biology letters
Marine biology

Biol. Lett. (2012) **8**, 438–441
doi:10.1098/rsbl.2011.1073
Published online 7 December 2011

Prey detection in a cruising copepod

Sanne Kjellerup[1,2] and Thomas Kiørboe[1,*]

[1]*Centre for Ocean Life and Section for Ocean Ecology and Climate, Technical University of Denmark, Kavalergården 6, 2920 Charlottenlund, Denmark*
[2]*Greenland Climate Research Centre, 3900 Nuuk, Greenland*
**Author for correspondence (tk@aqua.dtu.dk).*

Small cruising zooplankton depend on remote prey detection and active prey capture for efficient feeding. Direct, passive interception of prey is inherently very inefficient at low Reynolds numbers because the viscous boundary layer surrounding the approaching predator will push away potential prey. Yet, direct interception has been proposed to explain how rapidly cruising, blind copepods feed on non-motile phytoplankton prey. Here, we demonstrate a novel mechanism for prey detection in a cruising copepod, and describe how motile and non-motile prey are discovered by hydromechanical and tactile or, likely, chemical cues, respectively.

Keywords: prey detection; *Metridia longa*; hydromechanical signals; tactile signals; chemical signals

1. INTRODUCTION

Zooplankton live in a viscous and nutritionally dilute world. To cover their needs, they must daily clear a volume of sticky water 10^6 times their own body volume for microscopic prey [1]. Zooplankton have developed three ways of achieving this: they generate a feeding current and capture prey arriving in this current; they are ambush feeders that wait for prey to pass within their capture radius; or they cruise through the water and capture encountered prey [1]. Because of viscosity, filtering of water and direct interception of prey is often not feasible and in most copepods—the dominating zooplankton group in the ocean—remote prey detection and active prey capture is involved. In copepods that generate a feeding current, the cloud of organic solutes leaking from phytoplankton prey is drawn out in the sheared current, and a chemical signal arrives at the copepod approximately 0.5 s before the phytoplankton cell itself, allowing the copepod to redirect its feeding current and capture the cell [2–4]. Motile prey generate a hydrodynamic disturbance that may be perceived by the copepod and elicit an attack; this is how ambush feeding and some cruising copepods detect prey [5–7]. Some cruising copepods also feed on protists of limited or no motility. Such prey cannot be detected in front of the copepod, owing to the lack of hydromechanical signals and of a feeding current that can transport a chemical signal [4], and prey encounter has therefore consequently been described as by direct interception [8]. Interception feeding, however, is very inefficient because the cruising copepod pushes water away, allowing only a small fraction of the apparently encountered prey to be actually intercepted [1]. Such a mechanism would simply not allow sufficiently high feeding rates for survival.

Here, we use high-speed video and flow visualization to demonstrate a novel prey detection mechanism and show that both motile and non-motile prey are detected remotely and actively captured by a cruising copepod, *Metridia longa*.

2. MATERIAL AND METHODS

Copepods were collected at 200 m depth and 4°C in Disko Bay, Greenland. *Metridia longa* resides at depth during day, but feeds near the surface at night. All observations were made at 4°C with late copepodites or females (prosome length approx. 2.5 mm) after at least 1 day of acclimation. Five copepods were placed in an aquarium ($8.5 \times 10.2 \times 3.2\ \mathrm{cm}^3$) together with either recently hatched nauplii of the copepod *Acartia tonsa* (motile prey, approx. 150 μm), or dinoflagellates, *Akashiwo sanguine* (approx. 50 μm), that are essentially non-motile at this temperature. Feeding behaviour was recorded at a frame rate of 1600 Hz by a Phantom v210 (1280×800 pixels) high-speed camera equipped with optics to yield a field of view of $3.0 \times 1.9\ \mathrm{cm}^2$. Collimated light was provided by a halogen bulb that was shone through the aquarium directly towards the camera. Prey attacks/captures that occurred in focus were stored. We recorded nine and 14 attacks on dinoflagellates and nauplii, respectively. Prey positions and reaction, pursuit and handling times were measured using ImageJ software. Prey detection is defined by the copepod initiating an attack. Reaction time is defined as the time from when the prey jumps until the copepod initiates an attack (only motile prey), pursuit time as the time from when the copepod reacts until the prey is captured and handling time as the time from reaction until the copepod has resumed normal swimming. Not all parameters could be recorded in all attack events.

Longer sequences were recorded at 24 Hz and low magnification to measure copepod cruising speeds. Two-minute sequences were analysed using LabTrack software (DiMedia) to yield swimming tracks; 48 tracks were retrieved and used to compute swimming speeds (electronic supplementary material, figure S1).

The flow created by cruising copepods was visualized using particle image velocimetry (PIV). A sheet of light provided by an infrared-pulsed laser (808 nm, 3 W) was shone into the aquarium perpendicular to the camera and 10 μm tracer particles were added. Recordings were made at 400 Hz and sequences with animals swimming in the illuminated plane were analysed using standard PIV software (LaVision) to yield flow fields.

3. RESULTS

Metridia longa cruises through the water at an average speed of $11.1 \pm 1.7\ \mathrm{mm\ s^{-1}}$ (mean ± s.d.) while searching for prey. The fluid flow generated by the rapidly cruising copepods is modest (figure 1*a*). Obviously, there is no feeding current, i.e. a flow towards the animal. On the contrary, the translating animal pushes water away in front of itself. Hence, a chemical signal from a prey cannot be transported to reach the animal before the prey particle itself.

Both motile and non-motile prey were detected remotely and elicited attack responses in the cruising copepod, but the two types of prey were detected at different positions relative to the copepod (figure 1*b*). Dinoflagellate cells were detected only after the copepod had swum past them and when the prey was ventral or latero-ventral to the copepod, whereas nauplii were also detected in front of the copepod close to the antennules.

Nauplii prey were invariably detected subsequent to the nauplius performing an escape jump and with a delay of 16 ± 9 ms ($n = 13$). When the nauplius was

Electronic supplementary material is available at http://dx.doi.org/10.1098/rsbl.2011.1073 or via http://rsbl.royalsocietypublishing.org.

Received 2 November 2011
Accepted 16 November 2011

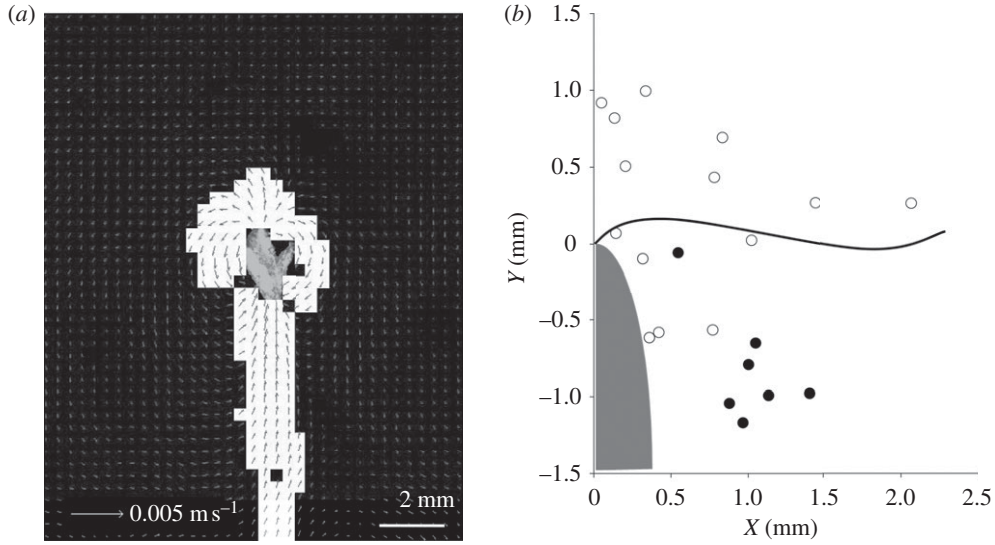

Figure 1. (*a*) Flow field induced by cruising copepod. The flow field is relative to a fixed frame of reference. Regions with velocities exceeding 0.5 mm s^{-1} are shaded white. The animal cruises at 11 mm s^{-1}. (*b*) Position of prey relative to the copepod (shown in grey shading with the antennule indicated). Note that all positions are two-dimensional projections and that real distances are thus underestimated (filled circles, dinoflagellate; open circles, nauplii).

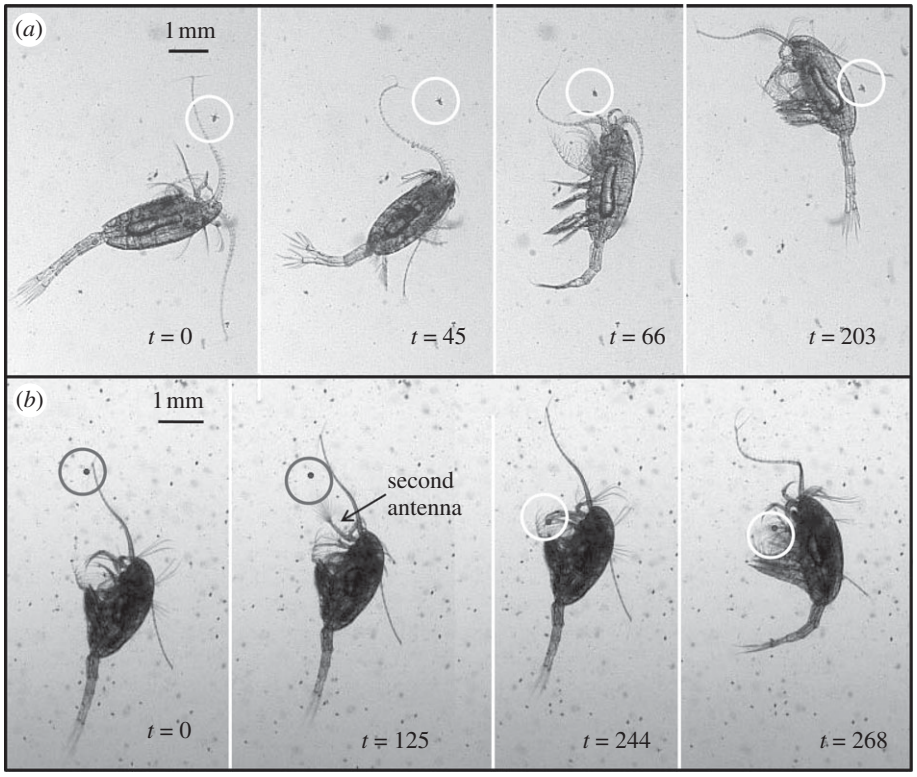

Figure 2. (*a*) Detection and capture of copepod nauplius or (*b*) dinoflagellate. Prey marked by ring. Video images frozen at various times (*t*, ms). (*a*) At $t = 0$, the nauplius jumps away from the cruising copepod that responds after 30 ms and jumps towards the prey ($t = 45$ and $t = 66$), but the prey manages to escape ($t = 203$). (*b*) At $t = 244$ ms, the prey cell is detected, which elicits a reaction. The prey is eventually captured just subsequent to $t = 268$ ms.

detected in front of the copepod, the copepod jumped forward by sequentially kicking its four pairs of swimming legs backwards; in the attack jump, the copepod may also rotate to turn its ventral side towards the prey (figure 2*a*; electronic supplementary material, video S1). The copepod then opened the feeding appendages, creating a suction that draws in the prey, either in the first or in subsequent appendage openings. For the successful attacks, the average pursuit time was 99 ± 44 ms ($n = 8$) and the handling time was 173 ± 69 ms ($n = 9$). In some cases, the nauplius managed to escape (figure 2*a*).

Non-motile dinoflagellates were detected only after the copepod had passed the prey. The prey had to be very close to one of the feeding appendages, typically the second antennae, to elicit an attack response.

In most cases, it looked as if the copepod had to actually touch the prey with one of the 0.75 mm long setae extending from the second antennae. The copepod did not show attack jump, but the prey was captured by the copepod opening the feeding appendages and pulling in the prey, similar to the behaviour described above (figure 2*b*; electronic supplementary material, video S2). The pursuit and handling times were 164 ± 88 ($n = 9$) and 270 ± 130 ms ($n = 9$), respectively, insignificantly longer than for nauplius prey (*t*-test, $0.1 < p < 0.05$ for both).

4. DISCUSSION

Interception feeding is very inefficient in small aquatic predators, which operate at low Reynolds numbers, owing to the viscous boundary layer that surrounds them [1]. For cruise feeding to be efficient, it therefore requires remote detection of the prey. This is well described for cruising fish larvae that localize prey visually [9] and for cruising copepods that perceive prey by fluid signals [5], as suggested here for the detection of escaping nauplii. Flagellates that were formerly believed to be interception feeders [10] have since turned out to encounter prey by other means [11]. Small aquatic predators approaching or capturing prey have to 'trick' viscosity in various ways to overcome the boundary layer effect. They do this either: (i) by accelerating out of the viscous regime in the moment of attack as in ambush feeding copepods [7], (ii) by performing asymmetric, 'flicking' movements of feeding limbs as in feeding–current feeding copepods [2], (iii) by creating a suction flow when opening the mouth as they lunge forward towards the prey as in suction feeding larval fish [12], or (iv) by shooting a harpoon-like structure that penetrates the viscous boundary layer, as in some pallium feeding dinoflagellates [13]. All these attack modes require prior detection of the prey.

Cruising *M. longa* does not intercept either motile or non-motile prey directly. Rather, prey cells are detected remotely. The response to escaping nauplii is consistent with the copepod detecting the fluid disturbance created by the jumping nauplius, and the reaction time is of the same order as the reported transmission time of signals through the antennules [14]. In the case of non-motile prey, detection takes place only after the copepod has passed the prey and at a very close distance to the second antennae. The presence of prey in the flow field created by the cruising copepod does create a very small fluid signal, but this is too small to be detected by the predatory copepod [15]. Thus, the cue for prey detection is either chemical or tactile. In copepods that generate a feeding current, the stretching of the chemical plume around the prey cell in the accelerating, sheared current allows prey detection at a distance that is of the order of the prosome length of the copepod [16]. In the absence of a feeding current, the plume is not similarly stretched [4], and the cell has to get very close to the feeding appendages for the copepod to detect a chemical signal. The detection area for non-motile prey is basically restricted to the region covered by the motion of the tip of the second antennae, an area that is approximately 1 mm wide and that begins outside the viscous boundary layer approximately 0.5 mm ventral to the copepod in the case of *M. longa*.

Remote detection of prey, even at a relatively short distance as that observed here for dinoflagellate prey, dramatically increases the encounter efficiency over that owing to direct interception. The clearance rate owing to direct interception or to remote detection of prey can be roughly approximated by $1.5\ \pi r^2 v$ and $\pi R^2 v$, respectively, where r is the radius of the prey, R the detection distance to the prey or the radius of the detection area and v the cruise speed of the copepod [1]. Inserting values relevant for the dinoflagellate prey ($v = 1.1$ cm s^{-1}, $r = 15 \times 10^{-4}$ cm, $R = 0.05$ cm) yields clearance estimates of 10^{-5} and 10^{-2} cm^3 cop^{-1} s^{-1}, or specific clearance rates (clearance rate per body volume) of approximately 10^3 and approximately 10^6 per day, for direct interception feeding and remote detection, respectively. The latter estimate is similar to that required for zooplankton to sustain a life in the ocean [1], and consistent with observed clearance rates of *M. longa* on dinoflagellate cells (K. Riisgaard 2010, unpublished data). Feeding on motile prey that is detected further away ($R \sim$ length of antennules, approx. 0.2 cm) leads to even higher potential clearance rates.

Here, we have described a novel prey detection mechanism and demonstrated that short-distance detection of the prey and not direct interception is involved in the feeding process of a cruise feeding copepod. Remote prey detection, even at a short distance, combined with high-cruising speeds explains how copepods with this feeding mode can survive in the ocean on algal diets.

We acknowledge support from the Carlsberg Foundation, the Danish Council for Independent Research and Arctic Station Qeqertarsuaq, University of Copenhagen.

1 Kiørboe, T. 2011 How zooplankton feed: mechanisms, traits, and trade-offs? *Biol. Rev.* **86**, 311–339. (doi:10.1111/j.1469-185X.2010.00148.x)
2 Koehl, M. A. R. & Strickler, J. R. 1981 Copepod feeding currents: food capture at low Reynolds number. *Limnol. Oceanogr.* **26**, 1026–1073. (doi:10.4319/lo.1981.26.6.1062)
3 Andrews, J. C. 1983 Deformation of the active space in the low Reynolds number feeding current of calanoid copepods. *Can. J. Fish. Aquat. Sci.* **40**, 1293–1302. (doi:10.1139/f83-147)
4 Jiang, H., Osborn, T. R. & Meneveau, C. 2002 Chemoreception and the deformation of the active space in freely swimming copepods: a numerical study. *J. Plankton Res.* **24**, 495–510. (doi:10.1093/plankt/24.5.495)
5 Doall, M. H., Strickler, J. R., Fields, D. M. & Yen, J. 2002 Mapping the free-swimming attack volume of a planktonic copepod, *Euchaetarimana*. *Mar. Biol.* **140**, 871–879. (doi:10.1007/s00227-001-0735-z)
6 Jiang, H. & Paffenhöfer, A. 2008 Hydrodynamic signal perception by copepod *Oithona plumifera*. *Mar. Ecol. Prog. Ser.* **373**, 37–52. (doi:10.3354/meps07749)
7 Kiørboe, T., Andersen, A., Langlois, V., Jakobsen, H. H. & Bohr, T. 2009 Mechanisms and feasibility of prey capture in ambush feeding zooplankton. *Proc. Natl Acad. Sci. USA* **106**, 12 394–12 399. (doi:10.1073/pnas.0903350106)
8 Uttieri, M., Paffenhöfer, G. A. & Mazzocchi, M. G. 2008 Prey capture in *Clausocalanus furcatus* (Copepoda: Calanoida). The role of swimming behaviour. *Mar. Biol.* **153**, 925–935. (doi:10.1007/s00227-007-0864-0)

9 Batty, R. S. 1987 Effect of light intensity on activity and food-searching of larval herring, *Clupea harengus*: a laboratory study. *Mar. Biol.* **94**, 323–327. (doi:10.1007/BF00428237)
10 Fenchel, T. 1984 The ecology of heterotrophic microflagellates. *Adv. Microb. Ecol.* **9**, 57–97.
11 Langlois, V. J., Andersen, A., Bohr, T., Visser, A. W. & Kiørboe, T. 2009 Significance of swimming. *Aquat. Microb. Ecol.* **54**, 35–44. (doi:10.3354/ame01253)
12 Holzman, R. & Wainwright, P. C. 2009 How to surprise a copepod: strike kinematics reduce hydrodynamic disturbance and increase stealth of suction-feeding fish. *Limnol. Oceanogr.* **54**, 2201–2212. (doi:10.4319/lo.2009.54.6.2201)
13 Hansen, P. J. & Calado, A. J. 1999 Phagotrophic mechanisms and prey selection in free-living dinoflagellates. *J. Eukar. Microb.* **46**, 382–389. (doi:10.1111/j.1550-7408.1999.tb04617.x)
14 Waggett, R. J. N. & Buskey, E. J. 2008 Escape reaction performance of myelinated and nonmyelinated calanoid copepods. *J. Exp. Mar. Biol. Ecol.* **361**, 111–118. (doi:10.1016/j.jembe.2008.05.006)
15 Visser, A. W. 2001 Hydromechanical signals in the plankton. *Mar. Ecol. Prog. Ser.* **222**, 1–24. (doi:10.3354/meps222001)
16 Paffenhöfer, G. A. & Lewis, K. D. 1990 Perceptive performance and feeding behavior of calanoid copepods. *J. Plankton Res.* **12**, 933–946. (doi:10.1093/plankt/12.5.933)