28. We measured the extensions by allowing the chain to reach its equilibrium extension and then digitizing 40 video frames with a delay (0.3 to 1.2 s) between each frame to allow the fluctuating chain to "explore" completely the phase space of accessible conformations. We measured the extension of the molecule along the direction of flow using a computer-generated cursor, and the average extension (x) and its standard deviation σ_x were calculated at each velocity from the 40 individual extension measurements.
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Muscle Efficiency and Elastic Storage in the Flight Motor of *Drosophila*

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Insects could minimize the high energetic costs of flight in two ways: by employing high-efficiency muscles and by using elastic elements within the thorax to recover energy expended accelerating the wings. However, because muscle efficiency and elastic storage have proven difficult variables to measure, it is not known which of these strategies is actually used. By comparison of mechanical power measurements based on gas exchange with simultaneously measured flight kinematics in *Drosophila*, a method was developed for determining both the mechanical efficiency and the minimum degree of elastic storage within the flight motor. Muscle efficiency values of 10 percent suggest that insects may minimize energy use in flight by employing an elastic flight motor rather than by using extraordinarily efficient muscles. Further, because of the trade-off between inertial and aerodynamic power throughout the wing stroke, an elastic storage capacity as low as 10 percent may be enough to minimize the energetic costs of flight.

Flight is an energetically costly form of locomotion, requiring metabolic rates as high as 100 times the resting rate (*1*). Most of the total energy required for flight is dissipated as heat in the flight musculature. For hovering animals, the remaining mechanical energy is divided into three components: induced power required to generate lift, profile power necessary to overcome drag on the wings, and inertial power required to accelerate and decelerate the wings during stroke reversal (*2*). Previous comparisons of total metabolic rate and estimated power output suggest that insects minimize the high cost of flight either by using highly efficient muscles or by recovering inertial power through elastic storage (*3*). It is not certain, however, which of these two strategies is actually used.

Female *Drosophila hydei* were tethered and flown in a flight arena that measured the frequency and amplitude of the wing stroke as well as the yaw torque produced by the animal (Fig. 1). The fly and the torque transducer were enclosed in a respirometry chamber and surrounded by a visual panorama consisting of a dark stripe on a bright background. All experiments were done under closed-loop conditions such that the yaw torque produced by the fly was used to control the angular velocity of the stripe. Under these conditions, tethered flies actively modulated yaw torque through changes in wingbeat kinematics in order to fix the position of the stripe in the front portion of their visual field (*4*). In order to increase the variations in wingbeat amplitude and stroke amplitude, sinusoid and square wave voltage biases were added to the control signal in some experiments. Under these conditions, flies actively stabilized the stripe position by modulating flight kinematics in order to generate a compensatory torque opposite to the imposed bias. Additional modulation of wingbeat kinematics in some experiments was achieved by modulating the gain of the closed-loop feedback. These active modulations in wing stroke amplitude and frequency produced by these manipulations provided a useful and rigorous means for comparing respirometric and kinematic estimates of mechanical power.

A representative flight sequence is displayed in Fig. 2 and shows the simultaneous measurements of metabolic cost, stroke amplitude (summed from the two wings), wingbeat frequency, and yaw torque during the application of a sinusoidal bias under closed-loop conditions. As in all experiments, the fly was capable of stabilizing the visual stripe by generating a sinusoidal yaw torque to compensate for the applied bias. During this modulation in torque, the metabolic cost oscillates at roughly twice the bias frequency and is highly correlated with changes in wingbeat frequency and stroke amplitude.

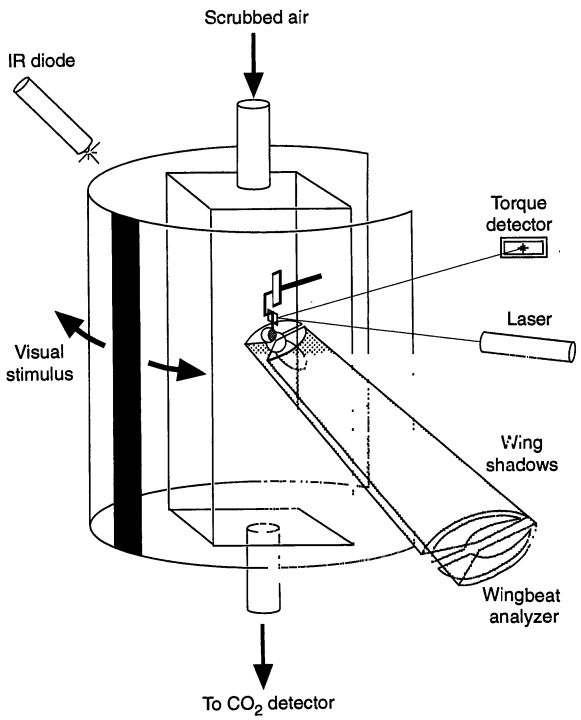

Fig. 1. Experimental apparatus for simultaneously measuring metabolic output and wingbeat kinematics of *Drosophila* during tethered flight. Flies were tethered with light-activated adhesive to a yaw torque transducer that optically tracks the angular deflection of a laser beam aimed at a small mirror mounted to the fly's tether. The fly was enclosed within a 30-ml rectangular acrylic and glass respirometry chamber. Room air was scrubbed of water and CO_2, pulled through the flight chamber at a rate of 150 ml min^{-1}, and sampled by a CO_2 analyzer (*11*). The wingbeat frequency and wing stroke amplitude of the flies were measured continuously by optical tracking of the shadows of the two wings cast by an infrared light source (*12*). The respirometry chamber was enclosed in a close-packed cylindrical array of 720 green light-emitting diodes that produced a 30° dark stripe on a bright background.

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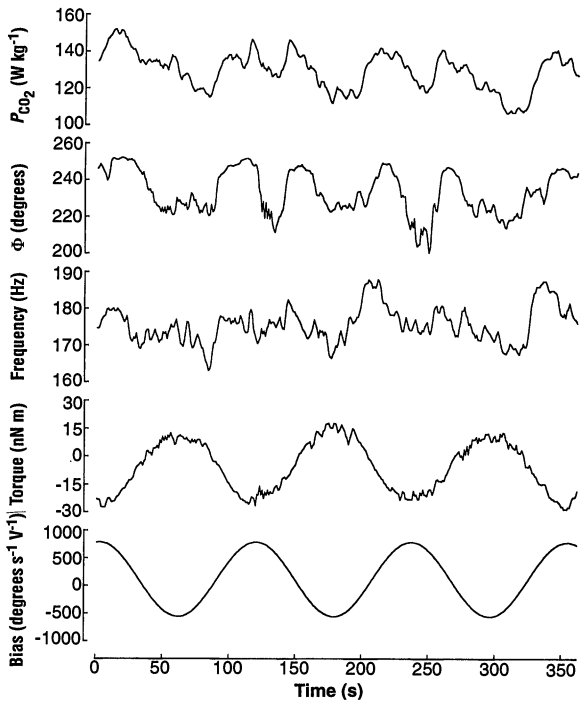

Fig. 2. Representative record showing measured metabolic rate during closed-loop conditions. In order to stabilize the vertical stripe, the fly produces compensatory yaw torque to counterbalance the sinusoidal rotatory bias. The generation of yaw torque requires modulation of both summed wing stroke amplitude (Φ) and wingbeat frequency, which in turn results in modulation of metabolic rate P_{CO_2}. The oscillations in metabolic rate are roughly twice the frequency of the applied rotatory bias, as is expected if the kinematic and metabolic responses to left and right biases are symmetrical. All data channels were sampled at 1 Hz. Bias units are given in degrees per second per volt.

Table 1. Morphological coefficients and mass-specific power calculations derived from respirometric and kinematic data. Values given are mean ± SEM and are derived from flight sequences of 30 individual flies. Flight sequences varied from 330 to 3260 s. The induced power estimate P_{ind} assumes that a fly supports 75% of its weight during tethered flight. Resting values of P_{CO_2} were measured on tethered animals several minutes after the cessation of flight.

Parameters	Values
Morphological coefficients	
C_{ind} (m^2 s^{-3})	10.1 ± 0.15
C_{pro} (10^{-8} m^2)	8.9 ± 0.21
C_{acc} (10^{-7} m^2)	3.7 ± 0.09
Respirometric power estimates (W kg^{-1} of body mass)	
P_{CO_2} (rest)	18.9 ± 1.46
P_{CO_2} (flight)	140.2 ± 6.09
Kinematic power estimates (W kg^{-1} of body mass)	
P_{ind}	4.6 ± 0.07
P_{pro}	10.0 ± 0.51
P_{aero}	14.7 ± 0.49
P_{acc}	15.2 ± 0.78

This rectification of the metabolic cost during induced steering maneuvers was typical and is expected from the basic kinematic symmetry required for production of yaw torque to the left and right.

The average mass-specific components of induced, profile, and inertial mechanical power (P_{ind}, P_{pro}, and P_{acc}, respectively) may be calculated from stroke amplitude Φ and wing beat frequency n by the following relations:

$$P_{ind} = C_{ind} \cdot \Phi^{-1/2} \quad (1)$$

$$P_{pro} = C_{pro} \cdot \Phi^3 n^3 \quad (2)$$

$$P_{acc} = C_{acc} \cdot \Phi^2 n^3 \quad (3)$$

The quantities C_{ind}, C_{pro}, and C_{acc} are constants derived for each fly from morphological parameters (5). The total aerodynamic power P_{aero} is simply the sum of P_{pro} and P_{ind}. Table 1 shows calculations of morphological parameters C_{ind}, C_{pro}, and C_{acc} along with the mean values of P_{aero}, P_{acc}, and P_{CO_2} from closed-loop flight sequences of 30 flies. As indicated in Table 1, the values of mean, inertial, and aerodynamic power were of comparable magnitude and were similar to previously published values for *D. melanogaster* (6). However, due to experimentally induced variations in wingbeat kinematics, 16 out of 30 flight sequences were such that aerodynamic power was greater during some portions and inertial power was greater during others.

Although the fly must generate aerodynamic power through the complete wing stroke, the situation with inertial power is somewhat different. Positive power is required during the start of each half stroke in order to accelerate the wings from rest. During the second portion of each half stroke, the wings must be decelerated. The energy yielded by this deceleration could be used to minimize the cost of flight in one of two ways. The flies could decelerate their wings by stretching elastic elements within the thorax. This work could then be recovered during the next half stroke and provide energy to accelerate the wings. Alternatively, the work of deceleration could be used directly as a source of aerodynamic power during the second half of each stroke. The fly cannot, however, do both. Any inertial energy stored in elastic elements is unavailable as an immediate source of aerodynamic power. Unless the excess inertial energy that is not stored while decelerating the wing exceeds that required for aerodynamic power, then any energy recovered with elastic storage is exactly offset by a loss in aerodynamic power savings. If α represents the elastic storage within the flight motor, and β is equal to 1 − α, the mechanical power P_{mech} is related to aerodynamic and inertial power as:

$$P_{mech} = 1/2[(P_{aer} + \beta P_{acc}) + R(P_{aer} - \beta P_{acc})] \quad (4)$$

$$R(x) = 0, \text{ for } x < 0.$$

A simple rectifying function, R, is necessary in Eq. 4 on the assumption that negative work requires negligible metabolic cost. Elastic storage has no effect on the net energy balance if P_{aero} exceeds P_{acc} or if β is greater than P_{aero}/P_{acc}. Because of the trade off between aerodynamic and inertial power, values of elastic storage above $1 - P_{aero}/P_{acc}$ do not cause further energetic savings. This theoretical relation between mechanical power and elastic storage is shown graphically in Fig. 3.

Mechanical power can also be derived from the respirometrically measured total metabolic output P_{CO_2} as:

$$P_{mech} = \zeta P_{CO_2}, \quad (5)$$

where ζ represents muscle efficiency. The respirometric and kinematic estimates of mechanical power (Eqs. 4 and 5), may be combined to solve for muscle efficiency. Under the condition that P_{aero} exceeds P_{acc}, elastic storage does not influence the power balance, P_{mech} is simply equal to P_{aero}, and muscle efficiency may be determined directly as:

$$\zeta = P_{aero}/P_{CO_2} \quad (6)$$

Muscle efficiency may be estimated from the mean value of the ratio P_{aero}/P_{CO_2} calculated at all points where P_{acc} exceeded P_{aero}. This method provides an estimate of muscle efficiency of just over 10% (Table 2).

With a value for mean muscle efficiency in hand, it is possible to estimate elastic storage within the flight motor, with the assumption that both muscle efficiency and elastic storage do not change substantially over time. Using our estimate of ζ, we determined the minimum value of elastic storage that provided the lowest mean square error (MSE) fit between kinematic and respirometric estimates of mechanical power over the entire flight sequence (Fig. 4B) (Eqs. 4 and 5). An example of the MSE between the two estimates of P_{mech} is plotted as a function of elastic storage in Fig. 4C. In all cases, the MSE decreased monotonically as α ap-

Table 2. Mechanical and physiological properties of *Drosophila* flight muscle. Values given are mean ± SEM. The sample size for minimum elastic storage is smaller because not all flight sequences contained portions in which $P_{acc} > P_{aero}$.

Properties	Values
(ζ) Efficiency (%)	11.0 ± 0.06 (N = 26)
(α_{min}) Minimum elastic storage (%)	11.3 ± 1.31 (N = 16)
Muscle power (W kg^{-1} of thorax)	39.9 ± 1.44 (N = 26)
Muscle stress (kN m^{-2})	40.4 ± 4.01 (N = 26)

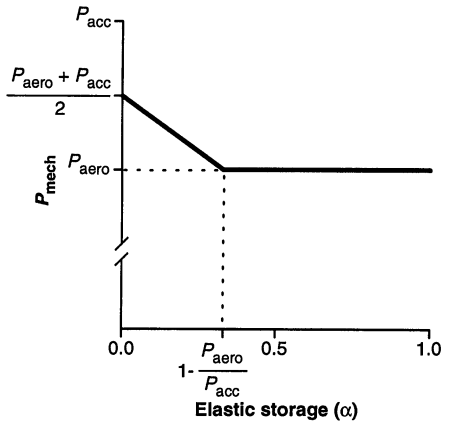

Fig. 3. Predicted mechanical power (P_{mech}) as a function of elastic storage. The graph plots Eq. 4 under the condition that P_{acc} is greater than P_{aero}. The maximal value of mechanical power is 1/2 (P_{acc} + P_{aero}) when α = 0. As elastic storage increases, P_{mech} decreases linearly toward P_{aero}. Mechanical power remains constant with increases in elastic storage above the critical value of $\alpha = 1 - P_{aero}/P_{acc}$.

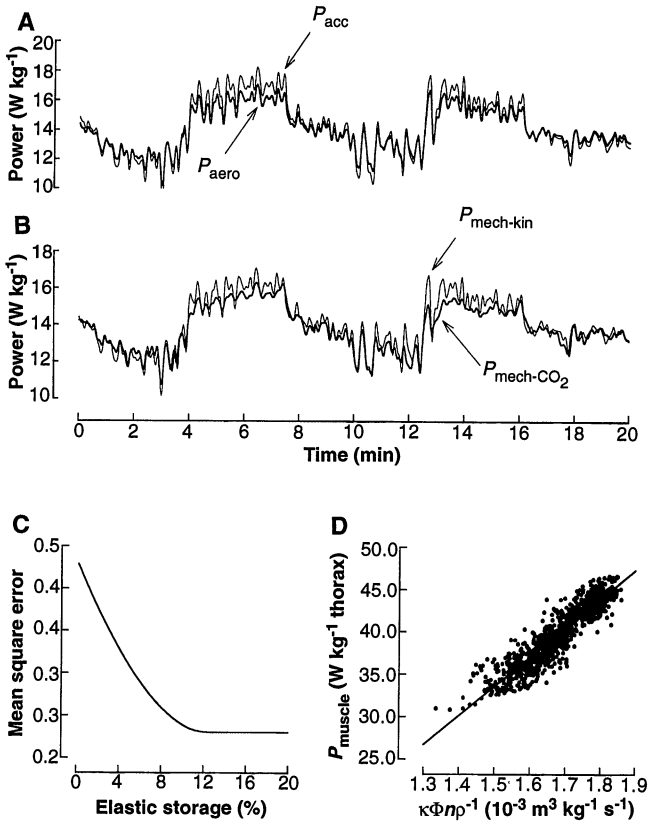

Fig. 4. (**A**) Comparison of predicted aerodynamic and inertial power during flight. The calculations are based on wingbeat frequency and stroke amplitude wave forms sampled at 1 Hz and so represent the power requirements averaged over many wingbeat periods. Although P_{acc} (thin trace) exceeds P_{aero} (thick trace) throughout most of the flight sequence, there are several sequences in which P_{aero} is larger. During these times, muscle efficiency may be estimated according to Eq. 6, yielding an average value of 11%. (**B**) Comparison of mechanical power based on respirometry ($P_{mech\text{-}CO_2}$, thick trace) and kinematics parameters ($P_{mech\text{-}kin}$, thin trace) for the same data set as in (A). The kinematic estimate of P_{mech} is based on an elastic storage of 12%, the minimum value of α that generated the lowest MSE with the respirometry data. (**C**) The MSE between the respirometric and kinematic estimates of P_{mech} as a function of percent of elastic storage [same data set as in (A) and (B)]. (**D**) Muscle power plotted against the product of strain, frequency, and density. Power was determined from the respirometric estimate of mechanical power, with the use of thoracic mass as an estimate of muscle mass [same data set as in (A), (B), and (C)]. Muscle strain was calculated by multiplication of stroke amplitude Φ by a scaling factor κ of 0.0037 rad^{-1}, which would generate a 1% strain at the mean stroke amplitude of 2.7 rad. The slope of this line gives a stress estimate of 34.3 kN m^{-2} (r^2 = 0.845).

proached the critical value of $1 - P_{aero}/P_{CO_2}$. The minimum elastic storage α_{min} is defined as the shoulder value of elastic storage above which the MSE remains constant. Values for minimum elastic storage determined by this method were typically about 11% (Table 2). The actual capacity for elastic storage could be higher, but it would not cause a further reduction in the power requirements for flight and would therefore not be detectable by this method.

In addition to allowing estimation of the degree of elastic storage, knowledge of muscle efficiency permits calculation of the specific power output of the flight muscle. Use of thoracic mass as an estimate of muscle volume yields an estimate of about 40 W kg^{-1} for the mechanical power of *Drosophila* asynchronous musculature (Table 2). The specific power output of muscle is thought to be linearly related to muscle stress (σ), stroke amplitude, and wingbeat frequency as (7):

$$P_{muscle} = \frac{\sigma \kappa \Phi n}{\rho} \quad (7)$$

where ρ is muscle density and κ is a constant relating stroke amplitude to muscle strain. By assuming that average wingbeat amplitude results in 1% muscle strain, we may use Eq. 7 to estimate the stress within the power muscles during flight. Respirometrically estimated muscle power output is plotted as a function of $\kappa\Phi n\rho^{-1}$ in Fig. 4D. The slope of this relation is muscle stress, which was on average 40 kN m^{-2} (Table 2). This value is low for insect muscle (8), but reduced stress is expected of muscles operating at high frequency because a large proportion of the internal space is taken up by mitochondria (7).

The results of this kinematic and respirometric analysis of *Drosophila* have general implications for the energetics of insect flight. First, we calculated a mechanical efficiency of about 10% for asynchronous muscle. Unless this value is radically different in other species, the results suggest that many insects must maintain an energy balance not through the use of extraordinarily efficient muscles but through elastic storage. The benefits of elastic storage are not as large in *D. hydei* as they might be in other species, because the difference between the average inertial and aerodynamic power requirements is quite small. However, in many other species, the requirements for inertial power may be up to six times those of aerodynamic power (9), and elastic storage would offer substantial energetic savings. Further, by consideration of the interaction between inertial and aerodynamic power, it appears that the amount of elastic storage required to minimize energy requirements during flight might be lower than previously expected. In *D. hydei*, we find that elastic storage greater than 10% would not affect the energy balance during flight. Taking the ratio of inertial and aerodynamic power for a variety of larger insects (9) yields minimum elastic storage values ranging from about 35 to 85%. The insect wing hinge is known to contain the protein resilin (10), which is among the most elastic materials known. It is quite reasonable to expect that, as in *Drosophila*, the thoracic structures of many insects are capable of the minimum elastic storage necessary to minimize the energetic costs of flight.

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Herbivory in Asymbiotic Soft Corals

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A zooxanthellae-free soft coral from the Red Sea feeds almost exclusively on phytoplankton, a mode of nutrition so far unknown for corals. Herbivory was also found in three other azooxanthellate soft corals. In tropical oligotrophic waters, phytoplankton biomass density may be an order of magnitude higher than that of zooplankton. Use of this resource allows these azooxanthellate cnidarians to be highly productive in flow-exposed oligotrophic reef waters.

Soft corals are an important group of sessile marine invertebrates in tropical and temperate waters. They are the second most common benthos component in coral reefs of the Indo-Pacific and the Red Sea, in which their abundance can be higher than that of hard corals (*1*). Their feeding organs are characterized by relatively poorly developed stinging cells (nematocysts) (*2*), and their tentacles are branched so that rows of narrowly spaced pinnules are arranged in a comblike structure around each of the eight polyp tentacles. Thus, the surface area used for passive suspension feeding in soft corals is much larger than in stony corals, whose tentacles do not carry pinnules.

We have studied the diet of the common reef-inhabiting soft coral *Dendronephthya hemprichi* from the northern Red Sea and assessed the composition of its food and rates of food intake in field experiments. Most reef-inhabiting corals live in symbiosis with unicellular algae (zooxanthellae), which translocate enough photosynthetically fixed carbon to the host to fully cover the host's carbon demand in its characteristically nutrient-depleted environment (*3*). *Dendronephthya hemprichi* does not contain zooxanthellae but is successful in coexisting with or even outcompeting symbiotic reef corals. The arborescent colonies embody dense filters with up to eightfold ramification, and the pinnules are the smallest filter elements, with diameters of only 45 to 55 μm. Gap width between the pinnules is 60 to 80 μm. These structures seem more suitable for suspension feeding than for predatory capture of prey. We demonstrate here that suspension feeding on phytoplankton is the principal mode of nutrition that fuels this rapidly growing (*4*) soft coral.

Three lines of evidence indicate that *D. hemprichi* feeds on phytoplankton: (i) Epifluorescence microscopy of the gastrovascular cavity of freshly collected *D. hemprichi* showed high concentrations of small (3 to 20 μm) phytoplankton cells (*5*). (ii) Chlorophyll a degraded to phaeopigments in actively feeding colonies, a process indicative of phytoplankton digestion (*6*). (iii) Phytoplankton gradually accumulated in starved corals after their reintroduction to natural seawater.

The observations under the epifluorescence microscope confirmed that *D. hemprichi* was free of autofluorescence and epiphytic algae and did not contain zooxanthellae. A great majority of the ingested algae were eukaryotes, whereas very few blue-green algae were taken in. This contrasts to the great proportion of blue-green algae in cell numbers and biomass in phytoplankton populations of tropical waters (*7*) and may be related to the small size of blue-green algae cells (<3 μm).

The concentrations of phytoplankton pigments (chlorophyll a and its degradation products, phaeopigments) in the corals were quantified in order to estimate rates of phytoplankton intake and decomposition. Concentrations were determined fluorometrically, after a standard acetone-extraction technique (*8*), in colony branches with a known number of polyps (*9*). For the experiments, colonies 4 to 5 cm tall growing on small polyvinyl chloride plates were kept in a flow chamber (18 cm by 15 cm in cross section) in continuously replaced seawater. The plates were suspended on metal-free wire away from the glass walls in such a way that each colony was exposed to unobstructed laminar flow of 4 to 10 cm/s (*10*).

The chlorophyll a gradually decomposed to phaeophytin in the gastrovascular cavities of the colonies. Ten colonies were kept in natural seawater in the flow chamber. After 3 days of feeding on the natural phytoplankton, the ratio of chlorophyll a to total photopigments in the colonies was 0.23 (±0.04 SD), as compared with 0.69 ± 0.02 SD in the seawater. The seawater in the flow chamber was then replaced by filtered water (filter pore width was 0.7 μm), and the changes in concentrations of plant-derived pigments in the colonies were recorded over 48 hours by random sampling of branch tips of the colonies for pigment extraction. Within the first 14 hours, chlorophyll concentrations decreased at a rate of 3.5% per hour in these starving colonies, whereas phaeopigment concentrations did not change. Around 14 hours after the ini-

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