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1 **Resolving the paradox of the ambush feeding cyclopoid copepod *Apocyclops royi***
2 **being microphageous**

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12 Running head: Feeding behavior of *Apocyclops royi*

13 Author contributions: AZ, BWH, TK, and FR conceived the study designed the experiments. AZ
14 and FR performed the experiments. All authors contributed to data analysis and interpretation. AZ
15 and FR wrote the manuscript with significant input from BWH and TK.

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17 **Keywords:** *Apocyclops royi*, prey-capture, ambush feeding, escaping capacity

18

19 **Abstract**

20 The cyclopoid copepod *Apocyclops royi* is assumed to be an ambush feeder that passively waits for
21 its prey and captures it by a fast surprise attack. This feeding strategy requires an acute sensibility to
22 hydromechanical signals generated by moving prey. However, *A. royi* in long-term cultures is able
23 to survive microphageously fed solely on Baker's yeast (*Saccharomyces cerevisiae*), a small, non-
24 motile prey. In this study, we investigate the feeding behavior of *A. royi* and how it senses *S.*
25 *cerevisiae* cells. Using high-speed video, we find that *A. royi* still exhibits an ambush feeding
26 behaviour when fed *S. cerevisiae*. Moreover, we characterise the distance and the duration of attack
27 jumps and evaluate the sensitivity of *A. royi* to fluid disturbances by filming its escaping behaviour
28 when caught in a suction flow simulating a predator e.g., a fish larva. We demonstrate that its
29 sensitivity to fluid disturbances is very similar to that of other copepod species. Thus, we find that
30 remote detection of *S. cerevisiae* cells due to hydromechanical signals is unlikely as the particles are
31 small ($3.8 \pm 1.3 \mu\text{m}$) and non-motile, and that *A. royi* likely senses *S. cerevisiae* cells by randomly
32 touching them with setae on their first antennae.

33 **Introduction**

34 The cyclopoid copepod *Apocyclops royi* is one of two dominant zooplankton species in brackish
35 Taiwanese aquaculture ponds (Jepsen *et al.*, 2021). It is well adapted to these waters that are
36 characterized by extreme fluctuations in salinity, oxygen, and food availability (Blanda *et al.*,
37 2017).

38 *A. royi* is able to survive and reproduce on very poor monospecific diets, such as Baker's yeast
39 (*Saccharomyces cerevisiae*) (Nielsen *et al.*, 2019, 2020). This is because *A. royi* can synthesise n-3
40 polyunsaturated fatty acids (PUFA) and produce docosahexanoic acid (DHA) even when fed low-
41 PUFA diets. These discoveries provide the metabolic reason why *A. royi* can survive on Baker's
42 yeast that is practically deprived of long-chained fatty acids, but do not provide any information on
43 how these copepods sense and catch these small (3–4 μm) non-motile particles acting
44 microphageously, i.e., feeding upon tiny particles. *A. royi* nauplii exhibit ambush feeding when fed
45 the motile microalga *Isochrysis galbana* ($\sim 6 \mu\text{m}$), one of its natural prey (Wu *et al.*, 2011).
46 However, there are no observations on the feeding behavior of later life-cycle stages of this
47 presumably ambush feeding copepod. Ambush-feeding copepods generally passively wait for
48 motile prey to swim within their sensory sphere, and then jump towards the prey and catch it by
49 creating a vacuum (Svensen and Kiørboe, 2000). *Oithona davisae*, an obligatory cyclopoid ambush
50 feeder, and *Acartia tonsa*, a calanoid partial ambush feeder, both elicit an attack when the prey
51 comes within ~ 0.2 mm of their first antennae (Kiørboe *et al.*, 2009). This suggests that the prey is
52 perceived by setae on their antennae acting as mechanoreceptors that perceives the fluid disturbance
53 generated by the motile prey (Strickler and Bal, 1973). However, as opposed to the microalgae
54 usually fed to ambush feeding copepods in cultures, *S. cerevisiae* cells are not motile and do not
55 generate a fluid signal. How, then, does *A. royi* manage to feed on Baker's yeast?

56 Here, we study the foraging and escape behavior of *A. royi* by direct observations using high-speed
57 videography. We find that *A. royi* elicits ambush feeding behavior even when fed the small non-

58 motile *S. cerevisiae*. We evaluate the capability of *A royi* to perceive fluid disturbances by
59 quantifying their escape response to artificial fluid signals and find that their sensitivity is similar to
60 that found in other copepods. We therefore propose that direct encounter, rather than a fluid signal,
61 triggers a feeding jump towards these small non-motile prey.

62 **Materials and methods**

63 **Experimental organisms**

64 We used *Apocyclops royi* from Donggang in Taiwan that were established in culture at LOG-
65 Marine Station of Wimereux in France (Pan *et al.*, 2016). The culture was initiated at Roskilde
66 University, Denmark and kept for 100+ generations in a 25 °C walk-in temperature controlled
67 room, with a 12:12 light:dark cycle (Jepsen *et al.*, 2021). Copepods were kept in 0.2 µm filtered 20
68 psu seawater and cultures were fed either the microalga *Rhodomonas salina* or Baker's yeast
69 (*Saccharomyces cerevisiae*) in excess.

70 *R. salina* was from a culture at Roskilde University and *S. cerevisiae* was from the yeast production
71 company De Danske Gærfabrikker A/S and available at most supermarkets. The equivalent
72 spherical diameter was 7.6 ± 1.2 µm and 3.8 ± 1.3 µm for *R. salina* and *S. cerevisiae*, respectively
73 (Fig. 1).

74 **Foraging experiment**

75 Between five and eight copepods (0.38 ± 0.06 mm prosome length, stages CII-CIII) were pipetted
76 into a 4.5 mL squared glass cuvette containing either *R. salina* or *S. cerevisiae* in excess. Filming
77 was conducted at 18–20 °C in a temperature controlled room in darkness. Foraging behavior was
78 filmed by a Phantom V210 high-speed camera (Vision Research, New Jersey, USA) equipped with
79 lenses to provide a 2.1×1.3 mm² field of view. Collimated infrared- (*R. salina*) or white light (*S.*
80 *cerevisiae*) shining through the experimental cuvette towards the camera was the only source of
81 illumination. The focal plane of the camera was in the middle of the experimental cuvette to

82 minimize wall effects. Whenever a feeding copepod was in focus, we recorded a 2.7 s video at 2000
83 frames per second (fps). Videos were analyzed using the software ImageJ version 1.53n (National
84 Institutes of Health, USA).

85 **Escape response experiment**

86 The setup and the protocol for the escape experiment were taken up from Kiørboe *et al.* (1999) with
87 some adaptations. A pipette sucked water from an aquarium, and the response of the copepods to
88 the flow generated was quantified. Our experimental container was a $15 \times 15 \times 20$ cm³ aquarium with
89 a mirror dividing it into two halves by the diagonal. We used the same camera as above, but with an
90 objective providing a 66×50 mm² field of view. The infrared light was placed perpendicular to the
91 camera and shined towards a mirror that reflected the light into the camera. The pipette was placed
92 on the bottom of the aquarium and was attached to a tube. The water flow was regulated by a faucet
93 and a clamp. The gravity-driven flow was fixed at $Q = 1.42$ mL s⁻¹ (Kiørboe *et al.*, 1999). The tip
94 of the pipette was 3 mm wide and the pipette extended 1.5 cm into the water. We recorded 143
95 second videos at 50 fps. During recordings we did not return water into the tank as to not generate
96 turbulence. We recorded escape behaviors only about 2 cm around the tip of the pipette. Some of
97 the copepods jumped multiple times to escape from the flow field but we only considered the first
98 jump. The experiment was repeated three times with different copepod size fractions. The videos
99 were analyzed using ImageJ. Due to the mirror in our experimental tank, we had both the (x, y) and
100 the (z, y) coordinate planes on the same image. Therefore, we could estimate the escape distances
101 from the x - y - z coordinates. We also determined the coordinates of the copepod at the end of its first
102 jump in order to estimate the average jump speed.

103 **Data analysis**

104 Using the escape distances measured in the pipette experiment we calculated the threshold
105 maximum deformation rate that elicits an escape. The maximum deformation rate (Δ) is the

106 deformation rate along the length axis that yields the highest absolute value (Kiørboe and Visser,
107 1999):

$$\Delta = \frac{Q}{2\pi r^3}, \quad (1)$$

108 where Q the volume flow (mL s^{-2}) and r the escape distance (cm). The maximum velocity
109 difference (signal strength, S) between the copepod and the ambient fluid due to fluid deformation
110 is:

$$S = \Delta \times L, \quad (2)$$

111 where L is the radius of the copepod. A potential limit to this experiment is that in the boundary
112 layer around the pipette, friction may be important and decelerate the flow, and thus we disregarded
113 responses occurring within that distance from the side of the pipette. To calculate its thickness (δ),
114 we used the same definition as (Kiørboe *et al.*, 1999) who considered it as the layer within which
115 the flow deviates more than 1 % of the free-stream fluid velocity. In our experiment, the thickness of
116 the boundary layer was estimated as $\delta \approx 0.25$ cm. The average speed of the first jump was
117 calculated with the coordinates at the beginning and the end of the jump. To test for statistical
118 differences between threshold deformation rates and jump speeds, bilateral and unilateral t-tests
119 were used ($\alpha = 0.05$).

120 **Results**

121 **Foraging experiment**

122 *Apocyclops royi* exhibits ambush feeding when offered both the motile microalga *Rhodomonas*
123 *salina* and the non-motile yeast cells *Saccharomyces cerevisiae*. The copepod sinks in the water
124 column, occasionally adjusting its position with short jumps. When prey is close to the first
125 antennae, *A. royi* jumps towards the prey and creates a vacuum using its feeding appendages to
126 ingest the prey (Fig. 2–3; Videos S1–S2). We were unable to determine whether or not prey cells
127 touch the setae of the antennules.

128 Jump distance, duration, and average speed are presented in Table 1. A jump is considered from the
129 detection of the prey to the opening of the feeding appendages (Kiørboe *et al.*, 2009).

130 **Escape response experiment**

131 Copepods drawn with the flow towards the tip of the pipette respond to the flow at a characteristic
132 distance to the pipette. These response distances increase with the length (L) of the copepods.
133 Consequently, the threshold deformation rate required to elicit an escape varied inversely with body
134 length (Table 2). The smallest size fraction reacted to a significantly higher deformation rate
135 compared to the two larger fractions (T-test, $p < 0.01$). Jump speed generally increased with body
136 length, and was significantly higher for the two larger size fractions compared to the smallest one
137 (T-test, $p < 0.001$). We also estimated the threshold strength of the signal (S) due to fluid
138 deformation (Eq. 3). We consider the copepod as a sphere, therefore its body length is twice its
139 radius. Our estimation of the average threshold strength of the signal is $S = 0.015 \pm 0.003 \text{ cm s}^{-1}$.

140 **Discussion**

141 **Feeding and prey perception**

142 *Apocyclops royi* displayed an ambush feeding behaviour when fed both *R. salina* and *S. cerevisiae*.
143 The prey attack mechanism in *A. royi* fed Baker's yeast is very similar to the one described for the
144 ambush feeding copepods *Oithona davisae* and *Acartia tonsa* by (Kiørboe *et al.*, 2009). Jump
145 distance, duration and speed are in the same range as for *O. davisae*, a obligatory ambush feeder
146 about the same size as *A. royi*. For both preys, *A. royi* elicited an attack when the prey was close to
147 or touching the first antennae (Video S1–S2). Thus, *A. royi* is capable of sensing smaller, non-
148 motile particles (*S. cerevisiae*) the same way it senses the motile *R. salina* cells. Remote prey
149 detection can be elicited by a chemical or a hydromechanical signal, however chemical detection of
150 individual prey is unlikely in ambush-feeding zooplankters (Svensen and Kiørboe, 2000; Kiørboe,
151 2011). While we cannot entirely exclude the possibility of chemical detection, we will provide

152 arguments to why we find it unlikely also for *A. royi* feeding on *S. cerevisiae*. Several previous
153 studies have addressed the issue of chemosensory prey detection in copepods, and has found it
154 improbable in both ambush- and feeding-current feeding copepods feeding on both motile and non-
155 motile prey (Légier-Visser *et al.*, 1986; Svensen and Kiørboe, 2000; Tiselius *et al.*, 2013;
156 Gonçalves and Kiørboe, 2015). This is because the ‘diffusion speed’ of the substances leaking from
157 the cell must be greater than the velocity of the cell travelling towards the predator, whether it does
158 so by swimming or sinking. Chemical signals leaking from smaller cells disappear almost
159 immediately due to molecular diffusion, and the estimated phycosphere, i.e., where the
160 concentration of solutes around the cell is 50% greater than the background, for a similarly sized
161 phytoplankton to *S. cerevisiae* (~5 µm) is estimated to protrude just a few microns from the cell
162 surface (Seymour *et al.*, 2017). This distance is similar to the sinking distance covered by
163 phytoplankton cells this size (Kiørboe, 2008). Thus, the cell would encounter the mechanoreceptors
164 on the setae extending from the first antennae before the first antennae itself. Even when entrained
165 in a feeding current, where the phycosphere is stretched out towards the grazer, the estimated lower
166 size limit for a cell to trigger chemical detection is in the range of 50–70 µm (Légier-Visser *et al.*,
167 1986; Tiselius *et al.*, 2013).

168 Rather, we suggest that *A. royi* perceives particles by the mechanoreceptory setae on the antennules,
169 similar to other ambush feeding copepods. Assuming that *A. royi* has a similar sensitivity to fluid
170 disturbances than the ambush feeding copepod *Oithona similis*, *R. salina* cells are clearly in the
171 size- and speed range of remote detectability (Kiørboe and Visser, 1999). However, it is not clear
172 how *S. cerevisiae* cells are perceived. In fact, *O. similis* can only perceive the fluid signal from non-
173 motile prey larger than 80 µm that create a sufficiently strong fluid disturbance by sinking (Kiørboe
174 and Visser, 1999). The escape response experiment suggests that *A. royi* does not have a sensitivity
175 to fluid disturbances different from that of other copepod species (Burdick *et al.*, 2007; Kiørboe *et*
176 *al.*, 2009). Therefore, remote detection of *S. cerevisiae* cells seems unlikely. Instead, *A. royi* most
177 likely senses single *S. cerevisiae* cells by randomly touching them with the first antenna. In a dense

178 culture, this presumably happens frequently enough to accomodate food intake needs. Once it has
179 located the prey, the copepod adopts the previously described ambush feeder behaviour. We were
180 from our videos unable to determine the fraction of attack-jumps that ended in a successful prey
181 ingestion, however, we believe the fraction to be high, given the inability of non-motile cells to
182 utilize escape behaviors commonly found in motile protists (Jakobsen, 2001). **The energetic cost of**
183 **jumping vs. the nutritional value of prey**

184 The energetic cost of swimming and jumping in copepods is considered relatively low (Titelman
185 and Kiørboe, 2003). However, in order to sustain growth on a diet of Baker's yeast, the energy
186 expenditure of the jump must be less than the gain from ingesting a cell. The energetic content of
187 the *S. cerevisiae* used here is roughly 4770 J g^{-1} (De Danske Gærfabrikker,
188 <https://oekologiskgaer.dk/>). Using a density of 1.0952 g mL^{-1} (Reuss *et al.*, 1979) one cell ($\sim 4 \mu\text{m}$
189 ESD) contains roughly $1.8 \times 10^{-7} \text{ J}$. This is an order-of-magnitude lower than the estimate for
190 *Rhodomonas* sp. using $47 \text{ pg C cell}^{-1}$ (Berggreen *et al.*, 1988) and a carbon to calorie ratio of 11.4
191 cal g C^{-1} (Platt and Irwin, 1973).

192 The energy expenditure ($\text{J, kg m}^2 \text{ s}^{-2}$) from a jump can be estimated from:

$$E = F \times d, \quad (3)$$

193 where F is the force (N, kg m s^{-2}) and d the jump distance (m). F is in turn estimated as:

$$F = 0.5\rho C_D U^2 A, \quad (4)$$

194 where ρ is the density of the water ($\sim 1 \text{ kg m}^3$), C_D is the drag coefficient, U is the jump speed (m
195 s^{-1}), and A is the cross-section area of the copepod (m^2). For simplicity, the copepod is assumed to
196 be spherical. The drag coefficient is estimated as (Massey, 1968):

$$C_D = \frac{24}{Re} \left(1 + \frac{3}{16} Re \right)^{\frac{1}{2}}, \quad (5)$$

197 where Re is the Reynolds number (~ 30 in our case). Using values from Table 1 gives $E = 5 \times 10^{-13}$
198 J if we assume an efficiency of 1%. If we assume that the attack-jump velocity scales to the same

199 power 0.6 as escape jumps (Kiørboe *et al.*, 2009), a large adult female (~0.95 mm length) still only
200 spends 1.9×10^{-10} J on an attack jump, three orders-of-magnitude less than the energetic content of
201 a yeast cell. Thus, the lower nutritional value of yeast compared to that of phytoplankton should not
202 be an issue for *A. royi*.

203 **Conclusions**

204 Our observations experiments demonstrates that *Apocyclops royi* use an ambush feeding strategy
205 even when microphageously fed small, non-motile Baker's yeast cells (*Saccharomyces cerevisiae*).
206 We also suggest that its foraging and escape behaviour are both elicited by fluid disturbances or
207 direct contact with the prey, thus, sensed by mechanoreceptors. Finally, we can confirm that *A. royi*
208 is not more sensitive to the presence of a predator than *Acartia tonsa*, a copepod suggested used as
209 live feed in aquaculture. Due to its high adaptability, self enriching fatty acid biosynthesis and the
210 fact that copepods are generally considered as a better live feed for fish larvae than the widely used
211 rotifers and *Artemia* sp., *A. royi* is indeed an interesting candidate for intensive aquaculture uses
212 (Abate *et al.*, 2016; Jepsen *et al.*, 2021). Evidently, the escape behaviour of *A. royi* would not be a
213 barrier for its aquaculture uses.

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220

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- 281

282

283 Table legends

284 Table 1. Overview of prey attacks in *Apocyclops royi* fed Baker's yeast (*S. cerevisiae*). Copepod
285 length refers to the prosome. n = number of observations.

286 Table 2. Escape response of *Apocyclops royi*. Reaction distance (mean \pm SD) to mouth of the
287 pipette for different developmental stages in a siphon flow (R), calculated threshold deformation
288 rate (mean and 95 % confidence interval) at the point of escape, and speed of the first escape jump
289 (mean \pm SD). n = number of observations.

290

291

292 Figure legends

293 Figure 1. Size spectra of Baker's yeast (*Saccharomyces cerevisiae*) and *Rhodomonas salina* as
294 measured by a Beckman Coulter Multisizer 4 (Brea, California, USA).

295 Figure 2. Prey capture in *Apocyclops royi* fed *Rhodomonas salina*. The position of the
296 phytoplankton cell is indicated by the red circle. Duration of the jump is indicated.

297 Figure 3. Prey capture in *Apocyclops royi* fed *Saccharomyces cerevisiae*. The position of the yeast
298 cell is indicated by the red circle. Duration of the jump is indicated.

299

300 Table 1

	Mean \pm SD	Range	<i>n</i>
Copepod length (mm)	0.38 \pm 0.06	(0.35 – 0.40)	18
Jump distance (mm)	0.42 \pm 0.20	(0.30 – 0.50)	10
Jump duration (ms)	26.3 \pm 5.91	(22.20 – 29.70)	10
Average jump speed (mm s ⁻¹)	16.0 \pm 5.23	(12.10 – 18.90)	10

301

302

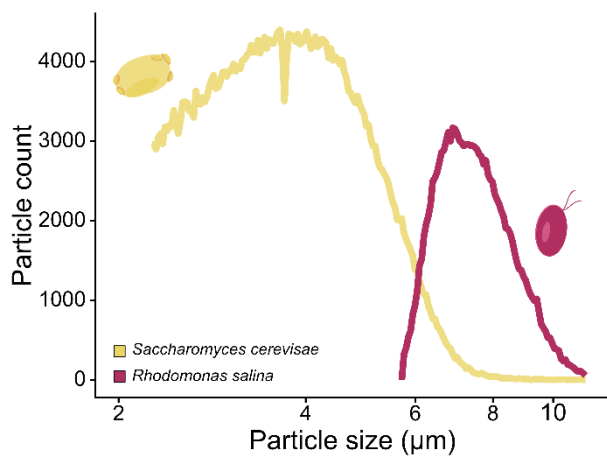
303 Table 2

Average length (μm)	Stage	R (cm)	Deformation rate (Δ) (s^{-1})	Jump speed (mm s^{-1})	n
117 ± 9	NI - NII	0.48 ± 0.08	2.16 (1.86 – 2.50)	12.6 ± 7.9	38
328 ± 78	CI - CIII	0.67 ± 0.21	0.88 (0.85 – 0.91)	28.0 ± 27.0	52
483 ± 25	CIII - CIV	0.69 ± 0.19	0.79 (0.61 – 1.01)	22.3 ± 9.9	45

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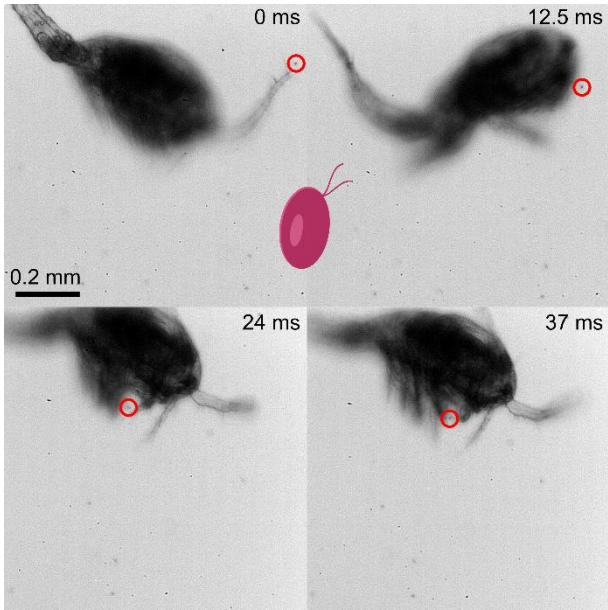
306 Figure 1



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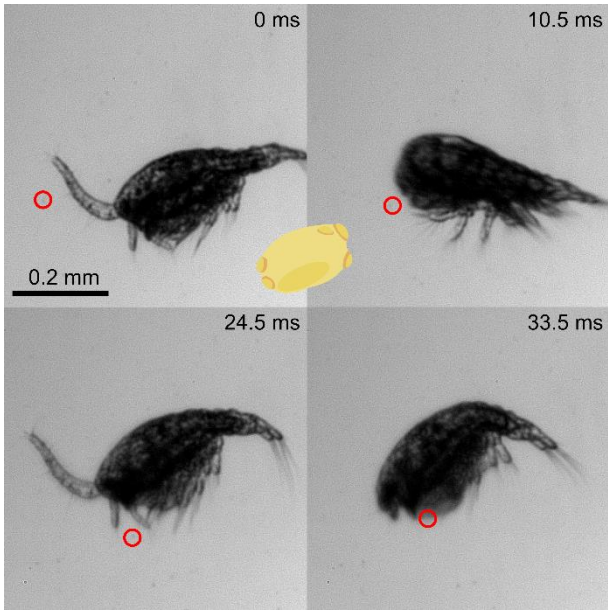
309 Figure 2



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312 Figure 3



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