An Interactive Fluid Model of Jellyfish for Animation

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Abstract. We present an automatic animation system for jellyfish that is based on a physical simulation. We model the thrust of an adult jellyfish, and the organism's morphology in its most active mode of locomotion. We reduce our model by considering only species that are axially symmetric so that we can approximate the full 3D geometry of a jellyfish with a 2D simulation. We simulate the organism's elastic volume with a spring-mass system, and the surrounding sea water using the semi-Lagrangian method. We couple the two representations with the immersed boundary method. We propose a simple open-loop controller to contract the swimming muscles of the jellyfish. A 3D rendering model is extrapolated from our 2D simulation. We add variation to the extrapolated 3D geometry, which is inspired by empirical observations of real jellyfish. The resulting animation system is efficient with an acceptable compromise in physical accuracy.

1 Introduction

As the field of computer graphics progresses, physics-based animation techniques are increasingly used to both improve realism and relieve animators of lower-level tasks. To this end, we propose a method of animating jellyfish locomotion that makes relies on computational fluid dynamics. We are interested in the unique mode of locomotion exhibited by jellyfish: namely, jet propulsion. Physiologically, jellyfish are not overly complex creatures: they are invertebrates with no significant cranial capacity [2]. However, their style of motion is largely not understood either by computer scientists or by marine biologists. As Beer et al. [3] discuss, we can learn much about motion and control systems by studying natural systems in the world around us. A general model of jellyfish would be difficult to attain because of differences in species of jellyfish, and even between individuals within the same species. In this paper, we seek to develop a means of generating animations of jellyfish that would be convincing to the general population. Figure 1 illustrates the kind of motion that we aspire to animate.

The combination of a jellyfish's elastic body and the surrounding incompressible fluids are difficult to simulate. Numerical methods for such coupled systems are quite computationally expensive [28]. We use simulation not for accuracy reasons, but so that our virtual jellyfish can physically interact with its environment, especially the water. Our simulations use a spring-mass model [30] to represent the elastic body of the jellyfish, and a semi-Lagrangian fluid solver [27] for the surrounding sea water. The two representations are coupled using the immersed boundary method [19].

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Fig. 1. Captured footage of a jellyfish swimming, as filmed by Cummins [4]

To animate jellyfish at interactive rates, we must simplify our simulation model. We simulate the jellyfish whose umbrella is axially symmetric in a coarse 2D plane, and extrapolate the results to higher resolutions and to 3D space. The result is a model whose motions are qualitatively similar to that of real jellyfish. However, if we naïvely extrapolate our simulations to a 3D model, the surface will lack the geometric complexity seen in real jellyfish. We propose a means of adding variation back to the 3D geometry of our model, based on observations from the biology community [10,25].

A further challenge in animating jellyfish is determining motor controls for the model. Jellyfish have only a small number of muscles, but those muscles are used in complex ways, and in manners that are not well studied. In this paper, we give one possible approach to a motor control for jellyfish, based on empirical observation of the organism. The resulting animations are appealing to a general audience, but may not be accurate enough for use by marine biologists.

2 Previous Work

Interactive animation techniques have been developed for a variety of characters, including snakes and worms [15], fish [31] and other marine vertebrates [9], as well as legged mammals [21]. Legged locomotion has also been studied by the robotics community [3]. A large amount of research has been aimed at animating various aspects of human motion [13]. However, little has been done to model marine invertebrates. Jellyfish have previously been animated with key-framing techniques [20], though without regard for the interaction between the organism and its environment.

To simulate elastic bodies like that of our jellyfish, particle-based approaches such as spring-mass systems [30] are commonly used. One might then be tempted to use a particle-based fluid representation, such as *smoothed particle hydrodynamics* [8,16], to simulate the sea water around our jellyfish. However, SPH systems approximate incompressibility with large pressure gradient forces, which makes the simulation numerically stiff, and thus computationally expensive. Grid-based fluid simulators are better suited for incompressible fluids. Classical grid methods are very accurate but slow because of stability restrictions [11]. As a compromise, the semi-Lagrangian method [27] is unconditionally stable, though it adds numerical dampening. To couple grid-based fluids with particle-based solids, the graphics community typically uses pressure gradients across fluid-solid interfaces. However, much care must be taken to ensure that fluid does not leak across thin solid regions [12]. An alternative is the immersed boundary method [19], which allows a minimal amount of leakage across solid boundaries [28]. A challenge in all simulation-based animation techniques is that we need to automatically control the bodies that are in motion. An adaptive method, such as a PID controller [7], is feasible; however, choosing the goal state of the system and tuning the controller's parameters are not trivial tasks.

The biology community has a fair body of literature on jellyfish. Megill [14] categorizes different gaits that jellyfish exhibit. Dabiri and Gharib [5] provide empirical data of a jellyfish's position and shape as it swims. Gladfelter [10] describes how the jellyfish will deform as it contracts. Aria [2], Gladfelter [10], and Megill [14] discuss the organism's elastic properties, and its distribution of muscles fibres. Megill [14] theorizes about how jellyfish achieve optimal thrust in several gaits. Sullivan et al. [29] provide data on the mechanics behind jellyfish movement and the reaction of the sea water surrounding the organism. Daniel [6] devised a differential equation for the organism's swimming thrust. However, Dabiri and Gharib [5] show that Daniel's equation is too sensitive to its parameters to be a good general model. Megill [14] determined the approximate resonant frequencies of the organism. However, Dabiri and Gharib [5] observed different resonant frequencies than those of Megill's theoretical predictions.

Dabiri and Gharib [5] exploit axial symmetry in a manner similar us, except that they rotate only one half of the lateral slice about the axis of symmetry. To add variation to our 3D volume, we take inspiration from Rasmussen et al. [22], who animated 3D explosions with 2D simulation and a cyclical 3D noise spectrum. Perlin [18] provides a continuous noise field which we find more suitable to our application.

3 A Numerical Model of Jellyfish

Jellyfish are essentially elastic volumes that activate muscles in order to contract their umbrellas, creating a jet of fluid that propels the organism. We build a model of jellyfish that accounts for the elastic flesh of the organism and the sea water that surrounds it.

3.1 Jellyfish Physiology

Jellyfish deflate their umbrella by contracting muscles that spread across the umbrella hull. The left side of Figure 2 highlights the anatomy of the organism that plays a role in locomotion. The right side of Figure 2 shows the muscular structure for one species of jellyfish. The left side of Figure 2 illustrates the different types of tissue within the umbrella itself. The chief muscle involved in locomotion is the circumferential muscle that lines the subumbrellar wall. This muscle contracts to pull the umbrella wall inward and creating a fluid jet at the aperture. The circumferential muscle has no opposing muscle, unlike muscles that rotate skeletal joints in other species. When the circumferential muscle relaxes, the umbrella is pushed outward by the elastic properties of the surrounding tissue [14] shows The organism also has tentacles along the aperture of the umbrella, which are passive, but cause additional drag.

Aside from muscles, the remainder of the umbrella is loosely categorized into two types of tissue: the *bell mesoglea* and the *joint mesoglea*. These mesogleae are essentially passive. However, the bell mesoglea does contain some sparsely placed *radial muscle fibres*, oriented normal the umbrella's surface. Megill [14] states that these radial muscles changes the symmetry of the umbrella when contracted, and so are used to



Fig. 2. Left: Cross-sections of an umbrella [10]. Right: Muscles in the umbrella [2].



Fig. 3. Horizontal cross-sections of umbrella deformation [10]. Left: the umbrella at its rest configuration. Centre: a contracted umbrella, and the deformation that occurs because of joint mesoglea. Right: the deformation that would occur if the entire umbrella was bell mesoglea.

reorient the organism as it swims. The joint mesoglea is so-called because it is much less elastically stiff than the bell mesoglea. When the umbrella contracts, the joint mesoglea deforms into sharp ridges or "joints", as is illustrated in Figure 3. Because of the joint mesoglea, the stress-strain curve for the umbrella is not linear. Megill [14] shows empirically that the elastic response of the mesoglea is essentially linear except for extremely large stresses, where the mesoglea becomes more stiff and thus compresses less. Thus, we ignore this non-linearity and assume linear springs. Lastly, the compression pattern given in Figure 3 suggests that a jellyfish has eight waves around its aperture. However, a survey of Canadian Atlantic species [25] shows that, some species commonly have different numbers and shapes of these segments.

Spencer [26] noted that the entire circumferential muscle is not completely synchronized. The neuronal impulses that tell the muscle to contract must travel across the nervous system of the organism, and a tiny delay is incurred at each neuronal synapse. The effect of this synaptic delay is that fibres which are further away from neuronal sources will receive the impulses at a slightly later time. However, in practice, we find that this delay pattern actually has little effect on the results of our model.

Many species of jellyfish are approximately axially symmetric, where the axis of symmetry runs from the apex of the umbrella through the centre of its aperture. Shih [25] lists a large number of jellyfish species, ranging in physical configuration, many of which are not axially symmetric. In this work, we only deal with the jellyfish that do have axial symmetry. We choose our simulation slice plane such that the organism's axis of symmetry lies on the plane.

3.2 2D Simulation Model

We want to model three aspects of the jellyfish's anatomy: the umbrella's mesoglea, the tentacles, and the circumferential muscle. The jellyfish will be a mass-spring system, and a grid-based fluid simulation will represent the fluids around the organism. We represent the subumbrellar surface of the mesoglea with a chain of Hookean springs, and further enforce the structure of the umbrella with angular springs. Instead of angular springs, one might be tempted to create small networks of Hookean springs to enforce relative orientations of the surface points, similar to the work of Miller[15] or Tu and Terzopoulos [31]. However, we found experimentally that the large number of short springs (relative to the resolution of our fluid grid) made the system more numerically stiff. Figure 4 shows the configuration of springs that we chose to use. We represent the tentacles in the same manner as the subumbrellar surface, with the same elastic modulus, but with a volume $1/100^{th}$ that of the umbrella springs.

The circumferential muscle is represented by linear springs going longitudinally across the umbrella, as shown in Figure 4. We contract the umbrella by reducing the rest lengths of these springs. Megill [14] measured the elastic strength of the bell mesoglea (including muscle fibres), finding that the mesoglea has an elastic modulus of approximately 1186 Pa, and that the joint mesoglea has an elastic modulus of 130 Pa. The modulus for the muscle fibres is significantly higher, at around 400,000 Pa.

We model sea water using the incompressible Navier-Stokes equations:

$$\frac{\partial \boldsymbol{u}}{\partial t} = \nu \nabla^2 \boldsymbol{u} - \boldsymbol{u} \cdot \nabla \boldsymbol{u} - \frac{\nabla p}{\rho} + \boldsymbol{F}, \qquad \nabla \cdot \boldsymbol{u} = 0, \tag{1}$$

where \boldsymbol{u} is a vector field that represents the fluid's velocity, p is a scalar field for pressure, ρ is the density of the fluid, ν is the coefficient of kinetic viscosity, and \boldsymbol{F} is a vector field for external forces that act on the fluid. The symbols ∇ and ∇^2 are spatial gradient and Laplacian operators, respectively. Griebel et al. [11] give an in-depth description of Equation 1. We integrate these equations numerically over time.

Of particular interest to our work with jellyfish, the second part of Equation 1 enforces constant density and incompressibility. Jellyfish exert large forces on the fluid within its subumbrellar cavity, and the high thrust achieved by the organism depends greatly on the fact that sea water is essentially incompressible. We choose the grid-based semi-Lagrangian method to simulate our fluids because it strictly upholds incompressibility. We immerse our spring-mass model in a square fluid volume that is ten times the jellyfish's diameter, and give the fluid cavity free-slip boundary conditions [11].

We use Peskin's immersed boundary method [19] to combine the particle-based spring-mass model with the grid-based semi-Lagrangian solver. In Peskin's method, the elastic point-masses are advected along the flow field of the fluid grid, and the elastic forces of the Hookean springs are applied to the fluid grid using the force term F in Equation 1. We diverge slightly from Peskin's method of distributing the elastic forces onto the fluid grid. Peskin uses a smoothing kernel to distribute the forces to several, possibly dozens, of grid cells near the point-mass. Doing so increases the cost of simulation, and effectively puts an upper limit on the frequency at which the force profile can vary over the fluid grid. Since we use relatively coarse grids (i.e., 50×50 or 100×100 cells), the frequency limitation of Peskin's smoothing kernel can make the fluid appear

artificially viscous. We instead distribute the elastic force of a point-mass onto its four closest grid cells with bilinear interpolation.

Peskin's method is known to be numerically stiff, and so can be slow if done naïvely. Semi-implicit integration schemes gain us approximately an order of magnitude in efficiency [28]. However, we find experimentally that we gain two orders of magnitude in speed-up simply by using Stam's semi-Lagrangian method [27] instead of an explicit scheme. Note, though, that Stam's method does not gain us larger time-steps, but rather decreases the cost of each step. Stam's method may be unconditionally stable when simulating fluids by themselves, but the elastic body can still introduce instabilities into the system when time-steps are too large. We are unaware of any stability conditions that we can apply to our model to determine an adaptive time-step. Even the commonly used *Courant-Friedrichs-Lewy* condition [11] does not control the stability of the elastic body. In the end, we use this CFL condition, but with a safety factor of 0.001.

For our 2D simulation, we use a Cartesian formulation of the Navier-Stokes equation over a plane. One may be tempted to use a cylindrical formulation [1], given that we are modeling a system with axial symmetry. However, the jellyfish may tilt itself and change the axis of symmetry. When this occurs (potentially on every frame), we would have to resample the fluid grid so that the axis of symmetry aligns itself with the grid lines. This effectively blurs the flow field across the grid, as well as adding to the cost of simulation. Thus, we use a Cartesian formulation, though at the cost of rigorous physical accuracy.

3.3 Muscle Activation

Megill [14] describes several jellyfish gaits. The majority of the biology research is on the *resonant gait*. We also limit our discussion to this gait. It is characterized by the organism contracting at (or near) the resonant frequency of itself and its surrounding sea water, giving the jellyfish optimal thrust during swimming. We simulate muscle contractions by modifying the rest lengths of the subumbrellar springs. Biology literature does not provide evidence that the organism uses closed-loop controllers such as those described by Dean [7] to induce muscle contractions. Instead, we suspect that jellyfish contractions are governed by a cyclical pattern that is quite predictable [26,14,5]. We thus define a function that describes the rest length of the springs over time. Specifically, we created a curve based on Hermite splines. We then normalize the contraction function to be between 1 and 0.56, since a jellyfish may contract to 56% of its maximum diameter when contracting, as seen in Figure 3.

When the jellyfish contracts, it will propel itself forward. However, when it expands, it also pulls itself backward. For a jellyfish to achieve a net positive movement over the course of a contraction cycle, the organism must incur less drag in the expansion phase of the cycle than it does in the contraction phase. This is analogous to how a human swimmer's arm must push more water during its downstroke than it does during its upstroke. We are unaware of any biology literature that details how jellyfish achieve this drag reduction. We suspect that jellyfish make themselves more flat to achieve higher drag, and more rounded to reduce their drag. To support our hypothesis, see Figure 1, which is a short image sequence of an actual jellyfish that expands, and then contracts. In the first three images, the jellyfish is expanding, and its umbrella's shape is relatively



Fig. 4. Our spring-mass network for a jellyfish slice, and the corresponding contraction functions that we use. The subumbrellar springs in the left image are colour-coded to correspond with the contraction function for that spring in the graph on the right.

curved. However, in the fourth frame of Figure 1, the jellyfish is contracting, and the umbrella appears less curved and resembles a cone shape. This conic resemblance is especially striking toward the aperture of the umbrella.

In order to achieve the sort of morphology that we see in Figure 1, we have to slow the expansion of springs that are at the bottom of the umbrella, relative to those at the top. We give each subumbrellar spring a unique contraction function so that springs close to the aperture expand more slowly than those closer to the apex of the umbrella. Figure 4 shows our spring-mass model of the jellyfish, but with the corresponding contraction functions for each spring. By using this staggered expansion mechanism, our jellyfish travels approximately 68% farther with each stroke than it did when all springs expanded in unison. Interestingly, the jellyfish still did have some positive net thrust when all springs moved in unison.

The frequency of the jellyfish's contractions has a direct effect on the thrust that is achieved by the organism, as well as the morphology of the organism. The resonant frequency of the system depends on the diameter of its umbrella. Megill [14] derives an approximate analytical model of the jellyfish, though his findings differ from empirical data [5]. Without further confirmation of either result, we experimented with different contraction frequencies to determine which ones were optimal for our model. Figure 5 shows the translational motion of our simulated jellyfish with different contraction frequencies. As seen in the right side of Figure 5, we get a large maximum for a frequency of 0.7 Hz, which agrees with data measured by Dabiri and Gharib [5].

3.4 2D Rendering Model

Our physics model is quite coarse, and we want to be able to resample it to a resolution appropriate for the rendering configuration. We also need a way to account for the thickness of the umbrella and the tentacles, since we are modeling both as piecewise linear curves. We first add a finite thickness to our model of the umbrella. In our simulation model that involved both linear and angular springs, the point-masses of the umbrella represent the subumbrellar surface. We can generate the exumbrellar side by computing



Fig. 5. Left: Trajectories of several simulated organisms with different frequencies of contraction. Right: Distance traveled with different frequencies of contraction. All results were simulated with a 4 cm organism, and the elastic modulus of the jellyfish's umbrella is $\lambda = 1186 Pa$.



Fig. 6. Simulation of a contraction cycle. Trace particles show the fluid flow around the jellyfish.

surface normals at each point-mass, and then projecting backward through the thickness of the umbrella. Figure 3 provides us with suitable thickness values. We can then generate an arbitrary resolution model for rendering by interpolating a cubic spline through the original point-masses and then the newly generated exumbrellar points.

3.5 3D Extrapolation

We must extrapolate our 2D rendering model to a 3D volume. However, our 2D slice may not be symmetric itself (i.e., the two sides of the umbrella may be different). Thus, we cannot merely rotate the results of the 2D slice about a single axis of symmetry. Our 3D interpolation proceeds by considering each pair of points x_i and x_j opposite to each other on the umbrella. On our simulation model in Section 3.2, these opposing points would be joined by a subumbrellar spring. However, since we have resampled our model for rendering, we use opposing pairs from the rendering model. We define an axis of rotation for each pair, which goes orthogonally through the centre of the line segment between the two points x_i and x_j . Note that each pair of points will potentially have

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Fig. 7. Example point pairs along the 2D umbrella slice that have been extrapolated to 3D discs



Fig. 8. Jellyfish that are only approximately axially symmetric. Left: courtesy of Mark Eramian. Centre: taken by the authors. Right: taken by the Florida Keys National Marine Sanctuary [24].

a different axis of symmetry. Figure 7 illustrates our process of extrapolating circular area from pairs of points in our 2D model. We use the same disc extrapolation scheme for generating tentacles along the 3D aperture of the umbrella.

The volume that will result from our disc-based extrapolation will be artificially smooth and perfect. Although a jellyfish may be roughly symmetric, they are not exactly so. Figure 8 shows example individuals whose umbrellas are approximately symmetric, but with some small-scale asymmetries. To add variation to our rendering model, we perturb each point $z_{i,j}$ on the surface by some scalar distance $c_{i,j}$ in the direction of its surface normal $n_{i,j}$. We use an two subscripts in our notation for the points because we are now dealing with points on two different axes (i.e., latitude and longitude).

Several factors can cause small-scale asymmetries in jellyfish. For one, a particular species may exhibit periodic structures in their umbrella's geometry [25]. For these structural patterns, we define simple functions to generate the desired appearance, such as $\alpha^{str} sin(f\sigma_j)$ or $\alpha^{str} |sin(f\sigma_j)|$, where α^{str} is a scale factor, f is the artistically chosen frequency that suits the target species, and σ_j is the longitudinal angle of points $\mathbf{x}_{i,j}$ for all values of i.

Another type of variation, seen in Figure 3, is caused by the nonuniform elastic properties of the jellyfish's mesoglea, which cause ripples across the umbrella as it contracts. This variation is roughly sinusoidal. We achieve the desired effect by normalizing the function $sin(f\sigma_j)$ to be between 0 and 1, and scale the result by a factor that linearly interpolates between 0 and $(1.51 - 1.36)\vartheta$ as each umbrella spring moves from being fully expanded to fully contracted. For this variation due to compression, we do not modify the subumbrellar points, as the effect is only seen on the exumbrellar surface.

Lastly, some variations are due to differences between individuals of the same species. We have no suitable model for this variation, and so we mimic it artistically by adding noise to the surface of the umbrella. We use Perlin's noise function [18], which yields a second-order continuous scalar field over a 3D space. We control the frequency of each parameter to the noise function independently, since different species display different frequencies of noise in the lateral and longitudinal axes. We chose parameters to qualitatively approximate the look of a target species. We also attenuate the amplitude of the noise function for points that are near the apex of the umbrella. This is partially done because the umbrella is thicker near the apex, and thus will ripple less. Also, the discs that we extrapolate from our slice data are smaller near the peak of the umbrella than the discs that are closer to the aperture. Thus, the noise function appears to have a higher frequency on the discs with smaller radii. By attenuating the noise function near the top of the umbrella, we remove these artifacts. Our expression for the displacement of the umbrella points due to non-periodic variation is as follows:

$$c_{i,j}^{unstructured} = \alpha^{unstr} d_i * Q_P(2d_i, 8d_j, 0.01t), \tag{2}$$

where (d_i, d_j) is a normalized latitude-longitude coordinate for each surface point, t is the simulation time, Q_P is the Perlin noise field, and α^{unstr} is again a scaling factor. We apply this displacement to both umbrella points, and also tentacle points, so that the tentacles themselves exhibit some variation.

4 Results

Figure 10 shows a series of frames from our system, rendered with a simple Lambertian surface lighting model. We find the motion of our jellyfish to be quite satisfactory and convincing. The model's movement is more closely tied to the contraction of the organism than previous animations of jellyfish such as in Disney's "Finding Nemo" [20]. Also, our model's morphology, motion, and resonant frequency shown in Figures 5 and 11 are similar to empirical results [5].



Fig. 9. The results of naïve 3D extrapolation for both an expanded (rest) and contracted state, and the three types of variation that we apply to the umbrella, as well as the combined variation



Fig. 10. A single contraction-expansion cycle for our virtual jellyfish, fully rendered



Fig. 11. The morphology of a 4 cm simulated jellyfish with a contraction frequency of 0.7 Hz. All other simulation parameters were the same as Figure 5.

Parameter	Value
Fluid Grid Height/Width (n)	100
Fluid Viscosity (ν)	1.304×10^{-3}
Fluid Density (ρ)	1
Safety Factor for Integration Step Size	0.001
Jellyfish Contraction Frequency	0.7Hz
Jellyfish Diameter	40mm
Jellyfish Height	28mm
Jellyfish Thickness (ϑ)	4mm
Hookean Elastic Modulus (λ)	1186Pa
Angular Elastic Stiffness	$1.186 \ N \cdot m/rad$
Tentacle Cross-sectional Area Factor	1/100
Structural Variation Scale (α^{str})	$0.375 \cdot \vartheta$
Unstructured Variation Scale (α^{unstr})	$2.25 \cdot \vartheta$

Fig. 12. Parameters of our animation system

However, one major difference between our model and empirical data is that our model yields more high-frequency movement than is seen with real jellyfish. Essentially, our model's position oscillates up and down more, relative to its overall translational motion. Thus, our model is suitable for entertainment purposes, but would not be accurate enough for the biology community.

We are able to achieve interactive rates of 30 to 40 frames per second on modest hardware (AMD Turion 1.6 GHz processor), depending on the resolution of our 2D simulation and of our 3D extrapolation. We experimentally find that time-steps of the order of 0.01 seconds begin to hit the stability limits of the system, and so several steps are taken between frames. Of course, the 3D extrapolation process is done only once per rendered frame.

5 Conclusions and Future Work

We numerically simulate a model of jellyfish that accounts for the elastic forces of the organism as it contracts its muscles, as well as the reaction of the sea water that surrounds the organism. We choose simulation as our animation technique because it allows us to model the interaction of the jellyfish and its environment. We restrict our model to species that are axially symmetric, so that we only need to simulate a 2D vertical slice of the organism. We also concentrate on the resonant gait of adult jellyfish.

In our simulations, we represent the jellyfish's flesh as a spring-mass system that consists of a combination of linear and angular springs. The muscles that line the under part of the umbrella are modeled as linear springs that span the subumbrellar cavity. We mimic the contraction of these muscles by shortening the subumbrellar springs' rest lengths based on an artistically chosen periodic function. To simulate the reaction of the sea water that surrounds the organism, we use a semi-Lagrangian [27] fluid simulator in conjunction with the immersed boundary method [19].

We generate a high resolution 2D rendering model by threading a cubic interpolant around the point-masses of our coarse simulation model. With this higher resolution slice model, we extrapolate to a 3D surface by defining discs that go through both sides of the 2D umbrella curve. We add several forms of variation to the resulting 3D surface. First, parabolic patterns are added, which run vertically down the surface of the umbrella. These patterns are specific to certain species of jellyfish. Second, vertically sinusoidal ridges are introduced as the organism contracts, due to its non-linear elastic properties. The amplitude of these ridges depend on the contraction of the umbrella. Lastly, we add continuous noise to the umbrella's surface to give each individual jellyfish a unique shape, artistically defined for lack of a concrete model of this variation.

Further work with respect to jellyfish animation could be done. We would like to remove the restriction of axial symmetry, possibly by simulating multiple 2D slices and interpolating between them. One challenge with this approach is to reconcile the simulated slices where they intersect. Rendering could be improved by considering translucency and bioluminescence. We are unaware of any literature that describes a jellyfish's optical properties. Similarly, one could model the venous structures that are present in some species, though again we are unaware of any relevant biology literature.

We still know little about how jellyfish control their muscles to achieve jet propulsion. Much work in this regard could be carried out by the biology community, but we could also make use of work in the field of computer animation. Specifically, we could experiment with different muscle control schemes in a manner similar to *sensor actuator networks* [17]. Also, jellyfish are capable of other locomotion modes besides the common resonant gait, and so these other modes could be investigated.

In our work, we have not discussed how some species of jellyfish are able to reorient themselves. Megill [14] states that jellyfish use sparsely placed radial muscle fibres in the bell mesoglea to change the symmetry of the umbrella and thus affect a course change for the organism as it swims. The exact process is not well understood. So far, we were not able to reproduce this phenomenon within our model.

With relation to fluid dynamics, there are a number of improvements that could be made to numerical techniques. Stability criteria could be derived for the immersed boundary method. Also, the numerical stiffness of SPH techniques for incompressible flows could be improved. Recently, Robinson-Mosher et al. [23] have introduced pressure-based elastic-fluid methods that are unconditionally stable, though we have not investigated these new results.

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