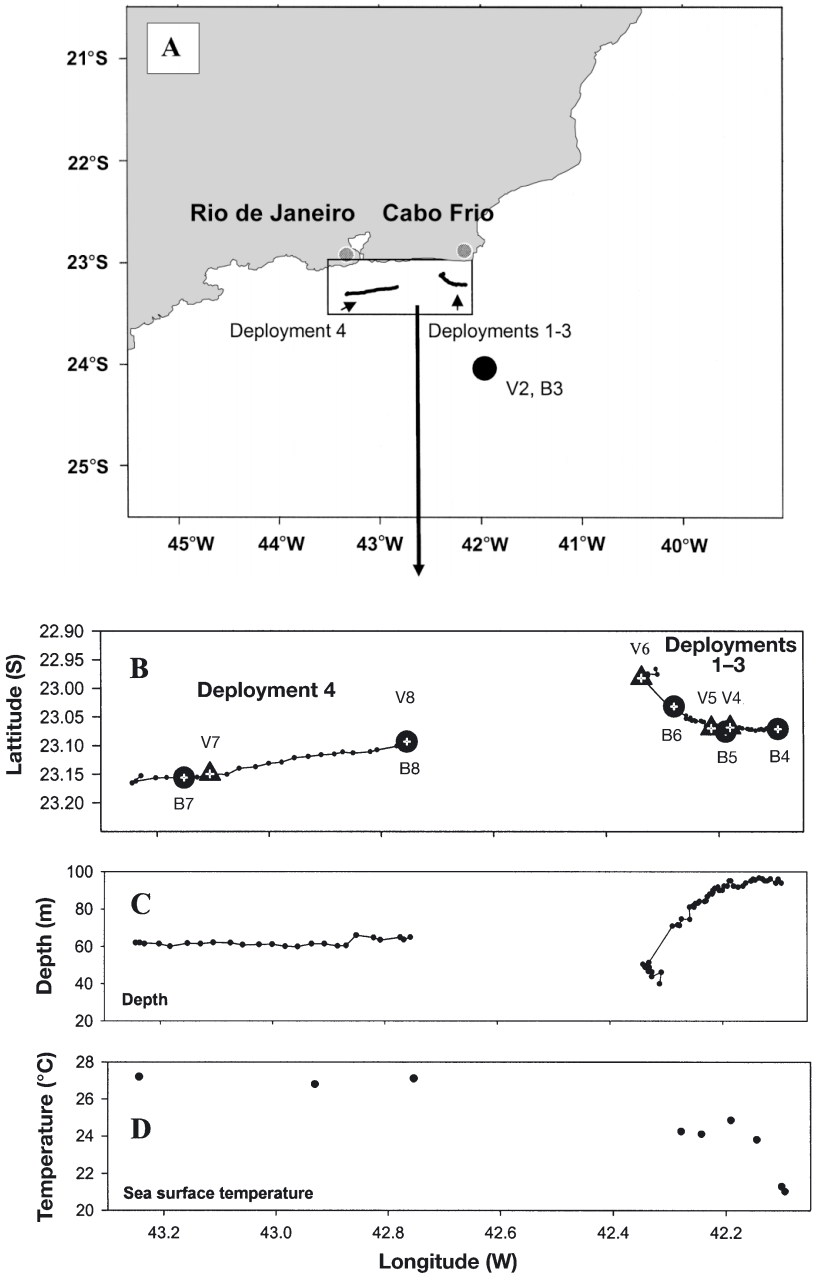

Fig. 1. (A) Map of study area, (B) buoy track and sampling stations, (C) water depth, and (D) sea surface temperature. Positions of buoy shown at 1 h intervals (small dots). Bottle profiles were taken at B-stations and video-profiles at V-stations. Three trap deployments were made on the eastern buoy-track and one trap deployment on the western track

MATERIALS AND METHODS

The experiment was conducted in neritic waters off the coast of Brazil between Rio de Janeiro and Cabo Frio during January and February 2002 (Fig. 1). Sampling was conducted about once per day as we followed a drifting buoy equipped with a drogue at 10 to 20 m depth and sediment traps suspended at 10 and 30–60 m depth. An off-shore station (without trap deployment) was, in addition, sampled for comparison. The mooring was deployed between 31 January and 3 February and between 3 and 4 February at water depths between 40 and 90 m (Fig. 1). Sampling included CTD casts, and collection of water with 12 l Niskin bottles from 5 depths between the surface and the deepest sediment trap. The water was sieved through 10 µm mesh and the numbers of adult and copepodid copepods (not determined to species), *Noctiluca scintillans*, and copepod fecal pellets were counted. A subsample (n = 30) of the fecal pellets was sized. Vertical profiles of *N. scintillans* and copepod abundances were also recorded by means of an *in situ* video camera as described by Tiselius & Kiørboe (1998). The camera views a volume of either 24 or 0.42 ml per frame. The higher magnification was used for enumeration of plankters, and about 6000 frames were analyzed per sampling depth. An *in situ* fluorometer was attached to the camera rig.

Fecal pellet fluxes were estimated by sediment traps. These were simple tubes, 7.2 cm inner diameter and 60 cm

high, and were equipped with 7 baffle tubes in the upper 10 cm to reduce resuspension of trapped material. Trap tubes were filled with water from the deployment depth and were deployed during 4 periods of 17 to 23 h duration. A 60 mm diameter petri dish filled with an 8% polyacrylamide solution was positioned at the bottom of each trap to collect and preserve settled material (Lundsgaard 1995, Kiørboe et al. 1998). Copepod fecal pellets were counted in 50 to 100 fields, 3 × 3 mm^2, of each petri dish under a dissecting microscope corresponding to 100 to 200 pellets, and 30 pellets were sized.

To estimate water column fecal pellet production, copepod assemblages were incubated on deck, in darkness at sea surface temperature. Copepods and other zooplankton were collected at night by a vertical haul with a 200 µm mesh size WP2 net (Tranter 1968) from the depth of the deepest trap to the surface. In each of the experiments varying fractions of the cod end contents were immediately diluted into 4 to 6 cylinders of 3 l that had a bottom made of 300 µm plankton net. The cylinders were submerged into 5 l jars containing water collected over the copepod collection depth range. After 3 h of incubation, the entire contents of the jars were filtered through a 10 µm plankton net, and copepods and fecal pellets were enumerated. Fecal pellet abundance was regressed on copepod abundance, and the slope represents an estimate of the per capita fecal pellet production over the duration of the incubation. One experiment was conducted for each of the 4 trap deployments.

Fecal pellet degradation rates were estimated from the observations by means of 2 simple models. The first model disregards vertical heterogeneity of fecal pellet concentration and degradation rate above the deepest trap:

Model 1:

$$\frac{dF}{dt} = pC - sF - rF = pC - (s+r)F \quad (1)$$

where F (m^{-2}) is the fecal pellet abundance integrated from the surface to the deepest sediment trap, C (m^{-2}) is the abundance of copepods over the same depth interval, p is the specific fecal pellet production rate (pellets copepod^{-1} d^{-1}), and s and r the specific sinking loss and remineralization rates of fecal pellets (d^{-1}), respectively. I assume steady state, thus $dF/dt = 0$, and:

$$F = \frac{pC}{s+r} \Rightarrow r = \frac{pC - J}{F} \quad (2)$$

where J is the pellet flux at the deep trap, and the specific sinking loss is estimated as $s = J/F$.

The alternative formulation takes vertical heterogeneity in concentrations and degradation rates into account:

Model 2:

$$\frac{dF(z)}{dz} = v\frac{\partial F(z)}{\partial z} + pC(z) - r(z)F(z) \quad (3)$$

where $F(z)$ and $C(z)$ are the fecal pellet and copepod concentrations at depth z, $r(z)$ is the depth-specific pellet degradation rate, and v is the fecal pellet sinking velocity [estimated for individual traps as $J(z)/F(z)$ and averaged over all traps]. At steady state:

$$r(z) = \frac{v\frac{\partial F(z)}{\partial z} + pC(z)}{F(z)} \quad (4)$$

The remineralization rate averaged over the water column to trap depth (h) is then

$$r = \frac{\int_0^h r(z)dz}{h} \quad (5)$$

RESULTS

Distributions and abundances

The upwelling center was off Cabo Frio near the initial deployment of the buoy, and sea surface temperature increased as the buoy drifted westwards and the plume aged (Fig. 1). Vertical profiles of *in situ* fluorescence revealed low chlorophyll concentrations at the off-shore station, but higher and rather similar concentrations and vertical distributions of chlorophyll at the coastal stations with a broad subsurface maximum between 25 and 50 m (Fig. 2). Bottle casts and *in situ* video-recordings yielded similar abundances and vertical profiles of copepods and *Noctiluca scintillans* (Fig. 3). Copepods were abundant in the upper 50 m at the coastal stations, with peak concentrations of 10 to 30 copepods l^{-1} at 15 to 30 m depth. Depth-integrated abundances were similar among coastal stations, but substantially less at the off-shore station (Table 1). The concentration of copepod fecal pellets generally increased with depth in the upper 30 to 50 m; at the off-shore station that was sampled deeper, there was a pronounced decline at depths exceeding 50 m. Fecal pellet abundances were substantially less at the 2 westernmost stations than at all other stations (Table 1, Fig. 3). *N. scintillans* were found on all stations, but only in substantial concentrations at the most westerly stations. There was a significant negative relation between the depth-integrated number of fecal pellets per copepod and the depth-integrated abundance of *N. scintillans* (Fig. 4), suggesting that *N. scintillans* play a role in turning over fecal material.

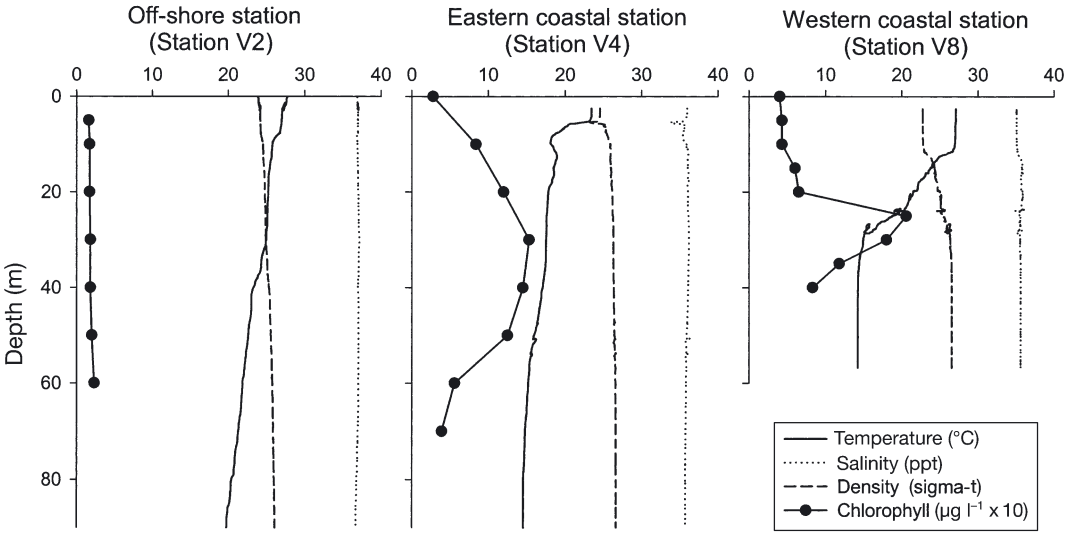

Fig. 2. CTD and fluorescence profiles at representative stations

Fecal pellet production, flux, and degradation

Per capita fecal pellet production rates (p) were similar in all 4 experiments and averaged 3.3 ± 0.4 pellets copepod^{-1} d^{-1} (Fig. 5). Fecal pellet fluxes (J) were similar among experiments, between 3 and 5×10^5 pellets m^{-2} d^{-1}, and constituted between 20 and 45% of the water column fecal pellet production rate (pC), corresponding to specific sinking losses of 0.5 to 2.9 d^{-1} (Table 1). Thus, between 55 and 80% of the fecal pellets produced were degraded within the upper 30 to 60 m. This leads to estimated specific pellet degradation rates by both approaches of between 1 and 13 d^{-1}. Pellet degradation rate was linearly related to the average concentration of *Noctiluca scintillans* in the upper water column (Fig. 6a,b).

Sizes of fecal pellets produced in the incubations (average volumes between 1.0 and 2.2×10^5 µm^3) were similar to those collected in the water column (averages between 1.0 and 1.5×10^5 µm^3), while pellets captured in the traps were slightly larger (averages between 1.8 and 2.7×10^5 µm^3).

DISCUSSION

Copepod fecal pellets are turned over rapidly in the upper ocean, both due to sinking losses and rapid remineralization. Here we found that turnover rate varied between 0.6 and 16 d^{-1}, corresponding to average residence times of between 1.5 and 40 h. During this time interval, the typical pellet has either left the upper

Table 1. Abundances of copepods and copepod fecal pellets, as well as estimates of flux, turnover, and specific sinking losses and degradation rates of copepod fecal pellets at 6 stations off the Brazilian coast. Station B3 was taken off-shore (Fig. 1) where no trap was deployed, whereas all other profiles were taken in neritic waters. Pellet production was computed applying an average production rate of 3.3 pellets copepod^{-1}; this value may not be valid for the off-shore station but was used anyway, hence the parenthesis

Station	B3	B4	B5	B6	B7	B8
Trap deployment number	–	1	1, 2	3	4	4
Integration depth (h) (m)	100	60	60	40	30	30
Copepod abundance (C) (# copepods m$^{-2} \times 10^3$)	150	647	340	373	610	337
Pellet production (pC) (pellets m^{-2} d$^{-1} \times 10^3$)	(500)	2130	1120	1230	2110	1110
Pellet flux (J) (pellets m^{-2} d$^{-1} \times 10^3$)	–	440	400	360	480	480
Pellet abundance (F) (# pellets m$^{-2} \times 10^3$)	831	745	601	639	127	160
Pellet turnover rate ($s + r$) (d^{-1})	0.6	2.9	1.9	1.9	15.9	7.0
Specific sinking loss (s) (d^{-1})	(0.3)[a]	0.7	0.5	0.6	2.9	2.9
Specific degradation rate (r) Model 1 (d^{-1})	(03)	2.2	1.4	1.3	13.0	4.1
Specific degradation rate ($\int r(z)dz/h$) Model 2 (d^{-1})	(0.5)	2.8	0.7	0.7	12.1	5.5

[a]Specific sinking loss for the off-shore station was computed as: (pellet sinking velocity × pellet concentration at 100 m depth)/F; the average sinking velocity computed from all trap deployments (as pellet flux/pellet concentration) was used (53 m d^{-1})

mixed layer due to sinking, or it has been degraded. In the present study, degradation rates were either similar to (off-shore station) or higher to much higher than specific losses due to sinking. Thus, only a relatively small fraction of fecal pellets produced in the upper ocean leave the euphotic layer in the study area, a typical observation for both neritic and more oceanic regions of the ocean (Smetacek 1980, Viitasalo et al. 1999).

Our observations suggest that *Noctiluca scintillans* may be responsible for a significant fraction of the mineralization of fecal pellets, particularly in the westernmost and oldest part of the upwelling plume, where the dinoflagellate occurred in high concentrations. The slope of the linear relations between *N. scintillans* concentration and specific pellet degradation rate, 0.6 l cell^{-1} d^{-1} from both approaches, can be interpreted as the rate at which *N. scintillans* clears copepod fecal pellets. This appears to be a very high clearance rate for a small organism (the cells measure ca. 0.4 to 0.6 mm in diameter). For example, *N. scintillans* clears small phytoplankton cells at rates of up to a few ml per day (Kiørboe & Titelman 1998). However, large (~0.5 cm) neutrally buoyant diatom aggregates may be cleared at rates of about 0.6 l d^{-1} (Tiselius & Kiørboe 1998). In these cases *N. scintillans* intercept prey particles as the cells ascend in the water. In the case of sinking fecal pellets, the encounters are, however, instead due to the sinking of the pellet, because pellet sinking velocity, averaging ca. 50 m d^{-1} in the present study (see legend of Table 1), exceeds the ascent rate of *N. scintillans* (about 20 m d^{-1}, Kiørboe & Titelman 1998). Because the smaller particle (the pellet) moves faster than the larger one (the *N. scintillans* cell), hydrodynamic effects can be ignored (cf. Kiørboe & Titelman 1998), and the clearance rate (β) can be estimated as:

$$\beta = \pi R^2 \Delta u$$

where R is the contact radius and Δu the velocity difference. *N. scintillans* intercepts its prey by means of a long mucus thread that it produces. *In situ* video recordings revealed the presence of such strings of up to several cm in length with food material attached. The nature of the food material could not be clearly identified on the video, but freshly caught cells had copepod fecal pellets in their food vacuoles. These mucus strings can be oriented in any direction from the cell (video observations) and enhance the size of the dining sphere of *N. scintillans*, although it is impossible to accurately estimate by how much. To account for the clearance rate estimated from Fig. 6 (600 ml d^{-1}), given the velocity difference between cells and fecal pellets (pellet sinking velocity + *N. scintillans* ascent velocity = 72 m d^{-1}), a contact radius of 1.6 mm is required. This estimate is

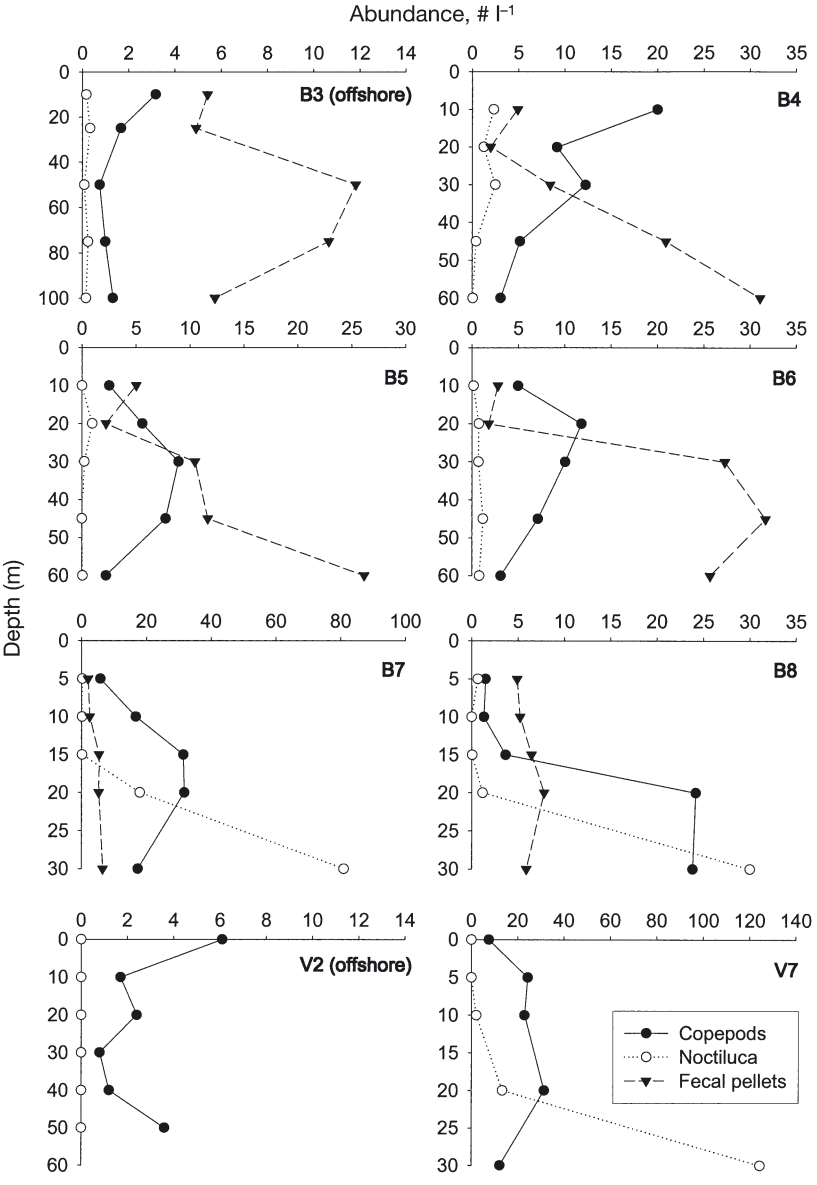

Fig. 3. Vertical concentration profiles of copepods, copepod fecal pellets, and *Noctiluca scintillans*. B3 to B8 are profiles obtained by bottle samples, V2 and V7 are profiles derived from *in situ* video recordings

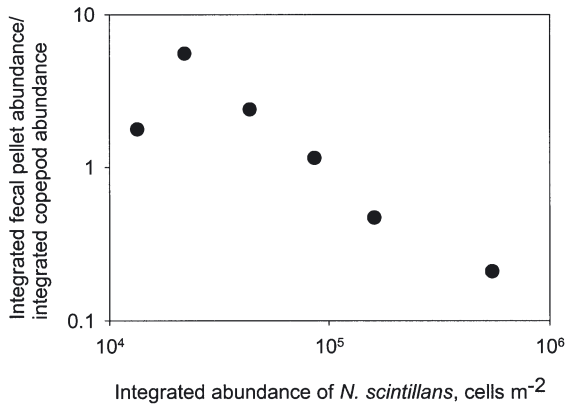

Fig. 4. Ratio of fecal pellet abundance to copepod abundance (both depth-integrated) as a function of depth-integrated abundance of *Noctiluca scintillans*

not inconsistent with the combined effect of cell size (0.5 mm), pellet size (average length 0.1 mm) and mucus string length (1 to 20 mm).

With a clearance rate of the estimated magnitude and water column peak fecal-pellet concentrations of 10 to 30 l^{-1}, this implies pellet ingestion rates of 6 to 18 pellets $cell^{-1}$ d^{-1}. With an average pellet volume of ca. 10^5 μm^3, and assuming a pellet carbon content of 10^{-7} $\mu g\,C\ \mu m^{-3}$ and a *Noctiluca scintillans* carbon content of 0.22 $\mu g\,C\ cell^{-1}$ (Kiørboe & Titelman 1998), this corresponds to specific ingestion rates of 0.3 to 0.9 d^{-1}. *N. scintillans* may grow at specific rates of up to 0.6 d^{-1} (Buskey 1995, Kiørboe & Titelman 1998), and assuming a growth yield of 33% the above estimate thus suggests that *N. scintillans* may obtain a significant fraction of its nutrition from sinking fecal pellets.

Noctiluca scintillans is distributed globally. The presence of *N. scintillans* is often evident from dense aggregations of cells at the surface during summer and fall in temperate waters. During such red-tide blooms, surface concentrations may exceed 10^4 to 10^5 cells l^{-1} (Schaumann et al. 1988, Huang & Qi 1997), and subsurface concentrations of 10^3 to 10^4 cells l^{-1} with depth-integrated abundances in excess of 10^7 cells m^{-2} have also occasionally been recorded (Huang & Qi 1997, Kiørboe et al. 1998). Apart from such spectacular bloom events, the abundance of *N. scintillans* is rarely reported from monitoring studies since they are normally not quantified in zooplankton samples, and they are too rare to be quantified in typical phytoplankton samples. However, a few monitoring studies aimed specifically at *N. scintillans* suggest that the highest cell abundances reported in this study are quite typical during the summer half-year over the shelf of temperate waters. Thus, Uhlig & Sahling (1990), Huang & Qi (1997),

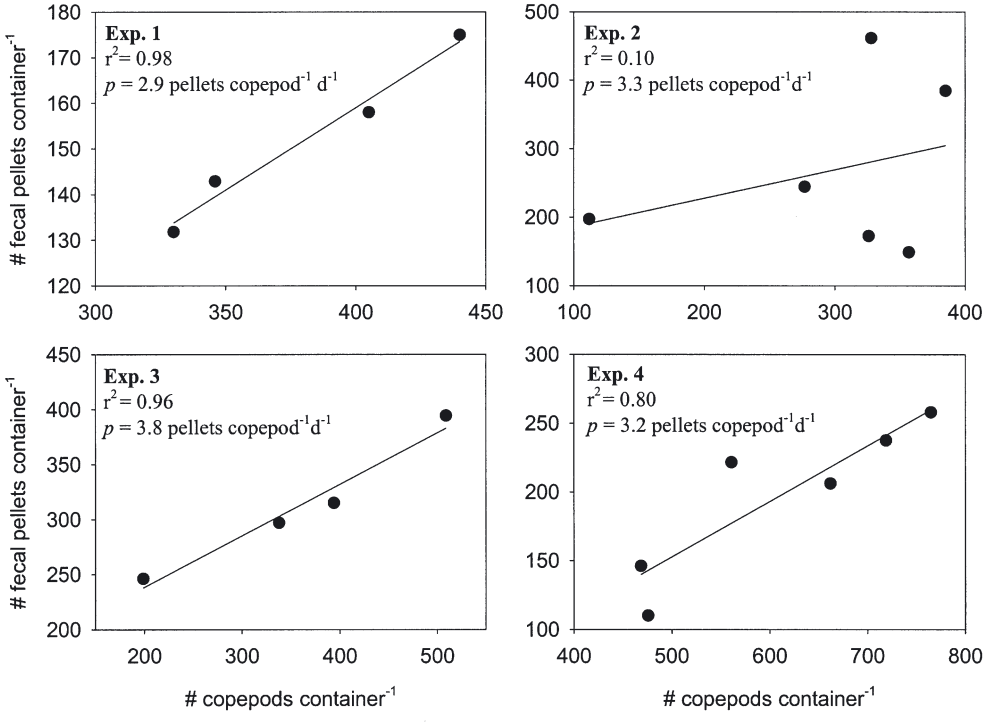

Fig. 5. Per capita fecal pellet production rate. Number of copepod fecal pellets per incubation container after 3 h of incubation as a function of the number of copepods per container in 4 experiments (one experiment per trap deployment). Estimates of daily per capita fecal pellet production rates (p; fecal pellets $copepod^{-1}$ d^{-1}) have been shown for each experiment

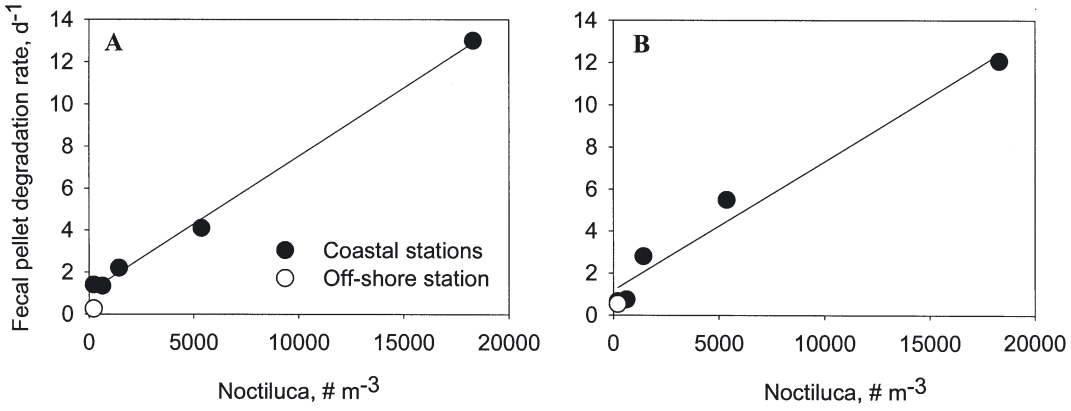

Fig. 6. Specific degradation rates of copepod fecal pellets (r; d^{-1}) in the upper 30 to 60 m of the water column as a function of depth-averaged concentration of *Noctiluca scintillans* at 5 coastal stations ([N]; cells m^{-3}) (●) estimated by Model 1 (A) and Model 2 (B). The regression lines have been shown. Model 1: $r = 1.0 + 0.6 \times 10^{-3}$ [N] ($R^2 = 0.99$); Model 2: $r = 1.2 + 0.6 \times 10^{-3}$ [N] ($R^2 = 0.97$). (○) approximate value for the off-shore station, which has been computed assuming identical pellet sinking velocity and copepod fecal pellet production rate as for the coastal stations (not included in regressions)

Nakamura (1998), and Murray & Suthers (1999) all found subsurface concentrations of 100 to 200 cells l^{-1} for extended periods (months) during spring, summer and/or fall in various shelf seas (North Sea, South China Sea, Seto Inland Sea, southeast Australian estuaries, respectively). These concentrations correspond to abundances of 2 to 10×10^6 cells m^{-2} if integrated over a 20 to 50 m euphotic zone. Copepods are often ascribed the major role in rapidly turning over their own fecal pellets in the upper water column (Smetacek 1980, Lampitt et al. 1991). However, if the above densities of *N. scintillans* are representative of the summer plankton of temperate waters, *N. scintillans* may be equally or more important in preventing loss of fecal pellet material from surface waters and, thus, in sustaining plankton production throughout the summer half year.

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