

SPEED, JET PRESSURE AND OXYGEN CONSUMPTION RELATIONSHIPS IN FREE-SWIMMING NAUTILUS

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Summary

1. Neutrally buoyant, ultrasonically telemetering, differential pressure transducers were attached to *Nautilus pompilius* L. to record mantle cavity pressures while the animals were induced to swim in a flume in response to food.

2. Synchronized videotapes and computer data files showed that jet pressures (p , Pa) increased linearly with swimming speed (u , m s^{-1}), $p=1565u-8$.

3. Because of their stereotyped responses to food, *Nautilus* could be induced to produce similar pressures in 51 respirometers, where oxygen consumption (\dot{V}_{O_2} , ml kg^{-1}) increased as a power function of pressure, $\dot{V}_{\text{O}_2}=3.85p^{0.584}$.

4. Combining these equations gave an oxygen consumption–speed relationship, $\dot{V}_{\text{O}_2}=283u^{0.584}$. We used this equation to show that the cost of transport for *Nautilus* is dramatically lower than that for squid and, at speeds below 0.05 m s^{-1} , even lower than that of an undulatory swimmer, the salmon.

5. Calculated power inputs and outputs suggest that squid have increased their power density (W kg^{-1}) 100-fold over their ectocochleate ancestors, and that *Nautilus* is very efficient in its low-speed, low-energy environment.

6. These laboratory ‘calibrations’ are a basis for field studies using telemetered pressure data to develop energy budgets for this unique living fossil as a reference for comparing the energetic requirements of ancient and modern seas.

Introduction

As the most primitive living cephalopod, *Nautilus* provides unique insights into both the evolution of the advanced jet-propulsion systems of modern shell-less coleoids and the life-styles of a vast array of shelled cephalopods that dominated the seas for hundreds of millions of years. We know something of the activities of *Nautilus* in nature, which can include daily vertical migrations of hundreds of metres and horizontal journeys of kilometres per day (Saunders and Ward, 1987), and the locomotory principles involved have been reasonably well detailed

Key words: *Nautilus*, jet propulsion, locomotion, bioenergetics, cephalopods, evolution, metabolic rate, swimming, power density.

(Chamberlain, 1987). Resting metabolic rates in *Nautilus* are much lower than those of comparably sized coleoids (Wells, 1990), suggesting that a conservative strategy accounts for the much longer life (Saunders, 1984), lower fertility (Arnold and Carlson, 1986) and iteroparous life-history (Saunders, 1984), which differ dramatically from those of the coleoids.

Since *Nautilus* is a purely jet-propelled animal, and all the locomotory and ventilatory work that it does is a result of pressurizing the water in its mantle cavity, a cannula placed in the ventral postbranchial chamber (see Fig. 1) can detect pressure produced by movements of the funnel wings in quiet respiration and slow swimming or by head retractions during rapid swimming (Packard *et al.* 1980). This makes it ideally suited for a study of a natural energy budget using ultrasonically telemetering, differential pressure transducers developed for squid (Webber and O'Dor, 1986). The present work was undertaken to 'calibrate' *Nautilus* for such a study so that telemetered jet pressure data can be interpreted in terms of oxygen consumption and speed as well as 'activity'.

Materials and methods

Animals

Nautilus pompilius L. were trapped at depths of 150–300 m off the sunken barrier reef east of Port Moresby and carried in cold boxes back to the Motupore Island Research Department of the University of Papua New Guinea. Fifty animals ranging from 0.450 to 0.650 kg total mass (0.300–0.450 kg flesh mass) were held in refrigerated aquaria at 15–20°C and observed during a 3-month period. Mantle cavity pressures were recorded from five free-swimming *Nautilus* averaging 0.614 kg total mass and 0.456 kg flesh mass.

Telemetered pressures

Mantle cavity pressures were monitored via cannulae and a differential pressure transducer/ultrasonic transmitter (Production model V3D-1L-R, Vemco Ltd, Shad Bay, Nova Scotia, Canada; similar to prototypes described in Webber and O'Dor, 1986) attached to the shell, as shown in Fig. 1. Transmitters weighed 25 g in air, but were covered with a cowling carved from 7 g of a foam-filled fishing float which made them neutrally buoyant and improved streamlining. One side of the differential transducer was left open to ambient pressure to compensate automatically for depth changes. At zero differential pressure an ultrasonic pulse was transmitted every 450 ms, while at a steady pressure of 10 kPa the interval was reduced to 30 ms. Pressure is linearly related to frequency and varying pressures are integrated as the voltage charges a capacitor. Ultrasonic pulses were detected with a Vemco VR-10 hydrophone, converted into TTL signals with a VR-60 receiver and intervals recorded with a timing routine on an Apple IIc computer. As seen in Fig. 2, this method allows pressure records to be reproduced which have low temporal resolution for low-pressure respiratory changes but provide much higher resolution of high-pressure jets. The maximum pressures during jets

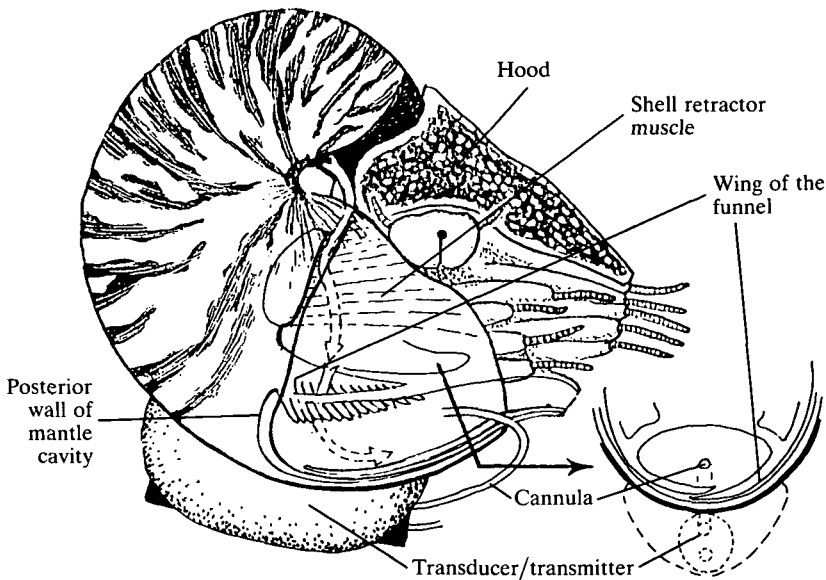


Fig. 1. Ultrasonically telemetering differential pressure transducers weighing 25 g in air were glued to the shells of *Nautilus*, enclosed in a 7 g buoyant cowling to make the whole assembly neutrally buoyant and to minimize added drag. Cannulae were bent around the lip of the shell to measure mantle cavity pressures during free swimming.

are underestimated to some extent, but the area under the pressure curve is representative of the total pressure produced over time, since the electronic package integrates the voltage produced by the strain gauge in the pressure sensor.

Swimming speed

Swimming speeds were determined by videotaping with a Panasonic WV-D5000 camera and an AG-2400 recorder with a 0.1 s time base superimposed. Three different facilities were used. (1) A large shallow tank (2.0 m × 1.0 m × 0.3 m deep) viewed from above. Unfortunately, available equipment would not cool this tank below 22°C, which is too warm to produce full activity in *Nautilus*. (2) A 1.0 m × 0.5 m × 0.5 m glass aquarium cooled to 15–17°C and observed from the side, which was too small to record full activity. (3) This aquarium was divided in half with a 0.5 m glass plate centred along the long axis, and a hand-turned outboard motor propeller was installed on the back side to produce a current. Upstream baffles produced a reasonably uniform flow profile in a 0.5 m (long) × 0.25 m (wide) zone in the front half of the aquarium. Dozens of small plastic vials, weighted with stones to make them neutrally buoyant, were released in the flume to allow flow speeds to be calculated from video recordings. Current speeds up to 0.5 m s⁻¹ were possible, and hand-cranking allowed the operator to push the animal gradually to higher speeds. Vertical stripes on the centre divider enhanced the optomotor response and usually held the animal in the zone.

Videotapes were synchronized with computer pressure data using computer-generated audio cues, allowing swimming speeds to be correlated with jet pressures. Segments of tape in which the animal swam steadily in the uniform zone were analysed. The speeds of bottles passing in front of, behind, above and below the animal were averaged to estimate relative speed. A typical speed:pressure datum is based on 10 bottles and 20 s of pressure record. Speeds in the static tanks were calculated directly from distance travelled and the time base for periods of steady movement. Average pressures (p) were calculated from the integrated area under the pressure curve.

Respirometry

Plexiglas cubes (0.25 m), divided in half, were modified for use as respirometers. The rear half housed an immersion cooler and the hydrophone, while the front half housed the *Nautilus*, isolated in 5 l of sea water. Floating lids held the oxygen electrode (either an Orion 97-08 or an EIL 7130) above a magnetic stirring bar in one corner, which kept the entire volume well mixed. *Nautilus* activities are so stereotyped that they would repeat entire behaviour sequences in a 5 l respirometer, even though they could go nowhere. Oxygen consumption and pressure data were synchronized to provide a direct measure of the metabolic cost of producing pressure.

Results

Swimming behaviour

Our observations of 50 *Nautilus* over a period of 3 months, including 6 animal-days of continuously monitored activity, generally confirm Zann's (1984) observations of bouts of swimming lasting a few minutes followed by rest (sleep?) periods about 10 times as long on an essentially random schedule which varied between individuals. Sleeping animals typically attached themselves to the tank walls with a few cirri and, if disturbed, usually withdrew into their shells rather than attempting to escape, making it impossible to have animals perform on demand. We had to adapt our experimental schedule to the animal's cycle. As the waking periods approached, a few cirri were extended, apparently to sample the environment, and, if bits of fish or lobster flesh were placed near the cirri, they produced a general arousal. Aroused animals extended all their cirri and explored the tanks by swimming about head first. When a current was produced in the flume, it was usually possible to get animals to swim head first against the current for several minutes; presumably this behaviour would lead an animal to food in nature. If animals were then given a few grams of food, they took it and moved rapidly away from the source, swimming backwards. In this orientation *Nautilus* exhibits a strong optomotor reflex and would hold its position against currents of up to 0.3 m s^{-1} for several minutes in front of the vertical bars in the flume. This may be the response that allows *Nautilus* to avoid being swept away by currents and remain near the reef face in nature (Saunders and Ward, 1987).

This suite of feeding-related behaviour seemed to be quite stereotyped, occurring reasonably reliably whenever the stimuli were applied after the animal had had adequate time to recover from the last activity bout. Similar patterns of activity were played out whether the animal was in the flume tank, the large static tank or the small respirometers. Thus, comparable levels of activity could be induced and quantified using the differential pressure transducer/transmitters under the three different circumstances.

Jet pressure

The average pressure (p , Pa), calculated from the area under the pressure curves, can be used to calculate work or power output and has been shown to be highly correlated with metabolic rate in squid (Webber and O'Dor, 1986). Fig. 2A shows a typical pressure record of a *Nautilus* swimming freely in the flume as reconstructed from data telemetered from a transducer/transmitter. It illustrates periods of steady swimming at various speeds, periods of rest while holding on to the side, and a sudden spontaneous burst of activity including a near-maximal jet (such bursts were relatively rare). The expanded trace in Fig. 2B contrasts respiratory pressures produced by the funnel wings with the powerful jets produced by head retraction and illustrates the frequency of ultrasonic pulses recorded at high and low pressures. The highest jet pressure we recorded was 7.5 kPa, but, considering the time averaging of the transmitter, this is probably comparable to the maximum of 11.3 kPa reported by Chamberlain (1987). The transducer range extended from 0.1 to 10 kPa and also resolved negative pressures produced by active extension of the retractors (Chamberlain, 1990) during refilling in the sequence of jets. In calculating average pressures, the absolute values of negative pressures were added to positive pressures since both are presumably produced actively.

Jet pressure at speed

Fig. 3 shows the average jet pressures, p (Pa), associated with movement at various speeds, u (m s^{-1}), for five *Nautilus* ranging from 0.571 to 0.639 kg total mass, m_t (0.614 ± 0.028 kg, s.d.; 0.456 ± 0.028 kg flesh mass). Speeds of animals in static water never exceeded 0.12 m s^{-1} , and it was difficult to produce steady currents below 0.05 m s^{-1} . There is no evidence of any consistent difference between the two types of measurement, however, and the data have been combined to span the full range of swimming speeds. Speeds of about 0.15 m s^{-1} were not sustained for more than a few minutes without rest. Resting respiratory pressures produced swimming at about 0.02 m s^{-1} , if the animal was not holding onto something with the cirri. Regression analysis indicates that the data are highly correlated ($r^2=0.88$) to a linear model (Fig. 3):

$$p = 1565u - 8. \quad (1)$$

This linear increase is probably caused by an interaction of drag forces, which

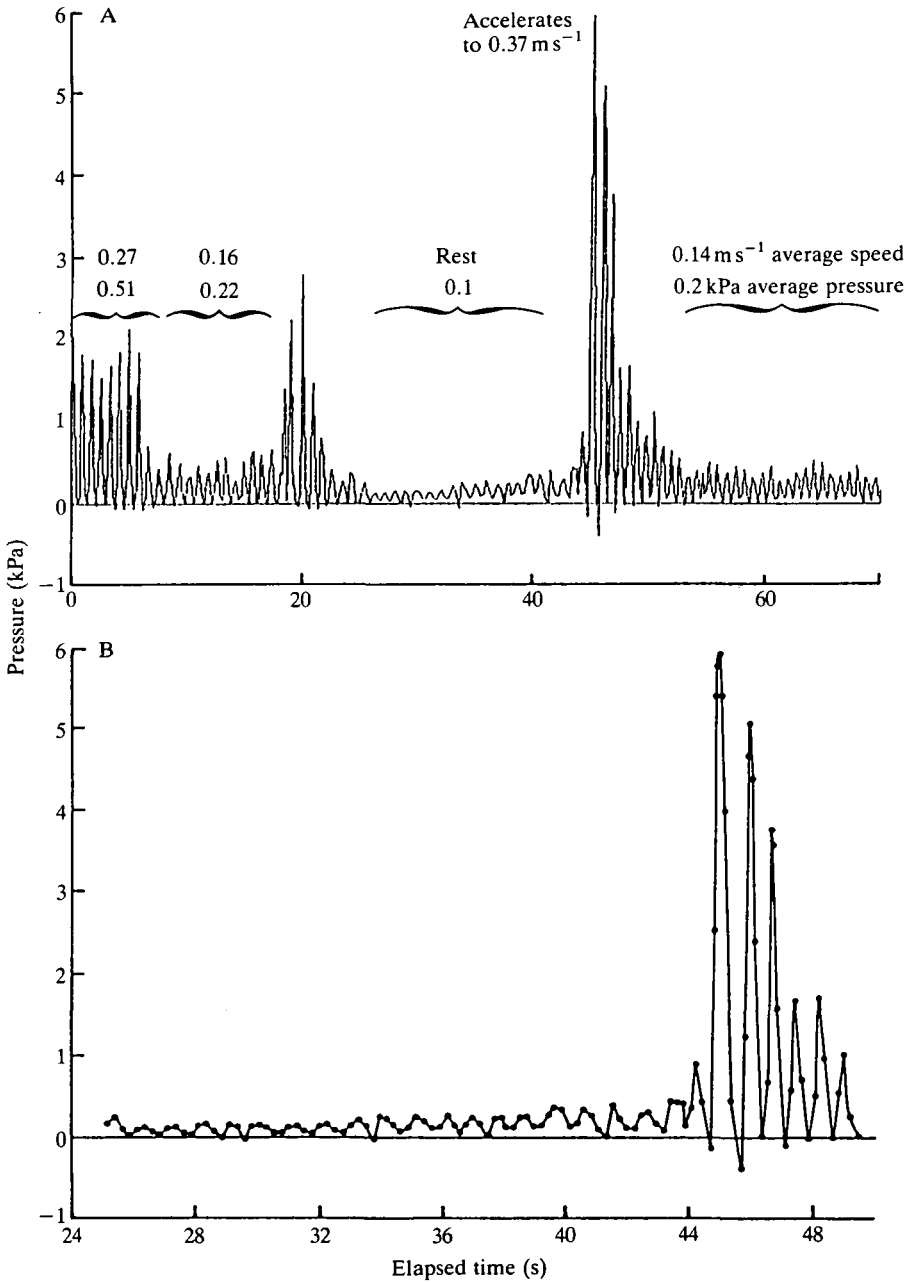


Fig. 2. (A) A pressure record of spontaneous activity of a *Nautilus* in a flume. Swimming speeds were calculated from videotapes, and average pressures calculated as the area under the pressure curve from synchronized computer files of telemetered data. (B) An expansion of the same record to show resolution of pressure data from telemetry for resting respiration and maximal jets.

diameter should be 50 % less than maximum, since the orifice must close as the wings lap over each other in low-speed swimming. Nor is it surprising that the data indicate higher speeds than predicted at higher pressures, since these jets are produced by head retraction and may well force the wings apart. The real relationship probably lies somewhere in between, since the approach used does not account for either Froude efficiency or propeller efficiency. Chamberlain (1987) indicates that films of funnels do show regular changes in diameter, as in squid (O'Dor, 1988*b*), and it should be possible to provide a much better model by relating a detailed analysis of these changes to our measured pressures and speeds. Unfortunately, we could not do this directly because we lacked the equipment to record swimming speeds and funnel orifices simultaneously, but *Nautilus* do appear to be able to alter both jet velocity and flow rate to adjust thrust and Froude efficiency.

Metabolic cost of jet pressure

Production of jet pressure requires muscular work which in most animals is ultimately fuelled from aerobic metabolism. Baldwin (1987) considers the muscles that move the funnel wings to be primarily aerobic and indicates that even the head retractor muscles have only moderate anaerobic capacity, suggesting that *Nautilus* is unlikely to be exceptional. Fig. 4 plots average jet pressures *versus* oxygen consumptions (\dot{V}_{O_2} , ml O₂ kg⁻¹ h⁻¹) over 2- to 4-min periods of activity following feeding for the same five *Nautilus* tested in the previous section.

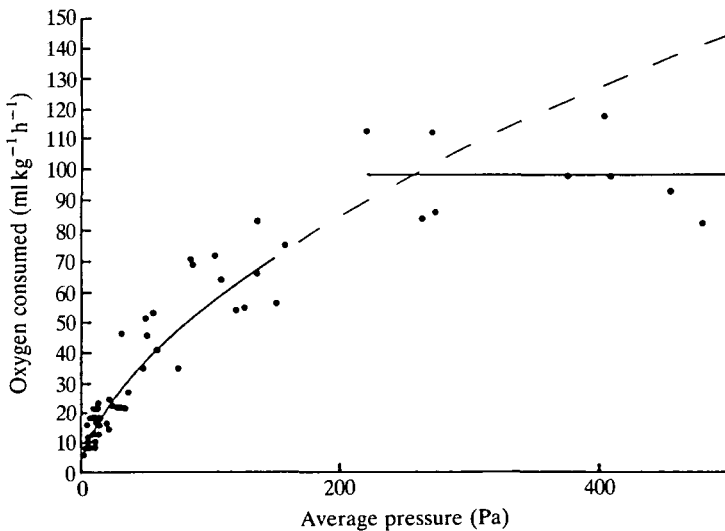


Fig. 4. The rates of oxygen consumption by *Nautilus* generating various pressures. The best-fitting power curve regression ($\dot{V}_{O_2} = 3.85p^{0.584}$) (dashed line) is calculated for pressures below 150 Pa; at higher pressures there is no correlation. The horizontal line is the estimated maximum aerobic capacity (see text).

Pressure records were continuous and oxygen measurements were made at 20-s intervals in the small respirometer. As in the flume, food-induced periods of active jetting were followed by periods of relative quiescence, both of which were included in a typical sample period, and the highest average pressures were about 150 Pa for an entire period. Bouts of extreme activity produced average pressures approaching 500 Pa, equivalent to those in the flume, which were usually followed about a minute later by drops in oxygen level equivalent to up to $115 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ over a 20-s period.

Without precise information on blood equilibration time and respirometer homogeneity, it was often impossible to relate a specific period of high pressure to a specific drop in oxygen level, but 10 fairly obvious cases failed to show any correlation between oxygen and pressure at pressures above 200 Pa. We conclude that higher pressures are probably fuelled anaerobically, in the short term. The average rate of oxygen removal in these 10 cases was $98 \pm 13 \text{ ml O}_2 \text{ kg}^{-1} \text{ h}^{-1}$ (s.d.), which is a reasonable estimate of maximum oxygen extraction rates in *Nautilus*, consistent with literature values (Wells and Wells, 1985; Redmond *et al.* 1978). The best-fitting regression equation ($r^2=0.87$), based on pressures below 150 Pa, is:

$$\dot{V}_{\text{O}_2} = 3.85p^{0.584} \quad (3)$$

Extrapolations of energy required to produce higher pressures may be reasonable, since similar extrapolations in squid ($\dot{V}_{\text{O}_2}=330p^{0.77}$, Webber and O'Dor, 1986) agree with measured oxygen debts. The pressure predicted at $98 \text{ ml kg}^{-1} \text{ h}^{-1}$ (255 Pa) would equate to a critical speed of about 0.16 m s^{-1} .

The exponent of the oxygen–pressure power curve for *Nautilus* is considerably lower than in squid. For squid exercised for long periods, the decrease in oxygen demand at higher pressures appears to reflect increasing muscle efficiency at higher tensions (O'Dor, 1988a), but this may not be the full picture in *Nautilus*. Since we were unable to induce *Nautilus* to any sustained activity beyond breathing, we cannot be sure that oxygen supply is keeping up with demand. We suspect that several minutes of recovery after a few seconds of activity probably restores most of the biochemical oxygen debt in cephalopods. Their anaerobic end-product, octopine, does not accumulate in such large quantities as lactate and is recycled more rapidly. *Nautilus*, however, appears to have the capacity to accumulate a significant oxygen reserve in its large blood space.

When the heart is cannulated and allowed to empty *Nautilus* of blood, the blood volume accounts for $15.8 \pm 1.3\%$ of flesh mass (M. J. Wells, J. Wells and R. K. O'Dor, in preparation). Assuming an oxygen capacity of $2.3 \text{ ml O}_2 \text{ 100 ml}^{-1}$, as reported by Johansen *et al.* (1978) for *Nautilus pompilius*, this means that the blood of a 0.5 kg flesh mass *Nautilus* contains at least 1.84 ml of O_2 . At an oxygen consumption rate of $10 \text{ ml kg}^{-1} \text{ h}^{-1}$, seen commonly in normoxic water, such an animal could survive for a minimum of 20 min, without opening its hood, on its blood reserve. This is a conservative estimate since total blood volume is probably larger, and we know that *Nautilus* can dramatically decrease oxygen consumption in hypoxia. Similarly, the reserve could fuel a 2-min bout of maximal aerobic

activity; since this is about as long as we ever observed *Nautilus* being active at this level, it is not really clear that there needs to be a tight linkage between oxygen supply and demand.

Metabolic cost of speed

The metabolic cost of speed in aquatic organisms is normally measured using swim-tunnel respirometry (e.g. Brett and Glass, 1973). *Nautilus* would require a very large swim-tunnel because of its large cross-section, and its low oxygen consumption and irregular swimming patterns would make satisfactory answers unlikely in such a swim-tunnel because of the large volume of water it would involve. Using pressure as an intermediate provides an alternative way of examining the cost of locomotion at various speeds. Combining equations 1 and 3 yields a relationship similar to that used for squid (Webber and O'Dor, 1986):

$$\dot{V}_{O_2} = 283u^{0.584}, \quad (4)$$

which can be used as a first approximation, at least, for comparing primitive cephalopods with modern ones and with fish competitors that presumably eliminated them from most niches.

Discussion

Although the indirect approach to the energetics of locomotion through mantle cavity pressure is less precise than direct swim-tunnel respirometry, it is, perhaps, the only approach possible given the low metabolic rate, large lateral dimensions and limited behavioural repertoire of *Nautilus*. The general pattern is clear; *Nautilus* is not a powerful animal compared with modern coleoids. The lowest oxygen consumptions ever measured in squid are double the highest in *Nautilus*. Even when estimated anaerobic equivalents at maximum pressure are included there is no overlap. The comparisons are clearest when made in terms of power per unit mass or power density.

Power density

Oxygen consumptions can be converted into power inputs (PI) using the factor 20 J ml^{-1} and pressure-flow power outputs (PO) can be calculated for jet-propelled animals such as *Nautilus* (Chamberlain, 1987) and *Illex* (O'Dor, 1988a) knowing only pressure and funnel orifice. Estimates of PO are not accurate because of the assumption of a constant orifice, as indicated in the Results, but provide a basis for comparison. Table 1 summarizes some key comparisons. Maximum PO and PI in squid exceed those in *Nautilus* by 90- and 33-fold, respectively; at critical speeds (maximum aerobic speeds) the factors are 32 and 11. At 0.16 m s^{-1} , the *Nautilus* critical speed, squid still use about three times as much power, largely to overcome negative buoyancy (O'Dor, 1988b), but they remain more efficient at pressure-flow power production. The advantage only comes to *Nautilus* at extremely low power; 80 Pa is enough to push *Nautilus* along

Table 1. Comparison of calculated power outputs (PO) and inputs (PI) and squid/Nautilus ratios at various levels of activity

		Nautilus				Squid			
	u ($m s^{-1}$)	p (Pa)	Power ($W kg^{-1}$)	PO/PI (%)	u ($m s^{-1}$)	p (Pa)	Power ($W kg^{-1}$)	PO/PI (%)	Squid/ Nautilus
PO	0.32	500	Maximum output 0.08	13	1.6	9000	Maximum output 7.2	36	90
PI			0.60				20		33
PO	0.32	500	Maximum output 0.08	13	0.16	500	Corresponding pressure 0.09	4.2	1.1
PI			0.60				2.1		3.5
PO	0.16	255	Critical speed 0.03	3.3	0.16	500	Corresponding speed 0.09	4.2	3.0
PI			0.90				2.1		2.3
PO	0.16	255	Critical speed 0.03	3.3	0.9	2300	Critical speed 0.95	14	32
PI			0.90				10.0		11
PO	0.05	80	Corresponding pressure 0.005	2.5	0	80	Minimum pressure 0.006	1.2	1.1
PI			0.208				0.500		2.4

PO/PI (%) is an index of muscle efficiency.

Squid/Nautilus power ratios indicate the relative power densities (power per unit mass) of the animals.

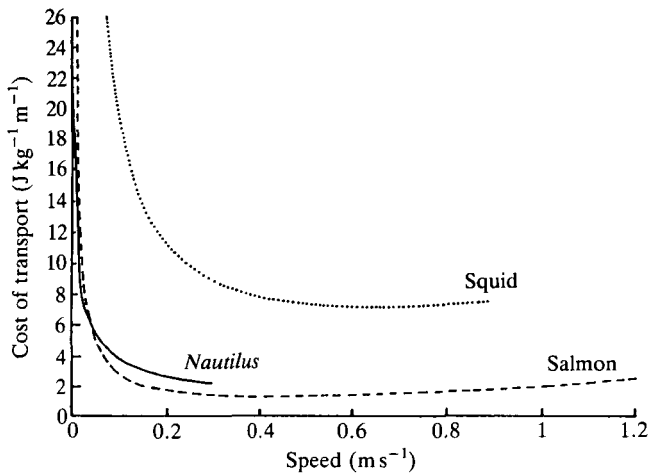


Fig. 5. Calculations of the gross cost of transport for *Nautilus* from combining equations 1 and 3 show that it is highly efficient at low speeds in comparison with other jet-propelled and even undulatory swimmers.

at 0.05 m s^{-1} , but squid use this much to respire without even moving off the bottom. Power production is about twice as efficient for *Nautilus* in this range.

Efficiency and cost of transport

Converting equation 4 to joules and dividing by speed gives the cost of transport for *Nautilus*, which is compared in Fig. 5 with similar plots for 0.5 kg squid and salmon (Webber and O'Dor, 1986; Brett and Glass, 1973). At its typical speed of 0.05 m s^{-1} (heavy breathing for a squid) *Nautilus* can search for food more economically than an undulating fish. This is remarkable considering the low Froude efficiency of jet propulsion, as illustrated by the squid. Neutral buoyancy and efficient use of muscles help. Jetting animals use more of their muscle more of the time than do undulatory swimmers (O'Dor, 1990), which should give them the edge over fish for very low-power swimming.

Packard (1972) explored examples of convergent evolution in coleoids and fishes and concluded that they have been shaped by competition. O'Dor and Webber (1986) argued that squid can only compete directly with fish by being more powerful, because their locomotor system is inherently less efficient but capable of greater power output and acceleration. If the coleoid ancestor was competitive with *Nautilus*, present results indicate that the coleoid model has proved to be quite adaptable, having increased its power density nearly 100-fold. Key elements have been the loss of the shell and a more open circulatory system, which collectively account for 42 % of the body mass of *Nautilus*. Increased muscle mass and mantle volume, as well as altered funnel design, have contributed to an increased ability to deliver power (Wells, 1990). On the input side, respiratory and circulatory systems have become completely realigned to supply dramatically

increased volumes of muscle mitochondria (Shadwick *et al.* 1990; O'Dor *et al.* 1990; O'Dor and Shadwick, 1989).

There were, of course, trade-offs in this pursuit of power. Although the buoyant shell is expensive to move around at high speed, it makes slow swimming almost free. *Nautilus* needs only to breathe to search its habitat for food. Moving the complex of muscles and collagen in the mantle walls of squid for resting respiration costs as much as cruising for *Nautilus*. Squid make 20 ml of blood deliver 33 times as much oxygen as 80 ml can deliver in *Nautilus*, but they cannot stop breathing or risk living in a hypoxic environment.

The extent to which *Nautilus* is a useful baseline for comparison with more recently evolved coleoids depends on how much like its fossil ancestors it really is. Perhaps, all the while squid have been evolving to be more powerful, *Nautilus* has been evolving to be more efficient. We suspect that this is not the case and that *Nautilus* was just lucky to occupy a niche in which its jet propulsion turned out to be more efficient than the propulsion of early undulatory fishes. Modern reef fishes often use undulatory fin propulsion, which appears to be more efficient at low speeds (Blake, 1983); perhaps this has contributed to *Nautilus* being relegated to deeper, less power-dense habitats.

Having measured locomotor efficiency in the laboratory, it should now be possible to see how this efficient machinery is applied in nature by using the ultrasonically telemetering tags to follow the activities and energy expenditures of *Nautilus* in the depths off the reef. Although we have not yet monitored jet pressures in nature, we have used the same system to monitor blood pressure and heart rate in *Nautilus* in the location where they were trapped (M. J. Wells, J. Wells, D. J. Wells, K. E. Wells and R. K. O'Dor, in preparation), which clearly demonstrates the feasibility of the approach.

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