Passive energy recapture in jellyfish contributes to propulsive advantage over other metazoans

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Gelatinous zooplankton populations are well known for their ability to take over perturbed ecosystems. The ability of these animals to outcompete and functionally replace fish that exhibit an effective visual predatory mode is counterintuitive because jellyfish are described as inefficient swimmers that must rely on direct contact with prey to feed. We show that jellyfish exhibit a unique mechanism of passive energy recapture, which is exploited to allow them to travel 30% further each swimming cycle, thereby reducing metabolic energy demand by swimming muscles. By accounting for large interspecific differences in net metabolic rates, we demonstrate, contrary to prevailing views, that the jellyfish (\textit{Aurelia aurita}) is one of the most energetically efficient propulsors on the planet, exhibiting a cost of transport (joules per kilogram per meter) lower than other metazoans. We estimate that reduced metabolic demand by passive energy recapture improves the cost of transport by 48%, allowing jellyfish to achieve the large sizes required for sufficient prey encounters. Pressure calculations, using both computational fluid dynamics and a newly developed method from empirical velocity field measurements, demonstrate that this extra thrust results from positive pressure created by a vortex ring underneath the bell during the refilling phase of swimming. These results demonstrate a physical basis for the ecological success of medusan swimmers despite their simple body plan. Results from this study also have implications for bioinspired design, where low-energy propulsion is required.

Significance

Jellyfish have the ability to bloom and take over perturbed ecosystems, but this is counterintuitive because jellyfish are described as inefficient swimmers and rely on direct contact with prey to feed. To understand how jellyfish can outcompete effective visual hunters, such as fish, we investigate the energetics of propulsion. We find that jellyfish exhibit a unique mechanism of passive energy recapture, which can reduce metabolic energy demand by swimming muscles. Contrary to prevailing views, this contributes to jellyfish being one of the most energetically efficient propulsors on the planet. These results demonstrate a physical basis for the ecological success of medusan swimmers despite their simple body plan and have implications for bioinspired design, where low-energy propulsion is required.


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form of passive energy recapture to enhance their swimming and reduce their COT further. Contraction of the bell generates a starting vortex at the bell margin and a stopping vortex with opposite-sign vorticity forms upstream of the starting vortex (11). After shedding of the starting vortex, the relaxation or refilling phase begins and enhances stopping vortex circulation and vorticity while drawing the fluid under the bell (Fig. 2A and Movie S1). Although medusae exhibit greater accelerations and peak velocities during contraction (Fig. 2B and Fig. S1), peak circulation of the stopping vortex (which is proportional to the thrust generated) can be significantly greater (ANOVA, $P = 0.01; n = 10$) than the starting vortex (Fig. 2C), illustrating the potential importance of stopping vortices during swimming. A study using computational fluid dynamics (CFD) has previously demonstrated that power can be generated during the refilling (relaxation) phase (18), but relative contributions to efficiency and distance are unknown.

The mesogleal tissue of jellyfish has both viscoelastic (19) and elastic properties (20). However, the refilling phase, responsible for the secondary thrust, is found to be powered exclusively from the elastic properties of mesoglea (20) (Fig. S2). The stress–strain relationship within this elastic tissue exhibits a nonlinear, $J$-shaped relationship (21, 22). This allows the tissue to strain easily at the beginning of the contraction when the potential for hydrodynamic output is high and to store most strain energy near the end of the contraction. This can aid in optimizing energetic efficiency because nearly all energy is devoted to thrust generation during periods of acceleration, whereas elastic strain storage occurs mostly at the end of the contraction cycle. Therefore, the large stopping vortex is produced and positioned under the bell using only stored strain energy and no additional energy from antagonistic muscle groups. An examination of multiple jellyfish species demonstrates that this translates to only a small proportion of each swimming cycle in jellyfish ($\sim 20\%$) requiring muscle contraction (Fig. 3A–C). The energy required to decelerate the contracting bell is translated to refilling the bell, similar to the mechanism demonstrated in flying insects, which greatly reduces energetic costs for thrust production (23).

Our results show that 32% (SD = 0.6%) of the total distance traveled per pulse can occur during the postrelaxation period (interpulse phase), where the animal produces no kinematic motion (i.e., coasting) and after inertial motion would have ceased (Fig. 2B and C). Anesthetized $A$. aurita were artificially propelled forward at natural swimming velocities to allow observation of the stopping vortex influence beyond the duration at which the subsequent contraction normally begins. We show that passive bell refilling can produce thrust for an extended period after bell motion ceases (Fig. S2). The force produced can carry a 4-cm $Aurelia$ an additional 10.1 mm (SD = 0.8, $n = 4$) each pulse, which is 80% of the measured 12.7 mm (SD = 3.5, $n = 5$) achieved during the kinematically active portion of normal swimming.

To elucidate how thrust is generated after refilling of the bell, we measured pressure around the body of the jellyfish using a combination of CFD and a newly developed empirical technique for pressure estimation from velocity field measurements. Oblate medusae are known to produce more complex pressure fields at the subumbrellar surface relative to jetting medusae (24). We find that during bell relaxation, the pressure is typically low as refilling occurs but that subsequent induced flow from the stopping vortex builds against the subumbrellar surface and creates a large region of positive pressure between the low-pressure cores of the vortex ring (Fig. 4 and Movie S2). The resulting high pressure creates enough force to cause an additional acceleration of the body after initial contraction and before the next cycle (Fig. 4B and C).

A simple, conservative estimate can be made to understand how passive energy recapture contributes to COT in $Aurelia$. Eliminating the interpulse duration (and thus any influence of passive energy recapture) will result in doubling of the pulse frequency as $f_{\text{new}} = 0.50$ (SD = 0.05, $n = 20$), where $T_p$ is the time of the interpulse duration and $T_{\text{tot}}$ is the total time of each pulse. Although the relationship between pulse frequency and respiration is unknown for jellyfish, it is exponential for fish (25). Conservatively, we assume a linear relationship between respiration...
rate and pulse frequency. By applying the measured velocity during the active phase ($V_A$) of the swimming cycle over the total velocity ($V_T$) for animals 2–10 cm in diameter ($V_A/V_T = 1.35, n = 12$), we find that COT will increase at least by 1.48-fold, or 48% in *Aurelia* if passive energy recapture is not used.

Although cnidarian swimming muscle structure and force production resemble those of other animal groups (16), the cnidarian muscle fibers are housed solely within epitheliomuscular cells. This single cell layer limits the thickness of swimming muscles within cnidarians, and thus force production during medusan swimming. Therefore, beyond a certain size, and unlike other animals, jellyfish do not continue to increase swimming velocity with size. As a result, the additional force required to continue increasing swimming speed with body size is limited to a specific range in jellyfish. This has consequences with respect to COT because jellyfish appear to have the greatest advantage over other metazoans when they are small. However, extrapolating the results from Fig. 1 indicates that fish only begin to exhibit a lower COT than *Aurelia* beyond a body mass of ~100 kg.

The ability of jellyfish to use passive energy recapture reduces metabolic demand while increasing fluid (and thus prey) encountered by feeding structures and translates to more energy available for growth and reproduction. Such energetic advantages would enable jellyfish populations to exploit environments with excess prey and contribute to the demonstrated ability of some jellyfish species to bloom rapidly over short periods and outcompete other species, such as fish (26). Our results show that because COT can vary by more than twofold in jellyfish alone, the species-specific influence of passive energy recapture should be taken into account when trying to understand bloom dynamics and trophic competition. In addition, the passive energy recapture demonstrated in *Aurelia* may be an important consideration in biomimetic design, where low-energy demands are required for efficient vehicle design. The fact that passive energy recapture appears to scale well with animal size also suggests there are important design implications to be explored over a wide range of size scales.

### Materials and Methods

**Swimming Kinematics.** Free-swimming jellyfish (1.5–6 cm) were recorded in a glass filming vessel (30 × 10 × 25 cm) by a high-speed digital video camera (Fastcam 1024 PCI; Photron) at 1,000 frames per second. Only recordings of animals swimming upward were used in the analysis to eliminate the possibility of gravitational force aiding forward motion of the animal between pulses. Detailed swimming kinematics (2D) were obtained using Image J v1.46 software (National Institutes of Health) to track the $x$ and $y$ coordinates of the apex of the jellyfish bell and the tips of the bell margin over time. Swimming speed was calculated from the change in the position of the apex over time as:

$$U = \frac{\left| (x_2 - x_1)^2 + (y_2 - y_1)^2 \right|^{1/2}}{t_2 - t_1} \quad [1]$$

Jellyfish were illuminated with a laser sheet (680 nm, 2W continuous wave; LaVision) oriented perpendicular to the camera’s optical axis to provide a distinctive body outline for image analysis and to ensure the animal
remained in-plane, which ensures accuracy of 2D estimates of position and velocity. Swimming kinematics of large (＞6 cm) A. aurita were obtained using a high-definition Sony HDV Handycam (model HDR-FX1) at a dedicated off-exhibit tank at the New England Aquarium. Here, a 500-mW laser (432 nm, Hercules series; Laserglow) was formed into a thin sheet to illuminate (from above) the outline of the animal for kinematic analysis.

COT. The metabolic COT per unit mass and distance (joules per kilogram per meter) for the moon jellyfish (A. aurita) was estimated from mass-specific swimming speeds and respiration rates. Mass-specific swimming speeds were obtained from kinematic data (current study) and supplemented with data from studies by Martin (27) and McHenry and Jed (28). Mass-specific active respiration data for A. aurita were obtained from Uye and Shimauchi (29). Conversion of metabolic respiration to energy expended (joules) is accomplished by using the conversion factor of 19 J·mL⁻¹·O₂⁻¹ (12). To obtain net COT, which accounts only for energy expended toward locomotion, basal energy consumption must be subtracted from the active rates. Because basal rates are found to be half of the active rates in medusae (12), we calculate the proportion of energy dedicated to location in Aurelia as 0.5-fold the active rate. It should be noted that this makes our net COTAurelia estimates conservative, because pulsation rates in Aurelia are lower than in species that were studied (12). This is because Aurelia spends proportionally less time actively contracting compared with many other species (Fig. S1), and because this is the only time energy is expended for swimming, due to passive relaxation (19), the proportion of the active-to-total metabolic rate in Aurelia (and COT) will likely be lower. The mass-specific respiration and swimming data for salmon (30) were used for comparative purposes.

Net COT was calculated using the equation:

$$ COT_{net} = \frac{\text{Energy}_{\text{res}}}{\text{Mass} \times \text{Velocity}} $$

[2]

Net COTs for runners, fliers, and other swimmers were obtained and re-plotted from studies by Larson (12), Uye and Shimauchi (29), and Schmidt-Nielsen (30), using graph digitizing software (GetData v2.25).

**Fluid Properties Around Swimming Jellyfish.** Fluid motion created by the jellyfish while swimming was quantified using 2D digital particle image velocimetry. Using the setup described above, the filtered seawater was seeded with 10-μm hollow glass beads. The velocities of particles illuminated in the laser sheet were determined from sequential images analyzed using a cross-correlation algorithm (LaVision software). Image pairs were analyzed with shifting overlapping interrogation windows of a decreasing size of 64 × 64 pixels to 32 × 32 pixels or 32 × 32 pixels to 16 × 16 pixels. Details on circulation and pressure estimates are provided in **SI Materials and Methods**.

Kinematic data were log-transformed and checked for normality using a Shapiro–Wilks test. Data were subsequently tested using one-way ANOVA to determine if a significant difference existed between means.

**CFD Model of a Swimming Jellyfish.** We developed a jellyfish model using the bell kinematics of an individual 3-cm diameter, free-swimming moon jellyfish (A. aurita). Digitized points along this half of the body were spatially interpolated using eighth-order polynomials, temporally smoothed using a Butterworth filter, and temporally interpolated using cubic-spline polynomials (Fig. S3).

The Fluent 13.0 commercial package (ANSYS) was used to solve the unsteady, incompressible, axisymmetrical Navier–Stokes equations. Swimming was modeled by coupling the forward motion of the jellyfish to the hydrodynamic forces exerted on the bell. Pressure and shear forces acting in the axial direction were integrated across the jellyfish surface at the end of each time step, and the resulting body acceleration was calculated. The discrete form of this force balance is given by the equation:

$$ \sum F_{ax} = \frac{\partial F_{ax}}{\partial t} $$

[3]

where \( \sum F_{ax} \) is the sum of all pressure and shear forces in the axial direction at time step \( n \), \( m \) is the mass of the jellyfish (fluid density assumed to be the same as the surrounding water: \( \rho \approx 998.2 \text{ kg m}^{-3} \)), and \( \frac{\partial F_{ax}}{\partial t} \) is the axial acceleration at the center of mass of the jellyfish. Using Taylor series expansions, the acceleration can be approximated by a second-order accurate, backward finite difference equation:

$$ \left( \frac{\partial^2 F_{ax}}{\partial t^2} \right) \approx \frac{2z^2 - 5z^n + 4z^{n-1} - z^{n-2}}{\Delta t^2} $$

[4]

where \( z \) is the axial displacement and \( \Delta t \) is the time step. Combining Eqs. 7 and 8, the displacement at time step \( n \) can be approximated:
\[ z^n = \frac{(\Delta t)^2}{2m} \sum \frac{5}{2} z^{n-1} - 2z^n + 1 z^{n-2}. \]  

Finally, to ensure stable coupling between the solver and the jellyfish displacement, we used an exponentially weighted moving average to smoothen the raw displacement, \( z^n \):

\[ \zeta^n = \begin{cases} \alpha z^n + (1 - \alpha) \zeta^{n-1}, & n = 0 \\ \alpha z^n + (1 - \alpha) \zeta^{n-1}, & n > 0 \end{cases} \]  

where \( \zeta \) is the smoothed displacement prescribed to the jellyfish and \( \alpha \in [0, 1] \) is the smoothing factor. We found \( \alpha = 0.25 \) was required for a robust simulation.

Verification and validation studies were performed to ensure the numerical and physical accuracy of our simulation. We first checked the sensitivity of our results to mesh and time step refinement (Fig. S4). A base mesh of 60,895 cells (64 and 58 cell faces on the top and bottom bell contours, respectively) was refined to 135,765 cells (86 and 82 cell faces on the top and bottom bell contours, respectively) and showed that the sum of forces acting on the jellyfish, and consequently its swimming performance, was insensitive to spatial refinement. Similarly, simulations run using a time step refined from \( \Delta t = 1/90 \) s to \( \Delta t = 1/180 \) s resulted in no appreciable change in the hydrodynamic forces acting on the jellyfish. Next, the instantaneous displacement of the numerical jellyfish was compared with that of the natural jellyfish used for the swimming kinematics (Fig. S5). Both show similar trends and indicate similar velocities throughout the swimming period, resulting in a nearly identical total displacement.

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vortex rings and aquatic propulsion mechanisms.