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Comment: On phytoplankton perception by calanoid copepods

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Abstract

Three publications recently reported that calanoid copepods, feeding on phytoplankton cells by using a feeding current, perceived such cells by mechanoperception. There was no evidence of remote chemically-mediated perception of those cells. These observations differ from earlier findings that feeding-current producing calanoids are able to detect phytoplankton cells by chemoperception at a distance from their particle-collecting setae of their cephalic appendages. The results on mechanoperception and the earlier published data on chemoperception will be presented and discussed. In addition, the concentration of chemicals within the phycosphere of food cells will be re-examined. We conclude that chemoperception of phytoplankton cells by calanoid copepods in a feeding current is feasible.

Usually planktonic copepods exist in an environment where food items are not highly concentrated (e.g., Conover 1968). For such species to persist they ought to possess, among other variables, means to obtain sufficient amounts of food. Planktonic copepods have developed means to persist at the lowest phytoplankton food levels encountered in the epipelagic ocean which are near 0.04 μg chlorophyll L^{-1} (e.g., Paffenhöfer et al. 2007). On the U.S. southeastern shelf where the copepod genera *Eucalanus*, *Centropages*, *Paracalanus*, and *Temora* occur abundantly (Bowman 1971) food concentrations can be as low as 0.2 and as high as 4.0 μg chlorophyll *a* L^{-1} (Yoder et al. 1983). To obtain food particles they need to recognize them among the often numerous nonfood particles, be they phytoplankton cells, protists, nauplii or fecal pellets, either as chemical signals as suggested by Friedman and Strickler (1975) or hydrodynamic ones (e.g., Strickler and Bal 1973).

Over the past decades numerous studies have been presented which support the assumption that phytoplankton cells were perceived by chemosensing of feeding-current producing calanoid copepods: This would be olfaction (at a distance), followed by capture, checked by gustation, and then ingested or rejected (e.g., Paffenhöfer 1998). Recent observations by Tiselius et al. (2013) and Gonçalves et al. (2014) are challenging this process of algal perception via chemosensing by calanoid copepods, and are suggesting from their findings that mechanosensing alone is the respective perception process. Gonçalves and Kiørboe (2015) provided a general review on the topic and additional data.

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The goal of this manuscript is to present the findings of Tiselius et al. (2013), Gonçalves et al. (2014), and Gonçalves and Kiørboe (2015) and discuss them according to an analysis of results from Strickler (1982) and Paffenhöfer and Lewis (1990). This is followed by a discussion how calanoids with a feeding current can persist depending only on mechanoperception. Finally, we will show how short-term leakage could result in above-threshold chemical concentrations in phycospheres, allowing chemosensing by calanoids at a distance.

Results and discussion

Food concentration matters

Tiselius et al. (2013) recorded feeding behavior of two calanoids *Paracalanus parvus* and *Pseudocalanus* sp. at 2200 Hz and 1280 by 800 pixels resolution. Filming occurred in 50 mL flasks at one copepod mL^{-1} offering eight different food species singly or in mixtures at *ad libitum* concentrations which were variable and for which no numbers could be given (P. Tiselius, pers. comm.). These authors reported that prey detection occurred within a few cell radii of the second antennae (A2) or the maxilliped (Mxp). They stated that "there is no evidence of remote chemically mediated sensing when feeding on algal cells up to a size of 35 μm." Gonçalves et al. (2014) used the same video camera as Tiselius et al. (2013) to observe particle perception and capture by late copepodids and adults of the calanoid *Temora longicornis*. A mixed phytoplankton diet (three species) and the ciliate *Mesodinium rubrum* were offered. Prey concentration was not quantified. Between 10 and 20 copepods were observed in small aquaria ranging from 5 mL to 200 mL. Here, as in Tiselius et al. (2013) prey perception occurred

when a prey cell was within a few cell radii of the setae of one of the food collecting appendages. Hollow glass spheres of a medium size of 10 μm "did not elicit capture reactions from the copepods." The authors stated "prey detection mechanisms appear to be the same for several (most?) species of copepods and depend on very close contact with prey cells."

Gonçalves and Kiørboe (2015) reviewed the available observations on algae perception in the literature and added new observations on *Calanus helgolandicus* and *Acartia tonsa* "to show that in most cases the prey …. has to be within a few cell radii from the setae of the appendages to elicit a capture response". No food concentrations were given.

Strickler (1982) had reported that a free-swimming calanoid *Eucalanus pileatus* reacted with its cephalic appendages to an incoming alga when the alga was 1.25 mm away, i.e., out of reach of the appendage setae. This led to the assumption that this cell was perceived chemically. Paffenhöfer and Lewis (1990) offered females of the calanoid *Eucalanus pileatus* a range of environmentally-oriented concentrations of the diatom *Thalassiosira weissflogii* (11 μm diameter) to determine the distance at which this diatom in the incoming feeding current was perceived. These females were preconditioned to this alga and the respective food concentrations for three days. The food concentrations ranged from 3 mm^3 L^{-1} (about 240 μg C L^{-1}) to as low as 0.03 mm^3 L^{-1} (near 2.4 μg C L^{-1}). Phytoplankton concentrations on the U.S. southeastern shelf where *E. pileatus* is often encountered ranged from 0.2. μg chlorophyll L^{-1} to 4 μg chlorophyll L^{-1} during a 5-day cruise in August 1978 (Yoder et al. 1983). One μg of chlorophyll *a* equals about 25 to > 50 μg of carbon. Paffenhöfer and Lewis (1990) found that *E. pileatus* females perceived the diatom at a significantly greater distance at cell concentrations of 0.03 mm^3 L^{-1}, 0.1 mm^3 L^{-1}, and 0.3 mm^3 L^{-1} than at 1.0 mm^3 L^{-1} and 3.0 mm^3 L^{-1}. This implies that when food became scarce (2.4 μg C L^{-1}, 8 μg C L^{-1} and 24 μg C L^{-1}) such diatom cells were perceived at a greater distance from the food collecting appendages than when food was abundant (80 μg C L^{-1} and 240 μg C L^{-1}). These authors showed that the average distance of cell perception of 220 μm at 1.0 mm^3 L^{-1} (from the tip of the Mxp to each perceived cell) was shorter than the length of most Mxp setae (between 200 μm and 320 μm length). Thus, at high food concentrations the perceived diatoms were in close vicinity of the appendage setae. This is similar to the results of Tiselius et al. (2013) and Gonçalves et al. (2014). The distances of diatom perception increased when food concentrations decreased: At 0.1 mm^3 L^{-1} of *T. weissflogii* (8 μg C L^{-1}) the cells were perceived at an average distance of 460 μm from the tip of the Mxp. This distance is beyond the average seta length of 320 μm. Thus, on average those cells were perceived out of range of the Mxp's setae. The actual perception of such a cell should have occurred prior to observing the motion initiation of the Mxp, i.e., at an even greater distance from the respective seta.

This increase of diatom perception is in line with Lohrenz (1951) who stated in his book *The Foundations of Ethology* that sensitivity thresholds decrease with decreasing food concentrations i.e., sensitivity increases with decreasing food levels. This increase in sensitivity allows an *E. pileatus* female to nearly compensate for decreases in food abundance: At 1.0 mm^3 L^{-1} the female would ingest daily 5.7 μg C, at 0.3 mm^3 L^{-1} 4.9 μg C and at 0.1 mm^3 L^{-1} 4.1 μg C (Paffenhöfer and Lewis 1990, using their Fig. 3).

Mechanosensing alone may not be sufficient

Should the described mechanoperception be the sole means for such calanoid copepods to perceive a non-moving particle to obtain sufficient food? Here, we try to understand this question using the stokeslet model for the feeding current created by a negatively buoyant copepod that hovers (Kiørboe and Jiang 2013). The clearance rate of a hovering copepod is

$$\Omega = \frac{F}{4\mu} R, \tag{1}$$

where μ is the fluid dynamic viscosity (= 1.390×10^{-3} kg m^{-1} s^{-1} for seawater with salinity 35 at 10°C at one normal atmosphere), R is the perceptive range of the copepod, and F equals the copepod's excess weight that is calculated as $F = \Delta\rho\ g\ V$ where $\Delta\rho$ is the excess density of the copepod, V the copepod body volume, and g the gravitational acceleration (= 9.81 m s^{-2}). Consequently, the body-volume specific clearance rate is

$$\frac{\Omega}{V} = \frac{g}{4\mu} \Delta\rho R \times 86400, \tag{2}$$

which is in the units of d^{-1}. For the copepod to sustain a life in the ocean, it is required that $\frac{\Omega}{V} > 10^6$ d^{-1} (Kiørboe 2011). Thus, it is required that R satisfies

$$R > \frac{10^6}{86400} \frac{4\mu}{g} \frac{1}{\Delta\rho}. \tag{3}$$

Based on the plot of the required minimum R as a function of $\Delta\rho$ in the range of [3, 30] kg m^{-3} (Fig. 1), we conclude: To obtain sufficient food, copepods that are 1–2 mm in prosome length and have an excess density in the range of [5, 15] kg m^{-3} require a perceptive range longer than 500 μm, which is beyond the reach of their Mxp setae. For those copepods, chemoperception is a more feasible mechanism to perceive phytoplankton cells remotely. Conversely, larger and denser copepods that generate strong feeding currents may rely solely on the short-ranged mechanoperception to detect phytoplankton cells and obtain sufficient food. However, strong feeding currents would likely bring greater predation risks from rheotactic predators.

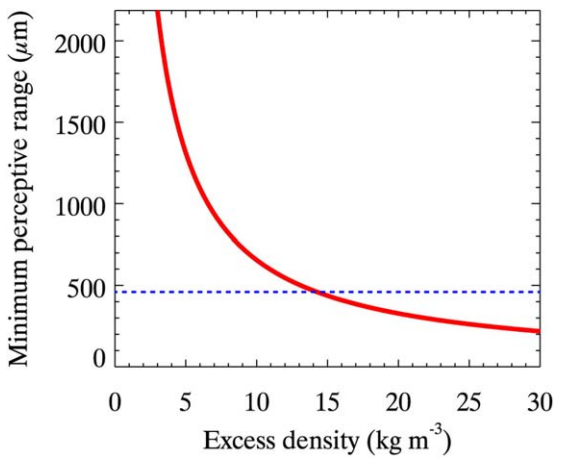

Fig. 1. Required minimum perceptive range, *R*, as a function of copepod excess density, $\Delta\rho$. If the actual perceptive range of a negatively buoyant copepod that hovers to create a feeding current is longer than the required minimum perceptive range, the resulting body-volume specific clearance rate will be larger than 10^6 d^{-1}. The dotted line indicates the observed perceptive range of 460 μm for the copepod *Eucalanus pileatus* females to detect the algae *Thalassiosira weissflogii* at 0.1 mm^3 L^{-1} (Paffenhöfer and Lewis 1990).

Will the suggested mechanoperception be sufficiently sensitive to perceive tiny and nutritious non-moving particles? *Temora longicornis* copepodids and adults did not perceive phytoplankton cells of near 7–9 μm diameter; they achieved 100% of a capture response for encountered cells of 15 to near 30 μm diameter decreasing beyond that size (Gonçalves et al. 2014, their Fig. 4). When environmental particle suspensions were offered to females of *Paracalanus parvus* clearance rates increased asymptotically from near 1 mL swept clear h^{-1} at 2 μm particle diameter to a maximum near 40–60 μm cell diameter (Bartram 1981); this implied that *P. parvus* was able to perceive a fraction of small cells and ingest them.

If mechanoperception is the only means of particle perception it should include living and nonliving particles as long as they possess a certain size (e.g., Gonçalves et al. 2014, their Fig. 4). Paffenhöfer and Van Sant (1985) offered phytoplankton cells and polystyrene beads of 18 μm diameter, separately and together, to adult females of *Eucalanus pileatus*: "Beads offered alone arrived at the second maxillae (M2) without flicks of the other mouthparts ….". They were rejected after three or more beads had arrived at the mouth. However, immediately after the diatom *Thalassiosira weissflogii*, then about 12 μm diameter, was added the copepods began to ingest large quantities of beads. What happened? As several diatoms arrived at the mouth they triggered the gustatory signal to be ingested (e.g., Paffenhöfer et al. 1982) while at the same time several beads were at the mouth. Each, beads and diatoms, were offered at 0.3 mm^3 L^{-1}. Other studies offering inert spheres to calanoids revealed similar findings: *Calanus pacificus* was reluctant to ingest plastic spheres unless nutritional particles were present (Frost 1977). For *Acartia clausii* the ratio of ingested phytoplankton cells to ingested beads was 198:1 (Donaghay 1980). However, Huntley et al. (1983) found that *C. pacificus* ingested spheres at similar rates in the presence and absence of phytoplankton. Gonçalves et al. (2014) used hollow glass spheres of 10 μm diameter to trace fluid motion, and found that those particles "did not elicit capture reactions from the copepods" (free-swimming *Temora longicornis*).

Short-term, high-intensity cell leakage may facilitate chemosensing

When calculating the stretching of the phycosphere surrounding an algal cell, Jiang et al. (2002) assumed a definition of the phycosphere to be the space between the cell surface and the concentric surface at 10 times the cell radius. An implicit assumption was that the chemical concentration within the defined phycosphere would be higher than the threshold concentration required by copepod chemosensing. However, the validity of this implicit assumption remained unexamined. Tiselius et al. (2013) and Gonçalves and Kiørboe (2015) pointed out in detail the limits of copepod chemosensing. This included various assumptions such as the threshold concentration of chemical detection, and leakage of molecules by potential prey cells. In particular, they examined the validity of the implicit assumption made by Jiang et al. (2002). They used a daily leakage rate, *Q*, of 5% d^{-1} of the algal cell mass. They assumed a threshold concentration of 5×10^{-8} mol L^{-1} for copepods to detect amino acids. For a spherical cell of radius *a*, they applied the steady state solution, $C(r) = Q/(4\ \pi\ D\ r)$, to calculate the concentration at the cell surface (where $D \sim 1.0 \times 10^{-9}$ m^2 s^{-1} the diffusivity of the cell mass solutes, and *r* the distance to the sphere center). Their calculations showed that the concentration within the phycosphere surrounding the algal cell was lower than the threshold concentration. Thus, they concluded that distant detection/olfaction of individual algal cells was only physically feasible for very large and leaky cells.

However, the steady state solution requires the cell to exude an infinite amount of solutes for infinite time to build up the steady state concentration field. Thus, the long-term leakage rate has to be kept low. In fact, Tiselius et al. (2013) and Gonçalves and Kiørboe (2015) used a low daily leakage rate of $\sim$ 5% d^{-1} of the cell mass to end up with the concentration within the phycosphere that was lower than their assumed threshold. Nevertheless, algal cells at times have considerably larger (e.g., 100-fold larger) short-term leakage rates than the daily leakage rate (Seymour et al. 2010). In the following, we re-examine the concentration within the phycosphere that is formed due to a short-term, high-magnitude leakage rate.

If chemical solutes leak at a constant rate Q (mol s^{-1}) over the surface of a sphere of radius a, starting at $t = 0$, the concentration at point r ($\geq a$) at time t is (Carslaw and Jaeger 1959, p. 263)

$$C(r,\ t)=\frac{Q}{8\pi aDr}\left\{\frac{\sqrt{4Dt}}{\sqrt{\pi}}\left[e^{-\frac{(r-a)^2}{4Dt}}-e^{-\frac{(r+a)^2}{4Dt}}\right]-(r-a)\mathrm{erfc}\left(\frac{r-a}{\sqrt{4Dt}}\right)+(r+a)\mathrm{erfc}\left(\frac{r+a}{\sqrt{4Dt}}\right)\right\}, \tag{4}$$

where erfc(x) is the complementary error function.

From Eq. 4, the concentration at the surface of the sphere (i.e., $r = a$) is calculated as

$$C_{r=a}(t)=C_0\left[\frac{1}{\sqrt{\pi}}\sqrt{t/\tau}\left(1-e^{-\tau/t}\right)+\mathrm{erfc}\left(\sqrt{\tau/t}\right)\right], \tag{5}$$

where

$$C_0=\frac{Q}{4\pi Da}, \tag{6}$$

which is the steady state ($t \to \infty$) concentration at the surface of the sphere, and

$$\tau=\frac{a^2}{D}, \tag{7}$$

which defines a diffusion time scale. The concentration at $r = 10a$ is calculated as

$$C_{r=10a}(t)=C_0\frac{1}{20}\left\{\frac{2}{\sqrt{\pi}}\sqrt{t/\tau}\left[e^{-\frac{81}{4}(\tau/t)}-e^{-\frac{121}{4}(\tau/t)}\right]-9\mathrm{erfc}\left(\frac{9}{2}\sqrt{\tau/t}\right)+11\mathrm{erfc}\left(\frac{11}{2}\sqrt{\tau/t}\right)\right\}. \tag{8}$$

Figure 2 shows the calculation results from Eqs. 5 and 8. It is shown that it will take $\sim 30\tau$ for the sphere surface to reach a concentration of $0.9C_0$, $\sim 110\tau$ for the sphere surface to reach a concentration of $0.95C_0$, and $\sim 110\tau$ for the surface at $r = 10a$ to reach a concentration of $0.05C_0$. For an algal cell of radius 25 μm, 30τ is $\sim$ 19 s and 110τ is $\sim$ 69 s. These results suggest that the phycosphere surrounding an algal cell forms quickly after the cell exudes its body solutes for only a short time on the order of 1 to a few minutes.

Next, we consider a short-term, high-magnitude leakage rate of 100% d^{-1} of the cell mass that lasts for only a short time on the order of 1 to a few minutes. We then follow the method of Tiselius et al. (2013) to calculate the resulting concentration at both the cell surface (i.e., $r = a$) and at the surface of $r = 10a$ at time $t = 110\tau$ after the leakage starts (Fig. 3). If the space between the cell surface and the surface of $r = 10a$ is defined as the phycosphere [i.e., the definition made by Jiang et al. (2002)], for an algal cell of radius 25 μm the resulting concentration within the phycosphere will be

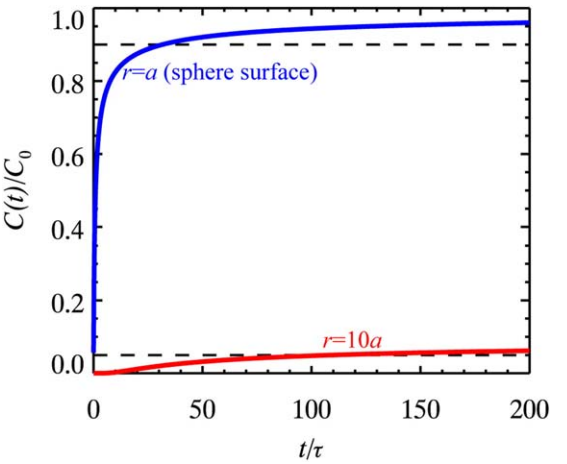

Fig. 2. Concentration, $C(t)$, as a function of time, t, at (1) the sphere surface ($r = a$, the blue line) and (2) $r = 10a$ (the red line). Concentration is normalized by the steady state surface concentration, C_0, and time is normalized by the diffusion time scale, τ.

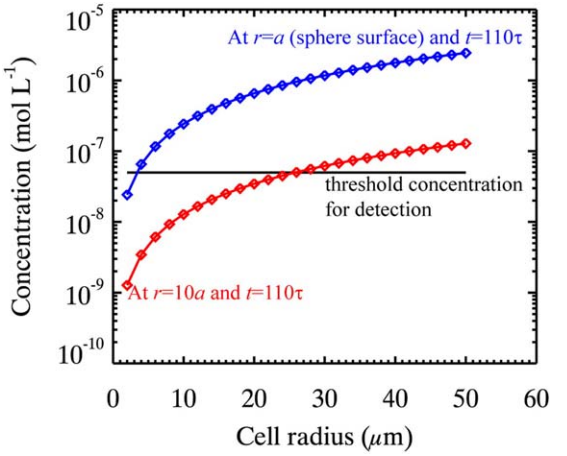

Fig. 3. Estimated sphere surface ($r = a$) and $r = 10a$ concentrations of amino acids for diatoms as functions of cell size, at time $t = 110\tau$ after the leakage starts.

higher than the assumed threshold concentration. Thus, from a point of view of diffusion physics, the calculations done by Tiselius et al. (2013) and Gonçalves and Kiørboe (2015) were not sufficient to invalidate the implicit assumption made by Jiang et al. (2002).

Empirical information on several aspects is still needed to inform our current debate on the topic. We are still not able to identify what chemical components allow copepods to detect individual algae and at what threshold concentrations. We also need to know more about cell leakage rates. Information on the long-term averaged cell leakage rates may not be enough. Short-term, high-magnitude cell leakage rates could potentially physically generate concentrations within the cell phycosphere that are high enough to trigger remote chemoreception of individual algal cells by copepods.

The temporal variability of cell leakage rates could potentially modulate the remote chemoreception by copepods of individual algae. This is related to algal quality, which is an important factor affecting copepod feeding on algae.

We have no idea how rapid the reaction of a calanoid would be once a molecule, triggering gathering motion of an appendage, has reached the tip of a seta of such an appendage (e.g., Paffenhöfer and Loyd 2000). We know from calanoids that reaction time to hydrodynamic signals can be as short as 2.5/1000 of a second (Lenz and Hartline 1999). We also do not know which molecules and how many would be needed to trigger such an olfactory reaction as a phytoplankton cell is perceived. So where would we go from here? Models alone will not do the job. If there is a model we need verification. As food levels and food composition differ in the ocean we (i.e., researchers interested in this topic) ought to conduct experiments/observations with calanoids and food particles at environmental conditions (e.g., a range of food concentrations) over time, having the feeders preconditioned in not so small vessels. This will take time and patience yet should lead to an understanding how calanoids perceive various phytoplankton species in the presence of environmental particles (e.g., detritus, fecal pellets), and actually can make a living at the often occurring low environmental food concentrations.

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