Don’t be jelly:
Exploring effective jellyfish locomotion

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Abstract  Jellyfish have been called one of the most energy-efficient animals in the world due to the ease in which they move through their fluid environment, by product of their morphological, muscular, and material properties. We investigated jellyfish locomotion by conducting in silico comparative studies and explored swimming performance in different fluids (e.g., changing viscosities) at different fluid scales (e.g., Reynolds Number), bell contraction frequencies, contraction phase kinematics, as well as bell morphologies and contraction amplitude. To study these relationships, an open source implementation of the immersed boundary method was used (IB2d) to solve the fully coupled fluid-structure interaction problem of a flexible jellyfish bell in a viscous fluid. Complex relationships between scale, morphology, and frequency lead to optimized forward swimming speeds for a particular bell composition, stemming from intricate vortex wake topology, interactions, and fluid mixing. Lastly, we offer an open source computational jellyfish locomotion model to the science community that can be used as a starting place for future numerical experimentation.

Keywords  jellyfish · aquatic locomotion · fluid-structure interaction · immersed boundary method · biological fluid dynamics

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1 Introduction

Scientists have long tried to understand aquatic locomotion in organisms ranging in size and scale from phytoplankton to whales. Oftentimes, an organism’s size and shape dictates what type of locomotive process it uses to move around its fluid environment (e.g., small invertebrates such as ctenophores use ciliary based motion [67], while larger organisms like fish may use fin-based propulsion [1]). One metric that quantifies aquatic locomotion scale is given by the a dimensionless number called the Reynolds Number, $Re$, which can be thought of as the ratio of inertial to viscous forces. It is given by

$$Re = \frac{\rho VL}{\mu} = \frac{\rho f L^2}{\mu},$$

where $\rho$ and $\mu$ are the fluid’s density and viscosity, respectively, $L$ is a characteristic length scale of the problem (e.g., such as the size of a fish fin or ctenophore’s cilia), and $V = fL$ is a characteristic velocity scale, which could be the speed of a fish fin or ctenophore’s cilia during it’s stroke cycle. In the natural environment, although a salt water fish and ctenophore are immersed within approximately the same fluid (e.g., same density and viscosity), they use significantly different mechanisms to move through their fluid environment. Certainly there are evolutionary processes which selected and developed particular locomotive mechanisms. Many such mechanisms are largely based on the size of the organism, e.g., length scale of the problem [86].

Recently, scientists have been trying to understand how jellyfish, the most energy-efficient animals in the world [36], swim. Jellyfish are soft body marine organisms composed of gelatinous bell, tentacles containing nematocists for prey capture, and either 4 or 8 oral arms [46,76]. Their nervous system typically consists of a distributed net of cells, which are concentrated into small structures called rhopalia. There are between four and sixteen rhopalia around the rim of the bell, which coordinate muscular contraction to propel the jellyfish forward [78]. Their relatively simple morphology and nervous systems make them attractive to robotocists [54,31].

Outside of laboratory settings, many computational scientists have developed sophisticated computational models of jellyfish that produce forward propulsion [3,48,51,50,73] and have compared swimming performance over a large mechanospace of bell flexibility, muscular contraction strength, and contraction frequencies [50]. Computational studies are attractive to scientists as it is easier (e.g., more cost and time efficient) to do widespread parameter studies using computational models rather than building many robots or physical models.

In this paper, we will use an open-source implementation of the immersed boundary method, $IB2d$ [7,12,11], to model jellyfish locomotion using a fully-coupled fluid-structure interaction framework. In particular we will expand upon the work of Hoover et al. 2015 [51] and perform comparative studies of jellyfish swimming in different fluids (e.g., changing viscosities), at different fluid scales (e.g., varying Reynolds Number), with varying bell contraction
frequencies, phase kinematics, and amplitudes. We are testing the hypothesis that not only does driving jellyfish bell contractions at their natural (resonant) frequency lead to increased swimming performance (forward speed), but also that this frequency will change depending on length scale of the problem (Reynolds Number, $Re$). Moreover, we posit that varying the contraction (and hence expansion) percentages of the overall contraction period will lead to non-linear behavior at higher $Re$ and that maximal contraction amplitudes leads to increased swimming performance for a variety of bell morphologies. However, all of these are governed by intricate relationships between vortex structure, interactions, and fluid mixing within the jellyfish’s vortex wake, which we will illustrate.

In addition, we offer the science community the first open-source jellyfish locomotion model in a fluid-structure interaction framework. It can be found at https://github.com/nickabattista/IB2d/matIB2d/Examples/Example_Jellyfish_Swimming/Hoover_Jellyfish/.

2 Mathematical Methods

To model a flexible jellyfish bell immersed in a viscous, incompressible fluid, we used computational methods. The mathematical frameworks used to couple the motion of a flexible object and the fluid it is immersed within are called fluid-structure interaction systems (FSI). The first numerical method developed to solve problems in FSI was conceived in the 1970s by Charles Peskin, a mathematical physiologist at the Courant Institute of Mathematics, and is called the immersed boundary method (IB) [70,71,72]. The immersed boundary method has since been improved upon numerous times [27,58,20,41,64,39,38,40] and is still a leading numerical framework for studying problems in FSI due to its robustness [12,11].

It has previously been applied to study problems ranging from cardiac fluid dynamics [61,37,9,8,6] to aquatic locomotion [16,17,45] to insect flight [62,63,53] to dating and relationships [12]. Additional details on the IB method can be found in the Appendix A.

Below we will discuss our jellyfish locomotion model implementation into the IB2d framework, e.g., the computational geometry, geometrical and fluid parameters, and model assumptions. Our model is based off the 2D jellyfish locomotion model of Hoover et al. 2015 [51] whose model was implemented in the IB software called IBAMR [38], which is parallelized IB software with adaptive mesh refinement [15,74,69].

2.1 Computational Parameters

In this study, we use the frequency-based Reynolds number, $Re_f$, to describe the locomotive processes of prolate jellyfish (Sections 3.1-3.3) and comparisons between prolate/oblate jellyfish (Section 3.4). The characteristic length, $D_{jelly}$,
| Parameter                      | Variable | Units       | Value          |
|-------------------------------|----------|-------------|----------------|
| Domain Size                   | $[L_x, L_y]$ | m           | [5, 12]        |
| Spatial Grid Size             | $dx = dy$ | m           | $L_x/320 = L_y/768$ |
| Lagrangian Grid Size          | $ds$     | m           | $dx/2$         |
| Time Step Size                | $dt$     | s           | $10^{-5}$      |
| Total Simulation Time         | $T$      | pulses      | 10             |
| Fluid Density                 | $\rho$   | kg/m$^3$    | 1000           |
| Fluid Dynamic Viscosity       | $\mu$    | kg/(m·s)    | varied         |
| Bell Radius                   | $a$      | m           | 0.5 (and varied) |
| Bell Diameter                 | $D (2a)$ | m           | 1.0 (and varied) |
| Bell Height                   | $b$      | m           | 0.75           |
| Contraction Frequency         | $f$      | 1/s         | varied         |
| Spring Stiffness              | $k_{spr}$| kg·m/s$^2$  | $1 \times 10^7$ |
| Beam Stiffness                | $k_{beam}$| kg·m/s$^2$  | $2.5 \times 10^5$ |
| Muscle Spring Stiffness       | $k_{muscle}$| kg·m/s$^2$ | $1 \times 10^6$ |

Table 1: Numerical parameters used in the two-dimensional simulations.

is set to the bell diameter at rest and the characteristic frequency, $f_{jelly}$, is set to the contraction (stroke) frequency. Therefore our characteristic velocity scale is set to $V_{jelly} = f_{jelly} D_{jelly}$, as in Eq. (1),

$$Re = \frac{\rho f_{jelly} D_{jelly}^2}{\mu}. \quad (2)$$

Fluid parameters (density and viscosity) can be found in Table 1. Note that for our studies in Sections 3.1-3.3, we will vary viscosity, $\mu$ and bell contraction frequency $f$, which will effectively change the Reynolds Number, $Re$ (see Eq. (1)). For our study in Section 3.4, we will vary the bell radius (diameter) and contraction amplitude.

For all studies, the computational width was kept constant as $L_x = 5$. Convergence studies were conducted that demonstrated low relative errors in swimming speeds for domain sizes from $L_x \in [3, 8]$ for $Re = \{37.5, 75, 150, 300\}$, see Figure 26 in Appendix C. In all cases, a similar trend was observed where narrower computational domains lead to slightly decreased forward swimming speeds while qualitative differences vortex formation were minimal, see Figure 27 in the same appendix. Additional grid resolution convergence studies were performed in Battista et al. 2019 [10] using the same computational model of a 2D jellyfish that demonstrate appropriate error tolerances for the numerical parameters described in Table 1.

2.2 Jellyfish Computational Model

The geometry is composed of a semi-ellipse of semi-major axis, $b = 0.75$, and semi-minor axis, $a = 0.5$, see Figure 1 for Sections 3.1-3.3. In Section 3.4, the semi-minor axis, $a$, is varied along with contraction amplitude. As shown, it is composed of discrete Lagrangian points that are equally spaced a
Don’t be jelly: distance $ds$ apart. We note that this Lagrangian mesh is twice as resolved as the background fluid grid, e.g., $ds = 0.5 dx$.

![Diagram of Jellyfish Model Geometry](image)

Fig. 1: Jellyfish model geometry composed of discrete points is a semi-elliptical configuration. The points are connected by virtual springs and virtual beams in the IB2d framework.

Although we view the jellyfish as being immersed in the fluid, the jellyfish (Lagrangian grid) and fluid (Eulerian mesh) only communicate through integral equations with delta function kernels (see Eqs. (12)-(13) in Appendix A for more details.) In a nutshell, the Lagrangian mesh is allowed to move around and change shape and as an observer we can see the motion of the body. On the Eulerian mesh we are only measuring what is happening in the fluid (velocity, pressure, external forcing) at discrete rectangular lattice points. In the latter, it is as though we have a number of measurement tools that are only checking the fluid at the locations the tools are placed; we are not tracking individual fluid blobs. The integral equations with delta function kernels simply say that the fluid points (on the rectangular Eulerian mesh) nearest the jellyfish (on the moving Lagrangian mesh) feel the movement of the jellyfish the most (via a force), as compared to locations in the fluid grid far away (Eq. (12)). A similar analogy describes how the jellyfish feels the effect of the fluid motion by the fluid grid points nearest the jellyfish (Eq. (13)).

Successive points along the jellyfish are connected by virtual springs and virtual (non-invariant) beams in the IB2d framework, as illustrated in Figure 1. Virtual springs allow the geometrical configuration to either stretch or compress, while virtual beams allow bending between three successive points. When the geometry stretches/compresses or bends there will be an elastic deformation force arise from the configuration not being in its preferred energy state, e.g., its initial configuration.

These deformations forces can be computed as below,

$$F_{spr} = k_{spr} \left( 1 - \frac{R_l(t)}{||X_A(t) - X_B(t)||} \right) \cdot \left( x_A(t) - x_B(t) \right) \cdot \left( y_A(t) - y_B(t) \right)$$

(3)

$$F_{beam} = k_{beam} \frac{\partial^4}{\partial s^4} \left( X_C(t) - X_{con}(t) \right),$$

(4)
where $k_{spr}$ and $k_{beam}$ are the spring and beam stiffnesses, respectively, $R_L(t)$ are the springs resting lengths (set to $ds$, the distance between successive points), $X_A = (x_A, y_A)$ and $B = (x_B, y_B)$ are the Lagrangian nodes tethered by the spring. Note that $R_L(t)$ indicates that the resting lengths could be time dependent. $X_C(t)$ is a Lagrangian point on the interior of the jellyfish bell and $X_{con}(t)$ is the corresponding initial (preferred) configuration of that particular Lagrangian point on the jellyfish bell. The spring stiffness are large to ensure minimal stretching or compression of the jellyfish bell itself, although via the beam formulation it is capable of bending and hence contracting. The 4th-order derivative discretization for the non-invariant beams is given in [11]. Note that the beams are deemed non-invariant because the preferred configuration is non-invariant under rotations, so if the jellyfish were to turn, the model will undergo undesired motion due to these artifacts.

Lastly, to mimic the subumbrellar and coronal muscles that induce bell contractions, virtual springs are used that dynamically change their resting lengths in a sinusoidal fashion. Rather than tether neighboring points with virtual springs to model the muscles, we tether points across the jellyfish bell, all Lagrangian points that are below the top hemi-ellipse. The deformation force equation does not change from Eq. (3) besides a different $k_{spr}$, which we call $k_{muscle}$, and now time-dependent spring resting lengths, $R_L(t)$, given by

$$RL(t) = 2a \left(1 - \sin(\pi t f)\right).$$  \hspace{1cm} (5)

Note that in Section 3.3 we vary the contraction (and expansion) percentage of the the bell contraction period and perturb Eq. (5) as described in Appendix B.

Upon running all simulations, we stored the following data in 5% increments during each contraction cycle:

1. Position of Lagrangian Points
2. Horizontal/Vertical forces on each Lagrangian Point
3. Fluid Velocity
4. Fluid Vorticity
5. Fluid Pressure
6. Forces spread onto the Fluid (Eulerian) grid from the Jellyfish (Lagrangian) mesh

We then used the open-source software called VisIt [19], created and maintained by Lawrence Livermore National Laboratory for visualization, see Figure 2, and the data analysis package software within IB2d [12] for data analysis. Figure 2 provides a visualization of some of the data produced from a single jellyfish locomotion at a single moment in time for simulation with bell contraction frequency of $f = 1.0 \text{s}^{-1}$ and Reynolds Number of 150.
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Fig. 2: A snapshot of a simulation at $Re = 150$ with $f = 1.0 s^{-1}$ after 6 contraction cycles illustrating some of the simulation data obtained at each time-step, e.g., positions of Lagrangian points, magnitude of velocity, the velocity vector field, and vorticity. Note other data not visualized is the fluid pressure and Lagrangian forces spread from the jellyfish onto the Eulerian (fluid) grid.

We stored 20 time points per contraction cycle in each jellyfish simulation and temporally-averaged data over the 10th (last) contraction cycle to compute average swimming speed in a particular simulation, $U_{avg}$. Moreover we computed the Strouhal Number, $St$,

$$St = \frac{fD}{U_{avg}}$$

where $f$ is the contraction frequency, $D$ is the maximum bell diameter during a contraction cycle, and $U_{avg}$ is the temporally-averaged forward swimming speed. By taking the inverse of $St$ we can get a normalized forward swimming speed based on driving frequency. Previous studies on animal locomotion have hypothesized that propulsive efficiency is high in a narrow band of $St$, peaking within the interval $0.2 < St < 0.4$ [83]. Hence we will explore the relationships between $St$ and $Re$, contraction frequency, $f$, the contraction phase kinematics, contraction amplitude, and bell diameter. Furthermore, we will also computed the cost of transport (COT) and investigated its relationship to the aforementioned parameters. The cost of transport has been used as a measure of aquatic locomotion efficiency and is a measure of energy (or power) spent per unit distance traveled [79-84]. We computed both a power-based COT and energy-based (work) COT, e.g.,
\[ COT_{work} = \frac{1}{N} \frac{1}{d_S} \sum_{j=1}^{N} |F_j||d_j| \]  
\[ COT_{power} = \frac{1}{N} \frac{1}{d_S} \sum_{j=1}^{N} |F_j||U_j|, \]

where \( F_j \) is the applied contraction force at the \( j^{th} \) time step by the jellyfish, \( U_j \) is the bell contraction velocity at the \( j^{th} \) time step, \( d_j \) is the lateral distance the bell contracted (or expanded) during the \( j^{th} \) time step, \( N \) is the total number of time steps considered, and \( d_S \) is the distance swam by the jellyfish traveled during during this period of time across all time steps considered.

Lastly, we computed the finite-time Lyapunov exponents (FTLE) which illustrate instantaneous Lagrangian Coherent Structures (LCS) [42, 80, 43]. In a nutshell, LCSs provide a systematic way to untangle the intricate, complex, and hidden dynamics of the system in a way that can be clearly visualized and interpreted. Within fluid flows, LCSs help reveal particle transport patterns that are of particular importance in biology. They can be used to understand various processes for jellyfish, including feeding and prey-capture [69, 77] and locomotion [32, 12, 88, 60, 44, 82]. FTLEs were computed using VisIt [19], where trajectories were computed using instantaneous snapshots of the 2D fluid velocity vector field on the entire computational domain using a forward/backward Dormand-Prince (Runge-Kutta) time-integrator with a relative and absolute tolerance of \( 10^{-4} \) and \( 10^{-5} \), respectively, and a maximum advection time of 0.02s with a maximum number of steps of 250. They were visualized using a colormap corresponding to the FTLE value on the background grid as well as FTLE contours.

3 Results

Below we present four differing studies, each complementing its former. First, we show how swimming performance varies across a spectrum of Reynolds Number, \( Re \), for particular bell contraction frequencies, \( f \). Next we selected four \( Re \) and varied the contraction frequency, illustrating that for a specific \( Re \) there exists a contraction frequency that will maximize forward swimming speed for a particular material composition. This extends the work of Hoover et al. 2015 [51] to multiple \( Re \).

Next we selected one \( Re \) (\( Re = 150 \)) and drove the bell at its preferred bell frequency, while varying the contraction (and hence expansion) phase percentage of the overall bell contraction period. Finally, we conducted a preliminary study varying the bell contraction amplitude for a variety of bell morphologies for the case with \( Re = 150 \). For each study we focused on quantifying differences in forward swimming speed (and Strouhal Number, \( St \)) and cost.
Don’t be jelly: 9 of transport. In addition we investigated differences in Lagrangian Coherent Structures (LCS) formation using finite-time Lyapunov Exponents (FTLE) analysis.

3.1 Results: Different $Re$, Uniform Frequencies

Fig. 3: Visualization comparing jellyfish swimming for a variety of $Re$ with a contraction frequency of $f = 1.0$ Hz. As $Re$ decreases (viscosity increases), less forward swimming occurs.

Previous studies of jellyfish locomotion have considered forward swimming performance over a range of $Re$ \cite{18, 91}; however, none have specifically investigated this over a range of $Re$ for a variety of bell contraction frequencies. As jellyfish are placed increasingly more viscous fluids while holding all other parameters constant, e.g., decreasing the $Re$, forward swimming performance decreases. This phenomenon can be seen in Figures 3 and 4 where the former visualizes distance swam for different numbers of bell contractions performed for a variety of $Re$, while the latter shows quantifies this data specifically for $Re$ ranging from 1 to 300. In agreement with previous models, forward swimming is negligible for $Re \lesssim 1$ and significant forward swimming begins around $Re \gtrsim 10$, when inertial effects become slightly greater than viscous dampening.
Fig. 4: Plot detailing distance swam against bell contractions performed for a variety of $Re$ when $f = 1.0 \text{ Hz}$. As $Re$ increases (viscosity decreases), distance swam increases. Moreover, as viscosity decreases (and $Re$ increases) forward swimming performance, e.g., swimming speed, increases for $10 \lesssim Re \lesssim 300$. For $Re \gtrsim 300$, forward swimming speed steadies out regardless of bell contraction frequency, see Figure 5. However, it is evident that different bell contraction frequencies lead to different forward swimming speeds, even if the speeds become uniform for large $Re$ for each individual frequency. Furthermore, there appears to be a non-linear relationship between swimming speed and contraction frequency, as illustrated that the cases of $f = 0.6$ and $1.5 \text{ Hz}$ are slower than the case with $f = 0.8 \text{ Hz}$. This nonlinear relationship is explored further in Section 3.2.
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Fig. 5: Illustrating average forward swimming speed against Reynolds Number, \( Re \), for a variety of different contraction frequencies, \( f \). Swimming speed is measured in (a) physical units (\( m/s \)) and (b) non-dimensional units (bodylengths/contraction). In both cases, as \( Re \) increases past a critical \( Re \), forward swimming speed steadies out, and there is a non-linear relationship between speed, \( Re \), and \( f \).

Next we investigated the relationship between \( Re \), contraction frequency, and Strouhal Number, \( St \). Note that by the way we defined forward swimming speed above as a non-dimensional speed given in bodylengths per bell contraction, it was just the inverse of \( St \). Exploring this data we find that slower bell contraction frequencies produce \( St \) in the biological regime of \( 0.2 < St < 0.4 \) for lower \( Re \) than cases with higher contraction frequency. In particular, for this jellyfish morphology, the lower contraction frequencies lead to swimming in this range of \( St \) for \( Re \gtrsim 50 \). Furthermore, in terms of scaling relations, for this jellyfish morphology, the \( St \) is a monotonically decreasing function of \( Re \) towards the biological \( St \) regime, suggesting that increasing \( Re \) maximizes propulsive efficiency in this instance [66].
Previous jellyfish studies have shown the cost of transport (COT) for jellyfish is much lower than other metazoans \cite{36}. However, they focused on passive energy recapture, similar to later studies by Hoover et al. 2019 \cite{73}, as the reason for lower COT in comparison. Nonetheless, we hypothesized that the cost of transport would show similar trends to those in Figure 6 where COT would decrease as $Re$ increases over the range where significant forward swimming is achieved. The COT data for both an average work-based and average power-based COT is provided for a variety of contraction frequencies over multiple orders of magnitude of $Re$, shown in Figure 7. Generally, COT decreases as $Re$ increases, with the highest COT attributes to the case with highest contraction frequency (similar to Figure 6). However, for $Re \gtrsim 200$, the COT increases slightly. Hence we remark that for this particular jellyfish morphology, optimal swimming performance occurs near $Re = 200$, where $0.2 < St < 0.4$ and COT is minimal for each contraction frequency.
Lastly, we performed Lagrangian Coherent Structure (LCS) analysis by computing the finite-time Lyapunov exponent (FTLE) \[42\]. Small values of the FTLE highlight regions where flow is attractive while large values indicate areas in which the flow is repelling. For jellyfish, LCSs can be used to highlight the regions of fluid in which the jellyfish is pulling towards or pushing away from its bell during contraction and expansion, respectively. Figure 8 compares the FTLE LCS analysis over one contraction cycle (between the 4\textsuperscript{th} and 5\textsuperscript{th}) between \(Re = \{37.5, 75, 150, 300\}\) for a contraction frequency of \(f = 0.75\) Hz. During bell contraction, high FTLE values are seen near the tips of the jellyfish bell, indicating regions of high fluid mixing in all cases. For cases with \(Re \gtrsim 75\), those regions on high fluid mixing are expelled downward by the time the contraction phase ends. The low FTLE values above the bell in each case suggest that fluid is being pulled downwards towards the end of the bell during contraction, rather than the jellyfish horizontally pulling in fluid. Within the bell, fluid is pulled inwards and towards the top during contraction and expansion. Moreover, as \(Re\) increases, the size of the regions with high FTLE also increases, suggesting a correlation with the amount of overall downstream fluid mixing.

As many scientists are now thinking of the effect of ocean mixing by marine animals \[57, 85, 55, 52\], this would suggest that smaller jellyfish (“smaller \(Re\)”) would contribute less to overall ocean mixing than larger jellyfish. However, ephyrae, larval jellyfish which have separated from the scyphistoma, swim at \(Re \sim 37.5\) while their adult counterparts swim at higher \(Re \gtrsim 100\) \[49, 28, 18\]. Hence adult jellyfish may contribute significantly more to ocean mixing than juvenile jellyfish.
Fig. 8: Visualization comparing Lagrangian Coherent Structures using finite-time Lyapunov exponents for $Re = \{37.5, 75, 150, 300\}$ between the $4^{th}$ and $5^{th}$ contraction cycle with a contraction frequency of $f = 0.75$ Hz.
3.2 Results: Same Re, Different Frequencies

In Section 3.1 we observed a non-linear relationship between Re, forward swimming speed, and contraction frequency, \( f \). Here we explore this relationship further and note that previous studies have investigated this relationship using the idea that the resonance properties of the jellyfish’s composition may be what is driving the system to prefer one bell contraction frequency over another to maximize forward swimming speed \[51\], \[73\].

First we explored how different contraction frequencies affect distance swam in the case of \( Re = 150 \), see Figure 9. We emphasize the importance of units in Figure 9; both sub-figures (a) and (b) show the same data of distance swam in bodylengths but against different measurements of time, either (a) bell contractions performed or (b) time in seconds. From both figures it is clear that there is a non-linear relationship between distance traveled and contraction frequency, as predicted from earlier Section 3.1. However, Figure 9a gives the illusion that over a bell contraction cycle, each waveform looks similar, while Figure 9b shows how different each waveform is. Moreover, what appeared to be the ideal contraction frequency for distance traveled per stroke (\( f = 0.1 \) Hz) is the worst if compared to distance traveled per second. Analogous observations may be made for other contraction frequencies as well.

Fig. 9: Plot detailing distance swam against bell contractions performed for a variety of contraction frequencies, \( f \), when \( Re = 150 \). Distance swam (bodylengths) is plotted against (a) non-dimensional time (bell contractions performed) and (b) physical time units (s).

Rather than focusing on possible resonant effects for one particular \( Re \), as studied previously, we chose to explore how contraction frequency affects forward swimming speed over numerous \( Re \) for jellyfish with the same material properties. In particular we chose \( Re = \{37.5, 75, 150, 300\} \), all within the range of where significant forward swimming occurs, before swimming speeds plateaus (in Section 3.1). An optimal contraction frequency, \( f_{opt} \) was
observed that maximizes forward swimming speed for all Re considered, see Figure 10a. Figure 10b provides the forward swimming speed in physical units (m/s) against frequency (Hz). The preferred contraction frequency appears to increase as Re increases. In addition, the forward swimming speed is symmetric about the optimal frequency in all cases. Interestingly, for Re \( \gtrsim 75 \), when contraction frequencies are less than the optimal frequency, all three Re cases have uniform forward swimming speed.

Similar to Figure 9, whether the data is presented using physical or non-dimensional units, different stories may unfold. Figure 10b provides the same data but as a non-dimensional swimming speed in bodylengths per contraction against frequency (Hz). For Re \( \gtrsim 75 \), swimming speed in bodylengths per stroke is equal and constant for \( f < 0.6 \ Hz \) between all cases. There does not appear to be an optimal frequency to maximize non-dimensional forward swimming speed; however, there is a critical contraction frequency, which is the optimal frequency seen in Figure 10a, \( f_{opt} \), in which for each Re when \( f > f_{opt} \), non-dimensional swimming speed strictly decreases.

![Fig. 10: Illustrating average forward swimming speed against contraction frequency, \( f \), for Reynolds Numbers, Re = \{37.5, 75, 150, 300\}. Swimming speed is measured in (a) physical units (m/s) and (b) non-dimensional units (bodylengths/contraction). (a) illustrates there is an optimal frequency, \( f_{opt} \), for forward swimming speed while (b) suggests that when \( f < f_{opt} \), non-dimensional swimming speed is uniform in each case of Re.](image)

While we did not vary jellyfish material composition or contraction strength properties (see [51, 73] for such studies), we observed preferred contraction frequencies that maximize forward swimming speed in physical units (m/s). We hypothesize that the complex, non-linear relationships observed are products of vortex formation and vortex shedding during each bell contraction cycle. Beyond relationships between resonance properties and driving bells at corresponding resonant frequencies, vortex formation among all cases appears unique. Complex vortex interactions occur which may lead to enhanced or
inhibited swimming performance, see Figure [11]. Figure [11] shows vortex formation and shedding over the fourth contraction cycle for the case of $Re = 150$ for differing contraction frequencies. In each case, formation formation and interaction are unique, in size, shape, and topology. Complex vortex dynamics have previously shown contributions to efficient propulsive mechanisms in jellyfish [22,34]. Moreover, vortices form within the bell during the relaxation phase of the contraction cycle at lower frequencies, similar to those observed in jellyfish during relaxation [24].
Fig. 11: Visualizations of complex vortex formation and interactions for a variety of contraction frequencies, $f$, in the case for $Re = 150$. Vortices overall topology and intricate interactions significantly vary for different contraction frequencies, $f$.

Furthermore, when $f < f_{opt}$ the Strouhal Number, $St$, the inverse of the non-dimensional swimming speed, is constant for each $Re$. Moreover, in this...
range of $f$, the $St$ falls within the well documented regime of $0.2 < St < 0.4$ for $Re \gtrsim 75$. For $f > f_{opt}$, $St$ strictly increases, see Figure 12. As $St$ is commonly used as a metric of swimming efficiency [74], we note that swimming at the $f_{opt}$ falls within the preferred range of $St$. If swimming at another contraction frequency, then $f < f_{opt}$ is preferred, when $f$ is closer to $f_{opt}$ the better (Figure 10). We note that the contraction amplitude also plays a role in efficiency swimming [75] and we explore that in Section 3.4 but in this study contraction amplitude is uniform.

![Fig. 12: Plot showing the relationship between Strouhal Number, $St$, and contraction frequency, $f$, for $Re = \{37.5, 75, 150, 300\}$. $St$ is the inverse of non-dimensional swimming speed.](image)

On the note of swimming efficiency, we compute the cost of transport (COT) using both a average work-based and average power-based COT. Swimming at lower frequencies has less COT, see Figure 13. When swimming near $f_{opt}$ for $Re \gtrsim 75$, the work-based COT is constant, while the power-based COT increases as $f$ increases. Swimming at higher $Re$ is generally less costly than lower $Re$, especially near $f_{opt}$. Moreover, the COT and $St$ are higher while forward swimming decreases as $f$ increases, again suggesting that swimming with $f < f_{opt}$ is preferred.
Fig. 13: Illustrating the relationship between cost of transport (COT) and contraction frequency, $f$, for $Re = \{37.5, 75, 150, 300\}$ when COT is computed using (a) average work and (b) average power.

Next we performed Lagrangian Coherent Structure (LCS) analysis via computing the finite-time Lyapunov exponent (FTLE). Figure 14 compares the FTLE LCS analysis over one contraction cycle (between the 4th and 5th) between $f = \{0.3, 0.5, 0.75, 1.0\}$ Hz for the case of $Re = 150$. In each case fluid from the top of the bell is pulled downwards towards the bell margin and thrust away from the jellyfish upon contraction. Moreover, there is downstream mixing in each case due to vortex ring propagation; however, for cases near the preferred contraction frequency, $f \sim 0.75$ Hz (Fig. 10) there appears to be significantly more mixing in the vortex wake. While enhanced swimming speed has been seen when driving the bell at resonant frequencies of its material properties [51][53], there appears to be another intricate dynamical relationship with vortex topology and interactions that increase vortex induced fluid mixing that may contribute to its enhanced speed.
Fig. 14: Visualization comparing Lagrangian Coherent Structures using finite-time Lyapunov exponents for \( f = \{0.3, 0.5, 0.75, 1.0\} \) Hz between the 4th and 5th contraction cycle for \( Re = 150 \).
While we have explored the relationship between forward swimming speed, $Re$, and frequency in further detail, there is much more open to be investigated. In particular, further study of these relationships with bell morphology, material properties, and contraction amplitude may lead to other non-linear relationships that could provide insight for more building more efficient biomimetic jellyfish robots [90,31,89,15,84].

3.3 Results: Varying contraction timing profile

All previous jellyfish simulations performed assumed a symmetric contraction cycle, e.g., 50% of the contraction cycle was contraction, 50% was expansion. Here we vary the ratio of contraction to expansion of each cycle for $Re = \{37.5, 75, 150, 300, 500\}$ when $f = 0.75\; Hz$. We investigated the following cases when the contraction percentage of the overall cycle was $\{5\%, 10\% \ldots 90\%, 95\%\}$. The remainder of each cycle was expansion. Note that other studies have assumed asymmetric contraction and expansion ratios [3,73]; however, no documented robust studies were performed investigating the role that the asymmetry itself may have on swimming performance. Moreover, Hoover et al. 2019 [73] included a passive coasting time between successive contractions, which we will neglect here. The model we used to induce bell contractions is described in Appendix B.

Fig. 15: Forward swimming speed (bodylengths/contraction) as a function of fraction that the contraction phase comprises of the overall contraction cycle for $Re = \{37.5, 75, 150, 300, 500\}$. For high enough $Re$, there is a non-linear relationship between speed and contraction fraction.

By varying contraction percentage across multiple $Re$, we discovered that for $Re \lesssim 75$ maximal forward swimming speed is achieved for quicker contractions (and longer expansions), see Figure 15. Interestingly this was not
the case for higher $Re$. For $Re = 150$, contraction percentages below 50% of the total bell contraction period, lead to approximately the same swimming speeds, before monotonically decreasing for slower contractions. However, for the cases of $Re = 300$ and $Re = 500$, a non-linear relationship between forward swimming speed and contraction percentage emerged, where contraction percentages of approximately 25% – 55% lead to faster forward swimming than quicker contractions, unlike the cases for lower $Re$. 
Fig. 16: Visualizations of vortex formation and interactions for a variety of contraction phase percentages of the overall contraction cycle for $Re = 150$. Vortex formation and interactions are different depending on contraction phase percentage. For the case when $Re = 300$, see Figure in Appendix B which illustrates similar complexities.
These results highlight a complex interplay between vortex formation and swimming speed. As the contraction-expansion ratio is varied, the resulting vortex structures also significantly differ, see Figures 16 and 25 (Appendix B) for snapshots from simulations of vortex formation over the course of a contraction period for cases of $Re = 150$ and 300, respectively, for multiple contraction-expansion ratios. In both figures, quicker contractions lead to a single vortex ring being pushed downwards, while slightly slower contractions lead to more intricate vortex ring-pair interactions. Complex vortex ring interactions in the wake have been previously observed in computational models of other sea invertebrates, such as sea hares (Aplysia) [93] and in fish, where propulsive efficiency can be controlled [1]. Moreover, optimal vortex formation has been observed in fast-swimming jellyfish where energy is minimized while maximizing forward thrust; however, vortex formation was controlled by the presence of complex morphology, velar structures [22].

Similarly, as in [93], we expect swimming speed to depend on contraction amplitudes, and so explore such relationship further in Section 3.4. Bell kinematics play a pivotal role in vortex formation, structure, and interactions, which can lead to discrepancies in swimming efficiency [35].

Fig. 17: Plot showing the relationship between Strouhal Number, $St$, and contraction phase fraction of the overall contraction cycle, for $Re = \{37.5, 75, 150, 300, 500\}$. $St$ is the inverse of non-dimensional swimming speed.

Moreover, for $Re \gtrsim 150$, we find that $0.2 \leq St \leq 0.4$ [34,75], as long as the contraction phase composes 70% or less of the overall contraction cycle, see Figure 14. Furthermore, for $Re \gtrsim 150$, the $St$ is not a monotonically increasing function of contraction phase length; however for other cases $St$ assumes its lowest value for the shortest contraction phases. We note that these relationships are expected as $St$ is the inverse of the normalized swimming speed given in Figure 15. Where $St$ is minimized corresponds to where cost of transport is minimized as a function of contraction phase as well, see Figure
In particular for $Re \gtrsim 150$, shorter (e.g. faster) contraction phases require more work/power to swim; however, cost of transport (and $St$) is minimized when the contraction phases are approximately 30% to 50% of the total stroke period, unlike cases at lower $Re$ ($Re < 150$).

Next we performed Lagrangian Coherent Structure (LCS) analysis via computing the finite-time Lyapunov exponent (FTLE). Figure 19 compares the FTLE LCS analysis over one contraction cycle (between the 4th and 5th) between for contraction phases that take of 10%, 25%, 60%, or 90% of the total contraction period when $Re = 150$. In all cases, fluid is pulled from around the top of the bell towards the bell and then expelled downwards as a vortex ring during contraction. In all cases there is considerable mixing near the bell margin throughout a contraction cycle. Downstream regions with high FTLE are observed in cases where contraction phases are shorter. Interestingly, in the 25% and 60% contraction phase percentage cases, horizontal mixing is more prevalent in the downstream vortex wake.

While the aforementioned non-linear behavior observed for higher $Re$ between contraction phases length and swimming performance is interesting, all models assumed uniform contraction amplitude. The computational models were run using the same jellyfish geometry with uniform material properties as well as contraction force and amplitude. Next we investigate how differing bell morphologies and contraction amplitudes affect forward swimming performance.
Fig. 19: Visualization comparing Lagrangian Coherent Structures using finite-time Lyapunov exponents for contraction phase percentages of the overall contraction-expansion cycle of \{10\%, 25\%, 60\%, 90\%\} between the 4\textsuperscript{th} and 5\textsuperscript{th} contraction cycle for $Re = 150$ and $f = 0.75$ Hz.
3.4 Results: Varying bell diameter and contraction amount

Previous studies may have explored how bell morphology affects forward swimming performance \cite{18,13,73}; however, deeper explorations of the relationship between the amount of contraction, bell morphology, and swimming speed have thus far been overlooked. Here we set \( Re = 150 \) and vary the bell radius, while keeping the jellyfish height constant, and also vary the amount the bell contracts (contraction amplitude). We did this for bell radii of \( 0.05 \leq a \leq 0.75 \) (overall aspect ratios of \( \frac{\text{width}}{\text{height}} = 2a/b \) of 0.133 to 2). To change the amount of bell contraction, we modified Eq.\((5)\), as follows

\[
RL(t) = 2a - A |\sin(\pi t f)|, \tag{9}
\]

where \( A \) is the amplitude of contraction and was selected to be \( A = 0.2, 0.4, \ldots, 1.0 \). Note that in simulations where the bell diameter was smaller than this amplitude, e.g., \( 2a < A \), we instead set \( A = 2a \), thus modeling maximum contraction possible. In general, we found that larger contraction amplitudes leads to increased forward swimming performance, see Figure 20. This figure illustrates that a jellyfish with bell radius \( a = 0.65 \) (diameter, \( D = 1.3 \)) swims farther for larger amplitudes of contraction. In particular if the bell contraction amplitude is 0.2 (e.g., bell occlusion of 0.2/1.3 = 15%), forwarding swimming is negligible.

Fig. 20: Contraction Amount: \( Re = 150 \) different contraction amounts vs distance swam for a jellyfish with bell diameter of \( d = 1.3 \).

This idea is detailed further in Figure 21a and b, which provide data pertaining to forward swimming speed in physical units and non-dimensional units, respectively, for a variety of different bell radii and contraction amplitudes. As bell radii and contraction amplitude increase, forward swimming...
speed increases. In particular forward swimming speed peaks near when bell diameter is equal to the contraction amplitude. Interestingly, it appears that this peak occurs when bell diameters are slightly larger than the contraction amplitude; however, this is much more pronounced in cases of smaller contraction amplitudes. Note that the dotted lines illustrate cases where the desired contraction amplitude was larger than the bell diameter and thus maximal contraction of the bell was used in Eq.(9).

Fig. 21: ContractionAmount: $Re = 150$ different contraction amounts vs swimming speed.

Moreover, for low contraction amplitudes, as bell radii increases, swimming speeds decrease. In the case of $A = 0.2$, for bell radii $a \gtrsim 0.4$, forward swimming speed is nearly zero. Similar trends are observed for larger contraction amplitudes. Comparing to the case when $A = 0.4$, we posit that when bell amplitude - diameter ratios (occlusion ratios) are less than approximately 25%, minimal forward swimming speeds are observed for our model. Furthermore, the Strouhal Number is within the assumed biological regime of $0.2 < St < 0.4$ for contraction amplitudes near the bell diameter of the jellyfish (see Figure 22). Moreover, as suggested by Saadat et al. 2017 [75], $St$ alone is insufficient in predicting optimal swimming performance and additional information about contraction amplitudes are required. Similarly, we find that for different jellyfish morphologies, there is an optimal range of contraction amplitudes that lead to more efficient swimming.

The associated cost of transport for both the work and power defined cases we higher for lower contraction amplitudes with minima occurring when contraction amplitude was approximately the bell diameter. For the case when $A = 1.0$ and bell radius $a \gtrsim 0.2$, the cost of transport is nearly constant, even though this was the case with the highest swimming speeds. Moreover, where peak forward swimming speed occurred, cost of transport was still nearly constant.
Next we performed Lagrangian Coherent Structure (LCS) analysis via computing the finite-time Lyapunov exponent (FTLE). Figure 24 compares the FTLE LCS analysis over one contraction cycle (between the 4th and 5th) between for contraction amplitudes of \{0.2,0.4,0.6,0.8,1.0\} for a bell diameter of \(D = 1.5\) for \(Re = 150\). In all cases, FTLE are high around the tips of jellyfish bell; however, for cases of low contraction amplitude, FTLE values are minimal elsewhere. For contraction amplitudes \(\gtrsim 0.6\), fluid is pulled from around the top of the bell towards the bottom of the bell and then expelled downwards during contraction. As contraction amplitude increases, so does FTLE. In particular, this suggests that larger contraction amplitudes lead to greater amounts of fluid mixing downstream in the vortex wake.

Recall that Section 3.3 illustrated the model’s sensitivity to varying the contraction phase percentage of the overall contraction period. Hence an idea that deserves further exploration is exploring the intricate relationships be-
Don’t be jelly: tween contraction phase kinematics, contraction amplitude, bell morphology, contraction frequency, and $Re$.

Fig. 24: Visualization comparing Lagrangian Coherent Structures using finite-time Lyapunov exponents for a jellyfish with bell diameter $D = 1.5$ with contraction amplitudes of $\{0.2, 0.4, 0.6, 0.8, 1.0\}$ between the $4^{th}$ and $5^{th}$ contraction cycle for $Re = 150$. 
4 Discussion and Conclusion

Experimental studies of the vortex wakes of oblate jellyfish have previously found that not only does bell morphology and scale [23] affect swimming performance [22] but also the bell kinematics itself [35]. Here we demonstrated through an elementary fluid-structure interaction model of jellyfish forward locomotion how complex the relationship between morphology, scale ($Re$), contraction frequency, contraction phase length, and contraction amplitudes (bell kinematics) is on the resulting forward swimming speed. Our model recreated similar swimming profiles from previous jellyfish locomotion models [26, 48, 91, 51, 50, 73]. We saw similar trends where forward swimming speed steadied out for high enough $Re$ [48] for all contraction frequencies considered (Section 3.1).

Moreover, nonlinear relationships between contraction frequency and $Re$ were observed and preferred contraction frequencies that maximized swimming speed were found for multiple $Re$, extending the work of Hoover et al. [51] (Section 3.2). From our data, we hypothesize that the preferred frequency will increase as $Re$ increases; however, further investigation needs to be pursued. On that note, in this work the material properties of the jellyfish were uniform and not varied. Varying the bell stiffness parameters will also affect swimming performance [73]. Similar to Hershlag et al. [48], we varied bell morphology but also varied contraction amplitude, which lead to significant differences in forward swimming speed (Section 3.4). Furthermore, we showed that varying the bell contraction frequency or contraction phase profile leads to significant qualitative differences in vortex formation and interactions in the wake of the jellyfish (Sections 3.2 and 3.3). It is known that vortex wake topology plays a critical role in swimming performance for a number of animals, not only jellyfish [22, 34], but also fish [25, 59, 11], and other sea invertebrates, such as sea hares [93], squid [5], nautilus [65], salps [83], and lampreys/eels [30, 45].

In addition, by performing Lagrangian Coherent Structure analysis on our jellyfish model, we determined parameter subspaces that lead to higher levels of fluid mixing around the jellyfish and downstream within the vortex wake. We observed that fluid is pulled from the top of the jellyfish bell towards its bell margin during forward swimming, rather than from the sides. Recently oceanic mixing via marine animals has gained attention [57, 85, 55, 52] and our analysis provides insight into the amount of mixing possible for a variety of jellyfish of various sizes (using $Re$ as a proxy), bell morphologies, and bell kinematics (contraction frequency, contraction phase profiles, contraction amplitude), see Sections 3.1, 3.4. We hypothesize that there may additional connections between vortex topology/interactions and fluid mixing that govern forward swimming performance (Section 3.2, 3.3).

Further investigation into how wake structure, and in particular vortex topology, structure, and interactions, may lead to more effective swimming performance are warranted. This data could prove beneficial for extending reduced models that describe collective behaviors in aquatic locomotion, such as fish schooling [2, 17, 83, 20], which are computational expensive and difficult to
resolve otherwise when using fully coupled FSI. The importance of wake structure and vortex interactions are not limited to solely locomotion processes; a deeper understanding of their governing principles may also be beneficial for inspiring innovative designs for biomimetic or bioinspired devices, such as vertical axis wind turbine (VAWT) farm configurations [87,21] or flow sensors in aquatic robotics for exploration based on vortex induced vibrations [13,14,56].

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A Details on IB

A two-dimensional formulation of the immersed boundary (IB) method is discussed here. The IB software used was IB2d [7,12,11]. The software has been validated [12] with specific convergence tests performed for the jellyfish model in [10] and below in Appendix C. For a full review of the immersed boundary method, please see Peskin 2002 [72] or Mittal et al. 2005 [64].

A.1 Governing Equations of IB

The conservation of momentum equations that govern an incompressible and viscous fluid are listed below:

\[
\rho \left( \frac{\partial \mathbf{u}}{\partial t} (x,t) + \mathbf{u}(x,t) \cdot \nabla \mathbf{u}(x,t) \right) = \nabla p(x,t) + \mu \Delta \mathbf{u}(x,t) + \mathbf{F}(x,t) \quad (10)
\]

\[
\nabla \cdot \mathbf{u}(x,t) = 0 \quad (11)
\]

where \( \mathbf{u}(x,t) \) is the fluid velocity, \( p(x,t) \) is the pressure, \( \mathbf{F}(x,t) \) is the force per unit area applied to the fluid by the immersed boundary, \( \rho \) and \( \mu \) are the fluid’s density and dynamic viscosity, respectively. The independent variables are the time \( t \) and the position \( x \). The variables \( \mathbf{u}, p, \) and \( \mathbf{F} \) are all written in an Eulerian frame on the fixed Cartesian mesh, \( x \).

The interaction equations, which handle all communication between the fluid (Eulerian) grid and immersed boundary (Lagrangian grid) are the following two integral equations:

\[
\mathbf{F}(x,t) = \int f(s,t) \delta (x - X(s,t)) \, dq \quad (12)
\]

\[
\mathbf{U}(X(s,t)) = \int \mathbf{u}(x,t) \delta (x - X(s,t)) \, dx \quad (13)
\]
where \( f(s, t) \) is the force per unit length applied by the boundary to the fluid as a function of Lagrangian position, \( s \), and time, \( t \), \( \delta(x) \) is a three-dimensional delta function, and \( X(s, t) \) gives the Cartesian coordinates at time \( t \) of the material point labeled by the Lagrangian parameter, \( s \). The Lagrangian forcing term, \( f(s, t) \), gives the deformation forces along the boundary at the Lagrangian parameter, \( s \). Equation (12) applies this force from the immersed boundary to the fluid through the external forcing term in Equation (10). Equation (13) moves the boundary at the local fluid velocity. This enforces the no-slip condition. Each integral transformation uses a three-dimensional Dirac delta function kernel, \( \delta \), to convert Lagrangian variables to Eulerian variables and vice versa.

Using delta functions as the kernel in Eqs. (12-13) is what gives IB its power. To approximate these integrals, discretized (and regularized) delta functions are used. We use the ones given from [72], e.g., \( \delta_h(x) \):

\[
\delta_h(x) = \frac{1}{h^3} \phi \left( \frac{x}{h} \right) \phi \left( \frac{y}{h} \right) \phi \left( \frac{z}{h} \right),
\]

where \( \phi(r) \) is defined as

\[
\phi(r) = \begin{cases} 
\frac{1}{8} (3 - 2| r | + \sqrt{1 + 4| r |^2} - 4r^2), & 0 \leq | r | < 1 \\
\frac{1}{8} (5 - 2| r | + \sqrt{9 + 12| r |^2} - 4r^2), & 1 \leq | r | < 2 \\
0, & 2 \leq | r |.
\end{cases}
\]

A.2 Numerical Algorithm

As stated in the main text, we impose periodic and no slip boundary conditions on the rectangular domain. To solve Equations (10), (11), (12) and (13) we need to update the velocity, pressure, position of the boundary, and force acting on the boundary at time \( n + 1 \) using data from time \( n \). The IB does this in the following steps [72].

Step 1: Find the force density, \( F^n \) on the immersed boundary, from the current boundary configuration, \( X^n \).

Step 2: Use Equation (12) to spread this boundary force from the Lagrangian boundary mesh to the Eulerian fluid lattice points.

Step 3: Solve the Navier-Stokes equations, Equations (10) and (11), on the Eulerian grid. Upon doing so, we are updating \( u^{n+1} \) and \( p^{n+1} \) from \( u^n \), \( p^n \), and \( f^n \). Note that a staggered grid projection scheme is used to perform this update.

Step 4: Update the material positions, \( X^{n+1} \), using the local fluid velocities, \( U^{n+1} \), computed from \( u^{n+1} \) and Equation (13).

B Varying the contraction/expansion ratio of the overall contraction period.

In this appendix we supply an additional figure illustrating complex vortex formation and interaction when the contraction phase percentage of the overall contraction cycle is varied for \( Re = 300 \). Figure 16 in Section 3.3 gives an analogous case for when \( Re = 150 \).
**Fig. 25:** Contraction: $Re = 300$ different contraction timing.
C Computational Grid Width Convergence Check

Here we perform a convergence test to determine how the width of the computational domain affects forward swimming speeds and moreover vortex formation and interactions. We investigated cases for $Re = \{37.5, 75, 150, 300\}$ and computed forward swimming speed and the subsequent error between cases of different widths of $L_x = \{3, 3.5, 4, \ldots, 8\}$. The height of the domain was fixed with $L_y = 12$ and we note we conserved spatial step-sizes, e.g., $dx = dy$, in every simulation.

Figure 26a and b provide the swimming speed for every $L_x$ and $Re$ considered and relative error between each case of $L_x$ against the widest case of $L_x$, respectively. Figure 26a shows that for every case of $Re$ considered, thinner width simulations produced slightly slower swimming jellyfish; however, the differences in speed were small. As the width gets larger, the relative error decreases, as illustrated by Figure 26b. Moreover, when $L_x = 3$, the relative error percentage is $\sim 5.5 - 6.5\%$ and by $L_x = 5$, the relative error decreases to $\sim 1 - 1.5\%$. We chose to run simulations at $L_x = 5$ in an attempt to minimize computational cost while preserving adequate accuracy.

![Figure 26](image)

**Fig. 26: ConvergenceCheck: $Re = 150$ for different computational mesh widths.**

Furthermore, Figure 27 illustrates that qualitative differences are negligible in vortex formation and vortex interactions near jellyfish contraction and expansion for $Re = 150$. Cases involving other $Re$ follow similarly. Subtle differences in vortex dynamics are only observed in down stream vortices when $L_x > 5$. 
Fig. 27: Convergence Check: $Re = 150$ different contraction timing.

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