<table>
<thead>
<tr>
<th>Title</th>
<th>Hydrodynamics of squirming locomotion at low Reynolds numbers</th>
</tr>
</thead>
<tbody>
<tr>
<td>Author(s)</td>
<td>Ishimoto, Kenta</td>
</tr>
<tr>
<td>Citation</td>
<td>Kyoto University</td>
</tr>
<tr>
<td>Issue Date</td>
<td>2015-03-23</td>
</tr>
<tr>
<td>URL</td>
<td><a href="https://doi.org/10.14989/doctor.k18770">https://doi.org/10.14989/doctor.k18770</a></td>
</tr>
<tr>
<td>Type</td>
<td>Thesis or Dissertation</td>
</tr>
<tr>
<td>Textversion</td>
<td>ETD</td>
</tr>
</tbody>
</table>
Hydrodynamics of squirming locomotion at low Reynolds numbers

Kenta Ishimoto
—Abstract—

Microorganisms such as *Paramecium* generate propulsion with attached appendages called cilia and flagella. The flow around the organisms is at low Reynolds numbers, i.e. the viscous force is dominating, and therefore the swimming is strongly restricted by the surrounding fluid motion, as illustrated by the scallop theorem. Thus morphology of appendages and the swimming strokes should be mechanically sophisticated through long history of evolution. In this thesis, a microorganism is considered as a self-propelled body with surface deformation, and hydrodynamics of swimming microorganisms is investigated with particular interest in swimming efficiency and swimming stability. As a fundamental and universal mathematical model for a deforming swimmer, James Lighthill first considered, in 1952, the squirmer model, which is originally a slightly deforming sphere in the steady Stokes flow, and the model is still frequently discussed for motion of microswimmers, in particular, ciliates such as *Paramecium* and *Volvox*. In this thesis, fundamental aspects of swimming microorganisms are explored by the use of extensions of the squirmer model from three perspectives: inertia, boundary, and large deformation.

First, the spherical squirming motion is considered in the unsteady Stokes flow to understand inertia effects on swimming, where the inertia is usually neglected in the studies of microswimming. Asymptotic expansion is performed with respect to small amplitude and small inertia of both fluid and a body to find out motion of a squirmer with time-periodic deformation, and an expression for the time-averaged swimming velocity after a long time is derived, which shows that the scallop theorem does no longer hold in the presence of inertia effect. Further, for a motion with metachronal wave, corrections due to inertia are found in deformation with wavenumber \( k = 1 \), which may correspond to flapping motion observed in tiny organisms with non-negligible inertia. With a more simplified squirmer, optimal strokes with respect to swimming efficiency for given energy consumption is obtained, being indicative of gradual transformation of the optimal stroke from a wavy motion to a flapping motion as the inertia effects increase.

Next, a model simplification is considered, and a spheroidal tangential squirmer, which is a rigid spheroid with tangential surface velocity, is discussed to investigate effects of the presence of a boundary such as a glass substrate. The motion of the simplified squirmer near an infinite flat plane boundary is reduced into two-dimensional dynamical system and the stability analysis is numerically performed, using the boundary element method for Stokes flow. Then the hydrodynamical interaction between a swimmer
and a boundary is characterised by boundary conditions on the flat plane and
geometry as well as the swimming strokes of the squirmer, and the surface accu-
cumulation phenomena observed in bacteria and spermatozoa are interpreted
as a stable fixed point of the dynamical system.

Finally, with improvement of the boundary element method for arbi-
trary volume-conserving swimmers, the Lighthill asymptotic expansions for
a squirmer with metachronal wave is numerically validated and extended for
a squirmer with large amplitude. It is found that the motion is well explained
by approximating the local surface deformation as a squirming plane, if the
wavenumber is sufficiently large. Nevertheless, the Lighthill theory is no
longer applicable to motion of a squirmer with small wavenumber and large
amplitude, which is found to give the most optimal swimming efficiency,
suggesting a novel type of microswimming.
## Contents

1 Introduction .......................... 1

2 Squirming locomotion with inertia .......... 10
   2.1 Introduction .......................... 10
   2.2 Formulation .......................... 12
      2.2.1 Fluid equations ...................... 14
      2.2.2 Boundary conditions .................. 15
      2.2.3 Body equation of motion ................. 18
   2.3 Fluid dynamic force ...................... 19
      2.3.1 Representation of $d_s$ ............... 20
      2.3.2 Fluid force due to deformation .......... 22
      2.3.3 Comparison with other studies .......... 23
   2.4 Motion of a swimmer ..................... 23
      2.4.1 Zeroth and first order of the expansion ... 25
      2.4.2 Second order of the expansion .......... 27
   2.5 Inertia effects on the surface wave pattern . 29
   2.6 Discussion .......................... 30
      2.6.1 Energy consumption .................... 30
      2.6.2 Example swimmer ..................... 33
   2.7 Conclusion .......................... 34

3 Squirming locomotion near a boundary .......... 36
   3.1 Introduction .......................... 36
   3.2 The model swimmer and its fluid dynamics .... 38
      3.2.1 The squirmer ........................ 38
      3.2.2 The far-field expression and singularity solutions ... 40
      3.2.3 Dynamical systems and time-reversal symmetry .... 42
      3.2.4 Numerical scheme ..................... 43
   3.3 Dynamics in phase space ........................ 45

iii
CONTENTS

C Details on the boundary element method 108
   C.1 Mesh generation ........................................ 108
   C.2 Boundary element integral ............................ 109
      C.2.1 Three-node flat triangle ......................... 109
      C.2.2 Six-node curved triangle ......................... 111
   C.3 Linear problem ....................................... 112

Acknowledgements 114

References 116
Chapter 1

Introduction

Swimming microorganisms.—

Ever since Van Leeuwenhoek and Hook founded microbiology over 300 years ago via improvements in microscopy, scientists have vigorously explored the fascinating biodiversity at the sub-millimetre scale. In turn, this has had an immense impact on our lives and our environment, for example driving a revolution in the understanding of infectious disease and recycling in the biosphere. One aspect of this biodiversity that has emerged in recent decades, with a resurgence of interest in the past few years, is cell motility and especially its underlying mechanics.

Microorganisms exist everywhere in life, and their locomotive motions are apparently different from our ways of swimming and those of other familiar visible organisms such as insects, birds and fish. Bacteria corkscrew with their flagella, and eukaryotic organisms such as Chlamydomonas and sperm cells achieve the locomotion with bending their flagella and beating surrounding fluid. Microswimmers seen by our naked eyes if looking carefully, which include, for example, Paramecium and Volvox, have their body surface covered with a number of tiny appendages, called cilia.

Size of a microorganism is literally the order of μm. For bacteria such as Escheria coli and Salmonella, the cell size is typically several μm with their flagella about 10μm long. Among ciliate organisms, the characteristic length is of the order of 100μm, with each cilia being typically of the order of 10μm [64, 14, 16, 57]. On such a micrometer scale, inertial effects can be negligible, namely a very small Reynolds number $Re = LU/\nu$, where $L$ is a characteristic scale of length of the organism, $U$ is a scale of velocity and $\nu$ is kinematic viscosity of the fluid. Indeed, the Reynolds number can be of the order of $10^{-5}$ or $10^{-4}$ for bacteria, and of $10^{-1}$ for Paramacium. In the world
1 Introduction

of low Reynolds numbers, viscous force is dominant, which is quite different from the world people live in.

Stokes dynamics.—

Let us introduce three dimensionless parameters, Reynolds number, oscillatory Reynolds number and Stokes number, to characterize the motion of a microorganisms in fluids. The Reynolds number \( Re = \frac{LU}{\nu} \) is defined as described above. The oscillatory Reynolds number \( R_\omega = \frac{L^2}{\nu T} \) is a ratio of the magnitude of time derivative term to that of viscous force term in the Navier-Stokes equation. Here \( T \) is a characteristic scale of time for which we employ an inverse frequency of a stroke of a swimmer. The Stokes number \( R_S \) represents the magnitude of body inertia defined as \( R_S = \frac{p_S}{\rho_F} R_\omega \), where \( p_S \) and \( \rho_F \) indicate averaged density of a swimmer and fluid, respectively. When all these nondimensional parameters vanish as often assumed for a swimming microorganism, the fluid equation is reduced to the steady Stokes equation, while the equations of motion of the body can be reduced to the force and the torque balance equations.

Let \( \mathbf{u} = \mathbf{u}(x) \) be the velocity vector of the fluid at the position \( x \), \( p = p(x) \) the pressure, and \( \mu \) a viscosity constant of the fluid. The steady Stokes equations are then expressed as

\[
\nabla p = \mu \Delta \mathbf{u},
\]

where \( \mathbf{u} \) satisfies the incompressible condition, \( \nabla \cdot \mathbf{u} = 0 \). If the body is immersed in the fluid obeying the above equations, the no-slip boundary conditions should be imposed on the body surface, \( S \), as for usual viscous flows, meaning that the fluid velocity \( \mathbf{u} \) equals to the surface velocity \( \mathbf{v} \) on \( S \).

One of the noteworthy mathematical properties of this partial differential equations is linearity. Thus, solutions of the equations are constructed by a superposition of fundamental solutions. The fundamental solution induced by a point force is called Stokeslet. The spatial derivatives of the Stokeslet are also solutions of this system. These are rotational solutions, i.e. \( \omega = \nabla \times \mathbf{u} \neq 0 \). The other type of the solutions are so-called potential flows, that can be expressed by gradient of a scalar function, \( \phi \). The potential flows correspond to the fundamental solutions of the Laplace equations, \( \Delta \phi = 0 \), and cover the irrotational part of the flow. The details of the fundamental solutions of the Stokes equations will be discussed in §3.2.2.

Furthermore, owing to the linearity, the solution of this equations is uniquely determined by the simultaneous boundary conditions.
Microswimmer changes their shape to propel in the fluid. Let us consider a single microswimmer is immersed in the fluid. The body surface velocity can be decomposed into linear velocity, angular velocity, and deformation velocity. One possible decomposition was shown by Ishimoto & Yamada [47], who introduced a virtual swimmer that possesses the same deformation as the real swimmer immersed in fluid but has no surrounding fluid. They showed that the force and the torque acting on the swimmer are represented by the sum of the drag and the reaction of swimmer’s propulsion. Now let $t$ be time and $s(t)$ label a point on the surface of the swimmer. The drag force is a linear function of the linear and the angular velocities of the swimmer, reflecting the linearity of the equations. The linear relation is described with a proportional coefficient matrix, $K$, called a grand resistive matrix, which is the function only of the simultaneous shape $s(t)$ of the swimmer, and the simultaneous position and direction. The reaction force to the propulsion is given in the form of the surface integral over $S$. The integrand is linearly dependent on the surface deformation velocity, with the coefficient matrix being a function of $s(t)$ and the position and the direction.

In this context, the swimmer’s dynamics is completely determined by the deformation or equivalently the shape and the surface velocity. The interaction between the shape and the fluid is the central issue of this system.

The scallop theorem.—

The second important property of this system is time-reversibility. This may be illustrated by a well-known theorem known as Purcell’s scallop theorem, which shows unavailability of reciprocal motions of a microswimmer [84]. The detailed mathematical proof of this theorem was given by Ishimoto & Yamada [47].

The scallop theorem states that a swimmer with a reciprocal motion in fluid which obeys the steady Stokes equation, returns to the same position with the same direction as the initial state, after one period of the stroke. The reciprocal motion can be characterized by the existence of one dimensional shape parameter $s \in [0, 1]$ which identifies the shape of the swimmer.

This theorem emphasises that the motion of swimmers in low Reynolds number flow is strongly restricted by the surrounding medium, and therefore stresses the significance of fluid dynamics on the morphology and ecology. The linear and the angular velocity of the microswimmers are determined solely by the simultaneous state of the swimmer if all the inertia is negligible, and thus, in such a situation, the problems can be reduced to the instant interaction between the fluid and the body with surface velocity.
The fact that microorganisms can swim in reality, means that swimmers avoid the theorem in one way or another. The easiest and most common way is to have multiple shape parameters to swim in a nonreciprocal manner. Corkscrew filaments of bacteria and *metachronal waves* in ciliate organisms (see figure 2.1 (b)) are the examples. Body flexibility and fluid viscoelasticity also break the theorem [59].

The breakdown of the theorem also occurs due to inertial effects. Childress & Dudley [17] first suggested the possibility of existence of a critical Reynolds number, above which the theorem breaks, and at which a transition of a stroke pattern of a mollusc occurs from ciliary to flapping. Some experimental and numerical studies [107, 108, 3, 68] support a transition driven by a dynamical instability at a critical Reynolds number. On the other hand, continuous breakdown of the theorem is suggested [56] for a non-deformable swimmer when $Re$ is nonzero but $R_\omega$ and $R_S$ are zero. For unsteady inertial effects, Wang & Ardekani [110] studied a sphere with surface velocity, which is referred as a tangential squirmer as explained later in details, when $Re$ is zero but $R_\omega$ and $R_S$ are nonzero, and they showed that a reciprocal swimmer can have a net displacement by an initial stroke, while the velocity eventually converges a harmonic function of time. For nonzero $R_S$ with other two Reynolds numbers vanishing, the continuous breakdown is analytically shown by [38, 46]. Spagnolie *et al.* [98] also supports experimentally and numerically when $Re = R_\omega = R_S$.

**The squirmer model.**—

As the fluid motion at the low Reynolds number obeying the Stokes equations is determined by the surface deformation of the swimmer, one of the most fundamental mathematical model of microswimmers consists of a simple geometrical object with slight surface deformation. There is a rich literature on the swimming by the surface deformation, especially on the relationship between the swimming stroke and swimming efficiency [93, 32, 27, 100, 22, 37, 71], nutrition transportation [69, 66, 72], hydrodynamical interaction with other cells and boundaries [44, 67, 99, 49], inertial effects [31, 38, 111, 110, 48], and viscoelasticity [58, 116, 117], as well as observational studies [25, 26, 15].

All these studies ultimately trace back to Lighthill’s inaugural exploration [63] of how swimming in a Newtonian fluid is induced by asymptotically small squirming shape deformations of a sphere, which has been dubbed the ‘Lighthill squirmer’, though the results of Lighthill’s [63] was later corrected by Blake [9, 10]. In this thesis, the squirmer model is considered for the ex-
ploration for fundamental aspects of microswimmers. Nevertheless, not only for the hydrodynamic aspects of microswimming, but the squirmer model has been studied for real biological swimmers such as ciliates, which is explained in the next section on the envelope approach. Further, the squirmer model has also been pursued for cell motility with a large deformation such as blebbing for neutrophils and *Dictyostelium discoideum* [4, 109]. These organisms have been investigated as a model of cancer locomotion and thus the squirmer model has potentials to shed light on a new aspect of cancer development and metastasis [102]. In addition, large amplitude deformations induced by pellicle motion of contractile motion of *Euglena* [103] have recently been shown to be sufficient to induce swimming [2], and this movement is also a potential application of the squirmer model.

The envelope approach.—

Blake [9, 10] has used the squirmer model to explore the swimming dynamics of the ciliates, a phylum of unicells that drive motility via a coordinated collective beating of a dense sheet of short cellular appendages on the cell surface, which are known as cilia and are schematically illustrated in Fig. 1.1. Note that each individual cilium has a cyclic beating (Fig. 1.1a), which contains two phases: the effective stroke, with the cilium extended from the cell surface which generates a larger propulsion force, and the recovery stroke, with the cilium traveling near the surface, inducing a smaller force in the opposite direction. On the whole, this cyclic beating induces a net propulsion for the cell. In addition, the collective wave of ciliary beating illustrated in Fig. 1.1(b) is referred to as the *metachronal wave* [14, 15] and, for planar beating, it exists in two main forms: symplectic and antiplectic. This classification depends on the phase between the ciliary beating and the wave progression: symplectic form require that the direction of the cilium’s effective stroke and metachronal wave propagation are in the same direction, whereas they are in opposite directions for antiplectic metachronism [13].

Whilst the validity of this model for antiplectic waves was questioned by Blake [9, 10], a later detailed study by Brennen [13] explicitly considered sufficient conditions for the validity of a squirmer model. Brennen’s sufficient conditions [13] requires that the entrainment radius of an individual cilium is much greater than the cilium separation, and that the ciliary separation is always less than the cilium length to ensure that wall effects do not change the cilium entrainment radius extensively. For typical parameters, as reported in [14], these conditions generally hold for symplectic waveform ciliates, but the requirement of a weak wall effect entails that there are $O(10)$ or more...
1 Introduction

(a) (b)

Fig. 1.1: (a) A schematic picture of an individual moving cilium attached to a cell surface. (b) A collective wave pattern of ciliary beating, whose envelope (solid) oscillates about a neutral surface (dashed) tangential to the cell surface substrate. The coordinates \((x, y)\), used in section B.1, are also indicated.

cilia per metachronal wavelength for antiplectic metachronism, though the envelope approximation is validated in many ciliates \([13]\). Thus in our study below we assume implicitly that an antiplectic swimmer represented by the squirmer model has a sufficient cilium density to fulfill this constraint.

The tangential squirmer. —

While the swimmer shape and its deformations can be arbitrary, axisymmetric bodies with tangential squirming are often assumed whereby the swimmer shape remains unchanged but an effective slip velocity is maintained on its surface. We here call this model a tangential squirmer. This is a standard abridged model of ciliate motility \([69, 71]\), whereby relatively large unicells, with a semi-axis lengthscale on the order of 50 microns, are motile due to a coating of relatively short actively beating cilia. These cilia drive a fluid flow around the cell, in turn inducing motility \([14]\); a classic pondwater example is \textit{Paramecium}, as illustrated in Fig. 1.2(a)(b). The slip-velocity swimming of the tangential squirmer is also used to model colonial algae such as \textit{Volvox carteri}, \([69, 44]\) with surface flows driven by flagella, and to model Janus particles \([99]\), which have the potential to induce slip velocities by many mechanisms, such as self-electrophoresis via asymmetric surface chemical reactions, \([78]\), as detailed in Fig. 1.2(c).

Aims and contents of this thesis. —

As James Lighthill has described the general motivation on the hydrodynamics in researches on swimming organisms, in his textbook \([65]\) (p.11),
Fig. 1.2: (Color online) (a), (b). Images of the ciliate, *Paramecium (Viri-doparamecium) chlorelligerum*. Upper Left, (a). An image from flash photomicrography of freely motile specimen after disturbance. Scale bar, 50 μm. Upper Right, (b). A scanning electron microscope image of the dorsal side, illustrating the density of cilia on the cell surface. Reproduced, with permission, from Kreutz et. al [54]. Lower (c). A schematic of a prospective self-electrophoretic propulsion mechanism for a conducting Janus particle within an acidic environment, whereby a slip-velocity is induced by the ion flows generated by a simultaneous catalytic oxidation of a fuel present in the solute, A, on one side of the particle and a catalytic reduction of a fuel, B, on the other. Reproduced, with permission, from Paxton et. al [78].
The subject so delimited is, however, of particular hydrodynamical interest, because about $10^9$ years of animal evolution in an aqueous environment, by preferential retention of specific variations that increase ability to survive and produce fertile offspring, have inevitably produced rather refined means of generating fast movement at low energy cost, which merit study.

the long history of evolution would sophisticate their swimming pattern and morphology. Particularly, swimming efficiency would be a main factor that should be optimised.

Maneuverability of locomotion is another important factor in competition for survival of swimming microorganisms. Signal pathways in control of locomotion have been investigated in terms molecular biology, in particular on bacterial chemotaxis [105]. However, we exclude the molecular regulation in this thesis, as such tiny organisms have less developed functions on sensing and regulating environment or surrounding fluid than higher animals such as fish and birds. In this context, we focus our discussion to dynamics, given the deformation or the surface velocity of a swimmer. Towards the mechanics of their regulation, we consider hydrodynamical interaction between a swimmer and environment and its mechanical stability of the swimming dynamics.

As the Stokes flow is completely determined by the surface velocity of the swimmer, the squirmer would provide fundamental aspects of microswimming, in particular, optimal strokes and stable swimming, in terms of interaction of surface deformation and fluid mechanics at low Reynolds numbers.

In this thesis, motions of the squirmer are investigated, targeting universal properties of microswimmers, in particular swimmers with inertia, adjacent boundaries, and large deformation, each of which is discussed in the separated chapters (Chapter 2 to Chapter 4), followed by the conclusions (Chapter 5).

In Chapter 2, the spherical squirmer in the unsteady Stokes flow is examined by the asymptotic expansions with respect to the small inertia and small deformation amplitude, and an explicit expression on the time-averaged swimming velocity is derived in terms of long time behaviour of time-periodic deformation of the squirmer. The results show that the scallop theorem is hold at the leading order of the expansion with respect to the amplitude, but the second order contribution gives non-zero swimming velocity in the case of reciprocal motion. When we consider deformation of metachronal wave, the major corrections due to the inertia are found in the deformation with metachronal wavenumber $k = 1$, which may correspond to a flapping deformation observed in tiny insects and molluscs as suggested in Childress
& Dudley [17]. With further simplification of the model, the optimal stroke, that provides the highest swimming efficiency given a power input, gradually changes from out-of-phase motion into in-phase motion as the inertia effects increase.

Chapter 3 is devoted to the squirmer dynamics near a boundary. The motion and the swimming stability of a tangential spheroidal squirmer near both a no-slip and a free-slip infinite plane are analysed. The stability is classified by the boundary conditions, cell geometry and the swimming strokes, after reduction of the dynamics to a two-dimensional dynamical system with time reversal duality derived from the Stokes equations. The squirmer dynamics near a no-slip boundary can possess a stable fixed point, which is expected to correspond to surface accumulation of microswimmers observed in bacteria and spermatozoa, whereby such a stable fixed cannot be observed in the case of free-slip boundary.

Effects of the large amplitude, which has not been handled in the squirmer model, are investigated in Chapter 4 with establishment of a numerical scheme based on the boundary element method. The numerical scheme is validated by the Lighthill asymptotic theory of the deformation with metachronal wave, and the dynamics of a spherical squirmer with large deformation is explored. In particular, the dynamics of a squirmer with small wavenumber and large amplitude cannot be predicted by the Lighthill theory, and it is shown that the best swimming efficiency is achieved by such large amplitude deformation with small wavenumber rather than the high wavenumber as observed in ciliary metachronal wave, shedding a light on a novel type of swimming motility at low Reynolds numbers.
Chapter 2

Squirming locomotion with inertia

2.1 Introduction

In this chapter, inertia effects on motion of microswimmers are considered with the spherical squirmer in the unsteady Stokes flows, which includes inertia of both the swimmer and the fluid motion, whereby the convective term in the flow equations is neglected. Contents of this chapter and Appendix A have been published as K. Ishimoto, J. Fluid Mech., 623 (2013) 163-189 [48].

We shed light on the case where $R_e$ and $R_S$ is nonzero but $Re$ still vanishes. This linearization has been considered for swimming microorganisms [81] and tiny insects in the air such as flapping thrips [7]. In terms of bottom-heaviness of algae microorganisms [79], $R_S/R_e$ is a slightly larger than unity, which means gravity affects locomotion of a swimmer. According to the experimental data of *Volvox* [25, 26], the swimming velocity decreases due to gravity force as the radius of the colony increases. We here introduce a nondimensionalised gravity/buoyancy force $R_g$, which corresponds to ratio of gravity/buoyancy force to viscous force, as $R_g = (R_S - R_e)gT/U$, where $g$ is the gravity acceleration constant. Suppose such a case where the swimming speed is smaller than the surface velocity of the swimmer, we can estimate the characteristic time $T$ and flow velocity $U$ as $T = 2\pi/\omega$ and $U \sim l\omega$ respectively, where $\omega$ is beat frequency and $l$ is length of a cilium. The ratio $Re/R_e$ then becomes the ratio of the cilium length and radius, $\epsilon = l/L$, which is usually small for ciliate swimmers. The condition we discuss here would be therefore satisfied. Considering *Volvox* for example, the radius of
2.1 Introduction

Fig. 2.1: Schematic pictures of metachronal wave pattern of ciliary microorganisms. (a): movement of each cilium. The trajectory of the tip of the cilium is often considered to be closed and modeled by a sphere or a spheroid. In this trajectory, the propulsion is generated during the part which travels farther from its body surface, which is so-called effective stroke. The backward stroke, corresponding to the lower arrow, moving near the surface in order not to cause the resistive force is called recovery stroke. (b): collective behaviour of cilia. The phases of the oscillation of cilia are different, depending their positions, which yields the wave like pattern. In the squirmer model, the envelope of each cilium is taken as the shape of the swimmer (dashed-line). When the direction of the wave is the same as the effective stroke, the pattern is called as symplectic, or antiplectic in the case of the opposite direction.

the body $L$ ranges about 200$\mu$m to 600$\mu$m [26]. We can evaluate $l$ and $\omega$ are $l \sim 10\mu$m and $\omega \sim 50s^{-1}$, which are estimated through experimental data of *Chlamydomonas* [40], noting that each cell with flagella on the surface of the colony looks like a cell of *Chlamydomonas*. Thus we have orders of the dimensionless parameters: $Re \sim 10^{-1}$, $Re_\omega \sim 10^0$, $Re_S \sim 10^0$ and $Re_g \sim 10^0$. From this estimation of the dimensionless numbers, the unsteady inertia might not be simply negligible for such swimmers, from which the study motivation in this chapter emerges from.

Inertia effects on swimming microorganisms were considered in Taylor’s swimming sheet [104] by Reynolds [87] and was later modified by Tuck[106] with taking convection effects into consideration. Brennen [13] presented an oscillating-boundary-layer theory and discussed the swimming sheet and the spherical swimmer as a non-accelerating body with oscillating boundary layer in terms of Reynolds number expansion. Nonetheless, these studies treated only steady oscillating motions and did not pay much attention to time evolution of the swimmer including inertia. The squirmer model in unsteady
Squirming locomotion with inertia

Stokes flow was introduced by Rao [86], which contains time evolution of the swimmer but confines to \( R_w = R_S = 1 \).

Wang & Ardekani [110] studied an unsteady spherical swimmer that propels itself by tangential surface deformation. Their study, however, was focused on unsteadiness effects during the small time period from the sudden start, assuming the decay of the inertial effects. In this chapter, asymptotically long time behaviours will be discussed with an assumption that the convective term is still irrelevant after long time.

We extend the unsteady squirmer model first introduced by Rao [86], to the envelop approach in the same way as [9] without any constraints on \( R_w \), \( R_S \), and its stroke under the gravity force, which is shown in §2.2. Combining the unsteady Stokes equations and Newton’s equation of motion, we expand the solution with respect to a small parameter \( \epsilon = l/L \). In §2.3, the fluid dynamic force on a deformable sphere is calculated up to the second order of the expansion. In §2.4, we focus on a long time behaviour of the swimmer. Time-averaged asymptotic velocity of the swimmer is shown under the assumption of a time-periodic stroke. In §2.5, using the obtained asymptotic correction we evaluate the unsteady inertial effects on the swimmer with a standing progressive wave pattern like a metachronal wave. In §2.6, we will give an example stroke to illustrate the inertial effects in terms of power consumption and swimming efficiency. §2.7 is devoted to conclusions.

2.2 Formulation

In this section, equations of motion of both fluid and the swimmer are introduced. We consider a spherical swimmer with swimmer-fixed coordinates whose origin is located in the center of a sphere with polar coordinates \((r; \theta, \phi)\) (See Fig.2.2).

Let us introduce a reference frame \( \{\mathbf{X}\} \) and a body-fixed frame \( \{\mathbf{\tilde{X}}\} \) whose origin corresponds to the centre of the undeformed sphere. In this chapter, we consider applications of the squirmer to a ciliary swimmer, and then assume the centre of mass of the squirmer is exactly the same as the centre of the swimmer itself, as cilia on the surface have negligible mass compared with that of the body. Let \( \mathbf{X}_0 \) be the position of the centre of the reference frame, the velocity of the swimmer is then derived as \( d\mathbf{X}_0/dt = \mathbf{V} \).

We use tildes for the variables in the body-fixed frame. The incompressible Navier-Stokes equations in the reference frame is given with the use of
the variables in the body-fixed frame by
\[ \frac{\partial \tilde{u}}{\partial t} + \frac{dV}{dt} + (\tilde{u} + V) \cdot \nabla \tilde{u} = -\frac{1}{\rho_F} \nabla p + \nu \Delta \tilde{u}. \] (2.1)

When this equation is non-dimensionalised, each term of the left hand side of (2.1) becomes \( O(R_c) \), \( O(R_c) \), \( O(Re) \) respectively. In this chapter, we focus our discussion to the case of negligibly small \( Re \) with non-zero \( R_c \) and \( R_S \).

From this assumption, the equations of motion of fluid in the body-fixed frame can be reduced to the unsteady Stokes equations,
\[ \frac{\partial \tilde{u}}{\partial t} = -\frac{1}{\rho_F} \nabla \tilde{p} + \nu \Delta \tilde{u}, \] (2.2)

where the pressure in the body-fixed frame \( \tilde{p} \) is defined by \( \tilde{p} = p + \tilde{X} \cdot dV/dt \).

The equations of motion of the swimmer can be given by the Newton equations for the position of the centre of mass of the body, which in this chapter corresponds to the centre of the sphere. Let us introduce mass of the swimmer \( M = (4\pi/3)\rho_P L^3 \), we have
\[ M \frac{dV}{dt} = \mathbf{d}. \] (2.3)

The fluid drag \( \mathbf{d} \) is given by
\[ \mathbf{d} = \int_S (\mathbf{n} \cdot \sigma) dS, \] (2.4)

where \( \mathbf{n} \) denotes an outward normal vector to the swimmer’s surface \( S \), and \( \sigma \) is the fluid stress tensor. The Newton equation in the body-fixed frame is obtained in the same way, noting that \( \tilde{\sigma} = \sigma - \tilde{X} \cdot (dV/dt) I \),
\[ \left( M - \frac{4}{3} \pi \rho_F L^3 \right) \frac{dV}{dt} = \mathbf{d}. \] (2.5)

The fluid force in the body-fixed frame is the surface integral in which the stress tensor is replaced by \( \tilde{\sigma} \). To derive the equation (2.5), we have assumed that the volume of the swimmer is conserved though the shape can change.

If we would like to take other external forces such as gravity and electromagnetic forces into consideration, the modification appears only in an extra force term \( \mathbf{F}_{ext} \) to the right hand side of (2.5). In this chapter, we suppose the swimmer under gravity for the application to real microorganisms. As mentioned in the introduction, some microorganisms have larger density than
that of surrounding water, and this fact is often of significance to individual and collective migration of such a bottom-heavy swimmer \cite{79, 45}.

The external force in the fixed-frame is given by the summation of the gravity and the buoyancy, 
\[ \mathbf{F}_{\text{ext}} = -(4\pi/3)(\rho_p - \rho_f)L^3 g e_z, \]
where \( g \) is the acceleration constant of gravity. From the well-known scaling of the fluid drag in the Stokes regime, \( \mathbf{d} \sim \rho_f \nu U L \), the dimensionless form of the equation may be obtained as,
\[ \frac{4\pi}{3}(R_s - R_\omega) \frac{d\mathbf{V}}{dt} = \mathbf{d} - \frac{4\pi}{3} R_g e_z, \tag{2.6} \]
where we define the dimensionless parameter \( R_g \) for the magnitude of the effective gravity force compared with the viscous force as \( R_g = (\rho_p - \rho_f) L^2 g / \nu U \).

The variables in (2.6) are dimensionless, which we should remark. In the case of \textit{Volvox}, for instance, \( R_g \) is at the order of unity.

We hereafter drop tildes for variables in the body-fixed frame, and discuss only with dimensionless variables.

\section*{2.2.1 Fluid equations}

The radial and polar components of the velocity fields \((u, v)\) are obtained from the Stokes stream function \(\psi\) such that
\[ \begin{align*}
    u &= -\frac{1}{r^2} \frac{\partial \psi}{\partial \mu}, \quad \text{and} \quad v = -\frac{1}{r \sqrt{1 - \mu^2}} \frac{\partial \psi}{\partial r},
\end{align*} \tag{2.7} \]
where \(\mu\) is defined as \(\mu = \cos \theta\), not the viscosity of fluid in this chapter. Throughout this chapter, we assume that strokes of the swimmer are purely axisymmetric, and thus the azimuthal component of the velocity fields is equivalent to zero. In this case, the Navier-Stokes equations are reduced to a partial differential equation,
\[ \left( \frac{\partial}{\partial t} - \nu D^2 \right) D^2 \psi = \frac{1}{r^2} \left[ \frac{\partial (D^2 \psi, \psi)}{\partial (r, \mu)} - 2D^2 \psi L \psi \right], \tag{2.8} \]
where \(D^2\) and \(L\) are derivative operators given by
\[ D^2 = \frac{\partial^2}{\partial r^2} + \frac{1 - \mu^2}{r^2} \frac{\partial^2}{\partial \mu^2}, \quad \text{and} \quad L = \frac{\mu}{1 - \mu^2} \frac{\partial}{\partial r} + \frac{1}{r} \frac{\partial}{\partial \mu}. \tag{2.9} \]
We nondimensionalise the equation (2.8), then it follows that
\[ \left( R_\omega \frac{\partial}{\partial t} - D^2 \right) D^2 \psi = \frac{Re}{r^2} \left[ \frac{\partial (D^2 \psi, \psi)}{\partial (r, \mu)} - 2D^2 \psi L \psi \right]. \tag{2.10} \]
2.2 Formulation

Fig. 2.2: Configuration of the spherical coordinates of the squirmer and the deforming boundary. The exact sphere without deformation (dotted line), which is labeled by the polar angle $\theta$, can change its shape (solid line) whose surface is expressed by the radius $R = R(\theta)$ and the new angle $\Theta = \Theta(\theta)$ as functions of the original label $\theta$.

Here $R_\omega$ and $Re$ are the oscillatory Reynolds number and the Reynolds number respectively. The assumption that $Re$ is equivalent to zero while $R_\omega$ is a finite number yields the governing fluid equation,

$$\left( R_\omega \frac{\partial}{\partial t} - D^2 \right) D^2 \psi = 0. \quad (2.11)$$

2.2.2 Boundary conditions

Next, we will discuss the boundary conditions of the fluid equation (2.11). According to the usual envelope approximation [9], we consider an end point of a flagellum whose original position is $(1, \theta)$, and we treat the envelop of such points as a surface shape of a swimmer (Fig. 2.2). Let us denote the
2 Squirming locomotion with inertia

end point as \((R, \Theta)\), defines as

\[
R = 1 + \epsilon \sum_{n=1}^{\infty} \alpha_n(t)Q_n'(\mu) \tag{2.12}
\]

\[
\Theta = \theta + \epsilon \sum_{n=1}^{\infty} \frac{n(n+1)}{\sqrt{1 - \mu^2}} \beta_n(t)Q_n(\mu). \tag{2.13}
\]

Here \(Q_n(\mu)\) is a polynomial induced by the Legendre function \(P_n(\mu)\) which is given by

\[
Q_n(\mu) = \int_{-1}^{\mu} P_n(x)dx, \tag{2.14}
\]

and the symbol ‘prime’ denotes the differentiation with respect to \(\mu\) of a function. This relates to Lighthill’s \(V_n[63]\) and the associated Legendre function of the first kind \(P_n^1\) such as

\[
Q_n(\mu) = -\frac{\sqrt{1 - \mu^2}}{2} V_n = -\frac{\sqrt{1 - \mu^2}}{n(n+1)} P_n^1. \tag{2.15}
\]

\(Q'_n\) is equal to the Legendre function \(P_n\). The time derivative of the equations (4.1) and (4.2) yields the velocity of the point on the surface:

\[
u(R, \Theta) = \dot{R} = \epsilon \sum_{n=1}^{\infty} \alpha_n(t)Q_n'(\mu) \tag{2.16}
\]

\[
\dot{\Theta} = R \dot{\Theta} = \sqrt{1 - \mu^2} \beta_n(t)Q_n(\mu). \tag{2.17}
\]

The equations (2.16) and (2.18) correspond to the no-slip boundary condition of the fluid equation (2.11). Since it is difficult to calculate exactly the solution of the fluid equation, we introduce alternative boundary conditions for the fluid equation given by

\[
\left( \frac{\partial \psi}{\partial \mu} \right)_{r=1} = -\sum_{n=1}^{\infty} A_n(t)Q_n'(\mu) \tag{2.18}
\]

\[
\left( \frac{\partial \psi}{\partial r} \right)_{r=1} = -\sum_{n=1}^{\infty} B_n(t)n(n+1)Q_n(\mu), \tag{2.19}
\]

16
which derive corresponding conditions for the velocity field as

\[(u)_{r=1} = \sum_{n=1}^{\infty} A_n(t)Q'_n(\mu) \quad (2.20)\]

\[(v)_{r=1} = \sum_{n=1}^{\infty} \frac{n(n+1)}{\sqrt{1-\mu^2}} B_n(t)Q_n(\mu). \quad (2.21)\]

Henceforth we assume \(\epsilon\) is a small parameter, and consider an expansion of \(A_n\) and \(B_n\) as

\[A_n = \sum_{k=1}^\infty \epsilon^k A_n^{(k)} \quad \text{and} \quad B_n = \sum_{k=1}^\infty \epsilon^k B_n^{(k)}. \]

The coefficients \(A_n^{(k)}\) and \(B_n^{(k)}\) are calculated order by order of \(\epsilon\) and the equations \((2.18)\) and \((2.19)\) are employed as the boundary conditions for the fluid equation.

Since the fluid velocity at infinity must be equivalent to the velocity of the swimmer, the boundary condition at infinity becomes

\[\psi \sim -\frac{1}{2} V(t)r^2(1-\mu^2) \quad \text{as} \quad r \to \infty. \quad (2.22)\]

For initial condition of the fluid equation, we impose

\[D^2 \psi = 0 \quad \text{at} \quad t = 0. \quad (2.23)\]

The solution of the fluid equation \((2.11)\) with boundary and initial conditions \((2.18) \sim (2.23)\) has been obtained by [86] with Laplace transformation,

\[
\bar{\psi} = \frac{-\nabla}{r R_\omega s} \left( 3 + 3\sqrt{R_\omega} \sqrt{s} + R_\omega s(1-r^2) - 3(1+\sqrt{R_\omega} \sqrt{s} r)e^{-\sqrt{R_\omega} \sqrt{s}(r-1)} \right) Q_1
- \sum_{n=1}^{\infty} \frac{1}{r^n} \left[ A_n + \frac{K_{n+1/2}(\sqrt{R_\omega} \sqrt{s}) - r^{n+1/2} K_{n+1/2}(\sqrt{R_\omega} \sqrt{s} r)}{\sqrt{R_\omega} \sqrt{s} K_{n-1/2}(\sqrt{R_\omega} \sqrt{s})} \times (nA_n + n(n+1)B_n) \right] Q_n, \quad (2.24)
\]

where the overlines denote Laplace transformed variables and \(K_n(x)\) is the \(n\)th order modified Bessel function of the second kind. Using the Laplace equation \(\Delta \bar{p} = 0\), the pressure \(\bar{p}\) has also been calculated by [86],

\[
\bar{p} = \left( r R_\omega s + \frac{3 + 3\sqrt{R_\omega} \sqrt{s} + R_\omega s}{2r^2} \right) \bar{V} Q'_1 + \sum_{n=1}^{\infty} \frac{n s}{r^{n+1}} \times \left[ \frac{A_n}{n(n+1)} + \frac{K_{n+1/2}(\sqrt{R_\omega} \sqrt{s})}{\sqrt{R_\omega} \sqrt{s} K_{n-1/2}(\sqrt{R_\omega} \sqrt{s})} \left( \frac{A_n}{n+1} + B_n \right) \right] Q_n' \quad (2.25)
\]
2.2.3 Body equation of motion

Owing to the axisymmetric fluid motion, the swimmer moves in $e_z$ direction. We take this velocity component as $V = V \cdot e_z$ and write down the equation of motion of the swimmer, i.e. Newton’s equation of motion, in the dimensionless form,

$$\frac{3}{2\pi} d(t) + (R_\omega - R_S) \dot{V}(t) - R_g = 0.$$  \hfill (2.26)

Here $d$ is the $z$ component of the fluid force, $d = d \cdot e_z$.

We will then solve both the body and fluid equations (2.26) and (2.11) with boundary and initial conditions (2.18), (2.19), (2.22) and (2.23), where these two equations are associated with $d(t)$.

With the axisymmetry, the integrand in the drag $d$ can be decomposed into four parts,

$$(n \cdot \sigma)_z = \mu n_r \sigma_{rr} - \sqrt{1 - \mu^2 n_r \sigma_{r\theta} + \mu n_\theta \sigma_{\theta r} - \sqrt{1 - \mu^2 n_\theta \sigma_{\theta\theta}}}.$$  \hfill (2.27)

The normal vector $n$ is obtained as the following. The position of the surface $\xi$ can be labeled by the angle $\Theta$:

$$\xi(\Theta) = (\xi \cdot e_r(\Theta)) e_r(\Theta) \equiv \xi_r e_r.$$  \hfill (2.28)

Remember that the tangent and normal vector, $t$ and $n$, are given by

$$t = \frac{d\xi}{d\Theta}, \quad n = \frac{e_\phi \times t}{|t|},$$  \hfill (2.29)

and we have the normal vector,

$$n = \begin{bmatrix} n_r \\ n_\theta \\ n_\phi \end{bmatrix} = \begin{bmatrix} 1 + \left( \frac{d\xi_r}{d\Theta} / \xi_r \right)^2 - \left( \frac{d\xi_\phi}{d\Theta} / \xi_r \right)^2 \\ \phi \sum_{\alpha\beta} \alpha_n Q_{n}^\alpha + O(\epsilon^2) \end{bmatrix}.$$  \hfill (2.30)

Under the assumption that the amplitude of deformation $\epsilon$ is small enough ($\epsilon \ll 1$), we finally obtain the expression of the normal vector up to the order of $O(\epsilon)$,

$$n = \left[ \begin{array}{c} 1 + O(\epsilon^2) \\ \epsilon \sqrt{1 - \mu^2} \sum_{\alpha\beta} \alpha_n Q_{n}^\alpha + O(\epsilon^2) \end{array} \right].$$  \hfill (2.31)
2.3 Fluid dynamic force

The fluid force element acting on the surface of the swimmer (2.27) is a value at the position \((R, \Theta)\) on the surface. Using the Taylor expansion, we have the expression as the value at \((1, \Theta)\) up to the second order,

\[
\frac{d}{2\pi} = \int_0^\pi (n \cdot \sigma \cdot e_z) R^2 \sin \Theta d\Theta
\]

\[
= \int_0^\pi (n_r \sigma_{rr} \cos \Theta - n_r \sigma_{r\theta} \sin \Theta) \sin \Theta d\Theta
\]

\[
+ \int_0^\pi \left( n_r (R - 1) \frac{\partial \sigma_{rr}}{\partial r} \cos \Theta - n_r (R - 1) \frac{\partial \sigma_{r\theta}}{\partial r} \sin \Theta \right) \sin \Theta d\Theta
\]

\[
+ \int_0^\pi (n_{\theta} \sigma_{\theta r} \cos \Theta - n_{\theta} \sigma_{\theta \theta} \sin \Theta) \sin \Theta d\Theta
\]

\[
+ \int_0^\pi (n_r \sigma_{rr} \cos \Theta - n_r \sigma_{r\theta} \sin \Theta) 2(R - 1) \sin \Theta d\Theta + O(\epsilon^3).
\] (2.32)

Note that \((R - 1)\) is \(O(\epsilon)\), and \(n_{\theta}\) is also the same order of \(\epsilon\). The first integral corresponds to the fluid force on the spherical squirmer \([86, 110]\) and it is found that the force depends on the first mode of the Legendre expansion \((A_1\) and \(B_1)\).

First of all, we calculate the second order expression of \(A_1\) and \(B_1\) and then the contribution of the first integral of the equation (2.32), which is denoted by \(d_s\) hereafter. The index \(s\) implies that the integral have been taken into consideration as the spherical squirmer model. The contribution from the remaining three integrals in the equation (2.32) which we denote by \(d_d\) are then calculated. The index \(d\) implies the explicit deformation of the swimmer. Let us rewrite the fluid force \(d\) as

\[
\frac{1}{2\pi} \int_S (n \cdot \sigma) z dS = \frac{d}{2\pi} = d_s + d_d + O(\epsilon^3).
\] (2.33)
2 Squirming locomotion with inertia

2.3.1 Representation of $d_s$

In the commonly used way as [63] and [9], we will obtain $A_1^{(2)}$ and $B_1^{(2)}$. With Taylor expansions up to $O(\varepsilon^2)$, the fluid velocity of the surface becomes

$$u(1, \theta) = u(R, \Theta) - (R - 1) \left( \frac{\partial u}{\partial r} \right)_{r=1} - (\Theta - \theta) \left( \frac{\partial u}{\partial \theta} \right)_{r=1}$$

$$= \epsilon \sum_{n=1}^{\infty} \alpha_n Q'_n + \epsilon^2 \sum_{n,m=1}^{\infty} \left( 2\alpha_n \alpha_m Q'_n Q'_m \right.$$

$$- m(m+1)\alpha_n \hat{\beta}_n Q'_n Q'_m + n(n+1)\beta_n \alpha_m Q_n Q''_m \left) \right)$$

$$v(1, \theta) = v(R, \Theta) - (R - 1) \left( \frac{\partial v}{\partial r} \right)_{r=1} - (\Theta - \theta) \left( \frac{\partial v}{\partial \theta} \right)_{r=1}$$

$$= \epsilon \left( 1 + \epsilon \sum_{n=1}^{\infty} \alpha_n Q_n \right) \sum_{n=1}^{\infty} \frac{n(n+1)}{\sqrt{1-\mu^2}} \hat{\beta}_n Q_n$$

$$+ \epsilon^2 \sum_{n,m=1}^{\infty} \left( m(m+1)\alpha_n \hat{\beta}_m \frac{Q'_n Q'_m}{\sqrt{1-\mu^2}} \right.$$

$$- m(m+1)\alpha_n \hat{\beta}_m \frac{Q'_n Q'_m}{\sqrt{1-\mu^2}} + \epsilon^{-1} \alpha_n R_m \frac{Q'_n Q'_m}{\sqrt{1-\mu^2}} \left) \right)$$

$$+ \epsilon^2 \sum_{n,m=1}^{\infty} \left( n(n+1)m(m+1)\beta_n \hat{\beta}_m \frac{\mu Q_n Q_m}{(1-\mu^2)^{3/2}} \right.$$

$$+ n(n+1)m(m+1)\beta_n \hat{\beta}_m \frac{Q_n Q'_m}{\sqrt{1-\mu^2}} \left) \right)$$

where $R_n$ is a part of the term from $\partial v/\partial r$, which is given by

$$R_n = \mathcal{L}^{-1} \left[ 3V \left( 1 + \sqrt{\Omega} \right) \right.$$

$$+ \sum_{n=1}^{\infty} \left( \frac{\sqrt{K_{n+1/2}(\sqrt{\Omega})}}{\sqrt{K_{n-1/2}(\sqrt{\Omega})}} \right) (nA_n + n(n+1)B_n) Q_n \left) \right]$$

(2.36)

Let us suppose $R_n \rightarrow R_n^0$ as the limit of the steady Stokes flow, i.e. $R_\omega \rightarrow 0$, and that $R_n$ can be described as $R_n = R_n^0 + R_n^\omega$, we then obtain

$$R_n^0 = 3V \delta_{n,1} + (2n-1)(nA_n + n(n+1)B_n)$$

(2.37)

$$R_n^\omega = X_n + \mathcal{L}^{-1} \left[ 3V \sqrt{\Omega} \delta_{n,1} \right]$$

(2.38)
2.3 Fluid dynamic force

where \( X_n \) is

\[
X_n = L^{-1} \left[ \left( \sqrt{\omega} \sqrt{s} \frac{K_{n+1/2}(\sqrt{\omega} \sqrt{s})}{K_{n-1/2}(\sqrt{\omega} \sqrt{s})} - (2n - 1) \right) (nA_n + n(n + 1)B_n) \right].
\]  
(2.39)

The coefficients of the Legendre expansion (2.20) and (2.21) are given by the following integrals:

\[
A_n = \frac{2n + 1}{2} \int_{-1}^{1} u(1, \theta) Q_n(\mu) d\mu \quad (2.40)
\]

\[
B_n = \frac{2n + 1}{2} \int_{-1}^{1} v(1, \theta) \frac{Q_n(\mu)}{\sqrt{1 - \mu^2}} d\mu. \quad (2.41)
\]

Some manipulations of Legendre integrals lead the coefficients up to the second order of \( \epsilon \). The results are

\[
A_1 = \epsilon \dot{\alpha}_1 + \epsilon^2 \sum_{n=1}^{\infty} \frac{3}{(2n + 1)(2n + 3)} \left( 2(n + 1) \dot{\alpha}_n \alpha_{n+1} + 2(n + 1) \alpha_n \dot{\alpha}_{n+1} 
- n(n + 1)^2 \beta_n \alpha_{n+1} - (n + 1)^2(n + 2) \alpha_n \beta_{n+1} 
- n(n + 1)(n + 2) \dot{\alpha}_n \beta_{n+1} - n(n + 1)(n + 2) \beta_n \dot{\alpha}_{n+1} \right), \quad (2.42)
\]

and

\[
B_1 = \epsilon \dot{\beta}_1 - \frac{3}{10} \epsilon V \alpha_2 - \frac{3}{10} \epsilon \sqrt{\omega} \left( \int_{0}^{t} \frac{\dot{V}}{\sqrt{\pi(t - x)}} \, dx \right) \alpha_2
+ \frac{3}{2} \epsilon^2 \sum_{n=1}^{\infty} \frac{\alpha_n X_{n+1} - X_n \alpha_{n+1}}{(2n + 1)(2n + 3)}
+ \frac{3}{2} \epsilon^2 \sum_{n=1}^{\infty} \frac{1}{(2n + 1)(2n + 3)} \left( - n(n - 2) \dot{\alpha}_n \alpha_{n+1} + (n - 1)(n + 1) \alpha_n \dot{\alpha}_{n+1}
- n(n + 1)(n + 2) \dot{\alpha}_n \beta_{n+1} + (n + 1)(n + 2)(2n + 3) \alpha_n \beta_{n+1}
+ n^2(n + 1)(n + 2) \beta_n \beta_{n+1} - n(n + 1)(n + 2)^2 \beta_n \dot{\beta}_{n+1} \right). \quad (2.43)
\]

We are now ready to write down the force \( ds \), which is expanded by \( \epsilon \) as

\[
d_s = \epsilon d_s^{(1)} + D_s^{(1)}[V] + \epsilon^2 d_s^{(2)} + \epsilon D_s^{(2)}[V] + O(\epsilon^3), \]

where \( D \) denotes a function of \( V \) while \( d_s^{(1)} \) and \( d_s^{(2)} \) are independent of \( V \). Noting that the \( O(\epsilon^2) \) contribution of \( B_1 \) which is independent of \( V \) includes remaining and vanishing parts when
$R_\omega = 0$, which we denote by $B_{1,0}^{(2)}$ and $B_{1,\omega}^{(2)}$ respectively. Each term of $d_s$ is given by

\begin{align}
    d_s^{(1)} &= -\left[ A_1^{(1)} + 2B_1^{(1)} + \sqrt{R_\omega} \int_0^t \frac{\dot{A}_1^{(1)} + 2\dot{B}_1^{(1)}}{\sqrt{\pi(t-x)}} \, dx + \frac{R_\omega}{3} A_1^{(1)} \right] \quad (2.44) \\
    D_s^{(1)} &= -\left[ 3V + 3\sqrt{R_\omega} \int_0^t \frac{V}{\sqrt{\pi(t-x)}} \, dx + R_\omega \dot{V} \right] \quad (2.45)
\end{align}

and

\begin{align}
    d_s^{(2)} &= d_s^{(2),0} + d_s^{(2),\omega} \quad (2.46) \\
    D_s^{(2)} &= \frac{3}{5} V \alpha_2 + \frac{3}{5} L^{-1} \left[ \nabla \sqrt{R_\omega} \sqrt{s} \right] \alpha_2 - \sqrt{R_\omega} \times \\
    &\quad \int_0^t \frac{1}{\sqrt{\pi(t-x)}} \frac{d}{dx} \left( \frac{3}{5} V \alpha_2 + \frac{3}{5} L^{-1} \left[ \nabla \sqrt{R_\omega} \sqrt{s} \right] \alpha_2 \right) \, dx \quad (2.47)
\end{align}

Here $d_s^{(2),0}$ and $d_s^{(2),\omega}$ are respectively

\begin{align}
    d_s^{(2),0} &= -\left[ A_1^{(2)} + 2B_1^{(2)} \right] \quad (2.48) \\
    d_s^{(2),\omega} &= -\left[ 2B_{1,\omega}^{(2)} + \sqrt{R_\omega} \int_0^t \frac{\dot{A}_1^{(2)} + 2\dot{B}_1^{(2)} + 2\dot{B}_{1,\omega}^{(2)}}{\sqrt{\pi(t-x)}} \, dx + \frac{R_\omega}{3} \dot{A}_1^{(2)} \right] \quad (2.49)
\end{align}

where $B_{1,0}^{(2)}$ is the first and the last term of the right hand side of equation (2.43), which remains nonzero after the limit $R_\omega \to 0$, and $B_{1,\omega}^{(2)}$ has to be vanishing at that limit which corresponds to the fourth term. We should note that $B_{1,\omega}^{(2)}$ depends on $\alpha_\omega$ and must disappear for a swimmer without a shape deformation from the sphere.

### 2.3.2 Fluid force due to deformation

Next, we calculate the remaining three integrals of the equation (2.32). Similarly to the calculation of $A_1$ and $B_1$, some manipulations of Legendre integrals are needed. Let us skip details of the calculation and show directly the result (For some details, see Appendix A.1),

\begin{align}
    d_d &= R_\omega \epsilon^2 \sum_{n=1}^{\infty} \frac{1}{(2n+1)(2n+3)} \left( 2(n+1)\alpha_n \ddot{\alpha}_{n+1} + 2(n+1)\ddot{\alpha}_n \alpha_{n+1} \\
    &\quad + 2(n+1)(n+2)\alpha_n \dddot{\beta}_{n+1} - 2n(n+1)\dddot{\beta}_n \alpha_{n+1} \right) . \quad (2.50)
\end{align}
This part has \( O(R) \) contribution and must be zero for the inertialess fluid. This fact is consistent with the classical discussions by [63] and [9] that the swimming velocity can be obtained from the expressions of the flow field when the inertia is neglected as the stokeslet term must vanish and that there is no need to calculate the fluid force. We would like to note again that \( d \) also comes from the shape variation and becomes zero when \( \alpha_n = 0 \) for all \( n \).

### 2.3.3 Comparison with other studies

In this subsection, we make some remarks on the obtained results in the previous subsections and its comparison with some literatures on the squirmer.

In the case of \( R = 0 \), it can be found that the second order representation of the usual squirmer model is recovered. To see this, we substitute (2.42) and (2.43) into the velocity of the swimmer with its shape being exactly a sphere, after taking the limit of \( R \to 0 \). We then recover the swimming velocity of the spherical tangential squirmer, \( V = -(1/3)A_1 - (2/3)B_2 \). Also some changes of variables are required to have the equivalent expressions in the literatures; for example, the results by [9] can be obtained when \( B_1 \to -B_1 \) and \( \beta_n \to -2\beta_n/n(n + 1) \), and those by [93] when \( B_1 \to -B_1 \) and \( \beta_n \to \beta_n/(n + 1) \).

With regard to the swimmer discussed in [86], we neglect all the \( O(\varepsilon^2) \) terms, which yields \( d = \varepsilon d^{(1)} + \varepsilon^2 d^{(2)} \) \([V]\). Assumption of the neutral buoyancy, or in other words \( R_w = R_s = 0 \) in (2.26) lets us find the equation (20) of [86] and its free-force condition, noting that \( A_1 = \varepsilon\dot{a}_1 \) and \( B_1 = \varepsilon\dot{\beta}_1 \) within this order of the expansion.

The reduction to the results by [110] may be achieved if we consider the swimmer only with tangential deformation, i.e. \( \alpha_n = 0 \) for all \( n \). It may be harder to see the correspondence in terms of the fluid force, but it would be rather easier after obtaining the swimming velocity of the swimmer, which will be considered in the next section.

### 2.4 Motion of a swimmer

In this section, we will derive the translational velocity of the swimmer from the equation of motion (2.26). Let us write \( d/2\pi \) as

\[
\varepsilon d^{(1)} + \varepsilon^2 (d_0^{(2)} + d_\omega^{(2)}) + D^{(1)} + \varepsilon D^{(2)}
\] (2.51)
with combining the contribution from $d_s$ and $d_d$. Here $d_0^{(2)}$ and $d_\omega^{(2)}$ represent the $O(\epsilon^2)$ term at the vanishing unsteady inertia and the leading correction due to the inertia, respectively. After we substitute (2.51) into the equation of motion of the swimmer (2.26), we have

$$
\left(3 + 3\sqrt{R_\omega} + \left(\frac{1}{3}R_\omega + \frac{2}{3}R_S\right) s\right) \overline{V} = \epsilon d^{(1)} + \epsilon^2 (d_0^{(2)} + d_\omega^{(2)}) + \epsilon \overline{D^{(2)}}[\overline{V}] - \frac{2}{3}R_g.
$$

From the right hand side of the equation (2.52) which depends on $V$, it is difficult to calculate $V$ directly as we can in the lowest order expansion [86]. Expansion of $V$ with respect to $\epsilon$, $V = V^{(0)} + \epsilon V^{(1)} + \epsilon^2 V^{(2)} + O(\epsilon^3)$, derives equations on the velocity order by order:

$$
\left(3 + 3\sqrt{R_\omega} + \left(\frac{1}{3}R_\omega + \frac{2}{3}R_S\right) s\right) \overline{V}^{(0)} = -\frac{2}{3}R_g
$$

(2.53)

$$
\left(3 + 3\sqrt{R_\omega} + \left(\frac{1}{3}R_\omega + \frac{2}{3}R_S\right) s\right) \overline{V}^{(1)} = d^{(1)} + \overline{D^{(2)}}[\overline{V}^{(0)}]
$$

(2.54)

$$
\left(3 + 3\sqrt{R_\omega} + \left(\frac{1}{3}R_\omega + \frac{2}{3}R_S\right) s\right) \overline{V}^{(2)} = d_0^{(2)} + d_\omega^{(2)} + \overline{D^{(2)}}[\overline{V}^{(1)}]
$$

(2.55)

Let us introduce a function $g$ which is defined by

$$
g(t) = \mathcal{L}^{-1}\left[\frac{1}{(\sqrt{a} + \sqrt{b})}\right] = \frac{1}{a - b}\left( ae^{a^2t} \text{erfc}(a\sqrt{t}) - be^{b^2t} \text{erfc}(b\sqrt{t}) \right),
$$

(2.56)

where $a$ and $b$ are given by

$$
\frac{9\sqrt{R_\omega} \pm 3\sqrt{5R_\omega} - 8R_S}{2(2R_\omega + 2R_S)}.
$$

(2.57)

The upper and the lower signatures respectively correspond to $a$ and $b$. The velocity of each order is described as a convolution of $g$ and a function $f$ which represents the right hand side of the equations,

$$
\frac{3}{R_\omega + 2R_S} [g \ast f](t).
$$

(2.58)

We would like to discuss a motion due to time-periodic deformation. We then focus our attention to a long time asymptotic form of the velocity of
a swimmer. We denote the time average of this velocity over a period by a bracket \( \langle \rangle \), which is defined by

\[
\langle V(t) \rangle = \lim_{n \to \infty} \frac{1}{T} \int_{nT}^{(n+1)T} V(t) dt
\]  

(2.59)

To evaluate the convolution, the following lemmas are useful. Proofs of the lemmas are shown in A.2.2.

**Lemma 1** Let a function \( f(t) \) have an asymptotic form \( f(t) \sim \tilde{f}(t) + O(1/\sqrt{t}) \) as \( t \to \infty \), where \( \tilde{f}(t) \) is a periodic function with period \( T = 1 \). Then the long time behaviour of the equation (2.58) is expanded with respect to the oscillatory Reynolds number \( R \) as

\[
\frac{3}{R_\omega + 2R_S} [g * f](t) \sim \frac{1}{3} \tilde{f} + \frac{1}{3} \sqrt{R_\omega} \frac{d_{1/2} \tilde{f}}{dt_{1/2}} + O(R_\omega, R_S, 1/\sqrt{t}).
\]  

(2.60)

**Lemma 2** Let \( f \) be a function that has the same asymptotic behaviour as Lemma 1, i.e. \( f(t) \sim \tilde{f}(t) + O(1/\sqrt{t}) \). Then we have

\[
\frac{3}{R_\omega + 2R_S} [h * f](t) = \frac{1}{3} \frac{d_{1/2} \tilde{f}}{dt_{1/2}} + O(\sqrt{R_\omega}, 1/\sqrt{t}),
\]  

(2.61)

where \( h = g * (1/\sqrt{\pi t}) \).

We should note that the fractional derivative of a periodic function is defined by the Fourier series;

\[
\frac{d^\gamma}{dt^\gamma} \tilde{f} = \frac{d^\gamma}{dt^\gamma} \sum_{n=-\infty}^{\infty} \tilde{f}_m e^{2\pi imt} = \sum_{m=-\infty}^{\infty} (2\pi im)^\gamma \tilde{f}_m e^{2\pi imt},
\]  

(2.62)

where \( \gamma \) is a real number.

### 2.4.1 Zeroth and first order of the expansion

We begin with the zeroth order of the perturbation (2.53). \( V^{(0)} \) is obtained when we apply \( f = -(2/3)R_g \) to Lemma 1, \( V^{(0)} \sim -(2/9)R_g + O(1/\sqrt{t}) \), which corresponds to Stokes’ law of drag.

The first order calculation is divided into two parts, namely contribution from \( d^{(1)} \) and \( D^{(2)}(V^{(0)}) \). The former part is reduced to the following convolution,

\[
-\frac{1}{3} \ddot{\alpha}_1 - \frac{2}{3} \ddot{\beta}_1 + g * \left( \frac{2 (R_S - R_\omega)}{3 (R_\omega + 2 R_S)} \ddot{\alpha}_1 + \frac{2}{3} \ddot{\beta}_1 \right).
\]  

(2.63)
This expression does correspond to the expression of the velocity obtained by [86]. The asymptotic behaviour of the former part is given by

\[
\frac{1}{3} \alpha_1 - \frac{2}{3} \beta_1 + \frac{2}{27} (R_S - R_\omega) \alpha_1 + \frac{2}{27} (R_\omega + 2 R_S) \beta_1 + O(R_\omega^{3/2}, R_\omega^{1/2} R_S, 1/\sqrt{t}).
\]

(2.64)

We may be interested in the comparison with Rao’s results, but we should note that there exists a difference that we have used here asymptotic analysis with respect to \( R_\omega \) and \( R_S \).

The latter part gives gravity effects on the deformed sphere. By the use of Lemma 1 and Lemma 2, each contribution from \( \mathcal{D}^{(2)}[V(0)] \) is obtained,

\[
\frac{3}{R_\omega + 2 R_S} \left [ g * \mathcal{D}^{(2)}_s[V(0)] \right ] (t) \sim -\frac{2}{45} R_\omega \alpha_2 + O(R_\omega, R_S, 1/\sqrt{t}) \tag{2.65}
\]

This shows only the \( n = 2 \) mode affects the velocity of the swimmer under gravity at the first order of \( \epsilon \). The squirming part (2.65) corresponds to classic results of resistance force on a slightly deformed sphere (p. 207 of [43]). The asymptotic time-averaged velocity becomes \( \langle V^{(1)} \rangle = -\langle 2/45 \rangle R_\omega \alpha_2 \) and it is found that the scallop theorem holds without external force in an asymptotic sense, which we here call the asymptotic scallop theorem. This results can be compared with [110], which says the net velocity of tangential squirmer converges to zero after a long time.

In order to illustrate the asymptotic satisfaction, let us consider what happens when the swimmer which is stationary at the initial time \( t = 0 \) deforms just over one period \( (0 \leq t \leq 1) \). We rewrite the convolution of the equation (2.63) as \( g \ast f \), where the function \( f(t) \) is expressed by Fourier series,

\[
f(t) = \sum_{m=-\infty}^{\infty} f_m e^{2 \pi i m t} H(t) H(1 - t).
\]

(2.66)

\( H(t) \) denotes Heaviside’s step function. Then the displacement \( X(t) \) \( (t \geq 1) \) is given by

\[
X(t) = \int_1^{t} \int_{t-1}^{t'} g(x) f(t' - x) dx dt' + \int_0^{1} \int_0^{t} g(x) f(t' - x) dx dt',
\]

(2.67)

because the first two terms of the equation (2.63) exactly follows to the standard scallop theorem. After we perform each integral over \( x \), we then
combine those integrals together,

$$X(t) = \int_{t-1}^{t} dt' \sum_{m=-\infty}^{\infty} \frac{f_m}{a-b} \left[ \frac{a}{a^2 - 2\pi im} \left( e^{2\pi imt'} \text{erfc}(at) + \frac{e^{2\pi imt'}}{\sqrt{2\pi imt}} \text{erf}(\sqrt{2\pi imt'}) \right) - \frac{b}{b^2 - 2\pi im} \left( e^{2\pi imt} \text{erfc}(bt) + \frac{e^{2\pi imt'}}{\sqrt{2\pi imt}} \text{erf}(\sqrt{2\pi imt'}) \right) \right], \quad (2.68)$$

which is found to go to zero as $t \to \infty$. Thus the swimmer approaches its original position after a long time.

### 2.4.2 Second order of the expansion

Now we consider the second order of the expansion $V^{(2)}$. According to the equation (2.55), we are required to perform three convolution integrals: $g * d_n^{(2)}$, $g * \mathcal{D}_n^{(2)}$ and $g * \mathcal{D}^{(2)}[V^{(1)}]$.

The $g * d_n^{(2)}$ contribution is given by $(1/3)d_n^{(2)}$. This term consists of represented by the form of summation of continuous two modes one of which is differentiated once with respect to time such as $\alpha_n^{(1)}\beta_{n+1}^{(1)}$, which does not break the scallop theorem.

Next, the $g * \mathcal{D}_n^{(2)}$ term is considered. Here we are interested in the time-averaged asymptotic velocity under the assumption of infinitesimal small inertia of fluid and body. To complete evaluation, we need to obtain an asymptotic expression of $X_n$, which is shown in A.2.1. Using (A.3) and (A.14), we have

$$\left\langle \frac{3}{R_\omega + 2R_S} [g * d_n^{(2)}](t) \right\rangle = \frac{1}{15} \sqrt{R_\omega} \left\langle \alpha_2 d_1^{1/2} (\alpha_1 + 2\beta_1) \right\rangle + O(R_\omega). \quad (2.69)$$

The leading order contribution of the $O(R_\omega)$ term in the equation (2.69), consisting of products of neighboring two modes one of which are differentiated twice such as $\alpha_n^{(1)}\beta_{n+1}^{(1)}$, is only proportional to the oscillatory Reynolds number and independent of the Stokes number.

We then investigate the $g * \mathcal{D}^{(2)}$ term of the equation (2.55). In the similar
2 Squirming locomotion with inertia

way to the evaluation of $g \ast D^{(1)}$, we have the expansion,

$$
\left\langle \frac{3}{R_\omega + 2R_S} \left[ g \ast D^{(2)}[V^{(1)}] \right] (t) \right\rangle = \frac{1}{5} \left\langle V^{(1)} \alpha_2 \right\rangle + \frac{\sqrt{R_\omega}}{5} \left\langle \frac{q^{1/2}V^{(1)}}{d^{1/2}} \alpha_2 \right\rangle
$$

$$
= - \frac{1}{15} \langle \dot{\alpha}_1 + 2\dot{\beta}_1 \rangle \alpha_2 - \frac{\sqrt{R_\omega}}{15} \left\langle \alpha_2 \frac{d^{3/2}}{dt^{3/2}} (\dot{\alpha}_1 + 2\dot{\beta}_1) \right\rangle + \frac{2}{135} (R_S - R_\omega) \langle \dot{\alpha}_1 \alpha_2 \rangle
$$

$$
+ \frac{2}{135} (R_\omega + 2R_S) \langle \dot{\beta}_1 \alpha_2 \rangle - \frac{2}{75} R_g \langle \alpha_2^2 \rangle + \text{h.o.t.} \quad (2.70)
$$

From the discussions above, we finally obtain the second order time-averaged asymptotic velocity,

$$
\langle V^{(2)} \rangle = \frac{1}{3} \langle \dot{q}_n^{(2)} \rangle - \frac{1}{15} \langle (\dot{\alpha}_1 + 2\dot{\beta}_1) \alpha_2 \rangle + \frac{2}{135} (R_S - R_\omega) \langle \dot{\alpha}_1 \alpha_2 \rangle
$$

$$
+ \frac{2}{135} (R_\omega + 2R_S) \langle \dot{\beta}_1 \alpha_2 \rangle + O(R_\omega) + O(R_\omega^{1/2} R_S, R_g), \quad (2.71)
$$

where the $O(R_\omega)$ expression is given by

$$
\frac{R_\omega}{45} \left( 4\alpha_1 \ddot{\alpha}_2 + 4\dot{\alpha}_1 \alpha_2 + 12\alpha_1 \dot{\beta}_2 - 4\dot{\beta}_1 \alpha_2 \right)
$$

$$
+ \frac{R_\omega}{3} \sum_{n=2}^{\infty} \frac{1}{(2n+1)(2n+3)} \left( \frac{(n+1)(4n-5)}{2n-1} \alpha_n \ddot{\alpha}_{n+1} + \frac{(n-2)(4n+3)}{2n-3} \alpha_n \ddot{\alpha}_{n+1} \right)
$$

$$
+ \frac{(n+1)(n+2)(4n-5)}{2n-1} \alpha_n \dot{\beta}_{n+1} - \frac{n(n+1)(4n-9)}{2n-3} \beta_n \alpha_{n+1} \right) \quad (2.72)
$$

The first two terms of the equation (2.71) have to vanish when the swimmer deforms in a reciprocal manner under no net gravity as the asymptotic scallop theorem says. The remaining terms, however, generate $O(R_\omega)$ and $O(R_S)$ net velocity for a reciprocal swimmer, which breaks the asymptotic scallop theorem.

We should make some remarks on the results by [110]. From (2.71) and (2.72), their swimmer without radial deformation ($\alpha_n = 0$) does not have any corrections due to the unsteady inertia on the net swimming velocity after a long time; $\langle V \rangle = -(2/3)B_1$. The other parts of the swimming velocity are oscillatory in time and the damping term with $O(1/\sqrt{t})$, both of which can be seen from the lemmas. This result can be compared with (3.15) in [110].

Effects of the body inertia appearing in the third and fourth term provide $O(R_S)$ net displacement which is compatible with the recent study [38, 39]. Both terms arise from the spheroidal deformation $\alpha_2$, which reflects the fact
that only the $a_2$ mode can change the resistance under an uniform back- 
ground flow as shown in the expression of $\langle V^{(1)} \rangle$. Under the neutral buoyancy 
condition, the leading correction is the fourth term and the $O(R_w)$ contribu-
tion from $a_2^{(2)}$ in the equation (2.69). We should remark once again that 
the net velocity is produced by the shape variation from the sphere for a 
reciprocal swimmer.

2.5 Inertia effects on the surface wave pattern

In this section, we consider the inertial effects on the swimmer with metachronal 
wave pattern. We assume the surface position is given by

$$R = 1 + \epsilon \sin \theta \cos(2k\theta - \omega t) \quad (2.73)$$
$$\Theta = \theta + \epsilon \sin \theta \cos(2k\theta - \omega t + \delta). \quad (2.74)$$

$\epsilon$ is the small parameter which represents the amplitude of the deformation, 
k is the wave number, and $\delta$ is the phase difference between radial and 
tangential components of the deformation ($0 \leq \delta \leq 2\pi$). The overall factor 
of $\sin \theta$ is assumed in order to remove the unphysical situation where the 
envelope of cilia intersects at $\theta = 0$ and $\pi$. In the following discussions, 
we fix the amplitude $\epsilon = 0.05$ as a physical realization for typical ciliary 
swimmers such as Volvox and Paramecium.

The deformation given here may correspond to the schematic pictures 
shown in Fig. 2.1. The trajectory of the tip of each cilium is circle when 
$\delta = \pi/2, 3\pi/2$ but it depends on the phase shift factor $\delta$. The wave number 
k implies the number of waves between $\theta = 0$ and $\theta = \pi$. We should note 
that the wave number of typical ciliary microorganisms with metachronal 
wave may be $k > 5$ [14]. The relation between the signature of $k$ and the 
phase shift is known as metachrony. For such a axisymmetric swimmer, when 
$0 < \delta < \pi$ and $k$ is positive, or $\pi < \delta < \pi$ and $k$ is negative, the configuration 
of stroke of cilia is called symplectic, otherwise antiplectic. An example of 
the symplectic swimmer is Paramecium and that of the other is Opalina [16].

We compute the Legendre coefficients of the deformation of (4.8) and (4.9) 
up to large enough modes, and evaluate the $O(R_w)$ term of (2.71) assuming 
the neutral buoyancy. The leading correction of the averaged velocity due to 
the small inertial effects is shown in Fig. 2.3.

The figure shows the inertial effects appear in the stroke with almost 
k = ±1 and $\delta = 0, \pi$, which corresponds to the flapping motion, while
the net velocity of the metachronal wave with a larger wave number is not modified by the leading inertia correction. This result suggests that the unsteady inertia may not have a significant role in the swimming velocity for the swimmer with wave-like deformation even when the oscillation of cilia is beyond the inertialess regime, but the flapping swimmer may utilise this to generate propulsion.

With regard to the unsteady inertial effects on real swimmers, the unsteady motility in emergency [51, 42, 60] has been recently reported. [110] have found that the Basset memory term and the added mass term account for a substantial fraction of the fluid force on the swimmer for the larger oscillatory Reynolds number above unity, employing the envelope model to the tangential squirmer with the lowest three modes [69], which does not change its shape from the sphere. Also they showed that the velocity decay of a jumping organism has good agreement with the experimental result of copepods by [51]. Compared with these unsteady effects, the obtained results in this chapter reflect the periodic swimming pattern of organisms, which we mean is the difference between the wave pattern and the flapping motion.

With regard to the metachrony, differences of the unsteady inertia corrections between the symplectic and antiplectic swimmers are so minor that we can not detect from the figure.

Compared with the analysis of the oscillating-boundary-layer theory for an inertialess squirmer [13], which shows the optimal net velocity is achieved at $\delta = \pi/2$ or $3\pi/2$ in this system, the chosen phase shift here reflects an advantage of a reciprocal motion in the unsteady Stokes flow. This characteristic of the unsteady inertial effects will be illustrated by a simple squirmer in the next section.

2.6 Discussion

In this section, we discuss the inertial effects on the squirmer by the use of a simpler mathematical model swimmer in terms of the energy consumption.

2.6.1 Energy consumption

Let us consider the power input into the fluid by the strokes of the swimmer. The power input is defined as

$$P = -\int_S (n \cdot \sigma) \cdot u \, dS = -2\pi \int_{-1}^1 [(n \cdot \sigma) \cdot u]_{r=1} \, d\mu + O(\epsilon^3), \quad (2.75)$$
Fig. 2.3: Contour of the leading correction of the averaged velocity when $R_\omega = 1$ in the wave number $k$ and phase shift $\delta$ plane. The peaks of the magnitudes of the corrections appear when $k \approx \pm 1$ and $\delta = 0$ and $\pi$. The correction due to the unsteady inertia becomes less and less for larger wave numbers.
where the normal vector is outward again. At the lowest order of $\epsilon$, $P$ becomes

$$
P = -2\pi \int_{-1}^{1} \left[ \frac{\partial\psi}{\partial\mu} + 2 \left( \frac{\partial^2\psi}{\partial r \partial\mu} - \frac{2\partial\psi}{\partial\mu} \right) \frac{\partial\psi}{\partial\mu} + \left( \frac{1}{1 - \mu^2} \frac{\partial^2\psi}{\partial r^2} - \frac{2}{1 - \mu^2} \frac{\partial\psi}{\partial r} - \frac{\partial^2\psi}{\partial\mu^2} \right) \frac{\partial\psi}{\partial r} \right]_{\mu = 1} \, d\mu. \tag{2.76}$$

Carrying out Legendre integrals as in §2.3, we obtain $P$ as series of the coefficients $A_n$ and $B_n$.

$$
\frac{P}{2\pi} = \sum_{n=1}^{\infty} \left( \frac{4n^2 + 6n + 8}{(n + 1)(2n + 1)} A_n^2 + \frac{24}{2n + 1} A_n B_n + 2n(n + 1)B_n^2 \right) \\
+ \sum_{n=1}^{\infty} \left( \frac{2X_n A_n}{(n + 1)(2n + 1)} + \frac{2X_n B_n}{2n + 1} + \frac{2R_\omega A_n \dot{A}_n}{(n + 1)(2n + 1)} \right) + (A_1 + 2B_1) V \\
+ \sqrt{R_\omega} (A_1 + 2B_1) \int_0^t \frac{\dot{V}(x)}{\sqrt{\pi(t - x)}} \, dx + R_\omega A_1 \dot{V}. \tag{2.77}
$$

At the limit of $R_\omega \to 0$, remember $V = (-1/3)(A_1 + 2B_1)$, the equation (2.77) can be reduced to the energy consumption obtained by [9]. When we neglect the gravity effect, we have finally

$$
\frac{\langle P \rangle}{2\pi} = \frac{8}{3} \epsilon^2 \left\langle (\dot{\alpha}_1 - \dot{\beta}_1)^2 \right\rangle \\
+ \epsilon^2 \sum_{n=2}^{\infty} \left( \frac{4n^2 + 6n + 8}{(n + 1)(2n + 1)} \alpha_n^2 - \frac{12n}{2n + 1} \alpha_n \dot{\beta}_n + 2n(n + 1)\beta_n^2 \right) \\
+ O(\epsilon^3, R_\omega^{3/2}, R_\omega^{1/2} R_S). \tag{2.78}
$$

At the lowest order of $\epsilon$, there are not any corrections due to the inertial effects up to $O(R_\omega, R_S)$.

Let us introduce commonly used [16, 71] efficiency for low Reynolds number swimmers $\eta = \langle V \rangle T / \langle P \rangle$, where the thrust $T$ is here given by $6\pi(V)$. This efficiency expresses the percentages of energy transformation from the work done by the deformation of the swimmer into the translation of the body whose energy is evaluated by an external force producing stationary movement with velocity $\langle V \rangle$. A swimmer with a reciprocal stroke has the efficiency $\eta = O(\epsilon^2 R_\omega)$, while the efficiency for a swimmer with a non-reciprocal stroke becomes at the order of $\epsilon^2$. 

32
2.6 Discussion

2.6.2 Example swimmer

In this section, we consider an example swimmer with a simplified stroke in order to illustrate the inertial effects. We assume

$$\alpha_1 = C_1 \cos(\omega t), \quad \alpha_2 = C_2 \cos(\omega t + \Delta), \quad (2.79)$$

where the amplitude factors $C_1$ and $C_2$ are positive constants, the frequency $\omega$ is $\omega = 2\pi$, and $\alpha_n$ ($n \geq 3$) and $\beta_n$ ($n \geq 1$) are zero i.e.

$$R = 1 + \epsilon (C_1 \cos(\omega t) P_1 + C_2 \cos(\omega t + \Delta) P_2). \quad (2.80)$$

Here $\Delta$ is a phase shift. The $\alpha_1$ mode gives displacement of the envelope, which does not mean the movement of the centre of the swimmer. The $\alpha_2$ mode corresponds to an ellipsoidal deformation. According to the results in §2.4, the time-averaged asymptotic velocity is given by

$$\langle V \rangle = \frac{\epsilon^2}{45} \left\{ 20\langle \dot{\alpha}_1 \alpha_2 \rangle + 15\langle \alpha_1 \dot{\alpha}_2 \rangle - R_\omega (4\langle \alpha_1 \dot{\alpha}_2 \rangle + \langle \dot{\alpha}_1 \alpha_2 \rangle) \right\} + O(\epsilon^3, R^{3/2}_\omega, R^{1/2}_S), \quad (2.81)$$

and the time-averaged power consumption $\langle P \rangle$ becomes

$$\langle P \rangle \frac{2\pi}{2\pi} = \epsilon^2 \left( \frac{8}{3} \langle \dot{\alpha}_1^2 \rangle + \frac{12}{5} \langle \dot{\alpha}_2^2 \rangle \right) + O(\epsilon^3, R^{3/2}_\omega, R^{1/2}_S). \quad (2.82)$$

Substituting the equation (2.79) to these representations, we obtain

$$\langle V \rangle = -\frac{\epsilon^2}{90} C_1 C_2 \omega \left( 3 \sin \Delta + 5 \omega R_\omega \cos \Delta \right) \quad (2.83)$$

and

$$\langle P \rangle \frac{2\pi}{2\pi} = \epsilon^2 \omega^2 \left( \frac{4}{3} C_1^2 + \frac{6}{5} C_2^2 \right). \quad (2.84)$$

The swimming efficiency is also calculated,

$$\eta = \frac{\epsilon^2}{360 \cdot 10C_1 + 9C_2^2} \left( 3 \sin \Delta + 5 \omega R_\omega \cos \Delta \right)^2. \quad (2.85)$$

We consider the optimal stroke which maximises the average velocity or the swimming efficiency with being subject to fixed average energy consumption.
\( \langle P \rangle = \langle P \rangle_{\text{max}} \). With the Lagrange multiplier method, it is found that both the maximum velocity and efficiency are achieved when \( C_2 = (\sqrt{10}/3)C_1 \) and \( \Delta = \tan^{-1}(3/5\omega R_\omega) \) \((\pi \leq \Delta \leq 2\pi)\). Then we have the maximum of the velocity,

\[
\langle V \rangle_{\text{max}} = \frac{\sqrt{10}}{1440\pi} \sqrt{9 + 25\omega^2 R_\omega^2} \langle P \rangle_{\text{max}},
\]

and of the efficiency \( \eta_{\text{max}} \)

\[
\eta_{\text{max}} = \frac{9 + 25\omega^2 R_\omega^2}{34560\pi} \langle P \rangle_{\text{max}},
\]

both of which are proportional to the input work rate \( \langle P \rangle_{\text{max}} \).

To see the reciprocity of the stroke, we consider an area \( W \) in the parameter space enclosed by the stroke, which is proportional to the magnitude of the net velocity when the inertia is neglected \([92]\). Given the oscillatory Reynolds number, the area \( W \) for an optimal stroke is obtained,

\[
W = \left| \int a_2 \, \text{d}a_1 \right| = \frac{1}{2} \epsilon^2 \omega C_1 C_2 \sin |\Delta|
\]

\[
= \frac{\sqrt{10}}{32\pi \omega} \sin \left[ \tan^{-1} \left( \frac{3}{5\omega R_\omega} \right) \right] \langle P \rangle_{\text{max}},
\]

which approaches zero as the oscillatory Reynolds number increases. Of course the expression when \( R_\omega \) is not small enough is beyond the asymptotic analysis given here. When \( R_\omega = 1 \), the area (2.88) is 9.5% of that when \( R_\omega = 0 \). This shows the optimal stroke, which must far from reciprocal in the case of the zero inertia, comes closer to the reciprocal motion when the inertia is taken into consideration. We can suggest that the unsteadiness effects of both the fluid and the body emphasise the flapping motion and become a key to the difference of the stroke pattern among the many varieties of swimmers.

2.7 Conclusion

Unsteady inertial effects on the motion of a spherical micro-swimmer with slight deformation of the surface are studied by the use of the squirmer model in the unsteady Stokes flow. The asymptotic expansions with respect to the small unsteady inertial effects and for the long time behaviour are
performed, and it is found that the inertial effects on the swimming velocity is significant for a flapping swimmer as contrasted with little influence on that of swimmer with wave pattern. The inertial effect is also illustrated with a simple squirmer so that the reciprocal motion can be the optimal stroke when the inertia is taken into account. This asymptotic analysis suggests the unsteady inertia is a key to understand the difference of the swimming morphology among microorganisms.

As shown in [110], the scallop theorem does not hold any more due to the unsteady inertia. We study the net motion of a squirmer with an arbitrary shape variation of the surface including the radial deformation. When we consider the long time behaviour at the first order of the expansion, the scallop theorem holds in an asymptotic sense, however the second order expansion gives rise to the breakdown of the ‘asymptotic’ scallop theorem in terms of the shape deformation from the sphere.

We have assumed that the convective term is always irrelevant compared with the unsteady term, but the effects of the small non-linearity are still unknown and might be important in the transition of the swimming motility and the breakdown of the scallop theorem. The recent experimental and numerical results [107, 108, 3, 68] suggest an existence of the dynamical bifurcation at a finite Reynolds number, while the results in this chapter show the continuous breakdown of the theorem. This contradiction may arise from suppressions by the non-linear term which is neglected here. Another possible reason is the symmetry of the stoke. As mentioned in [46], the magnitude of the displacement during one period depends on the symmetry of stroke and the scallop theorem still holds with a completely mirror symmetrical stroke even when the mass inertia is taken into consideration, which may occur in this case as well.

With regard to the real flapping swimmer, the amplitude of the deformation is not always small enough for the asymptotic analysis to be applied. Also the squirmer discussed in this chapter has axisymmetric stroke and spherical geometry, although a real swimmer, Paramecium for example, loses the axisymmetry of the stoke and has a spheroid or more complex cell geometry. From this context, computational researches on a deforming swimmer with enough accuracy is expected to be developed.
Chapter 3

Squirming locomotion near a boundary

3.1 Introduction

In this Chapter, the motion and the mechanical stability of the squirmer near a boundary is considered, using a spheroidal tangential squirmer from dynamical systems’ view points. The contents of this chapter have been published as K. Ishimoto and E. A. Gaffney, Phys. Rev. E., 88 (2013) 062702 [49].

Simply examining pond water under a microscope reveals a diversity of swimming microbes, thriving in a low Reynolds number world, where inertia is typically negligible [64, 14, 84, 16, 57, 41]. In many experiments, to assure more than a fleeting glimpse of motile microswimmers, the focal plane is typically set adjacent to the coverslip, where microswimmers often accumulate [89, 112, 55, 8, 24]. This boundary attraction initiates bacterial biofilms [76], which present major economic challenges and opportunities, such as biofouling, biohydrometallurgy and bioremediation [20, 34]. Boundary dynamics also clearly influences sperm motility [18, 113], with potential functional consequences, such as reducing the dimensionality of sperm guidance [23, 35] and encouraging sperm escape from reservoirs in the isthmus of the estrous mammalian female reproductive tract [101, 21].

This prevalence and importance of motile microswimmer boundary induced behaviours has encouraged numerous mechanical studies, from initial explorations of the extent of surface effects [52, 85] to the influence of a no-slip boundary on a flagellated bacterium’s circling behaviour, efficiency and entrapment [55, 8, 94]. Other examples include the confirmation that
detailed flagellar regulation is not required to bring a sperm cell close to a surface [30, 96], although a waveform regulation, known as hyperactivation, appears to encourage surface escape [21]. Further studies have also explored the boundary dynamics of idealised swimmers and prospective engineered swimmers [114, 19, 74], often via the use of dynamical systems ideas [74], and have for instance illustrated that height oscillations above the surface are possible for inertialess swimmers [74], though this has not been predicted by sperm or bacterial modelling to date.

In addition, a generic and detailed analytical study based on the far field structure of the flow field has been presented by Spagnolie and Lauga [99]. However, except as part of this generic context, and a brief consideration by Llopis et al [67], the boundary dynamics of one class of model microswimmer has not yet been considered, namely that of the squirmer [63, 9], which induces motility by non-reciprocal surface deformations.

Thus our first objective in this chapter will be to classify the behaviour of tangential squirmers with axisymmetric bodies and relatively simple slip velocities near no slip boundaries utilising dynamical system ideas, in particular a phase plane in the angle of attack and height from the surface. By exploiting boundary element methods for the solution of Stokes' inertialess fluid dynamical equations, which provide high numerical accuracy for low computational costs [44, 94, 39, 99], we will numerically explore phase space, considering fixed points and their bifurcations as parameters vary. We will also investigate whether more complex dynamics such as limit cycle behaviours and multiple fixed points occur, as well as considering surface scattering, enabling an assessment and characterisation of how swimming behaviours near surfaces vary in parameter space for this class of tangential squirmers. We note this generally takes us beyond the scope of Spagnolie & Lauga's [99] recent study of swimmer boundary dynamics using far field analytical approximation, except for aspects of scattering dynamics where the far field theory is used to provide an independent check of our simulations.

Of particular further interest is that modelling investigations of boundary swimming to date have almost exclusively focussed on no-slip boundaries. However, free surface boundary dynamics merit attention in that an air-water interface is an exploitable microenvironment, facilitating sperm accumulation for laboratory studies [12], as well as providing niche resource opportunities for ciliates [88] and strain dissemination for bacteria [62]. However, current modelling has been restricted to idealised two-dimensional studies including surface deformation [19] and a theoretical prediction that flagellated bacterial circling is reversed near a stress free surface [55], with a subsequent
3 Squirming locomotion near a boundary

empirical verification [62, 24]. The latter in particular relies on the dynamics of the rotating bacterial flagellum and the counter-rotation induced on the cell body, resulting in a far-field torque dipole, which clearly has an extensive influence on swimmer dynamics near surfaces.

Thus, our second objective will be to also characterise how squirmer boundary dynamics may differ in the presence of a stress free surface in parameter regimes characterised by low Capillary numbers, i.e. high surface tension, so that surface deformations are negligible [61], simplifying the analysis. The influence of swimmer strokes generating an additional torque dipole on squirmer boundary dynamics will also be explored, given its importance in bacterial surface behaviour.

In summary, microswimmers exhibit a diverse array of surface behaviours and differentiating between hydrodynamical and adaptive biological or chemical effects is fraught with difficulty. Hence we explore how dynamical systems principles provide a means of classifying purely hydrodynamical behaviours, both near no-slip and stress free surfaces for a simple swimmer, the axisymmetric tangential squirmer which is a common model for ciliates, colonial algae and Janus particles. The suggested prospect that the far field dynamics of swimmers may allow approximation of surface behaviours [99] indicates that such characterisations, with the inclusion of rotlet dipoles given the prevalence of rotary flagellated swimmers such as bacteria, may be more widely applicable. Thus in our study of squirmer boundary swimming, our final objective will be to suggest predictions of generic behaviours across parameter space that may be investigated in more specialised, geometrically faithful, studies of specific swimmers.

3.2 The model swimmer and its fluid dynamics

3.2.1 The squirmer

We consider an axisymmetric inertialess microswimmer with semi-axes $a, c$, initially above a no-slip wall, which generates propulsion by an axisymmetric tangential surface deformation, represented by a tangential slip velocity. The location of the swimmer is given by the height of its centre above the wall, $h$, and the angle between its axis of symmetry and the wall, $\varphi \in (-\pi/2, \pi/2)$, as illustrated in Fig. 3.1, noting that a unique symmetry axis exists even for the spherical swimmer, due to the squirming deformations. The squirmer surface
3.2 The model swimmer and its fluid dynamics

Fig. 3.1: A schematic picture of an inertialess tangential squirmer, with semi-axes $a, c$, located a height $h$ above a no-slip boundary at an angle $\varphi$, with the axis of symmetry corresponding to the unit vector $e$, directed positively with the swimming direction in the absence of a wall. The polar angle $\theta$ and the axisymmetric tangential slip velocity component, $u_\theta(\theta)$, are also depicted. The symmetry of the latter slip-velocity profile ensures the swimmer remains in a plane perpendicular to the wall, which in this chapter is taken to be the $x-z$ plane without loss of generality, as depicted.

is parameterised by a polar angle, $\theta \in [0, \pi]$ which is the angle between the swimmer surface normal and its axis of symmetry, as shown in Fig. 3.1, together with an azimuthal angle $\phi \in [0, 2\pi)$, which is the angle around the axis of symmetry, taken clockwise as seen from behind the swimmer.

We firstly consider a swimmer with a polar slip velocity relative to the body fixed frame. This is represented by a velocity component expressed in terms of an associated Legendre polynomial expansion

$$u_\theta(\theta) = \sum_{n=1}^{\infty} B_n V_n(\cos \theta), \quad (3.1)$$

in the polar tangential direction to the swimmer surface, as depicted in Figure 3.1, with

$$V_n(x) = \frac{2\sqrt{1-x^2}}{n(n+1)} \frac{d}{dx} P_n(x), \quad (3.2)$$

where $P_n(x)$ denotes the $n$-th order Legendre polynomial.
Squirming locomotion near a boundary

Given the symmetry of this surface velocity, the swimmer moves in a plane, which is perpendicular to the wall and denoted by the plane, as shown in Fig. 3.1. We non-dimensionalise so that the non-dimensional viscosity is \( \mu = 1 \), and the volume of the squirmer is given by \((4\pi/3)a^2c = 4\pi/3\) and hence the geometry of the swimmer is identified by the aspect ratio \( A = c/a \), and all length scales, for instance the height from the wall, are non-dimensionalised by \( A^{1/3} \). The swimming velocity of a spherical squirming \((a = c)\) in free-space is simply given by \( U = (2/3)B_1 \) on additionally noting an inertialess swimmer is subject to zero net force and torque [63, 9].

This highlights how the lower modes of the associated Legendre polynomial expansion strongly dictate the overall behaviour of the swimmer. Indeed these modes dominate the far field, which has a particularly simple structure any significant distance from the swimmer, as can be seen in Fig. 3.2, and thus these modes are likely to dictate initial swimmer-wall interactions as a squirming approaches a boundary. Hence, as observed in Spagnolie and Lauga [99], the consideration of the far field often leads to accurate predictions for overall swimmer behaviour. Consequently, to limit the dimensionality of parameter space that needs to be considered, we focus on the first three modes of expansion (3.1) in our explorations. Without loss of generality, we hereafter fix \( B_1 = 1.5 \) which generates a unit velocity in the case of a free-space spherical squirming, which is consequently the velocity scale used in the chapter. Thus to complete our characterisation of tangential squirming deformations, we introduce two further slip velocity parameters, \( \beta_2 = B_2/B_1 \) and \( \beta_3 = B_3/B_1 \).

### 3.2.2 The far-field expression and singularity solutions

The flow field obeys Stokes’ equation and can be expressed by the superposition of fundamental singular solutions, i.e. the Stokeslet \( G \), the potential source, \( H \) and their multipoles,

\[
    u_j(y) = \int dS_x \sum_{n=0}^{\infty} \frac{\partial^n}{\partial x_{i_1} \partial x_{i_2} \cdots \partial x_{i_n}} (a_{i_1, i_2, \cdots, i_n} G_{ij}(y, x) + \beta_{i_1, i_2, \cdots, i_n} H_{ij}(y, x)),
\]

where the integral is taken over a surface \( x \) located in the exterior of the flow [83]. The Stokeslet is also called the Oseen tensor and given by

\[
    G_{ij}(x, y) = \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3},
\]
3.2 The model swimmer and its fluid dynamics

Fig. 3.2: The flow field around a spherical swimmer with the direction $\theta = 0$ corresponding to the positive horizontal direction for a tangential squirming pattern that possesses only (left) a $B_1$ mode (centre) a $B_2$ mode and (right) a $B_3$ mode in the associated Legendre polynomial expansion, equation (3.1).

where $r = y - x$ and $|r| = r$. Similarly the potential dipole is given by

$$H_i(x, y) = \frac{r_i}{r^3}, \quad (3.5)$$

and it arises in the multipole expansions due to the presence of a boundary.

The flow far from the body is expressed by the first few modes, which is often used in the discussions of the fluid interaction of microswimmers, noting that both strengths of the Oseen tensor and the source singularity must be zero due to the free-force condition and the volume conservation of the swimmer. In particular, for an axisymmetric swimmer the flow field is of the form

$$u_l = \alpha e_i e_j G_{ijl}^D + \beta e_i H_{il}^D + \gamma e_i e_j e_k G_{ijkl}^Q + O(|r|^{-4}), \quad (3.6)$$

where the upper suffixes $D$ and $Q$ respectively denote the dipole and quadrupole of each singularity, and the vector $e$ is a unit vector along the swimmer’s axis of symmetry, in the same direction as the swimmer motion in the absence of a wall.

Since the swimmer geometry becomes irrelevant for the far-field velocity, the strengths of the singularities in (3.6) can be evaluated from the far-field expression around the spherical squirmer even though the swimmer is generally spheroidal. Compared with the flow around the spherical squirmer
3 Squirming locomotion near a boundary

[9], the strengths are respectively found to be

\[
\alpha = -\frac{3}{4} \beta_2, \\
\beta = \frac{1}{2} - \frac{1}{8} \beta_3, \\
\gamma = -\frac{5}{16} \beta_3.
\]  

(3.7)

The signature of \( \alpha \) is used to classify the slip-velocity of the swimmer; in particular, a swimmer with positive \( \alpha \) is a pusher while negative \( \alpha \) corresponds to a puller [99]. Microorganisms with tail-like flagella behind the cell, according to the direction set by the overall cell movement, such as bacteria and spermatozoa, can be categorised as pushers. Pullers may be seen in swimmers with their flagella ahead of the cell body, for instance \textit{Chlamydomonas} and \textit{Leishmania} promastigotes. Indeed, \( \beta_2 \approx 1 \) is reported for \textit{Escherichia coli}, whilst \( \beta_2 \approx 0 \) for \textit{Volvox carteri} and artificially created squirmers like a Janus particle, and \( \beta_2 \approx 1 \) for the algae genus \textit{Chlamydomonas} [29]. The potential dipole term, which is a fundamental solution for the Laplace equation of potential flow arises due to the presence of a boundary, while the Stokes quadrupole term typically reflects a fore-aft asymmetry of the swimmer. For instance the idealised, elongated, bacterial-like swimmers of Spanolie and Lauga [99] have negative \( \gamma \), with \( |\gamma| < 20 \), whilst spermatozoa also generate non-trivial values of \( \gamma \) due to their fore-aft asymmetry [97].

### 3.2.3 Dynamical systems and time-reversal symmetry

Given the surface velocity and the geometric aspect ratio, the force and the torque exerted on the swimmer are completely determined by the configuration of the body, i.e. the distance from the wall \( h \) and the direction of the symmetry axis \( \varphi \). Therefore the inertialess Stokes dynamics can be described in terms of the two-dimensional first-order ODE system,

\[
\dot{h} = F_h(h, \varphi) \\
\dot{\varphi} = F_\varphi(h, \varphi),
\]  

(3.8)

where the functions \( F_h \) and \( F_\varphi \) can be numerically obtained from Stokes’ equation. Determining the fixed points of the dynamical system (3.8) and their linear stability, by considering the associate fixed point eigenvalues, is fundamental as a stable fixed point of (3.8) may be regarded as a mathematical expression of stable boundary swimmer behaviour.
3.2 The model swimmer and its fluid dynamics

Furthermore, the dynamical system (3.8) possesses a time-reversal symmetry under the change of variables,

\[
\begin{align*}
    t & \rightarrow -t \\
    \varphi & \rightarrow -\varphi \\
    \beta_2 & \rightarrow -\beta_2 \\
    \beta_3 & \rightarrow \beta_3,
\end{align*}
\]

which demonstrates that the dynamical behaviour due to a slip-velocity with parameters \((\beta_2, \beta_3)\) is the same as a time reversed slip-velocity for the dual swimmer with parameters \((-\beta_2, \beta_3)\). Hence the behaviour of pushers can be understood from that of pullers. For instance, suppose that there exists a stable fixed point \((h^*, \varphi^*)\) for a given slip-velocity \((\beta_2, \beta_3)\). The symmetry (3.9) then implies that \((-h^*, -\varphi^*)\) is also a fixed point for the dual swimmer with \((-\beta_2, \beta_3)\), though stability is lost due to the time reversal in the duality.

3.2.4 Numerical scheme

The single layer boundary element method for an incompressible inertialess flow of a Newtonian fluid is used to compute the swimming trajectory. This is founded on an expression for the velocity field as an integral over the surface of the swimmer \(S\) [82],

\[
    u_i(x) = -\frac{1}{8\pi \mu} \int_S G_{ij}(x, x') q_j(x') \, dS_x,
\]

where \(q\) is a surface traction given by \(q = f - f_{int}\) with \(f, f_{int}\) respectively denoting the surface tractions due to the external and internal Newtonian flows associated with the swimmer surface velocities. This formalism entails that \(q\) possesses a gauge degree of freedom, namely an additive constant of the surface normal – this is removed by setting \(\int_S q \cdot n \, dS_x\) to zero. The Green function \(G\) is the Stokeslet in presence of an infinite no-slip rigid wall [11], known as the Blakelet, or in the presence of an infinite free-slip wall, according to the problem under consideration. For the integral kernel in the case of the free-slip wall, only the image singularity is required (see for example Appendix B of [99]), and the Green function is given by

\[
    G_{ij}^{slip}(x', x) = G_{ij}(x', x) \pm G_{ij}(x', x^*),
\]

where \(x^*\) is the mirror image of \(x\) with respect to the infinite wall, \(x^* = x - 2h\hat{z}\), and \(\hat{z}\) is an unit vector along the z-axis. The sign in (3.10) is taken to be positive when \(i = x, y\) and negative otherwise.
3 Squirming locomotion near a boundary

The boundary condition on the surface of the swimmer, $S$, is a continuity of velocity, so that the fluid velocity matches the local surface velocity of the swimmer. The position of the swimmer surface $\xi$ in the laboratory frame can be written as $\xi = X + B \cdot \xi'$ (Fig. 4.2), where $X$ is the origin of the body frame in the laboratory frame, corresponding to the centre of the swimmer, $\xi' = x' - X$ is the surface position in the body frame and, following [96], $B$ is a set of column basis vectors of the body frame. Let $U$ and $\Omega$ be the translational and rotational velocity of the origin of the laboratory frame $X$. Then the surface velocity of the swimmer in the laboratory frame is

$$v(\xi) = U + \Omega \times \xi' + B \cdot \dot{\xi}'.$$  (3.11)

The boundary condition that the velocity vector field does not slip relative to the swimmer surface deformation, $v(x') = u(x')$, thus becomes

$$u_j = U_i + \epsilon_{ijk} \Omega_j \xi_k' + B_{ij} \xi_j'$$

$$= -\frac{1}{8\pi\mu} \int_S G_{ij}(x', x'')(q_j(x'')) \, dS_{x''}. \quad (3.12)$$

Noting that the force and torque generated on the swimmer by the internal force, $f_{int}$, are both zero [82], the total force and torque balance equations can be written in the form

$$\int_S q(x') \, dS_{x'} = \int_S (x' - X) \times q(x') \, dS_{x'} = 0. \quad (3.13)$$

The unknown variables $q(x')$, $U$ and $\Omega$ are then obtained by solving the linear problem (4.19), subject to the balance equations (4.21).

For mesh generation, we have employed the BEMLIB library accompanying [83]. The number of mesh elements used here is $N = 512$ or $N = 2048$, depending on the accuracy that is required. At each time point, the problem then reduces to the solution of a dense matrix equation in $3N + 6$ unknowns, analogously to [44]. This yields the body velocity and angular velocity at each time point in terms of the surface deformations, which is sufficient to find phase space fixed points. When swimmer trajectories are required, there is a subsequent time-marching which proceeds via a Heun scheme, as presented by Smith et. al. [96].

Once the distance between the swimmer surface and the substrate is of the order of 0.1 microns or less, additional interaction forces manifest between a bacterial cell and the boundary, which are highly dependent on the details of the substrate, the swimmer surface and the solution media [53]. We do not
3.3 Dynamics in phase space

3.3.1 Swimming near a no-slip boundary

We proceed to numerically examine the fixed points for height, $h$, and angle, $\varphi$, using the standard Newton-Raphson method, which calls the boundary element solver to determine values of the functions $F_h$ and $F_{\varphi}$ in equation (3.8), in turn allowing the roots of $F_h = F_{\varphi} = 0$ to be found. The results are illustrated in Fig. 3.4 – the reflection symmetry and anti-symmetry with respect to $\beta_2$ is readily apparent in the phase diagram and is a consequence of the time-reversal symmetry of this system.

Note that by the consideration of the free space solutions, we anticipate straight line swimming trajectories as $h \to \infty$ due to negligible fluid inter-

Fig. 3.3: A schematic picture of the swimmer configuration – its surface and axis of symmetry are respectively given by $S$ and $e$, with the latter’s direction dictated by the swimming direction in the absence of a wall. A laboratory reference frame has Cartesian coordinates $x$, $y$, $z$ and the position vector of the swimmer’s centre, a point on its surface and an external field point, relative to this frame, are respectively denoted by $X$, $x'$ and $x$. Analogously, a point on the swimmer’s surface relative to a body fixed frame with origin at the swimmer centre, is denoted $\xi'$.
Fig. 3.4: Plots detailing the location and stability properties of phase-space fixed points for a given slip-velocity parameterisation \((\beta_2, \beta_3)\), with different swimmer aspect ratios \(A = 1, 2, 3\) and the presence of a no-slip boundary. If no colour is plotted there is no fixed point for the given parameter values. The upper row (a) presents the steady state angle between the axis of symmetry and the wall, \(\varphi^*\), associated with each fixed point in units of radians. When \(\beta_2 \approx 0\) and \(\beta_3 > 0\), there are multiple fixed points, though we only plot the one with the most negative \(\varphi^*\) when \(\beta_2 \geq 0\), and the most positive otherwise; these fixed points are nodes with nearby adjacent saddles, as illustrated in Fig. 3.5 and discussed further in the text. The central row (b) depicts the shortest distance between the swimmer and the wall for the plotted fixed point. The bottom row (c) gives the largest real part of the linear stability eigenvalues associated with the plotted fixed point.

actions with the wall; such regions of phase space are neglected below since the dynamics is trivial. In particular, since the time variation of \(h\) and \(\varphi\) becomes quite small when the swimmer is far from the wall \((h \gg 1)\), so
that $F_h$ and $F_{\phi}$ vary only weakly, the accuracy requirements in finding any prospective large-$h$ fixed point becomes extremely demanding. Furthermore, such a fixed point can be regarded as physically meaningless in terms of swimmer-boundary attraction. Thus we introduce a cut off for the height of the fixed point at $h_{far} = 15$, i.e. a scale of 15 swimmer lengths from the wall, where the squirmer-wall interactions are assured to be very small.

Achieving accuracy for any prospective fixed point very close to the wall is also computationally extremely demanding, due to difficulties in sufficiently resolving the singularities and their images when the swimmer surface is extremely close to the wall [94]. In particular, the boundary element scheme and discretisation used here lose accuracy when the distance $d$ between the wall and the nearest point of the swimmer, which is given by $d = h - A^{-1/\beta} \cos(\varphi) \sqrt{1 + A^2 \tan^2(\varphi)}$, decreases below 0.01 non-dimensional units. This is on the scale of 0.01 of the squirmer semi-axis: even for a swimmer as large as the ciliate depicted in Fig. 1.2 this is about 0.2 microns, which is approaching a scale necessitating the inclusion of non-hydrodynamic, molecular-level, details in the squirmer-surface wall interactions. Thus, once more, drawing any quantitative conclusions relying on the modelling predictions in this dynamical regime requires caution.

In Fig. 3.4, there is a region at the centre of the phase diagram where no fixed points exist. As the slip-velocity parameters ($\beta_2$, $\beta_3$) approach this region the steady state height, $h^*$, grows rapidly as can be seen in the middle row of Fig. 3.4. Thus, for example, the fully activated Janus swimmer, which is classified by $\beta_2 = \beta_3 = 0$ (Fig. 3.4, [99]) does not have a fixed point near a wall.

Now consider a swimmer with $\beta_2 = 0, \beta_3 < 0$ – there is a fixed point with zero steady state angle, $\varphi^* = 0$, and pure imaginary eigenvalues. More generally, if there is a fixed point with $\varphi^* = 0$, the real part of the eigenvalues must be zero due to the time-reversal symmetry discussed above. Such a fixed point is a centre, with the linear theory prediction that phase space trajectories form closed loops sufficiently close to the fixed point. While in general this need not reflect the behaviour of the full non-linear system, due to the breakdown of Hartman’s theorem, the time reversal symmetry ensures that such trajectories are indeed closed loops.

Except for $\beta_2 \sim 0$ with $\beta_3$ relatively large, which we discuss later below, there is a single fixed point; in this case, the eigenvalues have non-zero real parts when $\beta_2 \neq 0$ and thus the fixed point is a phase plane focus. Consequently, when the real part of the eigenvalue is negative, the swimmer progresses in one direction essentially parallel to the wall, with a damped height
oscillation that relaxes to the fixed point on approaching stable swimming and presents a growing unstable oscillation otherwise.

The presence or absence of this stability is highly sensitive to the swimmer aspect ratio \( A \), as can be observed from the lowest row of Fig. 3.4. First of all, let us consider the case of the spherical squirmer with \( A = 1 \). For a swimmer with positive \( \beta_2 \) (a puller), there are two regions with distinct stability behaviours in the figure: an unstable region with smaller \( \beta_3 \) and a stable region with larger \( \beta_3 \). Our computational results show that as the geometric aspect ratio, \( A \), is increased from 1 to 2, some fixed points are lost to infinity and the stable region with \( \beta_2 > 0 \) is compacted into a region with smaller \( \beta_3 \). There is also a new unstable region for larger \( \beta_3 \) and analogous dual changes occur for \( \beta_2 < 0 \). With a further increase in the aspect ratio to \( A = 3 \), boundary swimming with \( \beta_2 > 0 \) is now unstable, in distinct contrast to most of the parameter space for \( A = 1 \). Hence, both pushers and pullers can stably swim near a boundary with an appropriate slip-velocity pattern, which is generally contingent on the squirmer geometry. Furthermore, one can also observe that whenever a puller (\( \beta_2 > 0 \)) has a stable fixed point, its angle relative to the wall is negative, in contrast to a pusher, reflecting the duality imposed by time-reversal symmetry.

Remarkably, we can find regions containing multiple fixed points when \( \beta_2 \sim 0 \) and \( \beta_3 \) is relatively large. These do not contradict time-reversal symmetry as the two steady state angles and the associated linear stability eigenvalues differ by a minus sign while the steady state height is the same. In this parameter regime, with \( \beta_2 \geq 0 \), only the fixed point associated with the most negative angle is plotted in Fig. 3.4, whilst the fixed point associated with the most positive angle is plotted for \( \beta_2 < 0 \). In addition, we observe an adjacent saddle point. The dynamics in this regime is therefore more complicated than a phase plane focus that we observed above. Thus, to understand swimming behaviours in the presence of these multiple fixed points, and global behaviour more generally, the swimmer’s overall behaviour in phase space also needs to be explored. We therefore numerically examine swimmer trajectories in phase space and, more generally, the \((h, \varphi)\) phase plane portrait.

Firstly, we consider a parameter regime with multiple fixed points. With \( A = 1, \beta_2 = 0, \beta_3 = 10 \), the phase portrait is plotted in Fig. 3.5. Nodes are depicted by circles, and the node associated with a negative steady state angle, \( \varphi^- \), is unstable in contrast to the node associated with positive \( \varphi^+ \). Two saddle points are also present and close to the nodes so that local to each saddle-node pair the phase portrait is analogous to that of a saddle-node
3.3 Dynamics in phase space

Fig. 3.5: The phase plane portrait for $A = 1, \beta_2 = 0, \beta_3 = 10$ with arrows indicating flow in the dynamical system. Four fixed points can be observed with a duality in the sign of the steady state angle. The circles indicate two fixed points, one of which at $(h^*, \varphi^*) = (1.093, 0.231\pi)$ is a stable node, whereas the other at $(h^*, \varphi^*) = (1.093, -0.231\pi)$ is an unstable node. Also, two saddle points are depicted by stars, at $(h^*, \varphi^*) = (1.222, \pm 0.194\pi)$.

Bifurcation. In particular such fixed point pairs are not globally stable, as the saddle’s unstable manifold drives integral paths away from the fixed points, and thus the associated dynamics can be highly contingent on the approach to the fixed points, even when one of them is locally stable. In particular stable boundary swimming need not occur, and the swimmer can either approach the surface or be scattered from it, depending on initial conditions. However this dynamical system phase plane portrait relies on relative fine tuning as the saddle and node annihilate in a bifurcation as $\beta_2$ moves away from zero. Nonetheless, certain aspects of the phase plane are also present even with a single stable fixed point, such as the observation that the swimmer can approach the boundary or escape at sufficiently extreme angles for example.

We proceed to consider a swimmer’s trajectory for a slip-velocity associated with an unstable fixed point. As the slip-velocity parameters $(\beta_2, \beta_3)$ are changed along a curve in $(\beta_2, \beta_3)$ parameter space where the real part of the eigenvalues transition through zero without a change in the sign of
Fig. 3.6: A phase-space trajectory for $A = 2, \beta_2 = 6, \beta_3 = -2$. The colour contour shows the time after departure from an initial point adjacent to the unstable fixed point. Clearly, the trajectory ultimately converges to a limit cycle.

$\beta_2$, the fixed point undergoes a Hopf bifurcation. In the case of $A = 2$ for instance, when the parameters change from $(\beta_2, \beta_3) = (6, -10)$ to $(6, 5)$, the stable fixed point becomes unstable at $\beta_3 \sim -4$. We therefore explore the swimmer dynamics in phase space after the Hopf bifurcation has occurred by employing initial conditions which constitute a perturbation away from the unstable fixed point, and then computing the swimmer trajectory until it approaches the wall or moves away ($h \geq h_{far}$), or the large time dynamics is revealed. In particular, the Hopf bifurcation is supercritical and a stable limit cycle is observed as highlighted in Fig. 3.6 for parameters $A = 2, \beta_2 = 6, \beta_3 = -2$. Furthermore, as $\beta_3$ further increases, the limit cycle becomes larger and approaches the wall, eventually intersecting it. Thus this trajectory finally becomes globally unstable in the sense that the swimmer is brought sufficiently close to the wall by hydrodynamic interactions that surface-swimmer molecular interaction forces manifest, at which point the model presented here breaks down, as schematically illustrated in Fig. 3.7.
3.3 Dynamics in phase space

Fig. 3.7: A schematic picture of the Hopf bifurcation and its influence on global behaviour in the phase space. A stable fixed point becomes unstable as a parameter varies, together with the appearance of a limit cycle which finally approaches and intersects the boundary. The stability of the fixed point is characterised via (s) stable, (c) non-linear centre, (u) unstable, (u+sLC) unstable fixed point with a surrounding stable limit cycle, and (u+sLC+W) unstable fixed point with a surrounding stable limit cycle that intersects the wall.

In contrast, when $\beta_2$ is negated for this set of parameters, the stability is lost due to the time-reversal symmetry, which entails the appearance of an unstable limit cycle together with a stable fixed point at a subcritical Hopf bifurcation, as reported in [74] for a simple 3-sphere swimmer.

### 3.3.2 Swimming near a free surface

The swimmer near a free surface is investigated analogously, under the assumption that the Capillary number is asymptotically small, so that surface deformation is negligible [61]. The angle, $\varphi^*$, and distance of closest approach are depicted for fixed points in Fig. 3.8 as a function of the geometric aspect ratio, $A$ and the slip-velocity parameters $\beta_2, \beta_3$. Once more the signature of the angle between the axis of symmetry and the wall at the fixed point, $\varphi^*$, is determined by the sign of the slip-velocity parameter $\beta_2$ though fixed points are now lost into the wall when $\beta_2 = 0$ as the aspect ratio increases for example, in contrast to observations for a no-slip boundary. The most surprising and interesting difference though is the absence of stable fixed
Fig. 3.8: Plots detailing the properties of phase-space fixed points for a given slip-velocity parameterisation \((\beta_2, \beta_3)\), with different geometric aspect ratios \(A = 1, 2, 3\) in the presence of a free surface boundary at asymptotically small Capillary numbers, so that surface deformation is negligible. If no colour is plotted there is no fixed point for the given parameter values. The upper row (a) plots the angle, \(\varphi^*\) of each fixed point and the lower row (b) denotes the shortest distance between the swimmer and the wall at the fixed point. When there are multiple fixed points, all are still saddles though only the one with the most negative \(\varphi\) is plotted above when \(\beta_2 \geq 0\), otherwise the fixed point associated with the most positive \(\varphi\) is plotted; see text for further details.

points in the same parameter space surveyed for the no-slip boundary case; instead we only find saddle points, demonstrating that the swimmer cannot be stably trapped near the boundary in this substantial region of parameter space.

An illustration of the global behaviour in the presence of a free surface boundary is given by the dynamical system flow presented in Fig. 3.9 for a geometric aspect ratio of \(A = 2\) and slip-velocity parameters \((\beta_2, \beta_3) = (0, 0)\) corresponding to a fully activated Janus particle [99]. The only fixed point is highlighted by a star and is a saddle, with no stable boundary swimming.
3.4 Scattering behaviour

Fig. 3.9: The phase plane portrait for an aspect ratio $A = 2$, and slip-velocity parameters $\beta_2 = \beta_3 = 0$ in the presence of a free surface. The star highlights the location of a saddle point at $(h^*, \varphi^*) = (1.147, 0)$; note that no stable accumulation dynamics is indicated by the phase-plane trajectories.

Instead (except on the stable manifolds of the saddle), the swimmer either escapes to infinity or approaches the wall, respectively with a positive and a negative angle $\varphi$. We finally note that multiple saddle points can co-exist with opposite fixed-point angle, $\varphi^*$ for a large value of $\beta_3$; in such cases the squirmer can approach the wall with a positive angle though once more stable boundary swimming is not possible.

3.4 Scattering behaviour

To examine the difference in swimmer behaviours in the absence of fixed points and either a no-slip or a free surface boundary, we consider scattering trajectories for a spherical swimmer ($A = 1$), initially located at $(x, z) = (0, 2)$ and with tangential deformation parameters $(\beta_2, \beta_3) = (0, 0)$. In Fig. 3.10a the relation between the initial angle $\varphi_{init}$ and the final angle $\varphi_{fin}$
Fig. 3.10: Left, (a). A plot of the final angle, $\phi_{\text{fin}}$, in terms of the initial angle, $\phi_{\text{init}}$, for the scattering trajectory followed by a swimming spherical squirmer with aspect ratio $A = 1$ and slip-velocity parameters $(\beta_2, \beta_3) = (0, 0)$ in the presence of both a no-slip and a free surface boundary; the far-field theory predictions are also plotted (solid). Inset: a magnified view when the initial angle is near zero. Right, (b). The trajectory when this swimmer is initially located at $(x, z) = (0, 2)$ with initial angle $\phi = -0.05\pi$ for both a no-slip and a free surface boundary.

for both no-slip and free surface boundaries are plotted, using squares and triangles. Note that below an initial angle of $\phi \sim -0.09\pi$, the swimmer is not scattered by a free surface, whilst scattering occurs for a no-slip boundary until the initial angle is as negative as $\phi \sim -0.19\pi$. Furthermore, in Fig. 3.10b, where sample trajectories in physical space are plotted for an initial angle of $-0.05\pi$, there is clearly an extended residence of the swimmer in the vicinity of the free surface during scattering, compared to a no-slip boundary. Finally, in Fig. 3.10a, the solid curve represents the far-field approximation expression for scattering from the no-slip boundary, $\phi_{\text{fin}} = \sqrt{\phi_{\text{init}}^2 + 1/64}$, [99] and clearly agrees with the no-slip boundary computation, providing an independent validation of the numerical simulations.

### 3.5 A swimmer with a rotlet dipole

We proceed to briefly consider a rotary swimmer, such as a bacterium, which is driven by a torque motor rapidly rotating a flagellum or multiple flagella in one direction, and thus inducing a cell body rotation in the opposite
3.5 A swimmer with a rotlet dipole

Fig. 3.11: A schematic picture of a squirmer with an additional rotlet dipole. The illustrated scenario case has a positive orientation and thus possesses positive $\gamma_2$.

direction, as required for conservation of angular momentum. To consider such influences, we allow the squirmer to possess an axisymmetric tangential deformation in the azimuthal direction, with this component of the surface velocity expressed in terms of a streamfunction $\Psi$, via

$$u_\phi = \frac{\Psi}{r \sin \theta}.$$  \hfill (3.14)

Here the stream function $\Psi$ satisfies

$$\left[ \frac{\partial^2}{\partial r^2} + \frac{\sin \theta}{r^2} \frac{\partial}{\partial \theta} \left( \frac{1}{\sin \theta} \frac{\partial}{\partial \theta} \right) \right]^2 \Psi = 0 \quad (3.15)$$

and, similarly to the polar angle component (3.1), we introduce a series expression of the surface velocity,

$$u_\phi(\theta) = \sum_{n=1}^{\infty} C_n V_n(\cos \theta).$$ \hfill (3.16)

Separation of variables gives the azimuthal velocity, via the solution of (3.15), as

$$u_\phi(r, \theta) = \sum_{n=1}^{\infty} \frac{C_n}{r^{n+1}} V_n(\cos \theta),$$ \hfill (3.17)

which decays on the scale $O(r^{-1})$ in the far-field, where the resulting flow can be also expanded in terms of the fundamental singular solution of a point
Fig. 3.12: The swimming trajectories projected into the $x - y$ plane for the spherical squirmer $(A, \beta_2, \beta_3) = (1, 0, 0)$, with and without a positively oriented rotlet dipole, adjacent to a no-slip or a free surface with initial location $(x, y, z) = (0, 0, 2)$ and direction $\varphi = -0.05\pi$. The swimmer with $\gamma_2 = 5$ rotates clockwise close to a no-slip boundary and counter-clockwise near a free surface, whilst swimming in the absence of a rotlet dipole induces motion only in the $x - z$ plane.

torque, or rotlet, and its multipoles [82]. The rotlet is given by

$$ R_{ij} = -\frac{\epsilon_{ijk} r_k}{r^3}, \quad (3.18) $$

though the leading term in the rotlet multipole expansion must be trivial due to the torque-free condition. Thus the leading term of the far-field velocity due to the azimuthal tangential deformations is given the rotlet dipole, $R_{ijk}^D$, and takes the form

$$ u_k \sim \tau e_i e_j R_{ijk}^D, \quad (3.19) $$

where $e$ is the axis of symmetry in Fig. 3.1 and $\tau$ is a constant, measuring the magnitude of the rotary flow and signed via its orientation. It may be determined by comparison with equation (3.17) and is given by $(1/3)C_2$, 

56
3.5 A swimmer with a rotlet dipole

Fig. 3.13: The trajectory of a squirmer adjacent to a no-slip boundary, with aspect ratio $A = 3$, and polar slip-velocity parameters $(\beta_2, \beta_3) = (-4, -4)$, for a given value of the azimuthal slip-velocity parameter $\gamma_2 \in \{0, 4, 8\}$. Left, (a). The trajectories are plotted in physical, $xyz$, space together with the projection onto the $xy$ plane, constituting the boundary at $z = 0$. Central, (b). The time evolution of swimmer height $h$. Right, (c). A plot of the associated trajectory in the phase plane dynamical system. Note that (a) the swimmer with positive $\gamma_2$ rotates in a clockwise direction when viewed from above with (b) its height converging to a constant irrespective to the magnitude of $\gamma_2$ and (c) the time evolution of the orientation angle $\varphi$ is also independent of the rotlet dipole strength.

with positive $\tau$ corresponding to the front of the cell, towards $\theta = 0$, rotating clockwise and the aft rotating anti-clockwise when viewed from behind, as depicted in Fig. 3.11, which corresponds to the chirality of $E. \text{Coli}$, whilst the opposite chirality is exhibited by $R. \text{Sphaeroides}$ [1, 73].

We therefore introduce another slip-velocity parameter, $\gamma_2$, defined as $\gamma_2 = C_2/B_1$, to incorporate the rotary contribution of the tangential deformation. Its effect only influences the squirmer trajectory near a boundary. In particular, Fig. 3.12 illustrates the trajectories of the spherical swimmer $(A, \beta_2, \beta_3, \gamma_2) = (1, 0, 0, 5)$ viewed from above, with initial position $(x, y, z) = (0, 0, 2)$ and direction $\varphi = -0.05\pi$. Note that the no-slip boundary case induces anti-clockwise circling with a positively oriented rotlet dipole, as also observed in Fig. 3.13(a), and in the opposite direction for a free surface boundary, as discussed by [55, 24] for models of bacteria. Importantly, in Fig. 3.13, we can also observe that the rotlet dipole term just modulates the swimmer’s behaviour within the horizontal plane and does not change its height and orientation angle (Fig. 3.13 (b, c)). Hence the dynamics of the swimmer in the $xz$ plane is decoupled from the influence of the rotary dynamics.
3.6 Discussion and conclusion

We have considered how an axisymmetric tangential squirmer, together with in general a rotlet dipole, behaves near a no-slip boundary and, for an asymptotically small Capillary number, near a free surface, using dynamical systems ideas to characterise the swimmer dynamics. In particular, there is a well-defined two dimensional phase plane consisting of the height above the surface and the angle the axis of symmetry makes with the boundary, immediately demonstrating that chaotic dynamics is not possible. Nonetheless, the dynamics can be complex, as emphasised in Fig. 3.5 which demonstrates that a locally stable node in phase space does not necessarily entail stable global behaviour due to its proximity to a saddle point.

Fortunately, for most regions of parameter space associated with boundary swimming, the dynamics is not as complicated. Boundary approach and escape for extreme angles of attack are evident from the phase-plane (e.g. Fig. 3.5), and the potential for extensive microswimmer boundary approach within a population of cells is consistent with the fact that in observational studies, albumin is required to prevent human sperm sticking to microscope slides [97]. For no-slip surfaces, there is also frequently a stable fixed point, demonstrating a prediction that stable boundary swimming can occur, with a slight orientation between the swimmer and the boundary, of positive angle for a pusher and negative angle for a puller. This ability to swim stably near a surface is regularly reported and likely to feature in many observations of swimming cell behaviours, such as with sperm boundary navigation [23]. In addition, the presented results demonstrate that there is a decoupling of the dynamics perpendicular to the boundary in the presence of a rotlet dipole, so that the discussions of boundary swimming immediately apply for such swimmers, as in the context of modelling bacterial motility.

Recall that the dimensional lengthscale is given by $L = (a^2 c)^{1/3}$, where $a$, $c$ are the semi-axis lengths depicted in Fig. 3.1, with a geometric aspect ratio $A = c/a$; further note that the distance of closest approach at the fixed point in Fig. 3.4 is broadly the same order of magnitude across a range of parameter values. This entails that the dimensional distance of closest approach scales with $a A^{1/3}$ and thus we have the indication that the distance of closest approach for fixed point boundary swimming is relatively insensitive to the geometric aspect ratio, as long as the fixed point remains stable. This is also consistent with simulations of monotrichous bacteria [94], and gives a first indication that the results observed here may be more generally representative of boundary microswimming.
It also clear in addition that fixed point stability, as required for stable boundary swimming, is readily altered with the aspect ratio and, in particular, the beat pattern, which can be adaptively changed by a cell. Indeed the ability of biological swimmers to regulate their behaviour near a no-slip surface is likely to be functionally important. One example concerns the passage of sperm through the estrous mammalian female reproductive tract, with the observation that the release of epithelial-bound sperm from tract reservoirs coincides with hyperactivation [101], which induces flagellar waveforms with lower spatial wavenumbers, higher amplitudes and asymmetric beating. In particular, it is interesting to note that hyperactivation, and its associated reduction in flagellar wavenumber, is predicted in modelling studies [96, 21] to induce surface escape, as recapitulated here in the presented results, with the loss of fixed points to infinity on reducing the magnitude of $\beta_3$, representing a higher spatial wavenumber in the stroke. This is not the only trend in swimmer behaviour that can be readily deduced by an inspection of the fixed points in Fig. 3.4 and is reflected in more geometrically faithful simulation studies. In particular, there is a tendency to surface approach with reduced aspect ratio [94] and the positive angle between the swimmer and the boundary for a pusher [36, 94, 96].

A time reversal symmetry is readily apparent which means that pullers and pushers are dual swimmers and thus many aspects of puller dynamics can be understood from pusher dynamics. For instance, the fact pushers can switch to boundary escape behaviours with altered tangential deformations demonstrates that pullers are capable of regulating their boundary dynamics analogously. Indeed, flagellated *Leishmania* promastigotes are, in contrast to sperm, pulled by their flagellum, but similarly bind to and subsequently escape from mid-gut epithelia in their vector host, the sandfly [6]. We have demonstrated that stroke or slip velocity regulation, here at the level of the lowest modes in expansion (3.1), does indeed allow both pullers and pushers control over their behaviour near a no-slip surfaces. Analogously, one might tentatively anticipate that ciliates and colonial algae can control their behaviour near surfaces and that detailed surface patterning may alter, and yield some control over, the no-slip boundary behaviour of Janus particles.

One further aspect of the time reversal duality between pushers and pullers concerns their differences, in particular our observations of stable limit cycle dynamics. This occurs in substantial regions of parameter space, but for pullers only. Hence, by duality, pusher limit cycles are unstable for all the slip-velocities we have considered. This is also consistent with the absence of limit cycles for pushers such as sperm and bacteria in observations.
and geometrically faithful simulations, together with the damped oscillatory
decay to fixed points seen in simulations (e.g. [96, 94]).

Further, note that all non-degenerate fixed points can occur in the dynamical system phase plane, so that the lowest three modes of the tangential squirmer in expansion (3.1) can in principle describe any phase plane behaviour aside from fine-tuned bifurcation dynamics. Thus, the restrictions and trends we have observed concerning no-slip boundary behaviours, such as pushers do not undergo limit cycles and stably swim at positive angles relative to the boundary, may indeed be generic physically-based restrictions rather than due to the necessarily limited exploration of parameter space in a predominantly simulation based study. Certainly there are no discrepancies known to the authors on comparing more geometrically faithful simulations or observational studies with the trends and constraints highlighted in the discussion above, which therefore can be considered as generic predictions of this modelling framework and suggests simple model squirmers can be used to explore the range of axisymmetric no-slip boundary microswimming behaviours.

We have also investigated the behaviour of the axisymmetric tangential squirmer near a free surface for an asymptotically small Capillary number, so that surface deformations can be neglected. In terms of scattering when stable near surface swimming does not occur, the most extensive difference was in the extent of surface residence, though a reduction in the level of scattering was also observed. These observations can be concisely understood in terms of the reduced amount of shear and thus viscous torque near the free surface boundary compared to the no-slip scenario [33].

When attempting to consider stable near-surface swimming near a free surface with low Capillary number, we in fact found that its absence is universally predicted within our modelling framework. Interestingly, the precise converse is observed for both *Escherichia coli* [62, 24] and sperm [12]. The first of these bacterial studies also assessed interfacial properties and recorded bacterial-induced surface property changes even before trajectories were observed [62], which is consistent with substantial evidence that *E. coli* produce surfactants [115]. Similarly, for the sperm study, sufficient surfactant was added to generate a flat drop [12] in the microscopy preparation. Thus surfactants are present, or at least most likely to be present, which has the effect of reducing surface tension, invalidating the assumption of a small Capillary number regime, preventing a direct comparison of the theory presented here and observation. Nonetheless, this discrepancy does suggest that surface deformation is necessary for stable near-surface swimming as
deduced, together with sufficiency though not stability, in a two dimensional mathematical study of singularity swimmers, where the lengthscale of the swimmer in the 2D plane of interest is asymptotically small relative to the boundary-swimmer separation [19].

Finally, we note that our prediction of the lack of boundary accumulation near free surfaces in the absence of surfactants also represents a novel potential experimental test of the hydrodynamical theory studied here. Another novel opportunity for experimental testing would be an exploration of whether slip velocity swimmers such as Janus particles can be adjusted to undergo limit cycles in experiments. This is predicted to require a Janus particle that is a puller with a geometric polarity (e.g. $A = 2$ or $A = 3$ in Fig. 3.4) but a limited fore-aft asymmetry in the force generation to avoid a very large negative value of the force quadrupole weighting, $\beta_3$ which may instead induce simply stable swimming at moderate geometric polarities (e.g. $A = 2, \beta_2 > 0, \beta_3 \ll -1$ in Fig. 3.4). Our modelling in particular emphasises that these tests of swimmer hydrodynamical theory would be legitimate over large regions of parameter spaces, ensuring the comparison of theory and experiment is subject to less uncertainty than quantitative tests which require detailed control over swimmer parameters.

In summary, our exploration of axisymmetric tangential squirmers as models of ciliates, colonial algae and Janus particles has been characterised by phase plane behaviours and simplified by a time reversal duality. Whilst all phase plane behaviours (except subtle bifurcations) have been observed as possible for a no-slip boundary, there are nonetheless dynamical restrictions such as pushers do not undergo stable limit cycles. The fact all dynamical system behaviours are observed for no-slip boundaries, but these restrictions are still in place, suggests that model squirmers may be a simple framework to understand, or at least predict, generic trends and properties of axisymmetric boundary microswimming. Our observations of free surface dynamics at low Capillary number revealed that hydrodynamic changes can be understood in terms of reduced viscous torques arising on the swimmer due to the boundary, though this does not explain our predicted absence of stable near-surface swimming. This contrasts with experimental studies though the latter are complicated by the presence of surface active substances, in turn suggesting that stable motility for finite-size swimmers near a free surface in 3D is necessarily contingent on surface deformation in the absence of non-hydrodynamical effects.
Chapter 4

Squirming locomotion with large deformation

4.1 Introduction

The motion and the swimming efficiency of the spherical squirmer with large amplitude is considered for the extension of the Lighthill theory to the finite amplitude. The contents of this chapter and Appendix B have been published as K. Ishimoto and E. A. Gaffney, Phys. Rev. E, 90 (2014) 012704 [50].

In Lighthill’s original paper in 1952 [63], the swimming efficiency on the spherical squirmer with infinitesimal small amplitude was obtained by the asymptotic expansions as well as the swimming speed, though the expression was corrected by Blake [9]. Blake [10] also determined swimming speeds and power for the envelope of numerous waveforms on a flat plate. As briefly recapitulated in Appendix B.1, these results reveal that, for a fixed mechanical power consumption, both the antiplectic and symplectic stroke generate the same maximal swimming velocity and that this is power optimal. Such observations ultimately emerge from the translational symmetry of a planar geometry, which is broken by a finite cell size. However, ciliates are much larger than the metachronal wavelength and thus one would expect such symmetries to re-emerge in an asymptotic limit for these cells, but also the possibility of extensively different dynamics at lower wave numbers. In addition, for large deformation squirming no such limits will apply and thus one may readily expect fundamental differences in the relationships between deformation patterns, mechanical energy expenditure and swimming velocity.

Finally, large shape deformations may feature in prospective artificial ciliate swimmers [91]. Despite these emerging observations and possibilities,
the mechanical consideration of large amplitude surface deformation swimming has been limited to date. Theoretical studies have been restricted to tangential deformations, a major simplification in that the cell shape does not change [71], while numerical studies to date have only assessed the biomechanical feasibility of swimming given observed deformations [5, 2].

Consequently, our aim is to assess how squirmer swimming speed, power and efficiency change outside the classical squirmer parameter regime of ciliate swimming, especially exploring differences between the small and large amplitude theories and detailing how swimming performance may be improved in a study that includes the effects of non-tangential deformations.

In §4.2, we recapitulate the spherical squirmer model and how it may be explored in the small amplitude limit, as well as relevant results concerning its fundamental limitations and how it may be approximated using planar squirmer theory in the large wave number limit, facilitating analytical insights and numerical validation. We will also introduce the finite amplitude non-tangential stroke patterns that we will explore, together with a boundary element numerical method to allow large amplitude studies with radial deformations. Note that while such numerical methods have been very popular in the context of microswimming, to date they have only been implemented for collections of non-deforming bodies [44, 99, 36, 39, 94, 95], with the exception of Euglena simulations [2]. Results are presented in §4.4, with an exploration of the differences in the small amplitude symplectic and antiplectic strokes given the loss of translational symmetry, which dictates the observed duality between the optimal efficiencies observed for the planar swimmer. Subsequently, the accuracy of small amplitude theory is examined as the deformation amplitude is increased, together with an exploration for novel behaviours with extensive squirmer deformations.

4.2 Models and methods

4.2.1 The axisymmetric spherical squirmer

For brevity, we only consider axisymmetric deformations and we non-dimensionalise so that the sphere radius, the viscosity and the period of the deformation envelope wave are all unity. Hence, below the temporal frequency of the deformation wave is given by $\omega = 2\pi$.

Following [9], [71], we consider the deformation of the reference sphere, i.e. the neutral surface depicted in Fig. 1.1b, which is parameterised by the spherical polar radius, $r = 1$, and polar angle $\theta \in [0, \pi]$. During the surface
4 Squirming locomotion with large deformation

Fig. 4.1: A schematic picture of a spherical squirmer with axisymmetric shape deformations, depicting the Lagrangian polar angle $\theta$, and the reference sphere $r = 1$ (dotted). The deformed sphere is also illustrated (solid), together with the Eulerian coordinates $R, \Theta$, and the wavelength associated with the wave number $k$.

deforation $(r, \theta)$ is mapped to $(R, \Theta)$, given by

\begin{align}
R &= 1 + \epsilon \sum_{n=1}^{\infty} \alpha_n(t) P_n(\cos \theta) \\
\Theta &= \theta + \epsilon \sum_{n=1}^{\infty} \beta_n(t) V_n(\cos \theta).
\end{align}

(4.1)

(4.2)

Here, the $P_n(x)$ are Legendre functions, and thus orthogonal, whilst the $V_n(x)$ are the associated Legendre functions

\begin{equation}
V_n(x) = \frac{2\sqrt{1-x^2}}{n(n+1)} \frac{d}{dx} P_n(x),
\end{equation}

(4.3)

and hence also orthogonal. Throughout, we assume volume conservation for the swimmer and thus the series in (4.1) has no $\alpha_0$ term.

The flow field surrounding the small amplitude spherical squirmer has been obtained analytically by expanding the velocity field in terms of Legendre polynomials and determining the coefficients of the expansion using the boundary conditions on the squirmer, which is always approximately a sphere in the small amplitude limit. The final unknown, the swimming speed of the squirmer, is then determined by enforcing the physical constraint that
the swimmer is force-free; with full knowledge of the velocity flow field, the viscous power dissipation can subsequently be determined. The details can be found in [63], with errata corrections by [9]. In particular the swimming velocity is given by equation (18) of [9]; however $\alpha_1$ modes are not considered in Blake’s calculation, though they are required in the current context, since the position of the swimmer in this paper corresponds to the centre of the non-deforming reference sphere as depicted in Fig. 4.1. The resulting generalisation for the swimming velocity can be determined from equation (3.11), (3.12), (3.17), (4.21) of [48], noting that $n! \to n^2 \frac{n}{(n + 1)(2n + 1)(2n + 3)}$ to accommodate a different normalisation of the associated Legendre functions; this yields:

$$U = \left(\frac{\epsilon}{3} + \frac{\epsilon^2}{15}\alpha_2\right)(2\beta_1 - \alpha_1) + \epsilon^2\left(\sum_{n=1}^{\infty} \frac{4(n + 2)\beta_n\beta_{n+1} - 4n\beta_n\beta_{n+1}}{(n + 1)(2n + 1)(2n + 3)}\right)
$$

$$+ \sum_{n=1}^{\infty} \frac{(2n + 4)\alpha_n\beta_{n+1} - 2n\alpha_n\beta_{n+1}}{(2n + 1)(2n + 3)} - \sum_{n=1}^{\infty} \frac{(6n + 4)\alpha_{n+1}\beta_n + (2n + 4)\alpha_{n+1}\beta_n}{(2n + 1)(2n + 3)}
$$

$$+ \sum_{n=1}^{\infty} \frac{(n + 1)^2\alpha_n\alpha_{n+1} - (n^2 - 4n - 2)\alpha_n\alpha_{n+1}}{(2n + 1)(2n + 3)}).$$

(4.4)

The leading order power is given in equation (18) of [63], and corrected via equation (9) of [9] with a utilisation of the expansion in equation (13) of [9]. Further imposing our volume conservation constraint, $\alpha_0 = 0$, the power reduces to:

$$P = \frac{16}{3} \pi \epsilon^2 \left(\alpha_1^2 + \beta_1^2 + \alpha_1 \beta_1\right)
$$

$$+ \frac{3}{8} \sum_{n=2}^{\infty} \left\{ \frac{(4n^2 + 6n + 8)\alpha_n^2}{(2n + 1)(n + 1)}
$$

$$+ \frac{8\beta_n^2}{n(n + 1)} + \frac{24\alpha_n\beta_n}{(2n + 1)(n + 1)} \right\} \right).$$

(4.5)

These expressions readily enable the study of spherical squirming efficiencies in the small amplitude limit, as will be considered below.
Fundamental limitations on finite amplitude tangential squirmer swimming

For a tangential squirmer, with $\alpha_n = 0$ for all $n$, the squirmer surface remains spherical at all times. Hence large amplitude results can be obtained analytically, once more by expanding the velocity field in terms of Legendre polynomials [9, 71], which reveals the swimming speed of a tangential squirmer is exactly

$$\frac{2\epsilon}{3} \beta_1(t).$$

(4.6)

In particular, one must note that $\epsilon$ need not be a small parameter in this instance and also that the tangential squirmer cannot swim with an oscillatory stroke, but instead requires non-periodic deformations such as treadmilling [71], so that $\beta_1$ does not integrate to zero over a stroke period. This also illustrates the quadratic law of low Reynolds number propulsion: swimming by tangential slip treadmilling processes entails a swimming velocity of $O(\epsilon)$, whereas a general periodic body deformation induces a swimming velocity which scales with $O(\epsilon^2)$, as seen by time integration of equation (4.4) over a stroke period (See [92, 93] for more general discussions).

Further, with $\langle \rangle_S$ denoting the integral mean over the sphere surface, we also have for the tangential squirmer even with finite deformation that

$$\frac{U^2(t)}{\langle \tilde{\Theta}^2(t) \rangle_S} = \frac{\frac{4\epsilon^2}{9} \beta^2_1(t)}{\epsilon^2 \sum_{n=1}^{\infty} \frac{4\beta^2_n(t)}{n(n+1)(2n+1)}} \leq \frac{2}{3}$$

(4.7)

providing a constraint on the swimming speed in terms of the surface-averaged tangential deformation wave speed. Analogously, with the mechanical power defined by $P$ and $\langle \rangle$ denoting the temporal integral mean over a period, one can show that the Froude efficiency of a squirmer, $\eta = 6\pi \langle U \rangle^2 / \langle P \rangle$ is bounded by 1/2 for a tangential squirmer [71].

The local planar theory approximation at high wave number

For sufficiently large wave numbers of the metachronal deformation, $k$, the magnitude of the local velocity of the spherical squirmer reference sphere surface relative to the far field flow should match that predicted by considering the planar ciliary envelope model on the tangent plane to the sphere. This is
a useful simplifying approximation that will be implemented frequently below. The validity of this approximation is explicitly confirmed in Appendix B.3 for a small deformation amplitude, $\epsilon \ll 1$, with the non-dimensional wave number $k$, defined by $\pi/\lambda$ where $\lambda$ is the non-dimensional metachronal wavelength, satisfying $k \gg 1$. Explicit calculations of the swimming speed and efficiency using this approximation are given in Appendix B.4.

### 4.2.2 Characterising squirming deformations

Below, we restrict our considerations to a wave of deformation with a single mode to represent a metachronal wave. Nonetheless, the wave is modulated by $\sin \theta$ to ensure smoothness at the poles of the swimmer (though the detailed nature of this modulation does not change the qualitative details of the presented predictions). Hence the deformation of the swimmer is given by the stroke functions,

$$
R = 1 + \epsilon A_R \cos(2k\theta - \omega t) - \epsilon c_0(t) \quad (4.8)
$$

$$
\Theta = \theta + \epsilon A_\Theta \cos(2k\theta - \omega t + \delta), \quad (4.9)
$$

where $k > 0$ without loss of generality and the amplitude factors are given by

$$
A_R = \sin \theta \cos \left( (1 + A) \frac{\pi}{4} \right) \quad (4.10)
$$

$$
A_\Theta = \sin \theta \sin \left( (1 + A) \frac{\pi}{4} \right). \quad (4.11)
$$

The function $c_0(t)$ is introduced to ensure volume conservation; this stroke deformation has no zeroth mode, so that $c_0 \equiv 0$.

The stroke has four parameters: the wave number $k$, the angular phase shift between radial and tangential deformation $\delta$, the aspect ratio of the radial and polar deformation amplitudes, $A \in [-1, 1]$ and the stroke amplitude, $\epsilon$ and the latter satisfies $\epsilon \ll 1$ for small amplitude theories.

Furthermore, the optimal stroke for the squirming sheet exhibits elliptical trajectories for the cilia tips with the radial and tangential oscillations out of phase by $\pm \pi/2$, as described in Appendix B.1.2. Noting the need to restrict the stroke parameter space to match computational demands and resources, we only consider strokes with this angular phase shift below and thus we take either $\delta = \pi/2$, which is a symplectic stroke or $\delta = -\pi/2$, which is antiprolectic. We do however, consider the full range of the amplitude aspect ratio $A \in [-1, 1]$, which gives radial motion only when $A = -1$ and
4 Squirming locomotion with large deformation

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Interpretation</th>
<th>Value or Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>$k$</td>
<td>wave number</td>
<td>$k &gt; 0$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$\frac{1}{2} &gt; \epsilon k \sin\left((1 + A)\frac{\pi}{4}\right)$</td>
</tr>
<tr>
<td>$\delta$</td>
<td>Angular phase shift</td>
<td>$\pm \pi/2$</td>
</tr>
<tr>
<td>$A$</td>
<td>Aspect ratio of radial and polar directions</td>
<td>$[-1, 1]$</td>
</tr>
<tr>
<td>$\epsilon$</td>
<td>Stroke amplitude</td>
<td>$\epsilon &gt; 0$</td>
</tr>
<tr>
<td></td>
<td>(for small amplitude theory results)</td>
<td>$\epsilon \sin\left((1 + A)\frac{\pi}{4}\right) &lt; 1$</td>
</tr>
</tbody>
</table>

Table 4.1: A summary of the stroke parameters; the constraints on their values are discussed in the main text of section 4.2.2.

A tangential squirmer when $A = 1$. For these two extremes, there is no concept of metachrony, which requires that the effective and recovery strokes are distinct from the propagation direction of the surface deformation wave and we simply refer to such waves as either radial ($A = -1$) or tangential ($A = 1$).

We also constrain the surface from turning back on itself, which is forbidden in the continuous axisymmetric envelope model as the function describing the surface becomes multivalued and does not admit an expansion in terms of Legendre polynomials. This generates the bijectivity constraint $d \Theta/d \theta > 0$, which is also sufficient to prevent a self-intersection of the surface. As detailed in Appendix B.2, we therefore require both

$$ \epsilon \sin\left((1 + A)\frac{\pi}{4}\right) < 1, \quad \frac{1}{2} > \epsilon k \sin\left((1 + A)\frac{\pi}{4}\right), \quad (4.12) $$

by bijectivity. Note that as the stroke approaches radial only motion, $A \approx -1$, this constraint becomes weak, as expected.

In summary, the stroke that we consider in detail is given by equations (4.8), with four stroke parameters, as presented in Table 4.1, together with constraints on the stroke deformations, as discussed above. However, the analytical techniques of section 4.2.1 are only valid for asymptotically small deformation amplitudes once there is radial deformation. Thus to study finite amplitude deformations with radial contributions, $\epsilon \ll 1$, which requires imposing the no-slip boundary conditions on the deformed surface, a numer-
ical approach must be implemented and we utilise the Boundary Element Method (BEM).

### 4.2.3 The boundary element method for a swimmer with finite amplitude deformations

In this subsection, the numerical methods are described, though many parts duplicate the explanations in §3.2.4 for a rigid swimmer. The methods are improved and then applied into any deforming swimmer with volume conservation.

Let \( S \) denote a surface of a swimmer in an unbounded viscous Newtonian fluid at rest at infinity and in the inertialess limit. The foundation of boundary element methods is that the dimensional velocity field satisfies

\[
u_i(x) = -\frac{1}{8\pi\mu} \int_S G_{ij}(x, x') f_j(x') dS_{x'} + \frac{1}{8\pi} \int_S K_{ij}(x, x') u_j(x') dS_{x'}.
\]

(4.13)

Here

\[G_{ij}(x, x') = \left( \frac{\delta_{ij}}{r} + \frac{r_i r_j}{r^3} \right),\]

(4.14)

and \( K_{ij} = T_{ijk} n_k \), with

\[T_{ijk}(x, x') = -6\frac{r_i r_j r_k}{r^5},\]

(4.15)

and \( n \) the normal vector pointing outward from the surface of the swimmer \( S \), whilst \( f(x') \) is the traction at \( x' \in S \).

Providing the deforming body’s volume is conserved, so that \( \int_S u \cdot n \ dS = 0 \), the second integral on the right of (4.13) can be eliminated. Introducing \( f_{int} \) as the internal traction associated with the mathematical problem of solving the interior flow induced by the boundary deformation, one has

\[u_i(x) = -\frac{1}{8\pi\mu} \int_S G_{ij}(x, x') q_j(x') dS_{x'}.
\]

(4.16)

where \( q = f - f_{int} \). Note that \( q \) has a gauge freedom [82]:

\[q(x) \rightarrow q(x) + cn.\]

To complete the problem, we require no-slip boundary conditions on the surface. Let us introduce the set of laboratory fixed (inertial) basis vectors,
\{e_1, e_2, e_3\} and basis vectors \{B_1, B_2, B_3\} (Fig. 4.2), which are fixed relative to the undeformed reference configuration frame of the sphere and are referred to simply as body fixed below. Further, Latin indices are used for the laboratory frame and Greek indices are used for the body fixed basis, together with summation convention. Let \(X\) denote the origin of the body fixed frame, corresponding to the centre of the undeformed swimmer, relative to the origin of the laboratory frame, and let \(\xi'\) denote the position of a point on the surface relative to the body fixed frame origin. The position of this point relative to the laboratory origin, denoted \(x'\), thus satisfies

\[
x' = X + \xi' = X_i e_i + \xi'_i e_i = X_a B_\alpha + \xi'_a B_\alpha.
\]

We now consider velocities. Let \(U\) denote the translational velocity of the origin of the body fixed frame \(X\) and define \(\Omega\) to be the angular velocity of the rotation of the body fixed frame relative to the laboratory frame, so that

\[
\dot{B}_\alpha = \Omega \times B_\alpha.
\]

The surface velocity of the swimmer, as measured in the laboratory frame, is now readily determined to be

\[
v(x') := \frac{\partial x'}{\partial t} = \frac{\partial X}{\partial t} + \xi'_\alpha \Omega \times B_\alpha + \dot{\xi}'_\alpha B_\alpha = U + \Omega \times \xi' + B_\alpha \dot{\xi}'_\alpha,
\]

and hence, in terms of laboratory frame coordinates, \[96\]

\[
v_i(x') := e_i \cdot v(x') = U_i + \epsilon_{ijk} \Omega_j \xi'_k + B_{\alpha i} \dot{\xi}'_{\alpha},
\]

where \(B_{\alpha i} := e_i \cdot B_\alpha\). The no-slip boundary condition, \(v(x') = u(x')\), then gives

\[
U_i + \epsilon_{ijk} \Omega_j \xi'_k + B_{\alpha i} \dot{\xi}'_{\alpha} = -\frac{1}{8\pi \mu} \int_S G_{ij}(x', x'') q_j(x'') \, dS_{x''}.
\]

Noting that the force and torque enclosing solely fluid are zero, the total momentum balance equations are given by \[82\]

\[
F_{ext} = \int_S q(x') \, dS_{x'}
\]

\[
T_{ext} = \int_S (x' - X) \times q(x') \, dS_{x'}.
\]

The unknown variables \(q(x')\), \(U\) and \(\Omega\) are obtained by solving linear problem (4.19), subject to the balance equations (4.20) and (4.21) plus the
Fig. 4.2: A schematic picture of the two frames to describe a swimming body with deformation. The laboratory frame with basis vectors \( \{e_1, e_2, e_3\} \) and the body-fixed frame with basis vectors \( \{B_1, B_2, B_3\} \). The surface of the squirmer, \( S \), is described in grey, with the non-deformable reference sphere depicted by a dashed curve.

Usual inertialess requirement that the total force, \( F_{\text{ext}} \), and torque, \( T_{\text{ext}} \), are zero (though \( \Omega = 0 \) and the torque condition is automatically satisfied for axisymmetric swimmers, whereas the rotational motion of non-axisymmetric squirmers has only been discussed in detail very recently [77]).

**Numerical scheme**

The mesh generation of the reference spherical geometry utilises the Fortran 77 BEMLIB library codes accompanying [83], with the number of mesh elements \( N \) given by \( N = 2^{2N_{\text{div}}+3} \), where \( N_{\text{div}} \) is the number of refinement iterations. Equations (4.8)–(4.11) give a time-periodic function for the displacement of each node relative to the body fixed frame and parameterised by Lagrangian coordinates. At each time step, we scaled the sphere radius to ensure the volume of the swimmer is conserved.

Similarly to [44], the boundary condition including the force-free and torque free relations are reduced to the linear problem with \( 3N + 6 \) scalar unknowns and the gauge freedom is removed by setting \( \int_S q \cdot n \, dS = 0 \). We solve to obtain the traction and the translational and rotational velocity of the swimmer, using the LU decomposition within the Intel Math Kernel Library.
Using the translational and rotational velocity at time $t_n$, we determine the position $X$ and the body fixed basis vectors $\{B_1, B_2, B_3\}$ at time $t_{n+1}$ using the Heun method as detailed in (3.12) of [96], thus giving the swimmer trajectory. The velocity field surrounding the swimmer can be computed immediately via $u(x) = -\left(\frac{1}{8\pi \mu}\int_S G(x, x') \cdot q(x')dS_{x'}\right)$.

The power used by the cell is given by $\int_S u_i f_i dS_{x'}$, where the components of the traction $f_i$ are given by [82]

$$f_i(x_0) = n_j \sigma_{ij} = -\frac{1}{2} q_i(x_0) + \frac{1}{8\pi} n_k(x_0) \int_S^{PV} T_{ijk}(x_0, x)q_j(x)dS_x,$$

with the superscript PV denoting that the principal value of the integral is taken. The approximation

$$\int_S u_i(x_0) n_k(x_0) \left\{\int_S^{PV} T_{ijk}(x_0, x)q_j(x)dS_x\right\} dS_{x_0} \approx \int_S u_i(x_0) n_k(x_0) \left\{\sum_{x_p \neq x_0} T_{ijk}(x_0, x_p)q_j(x_p)\Delta S_p\right\} dS_{x_0},$$

is accurate enough for our study, as neglecting the element on which the singularity lies is nonetheless asymptotically accurate in the mesh resolution, for this contribution to the power integral of $u_i f_i$ over the whole surface.

### 4.3 Efficiencies at asymptotically small amplitudes

Note that the period averaged swimming velocity and power are homogeneous degree two in powers of $\epsilon$ at leading order since the $2\dot{\beta}_1 - \dot{\alpha}_1$ term in equation (4.4) integrates to zero by periodicity. Therefore we can fix the amplitude at $\epsilon = 0.05$ without loss of generality to within a simple scaling when specifically considering the predictions of asymptotically small amplitude theory. With this additional restriction, the constraints summarised in Table 4.1 entail there are two degrees of freedom in the deformation stroke, the wave number $k$, and amplitude aspect ratio $A$, together with the choice of an antiplectic or symplectic wave, in maximising the swimming velocity for a fixed power.

We explore swimming for asymptotically small amplitudes using the perturbation theory expressions for the spherical squirmer velocity and power, equations (4.4), (4.5). In Fig 4.3 the maximum absolute velocity to power ratio, which is one (of many) measures of efficiency, is plotted as a function
4.3 Efficiencies at asymptotically small amplitudes

Fig. 4.3: Predictions of maximal velocities for a finite size, small amplitude, spherical squirmer. As discussed in the main text, the deformation amplitude is fixed at $\epsilon = 0.05$; in addition the symplectic stroke ($\delta = \pi/2$, red) and the antiplectic stroke ($\delta = -\pi/2$, green) are considered separately in the plotted results. (a) Consider the variation in the remaining wave parameters, namely the wave number $k$ and aspect ratio $A$, subject to the constraint that $\langle P \rangle$ is fixed. The maximal ratio of the absolute stroke averaged velocity to power, $\langle U \rangle/\langle P \rangle$, attained during this variation is plotted for each $\langle P \rangle$, both for the symplectic stroke ($\delta = \pi/2$, red) and the antiplectic stroke ($\delta = -\pi/2$, green). (b) A plot of the wave number $k$ associated with the plotted maximal velocity-power ratio, $\langle U \rangle/\langle P \rangle$ at each value of the stroke averaged power for both the symplectic stroke ($\delta = \pi/2$, red) and the antiplectic stroke ($\delta = -\pi/2$, green).
of power output, where the maximum is that achieved in a variation over the deformation stroke parameters, \( k \) and \( A \). Results for both the symplectic stroke \((\delta = \pi/2)\) and the antiplectic stroke \((\delta = -\pi/2)\) are presented, along with Fig. 4.3b where the wave number \( k \) associated with the maximal velocity to power ratio is also depicted.

For a sufficiently high wave number, which is equivalent to high power consumption due to the extensive undulations and also illustrated in Fig. 4.3b, we have a recovery of the symmetry between symplectic and antiplectic efficiency together with, overall, a more efficient stroke. Furthermore, an estimate based on planar theory, requiring small deformations and high wave numbers as discussed in §4.2.1 and Appendices B.3-B.4, predicts that the efficiency asymptotes to \( 9/[256\pi\sqrt{2}] \approx 0.0079 \) at high wave number, which is consistent with Fig. 4.3a.

However, maximising the velocity to power ratio for a low power or wave number deformation stroke clearly reveals a symmetry breaking. The behaviour is complex with the antiplectic stroke more efficient in some power regimes and the symplectic stroke more efficient for others. While we have generally fixed the phase parameter to be either \( \delta = \pi/2 \) or \( \delta = -\pi/2 \), these restrictions do not in fact alter the velocity to power ratio, at least while \( (P) > 3 \). For the very low power regime, \( (P) < 3 \), the velocity to power ratio does exhibit a significant phase dependence, though the maximum of this ratio for fixed power still requires \( \delta \in \{-\pi/2, \pi/2\} \); the swimming direction is also reversed (results not shown). Also note that the discontinuity of the optimal wave number in Fig. 4.3(b) reflects the switch of the optimal mode from tangential \((A = 1)\) to non-tangential \((A \neq 1)\) deformation, which will be discussed in §4.4.3.

In summary, the distinction between the maximal velocity to power ratio in symplectic and antiplectic swimming is only manifested at low wave numbers, which does not reflect ciliate motility. However membrane deformation squirmers have larger amplitudes and smaller wave numbers and thus most likely different relationships between deformation waves, power and swimming velocity, as we now explore.

### 4.4 Finite amplitude results

#### 4.4.1 Numerical test case

As a validation test for the finite amplitude boundary element code, we compute the translational velocity averaged over a period of the stroke for
4.4 Finite amplitude results

Fig. 4.4: A numerical test case. Plots of numerical predictions for the period averaged velocity $\langle U \rangle$ along the vertical axis and $\epsilon^2$ along the horizontal axis, with volume conservation for a wave number $k = 3$, a phase shift $\delta = 0$ and different choices of mesh refinement $N_{\text{div}}$ and aspect ratio, $A$. Results for $N_{\text{div}} = 5$ are given for $A \in \{-1, 0, 1\}$ together with the case of $N_{\text{div}} = 4$ with $A = -1$. 
a squirmer with a deformation pattern characterised by a wave number of 
\( k = 3 \) and a phase shift \( \delta = 0 \), together with numerous choices of the ampli-
tude \( \epsilon \) and aspect ratio, \( A \). These resulting swimming speed predictions are 
compared with the small amplitude spherical squirmer asymptotic theory in 
Fig. 4.4 which demonstrates that the asymptotic analytical results converge 
to the computational results. For the mesh refinement \( N_{div} = 5 \), in most 
cases, the relative error is less than 1%. Even when \( N_{div} = 4 \), the relative 
error is determined to be a few per cent at most, which is sufficient accuracy 
for the aims of this paper.

The period-averaged velocity is smaller than the leading order asymptotic 
analysis predictions as the amplitude increases, and the breakdown of the 
asymptotic analysis arises at smaller \( \epsilon \) for reductions in the aspect ratio factor 
\( A \). We can consider higher order predictions in that the discussion of §4.2.1 
indicates that \( k = 3 \) is sufficiently large to use a local planar approximation 
for at least a coarse estimate of the local velocity of the squirmer reference 
surface relative to the far field \( \omega \). Blake [9] determined the local velocity 
of a planar squirmer relative to the far field up to \( O(\epsilon^4) \) which, for \( \delta = 0 \), 
is given by

\[
U = \frac{1}{2} \epsilon^2 \omega k \sin \theta \left[ (A_R^2 - A_0^2) - \epsilon^2 k^2 (A_R^2 - 2A_0^2)A_R^2 \right] + O(\epsilon^6) \tag{4.22}
\]

This is effectively the slip velocity of a tangential squirmer and thus the mag-
nitude of the predicted swimming speed can be determined via the projection 
of equation (4.22) onto the first associated Legendre polynomial \( V_1(\cos \theta) \), by 
appeal to (4.6), as illustrated in the calculations of Appendix B.4.

When the aspect ratio is \( A = -1 \), the corrected locally planar velocity 
simplifies to \( U = \epsilon^2 U^{(1)} (1 - \epsilon^2 k^2 \sin^2 \theta) \), where \( U^{(1)} = (1/2) \omega k \sin^3 \theta \) denotes 
the leading order coefficient. Projecting this onto the first associated Leg-
endre polynomial \( V_1(\cos \theta) \), we have that the velocity magnitude is reduced 
relative to the leading order prediction as \( \epsilon \) increases. In the case of \( A = 1 \), 
this higher order correction vanishes, whilst for \( A = 0 \) this next-order correc-
tion is found to reduce the velocity magnitude, all of which are compatible 
with Fig. 4.4. The initial breakdown of the linear relation shown in Fig. 4.4 
thus can be understood in terms of these higher order contributions of the 
planar theory and the planar approximation.

### 4.4.2 Flow field for large deformation

We have computed the flow field exterior to a spherical squirmer. As an 
example, the velocity vector in the plane containing the axis of symmetry
Fig. 4.5: The external flow field. Snapshots are presented for (a) the flow field and (b) contours for the momentum in the \( z \)-direction exterior to a spherical squirmer with a symplectic swimming stroke, \( \delta = \pi/2 \), wave number \( k = 3 \), amplitude \( \epsilon = 0.1 \) and aspect ratio \( A = -1/2 \). The plots are presented at time \( t/T = 5/20 \), where \( T \) is the period of the stroke, non-dimensionalised to unity. The flow field within the plane containing the axis of symmetry is depicted by blue arrows and the cell geometry is given by the red dots, which corresponds to the computational mesh vertex locations. The \( z \)-momentum contour is coloured by the signature of the \( z \) component of the fluid momentum: positive momentum (upward) is shown in red and negative momentum (downward) is shown in blue. The green dots denote the mesh vertices of the discretised cell geometry when \( N_{\text{div}} = 3 \) to illustrate the shape change of the swimmer, though the flow field computation is undertaken with \( N_{\text{div}} = 5 \).
4 Squirming locomotion with large deformation

of the swimming stroke is plotted in Fig. 4.5, together with contours for the $z$-component of momentum field. These plots correspond to a swimming stroke that is symplectic ($\delta = \pi/2$), with amplitude $\epsilon = 0.1$, wave number $k = 3$ and aspect ratio $A = -1/2$. Thus the metachronal wave, with its phase velocity given by $\pi/k$, travels downwards, towards $\theta = \pi$. Note that regions with a positive (upward) $z$-component of momentum are in red while regions with a negative component are shown in blue in the momentum contour plot. We clearly observe loops of momentum contours around the surface, due to the surface oscillations imparting momentum to the fluid, and hence the number of closed contours corresponds to the wave number $k$; analogous comments also apply for the $z$-component of the velocity field. Importantly, both the velocity and momentum fields illustrate the simple structure of the flows and this simplicity is not just restricted to the far field as can be seen from the interior flows, which also highlights how the flows deviate from the local velocity fields of the planar model. We proceed to explore swimming speeds, which are dictated by the stroke average of the flows induced by the squirmer.

4.4.3 Swimming efficiency for large deformation

We proceed to consider the swimming velocity, power and Froude efficiency, defined by $\eta = 6\pi \langle U \rangle^2 / \langle P \rangle$, for both a symplectic and an antiplectic swimmer. At the leading order of the asymptotic theory for small amplitudes ($\epsilon \ll 1$) and large wave numbers ($k \gg 1$), subject to the constraints of Table 4.1, we have that $\langle U \rangle = O(\epsilon^2 k)$, as illustrated in Appendix B.4 with the derivation of equation (B.25). Similarly, $\langle P \rangle = O(\epsilon^2 k)$ in this asymptotic regime and thus the Froude efficiency is of the scale $\eta \sim O(\epsilon^2 k)$. Hence an unconstrained variation of the wave number will achieve an optimum efficiency in the infinite wave number limit, though this is excluded due to the constraints summarised in Table 4.1. These scalings nonetheless illustrate that it is informative to consider the stroke averaged swimming velocity and power, $\langle U \rangle$, $\langle P \rangle$ plus the Froude efficiency, $\eta$, scaled with respect to $\epsilon^2 k$, as presented within Fig. 4.6. In particular, the differences observed as the amplitude, $\epsilon$, or wave number, $k$, change in this figure thus highlight deviation from the leading order small-amplitude, large-wave number theory, rather than the substantial effect of these parameter variations within this approximation regime.

In particular only subtle changes emerge in the plots of Fig. 4.6 at different values of wave number, $k$, and similarly for the asymptotic approxi-
4.4 Finite amplitude results

Fig. 4.6: (color online) Large deformation swimming at relatively small amplitudes $\epsilon \leq 0.2$. After rescaling by $\epsilon^2 k$ the stroke averaged velocity (upper row), power consumption (central row) and efficiency (lower row) are presented for $k = 2$ (left column), $k = 3$ (central column) and $k = 4$ (right column), as determined by the boundary element method, with a mesh refinement given by $N_{div} = 4$ iterations; see section 4.2 for details. Results for symplectic strokes ($\delta = \pi/2$) and antiplectic strokes ($\delta = -\pi/2$) are presented as indicated by the red and blue arrows, which point in the direction of change with increasing $\epsilon$. 

79
mation of velocities as $\epsilon$ increases, as illustrated by the top row of Fig. 4.6. Nonetheless, as one varies the amplitude aspect ratio, $A$, the value of $A$ that induces the maximum magnitude of the velocity changes substantially as $k$ is increased. This simply reflects the fact that distinguishing two approximately equal maxima of velocity magnitude requires a very accurate perturbation theory, whilst at $k = 2$ the asymptotics is, at best, crude, with relative errors larger than the relative difference in the peaks of absolute velocity. The Froude swimming efficiency exhibits an analogous behaviour with a dramatic switch in the amplitude aspect ratio, $A$, of the symplectic stroke ($\delta = \pi/2$) that maximises the swimming efficiency when comparing $\epsilon \ll 0.1$ with $\epsilon \sim 0.1$.

Nonetheless, in the central row of Fig. 4.6, one can observe that a deformation amplitude of $\epsilon = 0.1$ is sufficient to cause a breakdown of the leading order theory, with substantial and qualitative changes in how the power varies with the amplitude aspect ratio. This is not simply due to a refined choice between two peaks and thus genuinely illustrates that even qualitative predictions of the small-amplitude, large wavelength theory can breakdown in general at nominally small amplitudes.

4.5 Small wave number, large amplitude, swimming

As expected, the symmetry breaking between symplectic and antiplectic metachrony is exacerbated at smaller wave number in Fig. 4.6 and thus we consider smaller wave numbers. The bijectivity constraint, $d\theta / d\theta > 0$, which enforces $2\epsilon k \sin((1 + A)\pi/4) < 1$, becomes less demanding and extensively higher deformation amplitudes can be considered. This gives rise to parameter regimes far from ciliate motility but which instead constitute large amplitude membrane deformation swimming, as seen in neutrophils, *Dictyostelium discoideum* and *Euglena* [4, 103], and which also could be exploited for artificial swimmers.

For each wave number, $k$, and a selection of deformation amplitudes, $\epsilon \in \{0.1, 0.3, 0.5\}$, Fig. 4.7 plots the maximal Froude efficiency as the aspect ratio, $A$, is varied for both symplectic ($\delta = \pi/2$) and antiplectic ($\delta = -\pi/2$) strokes, together with the corresponding time-averaged velocity and power consumption. The local minimum in this plot at $k = 0.75$ corresponds to a switch in maximal efficiencies occurring for a symplectic stroke at smaller wave numbers, $k < 0.75$ and an antiplectic stroke for larger wave numbers,
4.5 Small wave number, large amplitude, swimming

Fig. 4.7: Maximal swimming efficiencies at each given wave number, together with the associated time-averaged velocity $\langle U \rangle$, and power consumption $\langle P \rangle$. For the presented values of deformation amplitude $\epsilon \in \{0.1, 0.3, 0.5\}$, we plot the maximal Froude efficiency for each wave number, $k$, as the aspect ratio, $A$ is varied for both symplectic ($\delta = \pi/2$) and antiplectic ($\delta = -\pi/2$) strokes, together with the associated time averaged velocity and power. The most efficient stroke is symplectic when $k \leq 0.75$ and antiplectic at higher wave numbers. Note that the bijectivity constraint, $d\Theta/d\theta > 0$, which enforces $2\epsilon k \sin((1 + A)\pi/4) < 1$, limits the wave number for $\epsilon = 0.3, 0.5$ preventing a continuation of these curves to larger wave numbers.
Fig. 4.8: An efficient large amplitude swimming stroke. The position of the swimmer is plotted for a symplectic stroke, \( \delta = \pi/2 \) with deformation amplitude \( \epsilon = 0.5 \), wave number \( k = 0.4 \) and aspect ratio \( A = -0.08 \). This is the most efficient stroke for this value of \( \epsilon \) on varying the wave number, \( k \), aspect ratio \( A \) and the choice between a symplectic and antiplectic stroke, \( \delta = \pm \pi/2 \). The squirmer shape and flow field in the plane possessing the axis of symmetry of the swimmer are also depicted for select points within the stroke cycle.

One can immediately observe that for larger \( \epsilon \) and smaller wave numbers, much larger efficiencies can be achieved, with a peak around the wave number \( k \approx 0.4 \). This parameter regime also corresponds to substantially larger absolute swimming velocities which are, on average, directed downwards in the negative-\( z \) direction though with movement in both directions during the swimming stroke. Furthermore, the peaked efficiency is also associated with a local minimum of the power consumption rather than a local maximum of the swimming speed.

The most efficient swimming stroke associated with the deformation amplitude \( \epsilon = 0.5 \) in Fig. 4.7 is detailed in Fig. 4.8. This presents the time evolution of the swimmer’s position over a stroke period, together with the
4.6 Discussion and conclusion

swimmer shape and flow field at selected points of the deformation cycle relative to an origin fixed at the centre of the reference, undeformed, spherical configuration. The swimmer’s position does not change monotonically during a stroke period. Instead there is a recovery stroke phase where the swimmer is oblate, with a larger drag and an upward movement at a relatively slow velocity. This is followed by an effective stroke phase, with a prolate swimmer geometry and reduced drag. Here, the swimmer rapidly moves downwards, at a much faster velocity than the swimming speed induced by deformation strokes possessing the larger wave numbers associated with ciliate swimmers.

By explicit evaluation, one can also readily determine that the surface average of the square tangential speed of the metachronal wave, \( \langle \hat{\Theta}^2(t) \rangle_S \), for the stroke depicted in Fig. 4.8 satisfies

\[
\langle \hat{\Theta}^2(t) \rangle_S = \frac{1}{4\pi} e^2 \omega^2 \sin^2((1 + A)\pi/4)
\times \int_0^\pi d\theta \sin^3 \theta \sin^2(2k\theta - \omega t + \delta) \int_0^{2\pi} d\phi
\]

\[
= \alpha + \beta \cos(4\pi t + \chi) \leq \alpha + \beta,
\]

(4.23)

where \( \alpha \approx 1.28, \beta \approx 1.19, \tan \chi \approx -3.1 \), on noting that \( \omega = 2\pi \). Thus the constraint on the tangential squirmer swimming velocity in terms of the deformation wave speed, given by (4.7) which is valid for finite amplitude tangential squirming as discussed in §4.2.1, reduces to a bound on the absolute swimming velocity of

\[
|U|(t) \leq \sqrt{\frac{2}{3}}(\alpha + \beta) \approx \sqrt{\frac{5}{3}} \approx 1.29.
\]

This is clearly exceeded during the effective stroke of the non-tangential deformation swimming depicted in Fig. 4.8, highlighting that large amplitude periodic radial deformations allow the escape of fundamental stroke-velocity limitations constraining tangential-only spherical squirmers.

4.6 Discussion and conclusion

In this investigation we have briefly reviewed efficiency calculations for surface deformation swimming associated with the small amplitude planar and spherical squirmer. We have proceeded to consider spherical squirmers with swimming strokes that are outside the parameter regimes of ciliate swimmers, possessing increased deformation amplitudes and reduced wave numbers in the context of a single mode metachronal wave. This has included
investigations of the large amplitude small wave number parameter regime with combined radial and tangential surface deformations. Consequently, our studies have required the use of boundary element methods, as the no-slip boundary conditions on the swimmer surface can no longer be imposed on the simple spherical reference configuration of the swimmer.

We firstly highlighted that for small amplitude deformations there is a degeneracy between maximally efficient symplectic and antiplectic swimming strokes for a planar squirmer. This has also been shown to apply for spherical squirmers at sufficiently high power consumption, or equivalently at sufficiently large wave number, which generally enforces small deformations due to the bijectivity constraint, $2\varepsilon k \sin ((1 + A)\pi/4) < 1$. However, at smaller power consumptions and thus smaller wave numbers, the degenerate duality is broken and the antiplectic stroke becomes more efficient, with a switch to a more efficient symplectic stroke as the power consumption drops further, together with a reversal in the swimming direction for a symplectic deformation wave. Consequently, there are fundamentally different and more complex relationships between swimming velocities, power and the surface deformation wave even at small amplitudes if the wave number is sufficiently low. Nonetheless, Appendix B.3 highlights that the large wave number constraint is relatively weak, requiring $k \gg 1$ whilst Fig. 4.3 highlights that even for $k \sim 2$ or 3 the large wave number theory is reasonably accurate.

Hence the ubiquitously studied colonial multicellular alga *Volvox carteri*, which is driven by low wave number ($k \approx 5/2$) symplectic flagellar waves rather than by cilia [15], still squirms in a parameter regime essentially appropriate to ciliates. Thus the swimming of *Volvox carteri* may be constrained and approximated in a relatively simple manner using planar theory approximations which, for instance, generates predictions that such a swimmer has a non-dimensional velocity to power ratio bounded by $9/[256\pi \sqrt{2}]$. In addition, the experimental data for *Volvox carteri* [25, 26, 15], indicates that the condition for negligible inertia, $Re \ll 1$, occurs for non-dimensional power consumptions satisfying $\langle P \rangle \ll 100$ if we suppose the cell propels in an optimal manner required for Fig. 4.3. This further confirms the usefulness of the planar theory as these observations ensure that such a squirmer approaches its high wave number efficiency asymptote before the high power consumption potentially jeopardises the constraint of inertialess swimming (though the effect of inertia can still be negligible at high power consumption given a sufficiently high wave number [48]).

However membrane deformation swimming, as seen in neutrophils, *Dictyostelium discoideum* and *Euglena* [4, 103], is more generally associated with
4.6 Discussion and conclusion

the more complex dynamics of larger deformation amplitudes and small wave numbers. In this parameter regime, the flow field still remains relatively simple with a simple interior Newtonian flow within the swimmer. The interior flows are not directly relevant for biological swimmers, due to the mechanically complex non-Newtonian intracellular environment. Regardless, the observations of flow field simplicity throughout the domain suggests that standard approaches for population level modelling, via the representation of the influence of individual swimmers on the stress tensor via truncated multipole expansions (e.g. [90]), may remain tractable for finite deformation squirmers.

Nonetheless, as the deformation amplitude, $\epsilon$, is increased from very small amplitudes linearised theory is not always qualitatively reliable even at relatively small values, $\epsilon \sim 0.1$, as illustrated for a wave number of $k = 4$ by symplectic waveform power calculations. In addition, for this scale of amplitude deformation, linearised theory is also inadequate for assessing the nature of the swimming stroke that generates maximal velocity or efficiency, due to the need to accurately choose between local maxima of efficiency. Hence, caution is merited in using small deformation theory when the deformation is not multiple orders of magnitude smaller than the size of the swimmer.

Dramatic changes are further observed as the deformation amplitude, $\epsilon$, is increased further, ($\epsilon > 0.3$ is sufficient), and the wave number reduced below one. A symplectic swimming modality emerges with an effective and recovery stroke that causes oscillatory rather than monotonic cell motion, but nonetheless with very fast stroke averaged speeds and high efficiencies. For instance, with $\epsilon = 0.5$ and $k = 0.4$, we have a Froude efficiency of $\eta \approx 0.275$ in contrast to efficiencies scaling with $O(\epsilon^2)$ for optimal Froude efficiencies in the linearised, small amplitude, regime. This is also much larger than the efficiencies of biological swimmers, which are typically 0.01-0.02 for ciliates and flagellates [84, 100, 57], and also for the large deformation Euglena motility [2]. It also greatly exceeds the maximum efficiency of 0.08 for the planar flagellum [57]. These heightened efficiencies allow a tentative suggestion that power optimisation is not an evolutionary constraint for the relatively inefficient membrane deformation swimming of Euglena. Furthermore, the observed extensive increase in efficiency may also be of note for potential artificial systems, where energy storage is a major technical constraint [70], especially given the efficiency optima are associated with local minima of the power consumption.

Large amplitude spherical squirmers limited to tangential deformations can swim given non-periodic deformations such as treadmilling and can ap-
proach very high efficiencies of $1/2$, though this also require deformations that
become singular \[71\]. This exceeds the efficiencies we have observed, though
not more than a factor of two even though our deformations have been re-
stricted to single mode periodic metachronal waves. Furthermore, theoretical
limitations on tangential squirmers in terms of the ratio of absolute swimming
speed to the speed of tangential surface deformations are readily exceeded by
the deformation waves we have considered. Thus metachronal wave spheri-
cal swimmers with simple large amplitude radial motions can readily attain
higher swimming speeds with a periodic stroke given stroke velocity con-
straints compared to any spherical tangential squirmer. We should also note
that the computation of an optimal large deformation constitutes interesting
further work. This would need to take into account that even the restricted
squirming deformation considered here has complicated constraints such as
$2\varepsilon k \sin \left(\left(1 + A\right)\pi / 4\right) < 1$, and that the optimal may be achieved by surface
deformations that are multi-valued with respect polar coordinates, which is
beyond the scope of the current framework.

In summary, while relatively low wave number small amplitude swim-
mers such as \textit{Volvox carteri} are predicted to behave like ciliates, small am-
plitude linearised theories in general can become unreliable even when the
deformation is a single order of magnitude smaller than the swimmer length-
scale. With further deformation increases, a highly motile and efficient large
deformation–small wave number swimming modality arises with a simple
single mode surface deformation with swimming dynamics that exceeds the
limits of surface velocity to swimming speed ratios for arbitrary spherical
tangential squirmers.
Chapter 5

Conclusions

In this thesis, we considered small squirming body in fluid for understandings of fundamental aspects of microswimmers in terms of interaction between a body with surface velocity and the surrounding fluid, including the effects of inertia, adjacent boundary, and large deformation. The squirmer is one of the fundamental mathematical models of microswimmers, which was first proposed by James Lighthill in 1952 [63] to describe propelling motions of microorganisms with shape deformation. As a more simplified version, a rigid body with tangential surface velocity is often considered which is called the tangential squirmer. Asymptotic analysis has been one of the most common and powerful tools in studying microswimmers from the era of Lighthill. This thesis also provides viewpoints from dynamical system theory and theoretical guidelines for direct numerical computations.

Inertia.— In Chapter 2, the spherical squirmer with small surface deformation is considered in the unsteady Stokes flow to understand effects of the inertia on microswimmers, in relation to the scallop theorem and its breakdown due to inertia [48].

Under the assumption of an axisymmetric surface deformation, the governing equations of motion of fluid, the unsteady Stokes equations, are given by a partial differential equations of a single scalar function, the Stokes stream function, with two independent variables. The solution of the equations with no-slip boundary condition on a sphere can be obtained by the use of Laplace transform. To match the solution with the no-slip boundary conditions on the slightly deformed surface, an asymptotic expansion is conducted with respect to a small amplitude parameter, $\epsilon$, up to $O(\epsilon^2)$. The Laplace inversions is then performed with time-periodic surface deformation for long
time asymptotic behaviours of the squirmer. The time-averaged swimming velocity is finally obtained in the form of asymptotic expansion in terms of a small dimensionless parameters of fluid and body inertia, $R_w$ and $R_S$. In particular, the asymptotic analysis shows that the correction due to the inertia is of $O(R_w, R_S)$, meaning that the scallop theorem is in general broken due to nonzero inertia effects. However, the obtained swimming velocity is of the order of $\epsilon^2$, and therefore the scallop theorem survives at $O(\epsilon)$, which does not include the effect of the surface deformation, even in the case of non-negligible inertia, which means that the surface deformation is essential for the breakdown of the scallop theorem.

To find out the inertial corrections, surface deformation in a form of traveling wave is considered as a model of a metachronal waves of ciliary microorganisms. The corrections are found to arise when the surface traveling wave has the wavenumber about $k = \pm 1$, which may correspond to a flapping deformation rather than a wavy motion observed in ciliary swimmers with $k \gg 1$. For illustrating this inertial effect, a squirmer only with the lowest two radial deformation modes in Legendre expansion is considered. The optimized swimming stroke with respect to Froude efficiency, which is a conversion rate of swimmer’s power-input into propulsion, is found to change in form; the phase difference between the two radial modes decreases when $R_w$ and $R_S$ increase. Remembering that in the limit of zero inertia, the motion with phase difference $\pm \pi/2$ gives an optimized propulsion with respect to Froude efficiency, we see that the optimized motion approaches to the in-phase or anti-phase state as the effect of inertia increases. These results suggest that the optimal swimming pattern of microorganisms depends on the inertia effect, or the size of the swimmer as suggested by Childress & Dudley [17].

Adjacent boundary.— Chapter 3 is devoted to study on the motion of tangential spheroidal squirmer in the presence of an infinite plane boundary [49]. When microswimmers are observed through a microscope, boundaries such as glass slide and cover glass as well as drop surface are inevitable environmental factors.

The axisymmetrical tangential spheroidal squirmer only with three lowest modes of Legendre expansion of surface velocity, is considered in steady Stokes flow as a universal model of microswimmers, where the dynamics is characterized by three nondimensional parameters: the aspect ratio of the spheroid $A$, and stroke parameters $\beta_2$, $\beta_3$, which are the ratios of Legendre expansion coefficients. The motion of the squirmer adjacent to the wall
boundary is described by a two dimensional dynamical system of the distance from the boundary $h$, and the angle $\phi$ between the horizontal plane and the swimming direction. We perform the stability analysis for this dynamical system to understand the swimmer-boundary hydrodynamical interaction at low Reynolds number, taking into account the pusher-puller duality of this dynamical system arising from the time reversibility of the Stokes flow. The duality states that the stability of a fixed point of the system for a pusher is opposite to those for a corresponding puller.

For accurate analysis of the stability, the direct numerical computation using the single-layer potential scheme of the boundary element method is implemented for a swimmer near both a no-slip and a free-slip boundaries. The boundary conditions on the infinite flat plane is satisfied by the use of Stokelet with image singularities.

The swimming trajectories are slightly different, depending on the boundary conditions on the infinite plane, due to the different magnitude of torque that the swimmer experiences near the boundary, and, however, the difference is so small that we cannot detect it in experiments.

The stability analysis for a swimmer near a no-slip infinite plane reveals the existence of a fixed point located near the boundary, in a wide range of parameters. For a spherical squirmer ($A = 1$), the fixed point is found to be linearly unstable for a pusher, and thus that of a puller becomes linearly stable due to the pusher-puller duality, though nearly neutral squirmers do not possess such a fixed point. The stable dynamics in this system here corresponds to the swimmer captured at a constant distance from the boundary. This stable fixed point may be a representation of cell accumulation behaviour near a boundary, which are observed in bacteria and spermatozoa. As the aspect ratio $A$ increases, the stability is inverted. The stability inversion with increasing aspect ratio is found to be associated with Hopf instability. A puller therefore realizes the oscillating motion corresponding to the limit cycle of the dynamical system.

Compared with the stability diagram in the presence of a no-slip planar boundary, the dynamics of the swimmer near a free-slip boundary is simpler. All the fixed points found in our parameter regime are saddle points, and therefore no surface accumulation would be observed. As a cell accumulation near an air-water surface is actually observed [24, 12], the mechanism for such accumulation would include more than the hydrodynamic interaction.

The chirality due to the helical beating of microswimmer can be considered with adding the rotlet dipole term, which is found to be a minor effect on the swimming trajectory. Thus the cell accumulations near a no-slip bound-
ary such as bacteria and spermatozoa are well explained by this squirmer model, and hydrodynamic interaction near the boundary is also classified.

**Large deformation.** — In Chapter 4, the spherical squirmer with large deformation is investigated in the steady Stokes flow, by the use of the boundary element method. The squirmer motion has been considered only with a small deformation since Lighthill first discussed this model.

The surface deformation was assumed to be of traveling wave as a model of a ciliary motion as discussed in Chapter 2. In this traveling wave deformation, the symplectic and the antiplectic squirmer has been known to have an equivalent optimal Froude efficiency if the surface of the microorganism is considered to be infinitely extended [10]. In the case of spherical surface, the asymptotic expansion with respect to the small deformation parameter, $\epsilon$, reveals that the difference of optimal efficiency between the symplectic and the antiplectic swimmers is negligible if the wavenumber is not small ($k > 5$ is sufficient). This results suggest that the local deformation of the spherical squirmer can be approximated by planar squirming motion (local planar theory) when the wavenumber is sufficiently large.

The single-layer potential formulation of the boundary element method is applied to a general microswimmer conserving its volume, and the numerical results of the scheme are checked in comparison with the asymptotic expansions by Lighthill and Blake. The swimming velocity and the Froude efficiency for a squirmer with $k = 2, 3, 4$ are obtained by this newly improved numerical scheme. These results can be explained by the local planar theory, which gives the exact solution when $k \to \infty$, even for the case of $k = 2, 3, 4$ if the deformation amplitude is not large ($\epsilon < 0.1$ is sufficient).

Nevertheless, the efficiency for a squirmer with large-amplitude deformation and small wavenumber cannot be predicted by the local planar theory. In this case, the most optimal stroke is found in a symplectic swimmer. Moreover, the Froude efficiency $\eta$ exceeds 0.2 when $\epsilon = 0.5$, which is found to be more efficient than the swimmer with higher wavenumber. This result suggests a new type of efficient swimming strokes and would be of significant knowledge for micro engineering, though the large surface deformation itself may require high-cost energy due to structural reasons.

**Concluding remarks.** — In this thesis, the effects of inertia, boundary, and large deformation on microswimmers are considered using the squirmer model from the viewpoint of interaction between a body with surface deformation and its surrounding fluid. Even though the shape deformation or surface
velocity was given, this study highlights that the dynamics of microswimmers is rich and full of diversity, which may reflect real ecosystem at micro-scales. For the analysis, the dynamical system theory is employed as well as the direct numerical computation and asymptotic analysis. As illustrated in this thesis, the different mathematical analyses are found useful to discuss dynamics of microswimmers.

Nonetheless, there are much more factors left undiscussed in this thesis of microswimmers, including viscoelasticity of fluid, elasticity of cell structure, nutrition uptake, population dynamics, and molecular motor regulation. Further, the important factors should be highly depending on the problem that we are interested in. From the viewpoint of the diverse ecology and long history of microswimmers, the hydrodynamical analysis of real biological problems should be supported by experimental experts in close collaboration. The analytic method should be chosen properly depending on the problem to be solved, and the active interaction between theorists and experimentalists should be indispensable, as described in the Lighthill textbook (p2, [65]),

Progress towards biofluiddynamic goal can occur only when workers from the biological sciences and from the mathematical and engineering sciences work closely together.
Appendix A

Some calculations on squirming locomotion with inertia

A.1 Second order calculation of the fluid force

In this section, some detailed calculation on $d_d$ is shown. To complete the contributing three integrals in the equation (2.32), we need some manipulations on similar Legendre integrals as the calculation of $A_1^{(2)}$ and $B_1^{(2)}$. Each term is written by infinite series of $n$. We show the coefficients of $n$th term of the series in the following matrices, whose components represent the coefficients of

$$
\frac{1}{(2n+1)(2n+3)} \begin{bmatrix}
\epsilon^2 \alpha_n \hat{\alpha}_{n+1} & R_\omega \epsilon^2 \alpha_n \hat{\alpha}_{n+1} & \epsilon \alpha_n X_{n+1} & \epsilon \alpha_2 V \\
\epsilon^2 \alpha_n \alpha_{n+1} & R_\omega \epsilon^2 \alpha_n \alpha_{n+1} & \epsilon \beta_n X_{n+1} & \epsilon \alpha_2 \mathcal{L}^{-1}[\sqrt{R_\omega} \sqrt{s} V] \\
\epsilon^2 \alpha_n \beta_{n+1} & R_\omega \epsilon^2 \alpha_n \beta_{n+1} & \epsilon X_n \alpha_{n+1} & \epsilon \alpha_2 \mathcal{L}^{-1}[R_\omega s V] \\
\epsilon^2 \beta_n \alpha_{n+1} & R_\omega \epsilon^2 \beta_n \alpha_{n+1} & \epsilon X_n \beta_{n+1} & \epsilon \alpha_2 \mathcal{L}^{-1}[R_\omega s V]
\end{bmatrix}
$$

(A.1)
A.2 Laplace inversion

Each coefficient of the series of the six terms in the integrals is following:

\[
\begin{bmatrix}
6(n+1)(n+5) & 2(n+1) & -2(n+1) & -12 \\
6(n+1)(n+4) & 2(n+1) & 0 & -12 \\
-2(n+1)^2(2n^2 + 13n + 18) & 0 & -2(n+1) & 0 \\
-2n(n+1)(2n^2 + 9n + 7) & 0 & 0 & 0 \\
2(n+1)(2n^2 + n - 12) & 2(n+1) & 2(n+4) & -24 \\
-2n(2n^2 - 3n - 11) & -2n & 0 & -24 \\
2(n+1)(n+2)(4n^2 + 15n + 12) & 2(n+1)(2n+2) & -2(n+3) & -6 \\
-2n(n+1)(4n^2 + 7n + 1) & -2n(n+1) & 0 & 0 \\
-6n(n+1) & 0 & 2n & 18 \\
-6n(n+2) & 0 & 0 & 18 \\
2n(n+1)(n+2)(2n+3) & 0 & 2(n+2) & 0 \\
2n(n+1)(n+2)(2n+1) & 0 & 0 & 0 \\
\end{bmatrix}
\]

After the summation over these six terms, we obtain the force due to the deformation (2.50).

A.2 Laplace inversion

A.2.1 Long time behavior of \(X_n\)

Let us consider the long time behavior of \(X_n\), remembering that \(X_n\) is defined as the equation (2.39).
Some calculations on squirming locomotion with inertia

\[
\begin{array}{cccc}
  n & 1 & 2 & 3 \\
  Y_n(x) & x & x^2 + 1 & x^2 + 3x + 3 \\
  & & x^3 + 6x^2 + 15x + 15 \\
\end{array}
\]

Table A.1: \(Y_n(x)\) for small \(n\), where \(x = \sqrt{s}\).

When \(n = 1\), \(X_n\) is

\[
X_1 = \sqrt{R_\omega} \int_0^t \frac{\ddot{x}(x) + 2\dot{\beta}(x)}{\sqrt{\pi(t - x)}} \, dx
\]

\[
= \sqrt{R_\omega} \sum_{m=-\infty}^{\infty} (-4\pi^2 m^2) (\alpha_{1m} + 2\beta_{1m}) \frac{e^{2\pi imt}}{\sqrt{2\pi im}} \text{erf} \left( \sqrt{2\pi imt} \right) (A.2)
\]

Using the asymptotic relation \(\text{erf} \left( \sqrt{2\pi imt} \right) \sim 1\) as \(t \to \infty\), \(X_1\) becomes

\[
X_1 \sim \epsilon \sqrt{R_\omega} \sum_{m=-\infty}^{\infty} (2\pi im)^3 (\alpha_{1m} + 2\beta_{1m}) e^{2\pi imt} = \epsilon \sqrt{R_\omega} \frac{d^{3/2}}{dt^{3/2}} (\alpha_1 + 2\beta_1),
\]

(A.3)

which indicates that only the oscillating term remains.

When \(n \geq 2\), we rewrite it for briefly \(X_n = Y_n(nA_1 + n(n + 1)B_1)\) where \(Y_n = \sqrt{s}K_{n+1/2}(\sqrt{s})/K_{n-1/2}(\sqrt{s}) - (2n - 1)\). \(Y_n(\sqrt{s})\) can be described by a rational function with respect to \(\sqrt{s}\), \(Y_n(x = \sqrt{s}) = x^2(\sum_{k=1}^{n-2} q_k x^k)/(\sum_{k=1}^{n-1} p_k x^k)\).

All the zeros of the denominator are simple and they have negative real parts. Thus the partial fractional decomposition of \(Y_n\) can be performed,

\[
Y_n = \sum_{k=1}^{n-1} \frac{c_k \sqrt{s}}{\sqrt{s} + a_k}. \quad (A.4)
\]

Here, the real part of \(a_k\) \((k = 1, 2, 3, \ldots, n - 1)\) is positive.

Let us introduce a function

\[
g_k(t) = \frac{1}{\sqrt{\pi t}} - a_k e^{a_k^2 t} \text{erfc}(a_k \sqrt{t}), \quad (A.5)
\]

which corresponds to the Laplace inversion of \(1/(\sqrt{s} + a_k)\), and we have

\[
X_n = \sum_{k=1}^{n-1} \int_0^t c_k g_k(t - x)(nA_n(x) + n(n + 1)B_n(x)) \, dx. \quad (A.6)
\]
A.2 Laplace inversion

For large $t$, the first term of the integral in the equation (A.5) is calculated in a similar way to (A.3) as

$$
\left( \sum_{k=1}^{n-1} c_k \right) \int_0^t \frac{n\dot{A}_n(x) + n(n+1)\dot{B}_n(x) - n\alpha_n(x) + n(n+1)\beta_n}{\sqrt{\pi(t-x)}} \, dx \sim \epsilon \sqrt{R_\omega} \frac{d^{3/2}}{dt^{3/2}} \left( n\alpha_n(x) + n(n+1)\beta_n \right),
$$

where we used the fact $\sum_{k=1}^{n-1} c_k = q_{n-2} = \sqrt{R_\omega}$. The second term integral is evaluated as follows. For simplicity, we consider long time asymptotic behavior of an integral

$$
I(t) = \int_0^t a_k e^{a_k^2 x} \text{erfc}(a_k \sqrt{x}) f(t-x) \, dx,
$$

where $f(t)$ is a periodic function with period $T = 1$. Solving the integral (A.8), we have

$$
\sum_{m=-\infty}^{\infty} \frac{a_k f_m}{a_k^2 - 2\pi im} \left( e^{a_k^2 t} \text{erfc}(a_k \sqrt{t}) + \left( \frac{a_k}{2\pi i m} \text{erf}(\sqrt{2\pi i m} t) - 1 \right) e^{2\pi i m t} \right),
$$

For large $t$, it follows that

$$
e^{a_k^2 t} \text{erfc}(a_k \sqrt{t}) \sim \frac{1}{a_k \sqrt{\pi t}} + O(1/t^{3/2}), \quad \text{and} \quad \text{erf}(\sqrt{2\pi i m t}) \sim 1 + O(e^{-2\pi i m \sqrt{t}}).
$$

We remark that the first asymptotic relation in the equation (A.10) is satisfied when the real part of $a_k$ is positive. Using these relations, long time behavior of $I(t)$ becomes

$$
I(t) \sim \sum_{m=-\infty}^{\infty} \frac{a_k f_m}{a_k + 2\pi i m \sqrt{2\pi i m}} e^{2\pi i m t} + O(1/\sqrt{t}).
$$

Within this order of $\epsilon$, the asymptotic form of the integral is obtained,

$$
\epsilon \sum_{m=-\infty}^{\infty} \sum_{k=1}^{n-1} \frac{-c_k a_k}{a_k + \sqrt{2\pi i m}} (\sqrt{2\pi i m})^3 \left( n\alpha_{nm} + n(n+1)\beta_{nm} \right) e^{2\pi i m t}.
$$

The summation over $k$ is evaluated when we consider asymptotically small $R_\omega$,

$$
\sum_{k=1}^{n-1} \frac{c_k a_k}{a_k + \sqrt{2\pi i m}} = \sum_{k=1}^{n-1} c_k - \sqrt{2\pi i m} \sum_{k=1}^{n-1} \frac{c_k}{a_k} + O \left( \frac{2\pi i m}{a_k^2} \right) = \sqrt{R_\omega} - R_\omega \frac{\sqrt{2\pi i m}}{2n - 3} + O(R_\omega^{3/2}),
$$
where the symbol “∼” here indicates the asymptotic form for small \( R \). The last identity follows from the fact that the summation \( \sum_k (c_k/a_k) \) is equivalent to \( q_0/p_0 = 1/(2n-3) \). Thus the \( O(\sqrt{R}) \) term vanishes, and we finally have

\[
X_n \sim \epsilon R \sqrt{n} a \left( \frac{n \tilde{a} + n(n+1) \tilde{b}}{2n-3} \right) + O(\frac{R^{3/2}}{\sqrt{t}}) \quad \text{for } n \geq 2. \quad (A.14)
\]

for asymptotic small \( R \).

### A.2.2 Proof of lemmas

In this subsection, proofs of Lemma 1 and Lemma 2 are shown. The function \( g(t) \), which is defined by the equation (2.56) and (2.57), is equivalent to

\[
\sum_{k=1}^{2} c_k g_k,
\]

where \( c_1 = -1/(a - b) \), \( c_2 = 1/(a - b) \), \( a_1 = a \) and \( a_2 = b \). Also the function \( h \) corresponds to the case when \( c_1 = a/(a - b) \), \( c_2 = -b/(a - b) \), \( a_1 = a \) and \( a_2 = b \).

Let us first consider the periodic part of a function \( f(t) \). According to the equation (A.11),

\[
\frac{3}{R + 2R} [g * \tilde{f}](t) \sim \frac{ab}{3} \sum_{m=-\infty}^{\infty} \sum_{k} \frac{c_k a_k \tilde{f}_m}{a_k + \sqrt{2\pi im}} e^{2\pi im t} + O(1/\sqrt{t}), \quad (A.15)
\]

where \( \tilde{f}_m \) (\( m = 0, \pm 1, \pm 2 \cdots \)) is Fourier components of \( \tilde{f}(t) \). When an infinitesimal small inertia of fluid and body is assumed, the oscillating part of the equation (A.15) becomes

\[
\frac{ab}{3} \sum_{m=-\infty}^{\infty} \left[ \sum_k c_k - \sqrt{2\pi im} \sum_k \frac{c_k}{a_k} + (2\pi im) \sum_k \frac{c_k}{a_k^2} + O \left( \frac{\sqrt{2\pi im}}{a_k^3} \right) \right] \frac{c_k \tilde{f}_m e^{2\pi im t}}{\sqrt{2\pi im}}, \quad (A.16)
\]

which is reduced to

\[
\sum_{m=-\infty}^{\infty} \left( \frac{1}{3} + \sqrt{R \sqrt{2\pi im}} + O(R, R_S) \right) \tilde{f}_m e^{2\pi im t}. \quad (A.17)
\]

Also substitution of the coefficients \( c_k \) into the equation (A.16) yields

\[
\frac{3}{R + 2R} [h * \tilde{f}](t) \sim \sum_{m=-\infty}^{\infty} \left( \frac{\sqrt{2\pi im}}{3} + O(R, R_S) \right) \tilde{f}_m e^{2\pi im t} + O(1/\sqrt{t}). \quad (A.18)
\]
The equations (A.17) and (A.18) argue the statements of the Lemma 1 and Lemma 2 when the function \( f \) is purely periodic.

Remembering that \( f(t) - \hat{f}(t) = O(1/\sqrt{t}) \) as time progresses, we have

\[
|g \ast (f - \hat{f})| \leq C \left| g \ast \left( \frac{1}{\sqrt{\pi t}} \right) \right| = C|g \ast h| \to 0 \quad (t \to \infty), \tag{A.19}
\]

where \( C \) is a positive constant. The limit is obtained by the use of the equation (A.18) with \( \hat{f} = 1 \). This completes the proof of the Lemma 1.

We have a similar relation for \( h \) as well,

\[
\left[ h \ast \left( \frac{1}{\sqrt{\pi t}} \right) \ast \hat{f} \right](t) \sim \frac{d}{dt} \left( g \ast \hat{f} \right) + O(1/\sqrt{t}), \tag{A.20}
\]

noting that \( h \ast (1/\sqrt{\pi t}) = \mathcal{L}[gs] \). This gives

\[
|h \ast (f - \hat{f})| \leq C \left| h \ast \left( \frac{1}{\sqrt{\pi t}} \right) \right| \to 0 \quad (t \to \infty). \tag{A.21}
\]

Thus the Lemma 2 also follows.
Appendix B

Some calculations on squirming locomotion with large deformation

B.1 The small amplitude squirming sheet

The infinite squirming sheet with planar undulations is one of the most parsimonious mathematical models for a low Reynolds swimmer and was first considered by [104] with further revision from [10], in the context of an envelope model for a ciliary swimmer.

B.1.1 Formulation

The governing equations are those of Stokes:

\[ \nabla p = \mu \Delta u, \quad \nabla \cdot u = 0, \quad (B.1) \]

coupled with the force free condition for a swimmer. Zero velocity boundary conditions are imposed asymptotically far from the squirming sheet, with the standard no-slip conditions on the squirming surface. The latter is denoted by \((X, Y)\), which is defined by

\[ X(x, t) = x + \epsilon \sum_{n=1}^{\infty} (a_n \sin n(kx + \omega t) - b_n \cos n(kx + \omega t)) \quad (B.2) \]

\[ Y(x, t) = Y_0 + \epsilon \sum_{n=1}^{\infty} (c_n \sin n(kx + \omega t) - d_n \cos n(kx + \omega t)), \quad (B.3) \]
where $Y_0$ is a constant (which may be set to zero without loss of generality) and the coordinates $(x, y)$ are indicated in Fig 1.1b. $\Delta X = X - x$ and $\Delta Y = Y - Y_0$ represent the deformation of the surface. At leading order in $\epsilon$, the velocity of the neutral surface is parallel to the surface and given by (31) of [10],

$$U = \frac{1}{2}\epsilon^2 \omega k \sum_{n=1}^{\infty} n^2 \left[ c_n^2 + d_n^2 - a_n^2 - b_n^2 + 2(a_n d_n - c_n b_n) \right].$$

(B.4)

To consider the energy consumption of the swimmer, we define the power output per unit area on the fluid due to the surface deformation as $P = \int_S \mathbf{n} \cdot \mathbf{\sigma} \cdot \mathbf{u} \, dS$. The lowest order expression of the energy consumption is also obtained by [10],

$$P = \epsilon^2 \omega^2 \mu k \sum_{n=1}^{\infty} n^3 \left( a_n^2 + b_n^2 + c_n^2 + d_n^2 \right).$$

(B.5)

The leading order expressions, (B.4) and (B.5), are both proportional to $\epsilon^2$ and $k$ and this linear dependence on the wave number reflects the fact that the wavelength of the deformation wave is the only characteristic length of this system.

### B.1.2 Symmetry and the power optimal stroke

The study of optimal strokes is a fundamental aspect of many theoretical studies of micro-swimming, as highlighted by [75, 80]. Here we determine the optimal strokes in terms of power, defined as those maximising absolute velocity, subject to the constraint of a fixed power consumption $W$ using the Lagrange multiplier method with the above leading-order expressions. Thus we consider

$$L[\{a_n, b_n, c_n, d_n\}] = U[\{a_n, b_n, c_n, d_n\}] - \lambda(P[\{a_n, b_n, c_n, d_n\}] - W)$$

(B.6)

and the extremal conditions

$$\frac{\partial L}{\partial a_n} = \frac{\partial L}{\partial b_n} = \frac{\partial L}{\partial c_n} = \frac{\partial L}{\partial d_n} = 0,$$

(B.7)

yielding

$$(1 - 2\lambda^2 \omega^2 \mu^2 n^2)a_n d_n = (1 - 2\lambda^2 \omega^2 \mu^2 n^2)b_n c_n = 0,$$

(B.8)
B Some calculations on squirming locomotion with large deformation

\[(1 + 2\lambda \omega \mu n)a_n = d_n, \text{ and } (1 - 2\lambda \omega \mu n)c_n = b_n.\] Since we consider the case \(W > 0\), there must be a unique \(n\) such that \(1 - 2\lambda^2 \omega^2 \mu^2 n^2 = 0\). Thus the stroke is reduced to a single mode which is constrained by \(a_n = (-1 \pm \sqrt{2})d_n\) and \(b_n = (1 \pm \sqrt{2})c_n\). Hence

\[
U = e^2 \omega k n^2 \left( (2 \pm 2\sqrt{2})c_n^2 + (2 \mp 2\sqrt{2})d_n^2 \right), \quad (B.9)
\]
\[
P = e^2 \omega^2 \mu k n^3 \left( (4 \pm 2\sqrt{2})c_n^2 + (4 \mp 2\sqrt{2})d_n^2 \right). \quad (B.10)
\]

Without loss of generality, we can set \(b_n = 0\), and we have the velocity,

\[
U = \mp \frac{1}{\sqrt{2} n \omega} W, \quad (B.11)
\]

which yields the optimal stroke for \(n = 1\) with \(a_1 = (-1 \pm \sqrt{2})d_1\) with the optimal velocity, \(U = \mp (1/\sqrt{2})(W/\mu \omega)\). Clearly, both the symplectic stroke \((a_n = (-1 + \sqrt{2})d_n)\) and the antiplectic stroke \((a_n = (-1 - \sqrt{2})d_n)\) maximise absolute velocity in this case and both optimal strokes require Lagrangian surface points (or cilia tips) to have ellipsoidal trajectories with the oscillation in \(x\) and \(y\) direction possessing a phase difference of \(\pm \pi/2\), as illustrated in Figure 1.1 (a). This degeneracy between the two metachronies originates from the simple relation in the change of variables \((\Delta X, \Delta Y) \rightarrow (\Delta Y, \Delta X)\). This reflects a translational symmetry of the underlying geometry and corresponds to the change of variables, \(a_n \leftrightarrow c_n, d_n \leftrightarrow b_n\) which does not change the leading term of the absolute value of the translational velocity or the power consumption. Thus, geometric symmetry induces a degeneracy in the waveforms that generate maximal speeds at fixed power consumptions.

Of course these results are restricted to a two-dimensional stroke: three-dimensional strokes are also observed and discussed by [14], [75] and [28].

B.2 Simplifying a constraint on the surface deformation

The constraint \(d\Theta/d\theta > 0\) for the surface deformation, equations (4.8), can be simplified. For a fixed value of the aspect ratio between radial and polar deformations, \(A\), we require

\[
1 + \epsilon \sin \left( (1 + A)\frac{\pi}{4} \right) [\cos \theta \cos \chi - 2k \sin \theta \sin \chi] > 0, \quad (B.12)
\]

\[100\]
B.3 The local planar theory approximation

where

\[ \chi := 2k\theta - \omega t + \delta, \]

for all \( \theta \in [0, \pi] \) and all \( \chi \), noting that \( t \in [0, \infty) \). If \( \epsilon \sin \left( (1 + A) \frac{\pi}{4} \right) \geq 1 \), this constraint is violated whenever \( \cos \theta = - \cos \chi = \pm 1 \). Thus we firstly require

\[ \epsilon \sin \left( (1 + A) \frac{\pi}{4} \right) < 1, \]

even for the finite amplitude deformations considered. Then the constraint given by (B.12) is automatically satisfied whenever \( \sin \theta \sin \chi \leq 0 \) since \( k > 0 \). Further, when \( \sin \theta \sin \chi > 0 \), we have the equivalent requirement that

\[ \frac{1}{2} \left( 1 + \epsilon \sin \left( (1 + A) \frac{\pi}{4} \right) \cos \theta \cos \chi \right) > k \epsilon \sin \left( (1 + A) \frac{\pi}{4} \right). \]

The minimum of the left handside as \( \theta, \chi \) are varied is readily determined to be attained at \( \cos \theta = \cos \chi = 0 \) and, in combination with the constraint \( \sin \theta \sin \chi > 0 \), we thus have \( \sin \theta \sin \chi = 1 \) at this point. Hence we also require

\[ \frac{1}{2} > k \epsilon \sin \left( (1 + A) \frac{\pi}{4} \right). \]

(B.13)

B.3 The local planar theory approximation

We non-dimensionalise as in the main text so that the squirmer radius is unity. The non-dimensional fluid dynamical equations for the axisymmetric streamfunction, \( \psi \), can be derived in terms of the operator

\[ E\psi := \psi_{rr} + \frac{2}{r} \psi_r + \frac{1}{r^2} \psi_{\theta \theta} - \frac{\cot \theta}{r^2} \psi_\theta. \]

For \( \eta, \zeta \) positive constants, we consider the rescaling

\[ \eta y = r - 1, \quad \zeta x = (\theta - \theta_0). \]

(B.14)

where \( \theta_0 \) is the polar angle where the tangent plane intersects the sphere (Figure B.1). With \( k \) defined by \( \pi / \lambda \) where \( \lambda \) is the non-dimensional metachronal wavelength (as in equation (4.9)), we have \( \psi_{\theta \theta} \sim 4k^2 \psi, \, \psi_\theta \sim 2k \psi \) since \( \psi \) must be oscillatory at least sufficiently near the sphere, whilst inheriting the wave number by virtue of being consistent with no-slip on the metachronal wave. We fix \( \zeta = 1/[2k] \), so that \( \psi_x = \zeta \psi_\theta \sim \psi \) and hence the scale of the
Some calculations on squirming locomotion with large deformation

Fig. B.1: A schematic picture of the local plane in the local planar approximation theory. The tangent plane, which intersects the sphere at angle $\theta_0$, is utilized for the dynamics at $(r, \theta)$ nearby the tangent point.

tangential derivatives is of order one and the size of these terms is determined from the scale of their coefficients. Rewriting the operator $E$ with respect to the new coordinates gives:

$$
\eta^2 E\psi = \psi_{yy} + \frac{2\eta}{1 + \eta y} \psi_y + \frac{4k^2 \eta^2}{(1 + \eta y)^2} \left\{ \psi_{xx} - \frac{1}{2k \tan (\theta_0 + \zeta x)} \psi_x \right\}.
$$

(B.15)

For $y$ sufficiently small, so that one is sufficiently close to the deformations, which is a sufficient region of validity to enable the approximation of swimming speeds and power consumption in Appendix B.4, one may apply the approximation $(1 + \eta y) \approx 1$. Further, for a dominant balance of the highest order derivatives, as required for non-trivial two dimensional flow, we require $4k^2 \eta^2 \approx 1$, and we thus set $\eta = \zeta = 1/[2k]$, which ensures that $\psi_{yy} \sim \psi_{xx} \sim \psi$ at dominant balance. Also, for $k \gg 1/2$, we have $\eta \ll 1$ and one may also drop the $\eta_y$ term relative to the $\psi_{yy}$ term. Hence

$$
\eta^2 E\psi \approx \psi_{yy} + \left\{ \psi_{xx} - \frac{1}{2k \tan (\theta_0 + \zeta x)} \psi_x \right\}.
$$

Thus neglecting the final curvature term relative to $\psi_{xx}$ induces a relative
error of not more than \( R_1 := 1/[2k \tan \theta_{00}], \) for \( \theta_{00} = \theta_0 - \pi/[2k], \) \( \zeta x \in [-\pi/[2k], \pi/[2k]], \) so that the domain contains a wavelength. Hence, there is no planar approximation for \( \theta_{00}, \) and thus \( \theta_0, \) sufficiently small – that is sufficiently close to the sphere north pole, with analogous reasoning near the south pole. However, for \( \theta_0 \) sufficiently large, the planar approximation holds except for the region \( \theta \in [0, \theta_0] \) of area \( 2\pi(1 - \cos \theta_0) \) near the north pole, with additional analogous errors near the south pole. For approximations based on integrating the planar approximation over the sphere surface, such as the swimming speed or power consumption as illustrated in Appendix B.4, these two pole errors are both counted to induce a relative error of order \( R_2 = (1 - \cos \theta_0), \) on noting the non-dimensional sphere surface area is \( 4\pi. \)

Note that one relative error is monotonic decreasing in \( \theta_0 \) and the other increasing. Hence, there is the prospect of choosing a polar cut-off, \( \theta^*_0, \) whereby \( R_1 \) is small, but also the relative error due to inaccurate polar expressions on integrating the planar approximation over the sphere surface, \( R_2, \) is also small, so that the planar approximation calculations in appendix B.4 are accurate. We take the cut-off to be

\[ \theta^*_0 = \left( \frac{\pi}{k} \right)^{1/3}, \]

whence \( R_2 = 1 - \cos \theta^*_0 \approx \theta^*_0^2/2 \ll 1 \) demands

\[ k \gg \frac{\pi}{2\sqrt{2}} \approx 1.11 \approx 1. \] (B.16)

Also, with \( q := \theta^*_0 - \pi/[2k], \) note that \( q \in (0, \theta^*_0) \) given \( k \gg 1, \) so that \( q \approx \tan q \) with a small relative error of \( q^2/3 < \theta^*_0^2/3 < R_2 \ll 1. \) Hence,

\[ 1 \ll \frac{1}{R_1} \approx 2kq = 2\pi^{1/3}k^{2/3} \left( 1 - \frac{1}{2} \left( \frac{\pi}{k} \right)^{2/3} \right) \]

\[ \approx 2\pi^{1/3}k^{2/3} (1 - R_2) \approx 2\pi^{1/3}k^{2/3}. \] (B.17)

We thus require \( k \gg 1/[2\sqrt{2}\pi^{1/2}], \) which is immediate from the stronger constraint (B.16). Thus, once we have small deformations, \( \epsilon \ll 1 \) and large wave numbers, \( k \gg 1, \) the curvature terms can be neglected close to the swimmer with \( \eta^2 E\psi \approx \psi_{yy} + \psi_{xx}, \) the planar Laplacian.

If we rescale the variables again so that \( \bar{x} = \zeta x = x/[2k] \) and \( \bar{y} = \eta y = y/[2k], \) the resulting approximation, \( E\psi \approx \psi_{\bar{y}\bar{y}} + \psi_{\bar{x}\bar{x}}, \) is accurate over all but an asymptotically small region of the sphere.
We also need to consider the waveform. The effectively planar dimensional waveform is given by equation (4.8) with the coordinate transformation (B.14) and similarly for Eulerian coordinates, written in terms of \( \bar{x}, \bar{y} \), and gives

\[
\begin{align*}
\bar{Y} &= \epsilon \cos((1 + A)\pi/4) \sin(\theta_0 + \bar{x}) \\
&\quad \times \cos(2k\bar{x} + 2k\theta_0 - \omega t) - \epsilon c_0(t), \\
\bar{X} &= \bar{x} + \epsilon \sin((1 + A)\pi/4) \sin(\theta_0 + \bar{x}) \\
&\quad \times \cos(2k\bar{x} + 2k\theta_0 - \omega t + \delta),
\end{align*}
\]  
(B.18)  
(B.19)

where \( \omega = 2\pi \) denotes the temporal frequency. The \( 2k\theta_0 \) terms can be absorbed by a translation of the time variable and thus do not alter the dynamics and are neglected without loss of generality. Recall the \( \epsilon c_0(t) \) term is not arbitrary but inherited from constraining the spherical squirmer volume to be constant. An exact expression is too complex to be tractable and informative, but a straightforward but tedious regular perturbation expansion in \( \epsilon \) reveals

\[
\begin{align*}
\epsilon c_0(t) &= \frac{\epsilon}{4} \frac{\sin(\pi k) \cos(\pi k - \omega t)}{k - k^3} \cos((1 + A)\pi/4) \\
&\quad + O(\epsilon^2) + O\left(\frac{\epsilon^2}{k^3}\right) \\
&\sim O\left(\frac{\epsilon}{4k^3}\right) + O(\epsilon^2),
\end{align*}
\]  
(B.20)

and thus we neglect this “breathing term” in estimates based on local planar approximations with \( \epsilon \ll 1, k \gg 1 \).

To simplify further we assume that over a wavelength \( \bar{x} \in [-\pi/[2k], \pi/[2k]] \) we have

\[
\begin{align*}
\sin(\theta_0 + \bar{x}) &= \sin \theta_0 \cos \bar{x} + \cos \theta_0 \sin \bar{x} \\
&= \sin \theta_0 \left[ 1 + \frac{\bar{x}}{\tan \theta_0} + O(\bar{x}^2) \right] \\
&\approx \sin \theta_0.
\end{align*}
\]  
(B.21)

The latter approximation induces a maximum relative error of approximately

\[
R_3 = \frac{\pi}{2k \tan \theta_0^*} \approx \frac{1}{2} \left( \frac{\pi}{k} \right)^{2/3} = \frac{1}{2} \theta_0^{*2} \approx R_2 \ll 1,
\]

where the approximation \( \tan \theta_0^* \approx \theta_0^* \) has been used on noting the relative error is given by \( \theta_0^{*2}/3 \approx 2R_2/3 \ll 1 \). Hence, dropping bars for convenience,
B.4 An estimate for the efficiency of a small amplitude spherical squirmer at low wavelength, high wave number

the effectively planar dimensional waveform is

\[
Y = \epsilon \cos((1 + A)\pi/4) \sin(\theta_0) \cos(2kx + 2k\theta_0 - \omega t),
\]
\[
X = x + \epsilon \sin((1 + A)\pi/4) \sin(\theta_0)
\]
\[
\times \cos(2kx + 2k\theta_0 - \omega t + \delta),
\]  
(B.22)

where \(\theta_0\) is the polar angle where the tangent plane meets the sphere.

In summary, when \(k \gg 1\), \(\epsilon \ll 1\) we can immediately use single mode planar calculations based on equation (B.22) to determine local fluid dynamics near the sphere for the stroke patterns we explore in this paper. This in turn allows the approximation of swimming speeds and power, as illustrated in the next Appendix for the optimal efficiency of a small amplitude spherical squirmer at high wave number and its associated swimming velocity.

B.4 An estimate for the efficiency of a small amplitude spherical squirmer at low wavelength, high wave number

Given a large wave number \(k \gg 1\), and small deformation amplitude \(\epsilon \ll 1\), we have from Appendix B.3 that the local velocity profile for a tangent plane touching the sphere at polar angle \(\theta_0\) is given by equation (B.22) with the phase shift given by \(\delta = \pi/2\) for a symplectic wave:

\[
Y = \epsilon \cos((1 + A)\pi/4) \sin(\theta_0) \cos(2kx - \omega t),
\]
\[
X = x + \epsilon \sin((1 + A)\pi/4) \sin(\theta_0)
\]
\[
\times \cos(2kx - \omega t + \pi/2).
\]  
(B.23)

A comparison of equation (B.23) with the \(n = 1\) contribution to equations (B.2–B.3) of the planar analysis reveals that they are equivalent if (i) \(\omega \rightarrow -\omega\), which just reverses the velocity direction but not its magnitude, (ii) \(k \rightarrow k/2\), and (iii) \(a_1 = -\sin((1 + A)\pi/4) \sin(\theta_0)\) and \(d_1 = -\cos((1 + A)\pi/4) \sin(\theta_0)\).

We therefore have from Appendix B.1 that this waveform is optimally efficient if

\[
\tan \left( (1 + A)\frac{\pi}{4} \right) = \frac{a_1}{d_1} = -1 + \sqrt{2} = \tan \left( \frac{\pi}{8} \right).
\]

Hence optimality occurs at \(A = -1/2\) in the planar approximation to the spherical waveform (which is consistent with the plots for \(k = 4\), \(\epsilon \ll 1\) in Fig. 4.6). At this optimality equation (B.11) reveals that the magnitude of
the local velocity of the squirmer reference surface relative to the far field flow, denoted $|U|$, is given by the planar theory via

$$|U| = \frac{W}{\sqrt{2\mu|\omega|}} = \frac{W}{2\pi\sqrt{2}}$$

(B.24)

where $W$ is the power dissipated per unit area at maximal planar stroke efficiency. The final equality in equation (B.24) arises as the viscosity, $\mu$ and frequency, $\omega$ are unity and $2\pi$ respectively in the non-dimensional form of the model used here.

From equation (B.10) $W$ is proportional to $\epsilon^2kd_1^2$ and thus proportional to $\epsilon^2k\sin^2\theta_0$, allowing us to write $W = J\epsilon^2k\sin^2\theta_0$, where $J$ denotes a positive constant which is independent of $\theta$, $k$, $\epsilon$ and whose evaluation is not required below. Since $U$ is in the $e_\theta$ direction tangent to the sphere, at least sufficiently close to the sphere, and assuming asymptotically small deformations, we can approximate the squirmer as possessing an effective tangential slip velocity in the $e_\theta$ direction. The magnitude of this slip velocity is given by

$$|U| = \frac{W}{2\pi\sqrt{2}} = \frac{J\epsilon^2k\sin^2\theta_0}{2\pi\sqrt{2}} := \sum_{n=1}^{\infty} \gamma_n V_n(\cos \theta_0),$$

where the final expression defines an expansion in terms of the associated Legendre polynomials $V_n(\cos \theta_0)$, as defined in equation (4.3).

In particular the tangential squirmer approximation immediately yields that the magnitude of the leading order swimming speed is simply $2|\gamma_1|/3$, by inspection of equations (4.2), (4.6) and as detailed in [9, 71]. Hence the magnitude of the swimming speed, denoted $U_*$, is given via a projection onto the first associated Legendre polynomial coefficient:

$$U_* = \frac{2}{3\pi\sqrt{2} J\epsilon^2k} \left| \int_0^\pi d\theta_0 \sin^2 \theta_0 V_1(\cos \theta_0) \sin \theta_0 \right|$$

$$= \frac{J\epsilon^2k}{3\pi\sqrt{2}} \int_0^\pi d\theta_0 \sin^4 \theta_0 = \frac{3J\epsilon^2k}{32\sqrt{2}}$$

(B.25)

This result can be alternatively derived without appeal to the results of the tangential squirmer via the sphere surface average of $e_z \cdot U$, which must be the swimming speed for the reference frame to be comoving. The total power output is the integral of $W$ over the sphere surface area and, on noting the non-dimensional sphere radius is unity, the velocity to power ratio reduces
B.4 An estimate for the efficiency of a small amplitude spherical squirmer at low wavelength, high wave number

\[ \frac{U_*}{\int_0^{2\pi} d\phi \int_0^\pi d\theta_0 \sin \theta_0 \ W} = \frac{3\pi J e^2 k}{64\pi \sqrt{2} J e^2 k} \frac{1}{\int_0^\pi d\theta_0 \sin^3 \theta_0} = \frac{9}{256\pi \sqrt{2}} \]  

(B.26)

as used in the main text. The calculation is essentially the same for an antiplectic stroke.
Appendix C

Details on the boundary element method

In this appendix section, more details on the boundary element method used in Chapter 3 and Chapter 4 are provided. The boundary element code is based on the program stokes/prtcl_3d in the BEMLIB Library, and the details are following the practical guide [83].

The boundary element method is composed of several steps; First, the boundary meshes are generated with relations between elements, then the boundary integral is performed with careful treatment for the Stokes singularity, a linear problem is finally numerically solved. Each step will be described in the following subsections.

C.1 Mesh generation

The mesh generation is based on the program grids/trgl in the BEMLIB Library. A sphere or an ellipsoid is divided into quadratic triangular elements defined by six nodes based on successive subdivisions of a regular octahedron. In the process of the subdivision, the mid-points of the edges of a parental triangle becomes vertex nodes of the descendant triangles. The descendant triangles are finally projected onto the surface of the ellipsoid (Chapter 3) or onto the squirming sphere (Chapter 4). Therefore the increase of the number of the iteration of the subdivision yields the finer meshes.
C.2 Boundary element integral

A quadratic triangular element with six nodes is the fundamental region for the surface integral in the boundary element equations. This six-node curved triangle is mapped to a right isosceles triangle, where the numerical integral is performed both in the presence or in the absence of the singularity from the Stokeslet.

C.2.1 Three-node flat triangle

For briefly, we first consider the case when the boundary is divided into the three-nod flat triangles. This flat triangle is mapped to a right isosceles triangle in $\xi \eta$ plane for the implement of the numerical boundary integral, as illustrated in the left of Fig. C.1.

Let the three nodes of the physical triangle be $x_i$ ($i = 1, 2, 3$), and consider a map $x(\xi, \eta)$ such that

$$x(0, 0) = x_1, \quad x(1, 0) = x_2, \quad x(0, 1) = x_3. \quad (C.1)$$

Let the mapping from physical to parametric space be given by

$$x = \sum_{i=1}^{3} x_i \phi_i. \quad (C.2)$$

The basis function is derived from the conditions (C.1), and we obtain

$$\phi_1 = 1 - \xi - \eta, \quad \phi_2 = \xi, \quad \phi_3 = \eta, \quad (C.3)$$

where $0 \leq \xi, \eta \leq 1$, $0 \leq \xi + \eta \leq 1$. From this mapping, the boundary integral over a flat triangle is reduced to the integral in the parameter space. Consider the integral of a function $f(x)$, we obtain

$$\int_{\text{Triangle}} f(x) dS_x = h_S \int_0^1 \int_0^{1-\xi} f(x(\xi, \eta)) \, d\eta \, d\xi, \quad (C.4)$$

where $h_S = |e_\xi \times e_\eta|$.

If the integrand, $f(x)$ does not contain a singular part over the boundary element, this integral can be straightforwardly performed by a standard numerical scheme such as the Gauss quadrature method. When the integrand contains a singular part, we need a special treatment. As far as the Stokes equations are considered, the singular part is weak and can be removed with
C Details on the boundary element method

Fig. C.1: A schematic picture of a flat triangle in three dimensional space and the mapping to a right isosceles triangle in the $\xi\eta$ plane.

proper treatment, as the singularity is of the order of $O(1/\rho)$, where $\rho$ is the distance from the singular point. We will suppose the singular point is the first vertex without loss of generality, and consider the following integral,

$$I = \int_{\text{Triangle}} \frac{q(x)}{|x - x_1|} dS_x.$$  \hspace{1cm} (C.5)

With the use of the mapping (C.2), the integral becomes

$$I = \frac{h_S}{|x_2 - x_1|} \int_0^1 \int_0^{1-\xi} \frac{q[x(x, \eta)]}{\sqrt{\xi^2 + 2B\xi\eta + C\eta^2}} d\eta d\xi,$$  \hspace{1cm} (C.6)

where $B$ and $C$ is the constants defined by

$$B = \frac{(x_3 - x_1) \cdot (x_2 - x_1)}{|x_2 - x_1|^2}, \quad C = \frac{|x_3 - x_1|^2}{|x_2 - x_1|^2}.$$  \hspace{1cm} (C.7)

For the removal of the weak singularity, we introduce the local polar coordinate, whose origin is located at the singular point, i.e. $\xi = \rho \cos \chi$ and $\eta = \rho \sin \chi$. Thus the integral finally becomes

$$I = \frac{h_S}{|x_2 - x_1|} \int_0^{\pi/2} \int_0^{R(\chi)} \frac{q(\rho, \chi) d\rho}{\cos^2 \chi + B \sin 2\chi + C \sin^2 \chi} d\chi,$$  \hspace{1cm} (C.8)

where $R(\chi)$ is the maximum radius in the polar coordinates, given by $R = (\cos \chi + \sin \chi)^{-1}$. The integrand is then non-singular, and the integral can be numerically computed by the Gauss quadrature method.
C.2 Boundary element integral

C.2.2 Six-node curved triangle

In this subsection, we describe the method for the boundary integral over a six-node curved triangle. Similarly to the previous section, we consider a mapping from physical to parameter space as depicted in Fig. C.2.

The mapping is constituted by the function,

$$\mathbf{x} = \sum_{i=1}^{6} \mathbf{x}_i \phi_i(\xi, \eta),$$

(C.9)

where the element-node cardinal interoperation function $\phi_i$ is given by

$$\begin{align*}
\phi_2 &= \frac{1}{1-\alpha} \xi \left( \xi - \alpha + \frac{\alpha - \gamma}{1-\gamma} \eta \right) \\
\phi_3 &= \frac{1}{1-\beta} \eta \left( \eta - \beta + \frac{\beta + \gamma - 1}{\gamma} \xi \right) \\
\phi_4 &= \frac{1}{\alpha(1-\alpha)} \xi (1-\xi - \eta) \\
\phi_5 &= \frac{1}{\gamma(1-\gamma)} \xi \eta \\
\phi_6 &= \frac{1}{\beta(1-\beta)} \eta (1-\xi - \eta) \\
\phi_1 &= 1 - \phi_2 - \phi_3 - \phi_4 - \phi_5 - \phi_6,
\end{align*}$$

(C.10)

so that the conditions

$$\begin{align*}
\mathbf{x}(0,0) &= \mathbf{x}_1, \quad \mathbf{x}(1,0) = \mathbf{x}_2, \quad \mathbf{x}(0,1) = \mathbf{x}_3 \\
\mathbf{x}(\alpha,0) &= \mathbf{x}_4, \quad \mathbf{x}(\gamma,1-\gamma) = \mathbf{x}_5, \quad \mathbf{x}(0,\beta) = \mathbf{x}_6
\end{align*}$$

(C.11)

are satisfied. Here, the geometrical parameters $\alpha$, $\beta$ and $\gamma$ are given by

$$\begin{align*}
\alpha &= \left(1 + \frac{|\mathbf{x}_4 - \mathbf{x}_2|}{|\mathbf{x}_4 - \mathbf{x}_1|}\right)^{-1}, \\
\beta &= \left(1 + \frac{|\mathbf{x}_6 - \mathbf{x}_3|}{|\mathbf{x}_6 - \mathbf{x}_1|}\right)^{-1}, \\
\gamma &= \left(1 + \frac{|\mathbf{x}_5 - \mathbf{x}_2|}{|\mathbf{x}_5 - \mathbf{x}_3|}\right)^{-1}
\end{align*}$$

(C.12)

For the integral over a non-singular element, the integral is computed by the Gauss quadrature method,

$$\int_{\text{Triangle}} f(\mathbf{x}) dS \approx \frac{1}{2} \sum_{k=1}^{N_Q} f[\mathbf{x}(\xi_k, \eta_k)] h_S(\xi_k, \eta_k) w_k$$

(C.13)
Fig. C.2: A schematic picture of a six-node curved triangle in three dimensional space and the mapping to a right isosceles triangle in the $\xi \eta$ plane. $x_0$ is the center of the curved triangle.

where $N_Q$ is the number of quadrature base points and $N_Q = 13$ is used. The parameters $(\xi_k, \eta_k)$ is the coordinates of the $k$th base point inside or along the edges of the right isosceles triangle, $h_S$ is again the surface metric, $h_S(\xi_k, \eta_k) = |e_{\xi_k} \times e_{\eta_k}|$, and $w_k$ is the integration weight for the $k$th base point.

We consider a singular point on the center of the curved triangle, $x_0$, as in illustrated in the left of Fig. C.2. This point is defined by considering $f(x) = x$ in the integral (C.13). The integral over a singular element is performed after approximation of the curved triangle as divided six flat triangles in Fig. C.2. The integral over each three-node flat integral is computed by the Gauss quadrature method with $N_Q = 4$ after the local polar coordinates is introduced for removal of the weak singularity as in (C.8).

C.3 Linear problem

Once the integral over the boundary elements is computed, the Stokes equations are reduced to a linear problem. For a general discussion, let us write the boundary element integral argued in Chapter 3 and Chapter 4 as

$$u_i(x) = \int_S G_{ji}(x, x_0)q_j(x_0)dS_{x_0},$$  \hspace{1cm} (C.14)

where $G_{ji}$ is the integral kernel depending on the specified problem, and $q_j$ is the traction including constant factors. The boundary condition on surface
of the swimmer, $S$, is given by $\mathbf{u} = \mathbf{U} + \mathbf{\Omega} \times (x_0 - \mathbf{X}) + \mathbf{u}'$, where $\mathbf{U}$ and $\mathbf{\Omega}$ are linear and rotational velocity, respectively, and $\mathbf{u}'$ is the deformation velocity. The force and torque free conditions are reduced to

$$\int_S \mathbf{q}(x_0)dS_{x_0} = \int_S (x_0 - \mathbf{X}) \times \mathbf{q}(x_0)dS_{x_0} = 0, \quad (C.15)$$

where $\mathbf{X}$ is the centre of the swimmer. We suppose the traction is constant over a single boundary element, and then the integral in (C.14) is approximated by

$$u_i(x) \approx \sum_{e=1}^{N_e} q_j(x_0(e)) \int_{triangle(e)} G_{ji}(x, x_0(e))dS_{x_0}. \quad (C.16)$$

The integral over each element can be computed by the scheme described in §C.2, and we then rewrite this as $u_i = \sum_{e,j} A_{ji,e} q_{je} \ (e = 1, \cdots, N_e \text{ and } j = 1, 2, 3)$, where $N_e$ is the number of the boundary element. This is finally reduced to a $3N_e + 6$ dimensional linear problem, which can be symbolically represented by

$$\begin{pmatrix} A_{ji,e} & -\delta_{ik} & -\epsilon_{ijk}(x_{0,k,e} - X_k) \\ \sum_e \delta_{ij} & 0 & 0 \\ 0 & -\sum_e \epsilon_{ijk}(x_{0,k,e} - X_k) & 0 \end{pmatrix} \begin{pmatrix} q_{je} \\ U_k \\ \Omega_k \end{pmatrix} = \begin{pmatrix} u'_{i,e} \\ 0 \\ 0 \end{pmatrix}. \quad (C.17)$$

This linear problem is solved, using LU decomposition and the time-marching is computed by the Heun method [94]. At each time step, the deformation velocity is obtained by a specified function (Chapter 3) or numerical derivative of the surface shape (Chapter 4).
Acknowledgements

I would like to express my appreciation to Prof. Michio Yamada for his great advice on the basis of comprehensive and deep knowledge of fluid mechanics as well as other fields of physics and mathematics. He has given me insightful comments and suggestions not only on specific problems of this study but also on attitude to science as a researcher from fairly broad perspectives.

I would also like to express my gratitude to Prof. Eamonn Gaffney, who kindly hosted my stay at Wolfson Centre for Mathematical Biology, Mathematical Institute, University of Oxford, and has provided invaluable advice that made it possible to complete this study. He has not only guided me to the research frontier, where mathematics and biology are merging, but also offered thoughtful advice on my philosophy as a scientist with warm words of encouragement.

I would also like to thank the senior members of our research group, Prof. Shin-ichi Takehiro and Dr. Youhei Sasaki for warm encouragement and fruitful discussions. I deeply appreciate my senior colleagues at Research Institute for Mathematical Sciences (RIMS), Drs. Kiori Obuse, Keiji Kimura, Eiichi Sasaki, and Masanobu Inubushi for continuous encouragements and stimulus discussions. I am always proud of spending my PhD life with them. I am also grateful to the RIMS staffs for providing me such a stimulating and brilliant research environment.

I am grateful to Dr. Dave Smith at School of Mathematics, University of Birmingham for his kind lectures on the boundary element method and fruitful discussion. I also appreciate Prof. Jacky Cosson at Research Institute for Fish Culture and Hydrobiology (RIFCH), University of South Bohemia, who has given me kind introductory lectures on sperm biology and wonderful opportunities to enjoy the collaboration between mathematics and biology. I also thank Prof. Masaru Okabe at Research Institute for Microbial Diseases (RIMD), Osaka University, who has given me a wonderful opportunity for collaboration and shown me a proper attitude to nature through fruitful discussions filled with deep insights. Let me sincerely appreciate all the other
researchers whom I met during my PhD life, though they are not listed.

My special thanks go to my friends and family, who have always supported me during my university life. Lastly, I would like to express my deepest appreciation to my wife, Haru, who always supported me with cordial encouragements. Her supports of my translation of some German and Latin literatures are also of great assistance.

Elements of the numerical calculations were performed by the computer systems of the Institute for Information Management and Communication (IIMC) of Kyoto University and of the Research Institute for Mathematical Sciences, Kyoto University.

I acknowledge the Japan Society for the Promotion of Science (JSPS) for a grant for JSPS Fellows (Grant Number 24-2077), which supported the researches during my PhD. I also acknowledge Iwadare Foundation for a scholarship for graduate students in 2011. Department Mathematics and Mathematical Sciences, Kyoto University is also acknowledged for a grant in GCOE program, “Fostering top leaders in mathematics - broading the core and exploring new ground”, which supported my stay in University of Oxford in 2012. The stays at the University of Oxford and University of South Bohemia in 2013 and in 2014 were financially supported by JSPS funding for excellent graduate schools.
References


REFERENCES


REFERENCES


REFERENCES


REFERENCES


REFERENCES


REFERENCES


REFERENCES


