INVERTEBRATE ATHLETES: TRADE-OFFS BETWEEN TRANSPORT EFFICIENCY AND POWER DENSITY IN CEPHALOPOD EVOLUTION

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Summary

Jet propulsion concentrates muscle power on a small volume of high-velocity fluid to give high thrust with low Froude efficiency. Proponents are typically escape artists with high maintenance costs. Nonetheless, oceanic squids depend primarily on jets to forage over large volumes of relatively unproductive ocean (low power density, $W m^{-3}$). A survey of locomotor performance among phyla and along an 'evolutionary continuum' of cephalopods (*Nautilus, Sepia, Loligo* and *Illex*) suggests that increasing speed and animal power density are required if animals are to compete effectively in environments of decreasing power density. Neutral buoyancy and blood oxygen reserves require unproductive volume, keeping drag high. Undulatory fins increase efficiency, but dependence on muscular hydrostats without rigid skeletal elements limits speed. Migratory oceanic squids show a remarkable range of anatomical, physiological and biochemical adaptations to sustain high speeds by maximizing power density. Muscle mitochondrial density increases 10-fold, but metabolic regulation is realigned to optimize both aerobic and anaerobic capacity. The origins of these adaptations are examined (as far as possible, and perhaps further) along the continuum leading to the most powerful invertebrates.

Introduction

In this Symposium, 'exercise' presumably means the production of mechanical power by animals, typically using muscle to induce movement. Muscle power comes in two forms: sustainable and burst. Sustainable power is produced aerobically using the Krebs cycle, making it up to 20 times as efficient as burst power, which is typically based on anaerobic glycolysis. Few animals can afford the waste of metabolic energy resulting from raw glycolysis, so most of them accumulate its metabolic end-products and recycle them when oxygen supply catches up with power demand. Increased power production capability appears to enable animals to acquire more energy by foraging over larger areas and capturing larger (and typically faster) prey. Thus, most metazoan groups include lines of

predators showing an evolutionary trend towards increasing power production and consumption. In aquatic media such predators must also minimize drag by concentrating power production in a minimal volume, leading to forms with a higher 'power density' ($W m^{-3}$)

Among the invertebrates, cephalopods show this 'athletic' trend more clearly than any group except the insects. The cephalopods trace their lineage back over 500 million years and have retained the same basic locomotor mechanism, jet propulsion, for the entire time. Since the propulsion system has changed relatively little, and in quantifiable ways, this group represents a unique continuum for examining the physiological adaptations required to increase the capacity to exercise, both aerobically and anaerobically. The most primitive cephalopod whose physiology can be studied directly, *Nautilus*, has probably remained relatively unchanged for only 200 million of these years. This is, however, more primitive than the most primitive traceable vertebrate or insect, and recent analyses suggest that it is reasonable to extrapolate further (Wells, 1990; Wells and O'Dor, 1991; Chamberlain, 1990, 1991).

This report will explore what is known and conjectured about power production by both aerobic and anaerobic means along the cephalopod continuum as a way of understanding where the constraints on exercise by animals really lie. The cephalopod example is made more interesting by the fact that in many, but not all, systems vertebrates have converged on similar adaptations.

Aerobic *versus* anaerobic power

Primitive metazoans were small and their locomotion was powered by cilia, as is still the case for the marine larvae of most phyla. As these larvae grow they must switch to other forms of locomotion because of the inherent limits of cilia (Sleigh and Blake, 1977). The fossil record from the ediacarian period suggests that Cnidaria dominated it, probably as a result of the development of nerve–muscle systems that allowed coordinated movements of large medusae to produce jet propulsion. The muscle layers in medusae are thin and lie just beneath their ciliated surfaces. Cilia are normally powered aerobically by associated mitochondria, and Larson (1987) suggests that the thin muscle layers are also fully aerobic. Larson also points out that, because medusae are just thin layers of tissue overlying a thick, elastic mesogloeal mass, their muscles can be fully aerobic without the need for separate respiratory and circulatory systems. The combination of direct oxygen delivery with a resonating (DeMont and Gosline, 1988a,b,c), metabolically inert gel skeleton allows medusae to move at speeds up to $0.15 m s^{-1}$ with a cost of transport (COT) as low as $1 J kg^{-1} m^{-1}$, even lower than that of undulating fish of similar size (Larson, 1987; see Fig. 1).

The cnidarian organization typifies aerobic exercise in its ability to deliver limited power continuously for nektonic animals that search for small prey in a dilute medium. Fig. 1 also includes a COT for 0.02 kg medusae for comparison with an anaerobically powered scallop to illustrate this point. Power output of the
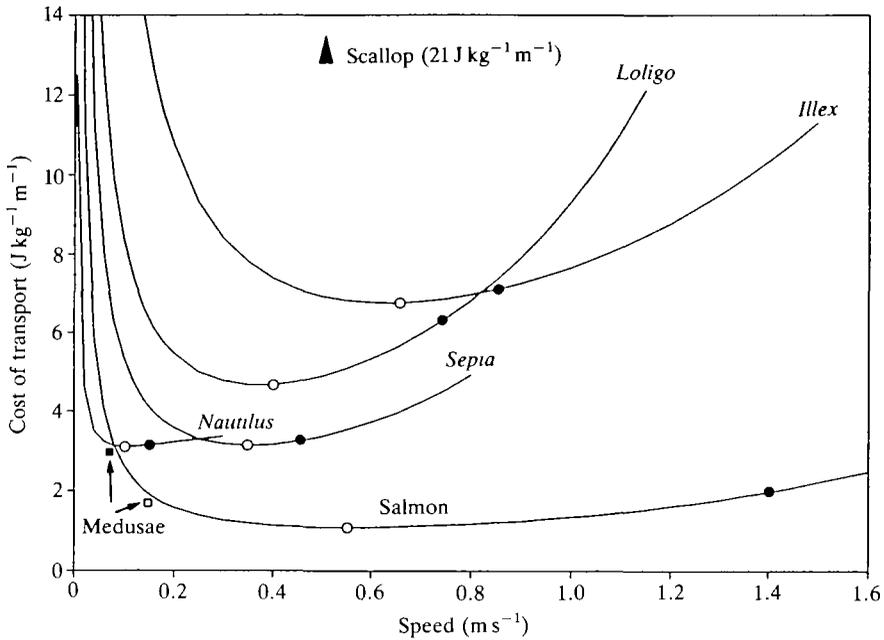
Fig. 1. Gross cost of transport (COT) over the speed ranges of the 'continuum' of 0.6 kg cephalopods compared to a generalist teleost (the salmon). COT values were calculated by converting oxygen consumption in $ml\,O_2\,kg^{-1}\,h^{-1}$ to $J\,s^{-1}$ (W), assuming $20\,J\,ml\,O_2^{-1}$, and dividing by speed. All *Nautilus* studied were near 0.6 kg, and we have no basis for scaling its COT. The other cephalopod COT values were scaled to 0.6 kg as $m^{0.75}$, where m is body mass, based on available information (Webber and O'Dor, 1986; O'Dor, 1988c; Johansen *et al.* 1982). Oxygen consumption equations used: *Nautilus pompilius*, $\dot{V}_{O_2}=10+726u^{1.2}$ (O'Dor *et al.* 1990b); *Sepia officinalis* (cuttlefish), $\dot{V}_{O_2}=43.5e^{2.85u}$ (P. Lee, D. M. Webber, J. Shears and R. K. O'Dor, in preparation); *Loligo pealei* (long-finned squid), $\dot{V}_{O_2}=69e^{2.68u}$ (D. M. Webber, E. Sim, J. Hoar and R. K. O'Dor, in preparation); *Illex illecebrosus* (short-finned squid), $\dot{V}_{O_2}=168.7e^{1.59u}$ (Webber and O'Dor, 1986); *Oncorhynchus nerka* (sockeye salmon), $\dot{V}_{O_2}=33.1\,m^{0.65}e^{1.81u}$ (calculated from Brett and Glass, 1973), where $\dot{V}_{O_2}$ ($ml\,O_2\,kg^{-1}h^{-1}$) is oxygen consumption and u ($m\,s^{-1}$ is swimming speed). Speeds at minimum COT (u_{opt}, ○) and maximum aerobic performance (u_{crit}, ●) are indicated and equations are extrapolated to maximum observed speeds. Values for 0.6 kg (□) and 0.02 kg (■) medusae (*Stomolopus meleagris*, Larson, 1987) and 0.20 kg scallops (arrow points to $21\,J\,kg^{-1}\,m^{-1}$, COT at $0.5\,m\,s^{-1}$; *Placopecten magellanicus*, Dadswell and Wiehs, 1990), as discussed in the text, are given for comparison.

medusa is about $0.016\,W\,kg^{-1}$ and efficiency about 10 % (DeMont and Gosline, 1988b; Daniel, 1985).

The scallop is at the opposite end of the spectrum, using an 'escape response' typical of benthic animals to 'vanish' into the third dimension. It maximizes power output with virtually no consideration of metabolic cost. Acceleration is more important than sustained speed, and anaerobic debts can be accumulated to be

paid off later. In the escape game even crustacean tail-flips turn out to be jets (Daniel and Meyhofer, 1989), but scallop swimming is perhaps the clearest example, as its geometry is simple and its power purely anaerobic.

There is, as yet, no comprehensive study of scallop locomotion, power output and input, but a composite is possible. Swimming speeds are maximal in *Placopecten magellanicus* of 0.055m shell height (0.02 kg) at $0.5\,\mathrm{m\,s^{-1}}$ (Dadswell and Weihs, 1990). Combining morphometric data from their study with pressure data for a 1.6s, four-'clap' swim by *Chlamys opercularis* (Moore and Trueman, 1971) predicts maximum pressure (p_{max}) and power output (see Table 2) similar to those of *Nautilus*. Livingstone *et al.* (1981) give the cost of a clap as 1.02 mmol $\mathrm{ATP\,kg^{-1}}$ muscle, allowing an estimate of power input and efficiency, assuming that ATP is ultimately made aerobically. At 28%, the efficiency appears high compared to aerobic values in the table, but is not unreasonable since losses related to the resynthesis of high-energy phosphate bonds are hard to determine and not included. Scallop muscle power is actually converted into jet power output reasonably efficiently by acting on a relatively large volume of water, using 'ram' refilling and taking advantage of resonance energy savings (DeMont, 1990). The COT (Fig. 1) is much higher than that for 0.6 kg squids, but is comparable to that for squid of similar size at similar speeds. Scallops of 0.6 kg seem incapable of swimming, but it is unclear whether this is a limitation set by the scaling of the jet propulsion mechanism or the demands of their life histories.

Dadswell and Weihs (1990) suggest that juvenile scallops may migrate to return to spawning areas. If so, they may do it efficiently but must do it with great patience. The biochemical data on adults in the 0.1 m shell height range indicate that, after a 30-clap swim covering 30 m over 60 s, scallops require 24 h to recover fully from anaerobiosis. This is a long-term power output of only 0.007 W $\mathrm{kg^{-1}}$ covering 11 km per year.

Fundamentals of jet propulsion

Jetting is a convenient form of exercise to quantify, but an inherently inefficient form to use (Alexander, 1977). Undulating and paddling, the swimming mechanisms used by nearly all evolving vertebrates, produce thrust by accelerating large masses (m_w) of an invisible fluid backwards at low speeds (u_w) in an exchange of momentum ($m_w u_w = mu$, $\mathrm{kg\,m\,s^{-1}}$) with the animal; neither the mass nor the velocity of the fluid is directly measurable. Jetters typically take a small mass of fluid into a body cavity, doing work against it, creating pressure and forcing it out through a small orifice at high speed. Because the energy invested in the accelerated mass is $0.5\,m_w u_w^2$, the cost of high jet velocity is exorbitant, but increasing the volume of the pressure chamber can cost even more, if it increases animal mass or drag.

With these design constraints, power jetters have a narrow window to evolve through, but the inefficient jet that is their problem provides an easy solution for

the scientist. As Trueman and Packard (1968) pointed out in their pioneering work on comparative jet propulsion, jet thrust ($kg\,m\,s^{-2}$), which equals jet velocity (u_j, $m\,s^{-1}$) times the flow (Q, $m^3\,s^{-1}$) and the medium density (d_w, $1025\,kg\,m^{-3}$ for sea water), can be defined (based on Bernoulli's equation, familiar to most physiologists from cardiovascular studies; jetting animals are just hearts set free) knowing only the pressure (p, Pa) and the area of the orifice (A, m^2) as:

$$u_j Q d_w = 2Ap. \tag{1}$$

Although this equation is a useful indicator, the orifice is variable, regulated and hard to view in most species, so it can rarely be applied accurately (O'Dor, 1988a). It is much easier to calculate flow from frame-to-frame changes in body dimensions, since the body *contains* the reaction mass. This yields power output (P_o, $W=Pa\,m^3\,s^{-1}=N\,m^{-2}.m^3\,s^{-1}$) directly as:

$$P_o = pQ, \tag{2a}$$

$$= (2/d_w)^{0.5}Ap^{1.5}. \tag{2b}$$

The second relationship can be used if only orifice area is known. In practice these relationships have proved quite robust as indices of jet power (O'Dor, 1988b) and can be useful even when data are limited, as illustrated in the examples above. Average pressures can be multiplied by average flows, and data from different studies can be combined. Acoustically telemetered, differential pressure transducers have been used to monitor jet pressures in swim-tunnels and in free-swimming animals with speeds calculated from video recordings (Webber and O'Dor, 1986; O'Dor *et al.* 1990b, 1991). The second approach eliminates artefacts associated with swim-tunnels when estimating the power required for speed.

Although, *a priori*, an allometric power function would be expected to describe the power–speed relationship best, regression analyses of pressure–speed data from cephalopods are typically more highly correlated as an exponential function. All relationships for the continuum in Fig. 2 are of the form:

$$p = ae^{bu}, \tag{3}$$

where a and b are constants. This shift from theoretical expectations probably reflects changes in funnel orifice with speed, which alter Froude efficiency, and changes in muscle efficiency with load (O'Dor *et al.* 1990b); similar shifts in power–speed relationships have been reported in fishes (O'Dor, 1982). However, over most of the speed range the differences between power outputs calculated from equations 2a and 2b are small. Thus, power outputs can be calculated for free-swimming animals using equation 2b, and the speeds and power outputs of animals in nature can be estimated from pressure data alone.

The aerobic power inputs (P_i, W) for jet propulsion can be measured in swim-tunnel respirometers (aquatic treadmills) by measuring oxygen removed from the water while it is recirculated past the animal at various speeds, as with other forms of swimming (e.g. Brett, 1964), and converted to comparable units by assuming
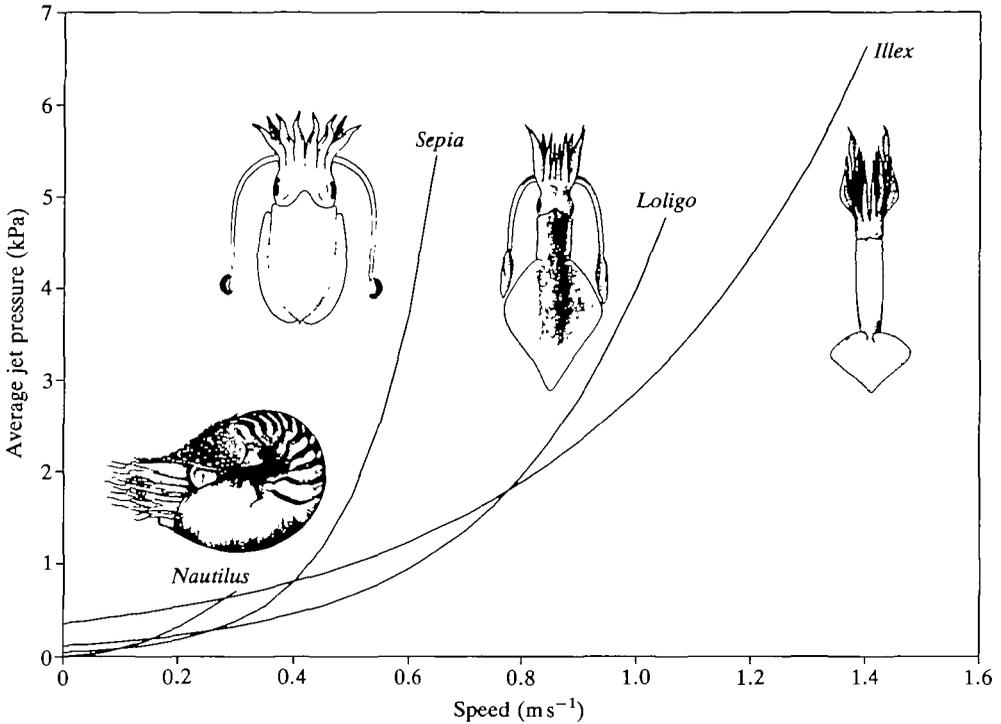
Fig. 2. Jet pressures required at various speeds by the 'continuum' of cephalopods. Equations used: *Nautilus pompilius*, $p=7883u^2$, where p is average pressure (Pa) and u is speed (m s^{-1}), (based on a fitted thrust–drag relationship from O'Dor *et al.* 1990*b*; Chamberlain, 1987); *Sepia officinalis*, $p=38e^{7.64u}$ (based on pressure records from Wells and Wells, 1991, fitted to speeds estimated from Fig. 1); *Loligo pealei*, $p=109e^{3.6u}$ (based on a regression from D. M. Webber, E. Sim, J. Hoar and R. K. O'Dor, in preparation); *Illex illecebrosus*, $p=350e^{2.1u}$ (Webber and O'Dor, 1986). (Illustrations modified from Roper *et al.* 1984.)

20 kJ l^{-1} O$_2$. Regressions of power on speed and animal mass typically yield relationships of the form:

$$P_i = ae^{bu}m^c , \qquad (4)$$

presumably linked to the pressure–speed relationship discussed above. The value of c is near 0.75 for animals in the 0.01–10 kg range; a and b are constant for a species. Power inputs and costs of transport can be calculated even for animals that will not perform in a swim-tunnel respirometer by combining free-swimming pressure–speed relationships (equation 3) with oxygen uptake–pressure relationships determined in small respirometers (O'Dor *et al.* 1990*b*). The typical form of such relationships is:

$$P_1 = am^c p^d , \qquad (5)$$

where $c=0.75$ and d varies. In all exercise experiments there is some contamination of aerobic power with anaerobic power as animals approach performance

limits; d is heavily influenced by anaerobic contributions in intense exercise. Some jet power estimates have included data on the size and payback period of 'oxygen debts' (O'Dor, 1982; O'Dor and Webber, 1986; Webber and O'Dor, 1985), but experiments using new nuclear magnetic resonance and microcalorimetric techniques are needed to monitor anaerobic metabolites directly.

Why exercise?

Before considering how jetters improved their power output it might be useful to consider why they needed to. Escape responses depend on rapid acceleration, which confuses the predator, puts distance between predator and prey and gives the prey time to hide or organize a defence. Since power output increases as $p^{1.5}$, escape is best effected using muscles producing maximum force and therefore maximum pressure, which means anaerobic muscles. Mitochondria can occupy up to 50 % of the cross-sectional area of aerobic muscles, reducing their force and power. If an animal has room for more escape muscle, it should make more anaerobic muscle, not dilute its force-producing machinery with mitochondria that do no work. One might argue that escape from a relentless predator would benefit from aerobic muscle, but this just makes it clear that sustainable power evolved first in relentless predators.

What creates a relentless predator? Competition for limited resources. Imagine a cambrian nautiloid, hanging from its neutrally buoyant chambered shell, bumbling over a sea bottom tasting everything with its cirri. Primary production at the surface yields $1 \, \text{W m}^{-2}$, which cycles through the lower levels of the food chain to produce $0.002 \, \text{W m}^{-2}$ of secondary and tertiary carnivores which die and sink to the bottom (values converted from Petipa *et al.* 1970). If it swims as efficiently as the *Nautilus* in Fig. 1 and tastes a path 0.2 m wide, the nautiloid can scavenge the $0.034 \, \text{W}$ it needs to move at $0.001 \, \text{m s}^{-1}$. If competition in the water column increased over a few million years, such that the supply of carrion dropped to $0.0002 \, \text{W m}^{-2}$, the nautiloid would have to increase its speed to $0.01 \, \text{m s}^{-1}$ to supply $0.034 \, \text{W}$. But, the power required to swim at this speed is $0.066 \, \text{W}$. The characteristics of the COT curves in Fig. 1 mean that the nautiloid could only break even by swimming at $0.05 \, \text{m s}^{-1}$. The nautiloid is still not a relentless predator, but it is certainly moving in that direction. An ecosystem with increasing competition should slowly and steadily reward any scavenger or predator that can search a larger area or search more efficiently. An extension of the same scenario could move evolution along the continuum of cephalopods, producing animals that can hunt more widely and survive in less power-dense environments, where less consumable energy is produced in a given volume of water in unit time. It is probably convenient and useful to think of both animals and environments changing in the same units (W m^{-3}) along an evolutionary continuum.

The cephalopod continuum

Fig. 1 summarizes what is known about cephalopod capacities for exercise

associated with locomotion in comparison to the capacities of a generalist fish. The graph was generated from relationships such as equation 4, based on swim-tunnel respirometry. Dividing the mass-specific metabolic rate at any speed by the speed gives the gross cost of transport (Schmidt-Neilsen, 1972). Standard metabolism, the extrapolated energetic cost of standing still, is included so that all curves are asymptotic at zero speed. The curves are extrapolated to the maximum speeds that have been observed, but are really only accurate to the aerobic limits, as indicated (u_{crit}, the critical velocity; Brett, 1964). Curves in this form emphasize the optimum speeds (u_{opt}), the relative minimum costs for different species and their ranges of effective speeds. The data for *Illex illecebrosus* and *Nautilus pompilius* are well documented (Webber and O'Dor, 1986; O'Dor *et al.* 1990*b*). The studies on *Loligo pealei* (D. M. Webber, E. Sim, J. Hoar and R. K. O'Dor, in preparation) and *Sepia officinalis* (P. Lee, D. M. Webber, J. Shears and R. K. O'Dor, in preparation) are still in progress, but the regressions used are based on several animals at a range of speeds and are certainly representative.

It is difficult to say whether this particular series of cephalopods has any real evolutionary significance because, while we do know that all cephalopods are related, the relationships between *Nautilus*, the only living representative of the vast diversity of ectocochleate fossils, and the endocochleate modern coleoids are not well defined in the fossil record. The best rationale for suggesting that ommastrephids, like *Illex*, have been more highly selected by competition in the water column (presumably from their arch rivals the fishes) may be that they have been competing longer. Sepiids, like *Sepia*, can be traced to fossils from about 70 million years ago, but ommastrephids appear to be very similar to *Plesioteuthis* from about 150 million years ago. If myopsids, like *Loligo*, diverged from the belemnoid line at some point in between then there is an evolutionary sequence.

Our premise is that the living coleoids diverged from a continuum of belemnoids with straight, conical, buoyant phragmacones that existed from 350 million years ago until 65 million years ago (Teichert, 1988; Donovan and Toll, 1988). *Sepia* has had 70 million years to become a good nekto-benthic predator, *Loligo* 100 million years to become a truly nektonic predator limited to continental shelves, and *Illex* and the ommastrephids over 150 million years to become truly oceanic. We assume the scavenger, *Nautilus*, has retained most of the locomotor characteristics of a more primitive cephalopod ancestor of the nautiloid and belemnoid lines. If the premise is wrong, we are just looking at the locomotor limitations of cephalopods adapted to a very wide range of lifestyles, which is still useful.

Nautilus

Nautilus has two distinct jet systems: (1) a 'piston' pump based on paired head retractor muscles used for escape and (2) a peristaltic pump based on the funnel wings used for respiration and cruising (Wells and Wells, 1985). The piston system is analogous to the scallop's jet and, like it, uses muscles low in mitochondria. This system is thought to be the origin of cephalopod mobility. Buoyancy provided by

closed shell chambers lightened the load of the 'archaemollusc' until the water displaced by head retraction produced a jet powerful enough to lift the animal off the bottom. The escape jet of the cephalopods was a natural consequence of an existing defence mechanism, just as the scallop's jet was a consequence of rapid valve closure. Once the primitive cephalopods got off the bottom, the typical molluscan foot could be modified to shape and direct the jet flow. A greatly extended and flattened foot could be rolled up to form a funnel and direct the jet.

Alternatively, modified peristaltic waves in the funnel could waft water over the gills and produce a low-speed, high-volume flow with enough momentum to propel the neutrally buoyant animal. In *Nautilus*, this system is driven by muscle fibres containing 20 % mitochondria (Hochachka *et al.* 1978) and may be analogous to the efficient, aerobic jet of the medusae; it could also be thought of as a fin undulating inside a duct, which could be very efficient. *Nautilus* may owe its long survival to this combination of an aerobic low-speed system having a lower COT than that of fish (Fig. 1) with a completely separate high-powered anaerobic escape system.

The problem with *Nautilus* is that the basic body plan only allows for muscle totalling 9 % of body mass (Chamberlain, 1987), which is divided equally between the two systems. Thus, its top speed is very low and probably more expensive than the extrapolation suggests, given the difficulty of measuring anaerobic metabolism. The body plan of all of the modern coleoids replaces the rigid shell, which merely *contains* pressure, with a muscular body wall that *generates* pressure. However, it is not clear what limits *Nautilus* to a maximum pressure of 11 kPa; retractor muscle loading is only 110 kPa and doubling of muscle volume would not seriously reduce stroke volume. Modern coleoids have funnels that fuse early in development; if the overlapping funnel design cannot withstand higher pressures, it would constrain *Nautilus* from using more retractor muscle effectively.

Illex

It will be easier to understand the compromises in *Sepia* and *Loligo* after considering the consequences of maximizing continuous power output in *Illex*. We should point out that in nature *Illex* is probably not quite as power hungry as these data suggest. An analysis of the forces acting on squid in a swim-tunnel (O'Dor, 1988*a*) showed that in forced, level swimming negatively buoyant squid use an inefficient lift-generating mechanism and that climb-and-glide swimming in nature could reduce the optimum COT by nearly 35 %. However, *Illex* is also not quite an oceanic squid and there may be even more powerful squid out there that no one has managed to exercise. In recent acoustic tracking experiments, *Ommastrephes bartrami* have averaged up to $0.5 \, \mathrm{m \, s^{-1}}$ in routine swimming in open ocean (Yoshida *et al.* 1990).

Like *Nautilus*, *Illex* is fully committed to jet propulsion with 40 % of its body mass in mantle muscle. The fins, only 12 % of body mass, are used for control and to smooth out the jet cycle, but alone they will not even allow the squid to hold

Table 1. *Design features and metabolic rates of jet-propelled invertebrates*

	Scallop[a]	Medusae[b]		Nautilus[c]	Sepia[c]	Loligo[c]	Illex[c]	I/N*
Body mass (BM, kg)	0.02	0.02	0.6	0.6	0.6	0.6	0.6	–
Density (kg m^{-3})	1220	–	–	1025	1025	1060	1076	
Muscle mass (%BM)								
Mantle or retractor	5.4	<1	<1	4.5	30	35	40	9
Fin or funnel	–	–	–	4.5	9	18	12	–
Mitochondria (%BM)	–	–	–	0.6[d]	–	–	6.5[e]	11
Funnel diameter (m)	–	0.02	–	0.011	0.006	0.012	0.012	–
Mantle volume (%BM)	88	32	–	15	25	50	45	3
Temperature (°C)	5	25	25	17	15	15	15	–
Resting rate of O$_2$ uptake (ml kg^{-1} h^{-1})	21[f]	24	24	10[g]	70[h]	100[h]	180[i]	18
Active rate of O$_2$ uptake (ml kg^{-1} h^{-1})	–	48	48	95	260	860	1090	11
Scope (ratio)	–	2	2	9.5	3.7	8.6	6.0	0.6

* *Illex* to *Nautilus* ratio.

Sources: (a) Dadswell and Wiehs (1990) *Placopecten magellanicus*; (b) DeMont and Gosline (1988a) (morphometrics, *Polyorchis penicillatus*), Larson (1987) (metabolic rates, *Stomolophus meleagris*); (c) Chamberlain (1991) (all cephalopod morphometrics, except *Sepia*, which are unpublished data); (d) Hochachka *et al.* (1987); (e) Mommsen *et al.* (1981); (f) MacDonald and Thompson (1986); (g) O'Dor *et al.* (1990b); (h) unpublished data as indicated in the legend of Fig. 1; (i) Webber and O'Dor (1986).

position whilst hovering (O'Dor and Balch, 1985). Tables 1 and 2 summarize some critical exercise parameters for the spectrum of cephalopods. As a simple estimate of maximum combined aerobic and anaerobic performance, a theoretical peak power output is calculated from equation 2a, assuming total mantle volume is ejected in 0.5 s while maintaining maximum pressure by contracting the funnel. There is a 14-fold increase from *Nautilus* to *Illex*. Because only the retractor muscles contribute directly to peak pressure in *Nautilus*, this results from a ninefold increase in muscle mass and a ninefold increase in mantle volume. Peak pressures increase less than muscle mass, so there is no evidence for inherent superiority of the endocochleate tubular pump over the ectocochleate 'piston' pump. However, the tube allows both muscle mass and mantle volume to increase relative to body volume; this increased power density yields more thrust with less drag.

Observed performances based on average pressures at maximum recorded speeds are considerably lower. Peak power should be at least three times swimming power at maximum speed, since refilling takes longer than the jet, but actual ratios range from 33 for *Nautilus* to 7.5 for *Illex*. Thus, the actual $P_{o,max}$ for *Illex* is 60 times that for *Nautilus*. This probably reflects the fact that *Nautilus* depends exclusively on anaerobic power for repeated escape jets and cannot restore energy substrates fast enough. Acceleration from a single escape jet by a well-rested animal would be a better measure of anaerobic power, but good data

Table 2. *Performance, pressures and power of jet-propelled invertebrates*

	Scallop[a]	Medusae[b]		Nautilus[c]	Sepia[c]	Loligo[c]	Illex[c]	I/N*
Peak pressure (kPa)	0.6	0.06	–	11	25	30	50	5
Peak power ($P_{o,peak}$, W kg^{-1})	2.8	–	–	3.3	12.5	30	45	14
Maximum speed (u_{max}, m s^{-1})	0.5	–	–	0.3	0.65	1.05	1.4	5
Average pressure (kPa)	0.4	–	–	0.46	5.5	4.8	6.6	–
Power out ($P_{o,max}$, W kg^{-1})	2.8	–	–	0.10	1.0	3.7	6.0	60
Power in ($P_{i,max}$, W kg^{-1})	10	–	–	1.0	2.6	10.7	14.4	14
Efficiency (P_o/P_i, %)	28	–	–	10	38	34	42	4
Critical speed (u_{crit}, m s^{-1})	–	0.09	0.15	0.15	0.45	0.75	0.85	6
Average pressure (kPa)	–	0.02	–	0.23	1.2	1.6	2.1	–
Power out ($P_{o,crit}$, W kg^{-1})	–	0.006	–	0.036	0.10	0.73	1.07	30
Power in ($P_{i,crit}$, W kg^{-1})	–	0.28	0.28	0.47	1.5	4.8	6.0	13
Efficiency (P_o/P_i, %)	–	2	–	8	7	15	18	2
Optimum speed (u_{opt}, m s^{-1})	–	–	–	0.10	0.35	0.40	0.65	7
Average pressure (kPa)	–	–	–	0.15	0.54	0.46	1.4	–
Power out ($P_{o,opt}$, W kg^{-1})	–	–	–	0.02	0.03	0.11	0.57	30
Power in ($P_{i,opt}$, W kg^{-1})	–	–	–	0.31	1.1	1.9	4.4	14
Efficiency (P_o/P_i, %)	–	–	–	6.1	2.8	5.9	13	2
Power at rest (W kg^{-1})	0.12	0.13	0.13	0.06	0.39	0.56	1.0	17

* *Illex* to *Nautilus* ratio.
Sources: (a) Moore and Trueman (1971) (pressure and power output, *Chlamys opercularis*), Livingstone *et al.* (1981) (metabolism, *Placopecten magellanicus*); (b) DeMont and Gosline, 1988*b* (pressure, *Polyorchis penicillatus*); Larson (1987) (metabolic rates, *Stomolophus meleagris*); (c) data derived from Figs 1 and 2.

are difficult to obtain. Much of the power for swimming at 'burst' speeds must come from aerobic muscle in *Illex*.

In *Illex*, $P_{o,crit}$, the maximum aerobic power output at the critical speed, is 30 times and $P_{1,crit}$ is 13 times those of *Nautilus*. From muscle masses and histological data (Hochachka *et al.* 1978; Mommsen *et al.* 1981; Bone *et al.* 1981), we estimate that the total mass of muscle mitochondria is 11 times higher in *Illex* (6.5 % of body mass *vs* 0.6 % of body mass), which accounts for most of the squid's extra power. There is also a 2.3-fold increase in efficiency, which accounts for most of the difference. This increase probably reflects the increased loading of squid muscles, where maximum stress was estimated at 250 kPa (O'Dor, 1988*b*), compared with 110 kPa in *Nautilus*, which may be limited by funnel design.

Aside from the patent funnel, the secret of jet power seems to be MORE: more muscle, more mitochondria, more water pumped to extract more oxygen, more distance covered to catch more food. There is no evidence for any fundamental changes in the properties of the power-generating machinery over the continuum or the hundreds of millions of years. Before turning to the critical question of how to keep the machinery working, however, we should consider how less became more along the continuum.

Sepia

Like *Nautilus*, *Sepia* has a chambered shell for buoyancy, but its light-weight, internal shell is less depth-resistant and occupies about half the mantle volume that the tubular pump could utilize. *Sepia* also have less muscle devoted to jet propulsion. Wells and Wells (1991) imply that, physiologically, it is just a floating octopus, using its jet as a secondary mode of locomotion. The only difference is that *Sepia*'s primary mode is undulatory swimming with a skirt of fin, while *Octopus*'s is walking with its arms. Our data for *Sepia* are the weakest, being based on an oxygen–speed relationship from a swim-tunnel combined with average pressures for hovering, cruising and escape swimming from separate experiments (Wells and Wells, 1991), with speeds estimated from swim-tunnel work. However, the results in Table 2 support the view that the jet is secondary and used primarily for escape. The apparent efficiencies at *Sepia*'s critical and optimal speeds are much lower than those of squids and even lower than those of *Nautilus*, because most of the oxygen consumption is supplying the fins. At its maximum speed *Sepia*'s P_o is 170 % of *Illex*'s at the same speed, but at its critical and optimal speeds its P_o values are only 30 and 15 %, respectively, of *Illex*'s. Fins clearly contribute more at low speeds. We estimate from electromyographic data on *Sepia* (Kier *et al.* 1989) that maximum fin-wave travel is about $0.15 \, \mathrm{m \, s^{-1}}$, which is comparable to rates in *Loligo opalescens* (O'Dor, 1988a).

Undulatory waves must move backward faster than the animal moves forward to be effective, so the speeds cephalopods can attain with fins are probably limited by the shortening speeds of their obliquely striated muscle in a muscular hydrostat system (Kier, 1988, 1989). Fishes using similar fin undulations have no such limits because bone–muscle systems with fractional mechanical advantages make the waves move faster than the muscles. However, O'Dor (1988a) pointed out that finning can complement jetting up to average speeds that are nearly double the wave speed because jetters slow down during refilling for part of each cycle. Jetting can also complement finning by providing acceleration during manoeuvres to avoid propeller slip. *Sepia* takes full advantage of its fins and jet for manoeuvring and to move nearly as efficiently as *Nautilus* at twice the speed. However, it is still not in the same league as real squid for speed and range.

Loligo

Although *Loligo*'s fins account for over one-third of its total muscle mass, compared to less than one-quarter for *Illex*, it has stepped over the line to become a real squid. It uses fin undulations at low speeds, for a u_{opt} only slightly higher than that of *Sepia*, but rolls up its fins to reduce frictional drag for higher speeds. It has sacrificed buoyancy for reaction mass by eliminating the shell, which probably accounts for much of the 50 % increase in COT over that of *Sepia*. While it cannot keep up with *Illex*, its u_{crit} is higher than *Sepia*'s u_{max}. These three have similar P_o/P_i ratios at u_{max}, so the value of the ratio relative to that of *Illex* at other speeds could be considered as a measure of dependence on jetting. This suggests th

jetting accounts for about 20 and 40 % of locomotor power at u_{opt} and u_{crit}, respectively, in *Sepia* and 50 and 90 %, respectively, in *Loligo*.

A tricky problem for committed jetters is the linkage between jetting and respiration (Wells, 1990). Once the mantle becomes an integral part of the jet engine it is impossible to breathe without moving nearly half of the body mass. This may be the critical factor that drives squids towards their power-hungry life-styles. As long as all those circular, radial and longitudinal muscles are stretching all those springs (Gosline and Shadwick, 1983) in a complex muscular hydrostat (Kier, 1988), they might as well go somewhere and find a bite to eat. There are dramatic physiological realignments associated with this commitment.

Respiratory and circulatory correlates

Committed jetters differ from most aquatic animals in that their exercise levels are not restricted by their access to oxygen. The volume of water pumped past the gills of swimming squids for reaction mass is so large that oxygen extraction is only 5–10 %; even in hypoxia or recovery from exhausting exercise the maximum is 17 % (Shadwick *et al.* 1990; Wells *et al.* 1988). Because it can decouple locomotion and respiration, *Sepia* is more like *Octopus* with normal extraction rates in the 35–45 % range, and occasionally higher. When swimming, *Nautilus* extracts only 5 %, like other committed jetters, but this can increase to 40 % at rest in hypoxic conditions (M. J. Wells, personal communication). The retention of separate high- and low-pressure pumps accounts, in part, for this flexibility, but the properties of the gas transport pigment, haemocyanin, also contribute.

The constraint on power output in squids is clearly not oxygen uptake, but oxygen transport in the blood. Although 'a considerable amount of evolutionary refinement of haemocyanin-oxygen transport appears to have occurred within the Class Cephalopoda' (Mangum, 1990), it is still the limiting process. The acellular protein, at concentrations approaching a gel in the blood (approximately 20 % w/v in *Loligo pealei*, Mangum, 1990), carries only about half the oxygen of the cellular haemoglobin-based bloods of vertebrates. A comparison of the power data above with the properties of haemocyanins from similar species (Fig. 3, Brix *et al.* 1989) makes it clear that these refinements have probably occurred in different ways in different groups. The authors group the cephalopod haemocyanins into three categories: (1) sluggish (lowest P_{50} and n_{50} values), (2) active and (3) *Sepia* (highest P_{50} and n_{50} values). This cannot simply be an activity cline, but must also reflect other adaptations, perhaps for being relatively active in hypoxic waters. Given *Nautilus*'s flexibility in oxygen extraction characteristics, it is tempting to suggest that its primitive low-P_{50}, low-n_{50}, no-Bohr-shift haemocyanin was as good as any and that, rather than optimizations, the differences are accidental mutations that are coped with. However, there is an impressive clustering of rather distantly related 'real squids' at what could be an optimum compromise for mass transport of oxygen from normoxic water. The truth is we still do not know enough about what these animals can do to be sure how good their adaptations are, and we
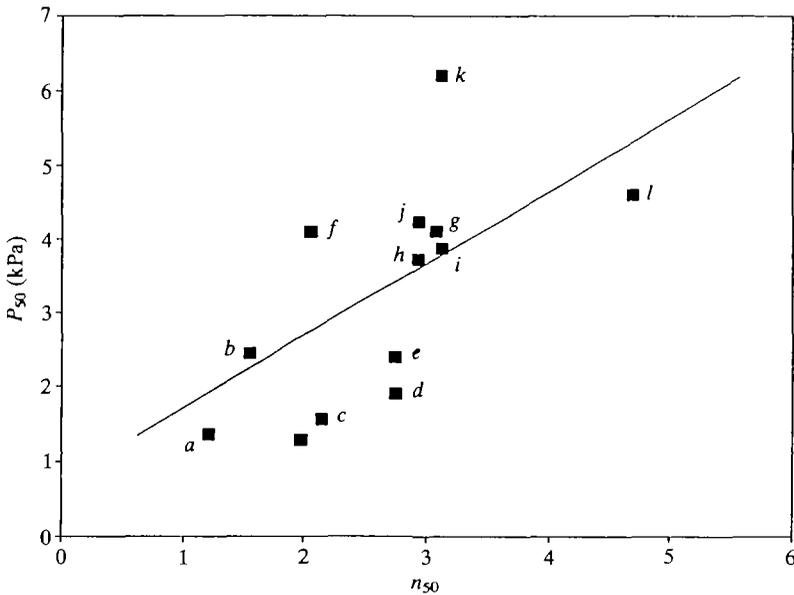
Fig. 3. The relationship between affinity and cooperativity in cephalopod bloods at habitat temperatures. (a) *Octopus dofleini*, (b) *O. vulgaris*, (c) *O. macropus*, (d) *Architeuthis monachus*, (e) *Nautilus pompilius*, (f) *Loligo vulgaris*, (g) *L. pealei*, (h) *Notodarus sloani philippinensis*, (i) *Sepioteuthis lessoniana*, (j) *Todarodes sagittatus*, (k) *Sepia latimanus* and (l) *S. officinalis*. The line is a regression: $n_{50}=1.01P_{50}-0.735$ with $r^2=0.6$. (From Brix et al. 1989.)

know even less about the actual *in vivo* blood parameters for most species (Pörtner, 1990).

Squids appear to use various forms of physiological 'magic' to bypass the limitations of haemocyanin. As swimming speeds increase, the calculated power output needed for a squid heart at 12°C to deliver the required volume of oxygen-carrying blood rises to over $40\,\mathrm{W\,kg^{-1}}$, exceeding the power output of mammalian hearts at 37°C, despite the fact that the heart becomes synchronized with the jet (Shadwick et al. 1990). The authors suggest that the mantle muscular hydrostat may, by a mechanism still not clarified, do much of the circulatory work, but they and others (Wells et al. 1988) also suggest that a major fraction of the oxygen consumed (20%?) comes directly through the particularly thin and fragile skins of squids. The most aerobic muscle fibres in squids (containing 50% mitochondria) are located in thin layers on the well-flushed inner and outer surfaces of the mantle (Bone et al. 1981; Mommsen et al. 1981). The first studies of blood gas parameters in cannulated, exercising squids (Pörtner, 1990; Pörtner et al. 1991) suggest that the functional properties of the haemocyanin are optimized to permit both the maximal removal of CO_2 from muscle mitochondria and the maximal delivery of O_2 per circulatory cycle, as indicated by the maintenance of a minimal venous reserve. Exercising muscle cells appear to retain protons to defend the transport

▐▶perties of the blood, occasionally reaching intracellular pH values as low as 6.8, while blood (anterior vena cava) pH values typically *increase*, as seen in exercising *Octopus* (Houlihan *et al.* 1986). Clearly more research on these athletes is required to understand how this system really works in extreme exercise, but it is interesting that the most powerful jetters may have reverted to the direct oxygen extraction system of the medusae. Even *Nautilus* may use this approach for its relatively thin, well-flushed and aerobic funnel.

The function of the circulatory systems in squids has clearly changed dramatically from that of *Nautilus* and the ancestral cephalopods. Assuming a blood volume of 15% of body mass (it is almost certainly more, as this is the amount one can collect) and an O_2 content of 2.0 vol%, blood O_2 would supply a *Nautilus* at $P_{i,max}$ for 1 min, which is about as much activity as it is likely to exhibit in 1 h (O'Dor *et al.* 1990*b*). Assuming a blood volume of 5% of body mass (it may be less) and 4.3 vol%, *Illex*'s blood O_2 would only last for 3 s. With *Nautilus*'s lifestyle it can apparently afford to carry around blood as an O_2 reserve; a heart rate much lower than the jet rate (M. J. Wells, personal communication), its low P_{50} and its lack of a Bohr shift all support this view. Squid, in contrast, use every bit of their anatomy to the limit to maximize power density, wringing out every watt of power while minimizing their drag.

Metabolic correlates

Although the efficiency of ATP conversion to pressure–flow power by muscle contraction increases between *Nautilus* and *Illex*, the committed jetters, an analysis of fin P_o and P_i is required to clarify the trend along the continuum. However, such a large increase in power output *must* involve increased rates of substrate breakdown, both anaerobically and aerobically. Octopine dehydrogenase activity, which reversibly links pyruvate to arginine as an alternative to lactate formation, increases from about 80 mmol min^{-1} kg^{-1} muscle in *Nautilus* to several hundred mmol min^{-1} kg^{-1} muscle in squids; alpha-glycerophosphate dehydrogenase activity increases from 2–5 to 20–50 mmol min^{-1} kg^{-1} muscle. Ratios of these activities have been used (Baldwin, 1982, 1987; Storey and Storey, 1983) to predict capacities for both 'sprint' and 'distance' exercise for a spectrum of cephalopods and their component parts. There are a number of inconsistencies in these data, but general trends correspond to measured performance. While there appear to be no major surprises in the pathways themselves, Storey and Storey (1983) indicate a shift in their regulation from octopuses (primarily AMP-based) to squids, which have an additional NADH-based regulation. This should couple energy consumption to *aerobic* energy production more tightly and may also influence the way squids activate their power delivery systems during rest-to-work transitions (Hochachka *et al.* 1983).

These most recent reviews (Storey and Storey, 1983; Hochachka *et al.* 1983) focused on carbohydrate metabolism, recognizing that cephalopods have little ▐▶acity for metabolizing or storing lipids (Mommsen and Hochachka, 1981). The

best data on glycogen reserves (24 mmol glucose kg^{-1} muscle) allow us to calcula█ that *Sepia* can manage aerobically at $P_{i,crit}$ for 3.7 h or at its maximum anaerobic power output for 70 s (assuming a maximum power cycle is one-third of $P_{o,peak}$, efficiency is 18 % and 3 anaerobic ATP molecules for 36 aerobic ATP molecules). *Illex* would last 1.2 h (aerobic) or 20 s (anaerobic) if its glycogen stores are as large. Carbohydrate stores alone seem to be inadequate for squids.

There is increasing evidence that amino acids are key substrates, particularly in the most active cephalopods. Oxygen/nitrogen ratios in *Octopus* vary from 10 to 35 (Boucher-Rodoni and Mangold, 1985), but *Illex* maintains a constant ratio of 15 over its full aerobic range (Hoeger *et al.* 1987), indicating a high proportion of amino acid fuel. As in insects, proline is an important substrate and arginine can also enter the Krebs cycle *via* 2-oxoglutarate (Mommsen and Hochachka, 1981). Meeting the demands of long-range squids like *Illex* and *Ommastrephes*, however, must require pathways for processing the mixed amino acids that result from the breakdown of proteins, which are ultimately the only permanent store of amino acids. Much work remains to be done on the efficient integration of mixed amino acids as substrates for aerobic metabolism.

The size of glycogen reserves appears to be linked to and limited by the amount of muscle phosphagen, arginine phosphate, because the principal anaerobic end-product, octopine, is retained in muscle as a 'depository' of arginine and pyruvate. Recovery from 'oxygen debt' seems to be largely a matter of rephosphorylating arginine and recycling pyruvate to glycogen *in situ* (O'Dor, 1988*b*). In *Sepia*, glycogen and arginine concentrations are approximately stoichiometric and decline in parallel during exhausting exercise or hypoxia as octopine forms (Storey *et al.* 1979). In extremes of exhaustion and hypoxia, *Sepia* muscle octopine levels rise to 13.4 mmol kg^{-1} and up to 18 % of tissue arginine is lost into the blood as octopine which may be processed in other tissues. However, this 'Storey' cycle (Storey *et al.* 1979) appears to be less important than the vertebrate Cori cycle. *Illex* swum to collapse at just supracritical speeds reached average tissue octopine levels of 8 mmol kg^{-1} (maximum 25 mmol kg^{-1}), and showed no depletion of the sum of arginine metabolites in the tissue and no increase in blood octopine. These animals retained protons in direct proportion to octopine production (Pörtner *et al.* 1991), indicating that, except in extreme duress, octopine is recycled within muscle. This anaerobic 'buffer' may be a unique adaptation of the molluscan system to maximize both aerobic and anaerobic performance in cells with a relatively long, enforced rest period in each duty cycle, resulting from the refilling requirement of the jet. This appears to be a question ripe for nuclear magnetic resonance studies and certainly implies strategies for maintenance of high-energy phosphate pools different from those of vertebrates (Hochachka, 1985).

Conclusions

The cephalopods have come a long way as athletes since *Nautilus* but, like most machinery tuned for maximum power, they have paid a high price in efficien█

▶e peak performers among them are a fascinating parallel to athletic vertebrates and deserve to be studied, if only to illustrate that vertebrate optimal adaptations are local, not global, optima. Squids have not been easy animals to work with, but techniques now exist that allow whole-animal studies in the laboratory (O'Dor *et al.* 1990*a*; O'Dor and Shadwick, 1989). It is even possible to buy them 'off-the-shelf' (Hanlon, 1990). Monitoring jet pressure as an index of power output allows laboratory observations to be tested directly in nature. We are currently examining data from experiments using acoustic telemetry of jet pressure and depth from the large Azorean *Loligo forbesi* to determine how inefficient real squid are in nature (O'Dor *et al.* 1991). The preliminary answer seems to be 'not very'. These squid appear to spend much of their time 'soaring' on mid-water currents, and pressure records suggest that they may not use much more energy here than when resting on the bottom. The prediction of Hochachka *et al.* (1983), that aerobic scope in squids was underestimated because 'squid in captivity may not reduce their metabolic rates down to the basal levels they may routinely reach in nature', seems to be true for *Loligo*, but we still need to 'road test' a real rocket like *Ommastrephes*.

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