

# Limitations on locomotor performance in squid

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O'DOR, R. K. *Limitations on locomotor performance in squid*. J. Appl. Physiol. 64(1): 128–134, 1988.—An empirical equation relating  $O_2$  consumption (power input) to pressure production during jet-propelled swimming in the squid (*Illex illecebrosus*) is compared with hydrodynamic estimates of the pressure-flow power output also calculated from pressure data. Resulting estimates of efficiency and stress indicate that the circularly arranged obliquely striated muscles in squid mantle produce maximum tensions about half those of vertebrate cross-striated muscle, that “anaerobic” fibers contribute to aerobic swimming, and that peak pressure production requires an instantaneous power output higher than is thought possible for muscle. Radial muscles probably contribute additional energy via elastic storage in circular collagen fibers. Although higher rates of aerobic power consumption are only found in terrestrial animals at much higher temperatures, the constraint on squid performance is circulation, not ventilation. Anaerobic power consumption is also among the highest ever measured, but the division of labor between “aerobic” and “anaerobic” fibers suggests a system designed to optimize the limited capacity of the circulation.

*Illex illecebrosus*; bioenergetics; obliquely striated muscle; jet swimming

THE CLASS Cephalopoda seems to be at the “cutting edge” of invertebrate evolution on a number of fronts. In addition to size and intelligence, cephalopods also appear to set records for power. Giant squid are obviously capable of greater total power output than smaller invertebrates, but recent studies indicate that squid also have higher mass-specific power outputs than other marine species (9, 21, 30, 31). Selection for high-power output probably resulted from the inefficiency of jet propulsion relative to the undulatory propulsion used by most of the competition (22). Although inherently inefficient, the jet system is easily studied since nearly all the locomotor power is used to pressurize the water in the mantle cavity. Ultrasonically telemetering differential pressure transducers placed inside the mantles of the squid swum in tunnel respirometers (aquatic treadmills) or filmed from above in schools in a large pool provide independent  $O_2$  consumption ( $\dot{V}O_2$ )-speed,  $\dot{V}O_2$ -pressure, and pressure-speed relationships over the full range of animal activities (30, 31). The  $\dot{V}O_2$ -pressure regression yields an index of power consumption at sustainable (aerobic) speeds, and the independent  $\dot{V}O_2$ -speed relationship confirms that the extrapolation of power consumption beyond actual aerobic capacity is reasonable.

Fundamental hydrodynamic relationships (e.g., the Bernoulli equation) allow prediction of power outputs

from intramantle pressures and the diameter of the funnel orifice. These have previously been shown to predict static forces produced by tethered cephalopods (29) and thrusts consistent with the forces required to overcome the low Froude efficiency and calculated rigid body drag (30). This report uses a comparison of projected power consumptions and power outputs over the full range of swimming activity to examine the mechanical organization of squid mantle and postulate the sources and limits of power production. A survey of other marine organisms suggests that squid operate close to physical and environmental limits.

## MATERIALS AND METHODS

The empirical estimates of power consumption used in this analysis are based on extensive experiments on adult squid, *Illex illecebrosus*, in the Aquatron Laboratory, Halifax, Nova Scotia, that included simultaneous measurements of  $\dot{V}O_2$  and average mantle pressure ( $\bar{P}$ ) for squid swimming at controlled speeds ( $u$ ) in a tunnel respirometer and records of mantle pressure for squid swimming freely in a 15-m-diam pool under video surveillance (30, 31). Although no direct measurements of power consumption beyond the critical speed ( $u_{crit}$ , the maximum speed which could be sustained for 1 h; typically assumed to be the limit of aerobic power production in swimming animals) were possible, combining the  $\dot{V}O_2$ -speed and  $\dot{V}O_2$ -pressure regressions from the respirometer yielded an equation which predicted the pressure-speed relationship of squid at higher speeds in the pool

$$\bar{P} = 0.35 e^{2.1u} \quad (1)$$

The slope of this equation was also shown to correspond closely to that of the exponential equation predicting drag forces at higher speeds, indicating that the required power was increasing in a predictable manner (31). Pressure data for freely swimming squid were collected using a differential pressure transducer implanted across the mantle wall such that external pressure due to depth was continuously offset. This transducer was linked to microcircuitry that integrated pressure generated by mantle contractions over time and emitted ultrasonic signals at intervals inversely proportional to pressure (31).

Since the major source of locomotor power for squid, particularly at higher speeds, is the jet produced by pressurizing the water in the mantle cavity, the intramantle pressure measured is also closely related to the work done by the mantle musculature and its power output. In this system, as in the heart, the work done by

the pump equals the pressure ( $P$ ) times the volume pumped and the power output (PO) equals  $P$  times flow rate ( $Q$ ). Thus the total  $PQ$  power output of the mantle muscle can be estimated at any instant from the single variable,  $P$ , as follows. If viscosity is negligible, the Bernoulli equation allows the jet velocity ( $u_j$ ) through the funnel to be calculated from  $P$  and the density of seawater ( $d = 1,023 \text{ kg/m}^3$ ) as

$$u_j = (2 P/d)^{0.5} \quad (2)$$

The flow rate can then be calculated, knowing the cross-sectional area ( $A$ ) of the funnel, as

$$Q = u_j A \quad (3)$$

Corrections for the effect of viscosity are usually made by including a "coefficient of discharge" in Eq. 3 that may be as low as 0.6 for right-angle, rigid orifices at Reynolds numbers in the range 10,000–40,000 which apply here; however, for "nozzles" shaped like a squid funnel, the required correction is usually in the range of 0.95–0.99 (24). The uncorrected equations have been used with reasonable success to predict the thrust produced by the jets of several tethered cephalopods (28). The present analysis differs from these earlier studies only in that the pressure used is the  $\bar{P}$ , but since this is calculated from the area under the pressure-time curve the result should be the same. The power output, then, should simply be

$$PO = PQ \quad (4)$$

## RESULTS

The power input line in Fig. 1 is based on the  $\dot{V}O_2$  (ml  $O_2 \cdot h^{-1}$ ) pressure ( $P$ , Pa) regression determined experimentally as described briefly in MATERIALS AND METHODS. Webber and O'Dor (31) studied squid with masses ( $M$ ) ranging from 0.204–0.672 kg and obtained the relationship

$$\dot{V}O_2 = 2.72M^{0.75}\bar{P}^{0.77} \quad (5)$$

When solved for a squid of 0.5 kg (the typical animals used throughout this analysis) and converted to mass-specific power using the common assumption that 1 ml  $O_2$  yields 20 J, this defines the power input (PI,  $W \cdot \text{kg}^{-1}$  animal) required to produce various pressures as

$$PI = 0.018P^{0.77} \quad (6)$$

This is the solid "input" line plotted in Fig. 1. Not all of this power goes to locomotion, but, even at rest, production of intramantle pressure for respiration ( $P = 80 \text{ Pa}$ ,  $PI = 0.5 \text{ W} \cdot \text{kg}^{-1}$ ) accounts for nearly half of the  $1.1 \text{ W} \cdot \text{kg}^{-1}$  consumed (30). This maintenance power, not associated with mantle muscle activity ( $0.62 \text{ W} \cdot \text{kg}^{-1}$ ), is <15% of the total power consumption at the swimming speed that minimizes the cost of transport ( $u_{\text{opt}}$ ,  $0.6 \text{ m} \cdot \text{s}^{-1}$ , see Table 1), and, since this analysis deals primarily with higher velocities, maintenance power has been ignored for simplicity, at some cost in accuracy (30). The second power scale in Fig. 1 converts power per unit animal mass to a per unit muscle mass basis by dividing by 0.4, the fraction of total mass in the mantle muscle.

There is also some error introduced by this assumption, since squid have fins that contribute some thrust. The error is small, however, since *I. illecebrosus* has relatively small fins (15% body wt) and usually rolls them tightly against the mantle at speeds  $>0.6 \text{ m} \cdot \text{s}^{-1}$ , presumably to reduce drag (31). The points plotted on the line are based on freely swimming animals with known pressures at known speeds back-calculated through regressions as described in MATERIALS AND METHODS to show that even though the line is based on aerobic power measurements its predictions of anaerobic power consumption are reasonable.

The dashed power output line in Fig. 1 was calculated as  $P$  times  $Q$  from the Bernoulli equation as described in MATERIALS AND METHODS. The funnel orifice is not perfectly circular and does vary in size during the jet (34), but, as a first approximation, the funnel diameter of an anesthetized 0.5-kg squid, 0.011 m, gives an  $A$  of  $0.000095 \text{ m}^2$ , assuming circularity. Using this value and substituting Eqs. 2 and 3 into Eq. 4 gives power output as

$$PO = 0.0000084P^{1.5} \quad (7)$$

Thus the efficiency of power production by the mantle musculature can be estimated as the ratio  $PO/PI$ , as plotted in percentages against the right-hand scale in Fig. 1. The frictional losses in a real, viscous fluid would reduce the real power output to some extent, but the mantle musculature would still have to produce the power required to overcome this friction. The output line is particularly interesting since it not only predicts average power output for  $\bar{P}$  but should also predict instantaneous power outputs at peak pressures during the cycle. It is less obvious why extrapolation of the input line should predict instantaneous power consumption, but the analysis that follows suggests that such extrapolation is consistent with all available information.

Table 1 summarizes some critical values from Fig. 1 needed for the analysis and includes values for squid (which are negatively buoyant by ~4% and must work to stay in the water column) at rest on the bottom, hovering ( $u = 0$ ), and at the average speed of schools of squid doing nothing in particular ("lolling") in the large pool. For speeds  $>0.6 \text{ m} \cdot \text{s}^{-1}$ , the optimal speed for long-range migrations, Table 1 includes both average pressure and maximum pressure attained during a typical cycle at each speed. Figure 2 shows a typical pressure record for a squid at  $0.6 \text{ m} \cdot \text{s}^{-1}$ . The total cycle for a 0.5-kg squid is ~1.5 s with pressure rising to maximum in 0.1–0.2 s and returning to a slightly negative value at the beginning of the refilling phase after ~0.6 s. At lower speeds a longer refilling phase increases total cycle time, but as speeds increase the duration of each phase is relatively constant, limiting the source of increased power primarily to increased peak pressures.

The efficiencies in Table 1 provide one test of the validity of the suggested power input and output relationships. The low efficiencies at low speed are not surprising since at these speeds the fins also contribute to locomotion and use  $O_2$  but produce no pressure. At optimum speed, the average efficiency of 8.4% compares

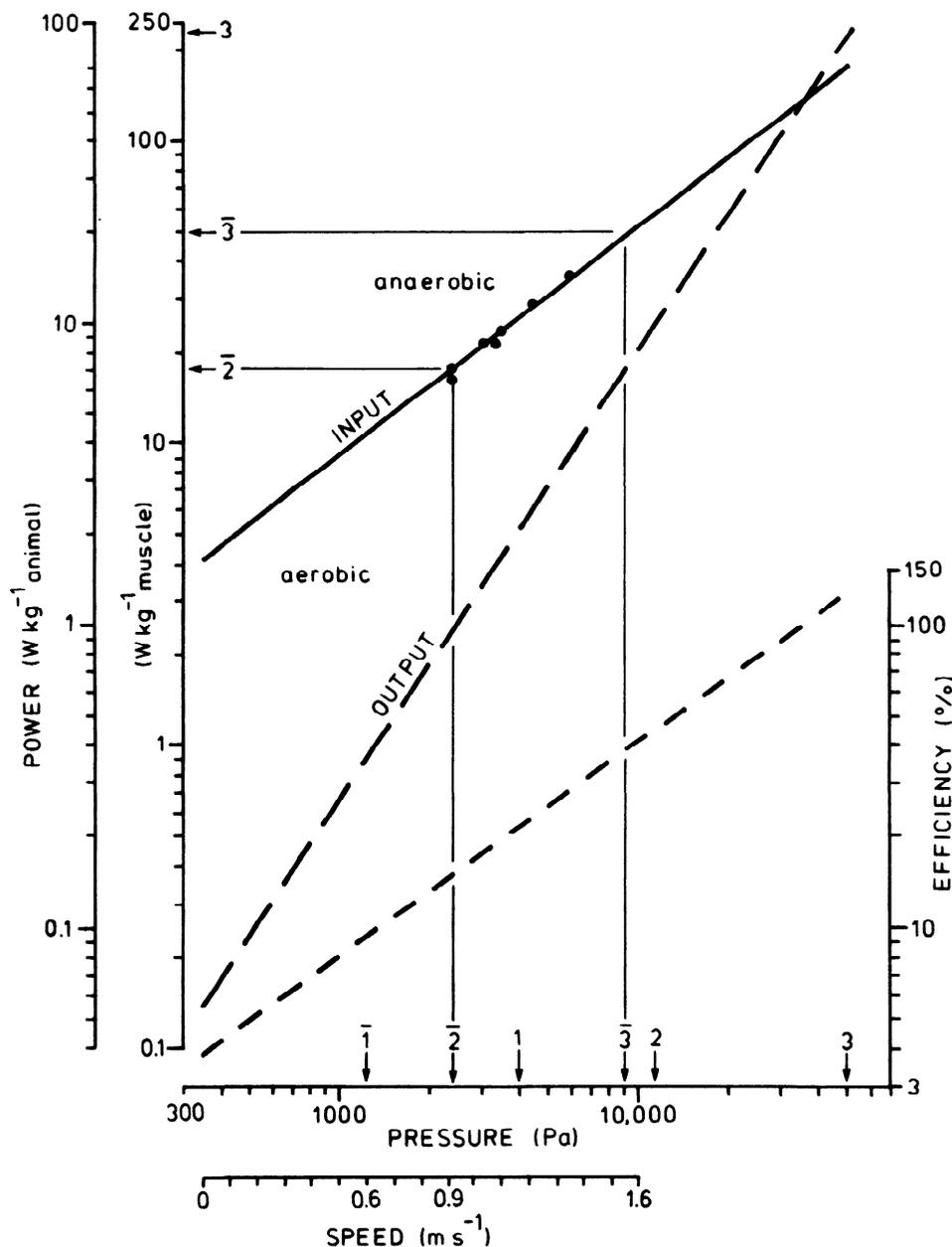


FIG. 1. A summary of power, pressure, speed, and efficiency relationships in swimming 0.5-kg squid (*Illex illecebrosus*). Power is presented based on both animal mass and mantle muscle mass (40% body mass). —, Based on regression analysis of data on  $O_2$  consumption and intramantle pressures of squid swimming at various speeds in a tunnel respirometer. ●, Projected values for freely swimming animals at known speeds and pressures (28). - - - - -, Pressure-flow power output calculated from Bernoulli equation. Ratio of these lines is plotted as efficiency below lower - - - - - against right-hand scale. Numbered ↓, average (bar) and peak (no bar) pressures at 1) optimum speed, 2) critical speed (maximum aerobic power), and 3) maximum speed (maximum anaerobic power).

reasonably well with values for other animals using their muscles below capacity (8) and during peak pressure production 20% is typical of maximal *in situ* muscle efficiencies (10). The efficiency of 14% at  $u_{crit}$  is relatively low, but it has been shown that part of the energy from powerful contractions of squid mantle go to load collagen "springs" which provide the energy to produce the negative pressures that draw water back into the mantle and accelerate it to the speed of the squid during the refilling phase (13). If this could be included, the overall efficiency would be close to expected values. The peak efficiency at this speed exceeds the maximum value for aerobically fueled muscle, but, since the contractile phase is only 40% of the cycle, such efficiencies could be achieved by fueling contraction directly from the phosphagen, phospho-L-arginine (P-Arg), and replenishing reserves aerobically during the refilling phase. The efficiency of conversion of high-energy phosphate compounds directly to

mechanical work can apparently be as high as 60% (10). The 36% efficiency predicted from average pressure at maximum speed, which is achieved by a series of maximal escape jets, is well within this limit, but obviously is drawing on reserves and cannot be sustained. Using the P-Arg concentration for *Loligo pealei* of  $10.5 \text{ mmol} \cdot \text{kg}^{-1} \text{ muscle}$  (27) and assuming  $30.5 \text{ J} \cdot \text{mmol ATP equivalent}^{-1}$ , the reserves would fuel only about six maximal jets, which is generally consistent with observations of squid behavior. The final paradoxical observation is that the calculated efficiency at peak pressure during an escape jet is  $>100\%$ , implying that during this brief period  $PO$  exceeds  $PI$ . This does not necessarily mean that the projections are wrong, however, since a careful look at the organization of the mantle can provide an explanation.

Squid mantle contains three collagen fiber systems. The two transverse fiber systems have been shown to

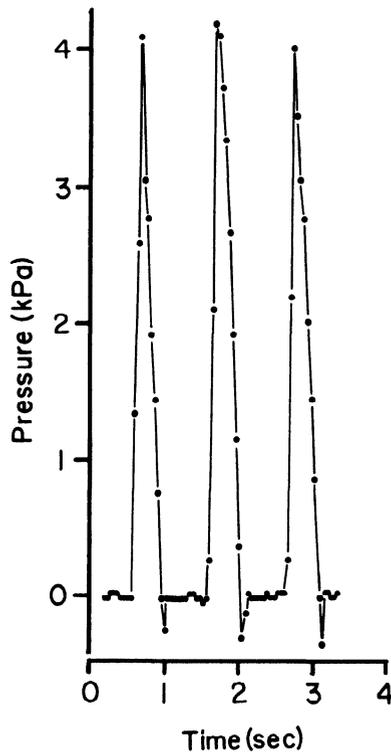


FIG. 2. A typical intramantle pressure record for a squid swimming at  $0.6 \text{ m} \cdot \text{s}^{-1}$ . This record is from a 0.3-kg squid and total cycle time is somewhat shorter than in a 0.5-kg squid (30).

TABLE 1. Calculated power inputs and outputs, efficiencies, and muscle stresses at various activity levels in squid

	Speed, $\text{m} \cdot \text{s}^{-1}$	Pres- sure, Pa	Power, $\text{W} \cdot \text{kg body}$ $\text{wt}^{-1}$	Effi- ciency, %	Stress, Pa
Rest		80	0.5	0.006	1.2
			1.1*		
Hovering	0	350	1.6	0.055	3.4
Lolling	0.15	480	2.1	0.088	4.2
$u_{\text{opt}}$	0.6	1,230	4.3	0.36	8.4
Peak		4,000	11	2.1	20
					40,000
					240,000†
$u_{\text{crit}}$	0.9	2,300	7.0	0.95	14
Peak		11,000	24	10	42
					68,000
					670,000†
$u_{\text{max}}$	1.6	9,000	20.0	7.2	36
Peak		50,000	73	94	129
					350,000

Pressure values include both average pressures over cycle and peak pressures during cycle as indicated.  $u_{\text{opt}}$ , optimal swimming speed;  $u_{\text{crit}}$ , critical swimming speed. \* Power calculated from resting  $\text{O}_2$  consumption directly using  $20 \text{ J} \cdot \text{ml} \text{ O}_2^{-1}$  rather than from pressure- $\text{O}_2$  regression used for other values. Difference provides an indication of non-presure-related power consumption. Input values for power on left; output on right. † Stress on aerobic fibers if they act alone.

store energy during mantle contraction to power refilling later and their angular arrangement is such that they should also store energy during the hyperinflation that precedes an escape jet (11–13). The third circular system should also be able to store energy during expansion. Hyperinflation is produced by a system of radial muscles running across the thickness of the mantle wall that

cause the mantle to thin when they contract. Since the volume of the mantle wall cannot change, the circumference and therefore the diameter of the mantle must increase. As these muscles contract, they not only cause active refilling of the mantle cavity, increasing the volume of water pumped out during the jet, but they should also stretch the collagen fibers, storing energy to be recovered during mantle contraction. This would result in part of the energy from radial muscle hyperinflation appearing as power output during the pressure peak and could explain the  $>100\%$  efficiency. This is indirect evidence for the hypothesized energy storage mechanism.

The maximum power output itself provides further, more direct evidence for energy storage. Maximum sustained power outputs in striated muscles (32) and insect asynchronous muscle (8) are suggested to range up to  $250 \text{ W} \cdot \text{kg}^{-1}$  muscle, with maximum power outputs about double this. However, lizards only approach maximum power outputs of  $500 \text{ W} \cdot \text{kg}^{-1}$  at  $45^\circ\text{C}$ , and their power outputs decrease with temperature with a  $Q_{10}$  of  $\sim 2$ , showing little acclimation (2). On this basis the calculated maximum power output of  $235 \text{ W} \cdot \text{kg}^{-1}$  in squid at  $15^\circ\text{C}$  is nearly four times the expected  $63 \text{ W} \cdot \text{kg}^{-1}$ . The obliquely striated muscle in squid may be uniquely adapted to be powerful at low temperatures, but a more reasonable conclusion is that part of the power comes from elastic recoil. The fact that the maximum sustained power output in squid of  $18 \text{ W} \cdot \text{kg}^{-1}$  is less than half the predicted maximum sustained power output is also consistent with energy storage. The enforced idleness of the circular muscles while the mantle refills may prevent squid from maximizing power output over a cycle, but short-term power production may be enhanced by optimizing the ATP production of mitochondria as outlined in the DISCUSSION. Thus squid muscle may not set any records for power, but squid are at least using sophisticated mechanisms for boosting short-term power output similar to those of mammals (18).

Since the radial muscles represent only  $\sim 9\%$  of the total muscle mass (3, 20), they seem an unlikely place to look for the source of large amounts of extra power. However, the orientation of these fibers across the mantle wall means that their length is much less and their cross-sectional area much greater than the circular fibers. For a 0.5-kg squid, resting mantle circumference is  $\sim 0.22 \text{ m}$  and the thickness only  $0.007 \text{ m}$ . In a theoretical 1-m-long tube of mantle the cross-sectional area of radial muscle is  $0.02 \text{ m}^2$ , over 3 times the cross-sectional area of circular muscle in the same tube, and the muscles themselves are presumably capable of producing three times the tension. Thus the recovery of energy from elastic storage only needs to be 33% efficient to double the tension, and the elastic system has a 75% efficiency when driving refilling (13). An elastic system can release energy more rapidly than muscle and, therefore, can maximize power output and peak pressure.

Muscles also have limited capacity to produce tension which provides another test of the two equations. From the peak pressures and dimensions of the mantle, the tension (T) produced can be calculated using the LaPlace

equation

$$T = Pr \quad (8)$$

During hyperinflation the outside radius of the mantle ( $r$ ) increases to 0.0375 m and a pressure of 50,000 Pa would require a tension of 1,725 N in a 1-m tube. Since hyperinflation would reduce the mantle thickness ( $t$ ) to 0.0063 m, the total stress would be 275 kPa and the stress on the circular fibers would be 300 kPa. Squid mantle contains "aerobic" fibers with ~47% mitochondria by volume on the inner and outer surfaces accounting for 17% of the circular muscle (in *I. illecebrosus*) and a central layer of "anaerobic" fibers with ~7% mitochondria (3, 20), so the actual stress on the area of myofibrils (excluding mitochondria) would be 350 kPa. If this is all met by muscle, it means this obliquely striated muscle outperforms most vertebrate-striated muscle but is not as strong as insect muscle with long myofilaments (1). If half of the tension is produced from recoil, the force produced by this obliquely striated muscle is quite routine.

The same calculation for maximum aerobic peak pressures (11,300 Pa), which involve less hyperinflation ( $r = 0.0365$  m,  $t = 0.0065$  m), requires a tension of 68 kPa on myofibrils if all circular muscles are involved and 645 kPa if only "aerobic" fibers are involved. The latter value seems very unlikely since it is twice the tension calculated for an escape jet, suggesting that a majority of the "anaerobic" fibers are, in fact, active during aerobic swimming. This idea is less contradictory when it is remembered that these fibers contain large reserves of P-Arg which could power contraction and be replenished from their small mitochondrial component during the 60% of the cycle when they are inactive. At  $u_{opt}$ , which may be optimal because it includes no anaerobic losses, aerobic fibers would need to produce only 240 kPa. This is probably the most reasonable estimate of the maximum stress in these obliquely striated muscles. If so, it indicates that elastic recoil contributes about one-third of the force during maximal contractions.

There are, then, no obvious inconsistencies in the comparison of PI and PO, as calculated, which cannot be resolved by consideration of the organization of the system to maximize power output at critical times. The comparison suggests several sophisticated adaptations to focus power on locomotion but does not require that squid have any unique mechanical properties. The discussion below compares squid performance with other animals on the assumption that the lines in Fig. 1 are perfectly accurate, but there is clearly a need for improved measurements and more direct experimental examination of the locomotor system.

## DISCUSSION

The performance of squid seems unlikely to be limited by ventilatory factors despite their high  $\dot{V}O_2$ 's. For 0.5-kg squid at a critical speed of 0.9 m·s<sup>-1</sup>, the PI of 7 W·kg<sup>-1</sup> corresponds to a  $\dot{V}O_2$  of 1,250 ml·kg<sup>-1</sup>·h<sup>-1</sup>. As Table 2 shows, this is more than twice the highest scope reported for a fish of this size at 15°C (4). Squid even use more aerobic capacity in swimming than birds (5)

and mammals (6) at body temperatures >20°C higher. These air breathers can consume much more O<sub>2</sub> during activities in air, but, in the underwater arena where they compete with squid, the squid have the edge in cruising power. This high aerobic scope is possible because large volumes of water must pass the gills to produce the jet. Eqs. 2 and 3 predict a total flow of 1,500 l·kg<sup>-1</sup>·h<sup>-1</sup>. For water containing 5.1 ml O<sub>2</sub>·l<sup>-1</sup> this means a total O<sub>2</sub> supply of 7,500 ml O<sub>2</sub>·kg<sup>-1</sup>·h<sup>-1</sup>, and the extraction efficiency need only be 17%, well below measured efficiencies of up to 60% in other cephalopods (22).

One potential limit is O<sub>2</sub> use by the mitochondria. The upper limit on mitochondrial consumption in homeotherms is 5 ml O<sub>2</sub>·cm<sup>-3</sup>·min<sup>-1</sup> (15). Discounting this by a factor of 4 to allow for a Q<sub>10</sub> of 2 and a 20°C temperature difference gives a value of ~75 ml O<sub>2</sub>·g<sup>-1</sup>·h<sup>-1</sup>. Available data (3, 20) given in RESULTS suggest that there are ~32 g of mitochondria associated with aerobic fibers per kilogram of locomotor muscle. The predicted 2,400 ml O<sub>2</sub>·kg<sup>-1</sup>·h<sup>-1</sup> would more than cover observed consumption if the mitochondria were continuously active. However, the aerobic fibers have much lower arginine and phosphoarginine kinase levels than the anaerobic fibers (20), and contraction may have to be fueled directly with mitochondrial ATP. If the mitochondria are active at the above rate during the contraction phase only (40% of the cycle), they could handle only 75% of the measured consumption, leaving 25% for the anaerobic fibers. This is well within the capacity of these fibers, which contain an estimated 22 g mitochondria per kilogram muscle, and is consistent with the observation that the stresses that develop at  $u_{crit}$  are too high to be borne by aerobic fibers alone. The optimum mix of the two fiber types may be determined by the relative lengths of the contraction and refilling phases in squid of various sizes and species. The distribution of these fibers is probably controlled by blood circulation, which is the most likely limiting factor.

The hemocyanin-filled blood of squid holds only 4.3 vol% O<sub>2</sub>, less than half that of vertebrates, and must restrict O<sub>2</sub> delivery and performance. Even with an extraction efficiency of 88% (22), squid require a cardiac output of 33 l·kg<sup>-1</sup>·h<sup>-1</sup> at  $u_{crit}$ . This is 10 times that of fish (16), higher than humans, and 70% of a similar-sized mammal. How squid manage even this is not really clear, although they do have high blood pressures and complex closed circulatory systems. The activity of the mantle musculature itself may aid in blood circulation, although the mechanism is unclear (22). Whatever the source of the power to drive the circulation, it is almost certainly the circulatory system that ultimately limits sustained performance, as in mammals (7).

At critical moments of escape or attack, squid, like most other animals, depend on anaerobiosis (14). From Fig. 1 the average PI over an escape cycle is 20 W·kg<sup>-1</sup>, indicating an anaerobic scope of 13 W·kg<sup>-1</sup>, nearly double the aerobic scope. As Table 2 shows, the anaerobic scope of fish (26), the highest ever calculated from glycogen breakdown rates, is lower. It is not clear that this is a fair comparison, however. The anaerobic capacity of squid is much smaller than that of fish and may largely

TABLE 2. Maximum power consumptions measured for various animals under water

Animal	Mass, kg	Temperature, °C	Power, W · kg <sup>-1</sup>	Source
<i>Aerobic</i>				
Squid	0.5	15	7.0	(30)
Penguin	4.6	38	5.5	(5)
Seal	40	37	4.4	(6)
Salmon	0.5	15	3.0	(4)
<i>Anaerobic</i>				
Squid	0.5	15	33	Fig. 1
Trout	0.2	11	30	(26)

Aerobic power was calculated per unit animal mass; anaerobic power was calculated per unit muscle mass.

reflect the breakdown of P-Arg as mentioned above. Glycolysis in squid appears to be coupled to the breakdown of the phosphagen in that the arginine released reacts with pyruvate to produce octopine rather than lactate. This reaction, however, does not appear to proceed to completion except in conditions of severe hypoxia (27). Nonetheless, squid swum to exhaustion accumulate an O<sub>2</sub> debt of ~165 ml O<sub>2</sub> · kg<sup>-1</sup>, which is just enough to produce the ATP needed to rephosphorylate the P-Arg and resynthesize glycogen from unoxidized pyruvate. This debt is only about one-third that possible in fish (21, 31). Although the detailed workings of these metabolic pathways during exercise remain unclear, it is remarkable that squid have managed to organize their musculature in such a way that they can be star performers in terms of both aerobic and anaerobic scope.

The use of obliquely striated muscle in the mantle does not appear to be an adaptation to maximizing power output per se. Squid use cross-striated muscle in tentacle extension, apparently because it contracts more rapidly (17), which would also yield more power. Obliquely striated muscles have a flattened length-tension relationship, however, allowing them to maintain tension in both elongated and shortened states (19). This would be essential if the circular muscles must produce maximal pressures during hyperinflation while retaining the ability to stretch the collagen springs as they near maximum contraction. Rosenbluth (25) has also suggested that obliquely striated muscle may be able to function both phasically and tonically since synchronous contraction along its length is not essential for force delivery. If squid mantle muscles can produce graded contractions, it might explain how the giant fiber nerve system which is supposed to have an "all or none response" (23, 33) can produce fully graded pressures with increasing speed. There remain many interesting unanswered questions about the function of the jet propulsion system in squid, but the analysis presented above indicates that the organization of squid is ideally suited to obtaining information about the flow of material and energy through the locomotor elements. Squid seem to have tried many unusual experiments in their quest for power and provide an ideal model for the assessment of performance.

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