Physics of low Reynolds number locomotion

Shen, Xinhui

2018

Shen, X. (2018). Physics of low Reynolds number locomotion. Doctoral thesis, Nanyang Technological University, Singapore.

<https://hdl.handle.net/10356/88610>

<https://doi.org/10.32657/10220/47021>

**NANYANG
TECHNOLOGICAL
UNIVERSITY**

SINGAPORE

**PHYSICS OF
LOW REYNOLDS NUMBER LOCOMOTION**

SHEN XINHUI

**SCHOOL OF MECHANICAL AND AEROSPACE
ENGINEERING**

2018

**PHYSICS OF
LOW REYNOLDS NUMBER LOCOMOTION**

SHEN XINHUI

School of Mechanical and Aerospace Engineering

A thesis submitted to the Nanyang Technological University
in partial fulfilment of the requirement for the degree of
Doctor of Philosophy

2018

Abstract

The propulsion of microscopic organisms and their mechanisms of detecting and responding to the environmental cues are the areas of interest to many physicists and biologists. Microorganisms of complicated geometries induce interesting flow patterns when swimming in a viscous fluid. Their swimming trajectories can be affected by the hydrodynamic interactions with nearby boundaries. Moreover, microorganisms, as a component in the food chain, consistently trace the nutrients or preys while in the risk of being captured by its predators. It is important to understand how the flow induced by the prey plays a role in activating the sensory mechanism of the predator. The objectives of this thesis are two folded: firstly, to understand the boundary effects on nearby microswimmers, and secondly, to analyze the role of the mechanoreceptional sensor of marine copepods in detecting the presence of phytoplankton.

The influence of a plane boundary on a low-Reynolds-number swimmer is investigated using the multipole expansion and wall traction approach. Previous research frequently studied the boundary effect using image systems for flow singularities. In the proposed model, the boundary effect is expressed using a boundary integral representation over the traction on the boundary. Examining the traction pattern caused by a swimmer is found to yield physical insights into determining when the far-field multipole model is accurate. As a demonstration, the swimming velocities and the traction of a three-sphere swimmer initially placed parallel to an infinite planar wall is investigated. In the far field, the instantaneous effect of the wall on the swimmer is well approximated by that of a multipole expansion consisting of a force dipole and a force quadrupole. On the

other hand, the swimmer close to the wall must be described by a system of singularities reflecting its internal structure. These limits and the transition between them can be independently identified by examining the traction pattern on the wall, either using a quantitative correlation coefficient or by visual inspection. Furthermore, for non-constant propulsion, correlations between swimming stroke motions and internal positions are important and not captured by time-averaged traction on the wall, indicating that care must be taken when applying multipole expansions to study boundary effects in cases of non-constant propulsion.

Copepods sense the hydrodynamic disturbances induced by the swimming planktonic preys through the bending of their setae on the first antennule pair. This thesis presents a mechanical model in the Stokes limit to address the fundamental characteristics associated with the setal deformation in the copepod-prey detection. The presence of the copepod is first demonstrated to have non-negligible contributions on the flow profile across the distal seta. A comparison between the proposed model and previous models for the sensed flow that consider the velocity field or far-field strain rate due to free-swimming prey shows that those approximations fail to determine the flow profile across the distal seta with a decent accuracy. Moreover, the setal deformations induced by the flow is evaluated as a function of oscillating frequencies of the prey; lower frequency signals are found to lead to larger setal bending, described by a low pass filter. Finally, the effects of setal length, velocity amplitude and frequency of the prey on the response time of the setal bending are investigated. The short response time is consistent with the rapid behavioral and neurological response of copepods.

Acknowledgement

First and foremost, I would like to extend my greatest gratitude to my main supervisor: Assistant Professor Marcos from the School of Mechanical and Aerospace Engineering, Nanyang Technological University, who always encourages me with enthusiasm, monitors my progress and helps me overcome all difficulties. His strong support makes my research meaningful and memorable, and is the biggest gift in my life.

I would also like to take this opportunity to express my heartfelt appreciation to my co-supervisor: Associate Professor Henry C. Fu from the Department of Mechanical Engineering, the University of Utah. He explains the basic concepts to me, constantly orients me the right research directions and gives his valuable advices over the course of my study as a Ph.D. candidate. Without his help, my research could be immeasurably more difficult.

I would like to say thank you to Dr. Kong Tian Fook for his explanations and guidance in microfluidic experiment setups and all his necessary help during the experiment. I am also grateful to Marcos Research Team members Dr. Yao Xin, Dr. Tran Ngoc Phu, Dr. Tran Duc Quang, Tan Pei Yen, Koh Boon Yong James, and Benjamin Tay Zikai for all fruitful discussions.

Last but not the least; I appreciate Nanyang Technological University for offering me the Nanyang President's Graduate Scholarship, providing me with stipends and allowances throughout the Ph.D. study.

Contents

ABSTRACT.....	I
ACKNOWLEDGEMENT	III
LIST OF FIGURES	IX
LIST OF TABLES.....	XXI
LIST OF ABBREVIATIONS	XXIII
LIST OF NOTATIONS.....	XXV
CHAPTER 1	1
1.1 BACKGROUND	1
1.2 OBJECTIVES AND SCOPES.....	5
1.3 REPORT ORGANIZATION.....	6
CHAPTER 2.....	9
2.1 STOKES EQUATION	9
2.2 SINGULARITY	11
2.3 MULTIPOLE EXPANSION.....	15
2.4 THEORETICAL MODELING OF MICROSCALE LOCOMOTION	18
2.4.1 <i>Resistive Force Theory</i>	18
2.4.2 <i>Slender body theory</i>	19
2.4.3 <i>The Method of Regularized Stokeslet</i>	23
2.5 MODELING OF THE WALL EFFECTS ON MICROSWIMMERS.....	29
2.5.1 <i>The Image System Method</i>	30

2.5.2 Wall Traction Approach.....	31
2.5.3 Wall Effect on Microswimmers.....	33
2.5.4 Neglecting the Wall Effect	36
2.6 MECHANORECEPTION OF COPEPODS.....	39
2.6.1 Setal morphology.....	40
2.6.2 Antennular and setal neurology	43
2.6.3 Theoretical model.....	45
2.6.4 Experimental studies on copepod setae	57
2.7 RESEARCH GAP	62
CHAPTER 3	65
3.1 INTRODUCTION	65
3.2 THE SWIMMER MODEL	66
3.3 RESULTS	71
3.3.1 Instantaneous Response	71
3.3.2 Time-Averaged Response.....	82
3.4 DISCUSSION.....	87
3.5 SUMMARY	89
CHAPTER 4	91
4.1 INTRODUCTION	91
4.2 THE NUMERICAL MODEL.....	93
4.3 FLOW PROFILE ON THE SETA	96
4.4 DEFORMATION OF THE SETA	102
4.5 SUMMARY	117
CHAPTER 5	121

5.1 CONCLUSION	121
5.2 FUTURE WORK	123
PUBLICATIONS	125
APPENDIX A	127
APPENDIX B	129
APPENDIX C	131
APPENDIX D	133
REFERENCES.....	139

List of Figures

- Figure 2-1: Streamlines (solid lines) and isotachs (dashed lines) induced by (a) a Stokeslet, (c) a Stresslet, (d) a Rotlet, and (f) a potential dipole. (b) A Stokeslet dipole of two forces of equal magnitude and opposite directions $\mathbf{f}$ and $-\mathbf{f}$, which is separated by a displacement vector $\mathbf{b}$. (e) A source and a sink separated by a displacement $\mathbf{b}$ generates a potential dipole. Adopted from Visser [40]. 13
- Figure 2-2: Sketch of the geometry of the particle in (a) the near field and (b) the far field when viewed from the point $\mathbf{x}^p$. $\mathbf{x}^R$ is the reference point of the particle. dS is an infinitesimal area on the surface of the particle centered at $\mathbf{x}^0$. $\mathbf{n}$ is the unit directional vector normal to the surface. $\mathbf{d}$ is the displacement vector from $\mathbf{x}^R$ to $\mathbf{x}^0$. In the far field, the position of $\mathbf{x}^R$ and $\mathbf{x}^0$ cannot be distinguished. 16
- Figure 2-3: Dimensionless displacement in the x -direction per cycle, using paddle length as the characteristic length, of a robotic two-paddle swimmer as a function of stroking angle predicted at slenderness ratios of 0.02 (dotted line), 0.06 (dashed line), and 0.1 (dotted-dashed line), compared with experimental measurements (circle markers) and values predicted using RFT (solid line without markers). Adopted from Huber, et al. [91]. 21
- Figure 2-4: Dimensionless velocity, power, and torque for three different strains of bacteria, namely, *V. alginolyticus* (left column), *C. crescentus* (middle

column) and *E. coli* (right column). Experimental data are indicated by the dashed line. Theoretical predictions computed by RFT and SBT are displayed as bars, with the uncertainties arising from the spreads in geometrical parameters of the bacteria. Adopted from Chattopadhyay and Wu [93].22

Figure 2-5: The resistive force coefficients $C_T = \mathbf{F}^D/\mathbf{v}$, $C_R = \mathbf{M}/\mathbf{\Omega}$, where $\mathbf{F}^D$ and $\mathbf{M}$ correspond to the total force and torque on the ellipsoid. The subscripts 1 and 2 indicates when the ellipsoid is moving parallel to the major and minor axis, respectively. The superscript *A* means analytical solution from [77]. ε is the regularization parameter. Δs is the average spacing between adjacent regularized Stokeslets. (a) C_{T1} , (b) C_{R1} , (c) C_{T2} and (d) C_{R2} are normalized by their corresponding analytical values and plotted against the number of regularized Stokeslets. Adopted from Hyon, et al. [36].25

Figure 2-6: (a) Bending energy, (b) Kinetic energy, (c) Twisting energy, (d) Total energy of an elastic rod, as computed by the Navier Stokes case with a virtual radius of $c = 2\Delta s$ (solid black line) and simulations of the Regularized Stokeslet formulation for the regularization parameter $\varepsilon = 5\Delta s, 6\Delta s, 7\Delta s, 8\Delta s$. Δs is the average spacing between the regularized Stokeslets. The energy is in units of kT , where k is the Boltzmann's constant and T is the temperature in degrees Kelvin, set to room temperature. Adopted from Olson, et al. [99].26

Figure 2-7: Dimensionless thrust for helical flagella as a function of dimensionless pitch λ , for helix length $l = 20a^{\text{flagellum}}$ and filament radius $a^{\text{filament}} = a^{\text{flagellum}}/16$ as obtained by: experiment (solid black circles), method

of regularized Stokeslet (solid black lines), slender body theory of Lighthill (solid blue lines), RFT of Gray and Hancock (green lines), and RFT of Lighthill (dashed blue lines). MRS and SBT results are very similar so the curves can be difficult to distinguish. Adopted from Rodenborn, et al. [100].
.....27

Figure 2-8: Error of (a, b) the centerline distribution of the regularized Stokeslets and (c, d) the slender body theory as compared to the surface distribution of the regularized Stokeslets. Panels (a) and (c) represent the case of a rotating flagellum pump while panels (b) and (d) present a swimming bacterium. The error (shown in the color bar) is proportional to the circle size. Isotachs (solid lines) show interpolated errors. Adopted from Martindale, et al. [38].28

Figure 2-9: A Stokeslet at $\mathbf{x}^0$ and its image system at $\mathbf{x}^{0*}$ with the infinite wall located at $x_1 = 0$ plane. An infinitesimal area dS on the wall is centered at $\mathbf{x}^w$.
.....31

Figure 2-10: (a) The experimental procedures: the mixture of *E. coli* and fluid is deposited between to glass slides with a separation distance of $2H = 100 \mu\text{m}$. The cells are counted as a function of distance z to the lower slide. (b) The distribution of cells is plotted against z for two experiments (blue and red colors). The markers represent the experimental data, the lines the multipole model prediction. Adopted from Berke, et al. [107].34

Figure 2-11: The horizontal, vertical, and rotational velocities (v_x , v_y and Ω_y) of (a) the four Janus swimmers and (b) the three polar swimmers are plotted against the normalized closest distance to the wall. The variable h is the distance from the swimmer' center to the wall normalized with the radius of the

swimmer, and l is the length of the cylindrical rod normalized with the radius of the swimmer. The lines present the full numerical solutions, the markers the multipole model approximations. Adopted from Spagnolie and Lauga [66].	34
Figure 2-12: Dimensionless swimming speed (circle markers) of <i>E. coli</i> as a function of the surface-to-cell distance, non-dimensionalized with respect to cell radius taken to be 1 μm . Also shown are the boundary element method solutions of Ramia, et al. [33] at cell orientation angles of 0° (solid line) and 45° (dotted line). Adopted from Frymier, et al. [50].	37
Figure 2-13: Normalized force $FD/F_\infty D$ as a function of normalized distance from the wall, for a sphere of radius A translating between parallel chamber walls where the half-depth H . Square markers indicate the results of Ramia, et al. [33], while cross markers indicate the computations by Gillies, et al. [110] corresponding to the half-depth of the chambers used. Adopted from Gillies, et al. [110].	37
Figure 2-14: Hair on the pedipalp of a scorpion. Adopted from Barth, et al. [117].	41
Figure 2-15: The first antennule of <i>Gaussia princeps</i> . Adopted from Fields, et al. [118].	41
Figure 2-16: Setae mechanoreception model proposed by Fields [126]. Left panel: the dendrites extend along the setal axis and are connected to the cuticle by linking proteins. Right panel: when the displacement is slow (in the order of 10 msec or more), the origin of the linking proteins can move within the	

membrane, reducing the tension on the ion channel and the sensitivity. If the angular displacement is rapid, the protein does not have enough time to respond and the channel is pulled open.44

Figure 2-17: Detection of (a) a sinking particle and (b) a self-propelled body by a raptorial copepod of antennular length L^{ant} . The head tip and the antennular tip are located at $[R^0, \theta^0]$ and $[R^b, \theta^b]$ with respect to the prey in the polar coordinate system. The prey of radius a^{prey} is sinking/swimming at the speed v^{prey} . $\mathbf{u}$ is the flow velocity induced by the prey, φ the swimming direction of the self-propelled body. Adopted from Visser [40].46

Figure 2-18: The spring damper system for modeled arthropod hair and pedipalpl. Adopted from Humphrey and Barth [70].49

Figure 2-19: Flow fluid velocity V_f above the cylindrical substrate, normalized with the background flow velocity U_0 , at (a) 10Hz and (b) 500 Hz. Other parameters are $\omega t = \pi/2$, preycopepod detection can be governed by the steady Stokes equation. $\nu_{air} = 1.59 \times 10^{-5} \text{ m}^2/\text{s}$ and $\nu_{water} = 8 \times 10^{-7} \text{ m}^2/\text{s}$. y is measured from the surface of the substrate. The solid and dashed lines are the flow profiles in air and water, respectively. Adopted from Devarakonda, et al. [68].54

Figure 2-20: (a) The maximum angular displacement of cylindrical seta of length 500 μm and diameter 7 μm attached to a cylindrical substrate when subjected to a background water oscillation with peak velocity of 5 mm/s. The damping constant of the seta is assumed to be 0, the spring constant 4×10^{-12} N. (b) bode plots for the maximum angular displacement of seta, normalized with the mean water displacement, for six setae with different lengths.

Adopted from Lenz and Hartline [73].	55
Figure 2-21: Extracellular recording system setup to measure the electric potential across the copepod due to the neural impulse transmitted along the first antennule. The copepod is clamped by forceps and immersed into mineral oil while its first antennule is in contact with sea water. Hydromechanical disturbance is generated by a vibration sphere connected to a transducer. Adopted from Gassie, et al. [142].	60
Figure 2-22: Threshold sensitivities for (a) <i>Pleuromamma xiphias</i> (crosses) and <i>Euchaeta rimana</i> (open symbols) females between 30 and 1,100 Hz and for (b) <i>Labidocera madurae</i> between 100 and 1800Hz. The vertical axis represents the maximum water displacement induced by a vibrating sphere. The horizontal axis represents the frequency of the vibrating sphere. (a) is adopted from Lenz and Yen [115], (b) from Hartline, et al. [60].	60
Figure 2-23: (a) Maximum angular displacement of distal seta on the antennule when subjected to a water jet. The letter A represents the seta orientation with no stimulation, and each subsequent letter represents a 2 msec increase in the length of time the solenoid remained open. The physiological responses of setae, when subjected to either distal or proximal oriented water jet, are plotted against (b) the angular displacement and (c) the water jet speed. Each physiological response curve is normalized with its maximum response. Adopted from Fields, et al. [118].	61
Figure 3-1: A three-sphere swimmer and its image system with respect to an infinite planar wall. Spheres with radius a are labeled $\alpha = 1, 2, 3$ from left to right. The two arms l^{12} and l^{23} perform periodic motions. Initially, the	

swimmer is placed parallel to the wall ($\theta = \pi/2$).....	67
Figure 3-2: The change in swimming velocity due to the wall (solid line), $v_{20} - v_0$, free, and the wall-induced velocity (dashed line), u_{20}^* , versus the (nondimensional) initial distance from the wall at (a) $t = \pi/2$ and (b) $t = 3\pi/2$. Note that both lines coincide.	71
Figure 3-3: The log-log plots of the magnitude of velocities versus the (nondimensional) initial distance from the wall at (a) $t = \pi/2$ and (b) $t = 3\pi/2$. The solid blue line represents the exact wall-induced velocity of (i) sphere 1, (ii) sphere 2, (iii) sphere 3, and (iv) the swimmer. The dashed green line represents the corresponding dipolar model. The dotted red line represents the corresponding combination of the dipole and quadrupole model.....	72
Figure 3-4: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 2.0$. In each panel, the values are scaled by the largest magnitude traction in that panel.	77
Figure 3-5: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 1.5$. In each panel, the values are scaled by the largest magnitude traction in that panel.	77
Figure 3-6: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.8$. In each panel, the values are scaled by the largest magnitude traction in that panel.	78

Figure 3-7: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.6$. In each panel, the values are scaled by the largest magnitude traction in that panel. 78

Figure 3-8: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.4$. In each panel, the values are scaled by the largest magnitude traction in that panel. 79

Figure 3-9: (a) The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.2$. (b) The instantaneous traction exerted by individual spheres at $h = 0.2$. In each panel, the values are scaled by the largest magnitude traction in that panel. 79

Figure 3-10: (a) The traction plot in the x_1 direction (left) and in the x_2 direction (right) of a Blakeslet dipole when the only nonzero component of dipole strength is $f_2 d_2 = 1$. The dipole is placed at a (nondimensional) distance $h = 1$ from the wall. In each panel, the values are scaled by the largest magnitude traction in that panel. (b) Instantaneous traction correlation coefficient, which quantifies the correlation between the instantaneous traction due to the swimmer and a Stokeslet dipole with corresponding dipole strength $\sum_{\beta} \mathbf{f}^{\beta} \mathbf{d}^{\beta}$ at $t = \pi/2$ (solid line) and $t = 3\pi/2$ (dashed line). 80

Figure 3-11: (a) Semilog and (b) absolute log-log scale of the normalized time-averaged wall-induced velocity of a three-sphere swimmer in the x_2 direction $u_2 * (\mathbf{x}_0)/v_{0, \text{free}}$ (solid blue line) and a Stokeslet quadrupole

model (dotted red line) versus the (nondimensional) initial distance from the wall.....82

Figure 3-12: The time-averaged traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at the (nondimensional) initial distance from the wall $h = 20.0$. In each panel, the values are scaled by the largest magnitude traction in that panel.84

Figure 3-13: The time-averaged traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at the (nondimensional) initial distance from the wall $h = 5.0$. In each panel, the values are scaled by the largest magnitude traction in that panel.84

Figure 3-14: The time-averaged traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at the (nondimensional) initial distance from the wall $h = 0.4$. In each panel, the values are scaled by the largest magnitude traction in that panel.85

Figure 3-15: (a) The traction plot in the x_1 direction (left) and in the x_2 direction (right) of a Blakeslet quadrupole when the only nonzero component of quadrupole strength is $f_2 d_2 d_2 = 1$. The quadrupole is placed at a (nondimensional) distance $h = 1$ from the wall. In each panel, the values are scaled by the largest magnitude traction in that panel. (b) Traction correlation coefficient quantifying the correlation between the time-averaged traction due to the swimmer and a Stokeslet quadrupole with corresponding quadrupolar strength $\sum_{\beta} \mathbf{f}^{\beta} \mathbf{d}^{\beta} \mathbf{d}^{\beta}$85

Figure 3-16: (a) Velocity correlation coefficient and (b) stress correlation

coefficient quantifying the correlation between the unbounded swimmer and a Stokeslet dipole at $t = \pi/2$ (solid lines) and $t = 3\pi/2$ (dashed lines). 89

Figure 4-1: The orientation of the prey (filled black circle), specified by the distance d and angles θ and ϕ in the copepod's body-fixed frame. The x_2 axis is pointed into the paper. The copepod consists of a ellipsoid of major axis length L^{maj} and minor axis length L^{min} , a long cylindrical first antennular pair of length $2L^{\text{ant}}$ and radius R^{ant} and a right distal seta (black line) of length L^{seta} and radius R^{seta} . The prey swims at a velocity of $\mathbf{v}^{\text{prey}}$. The figure inset shows the ventral view of *Acartia clausi*, modified from <http://investigacion.izt.uam.mx/ocl/Zooplankton/?M=A> (accessed 16 Jun 2018). 94

Figure 4-2: The lateral flow profile $u_{\perp}$ along the copepod's distal setal axis x when the prey is at four different orientations with respect to the copepod (specified as d , θ and ϕ). $u_{\perp}$ is scaled with the dipolar velocity at the copepod's center $v^{\text{prey}}(r^{\text{prey}}/d)^2$. x is scaled with the setal length L^{seta} . The solid lines represent the lateral flow velocity. The black dashed, dash-dot and dotted line represent the lateral velocity components due to the prey, first antennule and ellipsoidal body of the copepod, respectively. The grey dashed line represents the lateral velocity components due to the free swimming prey. Note that dashed black and dashed grey lines overlap with each other. The figure insets show the corresponding lateral flow velocities up to 5 times L^{seta} 97

Figure 4-3: Total error of Visser's model at (a) $d/L^{\text{maj}} = 0.9$ and (b) $d/L^{\text{maj}} = 10.5$ and (c) the error of the far-field strain approximation $d/L^{\text{maj}} = 10.5$. The size

of circles at each prey orientation is proportional to $\log_{10} (Er/100+1)$ 101

Figure 4-4: Shape of the distal seta normalized with $L^{\text{seta}} = 0.20$ mm when the prey oscillates at (a) $f = 0.1$ Hz and (b) $f = 100$ Hz. The time sequence over at the first cycle of oscillation is given by number 1 to 8. At (c)(e) $f = 0.1$ Hz and (d)(f) $f = 100$ Hz, the instantaneous curvature of the right distal setal root $\kappa(0,t)$ and its transient and steady-state response components are over the time t . The solid lines represent the instantaneous setal root curvature, the dashed lines the steady-state curvature component, the dash-dot lines the transient curvature component. The dotted lines are sine waves representing the swimming velocity of the oscillatory prey. 106

Figure 4-5: The loglog plot of the normalized minimum oscillation amplitude of the prey which triggers the detection threshold of the seta $v^{\text{prey,min}}/v^{\text{prey,0}}$ as a function of the oscillation frequency f , where $v^{\text{prey,0}}$ is the value of $v^{\text{prey,min}}$ for the 200 μm seta to hit the detection threshold. The solid black line represent the 200 μm seta, the dashed black line the 100 μm seta, and the dash-dot line the 50 μm seta. 110

Figure 4-6: (a) Semi-log plot of the response time t^r of the 200 μm distal seta as a function of the sperm number Sp (via varying frequency). The black, red and blue solid lines correspond to t^r at constant oscillation speed of the prey denoted as $v^{\text{prey}}/v^{\text{prey,0}} = 2, 10$ and 100 , respectively. (b,c) Loglog plot of t^r of the 200 μm distal seta (solid lines) as a function of v^{prey} normalized with the minimum velocity which triggers the detection threshold of the seta $v^{\text{prey}}/v^{\text{prey,min}}$ at $Sp = 0, 2$ and 5 , respectively. In all panels, the blue dashed and dash-dot lines represent $t^r = 1/(4f)$ and $t^r = 1/(2f)$, respectively; the green

dashed line represents $t^r = 1/(2\pi f v^{\text{prey}}/v^{\text{prey,min}})$; the red dashed and dash-dot lines represent $t^r = [\tau/(\pi f v^{\text{prey}}/v^{\text{prey,min}})]^{1/2}$ and $t^r = 1/[\pi f (v^{\text{prey}}/v^{\text{prey,min}})^{1/2}]$, respectively. 112

Figure 4-7: The curvature responses of the setal root in the simplified 1D model $\kappa(0, t)$ are plotted against the time t for (a) $Sp = 0.7$ and (b) $Sp = 5.0$. The solid, dashed and dash-dotted lines represents the solution of this 1D model, transient and steady-state pieces, respectively. The blue lines represent the cases that the maximum magnitude of driving force $\mathcal{F}$ equals to $\mathcal{F}^{\text{thr}}$, so the maximum magnitude of the setal root curvature in this 1D model hits the prey-detection threshold κ^{thr} . The green dashed lines in (a) represents the case that $\mathcal{F} \gg \mathcal{F}^{\text{thr}}$ and $\omega t^r/Sp^4 \gg 1$ such that the setal response happens close to 0 but after the transient response dies out. In contrast, the red lines represent the case that $\mathcal{F} \gg \mathcal{F}^{\text{thr}}$ and $\omega t^r/Sp^4 \ll 1$, so the setal root curvature needs much shorter time to reach κ^{thr} . The time taken for the setal root curvature to reach κ^{thr} is denoted as t^r 115

Figure B-1: (a) Instantaneous ($t = \pi/2$) and (b) time-averaged traction correlation coefficient by varying the square of side length Nh on the wall. 129

Figure C-1: The velocity convergence test results for (a) a free swimming prey and (b) a copepod under the flow induced by the prey. The horizontal axis and legend represent the number of regularized Stokeslets and the normalized regularization parameters of (a) the prey and (b) the copepod. 137

List of Tables

Table 1: Morphological characteristics of setae on the distal section of the first antennule of *Pleuromamma xiphias*. Adopted from Weatherby, et al. [54].42

Table 2: The hydrodynamic characteristics of planktonic preys.....56

List of Abbreviations

BEM	The boundary element method
EBT	The Euler beam theory
MRS	The method of the regularized Stokeslet
PIV	The particle image velocimetry
RFT	The resistive force theory
SBT	The slender body theory
TFM	The traction force microscopy

List of Notations

Chapter 2

Re	The Reynolds number
Sr	The Strouhal number
p	The fluid pressure
t	The time
T_f	The characteristic fluid time scale
f	The oscillation frequency of the fluid
ρ	The density of the fluid
ρ_{hair}	The density of arthropod's filiform hair
$\mathbf{x}^p$	An arbitrary point
$\mathbf{x}^R$	The reference point
$\mathbf{x}^0$	A singularity point
$\mathbf{x}^{0*}$	The image location of the singularity
$\mathbf{x}^c$	A point on the centerline
$\mathbf{x}^w$	The point on the infinite wall
$\mathbf{b}$	The displacement vector from one singularity to the other
$\mathbf{d}$	The displacement vector from the reference point to the singularity point
r	The distance between two points
r^*	The distance from the image location of a point to the other point
h	The distance from the Stokeslet to the planar wall
R	The distance to the prey

R^b	The distance from the antennular tip to the prey
R^0	The distance from the head tip to the prey
R^*	The distance when the prey is detected by the copepod
z	The distance measured from the lower plate
H	The half-depth of the chamber/two parallel plates
y	The distance from the arthropod's filiform hair base to a point on the hair
Δs	The average spacing between adjacent regularized Stokeslets
$\mathbf{e}$	The unit directional vector
$\mathbf{n}$	The unit directional vector normal to a surface
$\mathbf{e}_{ }$	The unit tangential vector of the flagellum
$\mathbf{e}_{\perp}$	The unit normal vector of the flagellum
$\hat{R}^b$	The unit direction vector from the prey to the antennular tip
$\hat{R}^0$	The unit direction vector from the prey to the head tip
a^{filament}	The radius of the filament
c	The virtual radius of the rod
A	The radius of the sphere
a^{prey}	The radius of the prey
d	The diameter of the arthropod's filiform hair
L	The characteristic fluid length scale
s	The curvilinear position along the centerline
λ	The pitch length of the flagellum
l	The length of the flagellum/hair/seta
L^{ant}	The length of the first antennule of the copepod
Amp	The oscillation amplitude of a pendulum

dS	An infinitesimal area
$\mathbf{F}$	The body force
$\mathbf{F}^D$	The drag force
F_{hair}	The force per unit length on the arthropod's filiform hair
$F_{\text{hair,D}}$	The force component on the cylinder due to the fluid drag
$F_{\text{hair,VM}}$	The force component on the cylinder due to the virtual mass of the fluid
$\boldsymbol{\sigma}$	The fluid stress
$\mathbf{M}$	The total moment
T_{hair}	The torque on the arthropod's filiform hair
$\mathbf{T}$	The traction on the wall
$\mathbf{f}$	The strength of a Stokeslet
$\mathbf{g}$	The strength of a Stokeslet dipole
$\mathbf{q}$	The strength of a potential dipole
Q	The strength of a source
$\mathbf{S}$	The kernel relates the fluid velocity with a Stokeslet
$\mathbf{D}$	The kernel relates the fluid velocity with a Stokeslet dipole
$\mathbf{P}$	The kernel relates the fluid pressure with a Stokeslet
$\mathbf{St}$	The kernel relates the fluid velocity with the image system of a Stokeslet
$\mathbf{T}$	The kernel relates the traction on the wall with the Blakeslet
U	The characteristic fluid velocity scale
$v_{\parallel}$	The tangential velocity component
$v_{\perp}$	The normal velocity component
$\mathbf{u}$	The fluid velocity

$\mathbf{u}^{\text{source}}$	The fluid velocity due to a point source
$\mathbf{u}^*$	The fluid velocity due to the image system of the Stokeslet
$\mathbf{u}^s$	The fluid velocity due to a Stokeslet
$\mathbf{u}^{s*}$	The fluid velocity due to an image Stokeslet
$\mathbf{u}^{\text{pd}}$	The fluid velocity due to an image potential dipole
$\mathbf{u}^{\text{sd}}$	The fluid velocity due to an image Stokeslet dipole
V_f	The velocity of the flow
V_c	The velocity of the cylinder
V_r	The relative velocity of the fluid defined as $V_r = V_f - V_c$
v_x	The velocity component of the swimmer parallel to the wall
v_y	The velocity component of the swimmer perpendicular to the wall
Ω_y	The angular velocity component of the swimmer
u^{thres}	The threshold detection speed of the copepod
$\delta u_{\perp}$	The velocity difference in the z direction
u^{prey}	The speed of the prey
$\mathbf{v}$	The linear velocity of the object
ω	The angular velocity of the fluid
Ω	The angular velocity of the object
μ	The dynamic viscosity
ν	The kinematic viscosity of the fluid
$\zeta_{\parallel}$	The tangential drag coefficient
$\zeta_{\perp}$	The normal drag coefficient
C_{T1}	Translational resistive force coefficient of the ellipsoid when the ellipsoid is moving parallel to its major axis
C_{T2}	Translational resistive force coefficient of the ellipsoid when the

	ellipsoid is moving parallel to its minor axis
C_{R1}	Rotational resistive force coefficient of the ellipsoid when the ellipsoid is rotating about to its major axis
C_{R2}	Rotational resistive force coefficient of the ellipsoid when the ellipsoid is rotating about to its minor axis
C	The damping coefficient of the hair/seta
C_μ	The damping coefficient contributed by the fluid medium
α	The angle between $\mathbf{f}$ and $\mathbf{b}$
θ^b	The angle between the swimming direction of the prey and R^b
θ^0	The angle between the swimming direction of the prey and R^0
θ	The angular displacement of the arthropod's filiform hair
I	The second moment of inertia
I_ρ	The moment of inertia contributed by the density of the fluid medium
I_μ	The moment of inertia contributed by the viscosity of the fluid medium
δ	The Dirac delta function
δ_{ij}	The Kronecker delta tensor
D_1	The constant defined in Appendix 1 of Humphrey, et al. (1993)
D_2	The constant defined in Appendix 1 of Humphrey, et al. (1993)
M	The total number of the regularized Stokeslets
N	The total number of Sperms
β	The parameter related to δ_{bl}
δ_{bl}	The thickness of the boundary layer
ε	The regularization parameter of the regularized Stokeslet
$\phi^\varepsilon(\mathbf{x})$	A blob function satisfying $\int \phi^\varepsilon(\mathbf{x}) d\mathbf{x} = 1$

T	The temperature in Kelvin
k	Boltzmann's constant
K	The spring constant
$\sim$	The non-dimensionalized variable

Chapter 3

α	The sphere label (used to denote the location and velocity of the sphere)
β	The sphere label (used to denote the force on the sphere)
L	The characteristic length of the swimmer
x_1	The axis perpendicular to the wall
x_2	The axis perpendicular to the plane of swimmer's motion
x_3	The axis perpendicular to the axis x_1 and x_2
t	The time
$\mathbf{x}^0$	The position of the center of mass of the three sphere swimmer
$\mathbf{x}^\alpha$	The position of sphere α
$\mathbf{x}^p$	An arbitrary point in the fluid domain
$\mathbf{x}^w$	An arbitrary point on the infinite planar wall
$\mathbf{x}^{\alpha*}$	The image position of the sphere α
$\mathbf{x}^{\beta*}$	The image position of the sphere β
$\bar{\mathbf{x}}^0$	The time-averaged position of the center of mass of the three sphere swimmer
$\bar{\mathbf{x}}^{0*}$	The time-averaged image position of the center of mass of the three sphere swimmer
$\mathbf{d}^\alpha$	The displacement vector from $\bar{\mathbf{x}}^0$ to $\mathbf{x}^\alpha$

$\mathbf{d}^\beta$	The displacement vector from $\mathbf{x}^0$ (or $\bar{\mathbf{x}}^0$) to $\mathbf{x}^\beta$
$\mathbf{d}^{\beta*}$	The displacement vector from $\mathbf{x}^{0*}$ (or $\bar{\mathbf{x}}^{0*}$) to $\mathbf{x}^{\beta*}$
h	The distance from the wall to the center of mass of the swimmer
a	The radius of the spheres
l^{12}	The length of the left arm of the three sphere swimmer
l^{23}	The length of the right arm of the three sphere swimmer
ζ	The amplitude of the harmonic motions of the two arms
S	The surface of the infinite planar wall
$\mathbf{f}^\beta$	The force acting on sphere β
$\mathbf{f}^{\beta,\text{free}}$	The instantaneous force on sphere β of the unbounded three sphere swimmer
$\mathbf{T}$	The instantaneous traction on the infinite planar wall due to the swimmer
$\mathbf{T}^{\text{BD}}$	The instantaneous traction on the infinite planar wall due to the Blakeslet dipole
$\mathbf{T}^{\text{BQ}}$	The instantaneous traction on the infinite planar wall due to the Blakeslet quadrupole
G^α	The kernel relates $\mathbf{x}^\alpha$ with $\mathbf{x}^0$
$\mathbf{S}$	The kernel relates the fluid velocity with a Stokeslet
$\mathbf{St}$	The kernel relates the fluid velocity with the image system of a Stokeslet
$\boldsymbol{\tau}$	The kernel relates the traction on the wall with the Blakeslet
$\mathbf{v}^0$	The instantaneous velocity of the center of mass
$\mathbf{v}^\alpha$	The instantaneous velocity of sphere α
$\mathbf{v}^{0*}$	The instantaneous velocity of the center of mass of the three sphere

	swimmer due to the three Stokeslets
$\mathbf{u}^{0*}$	The instantaneous velocity of the center of mass of the three sphere swimmer due to the image systems of the three Stokeslets
$\mathbf{v}^{0,\text{free}}$	The instantaneous velocity of the center of mass of the unbounded three sphere swimmer
$\mathbf{u}^*(\mathbf{x}^\alpha)$	The instantaneous velocity at $\mathbf{x}^\alpha$ due to the image system of the three Stokeslets
ω	The angular velocity of the three sphere swimmer
μ	The dynamic viscosity of the fluid
ϕ	The phase angle between the displacements of two arms
$\langle \rangle$	The time averaging
R	The traction correlation coefficient
N	The coefficient relates h to the side length of the square on the wall

Chapter 4

Re	The Reynolds number
Sr	The Strouhal number
Sp	The Sperm number
x_1	The axis parallel to the minor axis of the copepod and point to the right
x_2	The axis parallel to the minor axis of the copepod and point into the paper
x_3	The axis along the major axis of the copepod and point upward
x	The axis along the setal axis
y	The axis perpendicular to the setal axis

N^{prey}	The total number of the regularized Stokeslet on the prey
N^{body}	The total number of the regularized Stokeslet on the copepod body
N^{ant}	The total number of the regularized Stokeslet on the antennule
α	The α -th the regularized Stokeslet on the prey ($\alpha = 1, 2, \dots, N^{\text{prey}}$)
β	The β -th the regularized Stokeslet on the prey ($\beta = 1, 2, \dots, N^{\text{body}}$)
γ	The γ -th the regularized Stokeslet on the prey ($\gamma = 1, 2, \dots, N^{\text{ant}}$)
t	The time
Δt	The time step
f	The frequency of oscillation of the prey
$\mathbf{x}^{\text{p}}$	An arbitrary point in the fluid domain
$\mathbf{x}^0$	The position where $\mathbf{f}$ is exerted
$\mathbf{r}^\alpha$	The displacement vector from $\mathbf{x}^{\text{prey},0}$ to $\mathbf{x}^\alpha$
$\mathbf{r}^\beta$	The displacement vector from $\mathbf{x}^{\text{pred},0}$ to $\mathbf{x}^\beta$
$\mathbf{r}^\gamma$	The displacement vector from $\mathbf{x}^{\text{pred},0}$ to $\mathbf{x}^\gamma$
$\mathbf{x}^{\text{pred},0}$	The ellipsoidal center of the copepod
$\mathbf{x}^{\text{prey},0}$	The spherical center of the prey
$\mathbf{x}^{\text{root}}$	The location of the right setal root
r^{maj}	The distance from the origin of the body fixed frame to a point on the major axis of the ellipsoidal body
d	The distance from the ellipsoidal center to the center of the prey
$\hat{\mathbf{t}}$	The unit tangent vector on the spherical surface of the prey
$\tilde{l}$	The dimensionless active length of the prey
Δs_c	The average spacing between adjacent regularized Stokeslets on the first antennule

Δs_b	The average spacing between adjacent regularized Stokeslets on the ellipsoidal body
Δs^{prey}	The average regularized Stokeslet spacing on the prey
Δs^{ant}	The average regularized Stokeslet spacing on the first antennule of the copepod
Δs^{body}	The average regularized Stokeslet spacing on the ellipsoidal body of the copepod
Δx	The spacing between the uniformly distributed nodes on the seta
r^{prey}	The radius of the Janus particle
R^{ant}	The radius of the first antennule of the copepod
R^{seta}	The radius of the distal seta of the copepod
d_b	The diameter of the cross-section of the ellipsoidal body
L^{maj}	The length of the major axis of the copepod's ellipsoidal body
L^{min}	The length of the minor axis of the copepod's ellipsoidal body
L^{ant}	The length of the first antennule of the copepod
L^{seta}	The length of the distal seta of the copepod
$\mathbf{S}$	The kernel relates the fluid velocity with a Stokeslet
$\mathbf{f}^{\alpha}$	The force exerted on the fluid at the m th regularized Stokeslet on the prey
$\mathbf{f}^{\alpha, \text{free}}$	The force exerted on the fluid at the m th regularized Stokeslet on the free-swimming prey
$\mathbf{f}^{\beta}$	The force exerted on the fluid at the n th regularized Stokeslet on the copepod body
$\mathbf{f}^{\gamma}$	The force exerted on the fluid at the n th regularized Stokeslet on the copepod antennule

$f_{\perp}$	The force perpendicular to the setal axis
v^{prey}	The swimming speed of prey
$v^{\text{prey,min}}$	The minimum swimming speed of the prey that is able to elicit the response of the copepod at certain frequency
$v^{\text{prey},0}$	The value of $v^{\text{prey,min}}$ at the frequency $f = 0$ Hz
$\hat{\mathbf{e}}$	The swimming direction of the prey
$\mathbf{v}^{\text{prey}}$	The swimming velocity of the prey
$\mathbf{u}^{s,\alpha}$	The slip velocity at the point $\mathbf{x}^{\alpha}$ on the prey
$\mathbf{u}^{\text{prey}}$	The flow velocity induced by the force on the prey
$\mathbf{u}^{\text{prey,free}}$	The flow velocity induced by the force on the free-swimming prey
$\mathbf{u}^{\text{body}}$	The flow velocity induced by the force on the copepod body
$\mathbf{u}^{\text{ant}}$	The flow velocity induced by the force on the antennule
$\mathbf{u}^s$	The axisymmetric slip velocity on the surface of the prey
$u^{s,0}$	The constant slip speed used to determine $\mathbf{u}^s$
$\mathbf{u}$	The velocity of the fluid
$\mathbf{u}^{\alpha}$	The flow velocity at the m th regularized Stokeslet on the prey
$\mathbf{u}^{\beta}$	The flow velocity at the n th regularized Stokeslet on the copepod body
$\mathbf{u}^{\gamma}$	The flow velocity at the n th regularized Stokeslet on the copepod antenna
$\mathbf{v}^{\text{pred}}$	The translational velocity at the ellipsoidal center of the predator
$\mathbf{v}^{\text{prey}}$	The translational velocity at the center of the prey
$\boldsymbol{\omega}^{\text{pred}}$	The rotational velocity at the ellipsoidal center of the predator
$\boldsymbol{\omega}^{\text{prey}}$	The rotational velocity at the center of the prey
$u_{\perp}$	The flow velocity perpendicular to the setal axis

$v_{\perp}$	The setal velocity perpendicular to the setal axis
μ	The dynamic viscosity of the fluid
ν	The dynamic viscosity of the fluid
$\zeta_{\perp}$	The normal drag coefficient
E	The Young's modulus of the distal seta of the copepod
θ	The angle defining the orientation of the prey
ϕ	The angle defining the swimming direction of the prey
ζ	The zenith angle of the prey
η	The azimuthal angle of the prey
ω	The angular speed of oscillation of the prey
I	The second moment of inertia
A	The rigidity of the seta
ε	The regularization parameter
$\varepsilon^{\text{prey}}$	The regularization parameter for the regularized Stokeslets on the prey
$\varepsilon^{\text{body}}$	The regularization parameter for the regularized Stokeslets on the copepod body
ε^{ant}	The regularization parameter for the regularized Stokeslets on the copepod antennule
κ	The setal curvature
κ^{thr}	The threshold setal curvature to induce the copepod's response
t^{r}	The response time of the seta
$\epsilon^{\text{prey,free}}$	The strain rate of the fluid induced by the free-swimming prey
$\mathbf{x}^{\text{t}}$	The point on the copepod's first antennular tip
$\mathbf{x}^{\text{h}}$	The point on the copepod's head tip

Er^{visser}	The error of Visser's copepod hydromechanical reception model
Er^{strain}	The error of the far-field strain approximation
$\hat{\mathbf{n}}^{\text{ant}}$	the unit directional vector perpendicular to the antennular axis.
r	The radius of the oscillatory sphere
ψ	The angle between $\mathbf{x}^{\text{prey},0} - \mathbf{x}^{\text{root}}$ and the antennular axis
$\mathcal{F}$	The magnitude of the force in the 1D model
$\mathcal{F}^{\text{thr}}$	The threshold magnitude of the force which elicits the copepods mechanotransduction in the 1D model
χ	The phase lag of the steady curvature response in the 1D model

Chapter 1

Introduction

1.1 Background

The propulsion of microscopic organisms has been an area of recent interest. Microorganisms play an active role in nature [1-3], and many species swim through fluids. Due to their small size, they live in the low Reynolds number regime, where inertia is negligible. Thus, the locomotion adopted by large scale animals such as birds and fish, which relies on the inertial force, is proven to be ineffective at low Reynolds number regime [4]. Dominated by viscous force, the locomotion of microorganisms obeys the scallop theorem, which states a low Reynolds number swimmer will only be able to move on average when it deforms in a way that is invariant under time-reversal [5]. Therefore, in order to achieve a forward motion, a bacterium rotates its helical flagella [6] while a sperm propagates traveling wave on its flagellum [7-9]. Artificial microrobots capable of propulsion in fluids have also been studied and fabricated [10-18] with many potential applications, such as microsurgery [18, 19] and drug delivery [20, 21]. To understand how microscale locomotion can be achieved, one can use simplified models of microscale propulsion, including the Taylor sheet [22-24], the squirmer [25-27], Purcell's three-link swimmer [5], the three-sphere swimmer [28], and the two-sphere swimmer [29].

In the low-Reynolds-number regime encountered by microswimmers, fluid dynamics are governed by the Stokes equation, $-\nabla p + \mu \nabla^2 \mathbf{v} + \mathbf{f} = 0$, where p is the pressure, $\mathbf{v}$ the fluid velocity, μ the dynamic viscosity and $\mathbf{f}$ the body force on the fluid. Due to the linearity of the Stokes equation, a good approach to understand the behavior of microorganisms is to construct flow solutions as the superposition of a discrete set of or continuous distribution of fundamental singular solutions, such as the Stokeslet, which is the flow due to a point force acting on the fluid [30]. For instance, a bacterial flagellum can be modeled by a distribution of Stokeslets and Stokeslet dipoles [31, 32], or the entire swimmer can be modeled by a surface distribution of singular solutions [33] or a collection of regularized solutions [34-38]. Reduced order models composed of a discrete set of singular solutions have also been utilized, such as for *Chlamydomonas* [39]. Insight into the flows around swimming organisms can also be obtained by adopting the far-field approximation of a multipole expansion [30, 40]. The induced flow field of a bacterium at large distances decays as r^{-2} , indicating that it can be treated as a force dipole in the far field [4, 41, 42]. Similarly, in the far field, a swimming spermatozoon can be modeled as a combination of Stokeslet dipole and quadrupole [43]. The far-field swimming characteristic can also be altered on time averaging. For example, the flow induced by a three-sphere swimmer modeled as three Stokeslets switches from dipolar to quadrupolar on time averaging [44].

Microorganisms often swim in confined spaces near boundaries. Their locomotion can be significantly affected by the presence of the boundaries. Firstly, the boundary affects the spatial distribution of microorganisms. For example, the bull spermatozoa, when placed in between two glass plates, are

more likely to swim towards the plates, which results in the non-uniform cell distribution [45]. However, depending on the geometry of the cell body and the flagellum, there may exist a stable configuration in which the swimming microorganism maintains a constant distance to the wall [46, 47]. Moreover, the speed and trajectory of individual microswimmers can also be altered by the boundary. Evans and Lauga have found that the waveform of the spermatozoa flagellum is affected by the presence of the wall, which leads to a change in the propulsive force and swimming speed of the spermatozoa [48]. The helical flagellated bacteria, such as *Escherichia coli*, change their swimming trajectories from straight runs to clockwise circles when swimming close to a no-slip boundary [49, 50] and to counter-clockwise circles around a stress-free surface such as the liquid-air interface [51]. Lastly, the microorganism can be reoriented by the wall nearly. Microswimmers in general can be classified into two categories: a pusher which pushes the fluid around in the forward and backward directions and a puller which pulls the fluid in the forward and backward directions back to its body. When swimming near the wall, a pusher tends to align itself parallel to the wall while a puller tends to reorient perpendicular to the wall [4]. As microswimmers exhibit interesting phenomena near boundaries, there is a great interest in understanding the effects of boundaries on swimming microswimmers.

Living in a dynamic environment, the swimming of motile microorganisms is an important trait in exploring new environment, finding mates, and most importantly hunting for preys. Thus, it is important to understand how the microorganism as a predator detects the presence of the prey in the microscopic regime. As a concrete example, consider how marine copepods, a large

component in the zooplankton's family, detect the presence of planktonic preys. Marine copepods are equipped with chemoreceptional and mechanoreceptional setae [52-55] which are extended from the tubular sheath of their first antennule [56] and serve as the primary sensilla to respond to the environmental cues [57]. When predating for preys, they either beat appendages to generate a feeding current [58, 59] or stay ambush feeding. For both cases, they sense the chemicals and flow field emitted by the nearby swimming plankton. The mechanoreception, which is mainly due to the deformation of setae at the distal section of the copepod's first antennule under flow [60], is sufficient for remote prey detection in most circumstances [61-63]. The copepod-prey detection depends on two factors: the hydrodynamic characteristics of the prey's locomotion and the mechanoreceptional sensitivity of the predator. A rapid-swimming prey transmits larger disturbances to the surrounding, which leads to a higher chance to be detected and captured. On the other hand, this prey-induced flow disturbance decays over space. Only the copepod with high sensitivity is able to detect the suspicious signal at a large distance from the prey.

Marine copepods are capable of detecting and attack planktons at a distance much larger than the length scale of the planktons but in the same order as the length scale of the copepods. For example, the copepod *Acartia tonsa* (1 mm in prosome length) detects the swimming *Loboea strobila* (130 μm in length, 65 μm in width) at a distance of around 0.5 mm [64]. Up to the detection distance, the length scale of the prey and the inner structure is unimportant. Therefore, it is preferable to use the simplified models such as the squirmer or even the multipole model to treat the planktonic prey without considering its detailed swimming stroke. Visser (2001) modeled the self-sinking particle as a Stokeslet

and the self-propelled prey as a Stokeslet dipole [40], which greatly simplified the flow fields created by the different types of microorganisms. On the other hand, the prey-detection distance is in the same order as the length scale of the copepods, and hence it is important to consider the detailed mechanoreceptional sensory structure of marine copepods when analyzing their hydromechanical responses.

1.2 Objectives and Scopes

This thesis aims to provide substantial insights into the propulsion and feeding of microorganisms through theoretically modeling swimming microorganism and investigating the copepod-prey detection in the low Reynolds number regime. The objectives of this thesis are two-folded:

- **Seeking for an independent way to find the limit of validity of the multipole representation for boundary effects.**

The wall effect on microswimmers is usually studied by employing the image system method [65]. For large distances from the boundary, the inner structure of the microswimmer is no longer important so a far-field multipole expansion and its image system can accurately predict the effect of the boundary on pitching movement for the swimmer with a steady propulsion mechanism. However, the validity of the multipole approach is depends on geometry and mode of propulsion of the swimmer and could range from tenths of body lengths to approximately a single body length, with no *a priori* way of determining the range of validity [66]. This research is motivated to determine when the far-field multipole model is accurate

through examining the traction pattern on the boundary caused by a microswimmer.

- **Develop a theoretical model to study the mechanoreception of copepods under flow induced by the prey at its natural frequency range.**

Previous investigations into how flow disturbances lead to the setal deformations and mechanoreception of copepods have taken two main approaches. The first approach is based on the arthropod filiform model [67-70], which is valid on the condition that the copepod is treated as a stationary body subjected to the high frequency background flow. This assumption differs from the fact that: first, the flow induced by swimming prey is a low frequency signal, and second, the copepod moves under the prey-induced flow. The second approach considers that copepod detects the difference between the flow velocities at the body and the tip of the first antennule [40, 71] and the far field strain rate [40, 72, 73] induced by the free-swimming prey, without addressing how the flow causes the deformation of the copepod's mechanoreceptional seta. Therefore, the second part of this research aims to address the fundamental characteristics associated with the deformation of the copepod's seta under the prey-induced flow at its natural frequency range.

1.3 Report Organization

The report is organized in such an arrangement: Chapter 2 is a literature review on the basic theory in the low Reynolds number regime, the common approaches to model the swimming microorganism, and the existing theoretical and

experimental studies on the mechanoreceptor of marine copepods. In Chapter 3, the spatial pattern of traction on the wall induced by a swimmer in vicinity of an infinite planar wall is theoretically analyzed, which will be used to determine whether the far-field approximation applies to the microswimmer. Chapter 4 presents a theoretical model to study the fundamental characteristics associated with the setal deformation in the copepod-prey detection. Chapter 5 outlines the conclusions and the directions of the future works.

Chapter 2

Literature Review

This chapter begins with the Stokes equation governing the fluid motion at low Reynolds number, followed by the singularity solutions and multipole expansions. This chapter then presents three theories which are commonly used to model motile microorganisms in low Reynolds number regime, before the discussion of the two conventional methods to model the microswimmer near boundaries. The chapter ends with a review of the theoretical and experimental studies on the mechanoreceptor of marine copepods.

2.1 Stokes Equation

The Navier-Stokes equation, which governs the motion of incompressible Newtonian fluid substances, can be expressed in indicial notations:

$$\rho \left(\frac{\partial u_i}{\partial t} + u_j \frac{\partial u_i}{\partial x_j} \right) = -\frac{\partial p}{\partial x_i} + \mu \frac{\partial^2 u_i}{\partial x_j \partial x_j} + F_i, \quad (2.1)$$

where ρ and μ are the density and dynamic viscosity of the fluid, p is the flow pressure, u_i or u_j is the flow velocity, and F_j is the body force per unit volume acting on the fluid. For convenience, $\mathbf{x} = x_i e_i = x_j e_j$, $\mathbf{u} = u_i e_i = u_j e_j$ and $\mathbf{F} = F_i e_i$, where e_i and e_j are unit vectors, is used to convert the symbols from indicial notations to vector notations. The vector and indicial notations will be used

interchangeably throughout this thesis.

The Navier-Stokes equation can be nondimensionalized by using proper length and time scales denoted as L and T_f , respectively. Substituting $x_j = L\tilde{x}_j$, $t = T_f\tilde{t}$, $u_i = L\tilde{u}_i/T_f = U\tilde{u}_i$, $p = \mu U\tilde{p}/L$, and $F_i = \mu U\tilde{F}_i/L^2$ into Eq. (2.1), one can obtain

$$\text{Re Sr} \frac{\partial \tilde{u}_i}{\partial \tilde{t}} + \text{Re} \tilde{u}_j \frac{\tilde{u}_i}{\tilde{x}_j} = -\frac{\partial \tilde{p}}{\partial \tilde{x}_i} + \frac{\partial^2 \tilde{u}_j}{\partial \tilde{x}_i \partial \tilde{x}_j} + \tilde{F}_i, \quad (2.2)$$

where $\text{Re} = \rho UL/\mu$ is the Reynolds number, which is a dimensionless quantity representing the ratio between the inertia and viscous forces of the flow; the Strouhal number $\text{Sr} = UT_f/L$ is the dimensionless quantity which determines the relative importance of the forcing timescale to the flow timescale. In the low Reynolds number regime ($\text{Re} \ll 1$ and $\text{Re Sr} \ll 1$) where most microorganisms are living, Eq. (2.1) can be simplified to Stokes Equation, which is defined as

$$\frac{\partial p}{\partial x_i} = \frac{\partial^2 u_i}{\partial x_j \partial x_j} + F_i. \quad (2.3)$$

The Stokes Equation, shown in Eq. (2.3), is used to together with the continuity equation, denoted as

$$\partial u_i / \partial x_i = 0, \quad (2.4)$$

and the necessary boundary conditions to solve for the flow field around the microswimmer.

Locomotion of microswimmers in low Reynolds number regime satisfies two important properties which can be derived from the linearity and time independence of the Stokes equation. The first property is the rate independence. Since the Stokes equation is independent of time derivatives, the inertia effect is

negligible and thus the fluid responds instantaneously after the boundary condition changes. This indicates the distance travelled by the object when changing from one configuration to the other does not depend on the rate of deformation but the sequence of shape changes between these two configurations. For example, consider two identical swimmers. One swims faster than the other, but the sequences of their swimming strokes are the same from the geometrical point of view. Due to the rate independence, it is expected that both microorganisms generate the same displacement per swimming stroke. As the consequence, the geometry changes of a microswimmer can be utilized to address many locomotion-related problems in the low Reynolds number regime [74-76].

The second property derived the Stokes equation is the kinetic reversibility, which is well described using the Scallop Theorem [77]. The theorem states that the clapping motion of a scallop will not produce any net displacement over a cycle due to the fact that the motion is “reciprocal” [5]. The reciprocal motion here is not only restricted to be of the same forward and backward rate, but also extended to the cases when the sequences of shapes are the same if viewed forward or backward in time due to the rate independence as described above [4]. Thus, the Scallop Theorem should be strictly broken for the effective motion in low Reynolds number.

2.2 Singularity

The fundamental solution of the Stokes equation at low Reynolds number is the Stokeslet, or a point force. The flow field due to a Stokeslet can be obtained by

prescribing $\mathbf{F} = \mathbf{f}\delta(\mathbf{x}^p - \mathbf{x}^0)$ and applying Greens function to solve for Equations (2.3) and (2.4), where $\mathbf{f}$ is the strength of the point force exerted on the point $\mathbf{x}^0$; δ is a Dirac delta function; $\mathbf{x}^p$ is an arbitrary point. Mathematically, the velocity of the flow due to a Stokeslet is given by [30]

$$u_i^s(\mathbf{x}^p) = S_{ij}(\mathbf{x}^p, \mathbf{x}^0) f_j, \quad (2.5)$$

where the Stokeslet kernel $\mathbf{S}$ is given by

$$S_{ij} = \frac{\delta_{ij}}{8\pi\mu r} + \frac{(x_i^p - x_i^0)(x_j^p - x_j^0)}{8\pi\mu r^3}, \quad (2.6)$$

and $r = |\mathbf{x}^p - \mathbf{x}^0|$. The flow field generated by a Stokeslet is shown in Figure 2-1(a), with the solid line representing the streamlines and the dashed lines presenting the fluid with equal speed. One can imagine a Stokeslet flow as the flow field due to a sinking infinitesimal sphere, the drag force on the fluid generating a flow field similar to that shown in Figure 2-1(a) in the body fixed frame of the sphere. A Stokeslet is the lowest order of singularities to generate a net force.

Using the Stokeslet, the fundamental solution of the Stokes Equation, one can obtain higher order solutions by differentiation [78]. A Stokeslet dipole is obtained by taking a directional derivative of Eq. (2.5). The flow velocity due to a Stokeslet dipole is defined as

$$u_i^{sd}(\mathbf{x}^p) = b_k \partial_k u_i^s(\mathbf{x}^p) = \frac{f_j b_j (x_i^p - x_i^0) + f_j (x_j^p - x_j^0) b_i - b_j (x_j^p - x_j^0) f_i}{8\pi\mu r^3} - \frac{3f_j (x_j^p - x_j^0) b_k (x_k^p - x_k^0)(x_i^p - x_i^0)}{8\pi\mu r^5}. \quad (2.7)$$

Physically, a Stokeslet dipole represents two Stokeslets of equal magnitude but opposite directions placing apart by a vector denoted as $\mathbf{b}$ [Figure 2-1(b)]. The

Figure 2-1: Streamlines (solid lines) and isotachs (dashed lines) induced by (a) a Stokeslet, (c) a Stresslet, (d) a Rotlet, and (f) a potential dipole. (b) A Stokeslet dipole of two forces of equal magnitude and opposite directions $\mathbf{f}$ and $-\mathbf{f}$, which is separated by a displacement vector $\mathbf{b}$. (e) A source and a sink separated by a displacement $\mathbf{b}$ generates a potential dipole. Adopted from Visser [40].

angle between the Stokeslet strength $\mathbf{f}$ and the displacement $\mathbf{b}$ is defined as α . When $\alpha = 0$, the Stokeslet dipole is reduced to a Stresslet, the flow field of which has no radial component [as shown in Figure 2-1(c)]. On the other hand, when $\alpha = \pi/2$, the flow field due to the Stokeslet dipole is the combination of that due to a

Stresslet [Similar to the flow field shown in Figure 2-1(c) but rotated by $\pi/4$] and a Rotlet [as shown in Figure 2-1(d)]. A Rotlet is the lowest order of singularities to generate a net torque. Taking directional derivatives of Eq. (2.7) leads to higher order singularity solutions such as a Stokeslet quadrupole and a Stokeslet octupole.

In addition, the other type of singularities is related to a point source or sink or both. The fluid velocity due to a source of strength Q (in the unit of m^3/s , also known as volume flow rate or volume flux) is

$$u_i^{\text{source}}(\mathbf{x}^p) = \frac{Q(x_i^p - x_i^0)}{4\pi r^3}. \quad (2.8)$$

If a fluid source of strength Q and a fluid sink of strength $-Q$ separated by a displacement vector $\mathbf{b}$, the singularity is named as a potential dipole or a source dipole [as shown in Figure 2-1(e)], the velocity of which can be expressed as

$$u_i^{\text{pd}}(\mathbf{x}^p) = b_k \partial_k u_i^{\text{source}}(\mathbf{x}^p) = Q \left(\frac{b_i}{4\pi\mu r^3} - \frac{3b_j(x_j^p - x_j^0)(x_i^p - x_i^0)}{4\pi\mu r^5} \right). \quad (2.9)$$

The flow field due to a potential dipole is shown in Figure 2-1(f). High order singularities associated with a potential dipole, such as a potential quadrupole, can be obtained through differentiating Eq. (2.9), which is similar to what one can do to derive Eq. (2.7) from Eq. (2.5).

Due to the linearity of the Stokes equation, one can construct the solution of the Stokes flow by adding all necessary singularities together. This approach has been adopted by Lighthill [31] and Higdon [79] to formulate Slender Body Theory (SBT), and Phan-Thien, et al. [80] and Ramia, et al. [33] to develop Boundary Element Method (BEM), both of which will be discussed in Section 2.4.

2.3 Multipole Expansion

At a large distance from the particle, one cannot distinguish between the point on the surface of the particle $\mathbf{x}^0$ and the reference point placed inside the particle $\mathbf{x}^R$. Thus, The kernel $S_{ij}(\mathbf{x}^p, \mathbf{x}^0)$, which relates the velocity at the point $\mathbf{x}^p$ due to the force at $\mathbf{x}^0$ [Eq. (2.5)], can be approximated as $S_{ij}(\mathbf{x}^p, \mathbf{x}^R)$, provided that $|\mathbf{x}^p - \mathbf{x}^0| \gg |\mathbf{x}^0 - \mathbf{x}^R|$ (Figure 2-2). As a demonstration, consider the flow field induced by a solid particle. The flow velocity at any point $\mathbf{x}^p$ can be expressed as

$$u_i(\mathbf{x}^p) = \int_S S_{ij}(\mathbf{x}^p, \mathbf{x}^0) \sigma_{jk} n_k dS, \quad (2.10)$$

where $\mathbf{S}$ is the Stokeslet kernel defined by Eq. (2.6); $\boldsymbol{\sigma}$ is the fluid stress evaluated at the point $\mathbf{x}^0$; $\mathbf{n}$ is the unit normal vector perpendicular to the surface of the particle at $\mathbf{x}^0$; dS is an infinitesimal area centered at $\mathbf{x}^0$. When $\mathbf{x}^p$ is far from the solid particle, the kernel $S_{ij}(\mathbf{x}^p, \mathbf{x}^0)$ can be approximated as $S_{ij}(\mathbf{x}^p, \mathbf{x}^R)$ and taken out from the integrand, where $\mathbf{x}^R$ is assumed to be inside the particle. Thus, the first order approximation of Eq. (2.10) can be rewritten as

$$u_i(\mathbf{x}^p) = -S_{ij}(\mathbf{x}^p, \mathbf{x}^R) F_j^D, \quad (2.11)$$

where

$$F_j^D = -\int_S \sigma_{jk} n_k dS \quad (2.12)$$

represents the total drag force exerted on the particle, the negative sign due to the action and reaction forces. Physically, Eq. (2.11) represents that at a large distance from the particle, the fluid velocity is merely a function of the total drag force and the reference point of the particle and independent of its detailed shape. This is analog to the approximation in the electrostatics that being far from a conductor, the surface distribution of charges on the conductor is

Figure 2-2: Sketch of the geometry of the particle in (a) the near field and (b) the far field when viewed from the point $\mathbf{x}^p$. $\mathbf{x}^R$ is the reference point of the particle. dS is an infinitesimal area on the surface of the particle centered at $\mathbf{x}^0$. $\mathbf{n}$ is the unit directional vector normal to the surface. $\mathbf{d}$ is the displacement vector from $\mathbf{x}^R$ to $\mathbf{x}^0$. In the far field, the position of $\mathbf{x}^R$ and $\mathbf{x}^0$ cannot be distinguished.

reduced to a point charge [30].

In general, the multipole expansion simplifies the force distributed on the surface of the low-Reynolds number swimmer as singularities acting on its geometric center. This can be done by adopting the Taylor series to expand the force distribution around the reference point of the microswimmer, which leads to

$$u_i(\mathbf{x}^p) = -S_{ij}(\mathbf{x}^p, \mathbf{x}^R) F_j^D + \partial_l^{(2)} S_{ij}(\mathbf{x}^p, \mathbf{x}^R) \int_S d_l \sigma_{jk} n_k dS \\ + \partial_m^{(2)} \partial_l^{(2)} S_{ij}(\mathbf{x}^p, \mathbf{x}^R) \int_S \frac{1}{2} d_m d_l \sigma_{jk} n_k dS + \dots, \quad (2.13)$$

where $\partial^{(2)}$ denotes the derivative taken with respect to the second argument of the kernel $\mathbf{S}$; $\mathbf{d} = \mathbf{x}^0 - \mathbf{x}^R$. The first term on the right hand side of Eq. (2.13) corresponds to the flow field due to a Stokeslet of strength $-\mathbf{F}^D$ exerted on $\mathbf{x}^0$, while the second and third terms include the contributions of the Stokeslet dipole of strength $\int_S d_l \sigma_{jk} n_k dS$ and the Stokeslet quadrupole of strength $\int_S d_m d_l \sigma_{jk} n_k dS/2$, respectively. The multipole expansion can be continued further

to include higher order corrections for the disturbance field [30, 81].

As seen from Eq. (2.13), the flow field induced by a far field particle or microswimmer can be approximated as the superposition of “poles” such that the summation of flow field due to these “poles” satisfies the appropriate boundary conditions [30, 40]. Note that there is no systematic way besides try-and-error to determine types of “poles” required to model a far field particle or microswimmer [81]. For example, a translating sphere can be modeled as a Stokeslet and a potential dipole, the former satisfying the total drag force on the sphere while the latter conforming the no flow and no net stress conditions on the surface of the sphere [40]. For more complicated microswimmers such as a swimming bacterium, the propulsion on the tail and the drag on the head can be modeled as a Stokeslet dipole, the length asymmetry of the body as a Stokeslet quadrupole, the finite head size as a potential dipole and the counter-rotation of the head and the flagellum as a Rotlet dipole [66]. The decay of the flow field is defined by the leading order of the multipole expansion. The flow field being led by a Stokeslet, a Stokeslet dipole and a Stokeslet quadrupole decay as $1/r$, $1/r^2$ and $1/r^3$, respectively, where r is the distance to the singularity. It is worth to point out that although named as “dipole”, the flow field due to a potential dipole decays as $1/r^3$. Stokeslet dipolar flow field is the most common leading order for most self-propelling microswimmer [41]. Exceptions include *Clamydomonas*, the far field behavior of which is more like a Stokeslet [39].

2.4 Theoretical Modeling of Microscale Locomotion¹

In this section, the three fundamental theories: resistive force theory (RFT), the slender body theory (SBT) and the method of regularized Stokeslet (MRS) which used to model low-Reynolds number microswimmers in the number regime are presented. The accuracies of these theories are described by comparing the theoretical predictions with experimental results.

2.4.1 Resistive Force Theory

It is widely accepted that inertial effects can be ignored when dealing with microorganisms [82]. Self-propulsion due to a purely viscous force is first discussed by Taylor [22] in the form of a waving sheet with small amplitude, and subsequently Hancock [83] considered the propulsion of an infinite filament. This leads to RFT, in which a resistive coefficient [31] is used to linearly relate the viscous force to the fluid viscosity, relative fluid velocity, and the object's length scale. This model assumes that the flow field is not influenced by other parts of the filament (or flagellum), and ignores the presence of any cell body. The first application of RFT on microorganisms was by Gray and Hancock [84], who modeled the force acting on spermatozoa as the summation of independently determined viscous force acting on each infinitesimal segment of the flagellum in the normal direction, denoted by subscript $\perp$, as well as

¹ This section is published in J. B. Y. Koh, X. Shen and Marcos. "Theoretical modeling in microscale locomotion." *Microfluid. Nanofluid.*, vol. 20, pp. 1-27, 2016.

tangential direction, denoted by subscript $\parallel$:

$$\mathbf{F}^D = -\int_s (\zeta_{\perp} v_{\perp} \mathbf{e}_{\perp} + \zeta_{\parallel} v_{\parallel} \mathbf{e}_{\parallel}) ds, \quad (2.14)$$

where s is the curvilinear position along the flagellum, $\zeta_{\perp}$ and $\zeta_{\parallel}$ are the resistive force coefficients, $v_{\perp}$ and $v_{\parallel}$ are the velocity components, and $\mathbf{e}_{\perp}$ and $\mathbf{e}_{\parallel}$ are the unit vectors in the normal and tangential directions, respectively. Gray and Hancock [84] proposed an analytical relation for $\zeta_{\perp}$ and $\zeta_{\parallel}$ which was subsequently refined by Lighthill [31] to be:

$$\zeta_{\perp} = \frac{4\pi\mu}{\ln(0.18\lambda/a^{\text{filament}}) + 0.5} \quad (2.15)$$

$$\zeta_{\parallel} = \frac{2\pi\mu}{\ln(0.18\lambda/a^{\text{filament}})} \quad (2.16)$$

where μ is the fluid viscosity; λ is the wavelength; a^{filament} is the radius of the flagellum.

The solutions to analytical models depend on the dimensionless ratio $\zeta_{\perp}/\zeta_{\parallel}$. In the limit of infinitely long filaments, the ratio $\zeta_{\perp}/\zeta_{\parallel}$ approaches 2, which is the approximation used in some studies [85-87]. However, any real finite filament will have $\zeta_{\perp}$ less than twice the value of $\zeta_{\parallel}$. Experimental investigations have led to varying conclusions regarding the measured and computed ratio. Therefore, RFT may be insufficient if a high level of confidence is demanded. Nonetheless, it goes without a doubt that RFT serves as a decent estimate for a preliminary study, as its predictions match experimental observations to the order of magnitude.

2.4.2 Slender body theory

The premise of SBT requires the object modeled to be a slender body and have a

small filament curvature. Unlike the approach discussed in the RFT, hydrodynamic interactions are not ignored here. SBT was first introduced by examining the velocity of a long ellipsoid and a finite circular cylinder stationary under the uniform flow, and extended to general cases by Batchelor [41] and Cox [88]. The theory is then summarized by Lighthill [31] and Higdon [79] to relate the velocity distribution on the flagellum to the force per unit length, by considering the contribution of Stokeslet and potential dipole. SBT is then further developed to analyze the behavior of flagellum or filament by adding the contributions of higher order singularities [89]. When used to compute the swimming velocity of a helical swimmer, Lighthill's and Johnson's SBT actually provides very similar results regardless of the helix pitch angle [90]. For organisms with negligible rotational velocity, the flagellum can be replaced by a distribution of Stokeslets and potential dipoles along the centerline with force per unit length point $\partial \mathbf{f}(s)/\partial s$ and $\partial \mathbf{q}(s)/\partial s$, respectively, in order to satisfy the no slip on the surface of the flagellum. Without considering higher order singularities, as is commonly the case even in recent years, the flagellum velocity at the centerline $\mathbf{x}^p$ can be approximated, with an error in the order of the ratio of the flagellum radius to length, by its surface velocity through the following tensor equations [79]:

$$u_i(\mathbf{x}^p) = \int_0^l S_{ij}[\mathbf{x}^p, \mathbf{x}^c(s)] \frac{\partial f_j(s)}{\partial s} + D_{ij}[\mathbf{x}^p, \mathbf{x}^c(s)] \frac{\partial q_j(s)}{\partial s} ds, \quad (2.17)$$

with the Stokeslet kernel $\mathbf{S}(\mathbf{x}^p, \mathbf{x}^c)$ shown in Eq. (2.5) and the kernel of the potential dipole $\mathbf{D}(\mathbf{x}^p, \mathbf{x}^c)$ is similar to that in Eq. (2.9) and is given by

$$D_{ij}(\mathbf{x}^p, \mathbf{x}^c) = \frac{1}{4\pi\mu} \left[-\frac{\delta_{ij}}{r^3} + 3 \frac{(x_i^p - x_i^c)(x_j^p - x_j^c)}{r^5} \right], \quad (2.18)$$

where $\mathbf{f}(s)$ is the Stokeslet strength, $\mathbf{q}(s) = -Q\mathbf{b}$ is the dipole strength, $\mathbf{x}^c(s)$ is the

Figure 2-3: Dimensionless displacement in the x -direction per cycle, using paddle length as the characteristic length, of a robotic two-paddle swimmer as a function of stroking angle predicted at slenderness ratios of 0.02 (dotted line), 0.06 (dashed line), and 0.1 (dotted-dashed line), compared with experimental measurements (circle markers) and values predicted using RFT (solid line without markers). Adopted from Huber, et al. [91].

location of these two singularity distributions measured along the centerline of the flagellum, $r = |\mathbf{x}^p - \mathbf{x}^c|$, δ_{ij} is the Kronecker delta tensor, and l is the length of the flagellum.

Slender body theory provides better accuracy than RFT as it takes into consideration of the long-range interactions [92]. A numerical study using both SBT and RFT was done on two artificial swimmers, Purcell's swimmer and the two-paddle swimmer [91], and the displacement of the swimmer was plotted against the stroking angle which was defined as the angle that each paddle turns. The results were compared with experimental data, and it was found that RFT

Figure 2-4: Dimensionless velocity, power, and torque for three different strains of bacteria, namely, *V. alginolyticus* (left column), *C. crescentus* (middle column) and *E. coli* (right column). Experimental data are indicated by the dashed line. Theoretical predictions computed by RFT and SBT are displayed as bars, with the uncertainties arising from the spreads in geometrical parameters of the bacteria. Adopted from Chattopadhyay and Wu [93].

largely overestimates the time-averaged velocity of a two-paddle swimmer while SBT approaches the experimental results as the slenderness ratio ϵ , which is the diameter-to-length ratio, gradually increases toward the experimental value (Figure 2-3). Chattopadhyay and Wu [93] applied optical tweezers to measure the velocity of three bacterial strains processing only a single polar flagellum. The velocity of a bacterium swimming in a straight line was captured and compared to a mathematical model which treated the specific bacterium as a rigid helical flagellum attached to a spherical head and was solved by both SBT and RFT. For all strains of bacteria investigated, SBT agrees with the experimental data (Figure 2-4) better than RFT since the long-range hydrodynamic

interactions are captured, especially for a large cell body. They showed that the result from SBT deviated from the measured velocity by $\sim 7\%$ for a small cell (*E. coli*) and $\sim 17\%$ for a large cell (*V. alginolyticus*).

2.4.3 The Method of Regularized Stokeslet

To obtain the accurate results for the swimming velocity of a microswimmer and the flow field around, one could use the Method of Regularized Stokeslet (MRS), as one typical implementation of the Boundary Element Method (BEM) [33, 80]. MRS is a numerical method which relies on the rapid development of computational power over the past decades. Since first developed by Cortez [34], MRS has been used extensively to analyze swimming bacterium [35, 36], spermatozoa [94] and ciliated microorganisms [95].

MRS has an advantage over models using SBT as it provides information about the velocity, pressure and stress at any point of interest, in the fluid and on the surface of the microswimmer's body [96]. SBT, on the other hand, only allows the velocity along the centerline of the body to be computed. MRS also does not require the assumption of a slender body or small filament curvature.

The Stokeslet model relies on the surface smoothness of that object, in which the velocity expression is integrable and the flow is bounded on its surface. However, the validity is compromised in situations where the surface forces are concentrated along the curves or when the surface of that object is not smooth, which results in the singular velocity. MRS is therefore introduced to handle this limitation through de-singularizing the concentrated force $\mathbf{f}$ at the point $\mathbf{x}^0$ by a blob function in the kernel [34]:

$$F_i(\mathbf{x}^p) = f_i \phi^\varepsilon(\mathbf{x}^p - \mathbf{x}^0), \quad (2.19)$$

where $\phi^\varepsilon(\mathbf{x}^p - \mathbf{x}^0)$ is a radially symmetric smooth function of position $\mathbf{x}^p$ centered at $\mathbf{x}^0$ with $\int \phi^\varepsilon(\mathbf{x}) d\mathbf{x} = 1$. The pressure $p^\varepsilon(\mathbf{x}^p)$ and velocity $\mathbf{u}^\varepsilon(\mathbf{x}^p)$ of the regularized Stokeslet can be expressed as:

$$p^\varepsilon(\mathbf{x}^p) = \frac{1}{8\pi} P_j^\varepsilon f_j, \quad (2.20)$$

$$u_i^\varepsilon(\mathbf{x}^p) = \frac{1}{8\pi\mu} S_{ij}^\varepsilon f_j, \quad (2.21)$$

where $\mathbf{P}^\varepsilon$ and $\mathbf{S}^\varepsilon$ depend on the selection of the blob function $\phi^\varepsilon(\mathbf{x}^p - \mathbf{x}^0)$. There is no universal way to define the blob function. For a three-dimensional flow, a special choice of the blob function could be:

$$\phi^\varepsilon = \frac{15\varepsilon^4}{8\pi(r^2 + \varepsilon^2)^{7/2}}. \quad (2.22)$$

This leads to:

$$P_j^\varepsilon = \frac{(x_j^p - x_j^0)(2r^2 + 5\varepsilon^2)}{(r^2 + \varepsilon^2)^{5/2}}, \quad (2.23)$$

$$S_{ij}^\varepsilon = \delta_{ij} \frac{r^2 + 2\varepsilon^2}{(r^2 + \varepsilon^2)^{3/2}} + \frac{(x_i^p - x_i^0)(x_j^p - x_j^0)}{(r^2 + \varepsilon^2)^{3/2}}, \quad (2.24)$$

where $r = |\mathbf{x}^p - \mathbf{x}^0|$, δ_{ij} is the Kronecker delta tensor and ε is the regularization parameter. The pressure and velocity at any point due to M forces, $\mathbf{f}^k$, each located at the point $\mathbf{x}^k$, can be calculated by linear superposition and expressed as [35]:

$$p^\varepsilon(\mathbf{x}^p) = \frac{1}{8\pi} \sum_{k=1}^M P_j^\varepsilon(\mathbf{x}^p, \mathbf{x}^k) f_j^k, \quad (2.25)$$

$$u_i^\varepsilon(\mathbf{x}^p) = \frac{1}{8\pi\mu} \sum_{k=1}^M S_{ij}^\varepsilon(\mathbf{x}^p, \mathbf{x}^k) f_j^k. \quad (2.26)$$

Figure 2-5: The resistive force coefficients $C_T = \mathbf{F}^D/\mathbf{v}$, $C_R = \mathbf{M}/\mathbf{\Omega}$, where $\mathbf{F}^D$ and $\mathbf{M}$ correspond to the total force and torque on the ellipsoid. The subscripts 1 and 2 indicates when the ellipsoid is moving parallel to the major and minor axis, respectively. The superscript A means analytical solution from [77]. ϵ is the regularization parameter. Δs is the average spacing between adjacent regularized Stokeslets. (a) C_{T1} , (b) C_{R1} , (c) C_{T2} and (d) C_{R2} are normalized by their corresponding analytical values and plotted against the number of regularized Stokeslets. Adopted from Hyon, et al. [36].

The accuracy of MRS is mainly determined by two aspects, the number and location of the regularized Stokeslets, and the regularization parameter. Firstly, increasing the number of regularized Stokeslets improves the accuracy of MRS at cost of increased computational resources [97]. Hyon, et al. [36] compared the resistive force coefficients for a ellipsoid using the a surface distribution of regularized Stokeslets with those obtained analytically, and found that a total of 1712 Stokeslets is required to reduces the average error to 0.99 % if a proper

regularized parameter is chosen (Figure 2-5). One way to overcome this issue is to introduce a number of auxiliary Stokeslets around the area under the influence of a primary Stokeslet to compute the near-field velocity of that primary Stokeslet. For a translating sphere of unit radius in Stokes flow, 100 primary Stokeslets with 100 auxiliary Stokeslets leads to a smaller error (under 2%) as compared to that using 1600 regularized Stokeslets (around 2.3%) [98].

Figure 2-6: (a) Bending energy, (b) Kinetic energy, (c) Twisting energy, (d) Total energy of an elastic rod, as computed by the Navier Stokes case with a virtual radius of $c = 2\Delta s$ (solid black line) and simulations of the Regularized Stokeslet formulation for the regularization parameter $\epsilon = 5\Delta s, 6\Delta s, 7\Delta s, 8\Delta s$. Δs is the average spacing between the regularized Stokeslets. The energy is in units of kT , where k is the Boltzmann's constant and T is the temperature in degrees Kelvin, set to room temperature. Adopted from Olson, et al. [99].

Figure 2-7: Dimensionless thrust for helical flagella as a function of dimensionless pitch λ , for helix length $l = 20a^{\text{flagellum}}$ and filament radius $a^{\text{filament}} = a^{\text{flagellum}}/16$ as obtained by: experiment (solid black circles), method of regularized Stokeslet (solid black lines), slender body theory of Lighthill (solid blue lines), RFT of Gray and Hancock (green lines), and RFT of Lighthill (dashed blue lines). MRS and SBT results are very similar so the curves can be difficult to distinguish. Adopted from Rodenborn, et al. [100].

Secondly, the flow is usually discretized by a collection of regularized Stokeslets either on the boundary of the object or along its centerline [101]. The former usually offers higher accuracy, while the latter is more computationally efficient and still offers reasonable accuracy for a slender object. A semi-flexible fiber, 12mm long and $90\mu\text{m}$ in radius, modeled with regularized Stokeslets distributed along the centerline gave numerical results [102] which is in agreement with experimental observations. Cortez, et al. [35] modeled a microscale helix of finite body width by imposing regularized Stokeslet at the outer sheath of the helix, and calculated the number of rotations required for the helix to progress one body length to within the uncertainty range of experimental data.

Lastly, the error of MRS is largely dependent on the regularization parameter ϵ . There is no universal rule to determine the regularization parameter;

nonetheless, readers can refer to a number of justified and accepted selection approach [35, 103, 104]. By refining the regularization and discretization parameters, Cortez, et al. [35] also computed the resistance matrix for a sphere in flow and found the error can be less than 0.5%. As shown in Figure 2-6, the solutions obtained by MRS can be nearly identical to that obtained by solving the Navier-Stokes equation, given that a suitable regularization parameter is chosen [99].

Figure 2-8: Error of (a, b) the centerline distribution of the regularized Stokeslets and (c, d) the slender body theory as compared to the surface distribution of the regularized Stokeslets. Panels (a) and (c) represent the case of a rotating flagellum pump while panels (b) and (d) present a swimming bacterium. The error (shown in the color bar) is proportional to the circle size. Isotachs (solid lines) show interpolated errors. Adopted from Martindale, et al. [38].

A few researches compare the accuracy of the three models, RFT, SBT and MRS, with experimental data. One direct comparison is made for a helical flagellum, and it can be seen from Figure 2-7 that theoretical predictions using Lighthill's SBT and MRS match the data from experiment very well, but the same cannot be said for the case of RFT [100]. At this point, it is worth to take note that Martindale, et al. [38] tested the accuracy of RFT, SBT and centerline distribution of regularized Stokeslets two typical cases: a free swimming bacterium with a spherical head and a helical flagellum, and a flagellum pump with one end attached to an infinite planar wall, by setting the surface distribution of regularized Stokeslets as a benchmark. They found that the total error is inversely related to the ratio of the filament radius a^{filament} to the flagellum radius $a^{\text{flagellum}}$ and slightly affected by the flagellum pitch length λ (Figure 2-8).

2.5 Modeling of the Wall Effects on Microswimmers

The previous section has given a brief introduction about the methods used to model free-swimming microswimmers in the low Reynolds number regime. However, microswimmers do not always live in the unbounded environment. The presence of boundaries influences the swimming speed and trajectory of micro-swimmers. In this section, two methods which are used to model wall effects are introduced. The method to the wall effect on microswimmers is then presented, followed by the constraints which it is fair to neglect the wall effect are addressed.

2.5.1 The Image System Method

The fundamental solution of the Stokes equation at low Reynolds number is the Stokeslet [refer to Eq. (2.5)]. The image system method for a Stokeslet is commonly used to satisfy the no-slip boundary condition of an infinite planar wall at $x_1 = 0$ (Figure 2-9) [65, 105]. The entire space above the wall is filled with viscous fluid, and a Stokeslet $\mathbf{f} = [f_1, f_2, f_3]$ is placed at $\mathbf{x}^0 = [h, x_2, x_3]$, where h is the distance to the wall. A set of singular images consisting of an image Stokeslet, a potential dipole, and a Stokeslet doublet are placed at the image location $\mathbf{x}^{0*}$ such that $\mathbf{x}^{0*} = \mathbf{x}^0 - 2(\mathbf{x}^0 \cdot \mathbf{n})\mathbf{n}$, where $\mathbf{n} = [1, 0, 0]$ is the unit vector perpendicular to the wall. Thus, the velocity of a point $\mathbf{x}^p$ due to the image system of a Stokeslet, named as the wall-induced velocity $\mathbf{u}^*(\mathbf{x}^p)$, is

$$u_i^*(\mathbf{x}^p) = u_i^{s*}(\mathbf{x}^p) + u_i^{\text{pd}}(\mathbf{x}^p) + u_i^{\text{sd}}(\mathbf{x}^p), \quad (2.27)$$

where

$$u_i^{s*}(\mathbf{x}^p) = S_{ij}(\mathbf{x}^p, \mathbf{x}^{0*})(-f_j), \quad (2.28)$$

$$u_i^{\text{pd}}(\mathbf{x}^p) = \frac{q_i}{4\mu\pi r^{*3}} - \frac{3q_j(x_j^p - x_j^{0*})(x_i^p - x_i^{0*})}{4\mu\pi r^{*5}}, \quad (2.29)$$

$$u_i^{\text{sd}}(\mathbf{x}^p) = \frac{n_j g_j(x_i^p - x_i^{0*}) + n_j(x_j^p - x_j^{0*})g_i}{8\pi r^{*3}} - \frac{g_j(x_j^p - x_j^{0*})n_i}{8\pi r^{*3}} - \frac{3n_j(x_j^p - x_j^{0*})g_k(x_k^p - x_k^{0*})(x_i^p - x_i^{0*})}{8\pi r^{*5}}, \quad (2.30)$$

$\mathbf{q} = -h^2 [2(\mathbf{f} \cdot \mathbf{n})\mathbf{n} - \mathbf{f}]$, $\mathbf{g} = 2h [2(\mathbf{f} \cdot \mathbf{n})\mathbf{n} - \mathbf{f}]$, $r^* = |\mathbf{x}^p - \mathbf{x}^{0*}|$. The superscript s^* , sd , and pd correspond to the image Stokeslet, the Stokeslet dipole, and the potential dipole, respectively. For simplicity, since both $\mathbf{q}$ and $\mathbf{g}$ are functions of $\mathbf{f}$, $\mathbf{St}$ is defined using

$$u_i^*(\mathbf{x}^p) = St_{ij}(\mathbf{x}^p, \mathbf{x}^{0*})f_j, \quad (2.31)$$

where $\mathbf{f}$ is the strength of a Stokeslet so that $\mathbf{St}$ is the kernel of the image system of the Stokeslet, which only depends on the position of the Stokeslet's image system $\mathbf{x}^{0*}$ and the evaluation point $\mathbf{x}^p$. Incorporating the contribution of the original Stokeslet with its images, the net velocity due to a Blakeslet can be expressed as $\mathbf{u}(\mathbf{x}^p) = \mathbf{u}^s(\mathbf{x}^p) + \mathbf{u}^*(\mathbf{x}^p)$, or

$$u_i(\mathbf{x}^p) = [S_{ij}(\mathbf{x}^p, \mathbf{x}^0) + St_{ij}(\mathbf{x}^p, \mathbf{x}^{0*})]f_j. \quad (2.32)$$

Figure 2-9: A Stokeslet at $\mathbf{x}^0$ and its image system at $\mathbf{x}^{0*}$ with the infinite wall located at $x_1 = 0$ plane. An infinitesimal area dS on the wall is centered at $\mathbf{x}^w$.

2.5.2 Wall Traction Approach

An alternative approach to find $\mathbf{u}^*(\mathbf{x}^p)$ is to take advantage of the fact that the Lorentz reciprocal theorem implies that the flow field induced by a particular singularity and its images can also be expressed in terms of the traction exerted by the boundary on the fluid [30, 106]. This is analogous to how in electrostatics the electric field near a conductor can be represented using either image charges or a charge distribution on the conducting surface. $\mathbf{u}^*(\mathbf{x}^p)$ due to a Blakeslet can be evaluated by utilizing a boundary integral representation of the flow due to the

traction distribution on the wall. This approach is referred as the wall traction approach. The stress at any point in the flow $\mathbf{x}^p$ is

$$\sigma_{ij}(\mathbf{x}^p) = -p(\mathbf{x}^p)\delta_{ij} + \frac{\partial u_i(\mathbf{x}^p)}{\partial x_j} + \frac{\partial u_j(\mathbf{x}^p)}{\partial x_i} \quad (2.33)$$

where δ_{ij} is the Kronecker delta and $p(\mathbf{x}^p)$ and $\mathbf{u}(\mathbf{x}^p)$ are the pressure and velocity at $\mathbf{x}^p$.

The velocity at $\mathbf{x}^p$ due to a Stokeslet, an image Stokeslet, a potential dipole, and a Stokeslet dipole are shown in Eq. (2.5) and Eqs. (2.28)–(2.30), respectively. The corresponding pressure fields are given by

$$p^s(\mathbf{x}^p) = \frac{f_j(x_j^p - x_j^0)}{4\pi r^3}, \quad (2.34)$$

$$p^{s*}(\mathbf{x}^p) = \frac{(-f_j)(x_j^p - x_j^{0*})}{4\pi r^{*3}}, \quad (2.35)$$

$$p^{\text{pd}}(\mathbf{x}^p) = 0, \quad (2.36)$$

$$p^{\text{sd}}(\mathbf{x}^p) = \frac{n_i g_i}{4\pi r^{*3}} - 3 \frac{n_i (x_i^p - x_i^{0*}) g_j (x_j^p - x_j^{0*})}{4\pi r^{*5}}. \quad (2.37)$$

The overall traction on any infinitesimal area dS on the wall centered at $\mathbf{x}^w$ due to a Blakeslet is the net effect of the original Stokeslet itself located at $\mathbf{x}^0$ and its image system located at $\mathbf{x}^{0*}$. By setting $\mathbf{x}^p = \mathbf{x}^w$, the traction at $\mathbf{x}^w$ due to a Blakeslet can be expressed as

$$T_i(\mathbf{x}^w) = \left[\sigma_{ij}^s(\mathbf{x}^w) + \sigma_{ij}^{s*}(\mathbf{x}^w) + \sigma_{ij}^{\text{pd}}(\mathbf{x}^w) + \sigma_{ij}^{\text{sd}}(\mathbf{x}^w) \right] n_j \quad (2.38)$$

or

$$T_i(\mathbf{x}^w) = T_i^s(\mathbf{x}^w) + T_i^{s*}(\mathbf{x}^w) + T_i^{\text{pd}}(\mathbf{x}^w) + T_i^{\text{sd}}(\mathbf{x}^w), \quad (2.39)$$

where

$$T_i^s(\mathbf{x}^w) = -\frac{3n_j(x_j^w - x_j^0)f_k(x_k^w - x_k^0)(x_i^w - x_i^0)}{4\pi r^5} \quad (2.40)$$

$$T_i^{s*}(\mathbf{x}^w) = -\frac{3n_j(x_j^w - x_j^{0*})(-f_k)(x_k^w - x_k^{0*})(x_i^w - x_i^{0*})}{4\pi r^{*5}} \quad (2.41)$$

$$T_i^{pd}(\mathbf{x}^w) = -3\frac{q_j(x_j^w - x_j^{0*})n_i + n_j q_j(x_i^w - x_i^{0*})}{2\pi r^{*5}} - \frac{3n_j(x_j^w - x_j^{0*})q_i}{2\pi r^{*5}} + \frac{15n_j(x_j^w - x_j^{0*})q_k(x_k^w - x_k^{0*})(x_i^w - x_i^{0*})}{2\pi r^{*7}} \quad (2.42)$$

$$T_i^{sd}(\mathbf{x}^w) = -\frac{3n_j(x_j^w - x_j^{0*})n_k g_k(x_i^w - x_i^{0*})}{2\pi r^{*5}} - \frac{3[n_j(x_j^w - x_j^{0*})]^2 g_i}{4\pi r^{*5}} + \frac{15[n_j(x_j^w - x_j^{0*})]^2 g_k(x_k^w - x_k^{0*})(x_i^w - x_i^{0*})}{4\pi r^{*7}} \quad (2.43)$$

The traction expressed in Eq. (2.39) is linear in the force so it can be written as

$$T_i(\mathbf{x}^w) = \tau_{ij}(\mathbf{x}^w, \mathbf{x}^0)f_j \quad (2.44)$$

Viewing the traction as a distribution of Stokeslets on the wall, the wall-induced velocity on any arbitrary point $\mathbf{x}^p$ can be evaluated through

$$u_i^*(\mathbf{x}^p) = \int_S S_{ij}(\mathbf{x}^p, \mathbf{x}^w) T_j(\mathbf{x}^w) dS. \quad (2.45)$$

2.5.3 Wall Effect on Microswimmers

The most common approach to study the effect of an infinite planar wall on microswimmers is to apply the MRS which models the microswimmer as a collection of singularities [33, 47] and then utilize the image system method [65, 103] to satisfy the no-slip boundary condition on the wall. For example, to model the pumping of individual flagellum or a “flagellar forest” attached to infinite planar wall, Martindale, et al. modeled the flagellum as a collection of the regularized Stokeslets on the surface or along the centerline of the

Figure 2-10: (a) The experimental procedures: the mixture of *E. coli* and fluid is deposited between to glass slides with a separation distance of $2H = 100 \mu\text{m}$. The cells are counted as a function of distance z to the lower slide. (b) The distribution of cells is plotted against z for two experiments (blue and red colors). The markers represent the experimental data, the lines the multipole model prediction. Adopted from Berke, et al. [107].

Figure 2-11: The horizontal, vertical, and rotational velocities (v_x , v_y and Ω_y) of (a) the four Janus swimmers and (b) the three polar swimmers are plotted against the normalized closest distance to the wall. The variable h is the distance from the swimmer's center to the wall normalized with the radius of the swimmer, and l is the length of the cylindrical rod normalized with the radius of the swimmer. The lines present the full numerical solutions, the markers the multipole model approximations. Adopted from Spagnolie and Lauga [66]

flagellum, and applying the image system of the regularized Stokeslet to conform to boundary effect on the flagella [38, 108]. As such, the full numerical model relies on MRS and image system method must take into account of the detailed geometry and the swimming stroke of the microorganism.

However, since the far-field behavior of microswimmer can be well described by multipoles, the multipole expansion together with the image system method is useful to study the boundary effect on microswimmer. One of the advantages of such approach is that through the multipoles treatment, the inner structure of the microswimmer can be neglected and hence the complexity of the model is significantly reduced.

For example, to model the spermatozoa's density variation around two parallel glass slides plates, Berke, et al. [107] modeled the behavior of each spermatozoon as a dipolar pusher and utilize the image system for a Stokeslet dipole to satisfy the no-slip boundary condition on the plates. Through comparing their theoretical model with the experimental prediction, they concluded that the dipolar model is sufficient to describe the attractive force exerted by the boundary on the spermatozoa except for those very close to the boundary (Figure 2-10).

When the multipole expansion and its images well describe the effect of the boundary on a microswimmer has been investigated. Spagnolie and Lauga [66] studied the hydrodynamic interactions of the self-propelled microorganism with nearby boundaries with the help of the multipole expansion. Firstly, they used the BEM and the image system method to do the full numerical simulations on the two types of microorganisms: the Janus swimmer as the simplified model for

ciliated microorganisms and the polar swimmer as the representative of bacteria. The result is then compared with the reduced model to show validity of the multipole expansion. They found that for the full numerical solutions of 4 Janus swimmers [lines in Figure 2-11(a)], the multipole approximation is accurate down to one-tenth of the body radius distance from the wall. In the other case [Figure 2-11(b)], the range of validity of the multipole expansion is found to be also dependent on the geometry of the polar swimmer. Thus, although the multipole greatly reduces the complexity of the theoretical models, the validity of this reduced model depends on geometry and mode of propulsion of the swimmer and could range from tenths of body lengths to approximately a single body length, with no *a priori* way of determining the range of validity.

2.5.4 Neglecting the Wall Effect

In this subsection, the constraints under which it is fair to neglect the wall effect on microbes are discussed. The average velocity of a bacterium with a single helical flagellum rotating at a constant rate in the vicinity of a surface has been computed by the boundary element method. Having found the normalized velocity, force and torque experienced as a function of the relative separation distance, it is concluded that hydrodynamic interactions is significant only when the separation distance is no larger than the largest physical dimension of the organism [33]. The model was compared with experiments by Frymier, et al. [50], in which a three-dimensional tracking microscope was used to track the motion of a dilute sample of *E. coli* near a glass plate. Results show that wall effect is negligible when the bacteria are more than 10 μm from the surface (Figure 2-12), but significantly reduces the speed of bacteria within 10 μm from the planar surface. Frymier and Ford [109] reported that the speed of the wild-type *E. coli*

Figure 2-12: Dimensionless swimming speed (circle markers) of *E. coli* as a function of the surface-to-cell distance, non-dimensionalized with respect to cell radius taken to be 1 μm . Also shown are the boundary element method solutions of Ramia, et al. [33] at cell orientation angles of 0° (solid line) and 45° (dotted line). Adopted from Frymier, et al. [50].

Figure 2-13: Normalized force F^D/F_∞^D as a function of normalized distance from the wall, for a sphere of radius A translating between parallel chamber walls where the half-depth H . Square markers indicate the results of Ramia, et al. [33], while cross markers indicate the computations by Gillies, et al. [110] corresponding to the half-depth of the chambers used. Adopted from Gillies, et al. [110].

strain NR50, with a cell size of 1 μm , swimming perpendicular to the wall is

significantly affected by the wall when it is up to 10 μm away. However, the speed of those cells swimming approximately parallel to the surface remains constant regardless of the distance.

Similar results are obtained when the monotrichous bacteria *V. alginolyticus* is observed using inverted phase-contrast microscopy [111, 112]. They noted that, with all else kept constant, the wall effect on cells swimming toward the boundary differs from that of cells swimming away. Observing the swimming speed and pitching rate as a function of the distance away from the wall and the orientation, it was concluded that wall effect is negligible on the bacteria at a distance of at least 12.5 times the diameter of the cell body. This is in line with the cell distribution study of *E. coli* between two glass plates, in which there is a sharp spike in the population density within a distance of 10–12.5 times the cell length away from the wall but little variations at further distance [107].

Researchers have also looked into whether wall effects may be neglected for spermatozoa, which are much larger than the bacterial cells. Frymier, et al. [50] modeled two-dimensional spermatozoa with beating flagella as a distribution of the singularities to study its motion in the presence of two parallel boundaries. For the spermatozoa that was placed midway between the channel walls, the wall effect can be neglected when the ratio between the half channel width and the flagellum amplitude is around 5. The spermatozoa model has been extended to a more general case, comprising a distribution of regularized Stokeslet over an ellipsoid and along a slender filament [110]. The sperm motion in a slide chamber is computed, in which the walls are modeled as parallel plates and also discretized by a distribution of regularized Stokeslets. The force acting on the sphere-rod body as computed by them is in good agreement with the results by

Ramia, et al. [33], and it can be seen that the boundary effect becomes insignificant when half-depth of the chamber slide approaches 10 times the size of the swimmer (Figure 2-13).

Based on the results from studies discussed in this section, it is safe to conclude the wall effect can be neglected when the distance from the swimmer to the wall is over one order of magnitude greater than the body length of the swimmer. On the less conservative side, the wall effect can also be argued to be insignificant at a separation distance of slightly under 10 times the body length.

2.6 Mechanoreception of Copepods

The copepod belongs to the family of pelagic crustaceans. As opposite to the benthic crustaceans which spend most of their life cycles on land, pelagic crustaceans live in the aquatic environment. Both type of crustaceans are equipped with chemoreceptional and mechanoreceptional sensilla [52-55], which allow them to remotely locate preys, mate with each other, and avoid been caught by their predators. Research has shown that although copepod mating and conspecies identification may involve a combination of chemoreception and mechanoreception, the mechanical signals in most of the situations are sufficient for remote prey detection [61-63] and escaping from predators [113, 114]. Since the second half of this thesis addresses how copepods detect swimming preys, the mechanoreception of copepods is the focus here.

In this subsection, the morphology of copepod's mechanoreceptors and its neurological structures are first introduced, followed by a discussion on the two

existing theoretical models and experimental studies on the mechanoreception of copepods. Note that the second theoretical model is originally developed and applied to benthic crustaceans, but Lenz and Hartline [73] further expend it to predict the predating behavior of copepods.

2.6.1 Setal morphology

The morphologies and neurologies of benthic crustacean hairs and pelagic crustacean setae are almost the same except that pelagic crustacean setae are usually longer and harder to bend (Figure 2-14 and Figure 2-15). These setae protrude from the tubular sheath of the first antennule [56, 115], and detect the fluid deformation rate [40, 113, 114, 116] through the bending of the mechanoreceptional setae [52, 56]. Prior to determine the setal sensitivity to hydromechanical signals, the morphologies of the first antennule and attached setae in 9 species are analyzed by Yen, et al. [56] using light and scanning electron microscopies. The seta of marine copepods is classified into 4 categories:

- Smooth and tapered setae with length of 200 ~ 500 μm ,
- Short (<100 μm) and tapered setae with length < 100 μm ,
- Short setae with a blunt tip, and
- Feathered setae.

Figure 2-14: Hair on the pedipalp of a scorpion. Adopted from Barth, et al. [117].

Figure 2-15: The first antennule of *Gaussia princeps*. Adopted from Fields, et al. [118].

The first antennule of copepods are formed by antennular segments (23 segments for *Labidocera madurae*), which can be classified into three sections: the proximal section, in which one can observe all 4 types of setae, most projected anteriorly, the middle section, where there is usually one long seta and one to two short setae per segment, and the distal section, where extremely long (up to 1mm for *Gaetanus sp.*) setae grow on [56]. Paffenhöfer and Loyd [119] reported the seta length of *Temmorea styliifera* is around 105 μm . Fields, et al. [118] measured 8 setae lengths at the distal segment of *Caussia princeps* first antennule and found the setae lengths vary from 200 μm to 3032 μm , with the

longest seta at the distal region of the first antennule. Furthermore, Weatherby, et al. [54] did a detailed morphological study of sensory setae presented on the distal segments of *Pleuromamma xiphias* (Table 1). The diameters of the long setae (seta #1, #8) are usually larger than those of the short setae (seta #3, #5) but within the same order.

Segment	Seta #	Type	Position	Sensory function	Length (μm)		Diameter (μm)
XXXVII-XXXVIII					Male	Female	
	1	long stiff	posterior	mechano-	1100	1150	9.7
	2	short smooth	posterior	mechano-	55	55	7.0
	3	whip	posterior	mechano-	220	220	3.0
	4	creased	anterior	chemo-	110	70	6.4
	5	tapered smooth	anterior	mechano-	75	70	5.2
	6	small triangular	anterior	mechano-	9	11.5	2.1
	7	tapered smooth	anterior	mechano- /chemo-	82	73	4.6
XXVI	8	long stiff	anterior	mechano-	690	740	11.6
	9	plumose	posterior	mechano-	210	220	4.9

Table 1: Morphological characteristics of setae on the distal section of the first antennule of *Pleuromamma xiphias*. Adopted from Weatherby, et al. [54].

2.6.2 Antennular and setal neurology

The antennular structure of pelagic crustaceans is analyzed by scanning electron microscopy. The mechanoreception function of a crustacean is achieved by the neural signals transmitting in the dendrites, which are composed of closely packed microtubes (up to 3,000/dendrite) [54]. The dendrites are surrounded by scolopale cells, which are bundles of actin filament and acting as the rigid support for dendrites. Along the antennule, the dendrites and scolopale cells are connected by desmosomes [120]. At the distal region of the antennule, the dendrites are surrounded dendritic sheath, both of which are connected to the cuticle (the outermost structure of the seta) [121]

Research has analyzed the intracellular structure of the antennule of pelagic and benthic crustaceans; however, the structure of the distal seta and how it elicits copepod's neural response remains unknown. It is speculated that the setal motion or the deformation of the cuticle stretches the dendrite membrane hence activating the neural signals [122]. Copepod responds to external stimuli almost instantaneously. When the stimulus frequency is at 700 Hz, the nerve impulse of *Pleuromamma xiphias* is triggered within 1 msec [115] and its behavioral response is recorded to be as little as 6 msec [123]. The latter includes the time required for the mechanical and neural signal transduction, neural signal transmission and target motor action. Such short behavioral latency suggests a direct transduction between mechanical signals to neurophysiological signals through the opening of membrane bound ion channel, without a second-messenger cascade [124]. Deduced from a vertebrate hair model [125], the dendrites and cuticles are connected by linking proteins (Figure 2-16, left

panel). As the seta bends, the ion channels in the dendrites are stretched and opened via those proteins (Figure 2-16, right panel), after which the positive ions enter the channel and activate an action potential.

It is further hypothesized that the opening of the ion channel is more sensitive to fast setal deformation [126]. If the deformation is slow (in the order of 10 msec or more, by the definition of Holt and Corey [125] based on vertebrate hair), the linking proteins are able to move in the membrane, reducing the stress on the ion channel, and hence a larger setal displacement is required for eliciting the neural response. On the other hand, if the deformation is fast (in the order of less than 10 msec), the linking proteins do not have enough time to respond, and hence the ion channel is opened at a smaller setal deformation.

Figure 2-16: Setae mechanoreception model proposed by Fields [126]. Left panel: the dendrites extend along the setal axis and are connected to the cuticle by linking proteins. Right panel: when the displacement is slow (in the order of 10 msec or more), the origin of the linking proteins can move within the membrane, reducing the tension on the ion channel and the sensitivity. If the angular displacement is rapid, the protein does not have enough time to respond and the channel is pulled open.

2.6.3 Theoretical model

Since the hair of benthic crustaceans and seta of pelagic crustaceans is similar from the structure and neurological perspectives, a few research has been attempted to approach the flow field on hair/seta and further related it with the displacement of the hair/seta [118, 127]. In this section, two theoretical models are presented.

2.6.3.1 *Visser's Model on Copepod's Mechanoreception* [40]

Visser's model addresses the hydromechanical signal sensed by the copepod in common scenarios such as the flow induced by sinking particle, self-propelling body, and turbulence. Although the distal seta of the copepods serves the primary sensor, his work considers the flow velocity difference between the solid body and a seta positioned along its antennule as the stimulus to elicit the neural and behavioral responses of the copepod.

The model first considers an ambush-feeding copepod of antennular length L^{ant} , feeding on a settling particle of radius a^{prey} sinking at the speed v^{prey} [Figure 2-17(a)]. The flow field induced by the sinking particle is assumed to be within the Stokes limit, i.e., $Re \ll 1$ and $Re Sr \ll 1$. Thus, the far field behavior of the sinking particle can be approximated using the multipole expansion, composing of a Stokeslet and a potential dipole, the flow field of which in the polar coordinate is expressed as

$$\mathbf{u}(R, \theta) = \frac{3}{4} \frac{a^{\text{prey}} v^{\text{prey}}}{R} \begin{bmatrix} 2 \cos \theta \\ -\sin \theta \end{bmatrix} - \frac{1}{4} \frac{(a^{\text{prey}})^3 v^{\text{prey}}}{R^3} \begin{bmatrix} 2 \cos \theta \\ \sin \theta \end{bmatrix}, \quad (2.46)$$

where $\mathbf{u}$ is the velocity of the flow field at a distance of R from the particle and θ is the angle with respect to the particle's direction of motion. Assume the

presence of the copepod has no contribution on the flow field around, the velocity difference experienced by the seta is therefore $\delta \mathbf{u} = \mathbf{u}(R^b, \theta^b) - \mathbf{u}(R^0, \theta^0)$, where $[R^0, \theta^0]$ and $[R^b, \theta^b]$ are respectively the positions of the head tip and the antennular tip relative to the sinking particle. In the specific case that $\theta^b = \theta^0 = 90^\circ$, the flow velocity across the antennule in the direction perpendicular to the antennule is given by

$$\delta u_{\perp} = - \left[\frac{3v^{\text{prey}}}{4} \frac{a^{\text{prey}} L^{\text{ant}}}{R^0 (R^0 - L^{\text{ant}})} + \frac{3v^{\text{prey}}}{4} \frac{(a^{\text{prey}})^3 L^{\text{ant}}}{[R^0 (R^0 - L^{\text{ant}})]^2} + \frac{v^{\text{prey}}}{4} \frac{(a^{\text{prey}} L^{\text{ant}})^3}{[R^0 (R^0 - L^{\text{ant}})]^3} \right]. \quad (2.47)$$

As the detection happens when the magnitude of δu_z exceeds the threshold

Figure 2-17: Detection of (a) a sinking particle and (b) a self-propelled body by a raptorial copepod of antennular length L^{ant} . The head tip and the antennular tip are located at $[R^0, \theta^0]$ and $[R^b, \theta^b]$ with respect to the prey in the polar coordinate system. The prey of radius a^{prey} is sinking/swimming at the speed v^{prey} . $\mathbf{u}$ is the flow velocity induced by the prey, ϕ the swimming direction of the self-propelled body. Adopted from Visser [40].

sensitivity of the copepod u^{thres} , i.e., $|\delta u_z| > u^{\text{thres}}$, the distance R^* in which the sinking particle is detected by the copepod can be derived from Eq. (2.47). In the limit that the detection happens close to the seta with $R^* \ll L^{\text{ant}}$, R^* reduces to

$$R^* = \frac{v^{\text{prey}}}{4u^{\text{thres}}} a^{\text{prey}} \left[3 + \left(\frac{a^{\text{prey}}}{R^*} \right)^2 \right]. \quad (2.48)$$

Eq. (2.48) indicates that the length scale of the antennule L^{ant} is not important in the detection. The sensitivity of the seta u^{thres} is merely a function of the distance from the center of the particle to the root of the seta R^* . On the other extreme that the detection occurs far from the copepod $R^* \gg L^{\text{ant}}$, R^* becomes

$$(R^*)^2 = \frac{3v^{\text{prey}}}{4u^{\text{thres}}} a^{\text{prey}} L^{\text{ant}} \left[1 + \left(\frac{a^{\text{prey}}}{R^*} \right)^2 \right]. \quad (2.49)$$

Eq. (2.49) indicates the detection depends on the rate of strain of the flow induced by sinking particle $v^{\text{prey}} a^{\text{prey}} / (R^*)^2$ and the length scale of the copepod L^{ant} [Note that the flow velocity induced by a Stokeslet monopole scales as $v^{\text{prey}} a^{\text{prey}} / R^*$. Thus, the rate of strain scales as $v^{\text{prey}} a^{\text{prey}} / (R^*)^2$]. This far field strain approximation has been adopted in many studies such as Ref. [71-73].

Similarly, one can also analyze the flow velocity on the copepod's sensor induced by a self-propelled body which usually behaves as a Stokeslet dipole [Figure 2-17(b)]. The dipolar velocity in the polar coordinates is expressed as

$$\mathbf{u}_r(R, \theta) = \frac{3v^{\text{prey}}}{2} \left(\frac{a^{\text{prey}}}{R} \right)^2 (1 - 3\cos^2 \theta), \quad (2.50)$$

$$u_\theta(R, \theta) = 0. \quad (2.51)$$

Thus, the flow velocity difference across the sensor is

$$\begin{aligned}\delta \mathbf{u} &= \mathbf{u}(R^b, \theta^b) - \mathbf{u}(R^0, \theta^0) \\ &= \frac{3v^{\text{prey}}}{2} \left(\frac{a^{\text{prey}}}{R^b} \right)^2 (1 - 3\cos^2 \theta^b) \hat{R}^b - \frac{3v^{\text{prey}}}{2} \left(\frac{a^{\text{prey}}}{R^0} \right)^2 (1 - 3\cos^2 \theta^0) \hat{R}^0,\end{aligned}\quad (2.52)$$

where $\hat{R}^b$ and $\hat{R}^0$ are the unit directional vectors from the center of the self-propelled microorganism to the head tip and antennular tip of the copepod, respectively. Consider the two extreme cases, Eq. (2.52) can be reduced to

$$R^* \ll L^{\text{ant}} : R^* = a^{\text{prey}} \left(\frac{3}{2} \frac{v^{\text{prey}}}{u_{\text{thres}}} |3\cos^2 \theta^b - 1| \right)^{1/2}, \quad (2.53)$$

$$R^* \gg L^{\text{ant}} : R^* = \left[3(a^{\text{prey}})^2 L^{\text{ant}} \frac{v^{\text{prey}}}{u_{\text{thres}}} |3\cos^2 \theta - 1| \cos(\theta - \varphi) \right]^{1/3}, \quad (2.54)$$

where $\theta = \theta_b \approx \theta_0$, and φ is the angle between the swimming direction and the alignment of antennule. Eq. (2.53) indicates the flow velocity across the sensor is only dependent on the velocity at the antennular tip. Both Equations (2.53) and (2.54) shows the direction of motion of the microswimmer plays a role where it will be detected by the copepod.

The Visser's model illustrates the leading order of the flow field induced by a microswimmer in the prey-predator detection. It describes the relative importance of each parameter in determining the flow field experienced by the copepod's sensor and provides a fair estimation of if the prey will be detected by the copepod when the prey is extremely close to or far from the copepod. However, this model also exhibits a few limitations: firstly, the presence of the copepod body is neglected when determining the flow velocity across the sensor. In the near field which copepod-prey detection is most likely to occur, the vicinity of the copepod strongly affects the flow field at the mechanoreceptional sensor. Thus, one could expect the accuracy of the estimated velocity to be poor.

Secondly, as the copepod setae are the primary sensilla for the hydromechanical detection, using the velocity difference across the antennule instead provides a qualitative measurement of that across the seta but not quantitative. Lastly, the threshold velocity required to detect the prey is associated with the deformation of the seta. In this approach, where is no way to further evaluate the relationship between the flow velocity difference and setal deformation.

2.6.3.2 The Arthropod Filiform Hair Model

Although theoretical studies on the interaction between medium flow and the response of the hair and/or seta are limited, a well-accepted mathematical model has been frequently used to study the response of arthropod's hair subjected to the external flow. The arthropod filiform hair model [67-70] which was originally created for insect sensing in air [128, 129] and later applied to copepods in water [73]. Differs from Visser's model which assumes the flow dynamics is within the steady Stokes regime, the arthropod filiform hair model briefly discussed here is valid in the limit of oscillatory Stokes regime.

Figure 2-18: The spring damper system for modeled arthropod hair and pedipalpl. Adopted from Humphrey and Barth [70].

The arthropod filiform hair model assumes that first, the pedipalpl is a stationary body in the flow [130], and second, the arthropod hair is rigid and perpendicular to its pedipalpl, so the hair can be treated as a spring-damper system which rotates about its pivot point when subjected to the background flow (Figure 2-18). The arthropod hair is approximated as a cylinder with density ρ_{hair} , effective length l and diameter d ($l \gg d$). Note that arthropod hairs in reality are flexible and curved at their distal tip [117]. The equation of motion of such spring-damper system can be represented as

$$I \frac{d^2\theta}{dt^2} + C \frac{d\theta}{dt} + K\theta = T_{\text{hair}}(t), \quad (2.55)$$

where I is the moment of inertia of the cylindrical hair, C the damping constant, and K the spring constant; $T_{\text{hair}}(t)$ is the torque imposed by the external flow on the pivot point. Using the parallel axis theorem, the moment of inertia of the cylinder about the pivot point can be expressed as

$$I = \frac{\pi \rho_{\text{hair}} d^2}{48} \left(4l^3 + \frac{3}{4} l d^2 \right). \quad (2.56)$$

The total torque on the pivot can be related to the time dependent force per unit length acting along the cylinder as

$$T_{\text{hair}}(t) = \int_0^l F_{\text{hair}}(t) y dy. \quad (2.57)$$

To solve for F_{hair} in Eq. (2.57) for the case that the flow is oscillating parallel to the longitudinal axis of the cylinder, Humphrey, et al. [67] adopt the solution of the Stokes second problem [131] which describes the functional force of the force $F_{\text{hair}}(t)$ exerted on a pendulum oscillating with small angular displacement amplitude in a quiescent, incompressible, constant property fluid. This is because the boundary conditions on the hair are very similar to the

assumptions made in the Stokes second problem:

- The pendulum can be treated as a cylinder with length to diameter ratio much larger than 1, i.e., $l \gg d$,
- The displacement of pendulum measured from its neutral position is so small that the pendulum can be assumed oscillating only in the translational direction (normal to the cylindrical axis),
- The oscillation amplitude of the pendulum satisfies

$$Amp = \left(\frac{d}{4} \right) \left(\frac{2\pi f}{\nu} \right)^{1/2} \ll 1, \quad (2.58)$$

where f is the oscillation frequency of this pendulum; ν is the kinematic viscosity of the surrounding fluid.

The rationale of Eq. (2.58) is to ensure the Reynolds number associated with the oscillation of the pendulum is much smaller than 1. The mathematical proof is as follow. The Reynolds number for the flow passing a cylinder is defined as $Re = V_r d / \nu$, where V_r is the relative velocity between the flow velocity V_f and the cylinder velocity V_c . In quiescent fluid ($V_f \approx 0$), one could assume $V_r = -V_c$. The small amplitude constraint (as stated in the second assumption above) implies the displacement of the cylinder can be scaled with its diameter d . Since a typical displacement takes place in a quarter-period, $1/4f$, a characteristic relative velocity is $V_r = -V_c \sim d/(1/4f) = 4fd$. Substituting this result into the definition of Re , one can scale the Reynolds number as $Re \sim d^2 f / \nu$, which is equal to Amp squared times a constant in the order of one. Thus, Eq. (2.58) also indicates $Re \ll 1$. Note that the approximation here does not restrict the choice of the Strauhol number Sr . Thus, the convective acceleration term in the Navier-Stokes equation [the second term on the left hand side of Eq. (2.1)] is

non-negligible, and hence the fluid dynamics is governed by the time-dependent Stokes equation.

Following the above assumptions, Stokes [131] found that for the case of a fluid oscillating perpendicular to the cylinder, $F_{\text{hair}}(t)$ composes of two components, one due to fluid-induced stress forces along the axis of the cylinder $F_{\text{hair},D}(t)$, and the other due to the virtual mass of fluid $F_{\text{hair},VM}(t)$, or

$$F_{\text{hair}}(t) = F_{\text{hair},D}(t) + F_{\text{hair},VM}(t), \quad (2.59)$$

where

$$F_{\text{hair},D}(t) = 4\pi G V_r; \quad (2.60)$$

$$F_{\text{hair},VM}(t) = -\frac{\pi\mu G \dot{V}_r}{2gf} + \pi\rho \left(\frac{d}{2}\right)^2 \dot{V}_r; \quad (2.61)$$

$$g = 0.577 + \ln \left[\left(\frac{d}{4}\right) \left(\frac{2\pi f}{\nu}\right)^{1/2} \right]; \quad (2.62)$$

$$G = -\frac{g}{g^2 + \pi^2/16}; \quad (2.63)$$

$V_r = V_f - V_c$ is the local relative velocity between the flow and the cylinder; $\dot{V}_r$ is the time rate of change of V_f ; f is the oscillation frequency of the fluid in Hz. Since the rigid cylinder is oscillating about the pivot point, the velocity perpendicular to the cylinder axis can be expressed as $V_c = y\dot{\theta}$. Eq. (2.59) is then substituted into Eq. (2.55) via Eq. (2.57). Rearranging Eq. (2.55) with the help of $V_r = V_f - V_c$ to separate the terms involving hair motion from those involving fluid motion, one can obtain

$$(I + I_\rho + I_\mu)\ddot{\theta} + (C + C_\mu)\dot{\theta} + K\theta = 4\pi\mu G \int_0^L V_f y dy + \left(\frac{\pi\rho d^2}{4} - \frac{\pi^2\mu G}{2\pi gf} \right) \int_0^L \dot{V}_f y dy,$$

$$(2.64)$$

where the quantities I_ρ , I_μ and R_μ denote the fluid medium contributions to the moment of inertia and the damping constant of the hair associated with the fluid medium density and viscosity,

$$I_\rho = \frac{\pi \rho d^2 L^3}{12}, \quad (2.65)$$

$$I_\mu = -\frac{\pi \mu G L^3}{6 g f}, \text{ and} \quad (2.66)$$

$$R_\mu = \frac{4}{3} \pi \mu G L^3. \quad (2.67)$$

As the next step, the fluid velocity V_f around the surface of an infinite cylindrical substrate, which the arthropod's pedipalpl is approximated as, is determined in order to solve for Eq. (2.64). Humphrey, et al. [67] showed that for the case that the flow oscillation plane is parallel to the cylindrical axis, the curvature of cylindrical substrate can be neglected if $\text{Re Sr} > 10$, i.e.,

$$\frac{f d^2}{\nu} > \frac{20}{\pi}. \quad (2.68)$$

Eq. (2.68) is the constraint which it is fair to equate the flow velocity around the cylindrical surface to that around a flat surface. For fluid oscillating parallel to and far away from a flat surface with velocity $U_0 \cos(\omega t)$, the instantaneous fluid velocity at time t and a distance y perpendicular to the surface can be expressed as [132, 133]

$$V_f = U_0 \left[\cos(\omega t) - \cos(\omega t - \beta y) e^{-\beta y} \right], \quad (2.69)$$

where $\beta = (\pi f / \nu)^{1/2}$. When $y = 0$, the flow velocity is zero due to the no-slip boundary condition on the immobile cylindrical substrate surface; when $y \rightarrow \infty$, the flow velocity approaches the background flow velocity. This indicates the

presence of a viscous boundary layer around the cylindrical substrate, and the thickness of this boundary layer δ_{bl} , which is the location above the substrate with the viscous damping inducing 1% reduction in the amplitude of the far field velocity, is found to be $\delta_{bl} = 4.5/\beta$.

Figure 2-19: Flow fluid velocity V_f above the cylindrical substrate, normalized with the background flow velocity U_0 , at (a) 10Hz and (b) 500 Hz. Other parameters are $\omega t = \pi/2$, preycopepod detection can be governed by the steady Stokes equation. $\nu_{\text{air}} = 1.59 \times 10^{-5} \text{ m}^2/\text{s}$ and $\nu_{\text{water}} = 8 \times 10^{-7} \text{ m}^2/\text{s}$. y is measured from the surface of the substrate. The solid and dashed lines are the flow profiles in air and water, respectively. Adopted from Devarakonda, et al. [68].

Arthropods may live in air or water. The former is not relevant to our analysis. However, in order to analyze the effect of different mediums on the viscous boundary layer around the pedipalpl, it is worth to take two mediums as a comparison. Utilizing Eq. (2.69), the flow profiles above the cylindrical substrate due to air (solid lines) and water (dashed lines) are shown in Figure 2-19 for low (10 Hz) and high (500 Hz) frequency background flows. The boundary layer thickness δ_{bl} quantifies the region of flow affected by the presence of the substrate due to viscous effect. Since air has a larger kinematic viscosity compared to water ($\nu_{\text{air}} = 1.59 \times 10^{-5} \text{ m}^2/\text{s}$ and $\nu_{\text{water}} = 8 \times 10^{-7} \text{ m}^2/\text{s}$),

Figure 2-20: (a) The maximum angular displacement of cylindrical seta of length 500 μm and diameter 7 μm attached to a cylindrical substrate when subjected to a background water oscillation with peak velocity of 5 mm/s. The damping constant of the seta is assumed to be 0, the spring constant 4×10^{-12} N. (b) bode plots for the maximum angular displacement of seta, normalized with the mean water displacement, for six setae with different lengths. Adopted from Lenz and Hartline [73].

the boundary layer thickness is larger for air. Furthermore, δ_{bl} decreases with increasing background flow frequency f due to the relationship defined above.

With the medium flow profile given by Eq. (2.69) and the equation of motion of the spring-damper system shown in Eq. (2.64), the steady-state solution of the angular displacement of an arthropod hair can be derived as Humphrey, et al. [67]:

$$\theta = D_1 \cos(2\pi ft) + D_2 \sin(2\pi ft), \quad (2.70)$$

where the constants D_1 and D_2 are shown in Humphrey, et al. [67] Appendix 1. Eq. (2.70) used in the arthropod hair model is further extended by Lenz and Hartline [73] to predict that the setae of pelagic crustaceans are likely to be high

pass displacement filter. Although the maximum hair angle decreases as the background flow field frequency increases [Figure 2-20(a)], the maximum hair angle normalized with the mean water displacement shows a linear increase in the amplitude at the low frequency range, and become stabilized when the background flow frequency is more than a so-called “corner frequency” [Figure 2-20(b)]. The “corner frequency” and constant maximum hair angle are functions of the setal mechanical and geometrical characteristics [69, 134].

Plankton	Length (μm)	Swimming Speed ($\mu\text{m/s}$)	Beating Frequency (Hz)	Re	Sr
<i>L. strobila</i> [64]	130	500 - 1000	-	6.5E-2 - 1.3E-1	-
<i>S. reticulatum</i> [64]	43	500 - 1000	-	2.2E-2 - 4.3E-2	-
<i>C. deanei</i> [135]	7	45.6	40.5	3.20E-4	39
<i>C. fasciculata</i> [135]	11	54.3	60	6.00E-4	76
<i>L. major</i> [135]	13	36.4	24.5	4.70E-4	55
<i>C. reinhardtii</i> [136]	10	65.7	48 - 53	6.60E-4	46 - 51
<i>G. dominans</i> [137]	19	580	1.6	1.10E-2	3.30E-1
<i>B. designis</i> [138]	10	39	-	3.90E-4	-
<i>Spumella sp.</i> [138]	10	25	-	2.50E-4	-
<i>H. triquetra</i> [138]	17	97	-	1.60E-3	-
<i>B. comatum</i> [139]	16	220	-	3.50E-3	-
<i>G. lamblia</i> [140]	3	12 - 40	17	3.6E-5 - 1.2E-4	8 - 27

Table 2: The hydrodynamic characteristics of planktonic preys

There are two possible reasons why the arthropod filiform model may not adequately describe the setal deformation of untethered copepods. First, the hydrodynamic signal sensed by a moving object differs from a stationary object [71]. Second, the flow disturbances induced by planktonic preys such as ciliates and flagellates occur at low frequencies [141] contrary to the assumptions in the

arthropod filiform model, and hence the flow dynamics are well-treated in the steady Stokes regime. As shown in Table I, the typical body lengths of the preys are in $O(10^1)$ μm ; their beating frequencies range from 1.6 to 60 Hz; and their swimming speed falls in $O(10^2)$ $\mu\text{m/s}$. For detection of the prey by copepods, the flow field at the seta should be even smaller since it decays with distance, and typical setae have lengths of order 10^2 μm and much smaller diameters. Using these estimates, both the prey's swimming velocity field as well as the flow around the setae should satisfy $\text{Re} \ll 1$ and $\text{Re Sr} \ll 1$. Therefore, the hydrodynamics of the prey-copepod detection can be governed by the steady Stokes equation.

2.6.4 Experimental studies on copepod setae

The threshold stimulus displacement to elicit neural response is usually much lower than that to elicit the behavioral response [114]. The first experiment which analyzed copepod's neural and behavioral responses can be traced back to Yen, et al. [56], who recorded extracellular nerve impulses transmit along the first antennule of calanoid copepods. The nerve impulse is elicited by direct contact of a vibrator with copepod seta. The method is further improved by using a more "nature" stimuli: a sphere attached to a transducer which creates a Stokeslet dipolar flow field with controlled water displacement [115, 142]. In their experiments, either an ablated antennule or a copepod with one first antennule completely cut off was grasped by stainless steel forceps. The antennule/copepod was placed at the middle of a plastic ring, which was suspended on the water surface and then filled with mineral oil (Figure 2-21). This is to ensure the middle and distal section of the antennule is immersed into water while the copepod body and the tip of the forceps are surrounded by electricity-insulated oil. After

the vibrator/transducer started to vibrate with controlled displacement, the electric potential across the forceps and the ground (a reference wire placed in sea water), which was induced by the neural impulse travelling along the antennule, was recorded using a recording system.

Copepod setae are found to be ultrasensitive to hydrodynamic disturbance through the experiments conducted. Yen, et al. [56] found that the sensitivity of *Labidocera madurae* seta to water displacement ratio increases with increasing stimulation frequency. The threshold displacement to elicit *L. madurae*'s behavioral response is about 50 nm at the frequency range between 250 Hz and 1000 Hz; the threshold displacement decreases to 10 nm for frequencies above 1000 Hz. Thereafter, the grasped *Euchaeta rimana* and *Pleuromamma xiphias* were found to detect fluid displacement as low as 10 nm and 20 nm, respectively [Figure 2-22(a)], corresponding to fluid velocity of $\sim 20 \mu\text{m s}^{-1}$ and $40 \mu\text{m s}^{-1}$, the best sensitivity of which are all at around 1000 Hz [115]. Similar results is also discovered by Hartline, et al. [60], who found *L. madurae* physically respond to a sinusoidal wave with peak-to-peak displacement as low as 4 nm when the sinusoidal frequency is about 900 Hz, and the sensitivity was relatively low at low (< 100 Hz) and high (> 1200 Hz) frequency ranges [Figure 2-22(b)].

The first experiment which captures individual setal deformation was done by Fields, et al. [118], who recorded the angular displacement and neural response of four setae on the first antennule of *Gaussia princeps* when stimulated by a water jet. In their experimental setup, water was ejected out of the pipe by compressed air (344 kPa) using a micro-injection system (Picospritzer II). The water jet duration and head speed were controlled by the duration when the valve in the micro-injection system remained open. In Figure 2-23(a), the letter "A"

represents the seta orientation with no stimulation, and each subsequent letter represents a 2 msec increase in the length of time the valve remained open. Furthermore, the physiological responses of three setae were sorted out individually through connecting the antennule to a neural recording device [142]. The neural response of each seta, when subjected to either proximal or distal water jet, is plotted in Figure 2-23(b, c). The neural response of seta #8, the longest and stiffest seta at the distal section of the first antennule, is extremely steep at very small water jet speed. Seta #8, while the short seta, seta #7, is insensitive to water speed and offers a wider range of water speed information. Therefore, it is hypothesized that all setae at the distal section provide complementary information on the water speed.

The experiments described above have two limitations. First, the experiment setup forced the flow field on the antennule to be zero, which fails to mimic the flow field around the setae of copepods. Unlike benthic crustaceans whose pedipalpl (substrate) remains still under the flow, the copepods move together with the flow field induced by the prey, wind, etc.; therefore, the mechanoreceptional seta of copepods detects the velocity difference between the reference point of the copepod and the setal tip [114]. The grasped copepods in the experiments behave more like benthic crustaceans with a significantly increased hydromechanical sensitivity. Second, those experiments placed an oscillating sphere of radius 1.5 mm near a grasped copepod (first antennule) and recorded its behavioral (neurological) response at frequencies ranging from 50 to 2000 Hz, which is beyond the natural frequencies of the swimming strokes of the planktonic preys. Thus, these experiments described above fail to quantify the sensitivity of the copepod in detecting swimming preys.

Figure 2-21: Extracellular recording system setup to measure the electric potential across the copepod due to the neural impulse transmitted along the first antennule. The copepod is clamped by forceps and immersed into mineral oil while its first antennule is in contact with sea water. Hydromechanical disturbance is generated by a vibration sphere connected to a transducer. Adopted from Gassie, et al. [142].

Figure 2-22: Threshold sensitivities for (a) *Pleuromamma xiphias* (crosses) and *Euchaeta rimana* (open symbols) females between 30 and 1,100 Hz and for (b) *Labidocera madurae* between 100 and 1800Hz. The vertical axis represents the maximum water displacement induced by a vibrating sphere. The horizontal axis represents the frequency of the vibrating sphere. (a) is adopted from Lenz and Yen [115], (b) from Hartline, et al. [60].

Figure 2-23: (a) Maximum angular displacement of distal seta on the antennule when subjected to a water jet. The letter A represents the seta orientation with no stimulation, and each subsequent letter represents a 2 msec increase in the length of time the solenoid remained open. The physiological responses of setae, when subjected to either distal or proximal oriented water jet, are plotted against (b) the angular displacement and (c) the water jet speed. Each physiological response curve is normalized with its maximum response. Adopted from Fields, et al. [118].

The first experiment which analyzed behavioral response of pelagic crustaceans under the natural stimuli is done by Broglio, et al. [62]. They reported that the detection distance of *Acartia clausi* on its prey depends on prey's swimming behavior. They tested two prey species of almost identical size, *Metacylis sp.* and *Strobilidium spiralis*. *Metacylis sp.* (body length 59 μm , width 55 μm) which swims with a steep helical trajectory (mean velocity 0.78 mm/s) without jumps, is detected at a distance of 0.4 mm away the copepod's head tip. In comparison, *Strobilidium spiralis* (body length 52 μm , width 49 μm) which shows a slow upward and downward swimming (mean velocity 0.33 mm/s) interrupted by sudden jumps (mean jump length and velocity are respectively 0.36 mm/s and 3.93 mm/s), is detected at a distance of 0.69 mm away the copepod. *Strobilidium spiralis* is found to have a longer detection distance but a lower capture rate due to sudden jumps.

2.7 Research Gap

The far-field multipole expansion and its image system is a good approach to determine the boundary effect on microswimmers. However, the range of validity of the multipole expansion depends on geometry and mode of propulsion of the microswimmer. To find the limit of validity of the multipole representation for boundary effects, one must develop a model which includes the near-field geometry and detailed swimming strokes of the swimmer and do a full calculation of the boundary effects. Thus, it could be useful to seek an independent way to determine the validity limit of the multipole expansion without modeling the near-field details of the microswimmers.

To address copepod's mechanoreceptional system in prey detection, two theoretical frameworks are developed. The copepod model developed by Visser [40] is not capable of determining the actual flow profile on the distal seta and analyze its deformation. The other based on the arthropod filiform hair model [67-70] is valid for the background flow in a frequency range beyond the copepod realm. By assuming the substrate where the seta is attached is stationary, the model alters the physics that the seta serves as a velocity difference sensor and thus overestimates the mechanoreceptional sensitivity of copepods. Moreover, the maximum setal deformation is achieved after a few cycles of oscillation in the model, which is more than the time required for the copepod responds to the stimulus. Therefore, a new theoretical model which is capable of addressing the fundamental characteristics of the copepod's mechanoreception is required.

Chapter 3

Traction Reveals Mechanisms of Wall-Effects for Microswimmers near Boundaries²

3.1 Introduction

Understanding the effect of boundaries on swimming is the key to address the behaviors of microswimmers near boundaries [143-146]. Common approaches utilize singularities and far-field multipole expansions [107, 147, 148] to model microswimmers and adopt then the image system method [65] to satisfy the no-slip boundary conditions. As demonstrated in Section 2.5.3, when the swimmers are at large distances from the boundary, the far-field multipole expansion and its image system can accurately predict the effects of boundaries on pitching movements for swimmers with steady propulsion mechanisms. However, the closest approach to the boundary for which the approach is valid depends on geometry and mode of propulsion of the swimmer, with no *a priori* way of determining the range of validity [66].

² This section is published in: X. Shen, Marcos and H. C. Fu. "Traction reveals mechanisms of wall effects for microswimmers near boundaries." *Phys. Rev. E* vol. 95, p. 033105, 2017

The objective of this chapter is to show that the examining the traction on the wall induced by microswimmer provides an independent way to check when the multipole expansion is valid. The image system method is usually simpler and a more common approach, but the author suggests that examining the traction on the boundary can give additional insight into boundary effects which are harder to access by the image system approach. As a demonstration, the swimming velocities and the traction of a three-sphere swimmer [28], an artificial low-Re microswimmer, initially placed parallel to an infinite planar wall are investigated. The exact solutions are first obtained using the image system method to find the instantaneous forces acting on the three spheres and the instantaneous velocity of the swimmer. As a function of distance from the wall, the author then identifies when far-field approximations of the swimmer based on multipole expansions and image velocity fields are appropriate to describe the effect of the boundary. After that, the distribution of traction on the wall due to the swimmer and the multipole expansions are evaluated and compared to show that examining the traction pattern gives insight into whether the far-field approximation applies or, in contrast, the internal structure of the swimmer must be taken into account. The effect of time averaging is also discussed on the results section.

3.2 The Swimmer Model

For a low-Reynolds-number swimmer swimming in vicinity of a planar wall, conventional methods apply the image system approach to solve for the forces acting on a swimmer and the flow field generated by the swimmer. For a

three-sphere swimmer, the steps in Zargar, et al. [149] are followed to find swimming velocities using the image system approach. Using the same method, solutions for traction are generated. The author then compares this method to a method that relies solely on the traction on the wall and analyzes the traction patterns for insights.

Figure 3-1: A three-sphere swimmer and its image system with respect to an infinite planar wall. Spheres with radius a are labeled $\alpha = 1, 2, 3$ from left to right. The two arms l^{12} and l^{23} perform periodic motions. Initially, the swimmer is placed parallel to the wall ($\theta = \pi/2$).

A three-sphere swimmer [28] considered here is with spheres of equal radius a swimming in a fluid with viscosity μ near an infinite planar wall at $x_1 = 0$ (Figure 3-1). The three spheres from left to right are labeled as sphere 1, 2 and 3, respectively, and the prescribed lengths of the left and right arm, l^{12} and l^{23} , are,

$$l^{12}(t) = L + \zeta \cos(\omega t), \quad (3.1)$$

$$l^{23}(t) = L + \zeta \cos(\omega t + \phi). \quad (3.2)$$

Initially, the swimmer is placed parallel to and at a distance h from the infinite wall. In this paper, the characteristic length of the swimmer L , the angular frequency ω and the viscosity μ are used to nondimensionalize all physical

parameters are using. For example, the nondimensionalized arm length $\tilde{l}^{12} = 1 + \tilde{\zeta} \cos(t)$. For convenience, in the remainder of the paper, tildes are dropped and all variables refer to dimensionless quantities unless otherwise specified. All results presented are for sphere radii $a = 0.01$, amplitude of the harmonic motion $\zeta = 0.1$, and phase angle $\phi = \pi/2$. For $a \ll 1$ and as long as $a \ll h$, each sphere can be modeled as a Stokeslet placed at its geometric center. Note that the axis of the swimmer is set to be coincide with the plane $x_3 = 0$ so that the swimmer's motion remains in the x_2 - x_1 plane.

The position of each sphere can be related to the center of mass (CM) of the swimmer $\mathbf{x}^0$,

$$\begin{bmatrix} x_1^\alpha \\ x_2^\alpha \end{bmatrix} = \begin{bmatrix} x_1^0 \\ x_2^0 \end{bmatrix} + G^\alpha \begin{bmatrix} \cos \theta \\ \sin \theta \end{bmatrix}, \quad (3.3)$$

where $\mathbf{x}$ is the position vector, the superscript $\alpha = 1, 2, 3$ represents the sphere number, subscripts denote directional components, and

$$G^\alpha = \begin{cases} (-2l^{12} - l^{23})/3, & \alpha = 1 \\ (l^{12} - l^{23})/3, & \alpha = 2. \\ (l^{12} + 2l^{23})/3, & \alpha = 3 \end{cases} \quad (3.4)$$

Differentiating Eq. (3.4) relates the velocity of each sphere, $\mathbf{v}^\alpha$ to the swimmer's velocity $\mathbf{v}^0$, rotation rate $\dot{\theta}$, and arm lengths l :

$$\begin{bmatrix} v_1^\alpha \\ v_2^\alpha \end{bmatrix} = \begin{bmatrix} v_1^0 \\ v_2^0 \end{bmatrix} + \begin{bmatrix} -\sin \theta \\ \cos \theta \end{bmatrix} \dot{\theta} G^\alpha + \begin{bmatrix} \cos \theta \\ \sin \theta \end{bmatrix} \dot{G}^\alpha. \quad (3.5)$$

To find the velocity of the swimmer, the Blakeslet is utilized [65], which is the solution to a point force acting on a fluid in the presence of a no-slip boundary [149]. The Blakeslet consists of a Stokeslet (**S**) and a set of images (**St**) placed

below the boundary, which are explicitly defined in Section 2.5.1. Following the conventions of Section 2.5.1, the velocity of sphere α can be represented as,

$$v_i^\alpha = \sum_{\beta=1}^3 \left[S_{ij}(\mathbf{x}^\alpha, \mathbf{x}^\beta) + St_{ij}(\mathbf{x}^\alpha, \mathbf{x}^{\beta*}) \right] f_j^\beta, \quad (3.6)$$

where $\mathbf{f}^\beta$ is the force acting on sphere β , $\mathbf{x}^\beta$ is the Stokeslet location and $\mathbf{x}^{\beta*}$ the corresponding image location.

Since inertia is negligible at low Reynolds number, the total force and torque acting on the three-sphere swimmer are zero,

$$\sum_{\beta=1}^3 \mathbf{f}^\beta = 0, \quad (3.7)$$

$$\sum_{\beta=1}^3 -G^\beta \sin \theta f_1^\beta + G^\beta \cos \theta f_2^\beta = 0. \quad (3.8)$$

Equations (3.3)–(3.8) are a linear system which can be solved to obtain $\mathbf{v}^0$, $\mathbf{v}^\alpha$ and $\mathbf{f}^\beta$.

In the following the total velocity of the swimmer is decomposed into two parts, $\mathbf{v}^0 = \mathbf{v}^{0*} + \mathbf{u}^{0*}$. The first is due to the three Stokeslets,

$$v_i^{0*} = \frac{1}{3} \sum_{\alpha\beta} \left[S_{ij}(\mathbf{x}^\alpha, \mathbf{x}^\beta) \right] f_j^\beta, \quad (3.9)$$

and the other due to their corresponding images, which is named as the wall-induced swimming velocity,

$$u_i^{0*} = \frac{1}{3} \sum_{\alpha\beta} \left[St_{ij}(\mathbf{x}^\alpha, \mathbf{x}^{\beta*}) \right] f_j^\beta. \quad (3.10)$$

On the other hand, in the absence of the wall, the velocity of the free swimmer can be expressed as

$$v_i^{0,\text{free}} = \frac{1}{3} \sum_{\alpha\beta} [S_{ij}(\mathbf{x}^\alpha, \mathbf{x}^\beta)] f_j^{\beta,\text{free}}. \quad (3.11)$$

The change in swimming velocity due to the wall, $\mathbf{v}^0 - \mathbf{v}^{0,\text{free}}$, is not precisely equal to $\mathbf{u}^{0*}$ because the forces $\mathbf{f}^\beta$ differ from $\mathbf{f}^{\beta,\text{free}}$. However, they are quite close, meaning that most of the change in velocity is caused by the wall-induced velocity rather than changes in the internal forces of the swimmer (Figure 3-2). Thus, the focus in the following is how well the wall-induced velocity $\mathbf{u}^{0*}$ can be approximated by a far field approach, and how that is reflected in the traction. Lastly, the wall-induced velocity field at any point $\mathbf{x}^p$ is defined as

$$u_i^*(\mathbf{x}^p) = \sum_{\beta=1}^3 St_{ij}(\mathbf{x}^p, \mathbf{x}^{\beta*}) f_j^\beta. \quad (3.12)$$

The image system method is analogous to that used in electrostatics to find electric fields near conducting planes. In the electrostatic case, the field is physically produced by the combined effect of the original charge and the surface charge distribution on the conductor. Similarly, in the hydrodynamic case, the wall-induced velocity can be represented as that due to a force distribution (traction) on the boundary, which is the wall's portion of the single-layer representation of the velocity field [106]. Details are written explicitly in Section 2.5.2, but to summarize, the traction on the wall $\mathbf{x}^w$ due to a Blakeslet at $\mathbf{x}^\beta$ with force $\mathbf{f}^\beta$ is evaluated in this case, which is written as $\tau_{ij}(\mathbf{x}^w, \mathbf{x}^\beta) f_j^\beta$. For three spheres with forces $\mathbf{f}^\beta$ the traction at $\mathbf{x}^w$ induced by the three sphere swimmer can be obtained as

$$T_i(\mathbf{x}^w) = \sum_{\beta=1}^3 \tau_{ij}(\mathbf{x}^w, \mathbf{x}^\beta) f_j^\beta \quad (3.13)$$

Further substituting $\mathbf{T}(\mathbf{x}^w)$ into (2.45) allows us to evaluate the flow field at $\mathbf{x}^p$

by integrating the flow produced by the traction forces acting over the entire wall surface S ,

$$u_i^*(\mathbf{x}^p) = \int_S S_{ij}(\mathbf{x}^p, \mathbf{x}^w) T_j(\mathbf{x}^w) dS. \quad (3.14)$$

This is an alternative way to compute the result of Eq. (3.12) and suggests that analyzing the traction will give insight into the nature of the effect of the wall on swimming velocities.

Figure 3-2: The change in swimming velocity due to the wall (solid line), $v_2^0 - v_2^{0,\text{free}}$, and the wall-induced velocity (dashed line), u_2^{0*} , versus the (nondimensional) initial distance from the wall at (a) $t = \pi/2$ and (b) $t = 3\pi/2$. Note that both lines coincide.

3.3 Results

3.3.1 Instantaneous Response

In this section, the image system method is used to calculate the swimming velocity of the swimmer as a function of the distance from the wall. The wall contribution is then analyzed in terms of a multipole expansion. Comparing the two, the author determines when the multipole expansion is valid and the internal

Figure 3-3: The log-log plots of the magnitude of velocities versus the (nondimensional) initial distance from the wall at (a) $t = \pi/2$ and (b) $t = 3\pi/2$. The solid blue line represents the exact wall-induced velocity of (i) sphere 1, (ii) sphere 2, (iii) sphere 3, and (iv) the swimmer. The dashed green line represents the corresponding dipolar model. The dotted red line represents the corresponding combination of the dipole and quadrupole model

structure of the swimmer can be ignored. The author then turns to the traction and shows that the range of validity of the multipole expansion can be independently determined by observing when the spatial pattern of the traction resembles those expected from pure multipoles.

The image system method follows the results reported by Zargar, et al. [149]. To analyze the instantaneous flow field, the point of interest $\mathbf{x}^p$ is set to be at the instantaneous positions of the three spheres $\mathbf{x}^\alpha$. The average of the three velocities at these positions yields the instantaneous flow velocity at the CM of the swimmer due to its image system $\mathbf{u}^{0*}$. The focus here is the instantaneous velocity along the x_2 direction since $u_2^*(\mathbf{x}^\alpha)$ is significantly larger than the translational velocity in the x_1 direction and the rotational velocity. Since both forces on three spheres and sphere positions vary with time, the magnitude of wall-induced velocities and the multipole expansions both vary over a cycle. However, at all times the behavior of the three sphere swimmer throughout the cycle can be described below; as representative examples, the x_2 component of the instantaneous wall-induced velocities $u_2^*(\mathbf{x}^\alpha)$ and u_2^{0*} are plotted at two time points $t = \pi/2$ and $t = 3\pi/2$ in Figure 3-3(solid blue lines).

A multipole expansion is performed on Eq. (3.12) by defining $\mathbf{d}^{\beta*} = \mathbf{x}^{\beta*} - \mathbf{x}^{0*}$ as the image displacement vector from the image CM of the swimmer to the image sphere β . The expansion is expected to be valid when the swimmer is far away from the wall, or $|\mathbf{x}^\alpha - \mathbf{x}^{0*}| \gg |\mathbf{d}^{\beta*}|$ for any α, β . A Taylor expansion is performed around the image CM of the swimmer:

$$u_i^*(\mathbf{x}^\alpha) = \sum_{\beta=1}^3 St_{ij}(\mathbf{x}^\alpha, \mathbf{x}^{0*}) f_j^\beta + \partial_k St_{ij}(\mathbf{x}^\alpha, \mathbf{x}^{0*}) f_j^\beta d_k^{\beta*} \\ + \partial_l \partial_k St_{ij}(\mathbf{x}^\alpha, \mathbf{x}^{0*}) f_j^\beta d_k^{\beta*} d_l^{\beta*} + \dots, \quad (3.15)$$

where the derivatives act on the second argument of $\mathbf{St}$. The first three terms in the expansion represent the wall contribution of a Stokeslet, a Stokeslet dipole, and a Stokeslet quadrupole, respectively. The first term vanishes since the swimmer is force-free, so the subsequent dipolar term is the leading-order contribution to the wall-induced velocity. As seen from Figure 3-3(a) and Figure 3-3(b) in panels (i) and (iii) (dashed green lines), the dipole model matches well with the actual wall-induced velocity (solid blue lines) at $\mathbf{x}^1$ and $\mathbf{x}^3$ for $h > 2$, which indicates that the image system of a three-sphere swimmer at a large distance to the wall is well represented by that of a Stokeslet dipole. However, the velocity $\mathbf{u}^*(\mathbf{x}^2)$ is much smaller than $\mathbf{u}^*(\mathbf{x}^1)$ or $\mathbf{u}^*(\mathbf{x}^3)$ [note vertical scale on Figure 3-3(a) and Figure 3-3(b), panels (ii)]. This is due to the fact that $\mathbf{x}^2 - \mathbf{x}^{0*}$ and the image displacement vectors $\mathbf{d}^{\beta*}$ are almost perpendicular to the forces $\mathbf{f}^\beta$, and the wall-induced velocity of a dipole image vanishes in that direction. Therefore the subsequent term in the multipole expansion, the quadrupole, is needed to accurately describe the actual wall-induced velocity for sphere 2 [Figure 3-3(a) and Figure 3-3(b), panels (ii)].

The wall-induced contribution to the center-of-mass swimming velocity [Figure 3-3 (a) and Figure 3-3(b), panels (iv)] is the average of the wall-induced velocities of the three spheres. The dipolar wall-induced center-of-mass swimming velocity nearly vanishes because the contribution of sphere 2 is negligible and the contributions of sphere 1 and 3 nearly cancel: $\mathbf{x}^1$ and $\mathbf{x}^3$ are almost symmetric about $\mathbf{x}^0$ but the x_2 component of the dipolar velocity is odd in

the x_2 direction. Therefore, the multipole expansion of the center-of-mass swimming velocity requires the quadrupolar term to be accurate. At a given distance from the wall, the instantaneous validity of the multipole expansion holds for all times during the cycle. In summary, the multipole expansion is valid for $h > 2$ both for individual spheres and the center-of-mass velocity, as long as both dipole and quadrupole contributions are included.

The multipole expansion, however, is not suitable to describe a three-sphere swimmer close to the wall ($h < 2$). When the swimmer approaches the wall, distances from spheres to the image center-of-mass $\mathbf{x}^{0*}$ approach similar magnitude to the image displacements $\mathbf{d}^{\beta*}$. As a result, the assumption for the multipole expansion breaks down. Instead, one must use the full expression for the velocity field which for the three sphere swimmer includes a separate Stokeslet for each sphere. For a more complicated swimmer, this corresponds to contributions to the velocity field which depend on the detailed internal structure and movement of parts of the swimmer rather than a far-field representation as a series of point-like singularities.

As mentioned earlier, the wall-induced velocity can also be calculated using the wall traction approach. By comparing $\mathbf{u}^*(\mathbf{x}^\alpha)$ obtained using Eq.(3.12) and Eq. (3.14) (data not shown), it is verified that the wall traction approach yields the same results as the image approach. Here the spatial pattern of the traction on the wall is examined more closely. The traction on a fixed point $\mathbf{x}^w$ due to the Blakeslet system of all the three spheres β can be written as

$$T_i(\mathbf{x}^w) = \sum_{\beta=1}^3 \tau_{ij}(\mathbf{x}^w, \mathbf{x}^\beta) f_j^\beta. \quad (3.16)$$

When the swimmer is placed far from the wall, the traction expression above can

be expanded as

$$T_i(\mathbf{x}^w) = \sum_{\beta=1}^3 \tau_{ij}(\mathbf{x}^w, \mathbf{x}^0) f_j^\beta + \partial_k \tau_{ij}(\mathbf{x}^w, \mathbf{x}^0) f_j^\beta d_k^\beta, \quad (3.17)$$

where the derivative is taken on the second argument of $\boldsymbol{\tau}$, and the displacement vector $\mathbf{d}^\beta = \mathbf{x}^\beta - \mathbf{x}^0$. The first and second terms represent the contribution of the Blakeslet and Blakeslet dipole, respectively. The force-free condition eliminates the first term in the expansion. It is expected that the multipole expansion for the velocity to be valid if and only if the expansion in Eq. (3.17) is valid for the traction. Hence, examining when the traction resembles that of a pure dipole should provide a way to gain a diagnosis of validity for the multipole expansion that does not require calculating the exact result. In Figure 3-4 to Figure 3-9, the instantaneous traction exerted by the three-sphere swimmer is plotted at selected initial distance from the wall. For comparison, the Blakeslet dipole traction is plotted in Figure 3-10(a).

To quantify how much the traction due to the three sphere swimmer differs from that expected from a far-field Blakeslet dipole, the spatial distribution of these two tractions is analyzed using a traction correlation coefficient modified from the statistical two-dimensional correlation coefficient. The traction correlation coefficient, R , is defined as

$$R = \frac{\int_S \frac{T_i T_i^{\text{BD}}}{r^2} dS}{\sqrt{\left[\int_S \frac{T_i T_i}{r^2} dS \right] \left[\int_S \frac{T_i^{\text{BD}} T_i^{\text{BD}}}{r^2} dS \right]}}, \quad (3.18)$$

where T_i and T_i^{BD} are the spatial distribution of the traction in the i direction ($i = 1, 2, 3$) due to the swimmer and the Blakeslet dipole, respectively; $1/r$ is the

Figure 3-4: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 2.0$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-5: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 1.5$. In each panel, the values are scaled by the largest magnitude traction in that panel.

reciprocal of the three-dimensional distance from the point on the wall to the center of mass of the swimmer or multipole, which takes into account the decay of the Blakeslet velocity from the traction point to the swimmer; and S is the area of integration on the wall. $R = 0$ represents no correlation between the two tractions being compared while $R = -1$ and $R = +1$ represent perfect negative and

positive correlation, respectively. It is found that the correlation coefficient can be evaluated using S with linear dimension approximately one order of magnitude larger than h (details in Appendix B). Note that a correlation coefficient similar to Eq. (3.18) but without the $1/r$ factor yields similar results.

Figure 3-6: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.8$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-7: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.6$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-8: The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.4$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-9: (a) The instantaneous traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at $t = \pi/2$ when the (nondimensional) initial distance from the wall is $h = 0.2$. (b) The instantaneous traction exerted by individual spheres at $h = 0.2$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-10: (a) The traction plot in the x_1 direction (left) and in the x_2 direction (right) of a Blakeslet dipole when the only nonzero component of dipole strength is $f_2 d_2 = 1$. The dipole is placed at a (nondimensional) distance $h = 1$ from the wall. In each panel, the values are scaled by the largest magnitude traction in that panel. (b) Instantaneous traction correlation coefficient, which quantifies the correlation between the instantaneous traction due to the swimmer and a Stokeslet dipole with corresponding dipole strength $\sum_{\beta} \mathbf{f}^{\beta} \mathbf{d}^{\beta}$ at $t = \pi/2$ (solid line) and $t = 3\pi/2$ (dashed line).

As seen from Figure 3-10(b), the correlation coefficient in both directions approaches 1 as h passes 0.8 and becomes close to 1 at $h \approx 2$ ($R|_{t=\pi/2} = 0.91$ and $R|_{t=3\pi/2} = 0.93$ at $h = 2.0$). The same conclusion can be drawn by visually examining the traction pattern: For $h > 2$, the traction pattern (Figure 3-4) resembles that of a pure dipole with force and displacement in the x_2 direction [Figure 3-10(a)]. This traction results from the far-field superposition of the tractions from all three spheres. As the swimmer approaches the wall, the internal structure of the

swimmer becomes visible as individual contributions of the spheres become distinguishable and one can visually see that the traction becomes different from that of a pure dipole. This is shown from Figure 3-4 to Figure 3-9 for decreasing h : At $h = 1.5$ (Figure 3-5) the traction has visible distortion, at $h = 0.8$ (Figure 3-6) hints of the influence of sphere 2 appear as an additional positive peak at $x_2 \approx -0.75$, at $h = 0.6$ (Figure 3-7) the influence of sphere 2 causes an additional positive peak at $x_2 \approx -0.25$ in the x_1 component of traction, at $h = 0.4$ (Figure 3-8) the right lobe of the traction of sphere 2 (Figure 3-9, bottom middle panel) begins to be visible at $x_2 \approx 0.25$ in the x_2 component of traction and the left lobe is at $x_2 \approx -0.25$ in the x_1 component, and at $h = 0.2$ (Figure 3-9) the traction of all three spheres are clearly distinct.

In summary, because the dipole term is the first non-vanishing term of the multipole expansion, by calculating the correlation [Eq. (3.18)] or visually examining whether the traction resembles that of a pure dipole one can determine at what distance from the boundary the far-field multipole expansion treatment of images becomes an accurate representation of the effect of the boundary on swimming. Note that for a swimmer with complex geometry, if the traction can be observed (experimentally or numerically, see discussion), this avoids the need for a numerical model to calculate the exact boundary traction and opens the door to justify the use of simplified models of boundary effects. In that regard, however, one should keep in mind that higher-order terms (but perhaps not too many) of the multipole expansion may be necessary to accurately find the velocity, as can already be seen in the example of the three-sphere swimmer which have been investigated.

3.3.2 Time-Averaged Response

Section 3.3.1 has shown that traction patterns can be used to indicate when far-field approximations accurately represent boundary effects for instantaneous velocities. It has been suggested [66] that swimmers with a constant or time-averaged propulsion mechanism may have boundary effects that differ from those with time-varying strokes. This question is addressed here by examining whether the traction approach could be used to correlate time-averaged traction with time-averaged swimming velocities. To proceed, the image system method is utilized to calculate the exact time-averaged velocity of a swimmer as a function of distance from the wall. The angular brackets ($\langle \rangle$) is used to signify time averaging over one period of the swimming stroke.

Figure 3-11: (a) Semilog and (b) absolute log-log scale of the normalized time-averaged wall-induced velocity of a three-sphere swimmer in the x_2 direction $\langle u_2^*(\mathbf{x}^0) \rangle / \langle v^{0,\text{free}} \rangle$ (solid blue line) and a Stokeslet quadrupole model (dotted red line) versus the (nondimensional) initial distance from the wall.

Linear-log and absolute log-log plots of the x_2 component of the

normalized wall-induced average velocity of the swimmer ($\langle u_2^*(\mathbf{x}^0) \rangle / \langle v^{0,\text{free}} \rangle$) as a function of h are shown in Figure 3-11(a) and Figure 3-11(b) (solid blue lines), respectively. When $h > 16.8$, the swimmer is sped up by the wall. For $h < 16.8$, the swimmer is slowed down by the wall. The change in sign of the boundary effect around $h = 16.8$ manifests as the negative divergence of the logarithm in Figure 3-11(b).

At $h = 20$ (Figure 3-12), which is deep in the far field, the traction appears to be nearly the same as that produced by a pure quadrupole near a boundary [Figure 3-15(a)]. This is consistent with the fact that, due to the symmetry of the stroke, the time-averaged velocity field is quadrupolar, not dipolar [43]. Using this insight, the effect of the wall on the swimming velocity can be modeled by expressing it as the extra advection at the time-averaged CM location of the swimmer ($\bar{\mathbf{x}}^0$) due to the quadrupolar image system located at $\bar{\mathbf{x}}^{0*}$,

$$\langle u_i^*(\mathbf{x}^0) \rangle = \frac{1}{2} \sum_{\beta=1}^3 \partial_l \partial_k St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle f_j^\beta d_k^{\beta*} d_l^{\beta*} \rangle \quad (3.19)$$

where $\mathbf{d}^\beta = \mathbf{x}^\beta - \bar{\mathbf{x}}^{0*}$ is now defined as the image displacement vector from the time-averaged image CM to image sphere β , and the derivatives act on the second argument of $\mathbf{St}$. The last term in brackets is the quadrupole strength. For $h > 16.8$, the change in velocity due to the boundary predicted by this model (Figure 3-11, dotted red lines) agrees well with the actual wall-induced velocity (Figure 3-11, solid blue lines).

It is apparent that for $h < 16.8$, the quadrupolar model of Eq. (3.19) does not do well. In fact, the quadrupolar model always predicts an increase in swimming speed of the swimmer, while for $h < 16.8$, the swimming speed is decreased by the wall, so the quadrupolar model is qualitatively inaccurate. However, if one

examines the traction as h decreases, one finds that the traction pattern continues to resemble that of a pure quadrupole until $h \approx 5$ (Figure 3-13). The same traction correlation coefficient analysis defined in Eq. (3.18) is adopted here except using the time-averaged traction of the swimmer and the corresponding Blakeslet quadrupolar traction. As seen from Figure 3-15(b), it is only for $h \lesssim 2$ that the traction reveals signatures of the individual spheres, i.e., the internal structure of the swimmer in the near-field [e.g., Figure 3-14 at $h = 0.4$]. Thus, for

Figure 3-12: The time-averaged traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at the (nondimensional) initial distance from the wall $h = 20.0$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-13: The time-averaged traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at the (nondimensional) initial distance from the wall $h = 5.0$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-14: The time-averaged traction in the x_1 direction (left) and in the x_2 direction (right) exerted by a three-sphere swimmer at the (nondimensional) initial distance from the wall $h = 0.4$. In each panel, the values are scaled by the largest magnitude traction in that panel.

Figure 3-15: (a) The traction plot in the x_1 direction (left) and in the x_2 direction (right) of a Blakeslet quadrupole when the only nonzero component of quadrupole strength is $f_2 d_2 d_2 = 1$. The quadrupole is placed at a (nondimensional) distance $h = 1$ from the wall. In each panel, the values are scaled by the largest magnitude traction in that panel. (b) Traction correlation coefficient quantifying the correlation between the time-averaged traction due to the swimmer and a Stokeslet quadrupole with corresponding quadrupolar strength $\sum_{\beta} \mathbf{f}^{\beta} \mathbf{d}^{\beta} \mathbf{d}^{\beta}$.

time-averaged velocities, the traction does not seem to reflect the accuracy of a corresponding multipole model for the wall-induced velocity.

Why one must be careful in connecting time-averaged tractions to time-averaged swimming velocities is explained as follows. The wall-induced swimming velocity can be written as the average of the time-averaged wall-induced velocity over the three spheres:

$$\langle u_i^*(\mathbf{x}^0) \rangle = \frac{1}{3} \sum_{\alpha\beta} \langle St_{ij}(\mathbf{x}^\alpha, \mathbf{x}^{\beta*}) f_j^\beta \rangle. \quad (3.20)$$

In the far field, where $h \gg 1$, Eq. (3.20) can be expanded as follows:

$$\begin{aligned} \langle u_i^*(\mathbf{x}^0) \rangle = & \frac{1}{3} \sum_{\alpha\beta} St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle f_j^\beta \rangle + \partial_k^{(2)} St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle d_k^{\beta*} f_j^\beta \rangle \\ & + \partial_k^{(1)} St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle d_k^\alpha f_j^\beta \rangle + \frac{1}{2} \partial_k^{(1)} \partial_l^{(1)} St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle d_k^\alpha d_l^\alpha f_j^\beta \rangle \\ & + \partial_k^{(1)} \partial_l^{(2)} St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle d_k^\alpha d_l^{\beta*} f_j^\beta \rangle + \frac{1}{2} \partial_k^{(2)} \partial_l^{(2)} St_{ij}(\bar{\mathbf{x}}^0, \bar{\mathbf{x}}^{0*}) \langle d_k^{\beta*} d_l^{\beta*} f_j^\beta \rangle + \dots \end{aligned} \quad (3.21)$$

where $\mathbf{d}^{\beta*} = \mathbf{x}^{\beta*} - \bar{\mathbf{x}}^{0*}$, $\mathbf{d}^\alpha = \mathbf{x}^\alpha - \bar{\mathbf{x}}^0$, while $\partial^{(1)}$ and $\partial^{(2)}$ denote derivatives taken with respect to the first and second argument of $\mathbf{St}$, respectively. The last term in this expression gives the quadrupolar model. While the first and second term involve the total average force on the swimmer and the average dipole of the swimmer, respectively, and hence vanish, the averages in the third term do not vanish in general. These averages capture the correlation between the motion of the spheres and the hydrodynamic influence of one sphere on another, which are crucial to correctly determining average swimming speeds. On the other hand, the time-averaged traction is evaluated at a fixed point on the boundary [see Eq.(3.13)], hence cannot capture these correlations, and provides an inaccurate

picture of the contributions to the time-averaged wall-induced velocity. It is concluded that while the instantaneous traction is useful to understand when far-field models will be accurate representations for the effects of boundaries on instantaneous swimming speeds, one must be more careful about using time-averaged traction to make conclusions about time-averaged swimming speeds.

3.4 Discussion

In this chapter, the wall traction approach is adopted to determine when the far field multipole expansion and its image system are the good approximations of the wall effect on the three sphere swimmer. This work has some practical use since it demonstrates an independent way to find the limit of validity of the multipole representation for boundary effects. For numerical calculations, one can leverage our findings to determine whether the multipole representation of boundary effects is valid without having to do a full calculation of the boundary effects including near-field details, which was not possible in previous approaches [66]. The results in our approach suggest that simply analyzing the correlation between the velocity field for an unconfined swimmer and the corresponding multipole expansion is enough to make conclusions about the range of validity of using the multipole expansion for boundary effects. To test this, the velocity and stress fields due to an unbounded three-sphere swimmer on an imaginary plane parallel to the axis of the swimmer is analyzed here. Using a correlation coefficient similar to Eq. (3.18), but in the absence of a boundary, the author has determined how far away from the swimmer the stress or velocity

field of the swimmer is similarly to a multipole-like stress-velocity field. When the distance from the swimmer to the imaginary plane is more than $2L$, the unbounded swimmer behaves like a Stokeslet dipole (velocity: $R|_{t=\pi/2} = 0.97$ and $R|_{t=3\pi/2} = 0.97$; stress: $R|_{t=\pi/2} = 0.91$ and $R|_{t=3\pi/2} = 0.93$) (Figure 3-16). Therefore, even without calculating full boundary effects, one could diagnose whether to use images of a detailed discretization or of an image multipole to treat boundary effects accurately in a computation.

Experimentally, one could apply our results and test the correlation of the wall traction with that of a pure multipole by using traction force microscopy (TFM) [150] to directly measure the wall traction near a swimmer. In short, the forces on the boundary are quantified by the deformation of a thin layer ($\sim 20 \mu\text{m}$) of substrate on glass slides, and the strain on substrate is quantified through tracking the lateral displacement of nanoscale fiducial markers embedded in the substrate. TFM can measure the magnitude of the deformation down to tens of nanometers at submicrometer spatial resolution [151, 152] corresponding to nanonewtons of force. However, note that if the frequency of the swimming stroke is higher than or in the same order of the microscopy video frequency, TFM can only capture the time-averaged traction due to the microswimmer, resulting in qualitative conclusion of the wall traction approach. Experiments on traction measurement could be feasible for pelagic crustaceans with characteristic length up to several millimeters but would be technically challenging for microscale microswimmers. Following the observations made in the previous paragraph, an additional experimental way to apply our results is to measure velocity fields of freely swimming microorganisms away from boundaries via Particle Image Velocimetry (PIV) and compare those to pure

multipoles, which can be achieved for microorganisms as small as *Chlamydomonas* ($10 - 30 \mu\text{m}$) [39, 153]. The results would indicate whether models of wall effects on swimming behavior require detailed treatments of near-field hydrodynamics or could use simplified multipole representations.

Figure 3-16: (a) Velocity correlation coefficient and (b) stress correlation coefficient quantifying the correlation between the unbounded swimmer and a Stokeslet dipole at $t = \pi/2$ (solid lines) and $t = 3\pi/2$ (dashed lines).

3.5 Summary

The wall traction approach is proven to be an independent way to determine when the far field multipole expansion and its image system are valid to describe the effect of the boundary, or in contrast the inner structure of the microswimmer is important. The effect of a boundary on a three-sphere swimmer is investigated to exemplify the use of wall tractions for understanding boundary effects. For instantaneous swimming velocities, the boundary effect on the swimming velocity of the three-sphere swimmer is first calculated using the image system method, which allowed us to establish the limits of validity of a multipole representation of the boundary effects. It has been shown that the range of

validity of the multipole representation can be independently be diagnosed by comparing the wall traction to that of a pure multipole, either using a correlation coefficient or by visual inspection. When the wall traction is dissimilar to that of a pure multipole, the multipole representation is not valid and the inner structure of the swimmer is important for the swimmer-boundary interaction. However, it has been found that one should be cautious when using the time-averaged traction to draw conclusions about the validity of multipole approximations for boundary effects on time-averaged swimming speeds. Although the three-sphere swimmer is rather simple, it is a clear realization of a swimmer that, like many biological swimmers, has near-field velocity fields that differ considerably from a far-field multipole representation. Thus, it is expected that the insights gained can be applied to similar transitions in the validity of multipole expansions for more realistic swimmers compared to models that incorporate near-field details.

Chapter 4

Hydromechanical Reception of Marine Copepods: the role of mechanoreceptional seta³

4.1 Introduction

The success of marine copepods is highly dependent on their ability to adapt and respond to environmental cues [57, 154]. Previous investigation into how flow disturbances lead to setal deformation and sensing has taken two main approaches. The first approach is based on the arthropod filiform hair model [67-70] (refer to Section 2.6.3.2), which may not adequately describe the setal deformation of untethered copepods due to firstly, hydrodynamic signal sensed by a moving object differs from a stationary object [71], and secondly, the flow disturbances induced by planktonic preys such as ciliates and flagellates occur at low-frequencies [141] contrary to the assumptions in the arthropod filiform model. The second model is developed by Visser [40] (refer to Section 2.6.3.1) considers the Stokes flows due to nearby disturbances and postulates that the

³ This section has been submitted to X. Shen, Marcos and Henry C. Fu. "Hydromechanical reception of marine copepods: the role of mechanoreceptional seta" *Soft Matter*.

copepod detects the difference between the flow velocities at the body and the tip of the first antennule. However, such model neglects the effect of the presence of the copepod on the flow around the mechanoreceptional seta, and fails to address how this flow causes setal deformation in this low-Re regime.

The objective of this section is to develop such a model to provide insights to understand the fundamental characteristics of the copepod's mechanoreception under the prey-induced flow. The proposed model allows us to focus on the effect of the prey-induced flow on the mechanoreception of ambush-feeding copepods and provides the basis to develop more realistic models in the future. To address how the ambush-feeding copepod senses the prey in the low Reynolds number regime, a medium-sized copepod attacking a ciliated microorganism is considered as an example. First, the method of regularized Stokeslets (MRS) is used to solve for the flow profile along the distal seta caused by a swimming planktonic prey. The hydrodynamic effects of the copepod body and antennule on the flow is explicitly included, though how the seta itself alters the flow is neglected. Next, Resistive Force Theory (RFT) and Euler Beam Theory (EBT) are used to evaluate the setal deflection under the prey-induced flow oscillating at typical prey frequencies. It is found that the hydrodynamic effect of the body and antennule are required to accurately calculate the flow at the seta, that low frequency flow signals are more effective at bending the seta than high frequency signals, and that setal bending leading to mechanotransduction can occur on very short timescales due to transient and steady bending responses at low and high frequencies, respectively.

4.2 The Numerical Model

In our model, the first antennular pair of a calanoid copepod is simplified to two long rigid cylindrical substrates and the copepod body with other appendages and legs to an ellipsoid (Figure 4-1). The dimensions are chosen based on adult female *Acartia clausi* such that the cylindrical length $L^{\text{ant}} = 0.90$ mm, radius $R^{\text{ant}} = 10$ μm , ellipsoidal major axis length $L^{\text{maj}} = 1.00$ mm and minor axis length $L^{\text{min}} = 0.28$ mm (Refer to Appendix C for details). Note that the modeled copepod is a representative of typical calanoid copepods rather than targeting to any specific copepod species. The mechanoreception may involve the coordination [61, 155] of the four-point setal array at the proximal section of the first antennule [156] and the distal setae at the antennule tip [60]. To demonstrate the importance of the first antennule, the right distal seta is chosen to be the object of interest. The right distal seta is modeled as a thin filament of radius $R^{\text{seta}} = 1$ μm , length $L^{\text{seta}} = 200$ μm and Young's modulus $E = 10^6$ N m⁻² attached to the antennular tip and parallel to the major axis of the body (black line in Figure 4-1). The model intends to elucidate the physics underlying how hydrodynamic flow across the seta causes the setal deformation, and can be extended to evaluate the behaviors of any mechanoreceptional setae along the first antennule and their coordination in hydrodynamic reception [157].

In Table 2, the geometric parameters for a variety of planktonic preys are listed. Here the typical upper bounds of the hydrodynamic properties of planktonic preys are considered: diameter $d^{\text{prey}} \approx 50$ μm , swimming speed v^{prey} at $O(10^0)$ mm s⁻¹, frequency $f \approx 100$ Hz. The Reynolds number ($\text{Re} = v^{\text{prey}} d^{\text{prey}} / \nu$) and Strouhal number ($\text{Sr} = \omega d^{\text{prey}} / v^{\text{prey}}$) associated with swimming prey are

Figure 4-1: The orientation of the prey (filled black circle), specified by the distance d and angles θ and ϕ in the copepod's body-fixed frame. The x_2 axis is pointed into the paper. The copepod consists of a ellipsoid of major axis length L^{maj} and minor axis length L^{min} , a long cylindrical first antennular pair of length $2L^{\text{ant}}$ and radius R^{ant} and a right distal seta (black line) of length L^{seta} and radius R^{seta} . The prey swims at a velocity of $\mathbf{v}^{\text{prey}}$. The figure inset shows the ventral view of *Acartia clausi*, modified from <http://investigacion.izt.uam.mx/ocl/Zooplankton/?M=A> (accessed 16 Jun 2018).

$O(10^{-2})$ and $O(10^1)$, respectively. The detection of prey by copepod occurs at the length scale of the copepod's body, L^{maj} [62, 64, 158], much larger than the characteristic length of the prey. It is expected that varying details of the length scale and propulsion mechanism of the prey do not strongly affect our problem. Therefore, the far-field Stokeslet dipole model is useful to describe the hydrodynamic behavior of the self-propelled prey. The flow around a copepod due to a self-propelled prey obeys a dipolar decay [40, 158], scaled as $v^{\text{prey}}(d^{\text{prey}}/L^{\text{maj}})^2$. Thus, the Reynolds number ($\text{Re} = 2v^{\text{prey}}(d^{\text{prey}}/L^{\text{maj}})^2 R^{\text{seta}}/\nu$) and Strouhal number ($\text{Sr} = 2\omega R^{\text{seta}}/[v^{\text{prey}}(d^{\text{prey}}/L^{\text{maj}})^2]$) of the seta associated with the

prey-induced flow are $O(10^{-6})$ and $O(10^2)$, respectively. Therefore, quite conservatively, since $\text{Re} \ll 1$ and $\text{Re Sr} \ll 1$, the steady Stokes equation applies to the detection of prey for $f \leq 100$ Hz.

In order to be concrete while still using a representative geometry, a representative prey, *Metacylis* sp. swimming at $\mathbf{v}^{\text{prey}} = v^{\text{prey}} \hat{\mathbf{e}} = 0.78 \hat{\mathbf{e}}$ mm/s by wiggling the cilia at the back half of the body [62], is considered in this chapter. Here the *Metacylis* sp. is treated as a spherical particle of radius $r^{\text{prey}} = 25.25$ μm , and the swimming stroke is simplified to be an axisymmetric slip velocity $\mathbf{u}^s$ tangential to the surface of the spherical body in a squirmer-like model [66],

$$\mathbf{u}^s = u^{s,0} \sin(2\pi ft) \sqrt{(1 + \cos\xi)(\tilde{l} - \cos\xi)} \hat{\mathbf{t}}, \quad (3.22)$$

where $u^{s,0}$ is the constant slip speed to be determined such that the maximum swimming velocity is $\mathbf{v}^{\text{prey}}$; $\tilde{l} \in [-1, 1]$ defines the dimensionless active length; $\hat{\mathbf{t}}$ is the unit tangent vector on the spherical surface, which is a function of the zenith angle $\xi \in [0, \pi]$ and azimuthal angle $\eta \in [0, 2\pi]$. In our model, $\tilde{l} = 0$ indicates half of the body produces a slip velocity while the no-slip condition applies to the other half. In the analysis here, the origin of the copepod's body-fixed frame is set to be at the ellipsoidal center and prey's center coincide with the plane $x_2 = 0$. The parameters d , θ and ϕ are used to determine the orientation of the prey with respect to the copepod. The prey motion is restricted to the x_1 - x_3 plane for the ease of visualizing the flow patterns at the setae.

4.3 Flow Profile on the Seta

For the zero-Reynolds number Stokes regime, it is useful to apply the method of regularized Stokeslets [34, 35] to solve for the hydrodynamic flows induced by the prey in the vicinity of the copepod. Details of our implementation are presented in Appendix D, but briefly, the flow at a point $\mathbf{x}$ is obtained by superposing the flow produced by the discrete set of regularized Stokeslet solutions, which is expressed as

$$\begin{aligned} u_i(\mathbf{x}) &= u_i^{\text{prey}}(\mathbf{x}) + u_i^{\text{body}}(\mathbf{x}) + u_i^{\text{ant}}(\mathbf{x}) \\ &= \sum_{\alpha=1}^{N^{\text{prey}}} S_{ij}(\mathbf{x}, \mathbf{x}^\alpha, \varepsilon^{\text{prey}}) f_j^\alpha + \sum_{\beta=1}^{N^{\text{body}}} S_{ij}(\mathbf{x}, \mathbf{x}^\beta, \varepsilon^{\text{body}}) f_j^\beta, \\ &\quad + \sum_{\gamma=1}^{N^{\text{ant}}} S_{ij}(\mathbf{x}, \mathbf{x}^\gamma, \varepsilon^{\text{ant}}) f_j^\gamma \end{aligned} \quad (4.1)$$

where the superscripts prey, body and ant denote the contribution due to the prey, ellipsoidal body and first antennule of the copepod, respectively; the kernel $\mathbf{S}$ is defined in Eq. (D.1); $\mathbf{f}^\alpha$, $\mathbf{f}^\beta$, and $\mathbf{f}^\gamma$ represent the forces of regularized Stokeslets at the α -th, β -th, and γ -th collocation points of the prey, body, and antennule, respectively. The strengths of the $\mathbf{f}$ are determined from the boundary conditions and kinematic constraints on the copepod and prey (see Appendix C). On the other hand, in the absence of the copepod, the flow velocity at the point $\mathbf{x}$ due to the free swimming prey can be expressed as

$$u_i^{\text{prey,free}}(\mathbf{x}) = \sum_{\alpha=1}^{N^{\text{prey}}} S_{ij}(\mathbf{x}, \mathbf{x}^\alpha, \varepsilon^{\text{p}}) f_j^{\alpha,\text{free}}, \quad (4.2)$$

where $\mathbf{f}^{\alpha,\text{free}}$ represents the force distribution on the α -th collocation point of the unbounded prey.

Figure 4-2: The lateral flow profile $u_{\perp}$ along the copepod's distal setal axis x when the prey is at four different orientations with respect to the copepod (specified as d , θ and ϕ). $u_{\perp}$ is scaled with the dipolar velocity at the copepod's center $v^{\text{prey}}(r^{\text{prey}}/d)^2$. x is scaled with the setal length L^{seta} . The solid lines represent the lateral flow velocity. The black dashed, dash-dot and dotted line represent the lateral velocity components due to the prey, first antennule and ellipsoidal body of the copepod, respectively. The grey dashed line represents the lateral velocity components due to the free swimming prey. Note that dashed black and dashed grey lines overlap with each other. The figure insets show the corresponding lateral flow velocities up to 5 times L^{seta} .

The copepod's mechanoreception is mainly due to the bending caused by the lateral flow velocity in the direction perpendicular to the seta. This is because a very small bending of the seta is able to trigger the neurological and behavioral responses of the copepod. Therefore the lateral flow velocity at positions along the seta is calculated. Note that the regularized Stokeslets are not placed on the setae themselves; their hydrodynamic effects are neglected. Thus in the next section, the motion and deformation of the setae are caused by a background flow given by Eq.(4.1), but the setal motion itself does not change the flow. This assumption that the presence of the seta has negligible disturbance to the flow is analogous to the assumption made in the arthropod filiform hair model [67].

Figure 4-2 shows the lateral flow profile at the right distal setal position defined as $u_{\perp}(\mathbf{x}) = \hat{n}_i^{\text{seta}} u_i(\mathbf{x})$, where $\hat{\mathbf{n}}^{\text{seta}}$ is the unit vector perpendicular to the setal axis, i.e., in the x_1 direction. The distance d and the swimming direction of the prey ϕ vary while fixing the orientation angle $\theta = 0$ (see Figure 4-1). Note that θ and ϕ may induce asymmetric flow profiles on the two distal setae, which may allow the copepod to capture the directional information of the prey [40, 157]. The vertical axis represents the distance from the setal root to the point along the seta, $x = |\mathbf{x} - \mathbf{x}^{\text{root}}|$, normalized by the setal length L^{seta} . The horizontal axis shows $u_{\perp}$ normalized by the dipolar flow velocity at the copepod due to the swimming prey, $v^{\text{prey}}(r^{\text{prey}}/d)^2$. Strictly speaking, the presence of the copepod causes the lateral flow velocity contributed by the prey, $\mathbf{u}^{\text{prey}}(\mathbf{x})$, to be not precisely equal to $\mathbf{u}^{\text{prey,free}}(\mathbf{x})$, because the forces $\mathbf{f}^{\alpha}$ differ from $\mathbf{f}^{\alpha,\text{free}}$. However, when plotted in Figure 4-2, they are indiscernible (overlapping dashed black and dashed grey lines). On the other hand, the total lateral velocity

profile (solid lines) deviates strongly from the prey contribution, especially near the setal root. The velocity of the setal root is determined by the rigid-body motion of copepod body and antennule, and by the no-slip boundary condition the total fluid velocity must be equal to the setal root velocity. The fluid velocity contributions from the body and antennule add to the prey contribution to satisfy the boundary condition, and the overall lateral velocity profile on the seta is strongly affected by the force distributions on the first antennule (dash-dot lines), especially by those at the right distal section. This antennular effect decays away from the setal root. This is not surprising mainly due to two reasons: first, the distal section of the antennule is closer to where the seta is attached. Second, the distal section of the antennule, being furthest from the copepod center, usually experiences the largest velocity. In comparison, the ellipsoidal body has negligible effect on the flow across the seta, due to the larger distance to the seta and smaller magnitude of the force distribution (see the magnitudes of the dotted lines in Figure 4-2). Roughly speaking, the seta most easily senses flows that have a large difference in velocity between its tip and root. In general, it is observed that the velocity difference between tip and root increases as the length of the distal seta increases. It is also found that the presence of the antennule amplifies this velocity difference in most circumstances, as if the seta had a longer length.

Our findings are compared to the copepod mechanoreception model proposed by [40] and the strain rate approximation [72, 114] (refer to Section 2.6.3.1 for details of these two models). In Visser's model, the lateral flow across the seta is considered as due to the free swimming prey only, and since the copepod is not anchored in place, the seta is taken to sense the difference in

flow velocity between the antennular tip and head tip:

$$\Delta u_i^{\text{visser}} = u_i^{\text{prey,free}}(\mathbf{x}^t) - u_i^{\text{prey,free}}(\mathbf{x}^h), \quad (4.3)$$

where $\mathbf{x}^t = [0, 0, L^{\text{maj}}/2 + L^{\text{ant}} + R^{\text{ant}}]$ is at the tip of the antennular axis; the head tip $\mathbf{x}^h = [0, 0, L^{\text{maj}}/2 + R^{\text{ant}}]$. When the prey is far from the copepod, this difference can be approximated by the effective sensor length and strain rate $\epsilon^{\text{prey,free}}$ of the flow at the copepod's reference point $\mathbf{x}^0$:

$$\Delta u_i^{\text{strain}} = \epsilon_{ij}^{\text{prey,free}}(\mathbf{x}^0)(x_j^t - x_j^h). \quad (4.4)$$

These two approximations are examined to see if they are valid in our model, which takes into account hydrodynamic effects of the body and antennule. Note that our model directly evaluates the difference in the lateral flow velocity across the seta, $\Delta u_{\perp} = \hat{n}_i^{\text{seta}} [u_i(\mathbf{x}) - u_i(\mathbf{x}^{\text{root}})]$, where $\mathbf{x}^{\text{root}}$ is the coordinate of the setal root, while the other two approximate it as the difference in the flow on the antennule. To establish a fair comparison, the flow velocity component perpendicular to the sensor axis is considered here with the errors of the approximations as:

$$Er^{\text{visser}}(\%) = 100 \frac{|\Delta u_i^{\text{visser}} \hat{n}_i^{\text{ant}} - \Delta u_{\perp}|}{|\Delta u_{\perp}|}, \quad (4.5)$$

$$Er^{\text{strain}}(\%) = 100 \frac{|\Delta u_i^{\text{strain}} \hat{n}_i^{\text{ant}} - \Delta u_{\perp}|}{|\Delta u_{\perp}|}, \quad (4.6)$$

where $\hat{\mathbf{n}}^{\text{ant}}$ is the unit directional vector perpendicular to the antennular axis. Figure 4-3(a, b) show the total error evaluated using Visser's model for angular orientation of the prey at $d/L^{\text{maj}} = 0.9$ and 10.5, respectively. The error of Visser's model is not within a tolerable range ($>100\%$) in most prey orientations. The error of the far-field strain approximation at $d/L^{\text{maj}} = 10.5$ is evaluated

[Figure 4-3(c)]. The error of this method is similar to Visser's, but becomes even worse in some situations. Therefore, both methods are poor approximations of the flow velocity along the copepod's mechanoreceptional sensors. To determine the actual flow profile on the seta, one has to solve for the full hydrodynamics of the prey and copepod.

Figure 4-3: Total error of Visser's model at (a) $d/L^{\text{maj}} = 0.9$ and (b) $d/L^{\text{maj}} = 10.5$ and (c) the error of the far-field strain approximation $d/L^{\text{maj}} = 10.5$. The size of circles at each prey orientation is proportional to $\log_{10}(Er/100+1)$.

In the preceding section, the flow profile is calculated in the regime appropriate for copepods sensing prey, where $Re \ll 1$ and $Re Sr \ll 1$ so that the steady Stokes equation is valid. Our approach explicitly included the hydrodynamic effects of the copepod body and antennule, which is shown to have quite large effects on amplifying the flow over the mechanoreceptional seta. Previous approaches utilizing velocity difference approximations fail to estimate the flow profile with decent accuracy. In that regard, one should consider the full hydrodynamics including the swimming stroke of the prey and geometry of the copepod to determine the flow field around the distal seta in assessing the hydromechanical sensitivity of the copepod.

4.4 Deformation of the Seta

The arthropod filiform model mentioned earlier, which applies to high-frequency signals, addresses setal displacement by lumping the setal-antennular structure into a mass-spring-damper system [67-70], while Visser's hydromechanical reception model [40] does not explicitly treat setal deformation, instead postulating that the hydromechanical signal is related to the velocity difference at the antennule tip and the copepod body. Here the setal displacement due to an oscillatory flow caused by the prey is evaluated, considering signals within their natural frequency range. A seta which is initially straight at time $t = 0$ is considered here, which is disturbed by the prey's sinusoidally oscillating hydrodynamic signal for $t > 0$.

This section describes how the deformation of the seta is calculated. After obtaining the flow velocity distribution along the seta in the previous section,

RFT is used to find the forces on the seta due to hydrodynamic flow, then EBT is used to find the deformation due to those forces. Since the deformation angles of distal setae are less than 1° [73], only setal deformations and force distributions perpendicular to the setal axis are considered, which can be related to the lateral velocity difference between the seta and flow using

$$f_{\perp}(x, t) = \zeta_{\perp} [u_{\perp}(x, t) - v_{\perp}(x, t)], \quad (4.7)$$

where $\mathbf{f}_{\perp}$ is the instantaneous normal force per unit length exerted by the flow on the point of the setal axis $\mathbf{x}$, and $u_{\perp}$ and $v_{\perp}$ are the velocity component of the flow and seta perpendicular to the setal axis. For a cylindrical seta of length L^{seta} and radius R^{seta} , the normal drag coefficient is given by $\zeta_{\perp} = 4\pi\mu/[\ln(0.18L^{\text{seta}}/R^{\text{seta}}) + 0.5]$ [31]. Here a secondary coordinate system is set up such that the y axis is the setal deformation perpendicular to the setal axis represented by x and the origin is at the setal root. Utilizing EBT and neglecting inertial terms since the model is in the low Reynolds number regime [85, 159], the setal deformation can be described by [160]

$$A \frac{\partial^4 y(x, t)}{\partial x^4} = f_{\perp}(x, t), \quad (4.8)$$

where $A = EI$ is the rigidity of the seta [E is the Young's modulus, and $I = \pi(R^{\text{seta}})^4/4$ is the second moment of area]. Utilizing the no-slip condition at the setal root $u_{\perp}(0, t) = v_{\perp}(0, t)$, the velocity relation $\partial y/\partial t = v_{\perp}(x, t) - v_{\perp}(0, t)$, and substituting Eq. (4.7) into Eq. (4.8), the governing equation becomes

$$A \frac{\partial^4 y(x, t)}{\partial x^4} + \zeta_{\perp} \frac{\partial y(x, t)}{\partial t} = \zeta_{\perp} \Delta u_{\perp}(x, t), \quad (4.9)$$

where $\Delta u_{\perp}(x, t) = u_{\perp}(x, t) - u_{\perp}(0, t)$. Observations show that the seta is fixed and hardly deflects at the root (clamped boundary conditions) and while it is free at

the tip [118], and there is no deflection at $t = 0$. Thus the initial and boundary conditions are specified as

$$y(x, t = 0) = 0, \quad (4.10)$$

$$y|_{x=0} = \frac{\partial y}{\partial x}|_{x=0} = \frac{\partial^2 y}{\partial x^2}|_{x=L^{\text{seta}}} = \frac{\partial^3 y}{\partial x^3}|_{x=L^{\text{seta}}} = 0. \quad (4.11)$$

Eq. (4.9) is solved numerically by using the finite difference method. A convergence test performed on the seta of $L^{\text{seta}} = 0.2$ mm shows that 1000 uniformly distributed nodes in the space domain ($\Delta x = L^{\text{seta}}/1000$) and 500 uniformly distributed grids per cycle in the time domain [$\Delta t = 1/(500f)$] are sufficient to obtain a convergent setal shape.

To evaluate the time-dependent setal response, it is assumed that although the prey is moving and swimming, it does not change in position relative to the copepod appreciably during the time of interest since the timescale of the copepod's response in capturing the prey is very small. This allows us to focus on the frequency response of the seta while eliminating the effect of a time-dependent prey trajectory on the setal sensitivity.

The above assumption is also consistent with experiments in which a vibrating sphere oscillates at a fixed location [60, 142]. In the calculations here, the time-averaged power dissipated by the oscillating prey is kept as a constant, in contrast to experiments with oscillating spheres which keep the oscillation amplitude fixed [60, 115, 142]. The power dissipated by the prey is proportional to $[f \int_0^{1/f} \zeta^{\text{prey}} \mathbf{v}^{\text{prey}} \cdot \mathbf{v}^{\text{prey}} dt]$, where ζ^{prey} is the drag force coefficient of the prey. Note that the condition of constant power is equivalent to constant amplitude of

velocity (rather than displacement) oscillations, and so as when the frequency is changed, $u^{s,0}$ in Eq. (3.22) stays constant.

To quantify the setal deformation, the magnitudes of the terms in Eq. (4.9) are estimated by assuming the typical length scale of the seta is L^{seta} , the typical magnitude of setal displacement Y , the typical timescale of the setal deformation to be the timescale of the oscillatory flow $1/\omega$, the typical strain rate at the copepod's reference point $v^{\text{prey}}(r^{\text{prey}})^2/d^3$ and the corresponding typical scale of the velocity difference across the distal seta is $v^{\text{prey}}(r^{\text{prey}})^2 L^{\text{seta}}/d^3$. Therefore, the first term of Eq. (4.9) is scaled as $AY/(L^{\text{seta}})^4$, which represents the elastic forcing; the second term is scaled as $\zeta_{\perp}\omega Y$, representing the viscous forcing due to the setal displacement; the last term is scaled as $\zeta_{\perp} v^{\text{prey}}(r^{\text{prey}})^2 L^{\text{seta}}/d^3$, which representing the viscous forcing of the moving fluid. Taking the ratio of the viscous forcing and elastic forcing, $\text{Sp}^4 \equiv (L^{\text{seta}})^4 \zeta_{\perp} \omega / A$ is obtained, where Sp is known as the sperm number which quantifies the relative importance of the viscous force to elastic force, or the elastic timescale to viscous timescale. When $\text{Sp} \rightarrow 0$, the elastic term $A\partial^4 y/\partial x^4$ dominates the setal response, which is independent of the oscillation frequency of the prey. On the other hand, in the viscous limit $\text{Sp} \rightarrow \infty$, the setal response is dominated by the viscous term $\zeta_{\perp}\partial y/\partial t$, and thus the magnitude of the setal displacement decays with increasing ω for the fixed power dissipation.

As a demonstration, the deformation of the right distal seta is compared when the prey is fixed at $d/L^{\text{maj}} = 0.9$, $\theta = 0$ and $\phi = \pi/6$ and oscillating at two

Figure 4-4: Shape of the distal seta normalized with $L^{\text{seta}} = 0.20$ mm when the prey oscillates at (a) $f = 0.1$ Hz and (b) $f = 100$ Hz. The time sequence over at the first cycle of oscillation is given by number 1 to 8. At (c)(e) $f = 0.1$ Hz and (d)(f) $f = 100$ Hz, the instantaneous curvature of the right distal setal root $\kappa(0, t)$ and its transient and steady-state response components are over the time t . The solid lines represent the instantaneous setal root curvature, the dashed lines the steady-state curvature component, the dash-dot lines the transient curvature component. The dotted lines are sine waves representing the swimming velocity of the oscillatory prey.

distinct frequencies. When the prey oscillates at $f = 0.1$ Hz, the instantaneous shape of the right distal seta with $L^{\text{seta}} = 0.2$ mm (corresponding to $Sp = 1.4$) at selected time frames over the first cycle of oscillation of the prey is shown in Figure 4-4(a). Under such a low frequency sinusoidal wave induced by the prey, the seta is able to bend in response to the oscillatory flow. In comparison, when the oscillation frequency increases to 100 Hz (corresponding to $Sp = 7.9$), the setal response is dominated by the viscous term, and thus a notable phase lag between the flow and setal response is observed from the deformation pattern in Figure 4-4(b). In addition, the magnitude of setal deformation is smaller at the higher frequency [note horizontal scale change between Figure 4-4(a) and Figure 4-4(b)].

The fact that lower frequency signals lead to larger setal bending is opposite to the conclusions reached by Lenz and Hartline [73]. The difference stems from the fact that when the signal frequency is changed, the amplitude of prey oscillation decreases to keep the power constant. In comparison, Lenz and Hartline [73] assumes a vibrating source oscillating at a fixed *displacement* amplitude, which dissipates a time-averaged power that scales as the square of frequency. The author believes it is less realistic to imagine that prey would drastically increase power expended if they varied the frequency of their swimming stroke. Note that the condition of constant power is also equivalent to constant amplitude of velocity (rather than displacement) oscillations. Setal hydromechanical reception acts as a low-pass, not high-pass, filter for signals of constant velocity amplitude. Note that our low-pass filter conclusion does not violate the experimental findings in earlier experiments [60, 115, 142]. Those experiments placed an oscillating sphere of radius $r \simeq 1.5$ mm near a grasped

copepod (first antennule) and recorded its behavioral (neurological) response at frequencies ranging from 50 to 2000 Hz, which leads to $Re\ Sr \gg 1$, beyond the range of validity of our model. Therefore, the proposed model suggests that more experiments should be conducted to quantify the sensitivity of the copepod and validate our model within the physiological range of the flow induced by planktonic preys.

Here whether the mechanotransduction will occur on the copepod's seta due to the predicted complicated setal deformation patterns is quantified [for example, time sequence No. 6 in Figure 4-4(b)]. Bending of the seta is transduced to the neurophysiological signals through the deformation of the dendrites. These dendrites are firmly attached to the cuticle of the seta at the distal region [54, 121, 161-163]. The mechanotransduction is likely to occur through the opening of the stretch-sensitive ion channels populated in the dendrites [164, 165], which is associated with the curvature of the distal seta. Here the curvature of the instantaneous setal shape defined as

$$\kappa(x, t) = \frac{\partial^2 y(x, t)}{\partial x^2} \quad (4.12)$$

is used to quantify the setal deformation. The deformation of the right distal seta is evaluated when the prey is located at $d = 1.0, 1.5, 2.0$ mm and $\theta = 0$ and $|\mathbf{x}^{0, \text{prey}} - \mathbf{x}^{\text{root}}| = 1.0, 1.5, 2.0$ mm and $\psi = n\pi/18$ ($n = 0, 1, \dots, 14$) where ψ measures the angle of the vector $\mathbf{x}^{0, \text{prey}} - \mathbf{x}^{\text{root}}$ from the antennular axis. For all the cases being tested, the maximum magnitudes of the setal curvature over the first cycle of oscillation occur at the setal root $x = 0$. Note that in general, it is found that the curvature of the seta is not well-correlated with the angular displacement of the setal tip. For example, it is found that when the prey is

fixed at $d = 0.9$ mm, $\theta = 0$ and $\phi = \pi/6$, the angular displacement of the setal tip is correlated with curvature of the seta at $Sp < 2.7$ with a 95% confidence interval, corresponding to $f < 1.4$ Hz for the distal seta considered in this model. On the other hand, for $Sp > 2.7$, [$f > 1.4$ Hz, Figure 4-4(b)], the motion of the tip is decoupled from the direction of bending and curvature at the root. Therefore one should take care in assuming that tip displacement directly implies mechanotransduction, such as in Ref. [56, 60, 73, 118, 163]. Below, rather than the tip displacement, the focus of the model is the time-dependent curvature at the setal root.

The instantaneous curvature at the setal root, $\kappa(0,t)$, is analyzed for the first few cycle of the prey oscillation. The solid lines in Figure 4-4(c) and Figure 4-4(d) show $\kappa(0,t)$ as a function of time t for the 0.1 and 100 Hz signals, respectively. For the condition of constant velocity amplitude oscillation of the prey, the magnitude of the setal root curvature decreases as the sperm number gets larger. The dotted lines in Figure 4-4(c) and Figure 4-4(d) show the instantaneous speed of the prey particle; the curvature displays a slight lag relative to the hydrodynamic signal. Consequently in both Figure 4-4(c) and Figure 4-4(d) the maximum curvature of the setal root always occurs slightly after the first quarter cycle of oscillation.

These results can be explained by analyzing the time-dependent response of this first-order system [Eq. (4.9)] in terms of a transient response (homogeneous solution to the differential equation) and a steadily-oscillating response (particular solution). the transient (dash-dot lines) and steady (dashed lines) components of the responses of $\kappa(0,t)$ are shown for $f = 0.1$ Hz [Figure 4-4(e)] and 100 Hz [Figure 4-4(f)]. The steady curvature response follows a

Figure 4-5: The log-log plot of the normalized minimum oscillation amplitude of the prey which triggers the detection threshold of the seta $v^{\text{prey,min}}/v^{\text{prey,0}}$ as a function of the oscillation frequency f , where $v^{\text{prey,0}}$ is the value of $v^{\text{prey,min}}$ for the 200 μm seta to hit the detection threshold. The solid black line represent the 200 μm seta, the dashed black line the 100 μm seta, and the dash-dot line the 50 μm seta.

sinusoidal wave with a phase shift with respect to the sine wave input signal [dotted lines in Figure 4-4(c,d)]. The transient response decays exponentially over time, the timescale of which is characterized by $\zeta_{\perp} (L^{\text{seta}})^4/A$ [drawn from the homogeneous part of Eq. (4.9)], independent of oscillation frequency f . Thus, the transient response at high frequency range dies out much slower than the period of the signal [dash-dot lines in Figure 4-4(e,f)]. The linear superposition of the transient and steady components gives the largest magnitude of the curvature response before the first time that the steady response reaches its extreme, within the first cycle of prey oscillation.

It has been suggested that long setae might be responsible for detecting low frequency signals and short setae for high frequency signals, since long setae require longer time to respond to a stimulus than short ones [126]. Therefore,

the dependence of root curvature on setal length is examined. It is assumed that the root curvature detection threshold κ^{thr} which triggers the copepod's response is independent of the setal morphology and frequency. The constant power constraint imposed on the prey is then released in order to determine the minimum amplitude of oscillation, $v^{\text{prey,min}}$, required for the seta to reach the detection threshold κ^{thr} at the natural frequency range. Figure 4-5 shows the ratio $v^{\text{prey,min}}/v^{\text{prey,0}}$ as a function of the oscillation frequency f for the distal setae of length $L^{\text{seta}} = 50, 100, \text{ and } 200 \text{ }\mu\text{m}$, where $v^{\text{prey,0}}$ is the value of $v^{\text{prey,min}}$ for the $200 \text{ }\mu\text{m}$ seta to hit the detection threshold at $f = 0 \text{ Hz}$. At low frequency ranges $f \lesssim 2 \text{ Hz}$, the longest seta ($L^{\text{seta}} = 200 \text{ }\mu\text{m}$) requires the least $v^{\text{prey,min}}/v^{\text{prey,0}}$ to trigger its mechanotransduction [solid line in Figure 4-5]. At high frequency range ($f \gtrsim 50 \text{ Hz}$), although the difference in flow velocity across the short seta is less than that on the long seta, the shortest seta ($L^{\text{seta}} = 50 \text{ }\mu\text{m}$) requires the smallest $v^{\text{prey,min}}$ [dash-dot line in Figure 4-5], indicating short setae might be responsible for sensing time-variant swimming stroke and high-frequency trajectory signals while long setae sense time-invariant low-frequency signals. The first antennule of the copepod usually is equipped with long setae at the distal section and short setae at the middle and proximal sections. Although the flow profiles along the setae are not exactly the same, the coordination of setae of different morphologies may allow the copepod to maintain its sensitivity to a wide range of signals.

The time taken for a seta to start mechanotransduction is also investigated. The “response time” t^{r} is defined as the time taken from the start of the oscillation of the prey ($t = 0$) to when the setal root curvature hits the detection threshold. Figure 4-6(a) shows how the response time of a $200 \text{ }\mu\text{m}$ seta varies as

Figure 4-6: [color online] (a) Semi-log plot of the response time t^r of the 200 μm distal seta as a function of the sperm number Sp (via varying frequency). The black, red and blue solid lines correspond to t^r at constant oscillation speed of the prey denoted as $v^{\text{prey}}/v^{\text{prey},0} = 2, 10$ and 100 , respectively. (b,c) Log-log plot of t^r of the 200 μm distal seta (solid lines) as a function of v^{prey} normalized with the minimum velocity which triggers the detection threshold of the seta $v^{\text{prey}}/v^{\text{prey},\min}$ at $Sp = 0, 2$ and 5 , respectively. In all panels, the blue dashed and dash-dot lines represent $t^r = 1/(4f)$ and $t^r = 1/(2f)$, respectively; the green dashed line represents $t^r = 1/(2\pi f v^{\text{prey}}/v^{\text{prey},\min})$; the red dashed and dash-dot lines represent $t^r = [\tau/(\pi f v^{\text{prey}}/v^{\text{prey},\min})]^{1/2}$ and $t^r = 1/[\pi f (v^{\text{prey}}/v^{\text{prey},\min})^{1/2}]$, respectively.

the frequency of the signal is changed [via $Sp = L^{\text{seta}}(2\pi f \zeta_{\perp}/A)^{1/4}$] while keeping constant the time-averaged power dissipation. Since the response time is always within the first period, it tends to decrease as the frequency increases. Each curve terminates because as the frequency increases, $v^{\text{prey},\min}$ grows and eventually exceeds v^{prey} , so the detection threshold is not met. Figure 4-6(b, c)

show how the response time varies as the signal strength ratio $v^{\text{prey}}/v^{\text{prey,min}}$ changes for various constant Spm number (i.e. constant frequency). At both low and high Sp, for low signal strengths t^f is constant since around the threshold strength t^f occurs at either a quarter period or half period, respectively (see Figure 4-4). At higher signal strengths, t^f decreases since as signal strength increases, the threshold curvature is induced earlier and earlier in the first period.

The qualitative behavior of the response time as a function of signal strength and Sp (i.e., frequency) can be understood using a simple one-degree-of-freedom (1D) model of the curvature response at the setal root $\kappa(0, t)$ if it is postulated to obey the dynamic equation:

$$\kappa + \tau \partial_t \kappa = \mathcal{F} \sin(\omega t) \quad (4.13)$$

in which τ is a transient time corresponding to $\zeta_{\perp} (L^{\text{seta}})^4/A$ in the full model, and $\mathcal{F}$ is the magnitude of a driving force corresponding to the strength of the prey signal in the full model. Note that the quantity $\omega\tau = \zeta_{\perp} \omega (L^{\text{seta}})^4/A$ corresponds to Sp^4 in the full model, so the results below is expressed in terms of $\text{Sp}^4 = \omega\tau$ bring out the correspondence to the full model.

The solution to the 1D model is

$$\kappa = \frac{\mathcal{F}}{\sqrt{1 + \text{Sp}^8}} \left[\sin(\omega t - \chi) + e^{-t/\tau} \sin \chi \right], \quad (4.14)$$

where $\chi = \tan^{-1}(\text{Sp}^4)$. The first term in the braces is the steady (oscillating) part of the solution, and the second term is the transient. Figure 4-7 shows the full solution as well as steady and transient pieces in the limits of large and small Sp. This solution is used to analyze the response time, which is the time it

takes for $\kappa(0,t)$ to reach the threshold value κ^{thr} .

First consider when the signal strength is just enough to trigger the response within the first period, i.e., at $\mathcal{F} = \mathcal{F}^{\text{thr}}$. This occurs if κ^{thr} is at the maxima indicated in the blue dotted lines at the bottom panels of Figure 4-7. From the time of the maxima and Eq. (4.14), one can see that for $\text{Sp} \ll 1$, $\chi \approx 0$, $\omega t^r \approx \pi/2$, and $\kappa^{\text{thr}} \approx \mathcal{F}^{\text{thr}} / \sqrt{1 + \text{Sp}^8}$; while for $\text{Sp} \gg 1$, $\chi \approx \pi/2$, $\omega t^r \approx \pi$, and $\kappa^{\text{thr}} \approx 2\mathcal{F}^{\text{thr}} / \sqrt{1 + \text{Sp}^8}$. Therefore, as observed for the full model of the seta, near the threshold signal, the response time is approximately $1/(4f)$ or $1/(2f)$ for $\text{Sp} \ll 1$ or $\text{Sp} \gg 1$, respectively.

Now consider what happens if the signal strength is large, $\mathcal{F} / \mathcal{F}^{\text{thr}} \gg 1$. For $\text{Sp} \ll 1$, t^r can be obtained by solving

$$\frac{\kappa}{\kappa^{\text{thr}}} = \frac{\mathcal{F}}{\mathcal{F}^{\text{thr}}} \left[\sin(\omega t^r - \chi) + e^{-\omega t^r / \text{Sp}^4} \sin \chi \right] = 1. \quad (4.15)$$

For small t^r , Eq. (4.15) is solved by expanding to first order in ωt^r . There are two possible scenarios. First, ωt^r , while small, could be still be large enough such that $\omega t^r / \text{Sp}^4$ is still large. This corresponds to $t^r \gg \tau$, i.e., the response time is greater than the transient time [indicated by the green dashed lines in Figure 4-7(a)]. Then the second term in the braces is set to zero, and expand only the first term in ωt^r . Using $\sin \chi = \text{Sp}^4 / \sqrt{1 + \text{Sp}^8}$ and $\cos \chi = 1 / \sqrt{1 + \text{Sp}^8}$, $t^r = \mathcal{F}^{\text{thr}} / (\mathcal{F}\omega)$ is obtained. As the signal strength further increases, t^r continues to decrease and eventually $\omega t^r / \text{Sp}^4 \ll 1$, i.e., the response time is smaller than the transient time [indicated by the red dashed lines in Figure 4-7(a)]. In this

Figure 4-7: The curvature responses of the setal root in the simplified 1D model $\kappa(0, t)$ are plotted against the time t for (a) $Sp = 0.7$ and (b) $Sp = 5.0$. The solid, dashed and dash-dotted lines represents the solution of this 1D model, transient and steady-state pieces, respectively. The blue lines represent the cases that the maximum magnitude of driving force $\mathcal{F}$ equals to $\mathcal{F}^{\text{thr}}$, so the maximum magnitude of the setal root curvature in this 1D model hits the prey-detection threshold κ^{thr} . The green dashed lines in (a) represents the case that $\mathcal{F} \gg \mathcal{F}^{\text{thr}}$ and $\omega t^r / Sp^4 \gg 1$ such that the setal response happens close to 0 but after the transient response dies out. In contrast, the red lines represent the case that $\mathcal{F} \gg \mathcal{F}^{\text{thr}}$ and $\omega t^r / Sp^4 \ll 1$, so the setal root curvature needs much shorter time to reach κ^{thr} . The time taken for the setal root curvature to reach κ^{thr} is denoted as t^r .

regime, expanding both terms in the braces, $t^r = \sqrt{2\mathcal{F}^{\text{thr}}\tau / (\mathcal{F}\omega)}$ is obtained to lowest order in Sp^4 . Based on these two scenarios, since $\mathcal{F}/\mathcal{F}_{\text{thr}}$ corresponds to $v^{\text{prey}}/v^{\text{prey,min}}$, as $v^{\text{prey}}/v^{\text{prey,min}}$ increases, it is expected first a regime where the response time scales as $1/f$ and $1/v^{\text{prey}}$, then at the highest signal strengths a regime where the response time scales as $(f)^{-1/2}$ and $(v^{\text{prey}})^{-1/2}$.

On the other hand, for $Sp \gg 1$ [indicated by the red dash-dot lines in Figure 4-7(b)], t^r can be obtained by solving

$$\frac{\kappa}{\kappa^{\text{thr}}} = \frac{\mathcal{F}}{2\mathcal{F}^{\text{thr}}} \left[\sin(\omega t^r - \chi) + e^{-\omega t^r / Sp^4} \sin \chi \right] = 1. \quad (4.16)$$

In this limit, $\omega t^r / Sp^4 \ll 1$ is always satisfied, thus the response time is obtained by expanding both terms in the braces in ωt^r , yielding $t^r = \sqrt{\mathcal{F}_{\text{thr}} / \mathcal{F}} (2/\omega)$ to lowest order in $1/Sp^4$. Therefore, for $v^{\text{prey}}/v^{\text{prey,min}} \gg 1$ and $Sp \gg 1$, the response time scales as $1/f$ and $(v^{\text{prey}})^{-1/2}$.

The slopes of the scalings derived from the 1D model for the response time are plotted in Figure 4-6(b, c) and agree well with the results of the full model, except for the large v^{prey} limit $t^r = \sqrt{\mathcal{F}_{\text{thr}} / \mathcal{F}} (2/\omega)$ at $Sp = 7.9$ where a mismatch in the slopes of the solid and dash-dot lines is visible in Figure 4-6(c). It has been verified that at sufficiently large Sp , the slopes of these two match; however, the plot is not shown since the assumptions that $f \leq 100$ Hz and $Re \, Sr \ll 1$ break down at such high frequencies given actual setal dimensions. Thus the five regimes of the response time predicted by the 1D model qualitatively explain the observed response time of setae. The transient time figures prominently in delineating the two regimes of scaling at large signal strength and low Sperm number as well as the scaling for very large signal strength. In addition, note that a model with $\tau = 0$ is not adequate to explain even the threshold response time for small Sp . Hence incorporating the physics of the transient solution is the key to understanding the response of setae.

As a summary of the response time, when subjected to large signal strength, the setal response time can never be below the minimum timescale set

by transient response at small Sp and by the steady response at large Sp ; when signal strength approaching the copepod detection threshold, the response time is capped by the time taken for curvature response to reach its first peak. In either limit, mechanotransduction due to the opening of the ion channels is likely to occur within the first half cycle of oscillation and therefore the prey can be detected in a short time range. Our results contrast with the arthropod filiform hair model, which predicts that the maximum setal displacement is achieved only after a few cycles after the background flow starts to oscillate, which is inconsistent with the rapid neurological and behavioral responses observed in copepods. Therefore, at least in the Stokes limit, our model explains how a copepod is capable of responding to the external stimuli with a very short time lag.

4.5 Summary

In this chapter, a mechanical model in the Stokes regime is developed to evaluate the flow induced by the planktonic crustaceans on the deformation of the distal seta. The hydrodynamic effect of the ambush-feed copepod on the flow is explicitly included while neglecting the presence of the seta. The findings of the proposed model show that the antennule pair, especially the section where the seta is attached, has non-negligible contributions on the lateral flow profile along the seta. Therefore, the effect of the copepod itself on prey-induced flows causing setal bending and sensing should not be ignored.

Secondly, the maximum curvature of the seta, which is most likely to occur at the setal root, is utilized to predict whether the mechanotransduction

will be triggered. For large sperm numbers, the setal tip displacement may not be well-correlated with the setal root curvature. The setal response when the prey is oscillating at two distinct frequencies while maintaining the same power dissipation and are compared, which concluded that the setal root curvature is larger for smaller frequencies. Thus, the setal hydromechanical reception acts as a low-pass filter for signals of constant velocity amplitude. This work has some biological importance as it predicts which signal is most crucial in prey-copepod detection. The Fourier decomposition has been used to analyze the frequency spectrum of the hydrodynamic disturbances induced by smooth swimming planktonic crustaceans (data not shown here) and found two main signals emitted by the plankton: a dominant zero frequency signal due to its forward motion and minor high frequency signals due to the swimming stroke (e.g. flagellum beating and cilia wiggling). The seta characterized by a low-pass filter captures the main flow disturbance induced by the swimming prey.

Finally, the effects of the setal length, velocity amplitude and frequency of the prey on copepod-prey detection have been investigated. It is concluded that the long setae are responsible for detecting the threshold signal at low frequencies, and short setae at high frequencies, which is consistent with the previous predictions. The coordination of the setae of various morphologies may allow the copepod to maintain its sensitivity to both smooth swimming and fast jumping preys. A simplified 1D model has also used to qualitatively estimate the response time of the seta, which ranges from a short time approaching zero (subject to large signal) to the first half oscillation period of the prey (subject to threshold signal). In contrast to the previous arthropod filiform model, the proposed model is valid in the steady Stokes regime and explains why the

copepod response to the external stimuli rapidly. This model is particularly useful in predicting the setal deformation of the ambush-feeding copepod subjected to a small-scale source.

Chapter 5

Conclusion and Future Work

5.1 Conclusion

The main objectives of this research are to investigate the boundary effects on swimming microorganisms and the characteristics of the mechanoreceptional sensor of a copepod in detecting a swimming prey. This study contributes to our understanding of the engineered structures of microorganisms in a confined space and the strategies of stealthy swimming and detection in the low Reynolds number regime, which is beneficial to bio-inspired micro-robotics. To sum up, the major contributions made during this study are as follows:

a) Providing an independent way to validate when the far-field multipole expansion and its images can be used to represent the boundary effect

For instantaneous swimming velocities, the boundary effect on the swimming velocity of the microswimmer is first calculated using the image system. This is then compared with that obtained from the image system of the multipole representation to determine the range of validity of the multipole model. As the alternative, the range of validity can be diagnosed by comparing the spatial pattern of traction on the wall induced by the microswimmer with that by pure multipole, either using a correlation coefficient or by visual inspection. The range of validity obtained from the

two methods is found to be identical, indicating that the wall traction approach provides an independently way to validate when the multipole model is valid, or in contrast the inner structure of the swimmer is important for the hydrodynamic interaction with the boundary. However, for non-constant propulsion, it is found that the correlations between swimming stroke motions and internal positions are important and not captured by time-averaged traction on the wall. Thus, one should be cautious when using the time-averaged traction to draw conclusions about the validity of multipole approximations for boundary effects on time-averaged swimming speeds.

b) Revealing the mechanoreceptional seta of the marine copepod serves as a low pass velocity difference filter

A model is developed to quantify the flow velocity perpendicular to the distal seta and the setal deflection when the copepod is exposed to the flow field induced by an oscillatory prey. The model shows that at the natural frequency range experienced by the copepod, the lateral flow velocity is a function of the geometry of the copepod and the orientation and swimming velocity of the prey. The lateral flow at the base of the seta is non-zero in most circumstances. It is inappropriate to use the flow velocity induced by the prey only to approximate the flow velocity on the seta as the contribution from the antennule of the copepod cannot be neglected. The maximum curvature of the seta is always achieved within the first cycle of oscillation of the external stimuli. At low frequencies, the setal response is dominated by the elastic force, which shows large curvature and low phase lag. As the frequency gets higher, the viscous force takes over the dominance, which

leads to a small curvature and a long phase lag of the setal response. The model concludes that the mechanoreceptional seta of marine copepod is a low pass velocity difference filter from the physical perspective and explains the rapid mechanotransduction when responding to the stimulus.

5.2 Future Work

The future work of this study could be:

(a) Improving the ambushing-feeding copepod mechanoreception model

The current copepod mechanoreception model addresses the characteristics of the setal response under the prey-induced flow, while exhibits a few limitations. Firstly, this model assumes the densities of the copepod and surrounding fluid are the same. However, in reality, the copepod is slightly heavier than the fluid, and hence it slowly sinks during the ambush feeding. This causes the initial condition of the distal seta deviates from Eq. (4.10). Secondly, the existing model may not be accurate as it first evaluates the flow field on the “virtual” seta, which is then utilized to determine the setal deflection. The future work could implement Kirchhoff rod theory [166] together with the BEM to solve for the flow field on the seta and the setal deflection simultaneously while taking the density of the copepod into consideration. It is also recommended to explore whether the nerve impulse required to elicit the copepod’s physiological response is frequency-dependent.

(b) Developing a new theoretical framework to address how the copepod

attracts and detects the prey when generating a feeding current

Only a portion of copepods utilizes the ambush feeding strategy to detect and capture the swimming preys. In reality, other copepods actively search for the prey by generating a feeding current, which is achieved by the periodic motion of its second antennule, first maxillae and the maxillipeds or combinations [58, 167, 168]. In such case, the preys are attracted to the head tip of the copepod. Qualitative research is proven that the flow velocity differences across the distal seta are different with and without the prey, which are distinguished by the copepod to detect the presence of the prey [40]. In the future, a theoretical model could be developed to address the detailed motion of the appendages and to quantify how the deflection of the distal seta changes as the prey is gradually attracted by the feeding current.

Publications

1. J. B. Y. Koh, **X. Shen** and Marcos. "Theoretical modeling in microscale locomotion." *Microfluid. Nanofluid.*, vol. 20, pp. 1-27, 2016.
2. **X. Shen**, Marcos and H. C. Fu. "Traction reveals mechanisms of wall effects for microswimmers near boundaries." *Phys. Rev. E*, vol. 95, p. 033105, 2017.
3. T. F. Kong⁴, **X. Shen**⁴, Marcos, and C. Yang. "Lab-on-chip microfluidic impedance measurement for laminar flow ratio sensing and differential conductivity difference detection." *Appl. Phys. Lett.*, vol. 110, p. 233501, 2017.
4. J. B. Y. Koh, **X. Shen** and Marcos. "Supervised learning to predict sperm sorting by magnetophoresis." *Magnetochemistry.*, vol. 4, p. 31, 2018
5. **X. Shen**, Marcos and H. C. Fu. "Hydromechanical reception of marine copepods: the role of mechanoreceptional seta." *Soft Matter* (Submitted).

⁴ T. F. Kong and X. Shen contributed equally to this work.

Appendix A

Multipole Traction

The Blakeslet dipolar and Blakeslet quadrupolar traction on a fixed point $\mathbf{x}^w$ can be obtained by differentiating Eq. (2.44),

$$T_i^{BD}(\mathbf{x}^w) = \partial_k \tau_{ij}(\mathbf{x}^w, \mathbf{x}^0) f_j d_k, \quad (\text{A.1})$$

$$T_i^{BQ}(\mathbf{x}^w) = \partial_k \partial_l \tau_{ij}(\mathbf{x}^w, \mathbf{x}^0) f_j d_k d_l, \quad (\text{A.2})$$

where the derivatives act on the second argument of τ . The Blakeslet dipolar traction when the only nonzero dipolar strength component is $f_2 d_2 = 1$ is shown in Figure 3-10(a) while the Blakeslet quadrupolar traction when the only nonzero quadrupolar strength component is $f_2 d_2 d_2 = 1$ is shown in Figure 3-15(a). Both singularities are placed at a distance of $h = 1$ from the wall.

Appendix B

Traction Correlation Coefficient

Following the traction correlation coefficient defined in Eq. (3.18), convergence tests are performed to determine how large the sample area on the wall must be to find correlation coefficients that do not depend on the integration area size. Here the result is shown for the instantaneous traction at $t = \pi/2$ and the time-averaged traction. The same method can be extended to study the instantaneous traction at other time points (data not shown).

Figure B-1: (a) Instantaneous ($t = \pi/2$) and (b) time-averaged traction correlation coefficient by varying the square of side length Nh on the wall.

The total area to be examined is defined as a square centered on the projection of the center of mass of the swimmer on the x_2 - x_3 plane. The square has a side length of Nh . R is evaluated numerically for the traction due to the three-sphere swimmer and the corresponding Stokeslet dipole with strength $\sum_{\beta} \mathbf{f}^{\beta} \mathbf{d}^{\beta}$ using Eq. (3.18), plotted against N (Figure B-1). For a given h , the

correlation coefficients in both x_1 and x_2 directions converge when the side length of the area being examined is approximately 3–5 times larger than the distance from the wall to the three-sphere swimmer ($N \gtrsim 3-5$) and certainly for all cases when $N \gtrsim 10$.

Appendix C

Hydrodynamic characteristics of *Acartia clausi*

The geometry of copepod *Acartia clausi* (Calanoida) is used as a representative ambush-feeding calanoid copepod in the model. The size of *A. clausi* depends on the sex, development stage and habitat [169]. Here we use the approximate size of an adult female *A. clausi* of mean prosome length 0.87 mm, total length 1.13 mm and prosome width 0.28 mm [170]. The first antennular length L^{ant} is estimated to be 0.90 mm [171]. The antennular radius and the geometry and modulus of rigidity of the distal setae are scarcely documented. It is estimated that the antennular radius to be $R^{\text{ant}} = 10 \mu\text{m}$, distal setal length $L^{\text{seta}} = 200 \mu\text{m}$, radius $R^{\text{seta}} = 1 \mu\text{m}$, unless otherwise specified. The Young's modulus E has been empirically determined and estimated to be 10^7 N m^{-2} for a $2 - 5 \mu\text{m}$ thick and wide and $2 - 10 \text{ mm}$ long seta [172]. It has been observed that short and thin setae are usually softer than long and stiff ones [118], and hence E is chosen to be 10^6 N m^{-2} in our model.

Appendix D

The Method of Regularized Stokeslet (MRS)

The method of the regularized Stokeslet (MRS) discretizes the surfaces of the prey and copepod with regularized Stokeslets, which smoothens a point force with a localized distribution of force using a blob function. The velocity at any point $\mathbf{u}(\mathbf{x})$ due to the force $\mathbf{f}$ centered at $\mathbf{x}_0$ can be represented as

$$u_i(\mathbf{x}) = S_{ij}(\mathbf{x}, \mathbf{x}^0, \varepsilon) f_j^0, \quad (\text{D.1})$$

where the kernel $S_{ij}(\mathbf{x}, \mathbf{x}^0, \varepsilon)$ is given by Eq. 10(b) in the work of Ref. [35] and also shown in Eq. (2.24); ε is the regularization parameter related to the blob size of the regularized Stokeslets.

The regularized Stokeslets are distributed on the spherical surface of the prey using Cortez's discretization scheme [35], which in short first draws uniformly distributed grids on surfaces of a cube with the same side length as the diameter of the sphere, and then places the regularized Stokeslets at the intersection between the lines connecting the grids and cubic centers and the surface of the sphere placed inside the cube.

The copepod's ellipsoidal body and cylindrical antennule are discretized using our discretization scheme as described in [36]. The circular cross section of the cylinder with radius R^{seta} is approximated as the uniform n -gon. A total

number of n regularized Stokeslets are placed at the corner of the polygon such that the distance between successive Stokeslets is $\Delta s_c = 2R^{\text{seta}} \sin(\pi/n)$. To stagger the regularized Stokeslets uniformly on the cylindrical antennule, the successive cross sections are separated by a distance of Δs_c and rotated by an angle of π/n in radian. Two hemispherical caps discretized using the Cortez's scheme are added to both ends of the cylinder. The ellipsoidal body is also discretized in the same way, except that the number of regularized Stokeslets at each circular cross section depends on the radius of the circle. Given the separation distance between successive Stokeslets on the ellipsoid Δs_b , a number of $\pi d_b / \Delta s_b$ regularized Stokeslets are evenly distributed on the cross section, where the diameter of the cross section is $d_b = L^{\text{min}} [1 - (2r^{\text{maj}}/L^{\text{maj}})^2]^{1/2}$ with $2r^{\text{maj}} \in [-L^{\text{maj}}, L^{\text{maj}}]$. Similarly, successive circular cross sections of the ellipsoid are separated by Δs_b and rotated by $\Delta s_b / d_b$. The cylinder and ellipsoid are Δs_b apart to avoid the two surfaces being placed too close to each other.

To solve for the force distributions and velocities of the prey and copepod, the linearity of the regularized Stokeslet expression is utilized to express the flow velocity at a point as the superposition of a discrete set of regularized Stokeslets acting on the fluid. Assuming there are N^{prey} ($\alpha = 1, 2, \dots, N^{\text{prey}}$), N^{body} ($\beta = 1, 2, \dots, N^{\text{body}}$) and N^{ant} ($\gamma = 1, 2, \dots, N^{\text{ant}}$) collocation points on the prey, copepod's ellipsoidal body and antennule, respectively, the velocity at any arbitrary point $\mathbf{x}$ of the fluid, $\mathbf{u}(\mathbf{x})$, can be expressed as

$$u_i(\mathbf{x}) = \sum_{\alpha=1}^{N^{\text{prey}}} S_{ij}(\mathbf{x}, \mathbf{x}^\alpha, \boldsymbol{\varepsilon}^{\text{prey}}) f_j^\alpha + \sum_{\beta=1}^{N^{\text{body}}} S_{ij}(\mathbf{x}, \mathbf{x}^\beta, \boldsymbol{\varepsilon}^{\text{body}}) f_j^\beta + \sum_{\gamma=1}^{N^{\text{ant}}} S_{ij}(\mathbf{x}, \mathbf{x}^\gamma, \boldsymbol{\varepsilon}^{\text{ant}}) f_j^\gamma, \quad (\text{D.2})$$

where $\mathbf{f}^\alpha$, $\mathbf{f}^\beta$, and $\mathbf{f}^\gamma$ represent the force of regularized Stokeslets at the α -th, β -th,

and γ -th collocation points of the prey, copepod's body, and antennule, respectively.

Eq. (D.2) is used to relate the fluid velocity at any collocation point on the surfaces of the prey and copepod with the forces exerted by the regularized Stokeslets. After that, the no-slip boundary condition is applied to the copepod and the inert region of the prey. The velocity of the β -th collocation point on the copepod's body and γ -th collocation point on the antennule can be expressed in terms of the translational and rotational velocities at the ellipsoidal center of the copepod $\mathbf{x}^{\text{pred},0}$, $\mathbf{v}^{\text{pred}}$ and $\boldsymbol{\omega}^{\text{pred}}$, respectively using

$$u_i^\beta = v_i^{\text{pred}} + \epsilon_{ijk} \omega_j^{\text{pred}} r_k^\beta, \quad (\text{D.3})$$

$$u_i^\gamma = v_i^{\text{pred}} + \epsilon_{ijk} \omega_j^{\text{pred}} r_k^\gamma, \quad (\text{D.4})$$

where $\mathbf{r}^\beta = \mathbf{x}^\beta - \mathbf{x}^{\text{pred},0}$; $\mathbf{r}^\gamma = \mathbf{x}^\gamma - \mathbf{x}^{\text{pred},0}$; ϵ_{ijk} is the Levi-Civita symbol. Applying the boundary condition on the prey requires treating its inert and active regions separately. The fluid velocity at the α -th collocation point of the prey's surface can be expressed as

$$u_i^\alpha = v_i^{\text{prey}} + \epsilon_{ijk} \omega_j^{\text{prey}} r_k^\alpha + u_i^{s,\alpha}, \quad (\text{D.5})$$

where $\mathbf{v}^{\text{prey}}$ and $\boldsymbol{\omega}^{\text{prey}}$ are the translational and rotational velocities of the prey at its spherical center $\mathbf{x}^{\text{prey},0}$, respectively; $\mathbf{r}^\alpha = \mathbf{x}^\alpha - \mathbf{x}^{\text{prey},0}$. The last term $\mathbf{u}^{s,\alpha}$ prescribes the relative flow velocity with respect to the prey's velocity at the α -th collocation point. As such, $\mathbf{u}^{s,\alpha}$ at the active region is prescribed by Eq. (3.22) while $\mathbf{u}^{s,\alpha} = \mathbf{0}$ at the inert region.

It is further assumed the prey and copepod are neutrally buoyant since the density of the latter is usually within 5% of the surrounding fluid [173]. This allows one to focus on the effect of the prey-induced flow while neglecting the

role of the gravitational force on the copepod's mechanoreception. As the inertia effect is negligible in the low Reynolds number regime, the total forces and torques acting on both the prey and copepod are zero, hence

$$\sum_{\alpha=1}^{N^{\text{prey}}} f_j^\alpha = 0, \quad (\text{D.6})$$

$$\sum_{\alpha=1}^{N^{\text{prey}}} \epsilon_{ijk} r_j^\alpha f_k^\alpha = 0, \quad (\text{D.7})$$

$$\sum_{\beta=1}^{N^{\text{body}}} f_j^\beta + \sum_{\gamma=1}^{N^{\text{ant}}} f_j^\gamma = 0, \quad (\text{D.8})$$

$$\sum_{\beta=1}^{N^{\text{body}}} \epsilon_{ijk} r_j^\beta f_k^\beta + \sum_{\gamma=1}^{N^{\text{ant}}} \epsilon_{ijk} r_j^\gamma f_k^\gamma = 0. \quad (\text{D.9})$$

By solving Eqs. (D.2) to (D.9), the translational and rotational velocities of the prey and copepod, $\mathbf{v}^{\text{prey}}$, $\boldsymbol{\omega}^{\text{prey}}$, $\mathbf{v}^{\text{pred}}$ and $\boldsymbol{\omega}^{\text{pred}}$ can be obtained, which can further be substituted into (D.3) to (D.5) followed by Eq. (D.2) to evaluate the force distributions on the surfaces of the prey and copepod, $\mathbf{f}^\alpha$, $\mathbf{f}^\beta$, and $\mathbf{f}^\gamma$.

A convergence test is performed to determine the optimal ε and the number of necessary collocation points on the prey and copepod. The prey is isolated and assumed that $\mathbf{u}^{s,0} = 5$ mm/s to evaluate its free-swimming velocity [Figure D-1(a)]. The fastest convergence is achieved at $\varepsilon^{\text{prey}} = \Delta s^{\text{prey}}/3$. By fixing the number of regularized Stokeslets on the prey $n^{\text{prey}} = 2400$, $\mathbf{u}^{s,0}$ is adjusted to be 4.67 mm/s such that its free swimming speed $\mathbf{v}^{\text{prey}} = 0.78$ mm/s. The convergence of the copepod's velocity is then tested under the prey-induced flow when $d = 0.9$ mm and $\theta = \phi = 0$ [Figure D-1(b)]. The fastest convergence requires $\varepsilon^{\text{body}} = \Delta s^{\text{body}}$ and $\varepsilon^{\text{ant}} = \Delta s^{\text{ant}}$. The total number of regularized Stokeslets on the ellipsoidal body and antennule are selected as $N^{\text{body}} = 1797$

and $N^{\text{ant}} = 7440$, respectively, for the MRS calculation. The cross section of the first antennule in this case is a 16-gons.

Figure D-1: The velocity convergence test results for (a) a free swimming prey and (b) a copepod under the flow induced by the prey. The horizontal axis and legend represent the number of regularized Stokeslets and the normalized regularization parameters of (a) the prey and (b) the copepod.

References

- [1] C. A. Suttle, "Marine viruses—major players in the global ecosystem," *Nat. Rev. Microbiol.*, vol. 5, pp. 801-812, 2007.
- [2] M. E. Cortés, J. C. Bonilla, and R. D. Sinisterra, *Biofilm formation, control and novel strategies for eradication* vol. 2. Badajoz: Formatex Research Center, 2011.
- [3] M. R. Amieva and E. M. El-Omar, "Host-bacterial interactions in *Helicobacter pylori* infection," *Gastroenterology*, vol. 134, pp. 306-323, 2008.
- [4] E. Lauga and T. R. Powers, "The hydrodynamics of swimming microorganisms," *Rep. Prog. Phys.*, vol. 72, p. 096601, 2009.
- [5] E. M. Purcell, "Life at low Reynolds number," *Am. J. Phys.*, vol. 45, pp. 3-11, 1977.
- [6] R. M. Macnab, "Bacterial flagella rotating in bundles: a study in helical geometry," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 74, pp. 221-225, 1977.
- [7] J. Gray, "The movement of sea-urchin spermatozoa," *J. Exp. Biol.*, vol. 32, pp. 775-801, 1955.
- [8] Marcos, N. P. Tran, A. R. Saini, K. C. H. Ong, and W. J. Chia, "Analysis of a swimming sperm in a shear flow," *Microfluid. Nanofluid.*, vol. 17, pp. 809-819, 2014.
- [9] J. B. Y. Koh and Marcos, "The study of spermatozoa and sorting in relation to human reproduction," *Microfluid. Nanofluid.*, vol. 18, pp. 755-774, 2015.
- [10] Y. Wang, R. M. Hernandez, D. J. Bartlett, J. M. Bingham, T. R. Kline, A. Sen, *et al.*, "Bipolar electrochemical mechanism for the propulsion of catalytic nanomotors in hydrogen peroxide solutions," *Langmuir*, vol. 22, pp. 10451-10456, 2006.
- [11] A. Ghosh and P. Fischer, "Controlled propulsion of artificial magnetic nanostructured propellers," *Nano lett.*, vol. 9, pp. 2243-2245, 2009.
- [12] L. Zhang, J. J. Abbott, L. Dong, B. E. Kratochvil, D. Bell, and B. J. Nelson, "Artificial bacterial flagella: Fabrication and magnetic control," *Appl. Phys. Lett.*, vol. 94, p. 064107, 2009.
- [13] D. L. Fan, F. Q. Zhu, R. C. Cammarata, and C. L. Chien, "Electric tweezers," *Nano Today*, vol. 6, pp. 339-354, 2011.
- [14] S. Kim, F. Qiu, S. Kim, A. Ghanbari, C. Moon, L. Zhang, *et al.*, "Fabrication and characterization of magnetic microrobots for three - dimensional cell culture and targeted transportation," *Adv. Mater.*, vol. 25, pp. 5863-5868, 2013.
- [15] U. K. Cheang, F. Meshkati, D. Kim, M. J. Kim, and H. C. Fu, "Minimal geometric requirements for micropropulsion via magnetic rotation," *Phys. Rev. E*, vol. 90, p. 033007, 2014.

- [16] A. Ferreira, J. Agnus, N. Chaillet, and J.-M. Breguet, "A smart microrobot on chip: design, identification, and control," *IEEE-ASME T. Mech.*, vol. 9, pp. 508-519, 2004.
- [17] F. Meshkati and H. C. Fu, "Modeling rigid magnetically rotated microswimmers: Rotation axes, bistability, and controllability," *Phys. Rev. E*, vol. 90, p. 063006, 2014.
- [18] J. Edd, S. Payen, B. Rubinsky, M. L. Stoller, and M. Sitti, "Biomimetic propulsion for a swimming surgical micro-robot," in *Proc. IEEE/RSJ Int. Conf. Intell. Robots Syst.*, Los Alamitos, CA, 2003, pp. 2583-2588.
- [19] F. K. Nelson and D. L. Riddle, "Functional study of the *Caenorhabditis elegans* secretory - excretory system using laser microsurgery," *J. Exp. Zool. Part A*, vol. 231, pp. 45-56, 1984.
- [20] G. Dogangil, O. Ergeneman, J. J. Abbott, S. Pan é H. Hall, S. Muntwyler, *et al.*, "Toward targeted retinal drug delivery with wireless magnetic microrobots," in *IEEE/RSJ Int. Conf. Intell. Robots Syst.*, Los Alamitos, CA, 2008, pp. 1921-1926.
- [21] S. Fusco, G. Chatzipirpiridis, K. M. Sivaraman, O. Ergeneman, B. J. Nelson, and S. Pan é "Chitosan electrodeposition for microrobotic drug delivery," *Adv. Healthc. Mater.*, vol. 2, pp. 1037-1044, 2013.
- [22] G. Taylor, "Analysis of the swimming of microscopic organisms," in *Proc. R. Soc. A*, 1951, pp. 447-461.
- [23] H. C. Fu, V. B. Shenoy, and T. R. Powers, "Low-Reynolds-number swimming in gels," *Europhys. Lett.*, vol. 91, p. 24002, 2010.
- [24] S. A. Mirbagheri and H. C. Fu, "*Helicobacter pylori* couples motility and diffusion to actively create a heterogeneous complex medium in gastric mucus," *Phys. Rev. Lett.*, vol. 116, p. 198101, 2016.
- [25] J. Lighthill, "On the squirming motion of nearly spherical deformable bodies through liquids at very small Reynolds numbers," *Commun. Pur. Appl. Math.*, vol. 5, pp. 109-118, 1952.
- [26] J. R. Blake, "A spherical envelope approach to ciliary propulsion," *J. Fluid Mech.*, vol. 46, pp. 199-208, 1971.
- [27] J. R. Blake, "Infinite models for ciliary propulsion," *J. Fluid Mech.*, vol. 49, pp. 209-222, 1971.
- [28] A. Najafi and R. Golestanian, "Simple swimmer at low Reynolds number: Three linked spheres," *Phys. Rev. E*, vol. 69, p. 062901, 2004.
- [29] J. E. Avron, O. Kenneth, and D. H. Oaknin, "Pushmepullyou: an efficient micro-swimmer," *New J. Phys.*, vol. 7, p. 234, 2005.
- [30] S. Kim and S. J. Karrila, *Microhydrodynamics: principles and selected applications*. Boston, MA: Butterworth-Heinemann, 1991.
- [31] J. Lighthill, "Flagellar hydrodynamics," *SIAM Rev.*, vol. 18, pp. 161-230, 1976.
- [32] J. B. Y. Koh, X. Shen, and Marcos, "Theoretical modeling in microscale locomotion,"

- Microfluid. Nanofluid.*, vol. 20, pp. 1-27, 2016.
- [33] M. Ramia, D. L. Tullock, and N. Phan-Thien, "The role of hydrodynamic interaction in the locomotion of microorganisms," *Biophys. J.*, vol. 65, pp. 755-778, 1993.
 - [34] R. Cortez, "The method of regularized Stokeslets," *SIAM J. Sci. Comput.*, vol. 23, pp. 1204-1225, 2001.
 - [35] R. Cortez, L. Fauci, and A. Medovikov, "The method of regularized Stokeslets in three dimensions: analysis, validation, and application to helical swimming," *Phys. Fluids*, vol. 17, p. 031504, 2005.
 - [36] Y. Hyon, Marcos, T. R. Powers, R. Stocker, and H. C. Fu, "The wiggling trajectories of bacteria," *J. Fluid Mech.*, vol. 705, pp. 58-76, 2012.
 - [37] T. D. Montenegro-Johnson, D. A. Gagnon, P. E. Arratia, and E. Lauga, "Flow analysis of the low Reynolds number swimmer *C. elegans*," *Phys. Rev. Fluids*, vol. 1, p. 053202, 2016.
 - [38] J. D. Martindale, M. Jabbarzadeh, and H. C. Fu, "Choice of computational method for swimming and pumping with nonslender helical filaments at low Reynolds number," *Phys. Fluids*, vol. 28, p. 021901, 2016.
 - [39] K. Drescher, R. E. Goldstein, N. Michel, M. Polin, and I. Tuval, "Direct measurement of the flow field around swimming microorganisms," *Phys. Rev. Lett.*, vol. 105, p. 168101, 2010.
 - [40] A. W. Visser, "Hydromechanical signals in the plankton," *Mar. Ecol. Prog. Ser.*, vol. 222, pp. 1-24, 2001.
 - [41] G. K. Batchelor, "The stress system in a suspension of force-free particles," *J. Fluid Mech.*, vol. 41, pp. 545-570, 1970.
 - [42] T. Ishikawa, G. Sekiya, Y. Imai, and T. Yamaguchi, "Hydrodynamic interactions between two swimming bacteria," *Biophys. J.*, vol. 93, pp. 2217-2225, 2007.
 - [43] D. J. Smith and J. R. Blake, "Surface accumulation of spermatozoa: a fluid dynamic phenomenon," *Math. Scientist*, vol. 34, 2009.
 - [44] C. M. Pooley, G. P. Alexander, and J. M. Yeomans, "Swimming with a friend at low Reynolds number," *arXiv:0705.3612*, 2007.
 - [45] L. J. Rothschild, "Non-random distribution of bull spermatozoa in a drop of sperm suspension," *Nature*, vol. 198, pp. 1221-1222, 1963.
 - [46] D. Giacché, T. Ishikawa, and T. Yamaguchi, "Hydrodynamic entrapment of bacteria swimming near a solid surface," *Phys. Rev. E*, vol. 82, p. 056309, 2010.
 - [47] H. Shum, E. A. Gaffney, and D. J. Smith, "Modelling bacterial behaviour close to a no-slip plane boundary: the influence of bacterial geometry," in *Proc. R. Soc. A*, 2010, pp. 1725-1748.
 - [48] A. A. Evans and E. Lauga, "Propulsion by passive filaments and active flagella near boundaries," *Phys. Rev. E*, vol. 82, p. 041915, 2010.

- [49] H. C. Berg and L. Turner, "Chemotaxis of bacteria in glass capillary arrays. *Escherichia coli*, motility, microchannel plate, and light scattering," *Biophys. J.*, vol. 58, pp. 919-930, 1990.
- [50] P. D. Frymier, R. M. Ford, H. C. Berg, and P. T. Cummings, "Three-dimensional tracking of motile bacteria near a solid planar surface," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 92, pp. 6195-6199, 1995.
- [51] R. Di Leonardo, D. Dell'Arciprete, L. Angelani, and V. Iebba, "Swimming with an image," *Phys. Rev. Lett.*, vol. 106, p. 038101, 2011.
- [52] J. R. Strickler and A. K. Bal, "Setae of the first antennae of the copepod *Cyclops scutifer* (Sars): their structure and importance," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 70, pp. 2656-2659, 1973.
- [53] M. M. Friedman and J. R. Strickler, "Chemoreceptors and feeding in calanoid copepods (Arthropoda: Crustacea)," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 72, pp. 4185-4188, 1975.
- [54] T. M. Weatherby, K. K. Wong, and P. H. Lenz, "Fine structure of the distal sensory setae on the first antennae of *Pleuromamma xiphias* Giesbrecht (Copepoda)," *J. Crustacean Biol.*, vol. 14, pp. 670-685, 1994.
- [55] M. J. Weissburg, M. Doall, and J. Yen, "Following the invisible trail: kinematic analysis of mate-tracking in the copepod *Temora longicornis*," *Philos. T. Roy. Soc. B*, vol. 353, pp. 701-712, 1998.
- [56] J. Yen, P. H. Lenz, D. V. Gassie, and D. K. Hartline, "Mechanoreception in marine copepods: electrophysiological studies on the first antennae," *J. Plankton Res.*, vol. 14, pp. 495-512, 1992.
- [57] K. Singarajah, "Escape reactions of zooplankton: effects of light and turbulence," *J. Mar. Biol. Assoc. U.K.*, vol. 55, pp. 627-639, 1975.
- [58] J. R. Strickler, "Calanoid copepods, feeding currents, and the role of gravity," *Science*, vol. 218, pp. 158-160, 1982.
- [59] M. H. Bundy and G.-A. Paffenhöfer, "Analysis of flow fields associated with freely swimming calanoid copepods," *Mar. Ecol. Prog. Ser.*, pp. 99-113, 1996.
- [60] D. K. Hartline, P. H. Lenz, and C. M. Herren, "Physiological and behavioral studies of escape responses in calanoid copepods," *Mar. Freshw. Behav. Phy.*, vol. 27, pp. 199-212, 1996.
- [61] M. H. Bundy, T. F. Gross, H. A. Vanderploeg, and J. Rudi Strickler, "Perception of inert particles by calanoid copepods: behavioral observations and a numerical model," *J. Plankton Res.*, vol. 20, pp. 2129-2152, 1998.
- [62] E. Broglio, M. Johansson, and P. R. Jonsson, "Trophic interaction between copepods and ciliates: effects of prey swimming behavior on predation risk," *Mar. Ecol. Prog. Ser.*, vol. 220, pp. 179-186, 2001.
- [63] M. H. Bundy and H. A. Vanderploeg, "Detection and capture of inert particles by calanoid

- copepods: the role of the feeding current," *J. Plankton Res.*, vol. 24, pp. 215-223, 2002.
- [64] P. R. Jonsson and P. Tiselius, "Feeding behaviour, prey detection and capture efficiency of the copepod *Acartia tonsa* feeding on planktonic ciliates," *Mar. Ecol. Prog. Ser.*, pp. 35-44, 1990.
- [65] J. R. Blake and A. T. Chwang, "Fundamental singularities of viscous flow," *J. Eng. Math.*, vol. 8, pp. 23-29, 1974.
- [66] S. E. Spagnolie and E. Lauga, "Hydrodynamics of self-propulsion near a boundary: predictions and accuracy of far-field approximations," *J. Fluid Mech.*, vol. 700, pp. 105-147, 2012.
- [67] J. A. C. Humphrey, R. Devarakonda, I. Iglesias, and F. G. Barth, "Dynamics of arthropod filiform hairs. I. Mathematical modelling of the hair and air motions," *Philos. T. Roy. Soc. B*, vol. 340, pp. 423-444, 1993.
- [68] R. Devarakonda, F. G. Barth, and J. A. C. Humphrey, "Dynamics of arthropod filiform hairs. IV. Hair motion in air and water," *Philos. T. Roy. Soc. B*, vol. 351, pp. 933-946, 1996.
- [69] J. A. C. Humphrey, F. G. Barth, and K. Voss, "The motion-sensing hairs of arthropods: using physics to understand sensory ecology and adaptive evolution," in *Ecology of Sensing*, ed Berlin, Heidelberg: Springer, 2001, pp. 105-125.
- [70] J. A. C. Humphrey and F. G. Barth, "Medium flow-sensing hairs: biomechanics and models," *Adv. Insect physiol.*, vol. 34, pp. 1-80, 2007.
- [71] D. Takagi and D. K. Hartline, "Directional Hydrodynamic Sensing by Free-Swimming Organisms," *B. Math. Biol.*, vol. 80, pp. 215-227, 2018.
- [72] C. B. Woodson, D. R. Webster, M. J. Weissburg, and J. Yen, "Response of copepods to physical gradients associated with structure in the ocean," *Limnol. Oceanogr.*, vol. 50, pp. 1552-1564, 2005.
- [73] P. H. Lenz and D. K. Hartline, "Mechanoreception in crustaceans of the pelagic realm," in *Nervous Systems and Control of Behavior*. vol. 3, C. Derby and M. Thiel, Eds., ed Oxford, England: Oxford University Press, 2014, pp. 293-320.
- [74] A. Shapere and F. Wilczek, "Self-propulsion at low Reynolds number," *Phys. Rev. Lett.*, vol. 58, p. 2051, 1987.
- [75] A. Shapere and F. Wilczek, "Efficiencies of self-propulsion at low Reynolds number," *J. Fluid Mech.*, vol. 198, pp. 587-599, 1989.
- [76] A. Shapere and F. Wilczek, "Geometry of self-propulsion at low Reynolds number," *J. Fluid Mech.*, vol. 198, pp. 557-585, 1989.
- [77] J. Happel and H. Brenner, *Low Reynolds Number Hydrodynamics* vol. 133. Englewood Cliffs, NJ: Prentice-Hall, 1965.
- [78] A. T. Chwang and T. Y.-T. Wu, "Hydromechanics of low-Reynolds-number flow. Part 2. Singularity method for Stokes flows," *J. Fluid Mech.*, vol. 67, pp. 787-815, 1975.

- [79] J. J. L. Higdon, "A hydrodynamic analysis of flagellar propulsion," *J. Fluid Mech.*, vol. 90, pp. 685-711, 1979.
- [80] N. Phan-Thien, T. Tran-Cong, and M. Ramia, "A boundary-element analysis of flagellar propulsion," *J. Fluid Mech.*, vol. 184, pp. 533-549, 1987.
- [81] L. Leal, *Laminar Flow and Convective Transport Processes*. Boston, MA: Butterworth-Heinemann, 1992.
- [82] T. J. Pedley and J. O. Kessler, "Hydrodynamic phenomena in suspensions of swimming microorganisms," *Annu. Rev. Fluid Mech.*, vol. 24, pp. 313-358, 1992.
- [83] G. J. Hancock, "The self-propulsion of microscopic organisms through liquids," in *Proc. R. Soc. A*, 1953, pp. 96-121.
- [84] J. Gray and G. J. Hancock, "The propulsion of sea-urchin spermatozoa," *J. Exp. Biol.*, vol. 32, pp. 802-814, 1955.
- [85] H. C. Fu, C. W. Wolgemuth, and T. R. Powers, "Beating patterns of filaments in viscoelastic fluids," *Phys. Rev. E*, vol. 78, p. 041913, 2008.
- [86] J. B. Y. Koh and Marcos, "Effect of dielectrophoresis on spermatozoa," *Microfluid. Nanofluid.*, vol. 17, pp. 613-622, 2014.
- [87] M. Tournus, A. Kirshtein, L. Berlyand, and I. S. Aranson, "Flexibility of bacterial flagella in external shear results in complex swimming trajectories," *J. R. Soc. Interface*, vol. 12, p. 20140904, 2015.
- [88] R. G. Cox, "The motion of long slender bodies in a viscous fluid Part 1. General theory," *J. Fluid Mech.*, vol. 44, pp. 791-810, 1970.
- [89] R. E. Johnson, "An improved slender-body theory for Stokes flow," *J. Fluid Mech.*, vol. 99, pp. 411-431, 1980.
- [90] J. Liu, S.-H. Tan, Y. F. Yap, M. Y. Ng, and N.-T. Nguyen, "Numerical and experimental investigations of the formation process of ferrofluid droplets," *Microfluid. Nanofluid.*, vol. 11, pp. 177-187, 2011.
- [91] G. Huber, S. A. Koehler, and J. Yang, "Micro-swimmers with hydrodynamic interactions," *Math. Comput. Model.*, vol. 53, pp. 1518-1526, 2011.
- [92] R. E. Johnson and C. J. Brokaw, "Flagellar hydrodynamics. A comparison between resistive-force theory and slender-body theory," *Biophys. J.*, vol. 25, pp. 113-127, 1979.
- [93] S. Chattopadhyay and X.-L. Wu, "The effect of long-range hydrodynamic interaction on the swimming of a single bacterium," *Biophys. J.*, vol. 96, pp. 2023-2028, 2009.
- [94] S. D. Olson, S. S. Suarez, and L. J. Fauci, "Coupling biochemistry and hydrodynamics captures hyperactivated sperm motility in a simple flagellar model," *J. Theor. Biol.*, vol. 283, pp. 203-216, 2011.
- [95] H. Guo, J. Nawroth, Y. Ding, and E. Kanso, "Cilia beating patterns are not hydrodynamically optimal," *Phys. Fluids*, vol. 26, p. 091901, 2014.
- [96] K. Leiderman, E. L. Bouzarth, R. Cortez, and A. T. Layton, "A regularization method for

- the numerical solution of periodic Stokes flow," *J. Comput. Phys.*, vol. 236, pp. 187-202, 2013.
- [97] D. J. Smith, "A boundary element regularized Stokeslet method applied to cilia-and flagella-driven flow," in *Proc. R. Soc. A*, 2009, pp. 3605-3626.
 - [98] A. Barrero-Gil, "Weakening accuracy dependence with the regularization parameter in the Method of Regularized Stokeslets," *J. Comput. Appl. Math.*, vol. 237, pp. 672-679, 2013.
 - [99] S. D. Olson, S. Lim, and R. Cortez, "Modeling the dynamics of an elastic rod with intrinsic curvature and twist using a regularized Stokes formulation," *J. Comput. Phys.*, vol. 238, pp. 169-187, 2013.
 - [100] B. Rodenborn, C.-H. Chen, H. L. Swinney, B. Liu, and H. Zhang, "Propulsion of microorganisms by a helical flagellum," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 110, pp. E338-E347, 2013.
 - [101] H. Flores, E. Lobaton, S. Méndez-Diez, S. Tlupova, and R. Cortez, "A study of bacterial flagellar bundling," *B. Math. Biol.*, vol. 67, pp. 137-168, 2005.
 - [102] E. L. Bouzarth, A. T. Layton, and Y. N. Young, "Modeling a semi - flexible filament in cellular Stokes flow using regularized Stokeslets," *Int. J. Numer. Meth. Bio.*, vol. 27, pp. 2021-2034, 2011.
 - [103] J. Ainley, S. Durkin, R. Embid, P. Boindala, and R. Cortez, "The method of images for regularized Stokeslets," *J. Comput. Phys.*, vol. 227, pp. 4600-4616, 2008.
 - [104] H.-N. Nguyen and R. Cortez, "Reduction of the regularization error of the method of regularized stokeslets for a rigid object immersed in a three-dimensional stokes flow," *Commun. Comput. Phys.*, vol. 15, pp. 126-152, 2014.
 - [105] J. R. Blake, "A note on the image system for a stokeslet in a no-slip boundary," *Math. Proc. Cambridge*, vol. 70, pp. 303-310, 1971.
 - [106] C. Pozrikidis, *Boundary integral and singularity methods for linearized viscous flow*. Cambridge, United Kingdom: Cambridge University Press, 1992.
 - [107] A. P. Berke, L. Turner, H. C. Berg, and E. Lauga, "Hydrodynamic attraction of swimming microorganisms by surfaces," *Phys. Rev. Lett.*, vol. 101, p. 038102, 2008.
 - [108] J. D. Martindale and H. C. Fu, "Autonomously responsive pumping by a bacterial flagellar forest: A mean-field approach," *Phys. Rev. E*, vol. 96, p. 033107, 2017.
 - [109] P. D. Frymier and R. M. Ford, "Analysis of bacterial swimming speed approaching a solid-liquid interface," *AIChE J.*, vol. 43, pp. 1341-1347, 1997.
 - [110] E. A. Gillies, R. M. Cannon, R. B. Green, and A. A. Pacey, "Hydrodynamic propulsion of human sperm," *J. Fluid Mech.*, vol. 625, p. 445, 2009.
 - [111] T. Goto, S. Masuda, K. Terada, and Y. Takano, "Comparison between observation and boundary element analysis of bacterium swimming motion," *JSME Int. J. C-Mech. Sy.*, vol. 44, pp. 958-963, 2001.
 - [112] T. Goto, K. Nakata, K. Baba, M. Nishimura, and Y. Magariyama, "A fluid-dynamic

- interpretation of the asymmetric motion of singly flagellated bacteria swimming close to a boundary," *Biophys. J.*, vol. 89, pp. 3771-3779, 2005.
- [113] L. R. Haury, D. E. Kenyon, and J. R. Brooks, "Experimental evaluation of the avoidance reaction of *Calanus finmarchicus*," *J. Plankton Res.*, vol. 2, pp. 187-202, 1980.
 - [114] T. Kiørboe, E. Saiz, and A. Visser, "Hydrodynamic signal perception in the copepod *Acartia tonsa*," *Mar. Ecol. Prog. Ser.*, vol. 179, pp. 97-111, 1999.
 - [115] P. H. Lenz and J. Yen, "Distal setal mechanoreceptors of the first antennae of marine copepods," *B. Mar. Sci.*, vol. 53, pp. 170-179, 1993.
 - [116] L. A. van Duren, E. J. Stamhuis, and J. J. Videler, "Reading the copepod personal ads: increasing encounter probability with hydromechanical signals," *Phil. Trans. R. Soc. Lond. B*, vol. 353, pp. 691-700, 1998.
 - [117] F. G. Barth, U. Wastl, J. A. Humphrey, and R. Devarakonda, "Dynamics of arthropod filiform hairs. II. Mechanical properties of spider trichobothria (*Cupiennius salei* Keys.)," *Philos. T. Roy. Soc. B*, vol. 340, pp. 445-461, 1993.
 - [118] D. M. Fields, D. S. Shaeffer, and M. J. Weissburg, "Mechanical and neural responses from the mechanosensory hairs on the antennule of *Gaussia princeps*," *Mar. Ecol. Prog. Ser.*, vol. 227, pp. 173-186, 2002.
 - [119] G. A. Paffenhöfer and P. A. Loyd, "Ultrastructure of setae of the maxilliped of the marine planktonic copepod *Temora stylifera*," *Mar. Ecol. Prog. Ser.*, vol. 178, pp. 101-107, 1999.
 - [120] I. Altner, H. Hatt, and H. Altner, "Structural properties of bimodal chemo-and mechanosensitive setae on the pereopod chelae of the crayfish, *Austropotamobius torrentium*," *Cell and Tissue Res.*, vol. 228, pp. 357-374, 1983.
 - [121] E. E. Ball and A. N. Cowan, "Ultrastructure of the antennal sensilla of *Acetes* (Crustacea, Decapoda, Natantia, Sergestidae)," *Philos. T. Roy. Soc. B*, vol. 277, pp. 429-457, 1977.
 - [122] Y. Crouau, "Comparison of crustacean and insect mechanoreceptive setae," *Int. J. Insect Morphol. Embryol.*, vol. 26, pp. 181-190, 1997.
 - [123] D. K. Hartline, E. J. Buskey, and P. H. Lenz, "Rapid jumps and bioluminescence elicited by controlled hydrodynamic stimuli in a mesopelagic copepod, *Pleuromamma xiphias*," *The Biological Bulletin*, vol. 197, pp. 132-143, 1999.
 - [124] D. P. Corey and A. J. Hudspeth, "Ionic basis of the receptor potential in a vertebrate hair cell," *Nature*, vol. 281, pp. 675-677, 1979.
 - [125] J. R. Holt and D. P. Corey, "Two mechanisms for transducer adaptation in vertebrate hair cells," *Proc. Natl. Acad. Sci. U.S.A.*, vol. 97, pp. 11730-11735, 2000.
 - [126] D. M. Fields, "The sensory horizon of marine copepods," in *Copepods: Diversity, Habitat and Behavior*, L. Seuront, Ed., ed New York, NY, USA: Nova Science Publishers, 2014.
 - [127] L. Wilkens and J. Douglass, "A stimulus paradigm for analysis of near-field hydrodynamic sensitivity in crustaceans," *J. Exp. Biol.*, vol. 189, pp. 263-272, 1994.
 - [128] J. Tautz, "Reception of medium vibration by thoracal hairs of caterpillars of *Barathra*

- brassicae* L.(Lepidoptera, Noctuidae)," *J. Comp. Physiol.*, vol. 118, pp. 13-31, 1977.
- [129] J. Tautz, "Reception of particle oscillation in a medium—an unorthodox sensory capacity," *Naturwissenschaften*, vol. 66, pp. 452-461, 1979.
- [130] M. S. Triantafyllou, G. D. Weymouth, and J. Miao, "Biomimetic survival hydrodynamics and flow sensing," *Annu. Rev. Fluid Mech.*, vol. 48, pp. 1-24, 2016.
- [131] G. G. Stokes, "On the effect of the internal friction of fluids on the motion of pendulums," *Trans. Cambridge Philos. Soc.*, vol. 9, pp. 8-106, 1851.
- [132] R. L. Panton, *Incompressible Flow*. New York, NY: Wiley Interscience, 1984.
- [133] T. Shimozawa and M. Kanou, "The aerodynamics and sensory physiology of range fractionation in the cereal filiform sensilla of the cricket *Gryllus bimaculatus*," *J. Comp. Phys. A*, vol. 155, pp. 495-505, 1984.
- [134] D. K. Hartline and P. H. Lenz. (2014, February 4). *Hydrodynamics of arthropod cuticular setae in water* [Online]. Available: www.pbrc.hawaii.edu/~danh/seta-hydrodynamics/
- [135] C. Gadelha, B. Wickstead, and K. Gull, "Flagellar and ciliary beating in trypanosome motility," *Cytoskeleton*, vol. 64, pp. 629-643, 2007.
- [136] R. Kamiya and E. Hasegawa, "Intrinsic difference in beat frequency between the two flagella of *Chlamydomonas reinhardtii*," *Exp. Cell Res.*, vol. 173, pp. 299-304, 1987.
- [137] C. Svensen and T. Kiørboe, "Remote prey detection in *Oithona similis*: hydromechanical versus chemical cues," *J. Plankton Res.*, vol. 22, pp. 1155-1166, 2000.
- [138] A. W. Visser and T. Kiørboe, "Plankton motility patterns and encounter rates," *Oecologia*, vol. 148, pp. 538-546, 2006.
- [139] D. V. Holberton, "Fine structure of the ventral disk apparatus and the mechanism of attachment in the flagellate *Giardia muris*," *J. Cell Sci.*, vol. 13, pp. 11-41, 1973.
- [140] S. C. Lenaghan, C. A. Davis, W. R. Henson, Z. Zhang, and M. Zhang, "High-speed microscopic imaging of flagella motility and swimming in *Giardia lamblia* trophozoites," *P. Natl. Acad. Sci. USA*, vol. 108, pp. E550-E558, 2011.
- [141] H. Bleckmann, T. Breithaupt, R. Blickhan, and J. Tautz, "The time course and frequency content of hydrodynamic events caused by moving fish, frogs, and crustaceans," *J. Comp. Physiol. A*, vol. 168, pp. 749-757, 1991.
- [142] D. V. Gassie, P. H. Lenz, J. Yen, and D. K. Hartline, "Mechanoreception in zooplankton first antennae: electrophysiological techniques," *B. Mar. Sci.*, vol. 53, pp. 96-105, 1993.
- [143] L. Lemelle, J.-F. Palierne, E. Chatre, C. Vaillant, and C. Place, "Curvature reversal of the circular motion of swimming bacteria probes for slip at solid/liquid interfaces," *Soft Matter*, vol. 9, pp. 9759-9762, 2013.
- [144] N. Figueroa-Morales, G. L. Miño, A. Rivera, R. Caballero, E. Clément, E. Altshuler, *et al.*, "Living on the edge: transfer and traffic of *E. coli* in a confined flow," *Soft Matter*, vol. 11, pp. 6284-6293, 2015.
- [145] L. Ping, V. Wasnik, and E. Emberly, "Bacterial motion in narrow capillaries," *FEMS*

- Microbiol. Ecol.*, vol. 91, p. 1, 2015.
- [146] G. J. Li and A. M. Ardekani, "Hydrodynamic interaction of microswimmers near a wall," *Phys. Rev. E*, vol. 90, p. 013010, 2014.
 - [147] A. J. Mathijssen, D. O. Pushkin, and J. M. Yeomans, "Tracer trajectories and displacement due to a micro-swimmer near a surface," *J. Fluid Mech.*, vol. 773, pp. 498-519, 2015.
 - [148] K. Ishimoto and E. A. Gaffney, "Squirmer dynamics near a boundary," *Phys. Rev. E*, vol. 88, p. 062702, 2013.
 - [149] R. Zargar, A. Najafi, and M. Miri, "Three-sphere low-Reynolds-number swimmer near a wall," *Phys. Rev. E*, vol. 80, p. 026308, 2009.
 - [150] A. K. Harris, P. Wild, and D. Stopak, "Silicone rubber substrata: a new wrinkle in the study of cell locomotion," *Science*, vol. 208, pp. 177-179, 1980.
 - [151] B. Sabass, M. L. Gardel, C. M. Waterman, and U. S. Schwarz, "High resolution traction force microscopy based on experimental and computational advances," *Biophys. J.*, vol. 94, pp. 207-220, 2008.
 - [152] H. Colin-York, D. Shrestha, J. H. Felce, D. Waithe, E. Moeendarbary, S. J. Davis, *et al.*, "Super-resolved traction force microscopy (STFM)," *Nano lett.*, vol. 16, pp. 2633-2638, 2016.
 - [153] J. S. Guasto, K. A. Johnson, and J. P. Gollub, "Oscillatory flows induced by microorganisms swimming in two dimensions," *Phys. Rev. Lett.*, vol. 105, p. 168102, 2010.
 - [154] T. Kiørboe, "Attack or attacked: The sensory and fluid mechanical constraints of copepods' predator-prey interactions," *Integr. Comp. Biol.*, vol. 53, pp. 821-831, 2013.
 - [155] M. Doall, J. Strickler, D. Fields, and J. Yen, "Mapping the free-swimming attack volume of a planktonic copepod, *Euchaeta rimana*," *Mari. Biol.*, vol. 140, pp. 871-879, 2002.
 - [156] J. Yen and N. T. Nicoll, "Setal array on the first antennae of a carnivorous marine copepod, *Euchaeta norvegica*," *J Crustacean Biol.*, vol. 10, pp. 218-224, 1990.
 - [157] D. M. Fields, "Orientation affects the sensitivity of *Acartia tonsa* to fluid mechanical signals," *Mar. Biol.*, vol. 157, pp. 505-514, 2010.
 - [158] H. Jiang and G.-A. Paffenhöfer, "Hydrodynamic signal perception by the copepod *Oithona plumifera*," *Mar. Ecol. Prog. Ser.*, vol. 373, pp. 37-52, 2008.
 - [159] H. C. Fu, T. R. Powers, and C. W. Wolgemuth, "Theory of swimming filaments in viscoelastic media," *Phys. Rev. Lett.*, vol. 99, p. 258101, 2007.
 - [160] L. D. Landau and E. M. Lifshitz, *Theory of Elasticity*, 3 ed. Oxford, UK: Pergamon Press, 1986.
 - [161] A. Brandt, "Morphology and ultrastructure of the sensory spine, a presumed mechanoreceptor of *Sphaeroma hookeri* (Crustacea, Isopoda), and remarks on similar spines in other peracarids," *J. Morphol.*, vol. 198, pp. 219-229, 1988.
 - [162] M. Schmidt, "Ultrastructure of a possible new type of crustacean cuticular strain receptor

- in *Carcinus maenas* (Crustacea, Decapoda)," *J. Morphol.*, vol. 204, pp. 335-344, 1990.
- [163] T. M. Weatherby and P. H. Lenz, "Mechanoreceptors in calanoid copepods: designed for high sensitivity," *Arthropod Struct. Dev.*, vol. 29, pp. 275-288, 2000.
- [164] M. B. Goodman, E. A. Lumpkin, A. Ricci, W. D. Tracey, M. Kernan, and T. Nicolson, "Molecules and mechanisms of mechanotransduction," *J. Neurosci.*, vol. 24, pp. 9220-9222, 2004.
- [165] J. Árnadóttir and M. Chalfie, "Eukaryotic mechanosensitive channels," *Annu. Rev. Biophys.*, vol. 39, pp. 111-137, 2010.
- [166] E. H. Dill, "Kirchhoff's theory of rods," *Arch. Hist. Exact Sci.*, vol. 44, pp. 1-23, 1992.
- [167] M. A. R. Koehl and J. R. Strickler, "Copepod feeding currents: food capture at low Reynolds number," *Limnol. Oceanogr.*, vol. 26, pp. 1062-1073, 1981.
- [168] G. A. Paffenhöffer, J. R. Strickler, and M. Alcaraz, "Suspension-feeding by herbivorous calanoid copepods: a cinematographic study," *Mar. Biol.*, vol. 67, pp. 193-199, 1982.
- [169] J. M. Bradford, "Partial revision of the *Acartia* subgenus *Acartiura* (Copepoda: Calanoida: Acartiidae)," *New Zeal. J. Mar. Fresh.*, vol. 10, pp. 159-202, 1976.
- [170] D. V. P. Conway, *Identification of the copepodite developmental stages of twenty-six North Atlantic copepods*, 21 ed. Plymouth, United Kingdom: Occasional Publications, 2012.
- [171] K. Takahashi and P. Tiselius, "Ontogenetic change of foraging behaviour during copepodite development of *Acartia clausi*," *Mar. Ecol. Prog. Ser.*, vol. 303, pp. 213-223, 2005.
- [172] J. Yen and A. Okubo, "Particle and prey detection by mechanoreceptive copepods: a mathematical analysis," *Hydrobiologia*, vol. 480, pp. 165-173, 2002.
- [173] T. Knutsen, W. Melle, and L. Calise, "Determining the mass density of marine copepods and their eggs with a critical focus on some of the previously used methods," *J. Plankton Res.*, vol. 23, pp. 859-873, 2001.