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Reply to comment: Prey perception in feeding-current feeding copepods

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Abstract

We reply to the comments of Paffenhöfer and Jiang (2016) who argues that remote chemical prey perception is necessary for feeding-current feeding copepods to fulfill their nutritional requirements in a dilute ocean, that remote chemical prey detection may only be observed at very low prey concentrations, and that chemical prey perception is feasible if prey cells release dissolved organic material in short-lasting but intense bursts. We demonstrate that mechanoreception at a very short range is sufficient to sustain a living, even in a dilute ocean. Further, if chemoreception requires that prey cells have short intense leakage burst, only a very small fraction of prey cells would be available to the copepod at any instance in time and, thus would be inefficient at low prey concentration. Finally, we report a few new observations of prey capture in two species of copepods, *Temora longicornis* and *Centropages hamatus*, offered a 45- μm sized dinoflagellate at very low concentration. The observed short prey detection distances, up to a few prey cell radii, are consistent with mechanoreception and we argue briefly that near-field mechanoreception is the most likely and common prey perception mechanism in calanoid copepods.

Pelagic copepods can perceive and capture their prey individually. That has long been demonstrated for both feeding-current feeding and ambush feeding copepods (Koehl and Strickler 1981; Jiang and Paffenhöfer 2008). While it is well established that ambush feeders perceive their prey by the fluid mechanical disturbance that the swimming prey generates (Jonsson and Tiselius 1990; Yen and Strickler 1996; Svendsen and Kiørboe 2000; Jiang and Paffenhöfer 2008), the mechanism and distance at which feeding-current feeding copepods can detect non-motile prey remains a controversial issue. In a series of recent studies involving six different species as well as several developmental stages we observed that in all cases, prey had to be in the immediate vicinity of the feeding appendage setae in order to elicit a capture response (Bruno et al. 2012; Kjellerup and Kiørboe 2012; Tiselius et al. 2013; Gonçalves et al. 2014; Gonçalves and Kiørboe 2015). We also reviewed all available evidence of prey perception and found that, in most cases, cells as well as inert plastic

particles were detected within a few prey cell radii from the setae of the feeding appendages (Gonçalves and Kiørboe 2015). We further argued that near-field mechanoreception is the most likely detection mechanism. Paffenhöfer and Jiang (2016, this volume) (P&J) in a constructive rebuttal argue for the maybe more widely held traditional view, that cells are detected remotely by means of chemoreception. Mainly using the copepod *Eucalanus pileatus* as model species, they provide three main arguments: (1) remote detection is necessary for survival in a dilute environment; (2) remote detection is manifest only at low prey concentrations and can therefore only be observed under such conditions; (3) remote chemical detection is feasible and the main mechanism of remote detection. Below we examine their arguments, however, without repeating the evidence and reasoning in Gonçalves and Kiørboe (2015).

Remote detection necessary?

P&J argue that long detection distances are necessary for feeding-current feeding copepods to fulfill their requirements in a nutritionally dilute ocean environment. Thus, they calculate that a 1–2 mm sized copepod needs a prey detection distance, R , of at least 0.5 mm, which, they argue, implies

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

remote detection. However, in their model, R is the radius of the dining sphere and is measured from the center of the body, not from the tip of the feeding appendages. For the copepod species that they have in mind, *Eucalanus pileatus*, the distance from the centerline of the copepod to the tip of the extended maxillipeds is about 0.7 mm (measured on the drawing in Paffenhöfer and Lewis (1990)); if the estimate of this radius R is extended to the tip of the setae of the maxillipeds, it is more than 1 mm, well above the required 0.5 mm. Furthermore, they arrive at this estimate by assuming that the beating of the feeding appendages produces a force that exactly balances gravity such that the copepod is hovering and all the forces goes into producing a feeding current. However, most feeding-current copepods produce a force that exceeds gravity, and the additional force goes into propelling the copepod through the water at a speed which scales approximately with body length and is of order a few body lengths s^{-1} (Kiørboe et al. 2010). This increases the flow of water past the copepod and relaxes the need for a long detection distance. Thus, we argue that remote detection of prey is not a necessity for copepods to gather sufficient nutrition, even at dilute oceanic conditions.

Concentration matters?

P&J then revisit the study of Paffenhöfer and Lewis (1990) that showed that the detection distance of *Eucalanus pileatus* to small (11 μm) diatom cells increases with decreasing prey concentration. At high prey concentration, cells are perceived within reach of the setae of the maxillipeds and the second antennae, consistent with our observations, but at the lowest concentration, the copepods react to cells at a distance of 460 μm from the maxillipeds, thus exceeding the length of the 320- μm long setae of the maxillipeds. Thus, they seem to demonstrate remote detection, although the distance to the second antennae at the time of reaction is only ca. 300 μm and thus within reach of the setae here. Also, as pointed out in our synthesis paper (Gonçalves and Kiørboe 2015), the spatial resolution of their observations was as low as 100–200 μm due to the low frame rate of their recordings (125–250 Hz) and high beat frequency of the appendages (25 Hz). Anyway, P&J correctly argues that we have used unspecified and presumably high prey concentrations for all our observations and therefore only have seen short detection distances, with prey cells essentially touching or nearly touching the setae.

To examine this valid point, we have therefore made a few additional observations, using the copepods *Temora longicornis* and *Centropages hamatus* fed 45- μm sized dinoflagellate cells (*Akashiwo sanguinea*). In contrast to our previous observations on free-swimming animals, we tethered females of the two species to a hair straw and positioned them in front of the lens of a high-speed video camera in a 1-L aquarium with a dilute suspension of *A. sanguinea* (4 cells



Fig. 1. Frozen video image of a prey cell (*Akashiwo sanguinea*) arriving in the feeding current of *Temora longicornis* prior to a capture response is elicited. The distance between the tip of the setae of the 2 n antennae and the cell is about 100 μm . See also video in Supporting Information Appendix 1.

mL^{-1} or $0.2 \text{ mm}^3 \text{ L}^{-1}$). The animals were acclimated to the food concentration overnight before filming with infrared illumination at 500 frames per second with a Phantom v210 high-resolution (1280 \times 800 pixels) high-speed camera equipped with optics to yield a field of view of about $2.6 \times 1.6 \text{ mm}^2$. We observed two capture responses in *C. hamatus*, and three capture responses in *T. longicornis*. In all but one instance, the prey cells were near touching the setae before a capture response was elicited, as in our previous studies. In one case, however, *T. longicornis* responded to a cell at a distance of $\sim 100 \mu\text{m}$ from the setae (See Fig. 1 and movie in Supporting Information Appendix 1). Despite the scarcity of our data, this is then consistent with the idea of elevated sensitivity at low prey concentrations. Our observation is also consistent with several previous reports of detection distances of up to around 100 μm or a few cell radii, as summarized in (Gonçalves and Kiørboe 2015).

We argue that chemical detection is neither required nor likely for remote detection at such short distances. First, the $\sim 100 \mu\text{m}$ detection distance for a 45- μm sized prey cell reported here is in fact similar to that predicted (50–200 μm) by mechanoreception and the fluid mechanical mechanisms examined by Gonçalves and Kiørboe (2015). Second, the chemosensory apical pores on the setae of the feeding appendages, as found in copepods (Paffenhöfer and Loyd 2000) and many other crustaceans, are normally considered to have gustatory (taste) rather olfactory (smell) function; i.e., they only mediate chemical signals upon direct contact with the source (Hallberg and Skog 2012). Paffenhöfer and Loyd (2000) argued that in copepods, these sensillae do in fact have olfactory function, but their main argument was that mechanoreception could not explain the observations.

Chemical detection is feasible?

P&J finally develop an interesting model of diffusion of chemical signals from a prey cell that emits solutes during short bursts of high intensity, rather than continuously at low intensity. Previous models have assumed the latter (Légier-Visser et al. 1986; Tiselius et al. 2013) and argued that at characteristic low average exudation rates the solute concentration in the phycosphere would be insufficient to allow detection. P&J demonstrates that during exudation bursts, solute concentrations may be high enough to allow remote chemical detection at considerable distances by the mechanism suggested by Andrews (1983) and Jiang et al. (2002). However, such intensive leakage bursts must by necessity be rare and therefore only a small fraction of phytoplankton cells would be available for detection by this mechanism at any one point in time. If this were the main mechanism for prey detection at low prey concentrations, then the *available* concentration of cells would be even much lower and, thus, not be conducive to sufficient feeding in nutritionally dilute environments.

Conclusion

While early reports of far-field prey detection on the order of >1 mm within the copepod feeding-current (Strickler 1982) were exciting, subsequent reports have mainly been unable to verify such long detection distances that are rather on the order of <100 μm or a few prey cell diameters (Gonçalves and Kjørboe 2015). There seems to be no disagreement between us and P&J on this point. Here and elsewhere we have argued that hydromechanical detection can explain such detection distances, that chemical detection is unlikely at such short distances, and that mechanoreception therefore is the more likely mechanism. Thus, while we cannot entirely refute the possibility of chemical detection, we maintain the conclusion of Gonçalves and Kjørboe (2015), that “near-field mechanoreception is the common prey detection mode in pelagic copepods”.

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