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ENERGY EXPENDITURE OF SWIMMING COPEPODS

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ABSTRACT

The deceleration patterns following a leap by the calanoid copepod, *Labidocera trispinosa* were used to determine the parameters k and n in the proposed drag law $C_D = k(\text{Re})^{-n}$ where C_D is the drag coefficient and Re is the Reynolds number. This relation was used to calculate the rate of energy expenditure in constant velocity swimming and in accelerating from rest to a given velocity. At the velocities and accelerations observed, assuming 100% metabolic and propulsive efficiency, the rate of energy expenditure is slightly greater than 0.1% of the basal metabolic rate. It was also shown that at the swimming speeds observed during vertical migrations, the rate of energy expenditure is slightly less than 0.3% of the basal metabolic rate.

INTRODUCTION

Although the investigation of total energy requirements of marine planktonic copepods by oxygen consumption techniques has been rewarding (Anraku 1964; Conover and Corner 1968; Raymont and Gauld 1951) it is virtually impossible, by such techniques, to measure the amount of energy expended for swimming. This is due primarily to the small size of these organisms, their discontinuous motion while swimming, and the investigator's inability to determine which fraction of the total oxygen consumption is due to swimming alone. Therefore the determination of the energy required for this activity must be obtained from indirect evidence and an examination of the external physical limitations controlling swimming movement. The purpose of this study was to devise an indirect method for determining the energy required for swimming by the marine copepod *Labidocera trispinosa* and to compare it with its total energy requirement.

The basic approach to a study of the energy expenditure of bodies moving through a viscous fluid and having either an axis or a plane of symmetry parallel to the velocity of the approaching fluid is to evaluate the constant of proportionality C_D in Newton's quadratic resistance law,

$$D = C_D(\text{Re}) \frac{\rho}{2} V_\infty^2 A,$$

where D is the magnitude of the total drag force and points in the direction of the approach velocity of magnitude V_∞ , ρ is the fluid density, and A is the area of the projection of the body on a plane normal to the fluid stream. C_D , as indicated, is a function of the Reynolds number alone, neglecting effects of surface roughness and velocity fluctuations in the fluid flow. The nondimensional Reynolds number is defined as

$$\text{Re} = \frac{dV_\infty\rho}{\mu},$$

where d is a characteristic length of the body parallel to the approach velocity of magnitude V_∞ , ρ is the fluid density, and μ is the fluid viscosity. Knowledge of the functional relation between C_D and Re for a particular body allows determination of the drag force and hence the rate of energy expenditure at any given velocity.

The accurate determination of $C_D(\text{Re})$ beyond $\text{Re} = 10$ by mathematical analysis is extremely difficult for even the simplest of body configurations. For this reason, $C_D(\text{Re})$ is generally evaluated by the use of experimental data from wind or water tunnel tests using either the actual body of interest or a scale model. However, L .

trispinosa has a body length of less than 2 mm with a complex shape, making wind or water tunnel tests with the actual organism impractical and construction of accurate models for tunnel study too costly. These problems are circumvented by noting that *L. trispinosa* and most copepods rely only on hydrodynamic drag to arrest their motion after executing a leap. Thus by measurements of the deceleration patterns of leaps, coupled with a proposed functional relation for $C_D(\text{Re})$, the important parameters of the relation can be elucidated.

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THEORY

In ideal fluid theory, the external force on a body in potential flow is given by

$$M \frac{du_i}{dt} + m_{ik} \frac{du_k}{dt} = f_i, \quad (1)$$

where the summation convention is assumed and M is the mass of the body, u_i is the i -th component of velocity in rectangular cartesian coordinates, m_{ik} is the induced-mass tensor, and f_i is the i -th component of the external force. The derivation of this equation is given in Landau and Lifshitz (1959). Let x be the coordinate in the direction of motion of the body and let u_x be the component of velocity in that direction, then $u_y = u_z = 0$ and equation (1) becomes

$$M \frac{du_x}{dt} + m_{xx} \frac{du_x}{dt} = f_x,$$

or

$$(M + m) \frac{du_x}{dt} = f_x, \quad (2)$$

where $m_{xx} = m$, and depends on the body shape and orientation to the fluid stream. For a body moving in a viscous fluid medium the effects of viscosity are incorporated in equation (2) by the addition of viscous drag force D ; hence (2) becomes

$$(M + m) \frac{du_x}{dt} + \frac{1}{2} C_D \rho u_x^2 A = f_x. \quad (3)$$

Thus the equation of motion of a body decelerating in a viscous fluid under the influence of no external forces is

$$\frac{1}{2} \rho C_D u_x^2 A = -(M + m) \frac{du_x}{dt},$$

or

$$\frac{1}{2} \rho C_D u_x^2 A = -(M + m) u_x \frac{du_x}{dx}. \quad (4)$$

In the case of a leaping or swimming copepod the Reynolds number ranges between 10 and 500 and for this intermediate Re range we assume

$$C_D(\text{Re}) = k(\text{Re})^{-n}. \quad (5)$$

Substituting equation (5) into (4) yields

$$\frac{1}{2} \rho k (\text{Re})^{-n} u_x^2 A = -(M + m) u_x \frac{du_x}{dx},$$

and since $\text{Re} = d\rho u_x / \mu$

$$\frac{k}{2} \rho^{1-n} d^{-n} u_x^{2-n} \mu^n A = -(M + m) u_x \frac{du_x}{dx}. \quad (6)$$

Integrating equation (6) yields

$$\frac{k \rho^{1-n} d^{-n} \mu^n A}{2(M + m)} x_s = \frac{(u_x^i)^n - (u_x^f)^n}{n}$$

or

$$x_s = \frac{2}{k} \left[\frac{(u_x^i)^n - (u_x^f)^n}{n} \right] \frac{M + m}{\rho A} \left(\frac{\rho d}{\mu} \right)^n. \quad (7)$$

Thus the distance, x_s , required to decelerate from the initial velocity u_x^i to the final velocity u_x^f , assuming the drag relation (equation 5) is given by the right-hand side of equation (7). It should be noted that m , which is a constant for ideal fluid motion, is probably also a function of Re , but this is neglected in the present development as is the buoyancy force.

Measurements of x_s , u_x^i , and u_x^f combined with values of M , m , ρ , μ , A , and d allow the determination of k and n in $C_D(\text{Re})$ by a suitable procedure. The procedure used here is a parameter-searching computer subroutine (Beisinger and Bell 1963) that selects by trial and error the parameters which minimize a given function of those parameters. Regrouping equation (7) as

$$\frac{x_s \rho A}{2(M+m)} = \frac{1}{k} \left[\frac{(u_x^i)^n - (u_x^f)^n}{n} \right] \left(\frac{\rho d}{\mu} \right)^n, \quad (8)$$

and letting

$$\frac{x_s \rho A}{2(M+m)} \equiv X_1$$

and

$$\frac{1}{k} \left[\frac{(u_x^i)^n - (u_x^f)^n}{n} \right] \left(\frac{\rho d}{\mu} \right)^n \equiv X_2,$$

the parameters k and n are chosen such that the function

$$F(k, n) \equiv \sum_i \left[\log \frac{X_1}{X_2} \right]^2$$

is a minimum, where the index i refers to the individual measurements of x_s , u_x^i , u_x^f , M , m , ρ , μ , and A . The form of $F(k, n)$ is chosen to mitigate the influences of multicollinearity error in the calculations.

The value of m in the above equations is not evaluated directly but approximated by comparison with a similar geometric shape. Since the shape and motion of *L. trispinosa* is similar to a prolate spheroid moving parallel to its major axis, the value of m is taken as equal to the m of a prolate spheroid moving in a perfect fluid parallel to its major axis whose fineness ratio is equal to the equivalent fineness ratio of the animals. The fineness ratio for a prolate spheroid is defined as a/b where a is half of the major axis and b is the largest radius of the spheroid and the equivalent fineness ratio of a copepod is defined as $(d/2) \times (\pi/A)^{1/2}$. The value of m is calculated for the prolate spheroid by energy considerations and is given by Munk (1934) as

$$m = k_1 \rho V_D,$$

where

$$k_1 = \gamma / (2 - \gamma),$$

$$\gamma = 2 \left(\frac{1 - \epsilon^2}{\epsilon^3} \right) \left[\frac{1}{2} \log \left(\frac{1 + \epsilon}{1 - \epsilon} \right) - \epsilon \right],$$

$$\epsilon = \sqrt{1 - \frac{b^2}{a^2}},$$

$$V_D = \frac{4}{3} \pi a b^2.$$

With k and n known, the power expenditure P at a given constant velocity V is given by the drag force part of equation (6) with $u_x = V$, multiplied by V or

$$P = f_x V = (k/2) \rho^{1-n} d^{-n} V^{3-n} \mu^n A. \quad (9)$$

In addition, the average power expenditure in constant acceleration, a , from rest to the final velocity, V_f , is found by the following. The drag force for an accelerating body is given by equation (3) and the differential of work dW is given by

$$dW = f_x dx = f_x a t dt.$$

With the expression (5) for C_D ,

$$dW = \frac{1}{2} \rho^{1-n} d^{-n} \mu^n A (a t)^{3-n} dt + (M+m) a^2 t dt.$$

Integrating from time 0 to time t yields

$$W = \frac{\rho^{1-n} d^{-n} \mu^n A a^{3-n} t^{4-n}}{2(4-n)} + \frac{(M+m) a^2 t^2}{2}.$$

Substituting $t = V_f/a$ gives

$$W = \frac{k \rho^{1-n} d^{-n} \mu^n A V_f^{4-n}}{2(4-n)a} + \frac{(M+m) V_f^2}{2}.$$

Let $\rho^{1-n} d^{-n} \mu^n A = U_{(n)}$ then

$$W = \frac{k U_{(n)} V_f^{4-n}}{2(4-n)a} + \frac{(M+m) V_f^2}{2}. \quad (10)$$

The average power required to go from a velocity of 0 to V_f at the constant acceleration a is defined as

$$\langle P \rangle_0^{V_f} = \frac{W}{t} = \frac{W a}{V_f},$$

hence

$$\langle P \rangle_0^{V_f} = \frac{k U_{(n)} V_f^{3-n}}{2(4-n)} + \frac{(M+m) a V_f}{2}. \quad (11)$$

METHODS

A number of active *L. trispinosa*, collected from the Scripps Institution of Oceanography pier by dipnetting, were placed in an 8- × 10- × 8-cm aquarium filled with fresh seawater. A blackened glass plate was used to partition off a small front chamber about 4 cm in depth normal to the front of the tank. This provided a black background for good contrast and limited the swimming and jumping of the copepods to the plane of the front plate. The aquarium was illuminated from both sides of the narrow front chamber by 8-w fluorescent desk lamps. Animals were stimulated by touching them with a glass probe rounded at the end or by tapping the side of the aquarium. Movement was recorded with a 16-mm movie camera with a wide-angle lens and Tri-X film. Camera speed was 16 frames/sec, calibrated by photographing a stopwatch. A 10-cm reference ruler was mounted to the rear surface of the partition plate for measuring distances and copepod lengths. All lengths measured from the viewing screen were made using dial calipers read to 0.01 cm and corrected with the reference rule. The camera, mounted in a stationary position 60 cm from the center of the front chamber, was started when the animals became sufficiently disturbed and executed rapid leaps.

When a leap was recorded that showed little or no excursion normal to the plane of the front plate a measurement was made. The position of the copepod's head in sequences of 2-5 frames was marked on a paper viewing screen, resulting in a series of intervals progressively decreasing in length. The velocities u_w^i and u_w^f were taken as the average velocities in the first and last intervals of the sequence. The points at which these were taken as occurring was found to have a critical effect on the values of k and n . All leaps measured started from rest and thus the first point of the sequence was known to correspond to zero velocity. The deceleration of the copepod is proportional to u_w^{2-n} and in the Re range considered $0 < n < 1$; hence $u_w(x)$ is monotonically decreasing

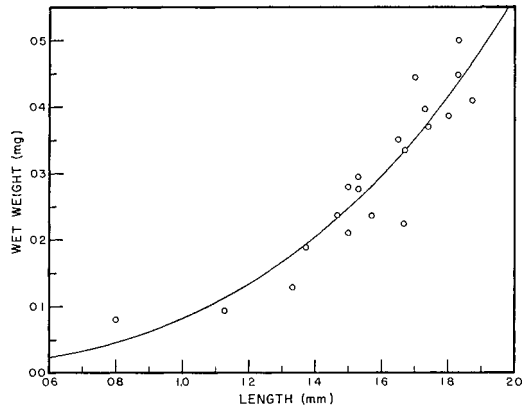


FIG. 1. Wet weight of 20 *Labidocera trispinosa* vs. metasome length. Animals washed in distilled water and weighed to ± 0.01 mg on Cahn electro-balance.

and convex in any length interval considered. Thus the choices made for the points representing the location of u_w^i and u_w^f was the right-hand end point for the first interval and the left-hand end point of the last interval, assuming a decrease in length of the intervals from left to right. These choices must lead to an estimate of $C_D(\text{Re})$ that is slightly higher than really exists. However, judging from the numerous drag-producing appendages of the animals, this estimate probably does not differ significantly from the true $C_D(\text{Re})$. In summary, if x_1, x_2, \dots, x_n represent consecutive head locations in a deceleration sequence and t is the constant time duration between points x_n and x_{n+1} then $u_w^i = (x_2 - x_1)t^{-1}$ and $u_w^f = (x_n - x_{n-1})t^{-1}$ where u_w^i is taken as occurring at x_2 and u_w^f at x_{n-1} . Thus x_s , the distance required to decelerate from u_w^i to u_w^f is $x_{n-1} - x_2$.

The mass of each organism was determined from the photographs by constructing a curve of wet weight versus length (Fig. 1). A least squares regression analysis yielded the relation $W = 0.08255d^{2.7469}$ where W is the wet weight in milligrams and d is the length of the carapace or metasome in millimeters. The metasome comprising the major length of the body was readily determinable from the photographs. The metasome length is also the

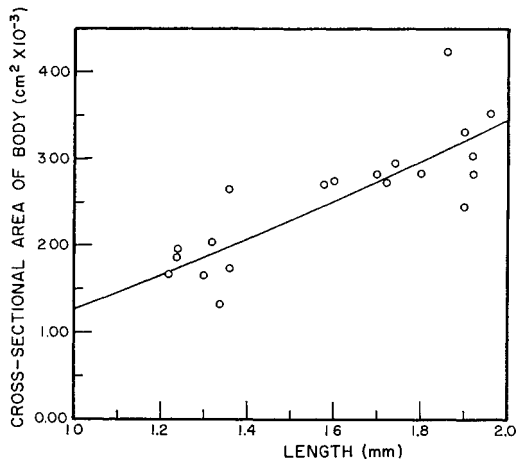


FIG. 2. Length of metasome vs. cross-sectional area.

characteristic length used in determining the Reynolds number.

The density, ρ , of the seawater came from tables published by the U.S. Navy Hydrographic Office (1956) using the temperature of the aquarium (17.0C) and a salinity of 33.7‰ and was 1.02454 g/cm³. These same values of temperature and salinity were also used to obtain the viscosity of the seawater (Sverdrup, Johnson, and Fleming 1942), which was 0.0119 g/cm-sec.

The projected area A was found by constructing a curve of projected area versus length (Fig. 2). This was accomplished by taking freshly killed animals and aligning them with the head facing upward in a petri dish containing a mixture of glycerine and nonresinous mounting medium. This kept the animals in a stationary position and allowed positional alignment by moving the mixture slightly. When properly aligned, projected body outlines were drawn on paper using a dissecting microscope (40 \times) with a camera lucida attachment. The areas of these outlines were computed with a compensating polar planimeter and corrected to the true area. Only the body projection was taken since the appendages are more or less flush against the body during leaping. A least squares regression analysis yielded the relation $A = 0.034003d^{1.4206}$ where A is the

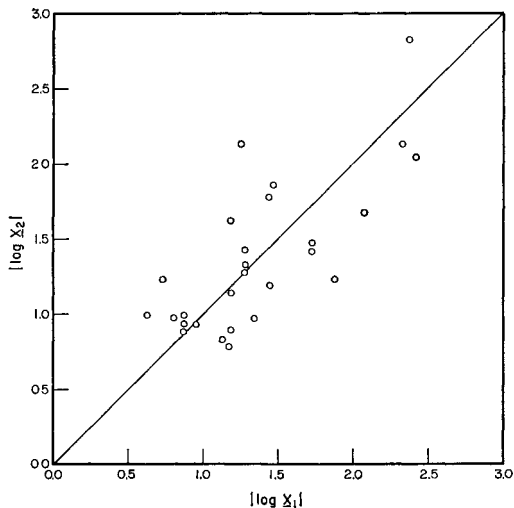


FIG. 3. Plot of $|\log X_1|$ vs. $|\log X_2|$ fitted to the data in Table 1.

projected area in square centimeters and d is the metasome length in centimeters.

RESULTS AND DISCUSSION

The measurement of u_w^i , u_w^f , x_s , M , and m was performed on 27 leaps of *L. tri-spinosa* ranging in size from 0.124 to 0.200 cm long. The sequences were chosen with regard to clarity and evidence of little or no excursion normal to the front plate (Table 1). Analysis of the data by the method already indicated yielded the values of $k = 85.2$ and $n = 0.80$, that is,

$$C_D(\text{Re}) = \frac{85.2}{\text{Re}^{0.80}}.$$

The degree of fit to the data can be seen from Fig. 3 where $|\log X_1|$ is plotted against $|\log X_2|$. The line drawn is of slope 1 and zero intercept, indicating perfect correlation. The relation indicates a drag coefficient of 85.2 at $\text{Re} = 1$. In comparison, a sphere for $2 \leq \text{Re} \leq 500$ is found by experiment to have the drag relation

$$C_D(\text{Re}) = \frac{18.5}{\text{Re}^{0.6}}$$

and a C_D of 24 at $\text{Re} = 1$ (Bird, Stewart, and Lightfoot 1960).

TABLE 1. *Measurements used in calculating the constants in the drag relation $C_D(Re)$*

A (cm ²)	M (g)	M + m (g)	d (cm)	x_g (cm)	u_g^t (cm/sec)	u_g^f (cm/sec)
0.00255	0.00028	0.00032	0.157	0.022	3.01	1.41
0.00163	0.00015	0.00017	0.124	0.020	3.53	1.53
0.00210	0.00021	0.00024	0.140	0.068	5.11	2.17
0.00210	0.00021	0.00024	0.140	0.063	5.69	2.02
0.00210	0.00021	0.00024	0.140	0.064	3.76	2.04
0.00140	0.00012	0.00013	0.113	0.023	3.98	0.90
0.00163	0.00015	0.00017	0.124	0.019	2.26	1.41
0.00362	0.00057	0.00063	0.200	0.060	5.92	3.20
0.00269	0.00031	0.00035	0.162	0.070	7.26	3.42
0.00240	0.00026	0.00029	0.152	0.055	4.06	1.97
0.00305	0.00034	0.00039	0.168	0.112	7.96	2.69
0.00285	0.00028	0.00032	0.156	0.039	4.49	1.30
0.00315	0.00041	0.00046	0.180	0.093	7.95	2.19
0.00315	0.00041	0.00046	0.180	0.086	8.20	1.99
0.00315	0.00041	0.00046	0.180	0.120	7.78	2.88
0.00315	0.00041	0.00046	0.180	0.120	8.47	2.88
0.00305	0.00034	0.00039	0.168	0.133	9.00	3.63
0.00315	0.00041	0.00046	0.180	0.074	6.85	1.99
0.00305	0.00034	0.00039	0.168	0.038	4.65	1.05
0.00305	0.00034	0.00039	0.168	0.059	3.63	1.56
0.00315	0.00041	0.00046	0.180	0.087	6.05	2.10
0.00315	0.00041	0.00046	0.180	0.067	5.36	1.64
0.00315	0.00041	0.00046	0.180	0.138	6.16	2.48
0.00315	0.00041	0.00046	0.180	0.110	8.12	2.88
0.00315	0.00041	0.00046	0.180	0.089	8.24	2.25
0.00315	0.00041	0.00046	0.180	0.118	8.64	3.40
0.00274	0.00032	0.00037	0.167	0.074	4.65	1.17

Apparently no experimental work has been done on prolate spheroids in the Re range of interest, but theoretical evaluation by Breach (1961) of $C_D(Re)$ has been made using matched asymptotic expansions valid at least to $Re = 1$. The form he gives is, in my notation

$$C_D = \frac{2\pi B}{3(1-\epsilon^2)Re} \times \left[1 + \frac{BRe}{24} + \frac{B^2}{360} Re^2 \log Re + O(Re^2) \right],$$

where

$$B = 24\epsilon^3 \left[(1 + \epsilon^2) \log \left(\frac{1 + \epsilon}{1 - \epsilon} \right) - 2\epsilon \right]^{-1}.$$

The value of $\epsilon = [1 - (b^2/a^2)]^{1/2}$ with a and b the same as noted previously. The factor of 3 in the denominator of the expression above for C_D is left out in the paper cited and appears to be a misprint as the expres-

sion must reduce to that of a sphere as $\epsilon \rightarrow 0$.

The average equivalent value of eccentricity for the *L. trispinosa* studied was $\epsilon = 0.94$ where $\epsilon \equiv [1 - (4A/d^2\pi)]^{1/2}$. With this value substituted in the above expression for C_D with $Re = 1$, we get $C_D = 77.6$. Thus at $Re = 1$ the $C_D(Re)$ for *L. trispinosa* is about 2.5 times higher than for a sphere and about 10% higher than the equivalent prolate spheroids. We would expect this higher value since *L. trispinosa* is similar to a rough-surfaced prolate spheroid with the addition of filamentous drag-producing appendages such as the antenna, legs, and tail.

The energy expenditure of *L. trispinosa* for five different wet weights and velocities ranging from 1–10 cm/sec, calculated using equation (9) and assuming a ratio of dry weight to wet weight of 0.25, appears in Table 2. The energy expenditure based on respiration is 3.53×10^{-6} cal \times

TABLE 2. Energy expenditure of five different wet weights (mg) of *Labidocera trispinosa* for velocities ranging from 1–10 cm/sec based on $C_D = 85.2/Re^{0.80}$

Velocity (cm/sec)	Energy expenditure [cal sec ⁻¹ (mg dry wt) ⁻¹] × 10 ⁻⁸				
	0.1	0.2	0.3	0.4	0.5
1.00	0.880	0.576	0.443	0.359	0.291
2.00	4.04	2.65	2.04	1.65	1.34
3.00	9.87	6.46	4.97	4.03	3.26
4.00	18.6	12.2	9.36	7.59	6.14
5.00	30.4	19.9	15.3	12.4	10.0
6.00	45.3	29.7	22.8	18.5	15.0
7.00	63.6	41.6	32.1	26.0	21.0
8.00	85.4	55.9	43.0	34.9	28.2
9.00	111.00	72.4	55.7	45.2	36.6
10.00	139.00	91.3	70.3	57.0	46.1

sec⁻¹ (mg dry wt)⁻¹ using the oxygen uptake for the cognate *L. aestiva* (Fleminger 1964) at 17C of 2.5 μ l O₂ (mg dry wt)⁻¹ hr⁻¹ (Anraku 1964), and a fat caloric equivalent of 5.0×10^3 cal/liter O₂. The values in Table 2, however, assume 100% metabolic and propulsive efficiencies, and this should be taken into account when relating these values to any real situation.

Comparison of the respiration figure quoted above with values in Table 2 shows that with the slightly higher estimate of $C_D(Re)$ used here, the energy expended by swimming is negligible compared to the total energy expenditure of the animal as calculated from oxygen consumption. A medium-sized animal of 0.3 mg wet wt and a metasome 0.16 cm long having a cruising speed of 1 cm/sec, equivalent to 6 body lengths/sec, consumes energy at a rate slightly greater than 0.1% of that used based on respiration.

Lasker (1966) stated that oxygen uptake remains the same for euphausiid shrimps whether or not the animal is swimming; euphausiids move their swimming appendages rapidly and continually, presumably to aerate their gills. My results with *L. trispinosa* appear to support Lasker's statement.

Because most copepods are similar in shape, the results for *L. trispinosa* probably approximate the energy expenditure for swimming of others, which may explain

the apparent ease with which copepods perform diurnal vertical migrations over great distances. *Calanus finmarchicus*, a larger copepod than *L. trispinosa*, has been observed (Nicholls 1933) to make vertical migrations of approximately 120 m in 6 hr, an average vertical velocity of 0.6 cm/sec. However, *C. finmarchicus* is more streamlined than *L. trispinosa* and while swimming, neglecting negative buoyancy, should expend energy at an even lower fraction of its total requirement than does a large *L. trispinosa*. If we include the effects of negative buoyancy in swimming toward the surface, the energy expenditure is $MG(1 - \sigma_{s.w.}/\sigma_a)V$ where M is the mass of the organism, G is the gravitational acceleration, σ_a is the specific gravity of the animal, $\sigma_{s.w.}$ is the specific gravity of seawater, and V is the vertical velocity. According to Parker (1901) the specific gravity of *Labidocera* is 1.082 and of seawater 1.025. Therefore, a medium-sized *L. trispinosa* of 0.075 mg dry wt, although not a migrating copepod, would expend 4.93×10^{-9} cal sec⁻¹ (mg dry wt)⁻¹ swimming upward at 1 cm/sec in addition to the 4.43×10^{-9} cal sec⁻¹ (mg dry wt)⁻¹ required to swim through the water. Thus, the total rate of energy expenditure required to swim upward is about 0.2% of the rate based on respiration, again a very small amount.

The results above seem consistent with the extensive vertical migrations observed for these animals but contradict the belief that an organism exhibiting vertical migration consumes a great deal of energy above a basal rate. Hardy (1956, p. 199) comments that it is an "extraordinary thing... that so many different animals will expend so much energy in climbing up towards the surface at night only to sink or swim down again in the daytime..." Similarly Marshall and Orr (1955, p. 140) ask "why *Calanus* should expend so much energy daily in swimming up and down in the sea." More recently Petipa (1966) calculated the coefficient a in the hydrodynamic drag force relation, $f = av^2$, where f is the force and v the velocity, by monitoring the

TABLE 3. Energy expended and average rate of energy expended in accelerating from 0 to V_f (cm/sec) for five different wet weights (mg) of *Labidocera trispinosa*

Accel- eration (cm/sec ²)	0.1 $V_f = 3.22$		0.2 $V_f = 5.07$		0.3 $V_f = 6.72$		0.4 $V_f = 8.34$		0.5 $V_f = 8.34$	
	ΔE^*	\overline{dE}/dt^\dagger	ΔE	\overline{dE}/dt	ΔE	\overline{dE}/dt	ΔE	\overline{dE}/dt	ΔE	\overline{dE}/dt
10	37.2	1.16	154	3.03	360	5.36	682	8.17	666	7.98
100	9.52	2.96	28.1	5.54	58.0	8.64	102	12.2	100	12.0
200	7.98	4.96	21.1	8.33	41.2	12.3	69.6	16.7	68.7	16.5
300	7.47	6.96	18.8	11.1	35.6	15.9	58.9	21.2	58.2	20.9
400	7.21	8.96	17.6	13.9	32.8	19.6	53.5	25.7	52.9	25.4
500	7.06	11.0	16.9	16.7	31.2	23.2	50.3	30.1	49.8	29.9
600	6.95	13.0	16.5	19.5	30.1	26.8	48.1	34.6	47.7	34.3
700	6.88	15.0	16.1	22.3	29.3	30.5	46.6	39.1	46.2	38.8
800	6.83	17.0	15.9	25.0	28.7	34.1	45.4	43.6	45.1	43.2
900	6.78	19.0	15.7	27.8	28.2	37.7	44.5	48.1	44.2	47.7
1,000	6.75	21.0	15.5	30.6	27.8	41.4	43.8	52.6	43.5	52.2

* ΔE in cal (mg dry wt)⁻¹ $\times 10^{-10}$.† \overline{dE}/dt in cal sec⁻¹ (mg dry wt)⁻¹ $\times 10^{-8}$.

consumption of fat in descending *Calanus helgolandicus*. Her method hinges on the same assumption made by the previously cited authors, that is, that the energy expenditure in swimming is so large compared to the basal metabolic rate that the latter can be neglected. Using Petipa's data and the drag coefficient relation obtained with *Labidocera* (similar in size and shape to *Calanus*), I calculate that her animals have a greater drag by 6 orders of magnitude—an impossible result. On the other hand, Hutchinson (1967) calculated the energy required by an organism of almost neutral buoyancy to migrate vertically 50 m and concluded that such migration would not be a serious drain on the biochemical economy of any known vertical migrator, even assuming efficiencies as low as 1%. Hutchinson neglected hydrodynamic drag in his calculations; in light of the evidence presented here which includes the effects of hydrodynamic drag, the vertical movements of *L. trispinosa* and presumably of all other copepods are truly not extraordinary or inexplicable from the standpoint of energy expenditure.

The energy expended and the average rate of energy expenditure in the short hops which the animals execute is calculated using equations (10) and (11) respectively. If we assume a constant acceleration in the first interval, that is,

$a = 2(x_2 - x_1)t^{-2}$ we find from film analysis that it ranges from about 10 to 1,000 cm/sec². Also the average velocity attained in the interval is $u_w^{\frac{1}{2}} = V_f$ and increases approximately linearly with weight. The energy expended, ΔE , and the average rate of energy expenditure, \overline{dE}/dt , during these hops for animals weighing 0.1–0.5 mg wet wt, taking V_f in equations (10) and (11) equal to the average hop velocity achieved for that weight, for accelerations ranging from 10 to 1,000 cm/sec² are summarized in Table 3. The rapid hops and leaps executed by *L. trispinosa* are seen to involve a small total as well as a small average rate of energy expenditure. In fact, as the acceleration of *L. trispinosa* increases for any given weight, the energy expended decreases and the average rate of energy expenditure increases. However, the rate of energy expenditure always remains small and it is probably to the animal's advantage to accelerate at the highest possible rate. *Labidocera trispinosa* uses this rapid acceleration to escape predators. High acceleration is to the copepod's advantage in minimizing total energy used and maximizing its chances for survival.

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