

# The physics of microbial feeding: mechanisms and trade-offs

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**OBJECTIVES:** Unicellular flagellated protists play a key role in the biological processes in the ocean. Through grazing on phytoplankton and bacteria they have major impact on global biogeochemical cycles, and by being grazed, they transfer primary production to higher trophic levels<sup>1–3</sup>. Yet, we do not understand the mechanisms of flagellate feeding, nor how their resource acquisition trades off against mortality and thereby shape the diversity and function of microbial communities. *We propose a cross-disciplinary project (microbial ecology, small-scale fluid physics) to examine the fluid dynamics of feeding and the associated mortality trade-offs in single celled protists through direct observations with high-speed video-micrography, novel flow visualisation techniques, novel holographic tracking to quantify encounter rates, as well as theoretical modelling.* An understanding of this fundamental process is essential to the understanding of microbial diversity, the role of microbial communities, and for the development of trait-based models of life in the oceans.

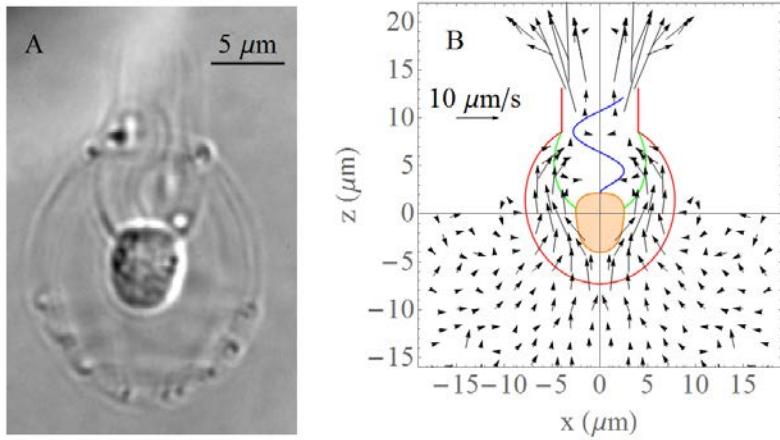
**BACKGROUND AND STATE OF THE ART:** Three decades ago, the pioneering work of Fenchel<sup>2–8</sup> progressed our understanding of the functional ecology of single celled protists significantly, but few studies have added to this since<sup>9,10</sup>. Therefore, the key process of resource acquisition, i.e., how unicellular protists capture their prey remains unexplored for most forms<sup>11–14</sup>. In the low Reynolds number world of protists, viscosity impedes predator-prey contact, and the physical mechanisms by which protists nevertheless clear huge volumes of water for bacterial and phytoplankton prey is not understood. We know, however, that bacteria and cyanobacteria - the main primary producers in the ocean - are consumed by unicellular protists at high rates and that the latter to a large extent control the populations of the former<sup>15</sup>. At the same time we have only vague ideas of the processes that govern the mortality of flagellates and, specifically, how resource acquisition trades off against mortality risk, despite knowing their predators. This is crucial, because the diversity of microbial communities is determined exactly by such trade-offs<sup>16</sup>, and microbial diversity, in turn, governs the functionality and “services” of microbial communities, and hence also their role in ocean biogeochemistry<sup>17,18</sup>.

In order to survive in the nutritionally dilute ocean, particle feeding protists need to daily clear a volume of water for sub-micron sized prey that is equivalent to one million times their own cell volume<sup>19</sup>. The protists have evolved two fundamentally different ways of achieving this<sup>4,19</sup>: (i) They

can be inactive ambush feeders that wait for motile bacteria to collide with their prey capture structures; this feeding mode only targets the larger motile bacteria, not the smaller non-motile phototrophic and heterotrophic bacteria that dominate the large oligotrophic regions of the ocean. Or (ii) they may swim or create a feeding current to encounter prey. Thus swimming and feeding are often intimately related processes, they are constrained by the fluid dynamics at the microscale in often non-intuitive ways<sup>20,21</sup>, and simple fluid dynamics arguments suggest that physically feasible feeding rates are often orders of magnitude lower than what is required for survival<sup>11</sup>. Thus, there is something fundamental missing in our understanding of flagellate feeding

Fluid dynamicists have a long tradition for examining the fluid dynamics of swimming – not feeding - in microorganisms at low Reynolds numbers in viscosity dominated environments<sup>22–30</sup>. The main scope of the literature has been fluid dynamical problems, and many of the problems studied, ranging from Purcell’s three-link swimmer<sup>20,31</sup> to the study of gyrotactic bioconvection and dense suspensions<sup>32–36</sup>, relate only remotely to the ecology and biology of “real” microorganisms in their natural environments. Yet, these studies have developed powerful analytical tools and models that we here use to address ecologically relevant questions.

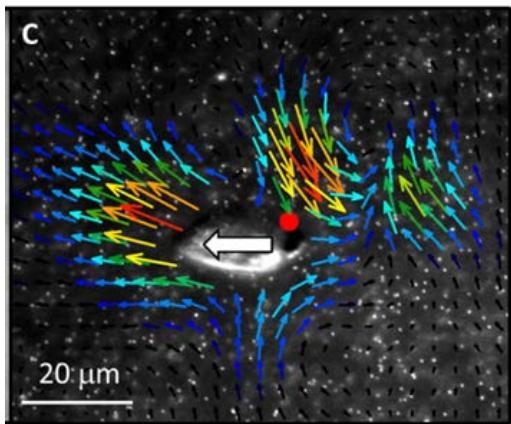
The optimal design of body plan and propulsion mechanism for efficient swimming, for stealth, and for feeding are typically in direct conflict with one another<sup>37</sup>. Consider, for example, a swimming flagellate that is pushed or pulled through the water by a beating flagellum. Many of such flagellates have been described as interception feeders, i.e., they capture their bacterial prey as the prey directly collide with the flagellate<sup>4,12</sup>. However, only prey that “sits” on streamlines that passes within one prey radius of the flagellate will be intercepted and captured<sup>38</sup>. This implies that the closer the streamlines come to the cell body, the more efficient is prey encounter. But the closer the streamlines, the larger is also the viscous drag. In fact, the drag penalty can be significant, increasing the energetic cost of swimming by more than an order of magnitude<sup>23</sup>. Streamline proximity is governed by the length and position of the flagellum: a long flagellum is optimal for swimming while a short flagellum optimizes feeding, so there is a direct conflict<sup>11</sup>. More important, even with a short flagellum, the clearance rates that can be calculated from simple Stokes flow models are about two orders of magnitude too low compared to what is necessary and what has been measured in some cases<sup>11</sup>. Thus, we miss something fundamental in our description, and the problem has been overlooked by previous studies of the fluid dynamics<sup>4,39,40</sup>.



**Fig. 1.** (A) Micrograph of freely swimming choanoflagellate and (B) flow obtained from particle tracking. The beating flagellum (blue) drives the feeding current through the filter (green) on which bacteria sized prey particles are caught. Modified from<sup>41</sup>.

Filter feeding choanoflagellates offer another example of confusion (Fig. 1). Their flagellum drives water through the surrounding collar filter that strains bacteria from suspension<sup>42</sup>. However, robust models demonstrate that the force that can be generated by the flagellum appears to be more than an order of magnitude too low to produce the necessary pressure drop over the finely meshed filter<sup>41</sup>, a fact that again has been overlooked or not examined by the numerous previous studies<sup>9,39,42–44</sup>.

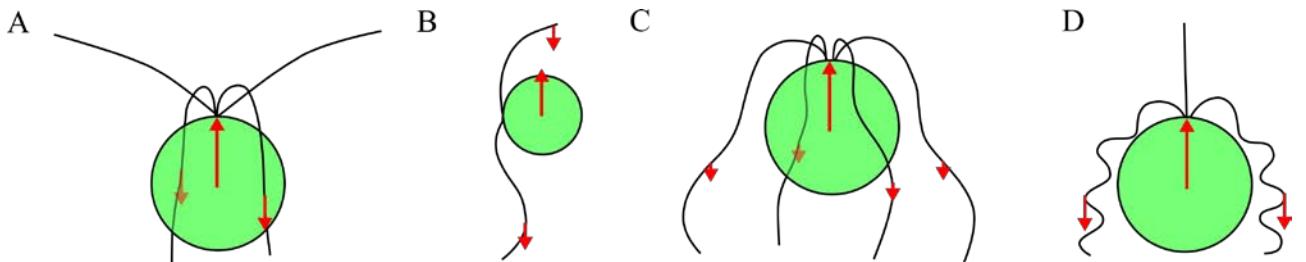
In addition to locomotion and feeding, the beating of the flagella also produces a fluid disturbance that exposes the flagellate to its rheotactic (flow sensing) predators. Small flagellates are grazed by microzooplankton many of which perceive their prey from the fluid disturbance the prey generates<sup>45</sup>. So, the flagellate is sandwiched between the need to feed and move, and the need not to be eaten. The fluid signal generated by a swimming cell depends strongly on the arrangement of the flagella or cilia: thus, an equatorial or breast stroke arrangement of the propulsion forces appears to be optimal for stealth, as suggested by both models and observations<sup>37,46,47</sup>.



**Fig. 2.** Snapshot of flow field generated by swimming and feeding dinoflagellate. Note how water is pushed in front of the cell in the swimming direction (white arrow), and how water is drawn towards the point on the cell (red dot) where prey is encountered and captured. Modified from<sup>48</sup>.

One way to resolve these apparent paradoxes are through visualization of the flow generated by the swimming and feeding protists. This has recently become feasible through the application of particle tracking and micro particle image velocimetry ( $\mu$ PIV). Flow fields are now available for a few freely swimming unicellular organisms<sup>37,49,50</sup>, and we have demonstrated how particle feeding

dinoflagellates have solved the conflicting needs of a long flagellum to optimize propulsion, and a short flagellum to optimize prey encounter: They are equipped with a long, trailing flagellum that is thought to mainly account for propulsion, and a transverse flagellum that encircles the cell body<sup>51,52</sup>. The transverse flagellum pulls the streamlines close to the cell and generates a feeding current that can account quantitatively for the observed clearance rates (Fig. 2), a feature not captured by previous modelling attempts<sup>53,54</sup>. However, for other particle feeding flagellates with diverse flagellar arrangements (Fig. 3), the flow fields that they generate are unexplored and the adaptive significance of the flagellar arrangements with respect to feeding, propulsion, and stealth remains unclear.



**Fig. 3.** Some of the diversity of position, number and beating of flagella in flagellates with two or more flagella. Modified from <sup>55,56,47</sup>.

**SPECIFIC HYPOTHESES:** We will pursue the general objectives through the testing of three interdependent hypotheses:

**Hypothesis 1:** *Particle feeding protists generate feeding currents to facilitate efficient prey encounter.* Flow fields and feeding currents have been observed in only very few motile protists (Figs. 1 & 2) Many protists are “mixotrophic”, i.e., they can perform both photosynthesis and particle feeding, and thus do not depend entirely on feeding, while others are purely heterotrophic. We hypothesize that the latter in particular should have efficient feeding currents.

**Hypothesis 2:** *Flagellar arrangements are optimized for efficient feeding.* The optimal design (number, position, length, kinematics of flagella) for feeding, propulsion, and stealth may be conflicting, but in purely heterotrophic protists, the design is optimized for feeding. In mixotrophic (and autotrophic), propulsion and stealth have relatively higher priority.

**Hypothesis 3:** *Prey encounter efficiency trades off against predation risk.* That is, the most efficient feeding strategies are also the most risky.

**APPROACH AND METHODS:** We will harness high-speed video-micrography, novel imaging and flow visualisation techniques, and novel fluid dynamical models to provide predictions of how

flagellar arrangement relate to the feeding-mortality trade-off, and test these predictions in incubation experiments.

*High-speed video-microscopy and holography:* We will record flagellar motion, swimming kinematics, and prey encounter behaviour for a diverse collection of particle feeding protists. This is an extension of the fundamental work by Fenchel<sup>4</sup> and will allow basic descriptions of the main forms, help formulate hypotheses on mechanisms, and provide input to fluid dynamical models. Through collaboration with Prof Roman Stocker (ETH Zürich) we will have access to a three-dimensional holographic observation system that allows three-dimensional observations of selected predator-prey interactions to help interpret the more numerous two-dimensional observations. This part is risky, and the fall-back position is the two-dimensional observations.

*Flow visualisation:* Flow visualisation will allow us to detect and describe feeding currents (**H1**), quantify fluid disturbances, their spatial extension and temporal and spatial attenuation (**H2+H3**). We have established and will use two-dimensional μPIV and particle tracking as the basic techniques<sup>37,41</sup>. In both, the fluid is seeded by tracer particles that allow quantification of flow fields. There is a limit to how small organisms can be studied because Brownian motion of tracer particles may overwhelm induced flow speeds, but we have successfully resolved flow fields generated by 5 micron sized flagellates<sup>57</sup>.

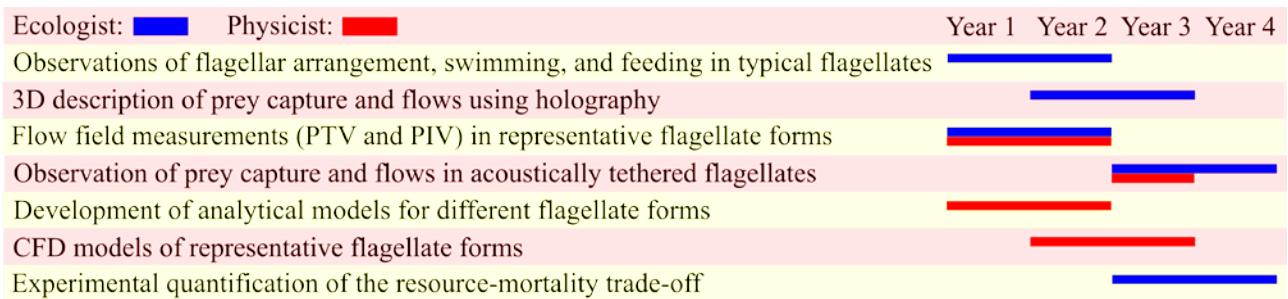
*Acoustic tethering:* We will develop an acoustofluidic “tweezers” to keep individual flagellates in microscopic focus without disturbing the dynamics of tracer and prey particles. On this we will collaborate with Prof Henrik Bruus (DTU Physics) who has extensive experience with the use of ultrasound for cell and particle manipulation in microfluidics<sup>58–60</sup>. This is a novel and risky approach, but if successful, it will allow us unprecedented observational details of prey interception and flow fields.

*Fluid dynamical models:* Together with observations, modelling will allow us to compare and quantify feeding currents (**H1**), fluid disturbances (stealth and predation risk) (**H3**), and propulsion efficiency for the various types of flagellar arrangements and kinematics observed, thus permitting test of **H2**. We will combine the use of analytical models employing Stokes flow solutions<sup>11,22,47,57</sup>, and computational fluid dynamics (CFD) models. The idealized analytical model will help yield fundamental insights in the underlying processes, while CFD may be more suitable for detailed description of complex geometries and kinematics and quantitative comparison with experiments. The combination of models will allow quantification of feeding currents and an understanding of

how they are generated by the combined action of one or multiple flagella. For CFD modelling, we will collaborate with the groups of Prof Jens H. Walter (DTU Mechanical Engineering) and Prof Stuart Humphries (Lincoln University, UK). We will combine CFD using the commercial software (STAR-CCM+) that allows simulations of flows in complex geometries and accurate modelling of beating flagella with a novel Boundary Element Method that can adapt to any cell morphology and provides accurate estimates of fluid movement around plankton with low computational costs<sup>61–63</sup>. Our initial trials with the latter have provided extremely promising results.

*Experimental quantification of the resource-mortality trade-off:* The above observations will allow theoretical estimates of clearance rates and fluid disturbances (predation risk). We will quantify both in simple incubation experiments with which we are familiar, using bacteria as prey, and rheotactic copepod (larvae) as predators. The theoretical predictions and the direct experimental estimates will both allow us to test and quantify the feeding-risk trade-off (**H3**).

**WORK PLAN AND MILESTONES:** We will recruit a post doc and a PhD student through international advertising and from our international network. We envisage an experimentalist (post doc) with a background in plankton ecology and a physicist (PhD student) with a modelling background in small-scale fluid dynamics. The plankton ecologist will mainly work with the experiments, and the physicist with the modelling, but they will collaborate on both activities, as described in the diagram below. We will also have master and project students working on the project and have the young researchers help with supervision.



**IMPLEMENTATION:** DTU Aqua will in January 2017 move into brand new facilities at DTU Lyngby Campus with relevant and necessary cold-rooms, cultivation facilities, video-laboratories, optical tables, and have access to high-speed cameras, microscopic setups and software for  $\mu$ PIV. Our collaborators have additional equipment, and we have access to CPU time at DTU Physics.

**THE RESEARCH GROUP:** The two PIs have complementary backgrounds in biology and physics. We have developed cross-disciplinary collaboration since 2007 and have jointly supervised one M.Sc. student, two PhD students, and two post docs. Our two laboratories master most – but not all – of the techniques that we plan to use. We will draw on collaboration with R. Stocker (ETH) for 3D holographic imaging; with H. Bruus (DTU) for acoustic tethering; and with J. H. Walter (DTU) and S. Humphries (Lincoln) for CFD modelling; commitment letters from international collaborators are enclosed. The two PIs will co-supervise the young researchers, and the PhD student will be enrolled in the PhD school at DTU Physics. The young researchers will receive cross-disciplinary training and be offered research stays with our collaborators, as relevant, and become members of the Small-Scale Ocean Biophysics community that organises student exchanges and international workshops every second year (by Kiørboe, Stocker, and Humphries at Aspen Physics Center: 2011 and 2015; Les Houches Physics School: 2013; Eilat Marine Lab 2016).

*Gender balance:* Unintentionally, the PI group is entirely male dominated. We will consider a better gender balance when recruiting, although scientific excellence will be the main criterion.

**EXPECTED OUTCOME AND PERSPECTIVES:** The main general outcome of the project is a quantification of the relations between flagellar arrangement and kinematics on one hand and the feeding-risk trade-off on the other. The mechanistic underpinning of this relation will allow us to generalize the results beyond the relatively few species that we can examine. The ideas and preliminary experiments described above have been developed at the Centre for Ocean Life (<http://www.oceanlifecentre.dk/>) to allow the development of trait-based descriptions and models of marine communities. Key to these models is a quantification of resource acquisition-mortality risk trade-offs, because these are what generates diversity (both in reality and in trait-based models). The project described here will not be part of the Centre for Ocean Life (expires ultimo 2017), but the results will be implemented in trait-based models in collaboration with our colleagues at the Centre (Profs. AW Visser and KH Andersen) to explore ocean biogeochemistry.

**PUBLICATION AND OUTREACH PLAN:** We will present our results at international meetings and publish them in high-impact, peer-reviewed journals. We aim at 3 and 6 first-authored papers by the PhD student and the postdoc, respectively. We also aim for several popular science articles as well as presentations to lay audiences, as we have done in the past. We will finally make our videos and animations available on a website as these may be useful for teaching.

## REFERENCES:

1. Azam, F. *et al.* The Ecological Role of Water-Column Microbes in the Sea. *Mar. Ecol. Prog. Ser.* **10**, 257–263 (1983).
2. Fenchel, T. Ecology of Heterotrophic Microflagellates. IV Quantitative Occurrence and Importance as Bacterial Consumers . *Mar. Ecol. Prog. Ser.* **9**, 35–42 (1982).
3. Fenchel, T. in *Flows of Energy and Materials in Marine Ecosystems; NATO conference series* (ed. Fasham, M.) **11**, 301–315 (Plenum Press, 1984).
4. Fenchel, T. The Ecology Of Heterotrophic Microflagellates. *Adv. Microb. Ecol.* **9**, 57–97 (1986).
5. Fenchel, T. Ecology of Heterotrophic Microflagellates. III. Adaptations to Heterogeneous Environments . *Mar. Ecol. Prog. Ser.* **9**, 25–33 (1982).
6. Fenchel, T. Protozoan filter feeding. *Prog. Protistol. J.O. Corliss D. J. Patterson* **1**, 65–113 (1986).
7. Fenchel, T. Ecology of Heterotrophic Microflagellates. I. Some Important Forms and Their Functional Morphology . *Mar. Ecol. Prog. Ser.* **8**, 211–223 (1982).
8. Fenchel, T. Ecology of Heterotrophic Microflagellates. II. Bioenergetics and Growth . *Mar. Ecol. Prog. Ser.* **8**, 225–231 (1982).
9. Dayel, M. J. & King, N. Prey capture and phagocytosis in the choanoflagellate *Salpingoeca rosetta*. *PLoS One* **9**, 1–6 (2014).
10. Eccleston Parry, J. D. & Leadbeater, B. S. C. A comparison of the growth kinetics of 6 marine heterotrophic nanoflagellates fed with one bacterial species. *Mar. Ecol. Prog. Ser.* **105**, 167–178 (1994).
11. Langlois, V. J., Andersen, a., Bohr, T., Visser, a. W. & Kiørboe, T. Significance of swimming and feeding currents for nutrient uptake in osmotrophic and interception-feeding flagellates. *Aquat. Microb. Ecol.* **54**, 35–44 (2009).
12. Boenigk, J. & Arndt, H. Particle Handling during Interception Feeding by Four Species of Heterotrophic Nanoflagellates. *47*, 350–358 (2000).
13. Boenigk, J. & Arndt, H. Comparative studies on the feeding behavior of two heterotrophic nanoflagellates: The filter-feeding choanoflagellate *Monosiga ovata* and the raptorial-feeding kinetoplastid *Rhynchomonas nasuta*. *Aquat. Microb. Ecol.* **22**, 243–249 (2000).
14. Christensen-Dalsgaard, K. K. & Fenchel, T. Increased filtration efficiency of attached compared to free-swimming flagellates. *Aquat. Microb. Ecol.* **33**, 77–86 (2003).
15. Calbet, A. & Landry, M. R. Phytoplankton growth, microzooplankton grazing, and carbon cycling in marine systems. *Limnol. Oceanogr.* **49**, 51–57 (2004).
16. Winter, C., Bouvier, T., Weinbauer, M. G. & Thingstad, T. F. Trade-offs between

- competition and defense specialists among unicellular planktonic organisms: the ‘killing the winner’ hypothesis revisited. *Microbiol. Mol. Biol. Rev.* **74**, 42–57 (2010).
- 17. Reiss, J., Bridle, J. R., Montoya, J. M. & Woodward, G. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* **24**, 505–514 (2009).
  - 18. Krause, S. *et al.* Trait-based approaches for understanding microbial biodiversity and ecosystem functioning. *Front. Microbiol.* **5**, 1–10 (2014).
  - 19. Kiørboe, T. How zooplankton feed: Mechanisms, traits and trade-offs. *Biol. Rev.* **86**, 311–339 (2011).
  - 20. Purcell, E. Life at low Reynolds number. *Am. J. Phys.* **45**, 3 (1977).
  - 21. Dusenberry, D. *Living at Micro Scale: The Unexpected Physics of Being Small*. (Harvard Univ. Press, 2009).
  - 22. Lauga, E. & Powers, T. R. The hydrodynamics of swimming microorganisms. *Reports Prog. Phys.* **72**, 96601 (2009).
  - 23. Guasto, J. S., Rusconi, R. & Stocker, R. Fluid Mechanics of Planktonic Microorganisms. *Annu. Rev. Fluid Mech.* **44**, 373–400 (2012).
  - 24. Goldstein, R. E. Green Algae as Model Organisms for Biological Fluid Dynamics. *Annu. Rev. Fluid Mech.* **47**, 343–375 (2015).
  - 25. Brumley, D. R., Rusconi, R., Son, K. & Stocker, R. Flagella, flexibility and flow: Physical processes in microbial ecology. *Eur. Phys. J. Spec. Top.* **224**, 3119–3140 (2015).
  - 26. Guasto, J. S., Johnson, K. a. & Gollub, J. P. Oscillatory flows induced by microorganisms swimming in two dimensions. *Phys. Rev. Lett.* **105**, 168102 (2010).
  - 27. Lauga, E. Bacterial Hydrodynamics. *Annu. Rev. Fluid Mech.* **48**, 105–130 (2016).
  - 28. Rodenborn, B., Chen, C.-H., Swinney, H. L., Liu, B. & Zhang, H. P. Propulsion of microorganisms by a helical flagellum. *Proc. Natl. Acad. Sci. U. S. A.* **110**, E338–E347 (2013).
  - 29. Eloy, C. & Lauga, E. Kinematics of the most efficient cilium. *Phys. Rev. Lett.* **109**, 1–5 (2012).
  - 30. Klindt, G. S. & Friedrich, B. M. Flagellar swimmers oscillate between pusher- and puller-type swimming. *Phys. Rev. E - Stat. Nonlinear, Soft Matter Phys.* **92**, 1–6 (2015).
  - 31. Tam, D. & Hosoi, A. E. Optimal Stroke patterns for Purcell’s three-link swimmer. *Phys. Rev. Lett.* **98**, 1–4 (2007).
  - 32. Pedley, T. & Kessler, J. Hydrodynamic Phenomena In Suspensions Of Swimming Microorganisms. *Annu. Rev. Fluid Mech.* **24**, 313–358 (1992).
  - 33. Bearon, R. N. Helical swimming can provide robust upwards transport for gravitactic single-cell algae; a mechanistic model. *J. Math. Biol.* **66**, 1341–1359 (2013).

34. Kirkegaard, J. B., Marron, A. O. & Goldstein, R. E. Motility of Colonial Choanoflagellates and the Statistics of Aggregate Random Walkers. *Phys. Rev. Lett.* **116**, 1–6 (2016).
35. Petroff, A. P., Wu, X. L. & Libchaber, A. Fast-moving bacteria self-organize into active two-dimensional crystals of rotating cells. *Phys. Rev. Lett.* **114**, 1–6 (2015).
36. Saintillan, D. & Shelley, M. J. Instabilities and pattern formation in active particle suspensions: Kinetic theory and continuum simulations. *Phys. Rev. Lett.* **100**, 1–4 (2008).
37. Kiørboe, T., Jiang, H., Gonçalves, R. J., Nielsen, L. T. & Wadhwa, N. Flow disturbances generated by feeding and swimming zooplankton. *Proc. Natl. Acad. Sci. U. S. A.* **111**, 11738–43 (2014).
38. Kiørboe, T. & Titelman, J. Feeding, prey selection and prey encounter mechanisms in the heterotrophic dinoflagellate *Noctiluca scintillans*. *J. Plankton Res.* **20**, 1615–1636 (1998).
39. Pettitt, M. E., Orme, B. a a, Blake, J. R. & Leadbeater, B. S. C. The hydrodynamics of filter feeding in choanoflagellates. *Eur. J. Protistol.* **38**, 313–332 (2002).
40. Shimeta, J. & Jumars, P. Physical mechanisms and rates of particle capture by suspension feeders. *Oceanogr. Mar. Biol. Annu. Rev.* **29**, 191–257 (1991).
41. Nielsen, L. T., Dölger, J., Kiørboe, T. & Andersen, A. Hydrodynamics of microbial filter-feeding. *Proc. Natl. Acad. Sci.* **Submitted**,
42. Leadbeater, B. S. C. *The Choanoflagellates Evolution, Biology and Ecology*. (Cambridge University Press, 2015).
43. Roper, M., Dayel, M. J., Pepper, R. E. & Koehl, M. a R. Cooperatively generated stresslet flows supply fresh fluid to multicellular choanoflagellate colonies. *Phys. Rev. Lett.* **110**, 228104 (2013).
44. Orme, B. a. a., Blake, J. R. & Otto, S. R. Modelling the motion of particles around choanoflagellates. *J. Fluid Mech.* **475**, 333–355 (2003).
45. Jakobsen, H. H., Everett, L. M. & Strom, S. L. Hydromechanical signaling between the ciliate *Mesodinium pulex* and motile protist prey. *Aquat. Microb. Ecol.* **44**, 197–206 (2006).
46. Jiang, H. & Paffenhöfer, G. A. Relation of behavior of copepod juveniles to potential predation by omnivorous copepods: An empirical-modeling study. *Mar. Ecol. Prog. Ser.* **278**, 225–239 (2004).
47. Andersen, A., Wadhwa, N. & Kiørboe, T. Quiet swimming at low Reynolds number. *Phys. Rev. E* **91**, 42712 (2015).
48. Nielsen, L. T. & Kiørboe, T. Feeding currents facilitate a mixotrophic way of life. *ISME J.* **9**, 2117–27 (2015).
49. Drescher, K., Goldstein, R. E., Michel, N., Polin, M. & Tuval, I. Direct measurement of the flow field around swimming microorganisms. *Phys. Rev. Lett.* **105**, 168101 (2010).

50. Drescher, K., Dunkel, J., Cisneros, L. H., Ganguly, S. & Goldstein, R. E. Fluid dynamics and noise in bacterial cell-cell and cell-surface scattering. *Proc. Natl. Acad. Sci. U. S. A.* **108**, 10940–10945 (2011).
51. Fenchel, T. How dinoflagellates swim. *Protist* **152**, 329–338 (2001).
52. Berdach, J. T. in Situ Preservation of the Transverse Flagellum of Peridinium Cinctum (Dinophyceae) for Scanning Electron Microscopy1. *J. Phycol.* **13**, 243–251 (1977).
53. Nguyen, H., Ortiz, R., Cortez, R. & Fauci, L. The action of waving cylindrical rings in a viscous fluid. *J. Fluid Mech.* **671**, 574–586 (2011).
54. Nakai, T., Shihira-ishikawa, I., Miyawaki, A. & Goto, T. Boundary Element Analysis and Three - Dimensional Observation of Propulsive Force and Torque of a Dinoflagellate Symbiodinium. *J. Aewro Aqua Bio-Mechanisms* **3**, 79–84 (2013).
55. Sleigh, M. a. Flagellar beat patterns and their possible evolution. *Biosystems*. **14**, 423–431 (1981).
56. Inouye, I. & Hori, T. High-speed video analysis of the flagellar beat and swimming patterns of algae: possible evolutionary trends in green algae. *Protoplasma* **164**, 54–69 (1991).
57. Dölger, J., Nielsen, L. T., Kiørboe, T. & Andersen, A. Swimming and feeding of mixotrophic biflagellates. *Sci. Rep.* **Submitted**,
58. Bruus, H. Acoustofluidics 10: scaling laws in acoustophoresis. *Lab Chip* **12**, 1578–86 (2012).
59. Antfolk, M., Muller, P. B., Augustsson, P., Bruus, H. & Laurell, T. Focusing of sub-micrometer particles and bacteria enabled by two-dimensional acoustophoresis. *Lab Chip* **14**, 2791–9 (2014).
60. Bruus, H. Acoustofluidics 7: The acoustic radiation force on small particles. *Lab Chip* **12**, 1014–21 (2012).
61. Cortez, R. The Method of Regularized Stokeslets. *SIAM J. Sci. Comput.* **23**, 1204–1225 (2001).
62. Shum, H., Gaffney, E. A. & Smith, D. J. Modelling bacterial behaviour close to a no-slip plane boundary: the influence of bacterial geometry. *Proc. R. Soc. A Math. Phys. Eng. Sci.* **466**, 1725–1748 (2010).
63. Smith, D. J. A boundary element regularized Stokeslet method applied to cilia- and flagella-driven flow. *Proc. R. Soc. A Math. Phys. Eng. Sci.* **465**, 3605–3626 (2009).