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## Transient pressure modeling in jetting animals

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## ABSTRACT

There are many marine animals that employ a form of jet propulsion to move through the water, often creating the jets by expanding and collapsing internal fluid cavities. Due to the unsteady nature of this form of locomotion and complex body/nozzle geometries, standard modeling techniques prove insufficient at capturing internal pressure dynamics, and hence swimming forces. This issue has been resolved with a novel technique for predicting the pressure inside deformable jet producing cavities (M. Krieg and K. Mohseni, J. Fluid Mech., 769, 2015), which is derived from evolution of the surrounding fluid circulation. However, this model was only validated for an engineered jet thruster with simple geometry and relatively high Reynolds number (Re) jets. The purpose of this manuscript is twofold: (i) to demonstrate how the circulation based pressure model can be used to analyze different animal body motions as they relate to propulsive output, for multiple species of jetting animals, (ii) and to quantitatively validate the pressure modeling for biological jetting organisms (typically characterized by complicated cavity geometry and low/intermediate Re flows). Using jellyfish (Sarsia tubulosa) as an example, we show that the pressure model is insensitive to complex cavity geometry, and can be applied to lower Re swimming. By breaking down the swimming behavior of the jellyfish, as well as that of squid and dragonfly larvae, according to circulation generating mechanisms, we demonstrate that the body motions of Sarsia tubulosa are optimized for acceleration at the beginning of pulsation as a survival response. Whereas towards the end of jetting, the velar morphology is adjusted to decrease the energetic cost. Similarly, we show that mantle collapse rates in squid maximize propulsive efficiency. Finally, we observe that the hindgut geometry of dragonfly larvae minimizes the work required to refill the cavity. Date Received: 10-18-2019, Date Accepted: 99-99-99999 \*kriegmw@hawaii.edu, UHM Ocean and Res Eng, 2540 Dole St, Honolulu, HI 96822

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## Introduction

Jellyfish, dragonfly larvae, salps, squid, octopi, nautilus, and other cephalopods all propel themselves through the water by ingesting water into an internal cavity and then expelling the fluid in the form of a high momentum propulsive jet, as illustrated in Fig. 1. Although this type of locomotion is often blanketly assumed to be inefficient (Lighthill, 1969; Vogel, 1994), recent studies have suggested that the high velocity, low volume propulsive jet does not negate a high propulsive efficiency (Anderson and Grosenbaugh, 2005; Bartol et al., 2008, 2009). At the heart of this misconception is the assumption that the jetting force is proportional to the jet velocity squared and that the energy scales with the veloc-

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https://doi.org/10.1016/j.jtbi.2020.110237 0022-5193/© 2020 Elsevier Ltd. All rights reserved. ity cubed, which is only accurate for steady, uniform flows. There are several complexities associated with unsteady propulsive jets which need to be taken into account to get an accurate picture; including, but not limited to, the thrust augmentation associated with vortex ring formation (Krueger and Gharib, 2005), the thrust augmentation associated with non-parallel jet flows (Krieg and Mohseni, 2013), and the acceleration of fluid both inside and outside of the cavity (Krieg and Mohseni, 2015). As such, models for pressure dynamics in these animals based on the Bernoulli approximation or 1D momentum transfer, do not match well with experimental data (Johnson et al., 1972; O'Dor, 1988; O'Dor and Webber, 1986; Trueman, 1968). In this study we investigate the use of a higher fidelity pressure model, which is applicable to this form of unsteady propulsive jetting (Krieg and Mohseni, 2015). Along with providing a more accurate internal pressure estimate throughout jetting, the innovative pressure model allows different animal body









**Fig. 1.** Diagram showing multiple types of marine jetting organisms and illustrating the common elements shared by these different animals; including a flexible internal cavity used to drive jet flow and the formation of a large vortex ring, which is a defining feature of unsteady fluid jets. Images of dragonfly larvae are taken from Roh and Gharib (2018).



Fig. 2. This diagram shows a hypothetical body layout for a jetting organism, and labels characteristic sources of vorticity in both the cavity and jet regions. (b) Also we show the path of integration referred to as a 'viscosity free path' used to calculate variation in internal pressure distribution.

motions to be analyzed individually with respect to propulsive output.

It was shown by Krieg and Mohseni (2015) that there is a direct link between the pressure inside bodies with cavities that deform to eject fluid jets and the rate of change of circulation in the surrounding liquid.<sup>1</sup> This relationship is summarized by,

$$\frac{P_b}{\rho} = \frac{d}{dt} \left( \Gamma_{Jet} + \tilde{\Gamma}_{Cav} \right) + \frac{1}{2} u_b^2, \tag{1}$$

where  $P_b$  is the pressure on the inner surface of the body,  $\rho$  is the fluid density,  $u_b$  is the velocity of the body surface,  $\Gamma_{Jet}$  is the total circulation in the jet region,  $\tilde{\Gamma}_{Cav}$  is a modification of the total cavity circulation ( $\Gamma_{Cav}$ ) which will be described in the **Methods** section (see Fig. 1 for a definition of the cavity and jet regions, respectively). The usefulness of this relationship lies in the fact that

total circulation can generally be considered a conserved quantity, with the exception of a few characteristic locations where vorticity is generated. Thus the circulation dynamics of a region of fluid can be calculated from the sum of all the vorticity generating sources in that particular flow. In turn, the pressure dynamics of cavity-jet systems can be determined without requiring the complete solution of the flow field. The relationship between internal pressure and mechanisms for generating system circulation was validated for a large test actuator, both during jetting and refilling, with a simple internal geometry in Krieg and Mohseni (2015), showing excellent agreement.

We identified four mechanisms by which vorticity is created in deformable cavity bodies that produce jet flows, which are depicted for a hypothetical body in Fig. 2. The rate of change of circulation in the surrounding fluid, and hence the internal pressure dynamics, can be fully described by the following sources:

 Vorticity Flux - This vorticity is created in the form of a shear layer that is attached to the animal's cavity opening (or nozzle) and extends into the surrounding fluid as it is carried outward

<sup>&</sup>lt;sup>1</sup> For those less well versed in fluid dynamics, total circulation of a region of fluid is the sum of vorticity in that region, and vorticity is similar to a measure of angular velocity of any differential element. For a 2D flow defined on a grid of positions [*x*, *y*] with velocity field given by [*u*, *v*], vorticity is defined,  $\omega = \frac{\partial v}{\partial x} - \frac{\partial u}{\partial y}$ 

with the jet flow. The rate vorticity is added to the system due to this term scales with the jet velocity squared, and the increase in pressure due to this term is associated with the momentum transfer taking place at the cavity opening, but it also allows us to quantify the effect of vortex ring formation and nozzle geometry.

- Half-Sink Vorticity Fluid internal to the cavity must be accelerated towards the opening to create the jet flow. This internal flow structure can be loosely modeled as that on one-half of a uniform circular velocity sink. The vorticity of this flow structure scales with the rate of change of the jet velocity. Modeling for this source of vorticity allows us to quantify the increase in pressure due to unsteady acceleration of internal fluid. In general forces associated with this increase in pressure are cyclical, and have little impact on total jet thrust, but have a significant effect on the energy required to create the jet.
- **Vortex Impingement** When the cavity is refilled, incoming fluid forms a shear layer similar to the vorticity flux terms during jetting. When the incoming vortex ring approaches the inner cavity boundaries it creates a shear layer of opposite sign attached to the cavity surface. The variation of pressure due to this term is largely dependent on cavity geometry and it provides a way to quantify recovery of incoming fluid momentum before the proceeding jetting cycle.
- **Boundary Stretching** Marine organisms that employ jetting propulsion are almost exclusively invertebrates, which allows them to deform and move water in and out of an internal cavity. In addition to bending, these animals can create deformation where a surface/appendage is elongated. If the cavity deformation includes stretching that is tangential to the cavity surface it creates an additional attached shear layer. However, as will be discussed in the **Methods** section this term does not directly affect the pressure/force dynamics, due to cancellation with an identical term.

Analytical models were derived for each of the vorticity generating mechanisms in Krieg and Mohseni (2015), and were verified using a prototype jet thruster and velocity field measurement techniques. The validity of the overall pressure model was also verified using the prototype thruster, which created jet flows with a Re on the order of 70,000. Since the Re of many jetting marine animals is significantly lower, we need to validate the accuracy of the model for lower Re jet flows. The squid Loligo pealei is reported to produce jets with  $Re > 10^4$  (Anderson and DeMont, 2000). Bartol *et al.* list the Reynolds number of Lolliguncula brevis to range between 1.000-16.000 through different developmental stages: whereas. Doryteuthis pealeii has a range of Re = 22,000 - 180,000 (Bartol et al., 2009). In another study (Bartol et al. (2008)) the same authors report that squid I. illecebrosus, S. lessoniana, and L. brevis in their paralarval stages produce jets with Re = 1 - 100. The jellyfish Sarsia tubulosa had its jet Reynolds number measured to be 302 in one study, while Aequorea victoria had Re = 672 (Sahin et al., 2009). It should be noted here that many of these organisms produce jets with low enough *Re* that viscosity starts to play a larger role. However, none of these animals get into the regime of very low Re where viscosity dominates and fluid inertia no longer plays a significant role (Also known as Stokes flow). Analysis of circulation based pressure modeling accuracy for flows in this regime will be left for future studies.

Swimming in marine organisms, especially jellyfish and cephalopods, involves both passive and active deformations of various body tissues. These biological systems have substantial complexity in their body morphology, and the effect these deformations have on animal locomotion can be difficult to investigate with standard analytical tools. On top of which limited experimental capabilities often make the exact body kinematics difficult to determine. Subsequently, many studies investigating these animal's swimming only consider basic aspects of body motion like volume change and funnel (opening) area (Anderson and DeMont, 2000; O'Dor and Webber, 1986; Trueman, 1968), or ignore the body morphology entirely and focus only on the qualities of the propulsive jet (Colin and Costello, 2002; Dabiri et al., 2005). The circulation based internal pressure model can help significantly in analyzing locomotion of jetting marine animals like squid and jellyfish, and help characterize the effect of each individual aspect of body deformation with respect to propulsive output.

In this paper we both demonstrate the accuracy of the novel pressure model for lower *Re* biological jet flows, and we show how different aspects of animal deformations and body morphology can be related to their effect on the characteristic vorticity generating mechanisms and subsequently identify the direct impact on propulsion (or other secondary objectives). We provide this analysis in the **Results** section of the paper for three representative animals with varying propulsive goals and jetting behavior, which include a prolate jellyfish (Sarsia tubulosa), dragonfly larvae (Aeshnidae sp.), and the longfin squid (Loligo pealei). The available velocity field data for the flow surrounding the jellyfish also allowed us to investigate the variation in pressure over the entire inner cavity surface. The Methods section gives a short summary of the circulation based pressure model, as well as other standard pressure models that are used for comparison, and provides the sources for data used in the analysis of biological jetting. Specifically the summary of the novel pressure model is presented to make it easily accessible and describe how it can be applied to various jetting animals. Finally, the overall determinations of the paper are listed in the **Conclusion**.

#### Results

One of the advantages of the circulation based pressure model is that it can be used as a powerful tool for more general analysis of swimming behavior, in addition to providing high accuracy calculations of internal pressure. The solutions for velocity field from that discrete numerical simulation are used to determine the rate of change of circulation, in addition to analytical inviscid circulation models. The pressure field from the CFD simulation is used as truth to validate the different pressure modeling.

In this section we examine the swimming of three representative jetting animals. We provide a quantitative comparison of pressure model accuracy for cases with sufficient data, and for all examples we analyze different aspects of body deformation observed in the jetting marine animals, qualitatively, in terms of how they affect the different sources of vorticity, and subsequently how they affect the overall propulsive output during jetting.

The different mechanisms for creating vorticity in jetting bodies and their functional dependencies were described in the introduction. Detailed analytical models are provided in the **Methods** section, and are summarized by Eqs. (3)-(9) for the vorticity flux, half-sink, and vortex impingement mechanisms, respectively. We start with the example of a prolate jellyfish (*Sarsia tubulosa*) because the extent of available data for this case allows the most in depth analysis. This is followed by a more qualitative analysis of dragonfly larvae and squid.

#### Analysis of jellyfish (Sarsia tubulosa) jetting locomotion

We start by analyzing the behavior of a swimming *Sarsia tubulosa*. The exact body shape was captured via high-speed filming and imported into a computational fluid dynamic (CFD) simulation, as summarized in the **Methods** section (and reported in Sahin and Mohseni, 2009), to generate the surrounding velocity and pressure fields. The solutions for velocity field from that direct numerical



**Fig. 3.** Internal pressure at the reference location (see Fig. 1) of *Sarsia tubulosa* as determined by various models. The pressure from the CFD simulation data (Sahin and Mohseni, 2009) is considered to be truth.

simulation are used to determine the rate of change of circulation, in addition to analytical, inviscid circulation models. The pressure field from the CFD simulation is used as truth to validate the different pressure modeling.

Jellyfish body deformations periodically cycle through jetting, refilling, and coasting phases, respectively. Depending on characteristic time and length scales associated with a given animal's jetting, the internal pressure distribution can range from nearly uniform to highly variable. We refer to a reference pressure,  $P_b$ , which is located on the inner surface on the axis of symmetry, and is indicative of the overall pressure dynamics and jet force. We will provide qualitative analysis of animal morphology with respect to this reference pressure, and will return to analyze the variation of pressure distribution on top of this reference in a later subsection. The reference pressure during the jellyfish jetting phase is shown in Fig. 3. During this period the circulation in the cavity can be described by a half-sink flow, and the jet circulation is given by the flux of shear flow carried with the expelled jet. Since we have access to the fluid velocity field, both inside and outside the subumbrellar cavity, the total cavity and jet circulation are calculated both from the velocity field and from analytical models derived for half-sink and vorticity flux sources, as derived in the **Methods** section. The circulation determined from both methods are then used to calculate pressure from (1). The internal pressure is also calculated with the standard Bernoulli equation approximation. Fig. 3 shows the pressure calculated by all three models, along with the pressure determined from the CFD simulation, which is considered to be truth.

It can be seen throughout this phase that the simple Bernoulli approximation (which is equivalent to calculating forces from momentum transfer at the jet opening) underestimates the actual pressure on the inner surface. One reason is the fact that the velar flap forms a conical nozzle during jetting which, along with the primary vortex ring formation, induces a converging radial velocity at the velar opening. This radially converging velocity results in downstream acceleration of the jet. The subsequent increase in pressure can be quantified by a non-zero gradient of the radial velocity in the axial direction, significantly increasing the vorticity flux rate as described in Krieg and Mohseni (2013) and summarized in Eq. (3). Previously, inabilities to sufficiently explain this increase in rate of vorticity and impulse transfer have led to heuristic coefficients like the additional 'discharge coefficient' (Johnson et al., 1972; O'Dor, 1988; O'Dor and Webber, 1986; Trueman, 1968),



**Fig. 4.** Refference pressure on the inner surface of the jellyfish cavity during the1/st refill phase.

requiring extensive empirical testing. Alternatively, by recognizing the coupled relationship between circulation and pressure dynamics, the effect that the radial velocity gradient has on vorticity flux can be incorporated using the parameterization employed by Krieg and Mohseni (2013) for different nozzle geometries.

Another reason for the large discrepancy between the Bernoulli approximation and actual pressure is that there are forces associated with accelerations of the unsteady flow; whereas, the standard Bernoulli equation assumes steady state flow. There is an unsteady form of the Bernoulli equation, but it requires solving for a velocity potential function, which is difficult in some cases, and impossible in others. The unsteady pressure forces correspond to the rate of change of half-sink circulation, which similarly scales with acceleration of the jet flow. The circulation based pressure analysis provides a quantitative measure of the effect these accelerations have on the internal pressure, as laid out in Methods. Other attempts have been made to quantify the effect of the fluid accelerations within biological jetting cavities. Anderson and DeMont, 2000 include an unsteady term in their model for squid mantle pressure. However, since this term depends on the axial location within the squid mantle, we will discuss accuracy of that modeling in a following subsection regarding pressure distribution throughout the inner surface.

It can be observed that the reference pressure predicted by (1) using the exact cavity and jet circulation drops below the actual reference pressure after about 0.15 s. Fortunately, if the system circulation is also predicted using analytical models of vorticity generation, the predicted reference pressure maintains accuracy throughout the jetting phase. This is because viscous dissipation in the jet results in a negative rate of change of circulation which contradicts an assumption of the pressure model that viscous forces are relatively small (large *Re*). Therefore, circulation dissipation doesn't directly affect the pressure dynamics the way that active generation of positive and negative circulation does; and the inviscid pressure model can be used on low *Re* jetting cavities with high accuracy, provided that the system circulation is also predicted using inviscid models.

Fig. 4 shows the actual reference pressure during the refill phase along with the accuracy of the three methods for calculating internal pressure. Note that an analytical model for impingement circulation is difficult to determine for the complex cavity geometry. Instead, for this analysis the circulation due to impingement is determined from the CFD velocity field for both circulation based

20

15

10

5

0

-5

Jetting Thrust (N)

models as discussed in Appendix A. It can be seen from this figure that the reference pressure is negative at the beginning of the refill phase due to the generation of negative vorticity in the incoming shear flow and the external half-sink flow. About halfway through the refill phase the formation of the impingement boundary layer reverses the direction of the pressure force corresponding to a transfer of momentum between the incoming flow and the cavity surface. The pressure predicted by the Bernoulli equation remains negative the entire refill phase, indifferent to the momentum transfer between internal fluid and the cavity.

The pressure predicted by Eq. (1) using the actual cavity and jet circulation again starts out significantly below the exact pressure at the beginning of the refill phase because of viscous dissipation in the previously expelled jet. However, later in the refill phase when dissipation in the jet region is less significant (the jet has settled to a more or less stable configuration), the increased pressure due to vortex ring impingement is well captured using the rate of change of actual cavity circulation. The technique utilizing analytical models for the characteristic sources of vorticity shows good agreement at the beginning stages of refill since dissipation in the jet is left un-modeled, and also shows good agreement when the jet first starts to impinge on the cavity boundary. However, towards the end of the refill phase this model drops below the actual pressure which can be attributed to vorticity cancellation between the internal vortex ring and the oppositely signed impingement boundary layer. Cancellation has no net effect on total cavity circulation, as positive vorticity eliminated in the impingement boundary layer is equal and opposite to the vorticity eliminated in the incoming vortex ring. This is the case in Krieg and Mohseni (2015) where the internal cavity geometry allows the impingement circulation to be modeled analytically. Despite the issues with vorticity cancellation, the accuracy of the modeled circulation technique is at all times better or equal to the accuracy of the Bernoulli approximation.

**Qualitative Analysis of Jellyfish Swimming** - Since the model quantifies dynamic pressure in terms of a specific set of vorticity generating mechanisms, isolated body motions of an animal can be analyzed with respect to how they drive the different mechanisms, and how this relates to the overall locomotion performance. In general there are two basic motions observed in the jellyfish body during the jetting cycle. The first is an almost uniform downward flexing of the bell, which comprises the majority of the jellyfish body. The second is an outward swinging of the velar flap, which is believed to be a passive process (Satterlie, 2002).

The velar flap, though not actively controlled, helps to increase the propulsive force at the onset of jetting, and reduce the energy expenditure at the peak of jetting. As can be inferred from (3) the circulation generation in the jet increases with increasing volume flux, but decreases with nozzle radius. Since the jetting in this species serves an escape purpose it is important to initiate a propulsive force as soon as possible and evade capture. At the beginning of jetting the velar flap extends straight in radially (refer to Fig. 7a) which keeps the nozzle radius at its minimum value at the start of jetting. Therefore, at the start of jetting even though the volume flux is still very low the rate of change of jet circulation is kept high by the small radius, and the required propulsive force is generated. At the peak of volume flux, the velar flap has extended outwards increasing the nozzle radius, relative to velar flap joint radius. At this stage the volume flux is more than adequate to generate the required propulsive force, so having the velar flap swing outward and increase the nozzle radius decreases the kinetic energy ejected in the wake (relative to the impulse transfer) and reduces the total energetic cost of locomotion.

The angle of the velar flap has an identical effect. At the onset of jetting, the flap is nearly a flat plate with a central opening which induces the maximum amount of converging radial velocity,



Circulation Pressure Model

CFD Solution

**Fig. 5.** Total jetting thrust, calculated from both the exact pressure distribution and the inviscid model for pressure distribution, during the first jet phase.

along with the maximum radial velocity gradient, which increases the rate of jet circulation growth and maximizes propulsive forces at the start of jetting. At the peak of volume flux, the velar flap forms more of an acute conical nozzle with a reduced radial velocity gradient. It was observed in Krieg and Mohseni (2013) that the rate of kinetic energy ejected in starting jets scales with both jet velocity cubed and the slope of the radial velocity gradient. Therefore, the more acute conical nozzle, like the increased nozzle radius, reduces the kinetic energy expelled in the wake relative to the impulse transfer, thus reducing the energetic cost once the required propulsive force has already been established.

The reference pressure on the inside of the cavity is indicative of the internal pressure dynamics, but from a practical standpoint many of the useful quantities when discussing jetting animal locomotion come from integrating terms involving the local pressure over the body surface. Two of the most important parameters are total thrust and propulsive efficiency. Here we will show how different pressure models influence the calculation of those two overall parameters, while an in depth qualitative discussion of internal pressure distribution is delayed until a following section.

Throughout the jetting cycle we compute the total jetting thrust from the predicted internal pressure distribution, using the reference pressure calculated from the inviscid circulation models, and compare it to the actual jetting thrust and that predicted by the Bernoulli approximation, all shown in Fig. 5. As might be expected the total jetting thrust and predicted jetting thrust have very similar features to the reference pressure. One notable difference is that the relative error of the Bernoulli approximation at the beginning of the jetting cycle is more significant for total jetting thrust. This is largely due to the non-uniformity of the internal pressure distribution during the initial phase, which will be discussed in the next section, but in general the accuracy of the total thrust calculation mirrors the accuracy of the reference pressure calculation for the jetting phase.

Throughout the rest of this paper we will discuss propulsive efficiency qualitatively in terms of increased/decreased propulsive output and increased/decreased total energetic cost. When it comes to the exact definition of propulsive efficiency there are several options to consider. However, given the unsteady thrust, unsteady velocity, and deformable body shape, an in depth discussion of appropriate efficiency parameter is beyond the scope of this work. Nevertheless, we calculate propulsive efficiency for the jellyfish during the jetting phase, which is most similar to tradi-

Table	1
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Table showing calculation of propulsive efficiency according to multiple methods. All values are given in percentages.

Method	Exact	Circulation model	Bernoulli	Froude efficiency	Rocket efficiency
1'st Cycle Efficiency	10.5	8.4	8.7	19.4	21.2
Quasi-Steady Efficiency	42.7	31.5	27.2	46.7	55.7

tional mobile vehicles, to examine the usefulness of different pressure models, and avoid the refilling phase which has more complex dynamics. As laid out in the **Methods** section the useful propulsive work is calculated as the product of total jet thrust and body velocity integrated over time, and the total work exerted by the jellyfish on the fluid is the product of the pressure distribution and the boundary velocity integrated over the inner surface and time. The efficiency is then the ratio of the two. We also calculate the efficiency according to Froude and rocket efficiency models, which are defined in terms of the ratio of jet to body velocity.

Table 1 shows the propulsive efficiency of a single jetting phase as calculated from different methods. Since the body velocity is critical to determining the efficiency we consider two cases: the efficiency of the first jetting cycle, where the body is accelerating from rest, and the efficiency of a jetting phase once the body has reached a quasi-steady forward velocity. As would be expected, the efficiency values show that the Froude and rocket efficiency models do significantly better for the case when the jellyfish has reached a relatively steady swimming speed, given that both models assume constant body velocity. However, even for this case both models overpredict the swimming efficiency, with the Froude efficiency model showing better accuracy than the Rocket efficiency model. When it is assumed that the internal pressure is uniform and equal to the pressure at the nozzle predicted by the Bernoulli equation, the total force is significantly underpredicted, as was shown in Fig. 5. However, the total work being done on the fluid is similarly calculated much lower than the average value. As a result the Bernoulli pressure approximation does a much better job at calculating propulsive efficiency than total force, and has roughly equivalent accuracy to the circulation based pressure model for the1/st pulsation case, but slightly worse at quasi-steady swimming speed. The refill phase invariable lowers the total propulsive efficiency for a full cycle, and likely decreases the accuracy of the Froude, rocket, and Bernoulli efficiency models due to the increased complexity of internal dynamics. That being said, examining the effect of the refilling phase on propulsive efficiency would require a more in depth analysis of energetics associated with the fluid doing work on the body surface and appropriate efficiency definitions, which is beyond the scope of the current investigation, so that will be left for future studies.

## Analysis of dragonfly larvae (Aeshnidae sp.) jetting locomotion

Roh and Gharib simultaneously measured thrust of a dragonfly larvae and the surrounding fluid velocity field, and examined the accuracy of circulation based pressure modeling of Krieg and Mohseni (2015) within the appendix, "Thrust Analysis" (Roh and Gharib, 2018). They started by calculating the pressure/thrust with just the circulation due to vorticity flux (3). Since the anal valve/prongs create essentially a straight tube nozzle, limiting any converging radial velocity, this is roughly equivalent to the Bernoulli approximation. As can be seen in figure S4 of Roh and Gharib (2018), this method is unable to capture the unsteady dynamics in the thrust profile, and largely over-predicts negative thrust during refill. They were able to very accurately calculate the thrust over the entire time by adding the circulation due to the half-sink vorticity (4) for both jetting and refilling, and removing the vorticity flux term during refilling (see figure S7



**Fig. 6.** Schematic diagram of a dragonfly larvae and the geometry of the hindgut which is used for jet propulsion. Anatomy not drawn to scale.

in Roh and Gharib (2018)). Here we present additional qualitative analysis of larvae morphology based on the thrust data from that appendix.

We argue here that the modeling accuracy during refilling with just the unsteady half-sink term is due to nozzle geometry of the larvae. During jetting the only two sources of circulation are vorticity flux and half-sink terms, which Roh and Gharib used in their study producing high accuracy calculated thrust. During refilling, impingement vorticity exists in addition to the other two sources. As can be seen from Fig. 6 the larvae has a bottleneck between the nozzle and the hindgut chamber. It is our contention that this geometry induces impingement right at the onset of refilling, effectively canceling the circulation due to vorticity flux throughout the remainder of the refilling phase. Thus Roh and Gharib were able to accurately calculate thrust with just the half-sink term.

It was observed in Krieg and Mohseni (2015) that the net impulse transfer to a prototype unsteady jet thruster over an entire refilling phase was nearly zero for every volume flux program tested. This was largely due to the fact that the incoming vortex ring impinged upon a flat wall perpendicular to its central axis. Since the vortex ring traveled very close to this boundary before being slowed down and expanded, the circulation growth in the impingement boundary layer was nearly equivalent to the internal vorticity flux, giving a zero net impulse. The equivalent circulation in the impingement boundary layer also resulted in total cancellation/annihilation of the internal vortex ring as the two regions merged together.

Although the net impulse transfer was zero, the total energy required to refill the cavity is not, because energy cannot be recovered through impingement the way that impulse is. Furthermore, it was shown that refill work decreased steadily as we reduced the distance for the incoming vortex ring to travel before impingement. In essence, there is a dynamic oscillation in internal pressure as the component of circulation dominating the pressure shifts from the vorticity flux term to the impingement term. By inducing the impingement at an earlier stage of the refill phase, the magnitude of the pressure oscillation is reduced, thus reducing the required energy input before impingement begins to assist in cavity deformation. Hypothetically, the minimum refill work would be achieved if the impingement occurs simultaneously with vorticity flux, in which case the refill work is just the product of pressure due to the unsteady half-sink circulation multiplied by small cavity deformation velocity at the onset of refilling. This is the case for the dragonfly larvae cavity/nozzle geometry.

In contrast, impingement circulation in the subumbrellar cavity of *Sarsia tubulosa* is significantly less than the vorticity flux circulation over the entire refill phase. For this species the incoming vortex ring begins to be slowed down by a weak impingement boundary layer on the outward edge of the cavity surface before it has a chance to come in close enough to the inner surface near the axis and create a substantial impingement boundary layer. This is bad for propulsion because it results in a net negative impulse transfer during refilling, but it allows the development of a stable vortex ring inside the bell cavity. We hypothesize that the internal vortex ring serves an additional purpose for *Sarsia tubulosa*, possibly, aiding in respiration.

Respiration in hydrozoans (and scyphozoans) does not take place in gills or lungs. Rather oxygen is absorbed through the skin of the subumbrellar cavity, and is either stored in the mysoglea or consumed in the coelenteron. As such, the water adjacent to the inner surface likely becomes oxygen depleted fairly quickly. Vortex rings are known to create significant mixing of source fluid and the fluid they are ejected into (James and Madnia, 1996; Sau and Mahesh, 2007). Having a persistent internal vortex ring would continually cycle the oxygen depleted water near the surface with water brought in with the ring refreshing the oxygen supply allowing for higher respiration rates. This hypothesis is supported by the relatively high rates of respiration observed in Sarsia tubulosa. As was observed in Møller and RiisgÅrd, 2007, the respiration rates of S. tubulosa are around five times the respiration rates of A. aurita and around ten times the respiration rates of A. vitrina and A. victoria. These three contrasting species all have oblate body shapes and propel themselves with more of a rowing process than jetting (Sahin et al., 2009) which does not result in a large persistent internal vortex. The more oblate species are also observed to have a higher propulsive efficiency (Sahin et al., 2009). In addition, Møller and RiisgÅrd, 2007 observed that S. tubulosa has respiration rates about five times greater than S. princeps. Despite the fact that both of these species have prolate body shapes, and produce distinct propulsive jets, S. princeps has an oral arm which extends along the axis of symmetry inside the subumbrellar cavity preventing any stable persisting internal vortex ring, which could explain the lower respiration rate.

#### Analysis of squid (Loligo pealei) jetting locomotion

In this section we provide a deeper examination of squid jetting, qualitatively, based on previously reported funnel/vent morphology (Anderson and Grosenbaugh, 2005) and previously reported data on mantle volume (Anderson and DeMont, 2000). Squid mantles contract radially to drive jet motion, and the contraction is observed to be nearly uniform along the length (Anderson and Grosenbaugh, 2005). When refilling, squid move their head away from the body, opening vents for fluid entering the mantle cavity. During jetting they retract the head closing the vents, forcing the jet through the funnel, which is known to actively contract during jetting. The refilling of squid mantle cavities takes place through vents behind the head, in addition to the funnel (refer to Fig. 1 from Anderson and Grosenbaugh (2005)). This increases the effective opening radius, R, reducing the circulation generated by both the vorticity flux (3) and half-sing (4) vorticity, thus reducing work required for refilling. It is also possible that the vents result in impingement at the onset of refilling similar to the dragonfly larvae, but that cannot be determined definitively without additional experimental data.

Squid also utilize a unique velocity program (meaning the time history of jet velocity over an entire cycle), whereby ejected fluid undergoes drastic acceleration when switching between jetting and filling, and maintains a nearly constant velocity otherwise. For the jellyfish, the rate at which volume is ejected is almost completely controlled by the collapsing bell, being negligibly affected by the motion of the velar flap. The bell contraction employed by *Sarsia tubulosa* corresponds to a nearly sinusoidal volume flux program. The sinusoidal program results in very large jetting forces at the peak volume flux but also requires substantial work to drive the flow since the peak in pressure occurs simultaneously with the peak in inner cavity surface velocity, as observed in Krieg and Mohseni (2015). For *S. tubulosa*, jetting propulsion is often used as an escape mechanism to avoid capture. This purpose matches well with the bell contraction driving a sinusoidal program with large propulsive force at the expense of required energy input, since the survival of the organism takes precedent over the efficiency of locomotion.

The squid Loligo pealei, on the other hand, is observed to have an impulsive jet velocity program. Figs. 5 and 6 of Anderson and DeMont, 2000 show measured values of squid mantle volume vs. time over multiple jetting cycles. It can be seen that the volume change has a nearly constant slope during both jetting and refilling, corresponding to a nearly constant jet velocity throughout each phase with massive acceleration when switching between phases. As was demonstrated in Krieg and Mohseni (2015), using an engineered jet thruster, an impulsive velocity program like this results in a peak pressure at the onset of jetting due to the half-sink circulation, which coincides with the minimum cavity deformation velocity, followed by a nearly constant pressure due to vorticity flux and nearly constant boundary velocity. Since the power required to create the flow is the product of pressure and cavity boundary velocity, the total work required is significantly reduced by offsetting the peak in pressure and velocity. Hence impulsive velocity programs have a higher propulsive efficiency (all other things being equal). Therefore, the unsteady pressure dynamics within squid helps to explain recent observations of propulsive efficiency in squid much higher than previously thought possible (Bartol et al., 2008, 2009).

#### Variation in internal pressure distribution S. tubulosa

In several cavity-jet systems the pressure inside the cavity can be considered uniform, as is assumed by most studies on biological jet propulsion, and is the case in synthetic jet actuators (Gallas et al., 2003). However, cavity-jet systems with a high degree of unsteadiness, relatively small openings, with respect to cavity volume, and relatively large time scales tend to exhibit larger variations in internal pressure. For the animals discussed in this study, the dragonfly larvae can be considered to have uniform pressure, given its small cavity volume and large anal valve, but squid and jellyfish cannot. In this section we discuss modeling techniques to determine the internal pressure distribution, using the jellyfish as an example since we have the exact pressure field calculated by CFD to use for validation.

Anderson and DeMont were among the first to discuss possible non-uniformity in the internal pressure of jetting marine animals (Anderson and DeMont, 2000). In that study they model the pressure internal to the squid Loligo pealei as the sum of the linear momentum transfer at the funnel (Bernoulli approximation) and an additional unsteady term which takes into account acceleration of fluid inside the mantle cavity. The authors of that paper strongly caution other researchers from treating internal pressure measurements as uniform cavity pressure measurements, suggesting that some previous experimental inconsistencies might have come from this assumption. In this section we calculate internal pressure by integrating the momentum equation along a viscosity free path along the cavity surface, as presented in Krieg and Mohseni (2015) and summarized in the Methods section, Eq. (5). We also describe the accuracy of the unsteady pressure term described by Anderson and DeMont, 2000. Although this term is ul-



**Fig. 7.** Snapshots of *Sarsia tubulosa* body shape, vorticity contours, and viscosity free path,  $\delta$ , at 0.04 s (a) 0.13 s (b) 0.17 s (c) and 0.27 s (d). Positive vorticity is given by red contours, and negative vorticity by blue contours. Position axes are given in cm. Vorticity field generated through CFD simulation (Sahin and Mohseni, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

timately shown to be less accurate than the integral equation proposed in Krieg and Mohseni (2015), there is a strong correlation shown between the unsteadiness (acceleration) of the jet flow and the non-uniformity of the internal pressure distribution, as predicted by Anderson and DeMont, 2000.

Fig. 7 shows the jellyfish body at 4 characteristic times during the jet phase, along with vorticity contours and the viscosity free path used to determine the full pressure distribution. It can be seen that during pulsation the viscosity-free path is mostly adjacent to the cavity surface except at the velar flap where there is a boundary layer associated with the half-sink flow which must be avoided.

The inner surface pressure distribution was calculated at the same instances depicted in Fig. 7. The exact pressure distribution is plotted alongside the calculated pressure distribution in Fig. 8. This figure shows very good agreement, suggesting that the thin boundary layer approximation is valid over this period. It can also be observed that during the initial and final instances of jetting, where the circulation and pressure dynamics are dominated by the acceleration/half-sink terms, the internal pressure shows the largest variation. Whereas during the middle of the jetting phase, when circulation dynamics are dominated by vorticity flux terms, the pressure distribution is more uniform. This reinforces the claim made by Anderson and DeMont, 2000 that the acceleration of fluid within squid mantle cavities leads to non-uniform internal mantle pressure distributions. Fig. 8a also has the pressure distribution

as calculated according to equation (16) in Anderson and DeMont, 2000 for comparison. It can be seen that the accuracy of that equation suffers from both the issues associated with the Bernoulli approximation, as described in the previous subsection, but also from the assumption that all fluid within the cavity at a given axial location accelerates together, which is likely more valid for prolate squid bodies than oblate jellyfish bodies. Despite the model accuracy issues, Anderson and DeMont, 2000 clearly identified the correspondence between non-uniformity in the internal pressure distribution and the existence of unsteady/acceleration terms. In fact the correlation is exact enough that quantifying the magnitude of non-uniformity has been used as a feedback method for determining relative contributions from half-sink vs. vorticity flux circulation to internal pressure of a jellyfish inspired soft robot (Krieg et al., 2015).

During the refill phase the fluid being ingested into the jellyfish rolls into a vortex ring which has little room to grow before impacting the inner surface of the jellyfish body. The existence and dynamics of this incoming vortex ring have a strong effect on the internal pressure dynamics. Fig. 9 shows the vorticity contours inside the jellyfish at four characteristic instances during the refill phase of the jetting cycle, as well as the viscosity free path near the cavity surface used to integrate the momentum equation and calculate the pressure distribution. At later stages of refilling the boundary layer on the cavity surface due to vortex ring impingement separates from the cavity surface in a small region violating



Fig. 8. Pressure distribution over the inner surface of the jellyfish Sarsia tubulosa at 0.05 s (a) 0.14 s (b) 0.18 s (c) and 0.28 s (d). The approximated pressure distribution is calculated from (5) along the path shown in Fig. 7 for each time step.

the thin boundary layer approximation, and the integration path must cut through this viscous layer (as depicted in Fig. 9). In general this decreases the accuracy of the pressure model, but not to a critical extent.

Fig. 10 depicts the pressure distribution over the cavity surface as well as the pressure distribution calculated by integrating the momentum equation along the path shown in Fig. 9 at every instance. Unlike the jetting phase, where the shape of the internal pressure distribution was generally coupled with the sign and relative magnitude of the internal half-sink circulation, the shape of the pressure distribution during the refill phase is closely related to the location and size of the primary internal vortex ring. We can see from Fig. 10a that at the start of refill there is a monotonic decrease in pressure along the surface towards the opening. As a vortex ring begins to form a local minimum develops in the internal pressure distribution, at the location closest to the ring, which grows in magnitude back along the inner surface in correspondence with the motion and growth of the internal vortex ring. In the later stages of the refill phase, Fig. 10c and d, the growth of the impingement boundary layer and transfer of hydrodynamic impulse to the jellyfish body result in a positive reference pressure, corresponding to forward thrust. Interestingly, even though the impingement boundary layer results in a reversal of reference pressure and total thrust, the pressure distribution relative to that reference pressure is nearly identical to previous stages, and dictated by the internal vortex ring. Here the circulation based pressure model allows a mechanism whereby thrust becomes positive during refilling to be quantified in terms of vorticity growth in the impingement boundary layer. However, this study is not the first to identify such a mechanism. Sahin et al., 2009 discuss how flexibility in the velar flap of the jellyfish *A. victoria* allows it to swing a forward facing surface into a low pressure zone behind the incoming vortex thus generating a positive thrust during refilling. Gemmel *et al.*, refer to this mechanism as passive energy recapture (Gemmell et al., 2013; 2018).

#### Methods and materials

#### Circulation based pressure model description

In the most general sense the biological jetting problem can be reduced to a flexible body with an internal cavity, and contraction of the body cavity ejects fluid through some opening as shown in Fig. 1. By the methodology of Krieg and Mohseni (2015) the pressure is first determined at a reference location on the body,  $P_b$  shown in Fig. 1, in terms of surrounding fluid circulation, and cavity boundary deformation. This is possible due to a simplification in the momentum equation along the central axis from symmetry conditions, and the realization that velocity integrals along this



**Fig. 9.** Snapshots of *Sarsia tubulosa* body shape, vorticity contours, and viscosity free path,  $\delta$ , at characteristic times during refilling 0.38 s (a) 0.44 s (b) 0.51 s (c) and 0.55 s (d). Positive vorticity is given by red contours, and negative vorticity by blue contours. Position axes are given in cm. Vorticity field calculated from CFD simulation velocity field (Sahin and Mohseni, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

path are contained in the total circulation of the jet and cavity regions.

$$\frac{P_b}{\rho} = \frac{d\Gamma_{\text{Jet}}}{dt} + \frac{d\Gamma_{\text{Cav}}}{dt} - \frac{d}{dt} \left( \int_{\sigma} \vec{u}_{\sigma} \cdot \hat{t} \, ds \right) + \frac{1}{2} u_b^2, \tag{2}$$

Here  $\rho$  is the fluid density,  $\Gamma_{\text{Jet}}$  is the total circulation in the jet region,  $\Gamma_{\text{Cav}}$  is the total circulation in the cavity region (see Fig. 1 for a definition of the cavity and jet regions, respectively),  $u_b$  is the velocity of the body surface at the reference point,  $\vec{u}_{\sigma}$  is the velocity vector at a point on the cavity surface boundary,  $\sigma$ , and  $\hat{t}$  is a unit vector tangent to that curve, as is shown in Fig. 2b. The term  $\frac{d}{dt} \left( \int_{\sigma} \vec{u}_{\sigma} \cdot \hat{t} \, ds \right)$  is the rate of change of circulation in the cavity specifically due to boundary stretching.

The benefit of the circulation based pressure modeling is that circulation can be considered constant throughout many flows, with the exception of small localized areas where viscosity plays a large role and leads to the creation of vorticity. For the rest of the flow vorticity is spread, but conserved. Circulation is the integral of vorticity in a given region, thus the rate of change of circulation can be modeled by a series of vorticity source terms. We described the 4 sources of vorticity common to any cavity jet system in the introduction, which include *vorticity flux* terms, *half-sink* terms, *boundary stretching* terms, and *vortex impingement terms*. A detailed description of each term along with analytical modeling and validation is provided in Krieg and Mohseni (2015). Here we summarize these models so that the circulation in a biological system can be modeled without completely solving the flow field. Let us start by discussing the component of circulation due to boundary stretching. This component, which is defined as  $\int_{\sigma} \vec{u}_{\sigma} \cdot \hat{t} \, ds$ , is part of the total cavity circulation. If we define a modified cavity circulation with this component removed,  $\tilde{\Gamma}_{\text{Cav}} = \Gamma_{\text{Cav}} - \int_{\sigma} \vec{u}_{\sigma} \cdot \hat{t} \, ds$  and insert into the full pressure Eq. (2), we are able to cancel the boundary stretching terms, resulting in the simplified Eq. (1), given earlier in the paper, where  $\tilde{\Gamma}_{\text{Cav}}$  is the circulation in the cavity due to vorticity flux terms, half-sink terms, and impingement terms alone. Therefore, those are the only components of circulation which need to be modeled from a pressure analysis standpoint.

When a fluid jet is forced through an opening into resting fluid, a viscous shear layer is formed at the edge of the opening and is carried into the resting fluid with the jet. The vorticity in this shear layer contributes to the vorticity flux component of circulation,  $\Gamma_{VF}$ ; and for circular openings, rolls into the leading vortex ring. On the other side of the opening fluid must converge towards the orifice before being ejected. This type of flow was modeled in Krieg and Mohseni (2013) as half of the flow created by a uniform plate of velocity sinks at the circular opening, hence the name *half-sink* circulation,  $\Gamma_{HS}$ . During jetting, vorticity flux terms contribute to circulation in the jet region and half-sink terms contribute to cavity circulation. During refill, this relationship is reversed. The rate of change of circulation due to vorticity flux was modeled for jet flows with non-zero radial velocity (like unsteady jets) in Krieg and Mohseni (2013) with respect to velocity profiles at the



Fig. 10. Pressure distribution over the inner surface of the jellyfish Sarsia tubulosa at 0.38 s (a) 0.44 s (b) 0.51 s (c) and 0.55 s (d). The approximated pressure distribution is calculated from (5) along the path shown in Fig. 9 for each time step.

nozzle plane. Those velocity profiles were also parameterized with respect to nozzle geometry, cavity deformation, and jet stroke ratio. Specifically these conditions can be uniquely defined by the volume flux,  $\dot{\Omega}$ , nozzle radius, *R*, and the non-dimensional slope of the radial velocity gradient,  $k_{2}^{*}$ .

In terms of these parameters the vorticity flux circulation can be approximated,

$$\frac{d\Gamma_{\rm VF}}{dt} = \frac{1}{2} \left(\frac{\dot{\Omega}}{\pi R^2} + V\right)^2 (1 + k_2^\star). \tag{3}$$

In this equation the velocity of the jellyfish, *V*, has been introduced to account for the motion of the flux boundary. An exact description of these parameters and their dynamic relationship to unsteady jet phenomena like vortex ring formation is provided by Krieg and Mohseni (2013). Here we provide a short summary of appropriate values for the biological examples.

For long tubular nozzles which make the jet flow parallel prior to ejection, the value of  $k_2^*$  rises to a peak at the onset of pulsation due to the induced velocity of the forming vortex ring, then drops to zero when the ring moves further downstream. Conical nozzles have a similar peak in  $k_2^*$  due to vortex ring formation but the peak is less observable since the geometry of the nozzle induces a constant radial velocity gradient, even after the primary vortex ring has traveled downstream, on the order of  $k_2^* \approx 0.8$ . The velar flap of *Sarsia tubulosa* is more conical, and for modeling purposes we will approximate the radial velocity gradient as a constant value throughout the jetting cycle,  $k_2^* = 0.8$ , for both jetting and refilling. The longer, less-steep, nozzles, such as squid funnels or dragon-fly larvae anal prongs, create a small degree of radial velocity. For those geometries the gradient slope can be approximated  $k_2^* \approx 0.4$ .

The circulation of one half of the uniform sink flow was derived and observed to be proportional to the total strength of the sink, which is equal to the volume flow rate at the nozzle exit,  $\dot{\Omega}$ . The rate of change of the half-sink circulation,  $\Gamma_{\text{HS}}$ , is given by,

$$\frac{d\Gamma_{\rm HS}}{dt} = -C_{\rm HS}\frac{\ddot{\Omega}R - \dot{\Omega}\dot{R}}{R^2},\tag{4}$$

where  $C_{\text{HS}}$  is a constant which depends on the opening geometry. For steep conical nozzles like the jellyfish velar flap,  $C_{\text{HS}} = 0.34$ ; whereas, longer nozzles like the squid funnel or dragonfly larvae anal prongs have  $C_{\text{HS}} = 0.15$ . These coefficients are determined from a numerical solver provided in Appendix A of Krieg and Mohseni (2015).

During jetting, the circulation due to vorticity flux contributes to the total jet circulation and the half-sink terms contribute to the cavity circulation. During refilling, their respective roles are reversed, but the velocity parameterization (i.e.  $k_2^*$  and  $C_{\text{HS}}$ ) at the opening remains the same.

The final component of cavity circulation which needs to be modeled is the circulation due to impingement of vortex rings on

the inner cavity surface. When the vortex ring comes close to the cavity surface it induces a very large tangential velocity, but this is opposed by friction on the surface (the no-slip condition) giving rise to a boundary layer of opposite sign vorticity. The circulation due to vortex ring impingement was modeled adequately with stream functions during the refilling of a synthetic pulsed jet thruster cavity (Krieg and Mohseni, 2015). However, that modeling is only valid when the vortex ring impinges upon a flat surface perpendicular to the central axis. Describing a model for circulation due to vortex ring impingement valid for any general cavity boundary geometry is beyond the scope of this manuscript. Instead we will leave modeling and validation of general impingement circulation for future publications, where all complications can be handled in full detail. However, for the analysis of the jellyfish example, the impingement circulation will be calculated directly from the available CFD flow field (see Appendix A), and we discuss impingement circulation qualitatively for the other examples.

With the vorticity source terms defined in (3) and (4), the reference pressure on the inner surface can be calculated by inserting these terms into (1) for cavity and jet circulation.

Understanding the evolution of circulation allows us to calculate the exact pressure at the reference location,  $P_b$ . In many cases the internal pressure can be considered uniform, but for cases where the nozzle/opening is large compared to the cavity characteristic length scale, the next step is to calculate the pressure distribution over the entire inner cavity surface, relative to the reference pressure. This is done, following the method in Krieg and Mohseni (2015), by integrating the momentum equation along a viscosity-free path,  $\sigma$ , which is at all points either adjacent to the cavity surface or adjacent to boundary layers attached to the cavity surface. An example of such a path is shown in Fig. 2b for a general body shape. By doing so the pressure at every location can be calculated by,

$$\frac{P(s)}{\rho} = \frac{P_b}{\rho} - \frac{1}{2} \left( \vec{u}_{\sigma} \cdot \hat{t} \right)^2 - \int_0^s \frac{\partial}{\partial t} \left( \vec{u}_{\sigma} \cdot \hat{t} \right) + \vec{u}_{\sigma} \cdot \hat{n} \frac{\partial}{\partial \hat{n}} \left( \vec{u}_{\sigma} \cdot \hat{t} \right) d\tilde{s}, \quad (5)$$

where  $\hat{n}$  is the unit vector normal to the curve  $\sigma$  at point *s* along its length and  $\tilde{s}$  is a dummy variable for the position *s*. These characteristic unit vectors are depicted in Fig. 2b.  $\vec{u}_{\sigma} \cdot \hat{t}$  is only non-zero at locations where the cavity surface has an attached boundary layer and  $\vec{u}_{\sigma} \cdot \hat{n}$  is provided by the body deformation.

By utilizing these models we are able to predict the pressure distribution within unsteady, complex geometry, biological, jetting cavities, throughout the entire locomotion cycle.

#### Available data for analyzing jetting propulsion in marine organisms

In this subsection we will describe the data available for different biological examples and how that data will be analyzed with respect to the new pressure model.

**Jellyfish Data** - By far the most complete data set we have to work with comes from a direct numerical simulation (DNS) of a *Sarsia tubulosa* jellyfish from Sahin and Mohseni, 2008. The exact body shape history of two species of jellyfish, *Sarsia tubulosa* and *Aqueoria Victoria*, were recorded at 60 Hz by Dr. Sean Colin and were discretized in Sahin and Mohseni, 2008 and Sahin et al., 2009. The flow-field around the jellyfish during locomotion was calculated by Sahin et al. (Lipinski and Mohseni, 2009; Sahin et al., 2009; Sahin and Mohseni, 2008, 2009) using an arbitrary Lagrangian-Eulerian Navier-Stokes solver. The code solved for pressure and velocity on a non-uniform  $1.8 \cdot 10^5$  point grid. Since data from this study includes both the full pressure/velocity field and body discretization, it allows us to calculate vorticity source terms from the analytical models, and the vorticity field to measure those terms directly.

#### Table 2

Summary of different methods that can be used to calculate the reference pressure inside jetting cavities. Specifically, the second method requires that the entire vorticity field in and around the body are known.

Method	Description
Bernoulli Equation	Reference pressure calculated from the Bernoulli equation assuming constant inner pressure and steady flow.
Exact Circulation	Reference pressure calculated from (1), with $d\tilde{\Gamma}_{cav}/dt$ and $d\Gamma_{Jet}/dt$ calculated from the vorticity field of the DNS flow solution (Sahin and Mohseni, 2009; Sahin et al., 2009).
Modeled Circulation	Reference pressure calculated from (1), with $d\tilde{\Gamma}_{Cav}/dt$ and $d\Gamma_{Jet}/dt$ calculated from inviscid circulation models (3) and (4).

The discretized body shape gathered for Sahin et al., 2009 is used at every step to describe the boundary curve,  $\sigma$ , in the cylindrical coordinate system. The total volume inside the cavity is  $\Omega = \pi \int_{\sigma} r(s)^2 \hat{t} \cdot \hat{z} ds$ , where *r* is the radial position of point *s* along the curve  $\sigma$ . The volume flux across the opening of the cavity is the rate of change of the cavity volume,  $\dot{\Omega}$ . The exact circulation in the jet region is calculated at any instant by integrating the DNS vorticity field,  $\omega$ , over the region,  $\Gamma_{\text{Jet}} = \int_{A_{\text{Jet}}} \omega dA$ , where  $A_{\text{Jet}}$  is the area of the jet region, and *dA* is a differential unit of area. The total circulation in the cavity region is determined from a similar surface integral of the vorticity field.

Given the wealth of available data for this case, we use it as a representative example to compare accuracy and advantages of three different techniques to model pressure which are summarized in Table 2. The first technique is the standard approach where pressure is calculated from jet velocity using the Bernoulli equation, and is equivalent to deriving the pressure from the axial momentum transfer at the nozzle. The second technique is to calculate pressure from (1) where circulation in the cavity and jet regions is integrated from the DNS vorticity field in those locations. Obviously this method requires a knowledge of the entire vorticity field, so it has little potential for application in practice, but it does allow us to draw useful conclusions about the circulation based pressure modeling. The third technique is to calculate pressure from (1) where jet and cavity circulation are calculated from analytical models for the characteristic vorticity sources (i.e. vorticity flux (3) and half sink (4) circulation).

**Dragonfly Larvae Data** - Roh and Gharib performed an excellent study on the jetting of dragonfly larvae, family *Aeshnidae* (Roh and Gharib, 2018), in which they measured jet flow properties with digital particle image velocimetry (DPIV) and directly measured thrust produced by the larvae. Although we do not have access to this raw data, the authors, fortunately, provided an appendix where they calculated thrust from pressure using methods 1 and 3 from Table 2, and validated against measured thrust. We summarize these results and use them in additional qualitative analysis regarding body morphology of jetting animals.

**Squid Data** - Of all the jetting organisms mentioned, squid have arguably the most impressive propulsive output (O'Dor, 1982; O'Dor and Webber, 1991). The analysis of squid mantle internal pressure dynamics within this study is mostly limited to a qualitative discussion of how body morphology and jet velocity characteristics create favorable pressure distributions to enhance propulsion. The jet velocity program of *Loligo pealei* can be determined from Anderson and DeMont, 2000. The existence of converging radial velocity in the jet can be inferred from DPIV data in Anderson and Grosenbaugh (2005). The shape and behavior of the funnel and mantle cavity are discussed in a number of studies including (Anderson et al., 2001; Anderson and DeMont, 2000; Johnson et al., 1972).

## Calculating propulsive efficiency

The propulsive efficiency of an organism/vehicle is the ratio of the useful propulsive work generated in an action to the total work required to create that propulsion. The useful propulsive work done is the integral of the propulsive force along a resulting trajectory (product of thrust and distance traveled for linear steady motion), which can alternatively be calculated as the product of propulsive force and body velocity integrated over time.

In this study propulsive efficiency is only calculated for the jellyfish, where exact, instantaneous body geometry is known. The body velocity,  $v_b$  is found by calculating the jellyfish body geometric center at each instant and then taking the derivative with respect to time. It is assumed that the body has a roughly uniform density so that the center of mass coincides with the centroid. The total thrust is calculated by taking the projection of internal pressure in the axial direction and integrating over the inner surface. The total instantaneous power required to create the propulsion, excluding any metabolic losses, is calculated as the internal pressure multiplied by the surface boundary velocity projected into the normal direction and integrated over the inner surface.

$$T_{prop} = 2\pi \int_0^s r P \hat{n} \cdot \hat{z} ds$$
  

$$P_{tot} = 2\pi \int_0^s r P u_{\sigma} \cdot \hat{n} ds$$
(6)

Here  $T_{prop}$  is the propulsive force,  $P_{tot}$  is the total power required to create propulsion, and  $\hat{z}$  is the unit vector in the axial direction. Therefore, the propulsive efficiency is,

$$\eta_{prop} = \frac{\int_{t_0}^{t_f} T_{prop} \nu_b \, dt}{\int_{t_0}^{t_f} P_{tot} \, dt} \tag{7}$$

Often, a moving body is assumed to have reached a steady state with a constant propulsive force. Under these assumptions the propulsive efficiency can be related to the ratio of the body velocity and the exhaust velocity,  $v_e$ . The two standard efficiency calculations based on this velocity ratio are the *Froude* efficiency, for vehicles that accelerate the surrounding fluid to generate thrust, and the *Rocket* efficiency for vehicles that accelerate an internal reservoir of material to generate propulsion.

$$\eta_{Froude} = \frac{2}{1 + \frac{v_e}{v_b}} \qquad \eta_{Rocket} = \frac{2\frac{v_b}{v_e}}{1 + \left(\frac{v_b}{v_e}\right)^2} \tag{8}$$

In order to provide the velocity ratio for these efficiency models, the exhaust velocity  $v_e$  is taken as the time average of the jet velocity over a period of time, and the body velocity  $v_b$  is also taken as the mean body velocity over the same period of time.

## Conclusion

Through this study we demonstrate that a novel methodology for modeling internal pressure of jetting cavities with respect to evolution of circulation of the system can be applied to low *Re* marine organisms including jellyfish, dragonfly larvae, squid, and other cephalopods. Despite the fact that the model is derived assuming no viscosity, it accurately predicts the pressure distribution inside the centimeter scale *Sarsia tubulosa*, provided that the circulation is likewise calculated from inviscid models. We demonstrate that the internal pressure distribution inside jetting organisms can actually be very non-uniform and accurately captured by the pressure model. During jetting the non-uniformity is dictated by the amount of fluid acceleration taking place, whereas, during refilling the non-uniformity is controlled by the location and strength of the internal vortex ring. Furthermore, we demonstrate that the model allows the purpose and propulsive function of isolated body motions to be identified independently. In the case of *Sarsia tubulosa* the bell contraction is optimized to generate a maximum propulsive force at the expense of efficiency for survival maneuvers, the motion of the velar flap is optimized to induce a large propulsive force at the onset of pulsation, but then reduce energetic cost once the propulsive force has been established. Additionally, the refilling, which results in a persisting internal vortex ring, is shown to not be optimized for efficient propulsion, and most likely serves to enhance respiration.

## **CRediT** authorship contribution statement

**Michael Krieg:** Formal analysis, Writing - review & editing. **Kamran Mohseni:** Funding acquisition, Data curation, Writing - review & editing.

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## Appendix A. Calculating Impingement circulation

We take advantage of the fact that the vortex ring created with the incoming fluid and the impingement boundary layer have opposite magnitude vorticity. The fluid simulation provides the entire vorticity field inside the cavity,  $\omega$ , and we subsequently map out regions which have either positive or negative vorticity. During the filling phase, the incoming vortex ring has negative vorticity; whereas, the impingement boundary layer has positive vorticity. During subsequent jetting phases, the remaining vortex ring from the refill phase and corresponding impingement boundary layer remain, but there is also a region of positive vorticity associated with the internal half-sink flow. During both phases there is both positive and negative vorticity associated with stretching and shrinking of the inner surface.

The total impingement boundary layer circulation,  $\Gamma_l$ , is determined by integrating the positive vorticity regions and subtracting off the positive circulation due to boundary layer stretching and subtracting off half-sink circulation during jetting phases.

$$\Gamma_{I} = \begin{cases} \int_{A_{\omega^{+}}} \omega \, dA - \int_{\sigma^{+}} \vec{u}_{\sigma} \cdot \hat{t} \, ds & : \text{ Refilling Phase} \\ \int_{A_{\omega^{+}}} \omega \, dA - \int_{\sigma^{+}} \vec{u}_{\sigma} \cdot \hat{t} \, ds - \Gamma_{HS} & : \text{ Jetting Phase} \end{cases}$$
(9)

Here the notation  $A_{\omega^+}$  denotes the area inside the avity with positive vorticity, and  $\sigma^+$  denotes the length along the cavity boundary,  $\sigma$ , with negative tangential velocity gradient,  $\partial \vec{u}_{\sigma} / \partial \hat{t}$  (which corresponds to positive stretching vorticity).

#### References

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- Anderson, E.J., DeMont, M.E., 2000. The mechanics of locomotion in the squid *loligo pealei*: locomotory function and unsteady hydrodynamics of the jet and intramantle pressure. J. Exp. Biol. 203 (18), 2851–2863.
- Anderson, E.J., Grosenbaugh, M.A., 2005. Jet flow in steadily swimming adult squid. J. Exp. Biol. 208, 1125–1146.
- Anderson, E.J., Wuinn, W., DeMont, M.E., 2001. Hydrodynamics of locomotion in the squid Loligo pealei. J. Fluid Mech. 436, 249–266.
- Bartol, I.K., Krueger, P.S., Stewart, W.J., Thompson, J.T., 2009. Hydrodynamics of pulsed jetting in juvenile and adult brief squid *Lolliguncula brevis*: evidence of multiple jet 'modes' and their implications for propulsive efficiency. J. Exp. Biol. 212 (12), 1889–1903.

- Bartol, I.K., Krueger, P.S., Thompson, J.T., Stewart, W.J., 2008. Swimming dynamics and propulsive efficiency of squids throughout ontogeny. Integr. Comp. Biol. 48 (6), 720–733.
- Colin, S.P., Costello, J.H., 2002. Morphology, swimming performance and propulsive mode of six co-occuring hyromedusae. J. Exp. Biol. 205, 427–437.
- Dabiri, J.O., Colin, S.P., Costello, J.H., Gharib, M., 2005. Flow patterns generated by oblate medusan jellyfish: field measurements and laboratory analyses. J. Exp. Biol. 208, 1257–1265.
- Gallas, Q., Holman, R., Nishida, T., Carroll, B., Sheplak, M., Cattafesta, L.N., 2003. Lumped element modeling of piezoelectric-driven synthetic jet actuators. AIAA J. 41 (2), 240–247.
- Gemmell, B.J., Colin, S.P., Costello, J.H., 2018. Widespread utilization of passive energy recapture in swimming medusae. J. Exp. Biol. 221, 168575.
- Gemmell, B.J., Costello, J.H., Colin, S.P., Stewart, C.J., Dabiri, J.O., Tafti, D., Priya, S., 2013. Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans. Proc. Natl. Acad. Sci. USA 110 (44), 17904– 17909.
- James, S., Madnia, C.K., 1996. Direct numerical simulation of a laminar vortex ring. Phys. Fluids 8 (9), 2400–2414.
- Johnson, W., Soden, P.D., Trueman, E.R., 1972. A study in jet propulsion: an analysis of the motion of the squid, *loligo volgaris*. J. Exp. Biol. 56, 155–165.
- Krieg, M., Mohseni, K., 2013. Modelling circulation, impulse and kinetic energy of starting jets with non-zero radial velocity. J. Fluid Mech. 719, 488–526.
- Krieg, M., Mohseni, K., 2015. Pressure and work analysis of unsteady, deformable, axisymmetric, jet producing cavity bodies. J. Fluid Mech. 769, 337–368.
- Krieg, M., Sledge, I., Mohseni, K., 2015. Design considerations for an underwater soft-robot inspired from marine invertebrates. Bioinspirat. Biomimet. 10 (6), 065004.
- Krueger, P.S., Gharib, M., 2005. Thrust augmentation and vortex ring evolution in a fully pulsed jet. AIAA J. 43 (4), 792–801.
- Lighthill, M.J., 1969. Hydrodynamics of aquatic animal locomotion. Annu. Rev. Fluid Mech. 1, 413–445.

- Lipinski, D., Mohseni, K., 2009. Flow structures and fluid transport for the hydromedusae Sarsia tubulosa and Aequorea victoria. J. Exp. Biol. 212, 2436–2447.
- Møller, L.F., RiisgÅrd, H.U., 2007. Respiration in the scyphozoan jellyfish Aurelia aurita and two hydromedusae (Sarsia tubulosa and Aequorea vitrina): effect of size temperature and growth. Mar. Ecol. Prog. Ser. 330, 149–154.
- O'Dor, R.K., 1982. Respiratory metabolism and swimming performance of the squid, *Loligo opalescens*. Can. J. Zool. 39 (4), 580–587.
- O'Dor, R.K., 1988. The forces acting on swimming squid. J. Exp. Biol. 137, 421–442. O'Dor, R.K., Webber, D.M., 1986. The constraints on cephalopods: why squid aren't
- O'Dor, R.K., Webber, D.M., 1986. The constraints on ceptatopods: why squid aren't fish. Can. J. Zool. 64 (8), 1591–1605.
   O'Dor, R.K., Webber, D.M., 1991. Invertebrate athletes: trade-offs between transport
- efficiency and power density in cephalopod evolution. J. Exp. Biol. 160, 93–112.

Roh, C., Gharib, M., 2018. Asymmetry in the jet opening: underwater jet vectoring mechanism by dragonfly larvae. Bioinspr. Biomim. 13, 046007.

- Sahin, M., Mohseni, K., 2008. The numerical simulation of flow patterns generated by the hydromedusa *Aequorea victoria* using an arbitrary Lagrangian-Eulerian formulation. In: Proceedings of the AIAA Fluid Dynamics Conference and Exhibit. Seattle, WA, USA.
- Sahin, M., Mohseni, K., 2009. An arbitrary Lagrangian-Eulerian formulation for the numerical simulation of flow patterns generated by the hydromedusa *Aequorea victoria*. J. Comput. Phys. 228 (12), 4588–4605.
- Sahin, M., Mohseni, K., Colin, S., 2009. The numerical comparison of flow patterns and propulsive performances for the hydromedusae Sarsia tubulosa and Aequorea victoria. J. Exp. Biol. 212, 2656–2667.
- Satterlie, R.A., 2002. Neural control of swimming in jellyfish: acomparative study. Can. J. Zool. 80 (10), 1654–1669.
- Sau, R., Mahesh, K., 2007. Passive scalar mixing in vortex rings. J. Fluid Mech. 582, 449-461.
- Trueman, E.R., 1968. Motor performance of some cephalopods. J. Exp. Biol. 49, 495–505.
- Vogel, S., 1994. Life in Moving Fluids, 2nd edn. Princeton University Press, Princeton, NJ.