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Perceiving the algae: How feeding-current feeding copepods detect their nonmotile prey

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Abstract

Feeding-current feeding copepods detect and capture prey individually, but the mechanism by which nonmotile prey is detected has been unclear. Early reports that copepods detect phytoplankton prey at distances of one body length or more led to the hypothesis that solutes leaking from the prey would be carried to the copepod by the sheared feeding current and arrive prior to the prey, thus allowing the copepod to adjust the feeding current to bring the prey within reach of the feeding appendages. Many subsequent studies have been interpreted assuming this mechanism, which appears currently to be the main accepted view. Here, we review the observations available in the literature and add our own data to show that in most cases the prey, whether phytoplankton cells or inert particles, has to be within a few prey radii from the setae of the feeding appendages to elicit a capture response. We further demonstrate that (1) long-range chemical detection is incompatible with known algal leakage rates and reasonable assumptions of sensitivity, (2) that near-field chemical detection is constrained by diffusion across the boundary layer of the sensor and takes longer than observed near-contact times, and (3) that most reported detection distances are well predicted by models of fluid mechanical signal generation and detection. We conclude that near-field mechanoreception is the common prey detection mode in pelagic copepods. Prey detection distances are thus governed mainly by the reach of the feeding appendages, in contrast to the strong prey size-dependency implied by remote chemical prey detection.

Pelagic copepods feed on suspended particles ranging in size from a few microns in diameter to mm-sized marine snow aggregates (Frost 1972; Berggreen et al. 1988; Koski et al. 2005). While the smallest prey are concentrated from the feeding current by an automated process not fully understood, prey larger than about 10 μm are perceived, captured and handled individually (Alcaraz et al. 1980; Koehl and Strickler 1981; Price et al. 1983). Pelagic copepods are well equipped with mechano- and chemosensors on the antennules and feeding appendages (Strickler and Bal 1973; Friedman and Strickler 1975; Heuschele and Selander 2014), and these mediate prey detection. It is well documented that motile prey cells can be perceived remotely from the fluid disturbance they generate while swimming; such prey detection has in particular been described for ambush feeding copepods (Svensen and Kiørboe 2000; Jiang and Paffenhöfer 2004; Kiørboe et al. 2009), but feeding-current feeding copepods may also perceive motile prey this way (Landry 1980; Jonsson and Tiselius 1990; Yen and Strickler 1996). It has also been hypothesized that even nonmotile prey may be detected hydrodynamically when entrained in a feeding current, from the distortion of the feeding current that the prey may cause (Bundy et al. 1998; Bundy and Vanderploeg 2002; Yen and Okubo 2002), although this is only efficient for very large prey (Visser 2001).

Chemical detection is also well documented in copepods. Not only may copepods change behavior in response to the presence of elevated concentrations of amino acids and other organic solutes indicative of a food patch (Poulet and Marsot 1978; Gill and Poulet 1988; Steinke et al. 2006), but they may also detect individual prey chemically. Sinking marine snow aggregates leak organic solutes that form a chemical trail in their wake, which may be detected by cruising copepods and guide them to this rich source of food (Kiørboe et al. 2001; Lombard et al. 2013). Copepods are also known to be able to discriminate between prey particles based on their chemical characteristics, e.g., between organically coated and non-coated polymer spheres (Poulet and

Additional Supporting Information may be found in the online version of this article

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Marsot 1978; DeMott 1988; Vanderploeg et al. 1990). It is also generally assumed that feeding-current feeding copepods may chemically detect leaky prey cells that are entrained in the feeding current. This idea stems mainly from Strickler (1982, 1984, 1985) that reported how phytoplankton prey cells are detected by the copepod *Eucalanus pileatus* at a distance of more than one body length away from the copepod (1.25 mm) and nearly 1/2 a second before the cell arrives at the copepod. The suggested mechanism was that the "phycosphere" surrounding a leaky cell would be stretched in the sheared feeding current. The leading edge of the phycosphere would therefore arrive prior to the cell, giving the copepod early warning and allowing it to redirect the feeding current to have the cell pass within reach of the feeding appendages (the capture area). Simple as well as more elaborate models of the feeding current subsequently confirmed the principal feasibility of the suggested mechanism (Andrews 1983; Jiang et al. 2002) and with certain implicit assumptions of cell leakiness and copepod sensitivity, the CFD model of Jiang et al. (2002) could even predict the reported 1.25 mm detection distance and 1/2 second lead time. Furthermore, experiments have demonstrated that, indeed, a spherical solute plume becomes stretched in the feeding current produced by real copepods (Moore et al. 1999). These early reports have been widely cited (mostly uncritically) and many subsequent observations of copepod feeding behavior have been interpreted in the light of this model of feeding (e.g., Cowles et al. 1988; Butler et al. 1989; Malkiel et al. 1999; Schultz and Kiørboe 2009). However, in most cases, remote detection was not required to explain the observations. Skeptical reports (e.g., Légier-Visser et al. 1986; DeMott and Watson 1991) have received less attention. Thus the uncertainty in our understanding of how copepods perceive their prey still remains but has not always been acknowledged.

However, our own recent high-speed video observations of the feeding of free-swimming copepods have made us doubt of the generality of the mechanism suggested by Strickler (1982). Some copepods cruise through the water while feeding, and these copepods do not generate a feeding current and thus are unable to perceive a chemical signal from the prey, yet they feed on the same type of prey as feeding-current feeders. Uttieri et al. (2008) suggested that the cruising copepod *Clausocalanus furcatus* simply intercepts prey, whereas the high-speed video observations of Kjellerup and Kiørboe (2012) demonstrated that the cruising *Metridia longa* indeed perceives prey cells individually, but only as these either touch or are very near the setae of one of the feeding appendages. This close contact then elicited a capture response. Our subsequent observations of feeding in free-swimming copepods of several species of feeding-current feeders (*Paracalanus parvus, Pseudocalanus* sp., *Temora longicornis* copepodites, *T. longicirnis* nauplii, *Calanus helgolandicus, Acartia tonsa*; Bruno et al. 2012; Tiselius et al. 2013; Gonçalves et al. 2014; see also Supporting Information 1–4) showed that prey perception and prey capture in all of these were identical to that observed in the cruising *M. longa*; i.e., no long-distance (chemical) detection and perception only on (near) touching of the prey.

Whether prey cells are perceived only within the reach of the feeding appendages or remotely by chemical cues has implications for the amount of water that a feeding-current feeding copepod can examine for prey: remote detection allows a much larger volume of water to be scanned. It also has implications for the prey size spectra of copepods: if individual cells are detected from the dissolved organics that they leak, large cells will be detected further away than small cells since large cells generally leak more material. In contrast, the detection distance will be independent of cell size if it is the reach of the feeding appendages that defines the dining sphere of the copepod. Thus, a correct understanding of prey sensing mechanisms may have implications to our quantitative interpretations of copepod trophic interactions and clearance rates (e.g., Kiørboe and Jiang 2013) and are also important for the development of size-based, mechanistic models of pelagic communities and ecosystems (Armstrong 1999; Banas 2011).

In this article, we review the evidence for remote chemical detection of individual microplankton prey by feeding-current feeding copepods, focusing on evidence based on direct observations. We also report a few original observations of prey detection in free swimming copepods to complement those already published.

Material and methods

While this article is mainly a review, we do provide a few new observations of prey perception and capture in feeding-current feeding copepods, i.e., *Calanus helgolandicus* (2.5 mm cephalothorax length) offered various species of 10–33 μm sized dinofalgellates, *Acartia tonsa* (0.8 mm) offered 23-μm *Lingulodinium polyedrum* and *Temora longicornis* copepodites ($\sim$ 0.8 mm) and nauplii ($\sim$ 0.3 mm) offered 20–30 μm plastic spheres. *C. helgolandicus* was collected in the Gulmar Fjord on the Swedish west coast, and the other species were taken from our culture. The copepods were placed in small aquaria (250 mL for *C. helgolandicus*; 70 mL for the others) with food or particles. We filmed free swimming specimens at a frame rate of 1000 or 2200 fps (Table 1) using a high resolution (1280×800) high speed Phantom camera equipped with optics to provide fields of view of $16 \times 25.5\,mm^2$ (for *C. helgolandicus*), $4.8 \times 3.0\,mm^2$ (for *A. tonsa*) and $7.7 \times 4.8\,mm^2$ (for *T. longicornis* nauplii and copepodites). We monitored the recordings continuously and saved sequences with prey capture events that happened in focus of the camera. We recorded additional capture events of *C. helgolandicus* glued onto a fine hair and positioned in front of the camera. Filming was conducted in a temperature-controlled room at

Table 1. Studies with quantitative data on capture and detection of prey by feeding-current feeding copepods. References: (1) Strickler (1984); (2) Paffenhöfer and Van Sant (1985); (3) Bundy et al. (1998); (4) Vanderploeg et al. (1990); (5) Bundy and Vanderploeg (2002); (6) This study; (7) Alcaraz et al. (1980); (8) Koehl and Strickler (1981); (9) Paffenhöfer et al. (1982); (10) Strickler (1982); (11) Price et al. (1983); (12) Cowles and Strickler (1983); (13) Price and Paffenhöfer (1984); (14) Koehl (1984); (15) Vanderploeg and Paffenhöfer (1985); (16) Paffenhöfer and Lewis (1990); (17) Kjellerup and Kiørboe (2012); (18) Bruno et al. (2012); (19) Tiselius et al. (2013); (20) Gonçalves et al. (2014)

Copepod species	Copepod size (mm)	Prey type	Prey size (μm)	Free-swimming or tethered	Film frequency (Hz)	Number of observations	Response distance (μm)	Distance measured to	Source
Eucalanus pileatus	NA	Glass particle	100	T	NA	NA; presumably several	"Within reach of mouthparts"	Tip of setae (presumably)	1
E. pileatus	NA	Polystyrene Beads	18	T	500	$\sim$ 15 (a)	Not perceived unless touched	Tip of mouthparts	2
Diaptomus sicilis	NA	Polystyrene beads	50	FS	60	10 (b)	1030 (c)	Eye of the copepod (d)	3
D. sicilis	1.2	Polystyrene beads	11–102	T	250–500	79	NA	NA	4
Skistodiaptomus oregonensis	1.1	Polystyrene beads	50	FS	60 (but digitized at 30)	4	1300–2300 (e)	Eye of the copepod?	5
Temora longicornis (nauplii + copepodids)	0.3–0.6	Plastic beads	20–30	FS	2200	71	Touched /within few cell radii	Setae of feeding appendage	6
Eucalanus crassus	NA	Algae	?	T	500				7
E. pileatus, *Centropages typicus*	NA	*Dinoflagellates and diatoms*	10–50	T	500	27 movies	Few cell radii (f)	Tip of setae	8
E. crassus, *E. pileatus*	2.6; 2.1	*Dinoflagellates and diatoms*	10–$\sim$ 200	T	500	NA	Nearly touches	Tip of setae	9
E. pileatus	NA	Algae	NA	T	100	1	1250	NA	10
E. pileatus	1.8	*Prorocentrum micans*	22	T	500	NA (several)	$\geq$ 70	"The closest seta of the maxilliped"	11
C. typicus	NA	*Gymnodinium nelsoni*	NA	T	500	NA (1 film of 8 s)	Few cell radii (g)	Tip of setae	12
E. pileatus	NA	*Thalassiosira weisflogii*	11	T	200	Five movies for four females	"The outermost extensions of the feeding appendages"	Tip of setae (h)	13

TABLE 1. Continued

Copepod species	Copepod size (mm)	Prey type	Prey size (μm)	Free-swimming or tethered	Film frequency (Hz)	Number of observations	Response distance (μm)	Distance measured to	Source
E. pileatus	NA	*G. nelsoni*	NA	T	NA	NA	Few cell radii (i)	Tip of setae (i)	1
E. pileatus	NA	*G.nelsoni* + *P. micans*	36–53	T	500	5	136±72	"Nearest setae"	14
C. typicus	NA	*G. nelsoni*	50–53	T	500	2	137±93	2nd maxilla	14
D. sicilis	~ 1.2	*Chlamydomonas* spp	4–12	T	500	66 (j)	Few cell radii (k)	Tip of setae (presumably)	15
E. pileatus	NA	Fecal pellets	20 × 90 to 30 × 300	T	500	Five movies	"Almost touching"	Tip of mouthparts	2
E. pileatus	NA	*T. weisflogii*	11	T	125–250	Six females	200–460 (l)	Tip of A2 or Mxp, excluding setae	16
Metridia longa	2.5	*Akashiwo sanguinea*	50	FS	1600	9	"Touch the prey"	Feeding appendage	17
T. longicornis (nauplii)	~ 0.16	*Heterocapsa triquetra*	14	FS	2200	10	"Detects prey as it touches the setae"		18
T. longicornis (nauplii)	~ 0.16	*Rhodomonas salina*	7	FS	2000			Setae of feeding appendage	18
Paracalanus parvus	0.64	Several algae, mostly	11–32	FS	2200	12	"Within a few cell	From prey center to	19
Pseudocalanus sp.	0.65	dinoflaellates		FS	2200	8	radii"	nearest feeding appendage (excluding setae)	19
T. longicornis (adults)	0.85	Nine different algae (m)	6–58	FS	2200	219	Touched /within few cell radii	Setae of feeding appendage	20
Calanus helgolandicus	2.5	*A. sanguinea*	33	FS	2200	9	Touched /within few cell radii	Setae of feeding appendage	6
Acartia tonsa	0.8	*Lingulodinium polyedrum*	23	FS	2200	38	Touched /within few cell radii	Setae of feeding appendage	6
C. helgolandicus	2.5	*L. polyedrum*	23	T	2200	12	Touched /within few cell radii	Setae of feeding appendage	6

TABLE 1. Continued

Copepod species	Copepod size (mm)	Prey type	Prey size (μm)	Free-swimming or tethered	Film frequency (Hz)	Number of observations	Response distance (μm)	Distance measured to	Source
C. helgolandicus	2.5	*Oxyhrris marina*	11	T	2200	8	Touched /within few cell radii	Setae of feeding appendage	6
C. helgolandicus	2.5	*Prorocentrum minimum*	10	T	2200	7	Touched /within few cell radii	Setae of feeding appendage	6
C. helgolandicus	2.5	*Scrippsiella trochoidea*	16	T	2200	8	Touched /within few cell radii	Setae of feeding appendage	6

Notes: (a) Total number of beads captured, from Table 7; (b) As inferred from Table 1 and mentioned in the text (page 2142); (c) Mean of last column in Table 1; (d) As inferred from Fig. 1; (e) only four observations with data (distance before attack, from Table 2); (f) inferred Figs. 2C,D; (g) Inferred from their Figs. 1, 2; (h) Although in their Table 1 they use distances of 273–345 to M2 to standardize the detection area; (i) Inferred from his Fig. 6, although author argues that the cell had been already detected; (j) total "active captures" from Table 1; (k) in fact, the authors state that "cells had to almost touch the appendages or be within the boundary layer around them before the active capture response was first apparent." Also it is evident from their Fig. 4; (l) Approximate values -only adult females, from Fig. 5; (m) Only cells with elicited a capture reaction, i.e., $E \neq 0$ in Table 1.

either 17 (*C. helgolandicus*) or 16 °C (*T. longicornis* and *A. tonsa*). Illumination was provided by an infrared LED that was shone through the aquarium toward the camera.

The first reports

Three interrelated papers are normally cited as the original evidence of remote, chemical detection of prey in copepods using a feeding-current to feed: Alcaraz et al. (1980), Koehl and Strickler (1981), and Strickler (1982). Alcaraz et al. is "a very personal account of thoughts and experiences" based on the first pioneering observations of feeding copepods using high speed cinematography (500 frames per second and several tens of meters of celluloid film!). The copepod, *Eucalanus crassus*, was tethered in front of the camera, hence altering the feeding current, but the authors were "most interested in the food handling of algal chains by the mouthparts…" The paper discussed chemical perception in very general terms, but the only observation reported is that "If it [the copepod] perceives the presence of an alga, it changes the movements [of the mouthparts] and uses viscous forces to bring the alga within reach of an appendage." No response distance or any other data on detection of algae is reported. The main contribution of the seminal paper of Koehl and Strickler (1981) was to demonstrate that copepods (*Eucalanus pileatus*) do not filter water, as was previously believed: the feeding current is a scanning current and prey entrained in this current is individually sensed and captured. This article does not talk about remote detection but simply notes that "when an algal cell is carried into the vicinity of the copepod, the feeding appendages [….] beat asymmetrically, redirecting the incoming current so as to draw water preferentially from the direction of the algae" and in conclusion talks about "the mechanical or chemical cues that stimulate copepods to flap asymmetrically." The initial asymmetrical flapping behavior of the feeding appendages and the following outward "fling" and subsequent closure of the 2nd maxillae to suck in and capture the prey cell is here described for the first time, and is similar to what we and others have subsequently described for a number of species (Price et al. 1983; Cowles et al. 1988; Tiselius et al. 2013). Again, no data are provided on how individual prey is detected. Strickler (1982) argues that the negative buoyancy of copepods allows the beating feeding appendages to produce a feeding current (had the copepod been neutrally buoyant, it would rather be propelled through the water), and that this is important for remote chemical detection of prey. The evidence for the latter is this: "Just before capture by second maxillae, other mouthparts direct algae into the capturing area […]. These observations suggested that calanoids perceive the approximate locations of nearby algae, and chemoreception probably assists in this recognition," and the observation is this: "Slight changes of the flow field near the mouthparts ensure that the alga comes close to the

second maxillae (Alcaraz et al. 1980; Koehl and Strickler 1981). *Eucalanus pileatus* executed such changes 430 msec before the alga reached the capture area or when the alga was approximately 1.25 mm away." The "slight changes of the flow field" refers to the asymmetrical flapping of the appendages described above. Thus, these early papers clearly demonstrated that prey cells that arrive in the feeding current are perceived and captured individually, not sieved out of suspension, and this is their main and very important contribution that has been verified by many subsequent observations. The evidence for remote chemical detection, however, is circumstantial, at best, and substantiated only by one ($n = 1$) observation of detection distance. Paffenhöfer et al. (1982) provided a more detailed account of the observations initially reported by Alcaraz et al. (1980) and notes for *E. pileatus* feeding on near spherical cells that "during the period of water/food transport toward the copepod the second maxillae usually remain motionless. Only when an alga nearly touches one of the mouthparts do the second maxillae start sweeping in the direction of the mouth." This latter description is consistent with our own much later observations on other species and provides no support for remote (chemical) detection.

Follow-up observations

Despite the weak evidence, the community to a large extent adopted the idea of remote chemical detection of individual, nonmotile prey, probably because it was an exciting idea and because a rather precise mechanism that was backed up by models could be suggested (Andrews 1983; Jiang et al. 2002). As a result, many later observations were interpreted with the implicit assumption of remote chemical detection.

Later observations of prey detection in feeding-current feeding copepods, by the same authors as above as well as by others, provided further insight and—in particular—more quantitative estimates of detection distances (Table 1). Many observations were conducted on one species, *Eucalanus pileatus* (ca. 2 mm), which was also the main target of the first studies. Thus, Price et al. (1983) examined capture of *Prorocentrum micans* cells (22 μm) using the same set-up as in Alcaraz et al. (1980). They report that "The distance from the cell to the closest seta of the maxilliped was at least 70 μm when the capture response was initiated,…." And "We have often observed initiation of capture responses when the individual cells were at least this far away." Koehl (1984) reported a mean minimum detection distance (from 36 to 53 μm prey cells to the nearest setae) of 136 μm (SD = 72, $n = 5$), and Price and Paffenhöfer (1984) reported mean distances from the 2nd maxilla to diatom cells (11 μm) of 273–345 μm, but the distance to any setae is unclear, and the authors note that they "observed the initiation of capture responses when cells are at the tips of either of these appendages, as well as throughout the interior of this region." Finally, Paffenhöfer and Lewis (1990) for the same copepod and prey reported average detection distances between ca. 200 μm and 460 μm, depending on prey concentration; however, the length of the setae were not included, and since these vary in length between 80 μm and 510 μm, it is difficult to evaluate whether the cells were near the setae when detected. These were average distances, and they report an observed maximum distance of 1.9 mm, well beyond the reach of the setae. In summary, observed detection distances in *Eucalanus pileatus* measured from the nearest seta vary between 0 μm and 140 μm, i.e., a few prey cell radii for cells varying in size between 11 μm and 57 μm. Distances measured to the nearest appendage (excl. setae) are clearly longer, up to 460 μm. And then there are a few extreme observations of substantially larger detection distances.

The above observations on *Eucalanus pileatus* were all conducted on tethered animals and with frame rates between 125 Hz and 500 Hz. The recorded detection distances must be interpreted in light of the temporal and spatial resolution of the detection and capture events. If the tip of the setae of the detecting feeding appendage moves at a speed of 25 mm s^{-1} (conservatively assuming that the total excursion is 1 mm per beat cycle and the beat frequency is 25 Hz; Paffenhöfer and Lewis 1990) then the spatial resolution of the prey detection observations range between 50 μm and 200 μm for the used recording frequencies (25 mm s^{-1} divided by a frame rate of 125–500 s^{-1}). This is of the same order as many of the observed detection distances, and consistent with the fact that the longest average detection distances were reported by Paffenhöfer and Lewis (1990) that also used the lowest recording frequencies (125–250 Hz).

The data in Table 1 also summarizes observations for other species, including our own observations reported here (Supporting Information 1–4). There is a somewhat similar diversity in reports of detection distances, however, with most values being on the order of < 100 μm for detection of phytoplankton cells. Also, the more recent observations recorded with the highest frame rates ($\sim$ 2000 fps) yield the shortest detection distances; these observations essentially all suggest that prey cells have to (almost) touch the setae of one of the feeding appendages to elicit a capture response, irrespective of species.

There are also reports on detection and active capture of inert particles, e.g., glass beads or washed polystyrene spheres (Table 1). In some cases such particles only elicit a capture response after being touched by the setae of the feeding appendages, as also observed for *Temora longicornis* copepodites and nauplii in our own experiments (Supporting Information 3). A (mistaken) capture reaction can be triggered by an accidental touch by the antennule of a nearby copepod (Supporting Information 4). However, in other cases, much longer detection distances have been reported. Thus, Bundy et al. (1998), and Bundy and Vanderploeg

(2002) reported instances of substantial apparent detection distances in the copepods *Diaptomus sicilis* (~ 1 mm) and *Skistodiaptomus oregonensis* (~ 2 mm) toward 50 μm plastic spheres (Table 1). These distances were measured from the eye of the copepod, so it is difficult to know how far from the antennules (length ~ 1 mm) or other sensors the particles in fact were. In the case of *D. sicilis*, prey attack was elicited while the target was outside the feeding current but embedded in the viscous boundary layer of the swimming copepod, whereas for *S. oregonensis*, the prey was entrained in the feeding current when the copepod made a reorientation jump at a distance of up to 2.3 mm from the particle; then the particle was pulled by the feeding current to within reach of the feeding appendages and captured.

Other evidence

Several pieces of indirect evidence from incubation and other experiments may throw further light on the relative significance of olfaction (smell), gustation (taste) and mechanoreception for prey detection. For example, DeMott and Watson (1991) measured clearance rates of *Diaptomus birgei* on various prey in the presence and absence of overwhelming concentrations of various odors (algal extracts, amino acids, sugars) and found no difference in clearance rates and prey selectivity, suggesting that olfaction was unimportant for prey detection. Remote chemical detection has been suggested to allow prey selection prior to capture (Alcaraz et al. 1980; Koehl and Strickler 1981; Schultz and Kiørboe 2009). However, Vanderploeg et al. (1990) found that toxic and nontoxic strains of the same algae were captured equally well, but that the toxic strain was subsequently rejected, suggesting that gustation rather than long-range olfactory cues were involved.

Gifford et al. (1981) offered two different clones of a diatom to *Calanus finmarchicus*. The two clones differed by one having long spines, the other not, with the spinose form appearing 10 times larger than the one without spines. Remote chemical detection would suggest similar clearance rates on the two forms as they presumably had similar solute leakage rates and, hence, phycospheres. However, the clearance rates were on average 1.7 times higher on the form with spines, consistent with touch reception of the form appearing much larger.

Mechanisms of remote detection of nonmotile prey

Remote prey detection can only be achieved through chemical and/or hydromechanical cues. It may be useful to consider how potential detection distances depend on sensitivity thresholds and cell sizes for the two potential mechanisms and to examine how predicted response distances compare with those observed.

Remote chemical detection requires that the solutes leak out of the cell and reach concentrations in the "phycosphere" that are high enough for detection. A minimum requirement for detection is that the concentration at the surface of the cell—before it enters the feeding current—should exceed the threshold concentration for detection. Légier-Visser et al. (1986) considered diffusion from a leaking sphere in the absence of flow and argued that likely leakage rates from a 50-μm cell would be insufficient to produce high enough concentrations for detection. Tiselius et al. (2013) expanded on their calculations and assuming that copepods would respond to amino acids or some other common organic solute they argued that the minimum diameter of a diatom cell for detection would be 70 μm, even under generous assumptions of leakage rates and detection thresholds. For detection to be remote, the solute concentration has to exceed the threshold, not only at the cell surface, but also far from the cell surface, and so a much larger cell size is required. Thus, the simulation model of Jiang et al. (2002), which reproduces Stickler's (1982) reported detection distance of 1.25 mm in *E. pileatus*, assumes that the undisturbed phycosphere with concentrations exceeding the threshold has a radius 10 times the cell radius. In the sheared feeding current, a phycosphere of this radius would be stretched to a distance of 1.25 mm. Because the solute concentration around a leaking cell, in the absence of flow, scales with Q/r, where Q is the leakage rate and r the distance from the cell center, then to get at threshold concentration 10 radii away requires a 10 times higher leakage rate than above and, hence, a cell size of approximately $10^{1/3}$ times larger diameter, ca. 150 μm. A limitation with these model calculations is that while estimates of bulk leakage rates from phytoplankton cells are rather well constrained by observations (Myklestad and Wangersky 2000; López-Sandoval et al. 2013), and may be high in senescent or damaged cells (Granum et al. 2002), we know little about the actual chemicals that the copepods may respond to or the threshold concentration for detection. Our calculations have assumed that the copepod would respond to leaking amino acids at concentrations of around typical background concentrations of amino acids in the ocean. However, some substances, such as DMS, may elicit responses at homeopathic concentrations in microorganisms (Strom et al. 2003) and also in higher animals (Nevitt and Haberman 2003; Nevitt and Bonadonna 2005; Savoca and Nevitt 2014), including copepods (Steinke et al. 2006). However, DMS production in phytoplankton is restricted to a few taxa (Keller et al. 1989) and thus it does not provide a consistent cue.

As mentioned above, it is well documented that motile prey can be detected remotely from the fluid disturbance that the swimming prey generates. However, even nonmotile prey entrained in a feeding current may give rise to a fluid signal that the copepod can detect, as suggested by some observations. Several models have been proposed to estimate signal strength and detection distances. The model of Légier-Visser et al. (1986) is flawed, not only because it had a

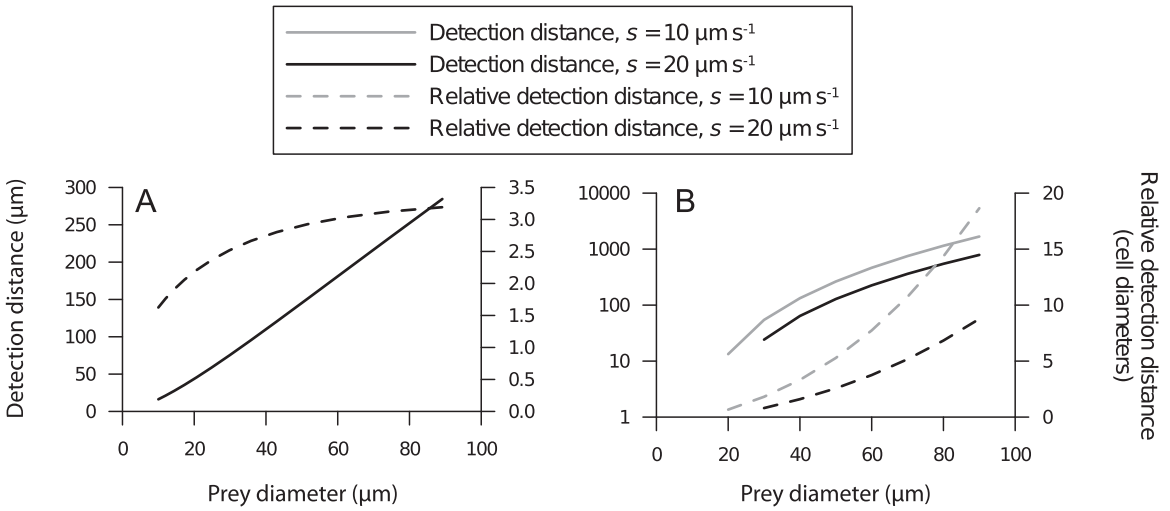

Fig. 1. Mechanoreception. Distances for fluid mechanical prey detection as a function of prey size for a nonmotile, neutrally buoyant prey particle predicted from Eq. 1 (A), and nonmotile but sinking particle with a density difference to the ambient medium of 0.05 g cm^{-3} predicted from Eq. 2 (B). Parameter estimates for (A) taken from *Eucalanus pileatus*, see text. The calculations in (B) have assumed two different copepod sensitivities to ambient fluid motion ($s = 10$ or 20 μm s^{-1}).

calculus error (Yen and Okubo 2002), but also because it considers the prey to be stationary rather than being entrained in the feeding current, and because it considers pressure signals rather than velocity signals; copepods respond to the latter rather than the former. The revision of Légier-Visser et al. (1986) by Yen and Okubo (2002), still considering pressure drop, concludes that a copepod would need 2 m long setae to perceive a 50 μm particle! The model of Bundy et al. (1998) is very idealized and considers a cruising copepod rather than one with a feeding current and also provides no basis for quantitative estimates. Visser (2001) considers a prey cell entrained in the feeding current of a copepod. He uses a stokeslet model to describe the feeding current of maximum speed U generated by a hovering copepod with effective radius a ($\sim$ half body width) and considers the perturbation of the fluid, $u(r)$, as a function of the distance from the prey (r) in the direction toward the copepod. The prey will be detected at distance R, if $u(R)$ exceeds the threshold velocity for detection, s. The detection distance (measured from the sensor) depends on where the prey enters the feeding current, but for a prey of radius b the maximum detection distance is approximated by:

$$R \approx \frac{a}{2}\left[1+\left(1+2\left(\frac{15b^3U}{a^3s}\right)^{1/2}\right)^{1/2}\right]-a \qquad (1)$$

Using parameters for *E. pileatus* (Paffenhöfer and Lewis 1990; $U = 6$ mm/s; $a = 0.5$ mm) and a threshold velocity of 20 μm s^{-1} (Yen et al. 1992) we find that predicted detection distances are a few prey cell diameters for a relevant range of cell sizes (Fig. 1a). The estimates are not hugely dependent on the parameters: doubling the feeding current velocity increase the detection distance by 25–40%; doubling the signal threshold strength decreases the detection distanced by 25–30%.

The stokeslet model used by Visser (2001) to describe the feeding current of the copepod simply assumes a stationary force working in a point in the water (corresponding to the copepods beating appendages) and is of course highly idealized, but it captures observed flow fields of hovering copepods surprisingly well (Catton et al. 2007; Kiørboe et al. 2014). A cruising copepod is better described by a stresslet, two oppositely directed forces of equal magnitude (Kiørboe 2011). Again this idealized model describes well observed flow fields of cruising zooplankton (Catton et al. 2007; Kiørboe et al. 2014), and one could use this model to evaluate detection distances for a cruising copepod. This would partly correspond to the observations of Bundy et al. (1998) (but see below). However, even without doing any calculations, one can argue that detection distances will be less than for the stokeslet model, simply because the flow velocity induced by the cruising copepod attenuates spatially much faster than that of the hovering one (with distance^{-1} and distance^{-2}, respectively), and so the estimates in Fig. 1 would be maximum estimates also for the cruising copepod.

Finally, some reports on particle detection use inert particles with a density different from that of the water, and such particles will sink and generate a fluid signal. For example, Bundy and Vanderploeg (2002) used 50-μm polystyrene beads with a density different form that of the ambient freshwater of 0.05 g cm^{-3}. Such particles will sink at 70 μm s^{-1} (Stokes law) and thus generate a significant fluid signal.

Kiørboe and Visser (1999) derived the detection distance to a sinking sphere as a function of its size and sinking velocity:

$$R = \frac{-b}{(2\times\cos((4\pi+\cos^{-1}(s/U))/3)),} \quad (2)$$

where b is the radius of the particle, U its sinking velocity, and s again the sensitivity of the copepod. Particles that sink faster than the threshold for detection (s) can be detected remotely. The detection distance depends strongly on the sensitivity of the copepod: for $s = 20$ μm s^{-1} a 50 μm particle can be detected at a distance of 0.13 mm, but at 0.26 mm with $s = 10$ μm s^{-1} (Fig. 1b). These are distances from the antennules and may potentially account for the observed detection distances from the eye of about 1 mm reported by Bundy et al. (1998).

Discussion

The pioneering work of Alcaraz et al. (1980) and Koehl and Strickler (1981) clearly demonstrated that feeding-current feeding copepods perceive and capture nonmotile prey individually. However, the way prey is perceived is less clear. Copepods possess two types of sensors relevant in this context: (1) aestetascs that only have chemosensory function and that pick up smell from the water; they occur mainly on the antennules; and (2) other sensilla that are spread over the body but mainly on the feeding appendages, and that both have chemosensory and mechanosensory function (e.g., Hallberg and Skog 2012). The unimodal aestetascs are olfaction organs (olfaction = smell), whereas the bimodal sensilla are believed to mediate chemical signals only on contact with the source (gustation = taste). Thus, this leaves four possible ways in which copepods can perceive their prey: remotely via chemical or hydromechanical signals using olfaction or mechanoreception, or by direct contact with prey cells, using gustation or mechanoreception. Note that these are not necessarily mutually exclusive.

Theoretical arguments and observations (Table 1) together suggest that mechanoreception is the general mode in which nonmotile prey are perceived. Most observed detection distances are within a few cell radii from the sensory hairs on the feeding appendages, consistent with detection distances predicted from the model of Visser (2001) (Fig. 1). In fact, distant chemoreception would be inefficient on these short distances, because the organic solutes in the phycosphere would still have to diffuse across the viscous boundary layer surrounding the setae to reach the sensor. The diffusion time across a, say, 20 μm thick boundary layer is on the order of $L2/6D = (20\times10^{-4}\ \text{cm})^2/(6\times10^{-5}\ \text{cm}^2\ \text{s}^{-1}) \sim 65$ ms, which is longer than the typical duration of an appendage beat cycle (e.g., 21 ms for *Paracalanus parvus*, Tiselius et al. 2013) and incompatible with observed near-contact times (see e.g., Supporting Information). In fact, it is more compatible with the post-capture handling time (61 ms in *P. parvus*; Tiselius et al. 2013), where gustation may play a role in deciding whether to reject or ingest a captured prey particle. In addition, phytoplankton cells and inert particles appear to be perceived equally well and at similar short distances. Whether the prey cell or particle is actually touched, or the mechanical signal is mediated through a relatively thin viscous boundary layer may vary from case to case depending on the prey size and the sensitivity of the copepod, but is often difficult to decide form movies and is probably of limited significance.

Some observations of long-range prey detection are inconsistent with our current understanding of mechanoreception and copepod sensitivity to fluid signals. This applies to the 1–2 mm detection distances reported by Strickler (1982, $n = 1$), Paffenhöfer and Lewis (1990; $n = ?$) and Bundy and Vandeploeg (2002; $n = 4$, but qualitative observations for 73 captures). There is no reason to disbelieve these observations, where in particular those of Bundy and Vanderploeg (2002) are very well documented, but one can discuss the interpretation of the observations. Bundy and Vanderploeg (2002), for example, describe how *Skistodiaptomus oregonensis* make a short reorientation jump toward a 50-μm particle entrained in the periphery of the feeding current, which positions the copepod such that the particle is in the center or the feeding current. The particle is subsequently drawn in and captured. However, one may question whether the reorientation is a response to the presence of the particle. Most copepods often make random and unprovoked reposition jumps; Jonsson and Tiselius (1990) recorded frequencies ranging from once per 2–3 min to once per second for a range of small neritic copepods. If, by chance, a jump positions the copepod such that a particle comes into the center of the feeding current, the particle may be captured. If the jump frequency is high relative to particle encounter frequency (0.6 min^{-1} in this case), all captures may be preceded by a jump that brings the copepod in a good position, while jumps that do not, are not followed by captures. The few other cases where very long detection distances have been reported (Strickler 1982; Paffenhöfer and Lewis 1990) may similarly be subsequent to random flicks of the feeding appendages, which were then interpreted as a response to a stimulus. The advantage of modern high-speed video technology is that it is high quality, cheap, and that many replicate observations can rather easily be made, while former time's video cinematography involved celluloid film that needed subsequent development; it was time-consuming and expensive and the possibility of many replicates was limited.

The implication of using near-field mechanoreception rather than long-range chemoreception to perceive nonmotile (and non-sinking) prey particles, as suggested here, is that prey perception distances are governed mainly by the reach of the setae of the feeding appendages and only to a very limited extent depend on the size of the prey cell (extended by the radius of the prey). The case of motile

prey, perceived remotely through hydromechanical cues, is different. The reaction distance to hydromechanical cues from motile prey scales approximately with $u(b/s)^{0.5}$, where u is the swimming velocity of the prey of radius b (e.g., Kiørboe 2011), and large and fast prey are therefore perceived at a further distance than smaller prey. Such differences in prey perception has implications to the prey size spectra of copepods and may explain why ambush feeding copepods that feed on motile prey appear to be targeting substantially larger prey than similarly sized feeding-current feeding copepods (Wirtz 2012; Saiz et al. 2014) and thus consistent with the prey perception mechanism suggested here.

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