

Simple models of the chemical field around swimming plankton

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The chemical field around swimming plankton depends on the swimming style and speed of the organism and the processes affecting uptake or exudation of chemicals by the organism. Here, we present a simple model for the flow field around a neutrally buoyant self-propelled organism at low Reynolds number and numerically calculate the chemical field around the organism. We show how the concentration field close to the organism and the mass-transfer rates vary with the swimming speed and style for Dirichlet (diffusion-limited transport) boundary conditions. We calculate how the length of the chemical wake, defined as being the distance at which the chemical field drops to 10% of the surface concentration of the organism when stationary, varies with the swimming speed and style for both Dirichlet and Neumann (production limited) boundary conditions. For Dirichlet boundary conditions, the length of the chemical wake increases with increasing swimming speed, and the self-propelled organism displays a significantly longer wake than the towed-body model. For Neumann boundary conditions, the converse is true; because swimming enhances the transport of the chemical away from the organism, the surface concentration of chemical is reduced and thus the wake length is reduced.

KEYWORDS: swimming; nutrient uptake; exudation; low Reynolds number

INTRODUCTION

Diverse swimming plankton interact with chemical fields in aquatic environments. The chemicals may be nutrients that are consumed or exudates that are produced by the organism. In both cases, we want to understand the chemical field generated around the organism, and the rate at which chemicals are transferred between the organism and the environment. For example, female copepods emit pheromones, generating trails which are tracked by their mates (Doall *et al.*, 1998) and many phytoplankton are motile which can enhance their uptake rate of inorganic nutrients (Karp-Boss *et al.*, 1996). Other organisms, such as *Phaeocystis*, a large motile phytoplankton which exudes

DMSP, may also alter the spatial distribution of chemicals that they themselves emit (Laroche *et al.*, 1999).

There have been extensive studies as to how fluid motion affects the chemical field around chemical sinks such as those reviewed by Karp-Boss *et al.* (Karp-Boss *et al.*, 1996) in the context of nutrient uptake by aquatic single cells. By modelling swimmers as towed bodies, these studies have predicted how swimming affects the chemical field surrounding the organism and the mass-transfer rate between the organism and the fluid environment. However, from simple force arguments, the towed-body model is not a self-consistent model of a self-propelled swimmer. To understand how propulsion affects the chemical field around a swimmer, it is

useful to examine simple self-consistent models for swimming, such as those by Visser (Visser, 2001) or Jiang *et al.* (Jiang *et al.*, 2002). Previous work has applied examples of these models to calculate the concentration of pheromone around a hovering copepod (Thygesen and Kjørboe, 2006), and the nutrient uptake by a model squirmer (Magar *et al.*, 2003) that was based on a model for low Reynolds number swimming analyzed by Blake (Blake, 1971).

The aim of this paper is to examine how the chemical field around a self-propelled organism is affected by the organism’s swimming speed and style and how this field is affected by the choice of surface boundary conditions. The two types of boundary conditions discussed here depend on the biochemical activities taking place within the organism.

METHODS

Models of self-propelled swimmers

We model a swimmer by a sphere of radius a moving with speed U and take a reference frame moving with the swimming organism. The key non-dimensional parameters of the problem are the Reynolds number (Re), which measures the relative importance of inertial to viscous forces, and the Péclet number (Pe), which represents the relative importance of advection (which here is due to swimming) to diffusion. Following Karp-Boss *et al.* (Karp-Boss *et al.*, 1996), we define these parameters as follows:

$$\text{Re} = \frac{aU}{\nu}, \quad \text{Pe} = \frac{aU}{D}, \quad (1)$$

where ν is the kinematic viscosity of the water and D is the molecular diffusivity of the chemical.

In our calculations, we will assume that the swimmer is sufficiently small and slow so that we can assume the flow is governed by the Stokes flow equations, i.e. zero Reynolds number flows (Acheson, 1990). Previous studies have investigated how the flow field and resultant chemical field around a sinking sphere are modified when this assumption is relaxed (Kjørboe *et al.*, 2001), but here the novelty is to focus on how self-propulsion modifies the chemical field and we restrict attention to the simple case of Stokes flow, for which analytic solutions are available. The Stokes flow equations are a reasonable approximation for planktonic microorganisms (Karp-Boss *et al.*, 1996), but are not valid in situations when plankton generate energetic, inertia-dominated events, e.g. the rapid escape jump of a copepod (Visser, 2001).

To simplify our analytic expressions for the flow field, we non-dimensionalize the system so that the swimmer is a sphere of unit radius moving at unit speed and take a reference frame moving with the swimming organism. We also assume the swimming behaviour is axisymmetric so the velocity field can be described by the radial and azimuthal components U_r and U_θ . The simplest model for swimming is to consider a rigid sphere moving steadily through the fluid which has flow field given by Visser (Visser, 2001):

$$\begin{aligned} U_r &= \left(-1 + \frac{3}{2r} - \frac{1}{2r^3}\right) \cos \theta \\ U_\theta &= \left(1 - \frac{3}{4r} - \frac{1}{4r^3}\right) \sin \theta. \end{aligned} \quad (2)$$

When visualizing the flow field, streamlines can be represented as contour plots of the stream function, ψ , defined as (Acheson, 1990):

$$\frac{\partial \psi}{\partial \theta} = r^2 \sin \theta U_r, \quad \frac{\partial \psi}{\partial r} = -r \sin \theta U_\theta, \quad (3)$$

which for the towed-body model is given by

$$\psi = \left(-\frac{1}{2}r^2 + \frac{3r}{4} - \frac{1}{4r}\right) \sin^2 \theta. \quad (4)$$

This flow field accurately represents a particle sinking under gravity, but is not a self-consistent model for a self-propelled body, as the hydrodynamic forces result in a net force acting on the body. Such a flow can only be realized if the drag force on the sphere is matched by an equal and opposite external force, e.g. gravity or some external “towing” force.

As discussed by Visser (Visser, 2001), the net force on a neutrally buoyant, self-propelled body moving at a uniform speed is zero, so that the thrust driving the body forward exactly matches the viscous drag. A simple model of this is the force dipole, or stresslet. The flow field generated by two equal and opposite forces \mathbf{F} and $-\mathbf{F}$ separated by a vector \mathbf{b} parallel to \mathbf{F} is given at leading order in $|\mathbf{b}|$ by the stresslet, or dipole, flow field. Given that we choose to work in a frame of reference moving with the swimmer, the far-field flow is a uniform flow of unit speed, giving the following total flow field:

$$\begin{aligned} U_r &= -\cos \theta + \frac{|\mathbf{F}||\mathbf{b}|}{8\pi\mu r^2} (3\cos^2 \theta - 1), \\ U_\theta &= \sin \theta. \end{aligned} \quad (5)$$

Note that for a sphere of unit radius moving with unit speed, the drag force is given by $|\mathbf{F}| = 6\pi\mu$,

furthermore, if we assume the drag and propulsive forces act at points on opposite sides of the surface of the sphere of unit radius, we can assume $|\mathbf{b}| = 2$, and thus obtain the result given by Visser (Visser, 2001):

$$U_r = -\cos \theta + \frac{3}{2r^2}(3 \cos^2 \theta - 1), \quad U_\theta = \sin \theta \quad (6)$$

with stream function

$$\psi = -\frac{1}{2}r^2 \sin^2 \theta + \frac{3}{2} \cos \theta \sin^2 \theta. \quad (7)$$

Although this model is a useful far-field representation of the flow around a self-propelled body, it does not represent the near-field behaviour. For example, the radial velocity on the surface of the body ($r = 1$) is typically non-zero.

In this paper, we investigate the effect of self-propelled swimming on chemical transfer for a model swimmer which is the simplest we can think of which has two important properties: (i) the swimmer is a neutrally buoyant, self-propelled organism in that there is no net force acting on the organism; and (ii) the organism has a well-defined shape that we can calculate the mass transfer across. The swimming model used by Magar *et al.* (Magar *et al.*, 2003) has these properties and generates the following flow field:

$$\begin{aligned} U_r &= \left(\frac{1}{r^3} - 1\right) \cos \theta + \frac{3q}{4} \left(\frac{1}{r^4} - \frac{1}{r^2}\right) (3 \cos^2 \theta - 1), \\ U_\theta &= \left(\frac{1}{2r^3} + 1\right) \sin \theta + \frac{3q}{2r^4} \sin \theta \cos \theta. \end{aligned} \quad (8)$$

with stream function

$$\psi = \frac{1}{2} \sin^2 \theta \left(\frac{1}{r} - r^2\right) - \frac{3q}{4} \cos \theta \sin^2 \theta \left(1 - \frac{1}{r^2}\right). \quad (9)$$

A key point for the purposes of this paper is that the radial component of the velocity field is zero on the surface of the sphere, and thus we can naturally consider the surface $r = 1$ to represent the surface of an organism whose surface is impenetrable to the surrounding fluid. The model swimmer moves its surface steadily and tangentially to itself to generate propulsion. Specifically, at the surface $r = 1$, the tangential velocity is given by

$$U_\theta = \frac{3}{2} \sin \theta + \frac{3q}{4} \sin 2\theta. \quad (10)$$

In this model, the parameter q adjusts the imposed surface velocities as shown in Fig. 1; intuitively, it measures how much the swimming stirs the water and

varying q allows an investigation of different swimming styles. The model can be thought of as approximating a highly idealized planktonic organism such as a ciliate with infinitely small cilia or *Volvox*. In the case of a ciliate, varying the stirring parameter can also allow investigation into how localization of the cilia alters the swimming pattern, e.g. in Fig. 1bii, the surface velocity is dominated by motions at the rear of the organism. However, the primary reason for studying such an idealized model is to investigate how a self-propelled organism can create quite a different chemical field than a towed rigid body.

The flow field given by Equation (8) was derived by considering imposed surface motions of the sphere and solving the flow field via an expansion in terms of Legendre polynomials and associated functions. Energy arguments were originally used to derive this flow field, based on the requirement that the total energy in the fluid is finite, which leads to formulae connecting the swimming speed to the surface velocities (Blake, 1971). Alternatively, the total force exerted by the swimmer due to the combination of pressure and viscous surface forces can be calculated as zero (e.g. Acheson, 1990), and thus the swimmer can be viewed as being self-propelled in the same sense as the stresslet model.

Equations describing the chemical field

In the presence of a velocity field, \mathbf{u} , generated by the swimming motions, around the organism the chemical is advected by the fluid and diffuses, and thus can be modelled by the following advection-diffusion equation with respect to non-dimensional variables:

$$\dot{C} = -\nabla \cdot (\text{Pe } \mathbf{u} C - \nabla C). \quad (11)$$

In this paper, we focus on computing the steady-state chemical field, found by setting $\dot{C} = 0$. The boundary conditions describing the chemical concentration or chemical flux on the surface of the organism are key in determining the concentration field. Because the surface of the organism is not well defined for the stresslet model, we calculate the chemical field only for the towed-body model and the squirmer. Here, we consider two possible boundary conditions, either the concentration is constant over the surface of the sphere (the Dirichlet boundary condition) or the total flux of chemical is constant over the sphere (the Neumann boundary condition). The Dirichlet boundary condition is valid when the transport of chemicals is limited by the rate at which the chemical can diffuse away from the concentration boundary layer. This boundary condition is useful to

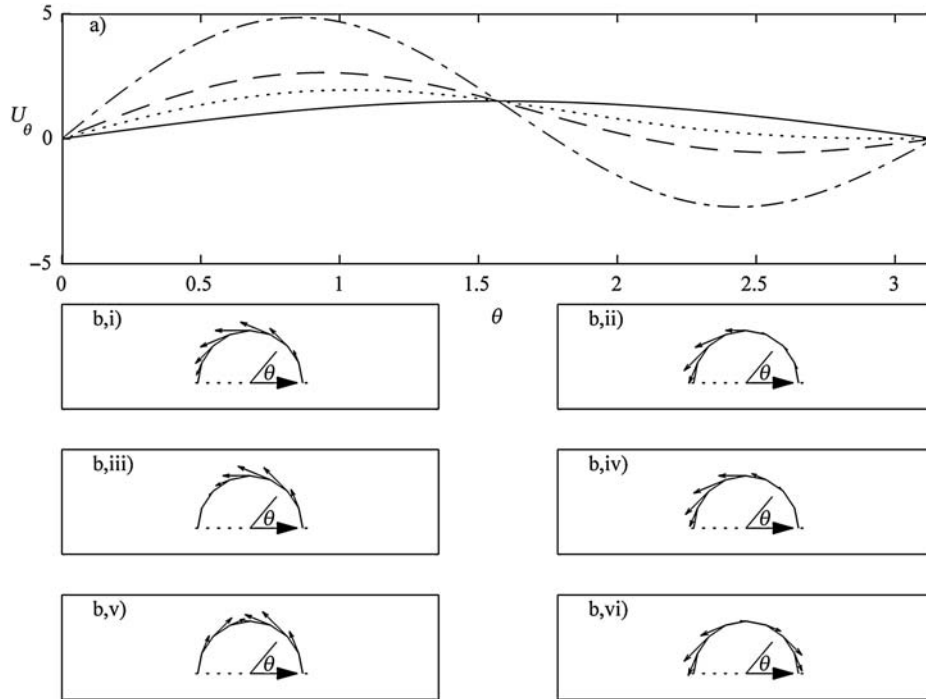


Fig. 1. Surface velocity of model squirmer. **(a)** Velocity on the surface of organism ($r = 1$) is purely tangential and given by U_θ [see Equation (10)], which varies with stirring parameter q : $q = 0$ solid line; $q = 1$ dotted line; $q = 2$ dashed line; $q = 5$ dashed-dotted line. Velocity for the negative values of q are obtained by reflecting about $\theta = \pi/2$ (not shown). **(b)** Example surface velocity vectors for the range of stirring parameters corresponding to flow fields shown in Fig. 2: (i) $q = 0$, (ii) $q = -2$, (iii) $q = 1$, (iv) $q = -1$, (v) $q = 10$ and (vi) $q = -10$. Angle θ is defined from the direction of swimming indicated by bold arrows. Only half the swimmer is shown as the model assumes symmetric behaviour.

compute an upper bound on the importance of fluid dynamic effects, e.g. obtaining a maximum estimate of how swimming can affect the nutrient uptake rate (Karp-Boss *et al.*, 1996; Magar *et al.*, 2003). The Neumann boundary condition corresponds to the situation when the flux of chemicals is limited by the rate of biological processes. In their model of pheromone production, Thygesen and Kjørboe (Thygesen and Kjørboe, 2006) assumed that the chemical was emitted from a point source at a constant rate Q independent of the flow field, which for a finite-sized organism would be most simply represented by a Neumann boundary condition. By considering the two boundary conditions as limiting cases, it is possible to assess the model predictions against experimental results to determine whether the underlying biology is transport or reaction limited (Kjørboe *et al.*, 2001).

For the Dirichlet boundary condition (diffusion-limited transport), we can calculate how swimming enhances the mass transfer between the organism and its environment. In this case, we can non-dimensionalize the concentration field so that $C = 1$ on $r = 1$ and $C = 0$ as $r \rightarrow \infty$, and then define the Sherwood number, Sh , which quantifies the

enhancement, as (Magar *et al.*, 2003)

$$Sh = - \int_0^\pi \frac{\partial C}{\partial r}(1, \theta) \sin \theta d\theta. \quad (12)$$

In the absence of flow, $C = 1/r$, giving $Sh = 2$.

For the Neumann boundary condition, the total flux across the surface is assumed to have a fixed value, Q , hence

$$- 2\pi \int_0^\pi \frac{\partial C}{\partial r}(1, \theta) \sin \theta d\theta = Q. \quad (13)$$

We choose to non-dimensionalize the concentration field so that the flux for both Neumann and Dirichlet boundary conditions are equal in the no-flow case, i.e. we take $Q = 4\pi$. This boundary condition is insufficient for obtaining a unique solution to the boundary value problem, and so we further assume that there is no angular variation in the surface concentration, i.e. we take

$$C(1, \theta) = C_0, \quad (14)$$

where the value C_0 varies with Pe , so as to ensure Equation (13) is satisfied. Thus, the chemical field for the

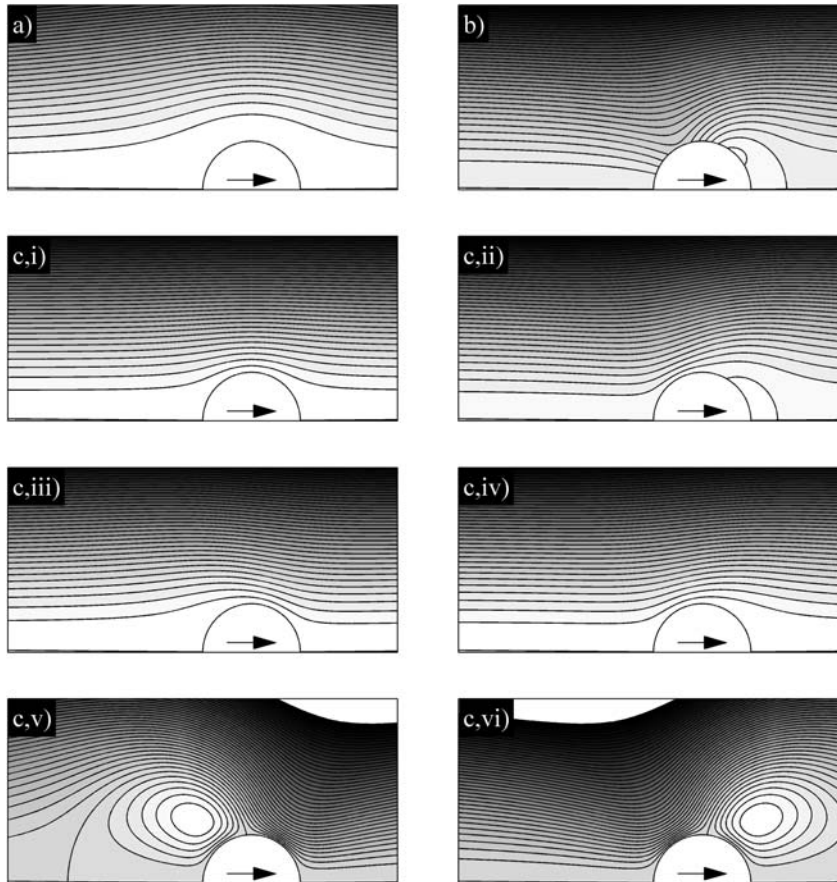


Fig. 2. Flow field around model swimmers. Streamlines computed as a contour plot of stream function for flow field generated by (a) towed body [Equation (4)], (b) stresslet [Equation (7)] and (c) squirmer [Equation (9)], with stirring parameter (i) $q = 0$, (ii) $q = -2$, (iii) $q = 1$, (iv) $q = -1$, (v) $q = 10$ and (vi) $q = -10$. Arrows indicate the swimming direction. Only half the swimmer is shown as the model assumes symmetric behaviour.

Neumann boundary condition is simply that calculated for the Dirichlet boundary condition rescaled by $2/Sh$.

The numerical solution for the chemical field is obtained using a finite volume method as described by Magar *et al.* (Magar *et al.*, 2003).

RESULTS

Flow field around self-propelled swimmers

The flow field generated by the model swimmers are plotted in Fig. 2. In order to compare the models, we note that the stresslet model agrees in the far-field (up to $1/r^2$ terms) with the squirmer model with stirring parameter $q = -2$ and can be compared in Fig. 2b and 2cii. In contrast to the towed-body model (shown in Fig. 2a), we note that these models have a fore-aft asymmetry and there is a recirculation region ahead of the swimmer.

If we compare the expression for the stresslet given by Equation (6) with the squirmer model, we see that these models agree up to $1/r^2$ terms for a much wider range of values of the stirring parameter q . For example, if we allow $|\mathbf{b}|$, the distance between the application of the point forces in the stresslet model, to take values other than the diameter of the sphere, we can obtain agreement for a much wider range of negative values of q . In Fig. 2ci–vi, we further investigate how the choice of stirring parameter, q , affects the flow field. For $q = 0$, the flow field is fore-aft symmetric; as we increase the magnitude of the stirring parameter, a recirculation region appears behind or ahead of the squirmer, depending on the sign of q .

Chemical field

The chemical field around the organism depends on the Péclet number (Pe), the choice of swimming model and the choice of boundary condition. Here, we

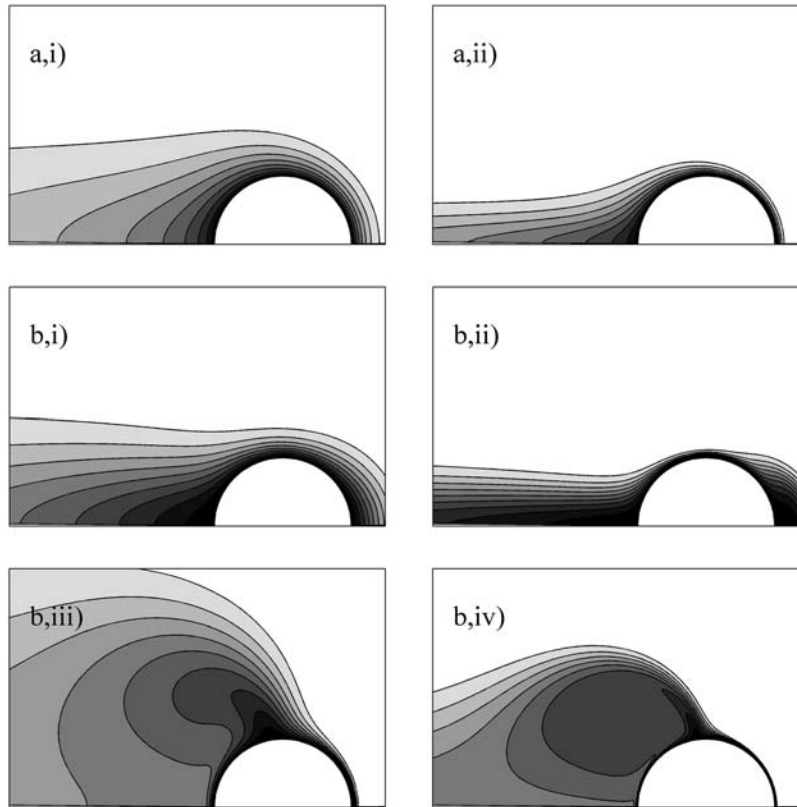


Fig. 3. Near-field chemical concentration with the Dirichlet boundary condition. Contour plot of chemical field surrounding swimmer for a range of Pe and swimming styles: **(a)** towed body for (i) $Pe = 10$ and (ii) $Pe = 100$; **(b)** squirmer for (i) $Pe = 10, q = -2$, (ii) $Pe = 100, q = -2$, (iii) $Pe = 10, q = 10$ and (iv) $Pe = 100, q = 10$. Only half the swimmer is shown as the model assumes symmetric behaviour.

compare how the squirmer model differs from the towed-body model for a range of stirring parameters, q . Concentration contour plots close to the organism for a range of Pe and q for the Dirichlet boundary condition are plotted in Fig. 3. As Pe increases, the diffusion boundary layer shrinks, and the chemicals are confined to a thin layer surrounding the organism except in the trailing wake. With increasing values of the stirring parameter, q , the point at which the concentration boundary layer detaches from the organism moves forwards and, as shown in Fig. 3biii and iv, there is a significant region of elevated concentration surrounding the rear half of the organism. Although the mathematical formalism is identical for both uptake and release of solutes from the swimming organism, we will separate our results to address two classical problems in plankton ecology, i.e. how swimming motions change nutrient uptake and how signal chemicals are spread from a swimming organism. In the first instance, we focus on how nutrient uptake is enhanced due to swimming, i.e. investigate how the Sherwood number is dependent on the swimming speed (as expressed by Pe) and style. This will be done by considering transport-limited (Dirichlet)

boundary conditions at the surface of the organism. In the latter case of chemical exudation, our results will focus on how the chemical wake is dependent on the swimming speed and style. For the problem of chemical exudation, we shall consider both the constant-leakage rate and transport-limited scenarios corresponding to Neumann and Dirichlet boundary conditions, respectively.

Nutrient uptake

When we assume that nutrient uptake is limited by the rate of diffusive transport across the concentration boundary layer, i.e. we impose the Dirichlet boundary condition, introducing fluid motion increases the rate of mass transfer as measured by the Sherwood number. In the basic case of a towed-body model, from Fig. 3ai and ii, we see how increasing the translational speed of the organism through the fluid sharpens chemical gradients near the surface, thus increasing the diffusive flux of chemicals into the organism. This explains why the Sherwood number (Sh) is an increasing function of the Péclet number (Pe), as depicted in Fig. 4. Furthermore,

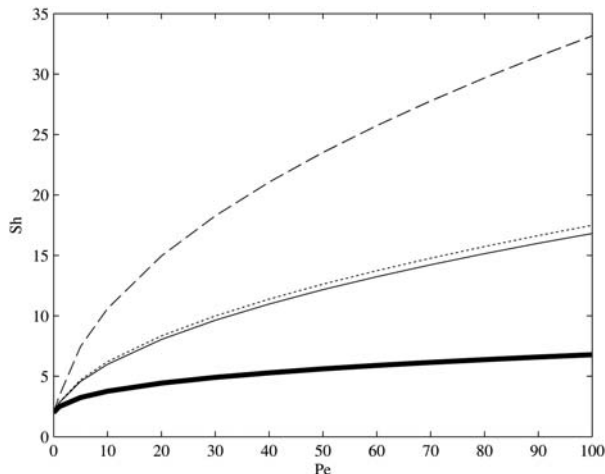


Fig. 4. Enhancement of mass transfer. Plot of the Sherwood number, Sh against Pe for the Dirichlet boundary conditions for different swimmers: thick solid line, towed body; thin solid line, squirmer, $q = 0$; dotted line, squirmer, $|q| = 2$; dashed line, squirmer $|q| = 10$.

the squirmer model introduces additional mixing near the surface of the organism which further enhances mass transfer relative to the towed-body model moving at the same speed. As the stirring parameter, q , is increased, the enhancement of mass transfer is increased further.

Chemical wake

For moderate and large values of Pe , the organism trails a long chemical wake, an example of which is shown in Fig. 5a. This wake may provide important chemical signals, e.g. to mates, and so it is of interest to understand how the shape of the wake is affected by the swimming speed and style of the organism. The wake length as a function of Pe for the towed-body model and the squirmer model for a range of stirring parameters are shown in Fig. 6. The length of the wake is defined as the distance behind the swimmer measured from the centre of the swimmer at which the non-dimensional concentration equals $C = 0.1$. For the Dirichlet boundary condition, where the surface concentration is fixed at $C = 1$ due to transport limitation, this corresponds to the concentration falling to 10% of the value specified at the surface of the organism. In this scenario, where fluid motions enhance the flux of chemicals away from the organism, the length of the chemical wake correspondingly increases for increasing values of Pe . Furthermore, the squirmer model shows a greater enhancement in wake length compared with the towed-body model because of the enhanced transport of chemicals away from the surface (Fig. 6). In contrast, we see that for the Neumann boundary condition, the

length of the chemical wake decreases with increasing Pe (Figs 5b and 6). This can be explained because in this scenario there is a constant-leakage rate of chemical, and so as fluid flow enhances the transport of chemicals away from the surface, the surface concentration is reduced for increasing values of Pe . Because of the reduction in the surface concentration with increasing Pe , we find that the wake length, defined as the distance behind the organism at which the concentration is given by $C = 0.1$ reduces with both increasing Pe and increasing values of q . Furthermore, for sufficiently high values of Pe and q , the surface concentration can drop below $C = 0.1$, and the wake disappears.

Our results show that the chemical wake length is dependent on Pe , i.e. it varies depending on the swimming speed of the organism. This is true even when assuming constant-leakage rate, i.e. taking the Neumann boundary condition. Previous authors, who modelled the organism as a point source emitting chemicals at a fixed rate, showed that the concentration distribution along the centre of the wake is identical to that of a non-moving point source; so that only the width and not the length of the chemical plume is affected by the swimming speed (Bagørien and Kjørboe, 2005). In contrast, by allowing the organism to have a finite size, our model produces a chemical plume with a length that is also dependent on the swimming speed.

DISCUSSION AND CONCLUSIONS

We have shown how the chemical field around swimming plankton depends on swimming speed, style, and the type of boundary conditions imposed on the surface of the organism. We have also shown how the simple squirmer model for a self-propelled swimmer is related to a previously proposed self-consistent model of a swimmer, the stresslet model, and shown how using the squirmer model allows one to examine the properties of chemical transport around a swimming organism.

For the Dirichlet boundary condition, the chemical transport is limited by the rate at which chemicals are transported across the diffusion boundary layer, and so fluid motion around the organism increases the flux of chemicals across the surface, as measured by the Sherwood number, and increases the length of the chemical wake. Furthermore, we have shown that, for a given swimming speed, the self-propelled swimmer can significantly enhance the chemical transport and increase the length of the chemical wake trailing the swimmer. Indeed, our results agree with previous analytic and numerical results showing how at large Péclet

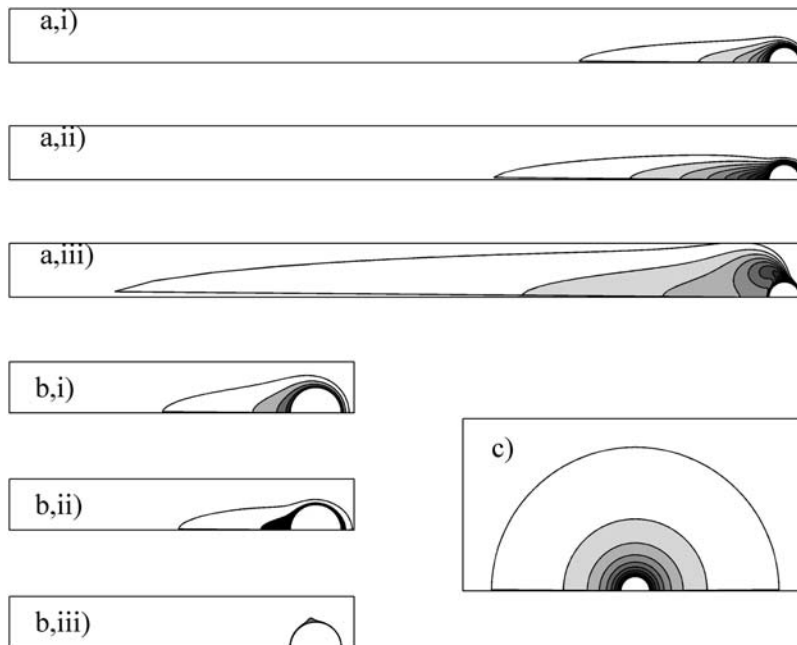


Fig. 5. Chemical wake following swimmer. Contour plot of chemical field surrounding swimmer for $Pe = 10$ for (a) Dirichlet boundary conditions showing long chemical wake, and for (b) Neumann boundary conditions: (i) towed body; (ii) squirmer with $q = -2$; (iii) squirmer with $q = 10$. (c) Chemical field surrounding stationary sphere, $C = 1/r$ for comparison. Contours are drawn every 0.1 from 0.1 through to 1. Only half the swimmer is shown, as the model assumes symmetric behaviour.

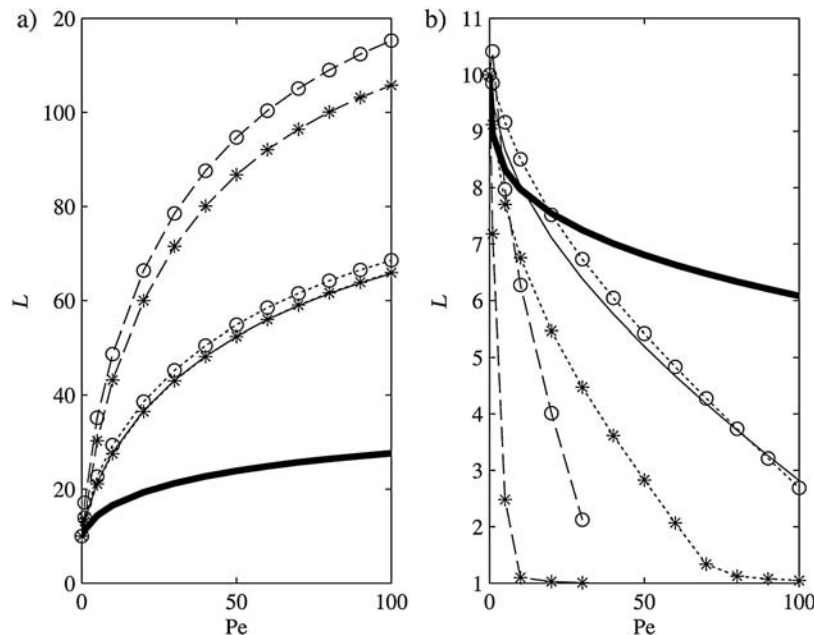


Fig. 6. Plots of wake length, L , against Pe for different swimmers: thick solid line, towed body; thin solid line, squirmer, $q = 0$; dotted line with circles, squirmer, $q = -2$; dotted line with stars, squirmer, $q = 2$; dashed line with circles, squirmer, $q = -10$; dashed line with stars, squirmer, $q = 10$. The length of the wake is defined as being the distance from the swimmer's centre at which the concentration in the wake has decayed to 0.1. (a) The Dirichlet boundary conditions and (b) the Neumann boundary conditions; note the wake is undefined in situations where the surface concentration, C_0 , is less than 0.1.

numbers, Pe , the Sherwood number increases as the square root of Pe for a squirmer rather than as the cube root of Pe for a towed body (Magar *et al.*, 2003).

In contrast, for the Neumann boundary condition, where transport is production limited and there is a fixed flux of chemicals across the surface, we see that

although the fluid motion around the organism transport chemicals away from the surface, this has the effect of decreasing the surface concentration of chemicals and hence decreasing the length of the chemical wake.

The models presented in this paper are relevant to recent discussions regarding the distribution of DMSP surrounding algal cells (Breckels *et al.*, 2010; Strom and Fredrickson, 2010). In particular, Breckels *et al.* (Breckels *et al.*, 2010) calculated the steady concentration field around a stationary DMSP-producing algal cell, which using the results of this paper, could be extended to study motile or sinking cells. A key point in their calculations was the timescale of exudation: the timescale over which a fixed amount of chemical is released will be inversely proportional to the exudation rate and thus significantly affect the (steady) concentration distribution (Strom and Fredrickson, 2010). Furthermore, if chemicals are released rapidly, what may be of more interest is the unsteady solution to the advection-diffusion equation which predicts the transient distribution of the chemical as it is emitted.

We note that the squirmer model presented here is highly idealized, and many plankton will have much more complicated morphologies and swimming patterns. However, simple models can often give useful insights, casting the problem in tractable terms and serving as a useful basis for comparison. Furthermore, recent work on the colonial algae *Volvox* suggests that the squirmer model can be used quite successfully to model real self-propelled organisms (Drescher *et al.*, 2009). Alternative simple models have recently been proposed to represent the motion of uni-flagellated organisms (Langlois *et al.*, 2009). These appear more biologically realistic for plankton propelled by a single flagellum, but are more complex than the model considered in this paper as analytical expressions are not available for the flow field generated by the swimmer. As in this paper, Langlois *et al.* (Langlois *et al.*, 2009) demonstrate that self-propulsion enhances nutrient uptake above the levels predicted for a towed body, although the enhancement is not as significant as the results presented here for the squirmer model. More complex models of the flow field around cilia have also been proposed which consider in detail the near-surface forcing generated by the cilia (Jiang and Paffenhoefer, 2008); it would be interesting to examine whether our results on the chemical field around a very simple swimmer hold for these more complex models of swimmers.

A major simplification in our model has been to assume the organism is neutrally buoyant. As discussed by Jiang *et al.* (Jiang *et al.*, 2002), typically plankton are denser than water and consequently will experience a

net external force acting on them. This is important for hydromechanical signalling, as in the far-field, the flow only decays as $1/r$ rather than $1/r^2$ which is the case for neutrally buoyant, self-propelled models. In the context of mass transfer and chemical wakes, it would therefore be interesting to consider how an external gravitational force affects the local flow field. Another major simplification we have made is to assume the flow field is symmetric; however, many organisms have an asymmetric physiology or swim with asymmetric beat patterns, e.g. which generate helical swimming paths (Crenshaw, 1996). Although our model cannot predict how asymmetries alter the chemical field, it is plausible that such motions induce a circulating component to the flow which may reduce chemical transport at large values of the Péclet number (Karp-Boss *et al.*, 1996).

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