

Sensitivity analysis of kinematic approximations in dynamic medusan swimming models

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Summary

Models of medusan swimming typically rely on kinematic approximations to observed animal morphology to make such investigations tractable. The effect of these simplifications on the accuracy of predicted dynamics has not been examined in detail. We conduct a case study of the scyphozoan jellyfish *Chrysaora fuscescens* to isolate and quantify the sensitivity of dynamic models to common kinematic approximations. It is found that dynamic models exhibit strong dependence on the nature of some

approximations and the context in which they are implemented. Therefore it is incorrect and potentially misleading to assume that achieving kinematic similarity in models of measured animal locomotion will necessarily provide dynamically correct models.

Key words: jellyfish, *Chrysaora fuscescens*, kinematics, medusan, swimming model, animal locomotion, dynamics, morphology, jet propulsion.

Introduction

The apparent simplicity of the medusan propulsive mechanism has enabled the development of models describing associated kinematics and dynamics. Daniel (1983) derived equations of motion for medusan jet propulsion, based on the principle that swimming thrust is produced by the flux of fluid momentum from the bell during the contraction phase of each propulsive cycle. This thrust is used to overcome drag on the bell surface, and to accelerate the medusa and surrounding fluid (i.e. added mass effect, cf. Batchelor, 1967; Webb, 1982). While a synergy of experiment and theory has been successfully implemented to further examine relationships between mechanics and energetics of medusan propulsion (Daniel, 1985; DeMont and Gosline, 1988a–c), studies of kinematics and dynamics have relied primarily on empirical data. The morphology of several species of medusae has been measured *in situ* (Gladfelter, 1972; Costello and Colin, 1994, 1995; Ford et al., 1997; Ford and Costello, 2000; Colin and Costello, 2002). However, with the exception of comparisons made by Daniel (1983) between dynamical model predictions and measured kinematics, few explicit comparisons between theory and experiment have been made.

Recently, Colin and Costello (2002) undertook this type of study in a comparative analysis of prolate and oblate forms of hydromedusae. They reported agreement between observed swimming acceleration and model predictions for a prolate medusa (*Sarsia* sp.), but significant discrepancy for an oblate form (*Phialidium gregarium*). They attributed this result to differences in swimming mode between oblate and

prolate medusae, where prolate forms may be more amenable to momentum jet models of swimming. Notwithstanding, there are substantial kinematic differences between prolate and oblate medusa that will be realized *via* kinematic inputs to the model, irrespective of swimming mode. This effect has not been examined. More generally, it is important in all comparative studies of animal locomotion models to contrast the effects of each kinematic approximation before attributing observed differences in the results of the model to behavior.

Specifically, there has been no complete, quantitative determination of the effects of various kinematic approximations employed in medusan swimming models. Two common assumptions are that the velar aperture area is constant throughout the propulsive cycle, and that the rate of bell volume change is constant during both the contraction and expansion phases of the cycle. Perhaps more prevalent is the use of a single-parameter ‘fineness ratio’ – the bell height divided by diameter – to completely describe the animal shape. Corollary to this parameter is the assumption that the bell can be approximated as a hemiellipsoid.

In sum, modeling of medusan swimming currently proceeds under the assumption that close kinematic approximation to observed animal morphology will necessarily yield corresponding approximate solutions to the dynamical equations of motion; this has not been verified. The mandate for this study is further amplified when one considers the prevalent use of this assumption in most models of animal locomotion. We report a quantitative case study of swimming

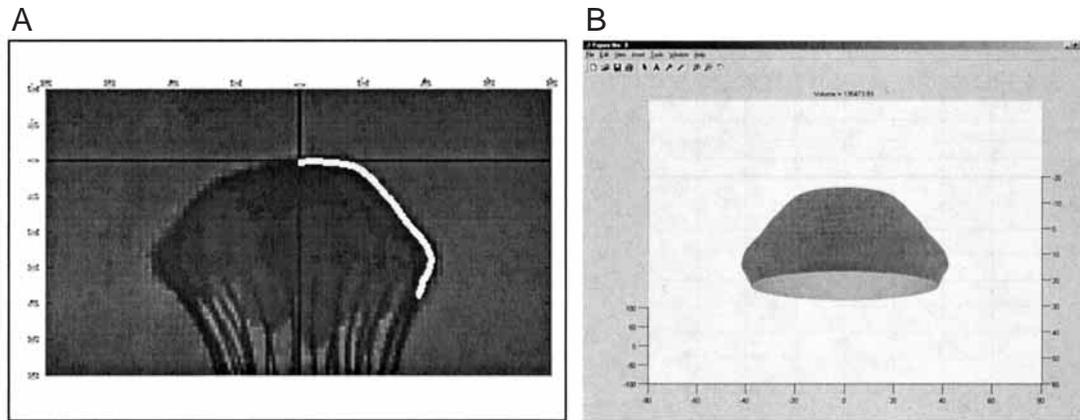


Fig. 1. (A) Video image frame with half-spline overlay. (B) Three-dimensional bell reconstruction generated by revolution of half-spline around axis of revolution.

scyphomedusae *Chrysaora fuscescens* that isolates the effect of each kinematic approximation mentioned above on the predictions of the dynamical model. As a baseline for comparison, an image-processing algorithm is developed to measure observed kinematics precisely.

Materials and methods

Video recording and image processing

Chrysaora fuscescens (Brandt 1835) were observed in an optically backlit kriesel facility at the Aquarium of the Pacific (Long Beach, CA, USA). Video recordings of swimming motions were captured using a three-channel (RGB) digital video CCD camera with 30 Hz frame speed. To resolve the surface of selected medusae with sufficient precision for subsequent image processing, a lens was used to enlarge each medusa image to the outer boundary of the CCD array. The camera was manually positioned to track translation of the medusa as it swam upward in a vertical plane of the kriesel. Video recordings of swimming medusae that did not occur in vertical planes were discarded, so that no scaling of the final video was necessary to correct for changes in depth of the viewing plane.

Each three-channel (by 8-bit) frame of a selected set of swimming contractions was converted to black-and-white using a binary threshold filter. The threshold level was selected such that pixels containing portions of the bell were assigned logic-0 (black) and all others were assigned logic-1 (white). An uncertainty of 3% was associated with binary conversion, due to limited resolution of the boundary between the medusa bell surface and surrounding water.

A search algorithm was created to identify pixels at the logic-0 to logic-1 transitions, corresponding to the bell surface. These pixels were connected using a cubic spline interpolation method (Hanselman and Littlefield, 2000). The spline data from one half of the bell (apex to margin) were then revolved around the medusa oral–aboral axis of symmetry to generate a three-dimensional, axisymmetric

description of the bell morphology. The appropriateness of the axisymmetric description is suggested by axial symmetry of the locomotor structure in medusae (cf. Gladfelter, 1972). User input was required to determine the location of the bell margin, due to optical obstruction by the tentacles and oral arms. Uncertainty of the user input was determined to be 3–4%, based on measurement repeatability. An example half-spline is displayed in Fig. 1 on a frame of the swimming medusa, along with the three-dimensional reconstruction.

Kinematic data were obtained from the reconstructed medusa, including bell volume (assuming a thin mesogleal wall), aperture diameter and fineness ratio. Wall thickness is not negligible near the apex. Bell volume measurements are not substantially affected, however, due to limited volume change in the apical region throughout the propulsive cycle. Total uncertainty in bell volume and aperture area measurements was calculated to be 8% and 5%, respectively.

Dynamical model

The implemented dynamical model for medusan swimming is principally that of Daniel (1983). The essence of the model is that thrust for swimming is generated by the flux of fluid momentum from the bell during each contraction phase. This thrust is used to accelerate the animal and surrounding fluid, and to overcome drag. By assuming a uniform profile of ejected fluid velocity, the generated thrust T can be computed as a function of time t , given the water density ρ , instantaneous bell volume V , and aperture area A :

$$T = \frac{\rho}{A} \left(\frac{dV}{dt} \right)^2. \quad (1)$$

Similarly, the drag and acceleration reactions can be computed from these parameters by utilizing the fact that medusae are nearly neutrally buoyant so that body mass can be neglected (Denton and Shaw, 1961). Therefore, the dynamical equation of motion for the translational velocity $u(t)$ can be expressed as nonlinear differential relationship:

Table 1. Data set definitions for kinematic inputs in first set of experiments

Data set title	$V(t)$	$A(t)$
mVmA (baseline)	Measured	Measured
aVmA	Approximate	Measured
mVaA	Measured	Approximate
aVaA	Approximate	Approximate

m, measured; a, approximate; V, volume; A, area; $V(t)$, $A(t)$, see text for explanation.

$$V(t) \left[1 + \left(\frac{3V(t)}{2} \sqrt{\frac{\pi}{A(t)}} \right)^{1.4} \right] \frac{du}{dt} + \left(\frac{12\pi^{0.35} A(t)^{0.65}}{2^{0.7}} \right) u^{1.3} = T(t). \quad (2)$$

The fractional powers in Equation 2 arise from expressions for drag and added mass coefficients. Equation 2 was solved using a fourth-order Runge–Kutta algorithm with time step equal to twice the temporal (frame rate) resolution of the data. The kinematic parameters $V(t)$ and $A(t)$ were input according to protocol described in the following sections.

Sensitivity analysis – bell volume and aperture area

The first set of experiments examined the effect of two common kinematic inputs to the dynamical model: approximating the aperture area as constant throughout the propulsive cycle, and assuming a constant rate of change of volume during both the contraction and expansion swimming phases. Table 1 indicates combinations of $V(t)$ and $A(t)$ that were input to the dynamical model.

The measured $V(t)$ and $A(t)$ refer to values obtained from the image processing algorithm. The approximate $V(t)$ was defined by assuming constant dV/dt during each contraction and expansion phase. The approximate $A(t)$ was defined as the average value of bell aperture area over several contractions.

Sensitivity analysis – fineness ratio

The second set of experiments examined the effect of using a fineness ratio (bell height h divided by diameter d) to characterize the bell morphology. The characteristic diameter d was measured by two methods, using the bell aperture diameter and the maximum bell diameter. A volume $V(t)$ and area $A(t)$ were assigned to each fineness ratio measurement using a hemiellipsoid geometrical approximation; the semi-major and minor axes of the hemiellipsoid correspond to the medusa bell height and radius, respectively. Based on these kinematic inputs, the results of the dynamical model (Equation 2) were then compared to the baseline case mVmA defined in Table 1.

The need to video-record swimming medusae in a non-inertial frame of reference (i.e. to achieve sufficient image resolution) meant that we were unable to record absolute position, velocity and acceleration of the animal. This limitation was circumvented in the comparative data analyses

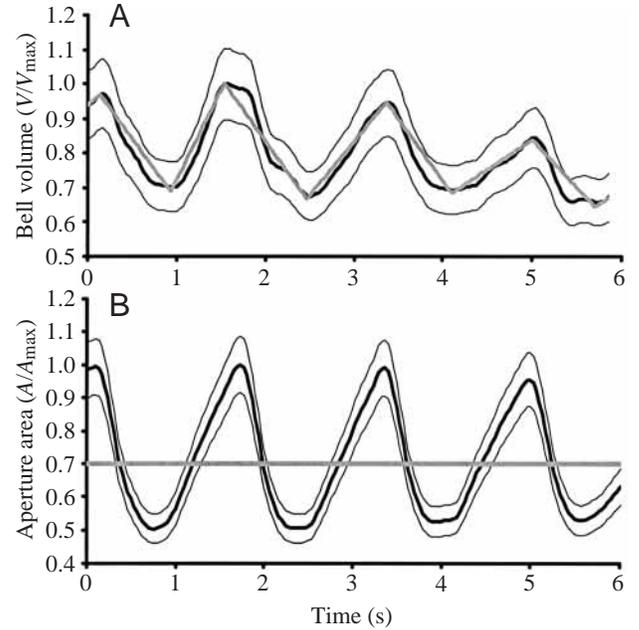


Fig. 2. (A) Measured volume *versus* time. Thick black line, curve fit; thin black line, uncertainty boundaries; gray line, approximate $V(t)$. (B) Measured aperture area *versus* time. Thick black line, curve fit; thin black line, uncertainty boundaries; gray line, approximate $A(t)$. Values are normalized by maximum in the plot.

by referencing these dynamic quantities to the relative *maxima* in each experiment.

Results

Bell volume and aperture area approximations

Fig. 2 plots measured bell volume V and aperture area A with their respective approximated curves. The amplitude of the volume curve is observed to decrease throughout the series of propulsive cycles, perhaps as a mechanism for drag reduction at higher speeds. Although this of no immediate consequence, it demonstrates the ability of the measurement technique to capture both transient and long-term effects.

Dynamical model predictions of medusa acceleration, velocity, and position for each data set defined in Table 1, are shown in Fig. 3. Data sets mVmA and mVaA show substantial peaks in acceleration at the beginning of each contraction. This is consistent with observations by Colin and Costello (2002) for hydromedusae with similar Bauplane. The remaining two data sets, aVmA and aVaA, do not realize the spikes in acceleration. They are more qualitatively similar to the acceleration simulated by Daniel (1983). The velocity and position predictions of the dynamical model, as expected, show a trend similar to the acceleration. The predicted medusa velocity and position for measured volume cases mVmA and mVaA show qualitative agreement with previous experimental measurements (e.g. Costello and Colin, 1994, 1995; Colin and Costello, 2002), whereas the approximated volume results correspond well with simulated dynamical predictions (e.g. Daniel, 1983).

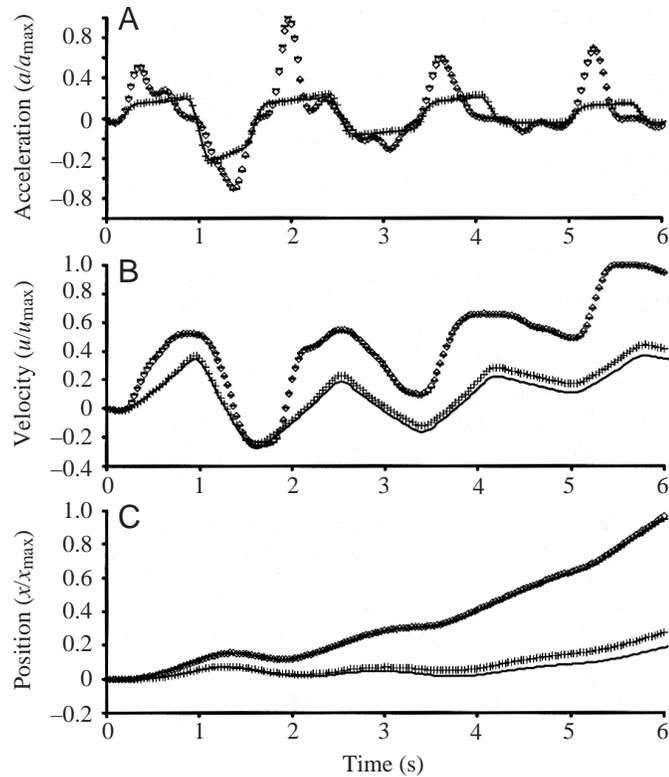


Fig. 3. Dynamical model of (A) acceleration *versus* time, (B) velocity *versus* time and (C) position *versus* time. Horizontal bars, mVmA; open diamonds, mVaA; solid black line, aVmA; +, aVaA (see Table 1). Values are normalized by maximum in the plot.

Finesness ratio approximation

Ultimately, the purpose of the finesness ratio in the dynamical model is to provide an estimate of bell volume, assuming the bell can be approximated by a hemiellipsoid. Therefore, it is useful to compare direct finesness ratio measurement with the corresponding finesness ratio computed from measured volume data.

Both data sets are plotted in Fig. 4. The direct measurement appears to provide a good estimate of the finesness ratio needed to satisfy the ellipsoidal approximation exactly. The trend of decreasing maximum finesness ratio in each propulsive cycle is similar to observations of *Mitrocoma cellularia* and *Phialidium gregarium* by Colin and Costello (2002).

Using the direct finesness ratio measurement and hemiellipsoid approximation, bell volume and aperture area were computed. This kinematic data was input to the dynamical model to compute swimming motions. They are plotted in Fig. 5 and compared with the baseline data set mVmA.

The swimming dynamics predicted using the finesness-hemiellipsoid approximation severely overestimate thrust generated by the swimming medusa. Accordingly, the velocity and position of the animal are also highly overestimated. This result is especially striking considering that measured finesness ratios appear to agree well with values computed from the hemiellipsoid approximation.

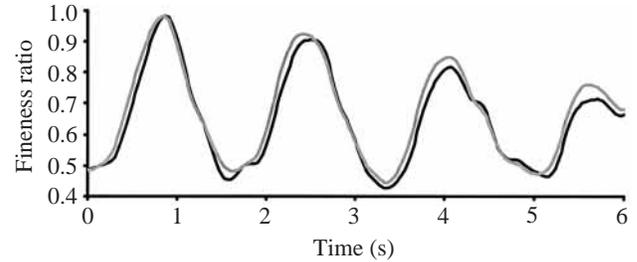


Fig. 4. Finesness ratio. Gray line, direct measurement; black line, values computed from bell volume and aperture measurements using hemiellipsoid approximation.

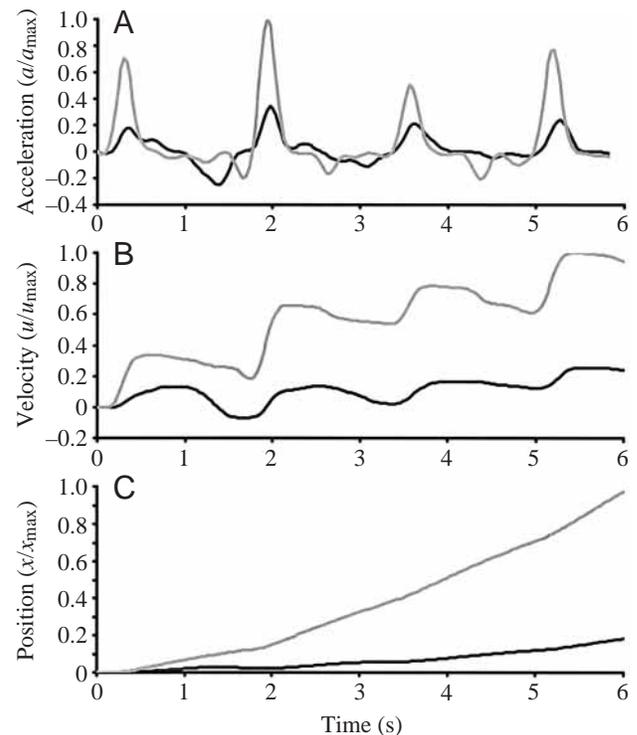


Fig. 5. Modeled swimming dynamics against time of (A) acceleration, (B) velocity and (C) position, from finesness ratio measurement inputs. Gray line, finesness ratio result; black line, mVmA baseline data set. Values are normalized by maximum in the plot.

Discussion

Two sets of experiments were conducted in this sensitivity analysis to deduce the effects of kinematic approximations on the accuracy of predicted medusan swimming dynamics in a momentum flux model of thrust generation. In both cases, bell volume approximations were observed to agree well with directly measured kinematic inputs to the dynamical model (e.g. Figs 2A, 4). By contrast, the area approximation was rough, both qualitatively and quantitatively (Fig. 2B). Interestingly, the crude area approximation was found to have negligible effect on the accuracy of dynamical model predictions, whereas the model was observed to be strongly

dependent on the volume approximation. The constant dV/dt approximation in the first set of experiments and the fineness-hemiellipsoid approximation in the second resulted in severe underestimation and overestimation, respectively, of thrust generation and associated swimming dynamics from the model.

Although this result might be unexpected from an *a priori* qualitative study of the approximations, immediate insight can be gained by examining the quantitative nature of the model in Equations 1 and 2. Here we see that thrust is dependent on the square of the rate of volume change, but only on the first power of area. The fact that the rate of volume change enters Equation 1 and not the volume itself suggests that a more appropriate qualitative check would be comparison of the time derivatives of Figs 2A and 4. There are substantial differences in this parameter between the measured and approximated volume, especially at the beginning of each contraction and expansion phase.

Errors in the fineness-hemiellipsoid approximation are more complex and depend on geometrical considerations. It is to be expected that this approximation is most accurate when the shape of the medusa bell resembles a hemiellipsoid. Fundamental to the fineness-hemiellipsoid approximation is the assumption that maximum bell diameter occurs at the bell margin. Under these circumstances, the volume and its rate of change can be accurately represented. For *Chrysaora fuscescens*, the bell shape approaches a hemiellipsoid when in its relaxed state. The maximum bell diameter occurs near the bell margin, and the fineness ratio can effectively describe the morphology. However, upon contraction the bell aperture diameter reduces substantially, and the location of maximum bell diameter is midway between the bell margin and apex. The shape can no longer be accurately described as a hemiellipsoid. If the bell aperture diameter is still used to define the fineness ratio, the volume of the medusa is significantly underestimated. The total volume change during each phase of the propulsive cycle is overestimated, as is the time rate of volume change. Such was demonstrated in these experiments. Alternatively, one might attempt to use the maximum bell diameter consistently to define the fineness ratio, but the volume would then be overestimated upon contraction and the time rate of volume change underestimated.

Using the measured bell volume and aperture area, it is possible to deduce the proper diameter that should be used to compute the fineness ratio *a priori* for an accurate hemiellipsoid approximation. The result is shown in Fig. 6, as the ratio between this reference diameter and the bell aperture diameter. In addition, the maximum value of bell diameter on the entire medusa is plotted at points of maximum contraction and expansion.

The variation in reference diameter relative to the bell aperture diameter is subtle, remaining within 10% of the aperture diameter throughout the series of propulsive cycles. Nonetheless, using the bell aperture in favor of the reference diameter has been shown to result in large errors, demonstrating the strong dependence on this parameter.

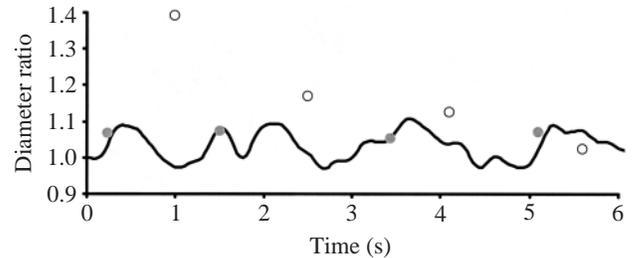


Fig. 6. Ratio of diameter for exact fineness-hemiellipsoid model to bell aperture diameter. Solid black line, diameter ratio; gray circles, maximum bell diameter at maximum expansion; open circles, maximum bell diameter at maximum contraction.

Consistent with the above arguments, the maximum bell diameter approaches the bell aperture diameter at points of maximum medusa expansion. By contrast, the maximum bell diameter is much larger than the reference diameter during phases of maximum contraction.

We are left with the dilemma of properly modeling medusan morphology and swimming in the general case, while maintaining the tractability of the problem. The measurement algorithm created for this sensitivity analysis presents an alternative, although it is cumbersome to implement relative to morphological models using geometrical approximations and a few descriptive parameters. It has been shown here that such models must have as a priority an accurate representation of medusa bell volume effects, especially their temporal variation. A single parameter can be insufficient to provide a robust, accurate description of the animal kinematics. It may be necessary to augment the fineness ratio description with a parameter to capture the effect of large deformations at the bell margin. An effective solution may be to incorporate information regarding the location of maximum bell diameter. This can be accomplished using a truncated-ellipsoid description of the bell, as a more general case of the hemiellipsoid model. Further examination of the relationship between volume transients and hydrodynamic forces may suggest more effective swimming models.

Generally, any dynamic model of locomotion that implements a combination of kinematic assumptions is vulnerable to a combined effect wherein competing errors of underestimation and overestimation may go unnoticed in the final result. In the present study, underestimation of swimming thrust due to the assumption of constant rate of volume change can be compensated by overestimation of thrust in the fineness-hemiellipsoid approximation. Should the two errors effectively cancel one another, one may be led to the spurious conclusion that because the measurements agree with the model, the theory is sufficient. Therefore it is critical in all animal studies of locomotion to isolate the error associated with each kinematic assumption before implementing them in combination.

An important step has been taken in this sensitivity analysis to isolate the kinematic parameters of greatest importance in medusan swimming and to quantify the sensitivity of the

dynamic model to these inputs. More generally, these results urge similar analyses of other animal locomotion models to avoid potentially misleading results that can arise by assuming an *ipso facto* link between kinematic and dynamic similarity.

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