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Benthic life in the pelagic: Aggregate encounter and degradation rates by pelagic harpacticoid copepods

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Abstract

We measured field abundances, feeding rates, swimming behavior, and particle colonization of two harpacticoids, the pelagic *Microsetella norvegica* and the semibenthic *Amonardia normanni*, to examine (1) if aggregates have a significant role in harpacticoid nutrition and (2) if harpacticoids contribute significantly to aggregate degradation. Neither of the harpacticoids was able to feed efficiently on suspended food, while both grazed well on attached food, indicating that pelagic harpacticoids depend on food attached to surfaces, such as those offered by marine aggregates. We estimated that the two harpacticoids are able to search substantial volumes of water for aggregates (up to 1.2 L d^{-1}), and that during bloom conditions in the North Sea, reported aggregate concentrations allow *M. norvegica* to daily encounter about three aggregates. High short-term hunger-induced feeding rates observed in *A. normanni* indicate that at least some harpacticoid species can fill their gut during few short visits to aggregates. Harpacticoids may cause substantial degradation of aggregates of <1 cm (5–100%) when their abundance exceeds 10^5 m^{-2}, which is not atypical during summer in temperate waters.

Macroscopic aggregates, generally referred to as marine snow, may constitute a significant source of organic carbon in the water column (Alldredge 1972; Alldredge and Silver 1988). Marine snow is colonized by a huge variety of microorganisms and metazoans (Shanks and Edmondson 1990; Bochdansky and Herndl 1992; Green and Dagg 1997), including copepods of the genera *Oncaea*, *Oithona*, and *Microsetella* (Alldredge 1972; Ohtsuka et al. 1993). These metazoans may at times be several orders of magnitude more concentrated on marine snow particles than in the surrounding water (Steinberg et al. 1994; Green and Dagg 1997; Kiørboe 2000).

Metazoans may use marine snow as nursery sites for their eggs and nauplii, as refuges from predation, and as vertical transport vehicles (Shanks and Edmondson 1990; Steinberg et al. 1994). Behavioral observations and studies based on fecal pellets produced on marine snow indicate that some metazoans may also feed on marine snow (Alldredge 1972; Lampitt et al. 1993; Dilling et al. 1998), thereby directly affecting the vertical flux of carbon out of the productive layer. Although quantitative studies on feeding rates of metazoans on marine snow are rare and limited to a few metazoan groups (Alldredge 1972; Rieper-Kirchner et al. 1991; Lampitt et al. 1993), calculations based on their abundances on marine snow and their metabolic rates indicate potentially high marine snow degradation rates due to metazoan activities (Kiørboe 2000).

Pelagic harpacticoid copepods, such as *Microsetella* spp., seem to be particularly adapted to feeding on aggregates (Steinberg et al. 1994; Green and Dagg 1997), and benthic harpacticoids may depend on aggregates for feeding if regularly suspended during, for example, storms (Thistle et al. 1995). Since *Microsetella* sp., as well as some meiobenthic harpacticoids, can be extremely abundant in the water column (Dugas and Koslow 1984; Nielsen and Andersen 2002) and are commonly observed in marine snow particles (Green and Dagg 1997), we can hypothesize that these harpacticoids contribute significantly to the degradation of marine snow (*see* Walters and Shanks 1996; Kiørboe 2000).

The contribution of harpacticoids to the degradation rates of marine snow depends on the ability of the harpacticoids to find the snow particles (search volume rate), on harpacticoid residence time and feeding rate on these particles, and on the abundance and vertical distribution of harpacticoids in the water column. The search volume, in turn, depends on harpacticoid motility (swimming behavior) and on their ability to remotely detect aggregates (Kiørboe and Thygesen 2001; Jackson and Kiørboe 2004). Feeding rate and residence time, on the other hand, are likely to be affected by the aggregate type. Although some studies have examined the effect of aggregate type on metazoan feeding rates (Rieper-Kirchner et al. 1991; Dilling et al. 1998), the ability of

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common harpacticoids to find, colonize, and feed on any type of aggregates is generally unknown.

Similarly, the importance of aggregates for harpacticoid ecology is unclear. Harpacticoid association with marine snow seems to vary with area (Shanks and Walters 1997), season, and depth (Steinberg et al. 1994) and with productivity of the water mass (Ohtsuka et al. 1993; Uye et al. 2002). It has been suggested that pelagic harpacticoids, such as *Microsetella* sp., would only be associated with marine snow in offshore areas where suspended food is scarce (Ohtsuka et al. 1993; Uye et al. 2002). On the other hand, it has been shown that even pelagic harpacticoids may feed more efficiently on food particles attached to a surface than on particles in suspension (Rieper 1978; Pace and Carman 1996; but *see* Decho [1986] for controversial observations). This indicates that harpacticoids in the water column would be dependent on surfaces, such as those offered by large particles, to obtain food (*see* Shanks and Edmondson 1990). The observed large number of harpacticoid nauplii and eggs on marine snow (Owen 1989; Steinberg et al. 1994) further indicates the importance of aggregates for harpacticoid reproduction and juvenile development.

The present study focuses on the importance of aggregates for harpacticoid nutrition as well as on the significance of harpacticoids for aggregate degradation. We used two harpacticoid species: *Microsetella norvegica,* the dominant pelagic harpacticoid in temperate waters (Daro 1988), and *Amonardia normanni,* which was used to represent benthic species that regularly emerge into the water column or are suspended during storms (*see* Thistle et al. 1995). We compare the ability of these species to feed on suspended versus surface-attached food, examine swimming patterns to calculate aggregate search volumes, and measure residence times and colonization and feeding rates on artificial aggregates. We show that even pelagic harpacticoids depend on surface-attached food to obtain enough nutrition and that the aggregate encounter and feeding rates are sufficiently high for pelagic harpacticoids to play a significant role in aggregate degradation.

Materials and methods

Experimental animals—All experiments with *A. normanni* were conducted with laboratory-reared animals, originally collected with plankton tows from Gullmarsfjord (western Sweden). *M. norvegica* was generally collected <1 week prior to experiments, either from Gullmarsfjord or from the central North Sea. Both species were fed *Thalassiosira weissflogii* in excess. The experiments were conducted at 18°C (*A. normanni*) or near in situ temperature (8°C and 18°C during spring and summer, respectively) at the collection site (*M. norvegica*).

Swimming behavior—Swimming behavior of *M. norvegica* and *A. normanni* was analyzed in the absence and presence of food (the diatom *T. weissflogii*), using females adapted for 24 h. The swimming behavior was recorded either in 90-mm–diameter Petri dishes (*A. normanni*) or in closed 50-ml tissue bottles (*M. norvegica*). A video camera connected to a timer and a VCR was mounted above the arena, and infrared light was provided from below. The two-dimensional projection of the motility pattern was evaluated by following at least 10 different individuals during 1 min or 10 swimming events each, and the duration of individual swim and pause events and swimming velocity were recorded. The motility parameters were then used to compute an equivalent diffusion coefficient (D), assuming random and isotropic motion pattern (Visser and Thygesen 2003):

$$D = \frac{\nu^2\tau^2}{2(\tau + \rho)} \quad (1)$$

where ν is the average swimming speed, τ is the average duration of swim events, and ρ is the average duration of pause events. From the diffusivity of the copepods, one can predict the rate at which a spherical aggregate will be encountered by copepod as βC, where C is the ambient concentration of copepods and β is the search volume rate given by

$$\beta = 4\pi Da \quad (2)$$

where a is the radius of the spherical aggregate (Berg 1993).

Colonization rates of agar spheres—Actual particle colonization of *A. normanni* was investigated using 2-mm (radius) agar spheres as model particles (Kiørboe et al. 2002). We used both agar spheres that were preincubated in 200-μm filtered water from Øresund (Denmark) for >1 week as well as newly produced agar spheres. Preincubated spheres were rich in potential food, e.g., bacteria, phytoplankton (mainly diatoms and cyanobacteria) at concentrations of 40 $\pm$ 20 ng Chlorophyll *a* cm^{-2} and in heterotrophic flagellates and ciliates (such as *Euplotes* sp. and *Vorticella* sp). The newly produced agar spheres did not contain any food.

Four colonization experiments with spheres containing food and one experiment with newly produced spheres (no food) were conducted by suspending ca. 40 agar spheres into a 30-liter bucket with a known concentration of *A. normanni.* The spheres were hanging on thin glass threads. During 3–4 d, ca. 10 spheres were carefully lifted up at 1–24-h intervals, the number of animals associated with the spheres recorded, and the spheres returned to the bucket. Similar experiments were attempted with *M. norvegica,* but the tendency of this species to get caught in the surface tension made the results unreliable.

Copepods both arrive and leave the suspended spheres. Assuming that the copepods search a constant volume of water for aggregates per unit time (β), that they attach to an encountered aggregate by a certain probability (p), and that they detach again at a constant specific rate (δ), then the number of attached copepods (N) changes with time as

$$\frac{dN}{dt} = p\beta C - \delta N \quad (3)$$

where C is the ambient concentration of copepods. Equation 3 integrates to

$$N_t = \frac{p\beta C}{\delta}[1 - \exp(-\delta t)] \quad (4)$$

This equation was fitted to the observed colonization data, and attachment probability × search volume ($p\beta$) and detachment rate (δ) were estimated. This allowed us to estimate the probability of attachment, p, as the ratio of $p\beta$ estimated from colonization experiments (Eq. 4), and β estimated from motility analysis (Eq. 2).

Grazing on surface versus in suspension—The functional response in weight-specific ingestion and fecal pellet production to the concentration of algal food were examined in *M. norvegica* and *A. normanni*, both when the diatom food (*T. weissflogii*) was offered in suspension and when settled on a surface. The food concentrations ranged from 0 to 8 μg C cm^{-2} on surfaces and from 0 to 4,000 μg C L^{-1} in suspension; 2 to 6 replicate experiments with *M. norvegica* and 2 to 12 replicate experiments with *A. normanni* were conducted for each food concentration. The surface carbon concentration in the experiments corresponded largely to natural marine snow aggregates: Alldredge (1998) reported carbon and chlorophyll contents of field-collected aggregates as a function of aggregate size, POC (μg) = 75a(cm)$^{1.5}$ and Chl (ng) = 225a(cm)$^{1.5}$, respectively (a is the equivalent spherical aggregate radius in cm). Kiørboe (2003) argued that the surface area of natural aggregates—which, as a result of their fractal nature, is difficult to measure directly—increases with aggregate size, such that area (cm^2) = 25a(cm)$^{1.5}$. This yields average surface area concentrations of 9 ng Chl cm^{-2} and 3 μg C cm^{-2} in natural aggregates. In contrast, the highest concentration of suspended phytoplankton in our experiments was one to two orders of magnitude higher than typical concentrations in even coastal oceans (Ferrari et al. 2003).

The surface feeding experiments were conducted in 10-ml vials with one female per vial (*A. normanni*) or in 50-ml airtight closed tissue bottles containing ca. 10 females (*M. norvegica*). Algae were allowed to settle at the bottom of the incubation chambers prior to the start of the experiments. The suspension feeding experiments were conducted in 330- or 140-ml airtight bottles, containing 10–50 females per bottle (depending on the food concentration) and rotated ca. 1 RPM. All animals were adapted to the food concentration for at least 24 h before the start of the experiment. Algal concentrations at the start and end of the experiments were counted using an ELZONE electronic particle counter, and ingestion rates were calculated according to Frost (1972). At the end of each experiment, fecal pellets retained on a 15-μm sieve were counted and, in one experiment with *A. normanni*, ca. 30 pellets per treatment were measured. The pellet volume of *M. norvegica* was obtained by measuring ca. 30 pellets produced in the stock culture.

Carbon contents of copepods, fecal pellets, and algae were used to compute specific rates. Carbon weights of *M. norvegica* (0.4 μg C ind.$^{-1}$) and *A. normanni* (2.2 μg C ind.$^{-1}$) females were calculated from length measurements and length-carbon regressions of Uye et al. (2002) and Tanskanen (1994), respectively. Fecal pellet carbon was computed from size measurements and by assuming a specific carbon content of 0.057 × 10^{-9} mg C μm^{-3} (Gonzalez and Smetacek 1994). The carbon content of *T. weissflogii* was assumed to be 218 pg cell^{-1}.

Grazing on aggregates—The grazing of *A. normanni* on the microbial community attached to the surface of preincubated agar spheres was estimated indirectly from fecal pellet production. Measured pellet production was converted to ingestion by using the linear regression between pellet production and ingestion of *T. weissflogii* obtained in the grazing experiments described above (r^2 = 0.64; data not shown). Five females (adapted for 24 h) were incubated with one agar sphere suspended on a glass thread in each of three replicate 0.5-liter bottles for 24 h. Triplicate control bottles with animals and fresh agar spheres (no food) or animals in filtered seawater were run simultaneously. Pellets were counted at the end of the incubations, and in one experiment ca. 30 pellets were sized.

In addition to agar spheres, the grazing of *A. normanni* was estimated on aggregates made from *T. weissflogii*. *T. weissflogii* cells (ca. 60,000 ml^{-1}) were heat-killed and slowly rotated on a rolling table for ca. 5 d. Then 20 small aggregates of ≤1 mm in radius (0.3 ± 0.2 mm; n = 20) were picked into five replicate 350-ml bottles containing filtered seawater, and five 24-h starved *A. normanni* females were added; the bottles were slowly rotated through the incubation. Triplicate controls were set up with *A. normanni* in filtered seawater only. After 24 h, the number of pellets was counted. The average cell number of *T. weissflogii* was 180 ± 240 cells aggregate^{-1}, corresponding to 0.04 ± 0.05 μg C aggregate^{-1} and 0.3 μg C cm^{-2}. Total aggregate volume in the experiments was 6 ppm.

Short-term grazing rates of adults and nauplii—Short-term ingestion rate of 24-h starved *A. normanni* females was estimated in six to nine replicate surface grazing experiments, using ca. 2 μg C cm^{-2} of *T. weissflogii* as food. Five females were incubated per 10-ml vial during 0.2–8 h. Short-term ingestion in *A. normanni* nauplii was estimated using a pellet produced by *A. normanni* female as food, from the disappearance of pellet carbon due to nauplii grazing. As a result of the problems associated with measuring grazing rates of small organisms by traditional means (counting produced fecal pellets or measuring the disappearance of algae cells), we used a pellet as a model particle instead of an agar sphere. Preliminary observations showed that *A. normanni* nauplii readily attach to pellets and consume them rapidly. A nauplius hatched within 24 h was positioned on a fecal pellet under an inverted microscope, and the cross-sectional area of the pellet was estimated from digital photographs taken at 1–5-min intervals for 2 h, during which time the nauplii remained attached to the pellet. Placing the nauplii on pellet was assumed to be reasonable, since most harpacticoid nauplii are unable to swim and are placed on a food source (such as an aggregate) by egg-carrying females (Owen 1989). The relative decline in pellet carbon was estimated from the change in cross-sectional area, assuming that carbon varies with (surface area)$^{1.5}$. The absolute decline in pellet carbon was then estimated from the initial pellet volume and carbon content.

Field sampling—Vertical day and night profiles of *M. norvegica* and other harpacticoids were taken in three locations and two seasons: Gullmarsfjord in western Sweden

Table 1. Swimming behavior of *Microsetella norvegica* and *Amonardia normanni*, described as swim duration, τ (s), pause duration, p (s), and swimming velocity, ν (cm s^{-1}) (mean ± SE), as well as equivalent diffusion coefficient, D (cm^2 s^{-1}). The potential search volume rate for 2-mm–radius spheres, β (ml d^{-1}), is computed from swimming behavior characteristics. FWS, filtered seawater; Tw, *Thalassiosira weissflogii*. n = 96–104 for *M. norvegica*, 64–87 for *A. normanni*.

	M. norvegica		*A. normanni*	
	FSW	Tw	FSW	Tw
Swim duration, τ (s)	4.8±0.3	4.1±0.3	4.5±1.0	4.3±0.9
Pause duration, p (s)	3.6±0.9	4.7±0.5	81±23	35±11
Swimming velocity, ν (cm s^{-1})	0.06±0.004	0.06±0.004	0.1±0.01	0.1±0.02
Diffusion, D (cm^2 s^{-1})	5.5×10^{-3}	3.0×10^{-3}	1.3×10^{-3}	2.4×10^{-3}
Search volume rate, β (ml d^{-1})	1,199	649	278	521

(58°16.00′N, 11°28.34′E; depth ca. 60 m) in May 2003 and Sta. 5 (56°02.93′N, 4°01.71′E; depth ca. 60 m) and Sta. 8 (55°49.47N, 4°13.70′E; depth ca. 40 m) in the central North Sea in August 2003. Samples were taken at 5–10-m intervals, using a 30-liter water sample filtered onto a 50-μm net, and were preserved in 4% acid Lugol's solution. CTD and Chl *a* or fluorescence samples were taken simultaneously. The abundance (nauplii, copepodites, and adults separately) and number of eggs per female of *M. norvegica*, as well as the total abundance of other (unidentified) harpacticoids in the samples, were determined. The egg production of *M. norvegica* was determined using the egg ratio method, assuming development times of eggs according to Uye et al. (2002).

Statistical analysis—The results were tested for significant differences by using a two-way analysis of variance (grazing experiments) or by using a Mann–Whitney sum rank test (swimming behavior).

Results

Swimming behavior—M. norvegica and *A. normanni* had similar swimming patterns, with swim events of 4–5 s in average duration interrupted by longer or shorter pauses (3–80 s), during which the animals were motionless (Table 1). The most striking difference between the species was the much longer pauses in *A. normanni* than in *M. norvegica*. Swimming velocities during swim events corresponded to about one body length s^{-1} in both species. In the absence of food *M. norvegica* had longer swim events ($p < 0.05$) and shorter pauses ($p < 0.05$) than in the presence of *T. weissflogii*. In contrast, swim duration in *A. normanni* was unaffected by food condition, although the average pause duration was higher in animals incubated without food than in animals incubated with food ($p < 0.05$). Search volume rates estimated from swimming patterns were substantial in both species (280 vs. 1,200 ml d^{-1} for 2-mm–radius particles) but lower in *A. normanni* than in *M. norvegica*, both in the absence (280 vs. 1,200 ml d^{-1}) and presence (520 vs. 650 ml d^{-1}) of food (Table 1).

Colonization of agar spheres—The abundance of *A. normanni* on agar spheres containing food increased during the initial 10–50 h and then saturated around one to three individuals $sphere^{-1}$ (Fig. 1A). The final abundance appeared independent of the ambient concentration of copepods. Very few copepods were observed on agar spheres without food (Fig. 1B).

The attachment probability × search volume rate ($p\beta$), computed by fitting Eq. 4 to the colonization data, ranged from 8 to 200 ml d^{-1} in experiments in which spheres contained food (Table 2). This was lower than the search volume rates computed based on the swimming behavior (Table 1). The attachment probability computed as the ratio of these two estimates varied inversely with ambient concentration of copepods, from 0.02 to 0.5 (Table 2). Detachment rate and residence time varied from 0.02 to 0.3 h^{-1} and from 3 to 50 h, respectively (Table 2). For agar spheres that did not contain any food, the fitted equation (Eq. 4) was not significant (Fig. 1B), and the search volume, attachment probability, detachment rate, and residence time could thus not be computed.

Surface versus suspension grazing—When feeding on a surface, both harpacticoid species obtained relatively high weight-specific ingestion rates corresponding to near 100% of the body weight already at a relatively low food concentration of 0.5 μg C cm^{-2} (vs. average surface concentrations of 3 μg C cm^{-2} in natural aggregates; *see Materials and methods*), whereas when feeding on suspended food, similar high rates were only obtained at ecologically irrelevant (high) food concentrations of close to 1,000 μg C L^{-1} (Fig. 2). The two species had similar weight-specific ingestion rates on surfaces (Fig. 2A), whereas *M. norvegica* appeared to be significantly better than *A. normanni* in terms of feeding from suspension ($p < 0.05$; Fig. 2B). The weight-specific pellet production of *A. normanni* reflected ingestion, with higher rates on surface and lower rates in suspension. The weight-specific pellet production of *M. norvegica* was unrealistically low in both treatments, indicating that the small pellets disintegrate when sampled.

Grazing on aggregates—With the exception of experiment 1, the weight-specific pellet production of *A. normanni* feeding on the surface of agar spheres containing food or on aggregates made from heat-killed *T. weissflogii* was close to maximum (cf. Fig. 2A), corresponding to a weight-specific ingestion rate of 0.2–1 μg C (μg C)$^{-1}$ d^{-1} (Fig. 3). Almost no pellets were produced on spheres that did not contain

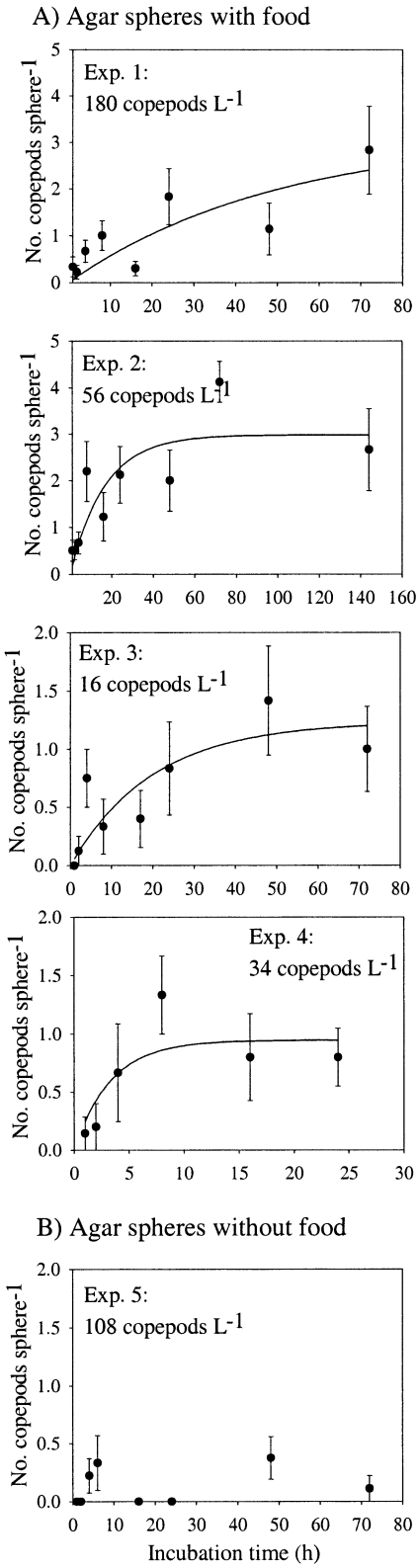

Fig. 1. Number of *Amonardia normanni* on agar spheres as a function of incubation time (mean ± standard error [SE]). (A) Agar spheres containing food, (B) agar spheres without food. The fitted equation is $N_t = (p\beta/\delta)[1 - \exp(-\delta t)]$ (*see Materials and methods*); for estimated parameters, see Table 2. The total concentration of *A. normanni* in experiments (ind. L^{-1}) is indicated in the figure. Note different scales of the axes.

food. Thus, *A. normanni* appeared to be able to find the suspended agar spheres and *T. weissflogii* aggregates and to feed significantly on the attached microbial communities.

Short-term ingestion rates—Short-term weight-specific surface ingestion rate of *A. normanni* females measured during the first hour following starvation was ca. 10 times higher [maximum, 0.4 ± 0.1 μg C (μg C)$^{-1}$ h^{-1}] than the average ingestion rate in 24-h incubations at similar food concentration (Fig. 4). After the first hour, the ingestion rate declined to the level corresponding to the 24-h average.

Similarly, 24-h starved nauplii of *A. normanni* were able to feed very efficiently in short-term incubations. Nauplii grazing removed >70% of the pellet surface area in less than 2 h (Fig. 5), corresponding to a consumption rate of ca 0.01 μg C (ind.)$^{-1}$ h^{-1} or a specific ingestion rate of ca. 1 h^{-1}.

Abundance and vertical distribution—M. norvegica occurred at all sampling locations with concentrations of copepodites and adults of up to 3 L^{-1} and nauplii up to 5 L^{-1} (Fig. 6). At the North Sea stations, this made *M. norvegica* the most abundant copepod species, the concentrations of other copepods being generally one order of magnitude lower (Jónasdóttir, Danish Institute for Fisheries Research unpubl. data). All developmental stages showed peaks in abundances in or below the pycnocline/Chl *a* maximum. Diel vertical migration was observed only in Gullmarsfjord, where all developmental stages occurred more deeply during day than during night. Other harpacticoids were occasionally observed near the bottom in low numbers. Twenty-five to thirty percent of the females of *M. norvegica* carried eggs, with average brood sizes of about nine eggs per brood (8.7–9.9) at all stations. The estimated egg production rate ranged between 0.4 eggs ind.$^{-1}$ d^{-1} in Gullmarsfjord to 1.0–1.3 eggs ind.$^{-1}$ d^{-1} in the North Sea.

Discussion

We wanted to address two questions: (1) can pelagic harpacticoids, mainly *M. norvegica*, take advantage of aggregates in the field?, and (2) do pelagic harpacticoids contribute significantly to aggregate degradation? The answer to the first question depends on the abundance of aggregates in the ocean, and the answer to the second question depends on the abundance of pelagic harpacticoids. Answers to both questions depend on the ability of pelagic harpacticoids to find aggregates and on the copepods' residence time and feeding once on an aggregate. These questions are discussed below.

Finding an aggregate—The observed swimming patterns indicate that the two species examined here may daily search 0.5–1.2 liters of water for 2-mm–radius aggregates. The actually observed particle colonization rates for one of the species is consistent with this prediction if one assumes an attachment probability of <1 in our experiments. There is proportionality between search volume and particle size (Eq. 2), and larger volumes of water can thus be searched for larger particles, and vice versa. These considerations assume purely random motility of the copepods and are therefore

Table 2. Copepod concentration, C (ind. L^{-1}); attachment probability × search volume, $p\beta$ (ml d^{-1}); attachment probability, p; detachment rate, δ (h^{-1}); and residence time, δ^{-1} (h), of *Amonardia normanni* on agar spheres in different colonization experiments (mean ± SE; *see* Fig. 2). Attachment probability was computed assuming β = 400 ml d^{-1} (average β in the presence and absence of food; Table 1).

Exp. No.	C (copepods L^{-1})	$p\beta$ (ml d^{-1})	p	Detachment rate, δ (h^{-1})	Residence time, δ^{-1} (h)
1	180	8±5	0.02	0.02±0.02	51
2	56	77±32	0.2	0.06±0.03	17
3	16	93±42	0.2	0.05±0.03	20
4	34	201±112	0.5	0.3±0.2	3
Mean		95±80	0.2±0.2	0.01±0.01	23±20

conservative if harpacticoids use chemical cues in locating the aggregates. The use of chemical cues in search of target particles has been demonstrated in copepods finding mates (e.g., Tsuda and Miller 1998), as well as in marine snow particles (Kiørboe 2001), and it may considerably increase the search volume rate (Kiørboe and Thygesen 2001; Jackson and Kiørboe 2004). The difference between the present search volume rate calculated based on the random motility only (ca. 1 L d^{-1} for 2-mm aggregate) and previous calculations based on the observed abundance of invertebrates on aggregates (6 L d^{-1} for 1-mm aggregate; Kiørboe 2000) may reflect the importance of chemical cues in locating the marine snow particles.

Residence time—Once on an aggregate, the copepod may start to feed on component particles for as long as they stay. The computed residence times of *A. normanni* estimated here were much higher than those observed previously for other aggregate colonizing zooplankton, on the scale of hours (3–50 h; Table 2) rather than minutes (Alldredge 1972; Shanks and Walters 1997). Meiobenthic harpacticoids, such as *A. normanni*, may be more hesitant to leave an aggregate than are truly pelagic species: for a meiobenthic harpacticoid with a relatively low search volume (cf. Table 1) and high energy consumption while in the water column (Thistle et al. 1995), it may be more advantageous to stay on the aggregate until it has been consumed. In contrast, a pelagic species with a higher chance of finding a new aggregate before the gut is empty may rather pay multiple short visits to aggregates to reduce the elevated predation risk experienced when attached to an aggregate (*see* Kiørboe and Thygesen 2001).

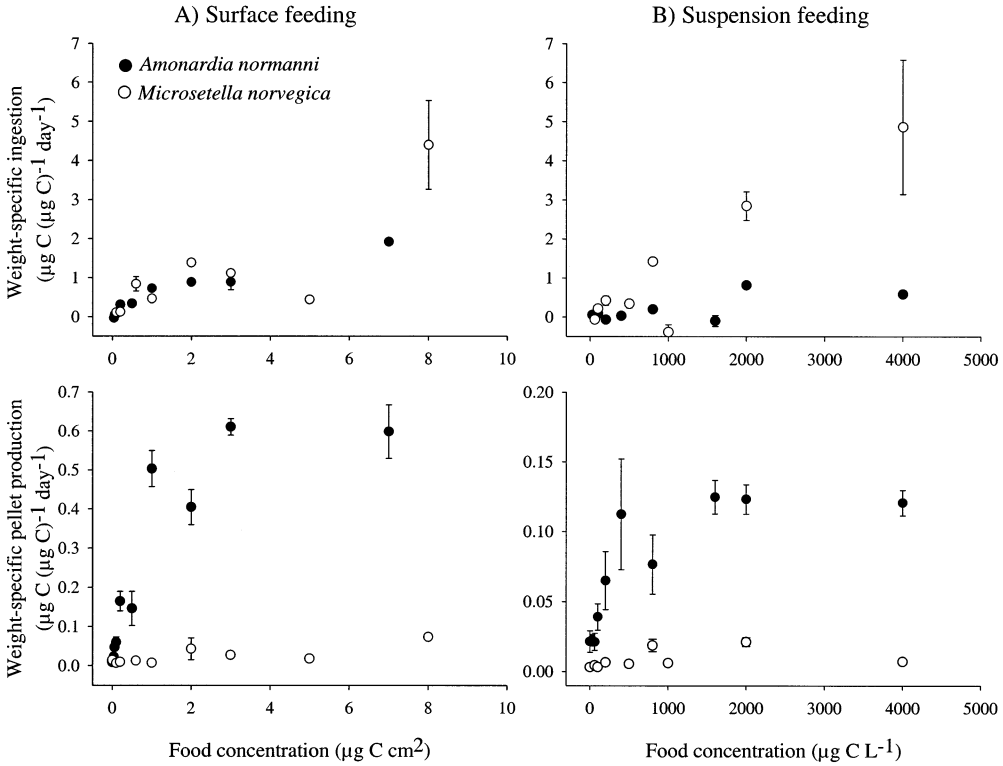

Fig. 2. Functional response of weight-specific ingestion [μg C (μg C)$^{-1}$ d^{-1}] and fecal pellet production [μg C (μg C)$^{-1}$ d^{-1}] in *Microsetella norvegica* and *Amonardia normanni* feeding on *Thalassiosira weissflogii* (A) on a surface or (B) in suspension (mean ± standard error [SE]). Note different scales of the axes.

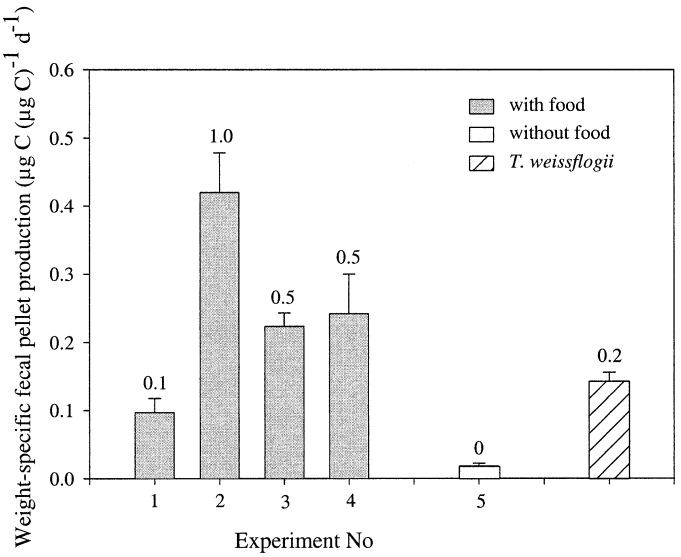

Fig. 3. Weight-specific fecal pellet production [μg C (μg C)$^{-1}$ d^{-1}] of *Amonardia normanni* on agar spheres with and without food and on *Thalassiosira weissflogii* aggregates (mean ± standard error [SE]). The weight-specific ingestion [μg C (μg C)$^{-1}$ d^{-1}] corresponding to pellet production (*see Materials and methods*) is indicated in the figure. The number of experiment refers to corresponding colonization experiments (Fig. 1; Table 2).

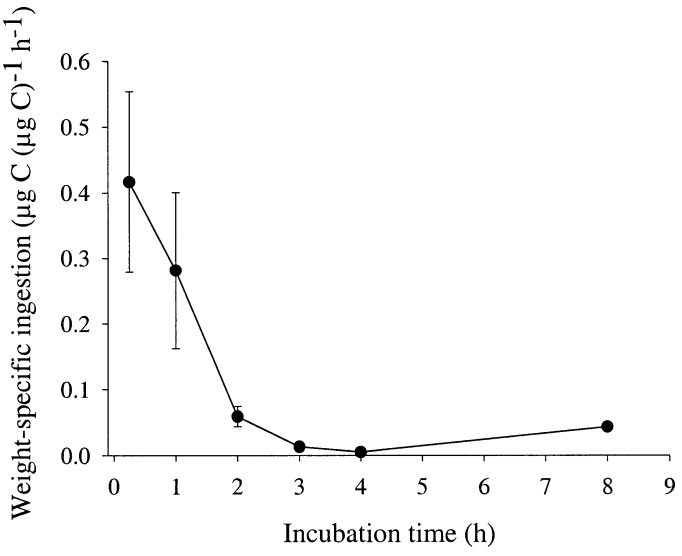

Fig. 4. Short-term weight-specific ingestion rate of *Amonardia normanni* [μg C (μg C)$^{-1}$ h^{-1}] feeding on *Thalassiosira weissflogii* (at a concentration of 2 μg C cm^{-2}), as a function of incubation time (mean ± standard error [SE]).

Unfortunately, we do not have estimates of the residence time for *M. norvegica*, but we may obtain an indirect rough assessment by comparing field observations of abundances of harpacticoid copepods attached to aggregates with abundances predicted from the present estimates of *M. norvegica* motility and search volume rates. Kiørboe (2000) compiled field data on abundances of harpacticoid copepods (mainly *M. norvegica*) attached to aggregates. The average normalized abundance of harpacticoids (i.e., the number of attached individuals divided by the ambient concentration of copepods) on a 2-mm–radius aggregate predicted from the relation found by Kiørboe (2000) is $\sim 10^2$ ml aggregate^{-1}. The normalized abundance can also be estimated as $p\delta^{-1}\beta$ (attachment volume × residence time × search volume) at steady state (i.e., after >20 h colonization). Putting $p\delta^{-1}\beta = 10^2$ ml aggregate^{-1}, assuming an attachment probability (p) equal to 1 and estimating β (search volume rate) from Eq. 2 (with D = 5×10^{-3} cm^2 s^{-1}, Table 1), yields an average residence time (δ^{-1}) of 2.2 h. We will use this value in subsequent considerations.

Feeding on aggregates—M. norvegica and *A. normanni* appeared to feed inefficiently on suspended food (Fig. 2B). Feeding on surfaces, on the other hand, appears to be efficient at concentrations typical for marine snow aggregates (Fig. 2A): the surface chlorophyll and carbon concentrations that supported maximum ingestion rates in our experiments (Figs. 2A, 3) correspond largely to average surface concentrations in natural marine snow aggregates (9 ng Chl cm^{-2} and 3 μg C cm^{-2}; *see Materials and methods*). The measured surface ingestion rates seemed to agree with previous observations: the weight-specific pellet production of *A. normanni* on agar spheres and on *T. weissflogii* aggregates was similar to the pellet production of *Calanus pacificus* feeding on diverse types of marine snow (Dilling et al. 1998).

The feeding rates of adult harpacticoids in our study, averaged over 24 h, are similar to rates measured in calanoid and other copepods (e.g., Paffenhöfer and Harris 1976). However, our observations indicate that the extremely intermittent availability of food on surfaces in the ocean can be utilized more efficiently than the average feeding rates suggest. Thus, *A. normanni* nauplii positioned on a fecal pellet were ingesting carbon at a specific rate of 1 h^{-1} for a short period of time (~1 h), more than 20 times the long-term average rates measured in adults. Similarly, in short-term incubations (15 min–1 h), surface-feeding *A. normanni* fe-

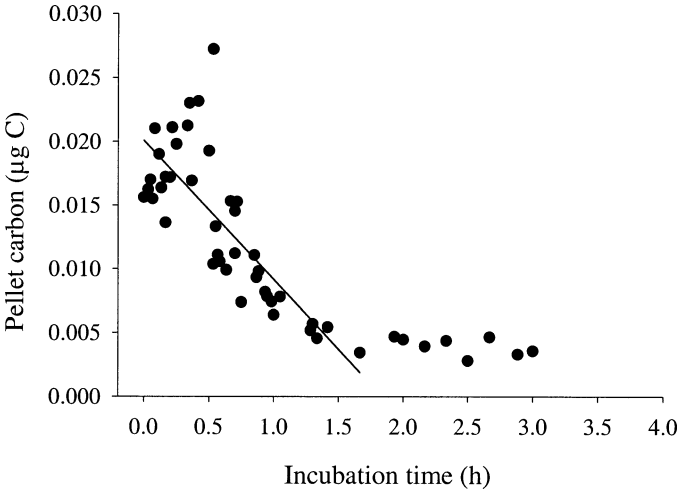

Fig. 5. Disappearance of pellet carbon (μg) due to grazing of a recently hatched *Amonardia normanni* nauplii, as a function of incubation time (h). The fitted line is $y = 0.02 - 0.011x$ ($n = 40$, $r^2 = 0.77$, $p < 0.001$).

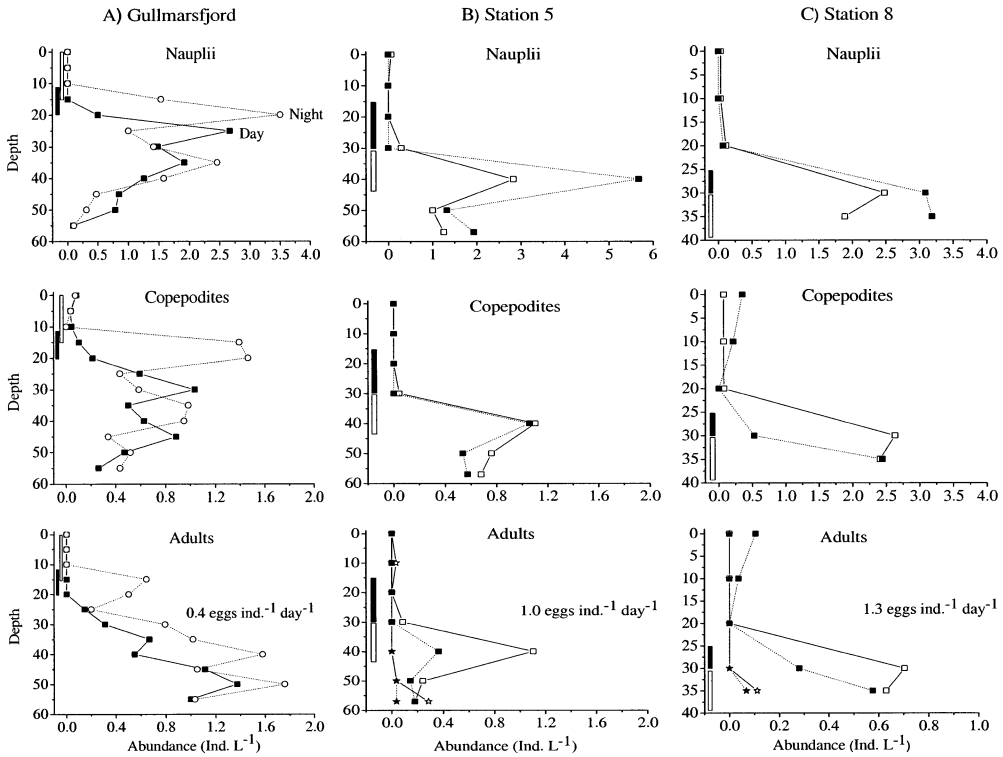

Fig. 6. Day- and nighttime vertical distribution of nauplii, copepodites, and adults of *Microsetella norvegica* (squares) and unidentified harpacticoids (stars) in (A) Gullmarsfjord in western Sweden in May and at (B) Sta. 5 and (C) Sta. 8 in the central North Sea in August (ind. L^{-1}). The solid lines and open symbols indicate day sampling, the filled symbols and dotted lines night sampling. The black bars indicate the position of the thermocline (9–6°C in Gullmarsfjord, 19–8°C in central North Sea) and the white bars the position of the Chl *a* maximum (2–4 μg L^{-1}). Average egg production of *M. norvegica* (eggs ind^{-1} d^{-1}) is indicated in the figure. Note different scales of the axes.

males were ingesting carbon at a specific rate of $\sim$0.4 h^{-1}, approximately 10 times the long-term average. A similar short-term (<6-h) hunger response to starvation has been shown for calanoid copepods (Hassett and Landry 1988). A rapid hunger-induced feeding allows harpacticoids to attain their daily maximum ration during few short visits to aggregates.

Significance of aggregates for harpacticoid nutrition—In addition to depending on the aggregate size-specific search volume (Eq. 2), the rate at which a copepod encounters aggregates depends on the size distribution and concentration of aggregates. Complete size spectra of aggregates are rarely reported in the literature, whereas volume concentrations of aggregates are. The size spectrum can, however, be estimated from the volume concentration if one assumes a power function to represent the aggregate size spectrum and assumes the exponent of the size spectrum to be three (Jackson et al. 1997; Kiørboe and Jackson 2001). Size spectra of aggregates can then be combined with the size-specific search volume rates to calculate for the total number of encounters with aggregates within a particular size range (*see* equations in Kiørboe and Jackson 2001; Kiørboe et al. 2002).

Riebesell (1991) and Tiselius and Kuylenstierna (1996) reported volume concentrations of aggregates in the North Sea and in the Gullmarsfjord—our two sampling locations—during and subsequent to phytoplankton blooms. Considering only aggregates in the size range of 0.05–1 cm (radius), peak concentrations in both areas were on the order of 100 ppm, whereas post-bloom concentrations were 1–10 ppm. Using the equations of Kiørboe and Jackson (2001) and Kiørboe et al. (2002), these aggregate concentrations imply that *Microsetella*-type copepods would encounter three aggregates per day during bloom conditions and 0.03–0.3 aggregates per day during postbloom conditions. Aggregate concentrations reported from other surface waters (reviewed by Alldredge and Silver [1988]) are variable, 10-7,000 ppm, but appear substantially higher than those reported above (geometric mean of 300 ppm). This geometric mean concentration of aggregates implies that *M. norvegica* would encounter nine aggregates per day. Therefore, during bloom conditions and in areas with high aggregate concentrations, *M. norvegica* may visit sufficient number of aggregates to fulfill their daily needs (e.g., three encountered aggregates in the size range of 0.05–1 cm would represent a potential food source of 2.5–225 μg C (*see* Alldredge 1998), which is sufficient to guarantee a maximum feeding rate of *M. norvegica* (*see* Fig. 2A).

In contrast, outside of bloom conditions, the significance of aggregates in *M. norvegica* nutrition seems to be minor. However, our laboratory experiments indicate that in the absence of aggregates, *M. norvegica* will be starving. The generally low egg production measured for *M. norvegica* in the field ($\leq$1 eggs $ind.^{-1}$ d^{-1}; Nielsen and Andersen 2002, this

study) could be connected to the low feeding rates in the absence of aggregates and indicate food limitation outside areas and seasons of high aggregate abundance. However, verifying this would demand a simultaneous seasonal sampling of both *M. norvegica* egg production and aggregate abundance, a sampling which, to our knowledge, has never been performed.

Harpacticoid impact on aggregate degradation—When considering the potential impact of *M. norvegica* and other pelagic harpacticoid copepods on aggregate degradation, the encounter rate of interest is the rate at which aggregates are encountered by copepods. This, of course, depends on the abundance of copepods. *M. norvegica* is very common in temperate waters, with typical abundances of >1–5 individuals (adults + copepodids) L^{-1} or 10^4–10^5 individuals m^{-2}, at times having densities of up to >100 L^{-1} or $>10^6$ m^{-2} (Dugas and Koslow 1984; Daro 1988; Uye et al. 2002). Combining these densities with the average search volume rates, residence times, and ingestion rates estimated here, and with literature values on aggregate sinking rates (Alldredge and Gotschalk 1989), we can estimate the potential degradation rates of aggregates due to harpacticoid feeding.

The number of copepods that a sinking aggregate of radius a will encounter (E) during its descent through a water column of depth h is

$$E(a) = \beta(a)C\frac{h}{u(a)} = \frac{\beta(a)A_{\mathrm{Cop}}}{u(a)} \tag{5}$$

where C is the average ambient concentration of copepods over depth h, A_{Cop} is the abundance of copepods integrated over this depth interval (numbers per unit surface area), and $u(a)$ is the size-dependent aggregate sinking velocity. The fractional degradation of an aggregate sinking through the water column (κ) is then

$$\kappa(a) = \frac{E(a)\delta^{-1}\cdot i}{POC(a)} = \frac{\beta(a)A_{\mathrm{Cop}}\cdot\delta^{-1}\cdot i}{POC(a)\cdot u(a)} \tag{6}$$

where δ^{-1} is the average residence time of a copepod on an aggregate and i the average carbon-ingestion rate of a copepod. Aggregate carbon is calculated based on Alldredge (1998) and Kiørboe (2003) (*see Materials and methods*). With parameters measured in this study or taken from the literature, this fraction is estimated to be significant during peak abundances of *Microsetella* (10^6 m^{-2}), particularly for aggregates of <0.5 cm radius, of some importance for the smallest aggregates at intermediate copepod densities (10^5 m^{-2}), and insignificant at low copepod densities (10^4 m^{-2}) (Fig. 7). Here we have ignored that some of the fecal pellets produced by the harpacticoids, which may constitute up to 40% of the ingested material (data not shown), may be returned to the aggregate. One the other hand, aggregates may sink substantially slower than assumed here (e.g., Pilskaln et al. 1998) and may slow down during passage of density discontinuities (MacIntyre et al. 1995), which may increase the fractional degradation rate due to longer residence times. Also, these estimates are based on averaged 24-h feeding rates (whereas short-term feeding rates may be up to 10 times higher; Figs. 4, 5) and on search volumes calculated based on random motility only (whereas using chemical trails to encounter aggregates may significantly increase the search volumes; Kiørboe and Thygesen 2001), and are therefore conservative. However, these calculations clearly show that, at moderate to high harpacticoid densities, the potential encounter and feeding rates of harpacticoids are sufficiently high to significantly influence aggregate degradation rates.

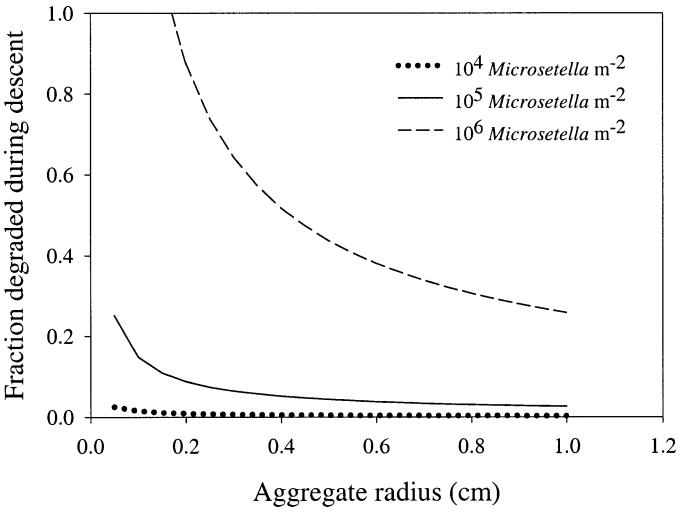

Fig. 7. The fractional degradation of an aggregate sinking through the water column as a function of aggregate radius and harpacticoid abundance (Eq. 6). The parameters used: $D = 5 \times 10^{-3}$ cm^2 s^{-1} for computation of β, $\delta^{-1} = 2.2$ h, $i = 0.4$ μg C $ind.^{-1}$ d^{-1}, POC based on Alldredge (1998) and Kiørboe (2003) (*see Materials and methods*), $u(a)$(cm s^{-1}) = 0.13 a(cm)$^{0.26}$ (Alldredge and Gotschalk 1988).

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