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Relationship between morphology and hydrodynamics during swimming by the hydromedusae *Aequorea victoria* and *Aglantha digitale**

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SUMMARY: Hydrodynamic forces acting upon adult swimming *Aglantha digitale* and *Aequorea victoria* were estimated by combining empirical kinematic data with the model of Daniel (1983). Forces varied in magnitude during bell pulsation and recovery. The acceleration reaction and inertial resistance were the dominant instantaneous terms. However, the net forces (each hydrodynamic force totaled over complete pulsation cycles) were different for the two species. *Ag. digitale* maximized acceleration rates and minimized the acceleration reaction: drag was the dominant net force. *Ae. victoria* minimized acceleration rates and maximized the acceleration reaction: the acceleration reaction was its dominant net force. A new finding of this work was that oblate medusae such as *Ae. victoria* may be efficient for continuous swimming due to a positive net contribution of the acceleration reaction to forward motion once the medusa has begun swimming.

Key words: medusae, foraging, morphology, swimming.

INTRODUCTION

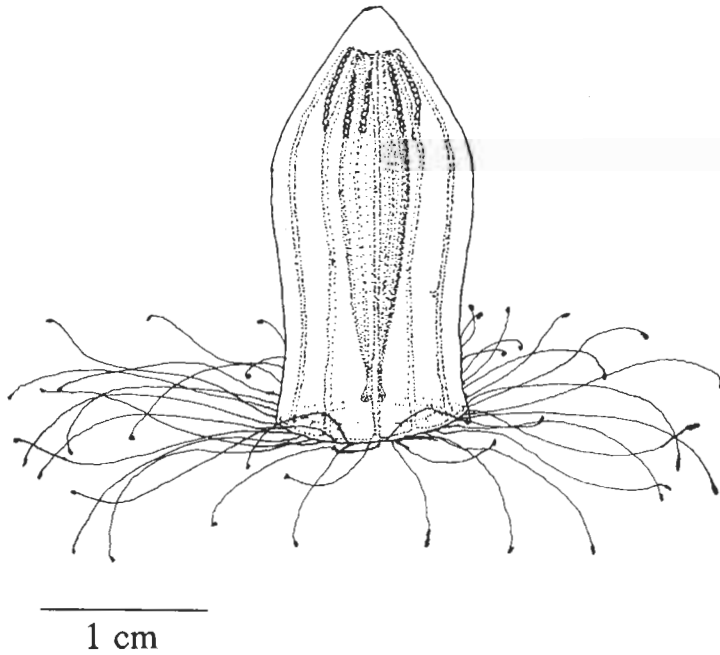
Hydromedusae exhibit a wide variety of bell morphologies and swimming behaviors (Mills, 1981). Because hydromedusae live and swim in a fluid, variations in morphology and swimming behavior should result in different hydrodynamic forces influencing motion of the medusae. These forces have been modeled (Daniel, 1983) and critical model parameters experimentally determined (Daniel, 1985). If, as proposed by Costello (1992), hydrodynamic forces are significant influences on the evolution of medusan body forms and foraging patterns, then divergent body morphologies might produce divergent hydrodynamic effects and these should relate to medusan foraging patterns.

Almost all hydromedusae generate thrust by periodic bell contraction and jetting of fluid through the velar aperture and away from the body. Essentially, hydromedusae throw fluid away from their bodies (Denny, 1983). The rate at which they add velocity to the fluid, thus altering its momentum, is defined as the rate of thrust production (Vogel, 1994). In order for forward motion to occur, there must be sufficient thrust to overcome variables which resist forward motion. Daniel (1983) defined three major hydrodynamic variables affecting the thrust necessary to accelerate a medusa. The first, drag, is determined by shape, surface area and velocity. Pressure or form drag is the dominant form of drag experienced by many medusae because fluid flow past swimming medusae is rapid enough to generate Reynolds numbers in the range of 10^2 - 10^3 (Gladfelter, 1973; Costello and Colin, unpublished data). The two other variables are related to inertial

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Aglantha digitale



Aequorea victoria

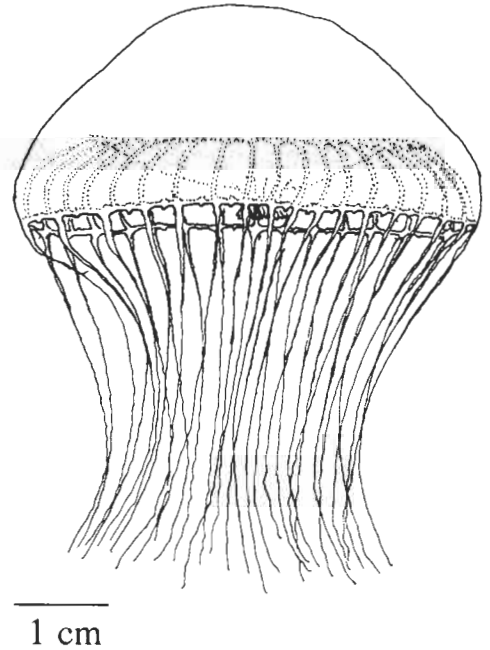


FIG. 1. – Representative bell shapes of adult *Aglantha digitale* and *Aequorea victoria* medusae.

properties of the medusa's body (inertial resistance) and the fluid surrounding the medusa (the acceleration reaction). The acceleration reaction is the force required to accelerate or decelerate a volume of fluid surrounding the medusa during swimming. The analytical description of this fluid volume, known as the added mass, is complex (for examples see Batchelor, 1967 and Newman, 1977). However, the magnitude of the added mass is estimated relative to the mass of the fluid displaced by the medusa and described by the added mass coefficient, α . α is dependent upon the shape of a form and forms with high drag coefficients will also have high added-mass coefficients (see Daniel 1983, 1984, 1985; Denny 1988, 1993, and Vogel, 1994 for a more extensive treatment). A major difference between drag and the acceleration reaction is that, while drag always opposes forward motion of a body, the acceleration reaction opposes any alteration in velocity including deceleration. Hence, once a body is in motion, the acceleration reaction may maintain the body's forward motion.

Our approach was to fit the swimming mechanics model developed by Daniel (1983) with empirical data collected from two hydromedusan species with widely divergent body forms. *Aglantha digitale* is a prolate trachymedusa (Fig. 1) with well documented swimming and escape patterns (Donaldson *et al.*,

1980). *Aequorea victoria* is an oblate leptomedusa (Fig. 1) commonly occurring along the northwest Pacific coast of North America. Both species co-occur in coastal regions such as the San Juan Islands in Puget Sound, where they were collected for this study. These results are preliminary findings of a large study encompassing a wider range of hydromedusa species.

METHODS

Collection and video

Individual *Aequorea victoria* and *Aglantha digitale* were hand collected from surface waters adjoining the dock off Friday Harbor Laboratories, San Juan Island, Washington, USA. Medusae were carried to the laboratory and placed in vessels with aerated seawater. Video recordings of swimming medusae were made within 48 hours of collection.

Video recordings (SVHS) were made following the methods of Costello and Colin (1994a). Medusan swimming and particle flow were recorded using a backlit optical system. A field-counter labeled sequential video fields and provided temporal data. Spatial characteristics of the optical field were determined from scale bars periodically included in

the recordings. Morphological measurements such as bell diameter and length were thus made directly from video recordings calibrated with scale bars.

Calculations

All calculations were based upon video recordings of normally swimming medusae starting from rest. Rapid escape response swimming sequences of *Aglantha digitale* were not used because of the unique nature of this type of swimming (Donaldson *et al.*, 1980). Instead, regular slow swimming sequences were used for both species. One representative sequence of swimming by each species was selected (from many representing a variety of individuals) and used in calculations. Measurements were made at 0.1 second intervals. Calculations of swimming mechanics relied upon the model of Daniel (1983). We refer interested readers to that work as well as to Daniel (1984, 1985) for a more thorough discussion of principles and explanations underlying these calculations.

Fineness ratio (F) was calculated as

$$F = h/d \quad (1)$$

where h is bell height and d is bell diameter. Velocity (u) for a time interval (i) was calculated as

$$u_i = \frac{x_{i+1} - x_i}{t_{i+1} - t_i} \quad (2)$$

where x represents the anterior most (aboral) bell position in space and t represents the time in seconds during which the position was measured. Acceleration (a) was calculated as

$$a_i = \frac{u_{i+1} - u_i}{t_{i+1} - t_i} \quad (3)$$

Reynolds number (Re) was calculated as

$$Re = \frac{du}{\nu} \quad (4)$$

where d is bell diameter, u is medusa velocity and ν is the kinematic viscosity of seawater. Volume (V) was calculated by fitting bell diameter and height to the volumetric equation for a hemiellipsoid

$$V = \frac{2}{3} \pi hr^2 \quad (5)$$

where r is the bell radius. Drag (D) was calculated as

$$D = C_D (.5 \rho) Su^2 \quad (6)$$

where C_D is the drag coefficient, ρ is the water density, S is the surface area exposed to flow and u is the medusa's forward velocity. C_D represents the resistance of the fluid to forward motion of a solid and is influenced by the flow regime around the solid. This relationship is proportional to Re as approximated by the equation

$$C_D = 24/Re^n \quad (7)$$

where the power n is 1.0 for Re less than 1 and .7 for Re from 1 to 500 (Daniel, 1983). Average Re values for replicate *Ae. victoria* and *Ag. digitale* were over 100 but less than 500 (Costello and Colin, unpublished data).

Medusae alter both shape and velocity during bell pulsation. These variations are reflected in C_D through changes in Re over the pulsation cycle. Exposed surface area (S) was expressed as that of a hemiellipsoid.

$$S = \pi hr/2 \quad (8)$$

During the contraction phase, fineness ratio (F) increases while volume (V) and projected area (S) decrease. Note that changes in volume (V) do not reflect compressibility of the body tissues but, instead, alterations in the fluid volume contained within the subumbrellar cavity. During the relaxation phase, F decreases while V and S increase. By combining equations 6-8, the drag experienced by a swimming medusa was expressed as a function of the pulsation phase.

The acceleration reaction (G) was described by Daniel (1983) as

$$G = -\alpha \rho V \frac{du}{dt} \quad (9)$$

where α , the added-mass coefficient for hemiellipsoids, has been empirically determined (Daniel, 1983, 1985) as

$$\alpha = (h/r)^{1.4} \quad (10)$$

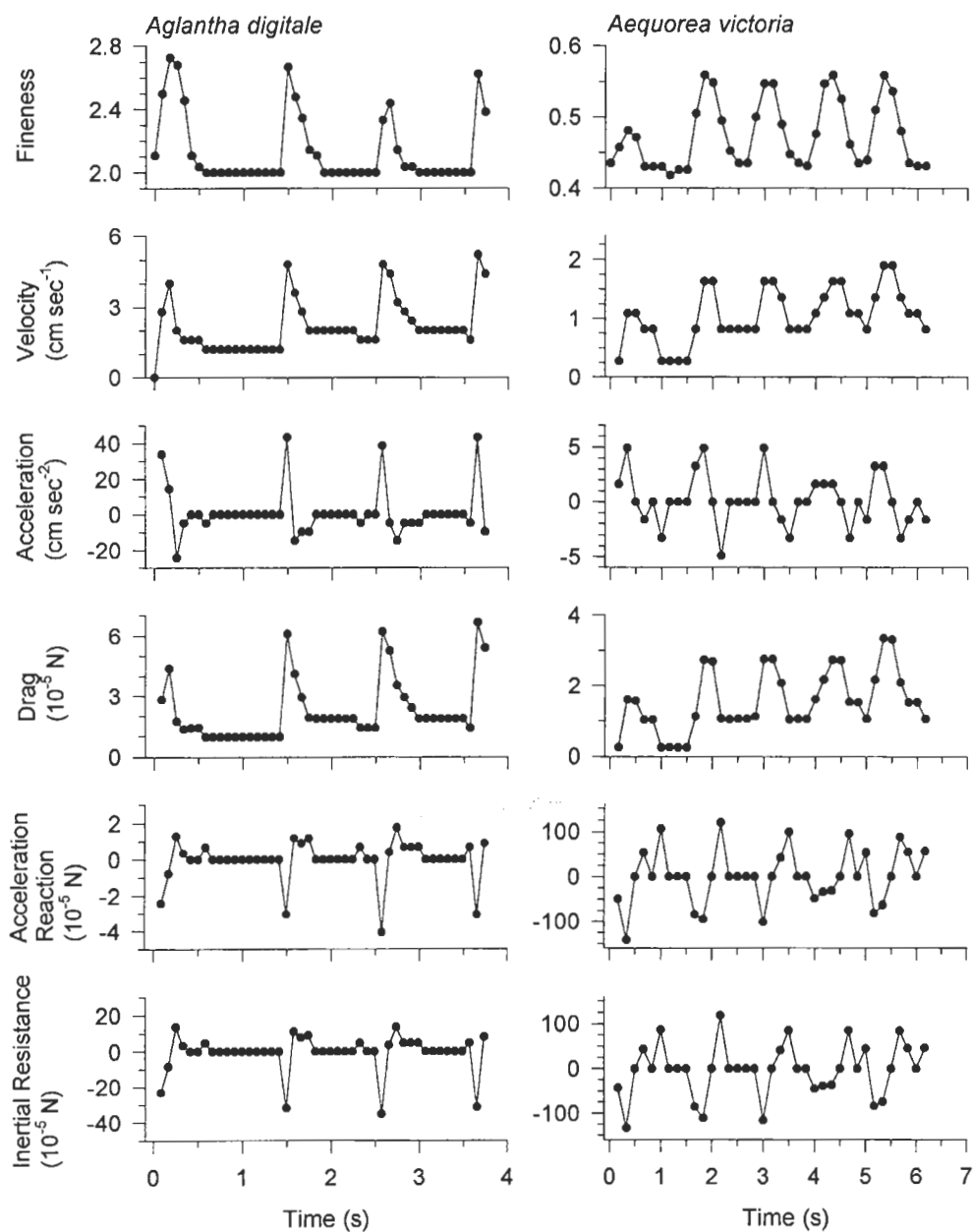


FIG. 2. – Kinematic and hydrodynamic force profiles during swimming by individual *Aglantha digitale* (1.9 cm height, 1.0 cm diameter) and *Aequorea victoria* (2.1 cm height, 5.0 cm diameter) medusae. All graphs in the left column relate to *Ag. digitale*, corresponding graphs in the right column represent *Ae. victoria*.

Thus, because α , V and u change during bell pulsation, the overall acceleration reaction (G) is also a time-dependent function which can be positive or negative depending on the pulsation phase.

The inertial resistance to acceleration of the medusa (I) is dependent upon the change in the medusa's volume (comprised of the medusa and the fluid contained in the subumbrellar cavity) and velocity.

$$I = -\rho V \frac{du}{dt} \quad (11)$$

I , unlike G , is independent of shape. The sign denotes the direction in which the force acts with reference to acceleration of the medusae. During bell contraction, acceleration is positive and inertial resistance opposes acceleration of the medusa. During bell relaxation, acceleration is negative and inertial resistance opposes deceleration of the medusa.

RESULTS

Representative kinematic and force profiles for *Aglantha digitale* and *Aequorea victoria* are illustrated in Figure 2. Bell pulsation altered the morphology of both species and resulted in cyclic variation in bell fineness. Bell contractions, indicated by increases in fineness, caused increased medusan velocities and accelerations. Similarly, bell relaxation, indicated by decreases in fineness, caused decreased velocities and decelerations. Drag is proportional to the square of velocity (Equation 6) and the drag profile patterns closely resembled those of the velocity profile patterns. In contrast, the acceleration reaction and medusan inertial resistance are negatively proportional to alterations in velocity, or acceleration (Equations 9,11). Drag forces, by convention (Daniel, 1983), were positive over the pulsation cycle because drag always acts as a negative force and resists forward motion of the medusa. However, acceleration reaction (G) and inertial resistance (I) forces alternated between positive and negative values. G and I were negative and resisted forward motion when the medusa accelerated, while they were positive and resisted changes in velocity when the medusa decelerated after peak contraction occurred.

Major hydrodynamic differences in swimming between the two species are apparent in the contrasting scales of the variables described in Figure 2. While a smaller medusa (1.9 cm length, 1.0 cm diameter), *Ag. digitale* attained higher velocities and accelerations with each pulsation than did *Ae. victoria* (2.1 cm height, 5.0 cm diameter). Peak drag forces experienced by each medusae were similar in magnitude (both less than 10^{-4} N). G and I values during pulsation were greater for *Ae. victoria* than for *Ag. digitale*. This difference was most apparent in the G force experienced by the medusae during consecutive pulsations. G was over an order of magnitude greater in *Ae. victoria* than *Ag. digitale*. The importance of this difference was apparent when contrasted with acceleration values. Figure 3 allows comparison of the relative values for the acceleration (a) and acceleration reaction (G) values for both medusae. *Ag. digitale*'s accelerations were high and acceleration reaction values low relative to corresponding values for *Ae. victoria*. Rephrased, *Ag. digitale* maximized acceleration and minimized the acceleration reaction; *Ae. victoria* minimized acceleration while maximizing the acceleration reaction.

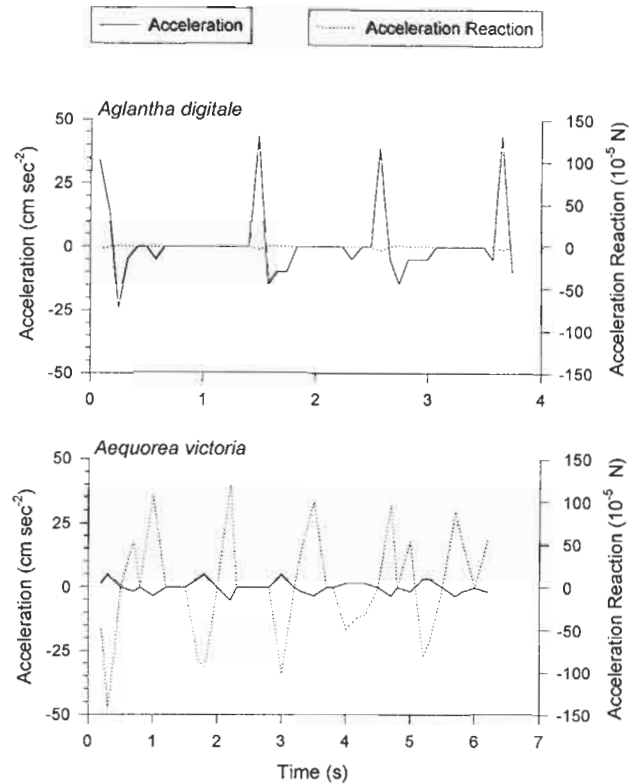


FIG. 3. — Comparison of the relative magnitudes of acceleration and the acceleration reaction in *Aglantha digitale* and *Aequorea victoria*. The data is the same as in Figure 2 but the axes (except Time) are identical for both species.

Figure 4 illustrates the influence of acceleration reaction minimization or maximization on the net (total over complete cycle) strength of hydrodynamic forces experienced during swimming. *Ag. digitale* minimized G and I through streamlined body form and low volume. This is apparent in the low net values of G and I over consecutive pulsation cycles. Whereas instantaneous values for I are of greater magnitude than those of D, the positive and negative I values largely cancel each other out after the first cycle and result in low net I over complete cycles. In contrast, D always acts to resist forward motion by the medusa so its force is additive over the pulsation cycle. Peak D values for *Ag. digitale* were approximately twice those of *Ae. victoria*. Because I and G forces were low while D was relatively high, D was the dominant net hydrodynamic force experienced by *Ag. digitale* over complete cycles. The relative contributions of these three variables were very different for *Ae. victoria*. *Ae. victoria* did not reach high velocities and, because D is a function of velocity squared (Equation 6), the relative contribution of D was low over consecutive cycles. In contrast, the large volume and high added-mass coefficients of

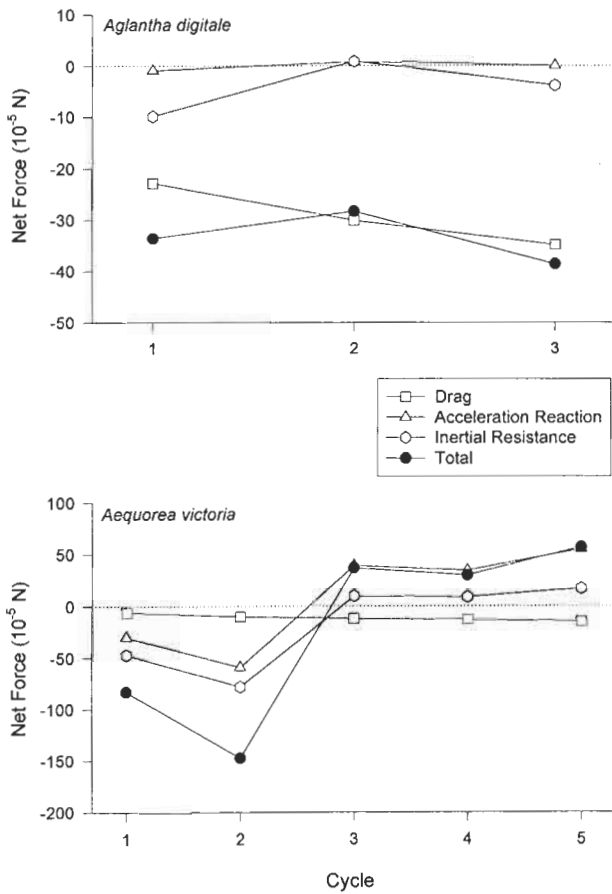


FIG. 4. – Net force over consecutive pulsation cycles for *Aglantha digitale* and *Aequorea victoria*. This figure uses the convention that forces impeding forward motion have negative values while those favoring forward motion have positive values. By this convention, values for drag are negative while those for inertia and the acceleration reaction vary in sign depending upon the sum of values for each time interval of the cycle.

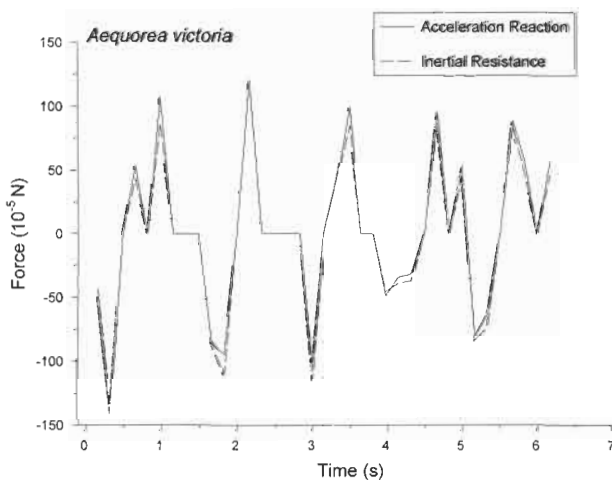


FIG. 5. – Enlargement of acceleration reaction and inertial resistance data for *Aequorea victoria* plotted in Figure 2. Note that, particularly for the last three cycles, the acceleration reaction values are more positive and less negative than those of inertial resistance.

Ae. victoria contributed to high relative I and G forces. The relative contributions of G and I switched after the second pulse. A more detailed examination of G and I data for *Ae. victoria* (Fig. 5) indicated that over consecutive cycles the positive values increased and the negative values decreased for G relative to I and resulted in G dominating the total force (Fig. 4). Each of the three hydrodynamic variables yielded net negative forces when totaled over *Ae. victoria*'s first two cycles. Therefore, the total or summed force during these cycles was dominated by G and I, strongly negative and opposing forward motion. However, by the third cycle, G and I shifted to net positive values, indicating that forward momentum of the medusa's body and the added-mass of surrounding fluid acted to maintain forward motion after the initial two cycles. Net total force values from the 3rd to 5th cycle resemble those of G because the negative net drag forces were approximately balanced by the positive net inertial resistance.

These results demonstrate that hydrodynamic forces acting during swimming contrasted sharply for the two species. The net total force experienced by *Ag. digitale* was always negative during swimming and increased in magnitude as the medusa increased velocity over several pulsation cycles. Therefore, the net total force always opposed forward motion by *Ag. digitale*. In contrast, *Ae. victoria* experienced initial highly negative net total force opposing forward motion but, after two cycles, this shifted to a net positive total force which acted to maintain forward motion.

DISCUSSION

Aglantha digitale and *Aequorea victoria* represent highly divergent evolutionary responses to hydrodynamic and trophic conditions imposed by a planktonic existence. *Ag. digitale* does not swim continuously. Instead, it swims sporadically and is well known for its rapid escape response (Donaldson *et al.*, 1980). Prey capture by *Ag. digitale* requires relatively motionless sitting within the water column while waiting for prey to swim into the medusa's extended tentacles. Therefore, swimming serves the purpose of either repositioning or rapid escape. Its body form and resulting hydrodynamic characteristics are well suited to its movement and foraging patterns. Low inertial resistance and acceleration reaction forces allow rapid forward motion on the first bell pulsation - a necessary con-

dition for rapid escape. We did not measure escape kinematics for *Ag. digitale*: rather, we measured slow swimming. We rarely observed more than 4 consecutive pulsations without rest, rapid escape or sudden turning. Only when agitated did these medusae swim frequently. When undisturbed, short bursts of swimming punctuated much longer motionless periods. While streamlining and low body volume reduce inertial resistance and acceleration reaction forces, *Ag. digitale* cannot avoid the energetic expense of drag. This cost is proportional to the square of velocity, so the energetic trade-off of rapid, high acceleration is high drag forces. However, this expense may be worth the investment if it results in successful predator avoidance by the medusa. Note that swimming by *Ag. digitale* always entails an expense due to the net total force opposing forward motion (Fig. 4). In contrast, *Ae. victoria* has negligible burst velocity capacity, but, after 1-2 pulses, a net total force which positively contributes to forward motion and opposes deceleration. The high energy input necessary to overcome initial inertia and acceleration reaction favors continuous swimming by *Ae. victoria*. This means that *Ae. victoria* must produce considerable thrust for the first two pulsation cycles, but much less during subsequent cycles. Even temporary cessation of swimming entails the high energetic costs of overcoming initial inertial and acceleration reaction forces. *Ae. victoria*'s foraging strategy is consistent with continuous swimming. Prey capture is often dependent upon swimming. Prey are entrained in vortices which are formed during bell pulsation and which pass through the tentacles trailed through the medusa's wake (Costello and Colin, 1994b). The acceleration of this fluid is part of the acceleration reaction. Thus, the acceleration reaction affects *Ae. victoria* both by maintaining forward motion during swimming and through the production of a current used to capture prey.

In addition to bell fineness, bell volume significantly affects medusan hydrodynamics. The relative importance of inertial resistance and the acceleration reaction increases with bell diameter more dramatically than does drag. This is because drag is a function of surface area (proportional to r^2) whereas inertial resistance and the acceleration reaction are both functions of volume (proportional to r^2h). Therefore, medusae adapted to function as acceleration reaction maximizers should theoretically be of larger relative size than medusae adapted to be acceleration reaction minimizers. The adult width of *Ae. victoria* is large among hydromedusae: however,

other oblate species such as *Mitrocoma cellularia* are also relatively large (>2 cm diameter) and function similarly to *Ae. victoria* (Costello and Colin, 1994b).

Whereas the shapes and sizes of oblate hydromedusae such as *Ae. victoria* and *Mitrocoma cellularia* bear similarities to scyphomedusae such as *Aurelia aurita* or *Chrysaora quinquecirrha*, phylogenetic affinities between the Hydrozoa and the Scyphozoa are not clear. Underlying morphological differences such as the absence of the velum in scyphozoan medusae indicate that basic propulsion mechanics are typically different in the two classes. Bell folding as well as musculature also differ (Gladfelter, 1973). Most hydromedusae are relatively small (< 2 cm diameter) and the number of large, oblate species is low. We suggest that these morphologies are a specialization among the hydromedusae for the use of swimming-generated flow in feeding. Therefore, similarities in bell form between oblate hydromedusae and scyphomedusae may represent a common morphological response arrived at convergently by the two cnidarian classes. Whereas this form is widespread among the Scyphozoa (Costello and Colin, 1994a, 1995), it is less so among the Hydrozoa. Previous reports have considered these large, oblate medusae to be less efficient swimmers than prolate forms (Daniel 1983, 1984, 1985; Costello 1992; Costello and Colin 1994a). However, the results of this paper indicate that, for continuously swimming foragers, oblate morphologies can produce substantial hydrodynamic advantages compared to those of prolate forms.

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