Anisotropic microswimmers in surface gravity waves

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Microswimmers (planktonic microorganisms or artificial active particles) immersed in a fluid interact with the ambient flow, altering their trajectories. By modelling anisotropic microswimmers as spheroidal bodies with an intrinsic swimming velocity that supplements advection and reorientation by the flow, we investigate how shape and swimming affect the trajectories of microswimmers in surface gravity waves. The coupling between flow-induced reorientations and swimming introduces a shape dependency to the vertical transport. We show that each trajectory is bounded by critical planes in the position-orientation phase space that depend only on the shape. We also give explicit solutions to these trajectories and determine whether microswimmers that begin within the water column eventually hit the free surface. We find that it is possible for microswimmers to be initially swimming downwards, but to recover and head back to the surface. For microswimmers that are initially randomly oriented, the fraction that hit the free surface is a strong function of shape and starting depth, and a weak function of swimming speed.

1. Introduction

The interactions between anisotropic microswimmers (or active particles) and an underlying flow field can have interesting consequences for microswimmer transport. In vortex lattice flows, microswimmers can become concentrated at the edges of vortices and escape depending on their shape and swimming speed (Torney & Neufeld 2007), while variations in swimming speed can alter the diffusivity of spherical swimmers (Khurana et al. 2011; Khurana & Ouellette 2012) and induce wildly oscillating transport properties of oblate swimmers (Berman et al. 2021; Berman & Mitchell 2020). Similarly, microswimmer shape and swimming determine whether it can escape an asymmetric vortex (Arguedas-Leiva & Wilczek 2020) or is ejected from a vortical flow (Sokolov & Aranson 2016). The effects of microswimmer shape and swimming on transport persists in turbulent flows, where anisotropic microswimmers can aggregate even in the absence of explicit inertial effects due preferential alignments with the velocity field and the local velocity gradients (Borgnino et al. 2019; Pujara et al. 2018; Zhan et al. 2013).

In nature, microswimmers (e.g., motile plankton) must often navigate through a complex flow environment that includes surface gravity waves. While the transport of passive spherical and anisotropic particles with waves have been previously examined (Bakhoday-Paskyabi 2015; DiBenedetto & Ouellette 2018; DiBenedetto et al. 2018; Eames 2008), here we examine trajectories of active particles.

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in surface gravity waves. Microswimmers are modelled as neutrally buoyant spheroids that swim with a constant velocity along their axis of symmetry that is co-planar with the flow field in progressive surface waves (figure 1).

We show that the system of equations can be reduced to a set of coupled ordinary differential equations (section 2) from which the wave-averaged trajectories of microswimmers can be found using a two-timescale expansion (section 3). We use these to identify regions of phase space in which microswimmers return to the surface and calculate the probability of this return as a function of body shape and starting depth (section 4). The wave-averaged microswimmer dynamics are determined by critical planes in the position-orientation phase space that confine swimmer motion. Within these planes, a microswimmer’s vertical position is coupled to its orientation and swimming, and there exist situations where the microswimmer begins swimming with a component in the downward direction, but recovers back to the surface. The probability of returning to the surface from an initial random orientation is a function of microswimmer shape, but increases monotonically as the starting depth decreases, for all shapes.

2. Model equations

A two-dimensional train of progressive, small-amplitude surface gravity waves travelling in the $x$ direction in deep water is described by

\begin{align}
\eta &= a \cos(kx - \omega t) \\
u_x &= a\omega e^{kz} \cos(kx - \omega t) \\
u_z &= a\omega e^{kz} \sin(kx - \omega t).
\end{align}

Here, $z = \eta$ is the free-surface position, $a$ is the wave amplitude, $k$ is the wavenumber, $\omega$ is the angular frequency, $u = (u_x, u_z)$ gives the fluid velocity field, and $\omega^2 = gk$ is the dispersion relation.

Within this flow field, we model the motion of a small, spheroidal microswimmer that swims at a steady velocity $V_s \mathbf{p}$ using

\begin{align}
\mathbf{v} &= \mathbf{u} + V_s \mathbf{p} \\
\dot{\mathbf{p}} &= \Omega \mathbf{p} + \lambda [S\mathbf{p} - (p^T S \mathbf{p})\mathbf{p}].
\end{align}

The microswimmer velocity $\mathbf{v}$ is taken as the vector sum of the local fluid velocity and its swimming
velocity, where \( \mathbf{p} \) is a unit vector that points along the microswimmers direction of swimming. The microswimmer angular velocity \( \dot{\mathbf{p}} = \frac{dp}{dt} \) is given by Jeffery’s (1922) equation (Eq. (2.2b)), where \( \Omega = \frac{1}{2} [\nabla \mathbf{u} - (\nabla \mathbf{u})^T] \) and \( \mathbf{S} = \frac{1}{2} [\nabla \mathbf{u} + (\nabla \mathbf{u})^T] \) are the local rotation rate and strain rate tensors, respectively. The particle shape is described by its aspect ratio \( \text{AR} \), which is defined to be the ratio of the diameter parallel to the axis of symmetry to the diameter perpendicular to the axis of symmetry. The aspect ratio enters the problem via the eccentricity the diameter parallel to the axis of symmetry to the diameter perpendicular to the axis of symmetry. The particle shape is described by its aspect ratio \( \text{AR} \).

We can simplify Eq. (2.2) by restricting the motion of the microswimmer to be in the two-dimensional plane of the flow field described by Eq. (2.1). To do so, we first note that the flow is irrotational (\( \Omega \equiv 0 \)) and that the strain rate tensor has components

\[
S_{xx} = -S_{zz} = - ka\omega e^{kz} \sin (kx - \omega t) \tag{2.3a}
\]

\[
S_{xz} = \quad S_{zx} = \quad ka\omega e^{kz} \cos (kx - \omega t). \tag{2.3b}
\]

The three components of Eq. (2.2b) are then given by

\[
\lambda^{-1} \mathbf{p}_x = S_{xx} \mathbf{p}_x (1 - (p_x^2 - p_z^2)) + S_{xz} \mathbf{p}_z (1 - 2 p_z^2) \tag{2.4a}
\]

\[
\lambda^{-1} \mathbf{p}_y = -p_y [S_{xx} (p_x^2 - p_z^2) + 2S_{xz} p_x p_z] \tag{2.4b}
\]

\[
\lambda^{-1} \mathbf{p}_z = S_{xz} p_x (1 - 2p_z^2) - S_{xx} p_z (1 + (p_x^2 - p_z^2)). \tag{2.4c}
\]

By restricting the axis of symmetry and the swimming direction to be in \( x-z \) plane, we can use the polar angle \( \phi \) to define the swimming direction

\[
p_x = \sin \phi, \quad p_z = \cos \phi. \tag{2.5}
\]

where \( \phi = 0 \) corresponds to swimming upwards, and \( \phi = \pi/2 \) to the right. Eq. (2.4) can then be reduced to a single equation for \( \phi \):

\[
\lambda^{-1} \dot{\phi} = S_{xx} \sin 2\phi + S_{xz} \cos 2\phi. \tag{2.6}
\]

We now have a dynamical system with 3 dependent variables:

\[
\dot{x} = a \omega e^{kz} \cos (kx - \omega t) + V_x \sin \phi \tag{2.7a}
\]

\[
\dot{z} = a \omega e^{kz} \sin (kx - \omega t) + V_z \cos \phi \tag{2.7b}
\]

\[
\dot{\phi} = \lambda k a \omega e^{kz} [\cos (kx - \omega t) \cos 2\phi - \sin (kx - \omega t) \sin 2\phi] \tag{2.7c}
\]

where \( (x, z) \) is the microswimmer position.

The system described by Eq. (2.7) can be made dimensionless by defining \( t' = \omega t, x' = kx \), where we immediately drop the primes, to give

\[
\dot{x} = \alpha e^{x} \cos (x - t) + \nu \sin \phi \tag{2.8a}
\]

\[
\dot{z} = \alpha e^{x} \sin (x - t) + \nu \cos \phi \tag{2.8b}
\]

\[
\dot{\phi} = \lambda \alpha \sin \phi \cos 2\phi. \tag{2.8c}
\]

Here, we have used the dimensionless groups \( \alpha = ka, \nu = k V_z / \omega \), and \( \lambda = (\text{AR}^2 - 1) / (\text{AR}^2 + 1) \). All variables are dimensionless from this point forth. Without loss of generality we can take \( \nu \geq 0 \), since the microswimmer orientation is captured by \( \phi \). Both \( \alpha \) and \( \nu \) are small and positive, and \( \lambda \in [0, 1] \).
in using the microswimmer model (Eq. (2.2)) we implicitly assume that the relative motion between the microswimmer and the fluid is characterised by a low Reynolds number, which requires that $\nu \ll \alpha$.

3. Two-timescale expansion

The trajectory of a microswimmer in surface waves depends on the interaction between its shape, swimming speed, and wave properties, as well as its initial conditions. Sample trajectories from numerical simulations of Eqs. (2.8) in figure 2 (computed using ode45 in MATLAB) show that a microswimmer that is initially near the free surface can end up back at the free surface, or continue swimming to infinite depth depending upon small changes in its initial orientation. The trajectory is shown in a coordinate system moving with the waves, so that the waves appear frozen and the microswimmer appears to be travelling backwards. The trajectories in figure 2 indicate that the solutions to Eqs. (2.8) consist of fast oscillations at the surface wavelength ($2\pi$ in dimensionless units) superposed with a slower trend at a longer timescale proportional to $1/\nu$. This suggests using a multiple timescale expansion to remove the fast oscillations.

3.1. Solution using two-timescale expansion

We rewrite the solution vector $V = (x \ z \ \phi)^T$ in terms of two timescales:

$$V(t) = V^\epsilon(t,T), \quad T = \varepsilon^2 t,$$

(3.1)
where the dependence on the fast timescale \( t \) is assumed periodic. Since \( \alpha \) and \( \nu \) are small, we express them in terms of a small parameter as \( \alpha \to \varepsilon \alpha, \nu \to \varepsilon^2 \nu \); Eq. (2.8) is then

\[
\begin{align*}
\partial_t x^e + \varepsilon^2 \partial_T x^e &= \varepsilon \alpha \varepsilon^e \cos (x^e - t) + \varepsilon^2 \nu \sin \phi^e \\
\partial_t z^e + \varepsilon^2 \partial_T z^e &= \varepsilon \alpha \varepsilon^e \sin (x^e - t) + \varepsilon^2 \nu \cos \phi^e \\
\partial_t \phi^e + \varepsilon^2 \partial_T \phi^e &= \varepsilon \alpha \varepsilon^e \cos (x^e - t + 2\phi^e).
\end{align*}
\tag{3.2a, b, c}
\]

We now expand the solution vector in the usual manner:

\[ V^e(t, T) = V_0(t, T) + \varepsilon V_1(t, T) + \varepsilon^2 V_2(t, T) + \ldots. \tag{3.3} \]

At order \( \varepsilon^0 \), Eq. (3.2) is simply \( \partial_t x_0 = \partial_t z_0 = \partial_t \phi_0 = 0 \), which indicates that the leading-order quantities are only a function of the slow time \( T \),

\[ x_0 = X(T), \quad z_0 = Z(T), \quad \phi_0 = \Phi(T). \tag{3.4} \]

At order \( \varepsilon^1 \), Eq. (3.2) is

\[
\begin{align*}
\partial_t x_1 &= \alpha \varepsilon^e \cos (X - t) \\
\partial_t z_1 &= \alpha \varepsilon^e \sin (X - t) \\
\partial_t \phi_1 &= \lambda \alpha \varepsilon^e \cos (X - t + 2\Phi).
\end{align*}
\tag{3.5a, b, c}
\]

Notice that the integral from \([0, 2\pi]\) of each right-hand side in Eq. (3.5) vanishes, which is the solvability condition at this order. The unique mean-zero solution to Eq. (3.5) is

\[
\begin{align*}
x_1 &= -\alpha \varepsilon^e \sin (X - t) \\
z_1 &= \alpha \varepsilon^e \cos (X - t) \\
\phi_1 &= -\lambda \alpha \varepsilon^e \sin (X - t + 2\Phi).
\end{align*}
\tag{3.6a, b, c}
\]

At order \( \varepsilon^2 \), Eq. (3.2) is

\[
\begin{align*}
\partial_t x_2 + \partial_T X &= \alpha \varepsilon^e (\cos (X - t) z_1 - \sin(X - t) x_1) + \nu \sin \Phi \\
\partial_t z_2 + \partial_T Z &= \alpha \varepsilon^e (\sin (X - t) z_1 + \cos(X - t) x_1) + \nu \cos \Phi \\
\partial_t \phi_2 + \partial_T \Phi &= \lambda \alpha \varepsilon^e (\cos(X - t + 2\Phi) z_1 - \sin(X - t + 2\Phi) (x_1 + 2\Phi_1)).
\end{align*}
\tag{3.7a, b, c}
\]

At this order there is a nontrivial solvability condition, obtained by averaging Eq. (3.7) over a period:

\[
\begin{align*}
\partial_T X &= \nu \sin \Phi + \alpha^2 \varepsilon^{2e} \\
\partial_T Z &= \nu \cos \Phi \\
\partial_T \Phi &= \lambda \alpha^2 \varepsilon^{2e} (\lambda + \cos 2\Phi).
\end{align*}
\tag{3.8a, b, c}
\]

This is the sought-after governing equations for the slow motion: the final term in Eq. (3.8a) is the Stokes drift. We shall need explicit solution to order \( \varepsilon^2 \) below, so we substitute the solvability condition Eq. (3.8) and solution Eq. (3.6) into Eq. (3.7), and obtain the simple set of equations

\[
\begin{align*}
\partial_t x_2 &= 0, \quad \partial_t z_2 = 0, \quad \partial_t \phi_2 = -\lambda^2 \alpha^2 \varepsilon^{2e} \cos 2(X - t + 2\Phi),
\end{align*}
\tag{3.9}
\]

whose unique mean-zero solution is

\[
\begin{align*}
x_2 &= 0, \quad z_2 = 0, \quad \phi_2 = \frac{1}{2} \lambda^2 \alpha^2 \varepsilon^{2e} \sin 2(X - t + 2\Phi).
\end{align*}
\tag{3.10}
3.2. Initial conditions for wave-averaged equations

Figure 2 shows that solutions to Eqs. (2.8) can be quite sensitive to initial conditions. Indeed, observe that the unaveraged trajectories start at (0, 0), whereas the averaged trajectories start below this point. In order that a solution to the averaged Eqs. (3.8) properly shadow its corresponding trajectory, the initial conditions for the unaveraged variables must be projected appropriately onto the slow variables, as we describe in this section.

The initial conditions for the full solution vector \( \mathbf{V}(t) \) are \( \mathbf{V}(0) = \mathbf{V}^e(0, 0) = (x(0), z(0), \phi(0)) \). From the two-timescale expansion Eq. (3.3) and its solutions (3.4), (3.6) and (3.10), we have

\[
\begin{align*}
x(0) &= X(0) - \epsilon \alpha e^{Z(0)} \sin X(0) + O(\epsilon^3) \quad \text{(3.11a)} \\
z(0) &= Z(0) + \epsilon \alpha e^{Z(0)} \cos X(0) + O(\epsilon^3), \quad \text{(3.11b)} \\
\phi(0) &= \Phi(0) - \epsilon \lambda e^{Z(0)} \sin (X(0) + 2\Phi(0)) \\
&\quad \quad + \frac{1}{2} \epsilon^2 \lambda^2 \alpha^2 e^{2Z(0)} \sin 2(X(0) + 2\Phi(0)) + O(\epsilon^3). \quad \text{(3.11c)}
\end{align*}
\]

We expand \( X(0) = X_0(0) + \epsilon X_1(0) + \ldots \), and similarly for \( Z(0) \) and \( \Phi(0) \), and equate terms at each order to successively solve for the initial conditions for the slow variables in terms of the initial conditions for the unaveraged variables. For instance, at leading order \( X_0(0) = x(0) \), \( Z_0(0) = z(0) \), and at order \( \epsilon \) we have \( X_1(0) = \alpha e^{Z(0)} \sin x(0) \), \( Z_1(0) = -\alpha e^{Z(0)} \cos x(0) \). Following this procedure, we eventually find that given initial conditions \( \mathbf{V}(0) = (x(0), z(0), \phi(0)) \), the initial conditions for the slow variables are

\[
\begin{align*}
X(0) &= x(0) + \epsilon \alpha e^{Z(0)} \sin x(0) + O(\epsilon^3) \quad \text{(3.12a)} \\
Z(0) &= z(0) - \epsilon \alpha e^{Z(0)} \cos x(0) + \epsilon^2 \lambda \alpha e^{Z(0)} \sin (x(0) + 2\phi(0)) + O(\epsilon^3) \quad \text{(3.12b)} \\
\Phi(0) &= \phi(0) + \epsilon \lambda \alpha e^{Z(0)} \sin (x(0) + 2\phi(0)) \\
&\quad \quad + \frac{1}{2} \epsilon^2 \lambda^2 \alpha^2 e^{2Z(0)} \sin 2(x(0) + 2\phi(0)) - 2 \sin 2\phi(0) + O(\epsilon^3). \quad \text{(3.12c)}
\end{align*}
\]

These corrections to the initial condition are small, but they are crucial, particularly when \( \phi(0) \) is near a critical angle \( \phi_{\text{crit}} \) (Sec. 4.1).

4. Analysis of wave-averaged trajectories

4.1. Critical planes

A striking feature of the wave-averaged equation for \( \Phi \) (Eq. (3.8c)) is that there exist critical angles \( \Phi_{\text{crit}} \) such that

\[
\lambda + \cos 2\Phi_{\text{crit}} = 0, \quad \text{(4.1)}
\]

which implies that \( \Phi = \Phi_{\text{crit}} \) for all time. (These critical angles are present even without swimming and were previously observed (DiBenedetto & Ouellette 2018; DiBenedetto et al. 2018).) We let \( \Lambda = \frac{1}{2} \arccos(-\lambda) \), where \( \arccos(x) \in [0, \pi] \) is the principal branch of \( \cos^{-1}x \), so that \( 0 \leq \Lambda \leq \pi/2 \). The four solutions for the critical angle in Eq. (4.1) can be expressed as a vector

\[
\Phi_{\text{crit}}(\lambda) = (\Lambda_1, \Lambda_2, \Lambda_3, \Lambda_4) = (\Lambda, \pi - \Lambda, \pi + \Lambda, 2\pi - \Lambda). \quad \text{(4.2)}
\]

The \( \Lambda_i \) are chosen such that \( \Lambda_i \in [0, 2\pi] \) and \( \Lambda_i \leq \Lambda_{i+1} \). The vector of solutions degenerates to

\[
\begin{align*}
\Phi_{\text{crit}}(-1) &= (0, \pi, \pi, 2\pi), \quad \text{(disc-shaped microswimmer)} \quad \text{(4.3a)} \\
\Phi_{\text{crit}}(+1) &= (\pi/2, \pi/2, 3\pi/2, 3\pi/2), \quad \text{(fibre-shaped microswimmer)} \quad \text{(4.3b)}
\end{align*}
\]
Figure 3: $\Phi$–$Z$ phase portrait for (3.8) for $\alpha = 0.1$ and $\nu = 0.005$, with (a) $\lambda = 0.6$ and (b) $\lambda = -0.6$. The vertical dashed lines indicate the critical angles (4.2). The shaded regions correspond to trajectories that end up at $Z = -\infty$ and the red curves are the bounding lines of these regions (4.9)-(4.12).

which are the only cases with fewer than four distinct solutions. We refer to the planes $\phi = \Phi_{\text{crit}}$ as critical planes within the three-dimensional phase space ($x$, $z$, $\Phi$). The average dynamics cannot cross those planes (at least for $t \leq O(e^{-2})$), so the motion is always confined between two planes, and the four planes delimit four invariant regions in the three-dimensional phase space. Note that solutions to the unaveraged system Eq. (2.8) may momentarily cross the critical planes when the average dynamics are near the boundaries due to the fast timescale oscillations.

4.2. Solutions to the wave-averaged trajectories

Observe that the $\partial_T Z$ and $\partial_T \Phi$ equations in Eqs. (3.8) do not depend on $X$, and so can be solved separately. This is because the problem is periodic in $x$ and Eq. (3.8) constitute the wave-averaged system. It is instructive to plot a phase portrait for the $\Phi$–$Z$ plane, as in figure 3, where the gray regions correspond to swimmers that end up at $Z = -\infty$.

The contour lines in this phase portrait can be solved for explicitly. The ratio $\partial_T Z$ over $\partial_T \Phi$ is

$$\frac{dZ}{d\Phi} = \frac{ve^{-2Z} \cos \Phi}{\lambda \alpha^2 (\cos 2\Phi - \cos 2\Lambda)}$$  \hspace{1cm} (4.4)

where $\cos 2\Lambda = -\lambda$. This can be rewritten as

$$\frac{d(e^{2Z})}{d(\sin \Phi)} = \frac{\nu}{\lambda \alpha^2} \frac{1}{\sin^2 \Lambda - \sin^2 \Phi}.$$  \hspace{1cm} (4.5)

If the initial condition $\Phi_0$ (0 subscripts here indicate initial conditions, not to be confused with the expansion in Sec. 3.2) is such that $|\sin \Phi_0| = \sin \Lambda$, then $\Phi$ is constant according to Eq. (4.2), and we cannot express $Z$ as a function of $\Phi$. This is the origin of the singularity in (4.5), which also corresponds to the critical angles (4.2). We may thus assume that $|\sin \Phi_0| \neq \sin \Lambda$. Eq. (4.5) can then be integrated...
\[ e^{2Z} - e^{2Z_0} = \frac{\nu}{2\lambda \alpha^2 \sin \Lambda} \log \left( \frac{\sin \Lambda + \sin \Phi \sin \Lambda - \sin \Phi_0}{\sin \Lambda - \sin \Phi \sin \Lambda + \sin \Phi_0} \right), \quad (4.6) \]

such that \( Z(\Phi_0) = Z_0 \). The solution (Eq. (4.6)) ceases to exist when \( |\sin \Phi| = \sin \Lambda \): this corresponds to solutions that asymptote to a critical angle.

To find equations for the trajectories that bound the regions where the swimmers end up at \( Z = -\infty \), we first let

\[ \Delta(x) := \tanh \left[ \frac{x \lambda \alpha^2 \nu^{-1} \sin \Lambda}{\sin \Lambda - \sin \Phi_0 \Delta(e^{2Z} - e^{2Z_0}) \sin \Lambda} \right]. \quad (4.7) \]

and solve Eq. (4.6) for \( \sin \Phi_0 \):

\[ \sin \Phi_0 = \frac{\sin \Phi - \sin \Lambda \Delta(e^{2Z} - e^{2Z_0}) \sin \Lambda}{\sin \Lambda - \sin \Phi \Delta(e^{2Z} - e^{2Z_0}) \sin \Lambda}. \quad (4.8) \]

We consider separately the case of positive and negative \( \lambda \).

Positive \( \lambda \): \( 0 < \lambda < 1 \)

To find the bounding curves, we consider final values of \( \Phi \) and \( Z \) in Eq. (4.8), guided by figure 3a. We then find \( \Phi_0 \) by inverting the sine, taking care to use the appropriate solution branch. Setting \( Z \to -\infty \) with \( \Phi = \pi/2 \) in Eq. (4.8) gives the curve bounding the gray region on the left:

\[ \Phi_0^{(\text{left})}(Z_0) = \pi - \arcsin \left( \frac{1 + \sin \Lambda \Delta(e^{2Z_0})}{\sin \Lambda + \Delta(e^{2Z_0}) \sin \Lambda} \right). \quad (4.9) \]

Setting \( Z \to 0 \) with \( \Phi = 3\pi/2 \) in Eq. (4.8) gives the curve bounding the gray region on the right:

\[ \Phi_0^{(\text{right})}(Z_0) = 2\pi - \arcsin \left( \frac{1 + \sin \Lambda \Delta(1 - e^{2Z_0})}{\sin \Lambda + \Delta(1 - e^{2Z_0}) \sin \Lambda} \right). \quad (4.10) \]

Negative \( \lambda \): \( -1 < \lambda < 0 \)

We proceed as for \( \lambda > 0 \), this time guided by figure 3b. Setting \( Z \to 0 \) with \( \Phi = \pi/2 \) in Eq. (4.8) gives

\[ \Phi_0^{(\text{left})}(Z_0) = \arcsin \left( \frac{1 - \sin \Lambda \Delta(1 - e^{2Z_0})}{\sin \Lambda - \Delta(1 - e^{2Z_0}) \sin \Lambda} \right). \quad (4.11) \]

Setting \( Z \to -\infty \) with \( \Phi = 3\pi/2 \) in Eq. (4.8) gives

\[ \Phi_0^{(\text{right})}(Z_0) = \pi + \arcsin \left( \frac{1 - \sin \Lambda \Delta(e^{2Z_0})}{\sin \Lambda + \Delta(e^{2Z_0}) \sin \Lambda} \right). \quad (4.12) \]

According to the bounding curves calculated above, assuming that \( \Phi_0 \) is uniformly distributed in \([0, 2\pi]\), for each starting depth \( Z_0 \) we can find the microswimmer fraction hitting the free surface (FHS)

\[ \text{FHS} = 1 - \frac{\Phi_0^{(\text{right})}(Z_0) - \Phi_0^{(\text{left})}(Z_0)}{2\pi}. \quad (4.13) \]

FHS is a function of shape parameter \( \lambda \) and starting depth \( Z_0 \). The results, plotted in figure 4, show that FHS increases monotonically as the starting depth \( Z_0 \) decreases. Strangely, at the special starting depth of \( Z_0 = -\log \sqrt{2} \approx -0.347 \), exactly half of the swimmers hit the surface regardless of their shape. For spherical swimmers (\( \lambda = 0.5 \)) and fibre-shaped swimmers (\( \lambda = 1 \)), exactly half hit the surface regardless of their starting depth.
Figure 4: The fraction (Eq. (4.13)) of microswimmers that hit the surface as a function of shape parameter \( \lambda \) for different starting depths \( Z_0 \) and uniformly distributed initial orientation \( \Phi_0 \) for \( \alpha = 0.1 \) and \( \nu = 0.005 \).

5. Conclusions

By using a two-timescale expansion, we have derived wave-averaged equations of motion for microswimmers in surface waves. The wave-averaged system reveals that there are critical angles of microswimmer orientation that correspond to wave-induced preferred orientations, and that these are independent of swimming speed and only functions of microswimmer shape. The wave-averaged system decouples the horizontal and vertical motions, with only the vertical component being coupled to the rotational motion. This is because the flow field is periodic in both time and the horizontal direction, and the two-timescale expansion explicitly removes the periodic motions in the slow variables. Additionally, the wave-averaged system shows that microswimmer trajectories are not too sensitive to the precise wave phase of the initial conditions, except when it is near the critical angles.

Our results also show that microswimmers that begin with a component of their swimming velocity in the downward direction can still return to the surface as a result of flow-induced reorientation. This return to the surface is a function of microswimmer shape, starting depth, and swimming speed, but interestingly it is possible for a microswimmer to swim arbitrarily deep and still return to the surface in a very slow process. The fraction of initially randomly oriented swimmers that return to the surface monotonically decreases with depth, with a special depth at which exactly half the swimmers return to the surface irrespective of shape or swimming speed. In general, there is more variability in the fraction hitting the surface for oblate microswimmers compared to prolate ones. For fibre-shaped (infinitely prolate) swimmers, exactly half return to the surface. Swimming speed enters the problem through the \( O(1) \) ratio \( \alpha^2/\nu \), and its effects are weaker compared to starting depth and shape. For swimmers that have an initial downward component of swimming, slower swimming speeds allow flow-induced
reorientations more time to redirect the microswimmers, and hence increase the size of the phase space region where swimmers recover back to the surface. These results are all in purely two-dimensional dynamics where the microswimmer axis is restricted to the flow plane. A full stability analysis of this plane remains to be done, but numerical simulations suggest that it is at least not too unstable.

Overall, our results show that flow-induced reorientations can affect the vertical transport of microswimmers in shape-dependent ways in surface waves. This has consequences for understanding how both natural and artificial swimmers navigate aquatic environments. It would be interesting to examine extensions where the presence of noise (e.g., rotational diffusion) or other reorientation mechanisms (e.g., gyrotaxis) causes deviations from the trajectories obtained here, and alters the ability of microswimmers to reach the surface or to reach large depths.

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