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Rowing jellyfish contract to maintain neutral buoyancy

Patricia J. Yang^a, Matthew Lemons^a, David L. Hu^{a,b,*}

^a Schools of Mechanical Engineering, Georgia Institute of Technology, Atlanta, GA 30332, USA
^b Schools of Biology, Georgia Institute of Technology, Atlanta, GA 30332, USA

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ABSTRACT

Jellyfish are easily carried by ocean currents, yet most studies on jellyfish focus on the kinematics in a quiescent fluid. In this experimental and theoretical study, we film six species of rowing jellyfish in a range of background flow speeds at the Georgia Aquarium. Each species has a unique contraction frequency, which is independent of both the body orientation and the background flow speed. Our mathematical model reveals that jellyfish contract to offset their sinking. This behavior is invariant: Despite the background flow conditions, jellyfish contract as if they are oriented upright in a quiescent fluid. Our study suggests that jellyfish operate in open-loop without feedback from their environment.

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Ocean currents vary in speed from regular currents of 0.08 m/s to a storm of 2.5 m/s [1, 2], which affect a number of aquatic organisms. Jellyfish are particularly susceptible because they swim relatively slowly by contracting and relaxing their bellshaped bodies. The magnitude of jellyfish contraction is associated with two propulsive modes: jetting and rowing. A jetting jellyfish fully contracts its bell, yet a rowing jellyfish only partially contracts its bell and paddle in a more relaxed manner [3]. In 1983, Daniel proposed that the bell contraction is the source of thrust for jetting jellyfish [4, 5]. Later studies accept this concept and further state that jetting jellyfish contract at the natural frequency of the bell, which reduces the energy cost of swimming [6-8] and maximize propulsive efficiency [9]. Besides jetting jellyfish, rowing jellyfish have been investigated by visualizing the full cycle of contraction [10-13]. However, these studies have been focused on jellyfish in a quiescent fluid. The goal of this study is to determine how background flow influences the kinematics of jellyfish.

Early theoretical studies have classified the forces on jellyfish as thrust, drag, added mass force, and inertia force [4]. The four forces provide a theoretical framework in later jellyfish studies [9, 14], which neglect the buoyancy force for simplicity. In 1981, Mills observed that most jellyfish sink in water. Jellyfish main-

* Corresponding author. E-mail address: hu@me.gatech.edu (D.L. Hu). tain themselves at a preferred depth by assuming a characteristic swimming pattern [15].

In this study, we incorporate the jellyfish sinking into a mathematical model and discuss its contribution to the kinematics of jellyfish. We first report the morphology of jellyfish and its kinematics in background flow. We then present the mathematical model for jellyfish swimming and compare its prediction to our observations. We lastly discuss the implications of our work and suggest directions for future research.

We model the shape of jellyfish as a section of a hemi-ellipsoid with density ρ_j , diameter *D*, height *H*, and mass m_j as illustrated in Fig. 2(a). Previous researchers have observed that most jellyfish are negatively buoyant [15, 16]. However, none have measured the density directly because measuring the volume of the soft and fragile jellyfish is challenging. Gemmell assumes that density of jellyfish *Aurelia aurita* is

$$\rho_i = 1.025 \text{ g/cm}^3, \tag{1}$$

and examine the sinking of static jellyfish in a numerical model [12]. Since the density of seawater is 1.020 g/cm^3 , jellyfish *A*. *aurita* are 0.5% denser than water [12]. For simplicity, we assume that all jellyfish species have the same density.

In 2007, Dabiri compiled the morphology of 660 jellyfish species [11]. Using Dabiri's and our data, the relationship between jellyfish bell height H and diameter D may be written

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Fig. 1. a *Aurelia aurita*. **b** *Chrysaora plocamia*. **c** *Chrysaora colorata*. **d** *Phyllorhiza punctata*. Courtesy of Marco Fumasoni in Wikimedia Commons. **e** *Chrysaora pacifica*. **f** *Catostylus mosaicus*. Courtesy of Steven Johnson in Wikimedia Commons. **g-h** The relationship between the diameter of jellyfish *D* and **g** the contraction amplitude ΔD **h** the contraction frequency *f*. Symbols represent experimental measurements, the dashed line represents best fit to the data, and the solid line represents the theoretical prediction.

$$H = 0.81D^{0.72} \ \left(N = 761, R^2 = 0.83\right), \tag{2}$$

where H and D are both in cm. The height of the bell increases disproportionally with body size as shown in Fig. 2(d). Consequently, small jellyfish are prolate (bullet-shaped), while large jellyfish are oblate (plate-shaped), as reported in previous studies [3, 17].

The wet mass of jellyfish m_j is complied from previous literature[18-20],. Its relationship to diameter D may be written

$$m_j = 0.08D^{2.77} (N = 22, R^2 = 0.99),$$
 (3)

where *D* is in cm and m_j is in grams. This trend indicates that the mass increases disproportionally with body size as shown in Fig. 2(e). Larger jellyfish are lighter than expected from isometry $(m_j \sim D^3)$. To understand the impact of morphology on the swimming kinematics, we turn to the filming of jellyfish.

We film six species of jellyfish at the Georgia Aquarium, including Aurelia aurita, Chrysaora plocamia, Chrysaora colorata, Chrysaora pacifica of the Order Semaeostomeae and Phyllorhiza punctata and Catostylus mosaicus of the Order Rhizostomeae (Fig. 1(a) to (f)). The jellyfish are of a broad range of size from 2 to 20 cm, which are identified as rowing jellyfish in previous litDownload English Version:

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