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1 **Can the mechanoreceptional setae of a feeding-current feeding**  
2 **copepod detect hydrodynamic disturbance induced by entrained**  
3 **free-floating prey?**

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13 Running head: Prey detection in feeding currents

14 Key Words: copepods, seta, mechanoreception, feeding-current feeding, prey detection,  
15 hydrodynamic sensitivity, setal deformation

16 ***Abstract***

17 Copepods that catch prey using feeding currents beat their cephalic appendages to generate flow  
18 entrainment, and detect the presence of nearby prey through the mechanoreceptional setae on the  
19 antennules and other appendages. It remains unclear whether the feeding current can be used by  
20 the copepod to gain information about its surroundings by sensing when the current is disturbed  
21 by nearby particles. In this article, we present a numerical model to address how much the  
22 presence of free-floating prey can alter the feeding current velocity field, and how these prey-  
23 induced disturbances modify setal deformation patterns. We prescribe the beating strokes of the  
24 feeding appendages, and quantify the changes in the bending flows across the setae and setal  
25 deformations due to the prey entrainment. We find that, first, the seta bends more due to the  
26 time-averaged velocity component of the feeding current, while filtering out the oscillatory  
27 component. Second, 100  $\mu\text{m}$  diameter free-floating prey do not induce any noticeable change in  
28 deformations of the proximal and distal setae unless they are less than 10 or 5.5 prey radii from  
29 the antennules, respectively. Larger prey cause bigger flow disturbances than small prey, which  
30 are expected to be even harder to detect. Last, if setae are responsive to changes in deformation  
31 *relative* to the deformations in the absence of prey, the distal seta may have long-ranged  
32 sensitivity to assist in detection of prey near the proximal seta, but if setae are responsive to  
33 *absolute* changes in deformation, both setae have very short-ranged sensitivity.

34 ***Introduction***

35 Feeding-current and cruise feeding copepods achieve prey detection by beating their cephalic  
36 appendages, pulling both motile and free-floating planktonic prey towards their mouthpart  
37 (Koehl and Strickler 1981; Strickler 1982), and sensing their presence through the  
38 mechanoreceptional and/or chemoreceptional setae protruding from the antennules and other

39 appendages (Paffenhöfer and Loyd 1999; Strickler and Bal 1973; Yen et al. 1992).  
40 Mechanoreception is postulated to be more efficient than chemoreception for feeding-current  
41 feeding copepods (Gonçalves and Kiørboe 2015). The mechanoreception of copepods starts  
42 when the prey-induced signal -- either hydrodynamic disturbance or direct contact (Kiørboe et al.  
43 2014; Kjellerup and Kiørboe 2012; Paffenhöfer and Van Sant 1985) -- bends the thin long  
44 mechanoreceptional seta to a certain extent (Fields et al. 2002). Setal deformation is then  
45 transformed into neurophysiological signals through mechanotransduction, in which opening of  
46 mechano-gated microchannels perforating the membrane of the dendrite attached to the cuticle at  
47 the setal root leads to an electric potential across the neuron (Weatherby and Lenz 2000;  
48 Weatherby et al. 1994). While motile prey can bend the setae via the larger flow disturbances  
49 generated by their swimming strokes, it is not clear if free-floating prey in the feeding current are  
50 hydrodynamically conspicuous (Visser 2001). It has been proposed that the feeding current could  
51 be used to aid detection of nearby particles; since the feeding current is a predictable background  
52 flow, any changes in the background flow due to the presence of prey particles in the feeding  
53 current could be detected by a copepod (Takagi and Strickler 2020; Visser 2001; Yen and  
54 Strickler 1996). Here, we study the case in which such changes arise because rigid prey particles  
55 cannot deform along with the deformations of the fluid (measured by shear or strain) in the  
56 complex flows of a beating current. Free-floating, neutrally buoyant prey particles generate this  
57 type of hydrodynamic disturbance without generating other hydrodynamic signals, such as from  
58 motility or gravitational forces. Therefore, we numerically study the flows around free-floating  
59 neutrally buoyant particles in feeding currents and their effect on the deformation of setae.

60 Our knowledge about whether free-floating prey entrained in the feeding current can be  
61 detected is largely dependent on microscopic observations; however, the findings of previously

62 reported experiments seem to contradict each other. First, it remains unclear which setae  
63 serve as the primary mechanoreceptors to detect the presence of prey entrained in the feeding  
64 current. The setae on the antennules, the primary focus in the past studies, seem  
65 most sensitive to hydrodynamic disturbances (Fields et al. 2002; Hartline et al. 1996) and motile  
66 prey are detected closest to those setae (Doall et al. 2002; Jonsson and Tiselius 1990).  
67 Nevertheless, most experiments conducted on free-floating prey observed that prey are detected  
68 closest to the setae on feeding appendages (Gonçalves and Kiørboe 2015). Second, it is unclear  
69 whether copepods are capable of detecting hydrodynamic disturbances induced by nearby prey,  
70 or instead the prey must be in contact with the seta. As summarized in table 1 of Gonçalves and  
71 Kiørboe (2015), a few studies reported that setae of copepods with  $O(10^0)$  mm prosome  
72 length have long-range sensitivity to  $O(10^{-2})$  mm diameter prey (Bundy et al. 1998; Bundy and  
73 Vanderploeg 2002; Strickler 1982). However, a majority of experiments report that prey  
74 detection occurs when  $O(10^{-2})$  mm diameter prey are within a few prey radii of the copepod  
75 mouthpart or tip of the feeding appendage (Gonçalves and Kiørboe 2015).

76 One key consideration for the long-range sensing of hydrodynamic signals is whether a  
77 copepod seta is able to distinguish the prey-induced hydrodynamic signal from its own feeding  
78 current, through a notable change in its deformation. The spatial distributions of the velocity of  
79 the background feeding current have been quantified in many experimental measurements  
80 (Catton et al. 2007; Fields and Yen 1993; Malkiel et al. 2003) and numerical simulations (Jiang  
81 et al. 1999; Jiang et al. 2002a; Jiang et al. 2002b), though not explicitly in the physical space  
82 occupied by setae. However, only a few studies (Bundy et al. 1998; Visser 2001; Yen and Okubo  
83 2002) have addressed how prey entrainment modifies the feeding current and deformation

84 pattern of the seta. This may be caused by technical difficulties in, first, measuring the small  
85 prey-induced hydrodynamic disturbance relative to the background feeding current, and second,  
86 quantifying setal displacement in the feeding experiment, as very small deformations of setae are  
87 capable of initiating the predatory response. As a result, many researchers (Jiang and Strickler  
88 2007; Kiørboe and Visser 1999; Visser 2001) have adopted simplified models which either treat  
89 the geometries of both prey and copepods as spheres (Happel and Brenner 1983), or which  
90 ignore the spatial extent of prey and copepods by representing the flows as due to a small set of  
91 multipoles, pointlike combinations of forces (Kim and Karrila 1991), which represent the flow  
92 induced by both prey and copepods in the Stokes limit, to quantify hydrodynamic disturbance  
93 sensed by the seta in feeding experiments.

94 For setal detection, the multipole model may often be a good representation of the flows  
95 caused by the entrained prey, if the prey radius is much smaller than the reported prey detection,  
96 hence allowing one to neglect the spatial extent of the prey. However, the spherical and  
97 multipole models are not adequate to describe the feeding current generated by the *copepod* for  
98 the following reasons. First, those models are only valid in the regime where the Reynolds  
99 number, which measures the relative importance of inertial and viscous effects in a fluid, is  
100 nearly zero. The Reynolds number is proportional to both the flow length scale and velocity. At  
101 the copepod's appendage and body length scales, the Reynolds numbers are  $O(10^{-1})$  and  
102  $O(10^0)$ , respectively (Jiang et al. 2002b; Koehl and Strickler 1981; van Duren and Videler 2003),  
103 outside the range of validity of those models. Second, since it ignores the spatial extent of the  
104 copepod, the multipole model only captures the characteristics of the feeding current far away  
105 from the copepod body. However, the prey detection happens at length scale smaller than the  
106 copepod's body length, where the spatial extent and the detailed geometry of the copepod

107 appears to be important (Jiang and Paffenhöfer 2008; Shen et al. 2020). Last, the multipole  
108 model does not link the fluid motion with setal deformation. Recently, we (Shen et al. 2020)  
109 have addressed how the bending of setae modulates detection capabilities of copepods using  
110 hydrodynamic signals approximated as oscillating simple shear flows, but it remains unknown  
111 how the deformation patterns of setae in a feeding current is altered by the presence of nearby  
112 prey.

113 In this article, we focus on understanding the distance at which free-floating prey can be  
114 detected by the mechanoreceptional setae due to induced changes in the feeding current. This  
115 article consists of two sections: first, we use the immersed boundary method to numerically  
116 calculate the flow across the setae on the antennules and other feeding appendages with and  
117 without the prey entrainment. This is the flow which bends the setae, and it is the change in this  
118 flow due to the presence of prey which could possibly be sensed hydromechanically by copepods.  
119 We explicitly take into consideration of the beating strokes of the feeding appendages, though  
120 we only account for the effect of setules and setae on appendages by increasing their effective  
121 thickness. Next, we utilize the method of regularized Stokeslets and inextensible Kirchhoff rod  
122 theory to calculate the setal deformations when subjected to the bending flows obtained in the  
123 previous section. We determine how the prey-induced hydrodynamic disturbances modify the  
124 deformation patterns of the distal and proximal setae on the antennules, and predict how close to  
125 the prey the setae on the antennules must be in order to gain information about the disturbance  
126 caused by the nearby prey, depending on the sensing mechanism of the setae. Our findings are  
127 compared with previous experiments to give insights into the possible range of the prey detection  
128 distance.

129 ***Bending flow across seta***

## 130 Copepod model

131 The geometry of our copepod model is based on copepods *Paracalanus parvus* and  
132 *Pseudocalanus sp.* in supplementary videos 1 and 3 of Tiselius et al. (2013), and described in  
133 detail in the “detailed copepod model” section in the Supplemental Information. The prosome  
134 length of the modeled copepod is assumed to be  $L_b = 1$  mm (Fig. 1). Such treatment is meant to  
135 represent a typical calanoid copepod rather than any specific species. The centerline of the  
136 longest appendage pair, the antennules, is fitted to a fifth-order polynomial of arc length  
137  $L_{AI} = 1.097$  mm.

138 The feeding appendage geometries and beating patterns are modeled as follows.  
139 Morphological examination shows that five pairs of feeding appendages are attached to the  
140 copepod cephalosome: antennae, mandibles, maxillipeds, first maxillae, and second maxillae  
141 (Conway 2006). The second maxillae stay almost stationary (Gill and Poulet 1986) and only  
142 move occasionally to handle food particles upon detection (van Duren and Videler 2003);  
143 therefore, we neglect the presence of the second maxillae in our model. To model the other four  
144 pairs of feeding appendages, we first determine the attachment points of the roots from Tiselius  
145 et al. (2013). We then find the projected motions of these appendages from supporting video 1 of  
146 Tiselius et al. (2013). Last, we recover the three dimensional beating patterns of these feeding  
147 appendages according to the copepod schematics as shown in fig. 2 of Koehl and Strickler  
148 (1981). Our obtained appendage motions and copepod beating strokes are animated in Videos S1  
149 and S2a,b in the Supplemental Information, respectively.

150 To generate a feeding current of comparable velocity to experimental measurements, we  
151 make two assumptions. First, the beating frequency of the feeding appendages,  $f$ , is set to be 30

152 Hz in our model, within the range of common copepods' beating frequencies of 20 to 40 Hz  
153 (Koehl and Strickler 1981; Svetlichny et al. 2020; Yen and Strickler 1996). Second, the setules  
154 and setae on the feeding appendages are not explicitly accounted for in the hydrodynamic model;  
155 instead, the root diameters of all appendages are 1.5 times the values obtained from the image  
156 analysis. We found that such treatment effectively increases the contact area with surrounding  
157 fluid and generates stronger power strokes (Koehl and Strickler 1981), and produce a feeding  
158 current similar to that in experiments (see the "Validation of numerical model" section of the  
159 Supplemental Information for details).

160 The positions of the anterior-posterior oriented setae on the antennules are constructed based  
161 on fig. 1 of Yen and Nicoll (1990). In our model, we consider the proximal seta on the 3rd  
162 segment of the antennule and distal seta, as shown in the black lines in Fig. 1. To evaluate if the  
163 setae on the feeding appendages are sensitive to the hydrodynamic signal, we also place setae at  
164 the tips of the endopods of the antennae and maxillipeds, pointing in the direction of the  
165 appendage centerline (see Fig. 1). Similar to our previous approach (Shen et al. 2020), we  
166 assume all setae are cylindrical-shaped with length  $L_{\text{seta}} = 200 \mu\text{m}$ , radius  $r_{\text{seta}} = 1 \mu\text{m}$ . Results  
167 are obtained for Young's modulus of  $E = 10^7 \text{ N/m}^2$  based on Yen and Okubo (2002), unless  
168 specified otherwise.

169 Feeding-current feeding copepods were tethered by forceps or hair for ease of microscopic  
170 observations in early experiments (Paffenhöfer and Lewis 1990; Vanderploeg et al. 1990; Yen  
171 and Strickler 1996) that quantified their behavior. In order to have a meaningful comparison with  
172 these experiments we therefore assume the body of the copepod is tethered and stationary.

### 173 **Prey model**

174 We consider a passive rigid spherical prey of the same density as the surrounding fluid. In a  
175 uniform flow, a sphere simply translates with the flow without altering it. Therefore, we expect  
176 that the free-floating prey would not generate a disturbance in a quiescent fluid or uniform flow.  
177 However, in a spatially non-uniform background flow, the finite extent of the sphere alters the  
178 flow and could be detected by the mechanoreceptional setae of copepods.

179 In selecting the prey size, we note that the food particles widely used in the experiments of  
180 copepod feeding on inert stimuli are non-motile algae and inert beads of diameter  $d$  varying from  
181  $O(10^0)$  to  $O(10^2)$   $\mu\text{m}$  (Broglia et al. 2001; Jiang and Paffenhöfer 2008; Vanderploeg et al.  
182 1990). In our model we choose the upper limit,  $d = 100 \mu\text{m}$  and assess if the copepod setae are  
183 equipped with long-ranged hydrodynamic sensitivity to this prey type. Since the flow  
184 disturbance arises from the spatial extent of the sphere interacting with non-uniform flow, we  
185 expect smaller food to cause even less disturbance, hence be harder for copepods to detect.

## 186 **Immersed boundary method**

187 The hydrodynamics are governed by the unsteady and incompressible Navier-Stokes  
188 equations, which we solve numerically by the immersed boundary (IB) method (Peskin 1972;  
189 Peskin 2002). We adopt the constraint IB version of IBAMR (Bhalla et al. 2013) to solve for  
190 and compare the feeding current across the setae with and without presence of the prey. The  
191 setup and validation of the numerics are briefly mentioned here but described in details in the  
192 “immersed boundary method” section of the Supplemental Information

193 We tether the copepod at the center of the computational domain and prescribe the beating  
194 strokes of the feeding appendages. Free-floating prey are treated as (net) force- and torque-free  
195 particles in IB simulations, allowing them to drift in the feeding current. The fluid is at rest at  $t =$

196 0, and accelerates due to the constraints provided by the no-slip boundary conditions specified by  
197 the copepod and prey geometry and motion. Similar to the approximations made in the arthropod  
198 filiform hair model (Humphrey et al. 1993) and our previous approach (Shen et al. 2020), we  
199 assume that the setae are far from each other and have negligible disturbance to the feeding  
200 current, and hence we do not explicitly include setae filaments as part of the immersed copepod.  
201 The flow profile obtained from the numerical model is validated by comparing the time-averaged  
202 steady-state flow with that measured experimentally in Fields and Yen (1997).

### 203 **Bending flow across feeding appendage setae**

204 Here we evaluate how the bending flows across the setae on the feeding appendages and the  
205 antennules are affected by free-floating prey. We find that there is little difference in flow with  
206 and without free-floating prey at setal locations on feeding appendages.

207 In our numerics, we first let the copepod's feeding appendages beat for 60 cycles so that the  
208 bending flows across all setae are within 2% of their corresponding steady state values (see the  
209 “steady state test” section in the Supplemental Information). We then center a free-floating prey  
210 at Point A and reset the time to be  $t = 0$ . Point A (Fig. 1) is on the sagittal plane of the copepod  
211 approximately 0.5 mm in front of the feeding appendages. Since the prey is force- and moment-  
212 free, it is entrained in the feeding current and moves towards the feeding appendages over time,  
213 as shown by the prey trajectory in Fig. 2a. In Figs. 2b and 2c, we plot the distance,  $D$ , from the  
214 prey center to the setae on the maxilliped and the endopod of the antenna as a function of time,  
215 respectively.

216 To analyze the prey-induced disturbance sensed by the setae, we evaluate the velocities of  
217 the bending flows along the setal axis relative to their corresponding setal root velocities,

218  $\Delta \mathbf{u}(s,t) = \mathbf{u}(s,t) - \mathbf{u}(0,t)$ , where  $s \in [0, L_{\text{seta}}]$  is a Lagrangian parameter along the centerline of  
219 the seta, with  $s = 0$  at the setal root. In Figs. 2d and 2e, we plot the  $x$ ,  $y$  and  $z$  components of the  
220 instantaneous bending flows across the setae on the maxilliped and the endopod of the antenna  
221 with and without a free-floating prey when their corresponding distances to the prey are the  
222 shortest. The shortest distance from the prey center to the seta on the endopod of the antenna is  
223 0.265 mm (equivalent to 5.3 prey radii), occurring at time  $t/T = 25.44$  (refer to Fig. 2c), and the  
224 shortest distance from the prey to the seta on the maxilliped is even smaller (0.163 mm,  
225 equivalent to 3.3 prey radii), occurring at time  $t/T = 21.91$  (refer to Fig. 2b). We find that the  
226 presence of the prey induces negligible difference in the sensed flow across these seta (note that  
227 the dashed lines coincide with the solid lines in Figs. 2d,e). The limited change in flow across the  
228 setae on feeding appendages is consistent with the conclusion reached by Gonçalves and Kiørboe  
229 (2015), which implies that feeding appendage setae may not be designed for prey detection  
230 through hydromechanical reception, as opposed to direct contact. As might be expected, we  
231 found that free-floating prey starting farther from the feeding appendages produce even less  
232 difference in flow across these setae (data not shown). Therefore in the remainder of this paper  
233 we focus on the setae on the antennule instead.

## 234 **Bending flow across the setae on the antennule**

### 235 *Without the presence of the prey*

236 First we evaluate the feeding current flow without prey across the setae on the antennule. The  
237 flow velocities at the roots of these setae should be zero due tethered boundary condition applied  
238 on the copepod. However, a known drawback of the constraint IB method is that the boundary  
239 conditions are satisfied only approximately, leading to a mild penetration of the flow through the  
240 copepod body (Kallemov et al. 2016).

241 To resolve this issue, we adjust the positions of the setae on the antennule in the  $x$  direction  
 242 (Fig. 1a) so that the setal root is about one computational grid into the antennule object, where  
 243 the calculated feeding current is the smallest. At these root locations, the feeding current is 5.7%  
 244 (13.8%) of the maximum magnitude of the flow across the corresponding distal (proximal) seta  
 245 on the antennule. To correct for this residual flow we use the quantity  $\Delta\mathbf{u}(s,t) = \mathbf{u}(s,t) - \mathbf{u}(0,t)$   
 246 to evaluate the velocities of the bending flows along the centerline  $s$  of the distal and proximal  
 247 setae on the antennule.

248 The steady-state bending flow across these setae is highly oscillatory (refer to Fig. S6 in the  
 249 Supplemental Information for the plot of the steady-state  $\Delta\mathbf{u}(s,t)$  across the distal and proximal  
 250 setae at selected times over one beating cycle). This is characteristic of all the feeding current  
 251 flows we examine, since they are generated by oscillatory movement of the feeding appendages.  
 252 Therefore, in what follows we quantify the bending flow by decomposing it into time-averaged  
 253 and oscillatory components during the  $N$ -th beating stroke ( $(N-1)T \leq t < NT$ ),

$$254 \quad \Delta\mathbf{u}(s,t) = \Delta\mathbf{u}_{\text{avg}}(s,NT) + \Delta\mathbf{u}_{\text{osc}}(s,t), \quad (1)$$

255 where  $\Delta\mathbf{u}_{\text{avg}} = (1/T) \int_{(N-1)T}^{NT} \Delta\mathbf{u} dt$  is the time-averaged velocity at centerline position  $s$  over one  
 256 oscillation cycle, and  $\Delta\mathbf{u}_{\text{osc}}$  represents the oscillatory velocity component of the bending flow.

### 257 Free-floating prey near the distal seta

258 In this section, we show that free-floating prey hardly affect the feeding current at the distal  
 259 setal locations unless they are quite close (less than 10 prey radii) to the antennules. After the  
 260 flow reaches steady state, we reset the time to be  $t = 0$  and start a free-floating at Point B (Fig.  
 261 1), in front of the distal of the left antennule and 0.5 mm from its centerline. Near the antennule,

262 the hydrodynamic interaction between the antennules and the free-floating prey can be seen to  
263 alter the prey trajectory (Figs. 3a-c). We show the time-averaged bending flows,  $\Delta\mathbf{u}_{\text{avg}}$ , across  
264 the left distal seta at four typical beating cycles with and without the free-floating prey in Figs.  
265 3d-h. From these results we make the following observations:

266 First, in the 1st beating cycle ( $0 \leq t/T < 1$ ), when the free-floating prey is 0.5 mm (10 prey  
267 radii) from the centerline of the antennule (Figs. 3a,b), we did not observe any difference in the  
268 average flow across the distal seta  $\Delta\mathbf{u}_{\text{avg}}$  due to the presence of the free-floating prey (note the  
269 solid and dashed lines coincide in Fig. 3d).

270 Second, in the 61st beating cycle, when the prey appears to be closest to the distal setal tip  
271 (0.160 mm away, equivalent to 3.2 prey radii from setal tip and 5.5 prey radii from the centerline  
272 of the antennule, Figs. 3a,b), we only observe a small change in the  $y$  component of  $\Delta\mathbf{u}_{\text{avg}}$   
273 (compare the solid and dashed lines in the middle panel of Fig. 3e). This is due to the fact that  
274 our hydrodynamic model neglects the presence of the distal setae and its hydrodynamic  
275 interaction with the prey; the change in  $\Delta\mathbf{u}_{\text{avg}}$  across the distal seta is induced by the relatively  
276 weak hydrodynamic interaction of the prey and the antennule.

277 Third, in the 91st beating cycle, when the prey is 0.171 mm (3.4 prey radii) from the  
278 centerline of the antennule (Figs. 3a,b), we observe the largest difference in  $\Delta\mathbf{u}_{\text{avg}}$  across the  
279 distal seta (compare the solid and dashed lines in Fig. 3f). In comparison, the free-floating prey  
280 initiated at Point A does not induce a noticeable change in the bending flow across the setae on  
281 feeding appendages when the distance from the prey to the maxilliped is about the same as the  
282 case here (3.4 prey radii). This demonstrates that the distal seta on the antennule has a higher

283 hydrodynamic sensitivity than feeding appendage setae, aided by the small magnitude of the  
284 feeding current across the distal seta, which creates a quiet hydrodynamic sensing environment.

285 Fourth, in the 112th beating cycle, when the prey is closest to the centerline of the antennule  
286 (0.138 mm away, equivalent to 2.8 prey radii, Figs. 3a,b), we find that the time-averaged prey-  
287 induced disturbance is smaller than that at the 91th beating cycle (compare the differences of the  
288 solid and dashed lines in Fig. 3f and in Fig. 3g). Thus there is no guarantee that the largest  
289 difference in bending flow occurs when the prey is closest to the centerline of the antennule.

290 Finally, in the last (140th) cycle of our simulation, when the prey is 0.183 mm (equivalent to  
291 3.6 prey radii) from the centerline of the antennule, we do not observe any difference in the time-  
292 averaged bending flow with and without the prey (Fig. 3h).

293 Next we examine the oscillatory portion of the flow across the distal seta  $\Delta \mathbf{u}_{\text{osc}}$ . In Fig. S7a  
294 of the Supplemental Information, we plot  $\Delta \mathbf{u}_{\text{osc}}$  across the distal seta with and without the  
295 presence of the prey during the 91st cycle (when the difference in  $\Delta \mathbf{u}_{\text{avg}}$  is the largest). In  
296 general, the oscillatory velocity component has the same order of magnitude as the time-  
297 averaged ones (compare the horizontal scales of Fig. 3f with Fig. S7a). This oscillatory flow  
298 velocity has not been revealed by the previous numerical models (Bundy et al. 1998; Jiang et al.  
299 1999; Jiang et al. 2002a) that either treat the hydrodynamic effect of the beating appendages as  
300 due to constant point forces, or assume the copepod swims at a constant speed; hence only  
301 capturing the time-averaged feeding current over a cycle of beating stroke. It is often argued that  
302 by analogy with the flow over an infinite oscillatory plate, oscillatory flows caused by the  
303 appendages should decay over a length scale set by viscous diffusion,  $L_d = \sqrt{\mu / (\pi \rho f)}$ , which

304 for appendage oscillations of frequency  $f = 30$  Hz is  $L_d \approx 103 \mu\text{m}$  (Jiang et al. 2002b).  
305 According to this argument, the oscillatory flow should have mostly decayed at the distance of  
306 the setae on the antennules. Interestingly, our full flow solution shows that the flow does not  
307 decay as much as expected, and that appreciable oscillatory component of the feeding current  
308 can be observed around the distal seta, more than 1 mm from the feeding appendages.  
309 Comparing velocities of bending flows across the distal seta with and without prey, we find that  
310 the oscillatory flow is nearly the same at all eight selected time frames over a cycle, so it is not  
311 much affected by the presence of prey. Since the presence of prey largely only affects the time  
312 averaged flows around the setae on the antennules, in the remainder of the paper we focus on the  
313 time-averaged feeding current,  $\Delta \mathbf{u}_{\text{avg}}$ , rather than the oscillatory flows.

314 To summarize, the hydrodynamic disturbance induced by free-floating prey at the distal seta  
315 induces small changes in the time-averaged background feeding current, with a notable change in  
316 the bending flow occurring when the prey is less than 5.5 prey radii away from the antennule.  
317 Note also that although the change in bending flow due to the prey-induced hydrodynamic  
318 distance is small in this example, the prey requires about 110 cycles ( $\approx 3.3$  s) to travel across the  
319 antennule, which gives the distal seta a relatively long time to sense its presence.

### 320 Free-floating prey near the proximal seta

321 Now, after the flow reaches steady state, we reset the time to be  $t = 0$  and start a free-floating  
322 prey at Point C (Fig. 1) in front of the proximal of the left antennule and 0.5 mm from its  
323 centerline. The prey trajectory relative to the centerline of the antennule and proximal (distal)  
324 seta is shown in Figs. 4a,b (Figs. 5a,b). Fig. 4c plots the distance from prey center to the  
325 centerline of the antennule over time. The prey-induced hydrodynamic disturbance is expected to

326 be stronger due to stronger flows and spatial variation in flows near the proximal compared to  
327 near the distal of the antennule. In this case, in addition to the proximal seta, the distal seta has a  
328 chance to sense the prey-induced flow disturbance, even though Point C is farther from the distal  
329 seta than Point B. Therefore, we consider the bending flow across both setae.

330 Similar to the case with prey near the distal of the antennule, we observe that the oscillatory  
331 portion of the flow across the proximal seta is hardly altered by the presence of the prey (Fig.  
332 S7b in the Supplemental Information). Consequently, we show the  $x$ ,  $y$  and  $z$  components of the  
333 time-averaged bending flows,  $\Delta \mathbf{u}_{\text{avg}}$ , across the proximal and distal setae at four typical beating  
334 cycles in Figs. 4d to 4g and Figs. 5c to 5f, respectively, and make the following observations:

335 First, during the 1st cycle, when the prey just departs from Point C (Figs. 4a,b and Figs. 5a,b),  
336 we find no difference in the bending flow across the proximal and distal setae with and without  
337 the presence of prey (note that the solid and dashed lines coincide in both Figs. 4d and 5c). This  
338 demonstrates that although the prey-induced disturbance near the proximal is larger than that  
339 near the distal of the antennule, both the proximal and distal setae are not capable of sensing  
340 free-floating prey when it is 10 prey radii away from the antennule.

341 Second, during the 17th cycle, when the prey is closest to the centerline of the antennule  
342 (0.153 mm away, equivalent to 3.1 prey radii, Figs. 4a,b and 5a,b), we observe some difference  
343 in  $\Delta \mathbf{u}_{\text{avg}}$  across the proximal seta with and without the presence of the prey (compare the solid  
344 and dashed lines in Fig. 4e) but did not find any noticeable difference for the distal seta (Fig. 5d).

345 Third, the largest difference in the sensed flow across the proximal (distal) seta occurs at the  
346 19th (23rd) beating cycle, in which the distance from the prey to the centerline of the antennule  
347 is about 0.189 mm (0.395 mm), equivalent to 3.8 prey radii (7.9 prey radii). Compare the solid

348 and dashed lines in Figs. 4f and 5e. This again shows that being closest to the antennule does not  
349 guarantee the largest difference in the bending flow. Both the second and third observations  
350 suggest that there may be a few beating cycles of delay between for the distal seta to receive prey  
351 information compared to the proximal seta.

352 Finally, in the last (30th) cycle of our simulation, when the prey is 0.567 mm (equivalent to  
353 11.3 prey radii) from the centerline of the antennule, we do not observe any difference in the  
354 time-averaged bending flow with and without the prey (note the solid and dashed lines coincide  
355 in Figs. 4g and 5f).

356 To summarize, we see that the prey entrained at the proximal region of the antennule  
357 generates a larger flow disturbance and is relatively easily sensed by the setae on the antennule  
358 when the prey is about 3 prey radii from the centerline of the antennule. This example  
359 demonstrates that prey can sometimes induce differences in the bending flows on multiple setae.  
360 Therefore, if the prey-induced hydrodynamic disturbance causes the neurons on more than one  
361 seta to fire, the prey detection may involve the coordination of the setal array on the antennule, in  
362 agreement with previous hypotheses (Fields 2014; Yen and Nicoll 1990). Last, we note that  
363 although the change in bending flow could be significant, the prey only requires 19 cycles ( $\approx$   
364 0.6 s) to move across the antennule, giving the proximal seta a relatively short time to sense its  
365 presence.

### 366 *Deformation of seta*

367 In this section, we analyze the change in the setal deformation due to the hydrodynamic  
368 disturbance induced by prey to evaluate if the setae are sensitive to their presence. To relate the  
369 hydrodynamic signal received by the setae on the antennule with their neurological responses,

370 we solve for the deformation of the seta when subjected to the bending flows described in the  
371 previous section. In previous work investigating the deformation of seta due to background shear  
372 flows, we solved for the time-dependent setal shape by assuming small two-dimensional setal  
373 deformations, and balancing elastic forces obtained from Euler beam theory against the  
374 hydrodynamic forces obtained from resistive force theory (Shen et al. 2020). In this paper, we  
375 must move beyond the Euler beam description of elastic forces, since the setal deformation is not  
376 necessarily small, and the flow and bending are inherently three-dimensional. Therefore we  
377 apply the more general Kirchhoff rod theory and method of regularized Stokeslets to solve for  
378 large scale setal deformations in three-dimensional feeding current flows.

### 379 **Method**

380 The method to solve for the setal deformation is as follows. We consider a seta which is  
381 straight at time  $t = 0$  and deforms when subjected to the feeding current obtained in the “bending  
382 flow across the setae on the antennule” section. At each cross section of the seta specified by  
383 centerline position  $s$ , we define a set of orthonormal basis vectors  $[\mathbf{d}_1(s, t), \mathbf{d}_2(s, t), \mathbf{d}_3(s, t)]$  to  
384 express the orientation of the filament cross section, where the unit tangential vector  
385  $\mathbf{d}_3 = \partial_s \mathbf{X} / |\partial_s \mathbf{X}|$ , while  $\mathbf{d}_1$  and  $\mathbf{d}_2$  are material unit vectors spanning the cross section. As a thin  
386 filament, the internal force and torque  $\mathbf{F}(s, t)$  and  $\mathbf{N}(s, t)$ , arising from the setal deformation are  
387 governed by Kirchhoff rod theory (KRT) (Jabbarzadeh and Fu 2018; Lim et al. 2008; Olson et al.  
388 2013), given by

$$389 \quad \partial_s \mathbf{F} + \mathbf{f} = 0, \quad (2)$$

$$390 \quad \partial_s \mathbf{N} + \mathbf{d}_3 \times \mathbf{F} + \mathbf{n} = 0, \quad (3)$$

391 where  $\mathbf{f}(s,t)$  and  $\mathbf{n}(s,t)$  are the hydrodynamic force and torque distribution exerted by fluid  
 392 along the setal centerline  $s$ , respectively. As the setal deformation is dominated by bending rather  
 393 than stretching (Fields et al. 2002), we utilize the inextensible version of the KRT (Jabbarzadeh  
 394 and Fu 2020) which implies that  $|\partial_s \mathbf{X}|=1$ , and  $N_i = \mathbf{N} \cdot \mathbf{d}_i$  ( $i=1, 2, 3$ ) can be expressed as

$$395 \quad N_1 = EI (\partial_s \mathbf{d}_2) \cdot \mathbf{d}_3, \quad (4)$$

$$396 \quad N_2 = EI (\partial_s \mathbf{d}_3) \cdot \mathbf{d}_1, \quad (5)$$

$$397 \quad N_3 = GJ (\partial_s \mathbf{d}_1) \cdot \mathbf{d}_2, \quad (6)$$

398 where  $I = \pi r_{\text{seta}}^4 / 4$  and  $J = \pi r_{\text{seta}}^4 / 2$  are the planar and polar second moment of seta,  
 399 respectively. The seta is treated as isotropic with Poisson's ratio  $\nu = 0.3$  (Yen and Okubo 2002),  
 400 hence  $G = E / [2(1 + \nu)]$ .

401 Due to the small length and velocity scales of the flow past seta ( $r_{\text{seta}} = 1 \mu\text{m}$  and  
 402  $|\mathbf{u}(s,t)| < O(10^0)$  mm/s), the Reynolds number is small enough that fluid motion is governed by  
 403 the Stokes equations:

$$404 \quad -\nabla p + \mu \nabla^2 \mathbf{u} + \mathbf{f}_b = 0, \quad (7)$$

$$405 \quad \nabla \cdot \mathbf{u} = 0. \quad (8)$$

406 Here we couple the Eqs. (2) and (3) with Eqs. (7) and (8), and apply the boundary conditions  
 407 that the seta is fixed and clamped at its root ( $\partial_t \mathbf{X}|_{s=0} = \partial_s \mathbf{X}|_{s=0} = \mathbf{0}$ ) and force- and moment-free  
 408 at the other end ( $\mathbf{F}|_{s=L_{\text{seta}}} = \mathbf{N}|_{s=L_{\text{seta}}} = \mathbf{0}$ ). Our numerical scheme implements the method of  
 409 regularized Stokeslets (MRS) (Cortez 2001; Cortez et al. 2005) to find the hydrodynamic forces  
 410 on the seta, and then solves Eqs. (2) and (3) for the deformed shape of the seta. Details of our

411 numerical scheme to implement the MRS (Hyon et al. 2012; Martindale et al. 2016) and KRT  
 412 (Jabbarzadeh and Fu 2020) and convergence test results are shown in the “numerical scheme for  
 413 setal deformation” section of the Supplemental Information, but briefly, we uniformly place a  
 414 total number of  $N$  regularized Stokeslets on the surface of the seta with physical coordinates  
 415  $\mathbf{X}_n$  ( $n = 1, 2, \dots, N$ ) . For each seta, the setal velocity  $\mathbf{v}(s, t)$  at  $\mathbf{X}(s, t)$  can be evaluated by using

$$416 \quad \mathbf{v}(s, t) = \partial_t \mathbf{X} = \Delta \mathbf{u}(s, t) + \sum_{n=1}^N \mathbf{S}(\mathbf{X}, \mathbf{X}_n, \varepsilon) \mathbf{F}_n(t), \quad (9)$$

417 where  $\Delta \mathbf{u}(s, t)$  is the bending flow (obtained in the “bending flow across the setae on the  
 418 antennule” section) prescribed at position  $s$  and time  $t$  without the presence of the seta, and  $\mathbf{F}_n(t)$   
 419 are the components of the strength of the regularized Stokeslet at position  $\mathbf{X}_n$  and time  $t$ ; the  
 420 regularized Stokeslet kernel  $\mathbf{S}$  is defined in Eq. S6 of the Supplemental Information.

### 421 **Setae are more sensitive to time-averaged feeding current**

422 Here we solve for the shape of the setal centerline,  $\mathbf{X}(s, t)$ , for the distal seta when placed in  
 423 the time-dependent bending flows. We use the magnitude of the setal tip displacement, defined  
 424 as

$$425 \quad \ell(t) = |\mathbf{X}(L_{\text{seta}}, t)|, \quad (10)$$

426 and the magnitude of the setal root curvature, defined as

$$427 \quad \kappa(t) = \left| \frac{\partial^2 \mathbf{X}(s, t)}{\partial s^2} \right|_{s=0}, \quad (11)$$

428 to relate the hydromechanical signal received by the seta (bending flow) with its  
 429 neurophysiological response (electric potentials). The tip displacement has been often used in the  
 430 previous experiments to estimate the angular displacement of seta (Fields et al. 2002; Yen et al.

431 1992). The root curvature has been hypothesized to be positively correlated with the chance of  
 432 sensing environmental signals, as discussed in Shen et al. (2020). In short, root curvature is  
 433 associated with shear displacement of the cuticle relative to the microtubule-filled dendrites  
 434 extending along the antennule and anchored to the inner wall of its cuticle at the setal root (fig. 5  
 435 of Shen et al. (2020)), opening the mechano-gated microchannels perforating the dendritic  
 436 membrane and leading to the transduction of mechanical signal into neurophysiological signal.

437 To determine the effect of the bending flow on the mechanical response of the seta, we first  
 438 consider the deformation pattern, tip displacement and root curvature of the distal seta when  
 439 subjected to the bending flow in the absence of prey (described in Fig. S6a in the Supplemental  
 440 Information). In Figs. 6a,b, we plot the distal setal shape at four selected time frames within a  
 441 beating cycle, after the time-averaged setal shape reaches steady state. We find that although the  
 442 magnitude of the oscillatory bending flow component ( $|\Delta\mathbf{u}_{\text{osc}}|$ ) across the distal seta is of the  
 443 same order as that of the time-averaged bending flow component ( $|\Delta\mathbf{u}_{\text{avg}}|$ ) the seta seems to  
 444 respond much more strongly to the time-averaged component, bending towards a fixed direction  
 445 while having a relatively small amplitude of oscillation.

446 To quantify the setal deformation, we plot magnitudes of the tip displacement ( $\ell$ ) and root  
 447 curvature ( $\kappa$ ) of the distal seta over 15 beating cycles in Figs. 6c,d. We characterize  $\ell$  and  $\kappa$  at  
 448 the  $N$ -th beating cycle by using their corresponding time-averaged responses over one beating  
 449 cycle of period  $T$ , denoted by

$$450 \quad \ell_{\text{avg}} = \frac{1}{T} \int_{(N-1)T}^{NT} \ell dt \quad (12)$$

451 and

452 
$$\kappa_{\text{avg}} = \frac{1}{T} \int_{(N-1)T}^{NT} \kappa dt, \quad (13)$$

453 and peak-to-peak amplitudes, denoted by  $\ell_{\text{pp}}$  and  $\kappa_{\text{pp}}$  (see Figs. 6c,d). The time-averaged setal  
454 responses,  $\ell_{\text{avg}}$  and  $\kappa_{\text{avg}}$ , are caused by the time-averaged bending flow component  $\Delta \mathbf{u}_{\text{avg}}$ , while  
455 the fluctuations around the average are induced by the oscillatory bending flow component  $\Delta \mathbf{u}_{\text{osc}}$ .  
456 When the response of the distal seta reaches steady state, we find from Figs. 6c and 6d that  $\ell_{\text{avg}}$   
457 is 2.86 times larger than  $\ell_{\text{pp}}$ , and that  $\kappa_{\text{avg}}$  is 1.45 times larger than  $\kappa_{\text{pp}}$ , in accord with the  
458 qualitative observation in the previous paragraph that the seta responds mostly to the time-  
459 averaged flow. This result is also consistent with our previous work (Shen et al. 2020), which  
460 explains why the bending response of setae behaves as a low-pass filter to flow velocity signals.

461 Our findings here have two implications on the prey detection of the feeding-current feeding  
462 copepods. First, at the most common range of beating frequencies ( $20 \text{ Hz} \leq f \leq 40 \text{ Hz}$ ), the  
463 effect of the oscillatory flow component on the hydrodynamic sensing is small. As the free-  
464 floating prey does not cause notable changes in the oscillatory flow components (see Fig. S7 in  
465 the Supplemental Information), the bending mechanism of the setae filters out less important  
466 hydrodynamic signals. Second, the time-averaged flow component is most important for prey  
467 detection. The presence of nearby prey does cause notable changes to the time-averaged flow  
468 across the setae (see Figs. 3f, 4f and 5e). The setal bending response, being a low-pass velocity  
469 filter (Shen et al. 2020), preserves the magnitude of this time-averaged signal and increases the  
470 chance of prey detection.

## 471 **Setal deformation due to free-floating prey**

### 472 *Free-floating prey near the distal seta*

473 We further examine how the proximal and distal setae respond to free-floating prey of  
 474 diameter  $100\ \mu\text{m}$ . We first consider the case in which the prey approaches the distal seta from  
 475 point B along the trajectory shown in Figs. 3a,b. Our results for setal bending are presented in  
 476 terms of three different prey detection criteria. The exact type of bending signal which leads to  
 477 copepod response remains unknown, and the different prey detection criteria correspond to  
 478 different possibilities.

479 The first criterion supposes that prey detection of copepods is related to the absolute change  
 480 in the tip displacement or root curvature of the seta due to the presence of the prey,  $|\Delta\ell_{\text{avg}}|$  or  
 481  $|\Delta\kappa_{\text{avg}}|$ , respectively defined as

$$482 \quad |\Delta\ell_{\text{avg}}| = |\ell_{\text{avg}}(NT) - \ell(0)| \quad (14)$$

483 and

$$484 \quad |\Delta\kappa_{\text{avg}}| = |\kappa_{\text{avg}}(NT) - \kappa(0)|. \quad (15)$$

485 The former has been widely used to relate the strength of external stimulus with setal  
 486 deformation (Fields et al. 2002; Yen et al. 1992), while the latter has been proposed by us to be  
 487 directly related to the physiological response of the copepods (Shen et al. 2020).

488 The second criterion supposes that the copepod seta adapts in sensitivity to the average level  
 489 of background signal caused by the feeding current. The seta only responds to the *relative*  
 490 change in deformation with respect to the background, expressed as

$$491 \quad R_{1,\text{disp}} = \frac{|\Delta\ell_{\text{avg}}|}{\ell_{\text{avg,w/o}}} \quad (16)$$

492 and

493 
$$R_{1,\text{curv}} = \frac{|\Delta\kappa_{\text{avg}}|}{\kappa_{\text{avg,w/o}}} \quad (17)$$

494 if the tip displacement and root curvature are used, respectively, where  $\ell_{\text{avg,w/o}}$  ( $\kappa_{\text{avg,w/o}}$ )  
 495 represents the magnitude of the time-averaged tip displacement (root curvature) without the  
 496 presence of the prey. Larger  $R_{1,\text{disp}}$  and  $R_{1,\text{curv}}$  are more likely to lead to prey detection.

497 The third criterion supposes that prey detection happens only when the change in  
 498 hydrodynamic signal induced by the prey can be distinguished from the time-dependent  
 499 fluctuations in signal due to the feeding current. We define this prey detection criterion in terms  
 500 of the setal tip displacement ratio as

501 
$$R_{2,\text{disp}} = \frac{|\Delta\ell_{\text{avg}}|}{\ell_{\text{pp,w/o}}}, \quad (18)$$

502 and in terms of the root curvature ratio as

503 
$$R_{2,\text{curv}} = \frac{|\Delta\kappa_{\text{avg}}|}{\kappa_{\text{pp,w/o}}}, \quad (19)$$

504 where  $\ell_{\text{pp,w/o}}$  and  $\kappa_{\text{pp,w/o}}$  are the peak-to-peak amplitudes of the tip displacement and root  
 505 curvature without the prey, respectively. It seems likely that copepods would not gain an  
 506 advantage by responding to these predictable fluctuations, so we hypothesize that the copepod  
 507 seta is more likely to sense the presence of the prey for  $R_{2,\text{disp}} > 1$  or  $R_{2,\text{curv}} > 1$ .

508 In Figs. 7a and 7b, we show the magnitude of the average tip displacement ( $\ell_{\text{avg}}$ ) and root  
 509 curvature ( $\kappa_{\text{avg}}$ ), respectively, as well as vertical bars representing their peak-to-peak ranges ( $\ell_{\text{pp}}$   
 510 or  $\kappa_{\text{pp}}$ ), along with the distance from the prey center to the centerline of the antennule over the

511 prey trajectory. Only results for the distal seta are presented, as the small hydrodynamic  
512 disturbance induced by the free-floating prey does not cause any notable change in the  
513 deformation pattern of the proximal seta.

514 We use the three aforementioned prey detection criteria to evaluate the hydrodynamic  
515 sensitivity of the distal seta. First, the detection of free-floating prey through absolute changes in  
516 the tip displacement or root curvature of the setae is feasible but highly unlikely. We find that the  
517 maximum changes in  $\ell_{\text{avg}}$  and  $\kappa_{\text{avg}}$  are 0.32 nm and  $1.2 \text{ m}^{-1}$ , respectively. According to past  
518 experiments performed on copepods, the threshold displacement to trigger setal response is at  
519 least 10 nm (Yen et al. 1992). Second, hydromechanical detection relative to average bending  
520 through  $R_{1,\text{disp}}$  or  $R_{1,\text{curv}}$  is feasible. The maximum  $R_{1,\text{disp}}$  and  $R_{1,\text{curv}}$  are 5.3% and 5.2%,  
521 respectively, which may give the copepod some information about the presence of prey. Last,  
522 detection relative to oscillatory background bending through  $R_{2,\text{disp}}$  and  $R_{2,\text{curv}}$  is unlikely; the  
523 peak-to-peak amplitudes of the tip displacement and root curvature without the prey are much  
524 larger than the changes in the corresponding time-averaged quantities.

#### 525 Free-floating prey near the proximal seta

526 We next consider the case in which the prey approaches the proximal seta on the antennule  
527 from point C along the trajectory shown in Figs. 4a,b. We expect that the stronger prey-induced  
528 disturbance in Figs. 4 and 5 may cause more changes in the deformation of each seta. In Fig. 8,  
529 we show the magnitude of the average tip displacement ( $\ell_{\text{avg}}$ ) and root curvature ( $\kappa_{\text{avg}}$ ), for both  
530 the distal and proximal seta, as well as vertical bars representing their peak-to-peak ranges ( $\ell_{\text{pp}}$ )

531 or  $\kappa_{pp}$ ), along with the distance from the prey center to the centerline of the antennule over the  
532 prey trajectory.

533 The tip displacement and root curvature of both setae follow similar trends. First, in the first  
534 beating cycle, we find that the prey, at Point C and 0.50 mm to the antennule, does not cause any  
535 notable changes in  $\ell_{avg}$  and  $\kappa_{avg}$  of the setae. This is due to the fact that even in the strong flow  
536 near the proximal of the antennule, the hydrodynamic disturbance induced by free-floating prey  
537 is too weak to be sensed by the nearest seta 10 prey radii away. Second, we note that the changes  
538 in tip displacement and root curvature induced by the entrained prey are not necessarily larger as  
539 the prey moves closer to the antennule. When approaching the proximal (distal) seta, the prey  
540 alters the surrounding current and reduces the deformation amplitude of distal (proximal) seta  
541 around the 15th (21st) beating cycle. Last, the maximum responses of the copepod setae may not  
542 occur at the shortest distance to the prey. This can be easily seen from the distal seta, for which  
543 the maximum changes in deformation occur at the 24th cycle, when the prey has travelled past  
544 the centerline of the antennule.

545 We again use the three prey detection criteria (Eqs. (14) to (19)) to assess whether free-  
546 floating prey near the proximal of the antennule can be detected. For the distal seta, we find that  
547 maximum changes in  $\ell_{avg}$  and  $\kappa_{avg}$  are very similar to those for prey near the distal of the  
548 antennule (compare Fig. 8c with Fig. 7a, and Fig. 8d with Fig. 7b). Therefore, we reach the same  
549 conclusions: prey detection through changes in setal deformation relative to average background  
550 bending is feasible, while detection through absolute changes in setal deformation and relative to  
551 oscillatory background bending is unlikely. For the proximal seta, we find that the maximum  
552 change in  $\ell_{avg}$  and  $\kappa_{avg}$  are significantly larger, while the maximum  $R_{1,disp}$  and  $R_{1,curv}$  are both

553 around 5%. Thus detection of absolute changes in setal deformation and relative to average  
554 background bending is possible, while detection through changes in setal deformation relative to  
555 oscillatory background bending remains unlikely.

## 556 *Discussion*

557 In this study, we have developed a numerical model that evaluates how the setae of a  
558 feeding-current feeding copepod respond to the hydrodynamic disturbance induced by the prey  
559 entrainment. We used the immersed boundary method to compute the feeding current induced by  
560 a tethered copepod by prescribing the beating strokes of its feeding appendages. We determined  
561 the changes in bending flows across the setae caused by free-floating prey. We found that the  
562 time-averaged component of the prey-induced flow disturbance is more relevant to the  
563 hydromechanical reception of copepods. The setae at the feeding appendage region suffer from  
564 the strongest background feeding current, and have the least relative change in bending flow  
565 induced by nearby prey. On the other hand, the distal seta on the antennule is subjected to the  
566 least background current, and is most sensitive to small changes in the prey-induced bending  
567 flow.

568 We used a relatively large prey size (100  $\mu\text{m}$  diameter) since smaller prey required finer  
569 numerical meshes and were not computationally feasible. However, our results can be used to  
570 gain insights into the sensed current caused by smaller free-floating prey in reality. In this study,  
571 100  $\mu\text{m}$  diameter free-floating prey do not cause any notable change in the bending flow across  
572 the setae on the antennule until the distance from the prey to the centerline of the antennule is  
573 less than 5 prey radii from the antennule. To estimate the prey detection distance for a prey of  
574 smaller radius ( $d/2$ ), we follow the approach of Visser (2001) to express the hydrodynamic

575 disturbance of a neutrally buoyant prey as  $\dot{\epsilon}(d/2)^3/r^2$ , at a distance  $r$  from the prey in a  
576 background flow characterized by strain rate  $\dot{\epsilon}$ . Assuming the same strain rate and the same  
577 disturbance magnitude needed for detection, this implies that detection distance scales as  
578  $(d/2)^{3/2}$ . This suggests that if the setae on the antennule are capable of detecting free-floating  
579 prey, the prey of 5, 10 and 25  $\mu\text{m}$  in radius will be detected within 1.6, 2.2 and 3.5 prey radii  
580 from the antennule, respectively.

581 We have evaluated the changes in deformation patterns of the setae on the antennule relative  
582 to those due to the background current, by coupling the method of regularized Stokeslets and  
583 inextensible Kirchhoff rod theory. We find that the copepod setae, as low pass velocity filters,  
584 are most sensitive to the time-averaged flow component of the feeding current. We proposed  
585 three prey detection criteria based on the changes in either tip displacement or root curvature to  
586 determine the copepod's prey detection capability. First, if characterized as an absolute change  
587 sensor, the copepod seta nearest to the prey is responsible for the prey detection. The small  
588 change in the deformation of the distal seta indicates that this detection mechanism is unlikely  
589 for the distal seta. Second, if characterized as a relative change sensor, the distal seta may be  
590 equipped with a long-ranged hydrodynamic sensitivity that assists the detection of the free-  
591 floating prey at the proximal region of the antennule. Third, if prey detection requires the prey-  
592 induced signal to be completely distinguished from the background fluctuations, both setae on  
593 the antennule have very short-range hydrodynamic sensitivity that requires the prey to touch or  
594 nearly touch the seta before being sensed.

595 Our three prey detection criteria imply different sensory mechanisms of the setae. Our results  
596 suggest that the mechanism of signal transduction can be better understood through experiments

597 that distinguish these criteria, which would ultimately shed light on how copepods sense their  
598 surroundings in the presence of not only self-generated noise such as the feeding current, but also  
599 environmental noise. For example, our results suggest that the proximal and distal setae have  
600 different amounts of changes in absolute magnitude compared to relative magnitude of bending  
601 and curvature. Both absolute and relative deflections of setae could be measured experimentally  
602 while observing triggering of physiological and behavioral responses of copepods, to see which  
603 is more important for sensing. If relative signals are more correlated with response, this implies  
604 that the distal setae are likely to be more important for sensing, even for particles that are closer  
605 to proximal setae. Interestingly, if  $R_{2,disp}$  or  $R_{2,curv}$  need not be greater than 1 for physiological  
606 and behavioral responses to be triggered, this implies that the triggering mechanism is somehow  
607 able to filter out the oscillatory signal of feeding current, which could be an important adaptation  
608 to allow sensing in the presence of noise.

609 We can also use the three prey detection criteria to assess the distance dependence of  
610 detection of free-floating prey. We find that free-floating prey generate minimal flow  
611 disturbances and are relatively hydrodynamically inconspicuous to copepods. They do not induce  
612 any changes in the responses of the distal and proximal seta unless they are less than 10 and 5.5  
613 prey radii away from the antennule, respectively. The short-ranged sensitivity of the setae on the  
614 antennule to free-floating prey may explain why most copepod feeding experiments using free-  
615 floating prey report that prey are missed by the setae and are detected upon reaching the vicinity  
616 of the feeding appendages (Gonçalves and Kiørboe 2015).

617 Finally, we point out the limitations of our current model and provide suggestions for future  
618 work. First, the copepod in our model is tethered in space, which only happens in laboratory  
619 setups. The prescribed swimming strokes of the feeding appendages do not guarantee that the

620 force- and moment-free conditions are satisfied automatically for a free-swimming and gravity-  
621 tethered copepods in nature, which might be investigated in further work. Second, the numerical  
622 method adopted in the our IB method relies on the fractional-step approach, in which the no-slip  
623 boundary condition is satisfied approximately and leads to a penetration of the flow into the  
624 copepod body and appendages. At zero to intermediate Reynolds number region, the prescribed  
625 boundary conditions could instead be satisfied exactly by using a direct forcing and unsplit  
626 method such as in Kallemov et al. (2016) and Usabiaga et al. (2017). Third, the setal deformation  
627 is solved in two steps, neglecting the presence of the setae filaments while determining the  
628 bending flows, then solving for setal deformation in the determined bending flow. Thus the  
629 accuracy of the setal deformation can be improved by incorporating its hydrodynamic effect on  
630 the flow through a finite element treatment and directly finding its deformation in the IB method.  
631 Last, we have focused on the sensing of hydrodynamic disturbances caused by the mismatch  
632 between the rigid body motion of a prey particle and the deformational flows of feeding currents.  
633 Another possible mechanism of sensing may be the phase mismatch of non-neutrally-buoyant  
634 particles with the oscillatory feeding current (Giuffre et al. 2019). In that case, additional  
635 hydrodynamic signals arising from the net force exerted on the fluid by the weight of the particle  
636 are unavoidable and could also be sensed by the copepod. Likewise, motile prey could be sensed  
637 not only through the disturbance to feeding current studied here, but also by sensing the flows  
638 caused by their motility. Detection of such particles that produce multiple hydrodynamic signals  
639 is worthy of future investigation.

640

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771 ***Acknowledgements***

772 **Authors' contributions**

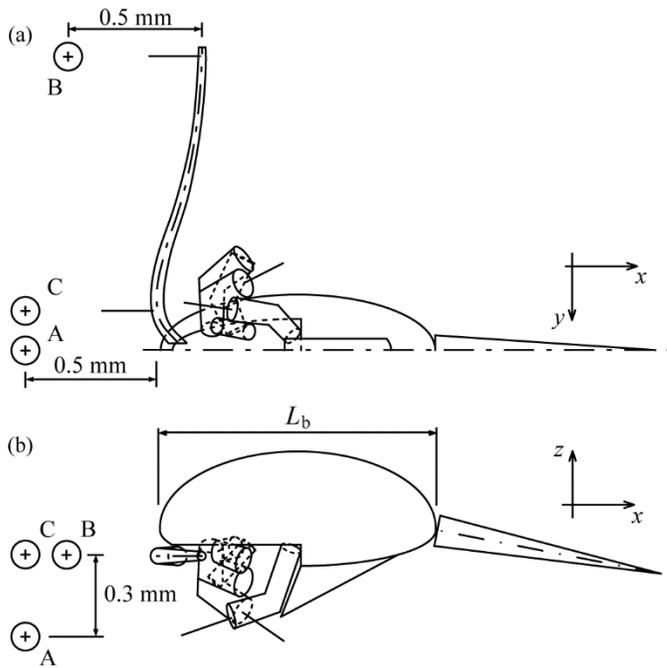
773 X.S. and H.C.F. conceived the study and wrote the manuscript; X.S. carried out the numerical  
774 simulations and performed data analysis; X.Y. assisted in the numerical simulation. M.  
775 coordinated the study and edited the manuscript. All authors participated in discussions and gave  
776 final approval for publication.

777 **Competing interests**

778 We declare we have no competing interests.

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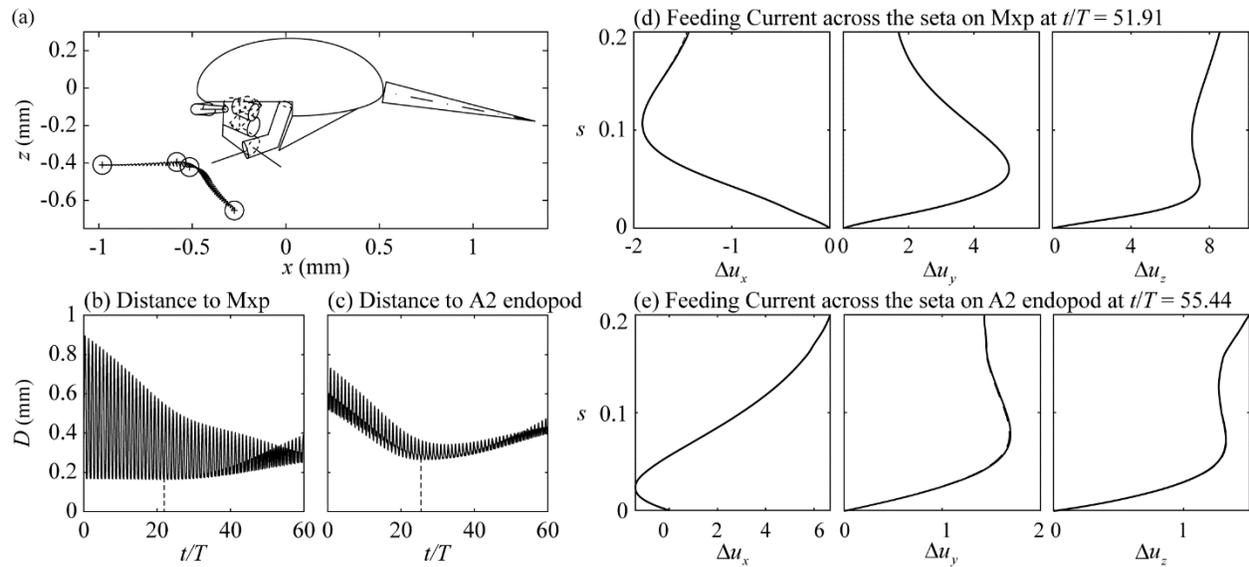
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782

783 Fig. 1. (a) Ventral-dorsal and (b) lateral views of the feeding-current feeding copepod model and  
 784 three starting prey positions. The cephalic appendages from left to right are the antennule,  
 785 antenna, mandible, first maxilla and maxilliped. Setae (all of length  $200 \mu\text{m}$ ) on the proximal and  
 786 distal of the antennule, the endopod of the antenna and the maxilliped, are indicated by straight  
 787 lines. Prey positions B and C are centered in front of the left distal and proximal antennule setae,  
 788 respectively, and A is on the sagittal plane.

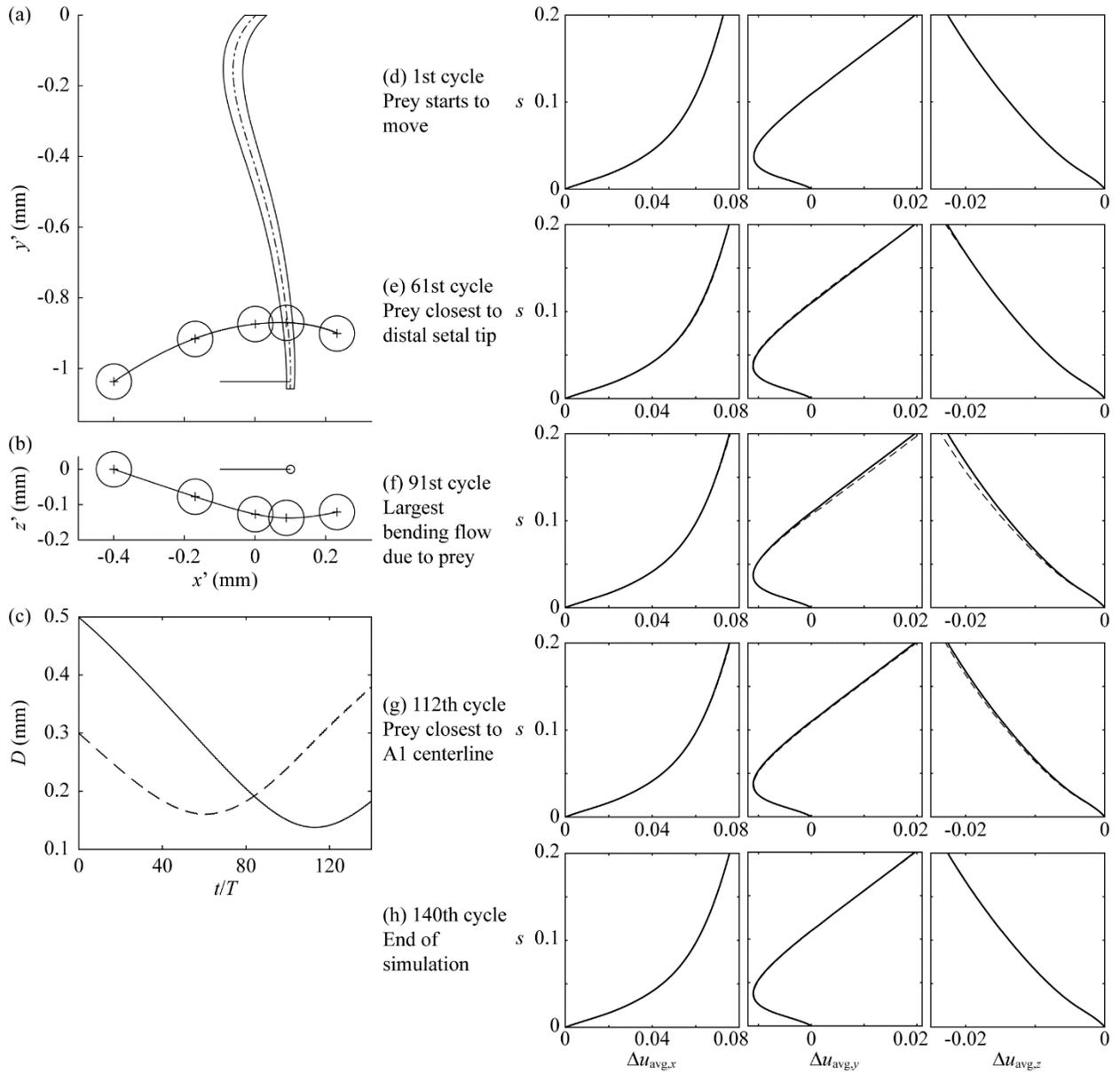
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790

791 Fig. 2. (a) Side view of the prey trajectory relative to the copepod over 60 beating strokes, for a  
 792 prey starting at Point A. The prey travels on the sagittal plane of the copepod. The distance from  
 793 the prey center to setae on (b) the maxilliped (Mxp) and (c) the endopod of the antenna (A2) as a  
 794 function of beating cycle. The instantaneous bending flow,  $\Delta \mathbf{u}(s, t)$ , plotted in terms of its  
 795 components in the  $x$ ,  $y$  and  $z$  direction in units of mm/s, across the setae on the (d) Mxp and (e)  
 796 A2 endopod, when the distance from the prey center to the corresponding seta is the smallest.  
 797 The arclength along the setal centerline ( $s$ , units of mm) is measured starting at the setal root.  
 798 The solid and dashed lines represent the feeding current without and with the presence of the  
 799 prey, respectively. Note that the dashed and solid lines show noticeable difference only in the  
 800 middle panel in (e).

801



802

803 Fig. 3. (a) Ventral-dorsal and (b) side views of the prey trajectory relative to the antennule (A1)

804 and distal seta over 140 beating strokes, for a prey starting at Point B. The large circles from left

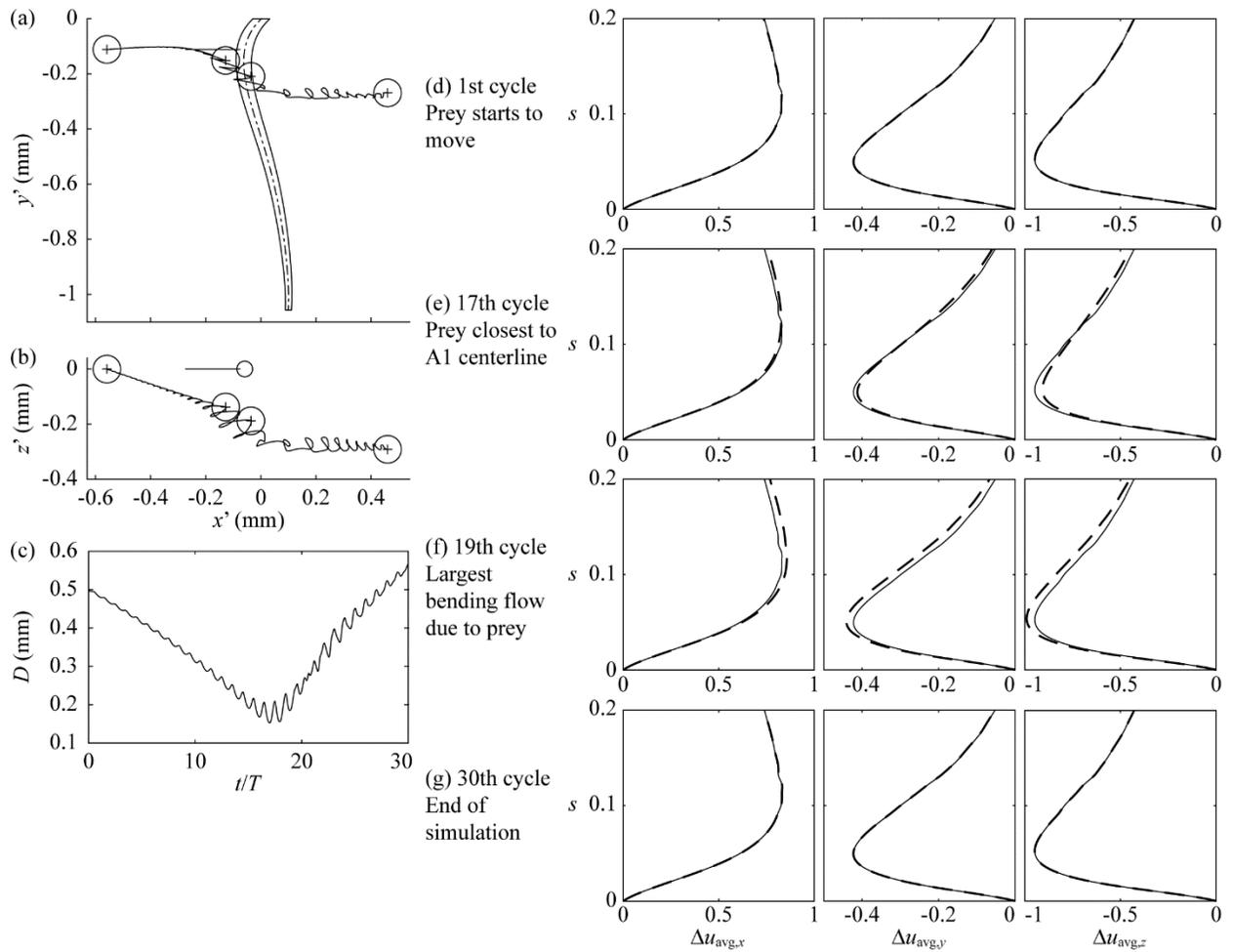
805 to right show the prey position at the end of the 1st, 61st, 91st, 112th and 140th beating strokes,

806 respectively. (c) The distance from the prey center to the tip of the distal seta on A1 (dashed line)

807 and A1 centerline (solid line) as a function of beating cycle. The time-averaged bending flow,

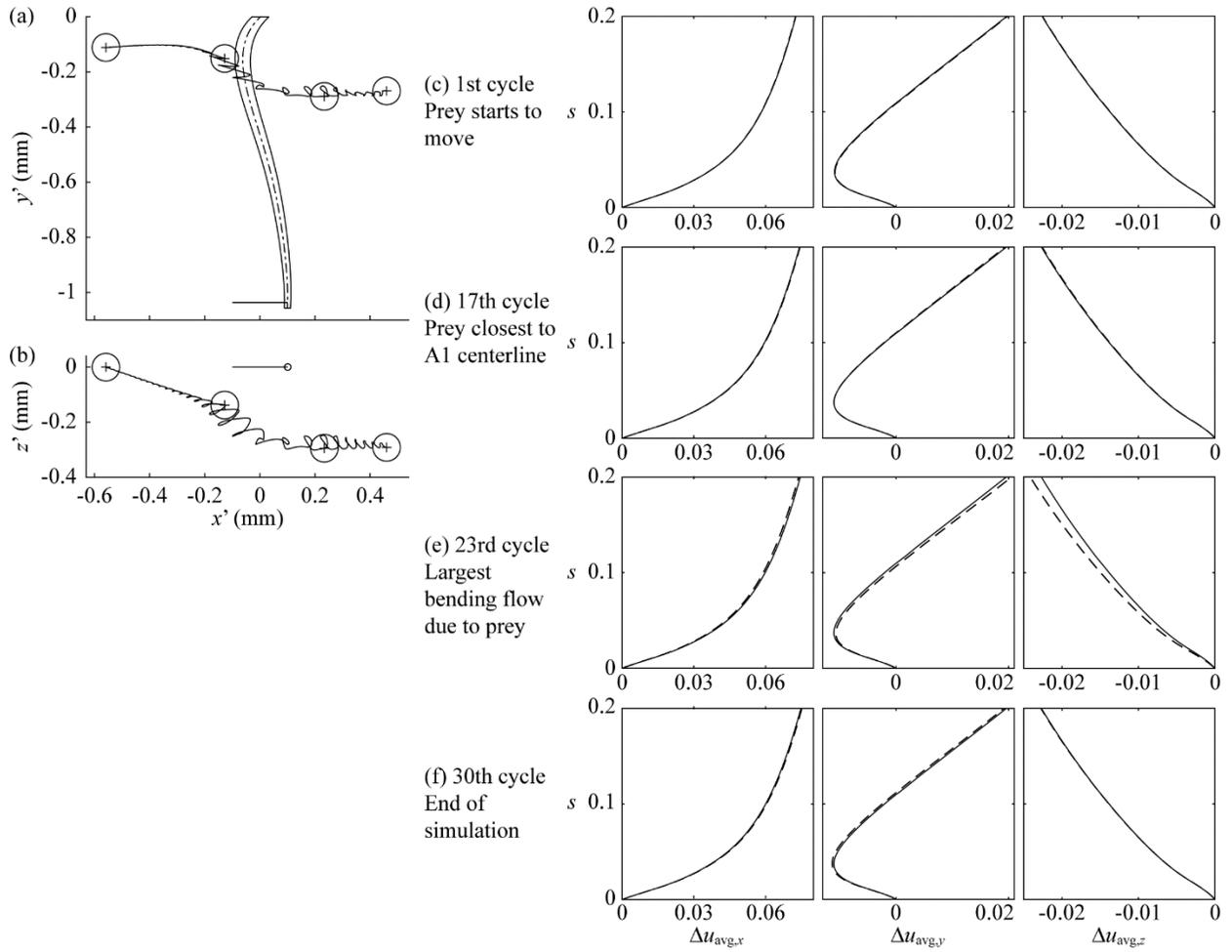
808  $\Delta \mathbf{u}_{avg}(s, NT)$ , plotted in terms of its components in the  $x$ ,  $y$  and  $z$  direction in units of mm/s,

809 across the left distal seta on A1 at the (d) 1st, (e) 61st, (f) 91st, (g) 112th and (h) 140th beating  
810 stroke. The arclength along the setal centerline ( $s$ , units of mm) is measured starting at the setal  
811 root. The black solid and dashed lines represent the feeding current without and with the  
812 presence of the prey, respectively.



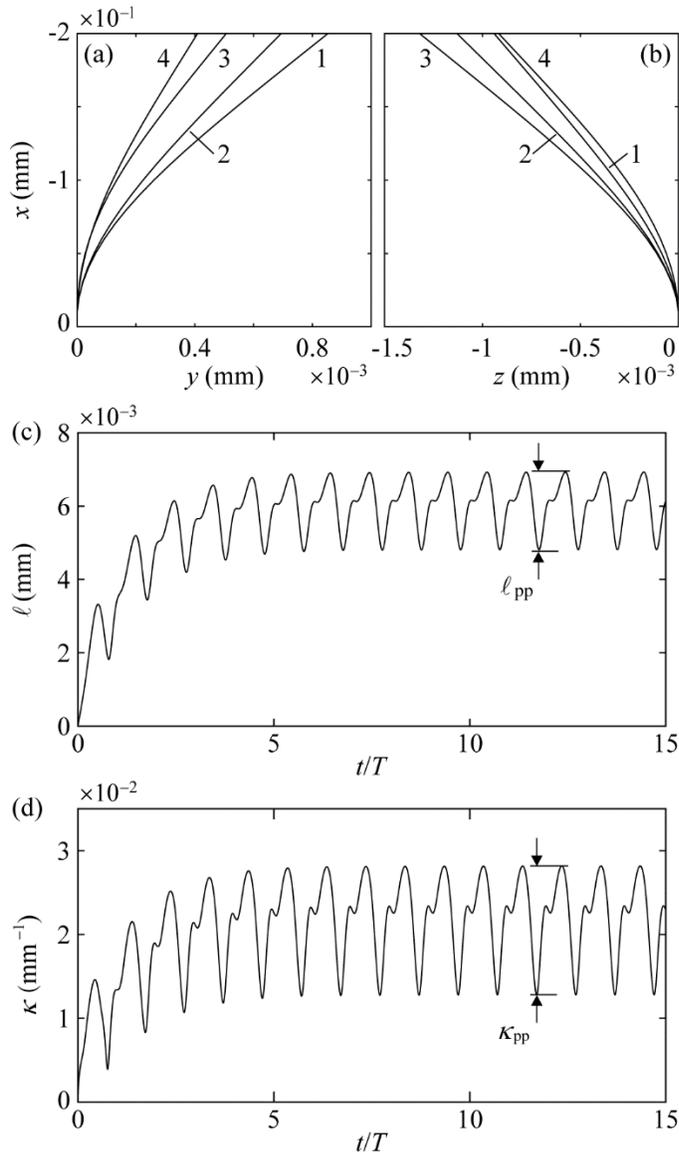
813

814 Fig. 4. (a) Ventral-dorsal and (b) side views of the prey center trajectory relative to the antennule  
 815 (A1) and proximal seta over 30 beating strokes, for a prey starting at Point C. The large circles  
 816 from left to right show the prey position at the end of the 1st, 17th, 19th and 30th beating strokes,  
 817 respectively. (c) The distance from the prey center to the A1 centerline as a function of beating  
 818 cycle. The time-averaged bending flow,  $\Delta \mathbf{u}_{\text{avg}}(s, NT)$ , plotted in terms of its components in the  
 819  $x$ ,  $y$  and  $z$  direction in units of mm/s, across the proximal seta on the left A1 at the (d) 1st, (e)  
 820 17th, (f) 19th, and (g) 30th beating stroke. The arclength along the setal centerline ( $s$ , units of  
 821 mm) is measured starting at the setal root. The black solid and dashed lines represent the feeding  
 822 current without and with the presence of the prey, respectively.



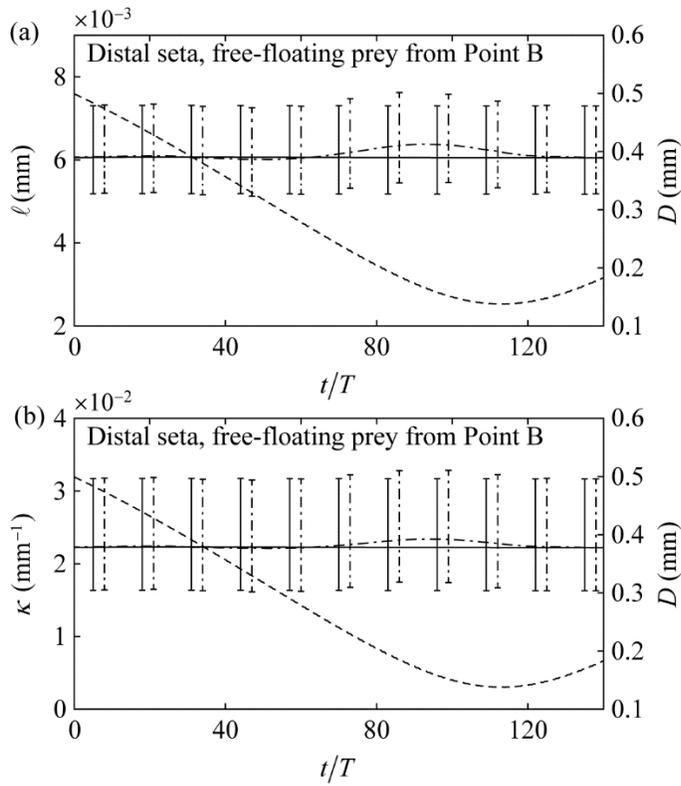
823

824 Fig. 5. (a) Ventral-dorsal and (b) side views of the prey center trajectory relative to the antennule  
 825 (A1) and distal seta over 30 beating strokes, for a prey starting at Point C. The large circles from  
 826 left to right show the prey position at the end of the 1st, 17th, 23rd and 30th beating strokes,  
 827 respectively. The time-averaged bending flow,  $\Delta \mathbf{u}_{\text{avg}}(s, NT)$ , plotted in terms of  
 828 its components in the  $x$ ,  $y$  and  $z$  direction in units of mm/s, the across the distal seta on the left  
 829 A1 at the (c) 1st, (d) 17th, (e) 23rd, and (f) 30th beating stroke. The arclength along the setal  
 830 centerline ( $s$ , units of mm) is measured starting at the setal root. The solid and dashed lines  
 831 represent the feeding current without and with the presence of the free-floating prey, respectively.



832

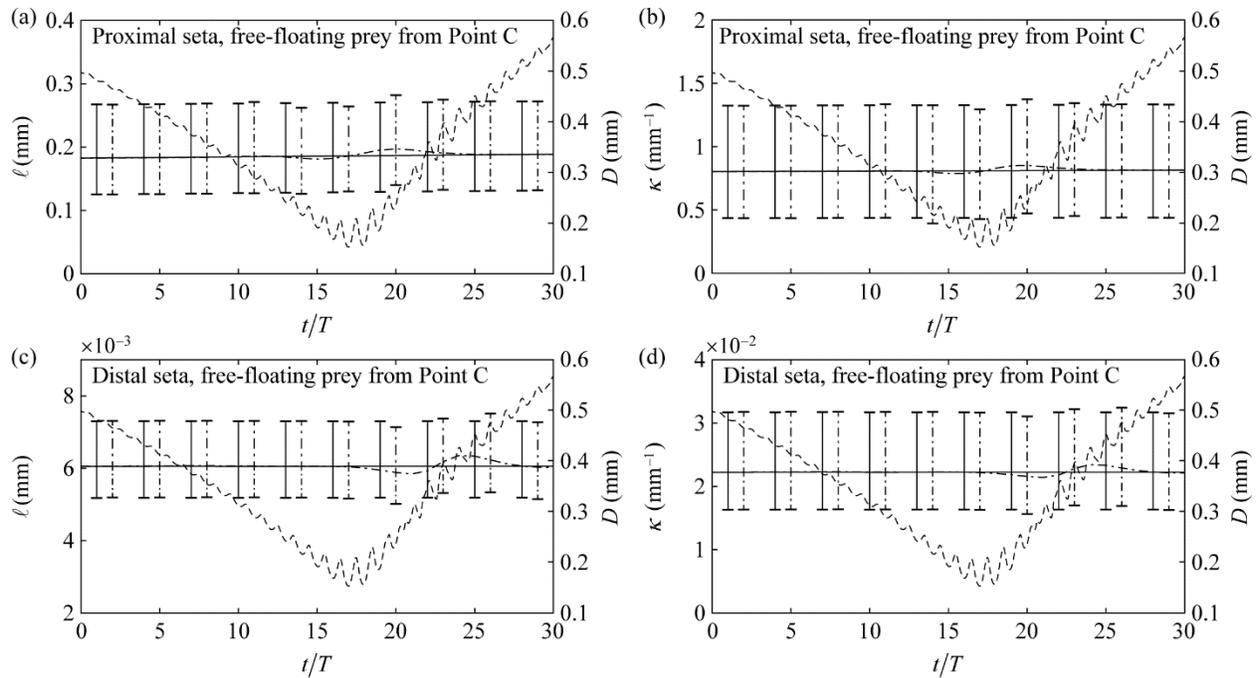
833 Fig. 6. (a,b) Projected views of the shape of the distal seta without the presence of the prey, after  
 834 the time-averaged bending flow,  $\Delta \mathbf{u}_{\text{avg}}(s, t)$ , across the distal seta reaches the steady state. A  
 835 sequence of shapes at equally spaced times during one cycle of the beating stroke are labeled by  
 836 the numbers 1-4. Plots of the magnitudes of (c) the tip displacement  $\ell$  and (d) root curvature  $\kappa$  of  
 837 the distal seta as a function of time  $t$  without the presence of the prey. The peak-to-peak  
 838 amplitudes of the tip displacement and root curvature are defined as  $\ell_{pp}$  and  $\kappa_{pp}$ , respectively.



839

840 Fig. 7. Plots of the (a) magnitude of tip displacement,  $\ell$ , and (b) magnitude of root curvature,  $\kappa$ ,  
 841 of the distal seta on the antennule (A1) as a function of beating cycle, for a free-floating prey  
 842 starting at Point B and moving along the trajectory shown in Figs. 3a,b. The solid lines in all  
 843 panels represent the setal response without the presence of the prey, while the dash-dotted lines  
 844 represent the setal response due to the entrained prey. The dashed lines in all panels denote the  
 845 distance from the prey to the A1 centerline,  $D$ . The vertical bars represent the peak-to-peak  
 846 amplitudes of the setal (a) tip displacement and (b) root curvature.

847



848

849 Fig. 8. Plots of the (a,c) magnitude of setal tip displacement,  $\ell$ , and (b,d) magnitude of root  
 850 curvature,  $\kappa$ , of the two setae on the antennule as function of beating cycle, for a free-floating  
 851 prey starting at Point C and moving along the trajectory shown in Figs. 4a,b and 5a,b. The solid  
 852 lines in all panels represent the setal response without the presence of the prey, while the dash-  
 853 dotted lines represent the setal response due to the entrained prey. The dashed lines in all panels  
 854 denote the distance from the prey to the centerline of the antennule,  $D$ . The vertical bars  
 855 represent the peak-to-peak amplitudes of the setal (a,c) tip displacement and (b,d) root curvature.