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A numerical study of the benefits of driving jellyfish bells at their natural frequency

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HIGHLIGHTS

- Driving the model jellyfish bell at or slightly below the resonant frequency led to a high amplitude of bell oscillation.
- The model jellyfish bell swam fastest at periodic steady state when driven at frequencies at or slightly above the resonant frequency.
- The optimal driving frequency for forward swimming was dependent upon the magnitude of the driving force.
- The advantage of driving the bell at its resonant frequency was reduced when additional fluid damping is introduced.

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ABSTRACT

A current question in swimming and flight is whether or not driving flexible appendages at their resonant frequency results in faster or more efficient locomotion. It has been suggested that jellyfish swim faster when the bell is driven at its resonant frequency. The goal of this study was to determine whether or not driving a jellyfish bell at its resonant frequency results in a significant increase in swimming velocity. To address this question, the immersed boundary method was used to solve the fully coupled fluid structure interaction problem of a flexible bell in a viscous fluid. Free vibration numerical experiments were used to determine the resonant frequency of the jellyfish bell. The jellyfish bells were then driven at frequencies ranging from above and below the resonant frequency. We found that jellyfish do swim fastest for a given amount of applied force when the bells are driven near their resonant frequency. Nonlinear effects were observed for larger deformations, shifting the optimal frequency to higher than the resonant frequency. We also found that the benefit of resonant forcing decreases for lower Reynolds numbers.

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1. Introduction

It has been suggested that locomotory efficiency and performance with flexible appendages is maximized when these structures are driven at their natural frequency (Alexander and Bennet-Clark, 1977; Ahlborn et al., 2006). 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 (Tytell et al., 2014), insect wings (Masoud and Alexeev, 2010), and jellyfish bells (DeMont and Gosline, 1988a). It is important to note that not every study has leant support to the idea that propulsive efficiency is maximized when the resonant and driving frequencies coincide. Ramananarivo et al. (2011) 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. (2014) 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.

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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 its elastic properties that store potential elastic energy (Ahlborn et al., 2006). 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 (Tytell et al., 2014; DeMont and Gosline, 1988a; Ramananarivo et al., 2011; Megill, 2002). One can then compare analytic solutions to experimental observations to test the accuracy and predictive ability of the model.

Jellyfish propulsion can be thought of as a complementary two phase process of active contraction and passive expansion of the bell. During a jellyfish swimming cycle, the coronally oriented subumbrellar swimming muscles contract and deform the jellyfish bell, expelling fluid. The mesoglea, an extracellular matrix composed fibers of a collagen-like protein, stores the potential elastic energy that drives the re-expansion of the bell when the muscles relax (Arai, 1996). The fluid mechanical mechanisms of jellyfish swimming depend upon the shape of the bell. Oblate jellyfish use a rowing or paddling motion (Dabiri et al., 2005) and prolate jellyfish use jet propulsion (Dabiri et al., 2006). 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 (DeMont and Gosline, 1988a). Resonant driving would maximize the potential elastic energy stored in the mesoglea that is then used to fill the bell. This is due to the fact that the amplitude of bell deformation is maximized when it is driven near its resonant frequency (see, for example, Ogata, 2005).

The effect of resonant driving of jellyfish bells has been previously examined using reduced models and experiments (Ahlborn et al., 2006; DeMont and Gosline, 1988a,b; Megill, 2002; Megill et al., 2005). DeMont and Gosline modeled the dynamics of the jellyfish bell as a linear damped harmonic oscillator with lumped parameters (DeMont and Gosline, 1988a). 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 (Megill, 2002).

The fluid flow around swimming jellyfish has also been studied using computational fluid dynamics (Huang and Sung, 2009; Zhao et al., 2008). Herschlag and Miller prescribed the kinematics of a 2D hemielliptical bell. The resulting forward motion of the jellyfish was similar to speeds measured in actual jellyfish (Herschlag and Miller, 2011). Mohseni et al. used an axisymmetric Lagrangian–Eulerian formulation of the fluid–structure interaction (FSI) problem to simulate the forward swimming of the jellyfish *Aequorea victoria* using the actual bell profiles as inputs (Sahin et al., 2009). Alben et al. used a combination of computational tools and analytical models to explore the kinematics of the bell for both high swimming and high efficiency movements (Alben et al., 2013). None of these studies, however, considered the effect of driving the bell at the resonant frequency.

This paper extends the idea of resonant driving of the jellyfish bell to an FSI framework using the immersed boundary method. Instead of prescribing the motion of the bell, a periodic force applied towards the centerline 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.

2. Methods

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 (Colin and Costello, 2002; Daniel, 1985; McHenry and Jed, 2003; Herschlag and Miller, 2011). 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

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

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

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

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.

2.2. The immersed boundary method

To solve the fully coupled fluid–structure interaction problem, a 2D formulation of the immersed boundary (IB) method was used. The IB method was originally developed by Peskin to study the fluid dynamics of blood flow in the human heart (Peskin, 2002). Since then, the IB method has been used to numerically solve a variety of fluid structure interaction problems that inhabit the low to intermediate Reynolds number regime here defined as 10^{-1} to 10^3 (Mittal and Iaccarino, 2005), including undulatory swimming (Fauci and Peskin, 1988; Fauci and Fogelson, 1993; Bhalla