Costs of Locomotion and Vertic Dynamics of Cephalopods and Fish[*]

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ABSTRACT

The world's oceans are three-dimensional habitats that support high diversity and biomass. Because the densities of most of the constituents of life are greater than that of seawater, planktonic and pelagic organisms had to evolve a host of mechanisms to occupy the third dimension. Some microscopic organisms survive at the surface by dividing rapidly in vertically well mixed zones, but most organisms, small and large, have antisinking strategies and structures that maintain vertical position and mobility. All of these mechanisms have energetic costs, ranging from the "foregone metabolic benefits" and increased drag of storing high-energy, low-density lipids to direct energy consumption for dynamic lift. Defining the niches in the mesopelagic zone, understanding evolution, and applying such ecological concepts as optimal foraging require good estimates of these costs. The extreme cases above are reasonably well quantified in fishes, but the energetic costs of dynamic physiological mechanisms like swim bladders are not; nor are the costs of maintaining vertical position for the chief invertebrate competitors, the cephalopods. This article evaluates a matrix of buoyancy mechanisms in different circumstances, including vacuum systems and ammonium storage, based on new data on the metabolic cost of creating buoyancy in *Sepia officinalis*.

Introduction

The purpose of this article is to emphasise the importance of the costs of buoyancy and vertical locomotion in the cephalopods in relation to their lifestyle and to compare these to

what is known about these costs in fishes. O'Dor and Webber (1986) provided the first quantitative comparison of locomotion costs of cephalopods and fish (O'Dor and Webber 1991). They focused on the use of high-power locomotion that cephalopods have evolved to become "invertebrate athletes" and the most aerobic marine animals of their size. The Atlantic short-finned squid, *Illex illecebrosus*, has the highest metabolic rates ever recorded for a 500-g poikilotherm (Webber and O'Dor 1986). Since then, telemetric measurements of jet-pressure power outputs for both nautiluses (O'Dor et al. 1993) and squid (O'Dor et al. 1994) in nature have shown that they actually expend more energy in vertical activity than horizontal.

Squid do not have swim bladders (Packard and Wurtz 1994). They have large eyes and excellent eyesight, along with fins that are used for soaring and maneuverability (Hoar et al. 1994). They also appear to be much less sensitive to acute temperature changes than most fish. We retrieve *Illex* from the ocean in 15°–18°C water, immediately immerse them in 0°C water, and transport them for 60 min to the lab, whereupon, once released in warmer water, they survive for many weeks. All of these characteristics suggest that squid, compared with most fish, are ideal candidates to exploit the vertical environment. These animals are well equipped to move through hundreds of meters of depth, competing and preying on many species of fish adapted to fairly strict vertical regimes.

Land animals can only move vertically dynamically. Various techniques, like gliding by birds and "parachuting" by spiders, allow them to take advantage of the dynamics of air itself, but there are no biological balloonists. The difference between the density of life and the density of air is too extreme (800-fold). There are organisms that make hydrogen, but, as far as we know, no life form, living or extinct, has ever conserved it for buoyancy. Buoyancy is a critical issue in the sea, where protoplasm is only slightly denser than the media and storage of small amounts of lighter material can give organisms complete vertical mobility.

There are numerous field studies that show that fish undergo vertical migrations that require adjustments to swim-bladder volume. While adjusting to a new depth, fish use hydrodynamic lift to compensate for the change in buoyancy (Gee and Holst 1992). Unfortunately, the costs of creating buoyancy and migrating vertically have never been quantified because of the difficulties in separating other metabolic costs (i.e., stress, maintenance, activity, digestion costs—specific dynamic action) from buoyancy costs over a long period (days) of buoyancy adjustment. Sticklebacks require up to 96 h of swim-bladder adjustment when abruptly exposed to percoll solutions in which water density is increased but tonicity is relatively unchanged

(Gee and Holst 1992). Goolish (1992) took the approach of subjecting killifish, *Fundulus heteroclitus*, to artificial lift or mass and observed changes in swim-bladder volume. Eventually, if costs can be quantified in the laboratory, it should be possible to use cardiac output (Webber et al. 1998), heart rate telemetry (Priede 1983), or a future alternative technique to predict buoyancy costs and vertical locomotion costs in the field; however, it is generally accepted that a good correlate to fish energetics for field applications is not currently available (Thorarensen et al. 1996; Webber et al. 1998). It will then be possible to quantify the proportion of the total energy budget that is allocated to buoyancy regulation and hydrodynamic lift during buoyancy adjustment. Until such time, we must rely on theoretical estimates of the cost of creating buoyancy in fish.

Alexander (1972) defined the bioenergetic costs of buoyancy while exploring the limitations on vertical migrations by fishes and later refined them (Alexander 1977). Gee (1983) reviewed fish buoyancy mechanisms, focusing primarily on gas bladders, and Phleger (1998) recently focused on storage of low-density lipids, particularly in deep-sea fishes. Figure 1, modified from Alexander (1990, 1993), summarises the situation. Scombroid fishes (e.g., tuna) have densities on the order of 1,080 kg m^{-3}, comparable to most life forms without special buoyancy systems, and they are well above the densities for most fish. These data tell us nothing about the cost of creating buoyancy. We

have found one buoyancy variable, measured as vacuum pressure, that can be telemetered with ultrasonic transmitters. When cuttlefish increase their buoyancy by pumping fluid out of their cuttlebones, they create a measurable vacuum. A similar process occurs in *Nautilus*, but gas pressure seems to equilibrate much faster in their large open chambers than in the minute capillary lamellae of the cuttlebone.

Vertical versus Horizontal Cost of Transport in Nature

We have tried several times to measure costs of vertical swimming using differential pressure telemetry in the controlled conditions of Dalhousie University's Aquatron Laboratory 10-m-deep tank, but 10 m is not much for animals used to the vertic scale of open ocean. This also limits us to species that we can transport to the Aquatron. However, we do have some data from field animals carrying multiplexed jet pressure–depth tags that allow us to compare the neutrally buoyant *Nautilus pompilius* with the negatively buoyant squid *Loligo forbesi*.

As mentioned above, the metabolic costs of creating buoyancy for neutrally buoyant fish is currently impossible to measure in nature. Fortunately, because jet propulsion is an excellent correlate to predict the rate of oxygen consumption ($\dot{V}o_2$) in *Nautilus* and many squids, we can telemeter jet pressure and depth and estimate vertical and horizontal swimming
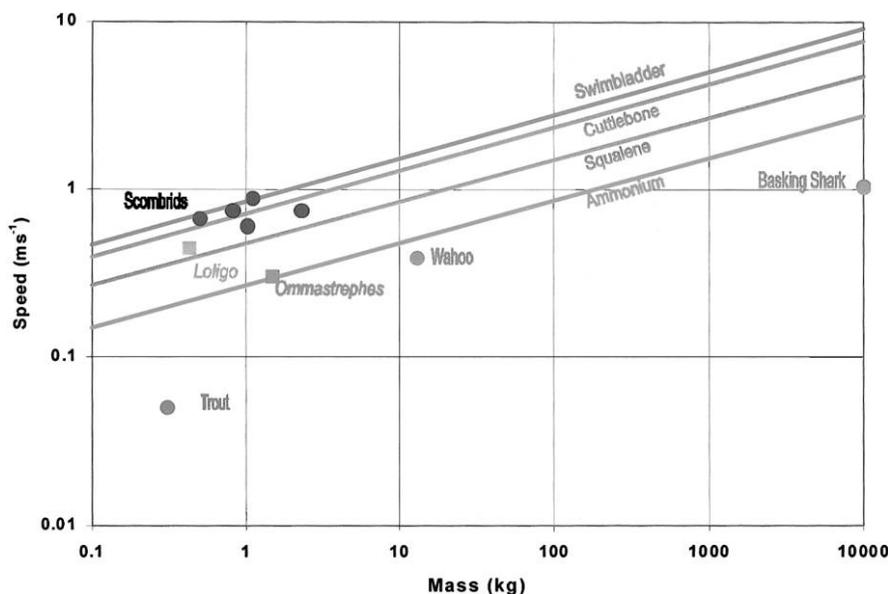
Figure 1. A graph on logarithmic coordinates of swimming speed (*u*) against body mass (*m*), with lines calculated from the equation $u > 0.34m\ 0.24(V/V_b)0.29$, where *V* is animal volume and V_b is the volume of a material required to neutralise buoyancy. Above the appropriate line, hydrofoils are more economical of energy than the buoyant material as an antisinking aid. Below, the buoyant material is more economical. The points show masses and typical swimming speeds for trout, wahoo, basking shark, and various scombroids. The scombroids have densities of 1,080–1,090 kg m^{-3}, but the others are neutrally buoyant. The original figure examined only swim bladders and squalene, but lines are added here for cuttlebone and ammonium storage. The black rectangle represents the best available data for squids from Nakamura et al. (1993) for 1.5-kg *Ommastrephes bartami* and Sauer et al. (1997) for 0.43-kg *Loligo vulgaris*. (Modified from Alexander 1990.)

costs in nature. O'Dor et al. (1993) tracked *N. pompilius* moving horizontally and vertically along reef faces in New Guinea and *L. forbesi* in deep water off the Azores, Portugal (O'Dor et al. 1994), using transmitters that monitored both depth and jet pressure. It is possible to derive reasonable estimates of vertical energetics by choosing periods when horizontal movements are minimal. Figure 2 shows depth changes of an *L. forbesi* with corresponding mantle jet pressures over 1.5 h, and Figure 3 illustrates the relationship between vertical displacement and jet pressure. These pressures can be used to predict $\dot{V}o_2$ based on laboratory calibrations. The figure very clearly illustrates that these negatively buoyant invertebrates pay a rather large price to be able to migrate vertically. Jet pressures are very high when ascending compared with descending.

A comparison of *L. forbesi* to *N. pompilius*, two species with very different lifestyles, reveals that, although these animals depend to a large extent on exploiting their vertical environment, their metabolic costs are quite different (Table 1). Climbing and diving in *Nautilus* costs almost the same as horizontal swimming. A negatively buoyant *L. forbesi*, on the other hand,

expends considerably more energy in holding its vertical position, and even more energy is consumed while vertically ascending. We maintain that these creatures use sophisticated climb and glide behaviours, timed with tidal and wind-driven currents, to reduce these relatively large metabolic costs incurred by being negatively buoyant (O'Dor et al. 1994). However, it is clear that exploiting the vertical environment requires a significant metabolic cost for a negatively buoyant animal.

Table 1 estimates the metabolic costs of various activities calculated from telemetered jet-pressure data and scaled to 0.22 kg and 15°C for comparison with the analysis in Table 4. For the negatively buoyant squid, the cost of vertical swimming is more than twice that of horizontal swimming and more than four times that for *Nautilus*. However, the actual cost of a 240-m climb is only 85 mg O_2 kg^{-1} for *Nautilus* and 324 mg O_2 kg^{-1} for the squid. If we assume a daily cycle of 12 h resting on bottom and 12 h hovering in the water column, this is 12% and 10% of their total daily budgets, respectively, and the squid can glide down for free, while *Nautilus* likely work equally hard in both directions. The big difference for squid is the cost of
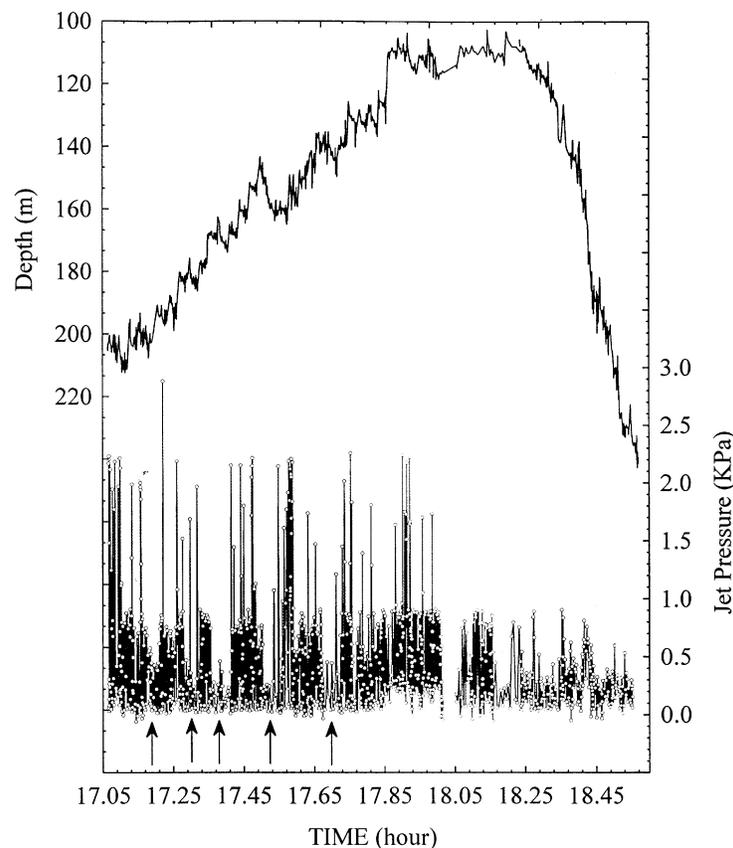
Figure 2. Depth and jet pressure changes of a 3.5-kg *Loligo forbesi* swimming up into high-density prey depths and then back down into deeper water. Note the overall increase in jet pressure during ascent and the decrease during descent. The arrows indicate very clear decreases in pressure during short periods of descent within an overall climb of 100 m.
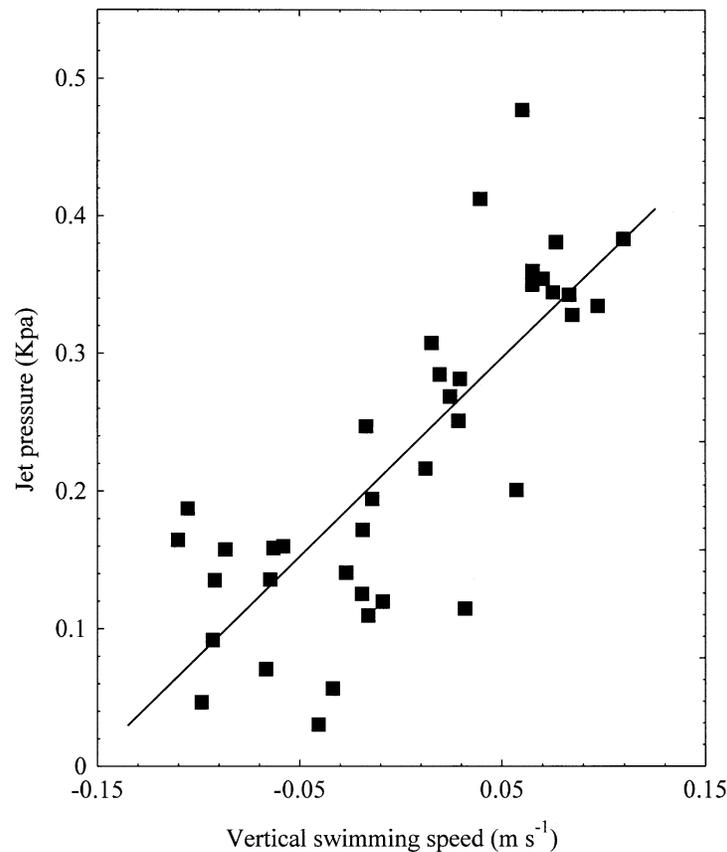
Figure 3. Average mantle jet pressure of climbing, hovering, and horizontal swimming of a 3.5-kg *Loligo forbesi* in nature. Average mantle jet pressure = 0.217 + 1.644. $N = 37$; $R^2 = 0.68$; $P < 0.0001$.

hovering, accounting for 36% of the total. Behavioural observations on the Azorean *L. forbesi* and, more recently, on the Australian reef squid *Sepioteuthis australis* indicate that they spend much of their time associated with seamounts or reefs "soaring" in upwellings created by tidal currents. Certainly, this is a familiar locomotor trick in the aerial realm, but it is much harder to monitor what animals are doing in the sea with its limited visibility.

Such behaviors put a real premium on being in the right place at the right time, however. Animals that neutralise their buoyancy can inhabit the vast, timeless, three-dimensional oceans. The problem has been that our jet-pressure tags for cephalopods and the tail-beat power output tags for fish tell us nothing about the cost of creating buoyancy. Fortunately, we have found one pressure-linked buoyancy variable that looks like it can be telemetered. When cuttlefish increase their buoyancy by pumping fluid out of their cuttlebones, they also create a measurable vacuum.

The Cuttlefish Model

Cuttlefish are an interesting intermediate between *Nautilus* and squid, and their cuttlebones are a functional approximation of fish swim bladders. They are also economically important (Nabhitabhata 1995), do well in captivity (Forsythe et al. 1994), and are well studied (Richard 1971; Boucaud-Camou 1990). During daylight they become more dense than water and bury themselves in the sediment, but at night they are nearly neutrally buoyant and hunt above the ocean floor or migrate upward in the water column to find prey (Denton and Gilpen-Brown 1961c). Buoyancy is regulated by manipulating fluid volume inside the cuttlebone, a modified internalised shell. As Figure 4 shows, the adult cuttlebone contains ~100 lamellae of calcified chitin, one above the other, held ~0.6 mm apart by pillars. The lamellae are divided into thin parallel chambers that hold cameral fluid and gas. The chambers are sealed laterally and anteriorly by the thick calcified layer forming the curved dorsal surface of the cuttlebone. This cuttlebone serves

Table 1: Metabolic rates of squid and *Nautilus* in nature, calculated from telemetered jet pressures

	Nautilus pompilius[a]	*Loligo forbesi*[b]
Resting	30	86
Hovering	30	183
Horizontal swimming	128	215[c]
Vertical swimming	128	572

Note. Values are in units of $\dot{V}O_2$ (mg O_2 kg^{-1} h^{-1}). Vertical and horizontal swimming calculated at ~0.12 m s^{-1}.

[a] Values from Table 1 in O'Dor et al. (1993), scaled to 0.22 kg with $m^{0.75}$ and to 15°C with $Q_{10} = 2$. $\dot{V}O_2 = 311p^{0.584}$, where p (kPa) is the mean jet pressure. For the neutrally buoyant *Nautilus* there was no evidence for any difference between hovering and resting or horizontal and vertical swimming.

[b] Values from Table 1 in O'Dor et al. (1994), scaled as above. $\dot{V}O_2 = 793m^{0.75}p^{0.77}$.

[c] Calculated as $\dot{V}O_2 = 99e^{0.269u}$, where u (m s^{-1}) is the squid speed (O'Dor and Webber 1991).

both as a skeleton and a buoyancy tank (Denton and Gilpen-Brown 1961*a*).

As in *Nautilus* (Ward et al. 1984; Ward 1987), the newest chamber of the cuttlebone is always incomplete and full of a solution containing potassium and sodium that is close to the concentration of seawater. In adjacent, relatively new chambers, the pressure of the gas is very low as gas slowly diffuses into the chambers following removal of liquid by osmotic pumps at the siphuncular (posterior) end of the chamber. Thus, the second newest chamber contains mostly gas space with some liquid. The third to about the tenth chambers are permeable to liquid and filled when the cuttlebone becomes dense. At densities of ~600 kg m^{-3} (approximate neutral cuttlefish buoyancy), the older posterior chambers are filled with liquid so that a horizontal position can be assumed without effort. When the animal becomes less dense, emptying these chambers tips the tail of the cuttlefish upward, a good posture for climbing and hunting. Gas pressure within the cuttlebone is less than atmospheric (~0.8 atm), and the volume of gas space changes little with external pressure. Similar to *Nautilus* (Ward et al. 1977), this buoyancy mechanism is almost independent of depth (Denton and Gilpen-Brown 1961*a*).

Posture and buoyancy are changed by altering the volume of fluid in the lamellae by exchange of cameral liquid at the siphuncular wall. This surface is separated from the viscera by a thick, yellowish, siphuncular membrane, rich in mitochondria. Cells located in this membrane pump sodium ions across the wall and out into the environment via the blood. As sodium ions leave the cuttlebone, water inside follows down the concentration gradient. The sodium pumps consume oxygen, including oxygen present inside the cuttlebone, and the gas left is primarily nitrogen (Denton and Gilpen-Brown 1961*a*).

More recent studies in *Nautilus* show that emptying of water

will only occur if the osmotic pressure between the cameral liquid and the blood within the siphuncular membrane is greater than the pressure difference between chamber pressure and ambient pressure. The cameral liquid is first made hypo-osmotic to body fluids, and water is thereafter removed by osmosis (Ward 1987). Cameral liquid osmolarity can serve as a clue to the normal depth of the animal (Ward 1987), as the hydrostatic pressure of the sea is balanced by an osmotic difference between the blood and the cuttlebone liquid, which can hold water out of the cuttlebone (Denton et al. 1961). At pressures lower than the natural habitat very little osmotic pressure is needed to empty the chambers and osmolarity rises (Ward 1987). In an aquarium, the cameral liquid is nearly isotonic to blood but with lower sodium and chloride ion concentrations. At depth, the liquid is markedly hypotonic to the seawater. If a cuttlefish changes depth, the salt concentration within the chambers also changes, so that within hours equilibrium between ambient pressure and osmotic pressure is regained (Denton et al. 1961). The siphuncular membrane is fairly impermeable to water and acts as a barrier to the penetration of liquid (Denton and Gilpen-Brown 1961*a*), but the cuttlebone is not completely impermeable, and there is continual pumping of cameral liquid.

These physiological mechanisms in the cuttlebone were originally worked out, in remarkable detail for the early 1960s, by Denton and Gilpen-Brown (1961*a*, 1961*b*, 1961*c*) at the Plymouth Laboratory, United Kingdom, primarily using cuttlebones extracted from recently dead animals. They observed nocturnal and diurnal density changes in the cuttlebones of live cuttlefish in laboratory tanks over 40 d. At night, the cuttlefish came to the surface of their tanks and became active, possibly looking for food. Weight measurements throughout the cycles confirmed that individual animals lost weight during the night and gained during the day. In daylight hours, the cuttlefish re-
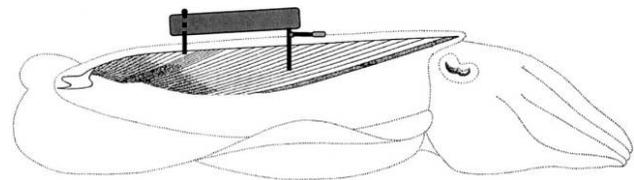
Figure 4. *Sepia officinalis*. The shell (cuttlebone) is shown in section with a typical distribution of liquid shown by stipple. The oldest and most posterior chambers are almost full of liquid, but liquid can be osmotically pumped out of the chambers to increase buoyancy and tip the tail upward. At night, sodium pumped out of the chambers by the siphuncular membrane increases osmotic pressure to exceed the hydrostatic pressure of the seawater until the excess weight of the diurnally buried animal is balanced and it rises to hunt. As illustrated, the vacuum telemetry transmitter was sealed in place in a small hole at the point of maximum depth so that it crossed the maximum number of lamellae. (Modified from Denton 1974.)

peatedly became heavy and sank to the bottom of their tanks (Denton and Gilpen-Brown 1961*c*). This regular cycle of buoyancy change makes it possible to monitor and quantify the costs of buoyancy using new technology to measure pressure changes occurring inside the cuttlebones of freely swimming cuttlefish while measuring their $\dot{V}o_2$.

Cuttlefish Buoyancy Costs

Cuttlefish obtained from cultured stocks reared at the Marine Biological Laboratory, Woods Hole (Forsythe et al. 1994), were maintained in the Aquatron for several months before experimental use. Male cuttlefish used for the experiments ranged from 0.655 to 1.09 kg. The cuttlefish were fasted approximately 24 h before and throughout the experiments to avoid the additional metabolic variable of digestion. Pressure changes occurring inside the cuttlebone were measured using a telemetering pressure tag (V16D-4H-R, VEMCO, Shad Bay, Canada). The cuttlefish were anaesthetised (Messenger et al. 1985), a small slit was made in the skin dorsally above the cuttlebone, and a 1-mm-diameter hole, 10 mm deep, was drilled into the cuttlebone. An 18-gauge needle coated in cyanoacrylate glue connected to the pressure-sensing membrane of the tag was inserted into the drilled hole, and additional cyanoacrylate glue was applied to make an airtight seal (Fig. 4). Light stitching to the tough collagenous tunic surrounding the posterior of the cuttlebone prevented the tag from rotating and breaking the seal.

After a 5-h recuperation period, the cuttlefish was placed into a 42.5 × 22.5-cm-diameter plastic cage and transported to a 230-L transparent cylindrical acrylic respirometry chamber 145 cm high × 45 cm diameter. The cage was hung from a balance on the outside of the chamber lid. The lid was then sealed except for a small hole for the line to the balance. The inflow was 65 L h^{-1}. Oxygen measurements were made by stopping the inflow and recirculating water over four pulsed polargraphic oxygen probes (ENDECO T1125). The $\dot{V}o_2$ was calculated as the decrease in oxygen concentration over time. Throughout the 14L : 10D cycle, time-lapse video recorded the balance readout to monitor changes in apparent weight (buoyancy) when the animal was at rest and active as indicated by rapid changes in balance readings. Cuttlebone pressure was telemetered acoustically four to five times per second and logged to a computer through a VR-60 receiver (VEMCO) via a hydrophone attached to the chamber. Pressures were averaged every 15 min and weights recorded at approximately 10-min intervals. The $\dot{V}o_2$ was measured for 2 h from 1400 to 1600 hours and 0200 to 0400 hours by measuring oxygen concentrations every 5 min.

Oxygen consumed in activity was distinguished from oxygen consumed for creation of vacuum using a "time-not-resting" activity index (DeMont and O'Dor 1984). Linear regressions provided average pressure changes from maximum to mini-

mum pressures. The pressure regressions were combined with the activity index in a multiple regression against $\dot{V}o_2$ to partition total oxygen consumption among rest, movement, and vacuum creation. Details will be presented elsewhere (Aitken et al. 2000), but Figure 5 shows the longest continuous observation of a 1.09-kg cuttlefish at 20.5°C. As expected, activity was consistently higher at night, and vacuum (negative pressure) increased by night and decreased by day. This was reflected in weight decreases by night and increases by day, as well as higher $\dot{V}o_2$ at night. Weight (in water) and $\dot{V}o_2$ of the cuttlefish showed a decreasing trend over the experimental period, while vacuum showed an increasing trend. The results of the change in vacuum, weight, and $\dot{V}o_2$ during three diurnal cycles are illustrated. The activity index (arbitrary, 0–3), vacuum (pressure in cm H_2O h^{-1}), and $\dot{V}o_2$ are given in Table 2. Changes in vacuum were referenced to the lowest calculated daytime vacuum change on day 2 by subtracting 2.34 from all other pressure values. The corrected vacuum changes in Table 3 give the multiple regression equation (with $\dot{V}o_2$ in units of mg O_2 kg^{-1} h^{-1})

$$\dot{V}o_2 = 77.0 + 4.5 \times activity + 5.5 \times vacuum \quad (1)$$

(adjusted $r^2 = 0.94$). The combined regression for all experiments was

$$\dot{V}o_2 = 76.1 + 6.6 \times activity + 4.7 \times vacuum \quad (2)$$

(adjusted $r^2 = 0.92$). The predicted oxygen equivalents for equation (2) are shown in parentheses in Table 3.

Buoyancy and activity are typically both elevated at night;
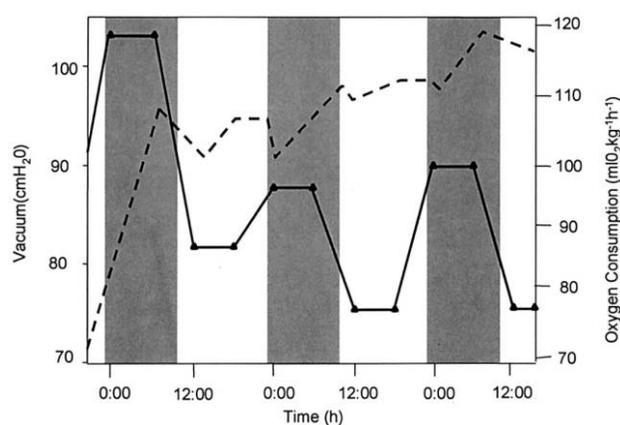
Figure 5. A 3-d experiment monitoring vacuum, weight in water, and $\dot{V}o_2$ in a 1-kg cuttlefish. Solid line shows vacuum regressions between maxima and minima. Dashed line shows weight changes over similar periods. Oxygen measurements were with water flow closed during 2-h periods between triangles, day and night.

Table 2: Activity index, change in vacuum, and $\dot{V}O_2$ of *Sepia officinalis*

	Activity Index (Arbitrary, 0–3)	Vacuum (cm H_2O h^{-1})	$\dot{V}O_2$ (mg O_2 kg^{-1} h^{-1})
Night 1	1.9	4.11	118.9
Day 1	1.4	−1.03	93.0
Night 2	1.7	.25	102.6
Day 2	1.4	−2.34	79.4
Night 3	.4	.67	95.9
Day 3	.15	−2.29	77.6

therefore, it is possible that our regression technique failed to adequately account for this covariance, overestimating the cost of ion pumping. However, it also seems likely that the assumption that pumps shut down completely in the day underestimates that cost. The average cost of nocturnal vacuum production after animal stabilization is ~13 mg O_2 kg^{-1} h^{-1}, ~10% of standard metabolism. Withers (1992) indicates that actual costs of fish osmoregulation are in the range of 20%–30%, so this is certainly not an extreme amount of energy to be consumed by an ion transport system. Thus, although there is still much to learn about the specifics of cuttlebone operation, it seems clear that these costs are neither trivial nor negligible, as has been suggested for swim bladders. The cost of creating neutral buoyancy actually appears higher than the cost of activity under these circumstances.

The $\dot{V}O_2$'s for the cuttlefish specimens here are lower than those found in the literature (e.g., 134 mg O_2 kg^{-1} h^{-1}, using the equation from O'Dor and Webber 1991 in Table 3). Johansen et al. (1982) give the resting $\dot{V}O_2$ of 114 mg O_2 kg^{-1} h^{-1} under these conditions, compared with our resting rate. The explanation is likely that our cuttlefish were truly at rest. Most experiments, including Johansen's, use cuttlefish that have been trawled from the ocean. Cuttlefish that have led a normal active life of jet swimming and migrating likely have higher metabolic rates than lab-hatched and reared *Sepia* that have never been in the ocean. These cuttlefish were grown in confined cages where jet swimming and active maneuvering are impossible, and they are unstressed by human presence and experimental procedures. During the latter 2 d they became quite accustomed to their surroundings and were virtually quiescent.

Denton and Gilpen-Brown (1961c) observed that feeding produced an immediate increase in density when cuttlefish behaviour was studied in a normal day and night cycle. The cuttlefish buried themselves in the day and only became buoyant again the following night, provided they were well fed. However, when cuttlefish were hungry, they stayed up in the water column in the day until they were fed and then hid again. Denton (1974) wrote that healthy cuttlefish can sink to the bottom, but when starving they usually pump liquid out of

their shells to such an extent that they float at the surface in an inconsistent fashion. The increasing trend of the negative pressure and decreasing trend of the weight of the cuttlefish in Figure 5 may be attributed to fasting. The low rates and overall decreasing trend in $\dot{V}O_2$ may also partly reflect fasting, as Wells et al. (1983) showed that the metabolic effect of a meal continues for several days in octopus.

Cuttlefish Vacuum Costs versus Other Antisinking Strategies

Prediction of the outcome of the cephalopod-fish competition will need questions answered concerning energetics and corresponding efficiencies (Clarke 1996). The analogy is sometimes used of fish being the "trees" of the ocean while cephalopods are the "weeds." Fish grow relatively slowly and are relatively efficient. Cephalopods grow rapidly and are relatively inefficient. As fish populations collapse in an ecosystem, the weeds take over. The conditions and time required for the trees to overcome or outcompete already established high populations of cephalopods are questions that need answers (Pauly et al. 1998). To understand how these populations compete, we must first understand energetics. Food consumption, respiration, growth rates, migrations, and buoyancy mechanisms all piece together a puzzle of an organism's behaviour and its expenses. Cephalopods compete with pelagic fish but have very different growth rates and life histories (O'Dor and Webber 1986).

Understanding the value of accurate physiological measurements of this sort to ecology and fisheries management requires some context. Packard (1972) presented an evolutionary scenario in which heavily shelled, primitive ectocochleate cephalopods like the nautiloids and belemnoids moved into deeper waters to avoid competition with more mobile fishes. At the same time, lighter-shelled ammonites were restricted to shallow water where they were outcompeted and went extinct. Whether the modern radiation of endocochleate cephalopods abandoned their chambered, buoyant shells in the depths or at the surface remains an open debate (Aronson 1991), but the two competing groups evolved a wide spectrum of buoyancy mechanisms to exploit the third dimension of the ocean habitat

Table 3: Observed activity, corrected change in vacuum, and rate of oxygen consumption for experiment 1

	Activity Index (Arbitrary, 1–3)	Vacuum (cm H_2O h^{-1})	$\dot{V}_{O_2}$ (mg O_2 kg^{-1} h^{-1})
Night 1	1.9 (12.5)	6.45 (30.3)	118.9 (120)
Day 1	1.4 (9.2)	1.31 (4.7)	93.0 (92)
Night 2	1.7 (11.2)	2.59 (12.2)	102.6 (100)
Day 2	1.4 (9.2)	.0 (0)	79.4 (85)
Night 3	.4 (2.6)	3.01 (14.1)	95.9 (93)
Day 3	.15 (1.0)	.05 (0.2)	77.6 (77)

Note. Oxygen equivalents in parentheses calculated from Equation (2).

(Clarke 1988). Both groups experimented with lipid storage and a variety of forms of dynamic lift, but sodium pumps to evacuate shells and hydrogen ion pumps to sequester light-weight ammonium ions are as characteristic of cephalopods as swim bladders are of fish (Clarke et al. 1979; Voight et al. 1994). Each mechanism has inherent limits within the niches where it can be applied. Alexander (1972) and Gee (1983) reviewed some of the trade-offs of mechanisms available to fishes, but additional comparisons of the fish systems to cephalopod systems are needed. The three principal niche constraints, which limit access to resources in the oceans, are maximum depth, maximum speed, and rate of change of depth. All are limited by metabolic cost, but depth is also limited by shell implosion strength. Speed and rate of change of depth determine the success between prey and predator. Table 4 allows a comparison of all of these costs. It includes applications of the approaches of Alexander (1972) to both a fish and a cuttlefish: (1) calculating the additional cost based on increased drag associated with the added volume occupied by the buoyant material and the accompanying increased surface area and (2) calculating the induced drag from the creation of dynamic lift.

The figures have all been adjusted to Alexander's (1977) standard 0.22-kg animal, using measured costs of locomotion at various speeds for salmon (Brett and Glass 1973), cuttlefish (O'Dor and Webber 1991), and Nautilus (O'Dor et al. 1990). They include measured costs for hovering, negatively buoyant fish (Blake 1979) and squid (Webber and O'Dor 1986) and for cuttlefish vacuum from above.

Another consideration in the balance of cost and benefit is the initial cost of creating the buoyant material. Alexander (1977) estimates the lightest lipids (e.g., squalene) must increase body volume by 32% to achieve neutral buoyancy. The cost of the "foregone benefit" of not using lipid for metabolism is easily estimated from its nutritional energetic value (40 MJ kg^{-1}/14 J mg O_2^{-1}; Alexander 1990). Although Alexander (1990) considered this negligible, it can be significant even when amortised over the relatively long life of a fish and would be quite dramatic over the short life of a cuttlefish. Similarly, the gas space in Nautilus occupies 25% of body volume (Chamberlain 1987),

and the initial cost of creating this relatively large vacuum reservoir in Nautilus is calculated based on the number of ions that had to be transported to create the total gas space. No estimate of the cost of making the shell has been included because there is no basis, and it is not exclusively a cost of buoyancy. These amortised costs have been added to the metabolic costs in the following columns of Table 4. The overall effects of the various components for cuttlefish and fish over the speed range are illustrated in Figure 4.

It is interesting to note that the Nautilus buoyancy system is approximately equal to squalene in volume (and therefore drag) efficiency but represents considerably less initial investment. Assuming that the operating costs for Nautilus shell are similar to the measured costs for cuttlebone, they account for over 90% of total Nautilus metabolism at rest. This may seem very large, but Boutilier et al. (1996) have shown that Nautilus can enter a hypometabolic state where it consumes only 4%–8% of normal rest metabolism. The cuttlebone costs suggest that this could be achieved simply by turning off the siphuncular ion pumps and temporarily operating on stored buoyancy.

The volume efficiency of cuttlebone, in terms of percentage of total body volume, is considerably better than Nautilus shell (or lipid). The cuttlebone is only 9% of total body volume, due to its light (but less robust) shell design; however, the swim bladder is even better because it is only 4%–6% of total body volume. This is seen in Table 4 from the incremental increases in estimated costs of producing cuttlefish vacuum (shown in bold because they are already included in the measured costs of standard and active metabolism on the line above) and, similarly, for a swim bladder. The basic cost of producing gas for the swim bladder is estimated as equal to that of the cuttlebone because it is not fully known. Alexander (1972) estimated an extremely small cost for filling a swim bladder, based only on work done by the gas, but gas secretion, like ion pumping, must involve additional unmeasured physiological costs, such as pumping blood to the bladder and producing the hydrogen ions to dissociate oxygen from haemoglobin. If we reflected these more realistic costs of buoyancy onto the lines in Figure 1 (which only account for increased drag costs), all of

Table 4: Oxygen equivalent costs of buoyancy mechanisms in cephalopods and fishes calculated at 15°C for 0.22-kg animals at various speeds and depths (m)

Animal/Mechanism	Amortised Metabolic Costs[a]		Speeds at 1-m Depth			Speed at 100-m Depth	Δ Depth (m)
	Years	Value	0	.1	.5	0	
Cuttlefish (measured)[b]	1		134	178	557	172[c]	
Vacuum:							
Ion pump		<1	13	13	13	52[d]	0
Drag			0	3	25	0	
Squalene		72	193	242	669	193	0
Dynamics[e]		0	186[f]	187	547	186	0
Ammonium[g]		1	122	227	1,961	122	0
Fish[h]	5		80	95	206		
Swim bladder:							
Gas pump		0	**13(?)**	**13**	**13**	**15[d]**	High
Drag			**0**	**1**	**5**	**0**	
Squalene		14	81	98	226	81	0
Dynamics[e]		0	193[i]	90	197	193	0
Nautilus (measured)[j]	5		14	80	467	53	
Vacuum:							
Ion pump		<1	**13**	**13**	**13**	**52[d]**	0
Drag			**0**	**13**	**78**	**0**	

Note. $\dot{V}o_2$ is expressed in units of mg O_2 kg^{-1} h^{-1}; speed is expressed in m s^{-1}; depth in m. The component costs are illustrated in Figure 4. Cost of drag at speed is the measured value less cost at 0 m s^{-1}; extra mechanism drag cost (D_e), as estimated from the increase in surface area associated with increased volume from the buoyancy mechanism (e.g., $1.09^{0.67}$ for cuttlebone), is deducted from this to estimate basic drag cost at speed (D_b). Costs for other mechanisms are similarly calculated and added back to totals. Basic standard metabolism (S) is calculated by subtracting mechanism maintenance cost (M; e.g., cuttlebone) from measured costs at 0 m s^{-1}. The amortised metabolic costs (A) of creating a reserve are estimated in O_2 terms and amortised over an assumed animal life. Thus, total costs $= S + M + A + D_b + D_e$.

[a] Energy sacrificed to create large lipid stores or vacuum spaces allocated over the life of the animal on an hourly basis.

[b] $\dot{V}o_2 = 39m^{0.75}e^{0.057T}e^{2.85u}$ (Wells and Wells 1990; O'Dor and Webber 1991).

[c] Osmotic pressure requires four times as many ions to be transported.

[d] Actual systems used by the animals, included in measured metabolic costs. Calculated costs for cuttlebone used for all, as other data are suspect (see text).

[e] Induced drag due to lift calculated after Alexander (1972, 1977); increased metabolic costs allocated in proportion to drag.

[f] From hovering cost of squid (Webber and O'Dor 1986).

[g] Assuming isosmotic NH_4Cl has a density 1.010 and H^+ is transported into cells to trap NH_3 on same basis as in note d.

[h] $\dot{V}o_2 = 47m^{0.65}e^{1.81u}$ (Brett and Glass 1973).

[i] From hovering cost of mandarin fish (Blake 1979); 0.75 W kg^{-1}/14 J mg O_2^{-1} = 193 mg O_2 kg^{-1} h^{-1}.

[j] $\dot{V}o_2 = 14 + 1037u^{1.2}$ (O'Dor et al. 1990), where mass $= m$ (kg), temperature $= T$ (°C), speed $= u$ (m s^{-1}).

the intercepts would be lowered and the advantages of dynamic lift for high-speed scombroids would become unambiguous. Lower overall metabolic rates of fish suggest that swim bladders may be cheaper to operate. Even though the cuttlebone has better volume efficiency than squalene, the higher locomotor efficiency of fish undulatory propulsion still gives fish, even those without swim bladders, an edge over "live fast, die young" cephalopods (O'Dor and Webber 1986). The cuttlefish does much better than its negatively buoyant, dynamic-lift relatives, the squids (O'Dor 1988*b*, 1988*c*). The best data for sustained swimming speeds in squids (Nakamura 1993; Sauer et al. 1997) suggest that due to the low efficiency of jet propulsion, squid

cannot reach the limit Alexander (1972) developed for fish, so that ammonium storage may be an acceptable option for slower animals.

The final critical trade-off illustrated in Table 4 is that of absolute depth and changing depth. The depth limits are well defined for shelled cephalopods from implosion depths, ca. 200 m for cuttlefish (Ward and Boletzky 1984) and 600 m for *Nautilus* (Ward 1987). Ward notes that it does not appear possible for *Nautilus* to generate an adequate osmotic pressure difference to create vacuum at its full depth range because the concentration of ions in seawater is not high enough, even if the gradient was against pure water. Similar calculations showed
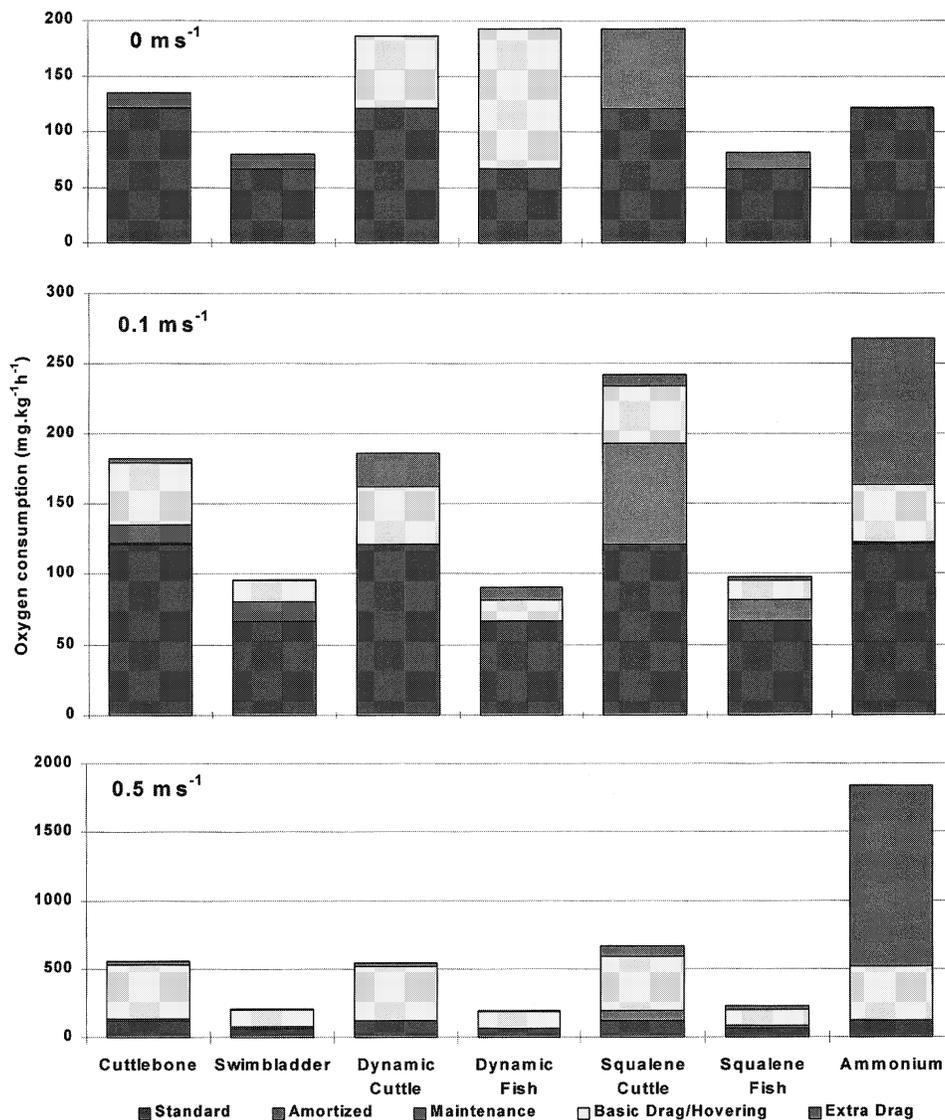
Figure 6. Partitioned metabolic cost estimates for cuttlefish and salmon, if they used various antisinking mechanisms as outlined in Table 3. Actual mechanisms are cuttlebone and swim bladder; hypothetical cuttlefish (*cuttle*) and salmon (*fish*) cost estimates using dynamic lift and lipid storage are calculated after Alexander (1977) based on added volume drag, as is the storage of ammonia by cuttlefish. Components are standard metabolism (*S*), the amortised costs of storing lipids (*A*), the maintenance costs for active buoyancy systems (*M*, i.e., cuttlebone and swim bladder), the costs above standard metabolism required to overcome drag when swimming at a speed or hovering (D_b), and the extra drag (D_e) that would be associated with moving the added volume of a buoyancy mechanism, calculated from the basic drag.

that cuttlefish should not be able to produce a vacuum below ~150 m. The likely explanation for this paradox is that these animals vertically migrate and create vacuums at shallower depths. The leakage rate for ions and gas are low enough that they can spend considerable time at depth without a significant loss of buoyancy. This ability to "store" vacuum buoyancy is probably the principal advantage that maintains an energetic edge for shelled cephalopods and perhaps the reason *Nautilus* has survived the competition with fishes.

Although fish always seem to have the edge in Figure 6, Alexander (1972) concluded that swim bladders became progressively more expensive with depth and that rates of gas secretion were sufficiently low as to make them essentially useless for rapid vertical migration. Thus, cuttlefish and *Nautilus* can competitively occupy "vertic niches" (O'Dor et al. 1993) in shallow seas that involve daily vertical migrations. Figure 6 shows vacuum costs of cuttlefish are lower than dynamic hovering for both squid and fish and lower than lipid storage for

cephalopods. This edge is important, as fish must rely on dynamic lift when their swim bladders collapse on descent, but clearly fish become competitive at very low, steady speeds. Ammonium storage is likely considerably less energetically expensive, but because of the huge volumes required, it probably only works for animals with nearly passive feeding strategies (Seibel et al. 1997). In a speculative review of squid migrations, O'Dor (1988a) suggested that, if optimal cruising speeds for a 100-kg giant squid scaled to a 1-kg smaller muscular squid, the giant squid could swim around the world in 80 d (at 6 m s^{-1}), but the present analysis shows that these ammoniacal creatures only have the muscles of a 25-kg squid to push them around. The limits set by Figure 1 make it unlikely that they can cruise at more than 0.6 m s^{-1}, which makes world cruises a matter of years, but this is good news for the teams of submariners currently trying to film them!

Acknowledgments

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