The flow field around a freely swimming copepod in steady motion. Part II: Numerical simulation

HOUHUI JIANG1,4, CHARLES MENEVEAU2,3 AND THOMAS R. OSBORN1,3

1DEPARTMENT OF EARTH AND PLANETARY SCIENCES, 2DEPARTMENT OF MECHANICAL ENGINEERING, 3CENTER FOR ENVIRONMENTAL AND APPLIED FLUID MECHANICS, THE JOHNS HOPKINS UNIVERSITY, BALTIMORE, MD 21218, USA
4CURRENT ADDRESS: MS #9, DEPARTMENT OF APPLIED OCEAN PHYSICS AND ENGINEERING, WOODS HOLE OCEANOGRAPHIC INSTITUTION, WOODS HOLE, MA 02543, USA

INTRODUCTION

In a companion paper (Jiang et al., 2002a), the flow field around a freely swimming copepod in steady motion was studied theoretically by using Stokes flow models, and the relationship between the flow field and the copepod’s swimming behaviour was investigated. The geometry of the flow field varies significantly with different swimming behaviours. When a copepod hovers or swims slowly in the water, the flow geometry is cone-shaped and wide, and a feeding current is generated. When a copepod sinks freely or swims fast, the geometry is not cone-shaped, but cylindrical, narrow and long, and the flow is not like a feeding current. However, the conclusions were made based on the strong simplifications of assuming a spherical body shape and neglecting the inertia effects. Numerical simulations to solve the steady Navier–Stokes equations with a realistic body shape are needed to consider the effects of finite Reynolds number (i.e. including the inertia effects), realistic morphology and body orientation, and to relate
energies and feeding efficiency to the swimming behaviour.

In Jiang et al. (Jiang et al., 2002a), the equations, which couple the Navier–Stokes equations with the dynamic equation for a copepod’s body and describe the flow field around a freely swimming copepod in steady motion, were obtained. The equations include the governing equations:

\[ \mathbf{p} \frac{\partial \mathbf{u}}{\partial t} = -\nabla p + \mu \nabla^2 \mathbf{u} + \mathbf{f} \]  

\[ \nabla \cdot \mathbf{u} = 0 \]  

(1)

(2)

for the quasi-steady flow field, with the no-slip boundary condition on the surface of the copepod’s main body, \( \Omega_{mb} \):

\[ \mathbf{u} = \mathbf{V}_{swimming} \text{ at } \Omega_{mb} \]  

and the boundary condition at infinity:

\[ \mathbf{u} \rightarrow 0, \text{ at infinity} \]  

(3)

(4)

Here, \( \mathbf{V}_{swimming} \) is the swimming velocity of the copepod. In equation (1), \( \mathbf{f} \) represents the force field (force per unit volume) that models the effect of the beating movement of the cephalic appendages. Since the appendages are spatially distributed (ventrally to the copepod), \( \mathbf{f} \) is interpreted as a distributed force field. If the copepod is assumed in a steady motion, i.e. either hovering at a same position (\( \mathbf{V}_{swimming} = 0 \)) or swimming at a constant velocity (\( \mathbf{V}_{swimming} = \text{constant} \)), the integral of \( \mathbf{f} \) can be evaluated from the force-balance of the copepod’s body:

\[ \mathbf{W}_{excess} + \int \mathbf{f} \mathbf{u} \cdot \mathbf{n} \, d\mathbf{S} = 0 \]  

(5)

where \( \mathbf{W}_{excess} \) is the excess weight of the copepod, and \( \mathbf{F} \) is the drag force exerted by the flow field on the copepod’s main body.

In the present work, a numerical method will be used to solve equations (1) to (5) with a realistic body shape of a copepod. The method comes from an improvement of the method used to simulate the flow field around a tethered copepod by Jiang et al. (Jiang et al., 1999).

The configuration of the flow field around a freely swimming copepod is controlled by three factors. The first is the body shape, which determines the stress applied to the water along the body-fluid interface through the no-slip boundary condition. The second factor is the complex motion pattern of the cephalic appendages, which has been simplified in the present work as a distributed force field modelling the effect of the beating movement of the cephalic appendages. The third factor is the motion of the copepod’s main body, including the body orientation, swimming speed and direction, etc. In the present work, a commercially available, state-of-the-art, finite-volume code, FLUENT™ (version 4.5) is used. FLUENT™ supports using curvilinear body-fitted coordinates. By using body-fitted coordinates, a realistic body shape can be smoothly portrayed without the jagged edges that would arise with Cartesian coordinates. 2 FLUENT™ allows the application of forces to any desired finite-volume cells. Thus, the distributed force field modelling the beating movement of the cephalic appendages can be rendered discrete and applied to the small computational cells located near where the appendages are known to exist. 3 FLUENT™ provides a wide variety of boundary-condition options. Among these options, suitable pressure and/or velocity inlet boundary conditions will be chosen on the boundaries of the computational domain, so that the constant swimming motion of a copepod with given body orientations can be simulated in a frame of reference fixed on the copepod’s body. In addition, FLUENT™ reports the drag forces by the water-flow acting on the body. Hence, if only steady motions are considered, finding numerical solutions to the coupling between the force-balance equation of a copepod’s body and the Navier–Stokes equations governing the flow field becomes possible. It has already been demonstrated that FLUENT™ provides accurate predictions of low Reynolds number flows (Jiang et al., 1999).

NUMERICAL METHOD

Model copepod and computational mesh

The body shape of the ‘model copepod’ consists of a prosome, a urosome and two antennules, which is designed after the external morphology of a species of coastal water copepods (i.e. Diaptomus minutus). The dimensions of the body parts are shown in Figure 1, which are in the range of a typical adult female copepod (J. R. Strickler, personal communication). The size and body shape used in the present work is more representative of the size and body shape of a real copepod than that considered in our previous work (Jiang et al., 1999). In the present numerical simulations, the model copepod is not referred to any specific copepod species, and various swimming behaviours will be attributed to this model copepod, only for the purpose of comparison.

A 6 × 6 × 6 cm cubic box is chosen as the computational domain with the model copepod located at the centre of the box (Figure 2a). The centre of the copepod’s ventral-side surface is chosen as the origin of the
Distributed force field and forcing index

Since the beating movement of the cephalic appendages plays a key role in shaping the geometry of the flow field in the vicinity of the appendages, it is crucial to include the effect of the beating movement in the numerical simulation. However, it is difficult to use the curvilinear body-fitted coordinates to depict the morphology and spatial distribution of the force field. Thus, it is necessary to introduce a forcing index to account for the effect of the beating movement on the terminal velocity.

Forced motion

The forcing index is defined as
\[ \vec{\Omega}_{\text{forcing}} = -\vec{g} \times \vec{\Omega}_{\text{model}} \]

where \( \vec{g} \) is the gravity acceleration, \( \vec{\Omega}_{\text{model}} \) is the angular velocity of the appendages, and \( \vec{\Omega}_{\text{forcing}} \) is the forcing index.

Excess density

The excess density \( \rho_{\text{excess}} \) is defined as
\[ \rho_{\text{excess}} = \rho_{\text{model}} - \rho_{\text{water}} \]

where \( \rho_{\text{model}} \) is the density of the copepod and \( \rho_{\text{water}} \) is the density of the surrounding water.

Terminal velocity

The terminal velocity \( V_{\text{terminal}} \) is defined as the velocity at which the net force on the copepod is zero.

\[ V_{\text{terminal}} = \frac{W_{\text{excess}}}{\rho_{\text{water}} g} \]

where \( W_{\text{excess}} \) is the excess weight and \( g \) is the acceleration due to gravity.

Beating movement

The beating movement of the cephalic appendages is modeled by applying a distributed force field to the body-fitted coordinates. The direction of the force field is along the negative z-direction, and the magnitude of the force is determined by the forcing index.

\[ \vec{F}_{\text{forcing}} = \frac{\vec{\Omega}_{\text{forcing}}}{\Delta \tau} \]

where \( \Delta \tau \) is the time step and \( \vec{F}_{\text{forcing}} \) is the force applied to the copepod.

Numerical simulation

The simulated swim data of the copepod is compared with the experimental data of the copepod's swimming. The simulation results show good agreement with the experimental data, indicating that the model is capable of accurately predicting the swimming behavior of the copepod.

Conclusion

The model copepod is designed to study the forces acting on the copepod while swimming. The model is able to accurately predict the terminal velocity and swimming direction of the copepod, and the results are in good agreement with the experimental data. The model can be further refined to include additional factors such as the effect of temperature and salinity on the swimming behavior of the copepod.
Fig. 2. (a) Outline of the cubical box-shaped computational domain with the model copepod located at the center of the box; (b) grid distribution along the grid slice I = 19; (c) magnified view of the grid slice I = 19 focusing on the model copepod.
two cases of swimming upward (Figures 4d and 4e), two
cases of swimming backward (Figures 4f and 4g), and
two cases of swimming forward (Figures 4h and 4i). The
swimming velocity of these swimming cases can be arbi-
trarily chosen. However, in practice, we choose it in
relationship to the terminal velocity of the freely sinking
copepod as shown in Figure 4a. As discussed in detail in
the companion paper (Jiang et al., 2002a), when a
copepod swims at a speed at least several times smaller
than its terminal velocity, the behaviour is termed the
Fig. 4. Schematics of the steady motions, considered in this study, of the model copepod: (a) The copepod sinks along its body axis at a terminal velocity of 4.187 mm s\(^{-1}\) with the anterior pointing upward, and the body axis of the copepod tilts ventrally at an angle of 1.131\(^\circ\); (b) The copepod sinks along its body axis at a terminal velocity of 3.941 mm s\(^{-1}\) with the anterior pointing downward, and the body axis tilts dorsally at an angle of 0.964\(^\circ\); (c) The copepod hovers (like a helicopter) in the water with the anterior pointing upward; A distributed force field of forcing index \(\phi = 2.304\) is applied to the water ventrally adjacent to the copepod, representing the effect of the beating movement of the cephalic appendages, and the body axis tilts ventrally at an angle of 2.242\(^\circ\); (d) The copepod swims upward vertically at a speed of 1.047 mm s\(^{-1}\) with the anterior pointing upward, the body axis tilts ventrally at an angle of 1.603\(^\circ\), and \(\phi = 2.537\); (e) The copepod swims upward along its body axis at a speed of 4.187 mm s\(^{-1}\) with the anterior pointing upward, the body axis tilts ventrally at an angle of 4.666\(^\circ\), and \(\phi = 4.044\); (f) The copepod swims backward at a speed of 1.047 mm s\(^{-1}\) with the anterior pointing upward, the body axis tilts dorsally at an angle of 5.554\(^\circ\), and \(\phi = 2.256\); (g) The copepod swims backward at a speed of 4.187 mm s\(^{-1}\) with the anterior pointing upward, the body axis tilts dorsally at an angle of 56.269\(^\circ\), and \(\phi = 2.821\); (h) The copepod swims forward at a speed of 1.047 mm s\(^{-1}\) with the anterior pointing upward, the body axis tilts ventrally at an angle of 9.558\(^\circ\), and \(\phi = 2.347\); (i) The copepod swims forward at a speed of 4.187 mm s\(^{-1}\) with the anterior pointing upward, the body axis tilts ventrally at an angle of 62.098\(^\circ\), and \(\phi = 3.141\).
slow-swimming behaviour. When a copepod swims at a speed equal to or greater than its terminal velocity, the behaviour is termed the fast-swimming behaviour. Here, a speed of 1.047 mm s\(^{-1}\) (i.e. \(V_{\text{terminal}} = 8.4\times10^{-8}\)) is chosen for the slow-swimming cases (as shown in Figures 4d, 4f and 4i); a speed of 4.187 mm s\(^{-1}\) (i.e. \(V_{\text{terminal}} = 8.4\times10^{-8}\)) is chosen for the fast-swimming cases (as shown in Figures 1e, 4g and 4h).

For a prescribed swimming speed, we must find the forcing index \(f\) and body orientation for which the force-balance is satisfied. For this purpose, for each speed the \texttt{FLUENT™} simulations are repeated for several body orientation angles \((\theta)\) and forcing indices \((f)\). Given the swimming speed, direction and body orientation of the model copepod and the magnitude of the forcing index \(f\) (so that the distributed force field is fully prescribed), the flow field around the copepod is calculated by solving equations (1) and (2) numerically with boundary conditions (3) and (4) using \texttt{FLUENT™}. Then the drag force \(F\) exerted by the computed flow field on the copepod’s body is calculated from \texttt{FLUENT™}. On the other hand, when the model copepod is applying a distributed force field with a forcing index \(f\) to the adjacent water (so that the total force applied to the water \(\mathbf{F} = -f \times 8.4 \times 10^{-8} \mathbf{k} \text{ N}\), the copepod itself simultaneously receives a reaction force from the water. The reaction force, which is actually the propulsion, is \(\mathbf{F}^r = f \times 8.4 \times 10^{-8} \mathbf{k} \text{ N}\) (in positive \(z\)-direction). When the propulsion \(F^r\) balances the excess weight \(W\), and drag force \(F\), the copepod is in a steady motion. By interpolation, we find the pair \((f, \theta)\) for which the force balance is satisfied. For more details, see Appendices A2–A1.

Finally, the flow field is computed for each case, using a frame of reference fixed on the model copepod (so that the flow field is steady). Then the drag force acting on the copepod’s body by the flow field is calculated from \texttt{FLUENT™} for each case. It is shown that the force-balance equation (5) is satisfied almost exactly in each case [with only a very small error, see Appendix 2 in Jiang, 2000c]. This indicates that the model copepod is a self-propelled body in the present work.

Owing to its complexity, we cannot deal with the balance of torques on the model copepod. We simply assume that choosing a suitable centre of mass relative to centre of volume enforces the torque balance. Note that in most situations centre of mass is not identical to centre of volume.

**NUMERICAL RESULTS**

**Flow geometry**

Particle tracking is used to construct the streamtube through the capture area of a copepod in order to visualize the computed flow field around the copepod. [The capture area of a copepod was defined previously (Strickler, 1985.)] Since in the \texttt{FLUENT™} simulations the frame of reference is fixed on the model copepod, the velocity field \(\mathbf{u}\) is steady and hence the fluid particle trajectory coincides with the streamline passing through a same position in the flow field. Based on the velocity field \(\mathbf{u}(x)\) computed from the \texttt{FLUENT™} simulations, fluid particle locations \(x(t)\) are determined by integrating numerically

\[
\frac{dx}{dt} = \mathbf{u}(x) \tag{7}
\]

The time integration scheme for equation (7) is a fourth-order Runge–Kutta method. At each time step velocity needs to be interpolated onto the current particle location. Since our \texttt{FLUENT™} simulations are based on a body-fitted coordinate system with non-rectangular cells, difficulties arise for the interpolation. In order to cope with the difficulties, we use a method for particle location and field interpolation on complex, three-dimensional computational meshes (Oliveira et al., 1997). The method is based on an iterative procedure that uses transformed coordinates defined by tri-linear isoparametric functions. For the particle tracking, 40 points located on an ellipse enclosing the capture area are chosen as the initial condition for the numerical integration. The ellipse is centred at \((0.22 \text{ mm}, 0.0, 0.16 \text{ mm})\), with a semi-major axis of 0.3 mm in the \(y\)-direction and a semi-minor axis of 0.14 mm in the \(x\)-direction. Then, backward integration of equation (7) in time determines the fluid particle trajectories leading to the capture area, i.e. we determine from where the fluid particles that end up in the capture area have come. For the present work, the time integration is from 0 s to \(-4.0\) s. The union of such trajectories forms the streamtube.

Streamtube plots are shown in Figures 5–9 for the nine cases considered in the present work. The streamtubes are calculated as a three-dimensional structure, however a two-dimensional lateral view is enough to show the difference in the flow geometry resulting from variations in the swimming behaviour, velocity and body orientation. Generally, in a frame of reference fixed on the copepod’s body, the streamtube through the capture area of a fast-sinking copepod is very thin and long and comes from below the copepod’s body (Figures 5a and 5b). The streamtube through the capture area of a hovering or slow-swimming copepod is cone-shaped and wide (Figures 6, 7a, 8a and 9a), while the streamtube through the capture area of a fast-swimming copepod is not cone-shaped but cylindrical, narrow and long (Figures 7b, 8b and 9b). In addition, the orientation of the streamtube is...
closely correlated to the body orientation and moving direction of the copepod.

**Velocity field**

Velocity vector plots along the median plane of a model copepod are shown in Figure 10. Here, the frame of reference is fixed on the copepod, so that the flow velocity reaches zero at the body surface. For a free-sinking copepod, the flow is coming from below its body. Since the copepod stops beating its cephalic appendages no velocity maximum is observed in the region near the body (Figure 10a). While a hovering or free-swimming copepod has to beat its cephalic appendages to counterbalance its excess weight as well as the drag force by water (i.e. to self-propel its body), so that there exist areas of high velocity (much larger than the swimming velocity) located ventrally (or anterior-ventrally) to and a short distance away from the body surface (Figures 10b, 10c, and 10d). These high velocity areas extend for about a body-length away from the copepod. Generally these results are comparable to the observations on freely swimming copepods by Bundy and Paffenhöfer (Bundy and Paffenhöfer, 1996). By comparing (for example) Figure 10b with Figure 10c, one can see that the spatial configuration of the velocity field around a slow-swimming copepod is quite similar to that around a hovering copepod. The velocity maximum of the two cases, swimming backward slowly and hovering, is similar (9.440 mm s\(^{-1}\) versus 9.640 mm s\(^{-1}\)). In contrast, the spatial configuration of the velocity field around a copepod swimming backward fast is different in that the velocity maximum is 11.790 mm s\(^{-1}\) and that there is a much stronger incoming flow around the body, especially around the antennules (Figure 10d). It is also shown that there exists some asymmetry in each flow field, which was not found in the companion paper (Jiang et al., 2002a). The anterior-posterior asymmetry is due to the finite Reynolds number in the numerical simulations and anterior-posterior asymmetry in the body shape. The dorsal-ventral asymmetry is mainly due to the dorso-ventrally uneven distribution of the
cephalic appendages and partially due to the dorsal-ventral asymmetry in the body shape. Furthermore, it is shown that the flow field is aligned with the body orientation and shaped internally by the body shape. These are the reasons that we need to solve the Navier–Stokes equations numerically with a realistic body shape.

Viscous dissipation rate

Any shearing motion in the fluid is inevitably accompanied by a one-way transfer of energy from the mechanical agencies causing the motion to internal energy of the fluid (Batchelor, 1967). The rate of this transfer of energy per unit mass of fluid is called the viscous dissipation rate defined for incompressible fluid as

$$\phi = \frac{2}{\rho} \mathbf{S} : \mathbf{S}$$

where

$$S_{ij} = \frac{1}{2} \left( \frac{\partial u_i}{\partial x_j} + \frac{\partial u_j}{\partial x_i} \right)$$

stands for the components of the strain rate tensor $\mathbf{S}$, and

Fig. 7. Lateral view of the streamtube through the capture area of a model copepod swimming upward. In (a), the copepod is swimming upward in positive $z$-direction at a speed of 1.047 mm s$^{-1}$. In (b), the copepod is swimming upward (along its body axis) at a speed of 4.187 mm s$^{-1}$. Note that the frame of reference is fixed on the copepod. The dashed line is the streamline passing through the centre of the capture area.

Fig. 8. Lateral view of the streamtube through the capture area of a model copepod swimming backward in negative $x$-direction. In (a), the copepod is swimming backwards at a speed of 1.047 mm s$^{-1}$. In (b), the copepod is swimming at a speed of 4.187 mm s$^{-1}$. Note that the frame of reference is fixed on the copepod. The dashed line is the streamline passing through the centre of the capture area.
The summation convention applies. The indicial notations are adopted with the $xyz$ axis referred to as $x_i$, $i = 1, 2, 3$. For a given viscosity, there is a one-to-one relation from the flow deformation rate $S^*$ to the viscous dissipation rate $\phi$.

$$\phi = \frac{2}{\rho} \left( \frac{\partial u_i}{\partial x_i} \right)^2$$

Neither the deformation rate $S^*$ nor the viscous dissipation rate $\phi$ depends on directional information, i.e. they do not change under any transformation of coordinate systems. Thus, they are both a useful measure of the magnitude of flow deformation. Usually the deformation rate $S^*$ is thought to be the hydrodynamic signal most likely detected by a copepod using mechanoreception. In this work, we choose to use the dissipation $\phi$ instead of the deformation $S^*$ so that it can be compared to the background dissipation associated with oceanic turbulence. In terms of Cartesian components, the viscous dissipation rate can be calculated according to

$$\phi = \frac{1}{2} \left( \frac{\partial u_i}{\partial x_j} \right)^2 + \frac{1}{2} \left( \frac{\partial v_i}{\partial y_j} \right)^2 + \frac{1}{2} \left( \frac{\partial w_i}{\partial z_j} \right)^2$$

where $(u, v, w)$ are the velocity components computed from the FLUENT™ simulations.

For the present work, the viscous dissipation rates are calculated on the plane 1 mm below the antennules of a model copepod sinking freely with the anterior pointing downward and the contour plot of the viscous dissipation rates shown in Figure 11a. For the hovering case and the active-swimming cases, in which a model copepod positions with the anterior pointing upward, the viscous dissipation rates are calculated on the plane 1 mm above the antennules. Figures 11b, 12a and 12b respectively show the contour plot for a model copepod hovering, swimming slowly or swimming fast. In order to be compared to the coastal oceanic energy dissipation rates in a turbulent regime, which are typically in the range $10^{-7} - 10^{-5}$ m$^2$ s$^{-3}$ (Gargett et al., 1984), the viscous dissipation rates calculated for each case are normalized by $10^{-7}$ m$^2$ s$^{-3}$, the lower bound of the coastal oceanic energy dissipation rates in a turbulent regime.

**Power, volumetric flux and relative capture volume**

The power $W_i$ applied by a model copepod to generate the flow field around itself is estimated using the formula

$$W = \sum_i f_i \cdot v_i$$

where the sum is taken over the $N$ cells on which the distributed force is applied, $\mathbf{f}_i$ is the force applied on the $i$th cell and $\mathbf{v}_i$ is the velocity at the centre of the $i$th cell. Here, the velocity is measured in a frame of reference fixed on the model copepod.
The volumetric flux $Q$ through the capture area of a model copepod is calculated as

$$ Q = \oint_{\mathbf{A}} \mathbf{v} \cdot d\mathbf{A} $$

(13)

where $\mathbf{A}$ is the capture area and $\mathbf{v}$ is the flow velocity relative to the copepod. For simplicity of the numerical integration, a rectangular region is chosen for the capture area. The area is 0.28 mm in the $x$-direction and 0.6 mm in the $y$-direction, centred at the point (0.22 mm, 0, 0.16 mm) in ($s$, $z$), the FLUENT frame of reference.

In a specified period of time ($T$), the volume of the water passing through the capture area is defined as the relative capture volume by the copepod for the period of time $T$ and calculated as

$$ Q_{\text{capture}} = T \int_0^T \mathbf{v} \cdot d\mathbf{A} $$

(14)
based on the volumetric flux $Q$ calculated from (13).

The second column of Table I lists the magnitudes of the power $W$ that a model copepod invests in generating the flow field around its body, for the nine steady motions. The magnitudes have been calculated according to equation (12). Also, the flow-induced volumetric flux $Q$ through the capture area and the relative capture volume $H$ have been calculated according to equations (13) and (14) and tabulated in Table I for the nine steady motions. In order to examine the feeding efficiency, we have calculated the magnitudes of $|Q/W|$ and listed them in the fifth column of Table I.

**DISCUSSION**

**Swimming behaviour and flow geometry**

Our results from the direct numerical simulations confirm the trends observed with the Stokes flow models presented in the companion paper (Jiang et al., 2002a) and show that the geometry of the flow field around a freely swimming copepod varies significantly with different swimming behaviours. Comparing the streamlines obtained from the Stokes flow models in Jiang et al. (Jiang et al., 2002a) with those from the direct numerical simulations in this paper (e.g. comparing Figure 7a in Jiang et al., 2002a with Figure 9a in this paper), one can see that the theoretical analysis using the Stokes flow models is actually quite good and can give much insight for general qualitative...
trends. The streamtube associated with a copepod swimming slowly (i.e. swimming at a speed at least several times smaller than the terminal velocity of the copepod, termed the slow-swimming behaviour) resembles the streamtube of a copepod hovering in the water. In both situations, the cone-shaped and wide streamtube transports water to the capture area of the copepod, and the copepod generates a feeding current (Figures 6, 7a, 8a and 9a). Conversely, when a copepod swims at a speed equal to or greater than the terminal velocity (termed the fast-swimming behaviour), the streamtube through the capture area is cylindrical, long and narrow and the generated flow field is not a feeding current (Figures 7b, 8b and 9b). In addition, when a copepod sinks freely, the flow comes from below relative to the copepod and the streamtube through the capture area is much narrower and longer than hovering and swimming slowly, but shorter than swimming fast (see Figures 5a and 5b). Again, the flow field around a free-sinking copepod is not like a feeding current.

The results suggest that the ecological functions of the flow field generated by a free-swimming copepod are different for different swimming behaviours. This probably explains why calanoid copepods exhibit a wide range of variable swimming behaviours. For a 'typical' feeding current copepod like *Eucalanus crassus* or *Paracalanus parvus*, the copepod adopts the slow-swimming behaviour (including the behaviour of hovering) to generate a cone-shaped and wide feeding current to transport food particles to the capture area, which benefits the suspension feeding of the copepod. Also, the feeding current probably enables the copepod to use chemoreception to detect in advance an algal particle entrained into the feeding current (Strickler,
A numerical study to compare copepods’ chemoreception ability associated with different swimming behaviours is presented in Jiang et al. (Jiang et al., 2002b). On the other hand, that a copepod adopts a fast-swimming behaviour and therefore generates a flow field around its body like those shown in Figures 7b, 8b and 9b is not because the copepod wants to transport water to its capture area. Actually, the fast-swimming behaviour enables a copepod to generate a flow field with strong flow rate and shear around the antennules of the copepod [see Figure 10d in this paper and Figure 10b in (Jiang et al., 2002a)], with which the copepod can use mechanoreception to detect inert particles (Bundy et al., 1998). Also, the fast-swimming behaviour enables a copepod to detect and capture moving prey located outside the influence of the feeding current (Kerfoot, 1978; Jonsson and Tiselius, 1990).

Swimming behaviour and body orientation

In the present work, the numerical methods for determining the steady motions of the model copepod have been successfully developed [see Appendices for detail]. The methods clearly show that given the swimming velocity (magnitude and direction) and the general pointing direction of the anterior, the tilting angle of the body axis against the vertical axis, i.e. the angle \( \theta \) shown in Figure 4, will be determined uniquely by solving equations (1) to (5). The practicability of the methods actually confirms that the body orientation and swimming velocity associated with a swimming behaviour are determined by the combined action of forces: gravity, buoyancy, thrust and drag [see also (Strickler, 1982)]. Our results show that the tilting angle is much larger for a fast-swimming copepod than for a hovering, slow-swimming or free-sinking copepod and that the body orientation is closely correlated to the swimming behaviour. When a copepod hovers, swims slowly or sinks freely, its body axis is prone to be aligned with the vertical direction, while for a fast-swimming copepod its body axis is prone to be aligned with the swimming direction. However, the methods developed in the present work do not consider the balance of torques associated with the forces, and the body shape and excess density are given parameters. If all these parameters are considered and varied, it is expected that the body orientation will depend on the swimming behaviour, morphology (especially the distribution of the cephalic appendages relative to the main body) and excess density, as well as the locations of

<table>
<thead>
<tr>
<th>Steady motion states</th>
<th>Power ( (\text{W, watt}) )</th>
<th>Volumetric flux ( (Q, \text{mm}^3 \text{s}^{-1}) )</th>
<th>Relative capture volume in 4.0 s ( (\text{mm}^3 \text{s}^{-1} \text{W}^{-1}) )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Freely sinking with anterior pointing upward</td>
<td>0</td>
<td>+0.102</td>
<td>0.408</td>
</tr>
<tr>
<td>Freely sinking with anterior pointing downward</td>
<td>0</td>
<td>+0.095</td>
<td>0.390</td>
</tr>
<tr>
<td>Hovering in the water</td>
<td>2.03 \times 10^{-9}</td>
<td>-1.87</td>
<td>7.48</td>
</tr>
<tr>
<td>Upward swimming at a speed of 1.047 mm s(^{-1})</td>
<td>2.44 \times 10^{-9}</td>
<td>-2.05</td>
<td>8.20</td>
</tr>
<tr>
<td>Upward swimming at a speed of 4.187 mm s(^{-1})</td>
<td>5.84 \times 10^{-9}</td>
<td>-3.05</td>
<td>12.2</td>
</tr>
<tr>
<td>Backward swimming at a speed of 1.047 mm s(^{-1})</td>
<td>1.95 \times 10^{-9}</td>
<td>-1.83</td>
<td>7.32</td>
</tr>
<tr>
<td>Backward swimming at a speed of 4.187 mm s(^{-1})</td>
<td>2.99 \times 10^{-9}</td>
<td>-2.26</td>
<td>9.04</td>
</tr>
<tr>
<td>Forward swimming at a speed of 1.047 mm s(^{-1})</td>
<td>2.11 \times 10^{-9}</td>
<td>-1.90</td>
<td>7.60</td>
</tr>
<tr>
<td>Forward swimming at a speed of 4.187 mm s(^{-1})</td>
<td>3.71 \times 10^{-9}</td>
<td>-2.51</td>
<td>10.0</td>
</tr>
</tbody>
</table>

For the hovering case and the active-swimming cases, the negative sign of volumetric flux indicates the flux is in the anterior-posterior direction. For the freely sinking case with the anterior pointing upward, the positive sign of volumetric flux indicates the flux is in the posterior-anterior direction. For the freely sinking case with the anterior pointing downward, the positive sign of volumetric flux indicates the flux is in the anterior-posterior direction.
centration of mass and centre of volume and will be species-

specific and stages-specific, which is consistent with the
observations on the motion behaviour of nauplii and early
copepodid stages of marine planktonic copepods by
Paffenhofer et al. (Paffenhofer et al., 1996).

Swimming behaviour and hydrodynamic conspicuousness

The general swimming locomotion of individual zoo-

plankton species can produce varying degrees of hydro-

dynamic conspicuousness (Brooks, 1968; Zaret, 1980).

Hydrodynamically conspicuous structures, such as feed-

currents, wakes and vibrations, may be perceived by both

prey and predators of the individual zooplankton gener-

ating the structures (Yen and Strickler, 1996). Thus, there

are at least two types of hydrodynamic conspicuousness:

one is to prey, and the other is to predators. Here, the

viscous dissipation rate fields calculated for copepods

with different swimming behaviours will be used to quan-

tify the hydrodynamic conspicuousness, both to prey and to

predators, for different swimming behaviours. For this

purpose, a threshold in the viscous dissipation rate (or flow

deformation) is needed to set the lowest level of hydro-

dynamic conspicuousness.

There is a large amount of literature on the detection

of prey (mostly copepod nauplii) of the deformation rate

inherent in copepod feeding currents (Fields and Yen,

1996, 1997; Vatsalu et al., 1998; Kienboe et al., 1999).

Many of these studies give measures of the threshold

deformation rate that elicits a prey escape. However, the

threshold deformation rate varies between species and

between studies. Above all, habituation to turbulent con-

ditions has been observed (Hwang and Strickler, 1994).

Thus, we may not be able to use these estimated threshold

deformation rates to set the lowest lever of hydrodynamic

conspicuousness. And all these estimates [ranging from

0.5 to 5 s−1, see (Kiørboe et al., 1999)] are larger than the

fluid deformation rates due to the weakest oceanic tur-

bulence (i.e. with energy dissipation rates of 10−7 m2s−3).

For ρ = 1.03 × 103 kg m−3 (density of seawater) and μ =

1.390 × 10−5 kg m−1 s−1 (dynamic viscosity of seawater),

simple algebra from equation (10) gives the fluid de-

formation rate (S) of 0.2 s−1 due to the oceanic turbulence

energy dissipation rate (Ω) of 10−7 m2 s−3. A necessary

condition for detection and escape of prey is that the

copred-generated viscous dissipation should exceed the

background turbulent energy dissipation. Thus, we use

10−7 m2 s−3, a reasonable lower bound of the coastal

oceanic energy dissipation rates in a turbulent regime to

set the lowest lever of hydrodynamic conspicuousness.

In practice, we calculate the viscous dissipation rates

along a certain plane in the flow field for each swimming

behaviour and draw the contour plots of the calculated

viscous dissipation rates normalized by 10−7 m2 s−3

(Figures 11 and 12). Such a plane is selected because the

food particles (prey) must first pass through this plane

before arriving at the capture area of the copepod (see

the upper panels in Figures 11 and 12). In order to compare

the hydrodynamic conspicuousness among different

swimming behaviours, we quantify the spatial extent of

the region on the plane (termed the detectable region) in

which the viscous dissipation rates exceed the background

turbulent energy dissipation rates, i.e. the region enclosed

by the contour line of unity. As can be seen in Figures 11b

and 12a the detectable region is very small for a hovering

or slow-swimming copepod, with a spatial extent less than

4 × 5 mm, i.e. about 3 × 4 body-lengths. Conversely, the
detectable region for a free-sinking or fast-swimming
copepod is very large (Figures 11a and 12b). Generally
speaking, a fast-swimming or free-sinking copepod may be

hydrodynamically more conspicuous to planktivores than

a hovering or slow-swimming copepod, provided that the

planktivores use the ‘searching-image’ based on prey

motion to search for prey (Zaret, 1980). It is more com-

plicated for the situations when prey perceives copepods.

Our results show that the flow field around a free-sinking

copepod is hydrodynamically more conspicuous than that

around a hovering or slow-swimming copepod, in terms

of the viscous dissipation rate (or flow deformation rate).

However, observations showed that when Acartia tonsa

sinks freely, the copepod can perceive prey (ciliates) which

itself can perceive a moving predator, while the ciliates

cannot perceive the free-sinking copepod; but the ciliates

can perceive the feeding current of a calanoid and there-

therefore jump away (G-A. Paffenhofer, personal commu-

nication). The explanation for this conflict is that the ciliates

may actually detect the hydrodynamic signal due to the
time-dependent components of the beating movement of

the ephippial appendages, Acartia tonsa when sinking is com-

pletely motionless and therefore does not generate a time-

dependent signal. Even when they can sense the flow

deformation due to the free-sinking motion of A. tonsa, the
ciliates probably cannot distinguish between a motionless

free-sinking A. tonsa and a big free-sinking particle. In con-

trast, a feeding-current-generating copepod generates a

time-dependent signal, which may be detected by the

ciliates. [However, in the present numerical simulations

the time-dependent components are neglected due to

their fast spatial decay; see the analysis in (Jiang et al.,

2002a)]. Observations also show that a fast-swimming

copepod is able to approach prey more closely than a

feeding-current generating copepod (Tiselius and

Jonsson, 1990). One of the reasons for this is that there is

a region of low flow deformations directly ahead of a fast-

swimming copepod (Figure 12b), if the copepod orien-

tates itself well towards the prey, the prey may not be able
to detect the approaching copepod. The other reason, and probably the most relevant, is that the copepod is able to outrun the prey. On the other hand, for a hovering or slow-swimming copepod, even the detectable region is small (as shown in Figures 11b and 12a), if the copepod cannot outrun an escaping prey that has powerful escape capabilities, it will not capture the prey. But, the mechanical signal generated by an escaping prey can be detected by a copepod using mechanoreception; if the copepod has the ability to respond to the signal by jumping towards the prey, the prey may be captured (Yen and Strickler, 1996). Some omnivorous species such as Diaptomus sicilis can combine bouts of slow swimming (including the behaviour of hovering) with intermittent hops, so that it can feed on non-motile prey or prey with limited escape capabilities during slow swimming and capture motile prey with well-developed escape capabilities by hopping (Bundy et al., 2002a)."}

Swimming behaviour and energetics, feeding efficiency

Our results of the power applied by a free-swimming model copepod to generate the flow field around itself (the second column of Table I) are of the same order of magnitude as the estimate by Yen et al. (Yen et al., 1991) of the viscous energy dissipation per Euchaeta rimana feeding current ($0.93 \times 10^{-9}$ watt). The differences between our results and their estimate may be due to the differences in the excess weight, body size and shape, swimming speed and distribution of the cephalic appendages between our model copepod and E. rimana. In Table I, the relative capture volume by a free-swimming copepod is shown to be much less than that by a copepod hovering in the water or swimming actively through the water. This indicates that the beating movement of the cephalic appendages contributes to most of the relative capture volume by a copepod. For the cases of hovering and swimming slowly, it can be seen that the values of the relative capture volume are quite comparable between each other. This is because for swimming slowly or hovering the volumetric flux through a copepod’s capture area is mainly due to the requirement to counterbalance the excess weight [as pointed out in (Jiang et al., 2002a)]. Also, it can be seen that the relative capture volumes for fast-swimming cases are significantly larger than those for the hovering and slow-swimming cases. Here, increases in the relative capture volume are due to the body orientation adopted by the fast-swimming copepods. When a copepod swims fast, it inclines its body axis with the swimming direction (see Figures 4g and 4i for the backward and forward swimming cases). Thus, the swimming direction is perpendicular or near perpendicular to the capture area. In these situations, swimming contributes significantly to the volumetric flux through the capture area. In contrast, when a copepod swims slowly, the body of the copepod is almost perpendicular to the swimming direction and hence the swimming direction is parallel to the capture area (see Figures 4f and 4h for the backward and forward swimming cases). In these situations, swimming contributes little to the volumetric flux through the capture area. Our results from the numerical simulations do not confirm the results from a simple theoretical analysis (Tiselius and Jonsson, 1990) which stated that a stationary copepod should do 50% better than a swimming one (in terms of clearance). Instead, our results (column 4 in Table I) show that a hovering or slow-swimming copepod scans less water volume than a fast-swimming copepod in a same period of time. Also, the conclusion that being stationary would be more efficient in terms of water flow per force than a swimming copepod is not confirmed. Simple calculations from our results show that $|Q_{fi}|$ is 0.812 $\text{mm}^3\text{s}^{-1}$ for a hovering copepod and 0.799 $\text{mm}^3\text{s}^{-1}$ for a forward-swimming copepod at a swimming velocity of 4.187 $\text{mm}\text{s}^{-1}$. Instead, our results (column 5 in Table I) show that the behaviour of hovering or swimming slowly is more energetically efficient in terms of relative capture volume per energy expended than the behaviour of swimming fast. That is to say, for the same amount of energy expended, a hovering or slow-swimming copepod is able to scan more water than a fast-swimming one. That our results are different from the previous work is because in the present work freely swimming copepods were considered to be self-propelled bodies [for the difference between a self-propelled body model and a towed body model, see the analysis in (Jiang et al., 2002a)] and also because the present numerical simulations have the ability to include the effects of body orientation. We point out that modeling freely swimming copepods as self-propelled bodies is imperative to correctly calculating the capture volume and understanding the efficiency of capture per unit of energy expended.

Also, the benefit of swimming slowly or hovering can be seen by comparing the energy gained in feeding to that expended in generating the flow and motion. The energy budget of a copepod requires

$$\Lambda \cdot E \cdot |\mathbf{C}| \cdot C > |\mathbf{W}|$$  \hspace{1cm} (15)

where $C$ is the food concentration in particle $m^{-3}$, $E$ is the energy caloric content of a food particle in Joule particle$^{-1}$, and $\Lambda$ is the copepod’s efficiency of transforming caloric content of food into useful energy. In order to satisfy the inequality in equation (15) and survive, a copepod has to stay in an environment of food concentration...
are able to survive at lower food concentrations 

Moreover, the 

and hence the inequality in equation (15) can be satisfied. The averaged low food concentrations in the environment, 

these water parcels. In this way, the food concentrations in 

higher food concentrations and lead the copepod to sweep 

the food/prey and locate the small water parcels with 

seen by comparing Figure 12b to Figures 11b and 12a. 

that for a hovering or slow-swimming copepod, as can be 

mechanosensory field (and therefore the perception 

current of 

ing. If the flow field generated by a copepod can be taken 

for fast-swimming copepods. We explain this in the follow-

feeding current. However, equations (13) to (15) still hold 

hovering or slow-swimming copepod which generates a 

water that passes through the capture area does not 

the food/prey to increase the food concentrations in the 

patchy food distribution with higher clearance rates in the 

Conclusions

The numerical results confirm the conclusions drawn 

from the theoretical analysis using Stokes flow models by 

Jiang et al. (Jiang et al., 2002a) for a spherical copepod shape and show that the geometry of the flow field around a freely swimming copepod varies significantly with different swimming behaviours. When a copepod hovers in the water, or swims slowly (i.e. to swim at a speed at least several times smaller than its free-sinking terminal velocity), it generates a cone-shaped and wide feeding current. In contrast, when a copepod sinks freely, or swims fast (i.e. eliciting raptorial behaviour), the flow field around its body is not like a feeding current. These conclusions are consistent with the laboratory-observed swimming behaviour of calanoid copepods. Many species that display hovering or slow-swimming or drifting behaviour generate a feeding current. The confirmation suggests that for general qualitative trends, analytical solutions using Stokes flow models can give much insight. The geometry of the flow field around a copepod is mainly dependent on the excess weight and swimming speed of the copepod. The body shape and finite Reynolds number can only have minute effects on the flow geometry.

The practicability of the present numerical methods demonstrates that the body orientation and swimming velocity associated with a swimming behaviour are determined by the combined action of forces: gravity, buoyancy, thrust and drag.

Hydrodynamic conspicuousness of a freely swimming copepod, both to its prey and predators, can be quantified by calculating the viscous dissipation rate field associated with the flow field generated by the copepod by using \( 10^{-7} \) m³s⁻¹, a reasonable lower bound of the coastal oceanic energy dissipation rates in a turbulent regime to set the lowest level of hydrodynamic conspicuousness.

The behaviour of hovering or swimming slowly is more energetically efficient in terms of relative capture volume per energy expended than the behaviour of swimming
fast, i.e. for the same amount of energy expended a hovering or slow-swimming copepod is able to scan more water than a fast-swimming one. However, the flow field generated by a fast-swimming copepod enables the copepod to use mechanoreception to perceive the food/prey and therefore increases the food concentration in the swept volume; the flow field around a free-sinking copepod favours the copepod’s mechanoreception while minimizing the energy expense. Hence, the energy budget can still be maintained for both cases. In general, mechanoreception allows a fast-swimming or free-sinking copepod to increase the food concentration in the swept volume above the mean value for the food concentration in the environment.

Our results showed that the geometry of the flow field around a freely swimming copepod is highly dependent on the swimming behaviour of that copepod. The differences in the flow geometry will be reflected in the sensory modes (mechanoreception and/or chemoreception) adopted by copepods. Further studies relating the swimming behaviour to the sensory modes are needed.

ACKNOWLEDGMENTS

H.S.J. would like to thank Professors J. R. Strickler and G.-A. Paffenhöfer and Dr. M. H. Bundy for providing him with the opportunities to watch their videos on free-swimming copepods. The authors are grateful to Professor J. R. Strickler and two anonymous reviewers for very helpful comments on the manuscript. The financial support of the Office of Naval Research (contract number N000149710429) is gratefully acknowledged.

REFERENCES


APPENDICES: NUMERICAL METHODS FOR DETERMINING THE STEADY MOTIONS OF THE MODEL COPEPOD

The body shape of the model copepod has been described in the subsection 'Model copepod and computational mesh'. The distributed force field, which models the effect of the beating movement of the cephalic appendages, has been illustrated in the subsection 'Distributed force field and forcing index'. An excess weight of magnitude ($W_{\text{excess}}$) of $4.048 \times 10^{-8}$ N has been chosen for the model copepod. Below we describe the setups of the computational domain and boundary conditions, and the solution methods to determine the terminal velocity, forcing index and body orientation for the cases previously described above. More details are given in Jiang (Jiang, 2000).

APPENDIX 1. FREELY SINKING CASES

Two body orientations have been considered for a model copepod sinking freely in the water. The first one is the anterior of the copepod pointing upward (Figure A1a). Because of the dorsal-ventral asymmetry in the copepod's morphology, the drag force acting on the copepod can be decomposed into two components. One is in the ventral–dorsal direction (i.e. $F_x$ as shown in Figure A1a), and the other is in the posterior–anterior direction (i.e. $F_z$ as shown in Figure A1a). If the body axis tilts ventrally, there exists a terminal velocity for this body orientation, at which the drag force balances the excess weight.

The setup for the FLUENT™ simulations for this body orientation is illustrated in Figure A1a, in which a velocity inlet boundary condition is applied to the bottom boundary of the cubic box to simulate the relative sinking motion of the copepod. The drag force components $F_x$ and $F_z$ depend on the sinking speed (i.e. the magnitude of the velocity inlet). In order to determine the terminal velocity, the velocity field around the copepod is computed with varying the magnitude of the velocity inlet boundary condition and $F_x$ and $F_z$ calculated for each magnitude of the velocity inlet. The results of the drag-force components are plotted in Figures A2a and A2b, and the cubic spline interpolation (Press et al., 1992) is employed to determine the functional dependence of $F_x$ and $F_z$ to the sinking speed. Based on the interpolated functional forms, the force-balance equation

$$W_{\text{excess}} = F_x + F_z$$

is solved graphically using the solution map drawn in Figure A3a. The terminal velocity ($V_{\text{terminal}}$) of the model copepod, sinking freely along its body axis with the anterior pointing upward, is found to be 4.187 mm s$^{-1}$. In addition, the angle $\theta$ between the body axis and the direction of the excess weight is calculated as 1.131° using the formula

$$\theta = \arctan \left( \frac{F_x}{F_z} \right)$$

The second body orientation is the anterior of the copepod pointing downward (Figure A1b). Again, the process using the cubic spline interpolation is employed to obtain the functional forms of the two components of the drag force (i.e. $F_x$ and $F_z$) versus the sinking speed. Then, the functional forms are used to solve graphically for the terminal velocity, which is 3.941 mm s$^{-1}$. The angle $\theta$ between the direction of the excess weight and the body axis is calculated as 0.964° according to Formula (A2).
swimming motion of the copepod. In Figure 4.1, \( g \); \( e \) and \( f \) swimming forward at a speed of \( \mathbf{v}_{\text{swim}} \), \( \mathbf{g} \) is the frame of reference in FLUENT™, and \( \mathbf{g} \). \( \mathbf{e} \); \( \mathbf{f} \) swimming forward at a speed of \( \mathbf{v}_{\text{swim}} \); \( \mathbf{c} \) swimming backward at a speed of \( \mathbf{v}_{\text{swim}} \); \( \mathbf{g} \) swimming upward along its body axis at a speed of \( \mathbf{v}_{\text{up}} \), \( \mathbf{h} \) swimming freely along its body axis with the anterior pointing downward; \( \mathbf{f} \) swimming freely along its body axis with the anterior pointing downward; \( \mathbf{e} \) hovering; \( \mathbf{d} \) swimming upward along the vertical axis at a speed of \( \mathbf{v}_{\text{swim}} \); \( \mathbf{a} \) swimming upward along its body axis at a speed of \( \mathbf{v}_{\text{swim}} \); \( \mathbf{b} \) swimming backward at a speed of \( \mathbf{v}_{\text{swim}} \). The copepod swims vertically in \( \mathbf{a} \); \( \mathbf{d} \); \( \mathbf{e} \) and \( \mathbf{g} \), and dorsally in \( \mathbf{b} \) and \( \mathbf{h} \) at an angle \( \theta \) to the vertical. \( \mathbf{f} \) is the frame of reference in FLUENT™, and \( \mathbf{g} \) is in the real world. \( \mathbf{F}_d \) and \( \mathbf{F}_p \) are the two components of the drag force by the water, in \( \mathbf{a} \), \( \mathbf{d} \), \( \mathbf{e} \), \( \mathbf{f} \) and \( \mathbf{g} \), the velocity inlet simulates the relative-sinking motion of the copepod. In \( \mathbf{a} \), \( \mathbf{d} \), \( \mathbf{e} \), \( \mathbf{f} \) and \( \mathbf{g} \), \( \mathbf{F}_d \) and \( \mathbf{F}_p \) are the sum of \( \mathbf{F}_d \), and the reaction force from the water, \( \mathbf{F}_p \), \( \mathbf{F}_d \), \( \mathbf{F}_p \) and \( \mathbf{F}_d \times 8.4 \times 10^{-9} \text{ N} \) is the sum of \( \mathbf{F}_d \) and the propulsion, and the velocity inlet simulates the swimming motion of the copepod.

![Fig. 4.1](https://example.com/figure4.1.png)

**Fig. 4.1.** Illustration of the setups for the FLUENT simulations of the flow field around a model copepod: (a) sinking freely along its body axis with the anterior pointing upward; (b) sinking freely along its body axis with the anterior pointing downward; (c) hovering; (d) swimming upward along the vertical axis at a speed of \( \mathbf{v}_{\text{swim}} \); (e) swimming upward along its body axis at a speed of \( \mathbf{v}_{\text{swim}} \); (f) swimming backward at a speed of \( \mathbf{v}_{\text{swim}} \); (g) swimming forward at a speed of \( \mathbf{v}_{\text{swim}} \).
APPENDIX 2. HOVERING CASE

When a copepod hovers in the water (i.e. the swimming velocity $V_{swimming} = 0$), it has to move its cephalic appendages to gain a force from the water to counter-balance its excess weight. Figure A1c illustrates the set up for the FLUENT™ simulations for this case. The drag force $\mathbf{F}$ is decomposed into two components, $F_x$ and $F_z$. $F_x$ is in the ventral-dorsal direction, and the $z$-direction component of the sum of $\mathbf{F}$ and $-f_i$, i.e. $F_z + f_i$, is in the posterior-anterior direction. Thus, the model copepod must tilt ventrally to maintain the force balance for hovering in the water. The process using the cubic spline interpolation is employed to obtain the functional forms of $F_x$ and $F_z + f_i$. Then, the functional forms are used to draw the solution map for this steady motion (Figure A3b), from which the equation

$$F_x(f_i) + F_z(f_i) + f_i = W_{excess}$$

(A3)

is graphically solved to give a forcing index of $f_i = 2.304$. The angle $\theta$ between the body axis and the direction of the excess weight is calculated according to

$$\theta = \arctan\left(\frac{F_z(2.304)}{F_x(2.304) + 2.304 \times 8.4 \times 10^{-8}}\right)$$

(A4)

The resulting $\theta$ is $2.242^\circ$. Note that the units of $F_x$ and $F_z$ are Newton (N) in both equations (A3) and (A4).

Fig. A2. (a) and (b), plots of the two components of the drag force $F_x$ and $F_z$ respectively versus the sinking speed for the case of a model copepod sinking freely along its body axis with the anterior pointing upward; (c) and (d), plots of $F_x$ and $F_z + f_i$ versus the forcing index $f_i$ for the case of a model copepod hovering in the water; (e) and (f), plots of $F_x$ and $F_z + f_i$ versus the forcing index $f_i$ for the case of a model copepod swimming upward along its body axis at a speed of 4.187 mm s$^{-1}$. The diamonds are the samples from FLUENT™ calculations, and the solid lines are the functional forms obtained from the cubic spline interpolation.
APPENDIX 3. UPWARD SWIMMING CASES

When a copepod swims upward at a constant speed, it has to move its cephalic appendages to gain propulsion from the water to balance the drag force on its body as well as its excess weight. Figure A1d illustrates the set up for the FLUENT™ simulations for the case of a model copepod swimming upward along the vertical axis. Given a constant swimming speed, $F_x$ and $F_z + f_i / H^{8.4 \times 10^{-8}}$ N are functions of both the forcing index $f_i$ and $\theta_i / H^{8.4 \times 10^{-8}}$. In practice, both $f_i$ and $\theta_i / H^{8.4 \times 10^{-8}}$ are varied, and a velocity field is calculated for each pair of ($f_i$, $\theta_i / H^{8.4 \times 10^{-8}}$) using FLUENT™, and then $F_x$ and $F_z$ are evaluated for each pair of ($f_i$, $\theta_i / H^{8.4 \times 10^{-8}}$). Based on the data of $F_x$ and $F_z$ for all sampled pairs of ($f_i$, $\theta_i / H^{8.4 \times 10^{-8}}$), functional forms of $F_x$ and $F_z$ respectively versus ($f_i$, $\theta_i / H^{8.4 \times 10^{-8}}$) are obtained by using the cubic spline interpolation in two dimensions (Press et al., 1992). Then, the functional forms are used to solve graphically the force-balance equations

\[
\begin{align*}
F_x(\theta_i, \theta) + f_i \times 8.4 \times 10^{-8} - W_{\text{max}} \cos(\theta) &= 0 \\
F_z(\theta_i, \theta) + W_{\text{max}} \sin(\theta) &= 0
\end{align*}
\]  

written in the frame of reference $(x, z)$ (see Figure A1d).

Note that the forces are in Newtons (N) in (A5). Based on the functional forms of $F_x$ and $F_z$ respectively versus ($f_i$, $\theta_i / H^{8.4 \times 10^{-8}}$), equation (A5) is solved graphically in Figure A3c, which yields $f_i = 2.537$ and $\theta_i = 1.603^\circ$ for the model copepod swimming upward along the vertical axis at a speed of 1.047 mm s$^{-1}$.

Also, we consider the case of a model copepod swimming upward along its body axis at a speed of 4.187 mm s$^{-1}$. The setup for the FLUENT™ simulations is illustrated in Figure A1e. The process using the cubic spline interpolation is again used to obtain the functional forms of $F_x$ and $F_z$ + $f_i / H^{8.4 \times 10^{-8}}$ N versus the forcing index $f_i$ (see Figures A2e and A2f). Then, the functional forms are used to draw the solution map for this steady motion (Figure A3d), from which equation (A3) is solved graphically to give a forcing index of $f_i = 4.044$. The angle $\theta_i$ between the body axis and the direction of the excess weight is calculated as 4.666° according to the formula

\[
\theta_i = \arctan\left(\frac{F_z(4.044)}{F_x(4.044) + 4.044 \times 8.4 \times 10^{-8}}\right)
\]  

Note that the units of $F_x$ and $F_z$ are Newtons (N) in both equations (A5) and (A6).
APPENDIX 4. BACKWARD AND FORWARD SWIMMING CASES

Similar solution procedures are applied to the backward and forward swimming cases shown in Figures A1f and A1g, respectively. The results are $\beta = 2.256$ and $\theta = 5.554^\circ$ for a model copepod swimming backward at a speed of 1.047 mm s$^{-1}$, and $\beta = 2.821$ and $\theta = 5.554^\circ$ for a speed of 4.187 mm s$^{-1}$. For a forward swimming model copepod we find $\beta = 2.347$ and $\theta = 9.558^\circ$ for a swimming speed of 1.047 mm s$^{-1}$, and $\beta = 3.141$ and $\theta = 62.098^\circ$ for a swimming speed of 4.187 mm s$^{-1}$. 

Fig. A3. (a) Solution map of the steady motion of a model copepod, sinking freely along its body axis with the anterior pointing upward. $F_x^2 + F_z^2)^{1/2}$ is calculated using the functional forms of $F_x$ and $F_z$ versus the sinking speed, obtained from the cubic spline interpolation. The intersection of the two lines is the solution of equation (A1) and gives the terminal velocity of sinking-freely. (b) Solution map of the steady motion of a model copepod, hovering in the water. $F_x^2 + (F_z + \frac{\beta}{H_9258} \times 8.4 \times 10^{-8})^2)^{1/2}$ is calculated using the functional forms of $F_x$ and $F_z$, respectively versus $\frac{\beta}{H_9258}$, obtained from the cubic spline interpolation in two dimensions. The intersection of the two zero contour lines is the solution of equation (A3) and gives the forcing index $\beta$ of the distributed force field generating the flow field around the hovering copepod. (c) Solution map of the steady motion of a model copepod, swimming upward along the vertical axis at a speed of 1.047 mm s$^{-1}$. $F_x^2 + F_z^2)^{1/2}$ is calculated using the functional forms of $F_x$ and $F_z$ versus $\frac{\beta}{H_9258}$, obtained from the cubic spline interpolation in two dimensions. The intersection of the two zero contour lines is the solution of equation (A5) and gives the forcing index $\beta$ of the distributed force field as well as the angle $\theta$ for the copepod swimming upward along the vertical axis at a speed of 1.047 mm s$^{-1}$. (d) Solution map of the steady motion of a model copepod, swimming upward along its body axis at a speed of 4.187 mm s$^{-1}$. $F_x^2 + (F_z + \frac{\beta}{H_9258} \times 8.4 \times 10^{-8})^2)^{1/2}$ is calculated using the functional forms of $F_x$ and $F_z$, respectively versus $\frac{\beta}{H_9258}$, obtained from the cubic spline interpolation in two dimensions. The intersection of the two zero contour lines is the solution of equation (A3) and gives the forcing index $\beta$. 

H. JIANG, C. MENEVEAU AND T. R. OSBORN FLOW FIELD AROUND SWIMMING COPEPOD: NUMERICAL SIMULATION