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Copepods use chemical trails to find sinking marine snow aggregates

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Running head: Copepods and marine snow chemical trails

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Abstract

Copepods are major consumers of sinking marine particles and hence reduce the efficiency of the biological carbon pump. Their high abundance on marine snow suggests that they can detect sinking particles remotely. By means of laboratory observations we show that the copepod *Temora longicornis* can detect chemical trails originating from sinking marine snow particles (appendicularian houses). The chemical cue was detected by copepods from a distance of > 25 particle radii, with the probability of detection decreasing with distance. The behavior of *T. longicornis* following the trail resembled the behavior of males tracking pheromone trails, although with a lower tracking velocity. Upon finding a house, the copepod would attach for a short period (10-30 s) and feed intensively. Due to short residence times, daily feeding rates were moderate. Our results demonstrate that even *T. longicornis*, a species usually considered a micro-particle feeder, is able to detect and feed on marine snow aggregates. If similar behaviors are displayed by the more dedicated aggregate-feeding copepods, a topic that remains unexplored, the effect of copepods on vertical flux attenuation may be significant.

INTRODUCTION

Sinking particles are the main vehicles for the vertical transport of biogenic carbon from the sea surface to the ocean interior and the seafloor (Fowler and Knauer 1986). The downward flux of particles, however, attenuates near exponentially with depth due to the degradation of the particulate material as it sinks (Martin et al. 1987). Bacteria and zooplankton are believed to be approximately equally important for the remineralization of sinking particles (Steinberg et al. 2008). Bacteria rapidly colonize sinking particles, facilitated by their chemotactic behavior (Stocker et al. 2008), and account for a surprisingly constant carbon-specific degradation rate of ca. 0.1 d^{-1} (Ploug and Grossart 2000). This quantitative understanding of the role of bacteria can readily be incorporated in models of flux attenuation (Buesseler and Boyd 2009). The contribution of zooplankton to flux attenuation is much more variable and the underlying processes are poorly known (Steinberg et al. 2008). The lack of knowledge of zooplankton processes has been cited as one of the main factors hampering the advances in modeling biogeochemical fluxes (Boyd and Trull 2007).

Zooplankton may occur in high abundances on marine snow aggregates in the upper ocean (Steinberg et al. 1994; Kiørboe 2000), and their grazing on aggregate constituents may be substantial (Koski et al. 2005). Likewise, large sinking particles may be a significant food source for many zooplankters (Dagg 1993). It is unclear, however, how the zooplankters find these particles. Random encounter is an insufficient process to explain observed abundance of zooplankton on aggregates and remote detection has been invoked to account for the high densities of zooplankton on snow particles (Kiørboe 2000; Kiørboe and Thygesen 2001; Jackson and Kiørboe 2004). Bacterial activity on the surface of sinking particles may cause a substantial leakage of dissolved organic material (Smith et al. 1992), and sinking particles therefore leave an organic solute trail in their wake (Kiørboe 2001). It has been hypothesized

that cruising zooplankters may encounter such trails, which, in turn, may lead the zooplankter to large, nutritious particles (Kiørboe and Thygesen 2001). Such behavior has been demonstrated in shrimps (*Acetes sibogae*) that follow scent trails left by sinking food particles (Hamner and Hamner 1977). Copepods are also known to be able to follow chemical trails. This has been demonstrated for copepod males in particular that follow pheromone trails left by receptive females (Doall et al. 1998), but copepodites and females may also be able to follow artificial trails of amino acids (Kiørboe 2001) or dextrane (Yen et al. 2004).

We here test the hypothesis that copepods may find and follow chemical trails left by sinking marine snow particles. We use discarded appendicularian houses as a source of particles, as it has been demonstrated that the sinking house leaves a trail in its wake (visualized in Lombard and Kiørboe 2010, their fig. 3). Discarded houses are an abundant type of marine snow (Alldredge and Gotschalk 1990) and they may contribute significantly to carbon export from the surface ocean (Robison et al. 2005). Appendicularian houses are loaded with, for instance, algae, bacteria and ciliates that are concentrated on houses up to 2-4 orders of magnitude relative to the ambient water (Hansen et al 1996; Lombard et al 2010). The houses are thus concentrated packages of food, likely to be of a high nutritional value (similar to its attached particles). Here, we demonstrate that even a typical suspension feeding copepod (*Temora longicornis*) can feed on sinking marine snow, and that it finds the particles by following the scent trail that marine snow leave in their wake.

METHODS

Origin and culture of animals

Experiments were conducted using both cultivated and freshly collected copepods and appendicularians ('culture' and 'wild' conditions). Cultured appendicularians (*Oikopleura dioica*) and copepods (*Temora longicornis*), originally collected in the Øresund (56°03'N;

12°39'E), western Baltic Sea, were grown in the laboratory (18°C; salinity 35) for > 10 generations following standard protocols (Lombard and Kiørboe 2010). The appendicularians were fed a mixture of diatoms (*Thalassosira pseudonana*) and phytoflagellates (*Isochrysis galbana* and *Rhodomonas salina*). Under these conditions *O. dioica* produces 7-8 houses d^{-1} (Fenaux 1985). *Temora longicornis* was fed a mixture of *R. salina*, *Thalassiosira weissflogii* and dinoflagellates (*Prorocentrum minimum* and *Heterocapsa* sp.) in excess, which allowed for relatively high ingestion and egg production rates.

Wild copepods and appendicularians were collected from a pier in the Øresund (55°45' N; 12°35.5' E) 24 h prior to the experiment. Animals were collected with a bucket, which ensured their good condition. Wild animals were only used for behavioral observations. Salinity at the time of collection was 17.

All experiments were conducted at 18°C.

Behavioral observations

We recorded the behavior of *Temora longicornis* in the presence of sinking houses with a black and white Charge-Coupled Device camera (Watex, WAT-535EX, 25 Hz frame rate) equipped with a 35 mm lens to yield a field of view of ca. 5 x 4 cm. The experimental arena consisted of a 500 mL transparent plexiglas chamber (dimensions 5 x 5 x 20 cm). The chamber was placed in a dark room and illuminated with collimated infrared light from a light-emitting diode that was shined through the chamber towards the camera. This way shadow images of copepods and sinking houses were obtained. Both the camera and the light were mounted on a motorized support which allowed moving the whole system in two dimensions. Individual particles could thus be followed as they were sinking through the water column without modifying the settings (size calibration) of the camera.

For behavioral observations we used either newly discarded houses (5-10 min), or houses that had aged for 1-2 h. Fresh and aged houses differ in their properties, because houses deflate rapidly once discarded. Thus, fresh houses leak internal water and food particles (Lombard and Kiørboe 2010). Prior to an experiment, the chamber was filled with filtered water from the appendicularian culture (or freshly collected sea water for wild conditions). 100-200 copepods were then added and allowed 24 h to acclimate. The high density of copepods was chosen to increase the number of encounter events during the video recordings and was assumed not to affect the swimming behavior (Dur et al. 2011).

Observations were made by gently introducing appendicularian houses (one at a time, up to 15 times) in the surface of the chamber, and then following the sinking house and nearby copepods with the camera until the house reached the bottom of the chamber (~5 min). Video sequences were later analyzed using a MatLab script that follows frame by frame the position of targeted objects. The following parameters were retrieved: sizes, sinking trajectories, and speeds of appendicularian houses; swimming trajectories and speeds of copepods that reacted to a house (before and after encountering the chemical plume of the house); and copepod residence time on the houses. A total of 232 copepod reactions were recorded and analyzed.

Feeding experiment

We estimated the feeding of copepods on discarded appendicularian houses by an indirect approach, by quantifying the number of fecal pellets that copepods produce when offered houses. Although dependent on food type, pellet production can be considered to be linearly related to feeding rate (Besiktepe and Dam 2002). Ten adult *T. longicornis* were incubated for 48 h in 600 mL screw-cap bottles in 0.2-μm filtered sea water, containing a variable number of aged 2-3 mm diameter houses (0; 5; 10; 20; 30; 40; 50 houses per bottle). The highest tested densities of houses are in the upper end of that observed in nature, representing bloom

conditions, where densities of appendicularians (each producing 13-26 houses d^{-1};Sato et al. 2003) may exceed 50, 000 m^{-3} (Uye and Ishino 1995). All incubations were done in triplicates. The bottles were mounted on a slowly rotating wheel (1 round per minute) and incubated in darkness. Water and houses were changed after 24 h and the pellets were counted at 24 and 48 h. For each counting, the content of the bottles was gently filtered onto a submerged 10 μm filter and the copepods were immediately transferred to the new water.

Pellet production was used to qualitatively verify feeding on houses. Pellet production was also converted to a crude quantitative estimate of feeding rate, by assuming a pellet volume of 3.75 10^5 μm^3 (Dutz et al. 2008), a carbon content of 0.052 pg μm^{-3} (González and Smetacek 1994), and a carbon assimilation efficiency of 0.75 (Besiktepe and Dam 20020). The obtained feeding rates should be taken as conservative, since pellets volume and in particular carbon content are strongly dependent on copepod diet and could be substantially higher than the values used here (*e.g.* Ploug et al. 2008). Carbon content of female copepods from our culture was 7.5 μg C individual (ind.)$^{-1}$ (Dutz et al. 2008).

RESULTS

Behavioral observations

We observed two different reactions of copepods to sinking houses (*see* also video A1 in the Web Appendix www.aslo.org/lo/toc/vol_xx/issue_x/xxxxa.xxx: 1) Direct encounter of a sinking house by a cruising copepod and subsequent attachment of the copepod to the house (as shown in video A1). This reaction was observed 86 times. 2) Remote detection and response to the house: When passing directly above the house the copepod abruptly changes its swimming direction and accelerates downward towards the house, following the presumed scent trail (as shown in video A1 and A2). The position where this happens is considered the detection point. While following the trail, the copepod doubles its swimming speed to 6-8 mm

157 s^{-1} (Table 1, Fig. 1) and swims in a zigzag course towards the particle. Of the 146 cases of
158 remote detection, the copepods were successful in actually finding and attaching to the
159 particle in only half of these (72).

160 The positions of detection points (Fig. 1) describe the extension of the chemical trail within
161 which the concentration of attractant exceeds the threshold for detection and response. The
162 length of the trail is about 35 mm, corresponding to more than 25 particle radii, its maximum
163 width about 4 mm, and it is tapered toward its distal part. If the copepod detects the chemical
164 signal with sensors at the tip of the antennules, then the 'real' width of the plume is 2 x
165 antennules length (~ 2 x 0.6 mm) less that suggested by the detection points, i.e., 2-3 mm. The
166 width of the plume can alternatively be estimated from the amplitude of the zigzag behavior
167 (~0.7 mm; Table 1) plus 2 x antennules length; again ca. 2 mm.

168 The probability of detection declines hyperbolically with the distance to the particle (Fig.
169 2). There was no difference in average detection distance between fresh and aged houses,
170 whereas there was a difference between the reactions in wild vs. culture conditions. Houses
171 from wild appendicularians, were detected at a shorter distance by wild copepods than
172 cultured copepods detected cultured houses (Table 1).

173 Copepods that managed to find a house attached to it and fed intensely from its surface as
174 evidenced by constant activity of the feeding appendages. Sometimes the copepod would grab
175 the house with its mandibles and apparently attempt to remove part of the house as evidenced
176 by vigorous kicking of the swimming legs (*see* the Web Appendix). The copepods resided on
177 the house for a relatively short (< 1 min) but intense period, which was more than twice as
178 long for wild than for cultured conditions (Table 1).

179

180 ***Grazing and fecal pellets production***

This feeding activity resulted in the production of fecal pellets, and the production of pellets increased with the concentration of houses. Fitting a Holling Type II response to the observations yields a saturated pellet production rate of 34 ±13 pellets ind.$^{-1}$ d^{-1} (Fig. 3). This rate was however not reached, even at the highest concentration of houses (83 L^{-1}). The maximum observed pellet production, ca. 15 pellets ind.$^{-1}$ d^{-1}, corresponds to an ingestion of ~0.45 μg C ind.$^{-1}$ d^{-1} (6% body weight d^{-1}). The saturated consumption rate of appendicularian houses would then be about 0.9 μg C ind.$^{-1}$ d^{-1} (12% body weight d^{-1}), a sufficiently high rate to support copepod metabolism, while not allowing for a high growth or reproduction rate (Hernandez-León and Ikeda 2005). Thus even in saturating concentration of houses those only partly fulfill this copepod needs.

DISCUSSION

Chemical or hydromechanical cues?

Our results demonstrate that the copepod *Temora longicornis* is able to remotely detect sinking appendicularian houses, to subsequently follow the sinking track to the particle, and eventually to grab the particle and feed on it. To our knowledge, our results constitute the first demonstration of such particle tracking behavior in a copepod using realistic particles produced both under laboratory and wild conditions. Similar observations have previously been reported for planktonic shrimps tracking sinking detritus (Hamner and Hamner 1977), while the general assumption of the ability of copepods to follow chemical particle trails has until present been mainly based on theoretical considerations (Jackson and Kiørboe 2004).

The detection distance to a sinking 0.25 cm radius house was up to 3.5 cm at a position that was left by the particle over 25 seconds earlier. This strongly suggests that the cue utilized by the copepod is chemical rather than fluid mechanical. All our observations correspond to Reynolds numbers (Re) between 1 to 6. Fluid disturbances at low Re dissipate rapidly due to

206 viscosity; thus, the viscous time scale (L^2/η, where L is the linear dimension of the disturbance
207 and η the kinematic viscosity of the water) for a fluid signal of a spatial extension similar to
208 the size of the sinking particles is ~6 s. The fluid disturbance also attenuates spatially, and the
209 signal generated by the sinking particle at a distance of 3.5 cm can be estimated assuming
210 Stokes flow for a translating sphere. Using the model developed by (Visser 2001), and
211 assuming that the fluid velocity signal has to be $\geq$ 100 μm s^{-1} to be detected (Kiørboe 2011),
212 the hydromechanical detection distance can be estimated as 0.4 cm; if a 10x smaller detection
213 signal is sufficient, this estimate increases to 1.2 cm.

214 The behavior of the tracking copepods is consistent with them following a chemical trail. It
215 resembles the behavior described for males tracking pheromone trails deposited by swimming
216 females, although tracking velocities observed here (< 10 mm s^{-1}; Fig. 1, Table 1) are
217 substantially lower than the swimming speed of female-tracking males of the same species
218 (15-40 mm s^{-1}; Doall et al. 1998) and thus cannot be confused. The constant zigzagging along
219 the invisible trail has been termed 'casting behavior' (Weissburg et al. 1998). It serves the
220 purpose of constantly checking the radial extension of the trail, and is a prerequisite for being
221 able to follow the trail. The tracking behavior of the copepods and the weakness of fluid
222 mechanical disturbances generated by the sinking particles lead us to conclude that the cue
223 used by the copepod to detect the sinking particle is chemical.

224 The spatial extension of the chemical plume, as evidenced by the distribution of detection
225 points, is only partly consistent with that predicted from a model that describes the flow and
226 concentration fields around a sinking sphere that leaks solutes (Kiørboe et al. 2001; *see* also
227 Fig. 1A). The predicted solute distribution depends mainly on the Péclet number (Pe = aU/D,
228 where a is the sphere radius, U the sinking velocity, and D the diffusivity of the leaking
229 substance). The slower the particle sinks, and the higher the diffusivity of the leaked
230 molecules, the broader the deposited trail. Assuming a diffusivity of $D = 10^{-5}$ cm^2 s^{-1}, which is

231 typical for small biological molecules, and the sinking velocities recorded for the discarded
232 houses (Table 1), we get a Péclet number of about 10^3, and a predicted solute distribution as
233 shown in Fig. 1A. Obviously, the observed plume is much broader than that predicted, even
234 when accounting for the length of the antennules of the copepods. The distribution rather
235 resembles a situation for a Péclet number of order 100 or less (Fig. 1A). We argue that this is
236 due to a much higher effective diffusivity of leaked substances in our experiments due to the
237 mixing effect of both the swimming copepods and of the unavoidable convection currents in
238 the experimental chamber. Observations and theory become consistent with one another if we
239 assume a 10-fold higher effective diffusivity due to our experimental setup.
240
241 ***Efficiency of particle detection***
242 From our observations, *T. longicornis* has almost twice the chance of remotely detecting a
243 sinking house rather than directly encountering it (146 vs. 86 observations). However, judged
244 from the observed ratio of direct collision-encounters to particle encounters facilitated by
245 remote detection of sinking particles (86 vs. 71), remote detection only has a rather modest
246 effect on the efficiency by which copepods can find sinking particles. However, we argue that
247 our experimental design leads to an underestimation of this efficiency due to the mixing
248 effects of the swimming copepods and small convection currents, but also that we can roughly
249 quantify the error and estimate the real efficiency from our observations.
250 We use the 'moving point source model' of Jackson and Kiørboe (2004) to evaluate our
251 results. According to this model, the length (L), maximum width (d; derived from Jackson and
252 Kiørboe 2004), and cross-sectional are (A_0) of the plume can be estimated as
253 $$L = \frac{Q}{4\pi DC^*} \quad (1)$$

$$d = 2.43\left(\frac{DL}{v}\right)^{0.5} \quad (2)$$

$$A_0 = \frac{0.24}{Dv^{0.5}}\left(\frac{Q}{\pi C*}\right)^{1.5} \quad (3)$$

where Q (mol s^{-1}) is the rate at which solutes leak from the particle, $C*$ (mol cm^{-3}) the threshold concentration for detection, and v (cm s^{-1}) the sinking velocity of the particle. Equation 2 allows us to estimate the effective diffusivity of the chemical substance from the observed length (3.5 cm) and width (0.2 cm) of the plume and sinking velocity of the particles (0.05-0.15 cm s^{-1}). The effective diffusivity thus estimated is about 1-3 10^{-4} cm^2 s^{-1}, one order of magnitude larger than the molecular diffusivity of small biological molecules, as also proposed above.

Kiørboe and Thygesen (2001) and Jackson and Kiørboe (2004) compiled empirical evidence to suggest that if the substance to which copepods respond is amino acids, then Q (mol s^{-1}) $\approx 10^{-12}a^{1.5}$ and $C* \approx 10^{-11}$ mol cm^{-3}, where a is the radius of the sinking particle (0.15 cm). If we accept these estimates and assume an effective diffusivity of 1-3 10^{-4} cm^2s^{-1} then the model predicts a plume length in our experiments of 1.67-5 cm, in the range of our observations (<3.5 cm). Thus, our experimental observations are internally consistent and moreover consistent with independent estimates of particle leakage rates and copepod chemical sensitivity.

The encounter cross section of the chemical plume can be estimated as

$$A = A_0 + 2SL \quad (4)$$

where S is the length of the antennules (0.6 mm). This may be compared to the encounter cross section of the sinking particle itself ($\pi(a+S)^2$) and used to estimate the enhancement in potential encounter rate due to chemical signals which are comparable to observed enhancement of encounter irrespectively to copepods or houses concentrations. Using the

numbers above and a diffusivity not affected by experimental mixing effect, the enhancement for 2.5 mm diameter sinking houses is about two orders of magnitude. This estimate does not take into account the decreasing detection probability with increasing distance to the particle (Fig. 2), and it does not consider the effect of turbulent mixing (Visser and Jackson 2004).

One may argue that the starved copepods used in our experiments were particularly responsive to food signals. As food in the ocean tends to be patchily distributed (Mitchell and Fuhrman 1989) and as starvation tolerance of neritic copepods such as *Temora longicornis* is limited (Koski and Klein Breteler 2003), an increased ability of starved copepods to detect food signals would be a relevant trait. However, our study was not designed to investigate the effect of starvation on behavior, but simply to demonstrate that chemical plumes behind sinking particles may significantly increase the possibility for zooplankters to find these nutritious particles.

Feeding on sinking particles

Jackson and Kiørboe (2004) explored the potential for zooplankters to find and feed on large sinking particles using the above model and parameter values consistent with those estimated here. While copepods are generally thought of as microphageous that mainly feed on microscopic phytoplankton and protozoans, the analysis of Jackson and Kiørboe (2004) suggested that large sinking particles may also be an important source of nutrition. The importance of sinking particles in the nutrition of zooplankton has also been suggested based on the metabolic demands of the zooplankton communities in the mesopelagic zone (Steinberg et al. 2008) and analysis of their gut fatty acid and pigment compositions (Wilson and Steinberg 2010).

The residence times of the copepods on the houses are short, consistent with earlier laboratory observations (Alldredge 1972). Reported residence times vary from minutes for

pelagic organisms (Shanks and Walters 1997) to hours for semi-benthic species (Koski et al. 2005). It has been suggested that the short residence times are the result of a trade-off between the good feeding conditions and the elevated predation risk when attached to an aggregate, and that a copepod should remain on the aggregate only long enough to fill its gut (Kiørboe and Thygesen 2001). From estimated house encounter rates (calculated from observed copepods swimming speed, and sizes of particles and chemical trail) and consumption for *T. longicornis*, one can estimate that each house encounter leads to the ingestion of 3-5 10^{-4} μg C, and an ingestion rate during attachment of 0.1-0.2 μg C h^{-1}. This is a very high instantaneous ingestion rate, but it would still take a copepod about 7-15 min to fill its gut (assumed to be the equivalent of one fecal pellet).

Our observations show that *T. longicornis* feed on discarded houses but even saturated feeding rates are only 10% of those reported for grazing on phytoplankton (Besiktepe and Dam 2002). The feeding rates (~4 x 10^{-4} μg C $encounter^{-1}$) extrapolated to natural concentrations of discarded appendicularian houses (e.g., max. 6 L^{-1} in the North Sea; Koski et al. 2007; encounter rate calculated with a normal case of effective diffusivity) would be low, around 0.5 μg C ind. d^{-1}. However, appendicularian houses are only one example of sinking particles, and copepods may also feed on other types of marine snow, such as diatom flocks or fecal pellets. Further, the feeding rates observed in the laboratory may underestimate those in the field. As suggested by the difference between cultured and wild copepods in our experiments, the wild copepods are more efficiently feeding on appendicularian houses. This may be due to the immediate history of the animals, e.g., hunger level or age, body size, or the different behaviors of the cultured and wild copepods (Tiselius et al. 1995).

T. longicornis is probably not a typical aggregate feeder and other zooplankters have morphologies and behaviors that make them particularly adapted to feed on marine snow aggregates. Copepods that are typically found on marine snow aggregates are harpacticoids,

such as *Microsetella norvegica*, and copepods of the genus *Oncaea* (Shanks and Walters 1997). These species are not able to feed efficiently on suspended food, but are dependent on aggregates for feeding (Koski et al. 2005), and behavioral observations suggest that they readily feed on appendicularian houses (Ohtsuka and Kubo 1991). *M. norvegica* and semi-benthic harpacticoids can have feeding rates ranging from 40% to 200% body weight^{-1} d^{-1} on appendicularian houses and settled diatoms (Koski et al. 2005; Koski et al. 2007), thus being considerably more efficient in aggregate feeding than *T. longicornis*.

Published estimates of the effect of copepods on the attenuation of sinking flux suggest potentially high degradation rates both in and below the euphotic zone, mainly depending on the abundance of potential grazers (Kiørboe 2000; Koski et al. 2005; Steinberg et al. 2008). Calanoid copepods, like *Temora longicornis*, are not normally considered feeders on large, sinking particles, and the feeding rates found here were lower than typically observed for *T. longicornis* feeding on suspended food (e.g., diverse phytoplankton). However, the degradation of sinking aggregates due to zooplankton grazing may be intense if typical detritivorous zooplankton exhibit similar aggregate-finding behavior as that reported here for *T. longicornis*. As calculations based on the abundance of some copepod species (typically *Microsetella norvegica* and *Oncaea* spp.) on marine snow suggest that random encounter is not sufficient to explain their high concentrations on aggregates (Kiørboe 2000), this seems likely. An efficient mechanism to find and colonize particles, together with their at times high abundances (up to 100 ind. L^{-1}; Uye et al. 2002), suggest a potentially high effect of particle-colonizing copepods on the attenuation of vertical flux.

We have here demonstrated a mechanism by which copepods may locate sinking marine snow aggregates. This mechanism may account for the high abundances of copepods observed on aggregates, and is consistent with copepods contributing significantly to the vertical attenuation of particle flux in the ocean. Our observation is one step further in

352 understanding the controls of flux attenuation and suggests that remote detection of chemical
353 cues can enhance the encounter and degradation rates by orders of magnitude from what
354 would be predicted based on the particle sizes and concentrations alone.

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Tables

Table 1 : Summary of copepod reactions to sinking aggregates at the different experimental conditions: Total number of observations (*n*), number of direct encounters, number of chemical tracking events (including copepods that lose the trail), mean house size and sinking speed, reaction distance of the copepods to the sinking house, mean zigzag amplitude, residence time, and swimming velocity before and after encountering the chemical trail (± SD). Differences between new and old houses have been tested as no significantly different for all observations (*t*-test, $p > 0.05$) except houses size (*t*-test, df = 230, $p < 0.001$). Differences between 'wild' and 'cultured' conditions are significant with respect to detection distance (*t*-test, df = 148, $p < 0.001$), residence time (*t*-test, df = 110, $p = 0.012$) and swimming and tracking velocities (*t*-tests, df = 109, $p = 0.048$ and df = 108, $p < 0.001$, respectively).

Observation conditions		*n*	Encounter		House size (mm)	House sinking speed (m d^{-1})	Mean reaction distance (mm)*	Mean zigzags amplitude (mm)	Time on particle (s)	Copepods speed (mm s^{-1})	
			direct	chemical (lose)						before encoutering the trail	following the trail*
culture	new	127	50	77 (37)	3.5 (±0.8)	129	12.7 (±8.3)	0.78	11.0 (±22.3)	4.1 (±1.8)	7.5 (±1.4)
	old	35	13	22 (9)	2.4 (±0.3)	132	12.3 (±9.8)	0.62	12.9 (±17.4)	4.4 (±1.9)	8.0 (±2.3)
	total	162	63	99 (46)	3.3 (±0.9)	130	12.6 (±8.7)	0.75	11.3 (±21.6)	4.2 (±1.8)	7.6 (±1.6)
wild	new	33	13	20 (12)	3.5 (±0.4)	48	7.9 (±5.6)	0.56	23.2 (±16.6)	3.6 (±1.4)	6.3 (±1.2)
	old	37	10	27 (16)	2.8 (±0.5)	57	8.6 (±6.6)	0.62	27.7 (±26.7)	3.5 (±1.5)	6.5 (±1.6)
	total	70	23	47 (28)	3.1 (±0.6)	54	8.3 (±6.2)	0.60	26.1 (±23.7)	3.5 (±1.5)	6.5 (±1.5)

* only consider chemical reactions

Figure legends

Figure 1 : (A) Relative position of *Temora longicornis* when it reacts to the chemical trail left by sinking discarded house (represented here as a large dot). The two inserted images represent the theoretical chemical plume assuming two different Péclet numbers (adapted from Kiørboe et al. 2001). (B) Example of *T. longicornis* swimming pattern and speed (mm s^{-1}) relative to position of sinking discarded houses. The detection point is marked with a black arrow. Note the increased speed and the zigzagging behavior when following the chemical trail.

Figure 2 : Frequency distribution of detection distance of *T. longicornis* to the sinking aggregates. Wild and culture conditions were plotted separately since they were tested as significantly different (χ^2-test $p>0.05$).

Figure 3 : *T. longicornis* fecal pellet production when offered discarded house at different concentrations (number L^{-1}). Error bars represent the standard error originating from triplicates. Relationship is: Y= 33.8 (±13.0)X/(X+133 (±73)) ($R^2 = 0.84$; $n = 27$) dotted lines represent the 95% confidence limits intervals of this relationship.

Figures

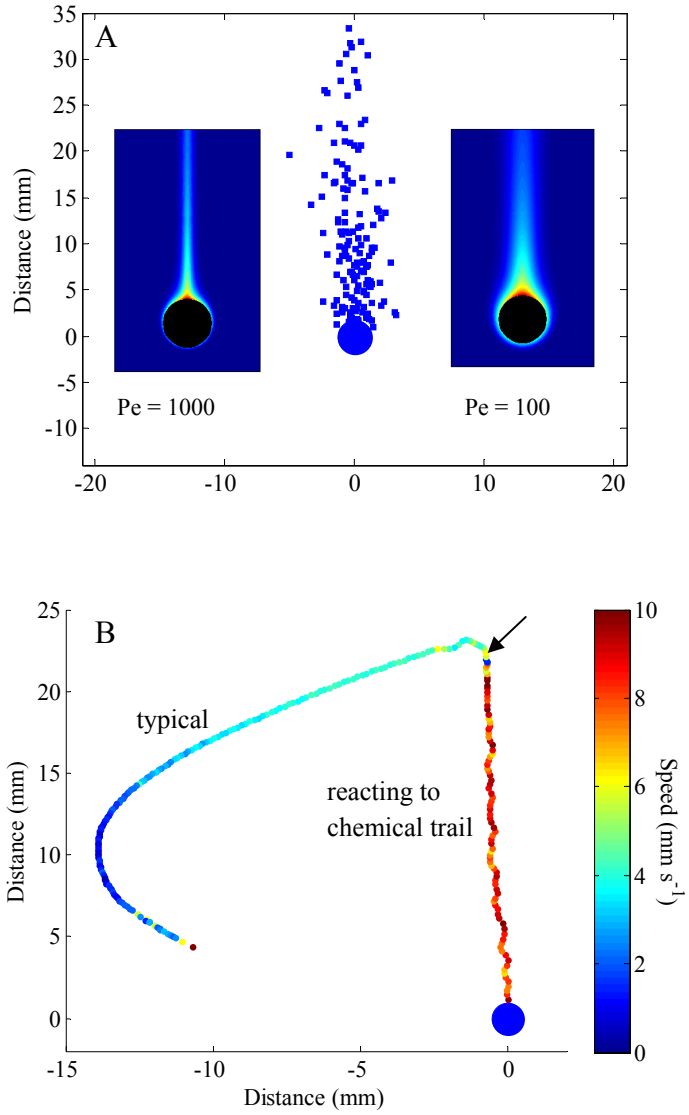


Figure 1

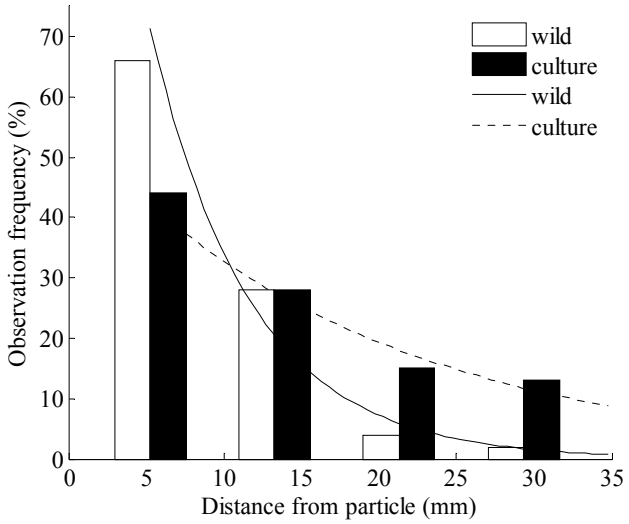

wild
culture
wild
culture
Observation frequency (%)
Distance from particle (mm)
0
10
20
30
40
50
60
70
0
5
10
15
20
25
30
35

Figure 2

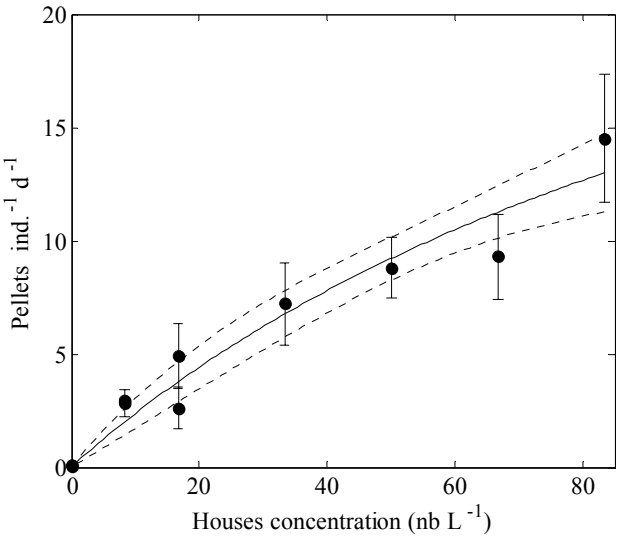

20
15
10
5
0
0
20
40
60
80
Pellets ind.-1 d-1
Houses concentration (nb L-1)

Figure 3

Web appendix

These three video sequences illustrate the different behavioral observations described in the accompanying manuscript.

Video A1: Example of *Temora longicornis* interacting with sinking marine snow (discarded appendicularian house) using infra red light. All the different behavior (chemical trail detection, direct encounter) are illustrated.

Available online at:

http://fabien.lombard1.free.fr/temoratrackIR2.wmv

Video A2: Example of *T. longicornis* following a chemical trail left by a sinking marine snow (discarded appendicularian house) using white light illumination inside a rotating tank:

http://fabien.lombard1.free.fr/temoratrackwhiteligth.wmv

Video A3: Close-up view of the feeding behavior of *T. longicornis* on marine snow (discarded appendicularian houses) using a binocular lens (inside a petri dish).

Available online at

http://fabien.lombard1.free.fr/closeupfeeding.wmv