A MODEL OF RAPID-START SWIMMING AT INTERMEDIATE REYNOLDS NUMBER: UNDULATORY LOCOMOTION IN THE CHAETOGNATH SAGITTA ELEGANS

BY CHRISTOPHER E. JORDAN

Department of Zoology NJ-15, University of Washington, Seattle, WA 98195, USA

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Summary

The mechanics and kinematics of accelerational undulatory locomotion by the chaetognath Sagitta elegans (Verrill, 1873) are studied with a combination of high-speed cinematography (200 frames s\(^{-1}\)) and mathematical modeling. The model is constructed such that it predicts body velocity for an organism starting from rest and accelerating rapidly by swimming with prescribed wave kinematics. The speed of the undulatory propulsive waves and the number of these waves on the body is highly conserved across 11 individuals, while the wave amplitude is positively related to distance traveled in the first 65 ms of swimming. There is excellent agreement between these data and predictions of body translations that are based on a mathematical model for this mode of locomotion. The model also shows that instantaneous forces generated by the undulating body are much larger than average forces and consist of non-trivial inertial terms, even for such small organisms. The model also shows that the distance traveled over a fixed time interval is limited by the maximum muscle stress that can be physiologically generated. Peak instantaneous force represents a mechanical upper boundary to thrust production and, hence, a limit to performance.

Introduction

Studies of aquatic locomotion have traditionally focused on extremes in body size and speed, emphasizing either relatively large fast organisms (>10 cm, >1 ms\(^{-1}\)) (Lighthill, 1975; Webb, 1983; Weihs, 1973) or rather small slow organisms (<1 mm, <1 cm s\(^{-1}\)) (Gray and Hancock, 1955; Wu et al. 1975; Purcell, 1977). This focus does not reflect a natural bimodal distribution of animal sizes or speeds, but is due to the simplifying assumptions made for the equations describing fluid motions in either case. In general, incompressible fluid flows are governed by a balance of three forces: pressure and inertial and viscous stresses. For simplicity, the physical realm of large fast organisms can be represented

Key words: intermediate Reynolds number, chaetognaths, swimming, acceleration, Sagitta elegans.
largely as a balance of pressure and inertial forces, while the balance of pressure and viscous forces dominates the realm of small slow swimmers.

A convenient way to distinguish between these two physical realms is with the Reynolds number \((Re)\), the dimensionless ratio of inertial to viscous forces given by \(Ul/v\), where \(U\) is a characteristic velocity, \(l\) is the characteristic length and \(v\) is the kinematic viscosity of the fluid. For high \(Re\) (>1000), the majority of thrust arises from organisms doing work against a fluid’s mass, while at low \(Re\) (<1), viscous forces dominate thrust production. In reality, inertial and viscous forces exist at all \(Re\) values, but the work done to one outweighs the other at the extremes in \(Re\). However, a significant fraction of aquatic life occurs in a physical realm where neither force dominates. In this intermediate \(Re\) range (1–1000), inertia and viscosity are both of similar magnitude and neither can be ignored. Although the intermediate \(Re\) range is not strictly defined, the choice of between 1 and 1000 as intermediate is physically appropriate. Below an \(Re\) of 1, drag coefficients are proportional to \(Re^a\) where \(a\) is derived from an approximation of first principles (e.g. Oseen and Blasius solutions, Schlichting, 1979). Above an \(Re\) of 1000, drag coefficients are predicted and measured to be roughly constant. However, for 1<\(Re<1000\), no simple rules exist for predicting force coefficients as functions of \(Re\). In this case, one must resort to approximate methods, such as those used in this study, to calculate the force generated by an undulating body.

In this study I combine high-speed cinematography and mathematical modeling to determine (1) the relative contributions of viscous and inertial forces to thrust, (2) the effect of changes in morphology and kinematics on force production and (3) a relevant measure of locomotory performance at intermediate \(Re\). The model combines elements of the more classical high \(Re\) reactive theories of Lighthill (1975) with those of the low \(Re\) resistive theories of Gray and Hancock (1955) to calculate the force generated by an accelerating undulating body. The situation that I have modeled is one in which an organism starts from rest and rapidly accelerates for a short time. I have also employed a mechanical boundary to performance, the maximum isometric stress of contracting muscle (Hoyle, 1983), to avoid the unrealistic situation whereby model predictions for generated forces exceed those that are physiologically possible.

Studies of organisms swimming at either high or low \(Re\) have identified different optimal shapes and behaviors imposed by the fluid environment’s respective balance of forces. At low \(Re\), the predominance of viscous forces implies a drag strongly dependent on surface area not shape. Also, since viscous flows lack any time dependence, oscillatory propulsors that are symmetrical in time produce no net thrust (Lighthill, 1975). At high \(Re\), shape becomes very important in minimizing the magnitude of the velocity gradient and separation (Wu, 1971). At intermediate \(Re\), both inertial and viscous constraints need to be met in order to develop optimal morphologies or kinematics.

As a consequence of the difficulties of solving the equations of fluid motion and of measuring the relevant flow variables at intermediate \(Re\), the effects of morphology and kinematics on force production for organisms inhabiting this
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Fig. 1. (A) Dorsal view of an adult Sagitta elegans (after Hyman, 1959). The specimen is 20 mm in length, with a maximum body width of 1.8 mm. In the model, the region of the body without fins is represented as a cylinder with sectional surface area $S_b = 2\pi r dx$ and projected area $A_b = 2\pi r dx$. The region with fins is represented as a cylinder with flat plates of height $f$, such that the sectional surface area is $S_f = 2(\pi r + 2f) dx$ and projected area $A_f = 2(\pi r + f) dx$. In the model, the fins are located on the body as depicted in this drawing. (B) Lateral view of an adult chaetognath. The animal is shown in normal swimming posture, moving at speed $U$ with propulsive wave speed $c$. The body wave amplitude grows from head to tail and can be described by its local displacement $h(x,t)$ and its limit $\epsilon(x)$. The enlarged section shows $\theta$, the angle a body section makes with the instantaneous direction of travel.

realm are very poorly understood. This study directly addresses the effect of variation in body morphology and kinematics on undulatory locomotion and defines a good measure of locomotory performance at this physical scale. Previous work on undulatory locomotion at intermediate $Re$ focused on the work required or the energetic efficiency of two swimming modes without discussing the corresponding variability in locomotory performance (Vlymen, 1974; Weihs, 1974).

I address the question of locomotion at intermediate $Re$ using the chaetognath Sagitta elegans (Fig. 1A). These animals swim in rapid 100 ms bursts of dorso-ventral undulatory propulsive waves that pass from head to tail (Fig. 2). Chaetognaths generate this mode of locomotion by rapid contractions of the body wall musculature that runs nearly from head to tail without opposing circular or
Fig. 2. Tracings made from high-speed 16 mm ciné films at 200 frames s\(^{-1}\). Every fourth frame is shown. The top tracing shows the frames superimposed.
radial muscles (Duvert and Salat, 1980). It is not known whether the longitudinal muscles contract locally to produce the body's undulations (Duvert and Savineau, 1986) or whether some type of moving buckling wave (C. E. Jordan, personal observation) is produced as a result of opposition to the muscles by a fiber-wound hydrostatic skeleton (Ahnelt, 1984).

A thorough understanding of the physical environment at intermediate Reynolds numbers is necessary in order to evaluate its role in constraining the morphology and kinematics of aquatic organisms at this scale. For example, the entire phylum Chaetognatha shows remarkable morphological similarity (Hyman, 1959). All 65 or so species of chaetognaths are similar to the *S. elegans* depicted in Fig. 1A, with a long slender body, a tail fin, one or two pairs of lateral fins and grasping spines on the head for which the phylum is named.

### Materials and methods

#### Specimens

Chaetognaths were collected in San Juan Channel (San Juan Island, Washington) at dusk from a depth of 75 m with a 1-m 635-μm mesh plankton net with a sealed cod end. To avoid damaging the specimens the net was pulled vertically at less than 0.5 m s\(^{-1}\). Healthy *Sagitta elegans*, roughly 20 mm in length (mean = 20.4 mm, s.d. = 2.2 mm, \(N=11\)), were separated from other zooplankters and maintained in 41 jars immersed in running sea water (12–15°C) at densities of one animal per liter. Individuals were used within 48 h of capture.

#### Kinematics

All filming was carried out with a Red Lake Locam (51003 with Nikon 55 mm 3.5f macro lens) at 200±10 frames s\(^{-1}\), using Ektachrome 7250 color film (ASA 400). Animals were filmed swimming in a 11 rectangular container cooled with a recirculating water jacket to keep the chamber temperature between 10 and 12°C. Illumination was provided by a Nikon MKII fiber light.

Chaetognaths were made to swim by tapping on the chamber or by direct contact with a pipet. Each swimming event, or sequence, was filmed for roughly 1 s. The powered swimming phase lasted less than 250 ms. Eleven sequences, representing seven individuals, were used in the analysis. Sequences were chosen in which the animals started from rest and remained in the plane of focus and field of view while swimming in a fairly straight path.

Sequential frame analysis was used to determine the three important kinematic variables: wave number, wave speed and wave amplitude. The first 50 frames (250 ms) of each sequence were digitized by drawing a line down the center of the image projected onto a digitizing pad (SummaGraphics). A 128-point cubic spline applied to these digitized data yielded a continuous curve describing body position in each frame. Each digitized frame was fitted with a principal component regression line, whose slope gave the instantaneous direction of travel and whose
grand mean gave instantaneous coordinates of the center of mass. Distance traveled, velocity and acceleration were thus determined by tracking the grand mean (center of mass) from frame to frame. The speed, number and amplitude of propulsive waves were determined by recording the maximum of each half-wave as it passed along the body.

**Theory**

A mathematical model of chaetognath locomotion was constructed by combining the existing high Reynolds number reactive theories of Lighthill (1975) with the low Reynolds number resistive theories of Gray and Hancock (1955). The fundamental idea underlying Lighthill’s theories is that propulsive forces, proportional to lateral body accelerations, arise from reactions to fluid accelerations normal to the surface of the animal. The resistive theories applied to undulatory swimming, as developed by Gray and Hancock (1955), assume that propulsive forces arise from viscous stresses generated by rearward components of the motion due to whole-body undulations.

Since resistive theories do not account for fluid inertial forces, and the reactive theories contain no viscous terms, any model of locomotion at intermediate Re must combine both theories in order to include the situation in which both viscous and inertial forces are of comparable magnitude. The model uses as a basis Newton’s law, \( F_t = M \frac{dU}{dt} \), where \( M \) is the animal’s mass, \( U \) is the forward speed and \( F_t \) is the sum of forces generated by the body acting on the fluid. In this case, force is calculated sectionally for both the inertial and viscous components, and then summed along the length of the body at each instant in time. Calculated in this manner, force can then be used to predict the body speed at the next instant in time by applying Newton’s law and solving the force balance equation numerically.

**Reactive forces**

Reactive theory for elongated body locomotion describes a body of length \( l \) that is displaced laterally by \( h(x,t) = \Gamma(t) \epsilon(x) \sin\left(\omega t - \left(\frac{x}{c}\right)\right) \), where \( x \) is the position along the length, \( \omega \) is the angular frequency, \( c \) is the wave speed, \( \Gamma(t) \) generates the growth in amplitude during the first 20 ms of swimming and \( \epsilon(x) \) is a function that describes the growth in amplitude along the length, or amplitude envelope (Fig. 1B; symbols for these and all following equations are defined in the Appendix). Thus, the lateral velocity \( V \) of any section of a body moving at a forward speed \( U \) is given by:

\[
V = \partial h / \partial t + U(t) \partial h / \partial x .
\]  
(1)

The sectional force (\( F_s \)) generated normal to the body at \( x \) is the product of the mass and lateral acceleration:

\[
F_s = \left[ \partial^2 / \partial t^2 + U(t) \partial^2 / \partial x^2 \right] \left[ m(x) V(x,t) \right] ,
\]  
(2)
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where \( m(x) \) is the sectional added mass (see for example Lighthill, 1975, chapter 4). Equations 1 and 2 give the instantaneous force in the direction of travel:

\[
F_x(t) = \int_0^1 \sin \theta(F_x) dx = \int_0^1 \sin \theta(m(x) \partial^2 h / \partial t^2 + 2m(x)U(t) \partial^2 h / \partial x \partial t + U(t) V dm / dx + m(x)U(t)^2 \partial^2 h / \partial x^2 + m(x)(dU/dt)(\partial h / \partial x)) dx, \tag{3}
\]

where \( \theta \) is the angle between segments of the body and the instantaneous direction of movement (Fig. 1B).

Resistive forces

For steady-state flows, the two components of drag on a section are given by:

\[
D_n = \frac{1}{2} \rho A C_{dn} V_n^2, \tag{4}
\]

\[
D_t = \frac{1}{2} \rho S C_{dt} V_t^2, \tag{5}
\]

where \( S \) is sectional surface area, \( A \) is projected area, the subscripts \( n \) and \( t \) represent normal and tangential, \( C_{dn} \) and \( C_{dt} \) are the sectional drag coefficients for normal and tangential flows and \( V_n (= V \cos \theta) \) and \( V_t (= V \sin \theta) \) are the normal and tangential components of velocity. Once the resistive terms are resolved into the direction of body translation, thrust and drag forces differ only in sign. Thus, equations 3, 4 and 5 can be combined to give the total instantaneous force generated by the body:

\[
F_x(t) = \int_0^1 \{ \sin \theta(\partial^2 h / \partial t + U(t) \partial h / \partial x)[m(x)V(x,t)] + \frac{1}{2} \rho (AC_{dn} V_n^2 + SC_{dt} V_t^2) \} dx. \tag{6}
\]

Equation 6 is numerically integrated along the body with \( m(x) \) constant within each body section. Also, since the angle that the body makes locally with the direction of travel is small \( (\theta < 10^\circ) \), the following trigonometric approximations were used:

\[
\sin \theta \approx \partial h / \partial x, \tag{7}
\]

\[
\cos \theta \approx [1 - (\partial h / \partial x)^2]^{1/2}. \tag{8}
\]

Thus, setting the force in the direction of travel as equal to the mass of the chaetognath times the change in body velocity and discretizing, equation 6 becomes:

\[
M \partial U / \partial t = \sum_{j=1}^N \left( \partial h / \partial x[\partial^2 h / \partial \partial t + U(t) \partial h / \partial x][m(x)V(x,t)] + \frac{1}{2} \rho (AC_{dn} V_n^2 \partial h / \partial x + SC_{dt} V_t^2 [1 - (\partial h / \partial x)^2]^{1/2}) \right) \Delta x. \tag{9}
\]

The body morphology of \textit{Sagitta elegans} is represented by the shape-dependent
terms, \( m, C_d, A \) and \( S \) of equation 9. In cross flow, the body approximates a cylinder of constant radius \( r \) or a rectangular flat plate of height \( 2(f+r) \) in the regions with fins or at the tail. For longitudinal flows, I treat the drag as purely frictional; thus, the body is represented by sectional flat plate coefficients with areas \( S_b \) in the regions without fins and \( S_f \) in the regions with lateral or tail fins (see Fig. 1 for a description of sectional geometry and location of fins). The expressions for describing the local cross-sectional shape-dependent terms are as follows. In the region without fins (curves fitted for cylinders in cross flow and flat plates in streamwise flow from White, 1974, and Vogel, 1981):

\[
C_{dn} = 1 + 10(Re_n)^{-2/3}, \quad Re_n = 2rV_n/v, \tag{10}
\]

\[
C_{dl} = 0.64(Re_{xl})^{-1/2}, \quad Re_{xl} = xV_l/v. \tag{11}
\]

In the region with fins (curves fitted to data for flat plates in cross flow from Hoerner, 1965):

\[
C_{dn} = 10^{[1.28-0.809(\log Re)+0.134(\log Re)^2]}, \quad Re_n = 2(r+f)V_n/v, \tag{12}
\]

\[
C_{dl} = 0.64(Re_{xl})^{-1/2}. \tag{13}
\]

The only drawback to this choice of force coefficients is that as the fin height goes to zero the two expressions for \( C_{dn} \), with and without fins, do not converge. At \( f=0 \) these two expressions differ by a factor of 1.8, primarily as a result of the inherent differences between flows around a cylinder and those around the sharp edges of a flat plate. Ideally, one should use the values of \( C_{dn} \) for a cylinder with appended flat plates; to my knowledge, however, no such geometry exists in the literature.

Equation 9 was rearranged to give \( dU/dt \) as the dependent variable. In this form, it is numerically integrated with respect to time by a fourth-order Runge-Kutta method to yield predictions of instantaneous body speed. Therefore, for a given set of kinematic variables, or initial conditions, the model predicts the forces generated by the propulsive wave and uses these to calculate body translations.

**Results**

**Kinematics**

The duration of the swimming bursts ranged from 65 to 240 ms (mean=128 ms, s.d.=65 ms, \( N=11 \)), during which time the individuals traveled from 3 to 17 mm (mean=8.19 mm, s.d.=4.78 mm, \( N=11 \)). To standardize for variation in time of powered swimming between individuals, I examined the kinematics only over 65 ms, the longest swimming duration common to all seven (Table 1). All measures of kinematic variables are scaled to the individual’s body length.

Over the first 65 ms, the animals swam at an average speed of 2.99 body length s\(^{-1}\) (BL s\(^{-1}\)), through an average distance of 4.1 mm (Fig. 3). Despite the variability in distance traveled, the kinematics of the propulsive wave were fairly well conserved, with an average wave speed of 12.0 BL s\(^{-1}\), approximately four
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Table 1. The observed kinematic variables for the first 65 ms of 11 swimming events

<table>
<thead>
<tr>
<th>Trial number</th>
<th>Size (mm)</th>
<th>Speed (BL s⁻¹)</th>
<th>Distance (mm)</th>
<th>Wave amplitude (BL)</th>
<th>Wave speed (BL s⁻¹)</th>
<th>Wave number</th>
</tr>
</thead>
<tbody>
<tr>
<td>01</td>
<td>21.5</td>
<td>2.042</td>
<td>2.9</td>
<td>0.030</td>
<td>9.3</td>
<td>1.2</td>
</tr>
<tr>
<td>02</td>
<td>21.5</td>
<td>1.199</td>
<td>1.7</td>
<td>0.027</td>
<td>11.5</td>
<td>1.4</td>
</tr>
<tr>
<td>03</td>
<td>18.2</td>
<td>2.221</td>
<td>2.7</td>
<td>0.038</td>
<td>12.5</td>
<td>1.4</td>
</tr>
<tr>
<td>04</td>
<td>22.5</td>
<td>3.650</td>
<td>5.3</td>
<td>0.050</td>
<td>8.8</td>
<td>1.2</td>
</tr>
<tr>
<td>05</td>
<td>22.5</td>
<td>2.208</td>
<td>3.4</td>
<td>0.036</td>
<td>15.3</td>
<td>1.4</td>
</tr>
<tr>
<td>06</td>
<td>18.0</td>
<td>5.492</td>
<td>6.8</td>
<td>0.037</td>
<td>15.0</td>
<td>1.3</td>
</tr>
<tr>
<td>07</td>
<td>15.8</td>
<td>2.329</td>
<td>2.4</td>
<td>0.034</td>
<td>10.0</td>
<td>1.3</td>
</tr>
<tr>
<td>08</td>
<td>22.1</td>
<td>2.466</td>
<td>3.7</td>
<td>0.035</td>
<td>11.0</td>
<td>1.3</td>
</tr>
<tr>
<td>09</td>
<td>22.1</td>
<td>2.541</td>
<td>3.8</td>
<td>0.042</td>
<td>10.3</td>
<td>1.4</td>
</tr>
<tr>
<td>10</td>
<td>19.9</td>
<td>3.848</td>
<td>5.1</td>
<td>0.037</td>
<td>10.6</td>
<td>1.3</td>
</tr>
<tr>
<td>11</td>
<td>19.9</td>
<td>4.966</td>
<td>6.7</td>
<td>0.028</td>
<td>18.0</td>
<td>1.3</td>
</tr>
<tr>
<td>Mean</td>
<td>20.4</td>
<td>2.997</td>
<td>4.05</td>
<td>0.036</td>
<td>12.0</td>
<td>1.3</td>
</tr>
<tr>
<td>s.d.</td>
<td>2.2</td>
<td>1.325</td>
<td>1.71</td>
<td>0.065</td>
<td>2.9</td>
<td>0.1</td>
</tr>
</tbody>
</table>

All values are scaled to the body length given in column 2.

Speed is calculated as the net displacement divided by 65 ms, and is thus an underestimate of final speed. All other values are taken directly from digitized high-speed cine film frames.

The amplitude height is the \( r \) term in the exponential wave amplitude envelope for each swimming event (see Fig. 4) and is calculated as the average wave height over the central 60% of the body.

The variable that showed the greatest variation between individuals, and the one that theory predicts can account for the variation in distance traveled, is the amplitude of the propulsive wave. In all cases the wave grew as it passed from head to tail (Fig. 4), but tended to be larger in those individuals that traveled farther (Kendall’s ranked correlation, \( r=0.51, \ P<0.05, \ N=10; \) Table 1).

Theory predicts that increased wave amplitude should produce increased thrust, if all other kinematic variables remain constant. Of the 11 swimming events analyzed, 10 exhibited fairly well-conserved kinematic variables, but one, no. 11 in Table 1, had a wave speed significantly different from the other 10 (\( t \)-test, \( t_s=2.82, \ P=0.02 \)). Hence, in comparing the dependence of performance on wave amplitude, I have not included this event since it violates my assumption of a constant wave speed over all swimming events, though it is still included in the data set as it represents the possible variation in kinematic variables. The model agrees with the theoretical prediction that an increased wave speed generates increased thrust, but I am limiting my study to the effect on performance by changing a single kinematic variable.

Comparison with theory

The kinematics of the wave form are incorporated into the model via a function describing the lateral displacements of the body. For this analysis, I chose an
Fig. 3. Observed distance traveled with time during 11 swimming events. All seven individuals started from rest, and swam when stimulated. No individual was used more than twice.

exponential function of the form $e(x) = a + \beta e^{\gamma x}$ (Fig. 1B) to generate an amplitude envelope with fairly constant height $\alpha$ and a sharp increase at the tail. To determine the coefficients $\alpha$, $\beta$ and $\gamma$ I fitted this function with a least-squares regression routine to the absolute value of the observed amplitude distribution (Fig. 4), ignoring the displacement of the head since it contributes negligibly to thrust (Lighthill, 1975). The amplitude measures ($\alpha$) specific to each swimming event, given in Table 1, were determined by averaging the wave heights measured over the central 60% of the body. This method does not include the large wave amplitude observed at the head. I chose to ignore the contribution to thrust generated by the larger amplitude over the first 20% of the body on experimental and theoretical grounds. In particular, Lighthill (1975) has demonstrated that the thrust generated by an undulating body at high $Re$ is determined primarily by the amplitude at the trailing edge, where momentum is shed into the wake. In the resistive case, Lighthill (1975) showed that thrust depends on the mean square cosine of $\theta$. This implies that resistive thrust is a function of the average wave height along the entire body and is less sensitive to localized peaks, such as in the head and tail regions. Additionally, the average wave height over the first 20% of the body differs by only 10% from $\alpha$, the average over the center 60% of the body.

Using the mean values for $\alpha$, $\beta$, $\gamma$, $\lambda$, $l$, $c$ and $\omega$, the model generated a predicted body translation (Fig. 5A) that was well within the range of observed values
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Fig. 4. Distribution of the absolute value of propulsive wave maxima for seven individuals during 11 swimming events, scaled to body length. Each circle represents the peak of a wave on the body during the powered phase of swimming. Values were taken from digitized high-speed ciné film frames shot at 200 frames s⁻¹. The heavy line is $e(x)$, the exponential curve fitted to represent the amplitude envelope in $h(x,t)$.

(Fig. 3). When the function $e(x)$ is fitted to the values for the individuals with the largest and smallest amplitude distribution, roughly corresponding to the steepest and shallowest curves in Fig. 3, comparing predicted body translations with those measured for these two individuals, very good agreement was obtained between the observed and predicted distances traveled (Fig. 5B,C). Furthermore, as the propulsive wave amplitude is varied, the model continues to be a good predictor of distance traveled in that there is no trend in the goodness of fit with amplitude height (Kendal’s ranked correlation of residuals vs observed, $P>0.5$).

Discussion

Because predicted and measured displacements are well correlated (Wilcoxon signed rank test, $P=0.02$), the model developed here gives reasonable estimates of average propulsive forces. To test the role of animal behavior and morphology in generating forces, I define distance traveled over a short interval of time as the most appropriate performance criterion for the chaetognath *Sagitta elegans*. However, whenever a performance measure increases without being limited by changes in behavior or morphology, as is the case here with increasing propulsive wave amplitude, limitations to force production must be considered in order to generate physiologically feasible motion (Daniel and Meyhöfer, 1989; Meyhöfer...
Fig. 5. Model predictions of distance traveled with time. (A) For this simulation, predictions were made based on the average kinematics shown in Table 1. (B) The bold line is the measured swimming performance of the individual with the largest propulsive wave amplitude (no. 4, Table 1). The solid line is the predicted swimming performance based on the kinematics of this individual. (C) A comparison of observed and predicted swimming performance for the individual with the smallest wave amplitude (no. 2, Table 1).

The model was originally developed to predict average forces generated by the body, but it does so by integrating sectional instantaneous forces and, thus, is a predictor of local instantaneous stresses generated by the body wall musculature. Amidst the scaling and evolutionary arguments, emerge rules for undulatory locomotion at intermediate $Re$ that apply broadly to many aquatic organisms.

Limitations to the model

I have made several assumptions to simplify the hydrodynamic analysis. While the reactive terms are fully unsteady and account for fluid accelerations, the resistive terms are calculated in a quasi-steady manner, ignoring the time dependence of their development. The coefficients of drag, both normal and longitudinal, are taken from published values for similar shapes moving through a fluid at a constant velocity (White, 1974; Hoerner, 1965). In reality, development of flow patterns, wake formation and separation are all time-dependent, and may
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affect the magnitude of the drag and added mass coefficients (Schlichting, 1979; Daniel, 1984). Additionally, fin–tail and fin–body interactions were neglected by assuming that fin wakes do not affect relevant flows about downstream structures. However, recent experimental work shows little difference between quasi-steady predictions and measured forces on an oscillating appendage at low and intermediate \( Re \) (Williams, 1990).

The choice of distance traveled over a short interval of time as the best criterion of performance stems from the assumption that chaetognaths swim rapidly either to avoid predation or to attack motile prey. There are few published observations of predation on chaetognaths by fishes or other zooplankters, though it has been noted that many chaetognath species are cannibalistic (Ghirardelli, 1968). \( S. \) elegans swims when disturbed either by direct contact or in response to an approaching object (C. E. Jordan, personal observation), indicating that they are capable of an escape response. Velocities of particles in the flow field of suction-feeding fish (Lauder and Clark, 1984) are similar to those observed for chaetognaths on the same time scale, implying that \( S. \) elegans is able to escape fish predation. There have been several studies of predation by chaetognaths focusing on prey detection (Feigenbaum and Reeve, 1977; Newbury, 1972), but with no reference to the whole-body kinematics of feeding. Until observations show otherwise, it is reasonable to assume that \( S. \) elegans swims in rapid bursts in order to escape predation or to capture prey. A rapid start-up would then be directly correlated to survival and, in an adaptationist sense, the behavior and morphology of \( S. \) elegans could be selected to optimize this measure of swimming performance.

Correlates of force, morphology and behavior

Despite any limitations and assumptions, the model, constructed by summing the instantaneous forces along the body, is a reasonable predictor of body translation as a function of the kinematics of the propulsive wave. The model accurately predicts the acceleration of a body started from rest by numerically extending existing constant body velocity theory into a time-dependent form. The model also predicts an increase in average thrust produced by the body with increases in wave amplitude corresponding to the increased performance measured in individuals with increasing wave amplitude.

The experimental observations of chaetognaths show a large variation in the distance traveled in the first 65 ms of swimming and, hence, a large variation in performance. What then are the mechanical determinants of locomotion such that a variation in performance can be correlated with a change in behavior or morphology? At low \( Re \), thrust is correlated positively with the square of wave amplitude and number (Gray and Hancock, 1955), while at high \( Re \), thrust is correlated with the square of wave amplitude (Lighthill, 1975; Daniel, 1988). However, the mechanical determinants of performance at intermediate \( Re \) are not necessarily a linear combination of these results. Average forces scale as the amplitude squared (see Fig. 8A,B), but viscous forces can predominate instantaneously (see Fig. 7). Fig. 6 shows the model’s prediction for distance traveled
Fig. 6. Comparison of the model (bold line) with a purely resistive (solid line) and a purely reactive (dashed line) case. Both A and B represent the same simulation; A is a detail of the first 100 ms. In this simulation, the model is run only with the average kinematic values (Table 1, Fig. 5A) and compared with both a run in which only the viscous terms (see equations 1, 5 and 6) are present (the resistive limit) and a run in which only the inertial terms (see equation 4) are present (the reactive limit). Note that the two limiting cases do not sum to the case in which all terms are present.

with time compared with the two limiting cases, either purely viscous or purely inertial. Two results are striking. (1) During the early phase of swimming (Fig. 6A), the situation can accurately be represented solely by inertial terms, but later (Fig. 6B), when the start-up force transients have decayed, the viscous model becomes a good approximation. (2) At all times the combination of viscous and inertial terms predicts more force than either the purely viscous, or purely inertial, limit.

The model predicts that resistive and reactive forces are of similar magnitude, although they have markedly different time histories during swimming (Fig. 7). Though the average force is a good predictor of distance traveled, the existence of transient peaks much higher than the temporal average suggests important mechanical limitations to force production.
There have been many studies of the kinematics of fast-start performance in fish (Webb, 1976, 1978, 1983), but the accompanying theory (Weihs, 1973) does not account for viscous flows and cannot be applied at this scale. The only other theoretical work on burst swimming at intermediate Reynolds numbers is that of Vlymen (1974) and Weihs (1974, 1980), whose formulations are in terms of the energetics of larval fish during locomotion. Vlymen’s model was unique in taking into account both inertial and viscous terms in undulatory locomotion, but he did not address the problem of force generation acting to accelerate the body. The work of Vlymen, therefore, is descriptive and not predictive. His formulation cannot be used to explore the mechanical determinants of locomotion. The work of Weihs addresses the relative efficiency of burst and glide versus continuous swimming through ontogenetic size and shape changes. His method does not involve calculating instantaneous force distributions along the body and, hence, cannot predict forward speed.

The theory presented here can be used as a means to explore the effect of morphological and behavioral variation on performance. For example, isometrically scaling a chaetognath to twice its original linear dimension, and prescribing
similarly scaled kinematics, will generate much greater forces and hence higher performance. Such morphological variation is well within the biological range, but the limiting factors may be the stress generated by muscle contractions. Although such stresses have not been measured for chaetognath body wall musculature, the maximum isometric stress of muscle is known and is fairly conserved across all muscle types examined (Prosser, 1973). The model generates instantaneous forces that can be equated with this isometric stress by dividing the maximum instantaneous force within the first 65 ms of swimming by the local cross-sectional area of muscle. Such a calculation yields a predicted stress of 0.32 MPa, comparable to the values published for striated muscle from organisms in other phyla (0.8–12.0 MPa; Prosser, 1973). This mechanical limitation of the chaetognath musculature provides a realistic boundary to the range of feasible morphologies and kinematics.

Fig. 8 represents level surfaces generated by simulating morphological variation to predict the effects on performance. For an array of body lengths and fin heights, wave amplitude (α) is increased until the mechanical boundary of the maximum isometric stress is reached. The corresponding distance traveled is recorded as performance (Fig. 8A). Fig. 8B represents the same result as Fig. 8A, but shows

Fig. 8. Predicted level surfaces generated by varying fin height, body length and propulsive wave amplitude and recording distance traveled in 100 ms if the mechanical limit, maximum isotonic stress, is not exceeded by the predicted instantaneous force. (A) Performance maximum corresponding to the amplitude maximum (B) for an array of body lengths and fin heights. Kinematic variables, with the exception of wave speed, were scaled isometrically; for example, fin height and wave length were expressed as constant fractions of body length. The propulsive wave speed was a constant, defined as the average value given in Table 1.
instead the wave amplitude at which the mechanical boundary was reached. The surfaces show a sharp tuning of the wave kinematics and maximum distance traveled that corresponds to a body length of roughly 2 cm. Fig. 8A also shows that, for a given body size, increasing fin height results in lowered performance with increasing amplitude. The general shape of Fig. 8A can be explained by the following scaling argument. Comparing Figs 8A and 8B, it is apparent that distance traveled during the initial 65 ms scales with the square of the wave amplitude, as predicted by the linear theory of Lighthill (1975). The lowered performance with increased fin height follows because the added mass coefficient scales linearly with body depth. For a given muscle stress, as fin height increases, sectional force production also increases. To remain below the maximum stress level in the muscle, the wave amplitude must decrease to conserve force. Any increase in thrust due to the presence of increased fin size is exceeded by the decrease in thrust due to reduced amplitude.

The prediction that increased fin height decreases performance seems counter-intuitive in the light of the extreme morphological conservation exhibited by the phylum, which includes a tail fin and at least one pair of lateral fins on all species (Hyman, 1959). However, the optimum of no fins may be explained by consideration of the body architecture. The longitudinal body wall musculature is arrayed in four discrete bundles just beneath the epithelium (Duvert and Salat, 1980), one in each quadrant of a cross section, such that the dorsal pair acts in opposition to the ventral pair. With the fins only in the frontal plane midway between the dorsal and ventral muscle masses, they would act to damp out any rotational components to the body motion introduced by a phase difference in contraction between the two muscle bundles within either the dorsal or ventral muscle masses. The fins would act to stabilize the swimming motion at the expense of performance because of their increased drag and added mass. Ultrastructural studies of S. hispida show the presence of transverse body wall musculature capable of deflecting the fins, raising the possibility that the fins could play an active role in directional control (Shinn, 1989). There may be an optimal fin size and height predictable from a species' behavioral pattern based on its need for stability versus maneuverability. To elucidate the role of fins of a given size, fin removal studies similar to those done on fish (Webb, 1977) could be performed. The model predicts increased performance with fin removal, and observation may show a corresponding loss of control.

### Appendix

<table>
<thead>
<tr>
<th>Symbol</th>
<th>Description</th>
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<tbody>
<tr>
<td>$A_{b}, A_{f}$</td>
<td>Sectional projected area of the body and of the body with fins</td>
</tr>
<tr>
<td>$c$</td>
<td>Propulsive wave speed</td>
</tr>
<tr>
<td>$C_{dL}, C_{dn}$</td>
<td>Drag coefficients of longitudinal and normal flow</td>
</tr>
<tr>
<td>$D_{L}, D_{n}$</td>
<td>Sectional longitudinal and normal drag force</td>
</tr>
</tbody>
</table>
C. E. JORDAN

\( f \)  
Fin and tail height

\( F_t, F_r, F_s \)  
Total, inertial and sectional force

\( h(x,t) \)  
Lateral body displacement

\( l \)  
Body length

\( m(x) = \rho \pi (r+f)^2 \)  
Sectional added mass; \( f=0 \) in areas without fins

\( M \)  
Mass of chaetognath \((1.006 \rho \pi^2 l)\)

\( r \)  
Radius of the body, constant along the length

\( Re \)  
Reynolds number

\( S_b, S_f \)  
Sectional surface area of the body and of the body with fins

\( t \)  
Time

\( U \)  
Forward body velocity

\( V, V_n, V_l \)  
Lateral velocity; normal and longitudinal components

\( x \)  
Position along the body

\( \alpha, \beta, \gamma \)  
Coefficients of the propulsive wave amplitude envelope

\( e(x) \)  
Propulsive wave amplitude envelope

\( \Gamma(t) = \text{erfc}(\tan(\pi [(t/b) - (1/2)])) \)  
Propulsive wave amplitude growth during \( b \), the start-up phase

\( \lambda \)  
Propulsive wave length

\( \nu \)  
Kinematic viscosity of sea water

\( \rho \)  
Mass density of sea water

\( \theta \)  
Angle made by a body section with the direction of travel

\( \omega \)  
Angular frequency of the propulsive wave

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References


contraction of the trunk musculature of *Sagitta setosa* (Chaetognatha). *Tissue & Cell* 18, 937–952.


