

MECHANICS OF JET PROPULSION IN THE
HYDROMEDUSAN JELLYFISH, *POLYORCHIS PENICILLATUS*
III. A NATURAL RESONATING BELL; THE PRESENCE AND
IMPORTANCE OF A RESONANT PHENOMENON IN THE LOCOMOTOR
STRUCTURE

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SUMMARY

The bell of the hydromedusan jellyfish *Polyorchis penicillatus* (Eschscholtz, 1829) was modelled as a harmonically forced, damped oscillator. The robustness of the model was tested and verified by comparing estimates of the work done during the contraction phase predicted by the model with analogous values measured in completely independent experiments. Data suggest that the animals swim at a frequency that is at or near the resonant frequency of the locomotor apparatus. The implications of this phenomenon for the mechanics and physiology of the system are discussed. If the swimming muscles force the bell at its resonant frequency, as opposed to a single contraction at the same rate of deformation, the amplitude of the oscillation will be increased by about 40 %, and the energetic requirement for the cycle will be reduced by about 24–37 % of the total cost of the cycle. The advantages of forcing the structure at its resonant frequency seem quite remarkable.

INTRODUCTION

The phenomenon of resonance has profound importance throughout physics. It can be observed when a physical oscillator is subjected to a periodic driving force by an external agency. A periodic force of fixed size produces very different amplitudes of oscillation, depending on its frequency. If the driving frequency is at, or near, the natural frequency of the driven oscillator, then the amplitude of the oscillation is very large for repeated applications of a small force. Driving frequencies above or below the natural frequency of the oscillator produce comparatively small amplitudes of oscillation for the same force.

The locomotor apparatus in metazoan animals is driven by muscles, the biological force generators, to obtain the maximum amplitude of oscillation, thus maximizing

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their mechanical function to propel the organism. The ability to increase the force generated by the muscle beyond some maximum value, however, is limited by its physiology (Alexander, 1985). Animals might therefore design locomotor structures that couple the frequency of activation of the muscles with the resonant frequency of the locomotor structure, thus taking advantage of the phenomenon of resonance. Animals working at the resonant frequency of the locomotor structure could then obtain a maximum amplitude of oscillation in the locomotor structure with the minimum mass of muscle to force the oscillator, while keeping the maximum force generated constant. A locomotor structure working at or near resonance can thus act as an energy conserving device. This idea is not new. McMahon (1975, 1985) has proposed that hopping kangaroos and galloping quadrupeds have a stride frequency that is the resonant frequency of the body. Taylor (1985) suggests that his recent experiments on human hopping show that the role of elastic strain energy is maximized and metabolic energy is minimized when subjects hop at their natural frequency.

This paper models the bell of the hydromedusan *Polyorchis penicillatus* as a moderately damped harmonic oscillator, and shows that the predicted resonant frequency of the oscillator is at or near the working frequency of the animal. The structure of the bell has been described in detail (Gladfelter, 1972; DeMont & Gosline, 1988a), but the information is summarized here. The swimming muscles line the surface of the subumbrellar mesoglea and are arranged to decrease the diameter of the bell during contractions. No muscles exist to antagonize this movement. The bell itself is made of noncellular mesoglea that is traversed by numerous radially arranged fibres. These fibres are loaded in tension during contraction of the bell, and rough calculations show that there are enough of the fibres present in the structure to store all the potential strain energy required to antagonize the contraction of the swimming muscles (DeMont & Gosline, 1988a). There is also evidence that the amount of energy required to power the refilling, and the amount provided by the energy storage system are closely matched, suggesting that the energy storage system is tuned to work at some optimum (DeMont & Gosline, 1988b). That is, mechanical energy is not wasted by storing more energy in the elastic storage system than is needed to just power the refilling phase.

MATERIALS AND METHODS

Experimental

Live *Polyorchis* were collected in Bamfield Inlet, British Columbia, and maintained in running seawater aquaria. Free damped oscillations of the locomotor structure of a single animal were recorded from the free oscillations following single spontaneous contractions of the swimming muscles. To record these data, a specimen was tethered to a flat Plexiglas plate at the apex of the bell (with cyanoacrylate adhesive). The bell is transparent, and it is possible to observe changes in the internal dimensions of the animal during contractions of the bell. A video system was used to monitor real time changes in the internal diameter of the tethered

animal. This system uses a video dimension analyser (Model 303, Instruments for Physiology and Medicine, San Diego, CA) that provides an electrical signal which is proportional to the separation of two contrast boundaries on any horizontal line in the video image. The free damped oscillations were recorded on a Hewlett–Packard instrumentation tape recorder (Model 3964A) and later printed on a Hewlett–Packard chart recorder (Model 7402A) for final analysis.

Most of the animals examined during these studies did not give clean, single spontaneous contractions followed by free damped oscillations, as seen for the individual observed in this study. This individual contracted in such a manner for the entire length of these experiments, and allowed adequate time to set up the video system and to collect very clean records of the free damped oscillations. It unfortunately did not cooperate by contracting in continuous trains at any time during the experiment. However, the working frequency of 11 freely swimming animals was measured by a frame-by-frame analysis of video records taken of other animals contracting in continuous trains.

Analytical

The locomotor structure of the jellyfish was modelled as a damped harmonic oscillator (see for example Kleppner & Kolenkow, 1973). The equation of motion for such an oscillator is:

$$m\ddot{X} + b\dot{X} + kX = 0, \quad (1)$$

where X is the displacement, and in this experiment, is the inside circumference of the bell. The other terms are the first (\dot{X}) and second derivative (\ddot{X}) of the displacement, and represent, respectively, the velocity and acceleration of the body wall. Each of the physical constants associated with the three terms in the equation has a biological analogy. The spring constant, k , is the structural stiffness of the bell. The damping coefficient, b , accounts for both the internal friction in the tissue itself, resulting from the viscoelastic properties of the mesoglea, and the external friction in the water resulting from the shear forces generated during the flow of water out of and around the bell. The mass of the system, m , is the effective mass of the bell. It includes both the actual mass of the animal and the mass of any water that is accelerated by the contraction of the bell.

Values for the three constants were obtained using separate methods. The spring constant, k , was obtained from an independent study (see below). The damping coefficient, b , was measured from the free damped oscillations recorded by methods described above. The mass of the oscillator, m , including the bell itself and any water entrained during the oscillation, was not known, but this mass could be calculated, as follows, from standard equations for damped oscillators.

It can be shown that the logarithmic decrement, the ratio of successive maximum displacements of a free damped oscillator, is defined by:

$$\ln (X'/X'') = b/4mf, \quad (2)$$

where X' and X'' are the displacements and f is the circular frequency. These

successive displacement maxima can also be used to calculate the resilience, R , of the oscillator per half-cycle as (Alexander, 1983):

$$R = (X''/X')^2. \quad (3)$$

Now the angular frequency, ω , for a damped harmonic oscillator can be defined as:

$$\omega^2 = k/m - b^2/4m^2. \quad (4)$$

Solving equation 2 for b and substituting into equation 4 yields an equation defining the mass of the spring in terms of experimentally measurable quantities:

$$m = k/\{\omega^2 + 4f^2[\ln(X'/X'')]^2\}. \quad (5)$$

The only unknown is the spring constant, k . However, the dynamic structural stiffness (E) for the swimming structure, where the strain is defined in terms of changes in the inside circumference of the bell, was shown in a previous paper (DeMont & Gosline, 1988a) to be between 400 and 1000 N m⁻². This structural stiffness can be converted to a spring constant with the following equation:

$$k = HEt/\pi R_o, \quad (6)$$

where H is the height of the bell, t is the resting thickness of the bell, and R_o is the resting inside radius. The derivation of this equation is shown in Appendix I.

These equations provide enough information to determine the equation of motion of the locomotor structure, modelled as a harmonic oscillator. One clear advantage of modelling the locomotor structure in such a manner is that it is possible to predict how the locomotor structure will respond to an applied driving force of any given frequency. A forced damped harmonic oscillator has a frequency-dependent amplitude of oscillation which is defined by:

$$A(\omega) = F_o/m[(\omega_o^2 - \omega^2) + (\omega\gamma)^2]^{1/2}, \quad (7)$$

where F_o is the maximum amplitude of the sinusoidal driving force and ω_o is the natural frequency of the undamped oscillator, defined by:

$$\omega_o = (k/m)^{1/2} \quad (8)$$

and γ is defined by:

$$\gamma = b/m. \quad (9)$$

The assumptions which were made in order to model the locomotor apparatus as a harmonically forced, damped oscillator cannot be verified experimentally. However, it is possible to make a specific prediction using the model and compare the prediction to experimentally measured values of the same quantity. The prediction made was the work done per cycle by the exciting force. The derivation of the equation used to make the prediction is summarized in Appendix II. The equation used was:

$$W = \pi F_o A \sin [\arctan (\gamma\omega/\omega_o^2 - \omega^2)], \quad (10)$$

where all symbols are as described previously.

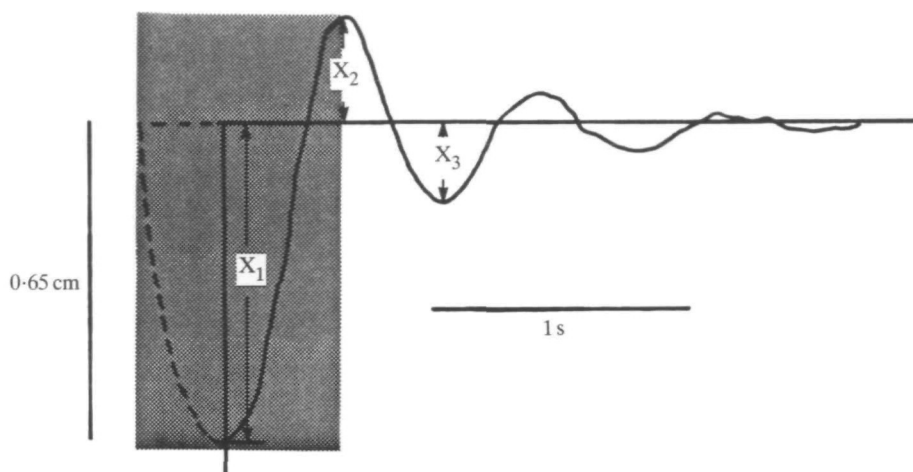


Fig. 1. A typical free vibration of the inside diameter of the bell of the hydromedusan *Polyorchis*. The maximum amplitude of oscillation is 6.46 mm.

RESULTS

The modelling of any system as a harmonically driven, damped oscillator requires values for three parameters: (1) the stiffness of the spring providing the elastic restoring force, (2) the damping in the system, and (3) the mass of the oscillator. The spring in the locomotor system of this animal is the mesogleal elastic structure containing a system of radial 'elastic' fibres. Certain morphometric data, and the estimate of the dynamic structural stiffness of the bell taken from DeMont & Gosline (1988a), can be used with equation 6 to calculate the spring constant of the elastic system in the locomotor apparatus. The necessary morphometric data from the animal used to measure the free damped oscillations include: the height of the bell, $H = 2.0 \times 10^{-2}$ m; the resting thickness of the bell, $t = 2.5 \times 10^{-3}$ m; the resting inside radius of the subumbrellar cavity, $R_0 = 8.6 \times 10^{-3}$ m. These morphometric data and the dynamic structural stiffness values given above substituted into equation 6 yield a spring constant of between 0.74 and 1.85 N m^{-1} .

The measurement of the damping parameters can be made directly from records of free damped oscillations. A typical free damped oscillation of the inside diameter of the bell is shown in Fig. 1. Eight such oscillations were recorded. Careful inspection of Fig. 1 shows that both the frequencies of oscillation and the relative amplitudes of successive oscillations differ between the first oscillation (shaded) and the subsequent oscillations. This suggests that two distinct processes are occurring, which become apparent by inspection of the pressure changes that occur during the jet cycle. Simultaneous measurement of pressure changes in the subumbrellar cavity and free damped oscillations of the internal diameter of the subumbrellar cavity of this animal were not made. Pressure-diameter records from DeMont & Gosline (1988b) can, however, be used to infer what processes are occurring during the free oscillations.

Table 1. *Numerical values of the parameters estimated from Fig. 1 for the first oscillation (shaded) or derived from the equations*

Parameter	Value	Units
f	1.17 (0.028)	Hz
ω	7.35 (0.15)	rad s ⁻¹
$\ln(X_1/X_2)$	1.078 (0.073)	
m	0.0123–0.0306	kg
k	0.74–1.85	N m ⁻¹
b	0.0618–0.154	N m ⁻¹ s ⁻¹

Values in parenthesis are standard deviations of the means, $N = 8$.

Figs 1 and 2 from DeMont & Gosline (1988b) show that pressures are large during the forced contraction but decay significantly during the refilling. Therefore, we expect pressure changes during the oscillations that follow the initial forced oscillation of Fig. 1 to be very small. Thus fluid flow will be large during the first oscillation (shaded), but comparatively small during the free damped oscillations that follow. This suggests that during the initial forced contraction in Fig. 1 the measured damping terms will reflect a complex interaction resulting from both the frictional losses associated with the flow out of the subumbrellar cavity and around the exterior of the bell and with mechanical hysteresis associated with the deformation of the bell mesoglea itself. The damping terms measured from the second and subsequent oscillations will mostly reflect the mechanical hysteresis associated with the deformation of the bell mesoglea. Thus, data from the first oscillation (shaded) will be used to estimate the parameters used in the model. Data from the second oscillation will be used as an independent measurement of the material properties of the bell mesoglea.

Data taken from the first oscillation of all eight damped oscillations, as illustrated in Fig. 1, are summarized in Table 1. All reported parameters that were measured from these records are averaged values. The errors associated with these measurements are standard deviations of the mean values. The ratio of successive amplitudes (X_1/X_2) can be substituted into equation 2 to give the logarithmic decrement. Eight of such measurements yield an average logarithmic decrement of 1.078. The circular frequency of the first oscillation is 1.17 Hz, corresponding to an angular frequency of 7.35 rad s⁻¹.

These data can be used in equation 5 to calculate the effective mass of the oscillator. The numerator on the right side of the equation is the stiffness of the spring, and is between 0.74 and 1.85 N m⁻¹. Substitution of these values into equation 5 gives an effective mass of between 0.0123 and 0.0306 kg. For comparison, the real wet mass of the entire animal was 0.005 kg, and the mass of the entire animal plus the mass of the water contained in the resting subumbrellar cavity is about 0.011 kg.

These data can also be used to measure the damping parameter, b , used in the equation of motion of the oscillator. Solving equation 2 for b , and substitution of the

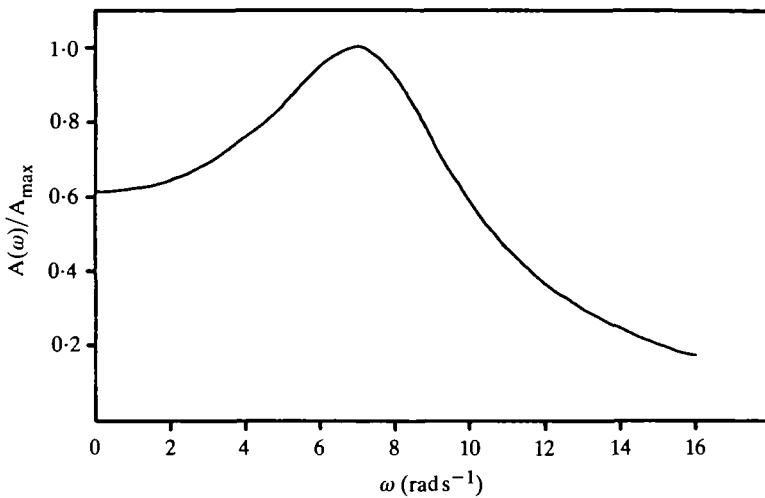


Fig. 2. The frequency-dependent relative amplitude of oscillation for a constant maximum amplitude of the exciting force. The maximum predicted amplitude was normalized to the maximum amplitude of oscillation measured in Fig. 1.

appropriate values yields a damping parameter of between 0.062 and $0.154 \text{ N m}^{-1} \text{ s}^{-1}$. These values can be used with equation 7 to predict the frequency dependence of the amplitude of oscillation for a sinusoidally varying force with some constant maximum amplitude. Fig. 2 shows this frequency dependence for a harmonic oscillator with the parameters defined above for the jellyfish. The maximum amplitude has been normalized to the maximum amplitude measured from the free damped oscillations from Fig. 1. For a constant maximum force, the maximum amplitude of oscillation is reached at a frequency of about 7 rad s^{-1} . This corresponds to a circular frequency of about 1.1 Hz . This, therefore, is the predicted resonant frequency of the locomotor system for this particular animal.

Continuous trains of contractions were not observed in this animal, and thus the natural swimming frequency for this individual is not known. However, Fig. 3 shows the waveform of continuous contractions for two other tethered animals measured using the video system described above. The working frequencies are about 0.8 Hz and 1.0 Hz . Free-swimming animals have a mean frequency of 1.1 Hz ($s = 0.43$) when contracting in continuous trains.

Data for the free oscillations following the initial forced oscillation (see Fig. 1) can be used to calculate the resilience of the mesogleal material. The ratio X_3/X_2 measured from all eight records of the free damped oscillations substituted into equation 3 give a mean value of 61% for the resilience of the mesogleal material.

DISCUSSION

The mesogleal bell of the hydromedusan jellyfish *Polyorchis* was modelled as a damped, harmonically forced oscillator. Four major assumptions were made in

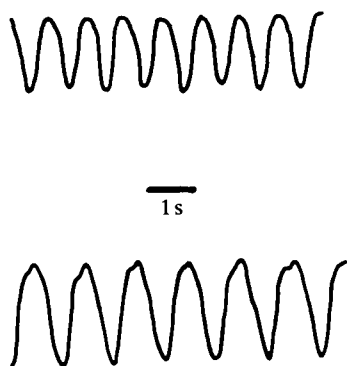


Fig. 3. Typical records of the inside diameter of the bell of a jellyfish contracting in continuous trains.

making this model. First, classical harmonic oscillators are modelled as massless springs with a known mass attached in series at one end of a spring. The 'spring' in the jellyfish is the bell mesoglea itself. The spring is therefore not massless, and the attached mass of the oscillator becomes, in part, the spring itself, as well as the mass of the rest of the bell and the mass of water entrained by the movement. Second, and somewhat related to the first assumption, a linear stress-strain curve was assumed to describe the mechanical properties of the elastic structure. Third, the damping term in the equation of motion, which includes both the internal damping of the tissue and the damping due to frictional losses within the moving fluid, was assumed to be proportional to the velocity of movement, thus ignoring any higher-order terms. Fourth, when predicting how the oscillator will respond to an applied driving force of any given frequency, for mathematical simplicity, the driving force was assumed to be sinusoidal. The force generators in this oscillator are the swimming muscles, and these do not generate tension sinusoidally (Spencer & Satterlie, 1981). However, the resulting displacement of the locomotor structure is very nearly a sinusoidal function (see Fig. 3). The validity of these assumptions is difficult to test, but a specific prediction made by the model is in excellent agreement with independent measurements made experimentally in a previous paper (DeMont & Gosline, 1988*b*). This implies that the model is robust and means that its validity is not seriously affected by moderate deviations from the underlying assumptions.

The robustness of the model was tested by using equation 10 to predict the frequency-dependent work output per cycle for the animal examined in DeMont & Gosline (1988*b*). This was then compared directly to the completely independent experimental measurements made of the same parameter in that paper. Morphometric data used in equation 10 were: the height of the bell, 2.7×10^{-2} m; the resting inside radius of the subumbrellar cavity, 1.0×10^{-2} m; the resting thickness of the bell, 2.5×10^{-3} m. These data, along with the damping parameters measured from Fig. 1, were used in the equations described in Materials and Methods to calculate all the parameters in equation 10. The amplitude of the oscillation was taken from fig. 1 of DeMont & Gosline (1988*b*) and is the change in the circumference of the bell. It

was calculated from half of the peak-to-peak change in diameter, and is 7.9×10^{-3} m. F_0 , measured from equation AII.8, has a maximum value of about 0.01 N. The angular frequency used was the measured frequency from fig. 1 of DeMont & Gosline (1988b), 5 rad s^{-1} . These calculations yield a predicted work output per full cycle of between 7.0×10^{-5} and 1.8×10^{-4} J. This represents the energy dissipated during an entire cycle. For a half-cycle, the predicted energy dissipated will be between 3.5×10^{-5} and 7.8×10^{-5} J.

This can be compared to data from DeMont & Gosline (1988b; see table 1), where the energy dissipated for the contraction phase was measured experimentally. The energy dissipated will be equal to the energy dissipated in generating the pressure in the subumbrellar cavity, 5.4×10^{-5} J, plus the energy dissipated in deforming the tissue. The latter value cannot be seen directly in table 1 (DeMont & Gosline, 1988b) but can be calculated from the dynamic test data in DeMont & Gosline (1988a). From the loss modulus of the mesogleal material, the energy dissipated during the deformation is between 0.4×10^{-5} and 0.9×10^{-5} J. The experimentally measured energy dissipated during the contraction phase of the cycle, therefore, is between 5.8×10^{-5} and 6.3×10^{-5} J. The predicted energy dissipated for a half-cycle nicely spans the values measured in independent experiments, implying that the model is robust; therefore any moderate violations in the assumptions stated previously will not invalidate the model.

An additional test of the robustness of the model is provided by a comparison of the measured and predicted force generated by the swimming muscles during the contraction. The maximum muscle force predicted by equation AII.8 used in the equations to predict the work done per cycle by the animal in DeMont & Gosline (1988b) is 0.01 N. This can be compared to the maximum force measured experimentally for the same animal. The maximum stress generated by the contraction of the muscle is shown in DeMont & Gosline (1988b) to be at least $1.25 \times 10^5 \text{ N m}^{-2}$. The cross-sectional area of the muscles is approximately $5.4 \times 10^{-8} \text{ m}^2$. Multiplication of these two values gives a measured force of about 0.007 N. Considering that this measured muscle force is only that which is required to account for the pressure generated in the bell chamber and that the true muscle force is probably somewhat larger (the muscles must also provide force to overcome the viscoelastic loss in the mesogleal material), the measured and predicted values of the maximum force generated by the muscles are in excellent agreement.

It should be noted that these data can be compared, as described in DeMont & Gosline (1988b), with previous estimates (Daniel, 1985; Bone & Trueman, 1982) of the power requirements of jet propulsion. Using the methods described in DeMont & Gosline (1988b), the measured power requirements for *Polvorchis* are between 0.27 and $0.29 \text{ W kg}^{-5/3}$. These calculations also agree with Daniel's estimates where the values range from 0.2 to $0.75 \text{ W kg}^{-5/3}$.

No mention has been made yet of the data collected for the second and following oscillations seen in the free damped oscillations of Fig. 1. These data are unimportant to the mechanics of the locomotor system, especially with regard to the

phenomenon of resonance, but they can be used to examine the material properties of the locomotor apparatus. Because pressures are very small in the subumbrellar cavity during these oscillations, water movement in and around the bell would be expected to be minimal. Thus, shear stresses in the water will be small, but certainly not zero. Any measure of damping will mostly reflect viscous damping in the mesoglea, and data can be used to measure the properties of the material comprising the mesoglea itself. Equation 3 was used to calculate the resilience of the material, and the mean value calculated was 61 %. This can be compared to the resilience of isolated mesoglea measured in dynamic tests in DeMont & Gosline (1988a). The average resilience of the isolated mesoglea is 58 %. These results are in excellent agreement, and suggest that the isolation of the mesoglea for the dynamic tests carried out in the previous study did not alter its mechanical properties.

The predicted resonant frequency of the locomotor structure for the animal used to collect the damping parameters is 1.1 Hz. The working frequency, i.e. the frequency of contraction for an animal contracting in a continuous train, was not measured for the animal described here. However, the mean value of the working frequency for eight free-swimming animals is 1.1 Hz. This fortuitous result certainly suggests that all *Polyorchis* swim at their respective resonant frequencies. This does not imply, however, that all these animals swim at exactly that particular frequency. In fact, variations in this working frequency certainly exist. For instance, the animals swimming in the trains of contractions shown in Fig. 3 have working frequencies of about 0.8 and 1 Hz. If the animal with the lower working frequency had a predicted frequency-dependent amplitude of oscillation as shown in Fig. 2, it would work at a frequency well to the left of the peak amplitude. But individual variations in the structural stiffness of the bell, the damping parameters, and the size of the animals could generate an entire spectrum of resonant curves. We suggest, therefore, that each individual, when contracting in continuous trains, is functioning at, or near, the resonant frequency of its locomotor apparatus.

What does the animal gain by forcing the locomotor structure at its resonant frequency? Taylor (1985) suggests, in human hopping at least, that the role of elastic energy storage is maximized and that metabolic energy consumption is minimized when subjects hop at their natural frequency. We did not carry out metabolic studies, so we cannot address the question of potential metabolic savings incurred by this animal working at resonance. However, data from DeMont & Gosline (1988a) suggest that there is a close matching between the quantity of elastic strain energy stored in the spring system, and the amount of energy needed from this storage system to power the refilling phase. It is shown that between 1.0×10^{-5} and 2.4×10^{-5} J of energy will be available from the energy originally stored in the system. Other mechanical measurements show that between 1.7×10^{-5} and 2.1×10^{-5} J of energy would be required to power the refilling phase. The animal that was examined was contracting in continuous trains, and presumably at or near the resonant frequency of its locomotor system. It would seem, then, that one advantage of working at resonance is that the animals can maximize the use of their elastic

energy storage system. Thus, mechanical energy that had been diverted from the metabolic energy of the contraction of the muscles will not be wasted by an inefficient storage system. Only that energy that is required to power the refilling will be diverted from other mechanical energies.

Fig. 2 shows that for a constant maximum force, the animals can increase the amplitude of the oscillations by about 40% above the amplitude for single contractions, if they force the bell at the resonant frequency. Increases in the amplitude of oscillation are important for jet-propelled animals, since larger volumes of water can be expelled for the same maximum force. It may, however, be more instructive to examine the work done by the muscles when they are forcing the bell at and off its resonant frequency.

Equation 10 can be used to calculate the work done by the exciting force for any frequency. It would seem appropriate then to use equation 10 to predict the work done near the resonant frequency, and far from the resonant frequency, and then compare the magnitudes of the predicted values. This comparison, however, cannot be made using equation 10. The physical model enforces a change in the rate of the deformation of the bell as the angular frequency varies. This comparison, therefore, would be quite arbitrary, since predicted changes in the work would mostly reflect changes in the dissipative forces created by changes in the rates of both deformation of the body wall and fluid flow. A more physiologically relevant comparison would be to compare the predicted work done by an animal swimming at resonance with the work done in completing a single contraction at the same rate of deformation without resonance.

For any oscillator functioning at resonance, such as a simple mass on a spring, potential and kinetic energies fluctuate sinusoidally between the energy stored in the spring, and the energy associated with the movement of the mass of the oscillator. At any point in time, the sum of the kinetic and potential energies is constant. That is, as the spring is compressed near the extremes of displacement of the oscillator, it stores potential energy that has been transferred from the kinetic energy associated with the movement of the oscillator. All of the energy in the system is stored as potential energy in the spring. Near the equilibrium position of the displacement, most of the energy has been transferred into kinetic energy, and little energy is stored in the spring. At resonance, the external force does work to counter only dissipative processes. This can be seen qualitatively with a closer examination of data in table 1 (DeMont & Gosline, 1988b). If the animal is working at resonance, the kinetic and potential energies should be about equal in magnitude. This is reflected in the approximately equal magnitudes of the energy required to deform the tissue and the energy associated with the inertia of the wall, summed for the contraction and refilling phase. The energy the swimming muscles generate, therefore, if the swimming muscles in this animal are forcing the bell to work at its resonant frequency, can be approximated as the energy to overcome the dissipative forces. This energy is shown above to be between 5.8×10^{-5} and 6.3×10^{-5} J. The energy to overcome the dissipative forces during the refilling should not be included in this

summation, since the swimming muscles do not directly do this work. The refilling phase is powered by the release of energy from the deformation of the tissue.

Off resonance, the kinetic and potential energies are not transferred from one to the other, and their sum is not constant at any time. For example, below resonance, where elastic forces dominate, the energy generated by the force can be approximated as the energy to counter the dissipative forces and the energy required to deform the spring. This can be measured from data presented in table 1 (DeMont & Gosline, 1988*b*). The energy required to counter the dissipative forces is between 5.8×10^{-5} and 6.3×10^{-5} J. The energy required to deform the tissue is between 1.8×10^{-5} and 4.1×10^{-5} J. Therefore, off resonance the energy generated by the swimming muscles is between 7.6×10^{-5} and 1.0×10^{-4} J. A comparison of these energies with the energies generated at resonance (5.8×10^{-5} and 6.3×10^{-5} J) gives an estimate of the potential energy savings of working at resonance. If the swimming muscles of these animals force the bell at a frequency that is near the resonant frequency of the bell, the energetic requirements for the cycle will be reduced by about 24–37% of the total energy generated by the swimming muscles. The advantages of forcing the structure at its resonant frequency are therefore quite remarkable.

We have not examined scaling phenomena related to resonance in this animal, although size-dependent variation in the resonant frequencies would be expected because mass is one of the parameters characterizing an oscillator. It is very interesting that one aspect of the physiology of the swimming muscles, however, seems to be functionally related to the scaling of the resonant frequencies. A positive correlation between the size of the animal (measured as the bell diameter) and the duration of the tension development has been shown to exist (Spencer & Satterlie, 1981). If the model presented here is valid, then it is tempting to infer that the size dependence of the duration of the tension development is an attempt to adjust the forcing frequency to accommodate for natural, requisite changes in the resonant frequency of the locomotor structure as the animal grows. Another physiological phenomenon potentially related to the idea of resonance is that the swimming muscles have a refractory period that exactly matches the swimming frequency (A. N. Spencer, personal communication). This would ensure that the muscles will not contract at frequencies above the resonant frequency. Thus, aspects of the animal's physiology appear to be elegantly designed to drive the locomotor system at its natural resonance (DeMont, 1986).

APPENDIX I

This appendix describes the derivation of equation 6. It is necessary to convert the dynamic structural stiffness measured from DeMont & Gosline (1988*a*) into a spring constant, k , for use in the equations of motion of damped harmonic oscillators.

The circumferential stress acting on a thin-walled cylinder due to an external pressure is defined by dividing the force acting on the cylinder by the area over which the force acts. The circumferential force is given by:

$$F = 2PRH , \quad (\text{AI.1})$$

where P is pressure, R is the radius, and H is the length of the cylinder, or in this case the height of the bell. The area over which this force acts is given by:

$$A = 2tH , \quad (\text{AI.2})$$

where t is the wall thickness. The circumferential stress is therefore:

$$\sigma_c = PR/t . \quad (\text{AI.3})$$

Strain in the bell was defined as the relative change in the circumference of the inside of the bell:

$$\epsilon = X/2\pi R_o , \quad (\text{AI.4})$$

where X is the circumferential deformation and R_o is the resting bell radius. By dividing equation AI.3 by equation AI.4 to give a stiffness, E , and rearrangement, the circumferential deformation becomes:

$$X = 2\pi PRR_o/Et . \quad (\text{AI.5})$$

The spring constant, k , required in this analysis is of the form, $k = F/X$. Thus, equation AI.1 divided by equation AI.5 will give:

$$k = HEt/\pi R_o . \quad (\text{AI.6})$$

APPENDIX II

This appendix describes the derivation of equation 10 (see Hansen & Chenea, 1952; pp. 96–97). It estimates the work done per cycle by the locomotor muscles contracting at any frequency. The driving force is assumed to oscillate sinusoidally, and is given by:

$$F(t) = F_o \cos(\omega t) , \quad (\text{AII.1})$$

where F_o is the maximum magnitude of the force, ω is the angular frequency of the contraction, and t is time. The total work done by such a force, over one period of oscillation (T), is given by the definite integral:

$$W = \int_{x=0}^{x=T} (F_o \cos \omega t) dx , \quad (\text{AII.2})$$

which can be changed to a time integral and becomes:

$$W = \int_0^T [(F_o \cos \omega t) dx/dt] dt . \quad (\text{AII.3})$$

For any sinusoidally driven oscillator, the displacement of the mass is given by:

$$X = A \cos(\omega t + \Phi) , \quad (\text{AII.4})$$

where A is the maximum amplitude of oscillation, and Φ is the phase shift between

the applied force and the displacement. This function, and its first derivative, substituted into equation AII.3 yields:

$$W = \int_0^T -FA\omega(\cos\omega t)[\sin(\omega t + \Phi)]dt. \quad (\text{AII.5})$$

With trigonometric identities, this equation can be transformed into the following equation:

$$W = \int_0^T -FA\omega[0.5\sin(2\omega t + \Phi) - 0.5\sin(\Phi)]dt. \quad (\text{AII.6})$$

Since $0.5\sin(2\omega t + \Phi)dt$ is equal to zero, equation AII.6 simplifies to:

$$W = F_o\pi\text{Asin}(\Phi). \quad (\text{AII.7})$$

The maximum force, F_o , is given by:

$$F_o = A(\omega_o)m\omega_o\gamma \quad (\text{AII.8})$$

and Φ by:

$$\Phi = \arctan(\gamma\omega/\omega_o^2 - \omega^2). \quad (\text{AII.9})$$

Thus,

$$W = \pi F_o\text{Asin}[\arctan(\gamma\omega/\omega_o^2 - \omega^2)]. \quad (\text{AII.10})$$

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