

FROM PACEMAKER TO VORTEX RING: MODELING JELLYFISH PROPULSION AND TURNING

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A dissertation submitted to the faculty at the University of North Carolina at Chapel Hill in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Mathematics in the College of Arts and Sciences.

Chapel Hill
2015

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ABSTRACT

Alexander Hoover: From Pacemaker to Vortex Ring: Modeling Jellyfish
Propulsion and Turning
(Under the direction of Laura Miller)

Jellyfish have been widely studied by disparate disciplines such as organismal biology, biooceanography, mechanical engineering, physics and mathematics. The jellyfish blooms of our warming oceans and their disruptions to industrial processes and fishing operations have garnered a high amount of attention from ecologists. More recently, the advent of drones has motivated engineers to look to jellyfish and other organisms for inspiration in the design of efficient underwater vehicles [18]. With their soothing motion to their impressive swarms, jellyfish are a creature that that both affixes the mind’s imagination and demands attention, whether from popular science articles on their ‘immortality’ [78] to the painful sting from the tentacles that can ruin a day at the beach.

Dating back to Romanes in the 1870s, biologists have studied this biomechanical system, using excision experiments to explore the nervous system and musculature [80]. One motivation for this work is that jellyfish are one the earliest examples of a motile, multi-cellular organism [23]. With a fossil record dating to the Middle Cambrian [16], one can gain insight into how the first cells organized into a moving system by studying the biomechanics of jellyfish locomotion. At its most general, the propulsion cycle of jellyfish is a result of the interaction of pacemakers, a decentralized nervous system, and the musculature driving the motion of an elastic bell. The resulting dynamics are robust enough to allow for both regular forward swimming gaits and complicated steering maneuvers resulting from asymmetrical activation of the musculature.

Relative to other organisms, mathematicians and physical scientists have focused a disproportional amount of attention to the mechanics of jellyfish swimming. This work has used both computational and analytical methods to reveal the optimal kinematics for vortex formation and fluid-structure interaction. There are few reasons that jellyfish have garnered the attention of mathematicians, with one of the simplest being its geometry. The smooth and simple geometry of a jellyfish bell

coupled with an assumption of radial symmetry allow for mathematically tractable simplifications. In terms of computational modeling, jellyfish are ideal for studying fluid-structure interactions due to their relatively simple kinematics and swimming in a non-turbulent fluid regime.

The main goal of this dissertation is to introduce a framework for studying locomotion using modern computational methods and high performance computing libraries that allow us to explore problems at the intersection of biology, fluid dynamics, and mechanics. Beginning with Chapter 1, I will introduce the body of work surrounding jellyfish biomechanics and point to open questions that are important and unaddressed. Chapter 2 will describe the methodology from which I will approach this problem, including the computational fluid-structure interaction framework of the immersed boundary-type methods, as well as the relevant dimensionless numbers. This framework will then be employed in Chapter 3 to examine resonant driving in simplified prolate bells. Chapter 4 follows and continues this work by introducing a 3-dimensional active tension model for forward locomotion using a hybrid finite difference/finite element version of the immersed boundary method. In Chapter 5, I will explore the scaling limits of oblate jellyfish propulsion. Finally, Chapter 6 will extend this framework to model the mechanics of turning.

To my parents, Daniela and Erkki, my grandparents, Dale and Jean, and
miei nonni, Gigi e Maria

ACKNOWLEDGMENTS

In a few words that are short, sweet, and possibly a little rushed, Id like to thank those that helped guide me in my early years (Greg and David), the UNC biomechanics group (Ty, Bill, and Dennis), my friends and colleagues who have helped me maintain a balance inside and outside of the department (Namdi, Agathe, Colin, Michael, Holly, Nate, Molly, Jacob, David, Charlie, John, Jesse, Nicole, Zane, and Mayukh), my parents and sister (Daniela, Erkki, and Rebecca), my lab (Shannon, Julia, Lindsay, Austin, Arvind, and especially Nick), the UNC IBAMR krewe that I cannot thank enough (Boyce and Amneet), my bedrock (Darin), and, of course, Laura.

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CHAPTER 1

Background

A large body of work in the field of biomechanics and fluid dynamics has focused on jellyfish and the nature of their propulsion. In many of these studies, the goal is to establish biologically-inspired design principles for what is considered a low cost-of-transport swimming mechanism. The focus of this work will be to understand how mechanical and physiological properties of the bell influence jellyfish swimming performance and maneuvering. In this introductory section, I will discuss the functional morphology that provides the basis for jellyfish propulsion. I will then review previous work on the fluid dynamics of jellyfish swimming using analytical and computational tools.

Before starting, it is helpful to define what I mean when I say ‘jellyfish.’ ‘Jellyfish’ is commonly used in reference to the planktonic medusae of the phylum Cnidaria, which includes scyphomedusae, hydromedusae, cubomedusae, and siphonophores. Additionally this definition is sometimes further expanded to include the planktonic, soft-body invertebrates known as comb jellyfish. These organisms are members of the phylum Ctenophora and have a mode of locomotion is substantially different from medusae. This broad definition arises from the similarities of their gelatinous structure and their presence as higher order carnivores in their ecosystems, as opposed to salps and other planktonic tunicates [68]. For the purpose of this work, I will use a narrower definition of the term ‘jellyfish’ that includes only the solitary, saucer-shaped organisms of the phylum Cnidaria with a defined subumbrellar region where the mouth is located. This definition includes the scyphomedusae, cubomedusae, and hydromedusae varieties, but excludes the paddling ctenophores and the multi-bell siphonophores. In this thesis, I will use the term jellyfish and medusae interchangeably.

1.1 Jellyfish morphology and physiology

Although there is a large amount of morphological variation among jellyfish, the mechanical process of generating thrust can be generalized for most medusae. The jellyfish locomotory cycle begins with the activation of the underlying muscular nerve net by pacemakers. The activation

then transmits signals to the swimming muscles present in the subumbrellar cavity to contract. This contraction in turn squeezes the bell, which pushes water out of its inner cavity and generates forward thrust. During the muscular contraction, the bell stores potential energy due to the elastic properties of the bell. Once the contraction has ended, the stored potential energy of the bell is released and the restoring force returns the bell to its original shape.

1.1.1 Neuronal organization and control

The movement of the bell is controlled via a decentralized nervous system whose primary function is to both generate a robust mode of locomotion and to respond to environmental cues. In scyphomedusae and cubomedusae, the pacemakers, also referred to as marginal centres, are evenly spaced around the bell rim, proximal to the sensory structures known as rhopalia [86]. These pacemakers maintain a tetra-radial symmetry, with the number of pacemakers present being a multiple of four. The pacemakers can fire independently and are weakly coupled. In hydromedusae, more complicated neural structures are manifested with compressed nerve rings that allow for a more coordinated response. All three medusan nervous systems are characterized by the presence of nerve nets into multiple, parallel conduction systems. The presence of these parallel conduction systems allows a robust control mechanism that can alter the swimming behavior of jellyfish in response to environmental cues.

In scyphomedusae, the diffuse nerve net (DNN) integrates environmental cues received throughout the bell. The motor nerve net (MNN) controls the activation of muscles. The scyphomedusan MNN has three major characteristics [85, 86]. First, the system is ‘through conducting’ such that action potentials generated in one part of the nerve net travel throughout the entire nerve net if unimpeded by other action potentials [81, 51]. Secondly, the MNN is diffuse throughout the subumbrellar epithelial layer where the main swimming musculature has no preferred orientation [85]. Lastly, the MNN has a non-polarized direction of excitation [81, 8]. The synapses present in the MNN are bidirectional wherein the terminal of the synapse can act as both the pre- and post-synaptic element of the traveling action potential [5]. The neurons that make up these nerve nets lack direct electrical coupling, and synaptic delays between pre- and post-synaptic neurons are consistent with those found in other animals [5, 7, 6].

The MNN and DNN interact with each other by modulating the pacemakers units present at the rim of the bell. Sensory information from the DNN is integrated and affects the pacemaker’s firing frequency of action potentials that travel the MNN. The MNN in turn allows for the transmission of action potentials across the subumbrellar epithelial layer that, if unimpeded by other action potentials, can depolarize and reset the pacemakers [52, 73]. The role of the DNN in muscular activation has also been the subject of research. In some scyphomedusae, the DNN facilitates muscular response through the process of ‘double innervation’ [51].

The pacemaker resetting mechanism present in scyphomedusans has been shown to reduce the interpulse duration between action potentials [52]. Through a series of excision experiments, the action potentials generated by pacemakers in a bell where all other pacemakers were removed displayed different firing frequencies than that of undamaged pacemakers that could experience resetting mechanisms [73]. This pacemaker response to other traveling action potentials has been shown to reduce the variability of interpulse durations and in turn allow for a more robust and regular swimming gait [70].

Cubomedusae can be characterized as having a nervous system that is very similar to scyphomedusae. Their bell movement is controlled through the interactions of pacemakers and a diffuse bipolar nerve net [88]. Some degree of centralization is present due to a higher concentration of neurons, referred to as neural condensation, that form a ring that connects the four pacemakers that control the bell [85]. The pacemakers themselves have complicated sensory structures, most notably the ocelli that processes visual stimuli and aid in hunting behavior. Similar to the scyphomedusae, the excision of the pacemaker units result in the absence of spontaneous movement [73].

In hydromedusae, the nerve nets and rhopalia give way to condensed nerve rings that can be characterized as more highly organized and integrated than those of the scyphomedusae and cubomedusae. Similar to the scyphomedusae, the hydromedusae nervous system is characterized by the presence of multiple, parallel, conduction systems. The number of systems varies among species, with the highest number identified being 13 systems in *Aglantha digitale*. Each conducting system can be associated with different behavioral responses to environmental conditions. These systems are generally organized within two nerve rings, the subumbrellar inner nerve ring and the exumbrellar outer nerve ring. Both systems are located towards the bell margin and the velum, an adjustable shelf of tissue found in hydromedusae that aids swimming and maneuvering. The

inner nerve ring has been characterized as the main control system for the swimming musculature, while the outer nerve ring integrates sensory information. The nerves present in these systems are electrically coupled, and gap junctions are present that allow for action potential conduction speeds that are much faster than those seen in the synaptic transmission of the scyphomedusae. Chemical synapses allow for the communication between the nerve ring systems and the epithelial cells that activate the musculature. The epithelial cells are also electrically coupled, which in turn means that the activity of a small portion of the nerve ring could allow for the uniform activation of the musculature. This was first observed by Romanes in 1885 when he noticed that it was necessary to excise the entire nerve ring to cease pulsations.

1.1.2 Musculature

The swimming musculature found in jellyfish performs the task of deforming the bell to propel and maneuver. This is done without the presence of an agonist-antagonist muscle pairing to return the bell back to its original shape. The bell's mesoglea, to which the swimming muscles are anchored, fulfills that role passively. The main swimming muscles are striated and form a thin layer in the inner cavity of the bell. The swimming musculature is predominantly circumferentially oriented, though scyphomedusae also have radial muscles. During the propulsive cycle, the activation of these circumferentially-oriented muscles drives the contraction and pushes fluid out of the bell.

Muscular activation varies between the different medusa types. In scyphomedusae, the musculature is activated within a unidirectional chemical synapse with the MNN, though there is evidence that the DNN plays a role by facilitating and amplifying the muscular response as well as controlling the contraction of non-swimming smooth musculature [51]. It's important to note the role that radial musculature is believed to play in turning. In scyphomedusae, and in all classes in the phylum Cnidaria except hydrozoa, there is an absence of gap junctions between the musculature [86]. The presence of gap junctions in hydromedusae allows for a rapid activation of the musculature once a signal has arrived from the nerve ring, though control of the swimming musculature in a fully functioning nerve ring is broken up into quadrants that allow for more coordinated muscular activity.

1.1.3 Mesoglea

The jellyfish bell is composed of the two epithelial layers, the epidermis and the gastrodermis, and a thick layer of gelatinous connective tissue known as the mesoglea, from which the dominant elastic properties are derived [9]. The mesoglea is thicker relative to the other layers and performs the skeletal function of the bell, maintaining shape and form.

The mesoglea itself is an extracellular matrix composed of a heterogeneous mix of mucopolysaccharides, elastic microfibrils, collagen fibrils, and other structural proteins that allow the bell to act as viscoelastic gel [63, 36]. Studies have found a large amount of variation among jellyfish mesoglea from species to species, with differences found in the elastic fibre structure’s composition and arrangement. Megill noted through a series of rheological experiments the presence of nonlinear elastic behavior at large deformations. He attributed this behavior to the presence of fibres that reinforced the bell during the large deformations that occur during contraction.[64]. Megill’s work also showed the presence of different swimming gaits for jellyfish through the tuning of the elastic properties of the muscle fibers. Generally, one can think of the bell as composed of primarily viscoelastic materials whose stiffness and elasticity is maintained through the presence and organization of collagen fibrils and microfibrils, respectively.

The concept of mesoglea as a reservoir for storing elastic potential energy comes from the necessity of returning the bell to its original form after contraction without the presence of a musculature to do so. Demont and Gosline [29, 28, 30] examined the energetic cycle of the hydromedusae *Polyorchis pencillatus* by measuring the mechanical properties of the mesoglea and the musculature. In that work, they introduced the concept of resonant driving of the bell where the muscular activation present in the bell is tuned to the elastic properties of the mesoglea and, if driven at resonant frequencies, can maximize the stored potential energy of the bell.

1.2 Fluid dynamics of jellyfish locomotion

The fluid dynamics of jellyfish propulsion has been the focus of current research in the fields of comparative biology, bioengineering, mathematics, and physics [62, 61, 48, 24, 25, 22, 23, 56, 18, 38, 37]. The unique and simple morphology of the bell and musculature has enabled careful study of swimming energetics (e.g. cost of transport) and the resulting flow structures [26, 62, 23]. One area

of research related to the fluid mechanics of jellyfish propulsion is to understand the vortex ring pairs generated during contraction and expansion. During the contraction of the bell, fluid is ejected from the bell in the form of a vortex ring that augments forward thrust. During the contraction, the momentum from the bell is transferred from the bell margin to the vortex ring that travels away from the bell. The vortex ring generated during this contraction phase is called the starting vortex. The bell then passively expands to its original position, and a stopping vortex ring forms in the bell cavity. Due to the complementary motion of the bell margin during the contraction and expansion, this stopping vortex spins in the opposite rotation of the starting vortex.

One of the fundamental questions in jellyfish propulsion is how bell design and shape are constrained by the single cell-layer thick muscles [61]. Work by Dabiri and others has revealed that jellyfish locomotion can be categorized as either jetting or paddling based on the bell's fineness ratio, which is defined as the ratio between bell height and diameter [23]. A high fineness ratio is indicative of prolate bell geometries and a low fineness ratio represents oblate bell geometries. In the jetting mode, forward thrust is generated primarily during the contraction phase with a strong expulsion of water out of the bell. This fast forward acceleration can be further enhanced with the presence of a velum to restrict the opening in the bell cavity [22]. This mode of transport is primarily found in jellyfish that are ambush predators and are of a small size. As the bell diameter and size increases, the muscular force necessary to create a comparable forward thrust through jetting is constrained by the thin swimming musculature as well as the increased drag of a larger bell [26, 62]. In contrast, at lower fineness ratios a paddling mode uses the stopping vortex in addition to the starting vortex to generate forward thrust [24]. The stopping vortex 'pushes' up against the bell, forming what can be described as a vortex ring 'motor' in the inner cavity of the bell. While the starting vortex generated during the contraction is lost in the wake and advected away from the bell, the force generated by the bell can be recaptured passively from the stopping vortex [38]. The efficient paddling mode allows larger jellyfish to effectively swim and filter feed even though their swimming muscles are only one cell layer thick [23]. Scaling also plays a role in determining swimming behavior, whether it be for small prolate jetters, which must produce enough thrust to escape the effects of fluid damping, to ephyrae (e.g. juvenile jellyfish), whose lappets allow for an effective drag based stroke at a size where inertial effects are minimal [35, 71].

The paddling and jetting modes of locomotion affect the feeding behavior of jellyfish [19]. For

jettors, many of which are hydromedusae, the fast forward thrust generated during the contraction phase makes them well suited for active prey capture and selective feeding [17]. Paddlers on the other hand satisfy their dietary needs during their swimming stroke by capturing prey in the vortex rings generated during their propulsive cycle [21, 20]. The large amount of entrained fluid present for their larger size and slower stroke allows them to cruise around their fluid environment, foraging for prey that are trapped in the bell cavity and then paralyzed by the cnidae that characterize the Cnidaria phylum and produce the infamous jellyfish stings. The implications of this cruising behavior extends outside the realm of feeding with evidence that Darwinian mixing due to the fluid entrainment by the jellyfish contributes significantly biogenic mixing and the transport of nutrients throughout the ocean [57].

A variety of analytical models have been used to examine jellyfish propulsion with respect to the energetic demands of propulsion [26, 62, 23, 29, 28, 30, 2, 64], and with this research comes the discussion of the role of the mesoglea in propulsion. If the jellyfish subumbrellar muscles were to have the same frequency of activation as the natural frequency of the bell, then it is thought that the swimming speed would be maximized for a fixed force amplitude [30]. Resonant driving would maximize the potential elastic energy stored in the mesoglea. This is due to the fact that the amplitude of bell deformation is maximized when it is driven near its resonant frequency. Demont and Gosline, in work that was later continued by Megill, showed that driving the bell at the resonant frequency can result in radial displacements that are significantly higher than those at other frequencies [64, 2, 30].

The fluid flow around swimming jellyfish has also been studied using computational fluid dynamics [53, 97]. Herschlag and Miller prescribed the kinematics of a 2D hemielliptical bell [48]. The resulting forward motion of the jellyfish was similar to speeds measured in actual jellyfish. Mohseni et al. used an axisymmetric Lagrangian-Eulerian formulation of the fluid-structure interaction problem to simulate the forward swimming of the jellyfish *Aequorea victoria* using the actual bell profiles as inputs [82]. Alben et al. used a combination of computational tools and analytical models to explore the kinematics of the bell for both high velocity and high efficiency movements [3]. Oblate swimming has also been modeled using a constraint-based immersed boundary method by Park et al. that accounted for some of the elastic properties of the bell [72]. Previous work by Hamlet et al. used the immersed boundary approach to examine the feeding mechanisms of the benthic jellyfish

Cassiopeia spp using a porous plate to model the effect of the oral arms on the flow [47, 84].

1.3 Concluding remarks

Using the scientific literature presented here as the inspiration of my work, 2-dimensional and 3-dimensional computational models were developed to explore how elastic properties affect the swimming performance of jellyfish. In Chapter 3, a simplified 2-dimensional prolate bell model is used to explore a large parameter space in the context of resonant driving with a full fluid model. In Chapters 4, 5, and 6, a 3-dimensional model is developed that incorporates morphological properties reported in the literature, as well as a turning mechanism derived from observations of the scyphomedusan nervous system. The goal of these studies is to create a theoretical framework from which many aspects jellyfish locomotion can be explored.

CHAPTER 2

Methods

In this chapter I will introduce the methods and equations used in the next chapters of this thesis. In the first section I will summarize the derivation of the Navier-Stokes equations, along with dimensionless numbers that arise during the nondimensionalization of these equations. I will then introduce the immersed boundary approach to fluid-structure interaction problems by first introducing the classical fiber-based approach to modeling elastic structures that is used for the study detailed in Chapter 3. Lastly I will discuss a hybrid immersed boundary formulation known as the hybrid immersed boundary finite element approach, or IBFE, that uses a finite element formulation to model the immersed elastic structure. This method is used in the studies introduced in Chapters 4, 5 and 6.

2.1 The equations of motion

To understand how an organism moves in fluid, I must first understand the movement of the fluid as a whole. The motion of fluid, whether it be gas or liquid, comes from the collective movement of the molecules that compose the fluid. At appropriate scales, a continuum assumption can be used to describe the motion of the fluid as continuous and differentiable, and it is not necessary to resolve the behavior of a discrete collection of molecules. Taking this assumption allows us to apply many of the tools from calculus and mechanics to the analysis fluid motion.

At its most basic, the movement of fluid is a consequence of Newton's second law of motion, $F = ma$. In fact, Newton's discussion on the nature of viscous fluids in *Principia* can be considered as one of the events that spurred the formulation of the equations of fluid motion. Further work by Bernoulli, Euler, Cauchy, and finally Stokes, just 158 years after Newton and preceded by erroneous molecular assumptions by Navier, produced the equations of fluid motion as used today [1]. The equations of fluid motion for a viscous incompressible fluid can be described using a compact form

of the incompressible Navier-Stokes equations for a parcel of fluid

$$\rho \frac{D\mathbf{u}}{Dt} = \nabla \cdot \sigma \quad (2.1.1)$$

with an additional incompressibility condition

$$\nabla \cdot \mathbf{u} = 0 \quad (2.1.2)$$

where $\mathbf{u} = \mathbf{u}(\mathbf{x}, t)$ is the velocity vector present at the coordinates of $\mathbf{x} \in \mathbf{R}^d$ at time t , ρ is the density of the fluid, $\frac{D}{Dt} = \frac{\partial}{\partial t} + \mathbf{u} \cdot \nabla$ is the material derivative (the rate of change of a quantity that "follows" where the quantity is being transported), and $\nabla \cdot \sigma$ is the divergence of the stress tensor of the fluid. By looking at this compact form of the Navier-Stokes equations, we note that how Eq. 2.1.1 is $F = ma$, where $\rho \frac{D\mathbf{u}}{Dt}$ is " ma " and $\nabla \cdot \sigma$ is " F ". This stress tensor can be thought of as the stress exerted on a parcel of fluid ($\sigma = \sigma^f$) and can be taken as

$$\sigma^f = p\mathbb{I} + \mu(\nabla\mathbf{u} + (\nabla\mathbf{u})^T) \quad (2.1.3)$$

where $p = p(\mathbf{x}, t)$ is pressure, and μ is dynamic viscosity. With this information we can expand Eq. 2.1.1 such that

$$\rho \left(\frac{\partial\mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} \right) = -\nabla p + \mu \Delta \mathbf{u} \quad (2.1.4)$$

where $\Delta = \sum_i^d \sum_j^d \frac{\partial}{\partial x_i} \frac{\partial}{\partial x_j}$. Note that the dynamic viscosity, μ , arises from the molecular properties of the fluid.

2.1.1 Reynolds number

Many times one is dealing with the movement of a fluid past a structure, the characteristic length ($\mathcal{L}$) of the structure, and the characteristic speed of the fluid with respect to the structure ($\mathcal{U}$) and the density and viscosity of the fluid determine the

dynamics. Let's nondimensionalize the Navier-Stokes equations using the following quantities:

$$\tilde{\mathbf{u}} = \mathbf{u}/\mathcal{U}, \quad \tilde{\mathbf{x}} = \mathbf{x}/\mathcal{L}, \quad (2.1.5)$$

$$\tilde{t} = t \frac{\mathcal{U}}{\mathcal{L}}, \quad \tilde{p} = p \frac{1}{\rho \mathcal{U}^2} \quad (2.1.6)$$

such that our differential operators become

$$\nabla = \mathcal{L}^{-1} \tilde{\nabla}, \quad \frac{\partial}{\partial t} = \frac{\mathcal{U}}{\mathcal{L}} \frac{\partial}{\partial \tilde{t}}, \quad \Delta = \mathcal{L}^{-2} \tilde{\Delta}. \quad (2.1.7)$$

Plugging equations 5-7 into the Navier Stokes equations yields

$$\frac{\rho \mathcal{U}^2}{\mathcal{L}} \left(\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + \tilde{\mathbf{u}} \cdot \nabla \tilde{\mathbf{u}} \right) = -\frac{\rho \mathcal{U}^2}{\mathcal{L}} \tilde{\nabla} p + \frac{\mu \mathcal{U}}{\mathcal{L}^2} \tilde{\Delta} \tilde{\mathbf{u}} \quad (2.1.8)$$

which in turn can be rearranged such that

$$\left(\frac{\partial \tilde{\mathbf{u}}}{\partial \tilde{t}} + \tilde{\mathbf{u}} \cdot \nabla \tilde{\mathbf{u}} \right) = -\tilde{\nabla} p + \frac{1}{Re} \tilde{\Delta} \tilde{\mathbf{u}} \quad (2.1.9)$$

where Re is a dimensionless quantity known as the Reynolds number that is defined as

$$Re = \frac{\rho \mathcal{U} \mathcal{L}}{\mu}. \quad (2.1.10)$$

This quantity gives the ratio of inertial forces to viscous forces in the fluid. When calculating the Reynolds number of objects whose characteristic velocity is not necessarily prescribed, but rather a frequency of motion is prescribed and one can define the characteristic speed with respect to this frequency, f , such that $\mathcal{U} = f\mathcal{L}$.

Note that for $Re \gg 1$, the viscous term is negligible and can be ignored. In this case the flow is called inviscid and is described using Euler equations. The equations have been used to analyze locomotion in fish, insects, birds, and other animals whose speed and length scales are appropriate for the assumption. Conversely, at $Re \ll 1$ viscous forces dominate such that the left hand side of the Navier-Stokes equations are negligible and can be ignored, leading to a Stokes flow formulation of fluid motion. This formulation is often used when describing flows at microscopic length scales,

such as bacterial or cellular locomotion [33, 89]. In the present study, the flows generated by jellyfish are firmly in the intermediate Reynolds number range with a lower bound of $O(1)$ and an upper bound of $O(1000)$, thus precluding the use of inviscid or Stokes flow assumptions.

2.2 The immersed boundary method

In my modeling work in Chapter 3, a 2-dimensional formulation of the immersed boundary (IB) method was used, though a similar formulation can be applied for 3-dimensional problems. The IB method was originally developed by Peskin to study the fluid dynamics of blood flow in the human heart [74]. Since then, the IB method has been used to solve numerically a variety of fluid structure interaction problems in the low to intermediate Reynolds number regime, here defined as 10^{-1} to 10^3 [69] including undulatory swimming [34, 15], insect flight [65, 66, 67], lamprey swimming [92], crustacean swimming [94], and jellyfish swimming [48].

The idea of the IB method is to describe fluid-structure interaction systems by separating the governing fluid and structural equations into Eulerian and Lagrangian frames, respectively. In the Eulerian frame, the viscous, incompressible fluid equations are discretized on a fixed Cartesian grid, $\Omega \subset \mathbb{R}^d$ for $d = 2, 3$, with appropriate boundary conditions. In the Lagrangian framework, the structure is defined as an elastic boundary with a material coordinate system, $U \subset \mathbb{R}^d$, that is allowed to move freely with reference to the Cartesian grid, but independent of the grid's node points. The interaction between the two frames is done via integral transforms with delta function kernels that couple the system by spreading the body forces generated by the elastic structure to the local fluid environment and by moving the elastic structure at the local fluid velocity.

The governing equations of motion for the fluid are the Navier-Stokes equations for a viscous, incompressible fluid with an additional force term to represent the contribution of the elastic structure

$$\rho \left(\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} \right) = -\nabla p + \mu \nabla^2 \mathbf{u} + \mathbf{f} \quad (2.2.1)$$

$$\nabla \cdot \mathbf{u}(\mathbf{x}, t) = 0, \quad (2.2.2)$$

where ρ is the fluid density, $p = p(\mathbf{x}, t)$ is the fluid pressure, μ is the dynamic viscosity of the fluid, $\mathbf{u} = \mathbf{u}(\mathbf{x}, t)$ is the fluid velocity, $\mathbf{f} = \mathbf{f}(\mathbf{x}, t)$ is the Eulerian force density acting on the fluid, $\mathbf{x}$ is the

position vector on the Cartesian grid, $\frac{D}{Dt}$ is the material derivative, and t is the time.

To determine the total force due to the elastic deformation of the boundary and the externally applied force, consider the boundary as a 1D fiber with a preferred curvature. For cases where an external force is applied, it is natural to separate the Lagrangian force density into the elastic force density, $\mathbf{F}_E$, and the driving force density, $\mathbf{F}_D$, such that the total force density is

$$\mathbf{F}(q, t) = \mathbf{F}_E(q, t) + \mathbf{F}_D(q, t), \quad (2.2.3)$$

where q is the curvilinear material coordinate of the elastic boundary. To determine $\mathbf{F}_E$, we take the assumption that the boundary is composed of an elastic fiber that resists compression, extension and bending. We then describe $\mathbf{F}_E$ with respect to the arclength, q , of the fiber as:

$$\mathbf{F}_E(q, t) = \mathbf{F}_E^{spring}(q, t) + \mathbf{F}_E^{beam}(q, t) \quad (2.2.4)$$

$$\mathbf{F}_E^{spring}(q, t) = \frac{\partial}{\partial q} T(q, t) \hat{\tau}(q, t) \quad (2.2.5)$$

$$\mathbf{F}_E^{beam}(q, t) = \frac{\partial^2}{\partial q^2} k_b \left(\frac{\partial^2}{\partial q^2} (\mathbf{X}(q, t) - \mathbf{X}_b(q)) \right) \quad (2.2.6)$$

where $\mathbf{X}(q, t)$ is the mapping of the Lagrangian material point q to the Cartesian grid, $T = k_s(|\partial\mathbf{X}(q, t)/\partial q| - 1)$ is the tension of the fiber, $\hat{\tau}(q, t) = \frac{\partial\mathbf{X}/\partial q}{|\partial\mathbf{X}/\partial q|}$ is the unit vector aligned with the fiber, $k_b, k_s \geq 0$ are respectively the bending and stretching stiffnesses of the fiber, and $\mathbf{X}_b(q)$ is the preferred configuration of the fiber. Both terms on the right hand side of the equation are derived by writing an expression for the stretching and bending energies of a fiber perturbed from its preferred configuration. The elastic forces are then determined by taking the Frechet derivative of the stretching and bending energies. More details of this formulation can be found in Peskin [74], Griffith *et al.* [41], and Bhalla *et al.* [15].

The interaction between the fluid and the structure is described by the equations

$$\mathbf{f}(\mathbf{x}, t) = \int \mathbf{F}(q, t) \delta(\mathbf{x} - \mathbf{X}(q, t)) dq \quad (2.2.7)$$

and

$$\frac{\partial \mathbf{X}}{\partial t} = \mathbf{U}(\mathbf{X}(q, t)) = \int \mathbf{u}(\mathbf{x}, t) \delta(\mathbf{x} - \mathbf{X}(q, t)) d\mathbf{x}, \quad (2.2.8)$$

where $\delta(\mathbf{x})$ is a d -dimensional delta function kernel and $\mathbf{U}(q, t)$ is the velocity of the Lagrangian material coordinate. Eq. (2.2.7) spreads the force exerted by the boundary onto the local fluid grid. After the Navier-Stokes equations are solved with this applied force for one time step, Eq. (2.2.8) is used to interpolate the local fluid velocity at each boundary point and update the boundary point position based on the local fluid velocity.

2.2.1 Eulerian discretization

Our discretization will be for the 2-dimensional case, though a similar discretization can be applied for 3-dimensions. Let Ω be a unit square that is discretised with a regular $N \times N$ Cartesian grid with uniform grid spacings $\Delta x_1 = \Delta x_2 = h = 1/N$. Label individual Cartesian grid cells with (i, j) for $0 \leq i, j \leq N$. A staggered-grid discretization is used to solve the Navier-Stokes equations, as described in [41]. This is done by determining at the center of each cell edge an approximation to the components of $\mathbf{u}(\mathbf{x}, t)$ and $\mathbf{f}(\mathbf{x}, t)$ that are normal to the edge. For $d = 2$, the components of the Eulerian velocity field are discretized as $\mathbf{u} = (u_1, u_2)$ that are approximated at the centers of x_1 - and x_2 -edges of the Cartesian grid cells, such that $\mathbf{x}_{i-1/2, j} = (ih, (j + \frac{1}{2})h)$ and $\mathbf{x}_{i, j-1/2} = ((i + \frac{1}{2})h, jh)$. The Eulerian body force $\mathbf{f} = (f_1, f_2)$ is also approximated using a staggered scheme. Cell-centered approximations are used for the approximations of p . Here $(u_1)_{i-1/2, j}$, $(u_2)_{i, j-1/2}$, $(f_1)_{i-1/2, j}$, $(f_2)_{i, j-1/2}$, and $p_{i, j}$ represent the discrete values of $\mathbf{x}$, $\mathbf{f}$, and p , respectively. We denote the approximations to the differential operators of the Eq. (2.2.1) as $\nabla_h \cdot u \approx \nabla \cdot u$, $\nabla_h p \approx \nabla p$, and $\nabla_h^2 u \approx \nabla^2 u$. We use standard second-order accurate finite difference approximations, where $\nabla_h \cdot u$ is defined at the cell centers and both $\nabla_h p$ and $\nabla^2 u$ are defined at the cell edges [41]. Using a staggered-grid discretization gives an added benefit of both reduced grid dependence (i.e. less sensitive to perturbations) and better volume conservation. More details on the performance of the staggered-grid discretization in the IB method can be found in Griffith [42].

The incompressible Navier-Stokes equations were discretized on a block-structured locally refined Cartesian grid as detailed by Griffith [46, 45, 43, 41, 42]. The Cartesian grid is composed of a hierarchy of nested grid levels that are labeled $\ell = 0, 1, \dots, \ell_{max}$, where $\ell_{max} \geq 0$ is the most refined level and $\ell = 0$ is the coarsest level. Each level consists of one or more rectangular Cartesian grids where the discretized fluid equations are solved. Each grid level ℓ has a grid spacing h^ℓ , which can

in turn be related to the grid spacing of the next coarser level $\ell - 1$ by an integer refinement ratio N^{ref} , such that $h^\ell = \frac{1}{N^{ref}} h^{\ell-1}$. For the Eulerian discretization described in the previous paragraph, let $h = h^{\ell_{max}}$. The immersed structure is placed at the finest grid level so as to accurately resolve the thin boundary layers present there. The finest grid level is also used to resolve areas where the magnitude of vorticity is above a threshold value, $|\omega^{Mag}|$, which is not necessarily close to the boundary due to vortex shedding. This hierarchical Cartesian grid structure allows one to solve the fluid structure interaction system with high spatial resolution in areas where it is necessary, while allowing for coarser resolutions in areas where the additional contributions of a higher resolution are negligible.

2.2.2 Lagrangian discretization

Computing an approximation to the Lagrangian elastic force requires the introduction of a finite difference operation for our curvilinear coordinates. For computing the stretching energies, we apply a central difference operator

$$D_q^0 \Phi_{q+1/2} = \frac{\Phi_{q+1} - \Phi_q}{\Delta q} \quad (2.2.9)$$

where $\Phi_{q+1/2}$ is an arbitrary quantity defined on the curvilinear mesh, and Δq is the spacing between mesh points. The fiber tension and unit fiber tangent vector are in turn approximated at "half-integer" values (here we use the notation $\mathbf{X}_q = \mathbf{X}(q, t)$ to separate discretization from formulation)

$$T_{q+1/2} = k_s(|D_q^0 \mathbf{X}_{q+1/2}| - 1), \quad (2.2.10)$$

$$\hat{\tau}_{q+1/2} = \frac{D_q^0 \mathbf{X}_{q+1/2}}{|D_q^0 \mathbf{X}_{q+1/2}|}. \quad (2.2.11)$$

These half integer values are then used to compute $\mathbf{F}_q$ of the curvilinear mesh nodes

$$\mathbf{F}_q^{spring} = D_q^0(T_q \hat{\tau}_q). \quad (2.2.12)$$

To resolve the beam equation of Eq. (2.2.4), we first define a forward and backward difference

operator

$$D_q^+ \Phi_q = \frac{\Phi_{q+1} - \Phi_q}{\Delta q} \quad (2.2.13)$$

$$D_q^- \Phi_q = \frac{\Phi_q - \Phi_{q-1}}{\Delta q}, \quad (2.2.14)$$

that will then be used to define a second order central difference operator

$$\begin{aligned} D_q^2 \Phi_q &= D_q^+ D_q^- \Phi_q \\ &= D_q^+ \left(\frac{\Phi_q - \Phi_{q-1}}{\Delta q} \right) \\ &= \frac{\frac{\Phi_{q+1} - \Phi_q}{\Delta q} - \frac{\Phi_q - \Phi_{q-1}}{\Delta q}}{\Delta q} \\ &= \frac{\Phi_{q+1} - 2\Phi_q + \Phi_{q-1}}{\Delta q^2} \end{aligned} \quad (2.2.15)$$

This is then used to approximate the bending energies present at the node q

$$\mathbf{F}_q^{beam} = D_q^2 (k_b D_q^2 X_q - C_q) \quad (2.2.16)$$

where $C_q \approx \frac{\partial^2}{\partial q^2} \mathbf{X}_b(q)$. More details of the Lagrangian structural discretization and several benchmark problems can also be found in [15].

2.2.3 Lagrangian-Eulerian coupling

In the Lagrangian-Eulerian coupling described Eq. (2.2.7) and Eq. (2.2.8), the regularized delta function, $\delta_h(\mathbf{x})$, is defined as

$$\delta_h(\mathbf{x}) = \delta_h(x) \delta_h(y) \quad (2.2.17)$$

where $\delta_h(x) = \frac{1}{h} \psi(\frac{x}{h})$ is a 1-dimensional regularized delta function. Here $\psi(r)$ is the four-point function of Peskin [74], which is defined as

$$\psi(r) = \begin{cases} \frac{1}{8}(3 - 2|r| + \sqrt{1 + 4|r| - 4r^2}), & 0 \leq |r| < 1, \\ \frac{1}{8}(5 - 2|r| + \sqrt{-7 + 12|r| - 4r^2}), & 1 \leq |r| < 2, \\ 0 & 2 \leq |r|. \end{cases} \quad (2.2.18)$$

This discretized delta function is then used to both spread the force from the Lagrangian force density of the curvilinear mesh, as well as to interpolate the velocity of the Lagrangian mesh based on the local fluid velocity of the Cartesian grid.

When spreading the force from the elastic boundary to the underlying cartesian grid, we discretize the transfer of elastic energy from a 1-dimensional fiber of Eq. (2.2.7) in the following manner

$$(f_1)_{i-1/2,j} = \sum_{q \in U} (F_1)_q \delta(\mathbf{x}_{i-1/2,j} - \mathbf{X}_q) \Delta q, \quad (2.2.19)$$

$$(f_2)_{i,j-1/2} = \sum_{q \in U} (F_2)_q \delta(\mathbf{x}_{i,j-1/2} - \mathbf{X}_q) \Delta q, \quad (2.2.20)$$

$$(2.2.21)$$

where $\mathbf{f} = (f_1, f_2)$ and $\mathbf{F} = (F_1, F_2)$. We can denote this discrete force-spreading operator with the shorthand $\mathbf{f} = \mathcal{S}\mathbf{F}$. Similarly for Eq. (2.2.8), updating of the boundary by interpolating the position of the boundary is discretized in the following manner

$$(U_1)_q = \sum_{\mathbf{x} \in \Omega} (u_1)_{i-1/2,j} \delta(\mathbf{x}_{i-1/2,j} - \mathbf{X}_q) h^2, \quad (2.2.22)$$

$$(U_2)_q = \sum_{\mathbf{x} \in \Omega} (u_2)_{i,j-1/2} \delta(\mathbf{x}_{i,j-1/2} - \mathbf{X}_q) h^2, \quad (2.2.23)$$

$$(2.2.24)$$

where $\mathbf{U} = (U_1, U_2)$ and $\mathbf{u} = (u_1, u_2)$. This in turn can be denoted $\mathbf{U} = \mathcal{R}\mathbf{u}$, where $\mathcal{R}$ is a velocity-restriction operator. Note that $\mathcal{S}$ and $\mathcal{R}$ are adjoint operators and therefore imply the conservation of energy in the coupling of the Lagrangian-Eulerian interaction.

2.3 Hybrid immersed boundary/finite element method

There are a number of limitations with classical IB methods, described in the previous section, that model the elastic Lagrangian structure as a collection of fibres that resist extension, compression, and bending. Fibers are well suited for structures that have a high degree of anisotropy and relatively simple geometries, and their implementation can be relatively straightforward. Their limitations become more apparent when one attempts to model materials where constitutive laws have been determined experimentally. Much research in the past decade has been directed towards the

formulation of IB-type methods that incorporate general material models to describe the structure [31, 39, 58, 96, 95]. For the work presented in Chapters 4, 5, and 6, we employ a hybrid version of the immersed boundary/finite element (IBFE) method that was formulated along these principles [44].

In the IBFE method, a Lagrangian elastic body is discretized in a finite element framework with material models from continuum mechanics describing its structural properties, while a finite difference formulation of the fluid equations are maintained in the Eulerian domain. Let $\mathbf{x} = (x_1, x_2, \dots) \in \Omega \subset \mathbb{R}^d, d = 2, 3$ be a position vector on a fixed Cartesian grid, where U denotes the Eulerian domain. We define $s = (s_1, s_2, \dots) \in U \subset \mathbb{R}^d$ to be the Lagrangian material coordinates of the structure in a Lagrangian coordinate domain, U . Let $\chi(s, t) \in \Omega$ denote the mapping of the Lagrangian coordinate s to a point in the Eulerian frame at time t , where the region occupied by the structure at time t is $\chi(U, t)$.

Returning to the stress tensor of Eq. (2.1.1), we now define σ in terms of the coupled fluid-structure interaction system

$$\sigma(\mathbf{x}, t) = \begin{cases} \sigma^f(\mathbf{x}, t) + \sigma^e(\mathbf{x}, t) & \mathbf{x} \in \chi(U, t) \\ \sigma^f(\mathbf{x}, t) & \text{else} \end{cases} \quad (2.3.1)$$

where $\sigma^f(\mathbf{x}, t)$ is the stress tensor of a viscous incompressible fluid that was defined in Eq. (2.1.3), and $\sigma^e(\mathbf{x}, t)$ is the tensor that describes the elasticity of the immersed structure. To relate the elasticity of the structure in current configuration, $\chi(U, t)$, to the Lagrangian material coordinate system, U , the first Piola-Kirchhoff elastic stress tensor $\mathbb{P}(s, t)$ is used such that

$$\int_{\nabla\Gamma} \mathbb{P}(s, t) N dA(s) = \int_{\nabla\chi(\Gamma, t)} \sigma^e(\mathbf{x}, t) n da(\mathbf{x}) \quad (2.3.2)$$

for any smooth region $\Gamma \subset U$, in which $N = N(s)$ is the outward normal along $\nabla\Gamma$, and $n = n(\mathbf{x}, t)$ is the outward unit normal along $\nabla\chi(\Gamma, t)$. Here $\mathbb{P}(s, t)$ is defined as the structural force in the deformed configuration per unit area of the undeformed (or reference) configuration. These stresses are calculated from the material properties prescribed to the elastic body. Using a hyper elastic constitutive model, we can define a strain-energy functional $W = W(\mathbb{F})$ where $\mathbb{F} = \nabla_s \chi(s, t) =$

$\frac{\partial \chi}{\partial s}(s, t)$ is the deformation gradient associated with the mapping $\chi : (U, t) \rightarrow U$. For such constitutive laws,

$$\mathbb{P}(s, t) = \frac{\partial W}{\partial \mathbb{F}}. \quad (2.3.3)$$

There are a number of possible mathematical formulations for the equations of motion for IBFE, which can be found in [44]. These formulations vary depending on whether strong and weak formulations of the elasticity equations are used, as well as how elastic forces are treated at the immersed body's interface. For this work, we use the following formulation

$$\rho \left(\frac{\partial \mathbf{u}}{\partial t} + \mathbf{u} \cdot \nabla \mathbf{u} \right) = -\nabla p + \mu \nabla^2 \mathbf{u} + \mathbf{f} \quad (2.3.4)$$

$$\nabla \cdot \mathbf{u}(\mathbf{x}, t) = 0, \quad (2.3.5)$$

$$\mathbf{f}(\mathbf{x}, t) = - \int_U \mathbf{F}(s, t) \delta(\mathbf{x} - \chi(s, t)) ds, \quad (2.3.6)$$

$$\int_U \mathbf{F}(s, t) \cdot d\mathbf{s} = - \int_U \mathbb{P} : \nabla_s \mathbf{V}(s) ds, \forall \mathbf{V}(s), \quad (2.3.7)$$

$$\frac{\partial \chi}{\partial t}(s, t) = \int_U \mathbf{u}(\mathbf{x}, t) \delta(\mathbf{x} - \chi(s, t)) d\mathbf{x}, \quad (2.3.8)$$

where $\mathbf{V}(s)$ is an arbitrary Lagrangian test function that does not vanish on ∂U . Similar to the fiber IB formulation, Eq. (2.3.4) and Eq. (2.3.5) are the incompressible Navier-Stokes equations and Eq. (2.3.6) and Eq. (2.3.8) are the Lagrangian-Eulerian interaction terms for spreading force from the boundary to fluid and interpolating the boundary with the local fluid velocity, respectively. The Lagrangian force density determined in Eq. (2.3.7), $\mathbf{F}(s, t)$, can be expanded using integration by parts

$$\int_U \mathbf{F}(s, t) \cdot d\mathbf{s} = \int_U (\nabla \cdot \mathbb{P}(s, t)) \cdot \mathbf{V}(s) ds - \int_{\partial U} (\mathbb{P}(s, t) \mathbf{N}(s)) \cdot \mathbf{V}(s) ds \quad (2.3.9)$$

where the first term of this expansion is the Lagrangian internal elastic force density evaluated throughout the immersed body, U , and the second term is the Lagrangian transmission elastic force density evaluated at the surface of the body, ∂U .

2.3.1 Eulerian discretization

For the Eulerian frame, we use the same spatial discretizations as described in Sec. 2.2.1. For the sake of further analysis during the Lagrangian-Eulerian interaction step, we wish to introduce

a discrete L^2 inner product for both Lagrangian and Eulerian frames. If $\mathbf{u}$ and $\mathbf{v}$ are discrete staggered-grid vector fields, let us define $[\mathbf{u}]$ and $[\mathbf{v}]$ to be the corresponding vectors at grid values. For periodic boundaries, the discrete L^2 inner product on Ω is defined by

$$(\mathbf{u}, \mathbf{v})_{\mathbf{x}} = [\mathbf{u}]^T [\mathbf{v}] h^2. \quad (2.3.10)$$

This definition can be adjusted for non-periodic physical boundary conditions [41].

2.3.2 Lagrangian discretization

Using the finite element discretization, define $\mathcal{T}_h = \cup_e U^e$ be a triangulation of U composed of elements U^e . Here $\{s_l\}_{l=1}^M$ denote the nodes of the mesh, and $\{\phi_l(s)\}_{l=1}^M$ are interpolatory Lagrangian basis functions. The IBFE formulation is independent of the nodal basis function, but the work here will only use first order linear nodal basis functions. Let $\{\chi_l(t)\}_{l=1}^M$ denote the time-dependent physical positions of the nodes of the Lagrangian mesh. Using the Lagrangian basis functions, we can approximate $\chi(s, t), \forall s \in U$ with

$$\chi_h(s, t) = \sum_{l=1}^M \chi_l(t) \phi_l(s). \quad (2.3.11)$$

Note that $\chi_h(s_l, t) = \chi_l(t)$. The deformation gradient is approximated by

$$\mathbb{F}_h(s, t) = \frac{\partial}{\partial s} \chi_h(s, t) = \sum_{l=1}^M \chi_l(t) \frac{\partial}{\partial s} \phi_l(s). \quad (2.3.12)$$

This approximation is then used to calculate $\mathbb{P}$ from the strain energy functional prescribed in our model's material properties. Note that because we are using first order nodal basis functions, χ_h is continuous while $\mathbb{P}$ is generally only piecewise continuous.

Using nodal basis function, we approximate our force density $\mathbf{F}(s, t)$ by

$$\mathbf{F}_h(s, t) = \sum_{l=1}^M \mathbf{F}_l(t) \phi_l(s) \quad (2.3.13)$$

where $\{F_l(t)\}_{l=1}^M$ are the Lagrangian force densities at the time-dependent nodal points. Restricting our Lagrangian test functions to be linear combinations of the Lagrangian basis functions such that Eq. (2.3.9) becomes

$$\begin{aligned} \sum_{l=1}^M \left(\int_U \phi_l(s) \phi_m(s) ds \right) \mathbf{F}_l(t) = & - \int_U \mathbb{P}_h(s, t) \nabla_s \phi_m(s) ds \\ & + \int_{\partial U} \mathbb{P}_h(s, t) \mathbf{N}(s) \phi_m(s) dA(s) \end{aligned} \quad (2.3.14)$$

for $m = 1, \dots, M$. By letting $[\mathbf{F}]$ denote the vector of nodal coefficients of $\mathbf{F}_h$, Eq. (2.3.14) can in turn be written as a linear system

$$[\mathcal{M}][\mathbf{F}] = [\mathbf{B}] \quad (2.3.15)$$

where $[\mathcal{M}]$ is the mass matrix composed of entries of the $\int_U \phi_l(s) \phi_m(s) ds$.

The mass matrix can also be used to define the L^2 inner product of the functions on U , such that for any $\mathbf{X}_h(s, t) = \sum_l \mathbf{X}_l(t) \phi_l(s)$ and $\mathbf{Y}_h(s, t) = \sum_l \mathbf{Y}_l(t) \phi_l(s)$

$$(\mathbf{U}_h, \mathbf{V}_h)_s = [\mathbf{U}][\mathcal{M}][\mathbf{V}]. \quad (2.3.16)$$

The choice of the mass matrix can induce different discrete inner products of U . From here on out, the h subscript is dropped when referring to the discretization of $\mathbf{U}$ and $\mathbf{V}$.

2.3.3 Lagrangian-Eulerian interaction

Similar to the fiber IB method, we apply an approximation for the singular delta function kernel of Eq. (2.3.8) and Eq. (2.3.6), using a d -dimensional delta function $\delta_h(\mathbf{x}) = \prod_{i=1}^d \delta_h(x_i)$, where $\delta_h(x_i)$ is defined from Eq. (2.2.18). The difference between this formulation and that seen in Sec. 2.2.3 is due to the finite element Lagrangian body discretization.

Due to our finite element discretization, the interaction terms will require the construction of quadrature schemes for each element $U^e \in \mathcal{T}_h$ with N^e quadrature points $s_Q^e \in U^e$ and weights ω_Q^e , $Q = 1, \dots, N^e$. We then calculate our Eulerian force density $\mathbf{f} = (f_1, f_2)$ on the edges of the

Cartesian grid cells via

$$(f_1)_{i-1/2,j} = \sum_{U^e \in \mathcal{T}_h} \sum_{Q=1}^{N^e} F_1(s_Q^e, t) \delta_h(\mathbf{x}_{i-1/2,j} - \chi(s_Q^e, t) \omega_Q^e, \quad (2.3.17)$$

$$(f_2)_{i,j-1/2} = \sum_{U^e \in \mathcal{T}_h} \sum_{Q=1}^{N^e} F_2(s_Q^e, t) \delta_h(\mathbf{x}_{i,j-1/2} - \chi(s_Q^e, t) \omega_Q^e, \quad (2.3.18)$$

where $\mathbf{F}(s, t) = (F_1(s, t), F_2(s, t))$. Remember, $\mathbf{F}_h(s, t)$ includes both the time varying node points as well as the interpolated values from Eq. (2.3.13). Similar to fiber IB method, we can view this as a linear system

$$\mathbf{f} = \mathcal{S}(\chi) \mathbf{F} \quad (2.3.19)$$

where $\mathcal{S}$ can be thought of as the equivalent force-spreading operator for IBFE. Similarly, we define our interpolation operator $\mathcal{R} = \mathcal{R}(\chi)$ as

$$\frac{d\chi}{dt} = \mathcal{R} \mathbf{u}. \quad (2.3.20)$$

We construct $\mathcal{R}$ by requiring that it satisfy the discrete power identity

$$\left(\mathbf{F}, \frac{d\chi}{dt} \right)_s = (\mathbf{f}, \mathbf{u})_x, \quad (2.3.21)$$

which implies the conservation of energy between the two frames, since they are ultimately L^2 inner products. With $\mathcal{S}$ known, the identity can be rewritten as

$$(\mathbf{F}, \mathcal{R} \mathbf{u})_s = (\mathcal{S} \mathbf{F}, \mathbf{u})_x. \quad (2.3.22)$$

Both of these inner products can be explicitly constructed using the matrix notation of Eq. (2.3.16) and Eq. (2.3.10). With the matrix form of $\mathcal{S}$ and $\mathcal{R}$ rewritten as $[\mathcal{S}]$ and $[\mathcal{R}]$ respectively, we can write Eq. (2.3.22) as

$$[\mathbf{F}]^T [\mathcal{M}] [\mathcal{R}] [\mathbf{u}] = ([\mathcal{S}] [\mathbf{F}])^T [\mathbf{u}] h^2. \quad (2.3.23)$$

Since our definition of $[\mathcal{R}]$ must be given for any $[\mathbf{F}]$ and $[\mathbf{u}]$, we arrive at the identity

$$[\mathcal{R}] = [\mathcal{M}]^{-1}[\mathcal{S}]^T h^2 \quad (2.3.24)$$

thus completing the derivation of the discrete interpolation operator.

2.4 Concluding remarks

In this chapter, I have discussed the theoretical and numerical framework of the immersed boundary and IBFE methods, as well as the derivation of the Navier-Stokes equations and dimensionless Reynolds number. The numerical methods discussed in this chapter will be subsequently used in Chapters 3, 4, 5, and 6 to model jellyfish propulsion. In Chapter 3, I will use the traditional fiber-based immersed boundary method to model a 2-dimensional prolate jellyfish bell to explore a wide parameter space in the context of resonant driving. In Chapter 4, I will employ a 3-dimensional finite element jellyfish bell with an oblate geometry, for which I will derive a material model that will be described using the first Piola-Kirchhoff stress tensor. This same model will then be used in chapters 5 and 6 to study scaling effects and turning maneuvers, respectively.

CHAPTER 3

Resonant driving of jellyfish bells

3.1 Introduction

A fundamental question in the biomechanics of swimming and flying is whether or not flexibility can be advantageous for performance. It has been suggested that locomotory efficiency and performance with flexible appendages is maximized when these structures are driven at their natural frequency [4, 2]. This argument is based upon the idea that if the animal's movements are tuned to the natural frequency of vibration of the propulsive structures, the potential energy stored by elastic deformation is maximized. Resonant driving has been examined for a range of different propulsive structures such as fish fins [91], insect wings [60], and jellyfish bells [30]. It is important to note that not every study has supported the idea that propulsive efficiency is maximized when the resonant and driving frequencies coincide. Ramananarivo et al. [77] used a self-propelled simplified insect model to show that flight performance may be maximized by tuning the temporal evolution of the wing shape to minimize drag rather than flapping the wings at their natural frequency. Tytell et al. [91] also noted that while fish with carangiform and thunniform swimming modes gain a propulsive benefit due to resonant effects, resonance is not critical for efficient swimming of anguilliform swimmers due the larger role that fluid dynamic damping plays in its movement. These studies and others have explored the nonlinear effects of the surrounding fluid environment, such as drag and added mass of the fluid, with the elastic properties of the propulsive structures. In this study, immersed boundary simulations of the fluid structure interaction problem of an elastic jellyfish bell driven at its natural frequency are used to examine swimming performance.

Mechanical systems that bend or flex have a natural frequency of vibration, defined as the frequency at which the system oscillates when no external forces are applied. This natural frequency is determined by the effective mass of the system and the elastic properties that store potential elastic energy [2]. Resonance occurs when the mechanical system responds with greater amplitude

when driven at its natural frequency of vibration, also known as the resonant frequency, as opposed to frequencies above and below it. When looking at propulsion studies in fluids, it is often useful to examine resonance by reducing the coupled fluid-structure system to a spring-mass model where the parameters incorporate the effective mass of the structure and the fluid as well as the effective stiffness [91, 30, 77, 64]. One can then compare analytic solutions to experimental observations to test the accuracy and predictive ability of the model.

The effect of resonant driving of jellyfish bells has been previously examined using reduced order models and experiments [2, 29, 28, 30, 64, 63]. DeMont and Gosline modeled the dynamics of the jellyfish bell as a linear damped harmonic oscillator with lumped parameters [30]. A linear damping parameter was used to account for both the internal damping of the viscoelastic mesoglea and the external damping due to shearing of the surrounding fluid. When a sinusoidal force was applied to this model, the result showed that there is a 40% increase in the amplitude of circumferential oscillation at the resonant frequency relative to significantly higher and lower frequencies. The resulting resonant frequency was also close to the observed frequency of pumping during swimming. Megill extended this work by modeling the elasticity of the bell with a nonlinear spring to more accurately describe the large strain ranges observed in jellyfish [64].

This chapter extends the idea of resonant driving of the jellyfish bell to an FSI framework using the immersed boundary method described in Chapter 2. Instead of prescribing the motion of the bell, a periodic force applied towards the centreline in a band spanning the lower quarter of the bell was used to drive the bell contractions. The results are used to determine the benefits of driving the bell at its resonant frequency in terms of forward swimming velocity and the amplitude of bell oscillation. The effects of changing the forcing magnitude and Reynolds number on the optimal driving frequency are also considered. Due to the computational costs of the FSI problem and the wide parameter space, this study will be restricted to consider only simplified prolate bells in two dimensions.

Table 3.1: Table of nondimensionalized, reference parameters related to the bell model. The reference values were chosen to roughly approximate swimming in *Sarsia*, and each of the parameters were varied above and below the reference states.

Parameter	Symbol	Value
Force magnitude	F_{Mag}^{ref}	.0406
Bending stiffness	$\bar{k}_b^{ref}$	0.0528
Spring stiffness	$\bar{k}_s^{ref}$	1.0563
Characteristic length	L	1
Reference resonance frequency	f^{ref}	.86
Reynolds number	Re^{ref}	172
Bell radius	a	$.5L$
Bell height (top)	b	$.75L$
Bell height (bottom)	d	$.25L$

Table 3.2: Table of all numerical parameters unless otherwise noted for simulations.

Numerical Parameter	Symbol	Value
Spatial step Cartesian grid	h	$L/64$
Spatial step Lagrangian grid	ds	$L/128$
Domain size	-	$8L \times 8L, 8L \times 40L$
Time step	dt	10^{-5}
Integer refinement ratio	N^{ref}	4
Maximum number of refinement levels	ℓ_{max}	4
Vorticity magnitude threshold	ω^{Mag}	.5

3.2 Model development

3.2.1 Jellyfish geometry

The jellyfish was modeled in two dimensions (not axisymmetric) as a hemielliptical bell with a specified cut-off for the lower portion of the bell. The idea of modeling the bell as a hemiellipsoid has been used in a variety of analytical and numerical studies [17, 27, 62, 48]. The bell is designed to resist bending and stretching, and the preferred configuration is initialized as a hemiellipse. The governing equation for the bell geometry is given by

$$\frac{(x - x_c)^2}{a^2} + \frac{(y - y_c)^2}{b^2} = 1 \text{ for } y \geq y_c - d, \quad (3.2.1)$$

where (x_c, y_c) is the center of the ellipse, a is the length of the half width of the bell, and $b + d$ is the height of the bell.

To drive the motion of the bell, an external forcing term, (F_D) , was applied to a portion of the bell. This forcing term is described by a simple sinusoidal function

$$F_D(t) = F_{Mag} \sin(2\pi ft), \quad (3.2.2)$$

where F_{Mag} is the amplitude of the forcing term, f is the driving frequency, and t is the time. During the contraction phase ($F_D > 0$), the forcing term pushes the bell towards the centerline. In the expansion phase ($F_D < 0$) the same process occurs except now the force is directed away from the centerline.

The choice of this forcing term is analogous to the forcing term present in DeMont and Gosline's model, which was in turn taken from observations of continuous trains of muscular contractions. It is important to note that the bell in this experiment does not have a fixed kinematic cycle but is instead subject to deformations caused by the forcing term and resulting fluid forces. Variations in the kinematics of the jellyfish bell during the contraction and expansion phase will be dependent upon the driving frequency, f , and magnitude, F_{Mag} , of the forcing term.

The driving force is applied to a subset of of the boundary, $\Omega_D \subset \Omega$:

$$\mathbf{F}_D(q, t) = \begin{cases} F_D(t)\hat{\tau}_s(q, t) & q \in \Omega_D \\ 0 & q \notin \Omega_D \end{cases} \quad (3.2.3)$$

where F_D was defined in Eq. 3.2.2 and $\hat{\tau}_s$ is the unit tangent vector of a fiber that cuts across the axis of symmetry to the other half of the bell, allowing for the bell to be driven by a horizontal force relative to the orientation of the bell. The force vector $\mathbf{F}_D(q, t)$ is 2D representation of the coronally oriented musculature found in the subumbrellar cavity of the bell [9]. During the contraction phase of forward swimming, the subumbrellar muscles squeeze the bell toward the center axis and expel fluid. I in turn flatten this 3D structure by applying the force magnitude $F_D(t)$ in the direction of the vector $\hat{\tau}_s$ to represent the contraction and expansion of the bell along the centerline of the bell.

3.2.2 Nondimensional numbers and parameters

Scaling effects on resonant driving are examined using the Reynolds number, which provides the ratio of inertial to viscous forces in the fluid and is derived through the nondimensionalization of the Navier-Stokes equations. There are many ways to calculate the Reynolds number, but for the purpose of this study I use the body kinematic based Reynolds number, defined as:

$$Re = \frac{\rho U_{body} L}{\mu} \quad (3.2.4)$$

where U_{body} is the characteristic pulsing speed of the bell, L is the characteristic length of the bell, ρ is the density of the fluid, and μ is the dynamic viscosity. Here L is defined to be the diameter of the bell in its preferred configuration. I define the characteristic speed with respect to the driving frequency, f , of Eq. 3.2.2, such that $U_{body} = fL$.

The stretching stiffness, k_s , and bending stiffness, k_b , are nondimensionalized in the following manner:

$$\bar{k}_s = \frac{k_s}{\rho U_{body}^2 L} \quad (3.2.5)$$

$$\bar{k}_b = \frac{k_b}{\rho U_{body}^2 L^3} \quad (3.2.6)$$

where $\bar{k}_s$ and $\bar{k}_b$ represent the dimensionless stretching and bending stiffnesses. Nondimensionalized parameter values for the reference configuration, where $f = f^{ref}$, are provided in Table 3.1.

3.2.3 Software implementation

The numerical study was implemented using the immersed boundary method with adaptive mesh refinement (IBAMR) [55]. IBAMR is a distributed-memory parallel implementation of the IB method that includes adaptive mesh refinement for Cartesian grids. Support for the distributed memory parallelism is provided by MPI and spatial adaptivity is implemented using the SAMRAI library [83, 49]. IBAMR functionality is also built upon the use of PETSc [10, 11] and hypre [54, 32] libraries, among others. Table 3.2 provides the numerical parameters used in this study.

3.3 Results

3.3.1 Free vibration study

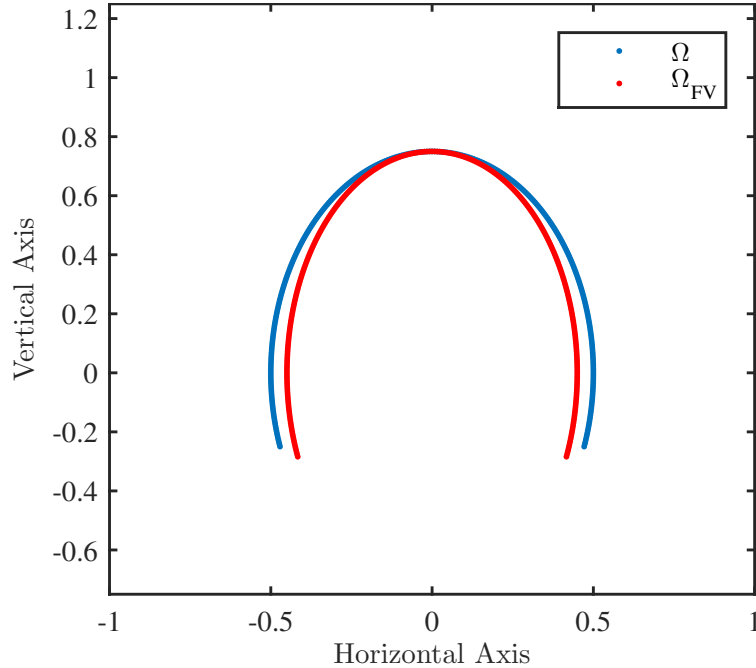


Figure 3.1: Numerical setup for the free vibration study. The bell initialized, Ω_{FV} , at 90% of its resting configuration, Ω . During this simulation, the bell freely vibrates until it returns to its equilibrium configuration due to passive elastic forces.

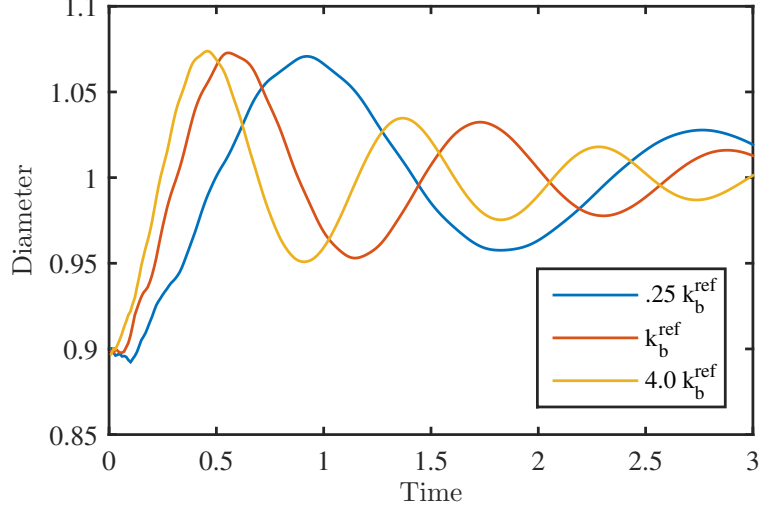


Figure 3.2: The oscillations of the diameter during the free vibration study as a function of time. The diameter is measured as the distance between two symmetric points at the widest cross-section of the bell.

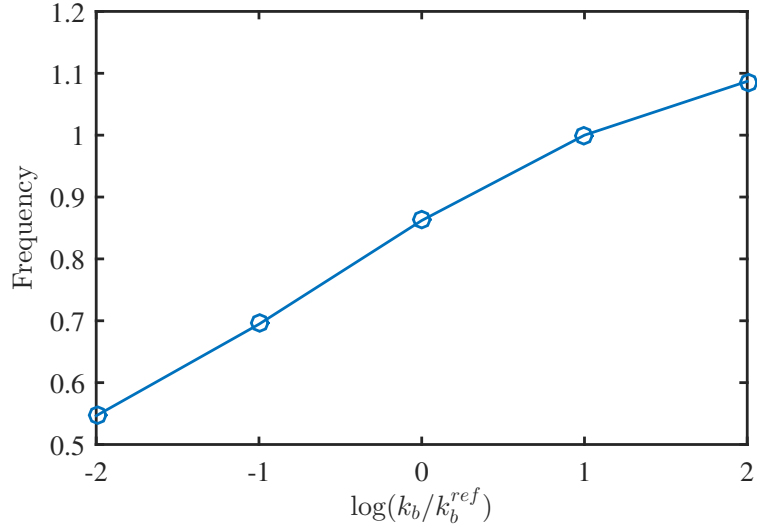


Figure 3.3: The natural frequencies recorded from the free vibration simulations of varying beam stiffness. The horizontal axis corresponds to $\log_2$ of the beam stiffness, k_b , relative to the reference beam stiffness, k_b^{ref} and the vertical axis is the recorded frequency. The natural frequency is defined as the inverse of the first period of contraction and expansion of the bell in free vibration.

To find the natural frequency, I ran a numerical study that set the initial position of the bell to have a diameter that was 90% of the diameter of the preferred configuration of the bell, effectively ‘squeezing’ the bell along its horizontal axis (Fig. 3.1). Note that the Lagrangian nodes were initialized with uniform spacing, ds , so that the spring forces would be minimized initially and the bell would be primarily driven by the bending forces. The simulation was then run so that the bell

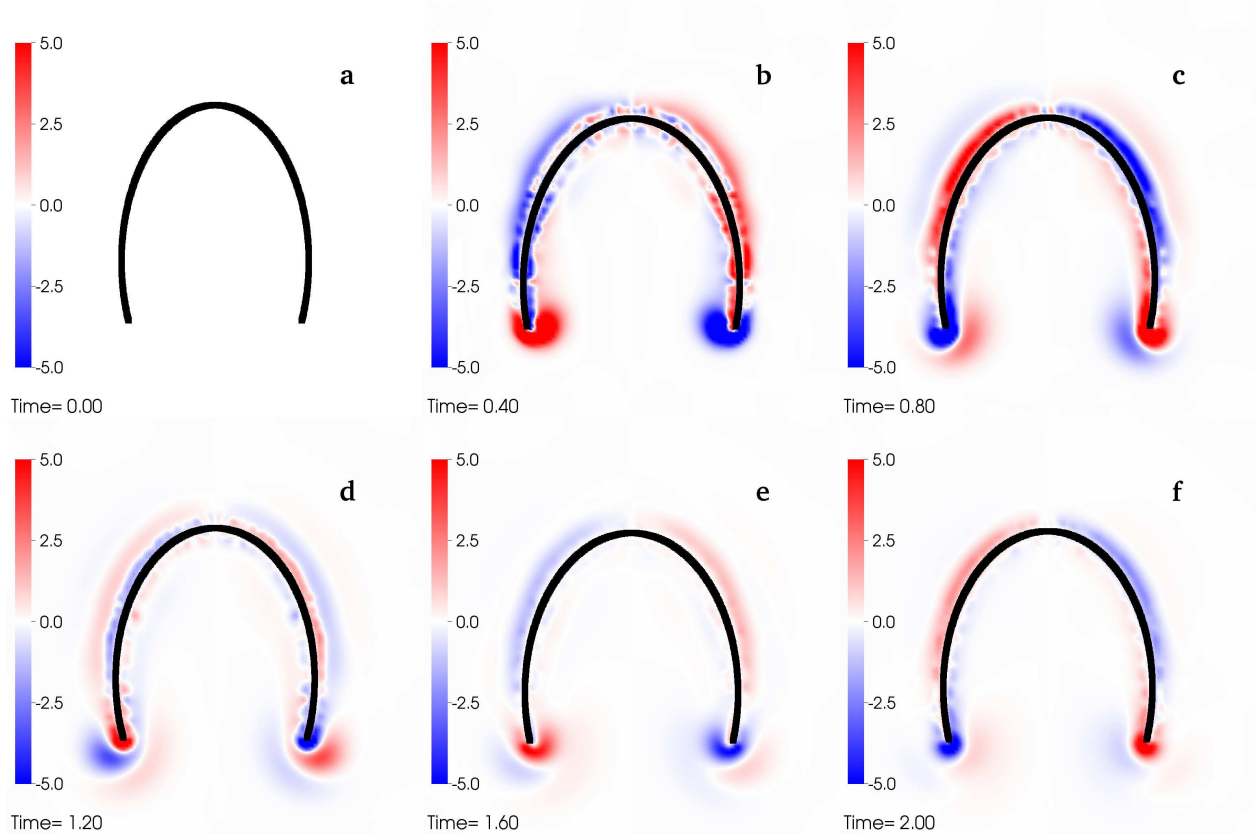


Figure 3.4: Vorticity plot of the free vibration simulation at $t= 0, .4, .8, 1.2, 1.6, 2.0$. Panels b, d, and e show times of expansion, and panels c and f show times of contraction.

was able to freely oscillate in the fluid. The oscillations of the diameter of the bell were recorded (Fig. 3.2) and the resonant frequency of the bell was calculated as the amount of time it took for one complete oscillation. To examine the relation between the natural frequency of vibration and the elastic properties, I varied the bending stiffness, k_b , and ran free vibration simulations for each stiffness to extract the new natural frequency. Simulations were run for $k_b = 2^n k_b^{ref}$ with $n = -2, -1, 0, 1, 2$. I found that increasing bell rigidity led to higher natural frequencies of vibration, as expected (Fig. 3.3). This rate scales roughly with the square root of the bending stiffness. Note that this scaling is similar to that of a straight, uniform beam undergoing small deflections with two free ends. In this case, the natural frequency of a beam, f_{beam} , with bending rigidity k_b , length L , and density ρ would be given by the equation

$$f_{beam} = \frac{22.373}{2\pi L^2} \sqrt{\frac{k_b}{\rho}}. \quad (3.3.1)$$

The recorded frequency of free vibration of the reference configuration was $f^{ref} = .86$, which is near the natural frequency observed for *Polyorchis pencillatus* [30]. Vorticity plots of the simulation at different points of expansion and contraction can be seen in Fig. 3.4. In those plots, I can see the alternating vorticity generated at the bell margin during the strong initial expansion and contraction after the initialization of the simulation, followed by the lower amplitude oscillations as the bell returns to its preferred configuration. It is important to note that the resonant frequency measured here is numerically determined by solving the fluid-structure interaction problem, as opposed to analytically deriving it from the beam equation. The reason for doing this is that the immersed elastic structure is effectively massless in the IB framework, with an effective mass due to the surrounding fluid. The effective mass is difficult to approximate in this context because jellyfish swimming is dynamic, both in terms of the temporal evolution of the fluid and in terms of the change in body shape. Steady state approximations of the boundary layer around the bell that could be used to estimate the effective mass are not appropriate, and modifications of steady state models may not be robust.

3.3.2 Driving frequency study

Using the forcing framework of Eq. (3.2.3), I defined Ω_D to be the lower quarter of the bell (Fig. 3.5) so as to model the musculature as concentrated towards the rim of the bell [9]. From an initial resting configuration, I then applied the sinusoidal driving force for a range of frequencies set to $f = .25, .50, .75, 1.0, 1.25, 1.50, 1.75, 2.0$ in addition to the recorded resonant frequency of the reference configuration, $f^{ref} = .86$. The performance of the different driving frequency studies was compared using the maximum amplitude of oscillation of the diameter (Fig. 3.6) and the averaged forward swim velocity of the bell (Fig. 3.7) at different pulse cycles, $P = 5, 10, 15, 20, 25$. Here a pulse cycle is defined as a full contraction-expansion period determined by the frequency, f , of the sinusoidal forcing term of Eq. (3.2.2), such that one pulse cycle is equal to $1/f$. Note therefore that the length of the propulsive cycle, $1/f$, is different for each of the driving frequencies. The horizontal axis in these figures represents the different driving frequencies, with a dotted red line to mark the recorded frequency of free vibration of the reference configuration. Plotting the forward swim velocities and maximum amplitudes of oscillation at different pulse cycles allows one to examine the

temporal evolution of swimming performance at different driving frequencies as they approach their steady state velocities from the initial state of zero forward velocity.

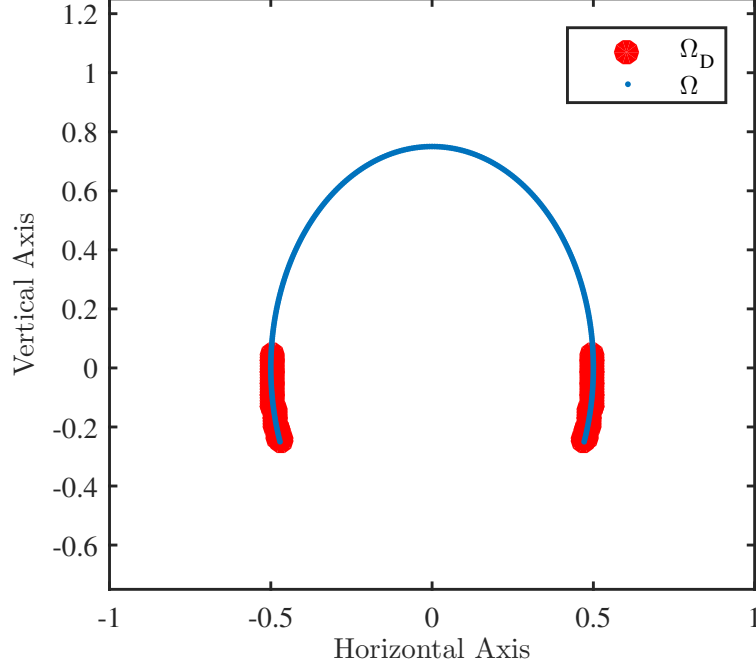


Figure 3.5: A sinusoidal driving force is applied to the mesh nodes in Ω_D (shown in red). These forces are applied in the direction normal to the centerline.

Varying force magnitude To understand the relationship between the magnitude of the applied force and the optimal swimming frequency, force magnitude was varied such that $F_{Mag} = nF_{Mag}^{ref}$, with $n = 1/6, 1/3, 2/3, 1, 4/3, 5/3$. I found that for low force magnitudes the highest maximum amplitude of oscillation occurred for the recorded frequency of free vibration, but that this shifted to a slightly lower frequency when force magnitude was increased (Fig. 3.6). This suggests that the effective resonant frequency decreases with increased applied force. This effect is likely due to additional fluid entrainment that increases the effective mass of the system and lowers the resonant frequency. In the case of applying the lowest force magnitude, the jellyfish had the fastest forward velocity when forced at the frequency of free vibration (Fig. 3.7). As the force magnitudes increased, the fastest steady state swimming velocities shifted to frequencies slightly higher than the recorded frequency of free vibration.

Using the amplitude and forward velocity data generated from the simulations, I introduce the

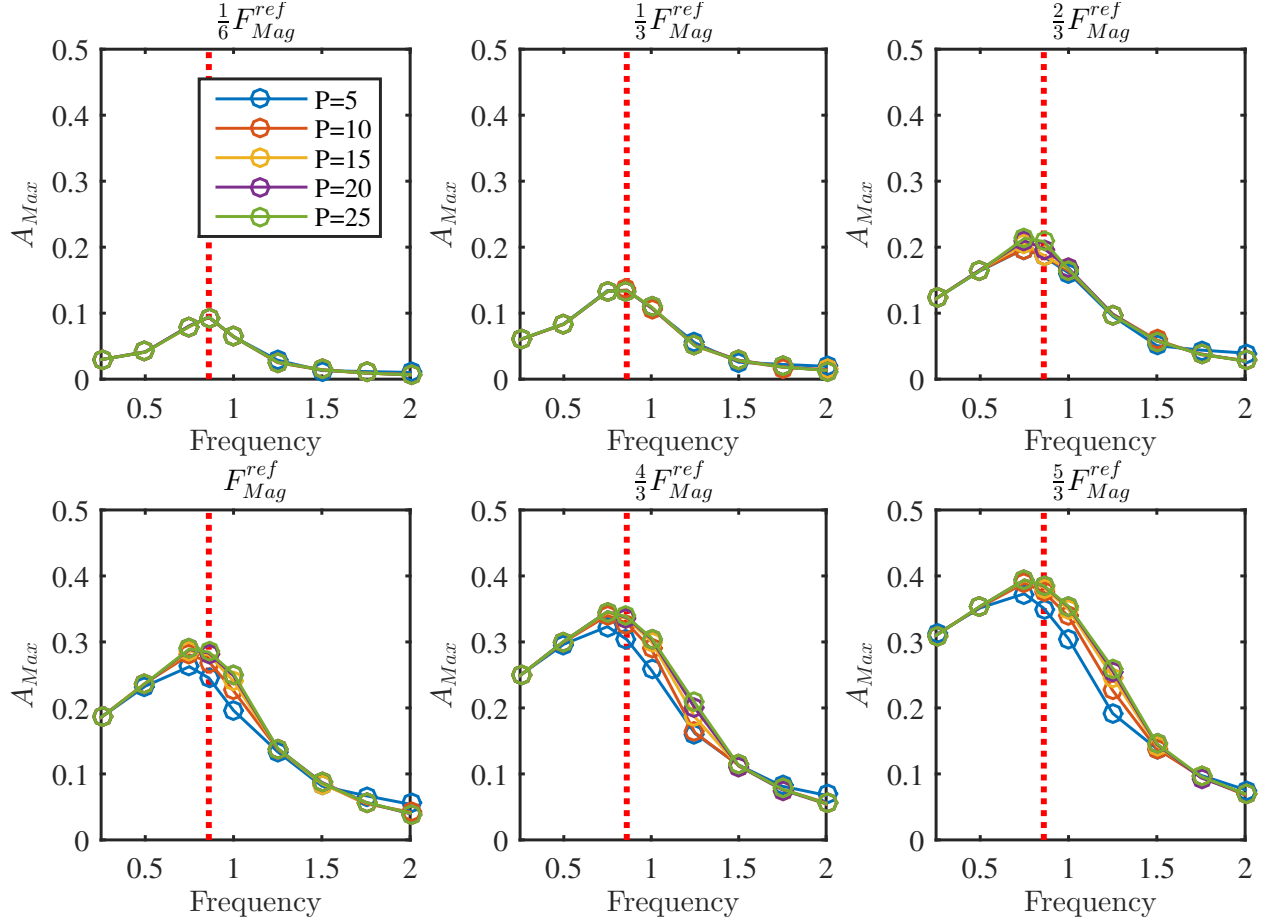


Figure 3.6: Comparing the maximum amplitude of diameter oscillation for each of the driving frequencies, f , at different force magnitudes, F_{Mag} , during the pulse cycle $P = 5, 10, 15, 20, 25$. The recorded frequency of free vibration is highlighted with the dotted red line. Notice that the frequency with the largest maximum amplitude is found for the largest force magnitude when $f = .75 \text{ s}^{-1}$, which is slightly below the measured frequency of vibration. The different values of P show how the maximum amplitudes change in time as steady state is approached.

non-dimensional Strouhal number

$$St = \frac{f D_s^P}{U^P} \quad (3.3.2)$$

where f is the driving frequency, D_s^P is the recorded maximum amplitude of the bell diameter during the pulse cycle P , and U^P is recorded average forward velocity (Fig 3.8). By looking at St^{-1} I get a normalized forward swimming velocity based on the driving frequency. It has been observed that propulsive efficiency in swimming and flying animals peaks within a range of $.2 < St < .4$ [90]. The model confirms that this optimal St range is reached for frequencies that are either slightly above or below the resonant frequency and that this range of optimal frequencies is in turn governed

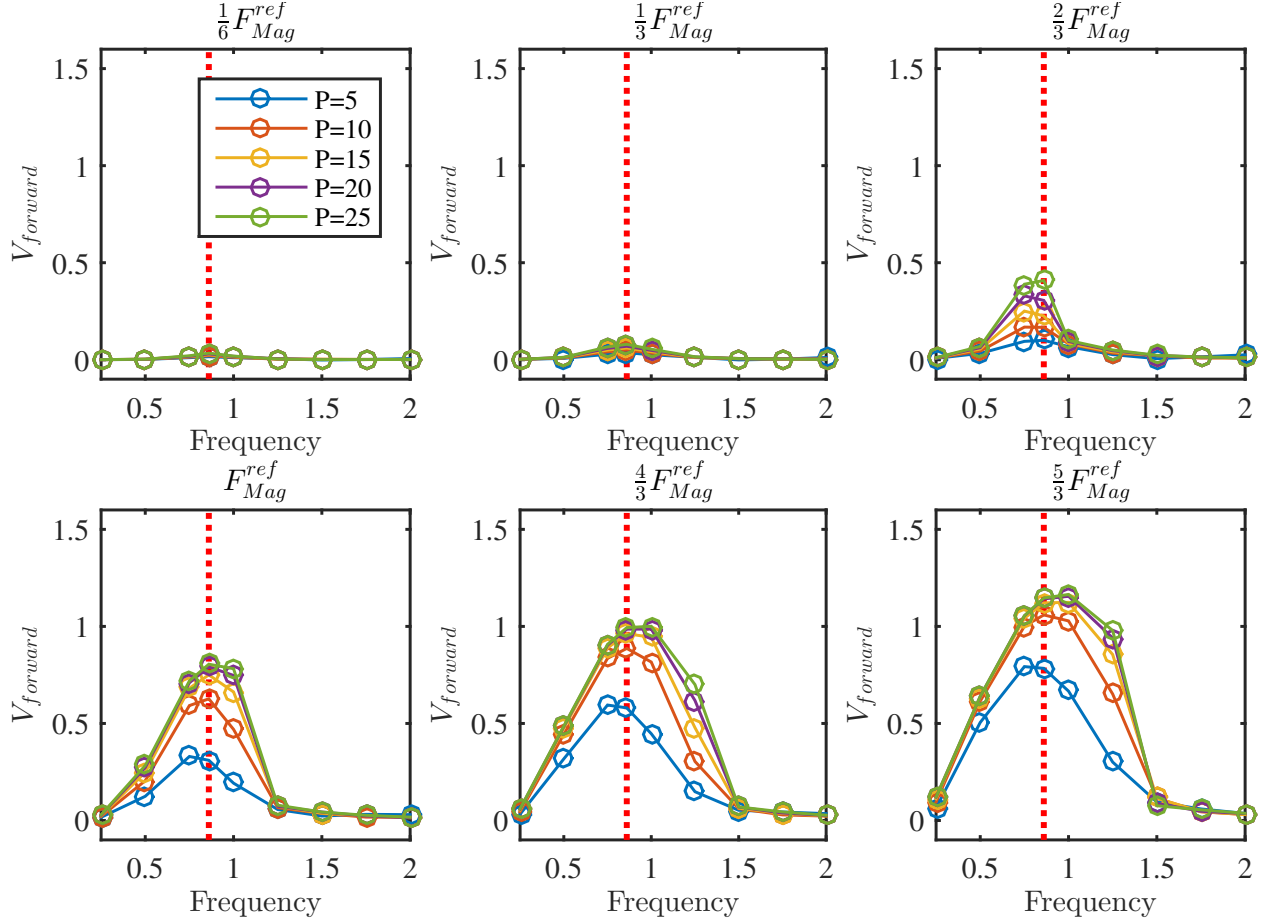


Figure 3.7: Comparing the average forward swimming velocity, $V_{forward}$, for each of the driving frequencies, f , at different force magnitudes, F_{Mag} , during the pulse cycle $P = 5, 10, 15, 20, 25$. The recorded frequency of free vibration is highlighted with the dotted red line. The best performing frequency shifts to higher frequencies as larger force magnitudes are used. The different values of P show how the swimming speeds change in time as steady state is approached.

by the force magnitude applied to the bell. As force magnitude increases, the range of frequencies that are within the efficient St range increases.

Differences in the wakes can also be observed for efficient and inefficient swimmers. For efficient swimmers, as seen in Fig. 3.9 for the 8th pulse cycle of a bell forced at the recorded resonant frequency of $.86s^{-1}$, pairs of starting and stopping vortices from the previous stroke are advected away from the bell. In panel a, the stopping vortices formed during the expansion are present inside the lower part of the bell. Once contraction begins (a-c), oppositely spinning starting vortices are formed that are advected away from the bell with the stopping vortices. During the subsequent expansion (d-f), a new pair of stopping vortices form that remain within the lower part of the bell

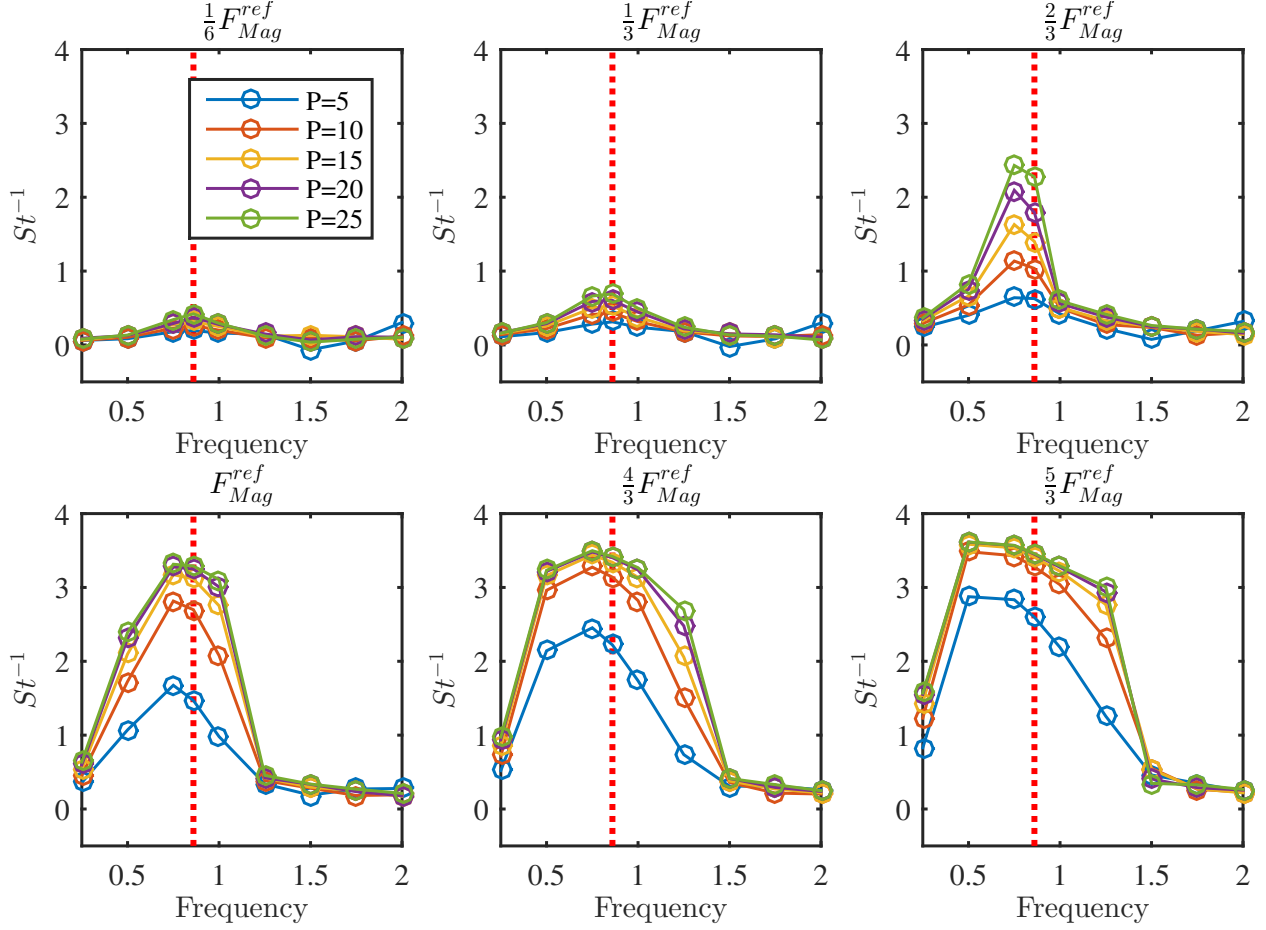


Figure 3.8: The inverted Strouhal number (St^{-1}) vs. driving frequency for several choices of force magnitude. St^{-1} was calculated using the maximum amplitude and forward velocity information taken from the driving frequency simulations. Although the best performing frequency is the recorded frequency of free vibration for small applied forces, the frequency that produces the largest deformations is shifted to lower force magnitudes as the force magnitude is increased. The different values of P show how the swimming speeds change in time as steady state is approached.

until the next contraction.

I also noted two pathological cases of swimming at frequencies that were significantly above and below the resonant frequency. The vorticity plots of Fig. 3.10 were generated by the inefficient swimming of a bell being driven at a higher frequency and show the lack of strong starting and stopping vortices during the pulse cycle. During the 8th pulse cycle of a bell being forced at a frequency of $2s^{-1}$, the contraction phase (a-c) does not produce a large enough change in amplitude to eject fluid from the bell. The subsequent expansion (d-f) in turn does not deposit stopping vortices in the bell cavity during the recovery phase. The resulting motion of the bell is a quick paddling motion that lacks the wake structures present in jellyfish locomotion. As can be seen the

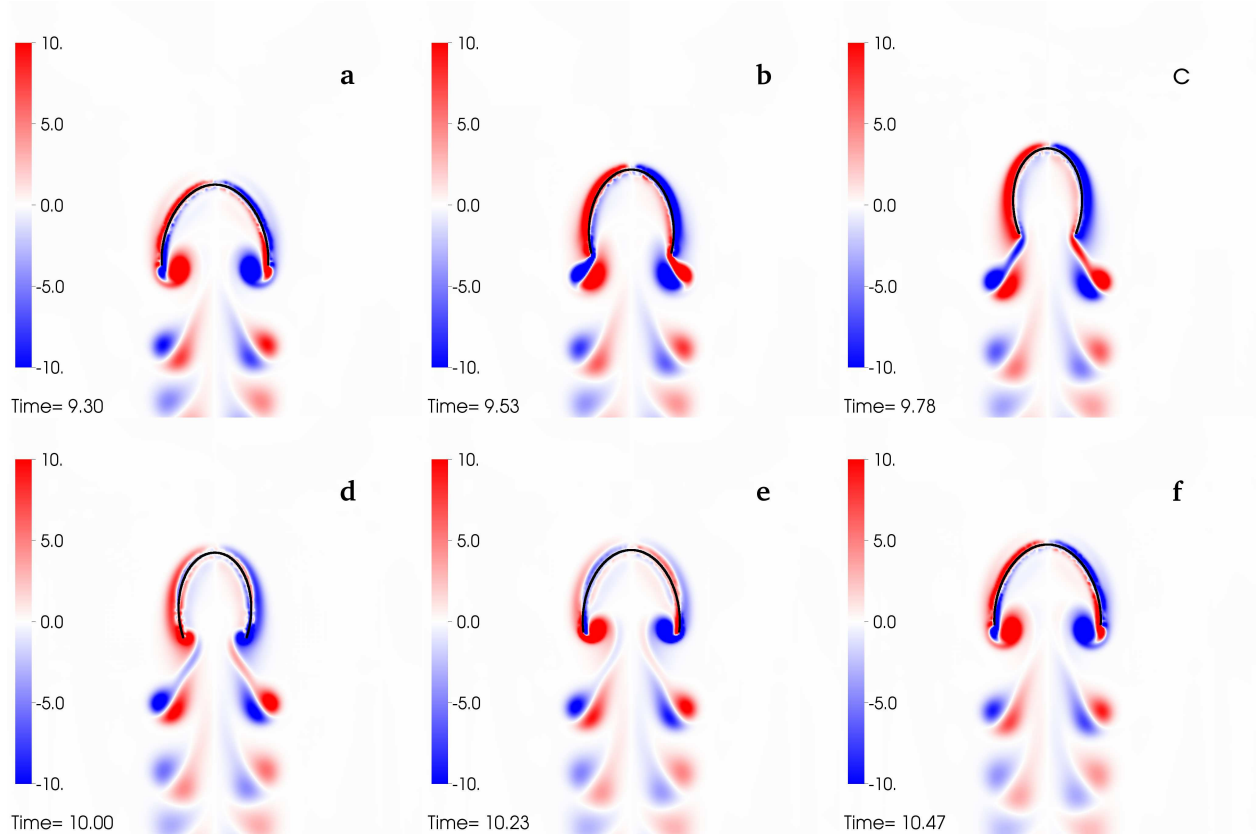


Figure 3.9: Vorticity plot of the 8th period of the propulsive cycle when the driving force magnitude was set to F_{Mag}^{ref} . The driving frequency is $.86 \text{ s}^{-1}$. A starting vortex is formed during the contraction phase that interacts with the previously formed stopping vortex (a-c) and is advected away from the bell. During expansion (d-f), a new stopping vortex is formed that remained near the lower inner portion of the bell until subsequent contraction.

vorticity plots of Fig. 3.11, when the bell is forced at a frequency that is significantly lower than the resonant frequency, it also lacks the starting and stopping vortex dynamics present in efficient swimmers. During the 8th pulse cycle of a bell being forced at a frequency of $.25 \text{ s}^{-1}$, the contraction phase (a-c) does not move fast enough to transfer enough momentum from the bell to the local fluid environment to generate strong starting vortices, nor does it generate sufficient pressure in the bell to eject fluid from the bell quickly. Likewise, the expansion (d-f) in turn does not generate significant stopping vortices in the bell cavity during the recovery phase. The slow motion of the bell during the contraction and expansion are a result of the driving force being damped by the viscous fluid. This in turn prevents the transfer of significant levels of momentum from the bell to the fluid to generate the vortices and jet of fluid necessary for forward movement.

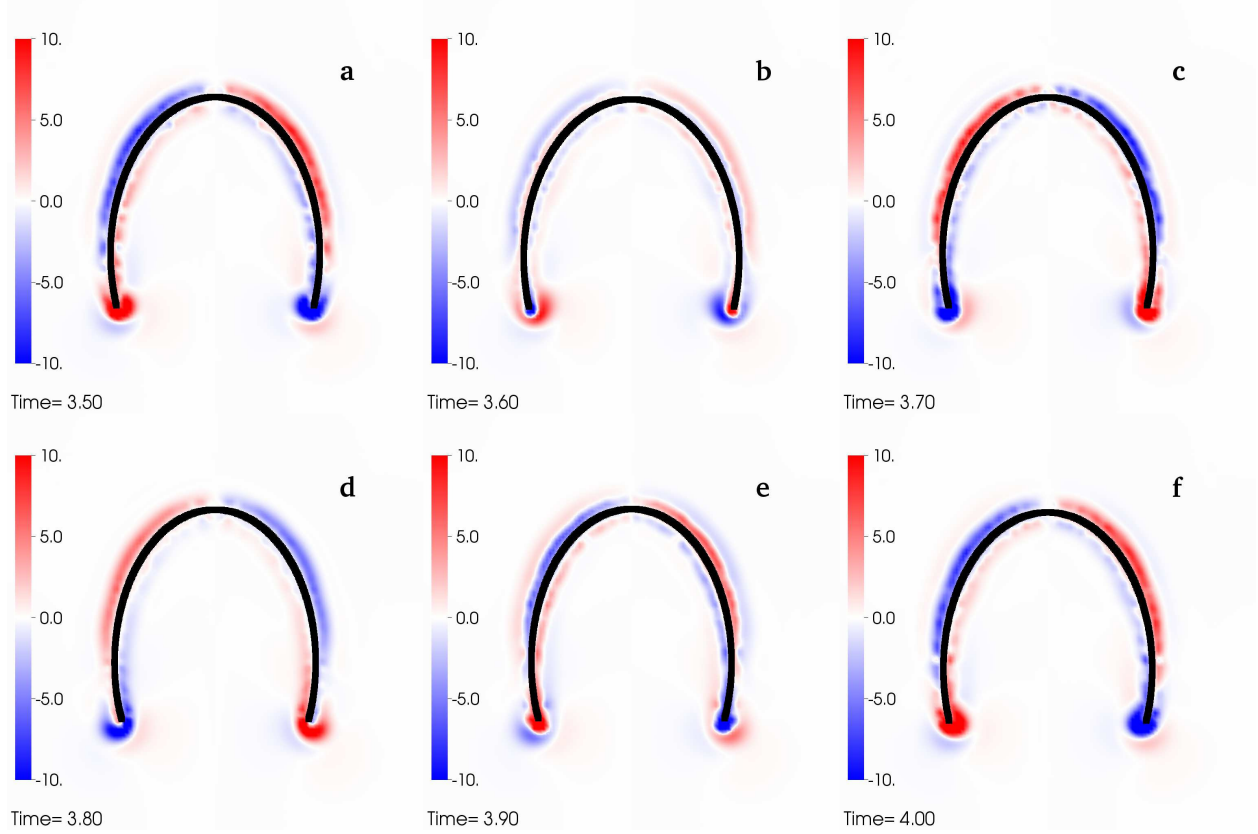


Figure 3.10: Vorticity plot of the 8th period of the propulsive cycle when the driving force magnitude was set F_{Mag}^{ref} . The driving frequency is 2 s^{-1} . Notice that the motion of the bell does not eject fluid from the bell and moves with a paddling motion. The contraction phase has a short inward paddle (a-c) , followed by an outward paddle during expansion phase (d-f). Vortex shedding does not occur in either phase.

3.3.3 Varying viscosity

The advantage of driving the bell at its resonant frequency is dependent upon the relative magnitude of fluid damping. The reference configuration swims at $Re = 172$ when driven at its resonant frequency, and this is used as a point of comparison for the lower Reynolds number simulations. The Reynolds number is lowered by adjusting the dynamic viscosity, μ . The free vibration and driving frequency studies were then performed for $\mu = 2^n \mu_{ref}$ with $n = -1, 0, 1, 2, 3, 4, 5, 6$. The force magnitude was set to F_{Mag}^{ref} .

In the free vibration study, increasing the dynamic viscosity of the system led to a decrease in the recorded frequency of free vibration (Fig. 3.12). Higher fluid viscosity increases both the amount of entrained fluid and the effective mass of the system. Increasing the viscosity also decreased the amplitude of the subsequent oscillations following the initial perturbation of the bell (Fig. 3.13).

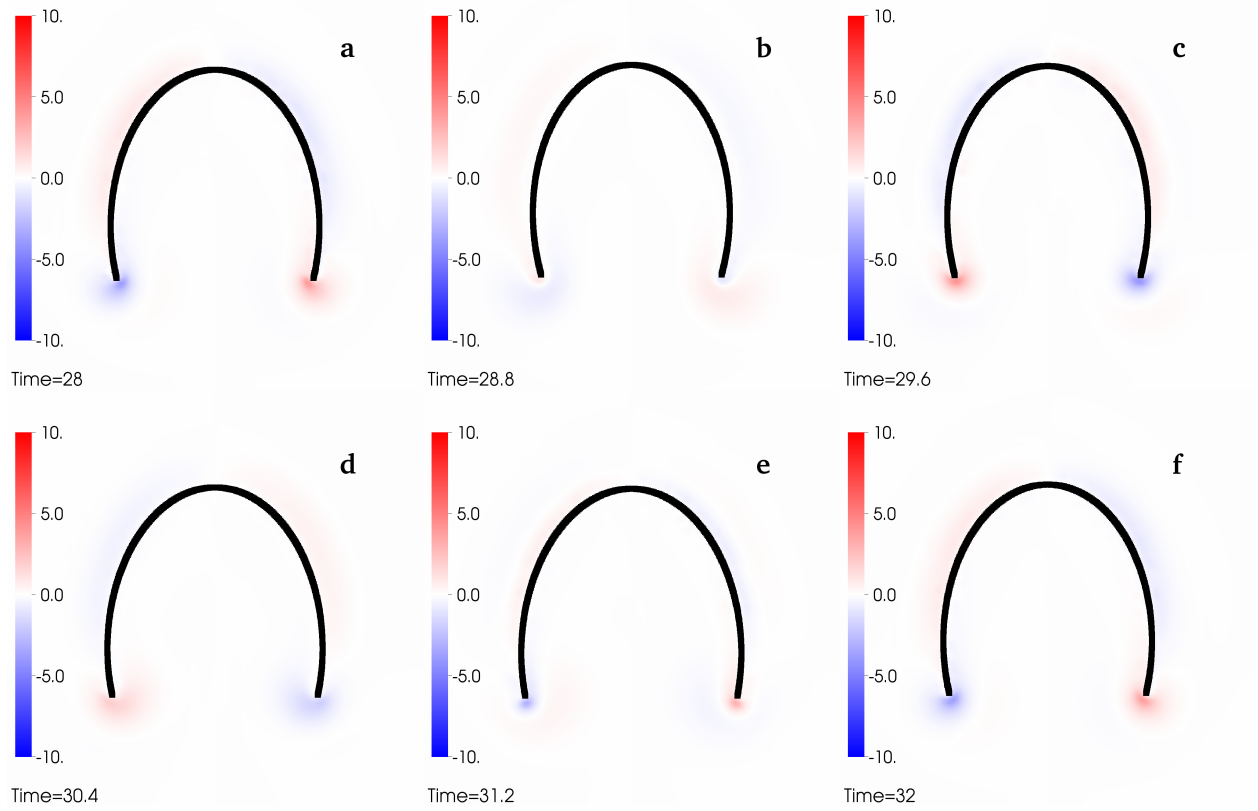


Figure 3.11: Vorticity plot of the 8th period of the propulsive cycle when the driving force magnitude was set F_{Mag}^{ref} . The driving frequency is $.25 \text{ s}^{-1}$. Notice that the motion of the bell does not generate significant starting and stopping vortices. The contraction phase has a slow inward motion (a-c) , followed by an outward motion during expansion phase (d-f). Vortices are only generate.

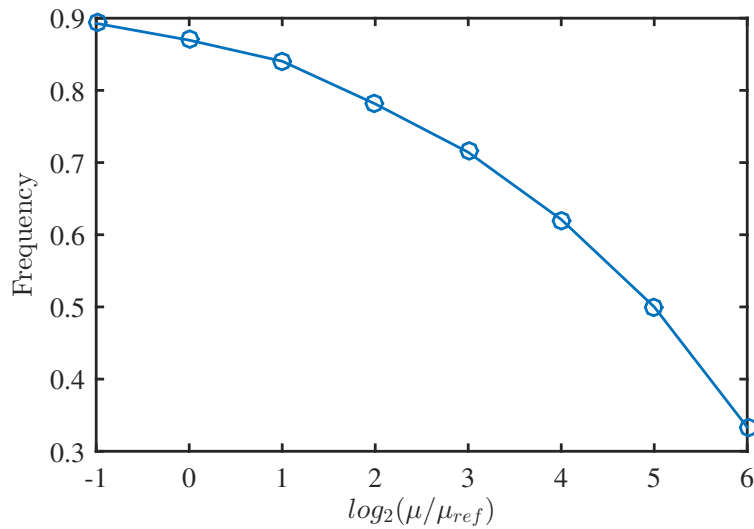


Figure 3.12: A free vibration study was done for different viscosities. As the viscosity was increased, the recorded frequency of free vibration decreased.

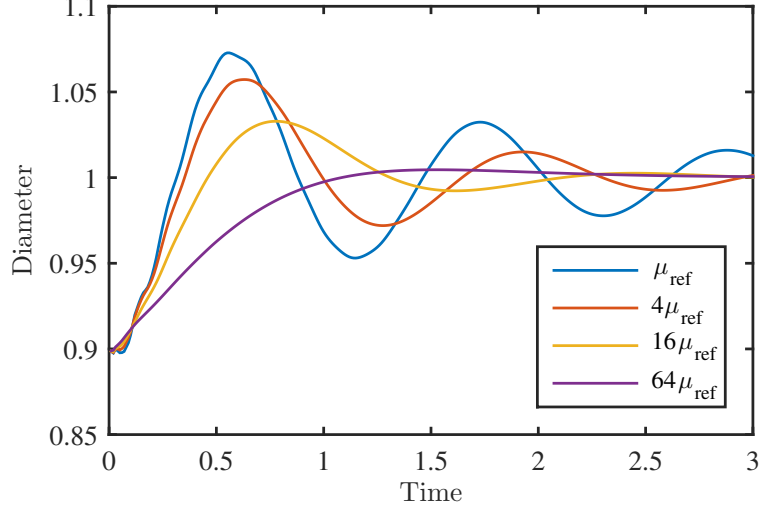


Figure 3.13: The trajectories of the diameter oscillation during the free vibration study for different viscosities. Notice that the subsequent amplitudes of the free vibration oscillation decrease for higher viscosities until the oscillations present are negligible, as in $\mu = 64\mu_{ref}$.

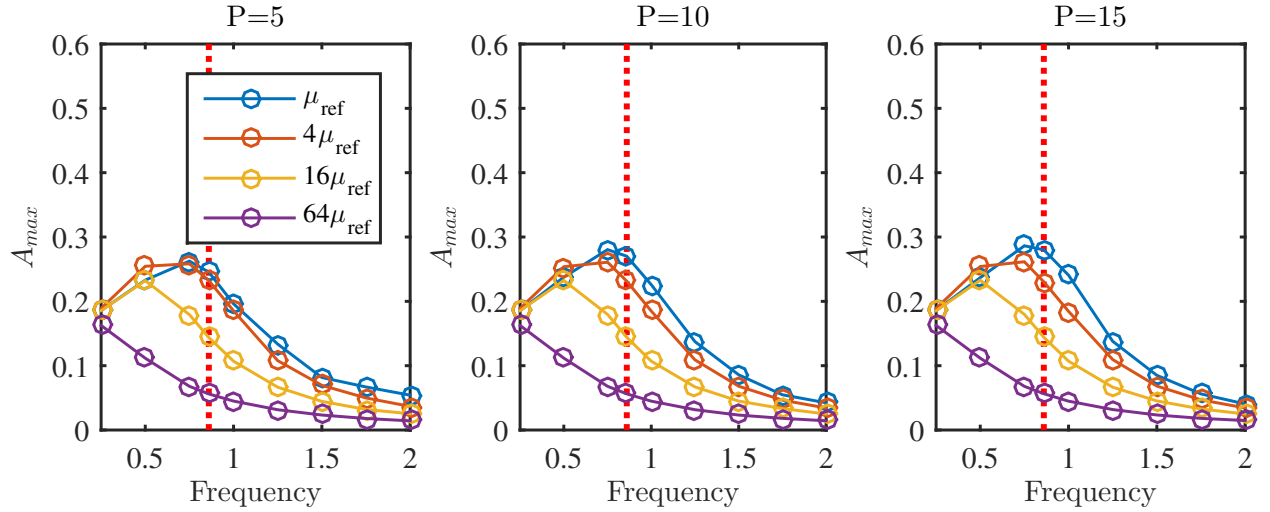


Figure 3.14: A comparison the 5th, 10th, and 15th propulsive cycles of the maximum amplitude of diameter oscillation during a driving force study with differing levels of μ . Notice that the peak frequency shifts lower frequencies as more fluid damping is added. Also note how the maximum amplitudes stay relatively fixed in more damped fluid environments.

Reynolds number effects were also noted in the driving frequency study, where the largest oscillations of the bell diameter occurred at the lower driving frequencies (Fig. 3.14). This coincides with the lower frequencies of free vibration found when viscosity was increased so that the effective resonant frequency shifts to lower frequencies. Looking at the average forward swimming velocity (Fig. 3.15), the increased viscosity both decreased the swimming velocity and reduced the advantage

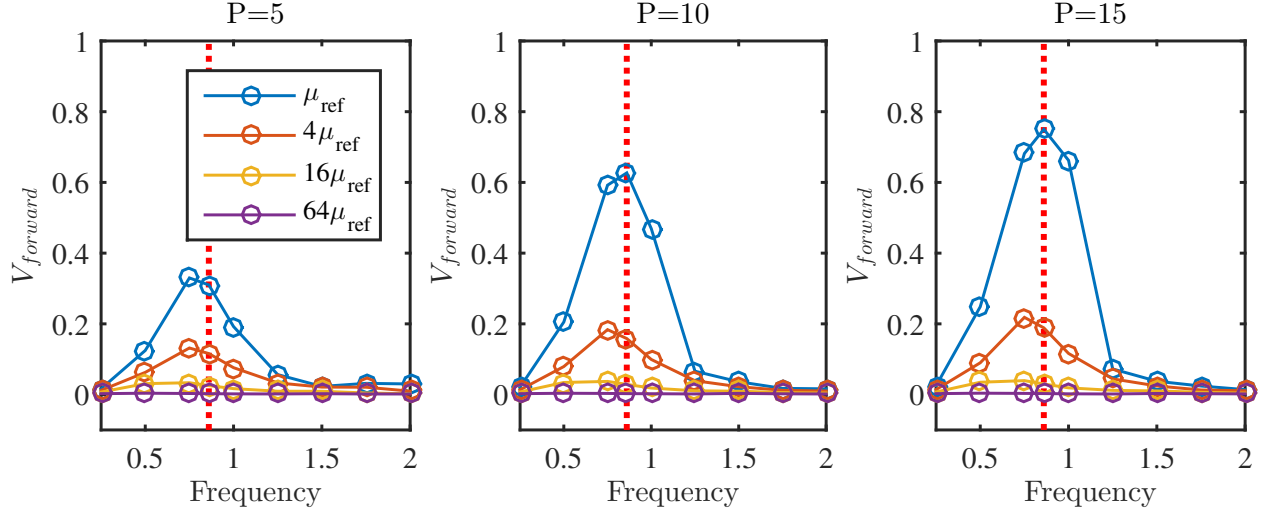


Figure 3.15: Comparing the forward swimming velocity of the bell at different periods with different amounts of viscosity. This allows oneto study the effects resonant driving at different Re . Notice that the highest speed per μ coincides with the highest amplitude of diameter oscillation, but the velocity does not change over time as seen in the reference viscosity case. At $\mu = 64\mu^{ref}$ the forward swimming velocity is near zero.

of driving the bell at the resonant frequency. This is due to the dissipation of the starting and stopping vortices at lower Re as well as the increased effective damping of the bell. In Fig. 3.16 I have plotted the vorticity generated by the bell when driven at the reference resonant frequency with F_{Mag}^{ref} . I observe that even though a nontrivial amount of vorticity is generated in the contraction and expansion phases of the stroke, no vortex shedding was observed in the low Re fluid environments where inertial forces were balanced by viscous forces. As Re approached 1, the average forward velocity in turn approached zero.

3.3.4 Cost of Transport

As another measure of swimming performance, the cost of transport (COT) was calculated for bells with the reference stiffness at $Re \approx 172$. The cost of transport gives a measure of the energy spent per unit distance traveled and has been used as a measure of the efficiency of swimming[87, 93, 12]. The force applied as well as the velocity of the bell margin can be readily calculated at each time step in the immersed boundary simulations. The COT was averaged over pulses 20-25 using the formula

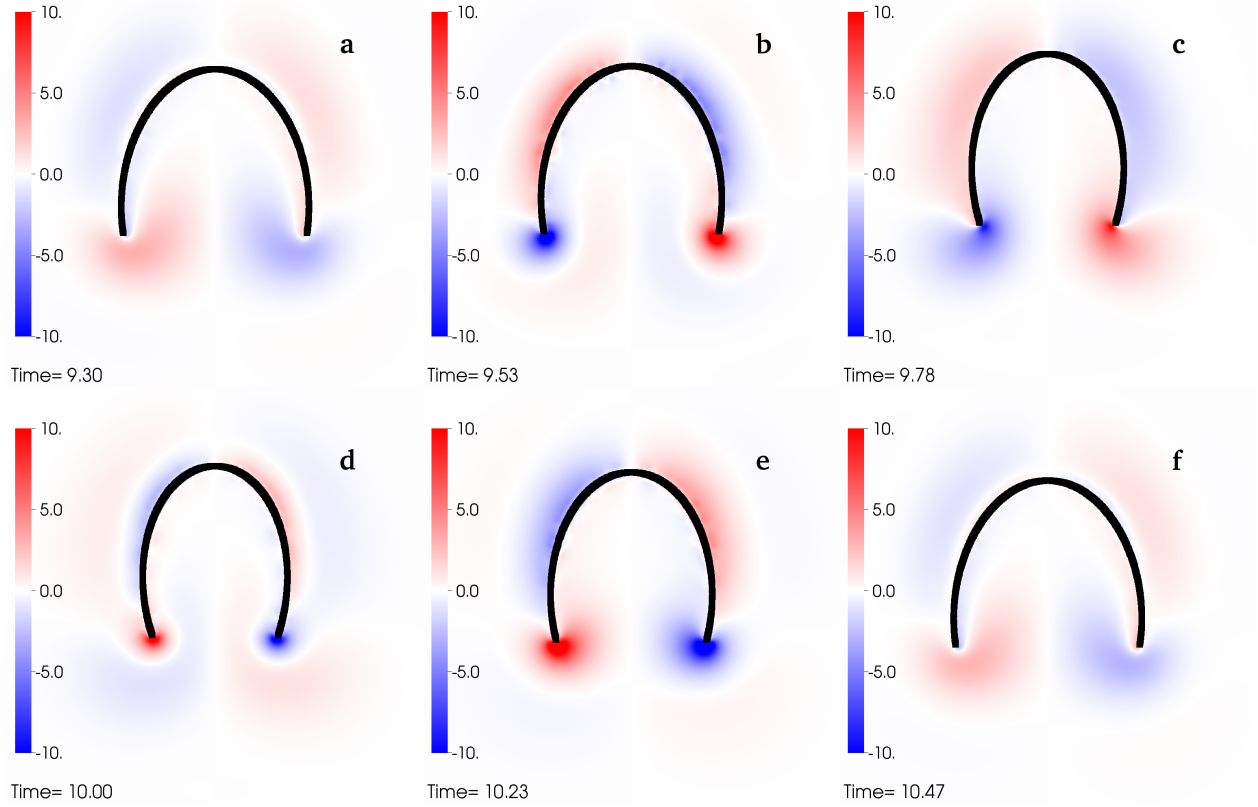


Figure 3.16: Vorticity plot of the 8th propulsive cycle of the driving frequency study with $\mu = 16\mu_{ref}$. The driving frequency is $.86 \text{ s}^{-1}$. Notice the absence of vortex shedding in both the contraction phase (a-c) and the expansion phase (d-f) of this lower Reynolds number regime.

$$COT = \frac{1}{N} \frac{1}{D} \sum_{i=1}^N |F_i| |U_{r,i}|, \quad (3.3.3)$$

where F_i is the applied force at the i^{th} time step, $U_{r,i}$ is the radial velocity of the margin at the i^{th} time step, N is the number of time steps, and D is the distance the jellyfish traveled during this time. Fig. 3.17 shows the distance that the jellyfish travels during each pulse for various forcing magnitudes and frequencies. Note that the jellyfish swims the farthest during each pulse when driven at frequencies slightly below the resonant frequency. Fig. 3.18 shows the average power input calculated as $P_{in} = \frac{1}{N} \sum_{i=1}^N |F_i| |U_{r,i}|$ for the same range of forcing magnitudes and frequencies.

Notice that the power input is highest at frequencies slightly above the resonant frequency due to the higher velocity of the bell margin at these frequencies. Finally, Fig. 3.19 shows the COT for the reference configuration over a range of driving frequencies and forcing amplitudes. The cost of transport is relatively low for forcing frequencies slightly larger than the resonant frequency. Above

the resonant frequency, the COT increases dramatically with increased frequency due to the small distance traveled per pulse. At lower frequencies, the distance travelled is also smaller than the resonant frequency, but the energy required is proportionally smaller.

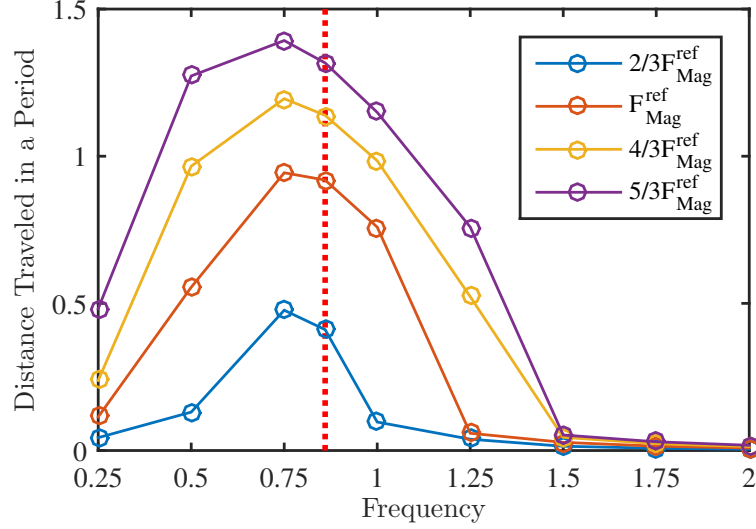


Figure 3.17: Comparing the average vertical distance (D) traveled per pulse cycle for different force magnitudes, F_{Mag} , during steady state swimming. This is averaged over the 20th to 25th pulse cycles.

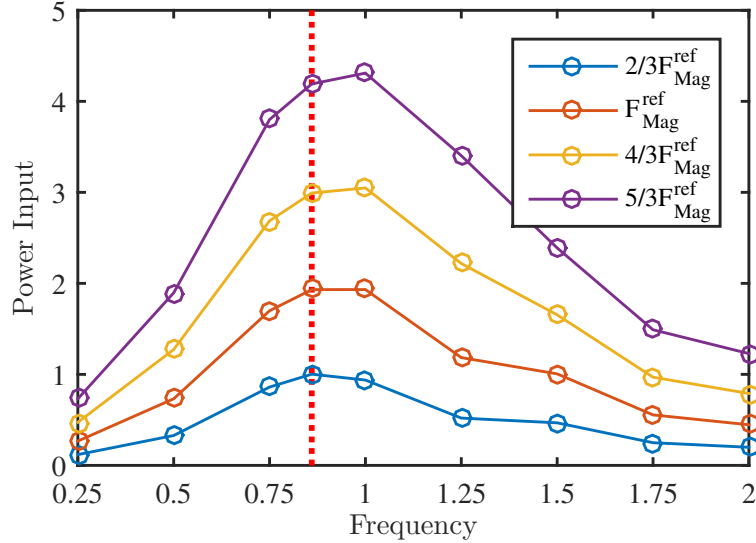


Figure 3.18: Comparing the power input $\mathcal{P}_{in}$ per pulse cycle for different force magnitudes, F_{Mag} , during steady state swimming. This is averaged over the 20th to 25th pulse cycles. The power input averaged over the cycle is calculated as $\mathcal{P}_{in} = \frac{1}{N} \sum_{i=1}^N |F_i| |U_{r,i}(q_D, t)|$ where $U_{r,i}$ is the radial velocity of the bell at time step i .

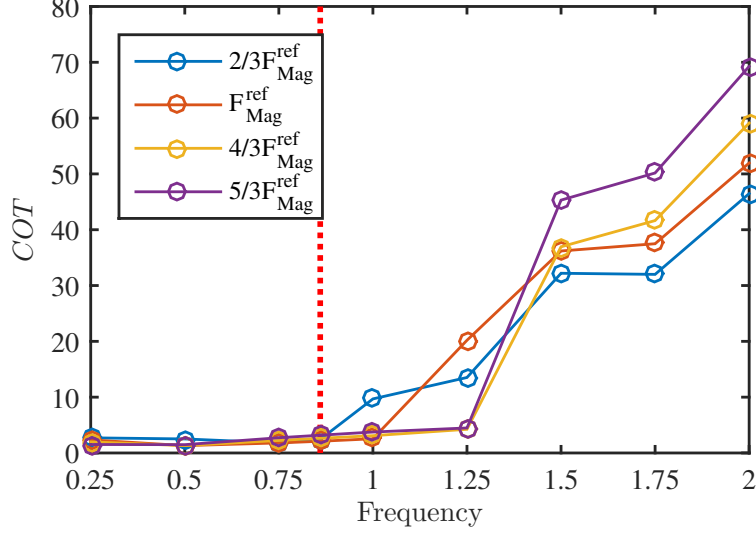


Figure 3.19: Comparing the cost of transport (COT) per pulse cycle for different force magnitudes, F_{Mag} , during steady state swimming. This is averaged over the 20th to 25th pulse cycles.

3.4 Discussion

In this numerical study, I found that driving the model jellyfish bell at, or slightly below, the recorded frequency of free vibration resulted in a higher maximum amplitude of bell oscillation. I also found that the model jellyfish bell swam fastest at periodic steady state when driven at frequencies at or slightly above the recorded frequency of free vibration. The optimal driving frequency for the largest forward swimming speed was in turn dependent upon the magnitude of the driving force, where nonlinear effects due to large deformations of the bell shifted the optimal frequency. When additional fluid damping was introduced into the model, the advantage of driving the bell at its resonant frequency was reduced. Finally, the cost of transport was lowest for driving frequencies below the resonant frequency, and increased dramatically for driving frequencies near the resonant frequency.

When comparing the results to the lumped parameter model of DeMont and Gosline [30], I found that driving the bell at the recorded frequency of free vibration generated the largest bell oscillations for a given force amplitude when that force was relatively small. For example, the maximum oscillation occurred when driven at the frequency of free vibration for $F_{Mag} = \frac{1}{6}F_{Mag}^{Ref}, \frac{1}{3}F_{Mag}^{Ref}$. For larger forces, the bell is deformed beyond the linear range. As the magnitude of the driving force was increased, the frequency that generated the largest oscillations shifted to $.75 \text{ s}^{-1}$. This suggests

that the actual resonant frequency is dependent on the forcing amplitude, which agrees with Megill's model prediction [64]. For some driving frequencies, the amplitude of the bell oscillation varies with the forward swim speed. This can be seen by comparing the amplitudes during different propulsive cycles (Fig. 3.6). As the swimming velocity increases, so to does the amplitude of bell oscillation. This effect is not observed for cases when the swimming speed quickly reaches steady state.

The driving frequencies that produced the fastest forward swimming velocities in the early propulsive cycles (Fig. 3.7) corresponded to the driving frequencies that also generated the largest oscillations of the bell diameter (Fig. 3.6). In the later propulsive cycles that approach the periodic steady state, the fastest driving frequencies are slightly above the recorded frequency of free vibration. In these cases the fastest driving frequencies do not correspond with the frequencies that produce the maximum amplitude oscillation. This effect is magnified for larger applied forces. This suggests that nonlinear effects play a role in determining the optimal driving frequency for forward swimming. One possible nonlinear effect is that successful swimmers with higher driving frequencies have faster forward swimming speeds because the shorter period of their propulsive cycle allows for the bell to recapture the momentum transferred to the fluid. In this case, the stopping vortex ring generated from the previous cycle would interact strongly with the new starting vortex, producing a larger flux of fluid away from the jellyfish. Though the expansion phase in the model is not fully passive, the benefit from coasting on vortices from previous propulsive cycles has been previously discussed in terms of passive energy recapture [38].

By examining how the harmonic response curves describing the forward swimming velocities and amplitudes change in time, the evolution of the system from rest to steady state swimming is revealed. One important observation is the presence of a threshold amplitude for frequencies higher than the recorded resonant frequency. If the amplitude of oscillation is close to or greater than 0.2, then significant forward swimming speeds are generated. If the amplitude of bell oscillation is lower than this value for a given driving frequency, then the forward swimming speed is dramatically lower. I observed (Fig. 3.6 and Fig. 3.7) that driving frequencies that generated bell oscillations with amplitudes near 0.2 had a relatively slower evolution to steady periodic swimming compared to driving frequencies that generated larger bell oscillations. As the forcing magnitude was increased, the amplitude of bell oscillations increased as well, and this also increased the frequency required to generate significant swim speeds.

When examining the Strouhal number (Fig. 3.8), I observed that for sufficiently high force magnitudes, frequencies that were close to the resonant frequency were within the optimal St range observed by Taylor [90]. The range of frequencies within this optimal St range was dependent on the force magnitude applied. As the magnitude of the applied force increases, driving frequencies slightly lower than or at the resonant frequency are within this optimal St range after fewer pulse cycles than those at frequencies slightly higher than the resonant frequency. Using a cost of transport measure for swimming performance, I found that driving the bell at frequencies significantly higher than the resonant frequency led to a much more elevated cost of transport (Fig. 3.19). Frequencies close to or lower than the resonant frequency had a lower cost of transport, though the distance traveled (Fig. 3.17) and power input (Fig. 3.18) per pulse were lower for lower frequencies.

In the Reynolds number study, the optimal driving frequency for the maximum amplitude of bell oscillation shifted to lower frequencies for lower Reynolds number (Fig. 3.14), as predicted by the free vibration studies (Fig. 3.13 and Fig. 3.12). This frequency also corresponded to the optimal driving frequency for the fastest forward swimming speed (Fig. 3.15), although the relative boost from resonant driving decreased as the Reynolds number decreased. At low Reynolds numbers the flows are reversible, and locomotion that uses reciprocal motions of the driving appendage is less effective. Purcell first introduced this idea as the famous “Scallop Theorem” and noted that a scallop could not swim at zero Reynolds numbers [75]. For low Reynolds numbers, the jellyfish moves forward during bell contraction and then moves almost back to its starting position during bell expansion.

CHAPTER 4

Active tension model for propulsion

4.1 Introduction

Although computational fluid dynamics has been used to examine jellyfish locomotion, many studies use prescribed kinematics to solve the fluid-structure interaction system [82, 47, 48, 3]. The limitation of these models is that they do not examine how the material properties and the morphology of the bell determines its motion and the resulting fluid dynamics. Further complicating matters is that many of these models use 2-dimensional or 2-dimensional axisymmetric implementations to describe the inherently 3-dimensional, non-axisymmetric vortex ring dynamics present in jellyfish. Herschlag et al. found that while flow profiles and swimming velocities of 2-dimensional prolate bell geometries could be validated with experimental data, the same is not true for oblate bells [48]. Park et al. attempted to tackle this problem by accounting for the elastic properties of a 3-dimensional bell in the equations of motion of an oblate jellyfish, but still imposed a penalty based immersed boundary method [72]. Sahin

When examining the fluid dynamics of animal propulsion, it is important to consider the functional morphospace, and specifically the mechanical design, of the organism in question. Recent work by Lucas et al. sampled a large number of flexible appendages and found that there were transcendental bending laws for enhanced thrust production regarding the flexion length and angle of the propulsive appendage [59]. With the use of experimental observations of *Aurelia* spp. and mechanical models, the flexibility of the jellyfish's bell margin has also been explored in context of enhanced thrust generation [18, 37]. In these studies, it was noted that the bell margin played a large role in secondary thrust generation. Stopping vortices are initially formed on the exumbrellar surface of the jellyfish during the contraction phase and are subsequently deposited in the bell cavity. If bell margin is too rigid, the vortices will not be deposited in the bell and this results in the loss of passive energy recapture and a higher cost of transport [38].

In this chapter, I present a model for a 3-dimensional forward swimming oblate jellyfish whose forward motion is solely determined by the active and passive material properties and morphology of bell. Using the IBFE framework discussed in Chapter 3, I have derived a material model for the bell that takes into account some of the spatially varying elastic properties found in the literature. The bell is driven by prescribing an active tension that takes into account the location, duration, and directionality of the muscle activation. The resulting forward motion emerges from the coupling between the elastic bell and the local fluid environment, rather than any form of prescribed kinematics. Once the bell model has been derived, I will then explore the parameters of the theoretical morphospace by examining how the bell's passive material properties and strength of muscular activation affect swimming performance.

4.2 Methods

4.2.1 Material model

An implementation of IBFE was used to perform the set of numerical experiments. In the numerical framework, I wanted to model the passive elastic properties of the bell and the active tension generated by the muscles. Using the IBFE framework, the stresses are calculated on the elastic body using the first Piola-Kirchoff stress tensor

$$\mathbb{P} = \mathbb{P}_p + \mathbb{P}_a, \quad (4.2.1)$$

where $\mathcal{P}_p$ is the first Piola-Kirchoff stress tensor of the passive elastic properties and $\mathcal{P}_a$ is the first Piola-Kirchoff stress tensor for the active tension prescribed on the body.

The passive elastic properties of the mesoglea are modeled using a material model based on the strain energy functional of Eq. (2.3.3). This was done by describing incompressible Neo-Hookean material model in terms of the first Piola-Kirchoff stress tensor

$$\mathbb{P}_p = \eta \mathbf{F} - \eta \mathbf{F}^{-T} \quad (4.2.2)$$

where $\mathbf{F}$ is the deformation gradient of the element and η is the elastic modulus of the material.

Here I make a simplifying assumption and do not model the bell as a viscoelastic material and neglect contributions of the viscous modulus [36].

The muscular activation of the coronal swimming muscles will be modeled by prescribing a time-dependent stress that is applied over the lower portion of the bell in a circumferential direction. Similar to the passive elastic stress, this stress will be described in terms of the first Piola-Kirchoff stress tensor as follows,

$$\mathbb{P}_a = JT\mathbf{F}\mathbf{f}_0\mathbf{f}_0^T \quad (4.2.3)$$

where J is the Jacobian of $\mathbf{F}$, T is the magnitude of prescribed tension, and f is the (fiber) direction vector of the prescribed tension with respect to the reference configuration. Note that because I am using the first Piola Kirchoff stress tensor, I am prescribing an active tension in the reference configuration as opposed to the current configuration.

To understand how this relates to a stress in the current configuration, I begin by looking at the Cauchy stress of an area

$$\sigma^{\mathbf{a}} = T\mathbf{f}\mathbf{f}^T, \quad (4.2.4)$$

where f is the fiber direction field of the tension in the current configuration, and $\sigma^{\mathbf{a}}$ is the Cauchy stress tensor. I can relate this to the first Piola Kirchoff stress tensor using Nanson's relation

$$\mathbb{P} = J\sigma^{\mathbf{a}}\mathbf{F}^{-T} \quad (4.2.5)$$

$$= JT\mathbf{f}\mathbf{f}^T\mathbf{F}^{-T} \quad (4.2.6)$$

$$= \frac{JT}{\|\mathbf{F}\mathbf{f}_0\|^2}\mathbf{F}\mathbf{f}_0\mathbf{f}_0^T\mathbf{F}^T\mathbf{F}^{-T} \quad (4.2.7)$$

$$= \frac{JT}{\|\mathbf{F}\mathbf{f}_0\|^2}\mathbf{F}\mathbf{f}_0\mathbf{f}_0^T, \quad (4.2.8)$$

where I relate the fiber direction fields between the current and reference configurations as $\mathbf{f} = \frac{\mathbf{F}\mathbf{f}_0}{\|\mathbf{F}\mathbf{f}_0\|}$.

4.2.2 Construction of the model

An approximate 3-dimensional model for the bell that accounted for variations in bell morphology was developed for use in the simulations. Previous models [26, 62, 48, 82] have described the bell geometry as a hemiellipsoid or by using functions fit to digitized bell shapes. These approaches

have been extended to immersed boundary simulations that model the bell as a collection of one dimensional fibers [48, 72]. The model presented here is an immersed body that has both exumbrellar and subumbrellar surfaces, as well as the flexible marginal flap. The bell shape was parametrized using a hemiellipsoid description for the exumbrellar(*ex*) and subumbrellar(*sub*) surfaces as follows

$$\frac{(x - x_c)^2 + (y - y_c)^2}{a_{sub,ex}^2} + \frac{(z - z_c)^2}{b_{sub,ex}^2} = 1 \text{ for } z \geq z_c, \quad (4.2.9)$$

where (x_c, y_c, z_c) is the center of the ellipse, $a_{sub,ex}$ is the radial axis of subumbrellar and exumbrellar surfaces of the bell, respectively, and $b_{sub,ex}$ is the vertical axis. As in [62], the bell was augmented with an additional ring of uniform thickness to model the bell margin described by the equations

$$\frac{(x - x_c)^2 + (y - y_c)^2}{a_{sub,ex}^2} + \frac{(z - z_c)^2}{b_{mar}^2} = 1 \text{ for } d \leq z < z_c, \quad (4.2.10)$$

where d is the length of the marginal flap and b_{mar} is the vertical axis associated with the bell margin.

The elastic bell model accounts for differences in stiffness between the flexible bell margin and other regions of the bell. In this case, the elastic modulus, η_{tot} , at a point (x, y, z) on the bell is dependent upon the angle it makes relative to the vertical axis

$$\gamma = \begin{cases} \frac{(\pi/2) - \tan^{-1}(\sqrt{x^2 + y^2}/z)}{\pi/2} & \text{if } z > 0 \\ 0 & \text{if } z \leq 0 \end{cases} \quad (4.2.11)$$

$$\eta_{tot} = \eta_{base} + \eta_{var}\gamma \quad (4.2.12)$$

where η_{base} is the elastic modulus of the bell margin, and η_{var} is the difference of the elastic modulus of the top of the bell and the elastic modulus of the bell margin. The elastic modulus of the bell margin is held constant throughout (see Fig 4.1a).

Since no kinematics are prescribed, care must be taken when choosing the area over which the tension is applied, as well as the duration and magnitude of the applied tension. My approach is to specify tension, T , as a function that depends on time, t , and the vertical spatial component of the

bell in its reference configuration, z , such that

$$T = T_{max}\alpha(t)\beta(z) \quad (4.2.13)$$

where T_{max} is the maximum applied tension, $\beta(z)$ is a spatial parametrization of the distribution of the subumbrellar musculature, and $\alpha(t)$ is a temporal parametrization of the activation and release of muscular tension. Note that $0 \leq \alpha(z), \beta(t) \leq 1$. A value of 0 implies that there is no muscle present or that the muscle is not activated.

The subumbrellar musculature does not extend throughout the bell cavity, and so I parameterize the region where active tension is applied to the rim of the bell. This region of activation is parameterized using the following function

$$\beta(z) = \begin{cases} 1.0 - \frac{1}{1+\exp(-\theta_s(z-d))}; & \text{if } z < 0.0350 \\ 0 & \text{if } z \geq 0.0350 \end{cases} \quad (4.2.14)$$

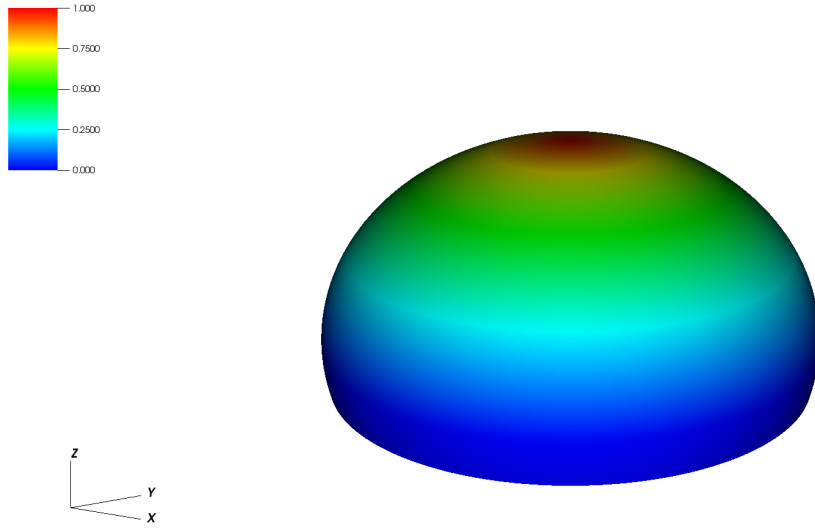
where θ_s characterizes the transition from an area of active tension to an area where no tension is applied (see Fig. 4.1b).

I make a simplifying assumption that a uniform tension is applied only during the contraction phase of forward swimming. The function describing the activation and release of tension draws inspiration from the recordings of muscular contraction in *Aurelia spp.* found in literature [50] and is parametrized in the following manner

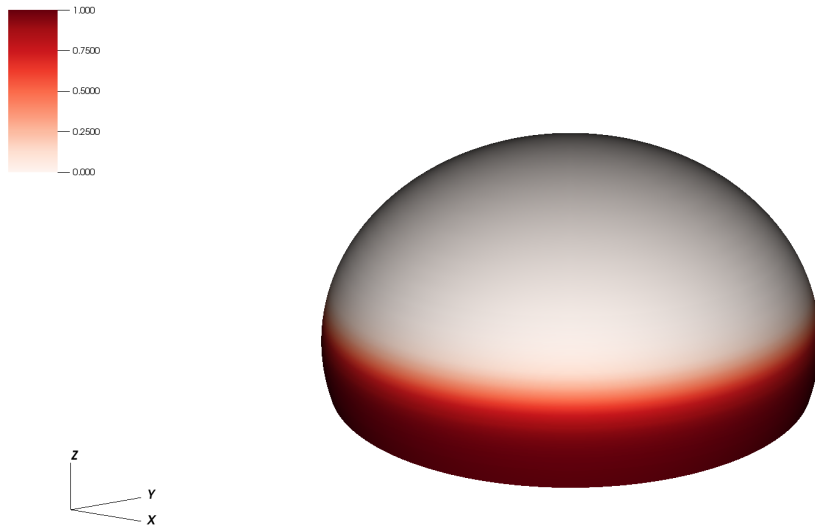
$$\alpha(t) = \frac{1}{1 + \exp(-\theta_a\tau)} - \frac{1}{1 + \exp(-\theta_r(\tau - \tau_{len}))} \quad (4.2.15)$$

$$\tau = \omega t - \lfloor \omega t \rfloor + t_0 \quad (4.2.16)$$

where ω is the frequency of the pulse cycle, t_0 is an offset time for the initial function, θ_a characterizes the speed of muscular activation, θ_r characterizes the release of tension, and τ_{len} is the length of contraction.



(a) Spatial organization of γ



(b) Spatial organization of α

Figure 4.1: Spatial organization of stiffness, γ , and activation α

Table 4.1: Table of nondimensionalized, reference parameters for the bell model. The reference values were chosen to roughly approximate swimming in *Aurelia*, and each of the parameters were varied above and below the reference states as specified in each study.

Parameter	Symbol	Value
Elastic modulus (base)	η_{base}	30
Elastic modulus (variation)	η_{tot}	150
Maximum tension	T_{max}	6000
Musculature variable (spatial)	θ_s	350
Musculature variable (activation)	θ_a	16
Musculature variable (release)	θ_r	6
Tension duration variable	τ_{len}	$.5T$
Horizontal axis (exumbrellar)	a_{ex}	$.6125L$
Horizontal axis (subumbrellar)	a_{sub}	$.5925L$
Vertical axis (exumbrellar)	b_{ex}	$.5L$
Vertical axis (subumbrellar)	b_{sub}	$.35L$
Vertical axis (margin)	b_m	$.5L$
Margin length	d	$.1L$
Frequency	ω	$1/(2T)$

Table 4.2: Table of all numerical parameters unless otherwise noted for simulations.

Numerical Parameter	Symbol	Value
Spatial step Cartesian grid	h	$10L/512$
Spatial step Lagrangian grid	ds	$10L/512$
Domain size	-	$10L \times 10L$
Time step	dt	5×10^{-4}
Integer refinement ratio	N^{ref}	4
Maximum number of refinement levels	ℓ_{max}	4
Vorticity magnitude threshold	ω^{Mag}	.06125

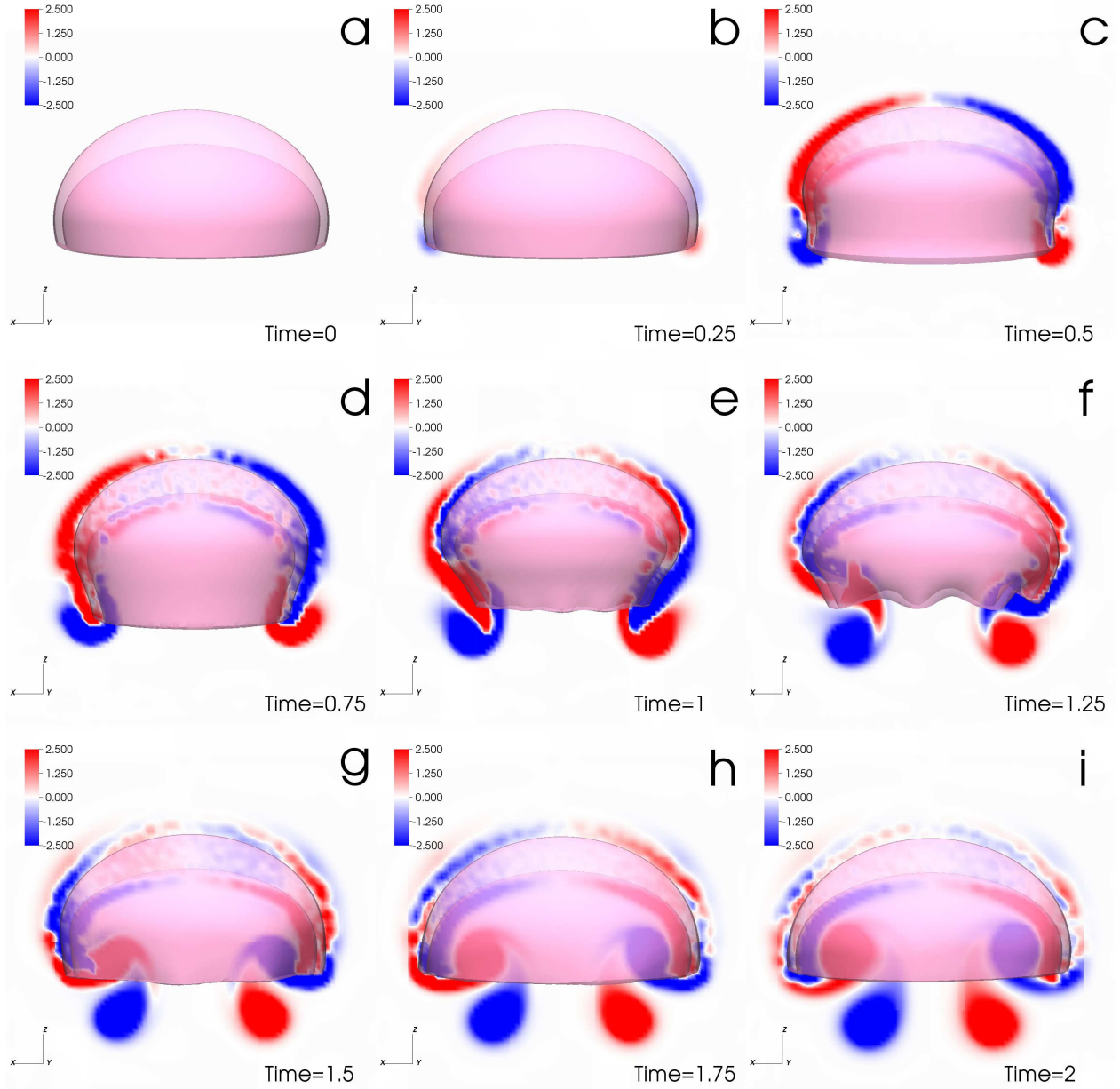


Figure 4.2: Plots of the y-component of vorticity on the XZ plane during one propulsive cycle at time=a)0, b).25, c).5, d).75, e)1.0, f)1.25, g)1.5, h)1.75. i)2.0. The active contraction phase (b-e) reaches its peak applied tension near d, and is then followed by the phase expansion phase (f-h). During the contraction phase, a starting vortex is shed from the tip of bell margin and is advected away from the bell. This is followed in turn by an oppositely rotating stopping vortex from the expansion of the bell that in turn occupies the bell cavity.

4.3 Results

In the following set of studies, I examine forward swimming in the oblate jellyfish model. The bell's contraction is initiated by applying a tension to the lower portion of the bell, referred to as

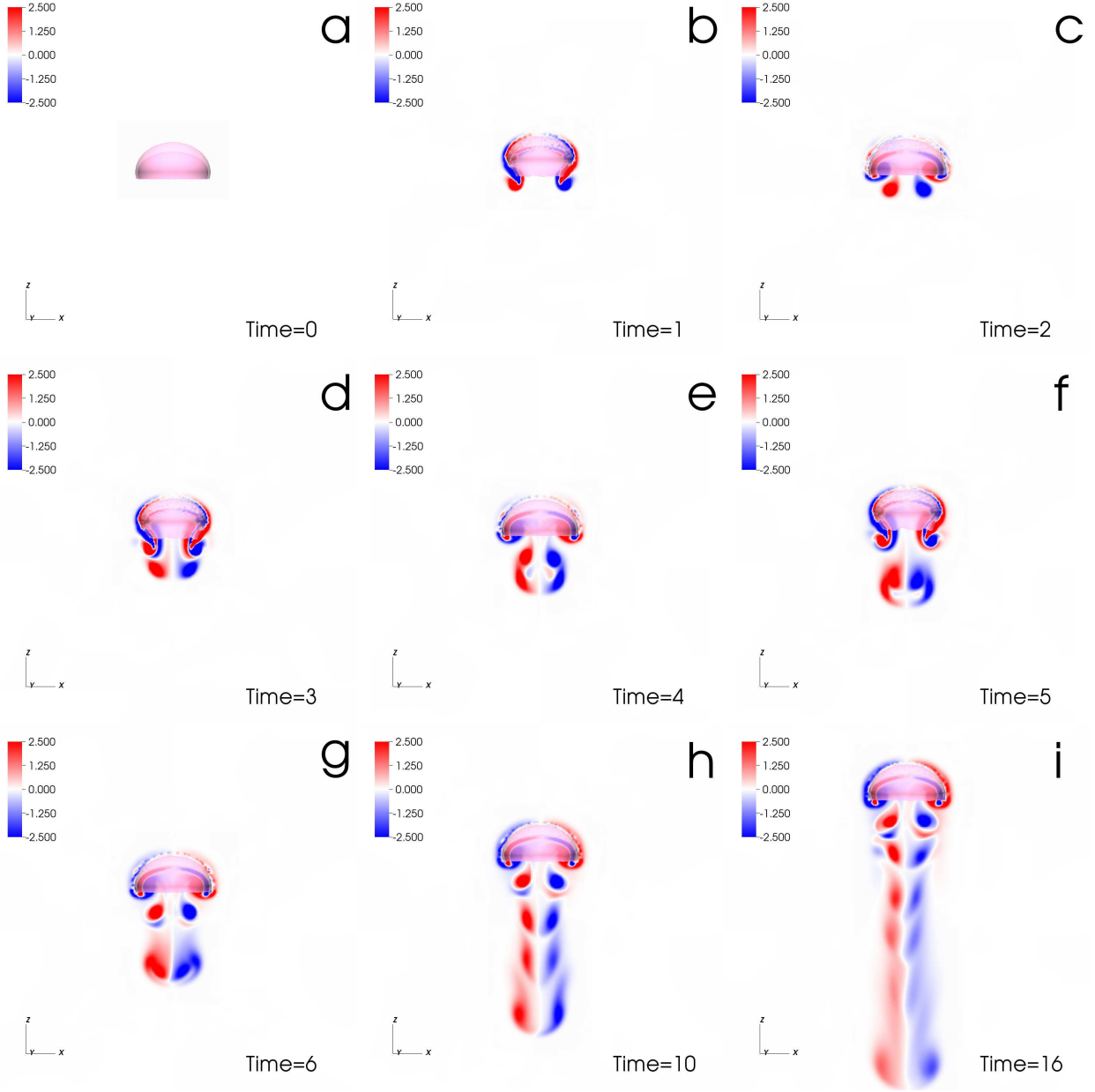


Figure 4.3: Plots of the y-component of vorticity on the XZ plane during the length of the simulation at time=a)0, b)1.0, c)2.0, d)3.0, e)4.0, f)5.0, g)6.0, h)10.0 i)16.0. In the vorticity plots of the bell after having completed a propulsive cycle (c,e,g-i), I can see the progression of shedding the starting vortices in the wake of the bell. Also present are the voriticity plots (b,d,f) of the bell mid-contraction for the first three propulsive cycles. The resulting starting vortices of previous cycles can be seen in the wake of the final plot (i), though note that the first and second starting vortices merge to form a large vortex wake (d-g). The stopping vortex is maintained in the bell following the initial expansion phase. The forward swimming here is a result of the fluid acting on the bell, as opposed to constrained kinematics.

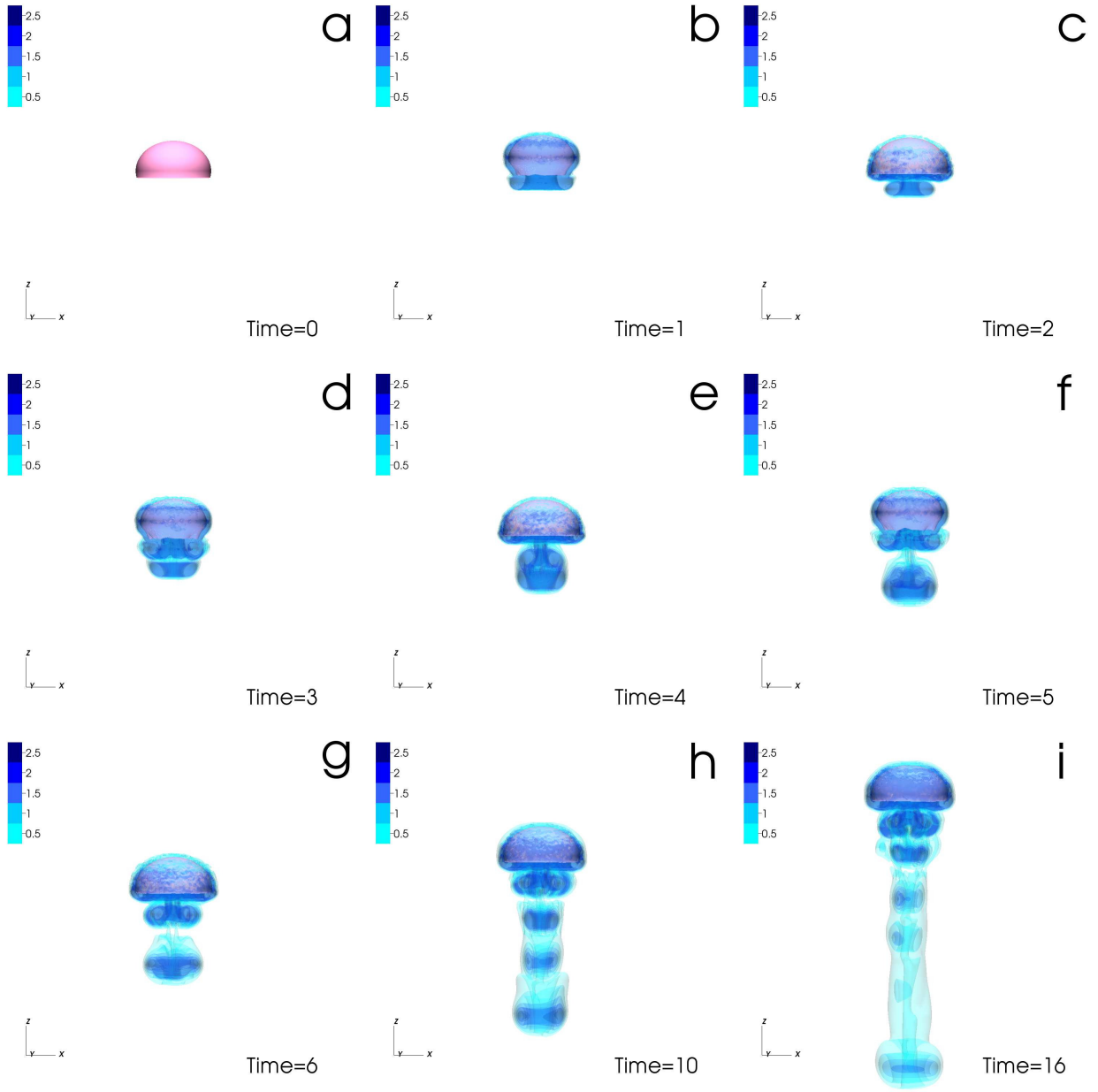


Figure 4.4: Plots of the vorticity magnitude during the length of the simulation at time=a)0, b)1.0, c)2.0, d)3.0, e)4.0, f)5.0, g)6.0, h)10.0 i)16.0. Looking at vorticity magnitude, I can see the emergence of the starting vortices during the contraction phase (b,d,f) and how they are advection away from the bell after the expansion ends (c,e,g-i). Interestingly, note that the second starting vortex leap frogs into the first starting vortex (d-g) and merges to form a large vortex wake that is sustained longer than the starting vortices of subsequent wakes (i).

the bell margin, using the reference parameters from Table 5.1 unless otherwise specified. The bell's expansion phase was initiated once the tension was released and the stored elastic energy drove the passive expansion of the bell. The complete contraction and expansion phase is driven at a

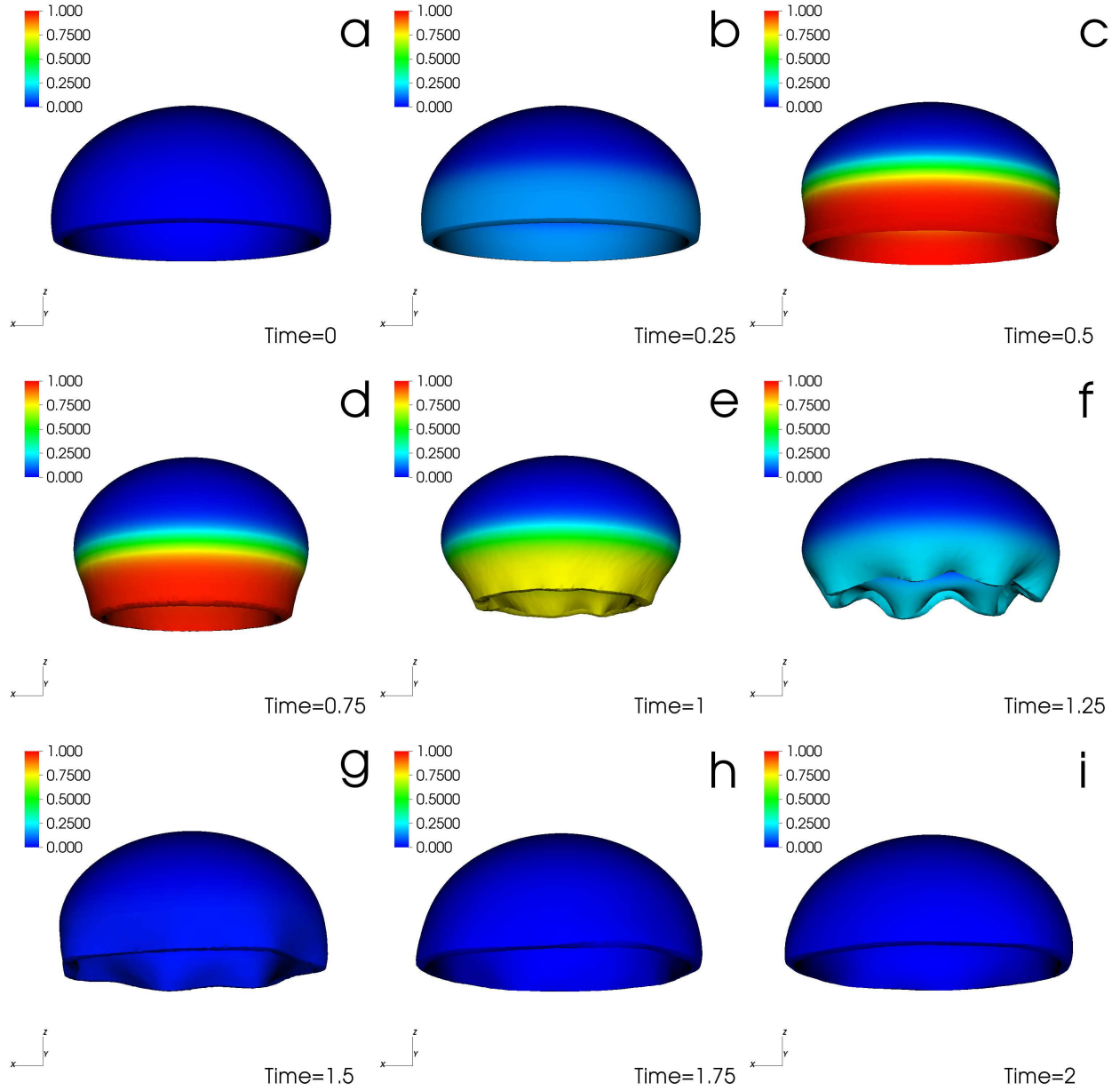


Figure 4.5: Snapshots of the bell during the propulsive cycle of the bell at time=a)0, b).25, c).5, d).75, e)1.0, f)1.25, g)1.5, h)1.75, i)2.0. The spatial activation of tension is plotted on the bell is mapped onto the bell. During the contraction phase (b-e), an active tension is applied circumferentially to the margin of the bell. The bell is then allowed to expand (f-i) passively to its resting state. Note the buckling of the margin (f) when the tension is released and the passive elastic properties push back from the contracted state in the presence of fluid, that in turn push back.

frequency of $.5s^{-1}$, and the totality of the period is referenced here as a propulsive cycle. Unless otherwise indicated, I drove the bell for 8 propulsive cycles for a total of 16 seconds of simulation time. My simulations were conducted at $Re = 500$ unless otherwise noted.

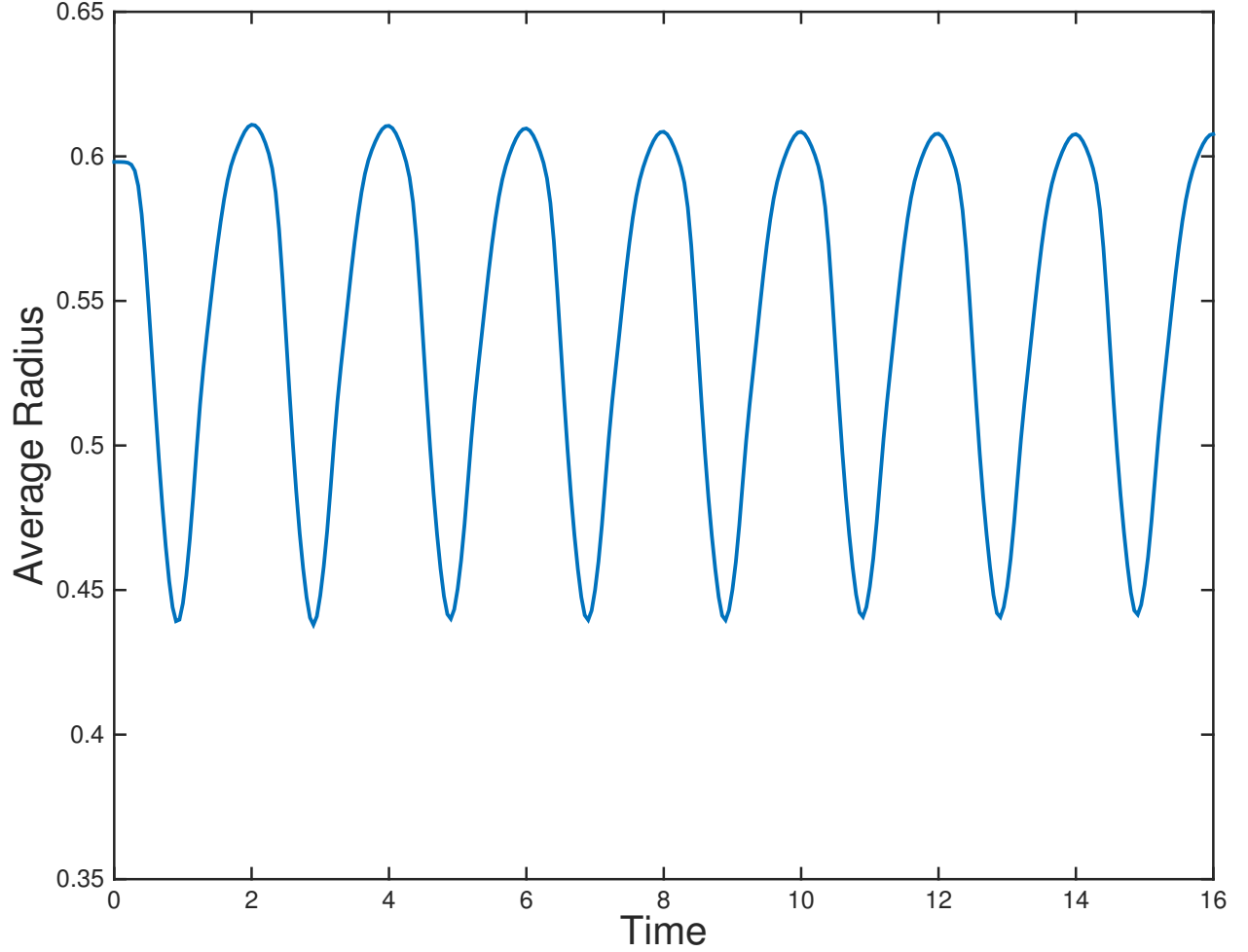


Figure 4.6: The circumferentially averaged radius of the reference case for the full simulation.

When parameters were set to the reference configuration, the bell achieved radial displacements and forward swimming velocities that were qualitatively similar to those reported for *Aurelia* spp. and *Polyorchis* spp. [38, 30]. Fig. 4.7 and Fig. 4.6 show that the radial displacement, due to the activation of the applied tension, corresponds with the fast forward swimming velocity associated with contraction. Fig. 4.8 shows the distance traveled vs. time. Note that the forward velocity during the passive expansion increase as the forward swimming speed is partially sustained during the passive expansion phase.

A sequence of plots of the y-component of vorticity on the xz-plane during one full propulsive cycle can be seen in Fig. 4.2. Note the presence of well defined starting and stopping vortices resulting from the active contraction and passive expansion, respectively. Fig. 4.3 and Fig. 4.4 show the y-component of vorticity and vorticity magnitude, respectively, at various times during the

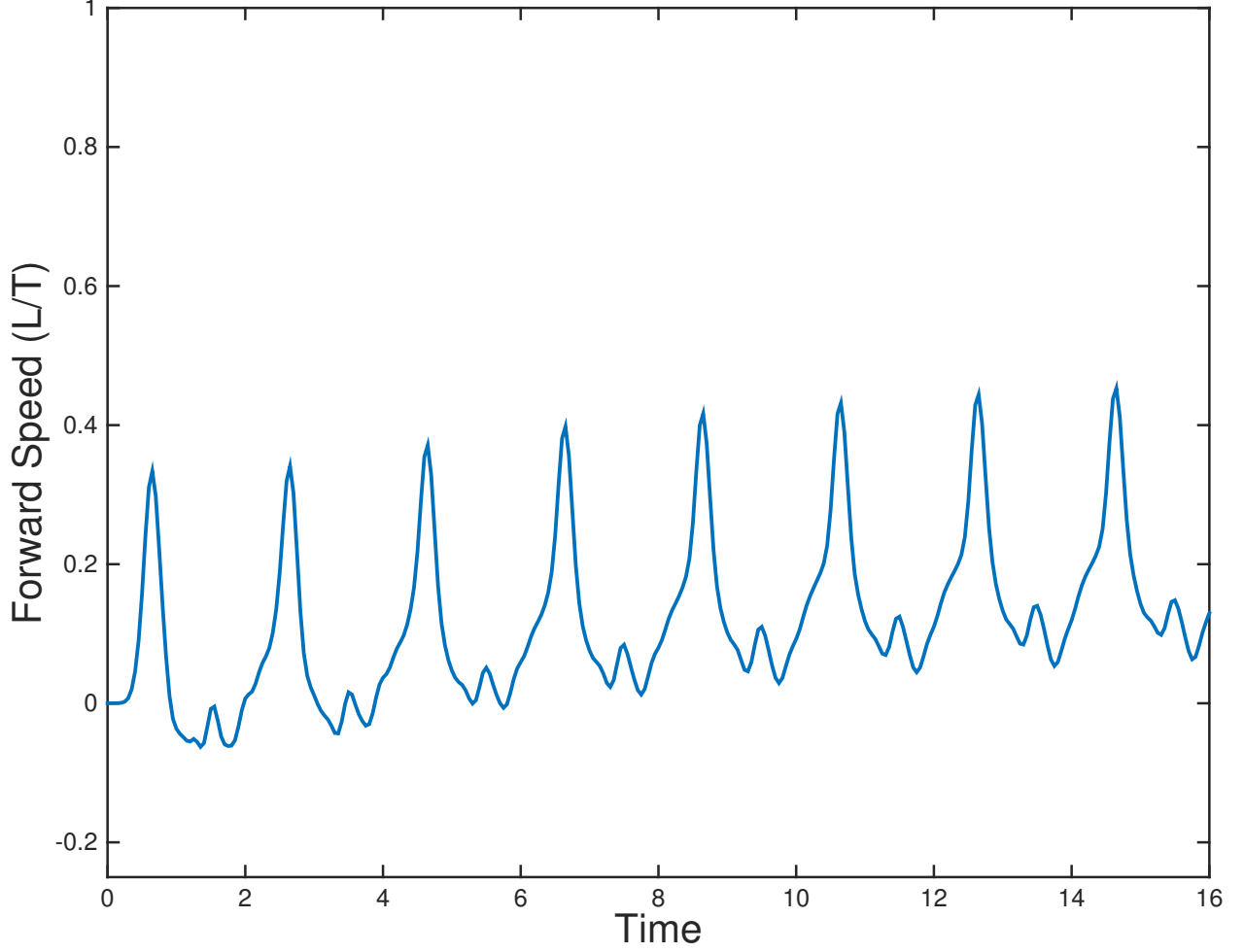


Figure 4.7: The forward swimming speed of the reference case for the full simulation.

simulation. Distinct starting vortices are seen for each of the propulsive cycles, with an interesting event occurring due to the interaction of the first and second starting vortices. The bell begins initially at rest, and the first starting vortex ring is advected downstream slower than the second starting vortex ring. The second vortex 'leap frogs' through the first vortex by passing through its center, eventually becoming one larger vortex ring that sustains itself longer than the subsequent vortices in the wake of the bell.

A spatial and temporal snapshot of the activation and release pattern of the bell can be seen for the reference configuration in Fig. 4.5. The bell contracts following the activation of tension along the bell margin. The bell then expands due to the release of tension. During the expansion of the bell, the bell margin buckles. In addition, this effect is dependent on the material properties of the bell, η_{base} and η_{var} , as well as the local fluid environment, both of which will be further explored in

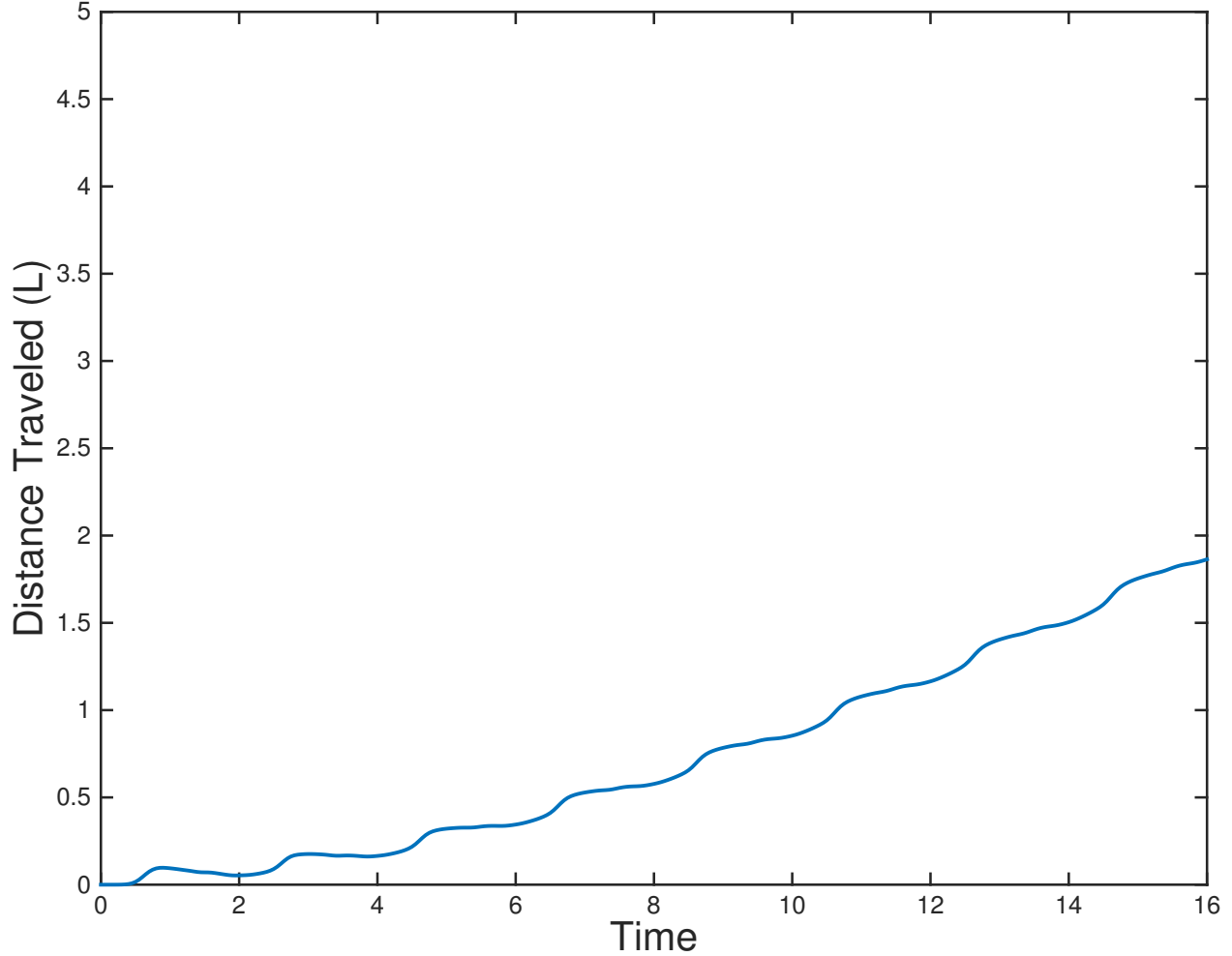


Figure 4.8: The displacement of the bell of the reference case for the full simulation.

this chapter.

4.3.1 Variable applied tension and constant elasticity

To understand the relationship between the elasticity of the bell and its locomotory performance, a series of studies were performed to examine the effects of bell elasticity and applied tension on swimming speed and cost of transport. In this section, the magnitude of the applied force on bell was varied to determine its effect on forward swimming speed. Here I varied the amount of tension applied on the reference configuration, keeping both η_{base} and η_{tot} fixed at 10 and 40, respectively, while setting $T_{max} = 2000, 4000, 6000, 8000, 10000$. The passive elastic properties of the bell were kept fixed to consider only the effect of increasing the activation strength.

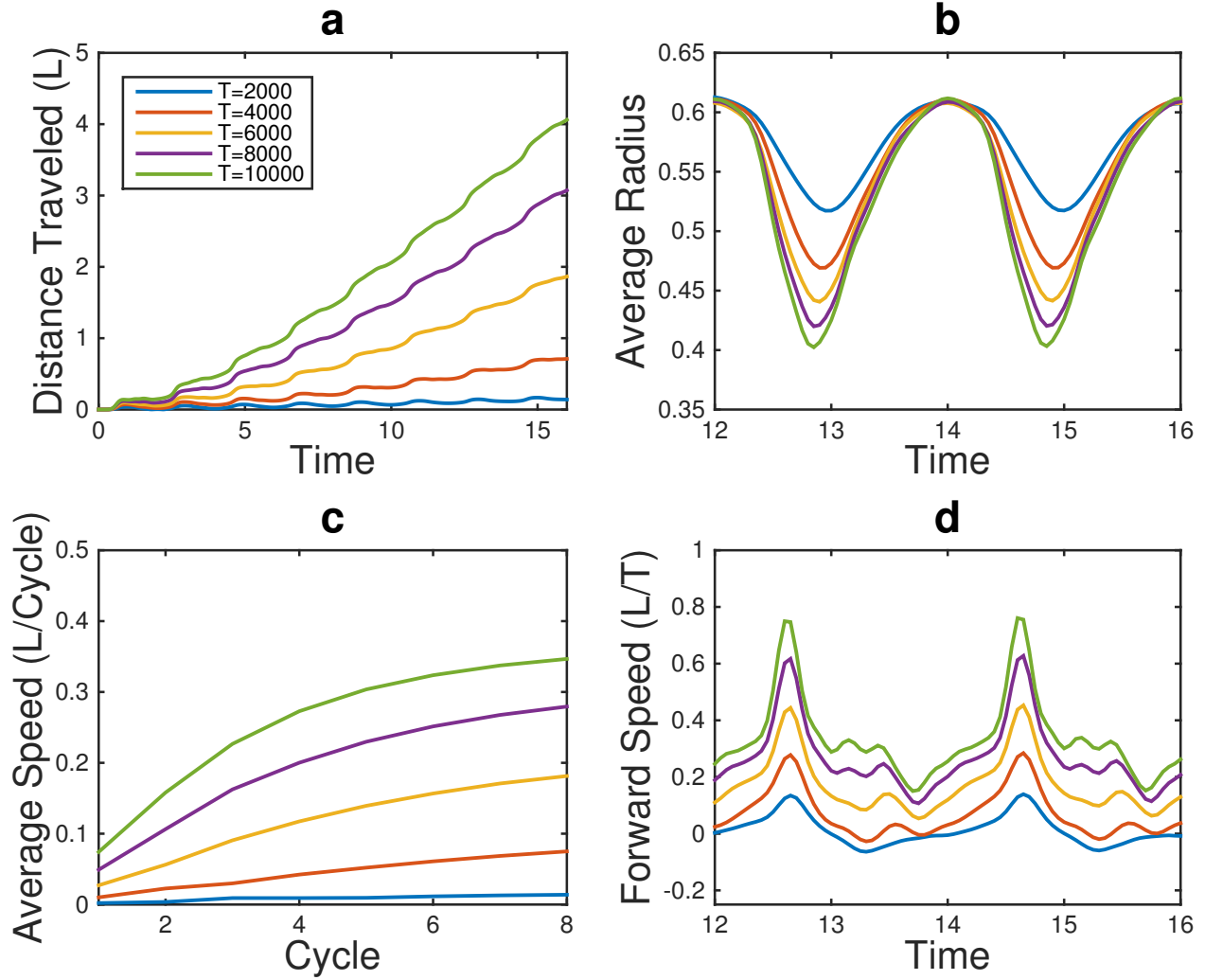


Figure 4.9: Plots for the varying applied tension study of a) the displacement of the bell, b) circumferentially averaged radius during the 7th and 8th propulsive cycle, c) average length traveled per propulsive cycle, and d) forward swimming speed of the bell during the 7th and 8th propulsive cycle. As tension was increased, the forward swimming speed increased and radial displacement increased. Note that the oscillations in forward swimming in to release were similar for varying levels of tension even if the resulting swim speeds vary.

In Fig. 4.9 shows the distance traveled, the average bell radius, and the average and instantaneous speeds. Note that as tension was increased, the forward swimming speed and the radial displacement both increased. The bell continues to swim forward after the release of tension, though the speed of this movement is dependent on the amount of tension applied. This demonstrates the role of the stopping vortex in maintaining forward momentum during the expansion phase of the bell.

Fig. 4.10 and Fig. 4.11 show the y-component of vorticity on the xz-plane and the vorticity magnitude for a range of applied tensions at time=16. As tension increased, the resulting vortex

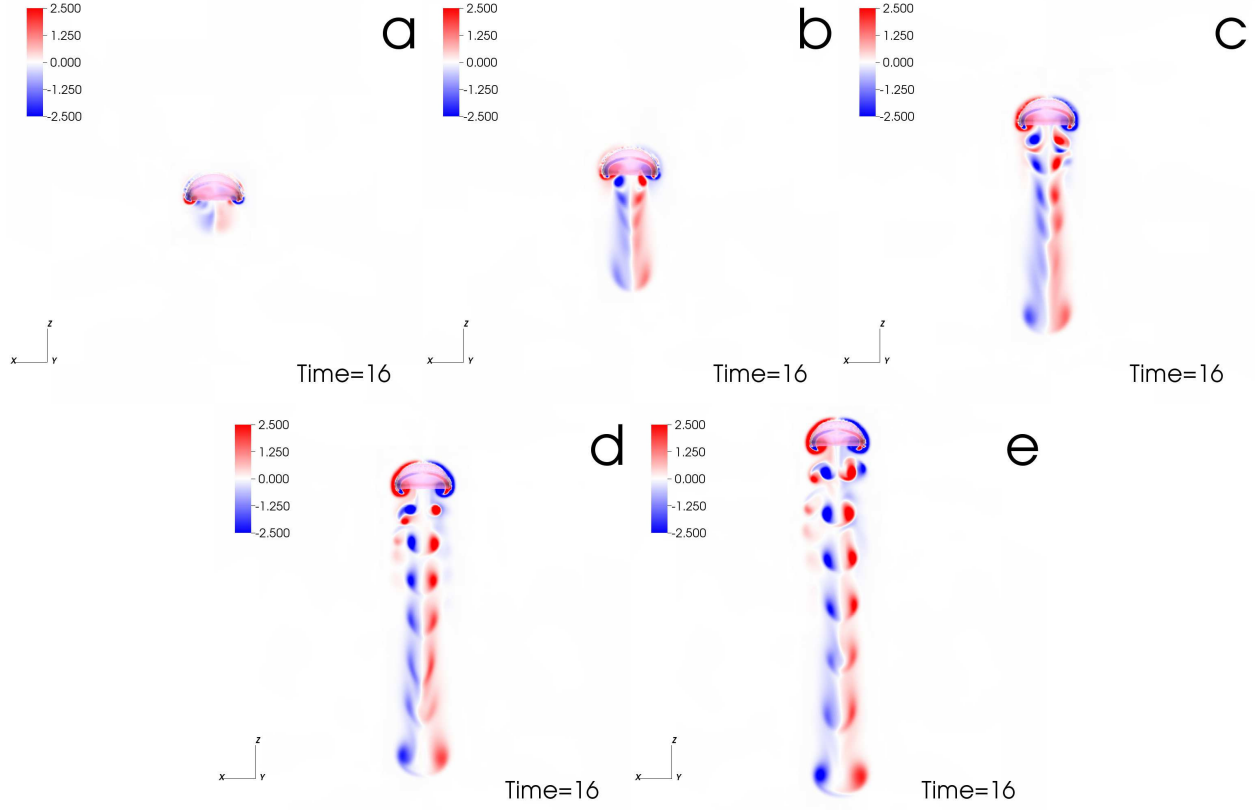


Figure 4.10: Plots of the y-component of vorticity on the XZ plane at time=16 with $T_{max} =$ a)2000, b)4000, c)6000, d)8000, e)10000. As tension is increased, the resulting wake of the vortex rings shed during the contraction became more defined and more distant from each other (d,e). In the low tension case (a), no clear vortex ring is present in the wake of the bell.

rings shed during the contraction became more defined. For the low tension case of $T_{max} = 2000$, neither stopping nor starting vortices were clearly observed. This results in a low radial displacement of the bell which also results in lower vorticity at the bell margin. As the maximum applied tension increases, so does the strength of the starting and stopping vortices. Note that the vortex rings become more defined and are advected more rapidly as the maximum tension increases. Examining Fig. 4.12 shows the vorticity magnitude for five values of applied tension. Note that the position of the shed starting vortex ring is proportional to applied tension, with the case of $T_{max} = 10000$ having a vortex ring farther from the bell than $T_{max} = 4000, 6000, 8000$. Note that $T_{max} = 2000$ lacks a clearly defined starting vortex.

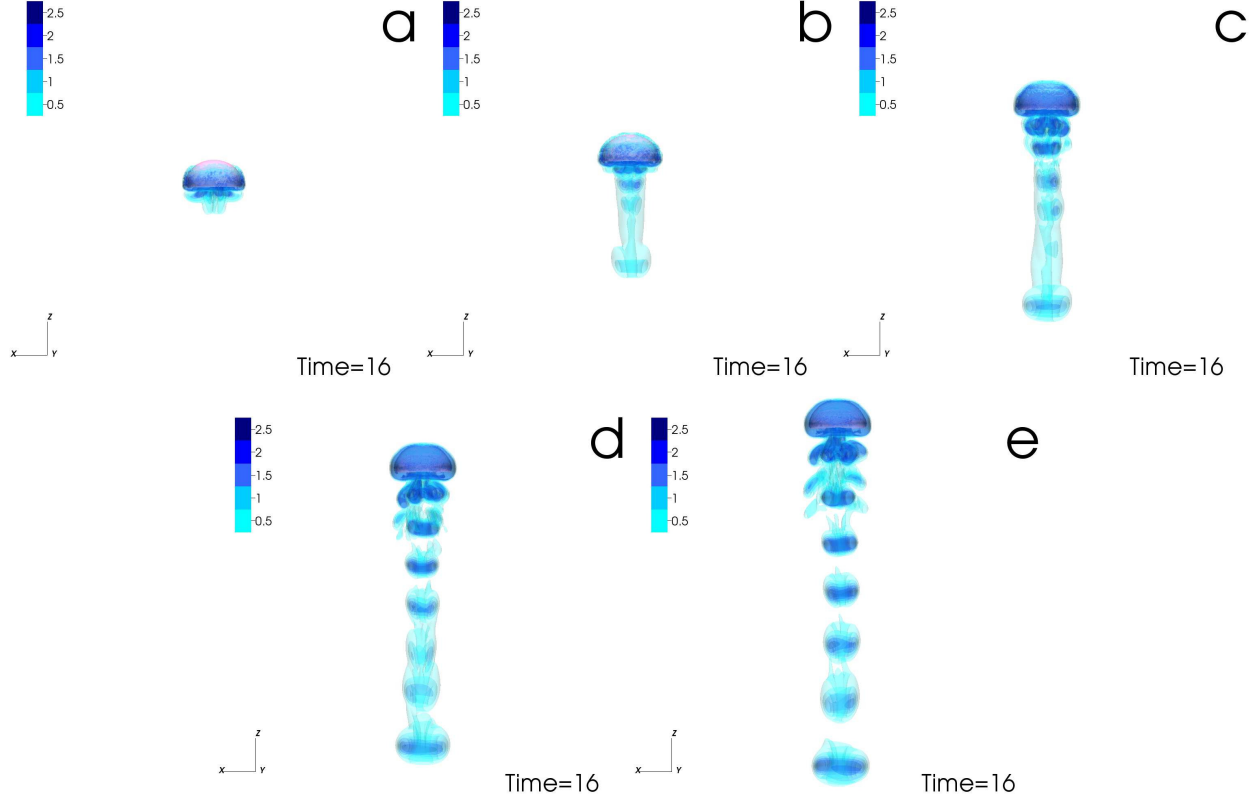


Figure 4.11: Plots of the vorticity magnitude at time=16 with $T_{max} =$ a)2000, b)4000, c)6000, d)8000, e)10000. As tension is increased, the resulting wake of the vortex rings shed during the contraction became more defined and more distant from each other (d,e). Note that in the low tension case of $T_{max} = 2000$, a well defined stopping vortex ring is not present in the bell cavity as it is in $T_{max} = 4000, 6000, 8000, 10000$.

4.3.2 Variable elasticity and constant applied tension

For this set of simulations, I will examine how the bending rigidity of the margin affects the resulting forward swimming speed when the applied tension is fixed. I will set $T_{max} = 6000$ and vary $\eta_{base} = 10, 20, 30, 40, 50$, adjusting η_{var} so that $\eta_{tot} = 150$ is fixed. This will allow me to examine the swimming performance of jellyfish bells with relatively flexible or stiff bell margins.

Fig. 4.13 shows the distance traveled, bell radius, and forward swimming speeds as functions of time. Note that as the bending rigidity is decreased, the resulting forward swimming speed increased. Similarly, the average radial displacement increased with decreased bending rigidity, and the amount of time it took to fully expand the bell after the contraction also increased. As η_{base} was varied, the oscillations of the forward swimming speed during the expansion phase shifted slightly due to changes in how the elastic modulus of the bell was adjusted via η_{var} .

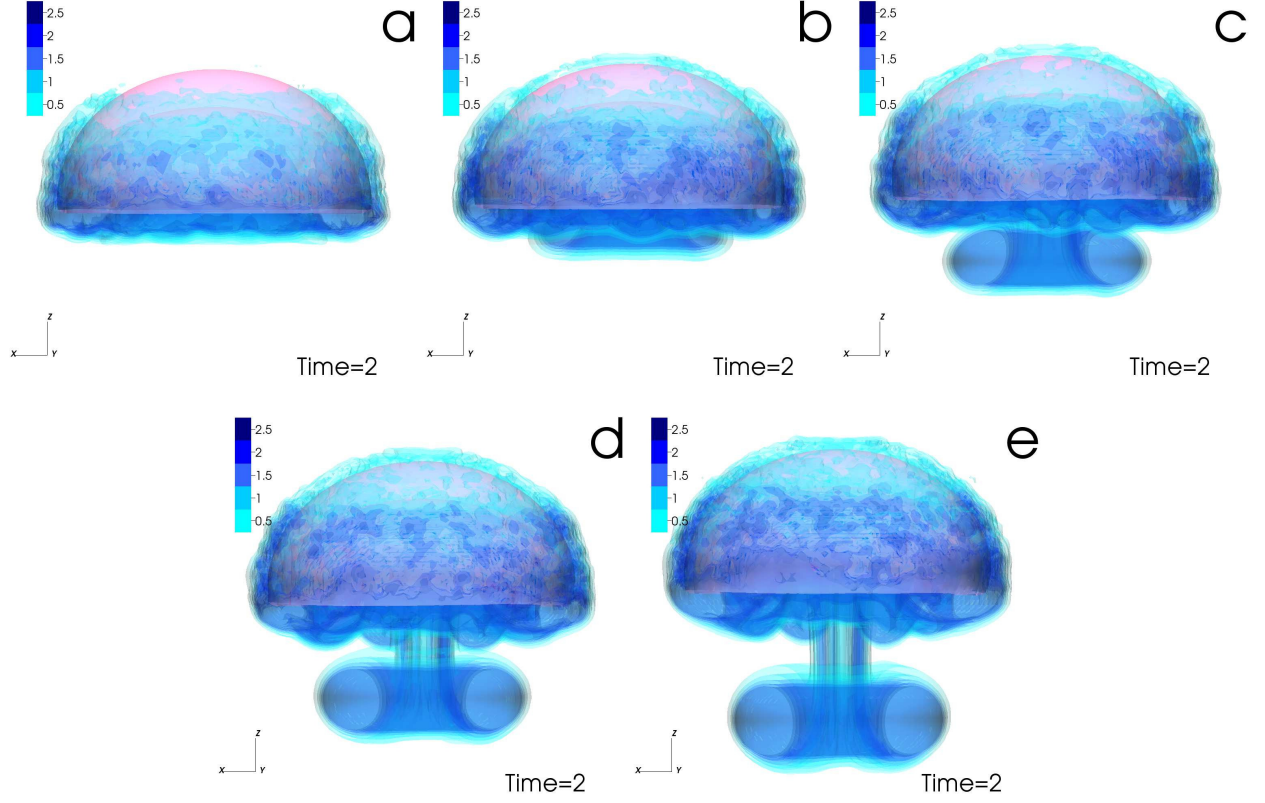


Figure 4.12: Plots of the vorticity magnitude at time=2 with $T_{max} =$ a)2000, b)4000, c)6000, d)8000, e)10000. Note that $T_{max} = 10000$ has a starting vortex ring farther from the bell than $T_{max} = 4000, 6000, 8000$. Note that $T_{max} = 2000$ lacks the presence of a defined starting vortex away from the bell.

Fig. 4.14 and Fig. 4.15 show the y-component of vorticity on the XZ plane and the vorticity magnitude for bell models with $\eta_{base} = 10, 20, 30, 40, 50$ at time=16. As flexural stiffness decreased, the starting vortex rings shed during the contraction became more defined. For the stiffer bell margins, in particular $\eta_{base} = 50$, the applied tension was resisted by the material properties of the bell resulting in a lower radial displacement and weaker starting and stopping vortices. Similar to the previous study, as the margin became more flexible the advection speed of the starting vortex increased (Fig. 4.16). The similarity between Fig. 4.16 and Fig. 4.12 suggests that the speed of the shed vortex ring and the resulting forward motion is a function of the distance traveled by on the bell margin.

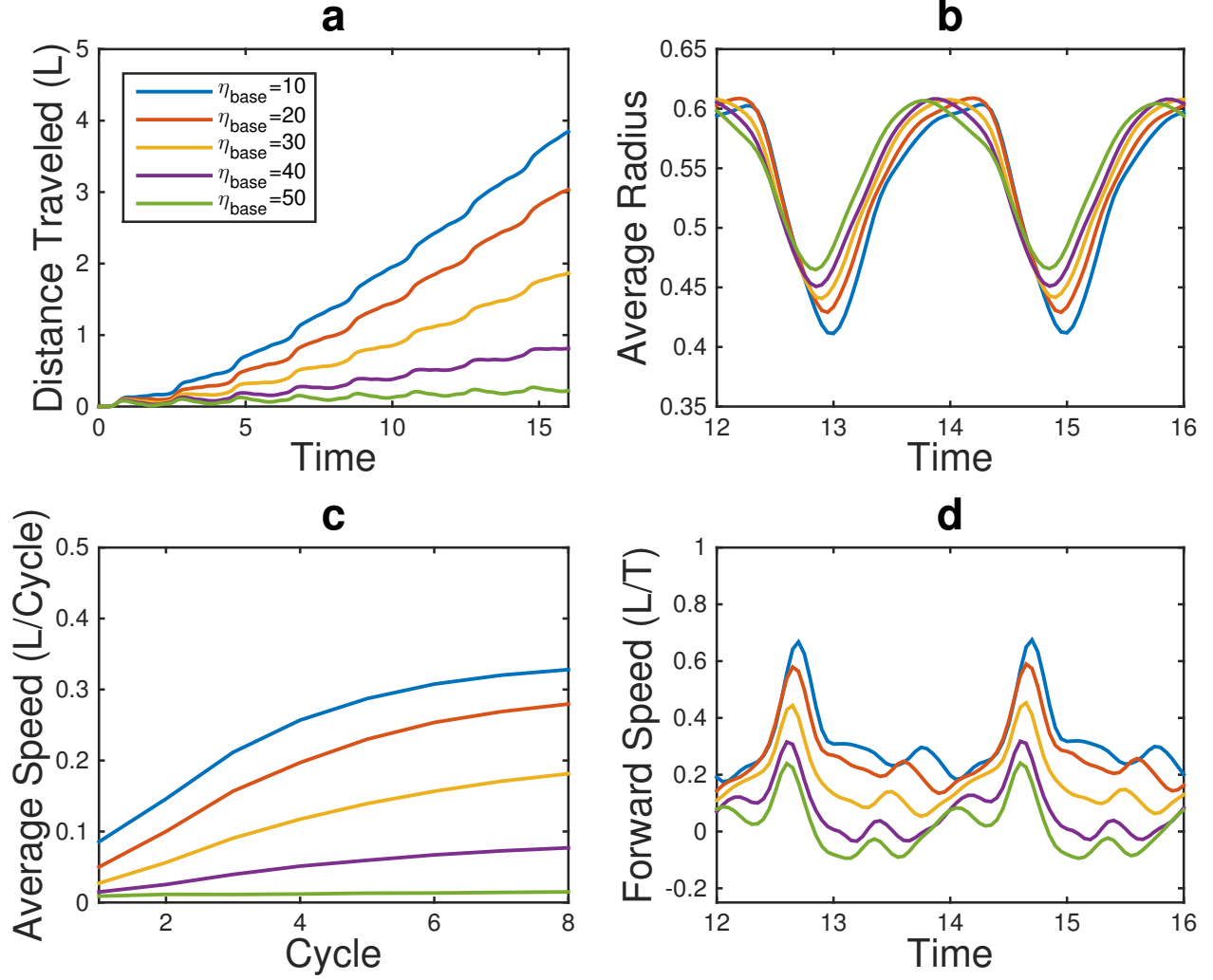


Figure 4.13: Plots for the fixed applied tension study of a) the displacement of the bell, b) circumferentially averaged radius during the 7th and 8th propulsive cycle, c) average length traveled per propulsive cycle, and d) forward swimming speed of the bell during the 7th and 8th propulsive cycle. As the stiffness of the bell margin, η_{base} , decreased, the forward swimming speed increased and radial displacement increased. Note that for different η_{base} , the oscillations of forward swimming speed during the release shifted slightly due to changes in how the elastic modulus of the bell was organized via η_{var} .

4.3.3 Varying effective margin stiffness study

I further explored the role of the margin by varying its flexibility and adjusting the magnitude of the applied tension to produce a fixed deformation of the bell. The total elastic modulus was fixed at $\eta_{tot} = 150$, while the margin's elastic modulus was varied such that $\eta_{base} = 10, 20, 30, 40, 50$. I then applied a tension that varied based on the magnitude of η_{base} , such that $T_{max} = c\eta_{base}$, where c is a fixed constant. Note that tension and the elastic modulus are nondimensionalized. The

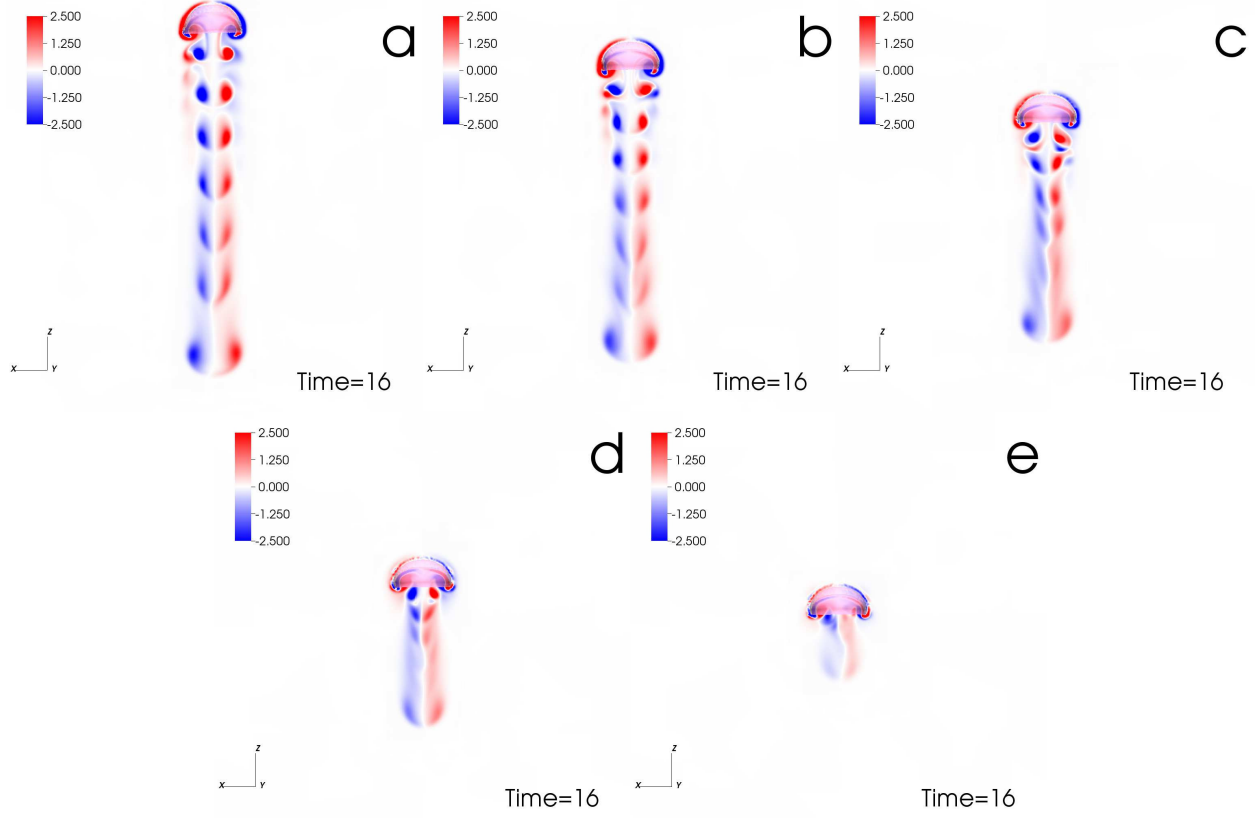


Figure 4.14: Plots of the y-component of vorticity on the XZ plane at time=16 with $\eta_{base} =$ a)10, b)20, c)30, d)40, e)50. As margin flexibility is increased, the starting vortex rings shed during the contraction became more defined and more distant from each other. In the $\eta_{base} = 50$ case, no clear stopping vortex ring is present in the bell cavity.

reasoning behind this choice is that if the tension is held and sustained uniformly on a cylinder with an elastic modulus equal to η_{base} , the deformation gradient, $\mathbf{F}$, would be linearly proportional to the choice of ν_{base} . By varying T_{max} and ν_{base} proportionally, one should produce similar deformations. This ignores the effects of the surrounding fluid, which will have a role in determining the radial displacement of the margin by pushing back against the bell due to the initial pressure generated inside the bell.

In Fig. 4.17 shows distance traveled, bell radius, average speed, and instantaneous speed as functions of time or the cycle number. The results show that by keeping the ratio between the magnitude of applied tension and the elastic modulus the same, similar average swimming speeds per propulsive cycles were produced, with $\eta_{base} = 10$ being the exception. Forward swimming velocity profiles were also similar, though the resulting oscillations of the top of the bell varied due to differences in η_{var} . The radial displacement of the bell was similar as well, with $\eta_{base} = 50$ having

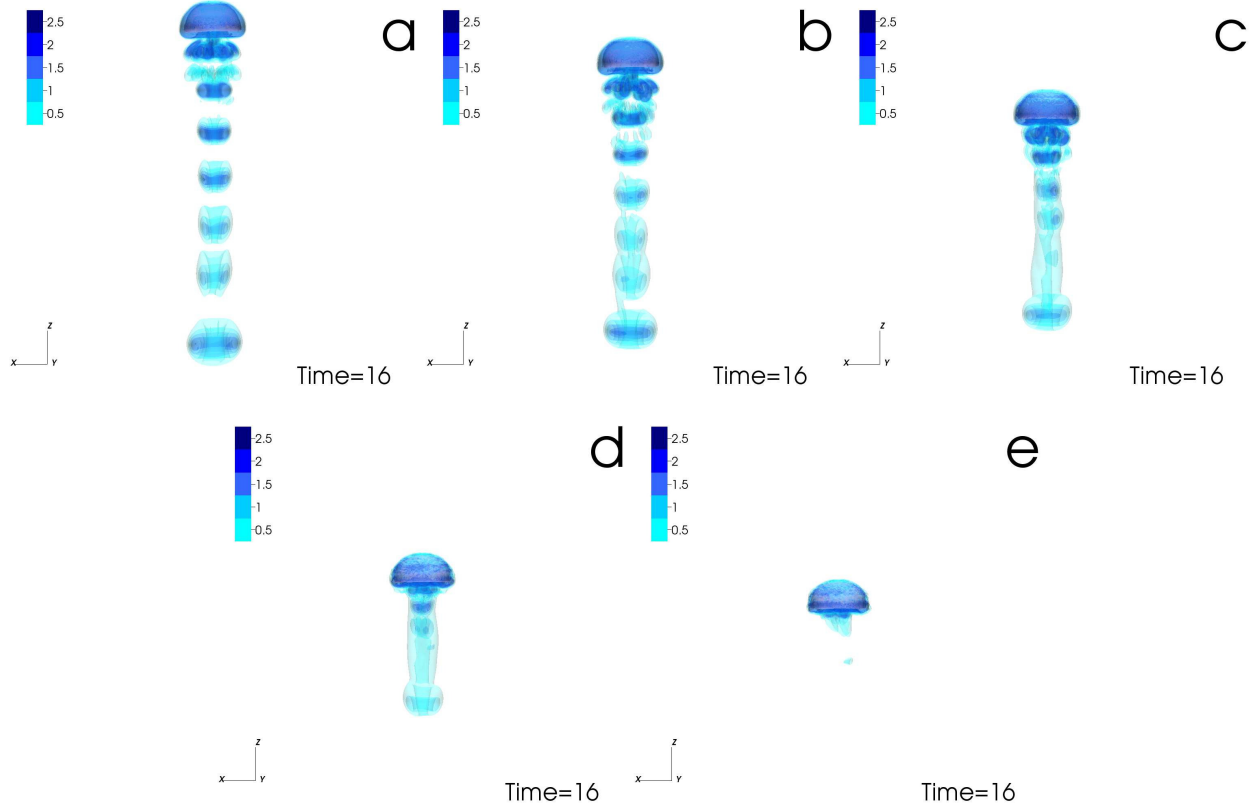


Figure 4.15: Plots of the vorticity magnitude at time=16 with $\eta_{base} =$ a)10, b)20, c)30, d)40, e)50. As margin flexibility is increased, the resulting wake of the vortex rings shed during the contraction became more defined and further from the bell. Note that in the more flexible case of $\eta_{base} = 10$, the vortex ring present in the wake are more defined than they are in $\eta_{base} = 20, 30, 40, 50$.

the largest radial displacement possibly due to the magnitude of the applied tension. The results suggest that forward swimming speed is primarily dependent on the strength of applied tension relative to the rigidity of the bell. The exception to this result is $\eta_{base} = 10$, which had a low forward swimming speed and small radial displacement. This suggests, along with the applied tension study where $T_{max} = 2000$, that there is a threshold of applied tension that must be produced to generate significant forward motion.

4.3.4 Varying the maximum bending rigidity of the bell

In this study, I wanted to examine the role of the bell's overall flexibility in swimming performance. To do this I varied η_{tot} while maintaining a fixed stiffness for the bell margin. I set the elastic modulus of the bell margin to $\eta_{base} = 30$ and varied the difference of the elastic modulus

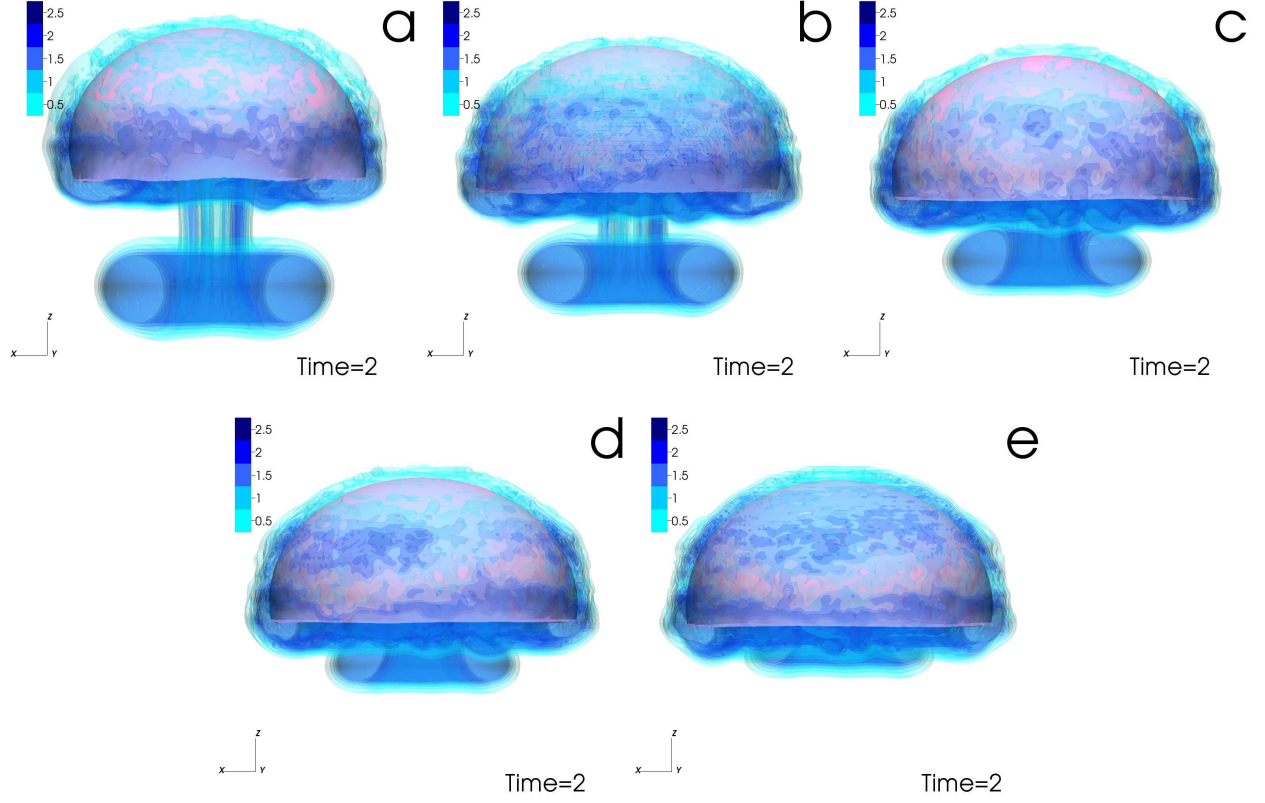


Figure 4.16: Plots of the vorticity magnitude at time=2 with $\eta_{base} =$ a)10, b)20, c)30, d)40, e)50. Note that for $\eta_{base} = 10$, the starting vortex ring is farther from the bell after one propulsive cycle than $\eta_{base} = 20, 30, 40, 50$.

of the top of the bell and the elastic modulus of the bell margin such that $\eta_{var} = 20, 70, 120, 170$. As a result, the top of the bell had a total elastic modulus of $\eta_{tot} = 50, 100, 150, 200$. The magnitude of the applied tension was kept fix amongst the different configurations with $T_{max} = 6000$.

I found that the bell with the lower total elastic modulus had the highest peak velocity during the contraction phase of the bell's propulsive cycle (Fig. 4.20). This peak also corresponded with largest average displacement of the bell radius. During the expansion phase, the bell decelerated but did not fully stop, though the bell did oscillate during the release of the tension. The frequency of oscillation was dependent on η_{tot} , where higher frequency oscillations were associated with the larger elastic moduli. For $\eta_{tot} = 50$, the frequency of bell oscillations were lower during the expansion phase, and the amplitude of oscillation during forward swimming was higher.

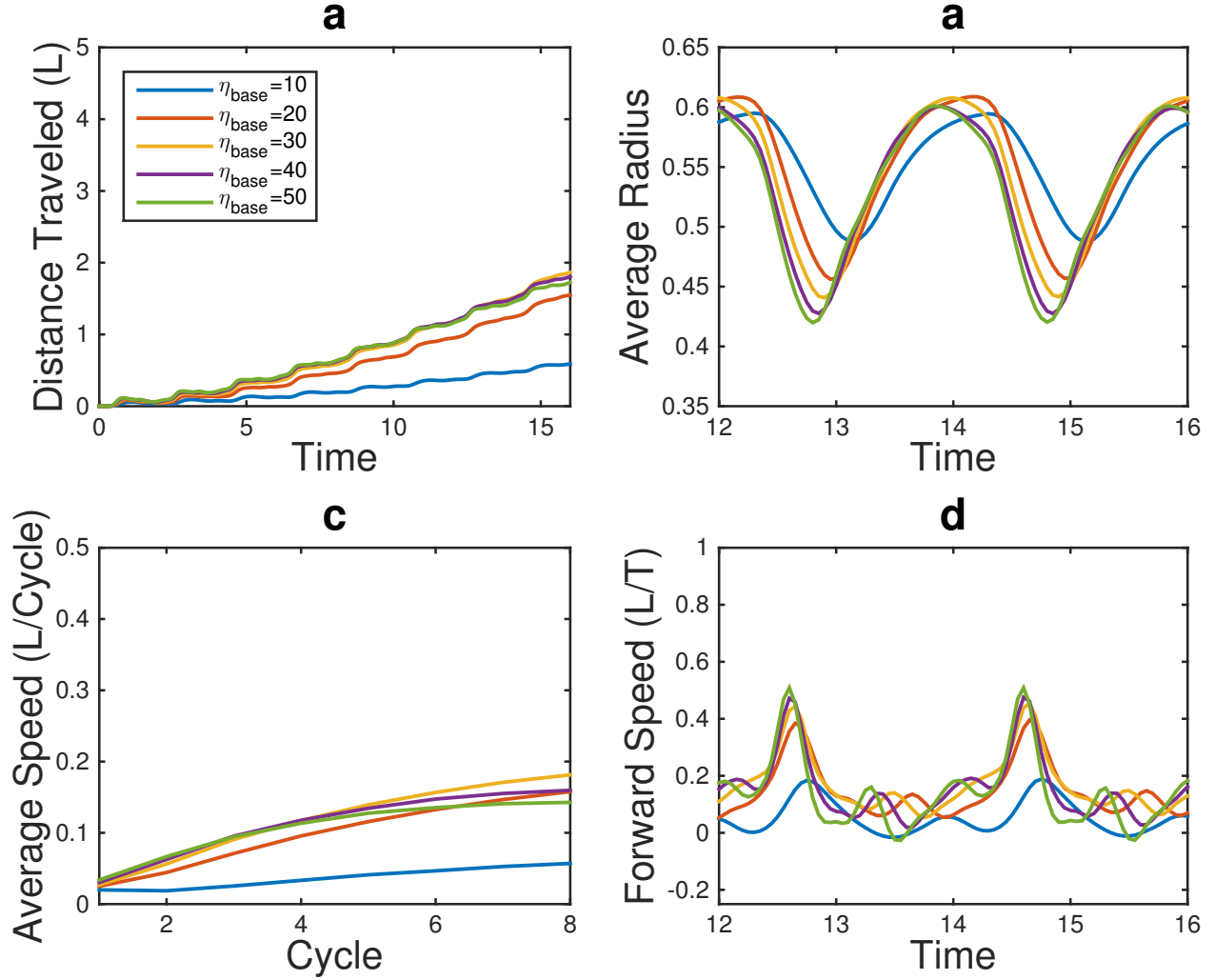


Figure 4.17: Plots for the the varying margin stiffness study of a) the displacement of the bell, b) circumferentially averaged radius during the 7th and 8th propulsive cycle, c) average length traveled per propulsive cycle, and d) forward swimming speed of the bell during the 7th and 8th propulsive cycle. As margin stiffness was increased, the ratio between the amount of applied tension and the elastic modulus was maintained. For $\eta_{base} = 20, 30, 40, 50$, the forward swimming speed between these case remained very similar to one another, even though there were significant differences in radial displacement. The exception was $\eta_{base} = 10$, where the radial displacement and forward swimming speed were much less than the other cases.

4.4 Discussion

In this chapter I have developed a 3-dimensional oblate jellyfish model within the IBFE framework. The forward motion of the bell is driven from the interaction of the material properties of the bell and the interaction with the fluid using a prescribed tension. The location and directionality of this applied tension is prescribed to model the circumferentially oriented subumbrellar musculature.

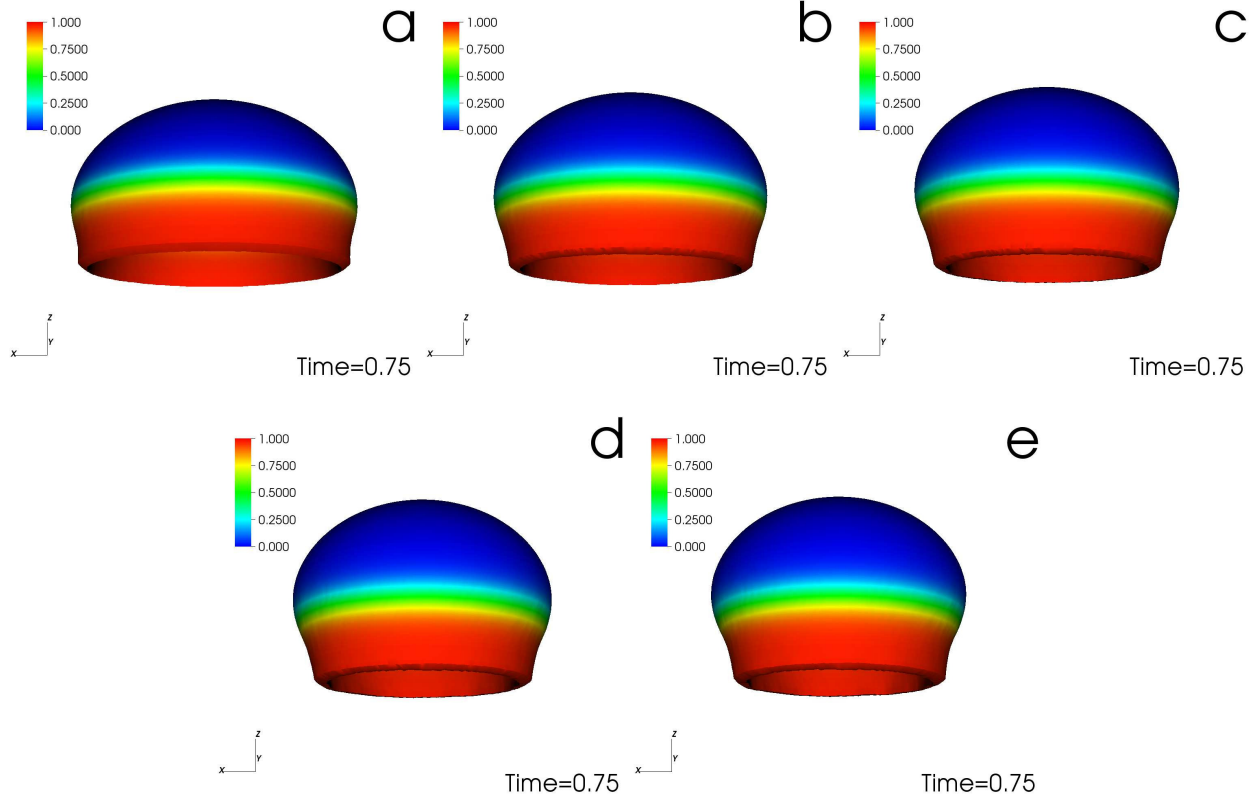


Figure 4.18: The bell during the contraction phase (time=.75) of the bell for $\eta_{base} =$ a)10, b)20, c)30, d)40, e)50, and T_{max} fixed proportionally to the elastic stiffness. The spatial activation of tension is mapped onto the bell. Note that $\eta_{base} = 10$ appears to have contracted significantly less than the other cases.

The passive material properties of the bell were spatially organized to account for a bell margin that has lower bending rigidity than the top of the bell. With the activation of a uniform applied tension at the bell margin, I generated a forward swimming motion for the bell with strong starting and stopping vortex rings.

A theoretical morphospace that included bell shape, a spatially varying bending stiffness, and the strength of applied tension was explored. In the first of the studies, the maximum applied tension was varied while the bell's passive elastic properties were held fixed. As the maximum applied tension was increased, the resulting forward swimming speed increased as well. In the second study, I held the maximum applied tension fixed and varied the bending rigidity of the margin, while also keeping the rigidity of the top of the bell fixed. I found that as the bending rigidity was decreased, the resulting forward swimming speed increased as well. In the third study, I kept the applied tension proportional to the elastic modulus of the bell margin. Both were varied

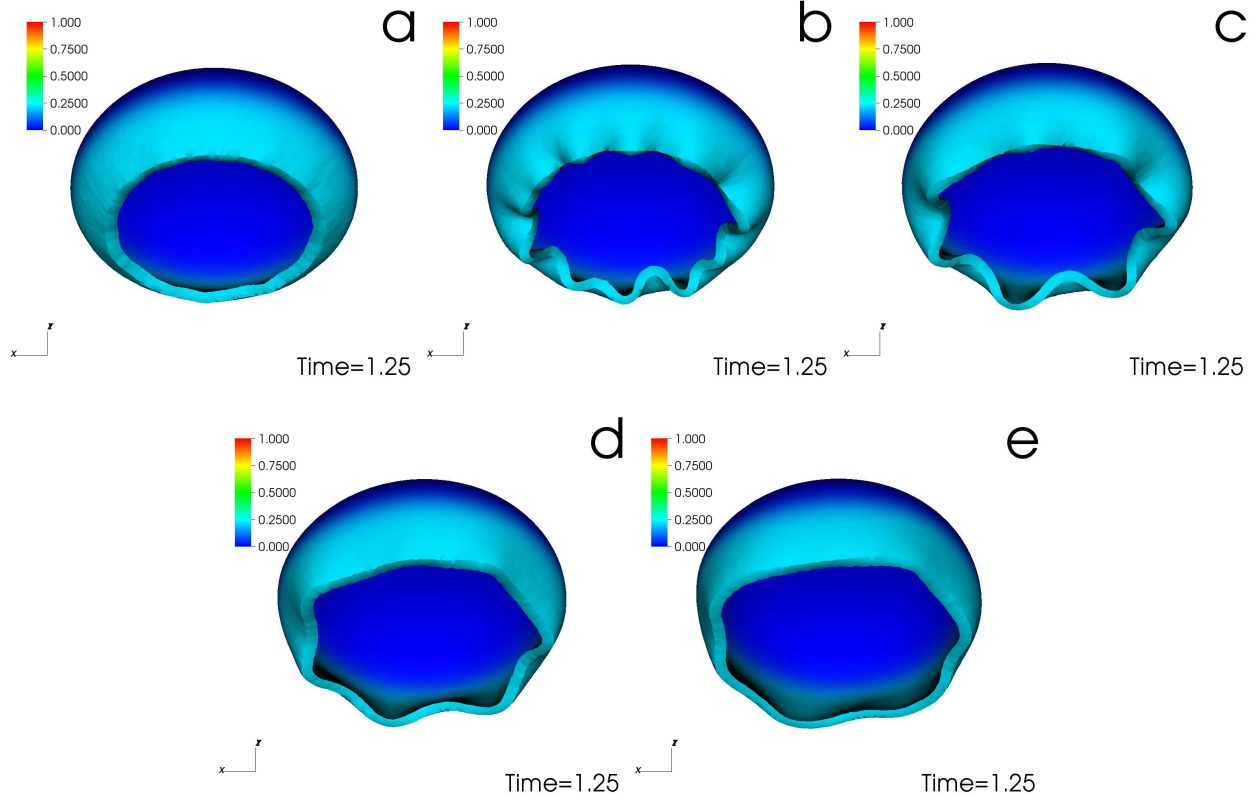


Figure 4.19: The bell during the expansion phase (time=1.25) of the bell for $\eta_{base} =$ a)10, b)20, c)30, d)40, e)50, and T_{max} fixed proportionally to the elastic stiffness. The spatial activation of tension is plotted on the bell is mapped onto the bell. Note that buckling decreases as η_{base} increases, though it also relatively absent for $\eta_{base} = 10$.

proportionally to generate similar deformations. The resulting velocity profiles revealed that bell configurations whose tension was above a threshold had similar swimming speeds. This suggests that forward swimming speed is dependent on the strength of applied tension relative to the rigidity of the bell. In the fourth study, the bell margin and magnitude of maximum applied tension was held fixed and the elasticity of the top of the bell was varied. For the parameter space considered, the most flexible bell top had the fastest swimming speed.

I have thus developed a idealized model for a forwards swimming jellyfish that accounts for some of the observed morphological organization of jellyfish bells. The model bell's elastic moduli span the range of observed in jellyfish. We nevertheless lack measurements of the elastic modulus of the bell margin, as well as how the bell rigidity is organized throughout the bell. Another limitation of these studies is that we ignore the viscoelastic properties of the mesoglea. The addition of a viscous modulus may dampen the oscillations observed during the passive expansion, and lead to more

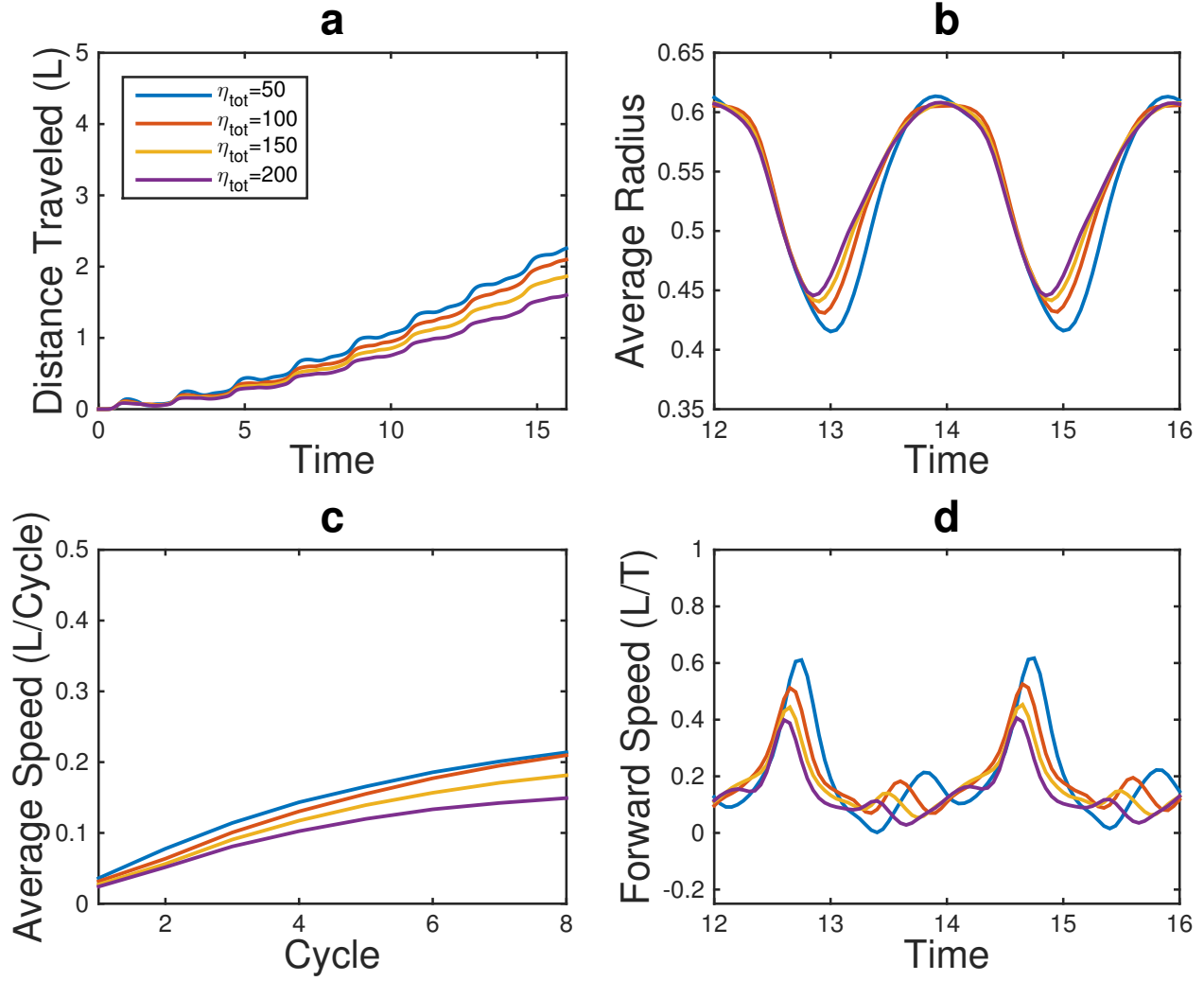


Figure 4.20: Plots for the the varying total stiffness study of a) the displacement of the bell, b) circumferentially averaged radius during the 7th and 8th propulsive cycle, c) average length traveled per propulsive cycle, and d) forward swimming speed of the bell during the 7th and 8th propulsive cycle. As the η_{tot} was increased, the oscillations present in the forwards swimming speed of the expansion altered their frequency and amplitude of oscillation. Note that the radial displacement during the start of contraction is identical among η_{tot} .

agreement between the model and literature.

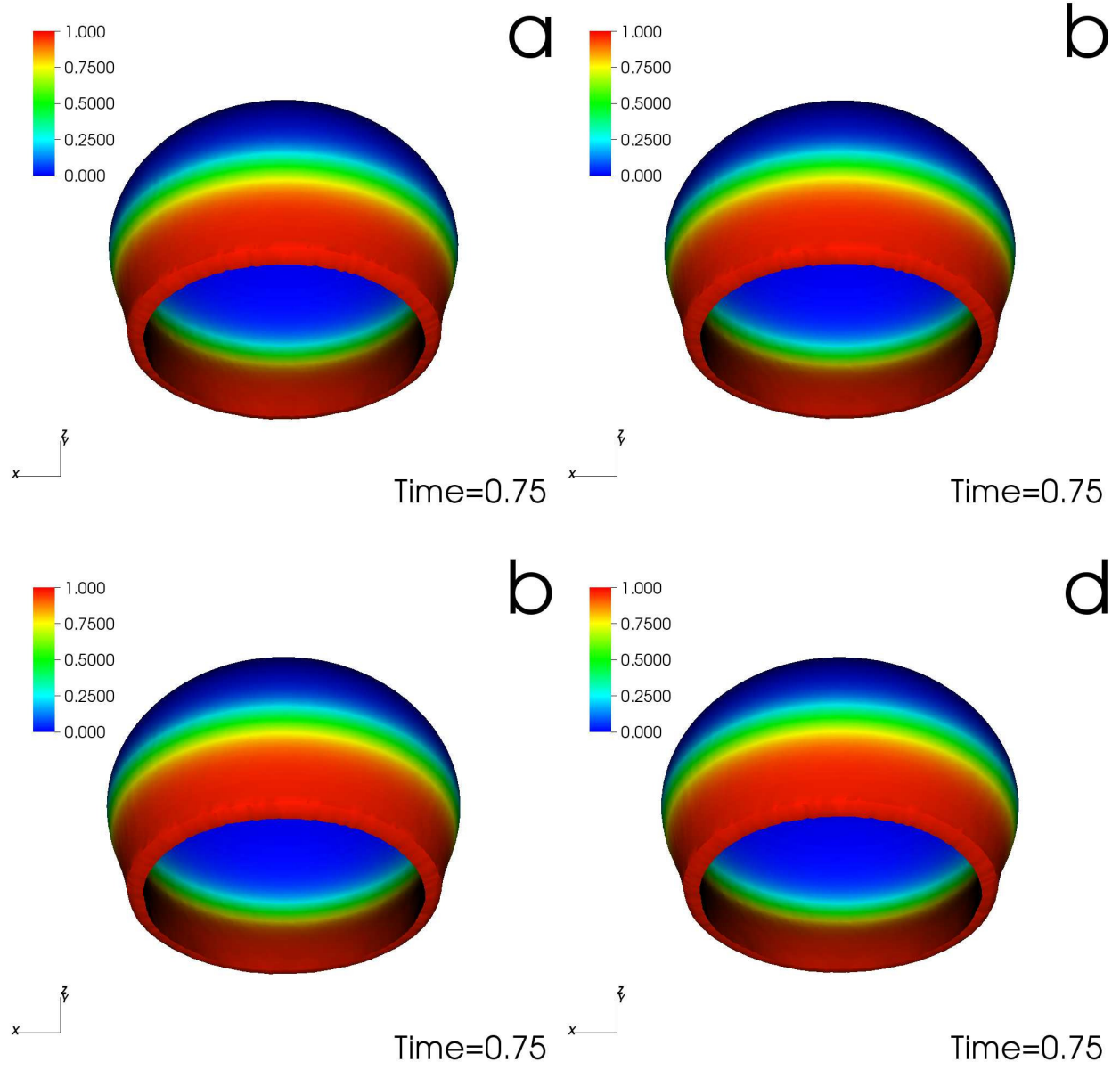


Figure 4.21: The bell during the contraction phase (time=.75) of the bell for $\eta_{tot} =$ a)50, b)100, c)150, d)200 and $\eta_{base} = 10$. The spatial activation of tension is plotted on the bell is mapped onto the bell. Note that contraction appears kinematics appear identical.

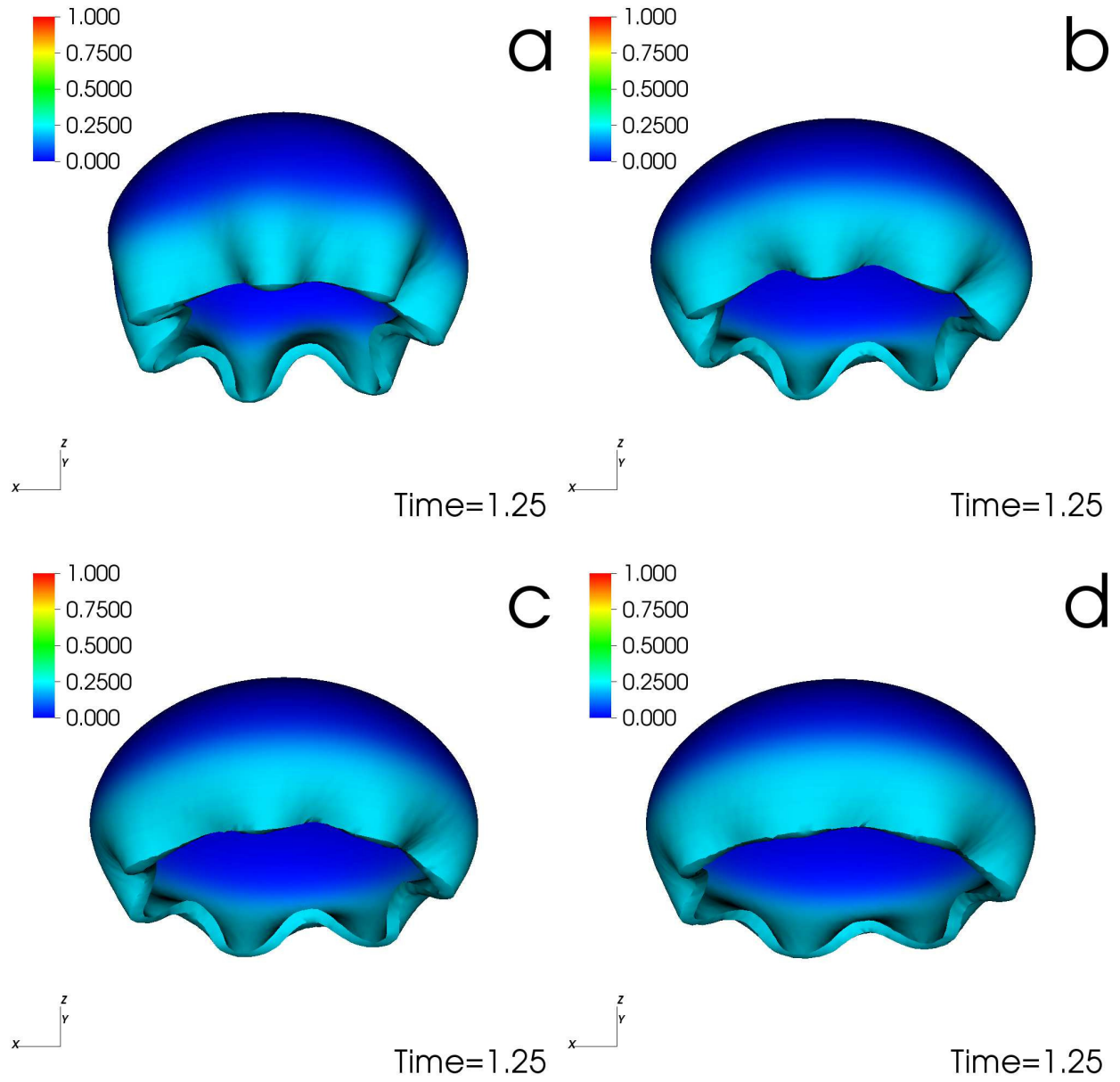


Figure 4.22: The bell during the expansion phase (time=1.25) of the bell for $\eta_{tot} =$ a)50, b)100, c)150, d)200 and $\eta_{base} = 30$. The spatial activation of tension is plotted on the bell is mapped onto the bell. Note that buckling decreases as η_{var} increases, though the buckling pattern is identical.

CHAPTER 5

Scaling limits for paddling swimmers

5.1 Introduction

Aquatic organisms must deal with the viscous and inertial forces of the fluid environment in which they inhabit in order to effectively locomote. As described in Chapter 2, the Reynolds number, Re , allows one to examine the scaling effects present in locomotion by considering the ratio between inertial forces and viscous forces. Re is frequently used when discussing scaling effects in fluid dynamics, where systems with the same Re are dynamically similar. At low Re , flows are reversible and as a consequence reciprocal motions yield no significant net fluid transport or forward movement. This insight into life at low Re was first introduced by Purcell, in a result that is called the Scallop Theorem [75]. Jellyfish also experience this Re limit. Ephyra, the juvenile form of a jellyfish, move at Re of about 5 and can grow into an adult jellyfish that swim at Reynolds numbers of the order of hundreds to thousands [62]. This large range of Re has consequences on the optimal morphology and swimming stroke, particularly for ephyra that move using a drag based motion [35].

Previous work by Herschlag and Miller examined the effects of scaling in jellyfish propulsion, using a series of 2-dimensional immersed boundary simulations that varied the Reynolds number of the system for both prolate and oblate bell geometries [48]. The model showed a significant decline in forward swimming speed for both bell shapes for $Re < 10$. This corresponded with an increase in work required to generate the pulsing motion for $Re < 10$. Although the forward swimming profiles of both bells were in agreement with literature, the vortex dynamics of the oblate bell did not match what had been measured experimentally. This is due to limitations of using a 2-dimensional formulation of the equations of fluid motion to describe the 3-dimensional interactions of the starting and stopping vortex rings. In particular, vortices cannot stretch in 2-dimensions, and the starting and stopping vortex rings of jellyfish are known to stretch. Finally, the radial movement of the bell was prescribed, and further insight based on how elastic properties affect swimming performance

could not be obtained with this model.

In this chapter, I will examine the scaling limits of oblate jellyfish swimming using the model introduced in Chapter 3. Drawing from the Herschlag paper, I will vary Re by adjusting the amount of fluid damping present in the environment to explore a large range of Reynolds numbers, while fixing the passive and active elastic properties of the bell. I will compare the forward swimming performance of the jellyfish at different Re , as well as the cost of transport and work associated with their movement.

5.2 Methods

In this chapter, I use the oblate IBFE bell described in Chapter 4. The geometry, passive and active elastic properties of the bell will be the same as the reference configuration used in the previous chapter. The only difference will be the amount of fluid damping present in the system. In this study I use the frequency based definition of the Reynolds number

$$Re = \frac{\rho f \mathcal{L}^2}{\mu} \quad (5.2.1)$$

where ρ is the fluid density, f the driving frequency, $\mathcal{L}$ is the characteristic length of the structure, and μ is the dynamic viscosity. The amount of fluid damping in the system is adjusted by varying μ and keeping the other parameters fixed. Re is varied from 1 to 5000, with jellyfish swimming occupying the Re range of $Re > 1$ for ephyra to a couple thousand in adult medusae [35, 17].

In this study, the effect of Re on the cost of transport (COT) for jellyfish locomotion are examined. Here the cost of transport is a measure of the energy spent per unit distance traveled. It is often used as a measure of the efficiency of swimming [12, 87, 93]. The COT is averaged for the eighth pulse using the following formula

$$\text{COT} = \frac{1}{N} \sum_{i=1}^N |\mathcal{E}_i| / \mathcal{D}_i^{\text{top}}, \quad (5.2.2)$$

where $\mathcal{E}_i$ is the energy at the i^{th} time step, and $\mathcal{D}_i^{\text{top}}$ is the vertical displacement of the top of the bell from the previous time step. Here $\mathcal{E}_i = |U_i^{\text{rad}}| T_i$, where U_i^{rad} is the radial speed of the margin, and T_i is the active tension at the i^{th} time step. T_i and U_i^{rad} is spatially averaged over the margin

Table 5.1: Table of nondimensionalized, reference parameters for the bell model. The reference values were chosen to roughly approximate swimming in *Aurelia*, and each of the parameters were varied above and below the reference states as specified in each study.

Parameter	Symbol	Value
Elastic modulus (base)	η_{base}	30
Elastic modulus (variation)	η_{tot}	150
Maximum tension	T_{max}	6000
Musculature variable (spatial)	θ_s	350
Musculature variable (activation)	θ_a	16
Musculature variable (release)	θ_r	6
Tension duration variable	τ_{len}	.5 T
Horizontal axis (exumbrellar)	a_{ex}	.6125 L
Horizontal axis (subumbrellar)	a_{sub}	.5925 L
Vertical axis (exumbrellar)	b_{ex}	.5 L
Vertical axis (subumbrellar)	b_{sub}	.35 L
Vertical axis (margin)	b_m	.5 L
Margin length	d	.1 L
Frequency	ω	1/(2 T)

of the bell, defined here as the region where the vertical coordinate of the bell is less than 0.1 L in the reference configuration.

The average work done by the bell per propulsive cycle, $\mathcal{W}$, is also calculated in the following manner

$$\mathcal{W} = \frac{1}{N} \sum_{i=1}^N |\mathcal{D}_i^{rad}| T_i, \quad (5.2.3)$$

where $\mathcal{D}_i^{rad}$ is the radial displacement from the previous time step. The non-dimensional Strouhal number is also examined

$$St = \frac{f \mathcal{D}_{max}^{rad}}{\mathcal{U}_{avg}^{top}} \quad (5.2.4)$$

where $\mathcal{D}_{max}^{rad}$ is the maximum radial displacement, and $\mathcal{U}_{avg}^{top}$ is the average forward velocity during the eighth propulsive cycle. Swimming and flying animals are typically known to have peak propulsive efficiencies within a range of $0.2 < St < 0.4$ [90].

5.3 Results

To compare the relative forward swimming velocity of the bell at different scales, I performed a set of simulations where I varied the Reynolds number. Our reference configuration is at a

Table 5.2: Table of all numerical parameters unless otherwise noted for simulations.

Numerical Parameter	Symbol	Value
Spatial step Cartesian grid	h	$10L/512$
Spatial step Lagrangian grid	ds	$10L/512$
Domain size	-	$10L \times 10L$
Time step	dt	5×10^{-4}
Integer refinement ratio	N^{ref}	4
Maximum number of refinement levels	ℓ_{max}	4
Vorticity magnitude threshold	ω^{Mag}	.06125

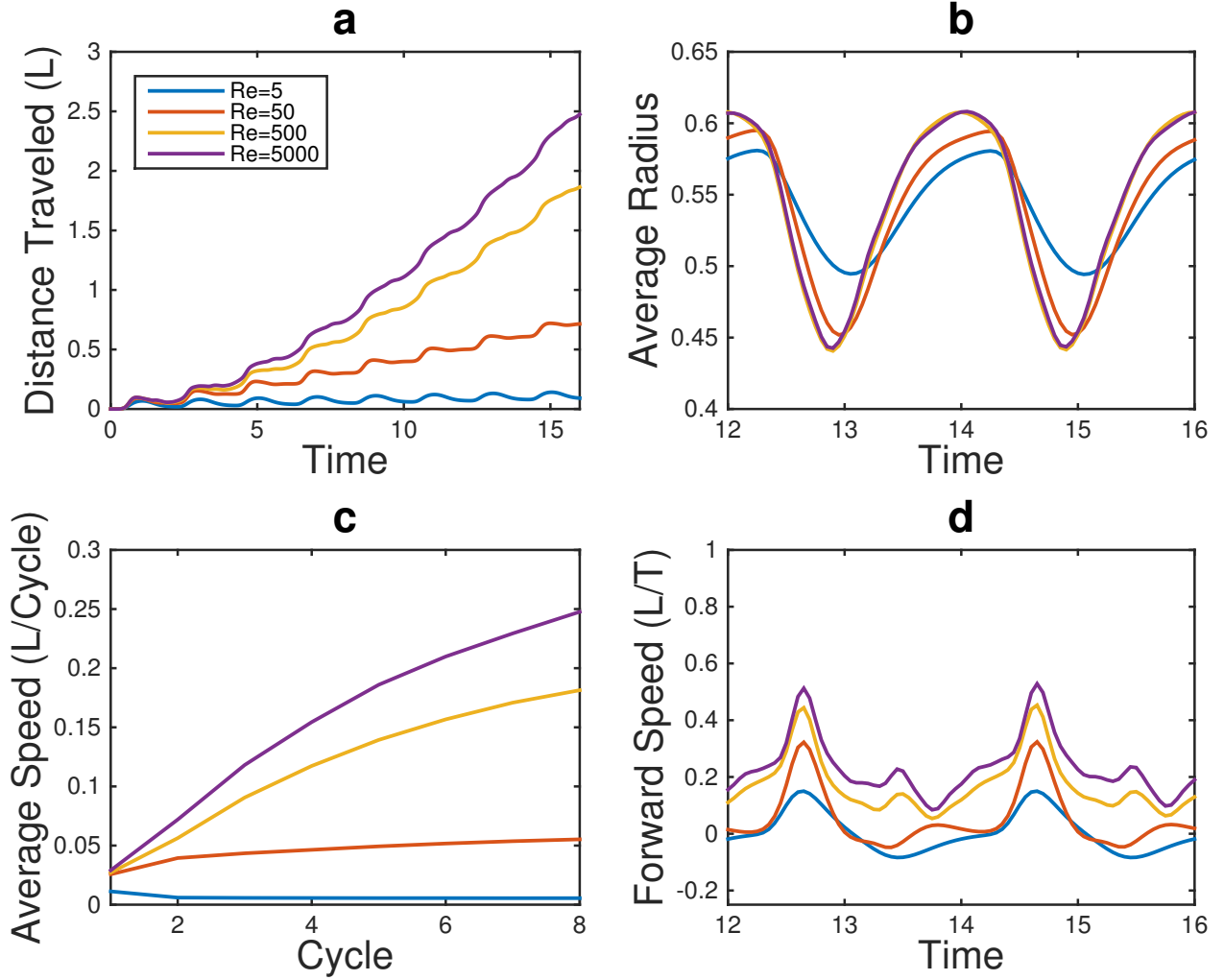


Figure 5.1: Plots for the the scaling study of a) the displacement of the bell, b) circumferentially averaged radius during the 7th and 8th propulsive cycle, c) average length traveled per propulsive cycle, and d) forward swimming speed of the bell during the 7th and 8th propulsive cycle. As the Reynolds number decreased, the forward swimming speed decreased.

Reynolds number of 500 using a frequency based calculation. The Reynolds number was varied, $Re = 1, 5, 10, 50, 100, 500, 1000, 5000$, by adjusting the dynamic viscosity, μ . All other variables

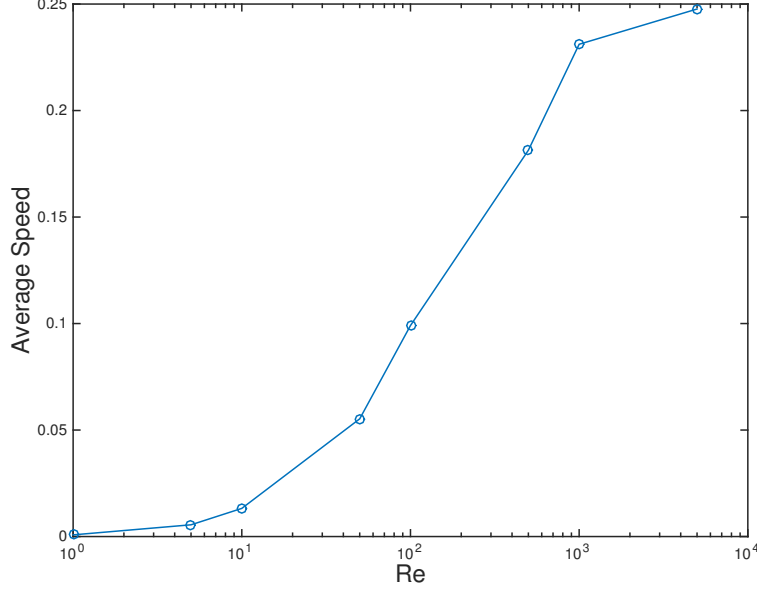


Figure 5.2: The inverted Strouhal number vs. the Reynolds number.

were held the same as our reference configuration. Since length scales are held fixed, I am directly comparing swimming speeds that are equivalent (e.g. the same amount of body lengths per second).

Figure 5.1a shows the distance traveled vs. time for four Reynolds numbers. Notice that for $Re = 5$, the bell moves forwards and then returns almost to its initial position during expansion. At the highest Reynolds numbers, the bell continues to move forward throughout the entire cycle. Fig 1b. shows the average radius of the bell over time. As the Reynolds number increases, the radial displacements of the bell increase until the displacement approaches a limit determined by the material properties of the bell rather than by the viscosity of the fluid. This can be seen by comparing the nearly identical radial displacements of $Re = 500$ and $Re = 5000$. Note that although the averaged radial displacements are similar, the resulting forward swimming speeds are not. At lower Reynolds numbers, effects of fluid damping are evident when comparing the slower expansion of the bell to the faster expansion at $Re = 500, 5000$.

Figure 1c. and 1d show the average speed per cycle and the instantaneous speed as a function of time. Notice that the average speed is slightly negative at $Re = 5$. The average speed increases with Reynolds number, and $Re = 500, 5000$ have not reached periodic steady state even after eight pulse cycles. Oscillations in the forward swimming speed are also observed for the higher Reynolds number cases where there is less damping. These oscillations are likely due to high frequency elastic

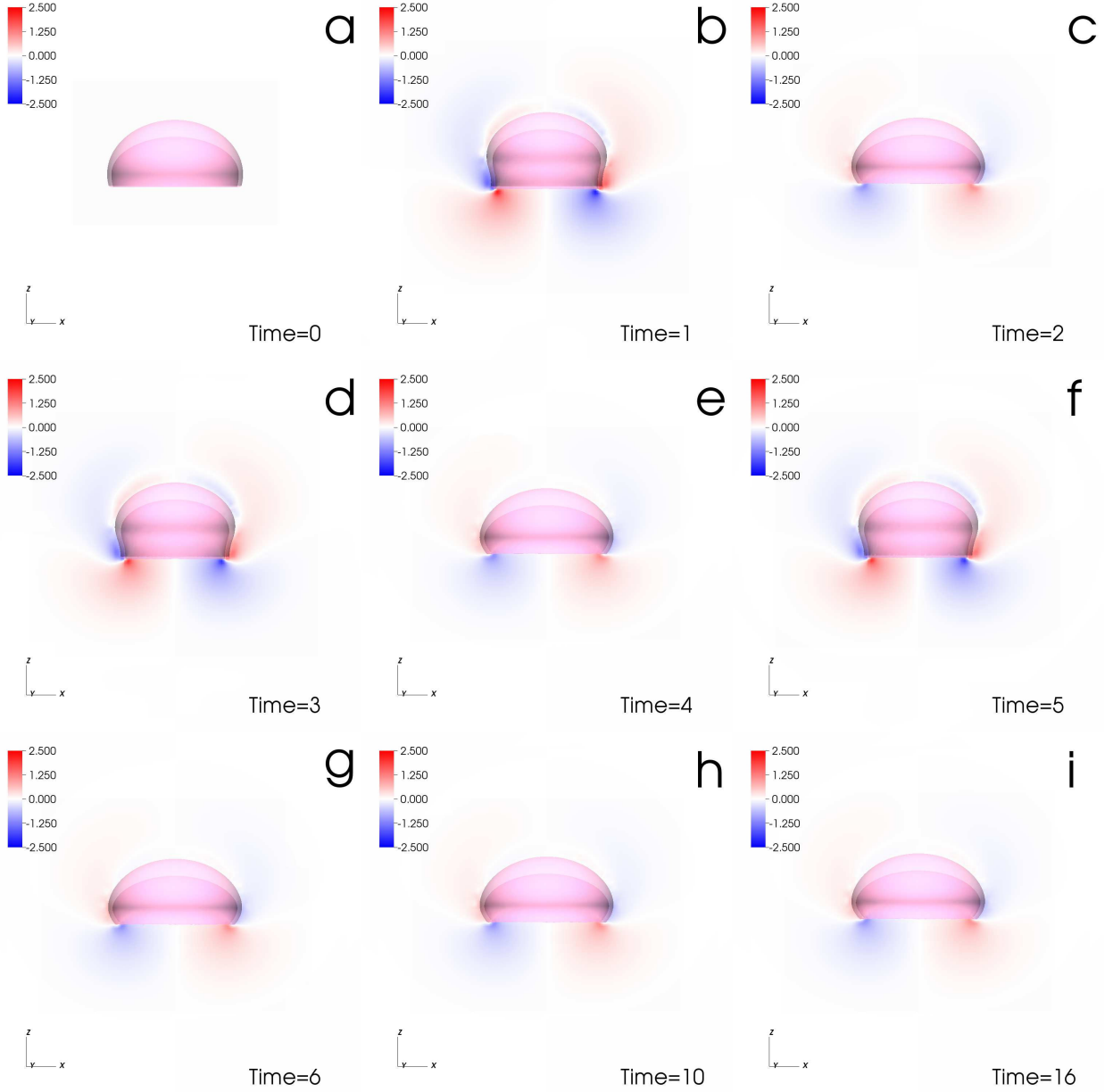


Figure 5.3: Plots of the y-component of vorticity on the XZ plane during the length of the $Re = 5$ simulation at time=a)0, b)1.0, c)2.0, d)3.0, e)4.0, f)5.0, g)6.0, h)10.0 i)16.0.

vibrations of the bell.

During the propulsive cycle of the low Reynolds number simulations, the inertial forces generated during the contraction are nearly balanced by the viscous forces, resulting in minimal forward movement during the expansion phase (Fig. 5.2). This effect can be seen in Fig. 5.3, where the y-component of vorticity at $Re = 5$ shows that although vorticity is generated during the contraction and expansion of the bell, no vortex shedding occurs. The vorticity snapshots of the contraction

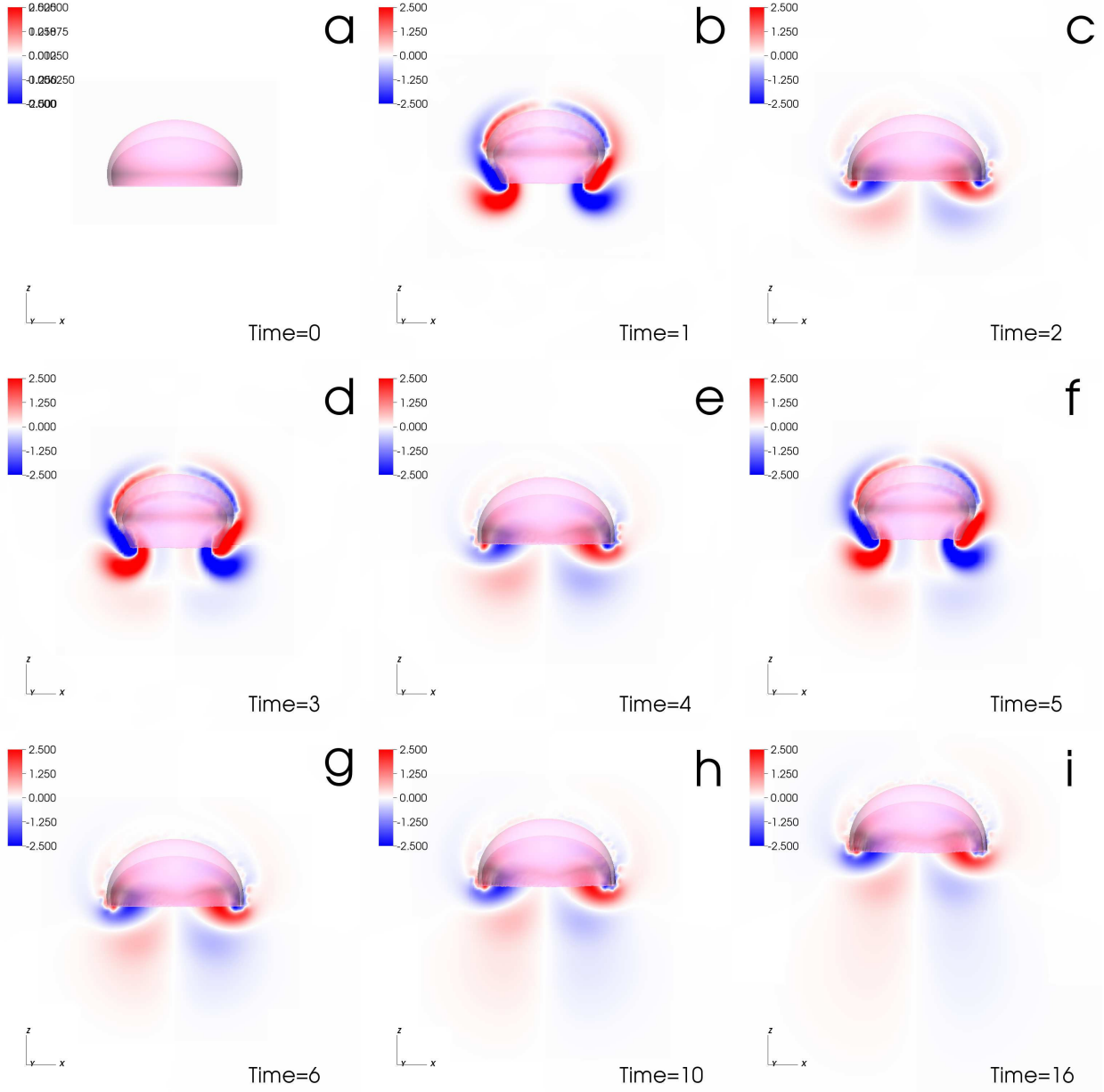


Figure 5.4: Plots of the y-component of vorticity on the XZ plane during the length of the $Re = 50$ simulation at time=a)0, b)1.0, c)2.0, d)3.0, e)4.0, f)5.0, g)6.0, h)10.0 i)16.0.

and expansion phases of the bell show the alternating rotations of the vortices, but note that no vortex separation is evident. The reciprocal bell motion for $Re = 5$ yields no significant forward motion. As Re approached 1, the forward swimming speed was minimal and quasi-reversible over the entire propulsive cycle, which agrees with Purcell's Scallop Theorem [75]. As the Reynolds number increased to $Re = 50$ (Fig. 5.4), the bell generated forward thrust during the contraction phase but had minimal forward motion during the expansion phase. Note that although the starting

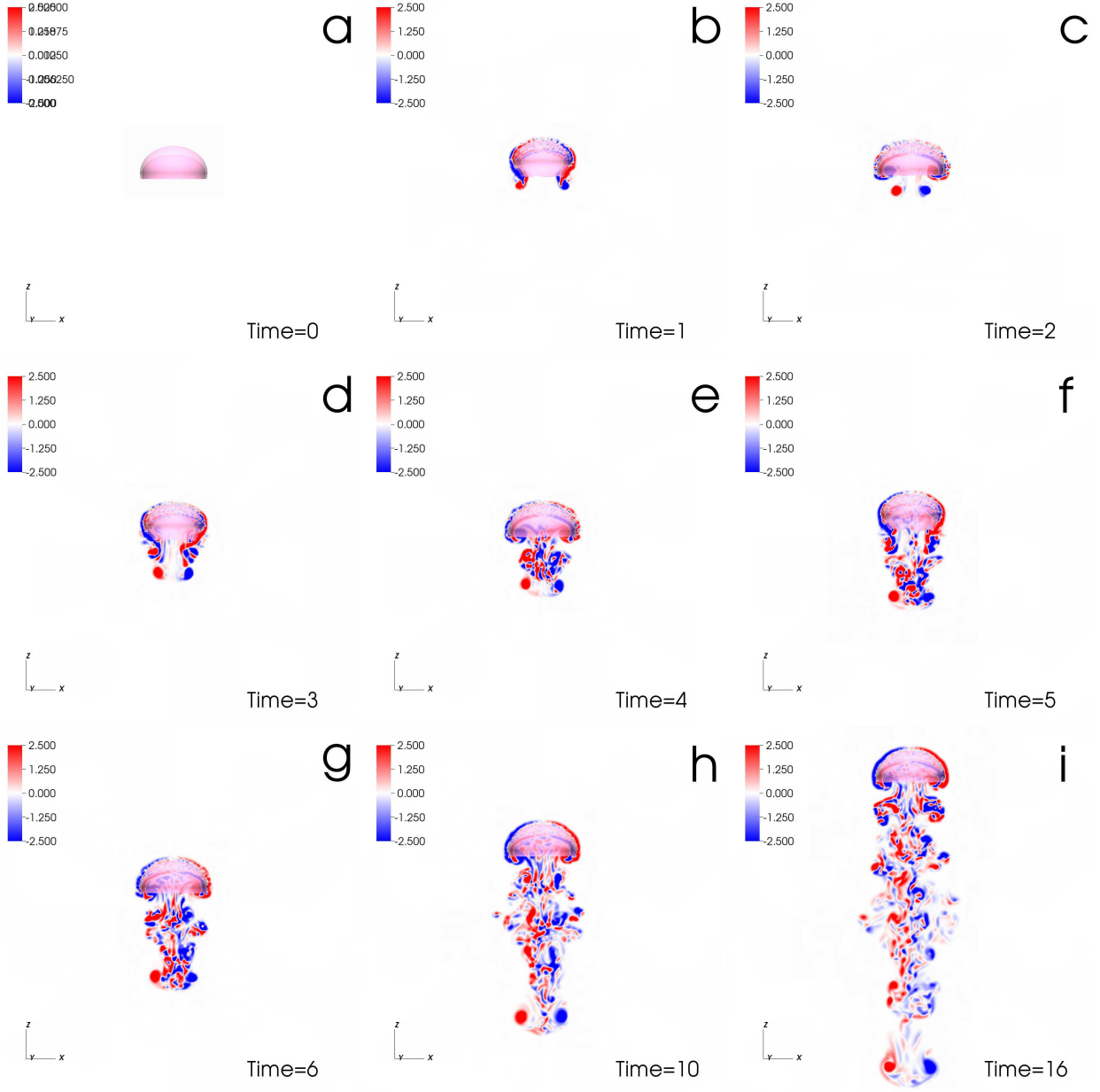


Figure 5.5: Plots of the y-component of vorticity on the XZ plane during the length of the $Re = 5000$ simulation at time=a)0, b)1.0, c)2.0, d)3.0, e)4.0, f)5.0, g)6.0, h)10.0 i)16.0.

vortex contributes to the wake of the bell and the stopping vortex is present in the bell cavity, significant forward swimming speeds only occur during the contraction phase of the bell. The bell ceases to move forward once the contraction phase has ended. Increasing the Reynolds number to $Re = 5000$ (Fig. 5.5) led to increased forward swimming velocities. Also at this high Re , the unconstrained elastic bell margin in part contributed to a more disorganized wake than what was observed at $Re = 500$ (Fig. 4.2). One can see the full transition from low to high Reynolds number

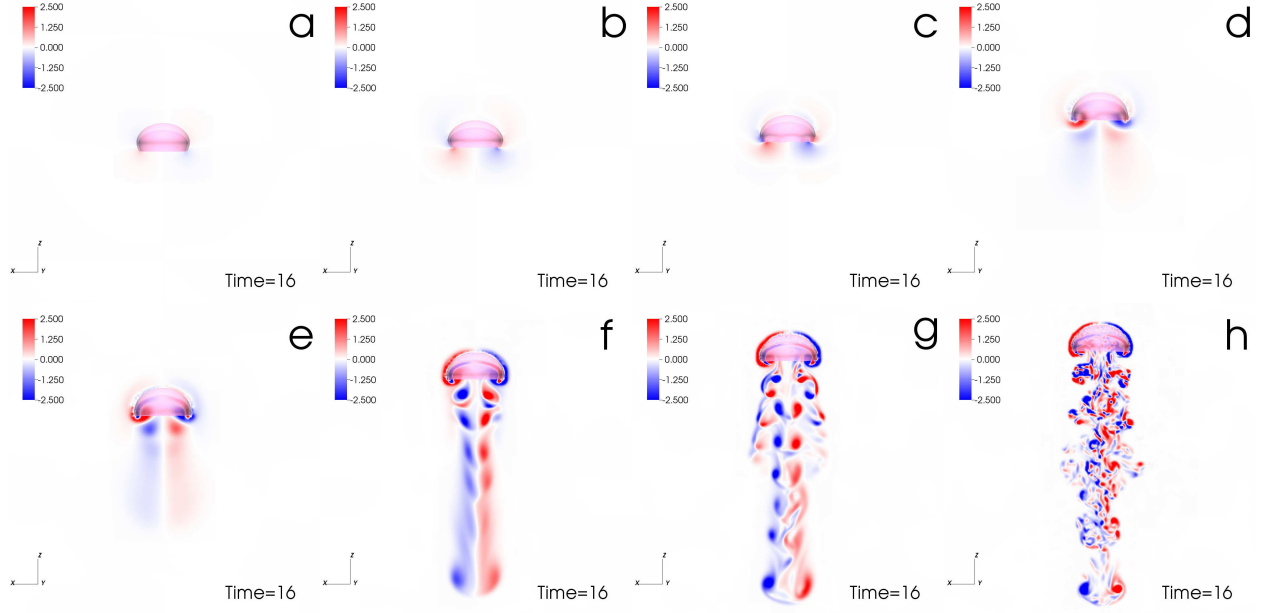


Figure 5.6: Plots of the y-component of vorticity on the XZ plane at time=16 at $Re =$ a)1, b)5, c)10, d)50, e)100, f)500, g)1000, h)5000.

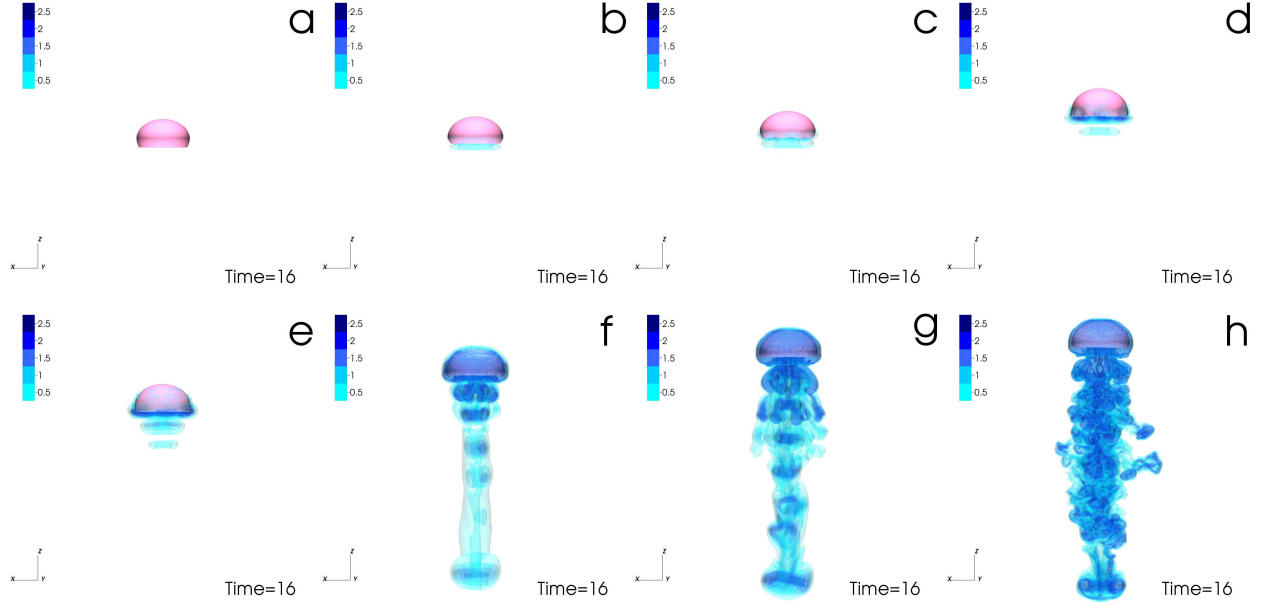


Figure 5.7: Plots of the vorticity magnitude at time=16 at $Re =$ a)1, b)5, c)10, d)50, e)100, f)500, g)1000, h)5000.

swimming after the 8th propulsive cycle in the vorticity plots of Fig. 5.6 and Fig. 5.7.

Fig. 5.8 shows the COT for the range of Re examined in this study. The COT significantly decreases as Re increases before leveling off when $Re \geq 1000$. Examining $\mathcal{W}$ in Fig. 5.9, I find that

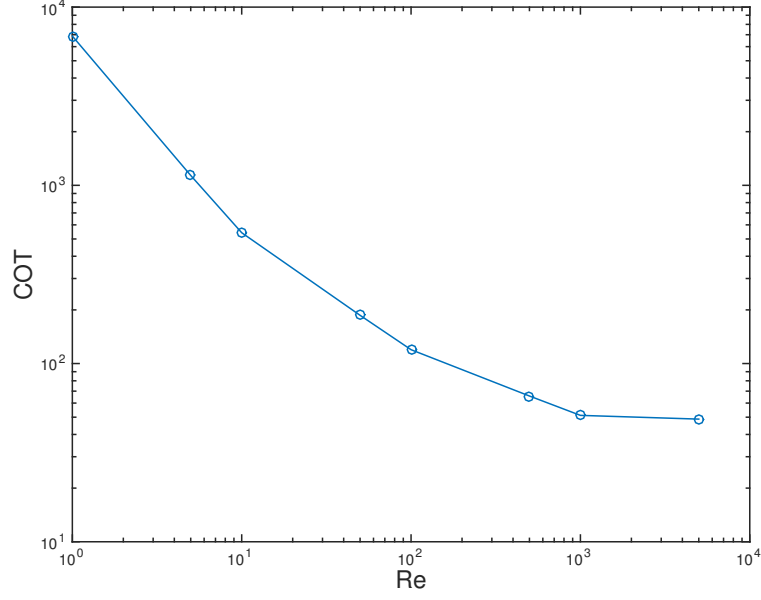


Figure 5.8: Cost of transport (COT) vs. the Reynolds number.

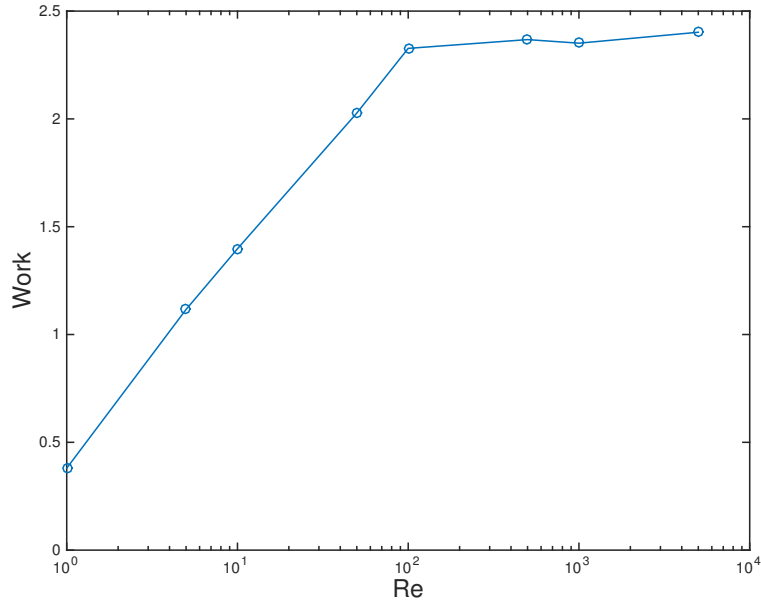


Figure 5.9: Work vs. the Reynolds number.

the work increases as Re increases. This is due to the fact that the bell margin is sweeping through a larger distance for the same given applied tension. As the amount of fluid damping decreases for lower values of μ , the force required to expell fluid from the bell decreases, and the average bell displacement increases. Once $Re \geq 100$, the average bell displacement and the work done plateau for increasing Re . For these Re , fluid damping plays less of a role in reducing the radial displacement of the bell during the propulsive cycle. The inverted Strouhal number, St^{-1} for the range of Re is

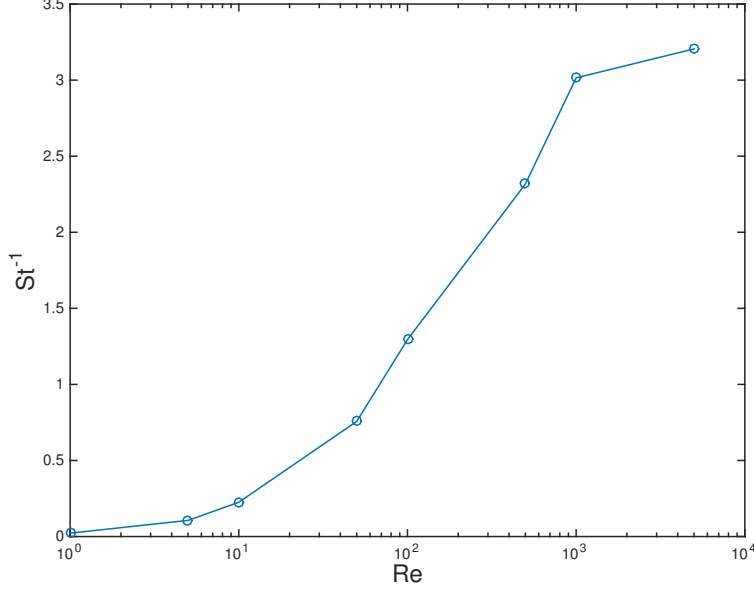


Figure 5.10: The inverted Strouhal number vs. the Reynolds number.

seen in Fig. 5.10. As Re increases, St increases to the optimal range for $Re > 500$.

5.4 Discussion

In order to effectively swim, jellyfish must contend with the viscous and inertial forces in their fluid environment. For low Re swimming, ephyrae employ a drag based stroke. It is possible that the lappets, or the clefts in their bells, allow for a very different swimming style than that of adults. Prolate jellyfish, who typically inhabit a lower Re than oblate jellyfish, use a quick muscular contraction to create a jet of fluid out of their bell and generate forward thrust. As seen in this chapter, oblate jellyfish take advantage of the morphology of their bell and the kinematics of its contraction to achieve sustained swimming in higher inertial regimes. By exploring the scaling limits of paddling propulsion, I examined at what point does this mode of transport become effective. In this chapter, I performed a scaling study on a 3-dimensional oblate jellyfish bell. The elastic properties and size of the bell remained fixed, and the Reynolds number was varied by increasing the amount of fluid damping present in the system. Examining the vorticity plots generated by numerical simulations, I found that the flows generated at $Re = 5$ were nearly reversible and yielded no significant net forward motion. At an intermediate range of $Re = 50$, the bell generated forward thrust during the contraction that was not sustained during the expansion phase of the bell. At

this Re , stopping vortices were present in the bell cavity, and a wake formed from the starting vortices of the contraction phase. A clear and sustained vortex wake due to previous contractions was not apparent. For $Re = 5000$, I found that the jellyfish was an effective swimmer, though the contribution of the asymmetries of the bell distorted the symmetric wake seen in the previous chapter for $Re = 500$. By calculating the energy expenditure per body length traveled at each Re , I found that the cost of transport dramatically decreased as Re increased. I also found that the work done during swimming increased as Re increased. This is due to the fact that the applied tension generated by the bell was held constant, but the distance swept by the bell margin increased with decreasing viscosity. The work done plateaus when the amount of bell contraction is determined by the material properties of the bell rather than by the viscosity of the fluid. Finally, the Strouhal number achieved during swimming approached the peak efficiency range described by Taylor [90] only when $Re > 500$. In this chapter, I performed a scaling study for a model of an oblate jellyfish to understand the scaling limits of paddling propulsion. To further examine how morphology and effective modes of transport are affected by scaling, other geometric and material models should be developed to for ephyrae. This would allow us to understand the effect of Re on juvenile jellyfish as they change over development. Finally, this scaling study only considered oblate bells, and one could extend the model to examine the effects of scaling on prolate jellyfish undergoing jet propulsion.

CHAPTER 6

Jellyfish Inspired Turning Mechanism

6.1 Introduction

In order for an organism to have an effective mode of locomotion, the underlying neuromuscular organization must be capable of controlling maneuverability in a changing environment. In scyphomedusae, the activation and release of muscular tension is governed by the interaction of the pacemakers, located near the rhopalia at the bell rim, with the underlying motor nerve net (MNN) that controls the musculature [85]. The pacemakers fire independently from one another, but are believed to interact via a resetting mechanism when depolarized by a traveling action potential. Under normal forward swimming conditions, where each pacemaker fires at the same intrinsic frequency, this has been shown theoretically to provide a measure of regularity in the swimming gait by decreasing the variance of the activation frequency and interpulse duration [51, 70]. The pacemaker units can respond to environmental cues from the diffuse nerve net and adjust their firing frequency. This distributed control mechanism in turn allows one pacemaker to set the rhythm of the bell's muscular contraction [9]. To induce turning, a pacemaker on the inside of the turn must actively fire and induce asymmetrical contraction, followed by the contraction of the rest of the bell [40]. The role of the diffuse nerve net (DNN) in turning has been examined through the process double innervation, where DNN activity increases the muscular response to activation. This increased response allows for quick and accentuated responses to motor nerve net output, but this phenomena has not been found in all jellyfish, such as *Aurelia* spp [51].

Though there are many numerical studies that model forward jellyfish propulsion, there are few studies of which I am aware that are focused on the solving the fluid-structure interaction during a turn. Numerical simulations have been, however, used to study the fluid dynamics of turning in other organisms. Turning in anguilliform swimmers has been examined by Bhalla et al. using a 2-dimensional eel immersed boundary model with prescribed changes in the preferred body

curvature [15]. Bergmann and Iollo have also examined the fluid dynamics of fish turning using level set based immersed boundary method [13]. Insect flight turning maneuvers have been examined in fruit flies, with 3-dimensional experimental data [14, 79] and computational studies [76]. None of these studies consider how an applied tension can deform and elastic body as it maneuvers in a fluid.

In this chapter, I extend the model presented in Chapter 4 to simulate the turning maneuvers of scyphomedusae by implementing a modified active tension function that allows for asymmetric contraction of the swimming musculature. The active tension function is modified so that a bidirectional wave of tension travels along the bell margin with a fixed circumferential velocity. This in contrast the uniform tension applied in Chapter 4. I then explore the effect of the speed of the activation wave on the resulting turn.

6.2 Methods

In this chapter, I employ a modified version of the IBFE bell described in Chapter 4. The material model, geometry, and passive elastic properties are similar to that previous study, though the active tension function is modified. The activation of the musculature from Eq. (4.2.13) is altered to take into account the angular coordinates of the bell in its reference configuration. Here $\beta(z)$ will remain unchanged from Chapter 4, though $\alpha(t)$ will now be dependent on the angular coordinate, ϑ , determined by $\vartheta = \cos^{-1}(\frac{x}{\|x+y\|})$, where x, y are the coordinates of the bell. The traveling activation wave is parametrized in the following manner

$$\alpha(\vartheta, t) = \frac{1}{1 + \exp(-\theta_a(\tau - v\vartheta/2))} - \frac{1}{1 + \exp(-\theta_r(\tau - v\vartheta/2 - \tau_{len}))} \quad (6.2.1)$$

$$\tau = \omega/2t - \lfloor \omega/2t \rfloor + t_0 \quad (6.2.2)$$

where ω is the frequency of the pulse cycle, t_0 is an offset time for the initial function, θ_a characterizes the initial activation of tension, θ_r characterizes the release of tension, τ_{len} is the length of contraction, and v characterizes the length of time it takes for the activation wave to reach the other end of the bell. Note that we are taking advantage of the $[0, \pi]$ range of $\cos^{-1}(\cdot)$ to model a bidirectional action potential that emanates from the inside of the turn and cancels itself out at the opposite side

Table 6.1: Table of nondimensionalized, reference parameters for the bell model. The reference values were chosen to roughly approximate swimming in *Aurelia*, and each of the parameters were varied above and below the reference states as specified in each study.

Parameter	Symbol	Value
Elastic modulus (base)	η_{base}	45
Elastic modulus (variation)	η_{tot}	180
Maximum tension	T_{max}	15000
Musculature variable (spatial)	θ_s	350
Musculature variable (activation)	θ_a	32
Musculature variable (release)	θ_r	32
Tension duration variable	τ_{len}	.4T
Horizontal axis (exumbrellar)	a_{ex}	.6125L
Horizontal axis (subumbrellar)	a_{sub}	.5925L
Vertical axis (exumbrellar)	b_{ex}	.5L
Vertical axis (subumbrellar)	b_{sub}	.35L
Vertical axis (margin)	b_m	.5L
Margin length	d	.1L
Frequency	ω	1/(3T)
Wave travel time	v	1.0

Table 6.2: Table of all numerical parameters unless otherwise noted for simulations.

Numerical Parameter	Symbol	Value
Spatial step Cartesian grid	h	10L/512
Spatial step Lagrangian grid	ds	10L/512
Domain size	-	10L $\times$ 10L
Time step	dt	5×10^{-4}
Integer refinement ratio	N^{ref}	4
Maximum number of refinement levels	ℓ_{max}	4
Vorticity magnitude threshold	ω^{Mag}	.06125

of the bell due to the normal refractory period of action potentials. This is done in absence of a full electrophysiology model.

6.3 Results

In the simulations that follow, the model and numerical parameters found in Tables 6.1 and 6.2 will be used unless otherwise noted. The bell’s contraction is initiated at $\vartheta = 0$, and an active tension wave travels along the rim of the turn. This traveling wave has a frequency of $\frac{1}{3T}$, which allows the bell return to its resting position after the release of tension. The frequency based Reynolds number for the simulations in this section was set to $Re = 3333.3$.

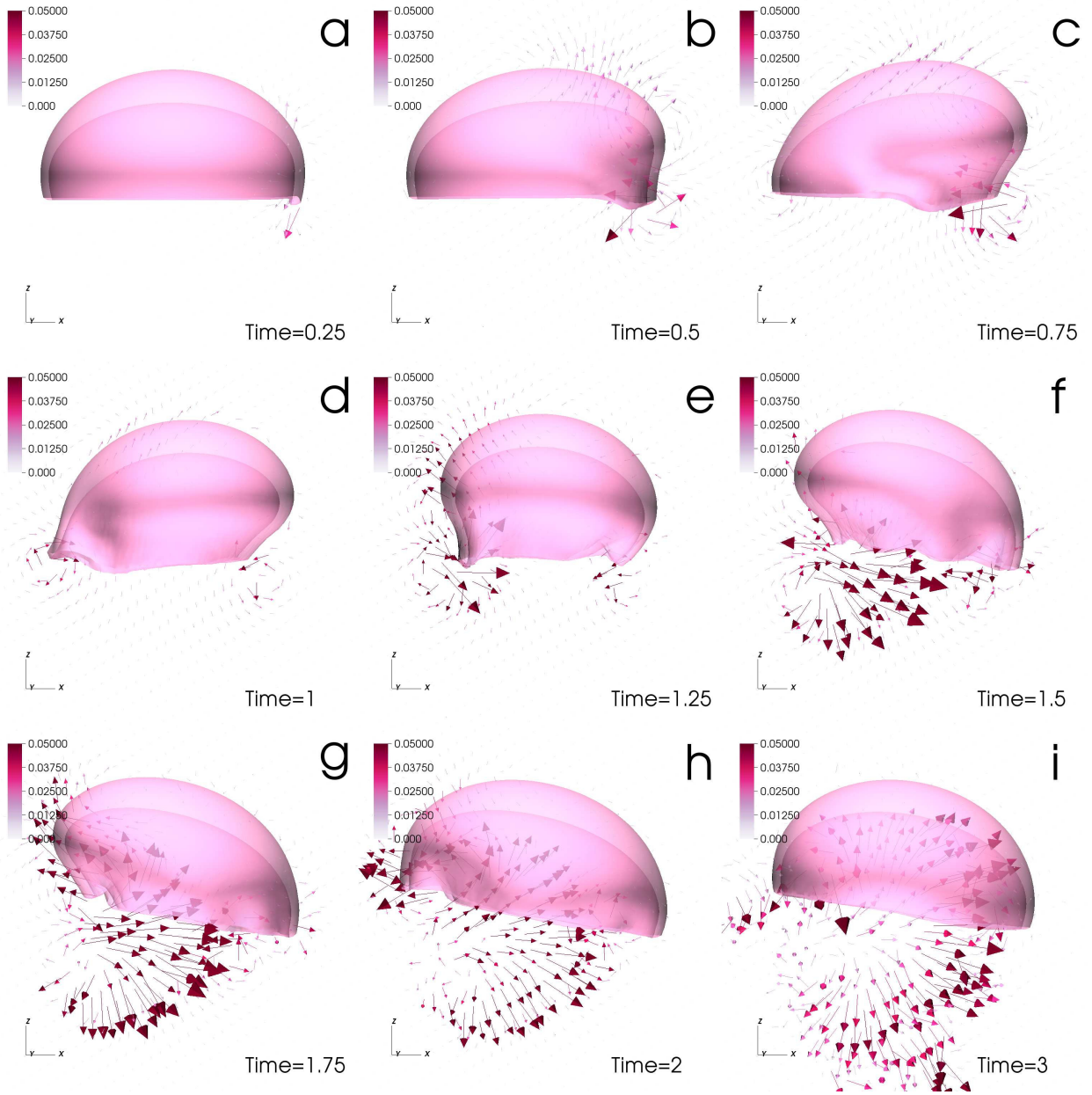


Figure 6.1: Plots of the velocity vectors on the xz -plane during a turning cycle at time= a).25, b).5, c).75, d)1.0, e)1.25, f)1.5, g)1.75, h)2.0, i)3.0 for $v = 1.0$.

Fig. 6.2 shows the jellyfish bell and resulting velocity field during an initial axisymmetric pulse using the reference configuration. The traveling wave of muscular activation begins at the inside of the bell, which is aligned with the positive x -axis, and travels along the bell margin until it reaches the opposite side of the bell. Fig. 6.2 shows the activation wave during the initial axisymmetric pulse. As the activation wave passes along the bell margin the fluid within the bell is forced to the outer side of the bell in the turn, causing this side of the bell margin to hyperextend prior to

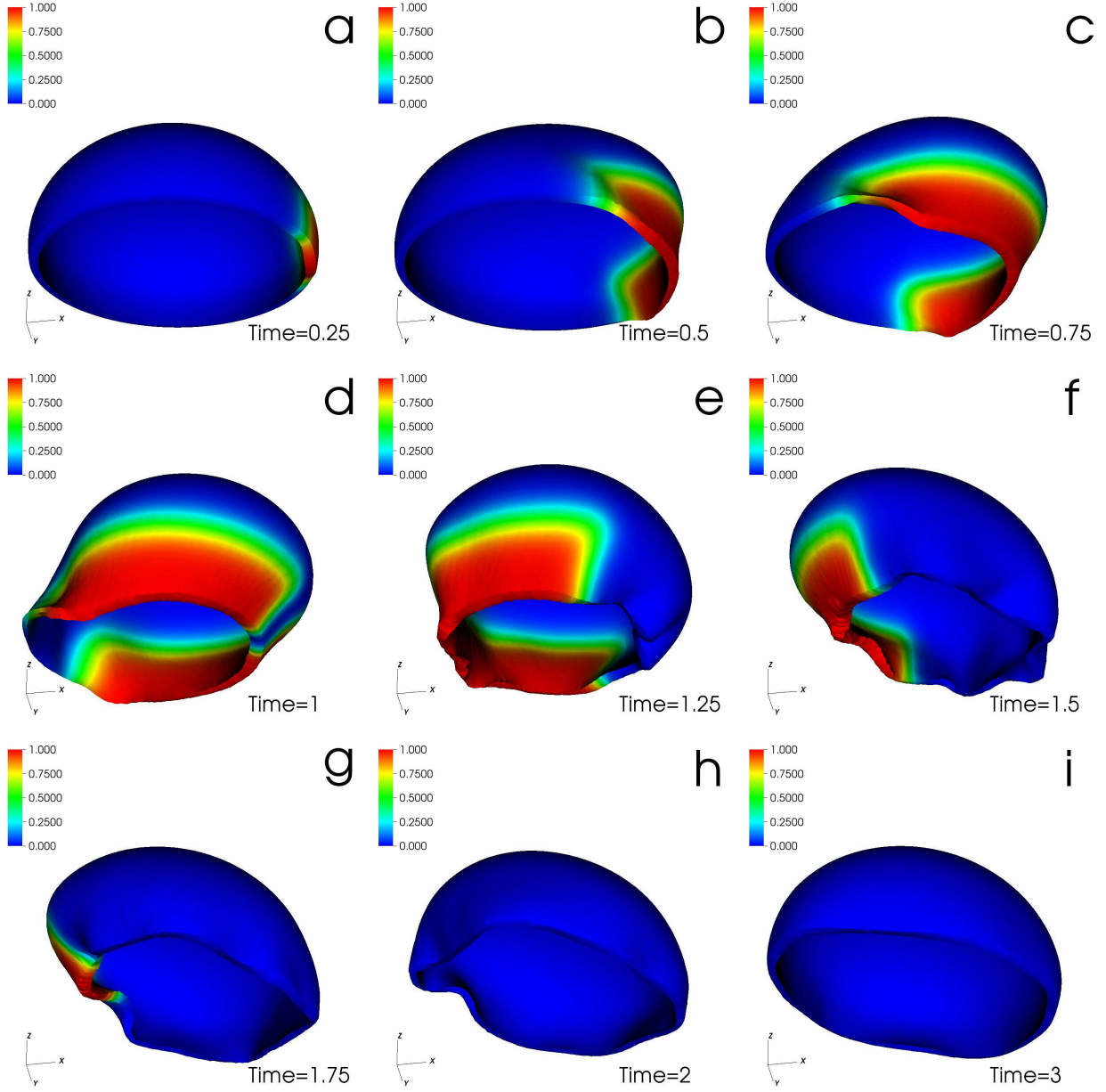


Figure 6.2: Plots of the activation pattern during a turning cycle at time= a).25, b).5, c).75, d)1.0, e)1.25, f)1.5, g)1.75, h)2.0, i)3.0 for $v = 1.0$.

contraction. When the outside of the bell contracts, the margin sweeps through a larger distance which accelerates the fluid towards the centerline and generates a torque that turns the bell.

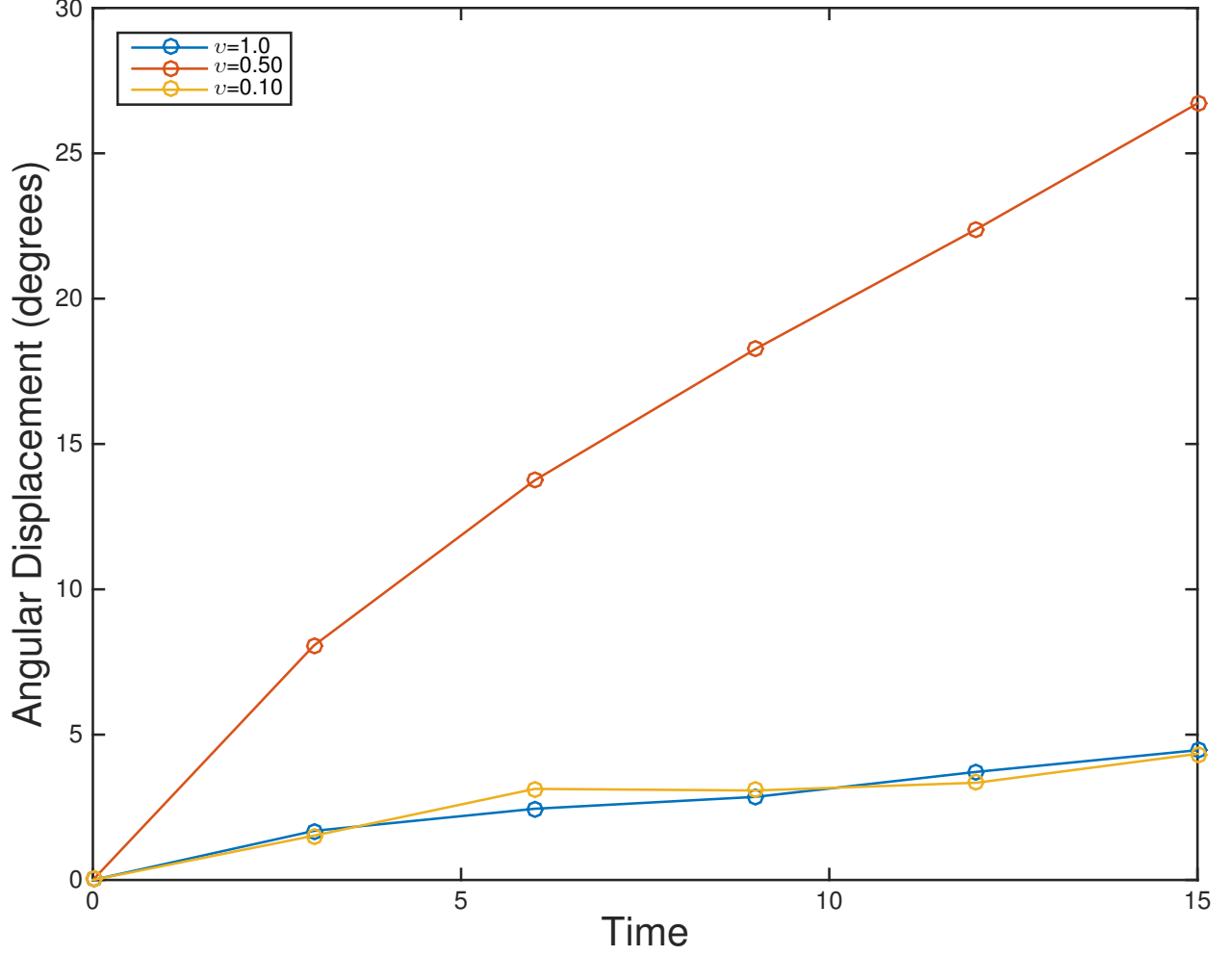


Figure 6.3: Angular displacement of the bell at the end of each turning cycle, using z-coordinate of the displacement between the inside and outside of the turn.

6.3.1 Varying active tension speed

This turning mechanism was explored by varying the speed of the bidirectional contraction wave. The length of time the activation wave took to reach the opposite side of the bell was set with $v = 0.2, 1.0, 2.0$. This range of values allowed us to compare how the reference configuration ($v = 1.0$) performed with respect to faster and slower contraction waves. The contraction wave of the reference configuration takes 1s to go from the inside of the bell to the other side, while for $v = 0.2, 2.0$ the wave will take 0.2s and 2.0s, respectively.

Fig. 6.3 show that neither the slow contraction wave, $v = 2.0$, nor the fast contraction wave, $v = 0.2$, generated significant turns by examining the angular displacement of vertical component between the inside and outside of the turn. The reference case, $v = 1.0$, generated consistent angular

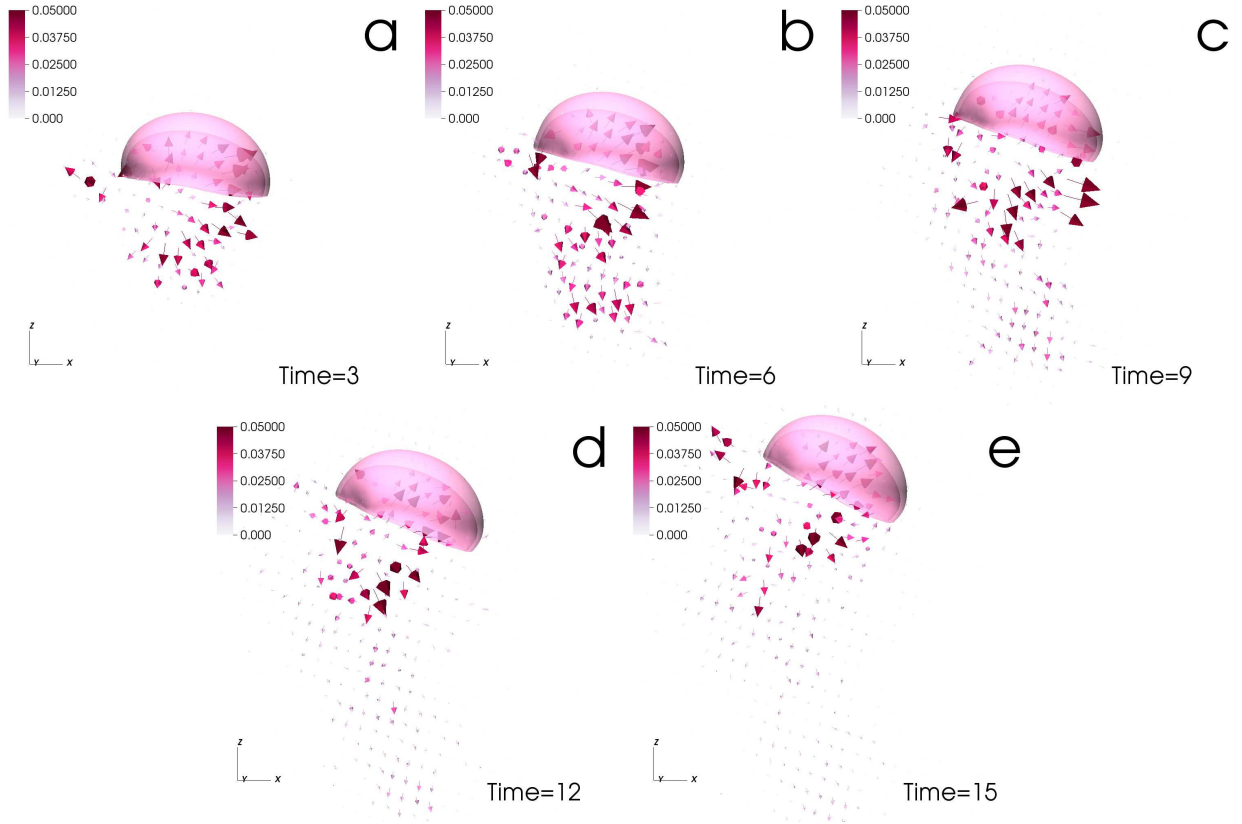


Figure 6.4: Plots of the velocity vectors on the xz -plane after a turning cycle at time= a)3, b)6, c)9, d)12, e)15 for $v = 1.0$.

displacements, such that the bell turned at a consistent angle for each pulse. Snapshots of the flow field at the end of each asymmetric pulse can be seen in Fig. 6.4.

The sequence of Fig. 6.5 shows the activation pattern of the fast contraction wave superimposed on the deformed bell. Absent is the hyperextension seen in Fig. 6.2c,d. The contraction wave reaches the other side of bell quickly and produces flow fields comparable to those seen within the forward swimming jellyfish of Chapter 4. In particular, one can observe well defined starting and stopping vortices. Fig. 6.6 shows the deformed bell and the velocity vector fields for the fast contraction wave, $v = 0.2$, at the end of each asymmetrical pulse. There is a slight angular displacement of the bell initially, but the resulting forward motion enforces the nearly symmetric movement of the bell that hinders any significant additional angular displacement. Note that as $v \rightarrow 0$, the activation function approaches the uniform applied tension function of Chapter 4.

Fig. 6.7 shows the activation pattern superimposed on the deformed bell for the slow contraction wave, $v = 2.0$. Note that this wave speed does not produce sufficient angular momentum during the

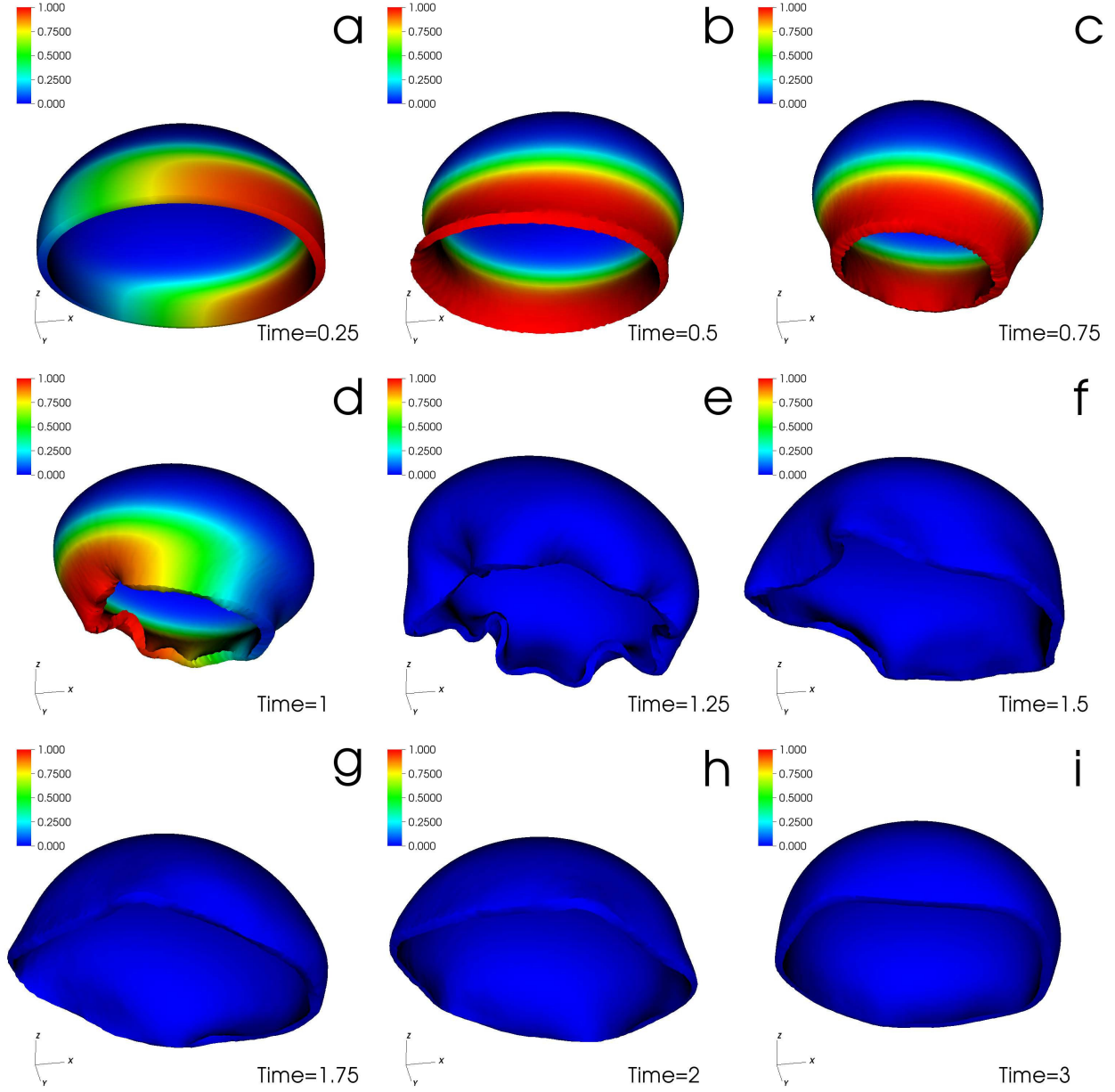


Figure 6.5: Plots of the activation pattern during a turning cycle at time= a).25, b).5, c).75, d)1.0, e)1.25, f)1.5, g)1.75, h)2.0, i)3.0 for $v = 0.2$.

contraction to turn the bell. The slow moving nature of the contraction wave produces negligible asymmetric flow. One can clearly observe a slow moving wave of deformation, but the flows generated are not sufficient to turn the bell. In particular, the bell does not hyperextend as in the reference case. The lack of hyperextension in turn reduces the angular momentum generated during the contraction of this portion of the bell margin. In contrast to the fast moving wave and the reference case, the bell also does not generate significant forward swimming (Fig. 6.8).

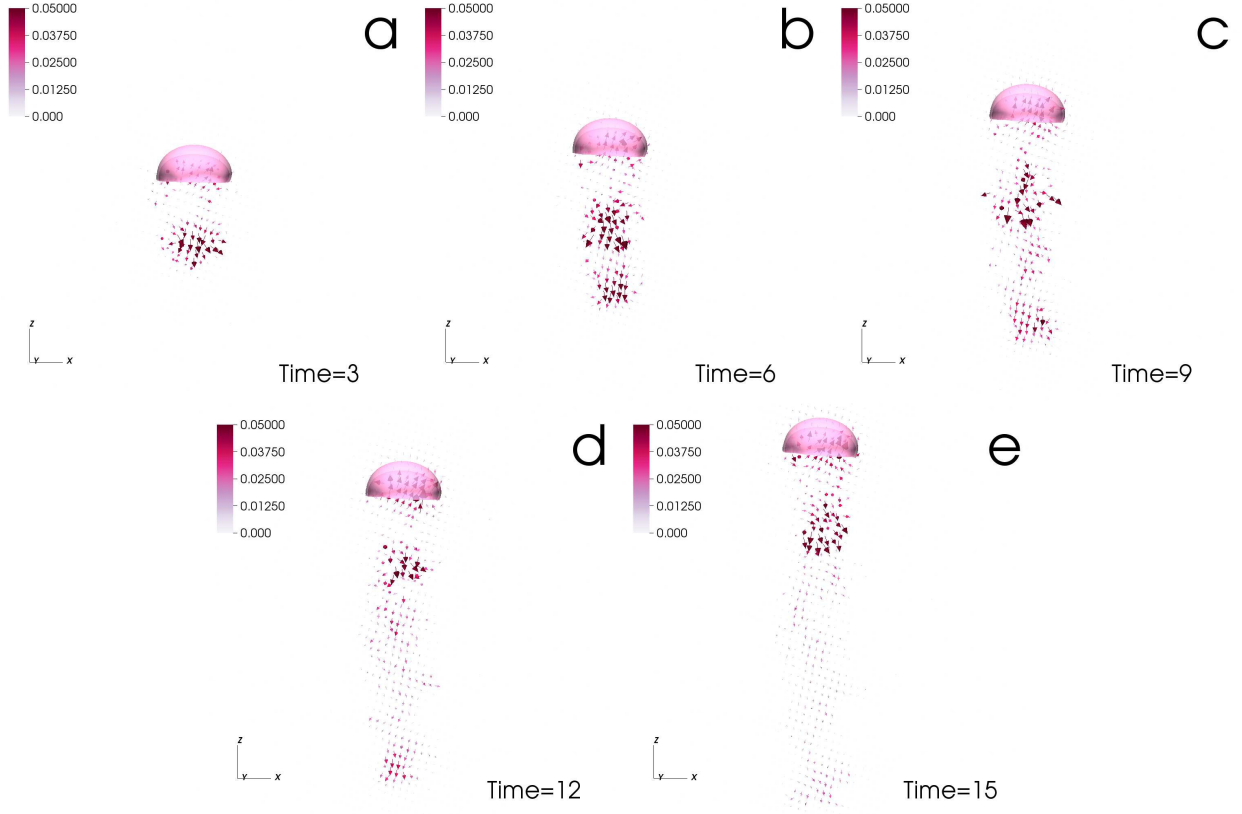


Figure 6.6: Plots of the velocity vectors on the xz -plane after a turning cycle at time= a)3, b)6, c)9, d)12, e)15 for $v = 0.2$.

6.4 Discussion

The capability of controlled turning is necessary for effective locomotion in response to a changing fluid environment. In this chapter I have developed a model for jellyfish turning that is inspired from the scyphomedusaen nervous system. In this model, I applied a traveling wave of tension to the margin of the bell and induced turning purely from the elastic properties of the bell. There were no prescribed kinematics. In the reference configuration, the application of an asymmetric contraction along the bell margin resulted in consistent angular displacement of the bell.

I also examined how the speed of the asymmetric contraction wave affects the resulting turn. I found that for a fast contraction wave, the resulting fluid flow and bell motion resembled the forward swimming jellyfish of Chapter 4. In contrast, the slow contraction wave produced neither significant turning nor forward swimming. This result suggests that the timing of the neuromechanical response and activation could be tuned for particular maneuvers. Furthermore, the elastic properties of the

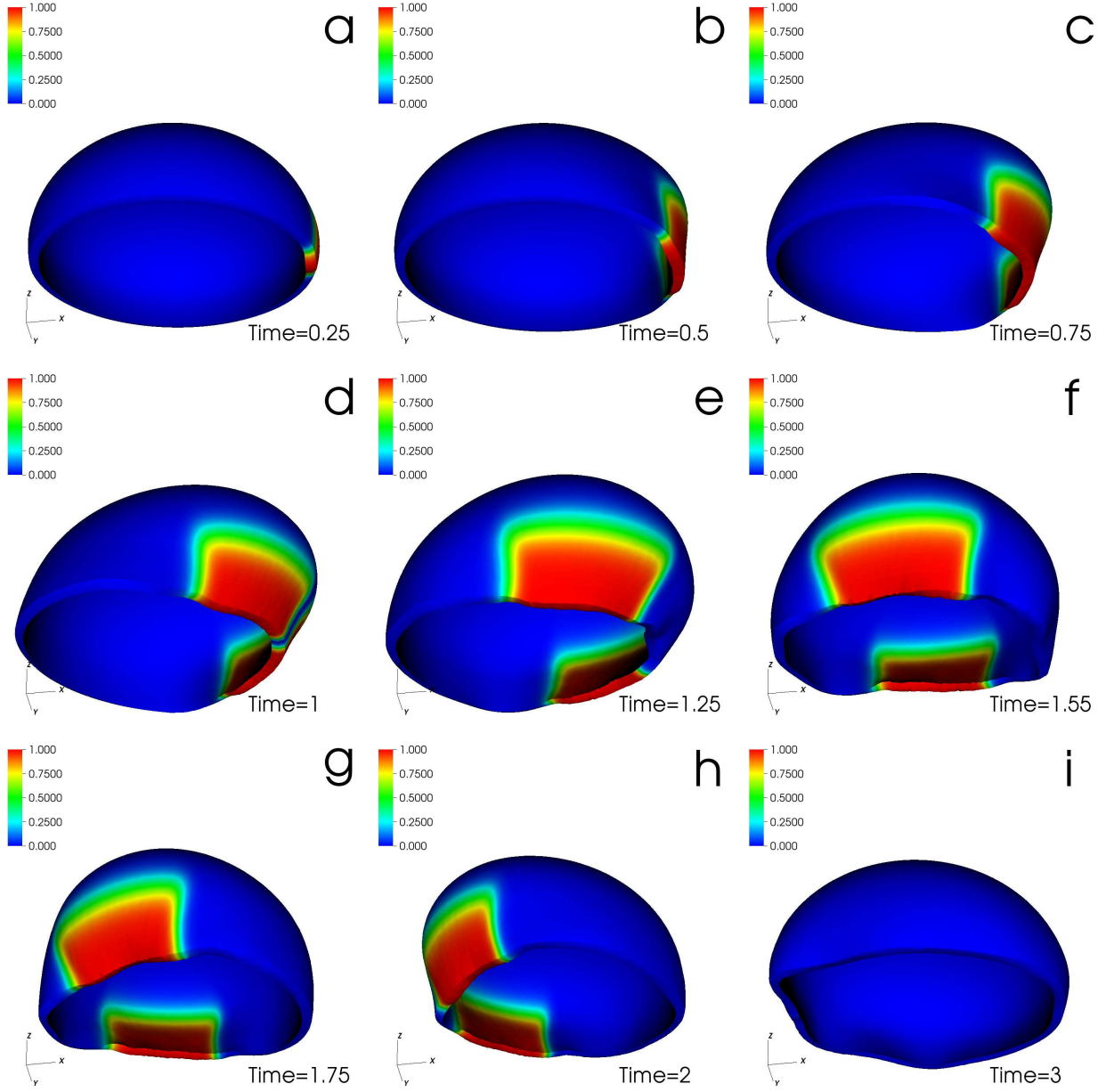


Figure 6.7: Plots of the activation pattern during a turning cycle at time= a).25, b).5, c).75, d)1.0, e)1.25, f)1.5, g)1.75, h)2.0, i)3.0 for $v = 2.0$.

bell coupled with the activation pattern can also affect the dynamics of the turn.

Our model has a few limitations for describing the neuromechanics of turning in actual jellyfish. First and foremost, we have simplified the neuromechanical system with a phenomenological mechanical model. The numerical jellyfish considered here could be extended with the inclusion of a muscle mechanics model to derive the tension. The underlying motor nerve net could also be incorporated using Hodgkin-Huxley type equations. One could also develop additional models that

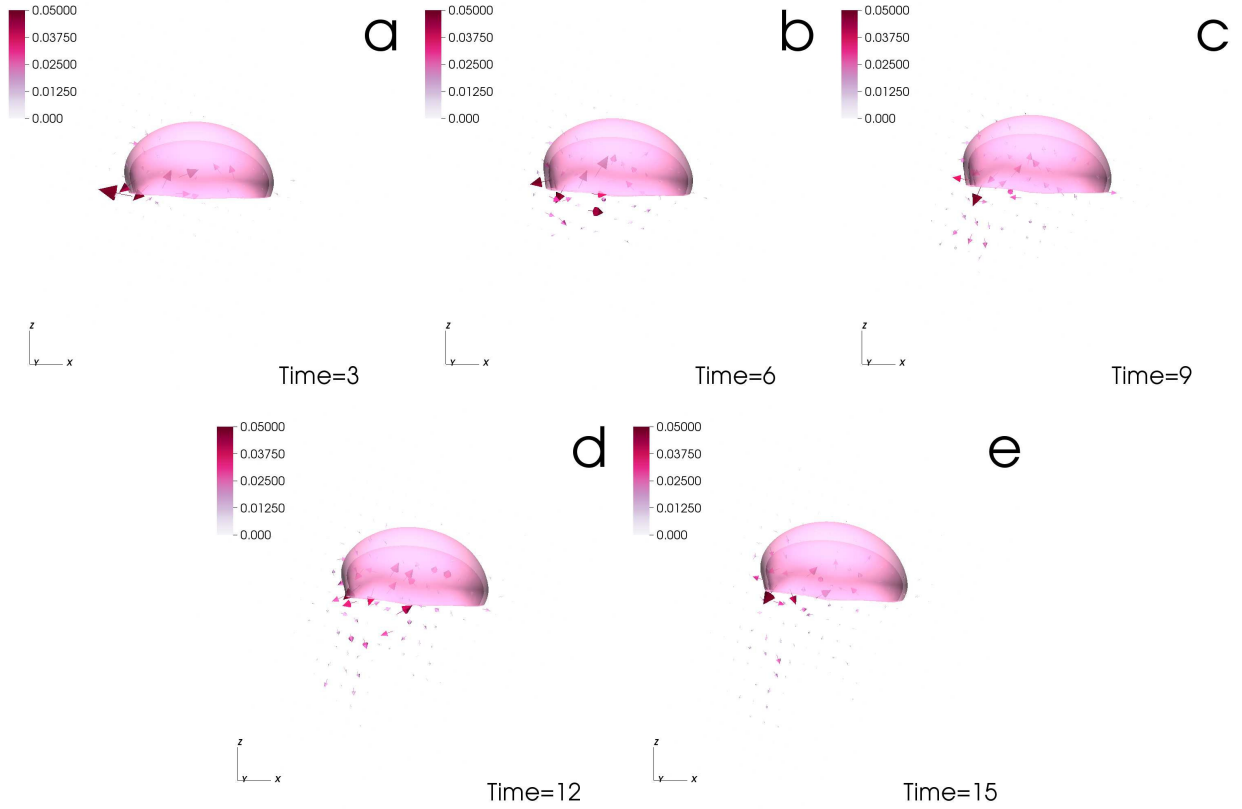


Figure 6.8: Plots of the velocity vectors on the xz -plane after a turning cycle at time= a)3, b)6, c)9, d)12, e)15 for $v = 2.0$.

account for the diffuse nerve net's role in facilitating muscular activation with double innervation. Furthermore, the morphospace (including fineness ratios and material properties of the bell) could be further explored in the context of turning. One possibility would be to vary the location of the applied tension in the bell. Another possibility would be to explore how the duration of the applied tension wave affects turning, with the inside of the turn being held longer than the outside of the turn.

CHAPTER 7

Conclusion

7.1 Conclusions

In this thesis I have introduced a framework for using modern fluid-structure interaction methods to explore the mechanics of an elastic jellyfish swimming through a viscous fluid. Using both the immersed boundary method and a hybrid finite difference/finite element immersed boundary method (IBFE), I have developed models for jellyfish propulsion and explored how the mechanical properties influence the generation of forward thrust and steering maneuvers. By exploring a theoretical morphospace, I can identify the mechanical constraints of this biological system and gain insights for bio-inspired design of underwater vehicles.

After describing in Chapters 1 and 2 the relevant literature and methods used, Chapter 3 presents a collection of studies that explored the effects of resonant driving on a simplified 2-dimensional elastic bell. In this chapter, I first extracted the resonant frequency of the model bell by performing a numerical free vibration experiment. I then drove the deformations of the bell with a sinusoidal force and found that driving the bell near the resonant frequency led to both a higher maximum amplitude of bell oscillation and faster forward swimming velocities. Nonlinear effects were noted when the magnitude of applied force was varied, with the optimal driving frequency shifting to account for added mass and nonlinear elastic properties. Additional fluid damping was introduced into the model to explore the scaling effects on resonant driving. With additional fluid damping, I found that the resonant frequency recorded during the free vibration study shifted to lower frequencies and that the advantage of driving the bell at the resonant frequency was reduced. Lastly, I found that the cost of transport was minimized for driving frequencies below the resonant frequency and increased for driving frequencies near the resonant frequency.

In Chapter 4, I developed a 3-dimensional forward swimming oblate jellyfish model that is implemented in an IBFE framework. With this bell model, I drove the forward motion of the elastic

bell by solely prescribing an applied tension that varied in time. This applied tension was isolated to the bell margin and was bi-directional. Both of these choices were made to approximate the mechanics of real jellyfish. The passive material properties of the bell were spatially organized to simulate a flexible margin with a relatively stiffer top of the bell. I then explored the morphospace by varying the passive elastic properties of the bell and the strength of muscular activation. I found that if the applied tension is varied proportionally with the elastic modulus of the bell margin, then the resulting velocity profiles are comparable. The results from these studies suggest that forward swimming speed is primarily dependent on the strength of applied tension relative to the rigidity of the bell. I also noted that the flexible bell margin enhanced the passive expansion phase as a stronger starting vortex generated continual forward motion.

In Chapter 5, a scaling study was performed by increasing the amount of fluid damping present. and showed a decline in swimming performance for the oblate jellyfish model as the Reynolds number decreases. As the Reynolds number decreased by increasing the dynamic viscosity of the fluid, the average forward velocity of the bell and the amplitude of bell deformation decreased. The cost of transport was examined and it was noted that the cost of transport dramatically decreased as the Reynolds number increased. Similarly the work done by the bell increased as Re increased, until the bell approaches a limit determined by the material properties of the bell rather than by the viscosity of the fluid. In this chapter, I found the Strouhal number approached the peak efficiency range described by Taylor [90] only when $Re > 500$.

In Chapter 6, I extended the model introduced in Chapter 4 to model jellyfish turning, drawing inspiration from the scyphomedusaen nervous system. This was done by applying a traveling bidirectional wave of active tension that allows for asymmetric contraction of the bell. The idea behind the formulation is that a dominant pacemaker drives the muscular response with a bidirectional action potential that travels along the bell margin and produces an asymmetrical muscular contraction. Using the model, I found that, at certain wave speeds, the application of an asymmetric contraction along the bell margin resulted in consistent angular displacement of the bell. If the wave speed was higher, the resulting fluid flow and bell motion resembled that of a forward swimming jellyfish. At slow speeds, the wave produced neither significant turning nor forward swimming. This study underscores the interplay between the timing of the neuromechanical response and the elastic properties of the bell.

7.2 Limitations and future work

In this thesis, I developed 2-dimensional and 3-dimensional models of elastic jellyfish bells to explore the biomechanics of jellyfish locomotion. When comparing the resulting velocity profiles and vortex structures of both models, there is good qualitative agreement with experimental data found in literature [38]. With the simplified 2-dimensional bell model of Chapter 3, I was able to explore a large parameter space of driving force frequencies and magnitudes, while maintaining the fundamental features of the bell structure. The main limitation of this approach is the absence of the vortex rings present in actual jellyfish locomotion, though previous computational studies have shown good agreement between the velocity profiles of prolate jellyfish and their 2-dimensional model counterparts [48].

This limitation is removed with the introduction of a 3-dimensional bell in Chapter 4. In this model, I was able to produce the vortex rings observed in the literature, though the focus shifted to oblate bells. In these studies, I accounted for a spatially varying elastic modulus that was flexible at the bell margin and stiff on top. This model was driven with applied active tension that was circumferentially oriented, as the swimming musculature in jellyfish has been observed to be. Although the spatial organization of the bell's elastic properties and geometry were idealized, I was able to explore fundamental aspects of jellyfish locomotion by varying the theoretical morphospace.

It is important to note, however, that there is much insight to be gained with measurements of the varying elastic and nonlinear properties of jellyfish that elucidate the structural organization of the bell. The elastic moduli used in this work are within the range observed for different jellyfish mesoglea, but measurements of the elastic modulus of the bell margin are lacking. Another limitation is that the viscoelastic mesoglea was modeled as a purely elastic structure taking some viscous properties from the immersed fluid. The addition of a viscous modulus within the bell itself could dampen the oscillations observed during the passive expansion, and may lead to more agreement between my model and observations. A resonance study for the 3-dimensional model would be beneficial to confirm the results observed in Chapter 3. Future work extending this modeling framework to prolate bells would further elucidate the differences in propulsion between paddlers and jetters.

The focus of future work should be directed towards the development of a full neuromechanical

model to drive the bell. The underlying scyphomedusan motor nerve net could be qualitatively modeled using reaction-diffusion electrophysiology models, such as the Hodgkin-Huxley and FitzHugh-Nagumo equations. This in turn could be extended with the addition of a diffuse nerve net model that could account for double innervation and its role in muscle activation. The application of tension to the margin in turn could be simulated using established muscle models, as opposed to the phenomenological active tension functions that describe forward swimming and turning in Chapters 4, 5, and 6. With the inclusion of a neuromechanical model in the bell, one could then further examine the control of muscular activation generated by the pacemaker interactions and their response to environmental cues.

In summary, 2-dimensional and 3-dimensional computational models were developed to explore how elastic properties affect the swimming performance of jellyfish. In both of these models the kinematics of the bell were not prescribed, allowing me to gain insight into the morphological constraints of jellyfish locomotion. By exploring a large parameter space with my 2-dimensional model, I was able to make significant observations about resonant driving. With my 3-dimensional model, a theoretical morphospace was developed and explored, allowing me to discern important factors in forward swimming and turning. Although more accurate structural models would allow me to better understand the mechanical design of jellyfish themselves, the insight gained in this study could be incorporated into the design of biologically inspired devices.

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