

Modeling a swimming fish with an initial-boundary value problem: unsteady maneuvers of an elastic plate with internal force generation

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Abstract

In order to model unsteady maneuvers in swimming fish, we develop an initial-boundary value problem for a fourth-order hyperbolic partial differential equation in which the fish's body is treated as an inhomogeneous elastic plate. The model is derived from the three dimensional equations of elastic dynamics, and is essentially a simple variant of the classical Kirchhoff model for a dynamic plate. The model incorporates body forces generating moment to simulate muscle force generation in fish. The initial-boundary value problem is reduced to a beam model in one spatial dimension and formulated computationally using finite differences. Interaction with the surrounding water is represented by nonlinear viscous damping. Two example applications using simple but physically reasonable physiological parameters are presented and interpreted. One models the acceleration from rest to steady swimming, the other a rapid turn from rest.

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1 Introduction

We use the elements of plate theory from mathematical elasticity to construct a model for the dynamics of a swimming fish. The fish itself is regarded as an elastic plate with stiffness that may vary over both the extent of the fish and over time. The model is relatively simple in that it is linear and can be written in two or one spatial dimension(s). Further, it can reconstruct the entire deformation of the fish in terms of the applied forces and the deflection of the centerplane (centerline, in the one dimensional case) of the fish. In contrast with prior work in this area, this approach allows us to examine how possible anatomical force generation patterns generate a range of maneuvers beyond steady swimming.

The idea of applying continuum mechanics to the study of fish locomotion dates back as far as the work of Gray [10, 11] at least and has flourished more recently. The idea of modeling the fish as an elastic plate goes back at least to Wu [28, 29, 30, 31], and was instrumental in much of Lighthill's work, summarized in [15], including the seminal "slender body theory." This work continues to find important application in the study of aquatic locomotion, *e.g.*, the recent work of Liu, *et al.* [16]. However, most of the work based on this ansatz to date assumes that the deformation of the elastic plate that models the fish is prescribed, and focuses on the motion of the water about the plate. Thus this paper is an important departure from previous work in that it focuses on the anatomical generation of the fish's deformation, and on how the interaction of the fish with the water affects its deformation. This is not entirely untrodden ground; Hess and Videler in their insightful papers [24, 14] brought a new level of rigor to Gray's original investigation of the fish's deformation under the action of internal and external forces, and Cheng and Blickhan [2, 3] have built on this analysis to obtain important results as well. Nonetheless, this work has been restricted to the analysis of steady swimming due to the lack of a comprehensive mathematical model. Our model takes the form of an initial-boundary value problem for a fourth-order hyperbolic partial differential equation, and is relatively simple in that it is essentially linear and can be written in one spatial dimension. Further, it can reconstruct the entire deformation of the fish in terms of the applied forces and the deflection of the centerline (roughly, the vertebral column) of the fish.

The derivation of this model is based on recent work in the mathematical theory of elasticity in which three dimensional behavior is reduced to two dimensional models by means of asymptotic analysis. The earliest efforts on this front of which we are aware is the work of Duvaut and Lions [6], on which the derivation of the model presented here is based. Since that time, this technique has proved very useful

in reaffirming the validity of a number of classical plate theories, while discrediting some others. Much of the work has been summarized in Ciarlet’s book [4]. The value of this technique in extending classical models to unusual situations has been demonstrated by one of the authors in [23], thus it seemed especially appropriate to carefully re-examine the classical linear Kirchhoff model for an elastic plate before applying it in the present rather novel situation. As we will show, the result includes some terms that don’t typically appear in the classical model, but whose presence is physically reasonable. Readers interested in a mathematical introduction to the theory of elasticity are encouraged to look at Marsden and Hughes [19] or Gurtin [12]. For an introduction directed at biologists, we suggest Vincent’s book [25].

In formulating the model numerically, we first reduced to one spatial dimension, to simplify the computations. Then, the finite differences technique is applied; this consists of essentially replacing the derivatives in the differential equation and boundary conditions by difference quotients, where the functions involved are evaluated only at prescribed points on a grid in the xt -plane. This transforms the initial-boundary value problem into a system of algebraic equations in the values of the unknown function on the grid. These equations can then be manipulated into a tridiagonal system, which allows us to apply the so-called “method of lines” to move forward in time, solving for the deflection of the fish’s centerline (the essential unknown in this model) at a given instant in time using as data the solutions for prior instants. Special equations must be formulated to treat the initial time step, which is determined from the initial conditions.

We apply the model to simulate two simple maneuvers, a transition from rest to steady swimming, and a so-called “fast start” in which the fish turns rapidly from rest and accelerates rapidly in a direction nearly opposite its resting orientation. Because of limitations in the model, the second example simulates only the first stage of the fast start maneuver.

1.1 Notation

Latin indices (i, j, k , etc., but not t) vary over 1, 2, and 3. Greek indices (α, β) vary over 1 and 2. Any term in which the same index appears twice is summed over that index, e.g., $u_\alpha v_\alpha = u_1 v_1 + u_2 v_2$; we will refer to this as our *summation convention* which must occasionally be suspended. Indices after a comma represent partial derivatives, while before the comma they represent components of a vector or matrix, e.g., $u_{i,\alpha t} = \frac{\partial^2 u_i}{\partial x_\alpha \partial t}$. We will denote by \mathbf{x} the position vector for a point in three dimensional space, $\mathbf{x} = (x_1, x_2, x_3)$. We will reserve upper case \mathbf{X} for points in the $x_1 x_2$ -plane, $\mathbf{X} = (x_1, x_2)$.

The symbol ε_{ijk} alternates the sign based on the order of 1, 2, and 3 in ijk . If 1, 2, and 3 don't all appear, $\varepsilon_{ijk} = 0$. If ijk can be rearranged into 123 by switching the position of two of the numbers, then $\varepsilon_{ijk} = -1$. Otherwise $\varepsilon_{ijk} = 1$. Some examples: $\varepsilon_{332} = 0$, $\varepsilon_{321} = -1$ (exchange the 3 and the 1 to get 123), $\varepsilon_{123} = \varepsilon_{312} = 1$. Notice that given two vectors \mathbf{x} and \mathbf{y} with cross product $\mathbf{z} = \mathbf{x} \times \mathbf{y}$, we may write $z_i = \varepsilon_{ijk}x_jy_k$.

The symbol δ_{ij} is the so-called Kronecker delta, and is 1 if $i = j$ and 0 otherwise.

2 Definitions and Assumptions

2.1 Geometry

We will use the following convention for coordinates to describe the fish in its undeformed state. The x_1 axis points from posterior to anterior, parallel to the fish's vertebral column; the x_2 axis points in the ventral to dorsal direction; and the x_3 axis points from left to right, for the fish. Assume the fish has profile Ω , a bounded open set in the x_1x_2 -plane with boundary $\partial\Omega = \Gamma$. The fish itself occupies the volume $\mathcal{V} = \{\mathbf{x} = (\mathbf{X}, x_3) | \mathbf{X} \in \Omega \text{ and } -h(\mathbf{X})/2 \leq x_3 \leq h(\mathbf{X})/2\}$ in its reference configuration, and we will call $H = \max_{\mathbf{X} \in \Omega} h(\mathbf{X})$ the thickness of the fish. It is essential for the analysis presented here that H be small. For convenience we use h to refer to $h(\mathbf{X})$ if it is clear where to evaluate the function. Notice that we are assuming that the fish is symmetric about its centerplane in its undeformed state.

We will often assume that quantities are roughly of the same magnitude as H^r , where r is an integer exponent. Such quantities will be called equal to $O(H^r)$. For a careful introduction to "big Oh" notation, see many Calculus texts, *e.g.*, Feroe & Steinhorn [9], section 3.5. For an application of this notation in the context of plate theory, see Duvaut & Lions, chapter 4. For instance, we will assume that h varies slowly over the extent of the fish, that is, $|\nabla h| = O(H^2)$.¹

Define the following functions of \mathbf{x} , and t (time):

u_i the displacement of the point \mathbf{x} in the i^{th} direction at time t .

\tilde{f}_i the density of applied forces at the point \mathbf{x} in the i^{th} direction at time t .

σ_{ij} the stress (internal force density) across the plane perpendicular to the i^{th} direction in the j^{th} direction at $(\mathbf{x}; t)$.

¹To make this rigorous, consider h to have the form $h(\mathbf{X}) = H(1 - H\eta(\mathbf{X}))$ with $|\nabla\eta|$ bounded by M . Then, as $H \rightarrow 0$, $|\nabla h| \leq MH^2$, and this is the definition of $|\nabla h| = O(H^2)$.

In addition we define the mass density to be $\rho(\mathbf{X})$, the mass per unit volume; for mathematical convenience it is assumed to be constant through the thickness of the fish. We will define some other functions as summed values across the thickness of the plate. The summed applied force is given by

$$f_i(\mathbf{X}; t) = \int_{-h/2}^{h/2} \tilde{f}_i(\mathbf{X}, x_3; t) dx_3. \quad (1)$$

The summed moments due to applied force are

$$m_i(\mathbf{X}; t) = \int_{-h/2}^{h/2} \varepsilon_{i3k} x_3 \tilde{f}_k(\mathbf{X}, x_3; t) dx_3. \quad (2)$$

There are corresponding summed displacements

$$U_i(\mathbf{X}; t) = \int_{-h/2}^{h/2} u_i(\mathbf{X}, x_3; t) dx_3, \quad (3)$$

and the “summed odd part,” which corresponds to the moment above,

$$V_i(\mathbf{X}; t) = \int_{-h/2}^{h/2} x_3 u_i(\mathbf{X}, x_3; t) dx_3. \quad (4)$$

The summed stress and its corresponding moment are defined by

$$\Sigma_{ij}(\mathbf{X}; t) = \int_{-h/2}^{h/2} \sigma_{ij}(\mathbf{X}, x_3; t) dx_3, \quad (5)$$

and

$$M_{ij}(\mathbf{X}; t) = \int_{-h/2}^{h/2} \varepsilon_{i3k} x_3 \sigma_{kj}(\mathbf{X}, x_3; t) dx_3. \quad (6)$$

2.2 Kinematics

Define $\mathbf{y}(\mathbf{x}; t) = \mathbf{x} + \mathbf{u}(\mathbf{x}; t)$ and $\mathcal{V}'_t = \{\mathbf{y}(\mathbf{x}; t) : \mathbf{x} \in \mathcal{V}'\}$ for any $\mathcal{V}' \subset \mathcal{V}$. Newton’s second law states that if \mathcal{V}'_t is regular, then

$$\int_{\mathcal{V}'_t} \tilde{f}_i d\mathbf{y} + \int_{\partial\mathcal{V}'_t} \sigma_{ij} n_j dS = \int_{\mathcal{V}'_t} \rho u_{i,tt} d\mathbf{y} \text{ for } i = 1, 2, 3,$$

where $d\mathbf{y}$ is the volume differential in \mathcal{V}'_t , dS is the surface area differential on $\partial\mathcal{V}'_t$, and n_j is the j^{th} component of the unit vector pointing outward perpendicular to $\partial\mathcal{V}'$ (the “unit outer normal ” to $\partial\mathcal{V}'$). We will assume that the deformations of the fish are sufficiently small that,

instead of integrating around the deformed region, it is reasonably accurate to integrate around the corresponding undeformed region. That is, we will use as our Newton's second law the equations:

$$\int_{\mathcal{V}'} \tilde{f}_i d\mathbf{x} + \int_{\partial\mathcal{V}'} \sigma_{ij} n_j dS = \int_{\mathcal{V}'} \rho u_{i,tt} d\mathbf{x} \text{ for } i = 1, 2, 3, \quad (7)$$

where $d\mathbf{x}$ is the volume differential in \mathcal{V} and dS is still the surface area differential, this time on $\partial\mathcal{V}'$. Under the same assumption that the deformations are not too large, conservation of angular momentum gives the comparable equations

$$\int_{\mathcal{V}'} \varepsilon_{ikj} x_k \tilde{f}_j d\mathbf{x} + \int_{\partial\mathcal{V}'} \varepsilon_{ikj} x_k \sigma_{jl} n_l dS = \int_{\mathcal{V}'} \rho \varepsilon_{ikj} x_k u_{j,tt} d\mathbf{x}, \quad (8)$$

for $i = 1, 2, 3$.

We will assume that $\Omega' \subset \Omega$ is regular with boundary Γ' , and that \mathcal{V}' has the form

$$\mathcal{V}' = \{\mathbf{x} = (\mathbf{X}, x_3) : \mathbf{X} \in \Omega' \text{ and } -h(\mathbf{X})/2 \leq x_3 \leq h(\mathbf{X})/2\},$$

so that \mathcal{V}' is a ‘‘cutout’’ of the fish, obtained by intersecting a solid cylinder $\Omega' \times \mathbf{R}$ (parallel to the x_3 axis) with \mathcal{V} . Then these equations can be reduced to equations in two spatial variables, x_1 and x_2 using the definitions above. Equation 7 can be rewritten

$$\int_{\Omega'} f_i + \Delta\sigma_i d\mathbf{X} + \int_{\Gamma'} \Sigma_{i\alpha} n_\alpha ds = \int_{\Omega'} \rho U_{i,tt} d\mathbf{X} \text{ for } i = 1, 2, 3,$$

where n_α are components to the unit outer normal to Γ , and

$$\Delta\sigma_i(\mathbf{X}; t) = \sigma_{ij}(\mathbf{X}, h/2; t) n_j^+ - \sigma_{ij}(\mathbf{X}, -h/2; t) n_j^- \quad (9)$$

is the difference in the stress in the i th direction acting across the right and left sides of the fish and

$$\mathbf{n}^\pm(\mathbf{X}) = \frac{1}{\sqrt{4 + |\nabla h|^2}} (-h_{,1}(\mathbf{X}), -h_{,2}(\mathbf{X}), \pm 2) \quad (10)$$

is the unit outer normal on the sides of the fish. Also, $d\mathbf{X}$ is the area differential in Ω' and ds is the arclength differential on Γ' . We can define the net of the external forces acting on the lateral faces of the fish and the body forces by $g_i = f_i + \Delta\sigma_i$ then we can rewrite this more simply as

$$\int_{\Omega'} g_i d\mathbf{X} + \int_{\Gamma'} \Sigma_{i\alpha} n_\alpha ds = \int_{\Omega'} \rho U_{i,tt} d\mathbf{X} \text{ for } i = 1, 2, 3. \quad (11)$$

Turning to Equation 8, we can reduce this to two dimensions as

$$\begin{aligned} \int_{\Omega'} m_i + \varepsilon_{i\alpha k} x_\alpha g_k + \varepsilon_{i3k} \frac{h}{2} \Delta \sigma_k d\mathbf{X} + \int_{\Gamma'} (M_{i\beta} + \varepsilon_{i\alpha k} x_\alpha \Sigma_{k\beta}) n_\beta ds \\ = \int_{\Omega'} \rho (\varepsilon_{i3k} V_{k,tt} + \varepsilon_{i\alpha k} x_\alpha U_{k,tt}) d\mathbf{X} \text{ for } i = 1, 2, 3, \end{aligned}$$

Applying the divergence theorem to Eq. 11, and recognizing that Ω' is an arbitrary regular set we arrive at our fundamental balance of forces equation,

$$g_i + \Sigma_{i\alpha, \alpha} = \rho U_{i,tt} \text{ in } \Omega. \quad (12)$$

The angular momentum equation can similarly be reduced to

$$\begin{aligned} m_i + \varepsilon_{i\alpha k} x_\alpha g_k + \varepsilon_{i3k} \frac{h}{2} \Delta \sigma_k + (M_{i\beta} + \varepsilon_{i\alpha k} x_\alpha \Sigma_{k\beta})_{,\beta} = \\ \rho (\varepsilon_{i3k} V_{k,tt} + \varepsilon_{i\alpha k} x_\alpha U_{k,tt}). \end{aligned}$$

Applying the balances of forces equation, Eq. 12, to this we arrive at the fundamental balance of angular momentum equation

$$m_i + M_{i\alpha, \alpha} + \varepsilon_{i\alpha k} \Sigma_{k\alpha} + \varepsilon_{i3k} \frac{h}{2} \Delta \sigma_k = \rho \varepsilon_{i3k} V_{k,tt}. \quad (13)$$

Notice that for $i = 3$ this equation merely states that Σ must be symmetric, while $i = \beta$ gives an equation involving $\Sigma_{3\alpha}$. These can be used to show that

$$\Sigma_{3\beta, \beta} = m_{2,1} - m_{1,2} + M_{2\alpha, \alpha 1} - M_{1\alpha, \alpha 2} + \frac{1}{2} (h \Delta \sigma_\alpha)_{,\alpha} - \rho V_{\alpha, \alpha tt}$$

Substituting this into the balance of forces equation, Eq. 12, with $i = 3$ yields

$$M_{2\alpha, \alpha 1} - M_{1\alpha, \alpha 2} + m_{2,1} - m_{1,2} + \frac{1}{2} (h \Delta \sigma_\alpha)_{,\alpha} + g_3 = \rho (U_{3,tt} + V_{\alpha, \alpha tt}), \quad (14)$$

which, when combined with the remaining balance of forces equations

$$\Sigma_{\alpha\beta, \beta} + g_\alpha = \rho U_{\alpha,tt} \quad (15)$$

forms our basic kinematic system.

The last equation is simply Newton's second law. It says that mass times acceleration is equal to the sum of the external forces being imposed on the fish (from the water, the fish's muscles, gravity, and any other sources) and the internal forces generated by the fish's current deformation. The second to last equation is also a balance of forces equation, but it has a very different form because of averaging across the thickness of the fish. It says that in the x_3 direction, in addition to

the component of external forces acting in that direction, the moments of the forces acting in the plane of the fish must be accounted for. It also says that the only internal forces that matter are the moments of the in-plane forces. Finally, in addition to mass times acceleration on the other side of the equation, there are additional terms that account for rotational acceleration caused by the spatial rate of change in acceleration in-plane.

2.3 Constitutive and Interface Assumptions

We assume that the fish is linearly elastic, and the stress strain relations are isotropic but inhomogeneous. That is, the relation between stress σ and strain γ is given by

$$\gamma_{ij} = \frac{1}{E} [(1 + \nu)\sigma_{ij} - \nu\sigma_{kk}\delta_{ij}] \quad (16)$$

or equivalently

$$\sigma_{ij} = \frac{E}{1 + \nu} \left[\gamma_{ij} + \frac{\nu}{1 - 2\nu} \gamma_{kk} \delta_{ij} \right], \quad (17)$$

where E and ν are functions of \mathbf{X} , and t , and δ_{ij} is the Kronecker delta. The constitutive parameters are: the Young's Modulus $E > 0$, a measure of the resilience of the fish's tissue in the same units as stress, force per unit area; and the Poisson's ratio $\nu \in (0, 1/2)$, a dimensionless measure of the degree to which stretching in one dimension results in compression in a perpendicular direction. We will use the linear strain tensor:

$$\gamma_{ij} = (u_{i,j} + u_{j,i})/2. \quad (18)$$

The most important of the assumptions regarding the interface between the fish and the water is the “no slip” condition of fluid mechanics. That is, the water is assumed to exert no shearing force on the fish. On the sides of the fish, this implies there is no force component parallel to the lateral face of the fish. In our notation this is just

$$\varepsilon_{ijk} n_j^\pm(\mathbf{X}) \sigma_{kl}(\mathbf{X}, \pm \frac{h}{2}; t) n_l^\pm(\mathbf{X}) = 0 \text{ for } i = 1, 2, 3.$$

Recalling the definition for \mathbf{n}^\pm , Eq. 10, and our assumption that $|\nabla h| = O(H^2)$, these equations give us that, on the left and right sides of the fish,

$$\begin{aligned} \sigma_{3\alpha} &= \frac{1}{2}(\sigma_{\alpha\beta} h_{,\beta} - \sigma_{33} h_{,\alpha}) \\ &= O(H^2) \end{aligned} \quad \text{for } \alpha = 1, 2. \quad (19)$$

One immediate consequence of this result is that $\Delta\sigma_\alpha(\mathbf{X}; t) = O(H^2)$.

By applying Hooke's Law, Eq. 16, the preceding equation 19 yields

$$u_{3,\alpha}(\mathbf{X}, \pm h/2; t) + u_{\alpha,3}(\mathbf{X}, \pm h/2; t) = O(H^2).$$

If we then use a Taylor expansion for u_i in the x_3 direction, that is,

$$u_i(\mathbf{X}, x_3; t) = u_i(\mathbf{X}, 0; t) + x_3 u_{i,3}(\mathbf{X}, 0; t) + \frac{x_3^2}{2} u_{i,33}(\mathbf{X}, 0; t) + O(H^3),$$

we see that

$$\begin{aligned} u_{3,\alpha}(\mathbf{X}, \pm h/2; t) + u_{\alpha,3}(\mathbf{X}, \pm h/2; t) &= u_{3,\alpha}(\mathbf{X}, 0; t) + u_{\alpha,3}(\mathbf{X}, 0; t) \\ &\quad \pm \frac{h}{2} (u_{3,\alpha 3}(\mathbf{X}, 0; t) + u_{\alpha,33}(\mathbf{X}, 0; t)) + O(H^2). \end{aligned}$$

So, by combining these expressions for $u_{3,\alpha} + u_{\alpha,3}$, we arrive at the important fact that

$$u_{\alpha,3}(\mathbf{X}, 0; t) = -u_{3,\alpha}(\mathbf{X}, 0; t) + O(H^2) \quad (20)$$

(as well as the less important fact that $u_{3,\alpha 3}(\mathbf{X}, 0; t) + u_{\alpha,33}(\mathbf{X}, 0; t) = O(H)$). This near equivalence is central to the theory of elastic plates, and deformations satisfying it are called Kirchhoff-Love deformations. By Taylor expansion we can apply this result to obtain the following expression for strains in a plane parallel to the centerplane of the fish passing through the point of interest, (\mathbf{X}, x_3)

$$\begin{aligned} \gamma_{\alpha\beta}(\mathbf{X}, x_3; t) &= \frac{1}{2} (u_{\alpha,\beta}(\mathbf{X}, x_3; t) + u_{\beta,\alpha}(\mathbf{X}, x_3; t)) = \\ &= \frac{1}{2} (u_{\alpha,\beta}(\mathbf{X}, 0; t) + u_{\beta,\alpha}(\mathbf{X}, 0; t)) - x_3 u_{3,\alpha\beta}(\mathbf{X}, 0; t) + O(H^2). \end{aligned} \quad (21)$$

We make a further assumption on the nature of the deformations: that the left-right displacement is nearly uniform across the thickness of the fish. Physically, this assumption, in conjunction with the basic linearity assumption, Eq. 7, states that the fish does not change thickness over time. Mathematically our assumption is that

$$u_{3,3}(\mathbf{X}, 0; t) = 0. \quad (22)$$

3 Assembling the Differential Equation

We are now in a position to create the central differential equation of our model. The equation has as its unknown d , the left-right deflection

of the centerplane of the plate. In terms of the quantities we have defined thus far, the definition is $d(\mathbf{X}; t) = u_3(\mathbf{X}, 0; t)$. Similarly we will define $\bar{\mathbf{u}}(\mathbf{X}; t) = (u_1(\mathbf{X}, 0; t), u_2(\mathbf{X}, 0; t))$. We will write these new functions without arguments if they are being evaluated at $(\mathbf{X}; t)$, as is usual.

We turn our attention to the component of stress on the left and right sides of the fish that we have not demonstrated to have negligible magnitude, $\Delta\sigma_3$. By applying the Taylor expansion for $(1+x)^{-1/2}$ to the definition for $\Delta\sigma_3$, Eq. 9, we find that

$$\Delta\sigma_3(\mathbf{X}; t) = \sigma_{33}(\mathbf{X}, h/2; t) - \sigma_{33}(\mathbf{X}, -h/2; t) + O(H^2).$$

By Hooke's law, Eq. 16; the definition of the linear strain tensor, Eq. 18; and Eq. 21, we can see that

$$\begin{aligned} \sigma_{33}(\mathbf{X}, \pm \frac{h}{2}; t) &= \frac{E}{1+\nu} \left(\gamma_{33}(\mathbf{X}, \pm \frac{h}{2}; t) + \frac{\nu}{1-2\nu} \gamma_{kk}(\mathbf{X}, \pm \frac{h}{2}; t) \right) \\ &= \frac{E}{(1+\nu)(1-2\nu)} \left[(1-\nu)u_{3,3}(\mathbf{X}, \pm \frac{h}{2}; t) + \right. \\ &\quad \left. \nu(\bar{u}_{\alpha,\alpha} \mp \frac{h}{2}d_{,\alpha\alpha}) \right] + O(H^2). \end{aligned}$$

Inserting the final expression for σ_{33} into the preceding expression for $\Delta\sigma_3$ we can conclude

$$\begin{aligned} u_{3,3}(\mathbf{X}, \frac{h}{2}; t) - u_{3,3}(\mathbf{X}, -\frac{h}{2}; t) &= \\ &= \frac{(1+\nu)(1-2\nu)}{E(1-\nu)} \Delta\sigma_3 + \frac{\nu h}{1-\nu} d_{,\alpha\alpha} + O(H^2). \end{aligned}$$

By Taylor expansion we know that $u_{3,3}(\mathbf{X}, \frac{h}{2}; t) - u_{3,3}(\mathbf{X}, -\frac{h}{2}; t) = hu_{3,33}(\mathbf{X}, 0; t) + O(H^3)$, so that, because of our assumption in Eq. 22,

$$\begin{aligned} \gamma_{33}(\mathbf{X}, x_3; t) = u_{3,3}(\mathbf{X}, x_3; t) &= \\ \frac{x_3}{h} \frac{(1+\nu)(1-2\nu)}{E(1-\nu)} \Delta\sigma_3 + x_3 \frac{\nu}{1-\nu} d_{,\alpha\alpha} + O(H^2). \end{aligned} \quad (23)$$

Now we have expansions of all of the components of strain, so we can compute the resulting expansions for components of stress; they are

$$\begin{aligned} \sigma_{11}(\mathbf{X}, x_3; t) &= \frac{E}{1+\nu} \left\{ \frac{1}{1-2\nu} [(1-\nu)\bar{u}_{1,1} + \nu\bar{u}_{2,2}] - \right. \\ &\quad \left. \frac{x_3}{1-\nu} [d_{,11} + \nu d_{,22}] \right\} + \frac{x_3}{h} \frac{\nu}{1-\nu} \Delta\sigma_3 + O(H^2), \end{aligned} \quad (24)$$

$$\sigma_{22}(\mathbf{X}, x_3; t) = \frac{E}{1+\nu} \left\{ \frac{1}{1-2\nu} [\nu \bar{u}_{1,1} + (1-\nu) \bar{u}_{2,2}] - \frac{x_3}{1-\nu} [\nu d_{,11} + d_{,22}] \right\} + \frac{x_3}{h} \frac{\nu}{1-\nu} \Delta \sigma_3 + O(H^2), \quad (25)$$

$$\sigma_{33}(\mathbf{X}, x_3; t) = \frac{E\nu}{(1+\nu)(1-2\nu)} \bar{u}_{\alpha,\alpha} + \frac{x_3}{h} \Delta \sigma_3 + O(H^2), \quad (26)$$

$$\sigma_{12}(\mathbf{X}, x_3; t) = \frac{E}{1+\nu} \left[\frac{1}{2} (\bar{u}_{1,2} + \bar{u}_{2,1}) - x_3 d_{,12} \right] + O(H^2), \quad (27)$$

$$\sigma_{\alpha 3}(\mathbf{X}, x_3; t) = O(H^2). \quad (28)$$

By substituting these expansions for stress into the definitions for the summed stress and moment given in Eqs. 1–6, and substituting the results into the basic kinematic system of equations, Eqs. 14–15, we arrive at the following system, in which we drop the $O(H^4)$ terms

$$\begin{aligned} \rho h d_{,tt} - \rho \left(\frac{h^3}{12} d_{,\alpha} \right)_{,\alpha tt} + [D(1-\nu) d_{,\alpha\beta}]_{,\alpha\beta} + (D\nu d_{,\alpha\alpha})_{,\beta\beta} &= F \quad (29) \\ \rho h \bar{u}_{1,tt} - \left\{ \frac{Eh}{1-\nu-2\nu^2} [(1-\nu) \bar{u}_{1,1} + \nu \bar{u}_{2,2}] \right\}_{,1} - & \\ \left[\frac{Eh}{2(1+\nu)} (\bar{u}_{1,2} + \bar{u}_{2,1}) \right]_{,2} &= f_1 \\ \rho h \bar{u}_{2,tt} - \left\{ \frac{Eh}{1-\nu-2\nu^2} [\nu \bar{u}_{1,1} + (1-\nu) \bar{u}_{2,2}] \right\}_{,2} - & \\ \left[\frac{Eh}{2(1+\nu)} (\bar{u}_{1,2} + \bar{u}_{2,1}) \right]_{,1} &= f_2 \end{aligned}$$

In these equations, $D = Eh^3/12(1-\nu^2)$ is the modulus of flexural rigidity, and

$$F = m_{2,1} - m_{1,2} + f_3 + \Delta \sigma_3 + \left(\frac{\nu h^2}{12(1-\nu)} \Delta \sigma_3 \right)_{,\alpha\alpha}$$

is the sum of the left-right forces acting on the fish. The equations are all in two spatial dimensions, and so solutions should be defined in the region Ω , the outline of the fish in the x_1x_2 -plane. Notice that the equations decouple d from the \bar{u}_α 's, allowing us to treat them independently. In the case when E , ν , and h are constant, the last two equations decouple further, leaving a single equation in each displacement. we will assume that $\bar{\mathbf{u}}$ is negligible, and work with only Eq. 29.

If we assume that the constitutive parameters ρ , E , ν , and h are constant with respect to x_2 and no applied forces act in that direction ($f_2 = m_1 = 0$), then we wish to search for deflections of the form

$d(x_1; t)$. Define the dorsal outline of the fish to be given by $x_2 = \tau(x_1)$ and the ventral outline by $x_2 = b(x_1)$. We may then average over the x_2 extent of the fish to get the equation:

$$\rho d_{,tt} - \frac{\rho h^2}{12} d_{,11tt} + (Dd_{,11})_{,11} = m_{2,1} + f_3 + \Delta\sigma_3 + \left(\frac{\nu h^2}{12(1-\nu)} \Delta\sigma_3 \right)_{,11}, \quad (30)$$

while the in-plane equations become

$$\rho h \bar{u}_{1,tt} - \left[\frac{E(1-\nu)h}{1-\nu-2\nu^2} \bar{u}_{1,1} \right]_{,1} = f_1.$$

Note that the forces are all assumed to be given as forces per unit area, because of the averaging. For instance, given a body force per unit length in the left-right direction $f(x_1; t)$, we would convert to the corresponding quantity in the Eq. 30 by assigning $f_3(x_1; t) = f(x_1; t)/(\tau(x_1) - b(x_1))$.

4 Boundary and Initial Conditions

4.1 Boundary Conditions

Appropriate boundary conditions derive from two physical assumptions about the fish's interaction with the water. First, the "no-slip" condition already used in section 2.3 is employed again. Second, we assume that water applies no bending moment upon the fish. It should be noted that fins, particular dorsal, pectoral, and caudal fins, might be regarded as mechanical devices for passing moment from water to fish and *vice versa*, so this assumption effectively makes the fish finless.

Recall that the "no-slip" condition states that there is no shearing force acting on the fish from the surrounding fluids. Examining the fish in its undeformed state, a shearing force can be decomposed most simply into two directions: The direction tangential to the boundary of the fish's profile, Γ and the x_3 direction. The shearing force in the tangential direction is

$$2n_1n_2(\bar{u}_{2,2} - \bar{u}_{1,1}) + (n_1^2 - n_2^2)(u_{1,2} + u_{2,1}),$$

an expression that does not involve the deflection d . The shear stress in the x_3 direction along Γ is $\Sigma_{3,\alpha}n_\alpha$, and we will specify that this stress is given only by the deformation. The moments of the deformation can be decomposed into two components, a twisting moment M_n about an axis normal to the boundary and a bending moment M_b about an axis tangential to the boundary. In terms of the summed moments $M_{\alpha\beta}$ defined in Eq. 6 the twisting and bending moments are defined as

$$M_n = M_{\alpha\beta}n_\alpha n_\beta \text{ and } M_b = M_{2\alpha}n_1n_\alpha - M_{1\alpha}n_2n_\alpha.$$

The shear force on the boundary generated by the twisting moment is $-\partial M_n/\partial s$, where $\partial/\partial s = \partial/\partial x_2 n_1 - \partial/\partial x_1 n_2$ represents the directional derivative in the counterclockwise tangential direction around the boundary. Thus our “no shear” boundary condition will be

$$\Sigma_{3\alpha} n_\alpha - \frac{\partial M_n}{\partial s} = 0.$$

The lack of bending moment passed from the water to the fish can be represented mathematically by the “no bending” condition

$$M_s = 0.$$

From the definitions in Eqs. 1–6 and Eqs. 24–28, we can express the moment term in the “no shear” boundary condition as

$$\frac{\partial M_n}{\partial s} = \frac{\partial}{\partial s} \{D(1-\nu)[d_{,12}(n_1^2 - n_2^2) + (d_{,22} - d_{,11})n_1 n_2]\}.$$

The stresses $\Sigma_{3\alpha}$ were shown to be $O(H^3)$ in Ω , but we do not wish to ignore them on the boundary. Using the fundamental equation for balance of angular momentum, Eq. 13, we see that

$$\Sigma_{3\alpha} n_\alpha = (m_2 + M_{2\alpha,\alpha})n_1 - (m_1 + M_{1\alpha,\alpha})n_2 - \rho V_{\alpha,tt} n_\alpha.$$

Once again applying the definitions in Eqs. 1–6 and the Eqs. 24–28, this gives

$$\begin{aligned} \Sigma_{3\alpha} n_\alpha &= [m_2 - (D(1-\nu)d_{,12})_{,2}]n_1 - [m_1 + (D(1-\nu)d_{,12})_{,1}]n_2 \\ &\quad - \{D[(1-\nu)d_{,\beta\beta} + \nu(d_{,\alpha\alpha} - q)]\}_{,\beta} n_\beta + \frac{\rho h^3}{12} d_{,\alpha tt} n_\alpha, \end{aligned}$$

where $q = \frac{1+\nu}{Eh} \Delta \sigma_3$. Thus the “no shear” condition in terms of the deflection d and the applied forces is

$$\begin{aligned} m_2 n_1 - m_1 n_2 - [D(1-\nu)d_{,\alpha\beta}]_{,\alpha} n_\beta - \frac{\partial}{\partial n} D\nu(d_{,\alpha\alpha} - q) + \frac{\rho h^3}{12} \frac{\partial d_{,tt}}{\partial n} = \\ \frac{\partial}{\partial s} \{D(1-\nu)[d_{,12}(n_1^2 - n_2^2) + (d_{,22} - d_{,11})n_1 n_2]\}. \quad (31) \end{aligned}$$

Here $\partial/\partial n = \partial/\partial x_\alpha n_\alpha$. In the same fashion, the “no bending” condition becomes

$$D \left((1-\nu) \frac{\partial^2 d}{\partial n^2} + \nu d_{,\alpha\alpha} \right) = D\nu q. \quad (32)$$

We will use Eqs. 32 and 31 as the boundary conditions in two dimensions. In one dimension the conditions simplify to

$$m_2 + [D(\nu q - d_{,11})]_{,1} \frac{\rho h^3}{12} d_{,1tt} = 0 \text{ and } d_{,11} = \nu q \quad (33)$$

4.2 Initial Conditions

To complete this mathematical model of the fish, we require knowledge of the starting deformation. The model theoretically requires only the data $d - \frac{b^2}{12}d_{,\alpha\alpha}$ and its time derivative, both evaluated at $t = 0$, but the initial data $d(\mathbf{X}; 0)$ and $d_{,t}(\mathbf{X}; 0)$ are physically easier to appreciate (initial deflection and velocity), and sufficient to allow solution.

5 Numerically Implementing the Model

5.1 Viscous Damping

To use the model to simulate the locomotion of fish, we must introduce the surrounding water into the model, and in particular, the passage of forces from water to fish and *vice versa*. The authors hope to integrate the fish model into a model for the surrounding water, along the lines of Liu, *et al.* [16], and Fauci *et al.* [8, 7]. However this is beyond the scope of the current paper. To allow a reasonable model without the added complication, we will consider simple viscous damping by the external fluid to dissipate the energy generated by the fish muscle. Following Denny [5], we assume that the damping force per unit length of the fish is jointly proportional to the square of the lateral velocity of the fish, and to the depth η of the fish. (Note that this is $\eta(x_1) = \tau(x_1) - b(x_1)$ in the notation introduced in Section 3, not the η introduced in the footnote in Section 2.1.) The principle inaccuracy in the model as it stands is the absence of inertial forces, although we see no impediment to incorporating them once the fish model is integrated with a model for the surrounding fluid. Thus we assume $\Delta\sigma_3$ has the form μd_t^2 , where μ depends on $\eta(x_1)$; note that this introduces a nonlinearity in the model.

5.2 A Numerical Scheme

In order to numerically solve the model, we apply the finite differences method to discretize the problem. In so doing we reduce the problem to approximating the value of d at a grid of points in the xt -plane having the form $(x_i, t_j) = (i\Delta x, j\Delta t)$ for $0 \leq i \leq N$ and $0 \leq j \leq M$. Thus $N\Delta x = L$ and $M\Delta t = t_{\max}$ and we have abandoned the limitation on Latin indices described in section 1.1. For brevity we use the notation f_i^j for $f(x_i, t_j)$. Readers unfamiliar with the finite difference technique may refer to any of a number of texts on partial differential equations and their applications; the authors offer Haberman's text [13] as an example. Having discretized the problem in this way, it can be solved most simply by means of the method of lines, in which the solution at t_j for all points on the x grid is computed in terms of the solution at

t_{j-1} , t_{j-2} , and t_{j-3} . This method is well-known as a stable method for solving initial-boundary value problems like the one at hand. In future work, the authors might employ the Crank-Nicholson method, which allows more rapid convergence without resorting to small Δt values. For the work presented here, the simpler method has been efficient, allowing run times of less than five minutes on a desktop computer for real-time simulations of 5 seconds of swimming.

The method requires special treatment of the nonlinearity to avoid having quadratic terms in the unknowns. In particular, we rewrite $\Delta\sigma_3$ as

$$\sigma_i^j = \mu_i(d_t \text{ centered})_i^j (d_t \text{ backward})_i^j,$$

using the centered finite difference approximation for one factor of the velocity, and using the backward finite difference approximation with the same order error for the other factor. This keeps the system linear in d values at the forward-most time step. To incorporate the boundary conditions into the scheme, we introduce “artificial” points at $i = -1, N + 1$ for 32, and at $i = -2, N + 2$ for 31. By combining the resulting equations in straightforward ways, we reduce the problem to tridiagonal system, which allows for rapid solution. This outlines the basic structure of the numeric scheme. The authors implemented this in the programming language C, adapting a well known tridiagonal system solver and other routines found in [22].

5.3 Evaluating Parameters

The model as presented has several parameters which need to be set in order to effectively model the swimming and maneuvering of fish. The primary goal of this stage of the research was to demonstrate the feasibility of this kind of model in reproducing or predicting fish kinematics with realistic parameters. We turn now to a discussion of the parameters.

The profile of the fish is shown in Figure 1. The profile is based roughly on a mackerel (*Scomber scomber*), but has dorso-ventral symmetry that no real fish has. The profile was chosen for its simplicity and passing resemblance to a carangiform fish. The dashed vertical line on the right indicates roughly where the fish’s head ends; we assume that the fish is much more rigid and has no muscle mass anterior to the line. The vertical line on the left indicates roughly where the fish’s tail begins; posterior to that line there is essentially no muscle mass. These demarcations are rough in that the Young’s modulus and proportion of muscle mass must vary smoothly to assure the stability of the numerical scheme.

For the Young’s modulus, the work of Long *et al.* [18] and McHenry *et al.* [20] was used; there a value of approximately 0.18 MPa was found as a Young’s modulus in the posterior region of a sunfish (*Lepomis*

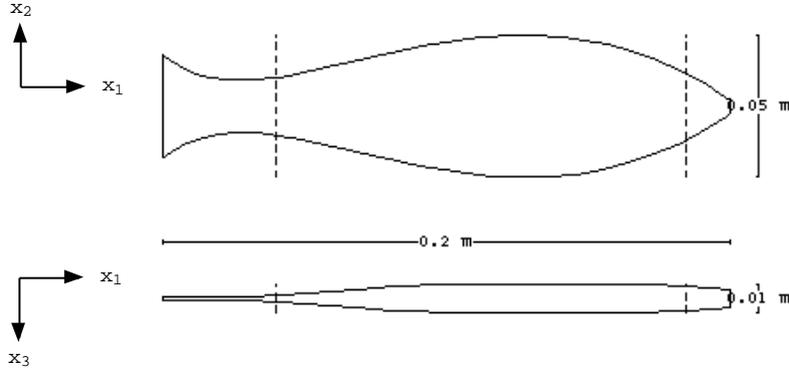


Figure 1: Lateral and top views of the profile for the virtual fish used in the model

gibbosus) and a gar (*Lepisosteus osseus*). The head’s Young modulus is not known, so we set it to be “much” (a factor of five) larger than that of the balance of the body. The authors expect that the dynamic modulation of Young’s modulus will prove instrumental in the accurate modeling of maneuvering fish—as the work in [17] suggests—but, to this point only temporally constant Young’s moduli have been used. The anisotropic nature of fish physiology is also expected to play a critical role in a comprehensive model, but the authors have chosen for this model to assume that the fish is isotropic in its elastic behavior. Thus we use a Poisson’s ratio of 0.3, which is in the range of physically measured ratios for organic structures. For the mass density a value of $1.07 \times 10^{-3} \text{ kg/m}^3$ is physically reasonable.

To model the actions of the muscles we have made some simplifying assumptions. We assume that essentially all the fish’s body mass posterior to its head and anterior to its tail is muscle. To determine the maximum tension that the muscles can generate we referred to Altringham *et al.*’s experiments [1] measuring the maximum tension generated in the course of *in vitro* work loop experiments; we use $1.5 \times 10^7 \text{ N/m}^2$ as the maximum possible tension that muscle fibers can generate.

In order to compute the force densities applied by the muscles at a point along the length of the body it is necessary to compute both the lateral force generated by the muscle and the rate of change of moment being exerted by the muscle. The force densities are specified by a lateral and a longitudinal component. The lateral component is a force density; the longitudinal component is determined by computing the difference in tension generated by all muscles posterior of a point, less the tension of all muscle anterior of that point. Note that this ignores any dissipation of muscle tension as it is transmitted down the length

of the fish; it also assumes that transmission occurs instantaneously. This quantity is integrated against the distance from the centerplane over the thickness of the fish to give a moment density. These in turn are integrated (using a Romberg method routine adapted from [22]) to obtain the net force or moment. A centered difference scheme is used to compute the derivative of the moment, except at the tail and head tips, where forward and backward differences, respectively, of the appropriate order are used.

Following Denny [5] we set the damping force for the external fluid acting on the fish to μAv^2 per unit area where $\mu = 9.9 \times 10^{-4}$ kg/m³ and A is the cross sectional area of the portion of the fish (assumed to be roughly rectangular) subjected to the specified velocity v .

In the second of the two examples below, the muscle fibers are assumed to be positioned parallel to the centerline of the fish. That is, all their contractile force is assumed to belong to the longitudinal component. In the first example, the model was modified to more accurately reflect the configuration of muscle suggested by the work of Westneat, *et al.* [27]. The muscle is assumed to have an angle of declination from the centerline of the fish that varies linearly from 60° at the head to 0° at the tip of the tail. This allows the introduction of a force component acting perpendicular to the centerline, and so generating deflection rather than twisting.

There are several other parameters that we vary from model to model; they are discussed in the following section.

6 Some Examples: Two Specific Models

6.1 Start to Steady Swimming

In this model we begin with the fish in its reference configuration and send traveling waves of muscle activation down the length of the fish. The goal was to create a transition from rest (still and straight) to steady swimming. The wavelength of the sinusoidal muscle activation waves is 0.4 fishlengths and the frequency is 3.45 Hz, chosen because the fish showed maximum deflection under a fixed amplitude of force at this frequency. That is the muscle force density had the form

$$A(x_1, t) \cos\left(\frac{1 - x_1}{2\pi 0.4} - \frac{3.45t}{2\pi}\right),$$

where the amplitude function A was a product of the cross-sectional area of the fish and the relative proportion of that area occupied by muscle at that position with a time scaled amplitude that went from nearly zero at $t = 0$ to a maximum of 15%; it achieves 99% of that maximum in less than 20 msec. The functions describing the distribu-

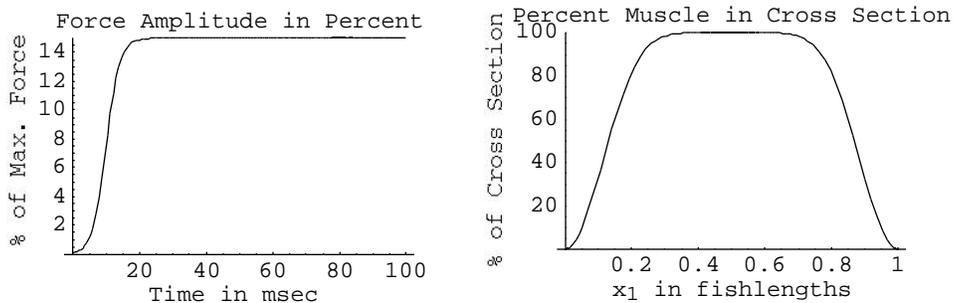


Figure 2: *Left:* The fish gradually increases its muscle force generation up to 15% of the maximum experimentally measured. The ramp is sigmoidal. *Right:* The fish is assumed to have most of its cross section occupied by muscle in the center of the fish, with less and less at the head and tail. This crude approximation is symmetric about the midpoint of the fish.

tion of muscle and the time ramp of amplitude are given in Figure 2.

Despite this the fish is able to quite effectively set its body into the recognizable pattern of traveling wave undulations of a carangiform fish swimming steadily. After the first traveling wave, the body transitions to a standing wave of deflection. It is easy to show that a linearly damped elastic plate subjected to a standing wave of force would have a steady state solution that would include a traveling wave. The steady state component would also include another component due to the interaction of the traveling wave with the boundary conditions. This latter component is not easily representable in closed form, but based on energetic considerations, it seems unlikely that its magnitude would cause it to mask the traveling wave portion of the solution. Thus the transition to a standing wave solution seems to be attributable to the nonlinearity of the damping. We expect that introduction of the external fluid's inertial forces will eliminate this artifact since it is not observed physically. It may be that the fish modulates speed of transmission of the traveling wave of tension down its body, as well. This possibility is discussed further in the Conclusion, section 7.

The fish's head also appears to be translated to its right in the course of the start. Given the balanced nature of the traveling waves of muscle activation, this is a very interesting asymmetric phenomenon, and may be a result of the initial ramp-up of amplitude, which could create a net force in the positive x_3 direction. The fact that the damping depends only on the square of velocity means that slow displacements of this sort are relatively unaffected.

The model simulates the first 1.2 seconds of the fish swimming away from rest; representative plots are shown in Figure 3. The plots show a series of snapshots of the deflection in the z -direction of the centerline of the simulated fish, which originally lies along the x -axis.

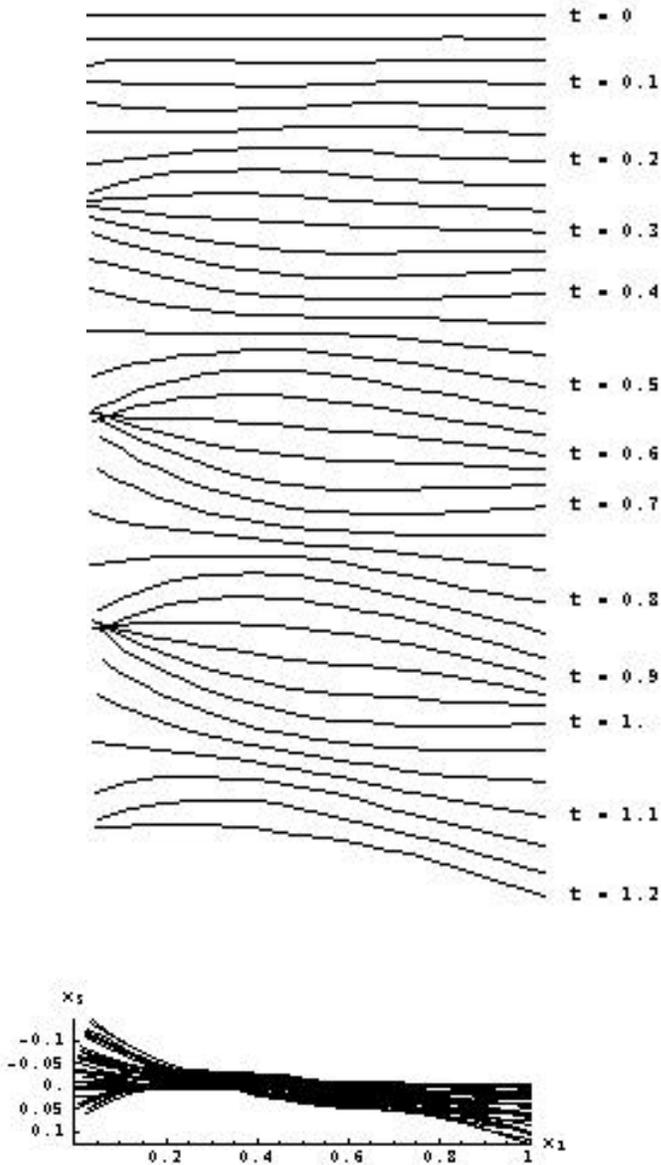


Figure 3: *Above:* A series of frames from an animation of a simulated start from rest. The time between frames is $1/30$ sec while in the figure the reference configuration of the fish is vertically displaced 0.05 fishlengths from one frame to the next. The times for every third frame are given to the right.

Below: The same frames without displacement, on axes scaled in fish-lengths. These offer an amplitude envelope, showing a node just anterior of the fish's tail, about 0.25 fishlengths from the tip of the tail. The second node, just posterior of the fish's head, about $x_1 = 0.85$, is masked by the slow translation of the head to its right visible in the sequence above.

6.2 A Rapid Rotational Start

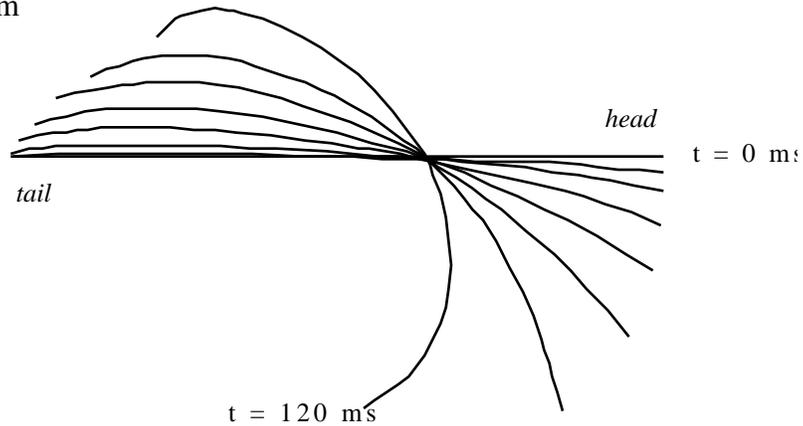
In this model we again begin in the reference configuration and simulate the first phase of the simultaneous turn and start known as a fast start. Because of the limitations of the model, we are unable to generate rotation and curvature as rapidly as live fish perform stage 1 of a fast start (120 v. 30 ms, Fig. 3). As a requirement for maintaining linearity, the model requires the centerline of the fish not to double back on itself, but in executing a fast start the fish closes about on itself, the centerline forming a nearly closed loop. In order to generate a meaningful portion of the fast start we do not allow the fish to exert all its muscle forces, restricting the model to 60% of the maximum. This lengthens the time before the fish doubles back on itself, and causes the centerline to form a slightly larger loop than is observed in experimentally. In this case, we simulate the application of a standing wave of muscle activity that runs from the head to the tail of the fish and has frequency 2 Hz. Representative plots from the first 150 milliseconds of motion, which include the first phase of the maneuver, are shown in Figure 4. Figure 4 offers a comparison with digitized centerline data taken from high-speed video of a sunfish executing a fast start. Simulations providing the virtual fish with a larger proportion of its maximum possible muscle force provided similar results, except that the loop was formed more rapidly and was more closed than the one shown in this animation. Thus they more closely approximated the behavior of a real carangiform swimmer, as shown in the figure.

7 Conclusions

Using a robust yet computationally simple linear model of the elastic behavior of a swimming fish, we have demonstrated that this approach simulates physically reasonable swimming maneuvers using experimentally observed parameters. The biologically-based inputs for the model include the following: muscle force magnitudes, pattern of muscle force development, muscle distribution along the body axis, body stiffness, and mass density. This model differs from others in that it produces swimming motions based on internally generated forces (to our knowledge, all other models of unsteady fish swimming prescribe the body motions *a priori*).

As we have mentioned, there are discrepancies between the model's simulated kinematics and those physically observed. In an effort to refine the model to more accurately reproduce physically observed phenomena, the authors have identified five mechanical roles for muscle tissue in fish locomotion. They are, in the authors' rough estimate of their relative importance,

Simulated
Carangiform
Swimmer



Real
Carangiform
Fish (Sunfish)

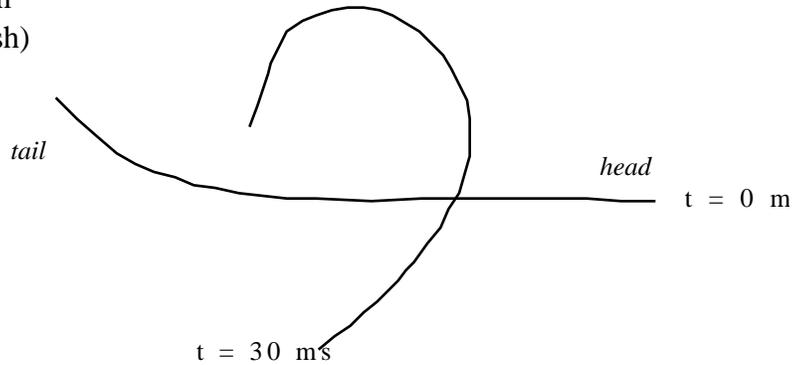


Figure 4: *Above:* A series of centerlines from a simulation of the first phase of a fast start. The time between frames is 25 msec, except that the last frame is 16.7 msec after the preceding one. The last frame demonstrates how the model breaks down when the fish forms a loop; the head and tail are parallel to one another although they should be curled toward one another. *Below:* Two outlines of the centerline of a pumpkinseed sunfish, *Lepomis gibbosus*, undergoing a fast start, in which the muscles operate at near 100% capacity and contract simultaneously on one side of the body (start and end of stage 1 figured).

- Generating force, both longitudinal and lateral for the purpose of laterally deflecting the fish.
- Varying the Young’s modulus of the fish to tune its response to the forces being generated. (See Long’s work [17].)
- Varying the loss of energy via dissipation as tension is transmitted down the length of the fish. (See Meyhofer and Daniels’ work [21].)
- Varying the pressure of the body cavity, which is likely to alter its constitutive properties, as well. (See Wainwright, *et al.*[26].)
- Varying the speed of transmission of tension down the length of the fish. (See McHenry, *et al.*[20].)

Only the first of these effects is incorporated in the model at hand. This clearly leaves considerable room for refinement. The model presented here is robust in that it will allow the straightforward inclusion of all the roles listed, as necessary to obtain physically verifiable motion. Beyond these physical phenomena lies the thorny issue of the performance of fish muscle, both constitutively, and as a force generator. The present model’s approximation of muscle tissue as linearly elastic and lossless is clearly crude. Further, the ability of muscle to generate power is known to depend on a number of variables, notably recovery time and pre-stressing. Future models will incorporate more physically reasonable assumptions of muscle behavior. In addition, the work of Westneat, *et al.* [27] strongly suggests directions for modeling the tendon structure of carangiform fish which might fruitfully be incorporated in the next iteration of the model.

Finally, the model requires more realistic modeling of the interaction between the fish and the water. The inertial forces are particularly important both in tuning the deflection of the fish, and determining the thrust the fish is able to generate, as a simple application of Bernoulli’s equation to models similar to those given here demonstrates.

Much work remains to create a model which will reproduce accurately the kinematics of undulatory swimming. Yet the first step in this process—to provide the theoretical and computational framework for more comprehensive models—is offered by our formulation of a swimming fish as a waving elastic plate. Because the motion of this system is not an *a priori* assumption but rather a consequence of interactions of muscle force, external fluid forces, and the body’s mechanical properties, models of this type offer the opportunity to analyze and reproduce dynamic whole-organism behaviors such as unsteady swimming maneuvers.

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