Pelagic copepods jump to relocate, to attack prey and to escape predators. However, there is a price to be paid for these jumps in terms of their energy costs and the hydrodynamic signals they generate to rheotactic predators. Using observed kinematics of various types of jumps, we computed the imposed flow fields and associated energetics of jumps by means of computational fluid dynamics simulations by modeling the copepod as a self-propelled body. The computational fluid dynamics simulation was validated by particle image velocimetry data. The flow field generated by a repositioning jump quickly evolves into two counter-rotating viscous vortex rings that are near mirror image of one another, one in the wake and one around the body of the copepod; this near symmetrical flow may provide hydrodynamic camouflage because it contains no information about the position of the copepod prey within the flow structure. The flow field associated with an escape jump sequence also includes two dominant vortex structures: one leading wake vortex generated as a result of the first jump and one around the body, but between these two vortex structures is an elongated, long-lasting flow trail with flow velocity vectors pointing towards the copepod; such a flow field may inform the predator of the whereabouts of the escaping copepod prey. High Froude propulsion efficiency (0.94–0.98) was obtained for individual power stroke durations of all simulated jumps. This is unusual for small aquatic organisms but is caused by the rapidity and impulsiveness of the jump that allows only a low-cost viscous wake vortex to travel backwards.

Key words: computational fluid dynamics, copepod jumping, viscous vortex ring, hydrodynamic camouflage, cost of jump, Froude propulsion efficiency.

INTRODUCTION

Planktonic copepods are a group of abundant, evolutionarily successful and ecologically important multicellular organisms found in the ocean and in fresh water (e.g. Mauchline, 1998; Miller, 2004). Most, if not all, of them are capable of jumping by sequentially striking the swimming legs posteriorly. Such jumps fall into four general categories as distinguished by their functioning: (1) powerful and rapid escape jumps for getting away from approaching danger (e.g. Singarajah, 1969; Strickler, 1975; Fields and Yen, 1997; Suchman, 2000; Buskey et al., 2002); (2) short and less powerful repositioning jumps for frequent relocation in the water column (e.g. Tiselius and Jonsson, 1990; Svensen and Kiørboe, 2000; Paffenöhfer and Muzzocchi, 2002); (3) accurately directed and carefully maneuvered attack jumps for capturing prey (e.g. Jiang and Paffenöhfer, 2008; Kiørboe et al., 2009); and (4) sequences of many consecutive small swimming jumps for traveling through the water (e.g. Strickler, 1975; Morris et al., 1990). All the jumps generate hydrodynamic disturbances, and a rheotactic predator may detect a jumping copepod by sensing the hydrodynamic disturbance the copepod generates (e.g. Strickler and Bal, 1973; Visser, 2001). Quantitative characterization of the jump-associated hydrodynamic disturbances allows a mechanistic understanding of the jump-related predation risk faced by the copepods. In spite of being a very common motility mode in copepods, jumping is generally believed to be energetically costly. Thus, it is also meaningful to assess directly the mechanical energy expenditure and propulsion efficiency of jumping by copepods.

We have recently examined the flow fields imposed by copepods that perform relatively weak repositioning jumps (Kiørboe et al., 2010a; Jiang and Kiørboe, in press). Flow visualization (particle image velocimetry; PIV) and simple analytical models have demonstrated that the flow field consists of two counter-rotating viscous vortex rings of similar intensity, one in the wake and one around the body of the copepod. These studies have suggested that the predation risk of ambush-feeding copepods that perform frequent repositioning jumps, and of copepods that swim by repetitive small jumps is less than that of copepods that produce a feeding current or cruise steadily through the water. Much less is known about the hydrodynamics of the powerful escape jumps. Although such jumps may allow a copepod to escape a predator, they also pose a risk: the jump-generated flow disturbance may inform the predator about the position of the copepod prey, and may elicit an attack (Williamson and Vanderploeg, 1988; Yen and Strickler, 1996). Therefore, the speed and distance of a jump becomes crucial. The specific force production during an escape jump is unusually high compared with that reported for any other organism (Lenz et al., 2004; Kiørboe et al., 2010b), but the propulsion efficiency is unknown. The simple analytical models are not applicable to escape jumps and PIV observations are not possible because, at the magnification required, the jump distance and the flow field will exceed the field of view. Schlieren (i.e. deflection of light by flow density gradient) observations have revealed a series of toroidal flow structures in the wake of an escaping copepod, probably frozen at several initial instants since the start of jumping (e.g. Yen and...
Strickler, 1996). However, nothing is known about the spatial configuration and temporal evolution of the flow field associated with these escape jumps, especially for the period following the completion of jumping, or of the energetics and efficiency. This is the focus of the present study.

Computational fluid dynamics (CFD) simulation has emerged as a suitable and useful approach for investigating small-scale hydrodynamic phenomena occurring at individual plankter scale and their interplay with plankton behavior and ecology (e.g. Jiang et al., 1999; Jiang et al., 2002; Gilmanov and Sotiropoulos, 2005; Jiang and Strickler, 2007; Latz et al., 2008; Musielak et al., 2009). Here we extend the CFD simulation approach to the investigation of the flow field associated with a jumping copepod. We validate the simulation approach using the PIV flow data measured for copepod repositioning jumps (Kiørboe et al., 2010a), and then apply the validated approach to simulate the flow field associated with copepod escape jumps. We use previously measured copepod jump kinematics (Kiørboe et al., 2010a; Kiørboe et al., 2010b) to drive our simulations. Based on the simulation data, we calculate Froude propulsion efficiency for both the repositioning jumps and the escape jumps.

MATERIALS AND METHODS
Copepod jumps

High-speed video observations of the kinematics of copepod jumps (i.e. the time-dependent copepod jump velocity) and PIV observations of associated flow fields were taken from Kiørboe et al. (Kiørboe et al., 2010a; Kiørboe et al., 2010b). Two species of copepod were studied: *Acartia tonsa* Dana 1849 (prosome length 0.7–1.1 mm) and *Calanus finmarchicus* Gunnerus 1765 (3 mm). Copepods jump by sequentially striking the four (*A. tonsa*) or five (*C. finmarchicus*) pairs of swimming legs posteriorly (Fig. 1). This pushes the copepod forward. Subsequently the swimming legs are recovered simultaneously. This beat cycle may be repeated after a few milliseconds. Repositioning jumps consist of one to several beat cycles, and escape jumps may consist of many beat cycles. The duration of the power stroke varies between 2 and 10 ms for *A. tonsa* and 5 and 20 ms for *C. finmarchicus* (both are absolute ranges), and the jump speed varies inversely with the stroke duration and may be up to ~500 mm s\(^{-1}\) for *A. tonsa* and ~800 mm s\(^{-1}\) for *C. finmarchicus*.

CFD simulation approach

At the onset of a jump and immediately before the striking of the swimming legs, a real copepod wraps its two antennules (A1) around its body, presumably to reduce drag. Modeling the copepod body as a prolate spheroid is therefore regarded as a good approximation. We simulated the flow field created by a prolate spheroidal model copepod of long axis equal to copepod body (prosome) length (2a) and short axes equal to ε×2a, where ε is the aspect ratio of the copepod. The model copepod was assumed to jump forward along its long axis (i.e. the x-axis; Fig. 2). Thus only a meridian plane was included as the computational domain (i.e. the finite geometric domain on which the flow field is to be solved numerically). A cylindrical polar coordinate system was used with r being the radial distance from the x-axis (Fig. 2). Symmetry boundary condition was specified on the upper boundary. Pressure-outlet boundary conditions were specified on both the left and right boundary. Because of axisymmetry, the flow patterns are identical in all planes containing the x-axis, independent of the azimuthal coordinate (θ). This is consistent with observational evidence that mushroom-like toroidal flow structures are left behind jumping copepods (Yen and Strickler, 1996; van Duren and Videler, 2003; Kiørboe et al., 2010a).

The computational domain is 90a in the x-direction and 30a in the r-direction (Fig. 2 upper panel). The domain was discretized into 6000 quadrilateral control volumes (CVs) immediately adjacent to the copepod body and into ~35,000 triangular CVs that were stretched radially outward from the outer boundary of the quadrilateral CVs. The model copepod body and the quadrilateral CVs travel together (Fig. 2) according to an observed time-dependent copepod jump velocity \([U(t)]\). \(U(t)\) was obtained by applying a
Savitzky–Golay smoothing filter (Press et al., 2007) to the data from Kiørboe et al. for repositioning jumps and from Kiørboe et al. for escape jumps (Kiørboe et al., 2010a; Kiørboe et al., 2010b) (Fig. 3). This filtering approach advantageously tends to preserve the relative maxima, minima and peak widths of the observed velocity time series. The outer zone consisting of the triangular CVs (i.e. the deforming mesh zone; Fig. 2) was remeshed every time step in order to accommodate the combined motion of the model copepod body (as an internal solid-wall boundary) and the adjacent quadrilateral CV zone.

There was no relative motion between the copepod body and the adjacent quadrilateral CV zone, and the quadrilateral CV zone remained un-deformed throughout the jump duration. It was therefore feasible to apply on the quadrilateral CV zone a spatially time-dependent field of body force \( F(x, r, t) \), to model the forcing due to swimming leg beating. That the forcing and the model copepod translate together in the CFD setup is analogical to the real world situation that the swimming legs translate with the copepod main body. The forcing was applied over the volume where the swimming legs are likely to sweep through in a real jump (indicated by the blue area in the lower panel of Fig. 2). The observations that all setae of the swimming legs were stretched out to achieve a maximal frontal area during a power stroke (Lenz and Hartline, 1999) [see also fig. 3K in Strickler (Strickler, 1975)] supports the use of an axisymmetric distribution of the swimming leg forcing in our simulation. The forcing magnitude applied at a specific CV is linearly proportional to the distance from the CV to the rear end of the model copepod prosome, and the forcing direction is perpendicular to the leg length. The linear relationship stems from our assumption that the flow surrounding the swimming legs remains in the low Reynolds number regime and hence the hydrodynamic force scales linearly with the velocity of a segment of the swimming legs. Thus, the mathematical descriptions of the axial component, \( F_x(x, r, t) \), and the radial component, \( F_r(x, r, t) \), of the forcing are:

\[
F_x(x, r, t) = -A(t) \frac{r}{L_{\text{leg}}},
\]

\[
F_r(x, r, t) = A(t) \frac{x - x_0}{L_{\text{leg}}},
\]

where \( x_0 \) denotes the time-dependent axial position of the rear end of the model copepod prosome (Fig. 2 lower panel), \( L_{\text{leg}} \) is the typical length of the swimming legs (\( \approx 1.5a \)), and \( A(t) \) is the forcing magnitude at the tip of the swimming leg (which needs to be determined at every time step, see below).

The flow field associated with a jumping copepod can be taken as laminar, incompressible and Newtonian, and is governed by the unsteady incompressible Navier–Stokes equations together with the...

Fig. 2. Axisymmetric computational fluid dynamics (CFD) model for simulating the flow field created by a prolate spheroidal model copepod jumping straight (arrow indicates direction of jump). The diagram at the top shows that the symmetry boundary condition specifies zero normal velocity and zero normal gradients of all variables at the symmetry line; the pressure-outlet boundary condition specifies a zero static (gauge) pressure at the two side boundaries.

Fig. 3. A. tonsa Jump 90 (see Table 1). Temporal variation in the velocity of the copepod. The kinematic data was obtained from high-speed video observation (Kiørboe et al., 2010b).
continuity equation (not shown for brevity). To obtain the flow field, these equations under the above-described forcing and boundary conditions were numerically solved by using the commercially available finite-volume CFD software package ANSYS FLUENT (version 12.0.16; Lebanon, NH, USA). The CFD simulation was conducted using a stationary frame of reference, so \( U(t) \) was explicitly included as a prescribed moving solid-wall boundary condition. This was implemented by writing a user defined function (UDF) using the dynamic mesh macro DEFINE_CG_MOTION (to define the motion of the center of gravity) in ANSYS FLUENT. To ensure that \( U(t) \) was a result of self-propulsion by the model copepod, the swimming leg forcing \( F(x, r, t) \) was determined at every time step by solving the dynamic equation of the model copepod jump:

\[
m_{\text{copepod}} \frac{dU(t)}{dt} = D(t) + T(t),
\]

where \( m_{\text{copepod}} \) is the body mass of the model copepod, \( D(t) \) is the instantaneous hydrodynamic resistance acting on the body surface of the model copepod and \( T(t) \) is the instantaneous thrust. \( D(t) \) was obtained by determining the axial component of the pressure force and shear stress over the body surface. \( T(t) \) was equal to the radial component of the volume integral of \(- F(x, r, t) \) over the volume where the swimming leg force was applied (the blue patch in the lower panel of Fig. 2). Because the general form of \( F(x, r, t) \) was prescribed (Eqn 1A,B; Fig. 2 lower panel), Eqn 2 was solved by determining the coefficient \( A(t) \), in front of the prescribed general form. The procedure for determining \( F(x, r, t) \) and coupling it to the flow solver at every time step was implemented by writing a UDF using the DEFINE_SOURCE (to specify the source terms, including the momentum source) macro in ANSYS FLUENT. In practice, at each time step \( F \) was first determined on the basis of the flow field information at the immediately previous time step, and then the determined \( F \) was coupled to the flow field solver, along with the moving and deforming mesh, to compute the flow field at the next time step. Therefore, a small time step was necessary for both accuracy and convergence (see below). Throughout this study, the fluid density (\( \rho \)) was 1.02695 \( \times 10^3 \) kg m\(^{-3} \) and the fluid kinematic viscosity (\( \nu \)) was 1.354 \( \times 10^{-6} \) m\(^2\) s\(^{-1} \); both are the values for seawater with a salinity value of 35 p.p.t. at 10°C at one normal atmosphere. The mass density of the model copepod was assumed to be equal to the fluid density.

As to the numerical schemes, the highly accurate third-order MUSCL (monotone upstream-centered schemes for conservation laws) scheme was used for spatial interpolation. The body force weighted scheme was selected as the discretization method for pressure. The PISO (pressure-implicit with splitting of operators) scheme was used for pressure–velocity coupling. Temporal discretization was a first-order implicit scheme. For the jumping phase when the model copepod was moving, the time step was \( \tau_j/50 \) where \( \tau_j \) is the sample time interval of the jump kinematics data obtained using the high speed camera. Three kinds of copepod jumps were simulated, namely, the repositioning jumps of \( A. \) tonsa with \( \tau_j=1/1000 \) s, the escape jumps of \( A. \) tonsa with \( \tau_j=1/3596 \) s, and the escape jumps of \( C. \) finmarchicus with \( \tau_j=1/2200 \) s. Using such a small time step was also a requirement by the dynamic (moving or deforming) mesh model in ANSYS FLUENT. At the end of the jumping phase, when the model copepod was no longer moving (in an approximate sense), the dynamic mesh model was switched off to allow for a much larger time step, e.g. \( \tau_s=200 \) where \( \tau_s=(\varepsilon d)^2/\nu \) (a viscous time scale based on half the body width of the model copepod). After the jumping phase the simulation was still continued for 20–40 \( \tau_s \) for the repositioning jumps and 100–130 \( \tau_s \) for the escape jumps. As a result, the time-dependent flow field at the decaying phase was also obtained. Good comparison between the simulated results and the PIV flow data measured for copepod repositioning jumps (see Results and discussion) validated the CFD simulation approach used.

### Circulation

At every time step, the instantaneous azimuthal vorticity field \( [\omega_k(x, r, t)] \) was calculated according to its definition:

\[
\omega_k = \frac{\partial v}{\partial x} - \frac{\partial u}{\partial r},
\]

where \( u_k \) and \( u_r \) are the CFD-simulated velocity components in the axial \((x)\) and the radial \((r)\) direction, respectively. Note that the vorticity sign conforms to the conventional right-hand rule. The time series of the wake vortex circulation \( [\Gamma(t)] \), was then obtained at every time step by area-integrating the negative vorticity in the wake of the jumping copepod:

\[
\Gamma(t) = \int \omega_k \, dr, \quad \text{for} \, \omega_k<0 \text{ in the wake}.
\]

For a simulated repositioning jump, the decay phase of \([\Gamma(t)]\) was fitted, subsequent to a virtual time origin \( (t_0) \), to the theoretical viscous decay of circulation, based on the impulsive stresslet model (Jiang and Kiørboe, in press):

\[
|\Gamma(t)| = \frac{M_{\text{fitted,CFD}}}{8\pi\nu (t-t_0)^{3/2}},
\]

where \( M_{\text{fitted,CFD}} \) is the fitted impulsive stresslet strength.

For a simulated escape jump event (consisting of multiple powerful jumps), besides the total circulation of all the wake vortices [i.e. \( \Gamma(t) \)], the time series of the circulation of the leading wake vortex generated by the first jump, \( \Gamma_1(t) \), was also calculated. \( \Gamma_1(t) \) was fitted, subsequent to \( t_0 \), to the theoretical viscous decay of circulation based on the impulsive Stokeslet model (Kiørboe et al., 2010a):

\[
|\Gamma_1(t)| = \frac{I_{\text{fitted,CFD}}}{4\pi\nu (t-t_0)},
\]

where \( I_{\text{fitted,CFD}} \) is the fitted hydrodynamic impulse (Saffman, 1992) of the leading wake vortex.

### Area of influence

Rheotactic predators are likely to respond to the velocity magnitude of the flow imposed by the copepod prey (Kiørboe and Visser, 1999) and we therefore computed the area (\( S \)) within which the velocity exceeds a threshold magnitude \( U^* \). For a simulated repositioning jump, the time series of the area of influence, \( S(t) \), was calculated at every time step by summing all the discretized areas in the meridian plane, within which the flow velocity magnitude was greater than \( U^* \). \( S(t) \) was then compared with a scaling relationship obtained from the impulsive Stokeslet model (Jiang and Kiørboe, in press):

\[
S(t) = 0.5 \pi R^* R^* \left \{ \frac{t}{\tau^*} \right \}^3,
\]

where:

\[
R^* = \left \{ \frac{3}{2\pi} \frac{M_{\text{fitted,CFD}}}{U^*} \right \}^{1/4}.
\]

\( \tau^* \) is the characteristic time scale of the jump (see Results and discussion).

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**Note:** The above text is a natural language representation of the content in the provided image. It is designed to be easily readable and understood, without altering the original meaning or context of the material. If you need further clarification or have specific questions about the content, feel free to ask!
mechanical work of $F$ applied by the swimming legs was calculated as the volume integral of $F$ over the volume where the swimming leg was applied (i.e. the blue patch in the lower panel of Fig. 2); here $u(x, r, t)$ was the CFD-simulated instantaneous flow velocity vector field. For this power stroke, the CFD-simulated total mechanical work $[W_{CFD}]$ was then calculated as the time integral of $P(t)$ over $\tau$.

The hydromechanical efficiency [or Froude propulsion efficiency (Lighthill, 1970)] for copepod jumping was calculated according to its definition:

$$\eta = \frac{\int_{\tau}^{\tau+\tau} T(t)U(t)dt}{W_{CFD}},$$

where the useful mechanical work was calculated as the time integral of the product of $T(t)$ and $U(t)$, over $\tau$, and $W_{CFD}$ was previously calculated as the total mechanical work that the swimming legs did against the surrounding water during the same power stroke duration.

Therefore, this definition reflects the highly unsteady nature of copepod jumping.

The fraction of $W_{CFD}$ expended to overcome the total hydrodynamic resistance (including the added mass effect) during the power stroke period was calculated as:

$$\eta_r = \frac{-\int_{\tau}^{\tau+\tau} D(t)U(t)dt}{W_{CFD}},$$

where $D(t)$ had been obtained at every time step by solving Eqn 2 and the flow field equations jointly.

According to Eqn 2 the fraction of $W_{CFD}$ used to accelerate only the model copepod body during the power stroke period was calculated as:

$$\eta_{body} = \eta - \eta_r.$$

RESULTS AND DISCUSSION

Flow field associated with a repositioning jump: validation of the CFD approach

The flow field associated with a weak repositioning jump consists of two counter-rotating viscous vortex rings of similar intensity, one in the wake of the copepod and one around the body. This was first revealed by a PIV observational study (Kiørboe et al., 2010) and then confirmed by a theoretical hydrodynamic model (Jiang and Kiørboe, in press). This can also be reproduced by the present CFD simulation approach. The simulated flow velocity field and vorticity field compare favorably with those obtained from the PIV observation (Fig. 4), despite some discrepancies that might be due to the three-dimensionality of a real copepod jump versus the model assumption of axisymmetry, especially at the initial stage of the jump when the leg forcing is somewhat three-dimensional (compare Fig. 4A with B).
The CFD-simulated results show that, at the initial stage of a repositioning jump, the spatial extension of the imposed flow field does not reach its maximum, even at the time when the thrust is at the maximum (compare Fig. 5A with B,C). It takes a very short time for the flow to reach its maximum spatial extension (Fig. 6) because the water surrounding the copepod receives momentum, although in opposite directions, during both the accelerating and decelerating phase of the jump. At the time when the jump stops, the vortex around the copepod body is stronger than the wake vortex because of the existence of a thin boundary layer surrounding the copepod body that hosts vorticity with sign opposite to that of the vortex around the body (Fig. 5B). However, in the decaying phase, the body vortex and the wake vortex quickly become similar in intensity because of viscous diffusion and mutual cancellation of the opposite-signed vorticities (Fig. 5C). The CFD-simulated circulation of the wake vortex also compares favorably with the PIV-measured circulation of the wake vortex, and the decaying phase of both conforms to the theoretical viscous vortex decay predicted from the impulsive stresslet model of Jiang and Kiørboe (Jiang and Kiørboe, in press) (Fig. 7). The CFD-simulated normalized area of influence follows the trend of the theoretical prediction from the impulsive stresslet model (Fig. 6). However, the CFD estimates of the areas of influence of different threshold velocities do not exactly collapse on to each other; rather, areas of larger threshold velocities decay faster than those of smaller threshold velocities, and they all decay slightly faster than the theoretical prediction. These discrepancies may be due to the fact that the model copepod body was included in the CFD simulations whereas the impulsive stresslet model neglects the body effect and use the Stokes approximation (i.e. zero Reynolds number). Nevertheless, these comparisons validate the present CFD simulation approach, and therefore we can confidently apply the validated approach to simulate the flow field...
associated with copepod escape jumps (for which no PIV flow data are available) and use the CFD output data to calculate several useful quantities that are often difficult to measure directly for both repositioning jumps and escape jumps.

A repositioning jump may involve a few kicks of the swimming legs (e.g. A. tonsa jump 73-2; Table 1, Fig. 7B). The CFD results show that all kicks create vorticity of the same sign as the leading wake vortex, which is associated with the first kick. However, only the leading wake vortex retains its integrity; the other wake vorticities are close to the opposite-signed body vortex (because a repositioning jump is of short distance) and therefore disintegrate quickly by vorticity cancellation. As a result, at the time when the jump stops, the vorticity configuration is still similar to that of a single-kick repositioning jump (not shown).

The flow field associated with an escape jump sequence
An escape jump is more powerful (fast power stroke) and may involve many beat cycles. However, at the initial stage of an escape jump, the spatial extension of the imposed flow field is still very limited even at the time when the thrust is largest (Fig. 8A, Fig. 9A); this is similar to a repositioning jump at the same stage (Fig. 5A). At the time when the copepod completes an escape jump sequence and stops (Fig. 8B, Fig. 9B), the associated flow field consists of two dominant vortex structures: one leading wake vortex ring located near the position where the copepod has executed its first power stroke of the swimming legs, and one vortex surrounding the copepod body. These two vortex structures are of opposite sign but have similar spatial extension. Between these two vortex structures lies an elongated patch of vorticity of the same sign as that of the
vortex around the copepod body. Along the edge of this elongated vorticity patch is a train of isolated blobs of vorticity of opposite sign (i.e., of the same sign as that of the leading wake vortex ring); each of these vorticity blobs corresponds to a power stroke of the swimming legs (subsequent to the first power stroke). However, this train of isolated vorticity blobs is short-lived; the vorticity blobs quickly disintegrate through vorticity cancellation with the nearby elongated vorticity patch of the opposite sign. As a result, in the decay phase the flow field evolves into one leading wake vortex ring plus a deformed vortex structure of opposite sign that surrounds the copepod body and trails behind (Fig. 8C, Fig. 9C). In other words, the major difference in terms of imposed flow disturbance between a slow repositioning jump and a fast escape jump is the elongated vorticity shed from the body in the escape jump. This is also evidenced by the fact that the total circulation of all the wake vortices eventually collapses with the time evolution of the circulation of the leading wake vortex (Fig. 10). The time evolution of the circulation of the leading wake vortex fits well with the theoretical prediction from the impulsive Stokeslet model of Kiørboe et al. (Kiørboe et al., 2010a) (Fig. 10). This is because the leading wake vortex ring is sufficiently isolated from the rest of the vorticity structures. It is therefore suggested that the impulsive Stokeslet model can be used to describe the behavior of the leading wake vortex ring, even for powerful escape jumps. This level of detailed description of the spatiotemporal evolution of the flow field associated with a copepod escape jump sequence has not been available previously.

In terms of the area of influence, the escape jump by a copepod of 0.67 mm prosome length (A. tonsa Jump 90) created comparable, yet stronger, hydrodynamic signals to those of the repositioning jump by a copepod of 1.11 mm prosome length (A. tonsa Jump 58). (Fig. 8 and Fig. 5 were plotted using the same length scale, so that the two areas of influence can be easily compared.) The former copepod achieved a much higher jumping velocity than the latter (compare Fig. 10A and Fig. 7A) even though it was smaller. The escape jump by a C. finmarchicus of 3.0 mm prosome length (C. finmarchicus Jump 212) created much stronger hydrodynamic signals than the two Acartia jumps, differing by orders of magnitudes in terms of both spatial extension and temporal duration. (Note that Fig. 9 was plotted using a different length scale from that used for Fig. 8 and Fig. 5.) An escape jump in general creates stronger and longer lasting hydrodynamic signals than a repositioning jump. For example, the escape of the 3-mm C. finmarchicus left a unidirectional flow trail with velocity vectors pointing to the location of the copepod; the trail was still persistent ~4.5 s after the completion of the jump and the length of the trail was ~5 cm with flow velocity magnitudes >350 mm s⁻¹ (Fig. 9C). Potentially, this allows a rheotactic predator to pursue its escaping prey at rather long distances, because the flow velocity threshold for rheotactic predator responses are in the order of 100 mm s⁻¹ (reviewed by Kiørboe, in press).

Hydrodynamic camouflage

In terms of the spatial configuration and temporal evolution of the jump-associated flow field, the difference between a repositioning
jump and an escape jump sequence can have consequences depending on whether or not an effective hydrodynamic ‘camouflage’ can be achieved. The flow field associated with a repositioning jump has a near mirror image of the wake vortex and the vortex around the copepod body (Fig. 5C), and therefore a rheotactic predator a short distance away may have to choose which side it should attack; this may reduce the probability at which the copepod prey gets caught. Such a near mirror image does not exist in the flow field associated with a copepod escape jump sequence. On the contrary, the flow velocity vectors behind the copepod are all pointing towards the location of the jumping copepod over almost the entire jumping path and over a long time period (Fig. 8C, 9C, 10).

---

**Fig. 9.** *C. finnarchicus* Jump 212 (see Table 1). Instantaneous flow velocity field and vorticity field associated with the copepod escape jump at (A) ~0.0007 s after the initiation of the jump, at which time the thrust was approximately maximal in the first jump, (B) ~0.232 s after the initiation of the jump, at which time the jump sequence was approximately completed, and (C) ~4.5406 s after the initiation of jump. Plotted in the meridian plane above the axisymmetric axis are equal-length flow velocity vectors showing flow directions only. For clarity, only a small fraction of the CFD-simulated vectors are shown. The line contours of the vorticity field overlap on top of the vector field: the grey contour lines indicate zero vorticity, the blue contour lines show negative vorticity, and the red contour lines indicate positive vorticity. In A and B, the negative vorticity range is [–6, –0.5] s⁻¹ with increments of 0.5 s⁻¹, and the positive vorticity range [1, 141] s⁻¹ with increments of 10 s⁻¹. In C, the negative vorticity range is [–3.56, –0.04] s⁻¹ with increments of 0.04 s⁻¹, and the positive vorticity range is [0.04, 0.28] s⁻¹ with increments of 0.04 s⁻¹. Plotted in the meridian plane below the axisymmetric axis are color contour lines of the flow velocity magnitude. A stationary frame of reference is used. The start (left) and stop (right) positions of the copepod are shown as the two ellipses labeled ‘C’.

**Fig. 10.** Time evolutions of the CFD-simulated total circulation of all the wake vortices and circulation of the leading wake vortex associated with two copepod escape jumps: (A) *A. tonsa* Jump 90 (see Table 1), and (B) *C. finnarchicus* Jump 212 (see Table 1). Also plotted is the fit of Eqn 6 to the CFD-simulated circulation data of the leading wake vortex.
Fig. 9C), and the flow structure may therefore efficiently inform a rheotactic predator about the position of the copepod. Thus, the escape jumps should only be executed as the last resort to avoid immediate predation. Also, as pointed out by Jiang and Kiørboe, viscous vortex rings created by copepod repositioning jumps may aid the copepod in hiding among those viscous vortex rings that are created by physical processes (turbulence) (Jiang and Kiørboe, in press). This is because the background flow field is likely to be made up of many such viscous vortices, as any unbounded flow that has net linear momentum (or momentum packet) eventually decays to the unique vortex ring solutions of the Stokes equations (Phillips, 1956; Stanaway et al., 1988; Saffman and Leonard, 1992; Afanasyev, 2004). This is, however, unlikely to be the case for the flow field associated with a copepod escape jump sequence, because the elongated, long-lasting, unidirectional flow trail behind the copepod may be more likely to be ‘read’ by a rheotactic predator as biologically generated.

**Mean thrust, cost of jump and Froude propulsion efficiency**

The mean thrust $T$ reported in Table 1 for each power stroke ranges from $1.66 \times 10^{-6}$ to $1.58 \times 10^{-4}$ N, varying greatly for different jump types, copepod body sizes and maximum jump velocities. The values for the escape jumps are similar to those measured experimentally (Alcaraz and Strickler, 1988; Lenz et al., 2004) or estimated from a previous simpler model (Kiørboe et al., 2010b). As pointed out by Kiørboe et al. the force production generated by the swimming legs, when normalized by the mass of the muscles, is much higher than reported for the muscle motors of any other organisms (Kiørboe et al., 2010b).

$W_{CFD}$ reported in Table 1 for each beat cycle ranges from $2.67 \times 10^{-9}$ to $9.84 \times 10^{-7}$ J, also varies significantly for different jump types, copepod body sizes and maximum jump velocities. For the three simulated repositioning jumps the cost of the jump corresponds to between 4 and 14% of the metabolic rate over the power stroke duration of the jump [metabolic rate computed from empirical size–metabolism relationships in Ikeda et al. (Ikeda et al., 2001)]. At a jump frequency of 1 Hz, which is high (Kiørboe et al., 2010a), the time-averaged cost of repositioning jumps is less than 1% of the total metabolic expenditure. The much more powerful escape jumps are of course energetically more expensive, corresponding to more than 400% of the instantaneous metabolic rate; however, such jumps are rare and similarly accounts for only a minute fraction of the metabolism of the copepod. These considerations suggest that jumps come at a very small energetic cost, consistent with most of the earlier estimates (e.g. Vlymen, 1970; van Duren and Videler, 2003). The total mechanical work is the mechanical work expended in moving the swimming legs through the water. Of the $W_{CFD}$, ~50–93% was used to overcome the hydrodynamic resistance (including the added mass effect) acting on the accelerating body of the copepod during the power stroke durations, and ~5–47% was used to accelerate the copepod body itself (Table 1). These two parts should be regarded as the useful mechanical work done by the copepod during the power stroke. Together they account for a significant share of the total mechanical work; the Froude propulsion efficiency was very high, ranging between 0.94 and 0.98 (Table 1). This result appears counter to our expectation because the calculated values of the Froude propulsion efficiencies are significantly greater than the known values (0.2–0.78) estimated for small swimmers as reviewed by Vogel (Vogel, 2003). We suggest that this difference is due to the unsteady nature of jumps as opposed to the steady cruising motion of the small swimmers examined by Vogel (Vogel, 2003) (see below). However, Morris et al. also obtained a low Froude propulsion efficiency (0.34) for the escape jump of the copepod *Pleuromamma xiphas* with the Reynolds number (>1000) similar to one of our simulated jumps (*C. finmarchicus* Jump 212; Table 1) (Morriss et al., 1985). This discrepancy is probably due to the different methods in calculating the hydrodynamic resistance acting on the accelerating copepod body. We directly calculated the hydrodynamic resistance from the area integral of pressure and shear stress over the copepod body surface, whereas empirical drag laws were used by Morris et al. (Morris et al., 1985). We note that the empirical drag laws were derived for well-developed steady-state boundary layer conditions, which might not be suitable for the copepod jump where only a very thin and highly unsteady boundary layer develops in the course of the few milliseconds power stroke duration.

Wasted mechanical work is the work that the backward traveling viscous wake vortex carries away in each power stroke. According to Saffman (Saffman, 1992), the kinetic energy of an axisymmetric distribution of vorticity is:

$$K = \pi \rho \int_0^L \psi_\phi dx \, dr.$$  \hspace{1cm} (12)

Based on the vorticity ($\psi_\phi$) and streamfunction ($\psi_\psi$) given by the impulsive stresslet model (Jiang and Kiørboe, in press), the kinetic energy of one of the two viscous vortex rings is:

$$K = \frac{\rho M^2}{20\sqrt{2\pi^{3/2}(4\nu t)^{3/2}}}.$$  \hspace{1cm} (13)

where $M$ is the strength of the impulse stresslet. The CFD simulation data have been fitted to Eqn 5 to determine $M$. Thus, the kinetic energy of the CFD-simulated wake vortex ring can be determined as:

$$K = \frac{\rho M^2_{final,CFD}}{20\sqrt{2\pi^{3/2}(-4\nu t)^{3/2}}}.$$  \hspace{1cm} (14)

(see Table 1 for data). Calculations using Eqn 14 show that the kinetic energy of the wake vortex ring is only a few percent of the total mechanical work, suggesting a high (>90%) Froude efficiency. This analysis is reassuring for our simulation results that suggest tiny wasted mechanical work. This is possible because the generated viscous wake vortex is of a very limited spatial extension and temporal duration (Kiørboe et al., 2010a; Jiang and Kiørboe, in press). As shown by Jiang and Kiørboe the rapidity and impulsiveness of the jump is necessary for generation of the wake vortex and therefore essential for such high Froude propulsion efficiencies (Jiang and Kiørboe, in press). This contrasts with steady self-propulsion where a spatially well-extended backward momentum jet is generated which probably costs much more mechanical energy to maintain, leading to a lower efficiency. Thus, not only are copepods capable of a force production during an escape jump that is unparalleled, but the unsteady and impulsive nature of the jump and the consequent high propulsion efficiency allows the copepod to get the most out of this force production in terms of velocity achieved and distance covered. We speculate that jumping copepods benefit from impulsive generation of viscous vortex rings by achieving maximized impulse generation while wasting only tiny amounts of mechanical energy in generating the wake vortices. These, of course, are essential features of a successful escape jump and are likely to be key to the evolutionary success of the copepods in pelagic environments.
LIST OF SYMBOLS AND ABBREVIATIONS

\( a \)  
half the prosome length

\( A(t) \)  
forcing magnitude at the tip of the swimming leg

\( \text{CFD} \)  
computational fluid dynamics

\( \text{CV} \)  
control volume

\( D(t) \)  
instantaneous hydrodynamic resistance

\( \text{F} \)  
field of body force

\( \text{F}_{\text{imp}} \)  
field of the impulsive stresslet

\( I_{\text{CFD}} \)  
fitted hydrodynamic impulse

\( L_{\text{imp}} \)  
typical length of the swimming legs

\( M \)  
body mass of the model copepod

\( t_{\text{imp}} \)  
fitted impulsive stresslet strength

\( \text{MUSCL} \)  
monotone upstream-centered schemes for conservation laws

\( \text{PIST} \)  
pressure-implicit with splitting of operators

\( \text{PIV} \)  
particle image velocimetry

\( r \)  
radial distance from the x-axis

\( R_{*} \)  
length scale for determining the scaling of area of influence

\( S_{*} \)  
area of influence

\( t_{*} \)  
time scale for determining the area of influence

\( T \)  
mean thrust

\( T(t) \)  
instantaneous thrust

\( U(t) \)  
velocity threshold

\( U^{*} \)  
velocity threshold

\( \text{UDF} \)  
user defined function

\( \text{W}_{\text{CFD}} \)  
fitted total mechanical work

\( \Gamma(t) \)  
time series of the wake vortex circulation

\( \varepsilon \)  
aspect ratio of the copepod

\( \eta \)  
Froude propulsion efficiency

\( \phi \)  
azimuthal coordinate

\( \omega_{\text{azimuthal}}(x, r, t) \)  
instantaneous azimuthal vorticity field

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REFERENCES


