NOTE

Fate of copepod faecal pellets and the role of *Oithona* spp.

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ABSTRACT: Because the downward flux of zooplankton faecal pellets (FP) measured in sediment traps is typically lower than FP production in overlaying waters, it is inferred that FP are recycled. One suggested explanation for low export fluxes of FP is retention through processes such as FP ingestion (coprophagy) and FP fragmentation (coprorhexy). It has become accepted that the globally important cyclopoid copepod *Oithona* spp. are one of the main organisms causing high retention of copepod FP, however, the experimental evidence supporting this hypothesis is limited. We conducted 3 experiments to test whether the raptorial feeding *Oithona* spp. removed sinking FP material produced by *Calanus finmarchicus* either by grazing or fragmentation. No such evidence was found. We therefore suggest that alternative explanations for pellet recycling should be sought. We believe that *Oithona* spp. may be indicator species for a 'retention ecosystem', but they are probably not the single factor explaining FP retention in the world oceans.

KEY WORDS: Faecal pellet · Faecal pellet retention · *Oithona* · Coprophagy · *Calanus finmarchicus* · Faecal pellet fragmentation

INTRODUCTION

The downward flux of intact faecal pellets (FP) measured in sediment traps is only a fraction of what is produced in the overlaying waters, both in coastal and open ocean environments (Small et al. 1987, Dam et al. 1995, Urban-Rich et al. 1999, Viitasalo et al. 1999, Wexels Riser et al. 2002, Sampei et al. 2004). The fate of FP and their role in the marine carbon budget has therefore frequently been debated. One suggested explanation for low export fluxes of FP is retention through processes such as coprophagy and coprorhexy (Smetacek 1980, Sasaki & Nishizawa 1981). Both processes imply decreasing FP sinking fluxes, as FP are either consumed (coprophagy) or modified (coprorhexy/coprochaly) by zooplankton (Lampitt et al. 1990, Noji et al. 1991). When FP are fragmented, sinking velocity decreases and the fragments contribute to the pool of suspended detritus (Smetacek 1980) and regenerated food web (Wassmann 1998).

Some zooplankton species are assumed to play key roles in the regulation of carbon export from the euphotic zone, and the most frequently cited species in this respect is the cyclopoid copepod *Oithona* spp. (Lampitt & Gamble 1982, Gonzáles & Smetacek 1994, Kiørboe & Visser 1999, Suzuki et al. 2003, Svensen & Nejstgaard 2003). This is mainly based on their raptorial feeding behaviour and preference for larger and moving prey particles (Lampitt 1978, Drits & Semenova 1984, Gonzáles & Smetacek 1994, Svensen & Kiørboe 2000, Paffenhöfer & Mazzocchi 2002). Both swimming prey and sinking FP produce a hydromechanical signal that can be detected by *Oithona* spp. (Svensen & Kiørboe 2000), potentially leading to attack and ingestion of the prey particle. The ubiquitous abundance and broad geographical distribution of *Oithona* spp. (Paffenhöfer 1993, Turner 2004) also suggests an opportunistic strategy, feeding on whatever is present. It has been suggested that populations of *Oithona* spp. may act as a 'coprophagous filter' (Gonzáles & Sme-

tacek 1994). Pulses of sedimented FP would then be a result of 'leaks' in the 'filter' that could be caused by patchiness in horizontal distribution or local decimation of the scavengers by predators' (e.g. Gonzáles & Smetacek 1994).

Experiments have demonstrated that *Oithona similis* may feed on pellets produced by *Calanus glacialis*, *C. finmarchicus* and *Temora longicornis* (Gonzáles & Smetacek 1994). However, these experiments were conducted in upright bottles where FP was sinking and *O. similis* were reported to graze FP from the bottom of the bottles. Based on the knowledge that *Oithona* spp. are raptorial feeders, we wanted to investigate their impact on FP in suspension. Furthermore, there are several pieces of evidence on significant FP retention from coastal regions of northern Norway and the Barents Sea (Urban-Rich et al. 1999, Wexels Riser et al. 2002), but we are not aware of any attempts to experimentally address the topic in this region. As *Oithona* spp. periodically are among the most abundant copepods in this region (Pasternak et al. 2000, Arashkevich et al. 2002), we therefore designed experiments with the purpose of testing the hypothesis that *Oithona* spp. are consuming FP produced by *C. finmarchicus* (hereafter referred to as *Oithona* and *Calanus*).

MATERIALS AND METHODS

Copepods and food. The fate of FP from the calanoid copepod *Calanus* was investigated during 3 experiments, 16 to 24 March 2004. Mesozooplankton was collected during a pre-bloom condition in the sea close to Tromsø, Norway (69° 40′ N, 18° 55′ E) ahead of each experiment. A WP-2 net (90 µm mesh size) with large cod-end was used for gentle sampling. The content was diluted at sea and acclimatised overnight in a cold room (8°C) in an aerated tank with additional food. Active female *Calanus* and *Oithona* females (*O. similis* dominated with a few *O. atlantica*) without any visible damage were selected for the experiments.

Thalassiosira weissflogi from an exponentially growing culture dominated by single cells (diameter = 10 µm) and a few shorter chains was used as food for *Calanus* to produce FP in all experiments. Algae were grown in F/2 medium (Guillard & Ryther 1962) in a 14:10 h day:night light regime (40 to 50 µE, 8°C) approximating the natural conditions in the region. *T. weissflogi* was selected as food to enhance the potential FP consumption by *Oithona* since this diatom is assumed to provide good food for *Calanus* and unsuitable food for *Oithona*, which prefer motile prey and larger cell sizes (Svensen & Kiørboe 2000). Algal concentrations in the incubation water were calculated from cell counts using an inverted microscope, and food concentrations of 0.5 to 2.0 mg C l^{-1} were offered (Table 1). The experiments were run in a temperature controlled room (8°C) in dim light. Copepods were incubated in 1000 ml bottles (sealed without bubbles) on a plankton wheel (1 rpm) to allow the FP to be suspended, thereby mimicking the natural feeding conditions of *Oithona*. Visual inspection showed that pellets were kept in suspension during the experiments.

We performed 3 experiments to investigate the effect of *Oithona* on FP produced by *Calanus*. Since stable FP production rates were crucial for our hypothesis, we first investigated the sensitivity of FP production rates to the copepod densities in Expt 1. This was to minimize the variability between replicates and ensure that indi-

Table 1. Experimental set up for Expts 1 to 3. Number of incubated copepods (*Calanus finmarchicus* female (Cf) and *Oithona* spp. female (O)) for treatment and control bottles is given with number of replicates (n). Incubation time is given in h, and food concentration in the incubation water is given as µg Chl *a* l^{-1}, concentration of *Thalassiosira weissflogi* cells (10^6 cells l^{-1}) and C content (µg C l^{-1})

Expt	Purpose	Experimental set up Treatment	Control	Incubation time (h)	Chl *a* conc. (µg l^{-1})	*T. weissflogi* 10^6 cells l^{-1} (µg C l^{-1})[d]
1	FP production[a]	2 Cf (n = 5) 4 Cf (n = 5) 6 Cf (n = 5)		6	12.2	1.8 (550)
2	Coprophagy[b]	6 Cf+20 O (n = 6)	6 Cf (n = 6)	22	29.4	6.5 (1980)
3	Coprophagy[c]	FP+40 O (n = 6)	FP (n = 6)	18	15.5	1.8 (550)

[a]Density dependent faecal pellet (FP) production
[b]*C. finmarchicus* and *Oithona* were incubated together in the treatment bottles
[c]Four *C. finmarchicus* females were incubated for 7.5 h in 12 bottles, and then removed from all bottles before *Oithona* spp. were added to the 6 treatment bottles for 18 h
[d]Carbon content of *T. weissflogi* measured average of 305 pg C cell^{-1}

vidually variable FP production rates did not affect the interpretation of the results. The potential removal of *Calanus* FP by *Oithona* was addressed using 2 different experimental set ups (Expts 2 and 3). In Expt 2 *Calanus* and *Oithona* were incubated in the same bottles, while in Expt 3 the *Calanus* were removed after FP production in order to eliminate potential disturbance of *Oithona* from the swimming and grazing *Calanus.*

Expt 1. We used 3 densities of *Calanus*, 2, 4 and 6 ind. bottle^{-1} to test whether FP production was affected by copepod density. Each copepod concentration was incubated in 5 replicates. Food was offered at a high and non-limiting concentration, ~550 µg C l^{-1}, corresponding to 2×10^6 *Thalassiosira weissflogi* cells l^{-1} (Table 1). After 6 h incubation on a plankton wheel (1 rpm), the contents of each bottle were gently sieved through a 20 µm Nitex mesh, fixed with buffered formalin (2% final concentration) and the FP were then analysed. FP fragmentation caused by *Calanus* through active grazing, destruction or by passive mechanical disruption was also recorded.

Expt 2. We incubated 6 *Calanus* and 20 *Oithona* together in 1 l bottles in 6 replicates for 22 h (Table 1) on a rotating plankton wheel. The control consisted of 6 bottles containing only *Calanus*. Food was offered in non-limiting concentrations corresponding to ~2000 µg C l^{-1} (Table 1). After incubation the animals were checked for viability and the total contents of the bottle were sieved through a 20 µm Nitex mesh to retain FP. The FP removal by *Oithona* was calculated from the difference in FP biomass in treatment and control bottles.

Expt 3. We incubated 4 *Calanus* in 1 l bottles with food concentrations corresponding to 550 µg C l^{-1} to produce pellets. After 7.5 h the *Calanus* were gently removed using a pipette and 40 *Oithona* bottle^{-1} were added (6 replicates). No *Oithona* were added to the 6 controls, leaving only pellets in these bottles. The bottles with pellets and *Oithona* and the controls with only FP were then incubated for another 18 h on a slowly rotating plankton wheel (1 rpm). After incubation the animals were checked for viability and the total contents of the bottles were sieved through a 20 µm Nitex mesh to retain FP.

Chlorophyll *a* and carbon determinations. Chl *a* concentrations in the incubation water were measured on a Turner Designs model 10-AU fluorometer after filtration (3 ×50 ml) on GF/F filter and extraction in 100% methanol overnight (Holm-Hansen & Riemann 1978). For POC analyses, incubation water was filtered on pre-burned GF/F filters (3 ×100 ml), frozen (–20°C), and analysed with a Leeman Lab 440 elemental analyser after fuming with HCl to remove inorganic carbon. Carbon content was also determined for *Calanus* females (n = 3) and FP (Table 2).

Table 2. Average width, volume and carbon content of intact faecal pellets (FP) produced by *Calanus finmarchicus* females in the experiment. Dry weight (dw), carbon (C), nitrogen (N) and C:N ratio of *C. finmarchicus* females from a North Norwegian fjord, March 2004. Variation is given as ±SD

Faecal pellets	
Width (µm)	61 ± 8
Volume (10^4 µm^3)	198 ± 95
Carbon content (µg C mm^{-3})	80.3
Carbon content (ng C pellet^{-1})	159
***Calanus finmarchicus* females**	
dw (µg ind.$^{-1}$)	262 ± 31
% C (µg dw^{-1})	37 ± 1
% N (µg dw^{-1})	7 ± 0
C:N (a:a)	6 ± 0

FP analyses. To obtain the best quantitative measure of the FP, volume was determined for all pellets. Entire samples were counted by the Utermöhl technique (Utermöhl 1931), using an inverted microscope (100× magnification) equipped with measuring ocular. The FP were sized (length and width measured) and categorised as a whole pellet, end piece or mid part. Total FP volume could then be calculated assuming a cylindrical shape (Edler 1979). The total pellet number in each bottle was calculated by adding up the whole pellets and the number of end pieces divided by 2. Mid parts contributed to FP volume, but not the number of pellets.

A FP carbon conversion factor was obtained by individually picking intact FP produced by *Calanus* during a 21.5 h incubation (conditions similar to Expt 2, Table 1). The pellets were rinsed twice in 0.4 µm filtered seawater, filtered onto a pre-burned GF/F filter in 3 replicates (100, 113 and 125 FP, respectively) and frozen (–20°C) until analysed. The average size of all unbroken FP (n = 917) produced by *Calanus* females during all experiments was used to calculate the carbon/volume ratio giving a C conversion factor of 80.34 µg C mm^{-3} (Table 2). Pellet production rates were calculated in terms of numbers (#FP ind.$^{-1}$ d^{-1}) and carbon (µg C ind.$^{-1}$ d^{-1}).

A 1-way ANOVA and *t*-test were run at the 95% level using Excel X to test the results for statistical significance.

RESULTS AND DISCUSSION

Did *Oithona* graze copepod FP?

No evidence was found that *Oithona* removed FP material in any of the experiments. In Expts 2 and 3 we evaluated the potential of 2 *Oithona* concentrations to remove *Calanus* FP (Fig. 1). In Expt 2, 20 *Oithona* were incubated with 6 *Calanus*. The total FP carbon or aver-
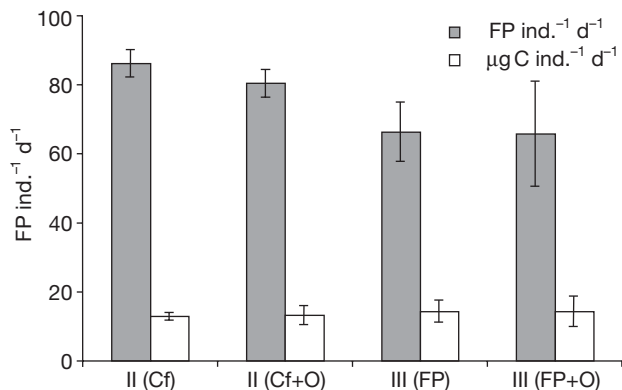
Fig. 1. Faecal pellet (FP) production in bottles with and without *Oithona* (O) in Expts 2 and 3 presented in terms of numbers and carbon. Bars represent 95% CI. FP were produced by *Calanus finmarchicus* (Cf) females
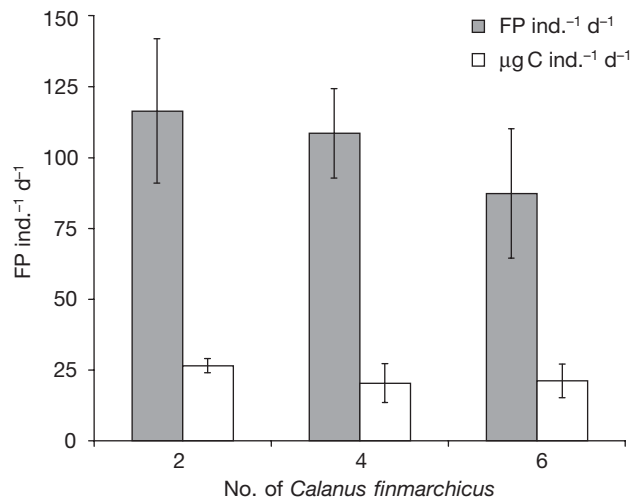

Fig. 2. Density-dependent faecal pellet (FP) production by *Calanus finmarchicus* in Expt 1. FP production presented in terms of numbers and carbon. Bars represent 95% CI

age number of *Calanus* pellets recovered after incubation in the bottles with *Oithona* did not differ significantly from the controls with no *Oithona* (2-tailed t-test; p = 0.82 and p = 0.42 for total carbon and number of FP, respectively) (Fig. 1). In Expt 3, 40 individuals of *Oithona* per bottle were offered 78 to 105 FP. Even with this high concentration of *Oithona* there were no differences between treatment and control bottles. This complete lack of FP removal by *Oithona* was in contrast to previous experiments (Gonzales & Smetacek 1994).

A daily food requirement of *Oithona similis* (160 ng C ind.$^{-1}$ d^{-1}, 19 to 21°C, Nakamura & Turner 1997) corresponds to the carbon content of 1 average sized FP from a *Calanus* female in this experiment (159 ng C pellet^{-1}). The *Oithona* females should thus be able to consume 40% of the present pellets to meet their daily C needs. If *Oithona* consumed FP, either through ingesting whole pellets or more likely by eating parts of the FP, this should have been detected as a reduced FP volume in the bottles with *Oithona*. This was not the case.

Stable FP production is of crucial importance when studying FP removal. *Calanus* demonstrated a relatively high and stable FP production of 4 to 5 FP h^{-1} in Expt 1 (Fig. 2), and the number of pellets produced per female and the pellet biovolume egested did not differ significantly as a result of changing *Calanus* density (1-way ANOVA; F = 3.69, p = 0.059). Generally, high FP fragmentation was observed during the experiments (23 to 40% of the pellets counted). The presence of 20 or 40 *Oithona* or the concentration of 2, 4 or 6 *Calanus* did not increase or change the fraction of broken/fragmented FP (2-tailed *t*-test; p > 0.05). Any minor increase in FP volume caused by the fragmentation would thus be similar for experimental and control

bottles, and would not influence our results and conclusions. A likely explanation for the high fragmentation is the combination of high food concentrations and small food particles used in the experiments which can result in less dense and faster degrading FP (Hansen et al. 1996, Feinberg & Dam 1998).

We argue that the lack of FP removal by *Oithona* was not a result of inappropriate experimental methods. A plankton wheel was used to ensure that the FP were suspended. The suspended and sinking FP were supposed to create hydromechanical signals and increase the detection by the raptorial feeding *Oithona*. Individuals of *Oithona* chosen were all active before and after the experiment, and most of them were carrying egg sacs when incubated, indicating active feeding mode.

Fate of FP in the field

The resulting lack of any indication of *Oithona* spp. feeding on or increasing fragmentation of the *Calanus* FP was surprising. Copepod concentrations used were all within the range observed in the field (Halvorsen & Tande 1999, Turner 2004) and so were the diatom concentrations (Eilertsen et al. 1981) and the FP production rates (Urban-Rich et al. 1999, Wexels Riser et al. 2002). We argue that these results imply that there is a need for further investigation on the FP retention mechanisms. Our results do not prove that *Oithona* do not feed on FP, but they demonstrate that they do not *always* feed on FP when present. Temperature dependent respiration for *O. similis*, measured by Castellani et al. (2005), suggests low energy demand at low temperatures, and they refer to *in situ* ingestion rates of 5

to 327 % body carbon d^{-1} from the cold sub-Antarctic regions (−1 to 6.5°C, Castellani et al. 2005, and references therein). For a female *O. similis* of 0.6 µg C ind.$^{-1}$ (Kiørboe & Sabatini 1994) the corresponding daily consumption is 0.03 to 1.96 µg C ind.$^{-1}$ or 0.2 to 12.3 *Calanus* FP. High variability in the retention potential by *Oithona* is therefore likely, especially in cold regions. Hence, predicting FP removal from *Oithona* abundance is obviously too simple. To explain the strong retention that evidently takes place in the field, also in low temperature regions (Gonzáles et al. 1994, Wassmann 1998, Urban-Rich et al. 1999, Viitasalo et al. 1999, Wexels Riser et al. 2001, 2002, Sampei et al. 2004), further attention is needed to search for alternative mechanisms and organisms that may shed light on the high retention of copepod FP reported.

Organisms other than *Oithona* have been suggested or shown to influence the fate of FP. High retention of FP has also been described where the abundance of *Oithona* have been low — in these cases larger mesozooplankton have been suggested to play a significant role (Urban-Rich et al. 1999, Sampei et al. 2004). *Calanus helgolandicus* (Paffenhöfer & Strickland 1970), *Calanus* nauplii (Green et al. 1992) and heterotrophic dinoflagellates (Kiørboe 2003) have all been shown to ingest FP. Mechanical destruction (coprorhexy) of FP (Noji et al. 1991) or degradation caused by wind induced turbulence (Viitasalo et al. 1999) are also described or suggested to fragment pellets and increase degradation and retention. Variability in the robustness of the FP based on diet or food concentration is another suggested mechanism (Hansen et al. 1996).

During periods or events when the food items cause more fragile pellets and reduced FP export, disintegration might be the most prominent retention mechanism. Our results indicate that this can also take place in early spring when small diatoms dominate. There is obviously a need for more work on how different food compositions influence the fate of zooplankton pellets. It is also necessary to investigate how different species and stages of zooplankton and physical factors contribute to retention. FP production experiments and simultaneous sedimentation measurements from contrasting regions such as off- versus on-shelf systems (Wexels Riser et al. 2001) and Atlantic versus Arctic regions of the Barents Sea (Wexels Riser et al. 2002) have revealed higher versus lower retention areas with regard to copepod FP. Some ecosystems are more retentive than others (Wassmann 1998), and *Oithona* might be an indicator species for high retention ecosystems without being the only causing agent in the system. It is therefore important that the coincidence of high *Oithona* abundance and high FP retention is not interpreted as an inevitable cause and effect mechanism.

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